

Poeciliid fish and color vision

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Abstract. Poeciliid fish have become model organisms for various studies over the past hundred years. Among the most recent studies that use the guppy fish as a model organism are the studies on the so-called opsin proteins. Opsins and color vision in poeciliid fish have become a topic of study that helps understanding the behavioral, ecological and evolutionary mechanisms of vertebrates. The paper discusses on relevance of understanding the poeciliid color vision for scientific development.

Key Words: color vision, opsin proteins, poeciliid fish, *Poecilia*.

Introduction. Poeciliid fish have become model organisms for various studies over the past hundred years (Papuc & Petrescu-Mag 2020), including studies of evolutionary biology, ethology, genetics, sexuality, ecology and ecotoxicology (Mag et al 2005a, b, c; Mag & Petrescu 2006; Petrescu-Mag 2007a, b; Miller et al 2010). Among the most current studies that use the guppy fish (*Poecilia reticulata*) as a model organism are the studies on the so-called opsins and those that follow color vision (Sandkam et al 2017; Sakai et al 2018; Chang et al 2020).

***Poecilia* genus, a good model for color vision studies.** First of all, we need to understand why guppy fish have been potential candidates for the study of color vision. It is known that in populations at low risk of predation, the male uses color signals on his own body (spots, lines, iridescence or even complex patterns with strong contrast, see Figure 1) to capture the female's attention and attract her for mating (Petrescu-Mag & Bourne 2008). In these populations, female guppy fish have the behavioral trait of attraction to red as a result of instinctual scanning of the environment to find food rich in carotenoids (Rodd et al 2002). Thus, the male uses red and other color patterns displayed on his own body as a sensory trap, to attract potential mating partners (Petrescu & Mag 2006; Petrescu-Mag 2009).

As a result of this "vicious circle" the fry resulting from such a mating will most likely inherit the attraction to red and other colored ornaments. So, young females will increase their chances of finding a male and will increase their chances of perpetuation. Also, young males will most likely inherit the potential to display red as well as other ornaments on their own bodies (Houde 2019). But all offspring, regardless of gender, will most likely inherit the ability to find new food sources rich in carotenoids and other nutrients associated with highly pigmented fruits and invertebrates.

It has been found that all these female preferences are genetically coded and even genetically linked. The physical linkage between genes responsible for the display of ornaments and genes responsible for the preference for a certain ornament (Lindholm &

Breden 2002) makes the guppy fish population have its own behavioral dynamics, in accordance with the environment and changes in the environment.



Figure 1. The guppy, *Poecilia reticulata* male (left), female (right) (photos provided by Petrescu-Mag I. V. from his personal collection).

The ability to distinguish colors and visual details in the aquatic environment involved an evolution of a very complex structure of the eye in poeciliid fish and especially in guppy fish (Hoffmann et al 2007). A study conducted five years ago on South American poeciliid species concluded that color vision (through the expression of opsins) varies more between populations than between species of poeciliid fish (Sandkam et al 2015). This fact illustrates the prompt evolution of fish populations in relation to local environmental factors, for a more efficient adaptation to local environmental conditions.

Opsins and color vision in vertebrates. In order to understand the color vision, we must understand first the opsins, which are special proteins involved in color vision. Both in human and other vertebrate groups, vision starts as photonic particles hit the photosensitive cells in the retina, the cone and rod cells more exactly (Bowmaker & Hunt 2006). This is the first step of a complex biochemical cascade that finally turns into a neurological process, a sensation that we call vision (Bloch 2016).

Cone and rod cells are distinct photoreceptors from morphological point of view (Ebrey & Koutalos 2001). This is because these different cells serve different systems in vision (Bowmaker & Hunt 2006). Rod cells, on one side, contribute to scotopic vision, useful at night, a highly sensitive process that lacks color information and has poor acuity (Bloch 2016).

Cone cells, on the other side, are only active in bright light (Bowmaker & Hunt 2006). They serve to photopic vision (vision during the daylight or bright light) and lies at the basis of color vision (Bloch 2016). Due to the fact vision in colors relies on comparing the output from different cone classes (Shevell 2003; Kelber et al 2003; Solomon & Lennie 2007), color vision requires a minimum of two cone types and an opponent mechanism wired into the nervous system that can compare the outputs of the different cone types (Bowmaker 2008; Bloch 2016).

The properties of spectral absorption of cone and rod photoreceptors are largely determined by the type of visual pigment they express (Bloch 2016). Visual pigments have the property of transforming the light energy into electrical potentials (Bowmaker & Hunt 2006). They are trans-membrane molecules contained in the exterior segment of photoreceptors. Visual pigments consist of an opsin protein moiety which is covalently bound to a light-sensitive chromophore. Opsins belong to the superfamily GPCR (which stand for "G-protein coupled receptor proteins"). This superfamily is involved in multiple processes of cell signaling (Arshavsky et al 2002). They are composed from seven α -helical trans-membrane regions which enclose the chromophore-binding pocket. The chromophores offer opsins their unique light-sensitive properties and are found in two variants (Bowmaker & Hunt 2006). Most of the vertebrate opsins bind an A1 chromophore, 11-cis-retinaldehyde (retinal) and some bind an A2 chromophore, 3,4-dehydroretinaldehyde (3,4-dehydroretinal) (Bowmaker 2008; Bloch 2016). The spectral

sensitivity of visual pigments depends on the type of chromophore they bind (chromophore A2 causes pigments to be slightly long-wavelength shifted), and on the identity of specific amino acids throughout the sequence of opsin protein which interact with the chromophore (Applebury & Hargrave 1986; Yokoyama 2000; Bowmaker 2008; Bloch 2016). At the moment when a photon hits a visual pigment, the chromophore switches from a 11-cis-retinal conformation to an all-trans-retinal, starting the process of phototransduction. This phototransduction cascade is translated to vision, which is a sensation resulted from this physiochemical cascade (Lamb et al 2007; Bloch 2016).

Cone and rod visual pigments differ in many ways (Hunt et al 2007). They differ in terms of their function and structure, and therefore they are active at different light levels and serve different purposes in the system of vision (Bowmaker & Hunt 2006; Bloch 2016). Besides the rod pigment, called Rhodopsin (RH1), there are also several types of cone visual pigments that differ in terms of their wavelength of maximum absorbance (λ_{max} , see Figures 2 and 3) and belong to four distinct spectral classes (Lamb et al 2007; Bowmaker 2008). The LWS-MWS family is maximally sensitive in the long to middle-wavelengths region of the spectrum ("reds" and "greens" between 490 and 570 nm) (Hunt et al 2007), the RH2 family is sensitive to middle-wavelengths (between 480 and 535 nm) (Hunt et al 2007), the short-wavelength sensitive SWS2 family ("blue-violet" between 410 and 490 nm) and the SWS1 family is also sensitive to short wavelengths generally, including ultraviolet (between 355 and 440 nm) (Yokoyama 2000; Yokoyama & Radlwimmer 1998, 2001; Bloch 2016).

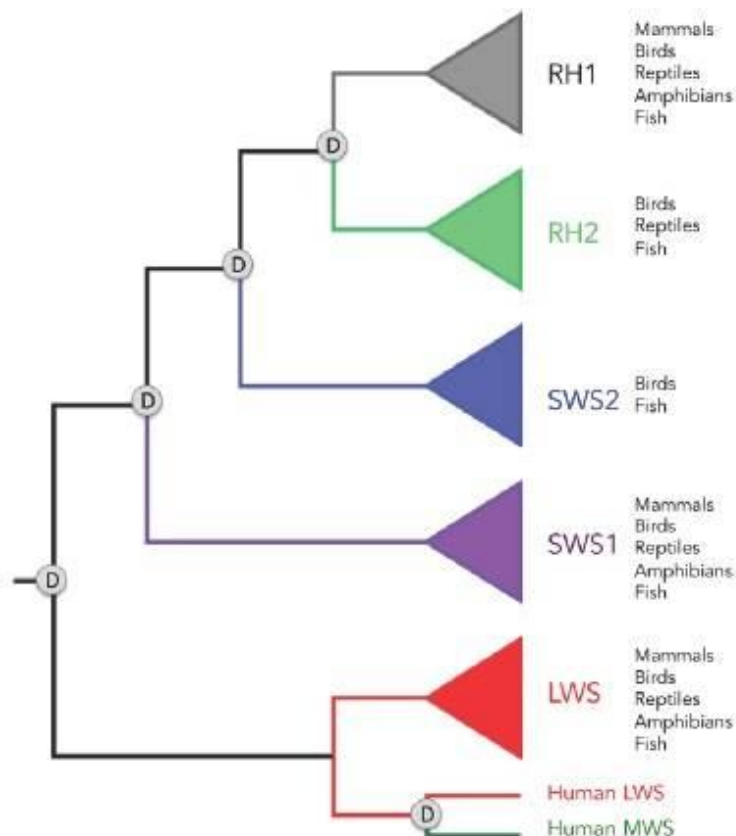


Figure 2. Relationships between spectral classes of opsins as presented by Bowmaker (2008). Duplications are represented by circles at relevant nodes. Except for the duplication that resulted in human MWS and LWS pigments, all duplications are believed to have occurred very early in evolution of vertebrates group (see also detailed explanation in Bloch 2016).

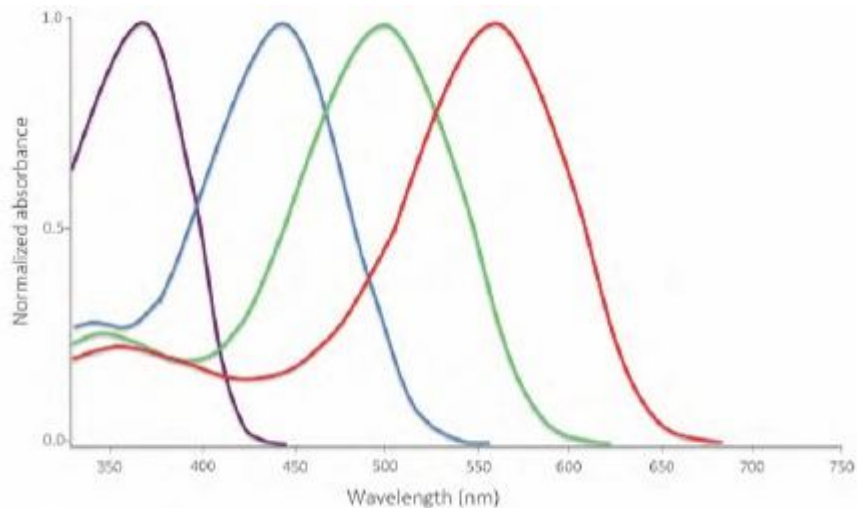


Figure 3. Vertebrate visual pigments and their spectral sensitivities according to Bloch (2016). LWS are represented in red, MWS/RH2 in green, SWS2 in blue, while SWS1 are represented in purple. These are just examples of the spectral sensitivities of visual pigments for each family. The real maximum sensitivity values and number of visual pigments in each family varies with species.

Why are so important opsins and color vision in poeciliid fish? Poeciliid fish have highly divergent visual systems. Guppy fish has photoreceptors with a broad range of spectral sensitivity indicating that the species has excellent capacity to detect subtle differences in color (Archer et al 1987; Archer & Lythgoe 1990).

Studies from the years 2000' indicates surprisingly high levels of genetic variability for visual pigment loci (opsin proteins), both within and between poeciliid populations, including variation in numbers of opsin loci (Weadick & Chang 2007; Hoffmann et al 2007). Guppy populations differ in terms of their behavioral response to colored objects, and this response covaries strongly with male color pattern and with female response to male color patterns (Endler & Houde 1995; Rodd et al 2002). This population covariation suggests that the visual system mediates both sexual and non-sexual behavior, and also provides the biological resources necessary to test such behavioral and evolutionary hypotheses.

"Sensory bias" models for the evolution of mate preference place a great emphasis on the importance of sensory system variation in mate preferences (Sandkam et al 2015). The "sensory-bias" hypothesis suggests that biases in female sensory or neural systems are important in triggering sexual selection and in determining which male traits will become elaborated into color patterns (Rodd et al 2002). However, the extent to which sensory systems vary across- versus within-species remains poorly known (Sandkam et al 2015). In their investigation, Sandkam et al (2015) assessed whether vision in colors varies in natural locations where guppies and the two closely related species, *Poecilia parae* and *Poecilia picta*, occur in extreme sympatry and school together. All these three species express mate preferences as preference for male ornamentation but differ in terms of colors mostly preferred (Sandkam et al 2015).

Measuring the intensity of opsin gene expression, Sandkam et al (2015) found that within sympatric locations these three species had very similar color vision and that color vision differed more across populations of conspecifics. Additionally, they found that all three poeciliid species differed across populations in terms of frequency of the same opsin coding polymorphism that influences visual tuning. They concluded on the basis of their results that sensory systems vary considerably across populations and this supports the possibility that sensory system variation is involved in population divergence of mate preference (Sandkam et al 2015).

Conclusions. Opsins and color vision in poeciliid fish have become a topic of study that helps understanding the behavioral, ecological and evolutionary mechanisms of vertebrates.

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