

Sex-limited coloration in guppy females: genetic and hormonal basis

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Abstract. Female guppies (*Poecilia reticulata*) generally lack the conspicuous ornamental pigmentation characteristic of males, although the underlying genetic determinants of coloration are present in both sexes. This mini-review examines the genetic, chromosomal, hormonal, developmental, and evolutionary mechanisms underlying sex-limited pigmentation in guppies, with particular emphasis on the relationship between sex linkage, recombination, and phenotypic expression. The guppy possesses an XY sex-determination system on chromosome pair 12, and current genomic, cytogenetic, and linkage evidence indicates that its sex chromosomes remain largely homomorphic and retain substantial regions capable of X-Y recombination. Rather than forming a simple nonrecombining block, chromosome 12 exhibits a recombination gradient, with strongly reduced exchange around the sex-determining region and progressively higher recombination toward the distal pseudoautosomal region. Classical genetic studies have demonstrated extensive Y-linked inheritance of male coloration, together with X- and Y-linked loci whose expression is restricted to males and a smaller contribution from autosomal loci. The absence of ornamental coloration in females therefore reflects predominantly sex-limited and hormonally regulated gene expression rather than the absence of pigmentation genes. Experimental androgen treatment can induce male-like coloration in females, further supporting a regulatory basis for sexual dimorphism. In domesticated ornamental strains, this regulatory restriction can be altered, allowing certain dominant sex-linked color patterns to be expressed in females. The developmental formation of pigmentation involves temporally distinct pigment-cell populations and signaling pathways associated with melanophore, xanthophore, and iridophore differentiation. Finally, female mate choice and predation jointly shape the evolution and maintenance of male coloration, while variation in visual sensitivity may contribute to coevolution between female perception and male ornamental traits. Overall, guppy pigmentation provides a particularly informative model for understanding how chromosome structure, recombination, hormonal regulation, and sexual selection interact to produce sexually dimorphic phenotypes.

Keywords: *Poecilia reticulata*, sexual dimorphism, pigmentation genetics, sex chromosomes, pseudoautosomal region, X-Y recombination, androgen regulation, pigment cells, ornamental strains, mate choice.

Introduction. Female guppies (*Poecilia reticulata*) are drab because ornamental color pattern genes, though present in both sexes, are sex-limited and expressed only in males (Khoo et al., 1999; Kottler et al., 2013; Dick et al., 2018). The guppy employs an XY sex-determination system with males as the heterogametic sex, and ornamental pigmentation develops only as males reach sexual maturity under hormonal control (Dick et al., 2018; Kottler et al., 2013). Both sexes share a reticulate black camouflage and light-yellow base coloration, but the polymorphic ornamental spots - comprising carotenoid, melanin, and iridescent pigments - are exclusive to males (Dick et al., 2018; Martínez et al., 2016). Transcriptomic analyses confirm that all differentially expressed color genes between the sexes are more highly expressed in males, with male-biased expression of melanin

synthesis genes correlating directly with the visual appearance of black ornamentation (Dick et al., 2018; Sharma et al., 2014).

The aim of this mini-review is to synthesize current and classical evidence concerning the mechanisms responsible for the predominantly male-restricted expression of ornamental pigmentation in *Poecilia reticulata*. Particular attention is given to the organization and recombination dynamics of the guppy X–Y chromosome pair, the inheritance of pigmentation loci, the distinction between sex-linked and sex-limited expression, and the hormonal and developmental mechanisms regulating pigment formation. The review also considers how domestication can modify the normal restriction of ornamental phenotypes to males and how female mate choice, predation, and visual-system variation contribute to the evolutionary maintenance and diversification of male coloration.

Guppy Sex Chromosomes and Recombination. In *Poecilia reticulata*, the sex chromosomes are an XY pair (chromosome pair 12) that remain largely homomorphic, with the Y retaining very similar gene content to the X rather than showing strong degeneration (Charlesworth et al., 2020ab; Charlesworth et al., 2021; Petrescu & Mag, 2006; Mag & Petrescu, 2006; Qiu et al., 2022; Nanda et al., 2022). Multiple recent genomic, linkage-mapping, and cytogenetic studies therefore converge on a model in which guppy sex chromosomes contain a substantial homologous, recombining component, rather than a long completely isolated male-specific chromosome (Fraser et al., 2020; Darolti et al., 2019; Nanda et al., 2022; Nanda et al., 2014).

The homologous segment is usually described as a pseudoautosomal region, and both cytological and genetic evidence show that crossing over does occur there in male meiosis (Charlesworth et al., 2020ab; Nanda et al., 2022; Nanda et al., 2014; Petrescu-Mag & Bourne, 2008). Classical and modern mapping place the sex-determining locus toward the distal end of linkage group 12, close to a terminal pseudoautosomal region where male crossovers are concentrated (Tripathi et al., 2009; Charlesworth et al., 2020ab; Charlesworth et al., 2024). One consistent estimate is that the principal terminal pseudoautosomal region lies in roughly the final 4–5 Mb of the chromosome, immediately adjacent to the male-determining region, and recombines at a high rate in males (Charlesworth et al., 2024; Charlesworth, 2018; Charlesworth et al., 2020ab).

At the same time, recombination is not uniform along the guppy XY pair. Several studies distinguish a region around the sex-determining locus in which crossing over is undetectable or extremely infrequent, and a more proximal region in which X–Y recombination still occurs but only rarely (Darolti et al., 2020; Kirkpatrick et al., 2022; Charlesworth et al., 2024). Darolti and colleagues delimit an older region around approximately 21–26 Mb, associated with the sex-determining locus and previously showing no detectable male recombination, whereas the adjacent interval at roughly 15–21 Mb shows very rare X–Y exchange rather than complete suppression (Darolti et al., 2020). This view is broadly compatible with mapping studies that identify occasional crossovers proximal to the male-determining region and use them to define a second pseudoautosomal region, sometimes termed *PAR2*, that recombines much less often than the highly recombining terminal *PAR* (Charlesworth et al., 2024; Charlesworth, 2018).

The strongest general pattern is therefore a recombination gradient along the guppy sex chromosome, not an abrupt dichotomy between a large fully male-specific block and a fully free-recombining remainder (Darolti et al., 2020; Qiu et al., 2022; Bergero et al., 2018). Near the sex-determining factor, recombination is least likely; somewhat farther away, in the partially sex-linked region, it is still rare but detectable; and at the terminal pseudoautosomal tip it becomes much more frequent (Darolti et al., 2020; Charlesworth et al., 2024; Charlesworth et al., 2020ab). This directly supports the formulation that the probability of crossing over increases with increasing distance from the fragment responsible for sex determination (Charlesworth et al., 2024; Charlesworth et al., 2020ab). Genome-scale analyses agree that much of chromosome 12 behaves as partially sex-linked rather than fully nonrecombining. Population resequencing found many variants showing strong but incomplete association with sex across most of the chromosome, while consistently male-specific variants remain elusive (Bergero et al., 2019; Charlesworth et

al., 2020ab; Qiu et al., 2022). The improved male reference genome likewise identified only two small regions with consistent male-specific signals and interpreted the overall pattern as a small Y-specific region plus rare male recombination, helping reconcile earlier conflicting inferences about extensive nonrecombining strata (Fraser et al., 2020). This is also consistent with the observation that the guppy Y chromosome retains integrity through incomplete recombination suppression, with occasional exchanges preventing the deep X–Y divergence expected under long-term total isolation (Darolti et al., 2020).

Cytogenetic and linkage data also show that this pattern is embedded in a broader regime of strong heterochiasmy in guppies. In females, recombination is distributed much more broadly across chromosomes, whereas in males crossover events are concentrated at chromosome tips, including on chromosome 12 (Charlesworth et al., 2020ab; Bergero et al., 2019; Bergero et al., 2018; Tripathi et al., 2009). For the sex chromosome, this means that the distal pseudoautosomal tip is the main zone of regular exchange, while the region extending inward toward the sex-determining locus experiences progressively lower male recombination (Charlesworth, 2018). GC-content analyses support the same interpretation indirectly, because chromosome ends show signatures expected for high recombination, matching the inference that male crossovers are highly localized in physically small terminal regions (Charlesworth et al., 2020ab).

There is still some disagreement about terminology and boundaries. Some authors accept strata on the guppy Y, with an older region of effectively absent recombination and a younger region of very rare exchange (Darolti et al., 2020; Kirkpatrick et al., 2020). Others argue that current evidence does not justify calling large parts of chromosome 12 a fully nonrecombining sex-determining region, and instead favor a model with a very small completely sex-linked segment, extensive partial sex linkage, and rare but real recombination across neighboring regions (Kirkpatrick et al., 2020; Charlesworth et al., 2024; Qiu et al., 2022). Even across this disagreement, however, the central empirical point is stable: guppy sex chromosomes are not completely isolated from one another, they retain a homologous region where crossing over occurs, recombination is strongly reduced around the sex-determining region, and the frequency of crossing over rises toward the distal pseudoautosomal end as one moves away from the sex-determining fragment (Nanda et al., 2022; Charlesworth et al., 2020ab; Charlesworth et al., 2024; Fraser et al., 2020) (Figure 1).

Sex Linkage and Inheritance of Color Pattern Genes. The guppy was the first species demonstrated to exhibit Y-linked inheritance of genes, and nearly all color pigmentation and patterning loci are sex-linked (Khoo et al., 1999). Early classical genetics documented 17 Y-linked genes passed exclusively from father to son (one-sided masculine inheritance), 15 X- and Y-linked genes found in both sexes but expressed only in males as sex-limited and hormone-mediated traits, and one autosomal dominant color gene (Khoo et al., 1999). Quantitative trait locus analysis has confirmed that most male color traits are controlled by multiple genes, including genes on autosomes (Kottler et al., 2013). The amount and size of male ornaments is highly heritable, with a substantial portion inherited in a Y-linked manner from the father (Kottler et al., 2014; Houde, 1992). High father–son regression slopes and strong response to selection for orange area indicate Y-linked inheritance of this sexually selected quantitative character (Houde, 1992). The table below (Table 1) summarizes the categories of color pattern gene inheritance documented in the guppy.

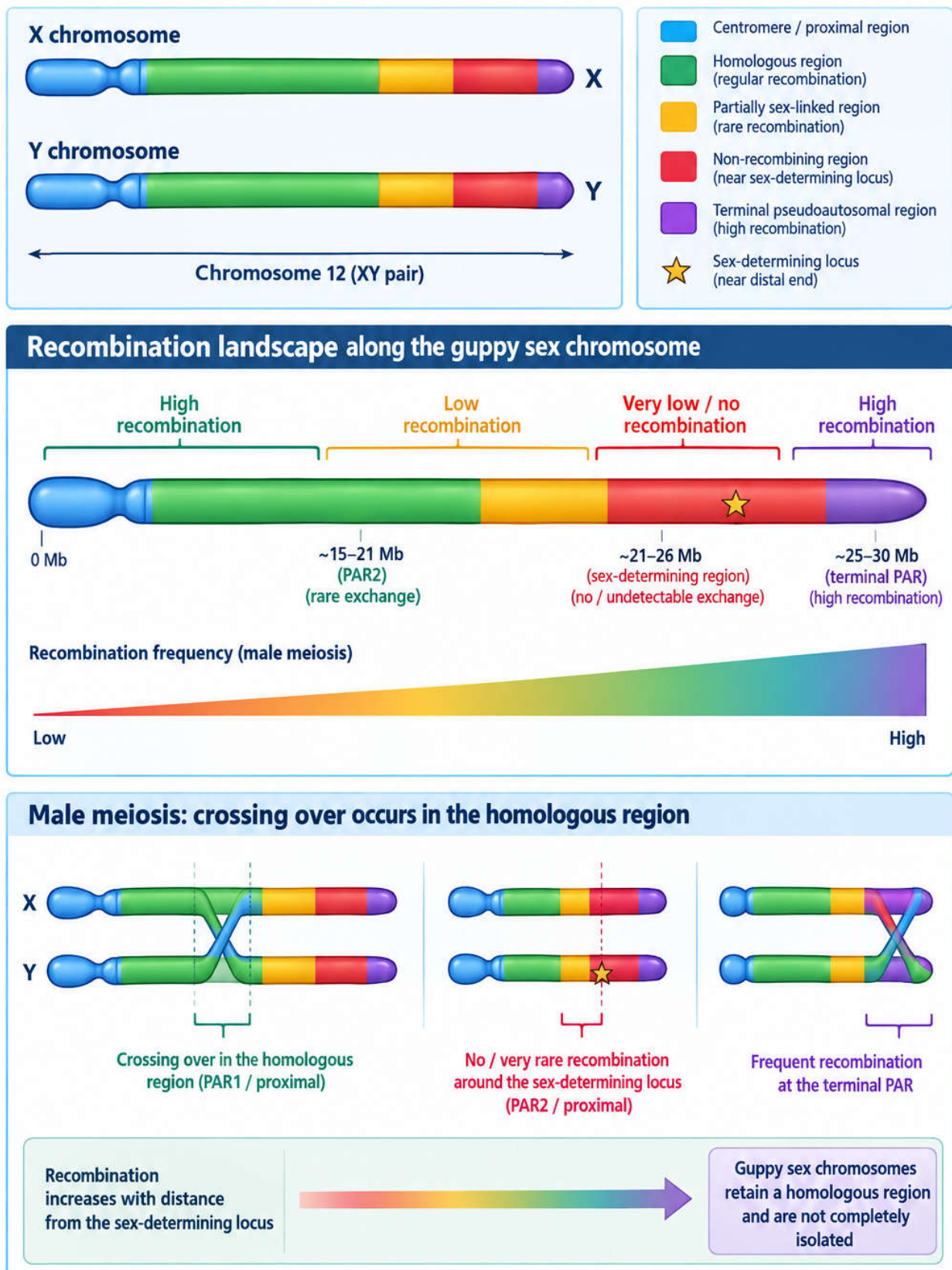


Figure 1. Guppy sex chromosome and recombination.

Table 1

Categories of color pattern gene inheritance in the guppy based on classical genetic documentation by Kirpichnikov (1981), as cited in Khoo et al. (1999)

<i>Inheritance category</i>	<i>Expression in males</i>	<i>Expression in females</i>	<i>Number of known genes</i>
Y-linked (one-sided masculine)	Expressed	Not expressed	17 (Khoo et al., 1999)
X- and Y-linked (sex-limited)	Expressed	Not expressed (hormone-mediated)	15 (Khoo et al., 1999)
Autosomal	Expressed	Not expressed	1 (Khoo et al., 1999).

At least 20 exclusively Y-linked color pattern alleles and at least 28 alleles that recombine between X and Y have been identified through traditional genetic studies (Sato & Kawata, 2020). Some of these color pattern genes, such as *Maculatus*, *Armatus*, and *Pauper*, influence sex determination and are located close to or within the sex-determining region (SdR) on the Y-chromosome (Khoo et al., 1999). An improved male-derived reference genome assembly identified two small regions with consistent male-specific signals, consistent with a small Y-specific region and rare recombination in male guppies (Fraser et al., 2020). Early genetics studies revealed that male color patterning genes are mostly but not entirely Y-linked, and that X-linkage may be most common in low-predation populations (Fraser et al., 2020). High-predation fish tend to have more Y-linked body coloration, while low-predation fish have more autosomal and X linkage (Dick et al., 2018).

Hormonal Control and Sex-Limited Expression. The absence of ornamental coloration in female guppies is attributable to sex-limited gene expression mediated by hormonal regulation, not to the absence of the color pattern genes themselves (Khoo et al., 1999; Kottler et al., 2013; Figure 2). Ornamental traits linked to the sex chromosomes are typically expressed only in males, but females can develop some male color patterns when treated with testosterone (Kottler et al., 2013; Mag et al., 2005abc). This experimental finding demonstrates that the color pattern genes are present in females but remain silent due to the absence of appropriate hormonal signaling. Only males develop highly polymorphic ornaments during puberty, and this development is under hormonal control (Kottler et al., 2013).

The developmental trajectory of male caudal fin coloration follows a fixed sequence: black melanin always appears first, followed by orange/yellow, then iridescence, regardless of predation regime (Dick et al., 2018). Increased expression of melanin synthesis genes correlates with the visual appearance of black coloration, but no correlation exists between carotenoid or pteridine synthesis gene expression and the appearance of orange/yellow (Dick et al., 2018). The lack of orange/yellow coloration in earlier developmental stages may stem from reduced expression of genes underlying xanthophore development (Dick et al., 2018). Orange spots appear to form through secondary differentiation of xanthophores rather than de novo generation, induced by *Csf1* and thyroid hormone signaling pathways (Kawamoto et al., 2021).

The molecular architecture of pigment pattern formation involves specific receptor tyrosine kinases. The autosomal loci blue and golden, which correspond to guppy orthologs of *csf1ra* and *kita* respectively, are both required for the development of black male ornaments (Kottler et al., 2013). Two temporally and genetically distinct melanophore populations contribute to the adult camouflage pattern expressed in both sexes: one early-appearing and *kita*-dependent, and another late-developing and *kita*-independent (Kottler et al., 2013). Multiple pigment cell types, including iridophores present in every

investigated color trait, contribute to black, blue, and orange ornaments (Kottler et al., 2014).



Figure 2. Androgen-induced expression of male traits in females: the same female before and after androgen treatment (Mag-Mureşan et al., 2004).

From a biomedical perspective, these mechanisms in guppies show some interesting similarities with human biology. In teleost fish, androgens such as 11-ketotestosterone are the main steroids involved in regulating secondary sexual characteristics, and they are generally more effective than testosterone in this role (Borg, 1994). A similar role of androgens can be seen in humans, where they are involved in the development of the male internal and external genitalia as well as secondary sexual characteristics (Amato et al., 2022). This shows that steroid hormones can act as important signals that activate specific genes. This is also supported by androgen receptor knockout studies, which have shown that AR signaling directly affects the expression of downstream genes (Chang et al., 2013). The role of *kita* in pigment cell development in guppies is also relevant to human biology (Kottler et al., 2013). Its mammalian counterpart, *KIT* (*c-KIT*), is important for the survival and migration of pigment cells that originate from the neural crest (Thomas & Erickson, 2008). In humans, mutations in *KIT* can cause piebaldism, a genetic condition characterized by localized areas of white skin and hair (Giebel & Spritz, 1991). Therefore, studying pigmentation in guppies can also help us understand how hormonal signals and conserved developmental pathways are involved in pigment cell development in vertebrates.

Ornamental Strain Expression in Females. Color pattern genes in domesticated ornamental guppy strains can show dominant expression in both sexes, a phenomenon not observed in wild populations (Khoo et al., 1999) (Figure 3). Genetic analyses of the Tuxedo strain revealed that the black caudal-peduncle (*Bcp*) and red tail (*Rdt*) color patterns are dominantly expressed in both males and females, sex-linked, and determined by different loci on the X- and Y-chromosomes (Khoo et al., 1999). The *Bcp*, *Rdt*, and variegated tail patterning (*Var*) genes showed single-gene inheritance and dominant expression in both sexes in crosses between Tuxedo and Green Variegated strains (Khoo et al., 1999). Their corresponding recessive alleles do not produce any color patterns (Khoo et al., 1999). The table below (Table 2) compares color pattern gene expression between wild-type and ornamental guppy strains.

Table 2

Comparison of color pattern gene expression in females between wild-type and ornamental guppy strains, illustrating that ornamental lines can break sex-limited expression

<i>Strain/population</i>	<i>Color pattern gene</i>	<i>Chromosomal location</i>	<i>Female expression</i>
Wild-type	Most ornamental loci	Y-linked or XY-linked	Absent (Khoo et al., 1999)
Tuxedo (ornamental)	<i>Bcp, Rdt</i>	X- and Y-linked	Present (dominant) (Khoo et al., 1999)
Tuxedo × Green Variegated	<i>Bcp, Rdt, Var</i>	X- and Y-linked	Present (dominant) (Khoo et al., 1999)
Domesticated strains	Various	X- and Y-linked	Present (sex-linked, dominant) (Khoo et al., 1999).

Genotypes of Tuxedo males are proposed to include combinations such as $X^{Bcp,Rdt}Y^{Bcp,Rdt}$ and $X^{Bcp,Rdt}Y^{Bcp+,Rdt}$, while females carry $X^{Bcp,Rdt}X^{Bcp+,Rdt}$ (Khoo et al., 1999). The expression of phenotypic color patterns in cultured guppy strains is determined by dominant sex-linked and sex-limited genes, which may consequently be used as genetic markers to map the X- and Y-chromosomes (Khoo et al., 1999; Mag & Bud, 2006). Map distances estimated from recombinants place the *SdR-Rdt* pair at approximately 3.1–3.4 map units, *SdR-Bcp* at 5.1 map units, and *Rdt-Bcp* at 2.3–2.4 map units (Khoo et al., 1999). The phenotypic map order of the guppy Y-chromosome is inferred to be *Var-SdR-Rdt-Bcp* (Khoo et al., 1999).

Sexual Selection and Female Preference. Female mate choice drives the maintenance and elaboration of male coloration despite the females' own lack of ornament. Females prefer males with the greatest development of both carotenoid and iridescent pigments, and this preference is consistent across genetic strains (Kodric-Brown, 1985). Females discriminate among males based on the relative area of orange pigment, and populations differ significantly in the degree of female preference for orange (Houde & Endler, 1990; Houde, 1987). The degree of female preference for orange is correlated with the population average orange area, indicating that male traits and female preferences evolve in parallel (Houde & Endler, 1990). Geographic variation in female preferences across 11 Trinidad localities reveals that mate-preference criteria vary in intensity, sign, and the number of traits used, with only orange, black, and color contrast showing correlations between male trait and female preference degree (Endler & Houde, 1995).

Colour vision tuning co-evolves with male coloration and female preference. Low-predation guppies invest more of their colour vision in detecting red/orange coloration, expressing higher levels of LWS-1 and LWS-3 opsins than high-predation populations (Sandkam et al., 2015). Visual pigment polymorphism in the long-wavelength cones may be related to the appreciation of the different yellow, orange, and red carotenoid color spots used in sexual display (Archer et al., 1987). Parasitic infection reduces the expression of carotenoid colors in males, and females discriminate against recently infected males, probably on the basis of color change (Houde & Torio, 1992). Colour polymorphism in male guppies results from a balance between natural and sexual selection, with female preference favoring conspicuous males while predation favors duller coloration (Martínez et al., 2016; Dick et al., 2018). In low-predation sites, males present a higher frequency of bright colors such as orange and iridescent, whereas in high-predation sites males tend to be drabber (Martínez et al., 2016). Different elements of any given color pattern are influenced by different modes of natural selection, with the relationship between predation

intensity and color pattern differing for melanin, carotenoid, and structural colors (Endler, 1983).



Figure 3. Female color patterns observed in domesticated guppies that have never been reported in wild females: Tuxedo (*Bcp*), Red Tail (*Rdt*), Variegated Tail (*Var*) and homozygous Magenta Black Tail. Note: *Nigrocaudatus*, *Bcp*, and Tuxedo are variations of the same trait. Photographs of the Tuxedo, Red Tail, and Variegated Tail female guppies were taken by Mircea Roșca at Professor Ioan Valentin Petrescu-Mag's guppy breeding facility, while the Magenta Black Tail females are fish photographed at the breeding facility of the author Grzegorz Prusinowski (<https://www.facebook.com/GenetykaGupika>).

Conclusions. The available evidence indicates that the predominantly drab appearance of female guppies is not attributable to the absence of genes responsible for ornamental pigmentation, but primarily to sex-limited regulation of their expression. The guppy X and Y chromosomes remain substantially homologous, and chromosome 12 displays a spatially heterogeneous recombination pattern characterized by strongly reduced exchange near the sex-determining region and more frequent recombination toward the distal pseudoautosomal region. Consequently, pigmentation inheritance cannot be adequately described by a simple model in which all ornamental genes are permanently restricted to a nonrecombining Y chromosome.

Classical genetic studies demonstrate that guppy coloration involves Y-linked, X- and Y-linked, and autosomal components, while many traits remain phenotypically restricted to males through hormonal regulation. The capacity of females to express male-associated patterns following androgen treatment provides direct evidence that the genetic machinery for pigmentation is present but normally transcriptionally or physiologically constrained in females. Domesticated ornamental strains further demonstrate that this restriction can be modified, allowing dominant sex-linked patterns such as black caudal-peduncle and red-tail phenotypes to appear in females.

At the phenotypic level, pigmentation results from coordinated developmental processes involving multiple pigment-cell types and signaling pathways, whereas at the

evolutionary level, male coloration is maintained through the interaction of sexual selection and natural selection imposed by predation. Female preferences for conspicuous coloration and population-specific differences in visual sensitivity can reinforce the diversification of male ornaments, while predation favors reduced conspicuousness. Thus, sex-limited pigmentation in the guppy represents an integrated phenotype arising from the interaction of chromosome architecture, recombination, genetic inheritance, hormonal regulation, pigment-cell development, and opposing selective forces.

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