

# Sex First—A New View of the Origins of Eukaryotes

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For wild, complex innovation one domain of life stands heads, shoulders, tentacles, tree bark and coral reefs above the rest: with full respect bacteria and archaea, many of evolution's most interesting inventions are a product of eukaryotic life.

"The complexity of life on earth can only be understood if we understand eukaryotes," says Neil Blackstone, a biologist at Northern Illinois University. But there's a problem. Most biologists believe that the last eukaryotic common ancestor (or LECA) had all of the complex features associated with modern eukaryotes: sex through meiosis and chromosomes held in a nucleus. That makes it very difficult to compare various eukaryotes a route to study how features arrived—as one might with tetrapods or land plants. It's all there from the start.

"So it's a tough problem to get at, yet it's crucial if we're going to understand life," says Blackstone. "I think right now we're seeing a lot of foment where people are coming to grips with the issue—realizing that we can't use methods of comparative biology."

If the field of evolutionary biology could use a new big idea to chew on, discuss and try to prove or try to disprove, they may perhaps have found a candidate in a richly detailed paper (Garg and Martin 2016) recently published in *Genome Biology and Evolution* by Sriram G. Garg and William F. Martin (Editor-in-Chief of GBE). In it they propose a somewhat radical idea:

"We're proposing that mitosis evolved from meiosis," says Martin, "which is exactly contrary to what everybody has always assumed." This happened, they believe, following the acquisition of the bacterial ancestor of mitochondria, as it established itself within the cytosol of its archaeal host.

Thinking back to high school biology you may remember, the purpose of mitosis and meiosis are very different, though at first glance the processes can seem very similar. In both, the function is to make new nuclei and ultimately cells. The names for steps in the nuclear cycle (prophase, metaphase, anaphase and telophase) are parallel between the processes (with a few additional steps for meiosis). However, their purpose is very different. Cells go through meiosis to make gametes, recombining genetic material (thereby creating genetic

diversity) and halving the number of chromosomes of the mother cell. Mitosis is purely for asexual reproduction. When it goes right, the daughter cells look just like the mother cell.

In great detail over more than 30 pages, Garg and Martin detail how they believe a proto-mitochondrial bacterium began living inside an archaeon and there developed meiosis. Only later, they believe, did mitosis start.

One of the reasons the authors believe this is sequence of events is Muller's ratchet: without genetic recombination, bad mutations pile up in an asexually reproducing population, making life difficult and eventually near-impossible. So the lineage giving rise to modern eukaryotes, they reason, had to have some method of recombining DNA. If this was the case, the authors write, "the lineage was necessarily recombining [...] leaving neither selective pressure to evolve anything as complicated as meiosis and sex, nor benefit from it once it arose. This line of thought actually renders the origin of meiosis from mitosis altogether unlikely."

A first step in their time line was the evolution of the nucleus: As individual proto-mitochondria died inside their host archaeal cells, the authors propose the mitochondrial genes released their DNA into the cell which then glommed on to the archaean genome. And, through nonhomologous recombination, these genes integrated. But this carried some consequences: the host had to deal with self-splicing introns which can copy themselves and reinsert into the genome.

"And that's what triggers the whole cascade," says Blackstone, who was not involved in the Garg and Martin paper. "It's really triggered by evolutionary conflict at the genomic level."

Because the self splicing introns were slow and translation in ribosomes was fast, it was dangerous to let the ribosomes get to the message RNA until the cell splicing introns had sort of finished their work of splicing themselves out. So, a physical barrier evolved to mediate these conflicts: the nucleus, and it became the hallmark of eukaryotes.

But, as often happens, the solution to one problem can create new ones. If chromosomes are confined to the nucleus they can no longer attach to the cell membrane. When the

cell divides the chromosomes don't and the whole prokaryotic system for making sure that the cell and the chromosomes replicate at the same time falls apart.

To address chromosome separation Garg and Martin propose something radically new—that the eukaryotic common ancestor was once coenocytic, having many many nuclei dividing in a long sack of cytosol.

“That’s much more primitive!” says Martin. “And you find it in all the eukaryotic supergroups.”

Importantly, chromosomes and nuclei divided in this state—whether in many diatoms, fungi, plants or animals, are pushed apart, not pulled apart by a spindle apparatus attached to a cell wall. The authors propose that meiosis was derived from the sort of reduction division seen in coenocytic cells, where chromosomes are separated out of heavily polyploid nuclei are separated by microtubules power by mitochondria.

“We’re saying that this is probably the ancestral state of nucleus division and chromosome division,” says Martin. “The process of cell division [and mitosis], that was solved

independently in independent lineages. And that would help explain why chromosome division is so conserved, whereas cell division in eukaryotes is not.”

The paper may attract some stiff criticism, Blackstone suspects. It is deeply rooted in natural history (rather than experiment) but that, he says, is its strength. “They offer a tapestry, it’s enormously rich and detailed, and I think conceptually satisfying,” Blackstone says. “How did eukaryotic complexity arise? All the rigorous tools of science can’t answer that very well.”

Martin, for his part, is also expecting some pushback. “Good ideas are supposed to be controversial,” he says. “They’re supposed to get people excited. That’s how progress unfolds in evolution.”

### Literature Cited

Garg SG, Martin WF. 2016. Mitochondria, the cell cycle, and the origin of sex via a syncytial eukaryote common ancestor. *Genome Biol Evol.* 8:1950–1970.