EVOLUTION OF SEX

Genomic health in an asexual fish

The genome of the Amazon molly (*Poecilia formosa*), a parthenogenetic fish species, shows little genetic decay and a high degree of diversity. The genetic health of this asexual vertebrate is surprising given the accumulation of genomic damage that is expected to follow from asexual reproduction.

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Sexual reproduction is nearly universal among higher organisms despite the expectation that sexual populations should be rapidly outcompeted by asexual competitors. Because only females contribute to population growth, the production of males effectively halves the reproductive output of sexual females. The proposed solutions to the paradox of this 'twofold cost of sex'[1] revolve around the fact that sex is associated with the mixing of genetic material through recombination and segregation[2]. Thus, sex could be favoured because recombination increases the variance in fitness, thereby enhancing the efficacy of directional selection or providing an escape from frequency-dependent selection. Inversely, the absence of recombination could select against asexuals because genetic linkage on a genome-wide scale can lead to the accumulation of deleterious mutations ('Muller's ratchet') and, ultimately, the extinction of asexual lineages.

In the absence of consensus on which main force drives the evolution of sex (or whether a single main driver even exists)[3], studying the rare asexual lineages can provide insights into the costs and benefits of asexuality. Writing in *Nature Ecology & Evolution*, Warren et al.[4] do just this by investigating the genomic features of a parthenogenetic fish species, the Amazon molly *Poecilia formosa* (Fig. 1). The main finding of the paper is that the species is in remarkably good genomic health. Based on the inferred age of the lineage, 100,000 years, significant genomic decay would be expected to have occurred, possibly even to the point of causing extinction. Surprisingly, however, Warren et al. found little evidence for an accumulation of deleterious mutations. In fact, the molly genome looks comparable to its sexual parents with regard to almost all population- and phylogenetic statistics analysed. Even genes involved in spermatogenesis and meiosis, a priori obsolete in an asexual species, are still intact and show little sign of decay. These results are remarkable and suggest that in this species, Muller's ratchet simply has not acted in the predicted way.

Fig. 1 | The Amazon molly (*P. formosa*) is an asexual fish with remarkable good genomic health. Credit: Manfred Schartl, University of Würzburg.

One area where the Amazon molly genome did prove exceptional is in the context of genetic diversity. As expected from its hybrid origin, the molly genome shows a high degree of heterozygosity. The high within-genome diversity also extends to immune genes, which not only show high levels of heterozygosity but also elevated allelic variation across paralogous gene families. This finding is important in the context of 'Red Queen' dynamics, where frequency-dependent selection would be expected to favour sexual recombination[5]. As Warren and co-workers argue, starting off with a great deal of genetic diversity and the associated broad immune defences might have allowed the Amazon molly to avoid the fate of other asexual lineages that serve as an easy, immobile target for pathogen specialization.

The genetic health of the Amazon molly provides an intriguing contrast to the prevailing idea of asexual boom and bust, where the initial advantage of escaping the twofold cost of sex is quickly outweighed by the accumulating genomic damage that follows from clonal reproduction. Accordingly, Warren et al. propose that part of the rarity of asexual species might be due to the difficulty of creating a functioning asexual organism from a sexual ancestor. This is an interesting thought that deserves consideration, but also requires further development. For example, one might wonder whether functional barriers to asexuality would not vary phylogenetically, in which case the frequency of asexual lineages should show some degree of clustering across the tree of life.

The lack of decay in the molly genome also contrasts with the idea of Muller's ratchet as a major cause of extinction of asexual lineages and suggests that rapid decay is not a foregone conclusion.

What preserves genome integrity in the Amazon molly is unclear, but obvious counteracting forces such as gene conversion or occasional paternal introgression could be ruled out[4]. One potentially important point worth adding is that a switch from sexual reproduction to female parthenogenesis eliminates males as a major source of mutation[6]. Owing to the high rate of cell proliferation in spermatogenesis, mutation rates in many organisms — including fish — are heavily biased towards males[7,8]. Converting to asexuality will therefore significantly reduce mutational input. As deleterious changes make up the majority of mutations, this would significantly slow down Muller's ratchet or could even make parthenogenesis advantageous in the medium term[6]. It would be interesting to analyse substitution patterns in more detail to investigate whether and to what extent the alleviation of mutation pressure explains the surprisingly low extent of genomic decay in the Amazon molly.

Warren et al.'s study has provided fascinating insights and interesting avenues for further research. The Amazon molly is the first asexual metazoan to have its genome analysed to such depth. More data of this type will allow us to assess the generality of the patterns described here and obtain a better understanding of the evolution of asexuality and the forces driving it. ❐

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Published online: 12 February 2018
https://doi.org/10.1038/s41559-018-0485-7

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Competing interests

The authors declare no competing financial interests.