

Eukaryotes, Endosymbiosis, and Complex Organisation

CHO-014 · Cosmic History and Its Observers

A Chronological Scientific History from the Early Universe to the Present

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Abstract

Background

Between approximately 1.8 billion and 720 million years ago, eukaryotic life acquired a fossil record that becomes progressively more informative about cell architecture, multicellularity, photosynthetic lineages, ecology, and trophic interaction. The record is discontinuous, and its apparent changes depend partly on preservation and sampling.

Evidence

This synthesis integrates controlled full-text palaeontological, biomarker, phylogenomic, and chronostratigraphic sources. It distinguishes possible from likely eukaryotes, total-group from crown-group assignments, fossils from molecular-clock estimates, organelle acquisition from lineage divergence, and local observations from broader interpretations. Claims supported only by abstracts, metadata, or an unconsulted primary source are not promoted in this synthesis.

Synthesis

Current evidence places the oldest convincingly eukaryotic fossils near 1.7 billion years ago, while several older candidates remain uncertain or have been weakened by later analysis. Macroscopic and multicellular organisation appeared in more than one form, including large cellular sheets, simple filaments, and coenocytic or colonial bodies. Proposed crown-group red-algal affinities near 1.6 billion years ago remain disputed, whereas later records provide more widely accepted crown-group assignments. Molecular-clock studies place major eukaryotic and endosymbiotic transitions across broad, model-dependent intervals and disagree about whether mitochondrial acquisition preceded or followed much of the assembly of eukaryotic cellular complexity. Late-Tonian body fossils and biomarkers show ecological and compositional change, but observed diversity remains entangled with sampling intensity. Perforated microfossils between 780 and 740 million years ago provide evidence of predation on eukaryotes without identifying the predator or implying cognition.

Conclusion

The interval records a mosaic of transitions rather than a single step toward complexity. By the Cryogenian boundary, eukaryotic life included diverse cellular architectures, several multicellular strategies, established photosynthetic lineages, and trophic interactions. The timing and order of organelle acquisition, the affinities of several early fossils, and the scale of Tonian diversification remain open or model-dependent.

Keywords: eukaryotes; LECA; mitochondria; plastids; multicellularity; Proterozoic; molecular clocks; biomarkers; Tonian; predation

1. Chronological orientation

This article follows the interval from 1.800 billion years ago to the base of the Cryogenian at approximately 720 million years ago [11]. A wider priority-topic overlay extends back to 2.800 billion years ago so that older published

candidates can be assessed rather than silently excluded. That overlay changes the search boundary, not the article's chronological spine.

Dates in this interval do not all describe the same kind of evidence. A radiometric age may constrain a bed above or below a fossil horizon; a molecular clock estimates a node under a model; a biomarker is a measured molecule whose biological producer requires separate inference; and a fossil's morphology does not by itself establish its exact phylogenetic position. The synthesis therefore uses intervals, one-sided constraints, and attributed interpretations where the evidence requires them.

2. The inherited initial state

At the opening of the interval, life had already altered Earth's environments, but a secure record of eukaryotic organisms was still sparse. Some historically influential signals no longer support the inferences once drawn from them. In particular, reanalysis of Archean hydrocarbon biomarkers found contamination and concluded that those compounds no longer provide valid evidence for eukaryotes at approximately 2.7 billion years ago [9]. This removes a former early anchor without demonstrating that eukaryotes were absent.

Morphological candidates older than the article window likewise require restraint. *Diskagma*, from a roughly 2.2-billion-year-old palaeosol, has been compared with lichens or fungi, but its affinities remain uncertain and a prokaryotic alternative is still viable [12]. Such fossils are evidence of unresolved biological structure, not secure milestones in eukaryote history.

3. From probable cells to differentiated organisations

A recent synthesis places the oldest convincingly eukaryotic fossils at about 1.7 billion years ago and treats still older forms such as *Grypania* as possible rather than likely eukaryotes [1]. The distinction matters. Eukaryotic affinity is not established by size alone, and a chronological priority claim is meaningful only within a declared comparison set.

The Limbunya Group in northern Australia preserves ornamented and process-bearing fossils in strata constrained to be older than 1642 ± 3.9 million years. The assemblage supports total-group eukaryotic affinity rather than a crown-group assignment. Within it, the authors describe *Limbunyasphaera operculata* as the oldest known operculate taxon [2]. The superlative is therefore an attributed statement about the published comparison set, not a universal claim that later discovery cannot revise.

Several records show that macroscopic size and multicellularity developed in forms that cannot be collapsed into one trajectory. In the Gaoyuzhuang Formation, carbonaceous compressions occur below a 1560 ± 5 million-year ash bed and above older volcanic units. Some reach 30 centimetres in length and nearly 8 centimetres in width, while preserved fragments contain closely packed cells approximately 10 micrometres across. The authors interpret them as likely photosynthetic multicellular eukaryotes with limited differentiation, but their precise position within Eukarya remains unresolved [16]. The same study provides a useful negative control: older North China compressions lacking diagnostic cellular structure may instead represent disrupted or redeposited microbial mats [16].

The filamentous fossil *Qingshania magnifica* comes from a horizon below an ash bed dated 1634.8 ± 6.9 million years ago. Its morphology supports simple multicellularity and likely photosynthesis, while its exact phylogenetic affinity remains uncertain [3]. This is not a contradiction with the Gaoyuzhuang material. Filamentous construction, cellular sheets, and differentiated tissues are different organisational characters, and no single specimen establishes a universal first appearance of multicellularity.

Horodyskia adds another organisational possibility. Tonian carbonaceous specimens preserve organic walls and have been interpreted as macroscopic organisms assembled through coenocytic or colonial organisation [13]. Biogenicity, eukaryotic affinity, and the specific mechanism of organisation remain separate questions; the interpretation does not license a claim about cognition, sentience, or evolutionary rank.

4. Crown groups and the problem of affinity

Fossils near 1.6 billion years ago illustrate why morphology and phylogeny must remain distinct. Three-dimensionally preserved *Rafatazmia* and *Ramathallus* were interpreted as probable crown-group red algae [5]. An integrated fossil-and-genomic analysis subsequently treated their assignment to crown Archaeplastida as not un-

equivocal [7]. The fossils and their cellular detail are real observations; their crown-group placement remains contested.

Later records support more stable, though still explicitly attributed, phylogenetic assignments. A current review describes *Bangiomorpha pubescens* as the oldest widely accepted crown-group eukaryote [1]. This formulation is deliberately comparative: it records present acceptance without turning consensus into direct observation or erasing older disputed candidates. In the Nanfen Formation, *Proterocladus antiquus* occurs within a stratigraphic bracket bounded by 1056 ± 22 and 947.8 ± 7.4 million years and was interpreted as a multicellular crown chlorophyte [6]. The bracket belongs to the formation, while the crown assignment is a phylogenetic interpretation of the fossil.

These cases show why a single ladder from small cells to large bodies to crown groups would be misleading. Size, multicellularity, cellular differentiation, and phylogenetic membership are different variables. They appeared in combinations that the surviving record reveals only unevenly.

5. Endosymbiosis and the assembly of the eukaryotic cell

Mitochondria and plastids are central to eukaryotic history, but their acquisitions are not preserved as ordinary fossil events. Their timing is reconstructed from gene histories, calibrations, and models. Different analyses therefore yield broad and partly incompatible results.

One gene-duplication analysis estimates the last eukaryotic common ancestor, LECA, at a mean age of 1.74 billion years, with a 95% interval from 1.80 to 1.67 billion years [4]. An integrated fossil-and-genomic analysis instead gives crown Eukaryota an interval of 1842 to 1210 million years [7]. These are model-dependent interval families, not two direct dates for the same observed event.

The chronology and ordering of mitochondrial acquisition are even less settled. The integrated analysis places mitochondrial symbiosis between 2053 and 1210 million years ago [7], while a cross-calibrated ATPase analysis suggests approximately 1200 million years with substantial deep-time uncertainty [14]. Gene-duplication studies also disagree about causal order. One infers that much eukaryotic cellular complexity assembled before mitochondrial endosymbiosis [4]; another concludes that mitochondrial gene transfer preceded the onset of eukaryotic cellular complexity [8]. The disagreement cannot be removed by averaging the estimates because the studies differ in data, calibration, and model structure.

Primary plastid endosymbiosis is similarly model-dependent. Published estimates include an interval of 1774 to 1118 million years [7], a mean estimate for the last plastid common ancestor of about 1.51 billion years with a 95% interval of 1.63 to 1.44 billion years [4], and an estimate near 900 million years from duplicated ATPase proteins [14]. Plastid acquisition, the last common ancestor of plastid-bearing lineages, and later red or green algal divergences are not interchangeable events. Fossil algae can calibrate parts of this history, but they are not direct fossils of the acquisition process.

6. Molecular fossils, ecology, and the Tonian record

Biomarkers complement body fossils but carry their own chain of inference. The molecule must be indigenous to the rock, its stratigraphic occurrence must be secure, and its producer must be assigned without treating a biosynthetic capacity as unique when it is not. The invalidation of the older Archean sterane record demonstrates why those controls are material [9].

In a complete accepted manuscript on Siberian strata, Rizzo and colleagues report late-Tonian sterane-to-hopane ratios below 0.05, contrasting them with Chuar Group ratios up to 0.38 and total organic carbon values of 1.3–5.6 weight percent. They interpret the low Siberian abundance in an oligotrophic setting and argue that C27-sterane dominance there supports the idea that the Tonian rise of algae occurred widely across the oceans [15]. The measurements are local. The wider-ocean conclusion is the authors' inference, and it does not by itself establish uniform abundance, productivity, or taxonomic diversity.

The body-fossil record provides a parallel warning. A compilation of 181 species and 713 occurrences from 145 formations found apparent eukaryote diversity strongly correlated with the number of sampled eukaryote-bearing formations and favoured sampling variation as a major explanation for the observed pattern [1]. Biomarker occurrence, local abundance, taxonomic richness, and sampling intensity therefore cannot be substituted for one another. Together they support change during the Tonian, but they do not define a single globally synchronous radiation.

7. Interaction and observer capacities

Perforations in organic-walled microfossils from the 780–740-million-year-old Chuar Group were interpreted as the oldest direct evidence for predation on eukaryotes [10]. The trace records an ecological interaction between prey and an unknown consumer; it does not identify the predator's clade.

For the observer-capacities framework used in this series, CHO-014 remains at OC1: living systems respond to and exploit their environments, but the evidence reviewed here does not establish sentience. Eukaryotic cell organisation, sex-related life cycles, multicellularity, macroscopic size, or predation cannot by themselves be converted into claims about subjective experience. “Complex” in this article describes organisation, not superiority or progress.

8. Contingency and contemporaries

The surviving record is compatible with several coexisting organisational experiments rather than a necessary march toward one outcome. Probable total-group forms, uncertain macroscopic problematica, simple filaments, cellular sheets, coenocytic or colonial bodies, and crown-lineage candidates overlapped in time. Some lineages persisted; others disappeared or left no recognised descendants. The present record cannot show how many comparable innovations arose and vanished without preservation.

Endosymbiotic history was contingent as well. Mitochondrial and plastid acquisitions joined formerly independent lineages and redirected later evolutionary possibilities, but the controlled evidence does not establish that their timing, host context, or sequence was inevitable. The disagreement among molecular models is itself evidence that plausible histories remain underdetermined by present data.

9. Competing interpretations and unresolved questions

Four unresolved families organise the present uncertainty.

First, the affinity of several early fossils remains open. Older macroscopic forms may be biological without being demonstrably eukaryotic, and some cellular fossils support eukaryotic affinity without locating a crown group. The proposed crown-red-algal status of the approximately 1.6-billion-year fossils remains a live dispute [5,7].

Second, molecular clocks do not yet provide a single chronology for FECA, LECA, mitochondrial acquisition, plastid acquisition, and subsequent lineage divergence. Their intervals and inferred order depend on datasets, calibrations, and models [4,7,8,14].

Third, biomarker records distinguish molecules more securely than producers. Local sterane abundance and composition can support an ecological interpretation without demonstrating global taxonomic richness [15].

Fourth, apparent diversification is inseparable from geological opportunity and research effort. Better sampling can enlarge a diversity curve even if biological diversity did not change at the same rate [1]. Future discoveries may therefore alter both the timing and the shape of the record.

10. Claim classes and evidential limits

The following statement distinguishes supported claim classes, speculative content and open questions.

- **Measured or observed:** fossil dimensions, cellular structures, biomarker ratios, stratigraphic relations, and radiometric measurements reported by the cited studies.
- **Reconstructed:** organismal affinity, ecological interaction, and the biological interpretation of morphological or molecular evidence.
- **Model-dependent:** molecular-clock ages and the inferred order of endosymbiotic and cellular events.
- **Contested:** early crown-group assignments, uncertain problematica, and the scale or synchrony of diversification.
- **Open:** the exact host and timing of organelle acquisitions, the affinities of several early fossils, and the fraction of evolutionary diversity lost to preservation and sampling.

The text does not promote claims whose controlled support remains limited to an abstract, metadata record, or unconsulted primary paper. Those candidates are not promoted in this synthesis and can be reconsidered if qualifying source access changes.

11. Boundary and exclusions

CHO-014 owns eukaryotic diversification, endosymbiosis, multicellular organisation, and protist ecology within its authorised spine and priority overlay. Earlier environmental and redox history is inherited only as context and is not re-adjudicated here. Environmental associations are not converted into single-driver causal explanations.

Animal-priority claims, including proposed Tonian animals, belong to CHO-015 and are not adjudicated in this article. The overlap permits eukaryotic and environmental context to pass forward without transferring ownership. The article also avoids treating fungal, sexual-reproduction, testate-amoeba, and several older macroscopic-priority candidates as closed where the controlled primary evidence is not yet complete.

12. Closing state at the Cryogenian boundary

At approximately 720 million years ago, the record supports a eukaryotic world containing diverse cell forms, multiple modes of multicellular organisation, established photosynthetic crown-lineage candidates, regionally variable biomarker signals, and trophic interaction. It does not support a single date for the origin of eukaryotes, a resolved order for all endosymbiotic events, a globally uniform diversification curve, or an inference of sentience.

CHO-015 inherits this biological and ecological context at the Cryogenian boundary. It will assess animal candidates and later capacity transitions under its own evidence and ownership rules.

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Disclosure

This document is a scholarly synthesis; it is not primary research and has not been peer reviewed. Juan Seguro is the sole author. He approved the final text and is responsible for its content.