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A search for origins of iridescence in modern domestic[A] guppies; if and when did introgression occur?

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Abstract. The source of genetic inputs in modern Domestic[2] Guppy strains has long been a controversial topic in breeder circles. Assumed by many to consist solely of *Poecilia reticulata*, and considered by others to have multiple inputs from closely related variant populations[B]. The attempt of this paper is to demonstrate that sum genotype, in particular for at least one identifiable trait known as Iridescens (Ir), stems from an amalgamation through interbreeding of native Guppy[C] populations in divergent stages of incipient speciation[6]; that are capable of interbreeding and surviving in either habitat, and are therefore non-cryptic[1]. Offspring should not be viewed as interspecific hybrids[5] (between different species in the same genus), as they are capable of viable reproduction, lacking any high degree of decrease in reproductive viability. Domestic strains, like wild counterparts in reproductive isolation[11] are not speciated. Results are based on 45 years breeding experience of which nearly thirty (30) years have been devoted to strains collectively known as "Swordtail Guppies", efforts of other professional breeders, and that of the scientific community.

Key Words: swordtail guppy, domestic strains, Vienna emerald, wild-type, guppy populations, reflective qualities, smaragd-iridescens, iridescence, *Poecilia reticulata*, *Poecilia obscura*, *Poecilia wingei*, Cumana' guppy, Campoma guppy, Endler's livebearer.

Hypothesis. Based on what we know today, it is likely early 1900's importations of the Guppy (*Poecilia reticulata*) made available to breeders contained "iridescent-reflective" genotype (Photo 1), as a result of admix of variant populations. Therefore, future introductions and usage of variants, by breeders, in domestic stocks should be viewed simply as "genetic tools" for improvement. Does phenotypical evidence exist to support admix?

Photo 1. Iridescent Asian Blau Schimmelpennig Platinum (Domestic Strain) (photo by A. S. Bias).

Introduction. What defines a species[12] from a related variety or population? Species; Quote: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942). Mayr formulated this statement as part of his belief in the concept of Biological Species (Dobzhansky 1935, 1950) which in brief states members of species can only breed among themselves.

This means since crosses between members of different populations produce fertile F1 and F2 offsprings, they cannot be considered interspecific crosses as they would fail to produce an F2. This concept is based on the assumption that while geographic isolation plays a large part in speciation, so does genetics in the form of an Isolating Mechanism[7].

The existence of the Guppy has been known to science since 1859 when German Zoologist Wilhelm C. H. Peters first published results based on preserved specimens collected in 1856 from the Guayre River outside of Caracas, Venezuela. This moment of stability would be lost for the next 50 plus years as *P. reticulata* would be re-classified and confused not only with other populations, but its own.

DNA results based on a single specimen taken from the 1856 collection suggest: "This sequence clusters with all present-day *P. reticulata* (Photo 2) including a fish taken in 2008 from a tributary to the Guayre…" (Schories et al 2009).

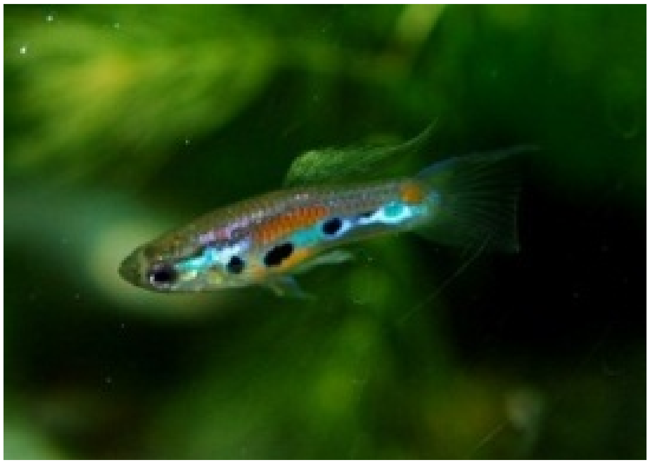

Photo 2. Wild-type *P. reticulata*, Brazil collection (photo courtesy of Shimpei Taniguchi).

Prior to 1910 there is little or no reference to the existence of Guppies in the realm of emerging stock breeders. During the years 1905-14 German breeders were just starting to develop their interest and means to collect and/or import wild guppies. Whether these live specimens came from Trinidad or mainland South America cannot be ascertained with any degree of certainty.

This is an important issue, as later it will be demonstrated that one location plays a larger role in potential source of iridescent qualities than the other. It is believed that all North American stocks were obtained from German breeders until the time of World War I.

During the period of 1918-1927 in a series of studies and resulting research papers, Prof. Ö. J. Winge of Copenhagen Denmark, published his findings involving the genetics of numerous Guppy phenotypes. While color photography was in its infancy and apparently not used to document results, we are fortunate to have accurate color representations of his findings. One trait in particular (Photo 3), Iridescens (Ir), is of particular interest for further discussion at a later point in this writing.

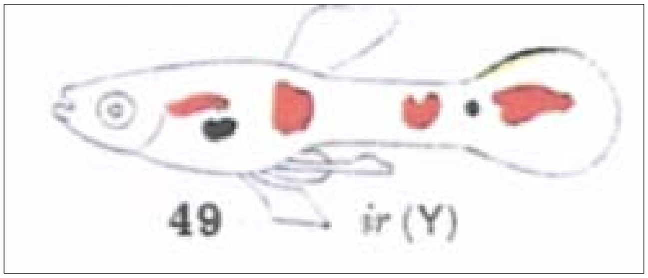

Photo 3. Winge (1927), Illustrations of Y-link gene for Iridescens (Ir).

***Definitions**:*

1. *Cryptic species complex*: similar on a phenotypic level, but DNA testing reveals genetically distinct. Interbreeding does not occur, otherwise there would be loss of distinction.
2. *Domestication*: to bring of keep (wild animals or plants) under control or cultivation (http://dictionary.reference.com).
3. *Founders*: individuals breeding members, initially responsible for founding a breeding population.
4. *Genetic drift*: gene frequencies within strains change over time due to random events by chance alone; resulting in a possible loss of certain traits. In small populations selection is often skewed and beneficial alleles may be lost.
5. *Hybrid*: (Life Sciences & Allied Applications/Biology) an animal or plant resulting from a cross between genetically unlike individuals. Hybrids between different species are usually sterile (http://www.thefreedictionary.com).
6. *Incipient speciation*: populations that are in the process of diverging to the point of speciation but still have the potential to interbreed (http://www.answers.com).
7. *Isolating mechanism*: something (as a geographical, ecological, physiological, anatomical, or psychological barrier) that limits interbreeding gene flow between groups and is thereby a major factor in the differentiation of biologic units (as races or species) (http://www.merriam-webster.com).
8. *Mutation*: a mutation is a permanent change in the DNA sequence of a gene. Mutations in a gene's DNA sequence can alter the amino acid sequence of the protein encoded by the gene (http://learn.genetics.utah.edu/archive/mutations).
9. *Natural selection*: the process by which plants and animals that can adapt to changes in their environment are able to survive and reproduce while those that cannot adapt do not survive (http://www.merriam-webster.com)
10. *Phylogeny*: the evolutionary development and history of a species or higher taxonomic grouping of organisms (http://www.thefreedictionary.com).
11. *Reproductive isolation*: the inability of a species to breed successfully with related species due to geographic, behavioral, physiological, or genetic barriers or differences (http://www.merriam-webster.com).
12. *Species*: a fundamental category of taxonomic classification, ranking below a genus or subgenus and consisting of related organisms capable of interbreeding (http://www.thefreedictionary.com).

Discussion

***Identification of wild-type Guppy populations**.* Part of the problem in classification of variants comprising *Acanthophacelus* (Eigenmann 1907) has been compounded by the inability of science to determine just what composes a common Guppy for lack of an accurate phylogeny[10]. Science has not provided a singular description entailing natural ranges, variation in color patterns, anatomical, behavioral variations, and historical processes.

Are variant populations truly incipient or cryptic? They freely interbreed with little or no evidence of lethal heterozygous alleles for environmental or hereditary conditions in offspring. Little in the way of MtDNA differentiation (Breden Labs) has been noted. Together this suggests incipiency.

If geographic barriers on mainland South America once existed, lack of genetic distance in variants (*P. reticulata* & *Poecilia wingei*) indicates any prior genetic differentiation towards speciation may be in the process of recombination (Webb et al 2011).

Support can be found in Schories et al (2009), quote: We hypothesize that *P. wingei* was the most western species but recently was circled by northwest colonizing populations of *P. reticulata.* We are left with sexual selection as the primary driving force behind variation in populations.

While the debate is ongoing and will likely be so for some years to come, in the last decade some clarification has been provided by science for the benefit of breeders. Findings suggest that the sub-genus *Acanthophacelus* (Eigenmann 1907) currently has at minimum three or more known variant populations: 1. The Orinoco (Common) Guppy; *P. reticulata* (Peters 1859)[E], 2. The Endlers/Cumana'/Campoma Guppy; *P. wingei n. sp.* (Poeser et al 2005), and 3. The Oropuche Guppy; *Poecilia obscura n. sp.* (Schories et al 2009).

In his description of *P. wingei*[G] as a distinct species Poeser et al (2005) states, quote: "Its closest relative is the common guppy, *P. reticulata*, sharing identical meristic data, but differing by its enhanced metallic body pigmentation. This brightness in body pigmentation is also noticed in the females to the distribution area of the common Guppy. *P. wingei* males exhibit a unique melanophore pattern, viz., a large band in the midsection of its body. The importance of this feature, i.e., the spatial distribution of melanophore patterns, is decisive for its recognition as a valid species…". *P. wingei* 2002 collections by Poeser and Kempkes were made in the vicinity of Cariaco, Venezuala.

To a large degree status as separate species has been determined by: morphological variation in gonopodium, geographic/geologic isolation, behavioral differences (courtship, foraging and habitat preferences), color pattern variation and iridescence.

With geographic limitations of *P. reticulata, P. wingei* has been able to maintain a distinct degree of speciation by sexual selection preferences. Thus, indicating that complexes for accumulated mutations[8] for iridescence can withstand the rigor of interbreeding in the wild. A parallel common to domestic strains has been confirmed with selection for iridescence in fishrooms. A converse is also apparent in domestic strains selected for "flat" color pigment in stocks of similar origins.

In Ludlow & Magurran (2006), regarding *P. obscura* (Photo 4) range, he states, quote: "populations in the Caroni and Oropouche drainages in Northern Trinidad exhibit marked genetic divergence". This shows that minimal geographic isolation, often results in reproductive isolation, as seen on Trinidad, within two populations of *P. reticulata* derived from similar origin; the eastern Quare-Orupuche drainage containing *P. wingei* and the western Caroni-Paría drainage containing *P. reticulata.*

Photo 4. *P. obscura* (photo by Tobias Bernsee).

All streams are on the same side of a local mountain range and gene flow between these two divergent populations likely has not been totally restricted as a result of seasonal flooding. Transport of fish and eggs by birds has long been acknowledged as a source of genetic migration between local populations.

Genetic analysis has shown that populations in the Paria drainage more closely resemble those of mainland South America. This you would expect as Paria region of Trinidad was recently connected to mainland South America during periods of reduced sea levels[F].

Morphological differences, confirmed by DNA testing, have been documented and populations on the eastern end of Trinadad in the Oropouche drainages have been described as *P. obscura* (Schories et al 2009).

Distribution of wild-type Guppy populations. It is accepted all three variants of Guppies naturally hybridize and/or share overlapping territories, as found in numerous studies. Yet, phenotypical variations when plotted on maps still show distinct regions of habitation.

Poeser et al (2005) further state, quote: "Distribution area. The common Guppy is presently circumtropical. However, it is believed to occur naturally only in the northeastern part of South America and on the Lesser Antilles. We consider only the mainland areas of Venezuela, east of Lago de Maracaibo, further east to the Guiana's, the adjacent part of Brazil, Para district, and upstream the Amazon river (Rio Solimões) as its natural area of distribution. Based on data presented in the discussion section, the occurrence on Trinidad is undisputed. The island of Barbados (cf. Boulenger 1912) is not considered part of its natural range."

In their description of *P. wingei* (2005) as a distinct species Poeser et al (2005) state, quote: "…Distribution. The Campoma Guppy occurs in fresh waters in the Campoma and Buena Vista Lagoons, unto Carúpano."

Schories et al (2009) adds, quote: "The subgenus *Acanthophacelus,* which so far included *P. reticulata and P. wingei* (Photos 5 and 6), has a wide range in northeastern South America and some Caribbean islands…. …The natural distribution of the common guppy is not exactly known, but we follow Rosen & Bailey (1963) listing the Netherlands Antilles, Venezuelan islands, Trinidad, Windward (Barbados) and Leeward (StThomas and Antigua) islands, Western Venezuela (and adjacent parts of Columbia in the Rio Orinoco drainage) to British Guiana (= Guyana). Magurran added Surinam and probably Tobago to the natural range and pointed out that it is unclear whether localities in Barbados, Cuba, and Brazil have been naturally colonized by *P. reticulata* or are the result of human introductions (Magurran 2005). *P. wingei* has been reported from brackish waters in the Campoma-Carúpano-region, Paría Peninsula, Venezuela. Our investigations show that *P. wingei* also occurs in the Cumaná region, Venezuela. Here, we describe the Guppies of North-East Trinidad, which so far were regarded as a population of *P. reticulata* as a separate species of the subgenus *Acanthophacelus."* In the last she is referencing *P. obscura*.

Photo 5. *P. wingei* (photo courtesy of Shimpei Taniguchi).

Photo 6. *P. wingei* (photo courtesy of Shimpei Taniguchi).

Speciation within Guppy populations has not been accepted across the board by all members of the scientific community. Magurran (1998) suggests multiple reasons for Guppies having diverse, visible phenotypical variation compared to many recognized species, yet having not speciated on a large scale. Quote: "molecular analyses of populations in the Caroni and Oropuche drainages indicate that reproductive isolation has not arisen even when there has been ample time for it to have done so."

Qualities of wild-type Guppy populations. When we view differences in reflectiveness of color in guppies Poeser (2005) has this to say, quote: "In the areas of stations 11-13, 15 (Carúpano region), the guppies exhibited similar colour patterns as the Orinoco variety, with the addition of metallic polychromatic patterns. Where in the Orinoco guppies the metallic sheen is restricted to areas around the black spots, in *P. wingei* all colours are a brilliant array of metallic colours: red, blue and green to yellow (= gold). … Females are greyish, with a bright sheen over their bodies. … where *P. wingei* and *P. reticulata* may co-occur, both populations have their most extreme phenotypes…" Note that this implies divergent selection.

In description of *P. obscura* Schories et al (2009), quote: "…body sides of adult males with red, blue, orange and yellow bright pigment spots, some reflecting iridescent, usually with 1 to 3 rounded black spots, sometimes with a series of irregularly thin and short or long brown or light black horizontal lines or with very short brown vertical lines sometimes crossing the horizontal bars; the caudal fin base often shows a lower or upper black spot surrounded by small dark and short dashes and yellow pigment, dorsal or ventral caudal fin rays sometimes pigmented and rarely elongated over the caudal margin of the fin, forming a short "sword"; dorsal fin often whitish, dark or polychromatic colored, sometimes flag-like elongated, all other fins hyaline. Male body coloration extremely polymorphic: in natural habitats no two males being alike. Body coloration and caudal appendix phenotype predominantly heritable characters, male offspring of a single male in laboratory crosses being very similar to their father and to each other."

Of interest Magurran (1998) notes Endler & Houde (1995) recognizing seven types of color in male guppies (Photo 7), quote: "fuzzy black, black, orange (including red), yellow, silver, blue and bronze-green". Magurran (1998) conclusions give further insight on how regional populations determine male coloration without direct speciation, thus establish mutation levels, quote: "This paper has highlighted two ways in which the battle of the sexes can inhibit speciation. First, the pursuit of copulations by males seems to be a potent force in maintaining gene flow between populations that might otherwise become reproductively isolated as a result of natural selection[9] and female choice. Second, sexual dimorphism, which is itself a consequence of sexual conflict, reduces the opportunity for the development of feeding polymorphisms that could open the door to sympatric speciation. …What is clear is that sexual conflict plays a major role in determining whether population differentiation does trans-late into speciation."

Photo 7. Seven types of Guppy color expressed in *P. wingei* (photo by Shimpei Taniguchi).

The iridescent and reflective qualities of *P. wingei* have been decribed by Schories et al (2009) as follows, quote: “longitudinal broad red band extending maximally from the operculum to the caudal fin base, along or above the lateral midline in the trunk and along or below the lateral midline in the peduncle, often interrupted by a vertical black bar originating around the anal fin base and extending to the dorsal fin base or anterior thereof. The red band often dissolved into oval or rarely round red spots, especially in the peduncle. A black stripe above the red band extending maximally to the eyes and the caudal fin base, sometimes missing in the trunk area. Additional dark black coloration of the ventral margin of the peduncle in many males. Caudal fin often with ventral and dorsal sword-like coloration (Photo 8), red, yellow or white, often with a black margin, frequently upper and/or lower rays of caudal fin prolonged to form colored swords or double-swords. Some males with large black shoulder spot with fuzzy margin, similar to the vertical bar. Perfectly round dark black body spots with sharp borders, which are typical for *P. reticulata* and *P. obscura* males, very rare. Large roundish or oval bright metallic blotches of, green, or more rarely yellow or light blue iridescent color following the basic longitudinal pattern interrupting the red band in the peduncle. White markings rare on the body sides. Rarely small black irregular spots on the belly. Dorsal fin hyaline, yellow and black coloration, sometimes anterior and dorsal margin black. …Nevertheless *P. wingei* males also share many components of their pigmentation patterns with males from the two other species, suggesting that this is an ancestral trait.”

Photo 8. *P. wingei* (photo by Shimpei Taniguchi).

Early 1900’s lab research focused on isolating single traits and later that in the field on behavioral studies of isolated populations. With advances in modern technology and understandings at the molecular level researchers are attempting to make sense out of fragments of information, singling out populations and describing them as distinct species. Classical definitions are being redefined as the result of advances in technology. Time will reveal if this approach is warranted. The amount of research in the last several decades is both revealing and often contradictory.

The approach of Breden Labs holds much promise not only for the scientific community, but to that of the world of domestic Guppy breeders to prove or dispel many long held and evolving beliefs. To date data suggest that *P. reticulata* has 4 mtDNA lineages associated with river drainages, yet only minimal mtDNA difference between *P. wingei* and *P. reticulata*.

Breden research identify isolating mechanisms that suggest that opsin, proteins in photoreceptor cells could be a driving force in sexual selection for *P. wingei* coloration, quote: "...the Cumaná guppy shows lowest variation in sensitivity. This may correlate with the male signals in Cumaná guppies, which are distinct in the purity of their orange coloration". Orange coloration and the ability to perceive it are evolving together. This indicates a selective advantage to isolation.

While we are left with the obvious hypothetical question: at what point would populations undergoing incipient speciation finally be considered closely related species? At this time Guppy variants still appear to rate classification not as distinct species, merely populations in the process of incipient speciation.

A breeder's perspective: domestic Guppy source of iridescence. Initially, basic identification of traits found in Guppy genotype was the product of scientific research and publication. While often lacking in formal documentation, identification of new traits, or at least assemblage of complex phenotypes, has been that of the breeder community.

As a domestic Guppy breeder, how would you react upon inquiry of your stocks, "Are they pure Guppies or Endler hybrids?" Such has occurred on several instances over the last decade. My initial thoughts were inclined toward apprehension not being aware of direct infusions of recent Endler genetics into my Vienna strains, nor had I deliberately done so.

Based on the phenotypes currently being producing in swordtail Guppies it is easy to perceive how one would suspect recent Endler influence. For over 25 years my breeding program has been nearly isolated with focus on; iridescence over color pigment, and patches of color over solid pattern when a choice presents itself. While periodically keeping Endlers and producing limited interbreeding, offspring are normally isolated from domestic Guppy stocks and disposed of when goals have been reached.

There has been an ongoing debate among breeders ever since the early-mid 1990's about the pros and cons of infusing Endler genetics into domestic Guppy strains. Many old time Guppy breeders take a negative stance to this approach. Yet, there is a greater level of acceptability in the reciprocal infusion of *P. reticulata* genetics into *P. wingei*/Endler stocks to create new strains by breeders attracted to brighter colors and patterns in a smaller body with minimal extension of finnage.

Domestic Guppy breeders have taken strides to concentrate intensity and density of color in strains around the world for over 100 years. Many show strains consist of color pigment in solid pattern, and minimal reflective iridophores. Possibly as a result of show circuits and fishrooms migration to the use of cheap "cool white" fluorescent illumination.

This set a course for development of "visible coloration" under these conditions. Allowing for production of strains with dense, solid, and often flat color pigment. Does the use of "cool white" fluorescent still pose a problem? Yes, when breeders make selections without the use of natural sunlight or hand held incandescent lighting.

A photo of the 1856 Berlin specimens (Photo 9), collected from outside of Caracas, Venezuela clearly reveals basal type melanophore striping. A trait more in common with reflective *P. wingei* phenotypes, and not that of *P. reticulata*. We are given notice by Poeser (2013) of this striping and also, quote: "großen runden Flecken (large round spots)".

Such spotting recognized as a *P. reticulata* trait, despite DNA results from a single 1856 Gollmer specimen indicating *P. reticulata* in Schories et al (2009). Thus, revealing co-expression of traits from two variants: *P. wingei* and *P. reticulata*.

Photo 9. 1856 Berlin Specimens (Poeser 2013) (Photo by J.H. Paeple).

Would this not suggest the 1850's collection made by Julius Gollmer, a German, were comprised of *P. reticulata* Guppies and/or *P. wingei* Cumaná Guppies? That the state of preservation inhibited identification of true colors by Peters? This seems very plausible given the nature of preservation techniques of the period, and extended length of time until formal identification was made. It has been observed that formalin and alcohol both dissolve out the carotenoid pigments and possibly iridescent blue.

For the first 70± years, after formal description of Berlin specimens (Peters 1859), the scientific community focused efforts on color pigment, and little documentation in regards to iridescence in either wild-type or domestic Guppies is found. Now would be an appropriate time to refer back to the often referenced research of Ö. J. Winge and two of his contemporaries. In his color plate illustrations (Winge 1927) we find reference to the Iridescens (Ir) gene pattern (Photo 10). Winge apparently focuses his description on the orange wild-type spots, though he clearly illustrates an individual Ir fish with highly reflective qualities of iridophore based pattern. Kirpichnikov does similar with this complex in 1981 (Photo 11).

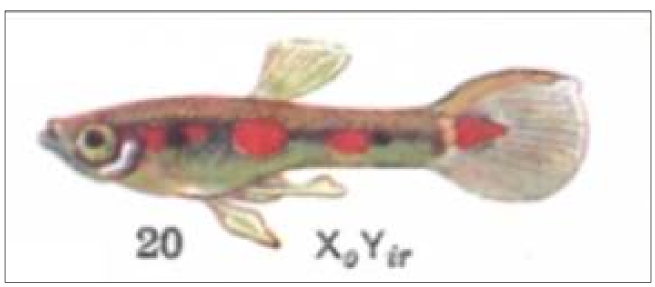

Photo 10. Winge (1927), illustrations of Y-link gene for Iridescens (Ir).

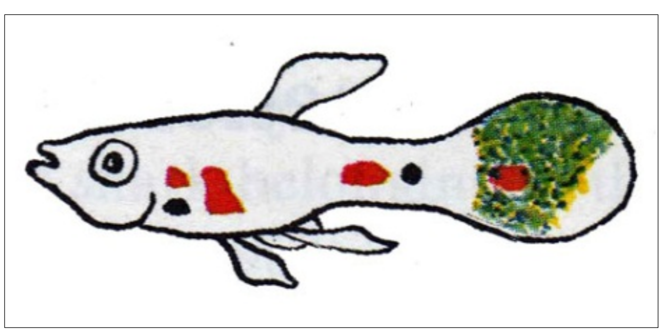

Photo 11. Kirpichnikov (1981), illustration of Y-link gene for Iridescens (Ir).

Dzwillo (1959) based his research, in part, on breeding experiments with a strain he named “Smaragd-Iridescens” (Photo 12), honoring the Winge Y-link Iridescens pattern it possessed. This strain was known for its recognizable Ir pattern of wild-type orange spotting, black caudal-peduncle spot and a vibrant (for the time) metallic silver/blue sheen of iridophores.

Photo 12. Dwzillo Smaragd-Iridescens Laboratory Strain (photo by Harold Auer).

Nearly identical to Winge’s #20 color plate illustrating the Ir gene pattern found in his own laboratory stocks. What is often overlooked in the Smaragd-Iridescens strain is the presence of iridophores in the form of white platina (leuchophores).

You will notice the trait in the caudal/peduncle juncture in the Dwzillo strain, not a common characteristic of wild-type *P. reticulata*.

In more recognizable form as a reflective patch of white leucophores (Photo 13), located just below the dorsal juncture in *P. wingei* and *P. wingei* * *P. reticulata* inter-breedings.

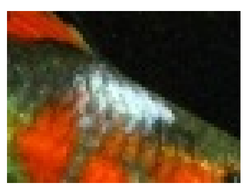

Photo 13. Wild-type strain *P. wingei* with Platina.

Often phenotypically blue in pure *P. wingei* stocks, close examinations reveals it to be comprised of an underlying collection of blue iridophores and/or white leucophores. Each expression being iridophore based. This expression is easily modified by the Metal (Mg) trait from white to yellow in appearance.

For ease of discussion we will identify “Platina” as initially being part of Y-link Iridescens (Ir) reflective coloration. This visible patch of iridophores (leuchophores) is present in many of the best modern iridescent strains (Photos 14-23). Enhanced by amplification through selective line-breeding, with autosomal concentration and sex-link combinations.

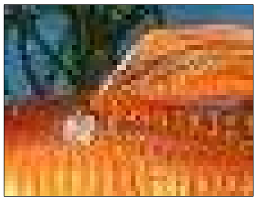
Photo 14. Coral Red DS


Photo 15. Full Gold


Photo 16. HB Blue Delta

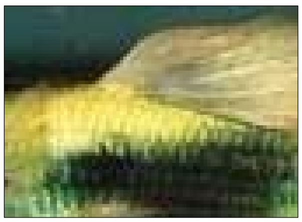
Photo 17. HB AOC Delta

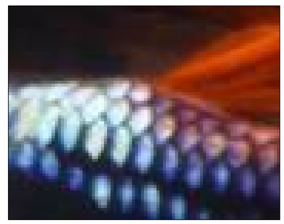
Photo 18. HB Red Delta

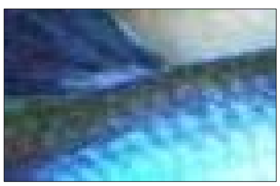
Photo 19. Lazuli Delta

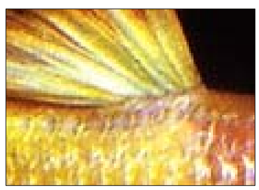
Photo 20. Micariff Delta


Photo 21.Blond Pb Schim DS


Photo 22. Grey Schim DS.

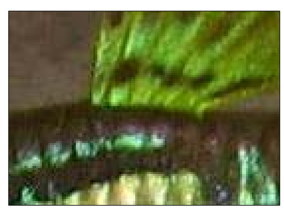
Photo 23. Ab Vienna DS.

A second reflective characteristic found in the Dzwillo strain is an underlying layer of silver/blue iridophores beneath wild-type orange and black circular spotting, creating a "circular ring effect". It is routinely absent in pure stocks of both *P. wingei* (Photo 24) and *P. reticulata*. It has been incorporated into many iridescent domestic Guppy strains. However, it is conspicuously absent in many solid color pigment strains.

Smaragd-Iridescens serves as the genetic foundation for one of the oldest established reflective domestic Guppy strains: Wiener Smaragd Doppelschwert (Vienna Emerald Doublesword). It is also the parent strain of an old established delta counterpart, The Old Fashioned.

Photo 24. *P. wingei* with reflective dorsal spot and lacking "circular ring effect" (photo by A. S. Bias)

Vienna Emerald (Photos 25-26) is often described as: predominantly metallic green color, with a series of posterior meandering (wavy) patterns, a peacock "eye-spot" with iridescent edge at the caudal/peduncle juncture, black spotting anterior, colors ranging from white, yellow, red, and blue/green, black outlines on fin edges.

Photo 25. Vienna Emerald Swordtail (domestic strain) (photo by A. S. Bias).

Photo 26. Smaragd-Iridescens as expressed in Asian Blau Vienna Emerald Swordtail (domestic strain) (photo by A. S. Bias).

As the name suggests, this phenotype derives it pattern and reflective qualities from those found in Dzwillo's Smaragd-Iridescens strain and owes its pattern to Winge's Iridescens (Ir).

Iridescent qualities in Guppies, while little mentioned, were re-affirmed by Kirpichnikov (1981), confirmed by Dzwillo (1959), and described by Winge (1927), as evidenced by his colored illustrations.

Now herein lies the dilemma. As previously discussed, such qualities were possibly overlooked in the very first recognized collection, used by Peters (1859), as evidenced by melanophore pattern striping common to reflective Campona Guppies, i.e. Endler-type guppies.

It is safe to assert domestic strains and wild-type laboratory strains of guppies had highly reflective qualities in the early 1960's and 1920's, respectively. This establishes a date for each well in advance of the documented 1970's–1990's arrival of the variants known as Endler's Livebearer[D] and later Cumaná/Compoma reflective strains in breeder tanks.

However, these dates do not identify a potential common source for reflective genotype in modern domestic strains. The two dates simply acknowledge existence of the Ir trait for reflectiveness in some *P. reticulata* based strains.

Continuing, assimilation of Endler and Cumaná/Compoma stocks into modern domestic strains likely precludes use of molecular level genetic testing, with such recent dates of infusion, to isolate a source(s) for reflective trait(s).

A similar reciprocal process is occurring in wild populations with reintroductions of both domestic stocks and relocations of non-native populations throughout the Guppies' native range.

All that is lacking to prove the hypothesis of early admix and co-mingling in founding members of domestic stocks is a means of verification, outside of classical DNA testing, in the form of phenotypical documentation.

Surprisingly, a means does exist. It is likely not in the living memory or our longest actively breeding members. Two identifiable traits are found in a photo taken by Wm. T. Innes, and published as part of an article of Stoye (1934). The two traits being: a reflective dorsal spot, and circular ring effect. Beneath the dorsal juncture of the male photographed in 1934 (Photo 27) is a distinctive trait recognized by reputable breeders world-wide as a sign of *P. wingei* * *P. reticulata* admix and/or Endler's Livebearer * *P. reticulata* admix in captive bred stocks (Note: see supporting breeder comments).

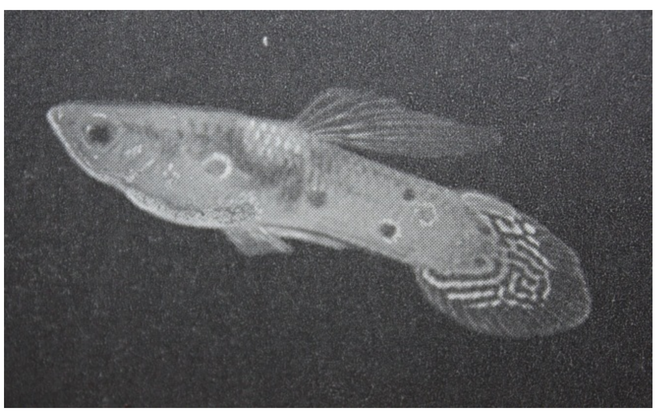

Photo 27. Lace Tail or Peacock Tail Guppy ca. 1934 with reflective dorsal spot and "circular ring effect" around spots (photo by Wm. T. Innes).

Even though a simple black and white photo, visible and verifiable traits are expressed. Evidence of a fish bred in the early 1900's by domestic Guppy breeders who regularly exchanged stock with other breeders.

As a result, this is compelling evidence for a founder[3], likely one of many, of specific origin with reflective admixture in modern domestic Guppies: that being *P. wingei.* This reveals a *P. wingei*[D] * *P. reticulata* hybrid Guppy, not in a classical scientific sense, but that in the realm of domestic Guppy breeders. Therefore, it should also be considered "De Facto" evidence of likely admix in wild stocks when the reflective dorsal trait is white instead of blue. This process is being duplicated to this day by modern breeders (Photo 28) via more recent importations of *P. wingei*.

Photo 28. F1 *P. wingei* * *P. reticulata* Top Sword with reflective dorsal spot (photo by Tobias Bernsee).

Conclusions. Provine (2004) concludes, quote: “the problem that (E. W.) Mayr threw to geneticists: How do these genetic isolating mechanisms arise during speciation, and not under the direct effect of natural selection?”

In a broad scope Provine’s statement may indirectly suggest many described traits found in Guppy genotypes are held in common within sum total populations of known variants. A trait need not have common ancestral origin, but rather may evolve in parallel evolution in populations of common origin (Breden Lab).

Does this not suggest at least some of the isolating mechanisms do result as the direct effect of natural selection? In example: the increasing use and/or preference for red coloration by *P. wingei*.

As a result of his population studies, Mayr believed reduced variability in geographically isolated populations was not solely the result of random genetic drift[4]. Quote: “The reduced variability of small populations is not always due to accidental gene loss, but sometimes to the fact that the entire population was started by a single pair or by a single fertilized female”. These “founders” of the population carried with them only a very small proportion of the variability of the parent population. This “founder” principle sometimes explains even the uniformity of rather large populations, particularly if they are well isolated and near the borders of the range of the species (Mayr 1942). This is the founder effect. It is covered in depth in Mayr (1963).

Does this suggest pattern and iridescence in modern domestic Guppies derives exclusively from interbreeding with *P. wingei* in the recent past? No, only a possible shared common genetic mutation for iridescence which can be the genetic basis used to create a host of recognizable phenotypes.

Ludlow & Magurran (2006) states, quote: “our study provides evidence for partial gametic isolation in Guppies by showing that sperm of males from the female’s own population have precedence over sperm from genetically divergent males.” In comparison Ludlow & Magurran based their observations between collections of *P. reticulata* from the Carona drainage with *P. obscura* from the Oropuche River and drainage.

Herein, lies good cause for plausible explanation of *P. wingei* accumulation and retention of iridescence in conjunction with uniform patterns on a population level, while *P. reticulata* has done so only in isolated individuals. When populations from two incipient species without complete reproductive isolation come into secondary contact, they tend to do one of two things: (1) inter-mate and produce a single population, or (2) undergo selection reinforcing current isolating mechanisms, or establishing new ones, until no gene flow continues between the two populations and speciation has become complete.

In conjunction with Breden’s Opsin studies, a pattern is demonstrated for reproductive isolation directed by sexual selection to concentrate reflective qualities, yet still allow dispersal into other populations. In the long run serving as a partial isolating mechanism.

As breeders we work with small isolated populations to create strains; this process does not lead to speciation as in the wild. There are a growing number of examples where species with differentiated gene pools do allow some introgression, by assumption of benefit from the addition of genetic variability.

Genetic introgression by breeders from one species to another should maintain the functionality of a co-adapted gene pool. Inbreeding results in homozygosity through genetic drift and loss of gene diversity. Beneficial genes must be "stripped" of accompanying deleterious genes during the process of introgression through selection for hardiness.

We isolate a genetic trait; in this case reflective quality of iridophores and attempt to maximize their value in phenotypical expression. In doing so we often bottleneck our strains, much in parallel with natural population crashes found in the wild.

So, what does this mean to the average domestic Guppy breeder of any of the acknowledged variant populations? Very little unless your emphasis is maintaining wild-type stocks with documented pedigrees based on collection locales.

The initial collections of Guppies and subsequent distribution to breeders were not well documented. Each variant in wild-form evolved primarily from isolation and preferences based on sexual selection. In documented ranges of each exists both natural overlap and inter-breeding to form new populations. Often as the result of single (limited) founders.

Each variant readily breeds with another in both wild and domestic settings. For this reason none meet the classical definition as distinct species; breedings produce viable offspring. Variants are only in the initial stages of incipient speciation and comprise founders in modern domestic Guppy strains. Any additional evidence of a cryptic species complex will also likely reveal it to be in process of reversal.

Magurran (1998) noted that laboratory hybridization of Trinidad stocks of *P. reticulata* and *P. obscura* resulted in documented male behavioral sterility and hybrid breakdown for embryo viability, brood size and sperm counts. Similar results are produced in breeder tanks not only between variants, but also between fixed strains in F1 offspring. This rarely manifests into later generations.

Domesticated strains (Photos 29-30) of Guppies are just that, domesticated. A fabrication of our imagination, accentuated by an ever increasing understanding of Guppy genetics as stock breeders. To assume all early genetic contribution in domestic stocks stems from *P. reticulata* Guppies would be presumptuous at best.

At least one recognized laboratory strain, Smaragd-Iridescens (Iridescens), has long been considered by breeders as the source for reflective qualities in Vienna Emerald Green Swordtails. A parent strain for many subsequent phenotypes. This trait may have existed in antiquity within *P. reticulata* populations from parallel evolution. Or it may have been a recent incorporation from a divergent population, as has been demonstrated with *P. wingei* reflective dorsal spotting.

Photo 29. Ginga Sulphureus (domestic strain) (photo by A. S. Bias).

Photo 30. Blond Schimmelpennig Platinum DS with Purple Body Mutation (Pb) (domestic strain) (photo by A. S. Bias).

If a trait from any recognized population or strain of Guppies can help a breeder obtain goals in a breed plan, it should be viewed as: "a genetic tool for creation of phenotype, after which you select for body traits found in preferred population type."

Domestic Guppy strains have long been recognized for specific characteristics based on breeder selection. As compared to other breeds of livestock, modern domestic Guppy strains are fluid in many aspects. There is little need for concern about continued infusions, as both wild-type and domestic strains are composed of multiple populations of Guppies.

Supporting breeder comments. Ronan Boutot (Beauvais, France): Angelfish in the hobby, are known to have originated from a hybrid cross of *P. scalare* and probably *P. eimeki.* For decades, all aquarium Angelfish were from this reproduction. We had to wait long time to have in our tanks authentic and pure (Angel) fishes of one or the other species. For our (domestic) Guppies, doubt is also possible. Examples from my breedings (Photos 31-33). I agree with your conclusions, together with the logic you followed, that I find particularly rational, scientific, and informed.

Photos 31-33. Endler Hybrid stocks with reflective dorsal spot (photos by Ronan Boutot).

Björn Lundmark (Gävle, Sweden): In my Metarika strain (Photo 34) the iridescent spot is clearly visible. The Metarika strain is considered a pure guppy strain, but I believe the iridescent spot shows that its origin is a *P. wingei* strain. This Metarika strain has never been crossed with *P. wingei*. At least not as long as it has been in Europe (ca. 2005). The strain has its origin in Asia, probably Yoshiki Tsutsui in Japan. I haven't found the spot in all of my *P. wingei* crossings with different strains. Probably the trait is Y-linked and there are *P. wingei* without this trait.

Photo 34. Metarika male with reflective dorsal spot (photo by Björn Lundmark).

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Notes:

A. The term "domestic Guppy" in this article shall collectively refer to any and all captive bred strains, regardless of genetic inputs from variant populations of *P. reticulata*, *P. reticulata (wingei), P. reticulata (obscura).*

B. The terms "variant populations" or "variant" in this article shall collectively refer to any and all described species of Guppy: *P. reticulata, P. reticulata (wingei), P. reticulata (obscura), P. reticulata (guppii).*

C. The term "Guppy" in this article shall collectively refer to any and all wild-type populations of *P. reticulata, P. reticulata (wingei), P. reticulata (obscura)*, or the offspring of inter-breedings in native range.

D. Endler's Livebearer (ELB) refers to initial collection of highly reflective Guppy by Prof. John Endler in the early 1970's. Fred Poeser suggests: 1. ELB, as collected by John Endler at Laguna de Patos, Cumaná, Venezuela, to be distinct species: *Micropoecilia endleri*. 2. Considered by some possibly extinct or a hybrid from release by man. 3. Likely a very homozygous result of limited founders.

E. The first Guppy collection from Venezuela described by Wm. C. H. Peters (1859) as *Poecilia reticulata*. Apparently Peters based his description only on the females of from a collection of both preserved sexes. A second collection from Trinidad was described by Albert C. L. G. Guenther (1866) as *Girardinus guppii*. Fred Poeser suggested *P. reticulata reticulata* and *P. reticulata guppii* as two distinct subspecies of the common Guppy, and based his studies as such.

F. Due to man-made and natural occurrence populations on Trinidad are losing historical distinctions. *P. obscura* population arose on Eastern side of Trinidad and the parent common Guppy *P. reticulata (guppii)* to the West.

G. *P. wingei*, not to be confused with Endler's Livebearer. Unfortunately the term "Endlers" has been used as a collective term for all highly reflective forms of Guppies. Named as "Cumaná Guppy" by Alexander and Breden (2004). Described as "Campoma Guppy", *P. wingei* by Poeser et al (2005).

References

Breden Lab, On-going Major Research Projects ... , http://www.sfu.ca/biology/faculty/breden/lab/ (last check 10.8.2013).
Dobzhansky T., 1935 A critique of the species concept in biology. Philosophy of Science 2:344-355.
Dobzhansky T., 1950 Mendelian populations and their evolution. American Naturalist 84:401-418.
Dzwillo M., 1959 Genetische Untersuchungen an domestizierten Stammen von *Lebistes reticulatus* (Peters) [Genetic studies of domesticated strains of *Lebistes reticulatus* (Peters)]. Mitt Hamburg Zool Mus Inst 57:143-186 [in German].
Eigenmann C. H., 1907 The poeciliid fishes of Río Grande do Sul and the La Plata Basin. Proceedings of the United States National Museum 32:425-433.
Kirpichnikov V. S., 1981 Genetic bases of fish selection. Springer-Verlag, Berlin, Germany, 410 pp. [in Russian].
Ludlow A. M., Magurran A. E., 2006 Gametic isolation in guppies (*Poecilia reticulata*). Proc Biol Sci 273:2477-2482.
Magurran A. E., 1998 Population differentiation without speciation. Philos Trans R Soc Lond B Biol Sci 353:275-286.
Mayr E., 1942 Systematics and the origin of species from the viewpoint of a zoologist. Columbia University Press, New York.
Mayr E., 1963 Animal species and evolution. Harvard University Press, 795 pp.
Poeser F. N., Kempkes M., Isbrucker I. J. H., 2005 Description of *Poecilia* (*Acanthophacelus*) *wingei* n. sp. from the Paría Peninsula, Venezuela, including notes on *Acanthophacelus* Eigenmann, 1907 and other subgenera of *Poecilia* Bloch and Schneider, 1801 (Teleostei, Cyprinodontiformes, Poeciliidae). Contributions to Zoology 74(1/2):97-115.
Poeser F. N., 2013 Apropos Guppys... In: VDA-Arbeitskreis Lebendgebärende Aquarienfishe (*Hrsg*.): viviparous. Das Lebengebärenden Magazin 1:36-40.
Provine W. B., 2004 Ernst Mayr: genetics and speciation. Genetics 167:1041-1046.
Schories S., Meyer M. K., Schartl M., 2009 Description of *Poecilia* (*Acanthophacelus) obscura* n. sp., (Teleostei: Poeciliidae), a new guppy species from western Trinidad, with remarks on *P. wingei* and the status of the "Endler's guppy". Zootaxa 2266:35-50.
Stoye F. H., 1934 Color breeding of Guppies. The Aquarium, vol. III, No. 2, June 1934.
Webb W. C., Marzluff J. M., Omland K. E., 2011 Random interbreeding between cryptic lineages of the Common Raven: evidence for speciation in reverse. Molecular Ecology 20:2390-2402.
Winge Ö. J., 1927 The location of eighteen genes in *Lebistes reticulatus*. J Genetics 18(1):1-44.
*** http://dictionary.reference.com
*** http://www.thefreedictionary.com
*** http://www.answers.com
*** http://www.merriam-webster.com
*** http://learn.genetics.utah.edu/archive/mutations

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