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Tree of Life Reshaped: The Discovery of Solarion arienae, the Phylum Caelestes, and the Rise of the Supergroup Disparia

Biology * Evolution * DNA

Introduction: The "Dark Matter" of the Eukaryotic World

The architectural reconstruction of the eukaryotic tree of life (eToL) has long been hindered by "orphan" lineages -- microbial eukaryotes that defy classification within the established supergroups of Amorphea, TSAR (Telonemia, Stramenopiles, Alveolata, Rhizaria), Archaeplastida, and Excavata. Often termed Protists with Uncertain Phylogenetic Affiliations (PUPAs), these deep evolutionary branches constitute the phylogenetic "dark matter" of eukaryotic biodiversity and hold critical clues to the biology of the Last Eukaryotic Common Ancestor (LECA).[2] The isolation and characterization of Solarion arienae, a novel, deep-branching, free-living heterotrophic protist, resolves a major sector of this evolutionary puzzle. Originally identified as a cryptic contaminant in a marine anaerobic ciliate culture, S. arienae has necessitated the erection of a new phylum, Caelestes, and provided the phylogenomic signal required to unify the orphan lineages Provora, Hemimastigophora, and Meteora into a massive novel supergroup designated as Disparia.[2][1]

Beyond its taxonomic significance, S. arienae exhibits ultrastructural and genomic features that challenge fundamental paradigms of eukaryotic evolution. Most notably, whereas traditional models assumed that proto-mitochondria rapidly transferred their genes to the nucleus and replaced bacterial protein export with the eukaryotic TIM/TOM import complex,[5] the mitochondrial genome of S. arienae encodes a functional SecA gene -- a direct relic of the ancestral alphaproteobacterial protein secretion pathway.[1] Shared only with the distantly related Mantamonas, this retention demonstrates that LECA possessed a chimeric mitochondrial transport apparatus blending bacterial export and evolving eukaryotic translocases. Combined with a dimorphic life cycle and a unique stalked extrusome used for predation, data from single-cell transcriptomics, high-pressure freezing transmission electron microscopy (HPF-FS TEM), and multi-gene phylogenomics portray the ancestral eukaryote as a metabolically versatile, sophisticated predator.

Discovery, Isolation, and Multi-Modal Methodology

Solarion arienae was discovered not through an open-ocean survey, but as an inconspicuous, free-living contaminant within a long-term laboratory culture of a marine anaerobic ciliate belonging to the order Metopida.[1] Within this anoxic, sulfur-cycling microcosm rich in bacteria and archaea,[6] Solarion persisted as tiny, slightly motile bacterivorous cells that evaded routine detection.[1] Because deep-branching protists often depend on complex syntrophic interactions that resist axenic monoculture,[7] the research team combined precise micromanipulation with cutting-edge molecular biology to bypass cultivation bottlenecks.

* Single-Cell Transcriptomics & Mitogenomics: Individual Solarion cells were manually isolated and lysed to amplify and sequence their expressed gene complement, yielding a comprehensive nuclear dataset alongside a complete mitochondrial genome assembly.[8]

* High-Pressure Freezing TEM (HPF-FS) & Tomography: To prevent the membrane distortion and axopodial retraction caused by standard chemical fixatives,[9] cells were frozen within milliseconds at 2,000 bar and substituted at -90 deg C to -60 deg C with acetone containing uranyl acetate and osmium tetroxide before embedding in EMbed 812 resin and sectioning at 90 nm.[10] Tilt-series electron tomography reconstructed 3D volumes of the internal cytoskeleton and predatory machinery.[1]

* Phylogenomic Architecture: A curated PhyloFisher dataset of 240 single-copy orthologous protein-coding genes across 87 taxa (77,133 amino acid sites) was analyzed under site-heterogeneous mixture models (LG+C60) to suppress Long Branch Attraction (LBA) and anchor the deep topology.[1][11][12]

Systematic Architecture: Phylum Caelestes and Supergroup Disparia

The inclusion of Solarion arienae (named from the Latin sol for its radiating, sun-like feeding projections) within the newly erected phylum Caelestes ("celestial") provided the missing evolutionary link needed to unify three enigmatic orphan clades -- Provora, Hemimastigophora, and Meteora -- into the supergroup Disparia.[2][1] Within Disparia, Hemimastigophora and Meteora form a robust sister clade supported by a gene concordance factor (gCF) of ~8.65%, comparable to established supergroups like Amorphea and CRuMs.[4] Provora branches sister to the Hemimastigophora+Meteora clade, while Caelestes branches at the base, anchoring the entire supergroup as an independent eukaryotic radiation alongside Diaphoretickes and Amorphea.[1][17]

| Feature | | Caelestes (Solarion) | | Provora (Nibbleromonas, Nebulomonas) | | Hemimastigophora (Hemimastix, Spironema) | | Meteora (Meteora sporadica) |

| Primary Morphology | | Sun-like (axopodial) & posterolateral flagellate | | Flagellates with ventral groove & cortical alveoli | | Multi-flagellated (two kinetid rows) & complex pellicle | | Gliding motility via lateral arms; intricate cytoskeleton |

| Predatory Organelle | | Stalked Extrusome (Bipartite) | | Toxicysts ("Nibbling" complex) | | Bottle-shaped Extrusomes | | Distinct/Cryptic extrusomes |

| Mitochondrial SecA | | Retains functional SecA | | Lost SecA (Standard) | | Lost SecA (Standard) | | Lost SecA (Standard) |

| Ecological Niche | | Marine anaerobic / microaerophilic | | Marine & freshwater predators | | Soil & sediment predators | | Marine sediments |

| Phylogenomic Support | | 240-gene dataset [1] | | Supergroup clade [1] | | Deep-branching clade [2] | | Sister to Hemimastigophora [4] |

Dimorphic Ultrastructure and the Stalked Extrusome

Solarion arienae alternates between two distinct morphological phases that balance sedentary feeding efficiency with spatial dispersal.[1] During its vegetative

trophont stage, the cell adopts a spherical, sun-like morphology with radiating axopodia-like projections supported by microtubule bundles originating from a central Microtubule Organizing Center (MTOC).[1] Time-lapse and TEM imaging confirm that these projections ensnare bacterial prey and draw them into phagosomes.[1] When local prey is depleted, Solarion transforms into an elongated, motile flagellate possessing a posterolaterally directed flagellum anchored by a basal body and striated fiber, accompanied by a trailing cytoplasmic tail for steering across sediment interstices.[1]

The defining cytological synapomorphy of Solarion is its bipartite "stalked extrusome."[1] Electron tomography reveals an organelle composed of a membrane-docked secretory body mounted atop a microtubule-supported stalk.[1] Unlike the lytic toxicysts of Provora that rip chunks from eukaryotic prey, TEM sections capture Solarion's extrusome body discharged and physically adhered to bacterial cells both extracellularly and within nascent food vacuoles, functioning as a microscopic harpoon that immobilizes bacteria for phagocytosis.[1] Together with the predatory arsenals of Provora and Hemimastigophora, this apparatus reinforces the "Phagotrophy First" hypothesis of eukaryogenesis.

Genomic Architecture and the Mitochondrial SecA Fossil

Despite inhabiting an anaerobic culture, Solarion retains cristate mitochondria surrounded by endoplasmic reticulum, indicating facultatively anaerobic versatility potentially regulated by ancient LYRM chaperone switches that maintain respiratory complexes across fluctuating oxygen gradients.[1] Its gene-rich mitochondrial genome -- comparable in coding capacity to Jakobids (60-66 proteins) and Mantamonas (62 proteins) -- harbors the landmark discovery of a mitochondrially encoded SecA gene.[1][14]

In free-living bacteria, the ATPase motor SecA binds pre-proteins in the cytoplasm and drives them across the inner membrane through the SecYEG channel.[15] During eukaryogenesis, as genes migrated to the nucleus, organelles evolved the reverse-oriented TOM and TIM23 import complexes, leading to the loss of SecA across almost all extant eukaryotes.[5] Phylogenetic analysis confirms that Solarion's SecA is a direct vertical descendant of the alphaproteobacterial endosymbiont rather than a horizontal gene transfer, and AlphaFold structural modeling identifies a unique transmembrane domain and divergent C-terminal domain that tether the motor to the inner mitochondrial membrane.[1] Because mitochondrial SecA is shared only with Mantamonas sphyraenae (in the distantly related CRuMs supergroup),[14] triangulation across the eukaryotic tree proves that LECA operated a hybrid protein transport system, and that SecA was lost independently across multiple post-LECA radiations.

| Evolutionary Stage | | Transport Machinery Configuration | | Representative Organisms |

| Alphaproteobacterial Ancestor | | Sec System (Export): SecA (ATPase motor) + SecYEG (Pore). No import machinery. | | Free-living Alphaproteobacteria |

| Proto-Mitochondrion (LECA) | | Hybrid System: SecA + SecYEG retained for inner-membrane export/assembly alongside evolving TIM/TOM import complexes. | | Inferred Last Eukaryotic Common Ancestor |

| Disparia / CRuMs Relicts | | Retained Hybrid: Functional SecA + SecY retained alongside complete eukaryotic TIM/TOM import system. | | Solarion arienae [1], Mantamonas sphyraenae [14] |

| Modern Crown Eukaryotes | | Derived Import System: SecA lost independently; canonical TIM/TOM complexes dominate protein sorting. | | Amorphea (Animals, Fungi), Archaeplastida, TSAR |

Conclusion: Reshaping the Deep Eukaryotic Tree

The elevation of an overlooked laboratory contaminant to the phylum Caelestes and the unification of the supergroup Disparia fundamentally reshape our view of the rare microbial biosphere.[1] By bridging long-branch orphan lineages and preserving a functional alphaproteobacterial SecA motor within a cristate mitochondrion, Solarion arienae demonstrates that the transition from endosymbiotic bacterium to canonical organelle was a protracted, mosaic process. Future metagenomic mining and targeted cultivation of micro-oxic transition zones promise to uncover additional relict lineages, further illuminating the predatory and metabolic complexity of early eukaryotic life.

Updates (November 14, 2026): Updated citations from ResearchGate author profiles, preprints, and thesis repositories to the peer-reviewed Nature (vol. 649, pp. 388-395), Current Biology, Systematic Biology, Current Protocols, and Figshare DOIs; corrected minor typographical errors in prose; and standardized unnumbered section headings.

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