The eukaryote root and chromist monophyly: evidence from ultrastructure, cell biology and sequence trees

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Eukaryotes are divisible into arguably ancestral protozoan subkingdom Eozoa (jakobids, *Tsukubamonas*, Percolozoa, Euglenozoa) and derived neokaryotes [all others, which ancestrally joined haem to mitochondrial c cytochrome apoproteins using a novel single-polypeptide haem lyase (HCCS) absent in prokaryotes, which use multiprotein Ccms instead]. Aerobic Eozoa retain mitochondrially-encoded Ccms (as do some neokaryotes: ciliates, *Malawimonas*), except for Euglenozoa that evolved novel unique machinery. The simplest interpretation is that Eozoa are ancestral to or sisters of neokaryotes and the eukaryote root is near jakobids, which alone retain mitochondrial α-proteobacterial SecY.

Microtubular pellicle morphogenesis/division suggests that discicristates (Euglenozoa, Percolozoa) are a clade. The eukaryote last common ancestor had two cilia, probably with a split right posterior centriolar root. Feeding grooves are not homologous across Eozoa. *Tsukubamonas* has the simplest eozoan flagellate cytoskeleton; unless secondarily simplified, the eukaryote root could lie between *Tsukubamonas* and other Eozoa. I present outgroup-rooted ribosomal multiprotein trees that put the root within Eozoa between Percolozoa and others, and discuss their limitations; they prove explosive basal eukaryote radiation.

Cytologically, kingdom Chromista is unified by a bypassing right microtubular band absent in other kingdoms and by derlin-based protein import into periplastid spaces. Derlin paralogue trees refute many hypotheses for the common ancestor of chromists being heterotrophic and multiple tertiary transfers of periplastid import machinery. HCCS trees give evidence for a eukaryote-eukaryote chimaera with four paralogues (likely photophagotrophic) being ancestral to all chromists with differential paralogue and plastid losses as lineages diverged in their (slightly more recent) explosive basal radiation. I discuss recent evidence that both chromist subkingdoms (Harosa; Hacrobia) are clades that ancestrally had excavate-like feeding grooves and vaned posterior cilia plus cortical alveoli that evolved in the common ancestor of superkingdom Corticata (Chromista, Plantae), and the likely homologies of the chromist bypassing root.

Scotokaryotes (all neokaryotes except Corticata) are a clade.