Trends in Genetics

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Spotlight

Clonal ants reveal a potentially hidden meiotic feature

Hugo Darras[1,*] and Qiaowei Pan[2,*]

Meiosis is essential for eukaryotic reproduction and provides the basis for Mendel's segregation laws. A recent study by Lacy *et al.* identified a significant deviation from these laws in a clonal ant, hinting at a potentially overlooked meiotic feature. This discovery may have broader implications for recombination in nonclonal eukaryotes.

Meiosis, the process by which haploid gametes are generated from diploid progenitors in preparation for reproduction, is a fundamental evolutionary driver of eukaryotic life. In most species, proper chromosome segregation during meiosis requires the formation of crossovers, which serve as physical anchors between homologous chromosomes. In addition, crossovers have evolutionary significance because they promote recombination, generating novel allelic combinations that can be subject to natural selection. Following the formation of these novel combinations, the alleles are distributed randomly into four haploid nuclei at the end of meiosis, giving each allele an equal chance of transmission to the next generation. This principle of random segregation is fundamental to Mendel's laws of inheritance, which remain foundational to modern genetics, even though they were established without the knowledge of chromosomes.

New research by Lacy *et al.* on the clonal raider ant revealed a significant deviation from Mendel's laws, characterized by a biased co-segregation of chromatids that have undergone recombination [1]. Unlike most ant species, the clonal raider ant establishes queenless colonies, where all individuals are worker females reproducing through parthenogenesis via central fusion automixis. In this mode of reproduction, which is frequent among insects, meiosis proceeds similarly to that in sexually reproducing species, but diploidy is restored not by fertilization but by the fusion of two haploid meiotic products descending from different maternal homologs. In principle, this process results in offspring genetically identical to the mother, except in recombined regions, where Mendelian segregation should lead to offspring being homozygous for one of the maternal haplotypes in two out of four instances [2] (Figure 1). Intriguingly, while such a mechanism is expected to cause loss of heterozygosity over generations, species reproducing via central fusion automixis, including the clonal raider ant, often maintain heterozygosity from mothers to daughters. Previously, the preservation of heterozygosity in these species was attributed to either a lack of recombination during meiosis or the selective mortality of offspring with reduced heterozygosity [3,4]. However, these explanations proved insufficient for the clonal raider ant. Using chromosome squashes and phased genome sequencing, Lacy *et al.* demonstrated that recombination is not impaired in this species, because numerous crossovers were observed across its 14 chromosomes. By carefully monitoring developmental lethality and modeling its potential impact, they further showed that mortality alone does not account for the preserved heterozygosity.

How can the clonal raider ant maintain heterozygosity across generations despite regular recombination occurring during meiosis? Lacy *et al.* suggested that this intriguing phenomenon requires a fundamental departure from Mendel's law of independent assortment. They proposed that chromatids undergoing recombination during meiosis must segregate nonrandomly, either consistently co-inherited or excluded together in the two meiotic products that will ultimately fuse to form the parthenogenetic offspring (Figure 1). This mechanism must rely on a low recombination rate, because multiple crossovers between different chromatid pairs could disrupt precise complementary sorting. Supporting this, Lacy *et al.* observed an average of only 0.4 crossovers per chromosome [1], a rate significantly lower than that found in other social Hymenoptera [5]. This discovery of a non-Mendelian segregation pattern in clonal raider ants parallels a recent finding in the nematode *Mesorhabditis belari*, where crossover chromatids were also found to co-segregate in parthenogenetic offspring, albeit involving incomplete meiosis in this case [6]. Notably, unlike typical meiotic drives, which manipulate meiosis outcomes to increase their transmission at the expense of the organism, drives in these two species do not favor any allele. Instead, they confer a fitness advantage by preserving genome-level heterozygosity across parthenogenetic generations, preventing the expression of recessive deleterious alleles.

The unique segregation bias observed during the meiosis of the clonal raider ant, which seemingly evolved as an adaptation to preserve heterozygosity in clonal reproduction, may originate from a more widespread mechanism linking crossover products during meiosis. Understanding this mechanism could reveal an overlooked, yet fundamental principle of meiosis, similar to how the study of selfish meiotic drivers in plants, animals, and fungi expanded our knowledge of crossovers, chromosome segregation, and centromere functions. Detecting segregation bias in female meiosis is challenging in most species. This is because, unlike clonal raider ants, where two meiotic products contribute to the next generation, only one of the four meiotic products is typically recoverable from the genome of the offspring in most species. As a result, the prevalence of such segregation bias remains largely unexplored.

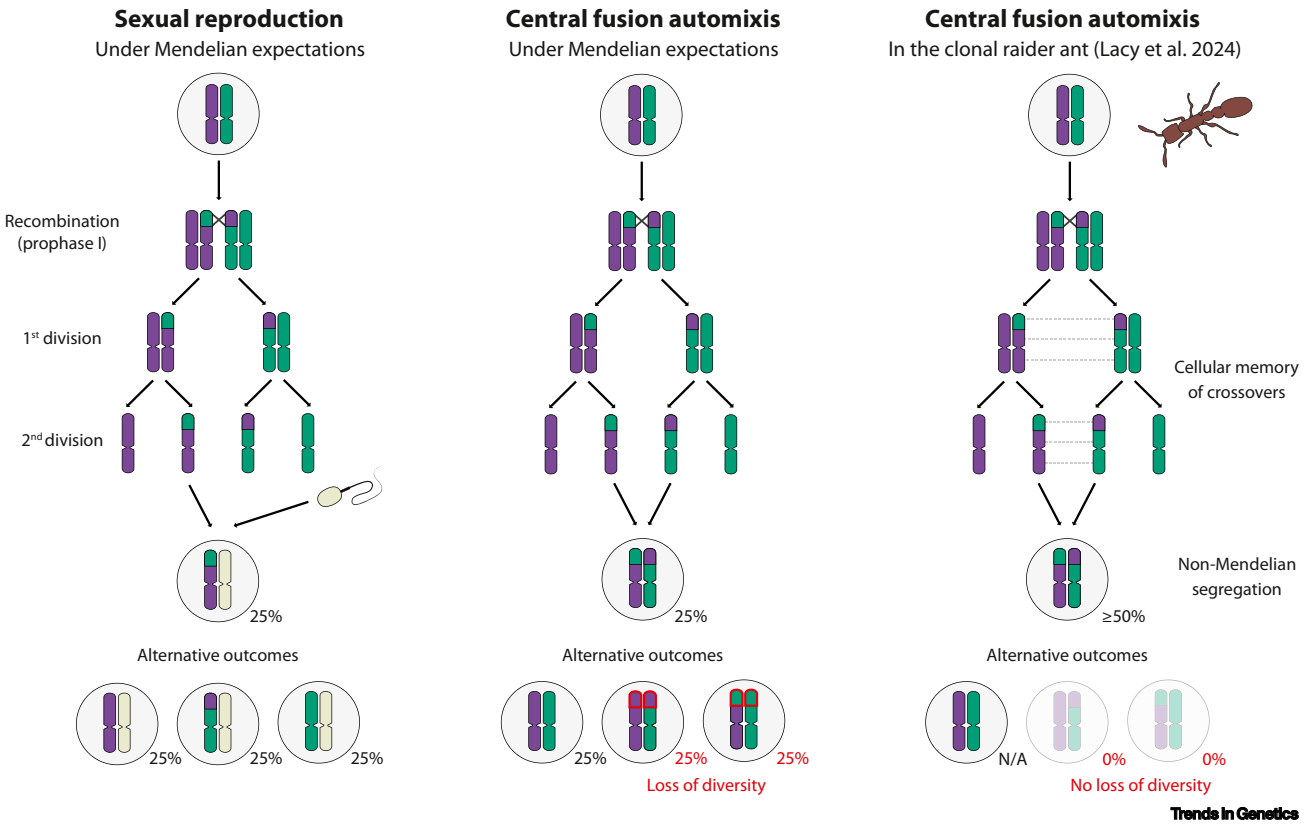

Figure 1. Overview of different types of female meiosis. Each panel illustrates a typical insect meiosis, resulting in a linear tetrad of haploid products, with two maternal homologs depicted in purple and green, and one crossover event illustrated. In canonical sexual reproduction, chromatids are randomly arranged into four haploid products, with one fusing with a male gamete. In central fusion automixis, meiosis proceeds as usual, but, instead of fusing with a male gamete, two of the haploid products derived from different homologs fuse to form a diploid zygote. According to Mendel's laws, a single recombination event during meiosis is predicted to cause a loss of diversity in 50% of the possible chromatid combinations in central fusion. However, Lacy *et al.* discovered that, in the clonal raider ant, chromatids involved in crossovers segregate nonrandomly, thereby preventing the loss of diversity across parthenogenetic generations [1]. It remains unclear whether only pairs of recombined chromatids contribute to the offspring or if pairs of nonrecombined chromatids also co-segregate half of the time. Abbreviation: N/A, not accessed.

However, research on two model organisms suggests these biases are more widespread than previously thought. In the fruit fly *Drosophila yakuba*, models propose that X chromatids with crossovers are favored, with 86% being chosen for fertilization [7]. Similarly, in humans, sequencing of all four products of female meiosis suggested that recombined chromatids are more likely (65%) to end up in the oocyte, although a recent study failed to replicate this pattern, underscoring the challenges in accurately studying the outcomes of meiosis [8,9]. The underlying mechanisms behind these reported segregation biases are not yet understood. Still, it was proposed that such cellular memory of crossovers may involve markers distinguishing recombined chromatids from no-recombined ones or persistent chromatin threads maintaining linkage between recombined chromatids throughout meiosis steps [6,10].

While further validation is needed, the hypothesis that nonrandom segregation of recombined chromatids may be more common than previously assumed could profoundly reshape our understanding of the forces influencing recombination. Recombination rates vary widely across species and are crucial in determining evolutionary rates and genetic diversity. Traditionally, recombination rates have been thought to be primarily influenced by crossover frequencies [11]. However, the existence of a widespread mechanism that could bias the segregation of recombined chromatids, thereby altering effective recombination rates, would prompt fundamental questions regarding the observed variation in recombination rates across taxa, the mechanisms of meiosis, and the origins of alternative reproductive modes.

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Declaration of interests

The authors declare no competing interests.

[1]Institute of Organismic and Molecular Evolution, Johannes Gutenberg University, Mainz, Germany
[2]Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

*Correspondence:
hdarras@uni-mainz.de (H. Darras) and
qiaowei.pan@unil.ch (Q. Pan).

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