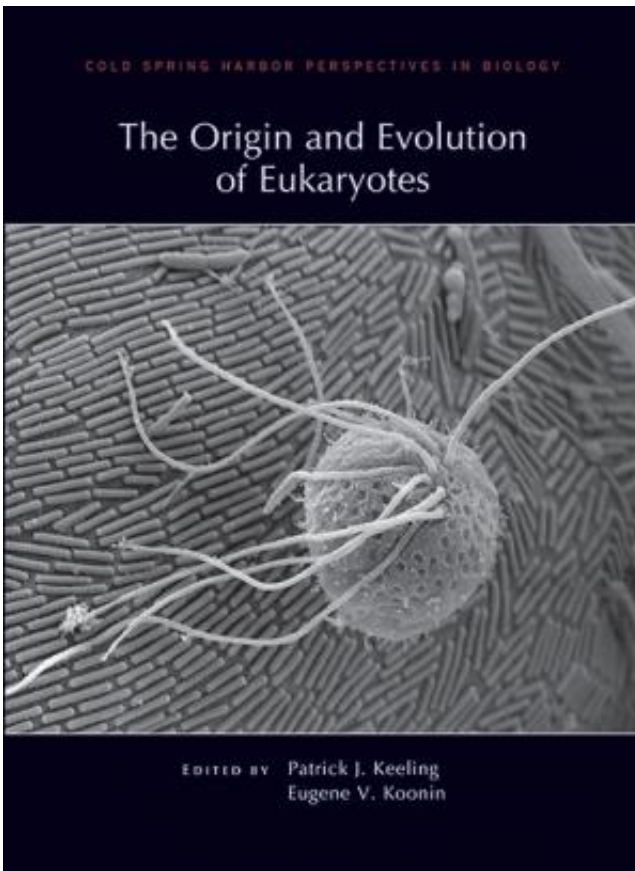


Origin of the Eukaryotic cell: Part II - Cytoskeleton, membranes, and beyond

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Credit: Cold Spring Harbor Press

(Phys.org) —In [Part I of our review](#) of the new book "The Origin and Evolution of the Eukaryotic Cell" we talked about the acquisition of endosymbionts by cells. While there we focused on some of the genetic

issues involved in acquiring mitochondria, here we want to focus on some of the other structural features that defined eukaryotic evolution. One approach that many of the chapter authors take is to examine the ways in which different bacterial and archaeal cells solve the universal problems of building membranes, organizing DNA, and constructing cilia or flagella to move things about. If prevailing intuitions are right, then once we are armed with sufficient knowledge regarding which primitive bacteria bear the rudimentary traces of the major innovations that define eukaryotic cells then the one true evolutionary path should be laid bare before us.

In the grand and timeless scheme of Cavalier-Smith, which [we discussed in Part I](#), the original bacterial "cenancestor" (and all later Eukaryotes) have largely employed bilayer membranes constructed with fatty acid chains linked through ester bonds to a glycerol 3 phosphate backbone. The highly contentious eukaryotic sister clade, the Archaea, inhabit more extreme environments and therefore do membranes a little bit differently. It appears they split from the main evolutionary trunk around the time they began to substitute in membranes made from isoprenoid chains linked through ether bonds to a glycerol 1 phosphate (G-1-P) backbone. A major mystery is hiding in the dry details of which cells use G-1-P and which use its [mirror image](#), G-3-P—namely, where did glycerol come from in the first place? A good explanation for the spontaneous formation of glycerol here on earth is still lacking. Just to whet the appetite, we offer that one new idea hints at the possible origins of glycerol deep within electron-irradiated [interstellar methanol ices](#).

One seeming paradox highlighted by Nick Lane's chapter is that while archaea and bacteria place similar values on fundamental issues like DNA transcription, ribosomal translation, and their ATP synthases, they differ in basic membrane-linked processes such as DNA replication. While the genetic, structural and phylogenetic data in general tends to address membrane or cytoskeletal homologies separately, the real story

doesn't contain evolution of two structures in isolated cellular vacuums. Membranes of ever increasing flexibility and selective permeability are only useful when mated to an equally nimble cytoskeletal apparatus that is capable of things like phagocytosis, or controlling organelle geometry, movement, and division.

Of central importance is the evolution of the cell is its centriole, which among other things serves as a cytoskeletal organizing center. The centriole conducts an orchestra that in many cells might still play flawlessly without it—at least through the first stanza. Over time however, cell harmony would inevitably be sacrificed if the cell can't quickly evolve sufficient compensations for the absent centrioles. In cells that have them, the centriole is intimately linked to the primary cilium or flagella, and much of the search for the ancestral eukaryote consists in defining [how centrioles are controlled](#) and replicated across successive cell cycles in different protists. Not only how many centrioles exist and where in the cell they are located, but also how many so-called "microtubule cones" each elaborates are important questions that need to be more fully defined.

A few key features of how cilia or flagella are built in bacteria, archaea and eukaryotes are probably worth mentioning here. The bacterial flagellum evolved not only to give creationists something to get worked up about, but also to give the origin of life sleuths a fascinating puzzle. Flagella on [gram positive bacteria](#) generally use two bearings in the lipid membrane while the gram negative versions have four bearings on account of the double membrane. All bacteria construct flagella by pumping individual flagellin protein subunits through a central bore out to the growing tip, but some are powered by hydrogen ions (proton motive force), while others instead by a sodium gradient. The unique forward and reverse motions of each these cellular appendages in space is yet another dimension to their character which seems to organize every aspect of their existence.

The archaea use their own archaeal flagellins (called archaellins), which are similar to bacterial type IV pilins. Archaea add successive protein subunits instead to the cell side of their growing flagellar chain, but power it using ATP just like the eukaryotes. The eukaryotes build their cilia from tubulin, an entirely different building block, and supply materials to the growing tip just like the bacteria do, except they use their own unique intraflagellar transport system to do it. The evolution of tubulins and actin from their hypothesized ancestral protein superfamilies —FtsZ and MreB respectively—is an interesting tale that contains many life lessons for us here.

One thing that is seen over and over again is that freedom to evolve new sequence, structure and function, as typically created by gene duplication, relaxes many of the requirements on the original protein and can therefore facilitate the wholesale replacement of subcellular forms and organelle designs. One example in the duplication of tubulin genes would be in the selection of an actin ring vs a tubulin-based Z-ring in various species for maintaining cell geometry and controlling division. Although the role of FtsZ in division is analogous to that of actin (and the actin-myosin ring) in eukaryotes, there is no known motor associated with it.

In this absence the fertile imagination has readily supplied potential [mechanisms for force generation](#). Chromosome pumps that behave like an osmotic contractile gel, expanding and constricting throughout mitosis, could be one such supplier of the mysterious "cytokinetic force" that researchers have previously shown must exist. With the case of FtsZ, a contractile force was found even in the absence of all other proteins. The use of an FtsZ ring in dividing chloroplasts and some mitochondria is suggestive of their deep their prokaryotic ancestry.

In the previous installment Torbjorn Larsson left us some insightful comments regarding the vertically inherited ATP importer of the

premitochondrion, as opposed a horizontally descended ATP-exporter, noting its ability function in low oxygen environments. The various milestones in eukaryotic evolution still require accurate placement in time with respect to the background eco-physiology of the Earth. Undoubtedly its oxygenation is the big one. A recent paper gives a tantalizing new hypothesis that would not only address these question but might also clear up doubts in our existing theories for the mitochondrion's origins.

The paper notes that although detailed images of the cellular structure of a class of alpha-protobacterial known as methaotrophs have been available for over half a century, apparently nobody has (until now) realized that they might be looking at [actual mitochondrial cristae in living bacteria](#). I asked author Mauro Esposito if these unique inner membrane structures of *Methylomonas* might contain cristae junction proteins that would be analogous to those now found in our mitochondria, and he indicated that a refined sequence analysis has yet to be done for these creatures.

In his chapter, Cavalier-Smith uses the shape of mitochondrial cristae (either tubular or flattened), the structure of the golgi (absent or with stacked dictyosomes), and the particular variety of intron splicing elements as important indicators of possible relatedness and ancestry in cells. Moving the field forward will undoubtedly require new links between these kinds of structures and the genetic sequence information that is now rapidly becoming available.

More information: The Origin and Evolution of Eukaryotes: [cshperspectives.cshlp.org/cgi/ ... lution_of_eukaryotes](http://cshperspectives.cshlp.org/cgi/...lution_of_eukaryotes)

Part 1 of the story is here: [phys.org/news/2014-12-eukaryot ... ll-endosymbiont.html](http://phys.org/news/2014-12-eukaryot...ll-endosymbiont.html)

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