

Genetics: Biased Transmission of Genomes According to Parents of Origin

A new study shows that wood ant queens selectively pass the maternally-inherited half of their genome to their daughters and the paternally-inherited half to their sons. This system, which most likely evolved from ancestral hybridization, creates distinct genetic lineages.

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Mendel's second law of genetics states that alleles of different genes assort independently of one another during gamete formation. This law usually holds true for genes not linked to each other on a chromosome. There are, however, some notable exceptions, such as hybridogenic frogs and fish, where females selectively exclude the paternal-inherited half of their genome during meiosis [1,2], or the platypus, which harbours five Y chromosomes that co-segregate during meiosis [3]. A recent genetic study [4] in wood ants of the genus *Formica* has revealed an even more unusual reproductive system whereby non-random assortment of chromosomes during meiosis leads to sex-specific genome transmission.

While conducting a population genetic study with 17 microsatellite markers and 81 amplified fragment length polymorphisms (AFLPs), Kulmuni *et al.* [4] found strong departure from the expected Hardy-Weinberg proportion of genotypes. A multilocus analysis revealed the presence of two distinct gene pools referred to as groups W and R. Although about 6% of the inferred mating occurred between individuals of the two groups, the high between-group genetic differentiation suggests that they do not translate into significant gene flow between the W and R groups.

The second and more striking finding of the study was an important difference in allele frequencies between males and females (queens and workers) in both the W and R groups. The difference was most remarkable in the R group, with a majority of the 17 microsatellites showing difference in allele frequencies between the sexes. To account for this difference, Kulmuni *et al.* [4] suggest

two alternative explanations. The first invokes genetic incompatibilities, with incompatible genotypes being eliminated. Such incompatibility effects have been reported in several ant species [5,6], but they pertain to the process of caste determination (the differentiation of female into either queens or workers). The alternative explanation invokes non-random assortment of chromosomes during meiosis: under this scenario, queens would pass on the maternally-inherited half of their genome to their daughters and the paternally-inherited half to their sons.

Two lines of evidence strongly militate against the first explanation. First, sex differences at almost all loci would require that the postulated genetic incompatibilities are extremely common throughout the whole genome (that for all the markers exhibiting sex-specific differences, there is at least one linked gene with incompatibility effects). This is highly unlikely. The other, and related problem, is that the presence of a large number of incompatible loci would translate into almost all offspring being non-viable because of the extremely low probability of having a 'compatible' combination of genes.

The finding that the maternally-inherited half of the genome is selectively transferred to daughters and the paternally-inherited half to sons has important evolutionary consequences. First, it translates into two distinct gene pools, the Maternally-inherited (*Mat*) and the Paternally-inherited (*Pat*) lineages. Thus, males, that develop from unfertilised eggs and are haploid (as usually is the case in ants), always have a *Pat* genome, while females have a *Mat/Pat* genome (the *Mat* lineage coming from their mother and the *Pat* lineage from their father). Consistent with this model, in the R group seven of the 17 microsatellites have common

alleles in females which are completely absent in males (these are alleles specific to the *Mat* lineage). Conversely, there are no male alleles absent in females, as expected from the fact that females also always have a copy of the *Pat* genome. (Similarly, females in the W group had four microsatellites with alleles common in females but wholly absent in males.)

Another consequence of all females having a *Mat/Pat* genome and all males having a *Pat* genome is brood inviability. Thus, given that a *Mat* genotype can apparently not give rise to viable haploid males, eggs with a *Mat* genotype would be viable only if fertilised (which would then give a viable *Mat/Pat* female). Conversely, because the *Pat/Pat* genotype can apparently not give rise to viable females, eggs with the *Pat* genotype would be viable only when unfertilised. In other words, this means that only half of the brood is viable unless a mechanism allows the selective fertilization of only eggs with a *Mat* genotype.

Finally, the selective transmission of the maternally-inherited half of the genome to daughters and paternally-inherited half to sons implies that males receive all their genes from their grandfather and none from their grandmother. Thus, males not only have no father (as usually is the case in ants), but they are clones of their grandfather!

Two lines of evidence suggest that this unusual mode of reproduction evolved by ancestral hybridization between *Formica aquilonia* and *Formica polyctena*. Morphogenic analyses of W and R workers and queens showed that their phenotypes are intermediate between *F. aquilonia* and *F. polyctena*. Second, many alleles present in only females of the R form can be found in the W form, and, inversely many alleles present in only females of the W form can be found in the R form. This pattern could be explained by the specific fixation of some alleles of *F. aquilonia* and *F. polyctena* in the *Mat* and *Pat* lineages of the W and R forms.

The system of reproduction discovered in these wood ants has similarities with two other unusual systems of reproduction recently discovered in ants. The first is in seed-collecting ants of the genus

Pogonomyrmex, where some populations contain two distinct genetic lineages [7]. Queens mate with both males of their own lineage and males of the other lineages. Eggs fertilized by males of the same lineage invariably develop into queens while eggs fertilized by males of the other lineage can only give rise to workers.

This reproductive system also results in there being a high proportion of unviable brood, because diploid intra-lineage eggs produced during the period of production of workers do not give rise to viable individuals [5,8,9]. Interestingly, these *Pogonomyrmex* systems with pairs of distinct lineages also evolved from ancestral hybridization, but there is currently no more gene flow between lineages or between the lineages and the parental species [7,10–12]. It remains to be investigated whether there is also a complete breakdown of gene flow between the *Mat* and *Pat* lineages of the *W* and *R* forms and between these gene pools and the two putative parental species *F. aquilonia* and *F. polyctena*.

The other unusual system of reproduction was uncovered in the little fire ant *Wasmannia auropuncta* [13]. In this species workers are produced by normal sexual reproduction but all queens are clonally produced from their mother and all males are clonally produced from their father. Interestingly, in this species there is no longer gene flow between males and females, as their genomes come

together only in the sterile workers. And, in a manner similar to maternally-inherited genomes of the *Formica* system, it seems that the *Wasmannia* female genome has lost the ability to produce viable males. In both cases the mechanism involved is unknown. Possible explanations include selective gene imprinting by one of the two parents, fixation of recessive deleterious alleles (expressed in haploid males), cyto-nuclear interactions, and/or fixation of allelic variants incompatible with the male-specific developmental pathway.

In conclusion, this new study [4] adds to the increasing number of unusual modes of reproduction recently discovered in ants. In addition to providing fascinating evolutionary enigma, these systems also provide unique opportunities to study the genetics of phenotypic plasticity, caste determination and incompatibilities.

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Cytokinesis: The Ubc of Positioning

A recent analysis of spindle positioning in yeast sheds light on how interactions between microtubules and the cleavage apparatus are modulated through mitosis to promote and maintain proper positioning of the spindle and cleavage plane relative to each other.

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During eukaryotic mitosis, proper positioning of the mitotic spindle and the site of cleavage relative to each other is a prerequisite for successful cell division. In animal cells, the spindle itself determines where the future cleavage plane will be and thereby positions the furrow machinery relative

to the mitotic spindle. Over decades, the mechanisms for cleavage furrow positioning in higher organisms have been strongly debated. Several models were proposed that appeared at first to be mutually exclusive because they propose opposite functions for the microtubules (Figure 1A). The first class of models implicates astral microtubules (aMTs) coming from

both asters in signaling the position of the future site of division at the spindle equator [1–4]. In these models, aMTs provide a positive signal for formation of the cleavage furrow. In the second class of models, aMTs relax the cortex around the asters, helping contraction to concentrate at the equator [5,6]. Here, the spindle midzone contributes to the process of furrow positioning by recruiting microtubules away from the cortex at the cleavage plane. Thereby, the cleavage plane is defined as a region of lower microtubule density. Therefore, in these models astral microtubules act as inhibitors of the furrowing process. Strong arguments exist for both