AACL BIOFLUX
Aquaculture, Aquarium, Conservation & Legislation
International Journal of the Bioflux Society

Crossing-over between Y chromosomes: another possible source of phenotypic variability in the guppy, *Poecilia reticulata* Peters

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Abstract. Genetic linkage acting through crossing-over between X and X chromosomes, X and Y chromosomes, and autosomal gene recombination are the most important sources of color pattern polymorphisms in animals. Variability in male color patterns and fin morphologies in the guppy, *Poecilia reticulata*, a livebearing fish is an example of extreme pattern polymorphism. We explored the possibility that crossing-over between Y chromosomes can also contribute to the high degree of pattern polymorphism in guppies because YY individuals are easily induced in the laboratory. However, note that YY individuals are also produced in natural populations. Our results indicated that YY crossing-over was another important source of phenotypic variability - probably because recombination may be possible over the entire length of Y chromosomes, and at very high frequencies due to high degrees of homology. Thus, crossing-over between Y chromosomes is yet another mechanism that can contribute to extreme pattern polymorphism in the guppy, a popular aquarium and important research model species.
Key Words: color pattern polymorphisms, genetic linkage, genetic recombination, guppy, variability.

Resumen. El entrecruzamiento entre los cromosomas X y X, X e Y o la recombinación genética autosómico son las mas importantes fuentes de polimorfismo en lo que se refiere a los patrones de colores del mundo animal. La variabilidad de los patrones del color y de la morfología de las aletas de los machos guppy, *Poecilia reticulata*, que es un pez ovovivíparo, es un ejemplo extremo de los patrones de polimorfismo de los colores. En este trabajo, hemos investigado la posibilidad de que el entrecruzamiento entre los cromosomas Y pueda contribuir en el alto nivel de polimorfismo en los guppy, esto porque en esta especie los individuos YY pueden ser fácilmente obtenidos en el laboratorio. De todos modos, es importante subrayar que los individuos YY aparecen también en poblaciones naturales. Nuestros resultados muestran que el entrecruzamiento entre los cromosomas Y representa una fuente de variabilidad fenotípica – probablemente porque la recombinación es posible, a lo largo de todo el cromosoma Y, y con alta frecuencia debido al alto grado de homología. Finalmente, la recombinación entre los cromosomas Y es otro mecanismo que puede contribuir con un papel importante en la formación del polimorfismo extremo de los patrones de color en los guppy, una especie popular de acuario y un modelo para la investigación científica.
Palabras clave: patrones de polimorfismo del color, ligamiento genético, recombinación genética, guppy, variabilidad.

Rezumat. Crossing-over-ul între cromosomii X şi X, X şi Y, sau recombinarea genetică autosomală, sunt cele mai importante surse de polimorfism în ceea ce priveşte tiparele coloristice în lumea animală. Variabilitatea tiparelor coloristice şi a morfologiei înotătoarelor la masculii de guppy, *Poecilia reticulata*, un peşte ovovivipar, este un exemplu de polimorfism extrem al tiparelor coloristice. În prezenta lucrare, am investigat posibilitatea ca crossing-over-ul dintre cromosomii Y să aducă un aport de polimorfism, la guppy, deoarece, la această specie, indivizii YY pot fi cu uşurinţă produşi în laborator. Oricum, este important de reţinut faptul că indivizii YY apar şi în sălbăticie. Rezultatele noastre au dezvăluit faptul că crossing-over-ul între cromosomii Y reprezintă o sursă de variabilitate fenotipică – probabil, pentru că recombinarea este posibilă pe toată lungimea cromosomilor Y şi cu frecvenţe foarte mari, datorită gradului înalt de homologie. Concluzionăm că crossing-over-ul dintre cromosomii Y este încă un factor care contribuie la polimorfismul extrem al tiparelor coloristice la guppy, o cunoscută specie de acvariu şi un peşte model pentru cercetarea ştiinţifică.
Cuvinte cheie: polimorfism coloristic, înlănţuire genetică, recombinare genetică, guppy, variabilitate.

Introduction.Currently there has been a renewed interest in color pattern polymorphism because a high degree of color pattern diversity is found in many animal taxa, and color polymorphism should confer adaptive benefits (reviewed in Basolo 2006; Gray & McKinnon 2007). Color pattern polymorphism has been defined as the presence of two or more distinct, genetically derived color morphs within an interbreeding population - the rarest morph occurring at a frequency too high to be only caused by recurrent mutations (Huxley 1955). The human drive to ″know″ is the motivation fueling the quest to answer the question, how is this within and between species color pattern diversity maintained in populations? Livebearing fish or poeciliids (Poeciliidae) have been popular models for polymorphic studies with the guppy or "millions fish", *Poecilia reticulata*, being the most popular model (Meffe & Snelson 1989; Houde 1997; Basolo 2006).

The guppy is also an economically valuable species ranking among the top 10 most popular ornamental fishes (Turan et al 2006; Karayücel et al 2006). This poeciliid, as many others (Liley 1966; Bourne et al 2003), exhibits a marked sexual dimorphism due to the more pigmented bodies and larger fins in males, with almost continuous color pattern polymorphism (Haskins et al 1961). In the ornamental fish trade, this results in guppy males commanding up to four times the price of females. Because of this pricing difference, the culture of all-male populations is of significant commercial advantage (Piferrer & Lim 1997). Additionally, fishes present a dazzling array of gender identity types ranging from synchronous hermaphroditism, protandrous, and protogynous hermaphroditism to gonochorism. At the same time, fish exhibit high variability in sex determination mechanisms - environmental, polygenic, and chromosomal sex determination. All of these factors influence the ornamental fish enterprise to invest in research that manipulates male biased sex ratios in guppies using several approaches such as: (1) thermal manipulation (Karayücel et al 2006; Petrescu-Mag 2007); (2) manipulation of pH levels (Petrescu-Mag 2007). However, neither thermal nor pH manipulations influenced sex ratio bias in meaningful ways; (3) conspecific stress was successfully used for sex ratio manipulation (Petrescu-Mag 2007); (4) hormonal induced masculinization of guppies was achieved by using natural or synthetic androgens (Kavumpurath & Pandian 1993a; Pandian & Sheela 1995; Piferrer & Lim 1997; Turan & Akyurt 2003; Turan et al 2006; Petrescu-Mag 2007); and (5) the most efficient manner for producing monosex guppy males is the use of YY males (supermales). YY guppy males are generally artificial produced using XY females, after a male to female sex-reversal induced by estrogen treatment (Takahashi 1975; Kavumpurath & Pandian 1993b; Petrescu-Mag 2007). Note that XY females and YY males occur naturally when XX-XY system is suppressed (Winge 1930).

Sex Chromosomes and Color Patterns. According to Traut & Winking (2001), three fish species are representative of the basic steps in sex chromosome evolution: (1) the zebrafish, *Danio rerio* (Hamilton), has environmental or polygenic sex determination without heterosomes; (2) the southern platyfish, *Xiphophorus maculatus* (Gunther), which has genetically defined sex chromosomes; and (3) the guppy, in which the acrocentric Y chromosome can be identified cytogenetically. Comparative genomic hybridization (CGH) indicated that a large part of the nonpairing region of the guppy Y chromosome comprises male-specific repetitive DNA. Only one-half of the Y chromosome pairs with homologous regions of the X in synaptonemal complexes. Orientation of guppy heterosomes allowed the recombination in only two of 49 observed synaptonemal complexes, suggesting that crossover is greatly reduced even in the homologous region (Traut & Winking 2001).

The color patterns of guppies are complex and often conspicuous combinations of orange, black, white, yellow, green, iridescent blues, occurring as spots, speckles, bars, and lines (Haskins et al 1961; Houde 1997). These color patterns are expressed mostly in males - only patterns that have never been reported from wild populations show weak expression in females. Lindholm & Breden (2002) reviewed literature on linkage of sexually selected male traits in guppies, and found that the inheritance of attractive male traits shows that color patterns, caudal fin size and shape, courtship rates, and general attractiveness are primarily sex linked. They also reported that 26 traits are Y-linked, two are X-linked, 24 are X and Y linked (Table 1), and nine are autosomal. Crossing-over makes possible recombination of some traits encoded by sequences located on sex chromosomes (Lindholm & Breden 2002). However, there is a restricted region of the chromosome where crossing-over cannot take place - the location of sex-determining genes. The genes situated close to the sex-determining locus can cross over but seldomly do so (Lindholm & Breden 2002). Rare crossing-over events at a frequency of < 1/3,800 have occurred between guppy genes for red and black elements in the *Maculatus* color pattern, which are believed to be located very close to the sex-determining locus (Winge 1934; Basolo 2006). Furthermore, a new and complex linkage map for the guppy based on phenotypic traits and genetic markers suggests that the sex determining region is flanked on both sides by recombining regions (Khoo et al 1999; Khoo et al 2003). However, experimental crossings made by researchers during the past century revealed that, even in the case of recombining patterns, crossing-over frequency is quite low (Lindholm & Breden 2002). The higher frequency of crossing-over known between the X and Y guppy chromosomes is 7.42 (in the case of pattern *Pigmentiert caudalis*, Table 1). Consequently, Y linkage of male traits is generally strong, but it can be broken from time to time by these rare events of crossing-over (Khoo et al 1999; Khoo et al 2003).

The extraordinary polymorphism of male guppy color pattern and fin form is maintained in populations and this persistence is perpetuated by evolutionary mechanisms such as those indicated by Hughes et al (1999). No two male guppies have identical color patterns in the wild even though crossing-over between X and X chromosomes, X and Y chromosomes, and autosomal gene recombination are the most important sources of variability of male guppy color patterns and fin morphology (Hughes et al 1999; Lindholm & Breden 2002). The question we raise here is how did male guppy color pattern polymorphism evolve so rapidly? And we focus on another suspected source of variability which is crossing-over between Y and Y chromosomes, where recombination should be possible over the entire length of chromosomes at high frequencies due to high degrees of homology. The overarching aim of this study was to determine whether meiotic crossing-over between Y and Y chromosomes has a higher frequency than crossing-over between X and Y chromosomes.

Materials and Methods. *Study organism and breeding crosses*. - We used captive bred guppies; half-black (or tuxedo) color pattern is generally determined by a dominant *Nigrocaudatus* II (*Ni* II) gene linked to the X chromosome (Figure 1 and 2). Three different YY males of wild-type phenotypes (non-mutant, non-tuxedo, or non-half-black) from our own biobase were used in this study. Their ascendants were Half-Black Guppy that have lost both their tuxedo pattern and X chromosomes. The sex-linkage of *Ni* II was used for easier genotype identification of the supermales (Figure 1). After their identification, they were progeny tested as described in Petrescu-Mag (2007).

Each of these three supermales (♂YY$_1$, ♂YY$_2$ and ♂YY$_3$) was crossed with five virgin Red Blond highly inbred females (♀XX$_1$ - ♀XX$_5$, ♀XX$_6$ - ♀XX$_{10}$, ♀XX$_{11}$ - ♀XX$_{15}$). Blond is an autosomal recessive gene that strongly reduces the melanin synthesis, but it cannot be expressed in heterozygote form (Goodrich et al 1944). However, this variety is the poorest guppystrain we ever had as regards body color elements. The only exception is the quantitative character Orange area, which is expressed in males only, being strongly linked to the Y chromosome (Houde 1992; Brooks & Endler 2001; Karino & Haijima 2001). The resulting number of different color patterns and fin forms were compared to results of 15 control crosses (♂XY x ♀XX, Table 2, Figure 2). These XY wild-type control males were produced in the same type of crosses (see Figure 1, 25%) but from different individual parents.

Table 1

Crossover frequency between X and Y chromosomes
in guppies (compiled by Lindholm & Breden 2002)

X and Y linked pattern	X to Y % (N)	Y to X % (N)	Reference
Maculatus-black	-	-	Winge & Ditlevsen 1947; Haskins et al 1961
Elongatus	4.31 (348)	6.43 (1,276)	Winge 1922,1927
Vitellinus	6.13 (1,321)	3.75 (800)	Winge 1927,1934; Haskins et al 1970
Coccineus	0.33 (1,198)	0.48 (414)	Winge 1927, 1934; Dzwillo 1959
Tigrinus	0.21 (938)	2.91 (206)	Winge 1927, 1934
Luteus	0.89 (1,012)	3.82 (157)	Winge 1927, 1934
Minutus	-	2.67 (487)	Winge 1927, 1934
Cinnamomeus	-	-	Winge 1927
Solaris	-	0 (20)	Kirpichnikov 1935
Caudomaculatus	-	-	Blacher 1928
Anterior rubra	20 (25)	-	Blacher 1928
Purpureus	-	0 (52)	Natali & Natali 1931; Kirpichnikov 1935
Lutescens	-	-	Natali & Natali 1931
Nigrocaudatus II	0 (74)	4.00 (25)	Dzwillo 1959; Nayudu 1979
Flavus	0 (77)	0 (17)	Winge & Ditlevsen 1947; Nayudu 1979
Pigmentiert caudalis	5.19 (270)	7.42 (364)	Dzwillo 1959; Schröder 1969a; Nayudu 1979
Sb	-	-	Haskins et al 1961
Red tail	2.06 (97)	1.64 (548)	Fernando & Phang 1990; Khoo et al 1999
Blue tail	1.79 (280)	-	Fernando & Phang 1990; Phang & Fernando 1991
Green tail	0 (312)	-	Phang et al 1989; Phang & Fernando 1991
Snakeskin body	-	0.36 (2,507)	Phang et al 1989, 1990; Phang & Fernando 1991
Snakeskin tail	-	0.11 (948)	Phang et al 1989 1990; Phang & Fernando 1991
Variegated tail	1.03 (679)	3.25 (462)	Khoo et al 1999
Black caudal peduncle	2.73 (549)	2.56 (260)	Khoo et al 1999

N is the number of offspring examined. In some cases, crossing-over was detected only outside of controlled crosses.

Husbandry. - Guppies were kept in aquaria at 25±1ºC under a 14/10 h light/dark cycle. They were fed with a commercial diet Tetramin® bioactive formula (Tetra Gmbh, Germany), with 48% protein, three times a day *ad libitum*. Water quality parameters (O_2, pH, ammonia, nitrite and nitrate) were monitored every 10 days during the experiment. Forty aquaria of different sizes, ranging from 5 to 100 L, and 30 net cages of 20 cm x 15 cm x 15 cm were used for fish keeping and reproduction. Water was well aerated and heated using a compressor and thermostatically controlled heaters (Aquael, Poland). All active aquaria were cleaned daily by siphoning excreta and uneaten food from the substrate. Color patterns were directly observed in progeny after attainment of sexual maturity at three months.

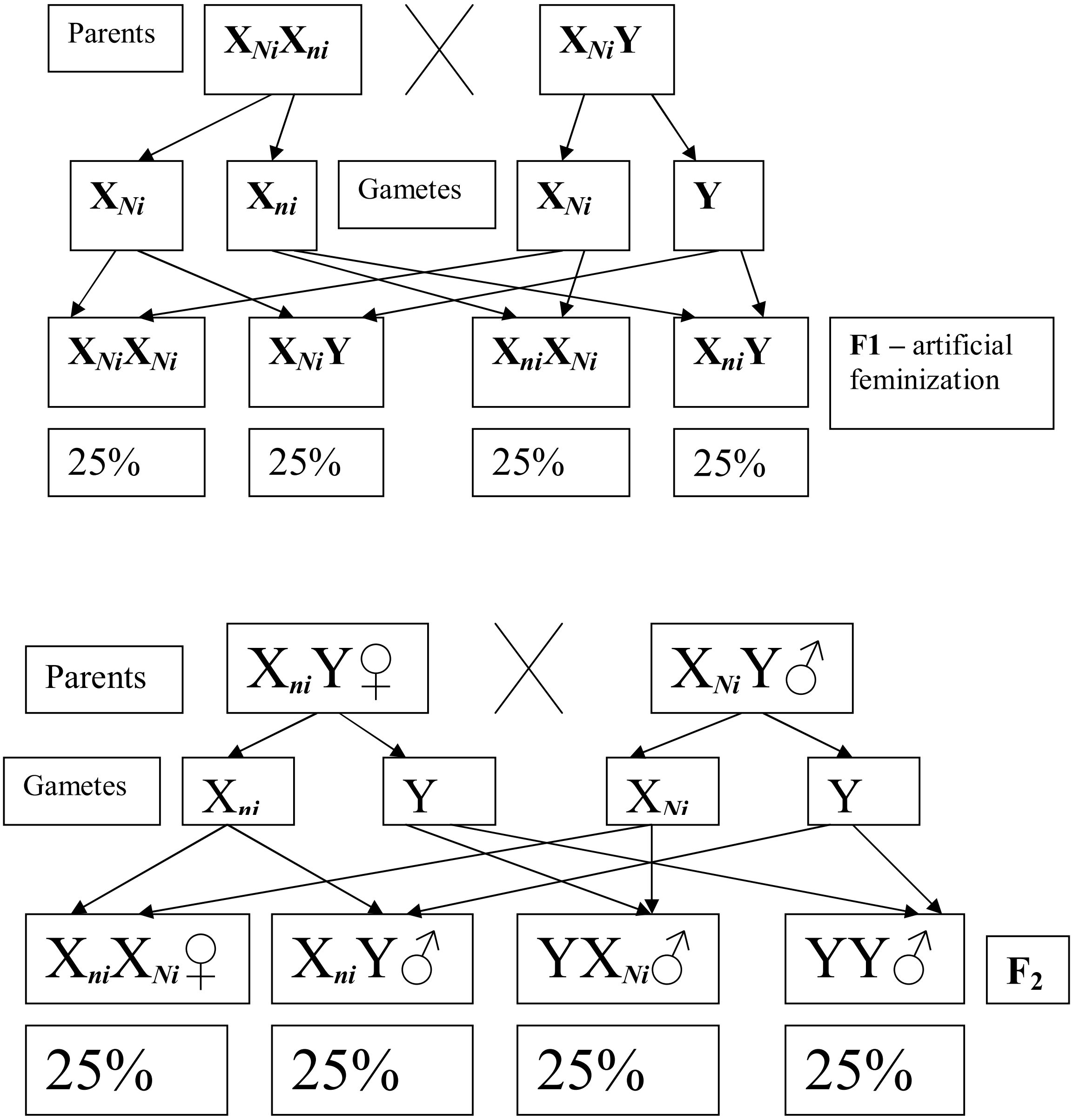

Figure 1. Sex-linkage paring design used for supermale production

Results and Discussion. Comparisons of tallies of experimental results to controls showed intense events of recombination when YY males were used as sires. Four to six polymorphic patterns were seen in the experimental F$_1$ generation for each male parent compared to only two patterns observed in F$_1$ control crosses for each male sire. Table 2 suggests a two- to three-fold higher frequency of recombination. The higher frequencies were due to Y chromosome separation on the one hand, and to a presumably crossing-over between the two Ys during meiosis on the other hand. Among the 15 different patterns that resulted from the ♂YY x ♀XX crosses none from the three original patterns was present. This indicated that several different loci (especially Y-linked ones) were often expressed in a single color pattern, resulting in high numbers of possible color pattern phenotypes. Winge (1930, 1934) studied the inheritance of a few color patterns, which he called morphs - today we know that the number of different color patterns in guppy populations is much higher than the number of described morphs. The new patterns obtained in our breeding experiment can be explained either as a result of crossing-over events between the two Y chromosomes during meiosis, or as caused by interaction of loci on the Y chromosome with loci on its paired X chromosome in the newly formed zygote. However, absence of this intense recombination in progeny that resulted from control crossings makes the second explanation less probable and crossing-over more probable. There is no other valid explanation for these results especially since the autosomes have fewer genes for pigmentation and fin morphology (see Lindholm & Breden 2002; Basolo 2006 and citations therein).

Table 2

Number of different patterns resulted in experimental/ control crosses and their observed frequencies

Male	*Female*	*Crossing*	*Number of different patterns resulted (frequencies)*		
♂YY_1	♀XX_1	♂YY_1 x ♀XX_1	3 patterns (33:25:4)	4 patterns (no original pattern was present; Figure 2, a-d)	A total of 15 different patterns (no original pattern was present; Figure 2, a-o)
	♀XX_2	♂YY_1 x ♀XX_2	2 patterns (42:37)		
	♀XX_3	♂YY_1 x ♀XX_3	2 patterns (27:25)		
	♀XX_4	♂YY_1 x ♀XX_4	3 patterns (23:18:2)		
	♀XX_5	♂YY_1 x ♀XX_5	2 patterns (30:26)		
♂YY_2	♀XX_6	♂YY_2 x ♀XX_6	2 patterns (12:11)	6 patterns (no original pattern was present; Figure 2, e-j)	
	♀XX_7	♂YY_2 x ♀XX_7	3 patterns (10:9:2)		
	♀XX_8	♂YY_2 x ♀XX_8	4 patterns (13:12:3:3)		
	♀XX_9	♂YY_2 x ♀XX_9	3 patterns (15:14:1)		
	♀XX_{10}	♂YY_2 x ♀XX_{10}	2 patterns (29:24)		
♂YY_3	♀XX_{11}	♂YY_3 x ♀XX_{11}	3 patterns (25:23:4)	5 patterns (no original pattern was present; Figure 2, k-o)	
	♀XX_{12}	♂YY_3 x ♀XX_{12}	2 patterns (32:27)		
	♀XX_{13}	♂YY_3 x ♀XX_{13}	3 patterns (26:23:3)		
	♀XX_{14}	♂YY_3 x ♀XX_{14}	2 patterns (22:22)		
	♀XX_{15}	♂YY_3 x ♀XX_{15}	3 patterns (17:15:3)		
♂XY_1	♀XX_{16}	♂XY_1 x ♀XX_{16}	1 pattern (15 pattern of the father)	2 patterns (the original pattern was present; Figure 2, p-q)	A total of 6 different patterns (The three original male patterns were present; Figure 2, p-u)
	♀XX_{17}	♂XY_1 x ♀XX_{17}	2 patterns (23 pattern of the father : 1 a new pattern)		
	♀XX_{18}	♂XY_1 x ♀XX_{18}	1 pattern (17 pattern of the father)		
	♀XX_{19}	♂XY_1 x ♀XX_{19}	1 pattern (13 pattern of the father)		
	♀XX_{20}	♂XY_1 x ♀XX_{20}	1 pattern (18 pattern of the father)		
♂XY_2	♀XX_{21}	♂XY_2 x ♀XX_{21}	1 pattern (14 pattern of the father)	2 patterns (the original pattern was present; Figure 2, r-s)	
	♀XX_{22}	♂XY_2 x ♀XX_{22}	1 pattern (14 pattern of the father)		
	♀XX_{23}	♂XY_2 x ♀XX_{23}	1 pattern (19 pattern of the father)		
	♀XX_{24}	♂XY_2 x ♀XX_{24}	2 patterns (16 pattern of the father : 2 a new pattern)		
	♀XX_{25}	♂XY_2 x ♀XX_{25}	1 pattern (12 pattern of the father)		
♂XY_3	♀XX_{26}	♂XY_3 x ♀XX_{26}	1 pattern (15 pattern of the father)	2 patterns (the original pattern was present; Figure 2, t-u)	
	♀XX_{27}	♂XY_3 x ♀XX_{27}	1 pattern (21 pattern of the father)		
	♀XX_{28}	♂XY_3 x ♀XX_{28}	1 pattern (18 pattern of the father)		
	♀XX_{29}	♂XY_3 x ♀XX_{29}	1 pattern (25 pattern of the father)		
	♀XX_{30}	♂XY_3 x ♀XX_{30}	2 patterns (17 pattern of the father : 1 a new pattern)		

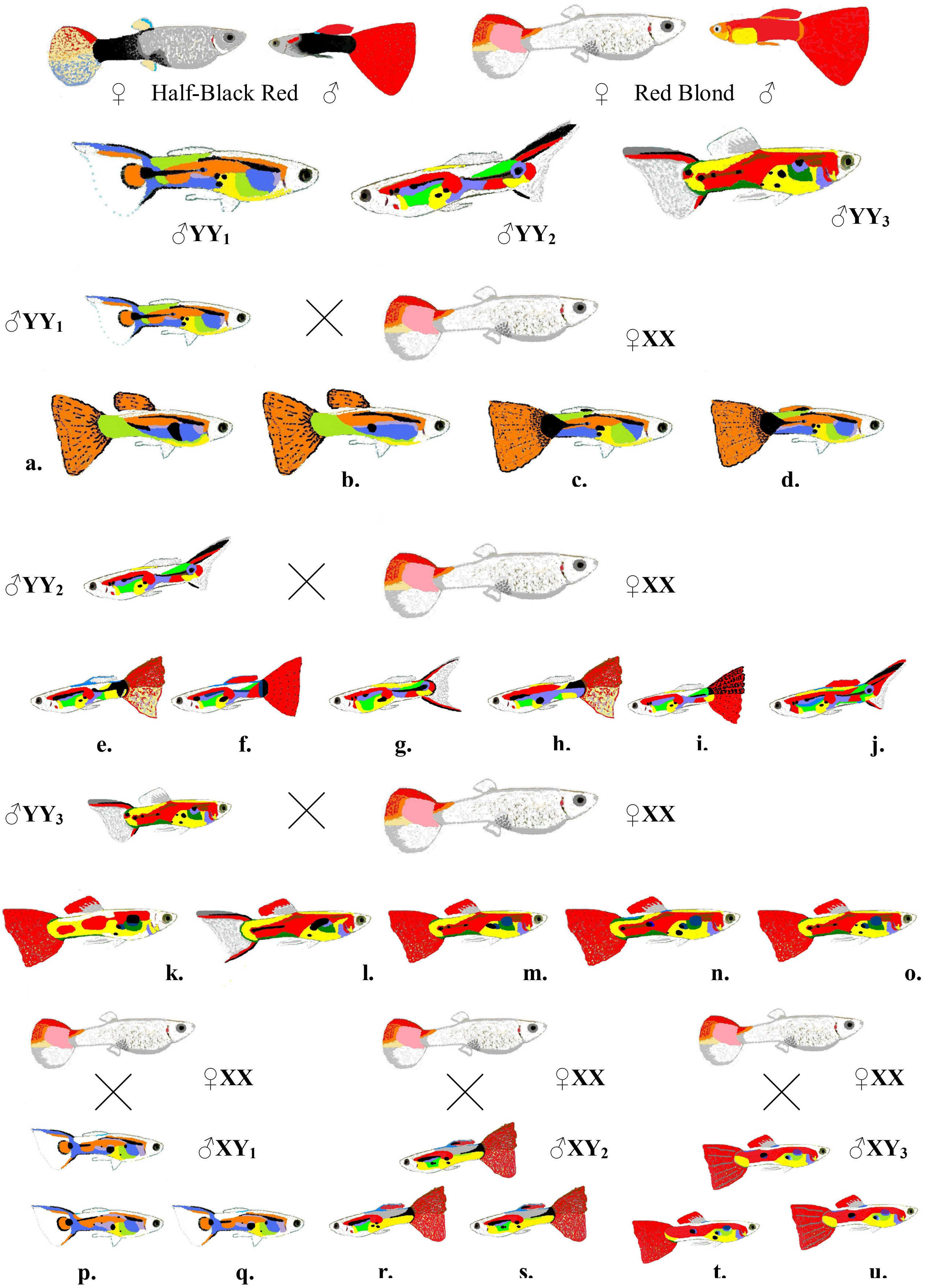

Figure 2. The breeding design, original (YY, XY, XX) and resultant phenotypes (a-u).

All three parental patterns from our ♂XY x ♀XX crosses were distributed among the six patterns expressed by their progeny. This demonstrates once again that most secondary male traits were encoded by sequences on the Y chromosome. Four males of 261 exhibited entirely new patterns, and 257 males had patterns similar to those expressed by their fathers. The small number of new patterns exhibited by our control crosses can be due either to low crossing-over frequencies between X and Y chromosomes during meiosis, and/or to low probabilities of new phenotypes caused by interaction of loci located on Y chromosome with loci located on its paired X chromosome in the newly formed zygote. Absence of the Y chromosome in XX males can be considered a possible cause of the new color patterns occurring in control crosses with a high probability that the new color pattern individuals could be pseudomales (♂XX; Reeve & Pfennig 2003).

The frequency of recombination between the Y and Y chromosomes is certainly higher than that occurring between X and Y and this event of genetic recombination is very probably another possible source of color pattern polymorphism variability in guppy populations. However, a long standing question still exists, what are the frequencies of spontaneous YY males in guppy populations? In conclusion, genes responsible for fish color pattern polymorphism located on sex chromosomes play a very important economic role in the ornamental fish industry. A new understanding of guppy genetics at the molecular level could help ornamental fish breeders to better exploit evolutionary and genetic models that constrain fish phenotypic expression. This knowledge will permit fish fanciers to choose optimal methods for genetic manipulation of color patterns in ornamental fish (see Basolo 2006; Bud 2002). The guppy is the primary and best model for such studies employing fish.

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Received: 01 July 2008. Accepted: 21 August 2008. Published: 30 September 2008.

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How to cite this article:
Petrescu-Mag I. V., Bourne G. R., 2008 Crossing-over between Y chromosomes: another possible source of phenotypic variability in the guppy, *Poecilia reticulata* Peters. AACL Bioflux 1:1-10.
Printed version: ISSN 1844-8143
Online version: ISSN 1844-9166 available at: http://www.bioflux.com.ro/docs/vol1/2008.1.1-10.pdf