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Review

Sex determination in the haplodiploid wasp *Nasonia vitripennis* (Hymenoptera: Chalcidoidea): A critical consideration of models and evidence

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Abstract

Sex determining mechanisms are highly diverse. Like all Hymenoptera, the parasitic wasp *Nasonia vitripennis* reproduces by haplodiploidy: males are haploid and females are diploid. Sex in *Nasonia* is not determined by complementary alleles at sex loci. Evidence for several alternative models is considered. Recent studies on a polyploid and a gynandromorphic mutant strain point to a maternal product that is balanced against the number of chromosomal complements in the zygote and a parent-specific (imprinting) effect. Research is now focused on the molecular details of sex determination in *Nasonia*.

Keywords: Genomic imprinting; Hymenoptera; *Nasonia*; Polyploidy; Sex determination

Contents

1. Introduction

An intriguing question is to what extent sex determining mechanisms are conserved during evolution. The fact that almost all multicellular sexual species reproduce with either separate

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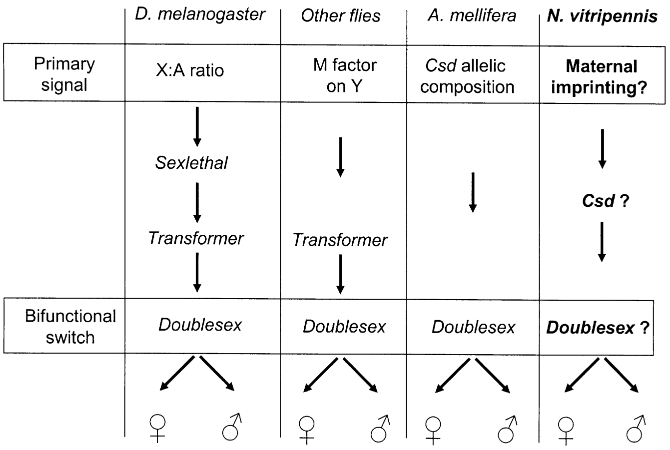

Fig. 1. Sex determination cascades in Diptera and Hymenoptera. Evolutionary conservation decreases from the bottom upwards. A: autosome sets, X: X-chromosome, Y: Y-chromosome, M: male determining factor, *Csd*: complementary sex determiner.

or combined male and female function, may suggest similar underlying genetic mechanisms for sexual differentiation. However, sex-determining mechanisms vary considerably and change rapidly in the course of evolution [1]. After elucidation of the genetics of sex determination in *Drosophila melanogaster* and *Caenorhabditis elegans* at the end of the last century [2], data have started to accumulate on the genetic regulation of sex determination in a large number of organisms. This allows for a more thorough consideration of the evolution of sex-determining mechanisms. An illustrative example is sex determination in a number of insects [3–16]. Consistent with Wilkins [17], these studies reveal evolutionary conservation at the basis of gene cascades, but divergence at the level of primary signals (Fig. 1).

There is a long-standing interest in sex determination of hymenopteran insects (ants, bees, sawflies and wasps) due to their haplodiploid mode of sex determination and the absence of heteromorphic sex chromosomes. Arrhenotoky is the most prevalent mode of reproduction among Hymenoptera: males are haploid and develop parthenogenetically from unfertilized eggs, whereas females are diploid and develop from fertilized eggs (Fig. 2). Sex determination is somehow triggered by the number of chromosome sets present in the embryo, but still little is understood about the molecular regulation. For over 60 years, it has been known that different sex determining mechanisms exist within the Hymenoptera [18]. Under complementary sex determination (CSD), gender is genetically determined by a single locus with multiple alleles: individuals that are heterozygous at this locus develop into females, whereas hemizygotes and homozygotes develop into haploid and diploid males, respectively [18]. This mode of sex determination has now been shown for more than 60 species [19]. It is considered ancestral although very few species from the basal taxonomic groups have been tested for CSD (Fig. 3) [20]. The *csd* locus was recently identified and cloned for the honey bee [8]. However, sex determination in some groups, such as the large parasitoid wasp group Chalcidoidea, can clearly not be explained by CSD because homozygous diploids develop into females nevertheless.

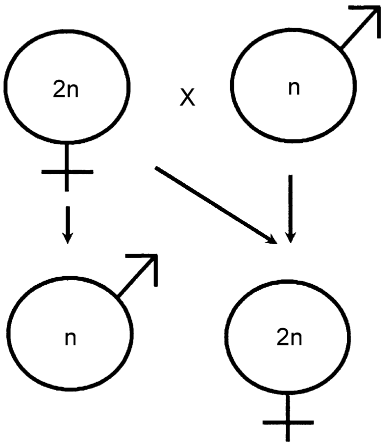

Fig. 2. Haplodiploid sex determination. Females are diploid and produce haploid eggs. Males are haploid and produce haploid sperm. Unfertilized eggs develop into haploid males and fertilized eggs into diploid females.

The parasitic wasp *Nasonia vitripennis* has been extensively studied genetically and is rapidly being recognized as a model system in evolutionary and developmental biology [21–25]. It has been known for a long time that its sex determination is not governed by CSD [26,27], but for many years progress has been made in elucidating its mode of sex determination [28]. Recently, several studies reported on the genetics of sex determination in *N. vitripennis* [29–32]. In this paper, we compile and interpret the currently available genetic data in relation to the proposed alternative models to CSD.

2. Mutant strains

Many of the discussions about sex determination in *N. vitripennis* have been prompted by attempts to accommodate observations on the ploidy level and sex of aberrant individuals. Whiting [33] reported spontaneous mutations to polyploidy in his stock cultures and one such strain has been maintained ever since. It has been used by Dobson and Tanouye [34] and Beukeboom and Kamping [29]. Triploid females have low fecundity and produce both haploid and diploid eggs, both of which normally develop into males if unfertilized, but into females if fertilized (Fig. 4). In the lab, it is possible to determine the ploidy level by using two different recessive eye-colour mutations, *scarlet* and *oyster* that do not recombine. Homozygosity at the mutant allele at either one of these loci results in a deviation from phenotypically “wildtype” (purple) eyes [35]. Diploid males are fully fertile. They produce diploid sperm mitotically, indicating that ploidy level does not determine the mechanism of spermatogenesis (meiotic or mitotic). They are mated to diploid homozygous *scarlet* females to re-obtain triploid females that carry two chromosome sets of the father and one set of the mother (see Fig. 4). Hence, it is important to realise that diploid males that are known from *N. vitripennis* do not arise from homozygosity under CSD (see below) but from unfertilized diploid eggs.

Males from some natural populations carry the paternal sex ratio (PSR) distorter [36]. PSR is a supernumerary chromosome