SUPERGENES

Y chromosome evolution spurs behavioural diversity in male fish

The Y chromosome of the freshwater fish *Poecilia parae* may have successfully evolved five haplotypes that are maintained in the population for alternative male reproductive strategies.

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Alternative male reproductive strategies have convergently evolved in a wide variety of species. They are manifested as large territorial 'aggressor' males, small female-mimicking 'sneaker' males and colourful 'dandy' males. These two or three types of distinctive colour and behavioural polymorphisms have been characterized in the ruff (a lek-breeding wading bird)[1], the side-blotched lizard (a small iguanid lizard in California)[2] and the livebearing fish *Poecilia parae*[3], to

mention just a few examples. The genetic determinants of such disparate male morphs have long intrigued biologists. They might be determined by supergenes, that is, multiple linked genes responsible for a series of complex phenotypes that are maintained in the population by reduced recombination[4]. Writing in *Nature Ecology & Evolution*, Sandkam et al.[5] report somewhat unexpectedly that the gene-poor Y chromosome of *Poecilia parae*, a special case of supergene, harbours five haplotypes

corresponding to five male morphs, and suggests different molecular mechanisms of male reproductive strategies that evolved independently.

Many poeciliids are popular aquarium fish found in the Americas and are also classic model systems for studying evolution of sexual selection and sex chromosomes. Unlike its well-known relative the guppy (*P. reticulata*) with continuous variation of male colours for female choice, *P. parae* males display five morph phenotypes
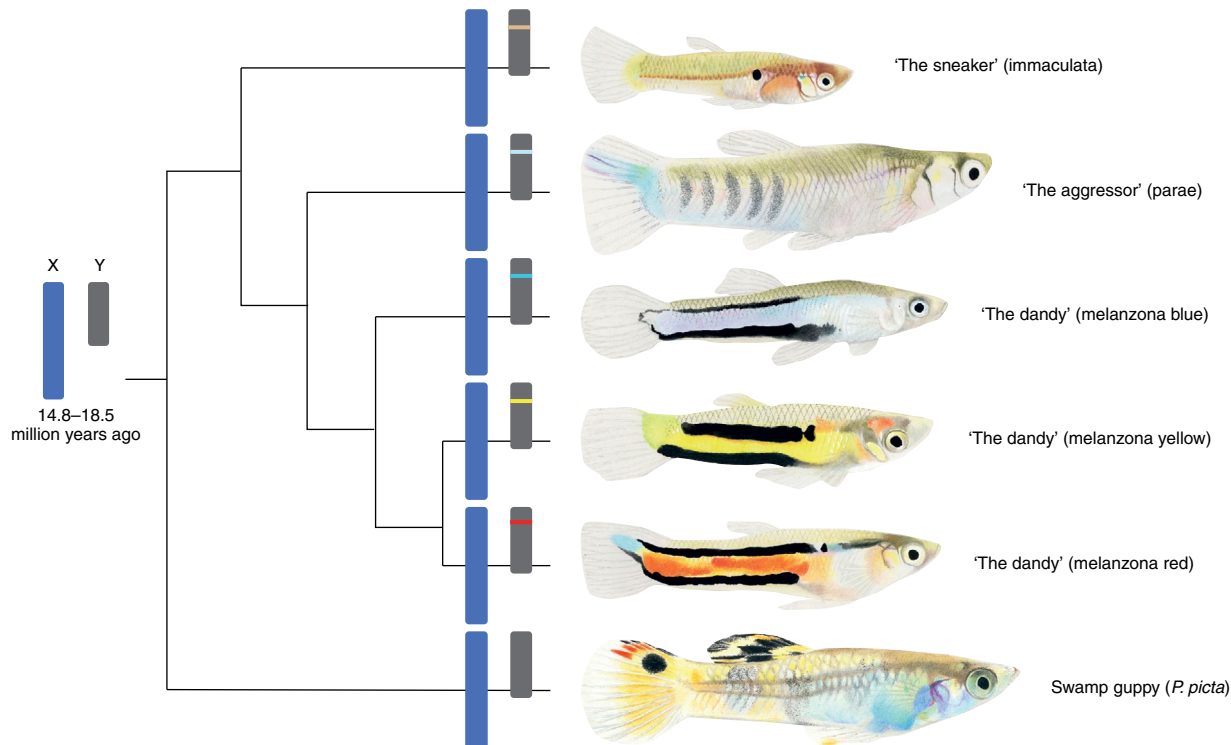

Fig. 1 | Five male reproductive morphs linked to the *Poecilia parae* Y chromosome. Phylogenetic relationships of five male morph phenotypes ('sneaker', 'aggressor' and three colour types of 'dandy') of the freshwater fish *P. parae*. Sandkam et al.[5] used this system as a model for studying sexual selection and evolution of supergenes. *P. parae* and *P. picta* share one pair of highly heteromorphic XY chromosomes that originated 14.8–18.5 million years ago. Since the morph phenotypes are passed from father to son, and are absent in other poeciliids, the five Y-linked alleles (indicated by different coloured bars) that control the respective morph probably emerged after recombination was suppressed on the Y chromosome. The 'dandy' and 'aggressor' alleles are closer to each other than to the 'sneaker' allele. Adapted with permission from ref. [5], Springer Nature Limited.

Labels in figure: 'The sneaker' (immaculata); 'The aggressor' (parae); 'The dandy' (melanzona blue); 'The dandy' (melanzona yellow); 'The dandy' (melanzona red); Swamp guppy (*P. picta*); X; Y; 14.8–18.5 million years ago

('aggressor', 'sneaker' and three 'dandies' of different colours, Fig. 1). Although the 'aggressors' are most abundant in the wild, female choice tests[3] have shown that they are, however, less attractive to females than the 'dandies'. Therefore, *P. parae* morphs provide a fascinating system for dissecting the genetic basis of the trade-off between natural selection and sexual selection.

What's special about *P. parae* is that all male morphs are strictly passed from father to son, that is, controlled by Y-linked alleles. Y-linked regions without recombination can be considered as a supergene and usually suffer from massive loss of genetic polymorphism and functional genes, as well as invasion of transposable elements due to lack of homologous recombination[6]. Nevertheless, some Y-linked genes may undergo adaptive changes in gene expression or copy numbers in response to the male-specific genetic environment, as previously demonstrated in *Drosophila*[7] and mice[8]. Given that the five Y-linked haplotypes have been stably segregating in *P. parae* populations, they might be under selection in the different male morphs.

Sandkam et al. found a reduced male read coverage to the same homologous chromosome of *P. parae* and its related species swamp guppy (*P. picta*), showing that both species share one pair of highly heteromorphic XY chromosomes that originated around 15 million years ago. Since *P. picta* and other poeciliids do not have the five morphs, the morph-associated alleles likely emerged after recombination became suppressed on the *P. parae* Y chromosome. Phylogenetic analyses using non-redundant male-specific sequence strings (called Y-mers) confirmed that individuals of the same or similar morph cluster together, and the three 'dandies' are closer to the 'aggressors' than to the 'sneakers'. Interestingly, this parallels the relationships between morphs of the ruff — the 'aggressor' (or 'independent') allele is also most divergent from the 'sneaker'

(or 'faeder') allele, while the intermediate 'satellite' ruff allele was speculated to be derived from recombination between the former two[1]. However, this evolutionary scenario seems unlikely for the Ys of *P. parae* if recombination was indeed suppressed very early on. The 'aggressor' haplotype might as well best represent the most ancestral one as it has the relatively least morph-specific Y-mers, while the derived 'dandies' were possibly driven by more extreme diversifying female choice and have the most unique Y-mers. The ancestral haplotypes, the sequence of events and the time of emergence of each morph still need to be determined.

Identifying Y-linked genes that account for the distinctive morphs is another open endeavour, since only one or two genes have been found to be unique to one of the three morphs. It is possible that some morph-specific genes are yet to be identified due to incomplete Y chromosome assemblies derived from Illumina sequencing. Another possibility is that Y-linked regulatory changes that alter the expression patterns of autosome or X-linked genes shared by both sexes through epistatic interactions may instead be responsible for the phenotypic differences between morphs. Previous studies in *Drosophila* attributed the genome-wide expression difference to the Y-linked variation of heterochromatic content among individuals that differ only by their Y chromosome origins, but not their Y-linked genes[9]. It will be very interesting to test this possibility with more complete Y chromosome sequences and gene expression data.

Regardless of the actual underlying genetic mechanisms, the case of *P. parae* morphs suggests a new trajectory by which not only alternative male reproductive strategies can arise but also for the evolution of supergenes. Chromosome inversion polymorphisms are ubiquitous among species but puzzling since their first report in *Drosophila* a century ago[10]. On one hand, recombination suppression is expected to

cause accumulation of deleterious mutations in the region, as evidenced by the Y chromosomes of many species. On the other hand, recombination suppression prevents the disruption of adaptive combination of multiple alleles that has been shown to be critical for dimorphic social organization in ants[11], mimetic wing patterns of butterflies[12] and local adaptation of different ecotypes of monkeyflowers[13]. The five Y-linked male morphs of *P. parae* probably emerged after recombination has halted, suggesting that recombination suppression made the Y chromosome a preferential environment for origination of novel supergenes related to the male-specific traits. ❐

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Competing interests

The author declares no competing interests.