Poeciliid Research

Sex chromosomes in fish. How sex chromosomes emerge and how they end

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Abstract. This paper aims to show, based on the latest studies in poeciliid fish and other fish species, how sex chromosomes appear, how they evolve and how they are supposed to end. Sex chromosomes originate from autosomes. Initially, the first differentiation appears in the form of minor genes specific to the male and female sex, scattered randomly along the length of the future sex chromosomes. Their abundance or frequency will influence the differentiation of the organism to one sex or the other. These minor genes tend to be concentrated in regions that are not predisposed to recombination through crossing-over, forming a major gene, more precisely the sex-determining locus. In this region, where genetic recombination is restricted, sexually antagonistic genes tend to accumulate. Such linkage of sexually antagonistic genes to the sex-determining locus will further promote the restriction of genetic recombination, rendering most of the sex chromosomes unable to recombine through crossing-over. The lack of genetic recombination will further promote the accumulation of non-functional DNA sequences and to the degeneration of the non-recombinant sex chromosome region. Sometimes, the decay affects the whole chromosome and the system is aborted. Therefore, some systems of sex determination have in the case of individuals of one sex, with a chromosome less than in the case of the opposite sex. In other cases, the obsolete sex-determining system is replaced by a new one, from a new pair of autosomes. We may conclude that emergence, evolution and replacement of sex chromosomes in fish is a cyclical process, which happens faster than we believed. Although mutations occur randomly, the evolution of sex chromosomes is directly correlated with the species history and ecological context.
Key Words: sex chromosomes, poeciliid fish, emerging, replacement, evolution.

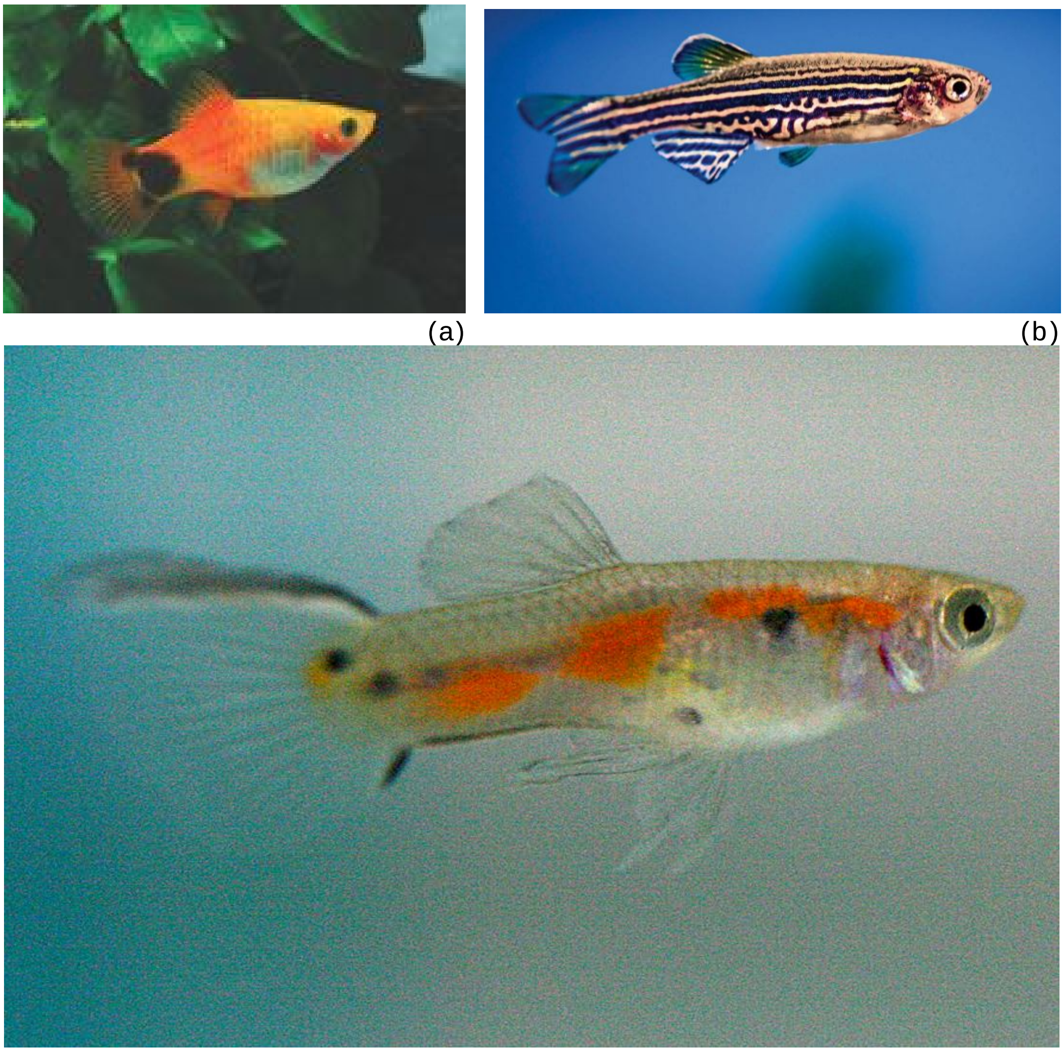
Introduction. The group of poeciliids is intensively studied in terms of the evolution of sex chromosomes (Mag & Petrescu 2006; Mag & Bud 2006a, b; Petrescu & Mag 2006; Mag et al 2006; Petrescu-Mag & Bourne 2008; Petrescu-Mag 2008; Miller et al 2010; Oroian 2015; Abbott et al 2017; Gordon et al 2017). Numerous studies have shown the coexistence within some poeciliid populations of two different chromosomal systems of sex determination (Nanda et al 2003), which denotes a rapid succession of these evolutionary processes (Petrescu-Mag 2018). This paper aims to show, based on the latest studies in poeciliid fish and other fish species, how sex chromosomes appear, how they evolve and how they are supposed to end.

Sex Chromosomes in Fish. Sex chromosomes originate from autosomes. Initially, the first differentiation appears in the form of minor genes specific to the male and female sex, scattered randomly along the length of the future sex chromosomes (Wang et al 2018; Kottler & Schartl 2018). Their abundance or frequency will influence the differentiation of the organism to one sex or the other. These minor genes tend to be concentrated in regions that are not predisposed to recombination through crossing-over, forming a major gene, more precisely the sex-determining locus. In this region, where genetic recombination is restricted, sexually antagonistic genes (i.e., genes that are beneficial to one sex but detrimental to the other sex) tend to accumulate (Lindholm & Breden 2002). In this way, genes that are detrimental to females, for instance, cannot be transmitted to female homogametic individuals (because homogametic females do not possess the Y chromosome) (Rice 1987a). This linkage of sexually antagonistic genes to the sex-determining locus will further promote the restriction of genetic recombination, rendering most of the sex chromosomes unable to recombine through crossing-over (Lindholm & Breden 2002; Rice 1987a). The lack of genetic recombination will further lead to the accumulation of non-functional DNA sequences and to the degeneration of the non-recombinant sex chromosome region (Charlesworth 1978; Rice 1987b). The three model species of fish represent basic steps of sex chromosome evolution: (i) the zebrafish, *Danio rerio* (Hamilton, 1822), with an all-autosome karyotype; (ii) the platy fish, *Xiphophorus maculatus* (Günther, 1866), with genetically differentiated sex chromosomes but no differentiation between X and Y detectable in the synaptonemal complexes or with comparative genomic hybridization in meiotic and mitotic chromosomes; (iii) the guppy fish, *Poecilia reticulata* Peters 1859, with genetically and cytogenetically differentiated sex chromosomes. This evolution of sex chromosomes was thought to be a slow process, but recent studies performed to genus *Xiphophorus* have shown that a change in sex determination system was possible over few generations through interspecific hybridization and introgression.

Basic Steps in Evolution of Sex Chromosomes. The three model species of fish represent basic steps of sex chromosome evolution (Figure 1): (i) the zebrafish, *D. rerio*, with an all-autosome karyotype; (ii) the platy fish, *X. maculatus*, with genetically differentiated sex chromosomes but no differentiation between X and Y detectable in the synaptonemal complexes or with comparative genomic hybridization in meiotic and mitotic chromosomes; (iii) the guppy fish, *P. reticulata*, with genetically and cytogenetically differentiated sex chromosomes (Nanda et al 1990, 1992; Traut & Winking 2001; Kottler & Schartl 2018). The acrocentric Y chromosome of the guppy consists of a proximal homologous and a distal differential segment (Traut & Winking 2001). The proximal segment pairs in early pachytene with the respective X chromosome segment (Traut & Winking 2001). The differential segment is unpaired in early pachytene but synapses later in an 'adjustment' or 'equalization' process (Traut & Winking 2001). The segment comprises a postulated sex-determining region and a conspicuous variable heterochromatic region whose structure depends on the certain Y chromosome line (Traut & Winking 2001). Investigation by comparative genomic hybridization differentiates a considerable fragment of predominantly male-specific repetitive DNA and a fragment of common repetitive DNA in that region (Traut & Winking 2001).

How fast? This evolution of sex chromosomes was thought to be a slow process, but recent studies performed to genus *Xiphophorus* have shown that a change in sex determination system was possible over few generations through interspecific hybridization and introgression (Franchini et al 2018; Petrescu-Mag 2018).

How long? As we stated above, the lack of genetic recombination will further lead to the accumulation of non-functional DNA sequences and to the degeneration of the non-recombinant sex chromosome region (Rice 1987a). Sometimes, the decay affects the whole chromosome and the system is aborted. Therefore, some systems of sex determination have in the case of individuals of one sex, with a chromosome less than in the case of the opposite sex. In other cases, the obsolete sex-determining system is replaced by a new one, from a new pair of autosomes (Almeida-Toledo et al 2000; Franchini et al 2018; Rodríguez et al 2019).



(a) (b) (c)

Figure 1. (a) *Xiphophorus maculatus* (original); (b) *Danio rerio* (www.genengnews.com); *Poecilia reticulata* (original).

Conclusions. We may conclude that emergence, evolution and replacement of sex chromosomes in fish is a cyclical process, which happens faster than we believed. Although mutations occur randomly, the evolution of sex chromosomes is directly correlated with the species history and ecological context.

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