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Winge's sex-linked color patterns and SDL in the guppy: genes or gene complexes?

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Abstract. In *Poecilia reticulata*, different phenotypes appear due to dominance, codominance, poligeny, or some demonstrated interallelic interactions. Recent (both molecular and classical) investigations suggest a mechanism of expression of several different loci in a single color pattern, resulting in high numbers of possible color pattern phenotypes. The color pattern seems to be determined by complex interactions of many genes (at the same locus or not, located on the same chromosome or not), under variable environmental conditions. For example, the *Maculatus* color pattern is due to the presence of both *Maculatus* red and *Maculatus* black elements. On their turn, having in view the latest definitions of the *gene*, both *Maculatus* red and *Maculatus* black could have a composite nature, too. Sex-determination in the guppy is studied since the 1920s. The deepest mechanism of sex determination is not clear yet, but classical studies of Winge early in the past century and recent molecular studies revealed a possible composite nature of the so called master sex determining gene, located at SDL of the Y chromosome.

Key Words: color patterns, guppy, sex genes, complex interactions.

Streszczenie. U gupika *Poecilia reticulata* różne fenotypy powstają w wyniku dominacji, współdominacji, polimorfizmu lub pewnych zaprezentowanych międzyallelicznych interakcji. Współczesne badania (zarówno klasyczne, jak i molekularne) sugerują obecność mechanizmu ekspresji kilku różnych loci w jednym wzorze ubarwienia, w wyniku czego powstaje wiele możliwych wzorów fenotypów. Ostateczny wzór ubarwienia wydaje się być wynikiem współdziałania wielu genów (w jednym locus lub w różnych loci, położonych na jednym lub kilku odrębnych chromosomach) oraz zmiennych czynników środowiskowych. Np. wzór ubarwienia *Maculatus* powstaje na skutek obecności zarówno elementów *Maculatus* czarny oraz *Maculatus* czerwony. Z kolei uwzględniając najnowsze definicje pojęcia *gen*, oba – *Maculatus* czerwony i *Maculatus* czarny – mogą mieć równiez złożoną naturę. Determincja płci u gupików jest przedmiotem badań od lat 20. XX wieku. Najgłębszy mechanizm determinujący płeć nie został do tej pory poznany. Jednak klasyczne doświadczenia Winge'a z początku ubiegłego stulecia oraz najnowsze badania molekularne sugerują złożoną naturę tzw. głównego genu determinującego płeć, umiejscowionoego w SDL na chromosomie Y.

Słowa kluczowe: geny determinujące płeć, gupik, wzory ubarwienia, złożone interakcje.

Rezumat. La *Poecilia reticulata*, diferitele fenotipuri cunoscute apar datorită dominanţei, codominanţei, poligeniei, sau datorită unor demonstrate interacţiuni interalelice. Studii recente (atât moleculare cât şi clasice) sugerează un mecanism prin care câţiva loci diferiţi se exprimă într-un singur tipar coloristic, rezultând un număr imens de tipare posibile. Tiparele coloristice par a fi determinate de interacţiunea complexă a mai multor gene (situate la acelaşi locus sau nu, pe acelaşi cromosom sau nu), sub influenţa variabilelor condiţii ambientale. Spre exemplu, tiparul *Maculatus* apare în prezenţa elementelor *Maculatus red* şi *Maculatus black*. Acestea, la rândul lor, având în vedere cele mai recente definiţii ale genei, ar putea avea şi ele o natură compusă. Determinismul sexelor la guppy a fost studiat încă din anii 1920. Cu toate acestea, mecanismul intim al determinării sexelor nu a fost complet elucidat, dar atât studiile clasice ale lui Winge de la începutul secolului trecut cât şi cercetările moleculare de ultimă oră sugerează o posibilă natură compusă a aşa-numitei gene dominante (epistatice) a sexului, situate la locusul SDL al cromosomului Y.

Cuvinte cheie: tipare coloristice, guppy, gene ale sexului, interacţiuni complexe.

Guppies. Ornamental fish production for aquarium, aquarists and aquariology is today a multimillion dollar industry in many countries (Bud 2002). The guppy *Poecilia reticulata* Peters, 1859 is considered by many authors to be the most popular aquarium fish, and it is also important for studies of genetics, behavioral ecology (as an excellent model system, see Houde 1997), ecotoxicology, evolutionary ecology (speciation, see Alexander & Breden 2004 vs. Poeser et al 2005) and conservation (as an invasive species, or as an endangered subspecies – Endler's livebearers).

Since the beginning of the 1900s *Poecilia reticulata,* at that time *Lebistes reticulatus,* has been the subject of scientific inquiry in a few disciplines and it has become dear to hearts of aquarists of all ages. Guppy is native to Venezuela, Guyanas, Northern Brazil, Trinidad and Barbados. They exhibit a marked sexual dimorphism due to the more pigmented bodies and larger fins, usually observed in males. Because of that there is a price discrepancy between the two sexes on the market. The color patterns of guppymales are complex and often conspicuous combinations of black, red, orange, yellow, white, green, iridescent, and other spots, speckles and lines. In the wild, they are expressed only in males and show a great deal of heritable variation among individuals (Houde 1997). Excepting cases of domesticated strains, where males of the same lot are often identical, each male is likely to have a unique color pattern. The well known geneticist Winge (1922ab, 1927), working at the Carlsberg Foundation in Denmark, had shown early in the past century that a number of shape and color pattern characters in males were sex-linked, and some color pattern features were autosomal. These observations brought the remarkable polymorphism of guppy color patterns in the attention of biologists and motivated work on the ecological genetics of color patterns. For a long period of time, it was difficult to understand how the polymorphism of color patterns originates and how it is maintained in guppy populations. The first steps ahead were related to understanding the concept of gene.

Concept of Gene. There are many definitions of the gene in the literature. Johannsen (1909) was the one who first used the term of gene to denote "... an internal something or condition upon whose presence an elementary morphological or physiological characteristic depends". The word *gene* was derived from De Vries' term *pangen*, itself a derivative of the word *pangenesis* which Darwin (1868) coined. Even not very precisely, the definition of Johannsen (1909, 1911) remained for a long time a good one for understanding the concept of gene. The nature of gene remained unknown even after Morgan's experiences (1919) who considered genes as "... material entities phisical linked into chromosomes".

Human Gene Nomenclature Committee (Wain et al 2002) in the paper "Guidelines for human gene nomenclature" gives the following definition based on phenotypic point of view: "… a DNA segment that contributes to phenotype/function. In the absence of demonstrated function a gene may be characterized by sequence, transcription or homology".

Gene Sweepstake Web Site - Sanger Institute gives us a definition centered on expression: "A gene is a set of connected transcripts. A transcript is a set of exons via transcription followed (optionally) by pre-mRNA (messenger RNA) splicing. Two transcripts are connected if they share at least part of one exon in the genomic coordonates. At least one transcript must be expressed outside of the nucleus and one transcript must encode a protein" (http://www.ensmble.org/Genesweep/).

Pollard & Earnshaw (2002) defined the gene as "... the nucleotide sequence required to make a protein or RNA product, including the coding sequence, flanking regulatory sequences, and introns, if present".

In the paper "Century of the gene" Morange (2001) stated: "... recent studies have impossible to give a functional definition of the gene".

But … what is a gene? Any definition is a logical compromise and an approximation of the reality (Dragoş 2004). One of the most accepted definition of the gene is that of Lodish et al (2000): "... a physical and functional unit of heredity, which carries information from one generation to the next. In molecular terms, it is the entire DNA sequence – including exons, introns, and noncoding transcription control regions – necessary for production of a functional protein or RNA". A gene is an ordered sequence of nucleotides located in a particular locus on a particular chromosome that encodes a specific functional product. The gene includes regions involved in regulation of expression and regions that encode a specific functional product.

Evolutionary Concept of Gene. The molecular gene *transcribes* as a unit, and the evolutionary gene *inherits* as a unit (http://en.wikipedia.org/wiki/Gene). Williams (1966) first explicitly advocated the gene-centric view of evolution in his book "Adaptation and Natural Selection". He proposed an evolutionary concept of gene to be used when we are talking about natural selection favoring some genes. The gene is "that which segregates and recombines with appreciable frequency". According to Williams (1966), even an asexual genome could be considered a gene, insofar that it have an appreciable permanency through many generations.

Sex Determination. *Poecilia reticulata* has a sex determination of *drosophila* type, with heterogametic (XY) males (Winge 1922ab). The female carries the setup XX and can therefore only produce sexual cells of one kind, X. The male has two different gender-defining cells and therefore produce gametes of two kinds, X and Y. If the male within the sperm donates one Y chromosome to its offspring, the offspring will become an XY individual, which is a son. If the male donates an X chromosome there the progeny will be a daughter. Minor sex genes are distributed throughout the autosomes and exceptional XX males or XY females appear occasionally by fortuitous combinations of autosomes or gene recombinations (Winge 1930, 1934; Winge & Ditlevsen 1947). However, in the majority of individuals, autosomal sex genes are more or less in balance, consequently, sex in most individuals is determined by the heterosomal combination. In spite of these statements, there are in *Poecilia reticulata* some environmental factors involved in the phenotypic sex determination (Petrescu-Mag 2007). However these factors seem to be less important.

Sex Chromosomes. Among most other vertebrates the Y chromosome is much reduced in size and does not carry any other information than the gender defining one. In the guppy, the Y chromosome contains many other functional genes which decide for example some coloring properties, fin forms, behaviour and some physiological processes (Nayudu 1979). The X and Y chromosomes of the guppy are both of the same size (Winge 1930, 1934). Many color patterns and fin morphologies recombine between the Y and X chromosomes, revealing a homology between guppy sex chromosomes (Lindholm & Breden 2002). Recombination is suppressed in the sex-determining region but increases with increasing distance from this region (Khoo et al 1999; Lindholm & Breden 2002).

It has been shown that there are some cytological and molecular differentiations between the X and Y chromosomes in the guppy (Traut & Winking 2001). Only one-half of the Y chromosome pairs with homologous regions of the X in the synaptonemal complexes. The orientation of the chromosomes allowed the recombination in only 2 of 49 observed synaptonemal complexes. This indicates that recombination is also greatly reduced even in the homologous region (Lindholm & Breden 2002).

Sex-Determining Region. A survey of the literature made by Lindholm & Breden (2002) indicates that, in the guppy, color traits and fin morphology are primarily Y and X linked. They found 16 Y-linked traits, 24 X- and Y-linked traits, two X-linked traits and two autosomal traits. Comparative genomic hibridization indicates a large part of the nonhomologous region of the Y chromosome comprising male specific repetitive DNA (Traut & Winking 2001). There is a structural variation among Y chromosomes in that region. Similar results from an *in situ* hybridization (Nanda et al 1990) show that Y chromosomes of domesticated guppies carry large numbers of simple repetitive sequences. These male-specific repetitive sequences are not observed in recent descendants of feral guppies (Hornaday et al 1994). A linkage map of the Y chromosome, based on phenotypic traits suggests that the sex-determining region is flanked on both sides by recombining regions (Khoo et al 1999). Suppression of recombination is probably not complete even in the non-pairing region of the chromosomes. Rare events of crossing-over occur even between the red and the black elements of the *Maculatus* pattern (Winge & Ditlevsen 1947), that are considered to be located near to sex-determining region (Winge 1934).

The male master sex-determining gene is located on Y chromosome, in the nonhomologous region at the specific locus SDL (Sex Determining Locus). Winge (1934), in his paper "The experimental alteration of sex chromosomes into autosomes and vice versa, as illustrated by *Lebistes*", demonstrated the fact that this gene may lose its epistatic function in the favor of some autosomal cofactors. According to Winge (1934), "… there are both masculine and feminine elements present in the autosomes. XX males may be produced by systematic selection of masculine autosomal elements. XY females can be produced by systematic selection of feminine autosomal elements". However, "even with respect to the major male SDL on Y we cannot tell whether it acts as a single locus or as a multifactorial complex that is almost never separated by recombination – as long as we do not know the molecular mechanism" (Dreyer 2008 - personal communication).

Variation of Male Trait. The extraordinary phenotypical variation and its dynamics in the guppy was often different and at different level explained by different scientists (see Table 1). The male polymorphism is perpetued by evolutionary mechanisms such those indicated by Hughes et al (1999). Carotenoid limitation in the environment and necesity of an alternative red pigmentation, mate choice, exposure to low or high risk of predation, high mortality due to some metabolic disfunctions, and accumulation of some color genes on the Y chromosome are all interdependent; the result: a great variation inside population, among populations, and an almost continuous dynamic of color traits in the population depending on environmental factors (see citations in Table 1, I.a-e). However, there are also many other factors affecting the male trait, acting at the individual level. Natural recombination of the chromosomes, crossing-over between autosomes and crossing-over between sex chromosomes are applicable to all eukaryotic species (see Table 1, II.a-III.a-d and citations therein). Nevertheless the same genetic factors express different under different environmental conditions, showing different possible phenotypes; some of them are temporary traits (Table 1, V.a and b, see also Figure 1).

The red color of the skin is chemical and is affected by the food the guppy eats. It has long been believed that foods with carotenoids, which the guppy cannot synthesize de novo, help the guppy store red pigment. Such an example is the brine shrimp, which is said to deepen the reds of some red guppy varieties. However, the scientific literature suggests that a redder guppy may simply be a healthier guppy. The other red chemical in guppy is the red pteridine, which can be synthesized de novo (see citations in Table 1, V.b). According to a compilation of Shaddock (2008a), "there are at least six different red genes, accounting for the variation you see in the color on different red guppies. Some believe the red is additive and multigenic. The more red genes involved, the redder the guppy. The fewer red genes, the pinker the strain" … "however, given that there are two red pigment organelles in red guppies, one containing carotenoids and the other containing pteridines, there must be more than one gene involved".

Different phenotypes appear due to dominance, codominance, poligeny, or demonstrated interallelic interactions. Petrescu-Mag & Bourne (2008) proposed, in the guppy, a mechanism of expression of several different loci in a single color pattern, resulting in high numbers of possible color pattern phenotypes. In the same year Tripathi et al (2008), based on earlier studies of Dreyer et al (2007), indicated that phenotypic and genotypic analysis of progeny from their mapping crosses and backcrosses suggests several genetic mechanisms that enhance natural variation, namely, additive effects of codominant alleles, suppressive actions of dominant alleles, and complex interplay between sex-linked and autosomal cofactors.

In the guppy, but also in many other vertebrates, the color pattern seems to be determined by complex interactions of many genes (at the same locus or not, located in the same chromosome or not), under variable environmental conditions. For example, the *Maculatus* color pattern is due to the presence of both *Maculatus* red and *Maculatus* black elements. On their turn, both *Maculatus* red and *Maculatus* black could have a composite nature, too.

Table 1

Factors contributing to variation of guppy male trait

		Factors contributing to variation of male trait	*Main references (year of publication)*
I.		Ecological/ethological/evolutionary	
	a)	Carotenoid limitation in the environment; necesity of the red pteridine alternative*	Kodric-Brown 1989; Long & Houde 1989; Brooks & Caithness 1995; Rodd & Sokolowski 1995; Grether et al 1999, 2001, 2004, 2005ab; Grether 2000; Rodd et al 2002; Hudon et al 2003; Karino et al 2005
	b)	Mate choice** (behavioral)	Haskins & Haskins 1950; Farr 1977; Bischoff et al 1985; Houde 1987; Stoner & Breden 1988; Darwall 1989; Crowley et al 1991; Nicoletto 1993; Breden et al 1994; Breden et al 1995; Gong 1995; Briggs et al 1996; Brooks 1996; Hughes et al 1999; Hoffmann et al 2007
	c)	Exposure to low or high risk of predation***	Seghers 1973; Endler 1980, 1983; Breden & Stoner 1987; Breden et al 1987; Breden 1988; Dugatkin & Alfieri 1991ab, Dugatkin 1992ab; Godin 1995; Nordell 1995; Godin 2003
	d)	High mortality due to some metabolic disfunctions**** (albino, half-black and transparent guppy)	Haskins & Haskins 1948; Nayudu 1979; Shaddock 2008 - personal communication
	e)	Accumulation of color genes on the Y chromosome*****	Fisher 1931; Charlesworth 1978, 2004; Bull 1983; Rice 1984, 1987ab; Lindholm & Breden 2002
II.		Genetic recombination in meiosis – extrachromosomal	
	a)	Natural recombination of chromosomes - applicable to all eukaryotic species	Morgan 1919
III.		Genetic recombination – intrachromosomal	
	a)	Crossing-over between autosomes - applicable to all eukaryotic species	Morgan 1919
	b)	Crossing-over between X chromosomes - applicable to most of eukaryotic species	Morgan 1919
	c)	Crossing-over between X and Y chromosomes	Winge 1922a, 1927, 1934; Blacher 1928; Winge & Ditlevsen 1947; Dzwillo 1959; Haskins et al 1961, 1970; Schröder 1969; Nayudu 1979; Fernando & Phang 1990; Phang & Fernando 1991; Khoo et al 1999; Lindholm & Breden 2002
	d)	Crossing-over between Y and Y chromosomes in accidental YY males	Petrescu-Mag & Bourne 2008
IV.		Different phenotypic expression of the genetic factors	
	a)	Additive effects of codominant alleles	Tripathi et al 2008
	b)	Suppressive actions of dominant alleles	Tripathi et al 2008
	c)	Expression of several different loci in a single color pattern, resulting in high numbers of possible color pattern phenotypes	Petrescu-Mag & Bourne 2008
	d)	Complex interplay between sex-linked and autosomal cofactors	Phang et al 1999; Petrescu-Mag et al 2007; Tripathi et al 2008
	e)	Interallelic interaction	Phang et al 1999; Petrescu-Mag et al 2007; Shaddock 2008b
	f)	Additive effects of some polygenes	Houde 1992; Brooks 2000; Brooks & Endler 2001; Karino & Haijima 2001
V.		Temporary traits	
	a)	Wide variation of some black patterns in male depending on its physiological condition	Petrescu-Mag, unpubl. data
	b)	A diet rich in carotenoids increases the red pigmentation of the skin (this trait is not hereditary, but the algal-foraging ability may be hereditary)	Grether 2000; Grether et al 2001, 2004, 2005b; Hudon et al 2003; Karino et al 2005; Shaddock 2008a; Petrescu-Mag, unpubl. data
VI.		Domestication and artificial selection	
	a)	Domestication, artificial selection, genetic modification, hybridization etc	Schmidt 1920; Dzwillo 1959; Shaddock 2008a

Note: *a, **b, ***c, ****d and *****e are all interdependent in the guppy.

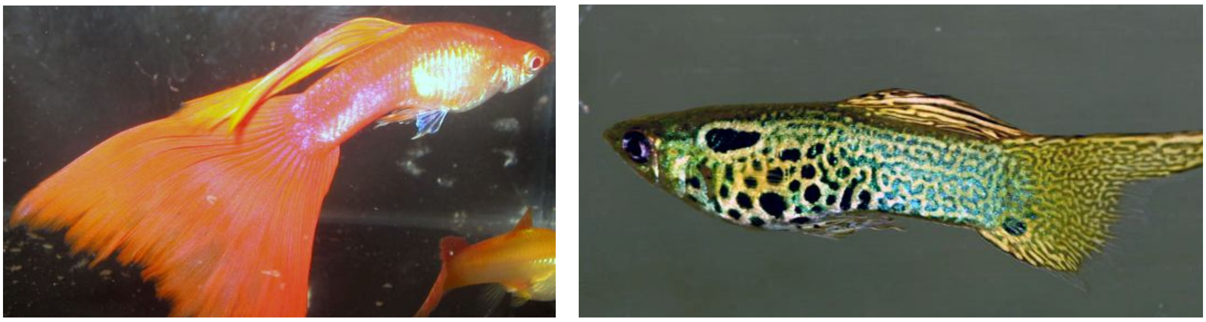

Figure 1. Temporary extreme coloration in Full Red Guppy (left; photo by Carlos Beserra) and nuptial black spots in Japan Blue Snakeskin (right; photo by Finn Bindeballe) (source: Shaddock 2008a)

Conclusions. Different phenotypes appear in the guppy due to dominance, codominance, poligeny, or some demonstrated interallelic interactions. Recent (both molecular and classical) investigations suggest a mechanism of expression of several different loci in a single color pattern, resulting in high numbers of possible color pattern phenotypes. These genetic mechanisms that enhance natural variation, are additive effects of codominant alleles, suppressive actions of dominant alleles, and complex interplay between sex-linked and autosomal cofactors. In *Poecilia reticulata*, but also in many other vertebrates, the color pattern seems to be determined by complex interactions of many genes (at the same locus or not, located in the same chromosome or not), under variable environmental conditions. For example, the *Maculatus* color pattern is due to the presence of both *Maculatus* red and *Maculatus* black elements. On their turn, having in view the latest definitions of the *gene*, both *Maculatus* red and *Maculatus* black could be composite, too.

The deepest mechanism of sex determination is not clear yet, but even with respect to the major male SDL on the Y chromosome we cannot tell whether it acts as a single locus or as a multifactorial complex that is almost never separated by genetic recombination – as long as we don't know the molecular mechanism. However, the classical studies of Winge early in the past century and recent molecular studies revealed a possible composite nature of so called master sex determining gene, located at SDL of the Y chromosome.

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References

Alexander H. J., Breden F., 2004 Sexual isolation and extreme morphological divergence in the Cumaná guppy: a possible case of incipient speciation. J Evol Biol 17:1238-1254.

Bischoff R. J., Gould J. L., Rubenstein D. I., 1985 Tail size and female choice in the guppy (*Poecilia reticulata*). Behav Ecol Sociobiol 17:253-255.

Blacher L. J., 1928 Materials for the genetics of *Lebistes reticulatus*. II. Transactions of the Laboratory of Experimental Biology of the Zoopark of Moskow 4:245-253.

Breden 1988 Sexual selection and predation risk in guppies. Reply. Nature 332:594.

Breden F., Stoner G., 1987 Male predation risk determines female preference in the Trinidad guppy. Nature 329:831-833.

Breden F., Scott M., Michell E., 1987 Genetic differentiation for antipredator behavior in the Trinidad guppy, *Poecilia reticulata*. Anim Behav 35:618-620.

Breden F., Gerhardt H. C., Butlin R. K., 1994 Female choice and genetic correlations. TREE 9:343.
Breden F., Novinger D., Schubert A., 1995 The effect of experience on mate choice in the Trinidad guppy, *Poecilia reticulata*. Environ Biol Fish 7:323-328.
Briggs S. E., Godin J.-G. J., Dugatkin L. A., 1996 Mate-choice copying under predation risk in the Trinidadian guppy (*Poecilia reticulata*). Behav Ecol 42:151-157.
Brooks R., 1996 Sexual selection by female choice in guppies ((*Poecilia reticulata*). PhD diss., University of Witwatersrand, South Africa.
Brooks R., 2000 Negative genetic correlation between male sexual attractiveness and survival. Nature 406:67-70.
Brooks R., Caithness N., 1995 Female guppies use orange as a mate choice cue: A manipulative test. SAJ Zool 30:200-201.
Brooks R., Endler J. A., 2001 Direct and indirect sexual selection and quantitative genetics of male traits in guppies (*Poecilia reticulata*). Evolution 55:1002-1015.
Bud I., 2002 [Aquariophilia]. Academicpres, Cluj-Napoca, Romania. [In Romanian]
Bull J. J., 1983 Evolution of sex determining mechanisms. Benjamin Cummings, Menlo Park, California.
Charlesworth B., 1978 A model for the evolution of Y chromosomes and dosage compensation. Proceedings of the National Academy of Sciences of USA 75:5618-5622.
Charlesworth B., 2004 Sex determination: primitive Y chromosome in fish. Curr Biol 14:R745-R747.
Crowley P. H., Travers S. E., Linton M. C., Cohn S. L., Sih A., Sargent R. C., 1991 Mate density, predation risk, and seasonal sequence of mate choice: A dynamic game. Am Nat 137:567-596.
Darwall W. R. T., 1989 Sexual selection in the guppy (*Poecilia reticulata*). M Sc Thesis. University of Utah, Salt Lake City.
Darwin C., 1868 The variation of animals and plants under domestication. John Murray, London.
Dragoş N., 2004 Structure and Evolution of the Genome. Course Notes (draft). Babeş-Bolyai University, Cluj-Napoca, Romania.
Dreyer C., Hoffmann M., Lanz C., Willing E.-M., Riester M., Warthmann N., Sprecher A., Tripathi N., Henz S., Weigel D., 2007 ESTs and EST-linked polymorphisms for genetic mapping and phylogenetic reconstruction in the guppy, *Poecilia reticulata*. BMC Genomics 8:269.
Dugatkin L., 1992a Sexual selection and imitation: Females copy the mate choice of others. Am Nat 139:1384-1389.
Dugatkin L., 1992b Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia reticulata*). Behav Ecol 3:124-127.
Dugatkin L. A., Alfieri M., 1991a Guppies and tit-for-tat strategy: Preference based on past interaction. Behav Ecol Sociobiol 28:234-246.
Dugatkin L. A., Alfieri M., 1991b Tit-for-tat in guppies: The relative nature of cooperation and defection during predator inspection. Evol Ecol 5:300-309.
Dzwillo M., 1959 [Genetic research on some domesticated strains of *Lebistes reticulatus* (Peters)]. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 57:143-186. [In German]
Endler J. A., 1980 Natural selection on color patterns in *Poecilia reticulata*. Evolution 34:76-91.
Endler J. A., 1983 Natural and sexual selection on color patterns in poeciliid fishes. Environ Biol Fishes 9:173-190.
Farr J. A., 1977 Male rarity or novelty, female choice behavior and sexual selection in the guppy *Poecilia reticulata* Peters (Pisces: Poeciliidae). Evolution 31:162-168.
Fernando A. A., Phang V. P. E. 1990 Inheritance of red and blue caudal fin colourations in two domesticated varieties of the guppy, *Poecilia reticulata*. Journal of Aquaculture in the Tropics 5:209-217.
Fisher R. A., 1931 The evolution of dominance. Biological Reviews 6:345-368.

Godin J.-G. J., 1995 Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). Oecologia 103:224-229.
Godin J.-G. J., 2003 Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. Behav Ecol 14:194-200.
Gong A., 1995 Costs and benefits of female choice in the Guppy (*Poecilia reticulata*). PhD diss, University of California, Los Angeles.
Grether G. F., Hudon J., Millie D. F., 1999 Carotenoid limitation of sexual coloration along an environmental gradient in guppies. Proc R Soc Lond B 266:1317-1322.
Grether G. F., 2000 Carotenoid limitation and mate preference evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulata*). Evolution 54(5):1712-1724.
Grether G. F., Hudon J., Endler J. A., 2001 Carotenoid scarcity, synthetic pteridine pigments and the evolution of sexual coloration in guppies (*Poecilia reticulata*). Proc R Soc Lond B 268:1245-1253.
Grether G. F., Kasahara S., Kolluru G. R., Cooper E. L., 2004 Sex-specific effects of carotenoid intake on the immunological response to allografts in guppies (*Poecilia reticulata*). Proc R Soc Lond B 271:45-49.
Grether G. F., Cummings M. E., Hudon J., 2005a Countergradient variation in the sexual coloration of guppies (*Poecilia reticulata*): Drosopterin synthesis balances carotenoid availability. Evolution 59(1):175-188.
Grether G. F., Kolluru G. R., Rodd F. H., de la Cerda J., Shimazaki K., 2005b Carotenoid availability affects the development of a colour-based mate preference and the sensory bias o which it is genetically linked. Proc R Soc B 272:2181-2188.
Haskins C. P., Haskins E. F., 1948 Albinism, a semilethal autosomal mutation in *Lebistes reticulatus*. Heredity 2:251-262.
Haskins C. P., Haskins E. F., 1950 Factors governing sexual selection as an isolating mechanism in the poeciliid fish *Lebistes reticulatus*. Proc Natl Acad Sci USA 36:464-476.
Haskins C. P., Haskins E. F., McLaughlin J. J. A., Hewitt E., 1961. Polymorphism and population structure in *Lebistes reticulatus*, an ecological study. P.320-395, In: Blair W. F. (ed.), Vertebrate speciation. University of Texas Press, Austin.
Haskins C. P., Young P., Hewitt R. E., Haskins E. F., 1970 Stabilised heterozygosis of supergenes mediating certain Y-linked colour patterns in populations of *Lebistes reticulatus*. Heredity 25:575-589.
Hoffmann M., Tripathi N., Henz S. R., Lindholm A. K., Weigel D., Breden F., Dreyer C., 2007 Opsine gene duplication and diversification in the guppy, a model for sexual selection. Proc R Soc B 274:33-42.
Hornaday K., Alexander S., Breden F., 1994 Absence of repetitive DNA sequences associated with sex chromosomes in natural populations of the Trinidad guppy (*Poecilia reticulata*). Journal of Molecular Evolution 39:431–433.
Houde A. E., 1987 Mate choice based upon naturally occuring color pattern variation in a guppy population. Evolution 41:1-10.
Houde A. E., 1992 Sex-linked heritability of a sexually character in a natural population of *Poecilia reticulata* (Pisces: Poeciliidae) (guppies). Heredity 69:229-235.
Houde A. E., 1997 Sex, Color, and Mate Choice in Guppies. Princeton University Press, Princeton, New Jersey.
Hudon J., Grether G. F., Millie D. F., 2003 Marginal differentiation between the sexual and general carotenoid pigmentation of guppies (*Poecilia reticulata*) and a possible visual explanation. Physiological and Biochemical Zoology 76(6):776-790.
Hughes K. A., Du L., Rodd F. H., Reznick D. N., 1999 Familiarity leads to female mate preference for novel males in the guppy, *Poecilia reticulata.* Animal Behavior 58:907-916.
Johannsen W. L., 1909 [Elements of an Exact Theory of Heredity]. Gustav Fischer, Jena. [In German]
Johannsen W. L., 1911 The Genotype Conception of Heredity. Am Nat 45(531):129-159.
Karino K., Haijima Y., 2001 Heritability of male secondary sexual traits in feral guppies in Japan. Journal of Ethology 19:33-37.

Karino K., Utagawa T., Shinjo S., 2005 Heritability of the algal-foraging ability: an indirect benefit of female mate preference for males' carotenoid-based coloration in the guppy, *Poecilia reticulata*. Behav Ecol Sociobiol 59:1-5.

Khoo G., Lim T. M., Chan W.-K., Phang V. P. E., 1999 Linkage analysis and mapping of three sex-linked color pattern genes in the guppy, *Poecilia reticulata*. Zoological Science 16:893-903.

Kodric-Brown A., 1989 Dietary carotenoids and male mating success in the guppy: an environmental component to female choice. Behav Ecol Sociobiol 25:393-401.

Lindholm A., Breden F., 2002 Sex chromosomes and sexual selection in poeciliid fishes. Am Nat 160:S214-S224.

Lodish H., Berk A., Zipursky S. L., Matsudaira P., Baltimore D., Darnell J., 2000 Molecular Cell Biology. 3th Ed., Freeman & Co.

Long K. D., Houde A. E., 1989 Orange spots as a visual cue for female mate choice in the guppy (*Poecilia reticulata*). Ethology 82:316-324.

Morange M., 2001. Century of the gene. ISUMA Can J Policy Res 2:22-27.

Morgan T. H., 1919 The Physical Basis of Heredity. JB Lippincott Company. Online Edition, Electronic Scholarly Publishing, prepared by Robert Robbins.

Nanda I., Feichtinger W., Schmid M., Schröder J. H., Zischler H., Epplen T. J., 1990 Simple repetitive sequences are associated with differentiation of the sex chromosomes in the guppy fish. Journal of Molecular Evolution 30:456–462.

Nayudu P. L., 1979 Genetic studies of melanic color patterns and atipical sex determination in the guppy, *Poecilia reticulata*. Copeia 2:225-231.

Nicoletto P. F., 1993 Female sexual response to condition-dependent ornaments in the guppy, *Poecilia reticulata*. Anim Behav 46:441-450.

Nordell S. E., 1995 Mechanisms of selection: Mate Choice and predator assessment in guppies (*Poecilia reticulata*). University of New Mexico Press, Albuquerque.

Petrescu-Mag I. V., 2007 [Research concerning possibilities of reproduction conducting for sex control in the varieties of *Lebistes reticulata* (*Poecilia reticulata*)]. Academicpres, Cluj-Napoca, Romania. [Edited in both Romanian and English]

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):1-10.

Petrescu-Mag I. V., Lozinsky R. L., Hărşan R., Csép L., Boaru A. M., 2007 Interallelic interaction between the autosomal Blond and the sex-linked *Nigrocaudatus* gene in the guppy (*Poecilia reticulata*). AIR 2(1).

Phang V. P. E., Fernando A. A., 1991 Linkage analysis of the X-linked green tail and blue tail color genes in the guppy. Zoological Science 8:975-981.

Phang V. P. E., Khoo G., Ang S. P., 1999 Interaction between the autosomal recessive *bar* gene and the Y-linked snakeskin body (*Ssb*) pattern gene in the guppy, *Poecilia reticulata*. Zoological Science 16:905-908.

Poeser F. N., Kempkes M., Isbrücker I. J. H., 2005 Description of *Poecilia* (*Acanthocephalus*) *wingei* sp from the Paría Peninsula, Venezuela, including notes on *Acanthocephalus* Eigenmann, 1907 and other subgenera of *Poecilia* Bloch and Schneider, 1801 (Teleostei, Cyprinodontidormes, Poeciliidae). Contributions to Zoology 74(1/2). Available online at: http://dpc.uba.uva.nl/ctz/vol74/nr01/art07

Pollard T. D., Earnshaw W. C., 2002 Cell Biology. Saunders Publ., p.74-83.

Rice W. R., 1984 Sex chromosomes and the evolution of sexual dimorphism. Evolution 38:735-742.

Rice W. R., 1987a The accumulation of sexually antagonistic genes as a selective agent promoting the evolution of reduced recombination between primitive sex chromosomes. Evolution 41:911-914.

Rice W. R., 1987b Genetic hitchhiking and the evolution of reduced genetic activity of the Y sex-chromosome. Genetics 116:161-167.

Rodd F. H., Hughes K. A., Grether G. F., Baril C. T., 2002 A possible non-sexual origin of mate preference: are male guppies mimicking fruit? Proc R Soc Lond B 269:475-481.

Rodd F. H., Sokolowski M. B., 1995 Complex origins of variation in the sexual behaviour of male Trinidadian guppies, *Poecilia reticulata*: Interactions between social environment, heredity, body size, and age. Anim Behav 49:1139-1159.

Sanger Institute - Gene Sweepstake Web Site http://www.ensmble.org/Genesweep/ (last view: 18.10.2004).

Schmidt J., 1920 Racial investigations. IV. The genetic behaviour of a secondary sexual character. Comptes Rendus des Travaux de Laboratoire Carlsberg 14(8):1-12.

Schröder J. H., 1969 Inheritance of fin characters in the guppy (*Lebistes reticulatus* Peters). Theoretical and aplied Genetics 39:73-78.

Seghers B. H., 1973 An analysis of geographic variation in the antipredador adaptations of the guppy, *Poecilia reticulata*. PhD diss, University of British Columbia, Vancouver.

Shaddock P., 2008a Guppy Color Bank. Electronic book, Edition 1.5, June, from: www.guppydesigner.com

Shaddock P., 2008b Blond: a regulatory gene in the guppy (*Poecilia reticulata* Peters 1859). AACL Bioflux 1(2):161-164.

Stoner G., Breden F., 1988 Phenotypic differentiation in female preferente related to geographic variation in male predation risk in the Trinidad guppy (*Poecilia reticulata*). Behav Ecol Sociobiol 22:285-291.

Traut W., Winking H., 2001 Meiotic chromosomes and stages of sex chromosome evolution in fish: zebrafish, platyfish and guppy. Chromosome Research 9:659-72.

Tripathi N., Hoffmann M., Dreyer C., 2008 Natural variation of male ornamental traits of the guppy, *Poecilia reticulata*. Zebrafish 5(4):265-278.

Wain H. M., Lovering R. C., Bruford E. A., Lush M. J., Wright M. W., Povey S., 2002 Guidelines for human gene nomenclature. Genomics 79:464-470.

Wikipedia, the Free Encyclopedia Web Site, http://en.wikipedia.org/wiki/Gene (last view: 20.01.2009).

Williams G. C., 1966 Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought. Princeton University Press.

Winge Ö., 1922a Crossing-over between the X- and the Y-chromosome in *Lebistes*. Comptes Rendus des Travaux du Laboratoire Carlsberg 14(20):1-20.

Winge Ö., 1922b One-sided masculine and sex-linked inheritance in *Lebistes reticulatus*. Journal of Genetics 12:146-162.

Winge Ö., 1927 The location of eighteen genes in *Lebistes reticulatus*. Journal of Genetics 18:1-43.

Winge Ö., 1930 On the occurrence of XX-males in *Lebistes*, with some remarks on Aida's so-called 'non disjunctional' males in *Aplocheilus*. Journal of Genetics 23:69-76.

Winge Ö., 1934 The experimental alteration of sex chromosomes into autosomes and vice versa, as illustrated by *Lebistes*. Comptes Rendus des Travaux du Laboratoire Carlsberg 21:1-49

Winge Ö., Ditlevsen E., 1947 Colour inheritance and sex determination in *Lebistes*. Heredity 1:65-83.

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