

## NEWS AND COMMENTARY

Sporadic sexual reproduction

# Sex to some degree

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The evolution of sex has been considered the queen of problems in evolutionary biology (Bell, 1982). The problem is why the male sex has not been discarded as it does not serve any short-term benefits. Males do not produce offspring and the energy saved on producing males could be allocated to females that can reproduce by themselves. On the other hand, sex may be beneficial in the long term because it creates new variation for selection to act upon (Weismann, 1889). A longstanding question is why there are so few organisms that solve this paradox with a little bit of sex (Green and Noakes, 1995), by combining the benefits of occasional sexual reproduction with low investment in male function? A recent study (D'Souza *et al.*, 2006) shows that a freshwater flatworm may thrive from predominantly parthenogenetic reproduction mixed with a little bit of sex.

Flatworms of the species *Schmidtea polychroa* do it quite differently. First, they are simultaneous hermaphrodites, meaning that every individual worm is both male and female during its entire lifespan. Second, they require sperm entering the egg to initiate egg devel-

opment, but the sperm chromosomes are typically expelled from the zygote and do not contribute genetically to the next generation. Hence, reproduction is parthenogenetic and sperm dependent. Third, parthenogens are polyploid, usually triploid, but sometimes tetraploid. They produce polyploid eggs, but haploid sperm (Benazzi Lentati, 1970). Finally, although each individual has male and female reproductive organs, they cannot fertilize themselves, but need to obtain sperm from a conspecific individual. Why go through all this hassle to reproduce?

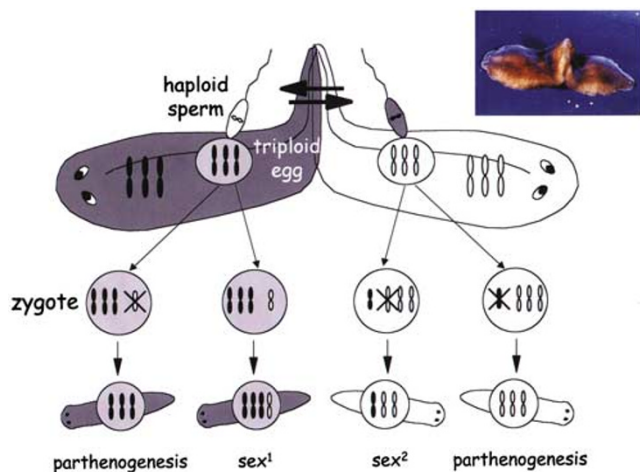
D'Souza *et al.* (2006) fingerprinted parental worms and their progeny to show that paternal DNA is sometimes inherited (Figure 1). They combined this with karyological analyses and showed that triploid mothers can produce tetraploid offspring with added paternal microsatellite alleles. Although such genome additions had been reported before, it is now clear that the added chromosome set need not be of maternal origin, for example, resulting from meiotic aberrations during oogenesis. Even more surprisingly, the authors also observed paternal inheritance with-

out an increase in offspring ploidy. In several crosses they found that addition of paternal alleles was compensated by loss of maternal alleles. Overall, the authors estimate that 5% of the offspring is not clonally produced. These observations alter our view of sperm-dependent parthenogenesis, it may be considered as a means of 'minimal sex'.

Although not a common mode of reproduction, sperm-dependent parthenogenesis has evolved multiple times within seven phyla (Beukeboom and Vrijenhoek, 1998). It may simply be considered as an evolutionary transition towards obligate parthenogenesis, but it has also been questioned whether such a reproduction mode would confer any selective advantage. For *S. polychroa* this question can now be answered positively; it allows for occasional sexual recombination that generates genetic variation. It remains to be seen whether this is a common phenomenon among sperm parthenogens in different taxa.

A number of intriguing follow-up questions remain. From a mechanistic point of view, how do these worms control paternal inheritance? Are the observed cases merely accidental by-products of an imperfect sperm expulsion mechanism or can the incorporation of paternal chromosomes be actively manipulated? Is paternal inheritance always involving complete chromosome sets, or is the process more intricate and allowing for replacement of single chromosomes or even recombination between egg and sperm chromosomes? Answering these questions requires more genetic experiments and detailed marker screening of parents and offspring. A first approach towards determining the potential adaptive significance of the process is to look for genetic variation for rare sex. Frequencies of paternal inheritance varied from 0 to 25% per investigated family. This suggests that selection for increased paternal inheritance may be effective. More challenging would be to show that populations that undergo paternal inheritance are selectively favoured over pure clonal ones. They may be better in preventing mutation accumulation or in resisting strong environmental perturbations, as predicted by general theories about the evolution of sex.

It has been a longstanding enigma why so few organisms exist that combine parthenogenetic and sexual reproduction. A number of recent studies have shown that parthenogens can have covert sex and suggest that rare sexual processes may be more common than previously thought. The flatworm



**Figure 1** Reproduction in *S. polychroa*. Hermaphrodites are polyploid and exchange sperm reciprocally. Sperm is either used for egg activation only and reproduction is clonal (sperm-dependent parthenogenesis, outer diagrams) or, occasionally, contributes genetically to offspring and reproduction is sexual (inner diagrams). Paternal inheritance can increase ploidy (type 1) or be accompanied by maternal chromosome displacement (type 2). Worm drawing and photo – Nico Michiels.

*S. polychroa* is a good example of an organism with, at first sight, an unnecessarily complicated reproductive mode, but at deeper insight it may well be efficiently exploiting the benefits of sexual and asexual reproduction.

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