Sex among eukaryotes is far more common than once believed

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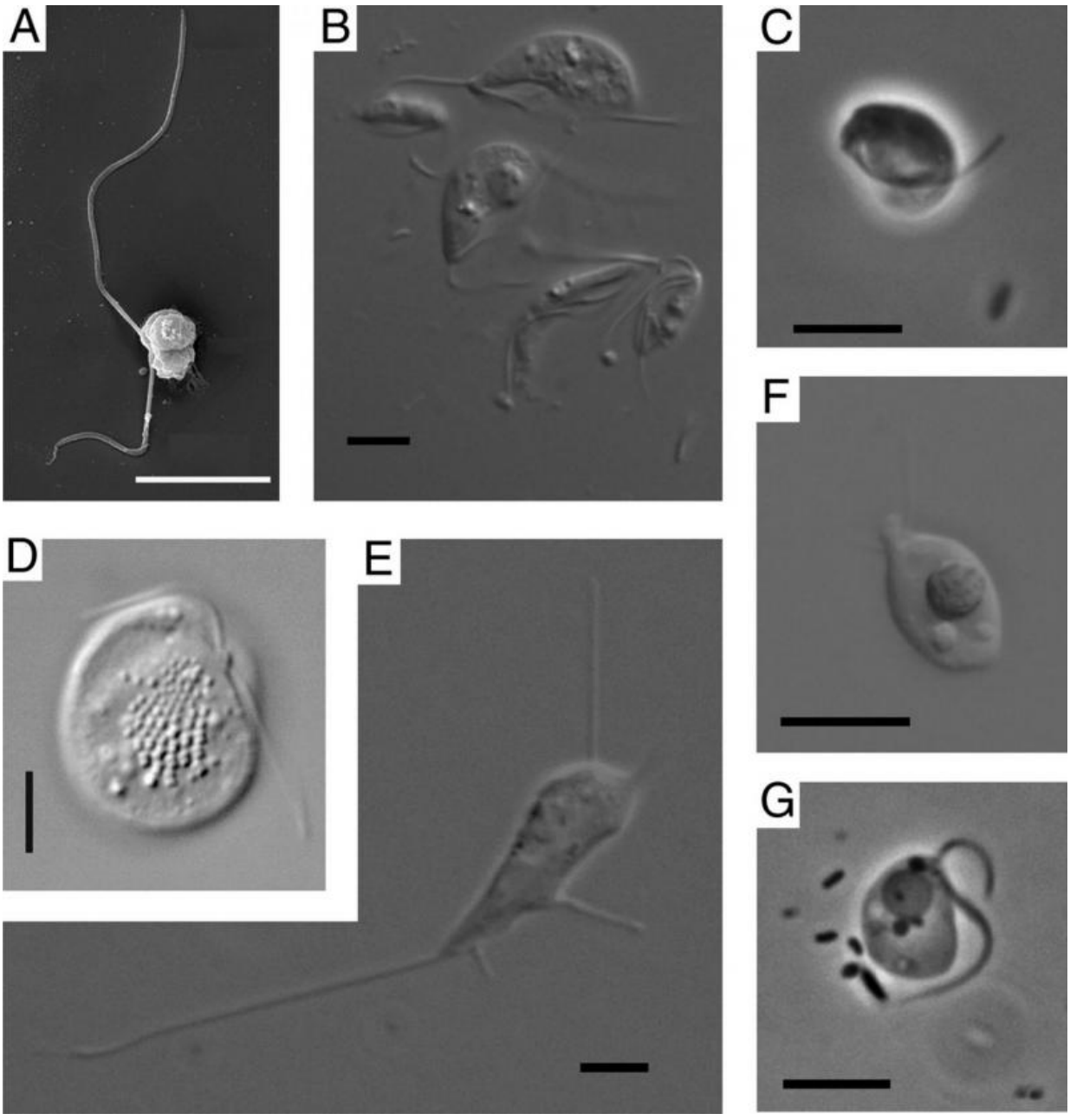

Representatives of deep eukaryotic lineages without published evidence for sex thus far. (A) Picomonas judraskeda (Picozoa). (B) Andalucia incarcerata and another, thus far undescribed jakobid (Jakobida). (C) Ancyromonas sigmoides (Ancyromonadida). (D) Roombia truncata (Katablepharida). (E) Breviata anathema (Breviatea). (F) Telonema subtilis (Telonemia). (G) An undescribed malawimonad (Malawimonadida). Images courtesy of Petr Táborský (B), Aaron Heiss (C, E, and G), and Akinori Yabuki (F); A and D were adapted from refs. 118 and 120. (Scale bars, 5 μm.) Credit: *PNAS* 2015 112 (29) 8827-8834; published ahead of print July 21, 2015, doi:10.1073/pnas.1501725112

(Phys.org)—For a long time, biologists have considered sex to be an inherent trait of multicellular life, while microbial eukaryotes were considered to be either optionally sexual or purely clonal. From this perspective, clonality in eukaryotes is seen as exceptional. However, a group of researchers Europe and Canada have recently published a paper examining this broad distinction more closely, and have suggested that it appears to stem from an improper comparison of unicellular and multicellular species.

The paper, published in the *Proceedings of the National Academy of Sciences*, points out that sex in multicellular organisms is simply clonal cell propagation among physically linked cells. "Hence," the researchers write, "from the perspective of cell lineage, sex in multicellular organisms is as episodic as it is in facultatively sexual unicellular eukaryotes." The authors' emphatic conclusion is that "sex is a ubiquitous, ancient, and inherent attribute of eukaryotic life."

Notably, the paper emphasizes that zoologists would be aghast at the absence of observed sex, while microbiologists are far more receptive to the lack of sex in protists. Many protist groups, including ciliates and green algae, propagate via sex, but direct observation of those processes

is lacking for the vast majority. Indeed, there are entire lineages of protists for which no evidence of sex processes exists. However, the authors screened scientific literature to find individual "signs of sex" in eukaryotic lineages, including physical observation of cell fusion or nuclear fusion, genetic evidence of meiosis or recombination, or changes in ploidy levels over the life cycle.

Among the individuals screened, Jakobida, Glaucophyta, and Malawaimonadida—putatively asexual eukaryotes— were all found to contain genes involved in gamete fusion and/or nuclear fusion. The authors suggest that sex among unicellular eukaryotes is likely to be far more common than currently believed, and the lack of evidence of sexual propagation attributable to the difficulty of microbiological observation. Highlighting this difficulty, they point out a famous example of a particular type of algae with two morphologically different life cycle stages, which had been wrongly considered to be two separate species. What we don't know about protist life forms still vastly outweighs what we've discovered. "...(W)e still have a tendency to underestimate how widespread sexual practices are in the different eukaryotic groups," the authors write.

Further, genome sequencing now supports the fundamentally sexual nature of eukaryotes. The authors cite numerous examples of putatively asexual eukaryotes found to express genetic traits associated with sex propagation. Giardia intestinalis was assumed to be asexual until genomic inspection revealed allelic differences indicative of sex. "The list of eukaryotic species that lack strong direct evidence for meiotic sex, but that seem sexual, as suggested by the presence of these meiosis-associated genes, is growing longer and longer," the authors write.

There are numerous adaptive benefits to sex: It creates genetic variation, repairs DNA breaks, and prevents the accumulation of disadvantageous mutations. Sexual reproduction is also associated with species survival

during adverse periods. Because of these advantages, the authors suggest, even asexual species overwhelmingly retain the option for meiotic sex propagation, even despite some of the disadvantages of sex for protists.

The paper goes on to speculate on the possibility that the evolution of meiotic sex was a defensive response to DNA-damaging effects of reactive oxygen species, and considers the possible influence of endosymbiotic organisms like chloroplasts and mitochondria on the evolution of sex.

More information: "Sex is a ubiquitous, ancient, and inherent attribute of eukaryotic life." *PNAS* 2015 112 (29) 8827-8834; published ahead of print July 21, 2015, DOI: 10.1073/pnas.1501725112

Abstract
Sexual reproduction and clonality in eukaryotes are mostly seen as exclusive, the latter being rather exceptional. This view might be biased by focusing almost exclusively on metazoans. We analyze and discuss reproduction in the context of extant eukaryotic diversity, paying special attention to protists. We present results of phylogenetically extended searches for homologs of two proteins functioning in cell and nuclear fusion, respectively (HAP2 and GEX1), providing indirect evidence for these processes in several eukaryotic lineages where sex has not been observed yet. We argue that (i) the debate on the relative significance of sex and clonality in eukaryotes is confounded by not appropriately distinguishing multicellular and unicellular organisms; (ii) eukaryotic sex is extremely widespread and already present in the last eukaryotic common ancestor; and (iii) the general mode of existence of eukaryotes is best described by clonally propagating cell lines with episodic sex triggered by external or internal clues. However, important questions concern the relative longevity of true clonal species (i.e., species not able to return to sexual procreation anymore). Long-lived clonal species seem strikingly rare. We analyze their properties in the light of meiotic sex

development from existing prokaryotic repair mechanisms. Based on these considerations, we speculate that eukaryotic sex likely developed as a cellular survival strategy, possibly in the context of internal reactive oxygen species stress generated by a (proto) mitochondrion. Thus, in the context of the symbiogenic model of eukaryotic origin, sex might directly result from the very evolutionary mode by which eukaryotic cells arose.