EUKARYOTE EVOLUTION

Engulfed by speculation

The notion that eukaryotes evolved via a merger of cells from the other two domains — archaea and bacteria — overlooks known processes.

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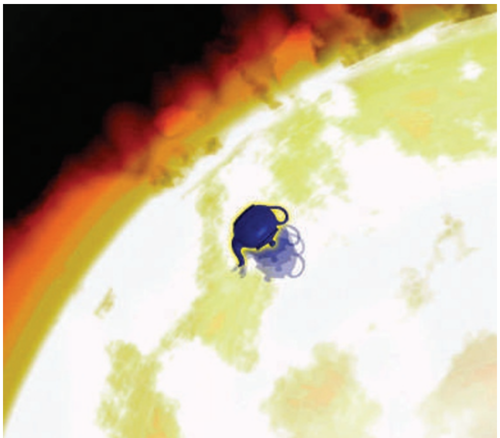

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In the absence of direct evidence, science should proceed cautiously with conjecture. Geologist Charles Lyell (1797–1875) warned us not to proceed like medieval scholars, who "often preferred absurd and extravagant positions, because greater skill was required to maintain them". Scientific speculation, Lyell emphasized, must take known processes into account. This has not happened with the debate on how eukaryotes (animals, plants, fungi, protists) arose. The conflicting hypotheses currently on offer show a curious disregard for mechanism.

One thing at least is agreed: the mitochondrion, powerhouse of the eukaryote cell, evolved from an engulfed bacterium. The question is 'who' did the engulfing. Did an archaeon engulf a bacterium? Did a bacterium, bacterial consortium, or RNA cell engulf first an archaeon (which became the nucleus) and then the mitochondrial ancestor? Perhaps nuclei emerged in a virus-infected archaeon, which then engulfed mitochondria. Which, if any of these, is right?

In the mid-1990s, a somewhat pedestrian view of eukaryotic origins, the 'archezoa hypothesis', held sway. This maintained that a protoeukaryote (with nucleus) engulfed the mitochondrial ancestor. Supporting the theory were 'archezoa', anaerobic eukaryotes with no mitochondria. Archezoa apparently populated the oldest branches of the eukaryote tree, suggesting that eukaryotes began diversifying before mitochondria entered the picture.

The archezoa hypothesis is thus composed of two independent hypotheses: (a) that a protoeukaryote host (PEH) engulfed the mitochondrial ancestor, and (b) that modern archezoa are 'missing links' that never possessed mitochondria. Hypothesis (b) is now unanimously rejected: every archezoan examined bears vestigial mitochondria, or genes inherited from mitochondria. Thus, all modern eukaryotes evolved from a mitochondrion-bearing ancestor.

But the baby was thrown out with the bath-water. Hypothesis (a) was also rejected, and because eukaryotes and archaea share a number of similar genes, the deposed PEH was replaced with archaea. Consequently, incorporation of the mitochondrion — not the origin of the nucleus — was hailed as the defining event in eukaryotic origins. This opened the floodgates of speculation, and numerous new hypotheses emerged. None is supported by observation: no archaea reside within bacteria, no bacteria reside within archaea, viruses have preposterously few similarities to the nucleus, and no RNA cells exist.

Of course, missing links might exist that could bolster one of the new theories. Because it is not possible to examine every cell on the planet for evidence, proponents could always argue that their theories are not disproved. Should we take them seriously, then?

No. Recall Bertrand Russell's (1872–1970) metaphorical teapot, orbiting the Sun but too small to be detected by telescopes. Without evidence, we cannot say the teapot is *not* there. Russell quipped, "if I were to go on to say that, since my assertion cannot be disproved, it is intolerable presumption on the part of human reason to doubt it, I should rightly be thought to be talking nonsense". In other words, the onus is on proponents, not sceptics, to find evidence for their theories.

If archezoa are not missing links, has evidence for the PEH theory also vanished? Are the various theories on equal ground? Again, no. First, phagocytosis — one cell engulfing another — is widespread among eukaryotes, but unknown in bacteria and archaea. Eukaryotes engulf bacteria as food, and some engulfed bacteria can evade digestion. There are conditional endosymbioses, in which one cell lives within another but escapes under adverse conditions, and stable endosymbioses, where host and guest are locked into the same evolutionary trajectory. Predatory eukaryotes even pilfer chloroplasts from their hosts. Second, every other organelle that evolved from a once free-living cell was initially engulfed by a eukaryote. This is, after all, how the chloroplast evolved.

The origin of mitochondria under the PEH theory is not some freak event requiring special explanation; mitochondria simply descend from an engulfed cell co-opted as an organelle. That this was an evolutionary success is clear: bona fide archezoa no longer exist. In contrast, archaea are not known to engulf bacteria (nor vice versa). So the alternatives to the PEH hypothesis require that bacterial or archaeal ancestors 'invented' engulfment, only to lose it again without trace — another assertion that cannot be disproved.

As Norman Pace pointed out (*Nature* **441,** 289; 2006), eukaryotes did not evolve from archaea; they share a common ancestor. This fits the PEH theory — the host was a direct ancestor of modern eukaryotes. If the host were, say, an archaeon, eukaryotes would appear on the tree of life as a subdivision of archaea — they would be phylogenetically part archaeon, part bacterium. The tree tells us they are part eukaryote, part bacterium, and sister to archaea.

Much uncertainty surrounds eukaryote origins. How did phagocytosis and the nucleus evolve? How was endosymbiosis between mitochondrion and host established? In answering these questions, we need the PEH theory. It is the only explanation based on a host capable of engulfing the mitochondrial ancestor by known processes — rather than by mechanisms founded in unfettered imagination. ■

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FURTHER READING
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CONCEPTS