

# An Extraordinary Sex Determination Mechanism in a Book Louse

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*In this commentary, Leo Beukeboom considers the findings of Hodson et al. in this issue of GENETICS, and their discovery of an unusual sex determination mechanism in a book louse, a little-studied group of insects.*

**M**OST biologists are familiar with male heterogamety, the mechanism of sex determination in most mammals, including humans. Males produce two types of gametes that carry either an X or a Y chromosome, whereas females produce only X-carrying eggs. The Y chromosome determines maleness. Female heterogamety is less widespread, but well known to scientists that work with birds and butterflies. In these taxa, the female carries two different sex chromosomes (Z and W) and the male is the homogametic sex (ZZ). Both sex determination systems occur frequently in insect species, but other types exist as well. All hymenopterans (ants, bees, wasps, and sawflies) lack sex chromosomes, as do thrips, and a number of smaller clades across insects. Many have haplodiploid sex determination in which haploid males develop from unfertilized eggs and diploid females develop from fertilized eggs. Additional mechanisms are known, but appear to be less common, of which one of the most peculiar is paternal genome elimination (PGE). In this issue of *GENETICS*, Hodson et al. (2017) report a case of PGE as the mode of sex determination in *Liposcelis sp.*, a species of book lice (Psocodea).

Insects are well suited for studying diversity in mechanisms of sex determination. They are one of the largest organismal groups on Earth, comprising almost one million described species, and occupying all terrestrial environments. At the

chromosomal level, the most abundant mechanisms are male heterogamety, female heterogamety, and haplodiploidy, whereas at the level of genes and gene regulation the diversity appears overwhelming (Beukeboom and Perrin 2014; Blackmon et al. 2017). Surprisingly, for some of the 29 distinguished insect orders, next to nothing is known about their mode of sex determination. Dipterans have been well studied, including the model species *Drosophila melanogaster*, as have species that are relevant to human diseases, such as mosquitoes (Krzywinska et al. 2016) and houseflies (Dübendorfer et al. 2002). Economically important insects such as the honeybee (*Apis mellifera*) (Beye 2004) and the silkworm (*Bombyx mori*) (Suzuki 2010) have also been investigated. The variation in sex determination regulation in these few studied species implies that much of the diversity in insect sex determination has not yet been described, which calls for more studies in other groups.

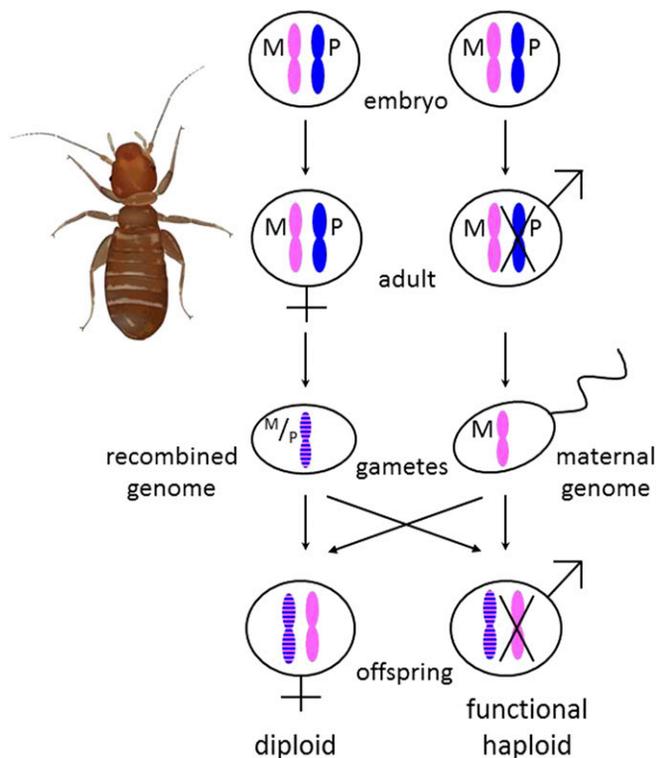
Hodson et al. (2017) investigated the reproduction of a species of woodlouse (Psocodea), representing an insect order for which no information on sex determination was previously available. They convincingly document the development of males from fertilized diploid eggs that eliminate half of their genome (Figure 1). All embryos begin as diploids, but soon after cell division those that will develop into males lose one of their chromosome sets, effectively becoming haploid. Those that become female remain diploid. This mechanism has previously been called parahaploidy (Nelson-Rees et al. 1980) or pseudoarrhenotoky (Sabelis and Nagelkerke 1988), but the term PGE is now being used (Herrick and Seger 1999). The term emphasizes that it is always the paternal genome that is lost in the male progeny. The result is effectively a haplodiploid mode of inheritance: mothers transmit a recombined copy of their genome to offspring,

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**Figure 1** Paternal Genome Elimination. Females and males develop from fertilized diploid eggs. Males are functionally haploid because the paternally-inherited genome is eliminated early during development. Females transmit a recombined genome to their offspring, but males transmit only the maternal copy. M = maternal, P = paternal. Book louse drawing by Jeannette Steenmeijer, Illustratiedesk.

but fathers transmit only their maternal genome copy, which is passed on by their daughters but not by their sons in the next generation.

How can one detect PGE? Traditionally, this required cytogenetic examination of early fertilized eggs. In other instances, visible markers may be used to demonstrate that it is always the maternal genome that is retained. Hodson *et al.* (2017) used both methods, but also applied modern genomic techniques. Fluorescent microscopy with markers for heterochromatin revealed condensed chromatin bodies in somatic cells of male but not female embryos. Crosses of two lines with polymorphic markers demonstrated that heterozygous females may transmit either allelic copy to progeny, but males transmit only the allele of maternal origin. These observations are consistent with transcriptional silencing of the paternal genome through extensive heterochromatinization. The authors also used the novel genomic technique of differential read coverage for identification of sex chromosomes (Vicoso and Bachtrog 2015). The read coverage of female and male genomes did not differ, suggesting the absence of differentiated sex chromosomes.

PGE has evolved multiple times independently, but it is not a common mode of sex determination (Lohse and Ross 2015). It has been recorded from several invertebrate orders, including phytoseiid mites (Acari), spring tails (Symphyleona and

Collembola), bark beetles (Cryphalini and Coleoptera), fungal gnats and gall midges (Sciaridae and Cecidomyiidae, both Diptera), scale insects (Neococcoidea and Hemiptera), and parasitic lice (Phthiraptera), the last being a sister group to Psocodea. Interestingly, these groups differ in the details of the PGE mechanism in terms of the degree and timing of paternal genome loss. In some scale insects and mites, the entire paternal genome is lost during early embryonic development. In bark beetles, some other scale insects, and *Liposcelis sp.*, it is retained in an inactive form in the adult male, but excluded from the dividing spermatogonia, resulting in sperm that carry only the genome of maternal origin (Nur 1980). In contrast, in sciarid and cecidomyiid flies only one or two paternally-inherited X chromosomes are excluded during embryogenesis, rather than the entire paternal genome (Goday and Esteban 2001).

Why did certain groups evolve PGE and others not? Bull (1983) suggested that diploid species with a high proportion of genes that are X-linked and haploid in males, *i.e.*, species with heteromorphic sex chromosomes and few autosomes, might transition to haplodiploidy more easily. There is some evidence for this hypothesis from mites (Blackmon *et al.* 2015). Several authors have tried to identify ecological conditions that are specific to PGE species. Such species often have limited dispersal ability and high inbreeding, which may select for a haplodiploid mode of reproduction (Normark 2003; Gardner and Ross 2014). Another selective benefit may be that PGE allows maternal control over progeny sex ratio in response to environmental conditions (Ross *et al.* 2011). Hodson *et al.* (2017) found that females of *Liposcelis* produce on average one son for every two daughters, and that this ratio becomes more female biased with age. They also found an effect of density at which females are reared, consistent with the evolution of sex determination where maternal effect is a strong driving force.

PGE requires distinguishing between the genomes of maternal and paternal origin, a process known as genome imprinting. Studies of PGE may thus be instructive about developmental processes, such as parent-of-origin recognition, epigenetic regulation of genome stability, heterochromatinization, and chromosome behavior during mitosis and meiosis. There is still very little known about the molecular genetic regulation of PGE. Application of modern genomic techniques may be the way forward, such as whole-genome sequencing for detecting the presence and possible loss of sex chromosomes, and transcriptomics for demonstrating genome inactivation during development. Given the variation in mechanisms of paternal genome loss among taxa, it is to be expected that a diversity of gene regulatory mechanisms underlie this extraordinary mode of sex determination.

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