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► **To cite this version:**

Emmanuelle J. Javaux. Patterns of diversification in early eukaryotes. Carnets de Géologie / Notebooks on Geology, 2007, CG2007 (M01/06), pp.38-42. hal-00168238

HAL Id: hal-00168238

<https://hal.science/hal-00168238>

Submitted on 25 Aug 2007

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Patterns of diversification in early eukaryotes [Modes de diversification des premiers Eucaryotes]

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Citation: JAVAUX E.J. (2007).- Patterns of diversification in early eukaryotes. *In*: STEEMANS P. & JAVAUX E. (eds.), Recent Advances in Palynology.- [Carnets de Géologie / Notebooks on Geology](#), Brest, Memoir 2007/01, Abstract 06 ([CG2007_M01/06](#))

Key Words: Proterozoic; early eukaryotes; diversification

Mots-Clefs : Protérozoïque ; premiers eucaryotes ; diversification

1 - Introduction

The Precambrian includes: the Hadean (4.6 to 4 Ga), the period of solar system formation and Earth accretion; the Archean (4 to 2.5 Ga) when life appeared, and the Proterozoic (2.5 to 0.56 Ga) subdivided into the Paleo-, Meso-, and Neoproterozoic. During this major part of Earth history (about 90%), major environmental changes were registered in the geological record. These events include the step-wise oxygenation of the atmosphere and oceans, meteoritic impacts, supercontinent formation and breakup, and severe glaciations; they may have had a profound effect on the early evolution of the eukaryotes. Several lines of evidence from the geological record, the fossil history and molecular phylogenies can be used to decipher the early record of the domain Eucarya and its evolution.

Genetic material is rarely preserved in the rock record, so paleontologists have to rely on other features to identify microfossils as members of the domain Eucarya. Fossils provide direct evidence of early cells, and document steps in biological and biochemical innovations. Organisms can be preserved by a variety of processes in a range of substrates. Early eukaryotic fossils include: carbonaceous compressions (the organisms are preserved as a thin film of carbon); acritarchs (organic-walled vesicles with unknown biological affinities, they can be extracted from shales using strong acids, or observed in thin sections of shale, chert or phosphorite); multicellular organic-walled organisms (chert, shale); vase-shaped microfossils; molds and casts in sandstone or shale; skeletons preserved in carbonates or phosphorite; and phylogenetically informative molecules (biomarkers and biopolymers preserved in the rocks that provide information about past ecosystems and the evolution of biosynthetic pathways).

Molecular phylogenies yield important information or hypotheses about relationships between clades and their order of branching. However paleobiological data are essential for testing these trees and for constraining the (minimum age of) timing of diversification.

Fossils may also record ancestral forms (and steps in evolution) that might not have any extant relatives. The position of the root of the tree of life is not yet understood. Within the eukaryotic tree, the eukaryotes are divided into several supergroups whose relationships are not well resolved. Lineages thought to have branched early because they seemed to lack mitochondria, actually host derived mitochondrial organelles (EMBLEY & MARTIN, 2006). Nevertheless, calibration of phylogenies using dates from fossils, biomarkers, and isotopes, shows that a major diversification of extant clades occurred in the Neoproterozoic, preceded by a long evolution of eukaryotic fossils starting in the late Archean -as suggested by biomarkers- or in the late Paleoproterozoic, when the oldest eukaryotic microfossils are found (see reviews in JAVAUX, 2006; KNOLL *et alii*, 2006; PORTER, 2004). Superimposing the record of biological innovations and environmental changes on the fossil record might reveal possible explanations of the pattern of diversification in the middle Neoproterozoic, long after the origin of the domain and possible early divergence of major clades in the Paleo- and Mesoproterozoic when eukaryotic fossils of unknown biological affinities are preserved.

As discussed elsewhere (JAVAUX & MARSHALL, 2006; JAVAUX *et alii*, 2003, 2004; MARSHALL *et alii*, 2005), in order to determine the biological affinities of these fossils at the level of domain or beyond, we have defined a set of criteria to differentiate prokaryotic from eukaryotic microfossils and have formulated a methodology combining microscopy and microchemistry of single acritarchs. Fossils can display morphological and ultrastructural features showing a degree of complexity and/or particular features unknown in prokaryotic organisms, therefore pointing to a eukaryotic affinity. Indeed, the wall structure and ornamentation, the presence of processes that extend from the vesicle wall, the presence of excystment structures (openings through which cyst liberate their content), wall ultrastructure and wall chemistry can clarify the biological affinities of organic-walled microfossils at the

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Manuscript online since March 22, 2007

level of the domain, and in some cases even at the level of class. Microchemical analyses such as micro infra-red and Raman spectroscopy, secondary ion mass spectrometry, and other techniques applicable to very small samples such as one acritarch can be used to characterize the chemistry of organic microfossils and might even reveal biomolecules specific to extant clades.

One limitation of this approach is the limited knowledge that we have about extant organisms producing fossilizable structures and their morphological, ultrastructural and chemical properties. This approach requires investigation of preservable biological properties and comparative actualistic studies of taphonomic processes affecting diverse organisms in diverse environments (JAVAUX & MARSHALL, 2006).

2 - The fossil record of biological innovations in early eukaryotes

Fossils can inform about the evolution of biological innovations, regardless of their biological affinities, as briefly summarized below (see reviews in JAVAUX, 2006; KNOLL *et alii*, 2006 and reference therein).

- Biomarkers in 2.7 Ga kerogens of the Fortescue Group, Australia, indicate that contemporaneous cells were able to synthesize sterols, requiring a minimum of oxygen.

- Paleo- and Mesoproterozoic macroscopic compressions or mold and cast structures have been compared to algae but this interpretation remains controversial.

- The first ornamented acritarchs are populations of *Valeria lophostriata* recorded in the Paleoproterozoic of China (~1.8 Ga) and Australia (+1.65 Ga). Early Mesoproterozoic acritarchs *Shuiyousphaeridium macroreticulatum*, *Valeria lophostriata*, *Tappania plana*, and *Satka favosa* exhibits a complexity of form observed with TEM, SEM, and light microscopy that is unknown in prokaryotes. Prokaryotes can be large, they can have ornamentation, and they can have preservable walls (at least cyanobacterial sheaths), but no prokaryote currently known has all three (large size, ornamentation, preservable acid-resistant walls) at once. Many eukaryotes do. Therefore, these early microfossils display the characteristics of a eukaryotic grade of organization, and are interpreted as eukaryotes with a sophisticated cytoskeleton. These 1.65-1.3 Ga fossil assemblages record biological innovations such as reproduction by budding, complex ecology, vegetative and resting stages, synthesis of resistant polymers, synthesis of various wall ornamentation including processes, and a moderate diversity.

- The bangiophyte red alga *Bangiomorpha pubescens* is so far the oldest taxonomically resolved eukaryote, and records the evolution of complex multicellularity, cell differentiation, and sexual reproduction, eukaryotic photosynthesis, primary endosymbiosis of a chloroplast ancestor by 1.2-1 Ga. Note that these biological innovations are recorded in this one fossil population of bangiophyte red algae that chronostratigraphy dates at 1.2 Ga-750 Ma. Chemostratigraphy and lithostratigraphy indicate an age closer to 1.2 Ga. However other multicellular photosynthetic eukaryotes also appeared around 1 Ga.

- Upper Mesoproterozoic / Lower Neoproterozoic rocks (and possibly Paleoproterozoic rocks) have yielded biomarkers of alveolates (which include dinoflagellates and ciliates, among other groups).

- *Palaeovaucheria*, a 1 Ga xanthophyte alga, indicates the appearance of stramenopiles (which include diatoms, xanthophytes, and brown algae) and of secondary symbiosis (involving a red alga-like endosymbiont).

- The 750 Ma vase-shaped microfossils provide a firm calibration point for the opisthokonts, the clade that includes animals, fungi and the amoebozoans not to mention direct evidence for heterotrophic eukaryotes and eukaryotic biomineralization, and possibly predation. Cladophorales green algae also appeared, recording again multicellular photosynthetic eukaryotes, and implying earlier evolution and diversification of green algae, as clearly underlined by BUTTERFIELD *et alii* (1994), KNOLL (2003) and other Precambrian paleontologists, but recently misunderstood by TEYSSEDRE (2006).

- The late Neoproterozoic appearance of animals preserved as calcareous skeletons forming large reefs or as possible animal embryos in phosphorites added another dimension to ecosystems and predation pressure.

- Florideophyte red algae at ~600 Ma record the evolution of a tissue-grade organization (cell differentiation in three dimensions to form a tissue with a specific function).

3 - Diversity patterns

So fossils do provide evidence for the evolution of eukaryotic biology, but their change in diversity might also tell us something about the factors controlling the patterns we see in the fossil record. What are those patterns?

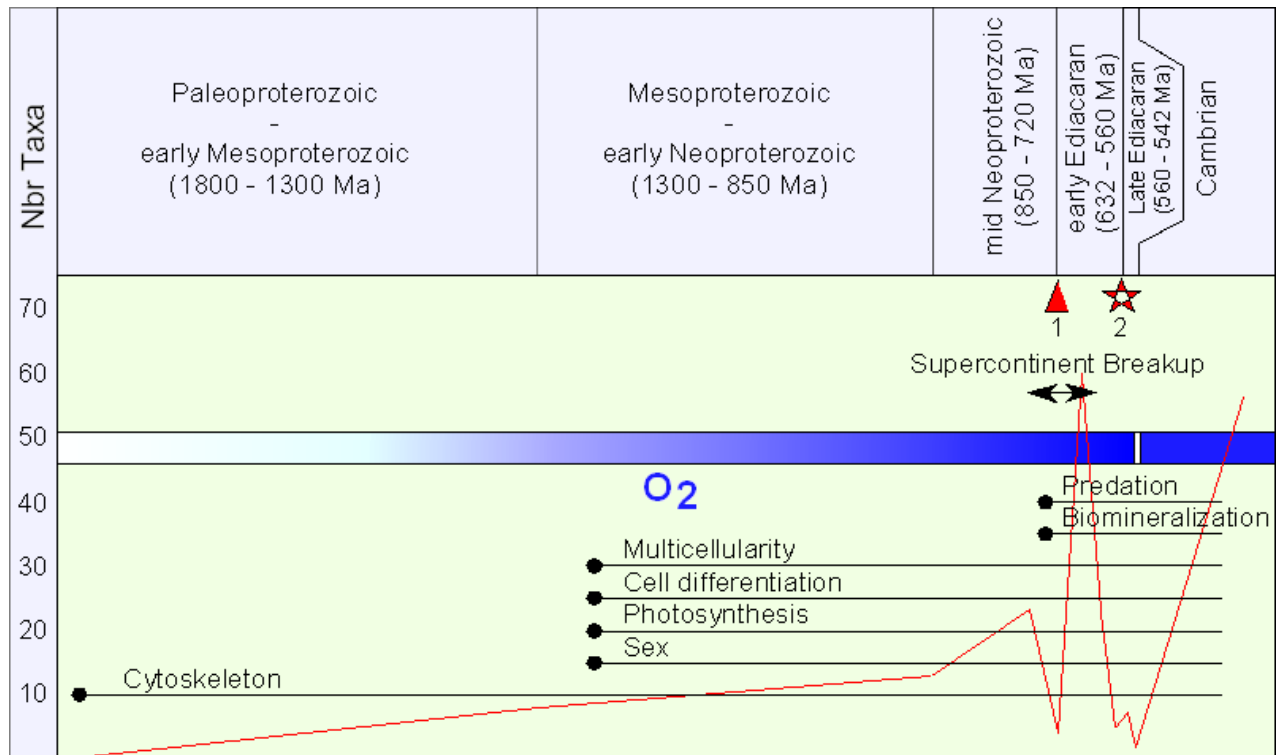


Figure 1: Patterns of early eukaryotic diversification, biological innovations and environmental changes (modified from KNOLL *et alii*, 2006).

This figure shows the general trend of variation in number of eukaryotic taxa (compilation of acritarchs, VSMs, multicellular fossils and macroscopic compressions, data in KNOLL *et alii*, 2006) through the Proterozoic, and the timing of major environmental changes (supercontinent formation and breakup, widespread glaciations, meteorite impact in Australia, and change in oxygenation), and of biological innovations evidenced by the fossil record (JAVAUX, 2006). 1: Glaciations. 2: Acraman impact.

The Figure 1 is a schematic curve drawn from a recent compilation of the number of taxa per assemblage throughout the Proterozoic, including the acritarchs, the VSMs, multicellular microfossils and macroscopic remains (data and references in KNOLL *et alii*, 2006). Of course, the fossil record is incomplete and more discoveries will undoubtedly improve our understanding. Nevertheless, there is a clear trend toward increasing diversity, starting with a low rate of diversity in the late Paleoproterozoic, a modest rate in the Mesoproterozoic-early Neoproterozoic, followed by a sharp increase in the mid and late Neoproterozoic (or early Ediacarian). In the late Ediacarian, diversity decreases before rising again at the Phanerozoic boundary. Between "global" glaciations, the fossil record is sparse and seems to show a big drop in diversity, although this might also result from insufficient sampling and/or gaps in the fossil record.

A closer look at the composition of acritarch assemblages (KNOLL *et alii*, 2006) reveals that earlier assemblages include mostly smooth and ornamented sphaeromorphs, along with a few forms with asymmetrically distributed processes whereas younger assemblages include more diversely ornamented acritarchs and acritarchs with symmetrically distributed processes. In the

Late Ediacarian, acanthomorphs disappear and large leiospheres dominate assemblages. Cambrian assemblages include a renewed diversity of ornamented forms and small acanthomorphs, generally assumed to represent planktonic algal cysts.

4 - Controls on diversification

To understand the factors controlling this pattern of fluctuations in diversity, we can superimpose on the diversity curve, the timing of environmental changes registered in the rock record and the timing of biological innovations evinced in the fossil record.

Three main factors are generally proposed to explain changes in diversity: genetic innovations, ecological innovations and environmental changes.

Since early cells had already all the eukaryotic features typical of their domain by the late Paleoproterozoic and possibly earlier, why did diversity stayed modest until the mid-Neoproterozoic?

Sex, complex multicellularity (and cell differentiation) and eukaryotic photosynthesis appeared around 1.2 Ga, well before the increase in diversity around 850 Ma. Glaciations (poorly constrained at ~720-710 and 650-635

Ma) and possibly a transient shallow-water anoxia event at the Precambrian-Cambrian boundary might have cut down some of the diversity, but most clades (the red, green, xanthophyte algae, the fungi, and the amoebae) survived and diversified again in the Phanerozoic. Supercontinent breakup might have increased the surface area of epicontinental seas and modified the cycle of nutrients, thus providing new niches and altering the chemistry of the early oceans. Animal predation pressure might also have played a role in forcing diversification. Some authors suggested that spines on acritarchs could be a defense mechanism against metazoan grazers, and that the modest early acritarch diversity could have resulted from the absence of animals before the Ediacaran (PETERSON & BUTTERFIELD, 2005). However it is also possible that some of these acritarchs record directly the presence of animals as some of them resemble metazoan eggs (KNOLL *et alii*, 2006), but the wall of at least one species (*Tanarium conoideum*) was made of a biopolymer similar to algaenan, thus indicating a green algal affinity (MARSHALL *et alii*, 2005). Finally in Australia a meteoritic impact (so-called Acraman impact) occurred at ~570 Ma, and acritarch assemblages before and after the impact seem to differ (GREY, 2005).

So far, not any one event seems to explain the observed pattern of early eukaryote diversification. More precise dating constraints on environmental changes and the fossil record are needed before drawing conclusions, but probably the three factors (genetics, ecology, environmental changes) were involved.

5 - Conclusions

Early eukaryotes had developed many complex and characteristic cellular and molecular mechanisms by 1.2 Ga, but the diversity of microscopic forms increased only in the middle Neoproterozoic, and a high diversity of macroscopic forms appeared at the end of the Proterozoic era. Despite the unavoidable incompleteness of the fossil record, the observed pattern seems to reflect natural trends. The causes of this relatively late or delayed diversification are probably multiple, including changes in the chemistry of the early atmosphere and oceans and a lack of (or reduced) predation pressure until the Ediacaran when increased oxygenation permitted the evolution of animals (possibly already present) and consequently the complexification of ecosystems (see discussions in PORTER, 2005; PETERSON & BUTTERFIELD, 2005; KNOLL *et alii*, 2006). HUNTLEY *et alii* (2006) examined the evolution of variations in the morphology of acritarch vesicles, processes, process tips, and ornamentation: broadly correlating the observed pattern with environmental (glaciations) and ecological changes (appearance of Ediacaran metazoans and

"Cambrian explosion") but as pointed out above, cause-and-effects relationships may not be so closely connected. Moreover, the authors do not explain the rise in diversity around 850 Ma also detected in their study.

A multidisciplinary approach combining microscopy and microchemistry on both fossils and extant cells may permit a better understanding of the paleobiology of the fossils, and might clarify this pattern of diversification by identifying members of early and later clades, such as the late Neoproterozoic acritarchs (were they animal eggs and/or phytoplankton cysts or something else?). One crucial point to elucidate is whether or not the late diversification reflects diversification between or within clades. Collating the paleobiological data with information from geology and geochemistry regarding paleoenvironments and their evolution, and with insights from molecular phylogeny, we can better understand the evolution of life on our planet and characterize the biosignatures needed for paleobiology and astrobiology.

Acknowledgments

This extended abstract has benefited from discussions and/or previous published work in collaboration with A.H. KNOLL, C.P. MARSHALL, and K. GREY.

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