

Pigments and pigment cells underlying coloration in the guppy *Poecilia reticulata* Peters, 1859

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Abstract. Coloration in the guppy (*Poecilia reticulata*) represents one of the most intensively studied model systems for understanding the cellular, biochemical, genetic, and ecological bases of vertebrate pigmentation. This mini review synthesizes current knowledge on the pigment cells and pigments responsible for guppy coloration, emphasizing the structure, function, and interactions of chromatophore classes. Guppy skin contains five major chromatophore types - melanophores, xanthophores, erythrophores, iridophores, and leucophores - each contributing distinct optical properties through pigment absorption, reflection, or scattering. Melanophores generate black and brown coloration via eumelanin, while xanthophores and erythrophores produce yellow to red hues through carotenoids and pteridines. Iridophores, containing ordered guanine crystals, create structural coloration and enhance brightness and contrast by interacting with overlying pigment cells, whereas leucophores contribute to white coloration and reflective backgrounds. Recent ultrastructural and genetic studies demonstrate that guppy ornaments result from multilayered chromatophore arrangements regulated by gene expression, intercellular signaling, and neural crest-derived developmental pathways. Environmental factors, including diet, endocrine disruptors, and pollutants, further modulate pigment deposition and chromatophore physiology, influencing coloration intensity and pattern expression. The integration of pigment cell biology, molecular genetics, and environmental influences underscores the guppy as a powerful model for investigating the mechanisms underlying complex vertebrate coloration and its evolutionary and ecological significance.

Key Words: carotenoids, chromatophores, coloration, environmental modulation, erythrophores, guanine, guppy, iridophores, leucophores, melanin, melanophores, pattern formation, pigments, pigment cell interactions, *Poecilia reticulata*, pteridines, structural coloration, xanthophores.

Aim of the study. The aim of this study is to review and integrate current knowledge on the pigment cells, pigments, and cellular interactions responsible for coloration in the Trinidadian guppy (*Poecilia reticulata* Peters, 1859), highlighting their structural organization, genetic regulation, and environmental modulation.

Overview of guppy coloration as a model system. The Trinidadian guppy, is a classical model for investigating vertebrate coloration, because males display conspicuous black, orange, yellow, white and blue-green iridescent spots (Figures 1 and 2) whose size, number and position are under strong sexual and natural selection (Kottler 2015; Dick et al 2018). Female guppies, which are more cryptically colored, prefer males with large areas of orange and iridescent coloration, while predators select against highly conspicuous patterns, generating complex evolutionary trade-offs (Kottler 2015; Dick et al 2018). At the cellular level, these colors arise from specialized pigment cells (chromatophores) originating from the neural crest and organized in distinct layers of the skin (Shaddock 2008; Shaddock 2009a, b; Kottler 2015; Luo et al 2021). Guppies possess more chromatophore types than most vertebrates, and have become a key system for linking pigment cell biology, genetics and evolutionary ecology (Kottler 2015; Dick et al 2018; Luo et al 2021).

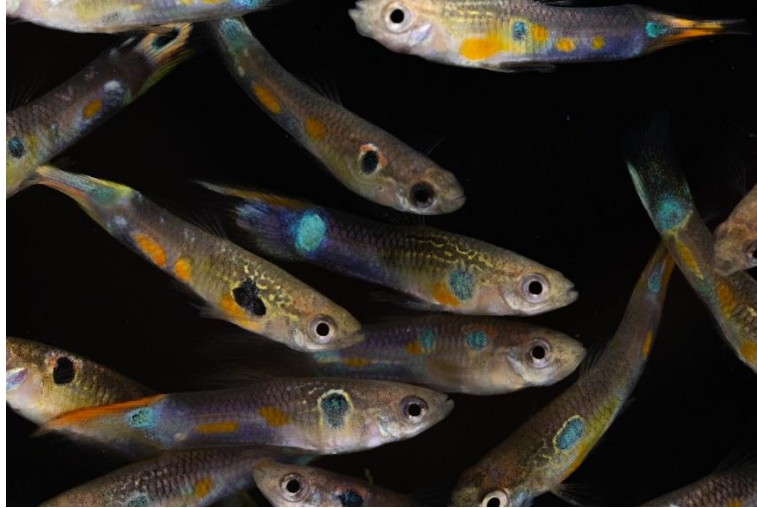


Figure 1. Colors of wild type guppy males
(source: <https://science.ubc.ca/sites/default/files/feature-images>).



Figure 2. Colors of some selected aquarium strains of guppy males
(source: <https://a-z-animals.com/media/guppy-5-600x374.jpg>).

Chromatophore classes in guppy skin. Five major chromatophore types have been described in guppy skin: melanophores, xanthophores, erythrophores, iridophores and leucophores (Kottler 2015; Dick et al 2018). Transmission electron microscopy of male ornaments reveals that at least three chromatophore types contribute to each of the main color traits (black, blue and orange) and that pigment cells are arranged in two principal layers, one within the dermis and one in the hypodermis (Kottler 2015). Melanophores contain dark melanin granules (melanosomes) that absorb light and generate black or dark brown areas; they occur as superficial dendritic cells associated with scales and deeper “corolla” melanophores in underlying skin layers (Kottler 2015; Dick et al 2018). Xanthophores and erythrophores contain carotenoids and pteridines in vesicles, producing yellow to orange and red hues respectively (Kottler 2015; Kottler et al 2015; Dick et al 2018).

Iridophores house stacks of thin guanine crystals that reflect light by thin-film interference and refraction, generating structural blue, green and silvery iridescence that can also modulate the appearance of overlying pigments (Kottler 2015; Dick et al 2018). Leucophores appear white because their organelles scatter incident light in many directions; their granules may contain uric acid and are thought to provide neutral, reflective backgrounds for other chromatophores (Dick et al 2018). Comparative work across teleosts emphasizes that such combinations of multiple chromatophore types,

interacting in space and time, underlie the extraordinary diversity of coloration patterns seen in ornamental fishes including guppies (Luo et al 2021).

Melanophores and melanin-based coloration. Black and dark brown ornaments in guppies are generated by melanophores containing the polymeric pigment eumelanin. In male trunk spots and fin patterns, melanophores are abundant both in the dermis above the scales and in the hypodermis below the scales, often intermingled with iridophores and xanthophores (Kottler 2015). During ontogeny of caudal fin coloration, black coloration appears first, coincident with increased expression of melanin synthesis genes such as tyrosinase and tyrosinase-related proteins, indicating tight coupling between melanogenic gene expression and visible melanin patterning (Dick et al 2018).

Genetic studies have begun to dissect the control of melanophore development and function (Petrescu-Mag 2009; Petrescu-Mag et al 2011; Țălu et al 2012). A spontaneous blond phenotype, characterized by reduced melanophore number and lighter overall coloration, was traced to a two-base-pair deletion in the guppy ortholog of adenylate cyclase 5 (*adcy5*), causing aberrant splicing and a premature stop codon (Kottler et al 2015). Loss of *adcy5* function not only reduces melanin-based pigmentation but also affects the development of orange ornaments, demonstrating the central importance of melanophore signaling pathways for pattern formation (Kottler et al 2015). Variants of the melanocortin 1 receptor (MC1R), a key G-protein coupled receptor regulating melanin synthesis, also show genotypic and phenotypic polymorphism in guppies, supporting its role as an upstream regulator of melanophore activity and color variation (Mohideen et al 2015).

Xanthophores, erythrophores and carotenoid-pteridine pigments. The intense orange and red spots of male guppies result from the combined action of xanthophores and erythrophores, which accumulate dietary carotenoids and de novo synthesized pteridines in their pigment organelles (Mag & Bud 2005; Kottler 2015; Dick et al 2018). Early work showed that orange ornaments contain both dietary carotenoids, largely derived from unicellular algae, and endogenously produced pteridines; the balance between these two pigment classes determines the exact orange hue and can be modulated by environmental carotenoid availability (Kottler 2015). Pteridine synthesis within orange spots decreases when carotenoids are scarce, maintaining a relatively constant carotenoid:pteridine ratio and hence a stable hue across populations, a pattern driven in part by female preference for a specific orange color (Kottler 2015).

Developmental studies of caudal fin coloration show that orange/yellow pigmentation appears after the initial establishment of black melanin, and that early stages lack strong expression of genes associated with xanthophore development, suggesting that delayed differentiation or recruitment of xanthophores underlies the temporal sequence of color appearance (Dick et al 2018). At finer scale, orange trunk and fin spots typically contain dense layers of xanthophores/erythrophores interspersed with underlying iridophores, whose reflected light enhances brightness and saturation of carotenoid-pteridine colors (Kottler 2015). Environmental and endocrine factors can modulate these pigment stores: for example, exposure of female guppies to the androgenic compound 17 β -trenbolone increases pteridine and melanin levels in the skin, brightening body coloration and partly masculinizing the pigment phenotype (Zhang et al 2021).

Iridophores, guanine-based structural coloration and leucophores. Structural blue and green iridescence in guppies is produced by iridophores containing ordered arrays of thin guanine crystals, which generate color through interference and refraction rather than absorption (Kottler 2015; Dick et al 2018; Bias & Squire 2017a, b, c, d). Electron microscopy of male trunk spots and fins shows that iridophores are present in all major ornaments examined, often as a continuous or patchy layer underlying melanophores or xanthophores (Kottler 2015). In blue ornaments, iridophores are especially prominent and densely packed, giving rise to intense, angle-dependent blue-green reflections; in black and orange spots, iridophores contribute less overtly to hue but strongly influence

brightness and contrast, for example by reflecting light through overlying orange xanthophores or providing a reflective backing under melanin (Kottler 2015).

Leucophores, characterized by light-scattering organelles and likely containing uric acid, create whitish areas and can serve as neutral reflectors or contrast enhancers. Earlier histological work detected leucophores in guppy fins, but a comprehensive ultrastructural survey of male ornaments in three genetically divergent strains failed to identify unequivocal leucophores in the analyzed spots and fin patches, suggesting that their distribution may be more restricted or variable among lines than other chromatophore types (Kottler 2015; Dick et al 2018). Beyond guppies, recent reviews emphasize that interactions between iridophores, leucophores and pigmentary cells are critical for both static patterns and rapid physiological color change in fishes (Luo et al 2021).

Cellular interactions, pattern formation and environmental modulation. Pigment cell lineages in guppies, as in other teleosts, originate from neural crest cells that migrate and differentiate under the influence of complex genetic networks and intercellular signals (Dick et al 2018; Luo et al 2021). Work in zebrafish has shown that short- and long-range interactions among melanophores, xanthophores and iridophores are essential for proper stripe formation. Analogous interactions appear crucial for guppy male patterns: guppy males lacking xanthophores because of mutations in colony-stimulating factor 1 receptor a (*csf1ra*) show severe defects in melanophore localization, indicating that xanthophores guide or stabilize melanophore patterning (Kottler 2015). The consistent presence of iridophores in all major ornaments further supports a key organizational role for this chromatophore type in guppy color pattern formation (Kottler 2015).

Guppy coloration is also sensitive to environmental factors that act on pigment cells or their pigments. Dietary supplements rich in phycocyanin or carotenoids, such as *Spirulina* or *Tubifex*-based feeds, increase total skin pigment content and enhance color brightness, reflecting increased deposition of carotenoids and perhaps secondary effects on chromatophore physiology (Asrami et al 2019; Gultom et al 2024; Nurjihan et al 2024). Background tank color can influence growth and skin carotenoid levels, with transparent or green backgrounds promoting higher carotenoid content and more intense orange-red coloration than red or blue backgrounds, implying that visual environment modulates pigment cell activity or pigment allocation (Barua et al 2021). Pollutants, including sodium fluoride, microplastics and organotin compounds, can disrupt chromatophore structure, induce oxidative stress and alter pigment distribution, leading to dull or abnormal coloration, often via effects on melanosome function, guanine metabolism or pteridine synthesis (Hou et al 2022; Hawari et al 2024; Ren et al 2025).

Conclusions. Coloration in guppies arises from the coordinated action of multiple chromatophore classes - melanophores, xanthophores, erythrophores, iridophores and leucophores - and their associated pigments, primarily eumelanin, carotenoids, pteridines, guanine and possibly uric acid. Recent ultrastructural and genetic studies demonstrate that each visible ornament typically incorporates several chromatophore types arranged in layered architectures, with iridophores playing a central, often underappreciated, role in pattern formation and signal amplification. The interplay between pigment cell genetics, environmental inputs and sexual and natural selection makes guppy coloration a powerful model for understanding how pigment cells and pigments are integrated to produce complex, evolutionarily labile visual traits.

Conflict of interest. The authors declare that there is no conflict of interest.

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