

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

^{1,2,3,4}I. Valentin Petrescu-Mag

¹SC Bioflux SRL, Cluj-Napoca, Romania, EU; ²USAMV Cluj, Romania, EU;
³SC 3M AGC SRL, Cluj-Napoca, Romania, EU; ⁴guppydesigner.com, Canada;
e-mail: zoobiomag2004@yahoo.com

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 również złożoną naturę. Determinacja płci u gupików jest przedmiotem badań od lat 20. XX wieku. Najgłębszy mechanizm determinujący płć 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 płć, umiejscowionego w SDL na chromosomie Y.

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

Rezumat. La *Poecilia reticulata*, diferitele fenotipuri cunoscute apar datorită dominantei, codominanței, poligeniei, sau datorită unor demonstrate interacțiuni interalelice. Studii recente (atât moleculare cât și clasice) sugerează un mecanism prin care câțiva loci diferiți se exprimă într-un singur tipar coloristic, rezultând un număr imens de tipare posibile. Tiparele coloristice par a fi determinate de interacțiunea complexă a mai multor gene (situat la același locus sau nu, pe același cromosom sau nu), sub influența variabilelor condiții ambientale. Spre exemplu, tiparul *Maculatus* apare în prezența elementelor *Maculatus* red și *Maculatus* black. Acestea, la rândul lor, având în vedere cele mai recente definiții ale genei, ar putea avea și 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 și cercetările moleculare de ultimă oră sugerează o posibilă natură compusă a așa-numitei gene dominante (epistatice) a sexului, situate la locusul SDL al cromosomului Y.

Cuvinte cheie: tipare coloristice, guppy, gene ale sexului, interacțiuni 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 *pangensis* 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 physical 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 coordinates. At least one transcript must be expressed outside of the nucleus and one transcript must encode a protein" (<http://www.ensembl.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 hybridization 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 perpetuated by evolutionary mechanisms such those indicated by Hughes et al (1999). Carotenoid limitation in the environment and necessity 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, polygeny, 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

<i>Factors contributing to variation of male trait</i>	<i>Main references (year of publication)</i>
I. Ecological/ethological/evolutionary	
a) Carotenoid limitation in the environment; necessity 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.

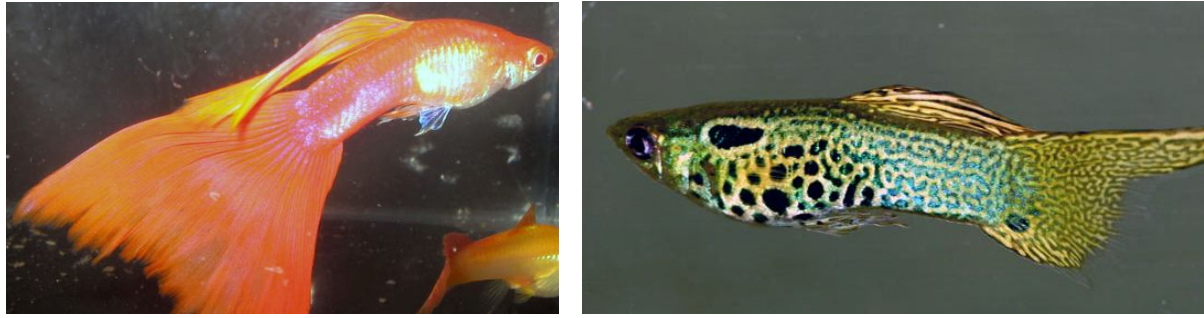


Figure 1. Temporary extreme coloration in Full Red Guppy (left; photo by Carlos Beserra) and nuptial black spots in Japan Blue Snakeskin (right; photo by Finn Bindeballe) (source: Shaddock 2008a)

Conclusions. Different phenotypes appear in the guppy due to dominance, codominance, polygeny, 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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Authors:

Ioan Valentin Petrescu-Mag, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Faculty of Animal Husbandry, Department of Aquaculture, Calea Mănăştur 3-5, 400372, Cluj-Napoca, Romania, EU;

SC Bioflux SRL, Ceahlău Street no 54, 400488, Cluj-Napoca, Romania, EU;

SC 3M AGC SRL Cluj-Napoca, Piața 1 Mai, no 3, 400058, Cluj-Napoca, Romania, EU;

Guppydesigner.com, Canada;

e-mail: zoobiomag2004@yahoo.com

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