# The Phenotypic Expression of Purple Body (*Pb*) in Domestic Guppy Strains of *Poecilia reticulata*

## Alan S. Bias<sup>1</sup> and Richard D. Squire<sup>2</sup>

<sup>1</sup>Swordtail Guppy Breeder, Show Judge and Independent Researcher. Mailing address: P.O. Box 1508, Lewisburg, West Virginia 24901, USA. orcid.org/0000-0002-9093-619X. <u>alansbias@aol.com</u>

<sup>2</sup>Biology Department (retired), University of Puerto Rico, Mayaguez campus, Mayaguez,
 Puerto Rico, USA. Mailing address: P. O. Box 3227, Mayaguez, P.R., USA 00681-3227.
 orcid.org/0000-0002-3916-0672. <u>rickdsquire@gmail.com</u>

**Abstract.** Modification of wild-type carotenoid orange and pteridine red coloration and spotting of male ornaments in modern Domestic Guppy Strains (*Poecilia reticulata reticulata*) by the naturally occurring Purple Body gene (Pb) has been long incorporated into their strains by Pedigree Stock Breeders. It is inherited as an autosomal incompletely dominant trait. Its existence has allowed breeders to produce a vast array of Purple based phenotypes. Photographic evidence demonstrates that Purple Body is a normal polymorphism in domestic guppies modifying color pigmented regions. When combined with currently used mutant genes such as Albino, Blond, Golden, Asian Blau, Coral Red, Magenta, Grass, Moscow, Pink, Platinum, Red Mosaic, Multicolor, and Full Red, startling new phenotypes are created. The recently described Purple Body gene (Bias and Squire 2017a, 2017b, and 2017c) has long been overlooked in research articles and little understood in breeder publications.

**Key Words:** Guppy color and modification, Domestic Guppy Strains, chromatophore, violet iridophore, blue iridophore, violet-blue iridophore, xanthophore, xantho-erythrophore, Purple Guppy, Purple Body gene, Metal Gold Iridophore, Purple Body gene, Vienna Emerald Green (*VEG*), Albino, Blond, Golden, Asian Blau, Coral Red, Magenta, Grass, Moscow, Pink, Platinum, Red Mosaic, Multicolor, Full Red, *Poecilia reticulata*.





Fig 1. Purple Delta (*Pb/Pb*), photo courtesy of Terry Alley

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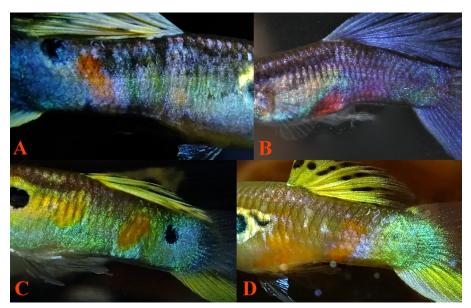
#### 32 Introduction

The Purple Body gene is located on an autosome. Breeding tests, involving this modification of orange spotting, reveal this trait to have an incompletely dominant mode of inheritance. As such a formal name and nomenclature of **Purple Body** (*Pb*) has been suggested (Bias and Squire, 2017a). [*Note: Hereafter Purple Gene, or Purple Body Gene used interchangeably in reference.*]

The intent of this brief paper is to provide spectral distinction, for ease in identification, between Pb and non-Pb in many of the more commonly produced modern Domestic Guppy strains. Emphasis is on the primary color traits, and several common pattern traits. Groupings are presented by Grey (*wild-type*), autosomal and sex-linked modifiers. These should not be considered inclusive of all known phenotypes. The number of strains and phenotypes being produced for color and pattern continues to increase, and is a testament to the efforts of both professional and amateur breeders around the world.

Autosomal incompletely dominant Pb, similar to identified autosomal recessives found in *Poecilia reticulata*, is a modifier of total existing body color and pattern pigmentation (involving xantho-erythrophores, structural iridophores and melanophores) in both males and females. Purple Body is capable of modifying extent color and pattern found in any Domestic Guppy strain.

Pb modification is most noticeable in Domestic Strains as a modifier of ornaments 50 comprised of orange carotenoid color pigment, in both males and females (Fig 2). Visually, 51 52 coloration is modified from a highly reflective orange to a "pinkish-purple" coloration in Grey 53 ("wild type" alleles A, B, G, R, and ab) corresponding to autosomal genes Albino (a, Haskins 54 and Haskins 1948), Blond (b, Goodrich 1944) Golden (g, Goodrich 1944), European Blau (r, Dzwillo 1959) Asian Blau (Ab, Undescribed - see Bias 2015). It is also modified in various 55 ways when combined with autosomal genes Pink (p, Luckman 1990, Förster 1993, pi, 56 57 Kempkes 2007), Ivory (I, Tsutsui 1997, Magenta (M, undescribed), and Zebrinus (Ze, 58 Winge 1927). It combines as well with sex-linked genes such as Coral Red (Co, undescribed) Y-linked, Grass (Gra, undescribed) X- and/or Y-linked, Moscow (Mw, Y-linked, Kempkes 59 2007]), Nigrocaudautus, X and/or Y-linked (Nil, Nybelin 1947] and Nill, Dzwillo 1959). 60 Platinum (P, undescribed) X- and/or Y-linked, Mosaic (Mo, Khoo and Phang 1999) X- and/or 61 62 Y-linked, Multicolor (no gene symbol) X-linked, and Schimmelpennig Platinum (Sc, described 63 as Buxeus by Kempkes 2007), Y-linked. Examples provided in this paper are primarily limited to Delta Tail and Swordtail phenotypes. 64



67 **Fig 2. (A)** Homozygous Pb (*Pb/Pb*) modified ornaments, expressing removal of

xanthophores and increased violet-blue iridophores. (B) Homozygous Pb (*Pb/Pb*) modified
 ornaments, expressing reduced xanthophores and increased violet-blue iridophores. (C-D)
 non-Pb ornaments (*pb/pb*) expressing no alteration of xantho-erythrophores.

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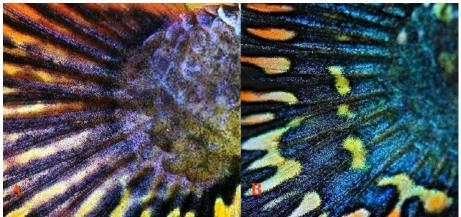
In heterozygous condition (*Pb/pb*) a distinct result is generated while in homozygous condition (*Pb/Pb*) these results are further amplified. Pb is capable of pleiotropic effect on all existing color and pattern elements at multiple loci. The purple phenotype has been present in hobbyist stocks for decades, but has been largely unrecognized by many breeders, except in the case of pure-bred all-purple strains.

Pb modification, zygosity dependent, removes certain classes of yellow-orange-red color pigment over silver iridophores or white leucophores. Pb modifies "other existing" color in both body and fins, thus suggestive of being a "full body" modifier, in homozygous condition. Dark red pteridine color pigment does not seem to be modified by Purple Body in fins lacking an underlying silver iridophore or white leucophore pattern. Modification by Pb seems limited predominantly to wild-type orange color pigment; i.e. that which also contains yellow carotenoids in addition to red pteridines, over an iridophore pattern.

84 Pb is always found in all-purple fish, but is not by itself sufficient to produce the all-85 purple phenotype in heterozygous expression. Homozygous Pb expression results in the further removal of xantho-erythrophores, in conjunction with both increased populations 86 87 and/or greater visibility of modified melanophores and naturally occurring violet and blue 88 iridophores. It is required for the production of the all-purple phenotype (Fig 1 and Fig 89 **2A).** Pb causes a large reduction of yellow color pigment cell populations (xanthophores). 90 It thus produces a modified pinkish-purple expression from what would have been orange 91 color pigment cells (xantho-erythrophores).

92 High resolution photography and microscopic study shows the co-existence of varying 93 populations of both violet and blue structural iridophores in all individuals, both male and female (Bias and Squire 2017a, Pb Cellular Description; 94 2017b, Pb Microscopy Study; 95 2017c, Ocular Study). Violet and blue structural iridophores and melanophores are always 96 found in close proximity with one another, forming a type of chromatophore unit [Note: 97 hereafter referenced as violet-blue (iridophores) for ease of discussion]. Violet-blue 98 iridophores (Fig 3A-B) are most visible along the topline and in between regions lacking a 99 clearly defined silver iridophore pattern, often including the caudal-peduncle base. Βv nature, yellow color pigment in Guppies is highly motile and mood dependent while red 100 color pigment is considered non-motile. Red color pigment (from erythrophores) is not 101 altered by Pb, or at least altered to a lesser degree, and a corresponding noticeable increase 102 103 in the visibility (possibly increased population levels) of structural violet and blue 104 iridophores is evident (Fig 2A-B and Fig 3A-B), resulting in the increased reflective 105 qualities of individuals.

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109 Fig 3. (A) Pb/Pb modified caudal base expressing increased violet iridophores. (B) Non-Pb
110 pb/pb caudal base expressing balanced violet-blue iridophores, photos courtesy of Christian
111 Lukhaup.

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113 When not masked by additional color and/or pattern traits, the identification of Purple 114 Body (*Pb*) in both wild-type and domestic males can be easily accomplished through visual 115 phenotypic observation. In non-Purple Body (*pb/pb*) individuals carotenoid orange color 116 pigment can be described as being vivid, bright orange spots structurally comprised of 117 densely packed yellow and orange xantho-erythrophores, normally extending to the very 118 edge of the spot. Though coverage over additional iridophore patterns may appear 119 incomplete.

120 Heterozygous Purple Body (*Pb/pb*) alters orange spots in select regions of the body and in finnage to "pinkish-purple". Thus, it may not act as a "full body" modifier in 121 122 heterozygous form. Heterozygous Pb does not appear to greatly reduce visible structural 123 yellow color pigment cells over white leucophore or reflective clustered yellow cells, known in breeder circles as Metal Gold (Mg) (Undescribed - Bias 2015), in body and finnage. A 124 125 slight increase in visibility of violet and blue iridophores is often detected. Additionally 126 noted is an increase and modification in existing melanophore structure and possibly population numbers, as compared to heterozygous Pb. In non-solid colored strains, a 127 128 reduction in the number of yellow xanthophores results in a corresponding reduction in 129 overall size of individual spotting ornaments. This reveals a "circular ring" around remaining 130 color pigment produced by an underlying iridophore layer. This well-defined layer of iridophores is an underlying precursor required for definition of shape over which color 131 132 pigment cells populate during maturation.

133 Homozygous Purple Body (Pb/Pb) alters all orange spots found in the body and in 134 finnage to "pinkish-purple", though modification may not be so readily visible in regions of 135 red solid color. It therefore should be considered a "full body" modifier. Homozygous Pb 136 can also produce a purple guppy phenotype. Homozygous Pb removes all visible yellow over white leucophores, but not Mg in body and finnage. This in turn, 137 color piament 138 produces a dramatic increase in the visibility of wild-type violet-blue iridophores. The 139 number of melanophores does not appear to drastically increase in any given individual as 140 compared to homozygous Pb, but the size of the melanophores themselves was greater.

Heterozygous Pb exhibits partial reduction in collected xanthophores, and homozygous
 Pb has a near complete removal of collected and clustered xanthophores. However, yellow
 color cell populations consisting of isolated "wild-type" single cell xanthophores remain
 intact.

145Further descriptions of Guppy Traits are available for download in:Bias and146Groenewegen (2016, with periodic updates) Poecilia reticulata:Domestic Breeder Trait147MatrixReferenceGuide.

- <u>https://www.academia.edu/29928596/Poecilia\_reticulata\_Domestic\_Breeder\_Trait\_Matrix\_R</u>
   <u>eference\_Guide</u> (last checked 1.21.2017).
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#### 152 Phenotypic expression of Pb and non-Pb modification in

153 Grey (wild-type)



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Fig 4. (A) Purple Delta (*Pb/pb*) males. Results of a homozygous Green (*pb/pb*) male x
 homozygous Purple (*Pb/Pb*) female breeding. (B) Homozygous Purple (*Pb/Pb*) male x

157 homozygous Green (pb/pb) female breeding. This type male will express as either blue or 158 purple depending upon the angle of light.

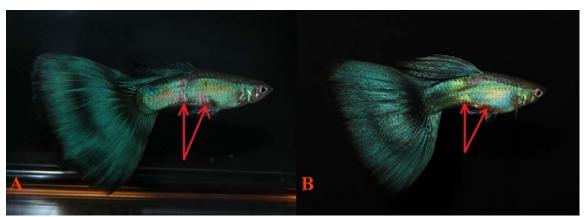
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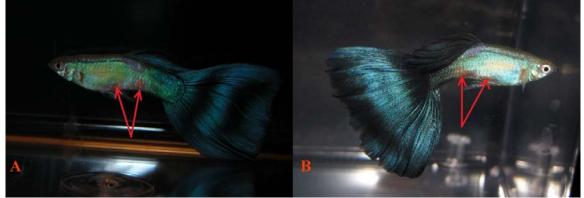
Fig 5. (A) Purple Delta Female (*Pb/Pb*) and (B) Green Delta Female (*pb/pb*), photos
courtesy of Bryan Chin. Note the dark violet-blue color of the caudal fin with Pb, green
reduced through xanthophore removal.

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- **Fig 6.** (A) Green Delta expressing Pb modified ornaments (*Pb/pb*). (B) Green Delta
- (*pb/pb*), photos courtesy of Bryan Chin. Note the deepening of the orange body spots topinkish-purple with Pb through xanthophore removal (arrows).

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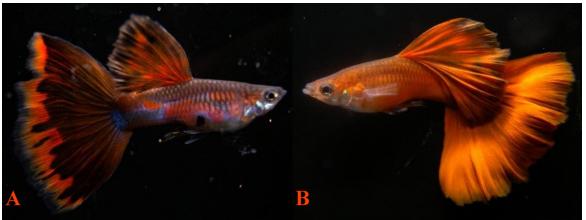
Fig 7. (A) Blue Delta expressing Pb modified ornaments (*Pb/pb*). (B) Blue Delta (*pb/pb*), 172 photos courtesy of Bryan Chin. Note the deepening of the orange body spot to pinkish-173 purple with Pb through xanthophore removal (arrows).

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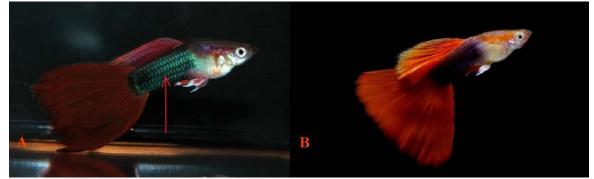
176 **Fig 8.** (A) Purple Moscow (Mw + MBAG) Delta expressing Pb modified ornaments (Pb/Pb). 177 **(B)** Blue-Green Moscow (Mw + MBAG) Delta expressing Pb modified ornaments (Pb/pb). Note violet-blue iridophore based pattern and reduction of xanthophores in heterozygous Pb 178 condition. Unmodified anterior orange body spot partially masked by MBAG in peduncle 179 (arrows). (C) Green Moscow (Mw + MBAG) Delta (pb/pb). Note absence of Pb effects. 180 Unmodified anterior and posterior orange body spots partially masked in peduncle by MBAG 181 182 (arrows), photos courtesy of Igor Dusanic. 183



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Fig 9. (A) Red Delta expressing Pb modified ornaments (Pb/pb). (B) Red Delta (pb/pb), 185 photos courtesy of 黃啟閔 Kiddo Huang. Note how Pb darkens deep orange to dark red 186 through xanthophore removal, and modifies body spots from orange to pinkish-purple with 187 increase violet-blue iridophore expression. 188

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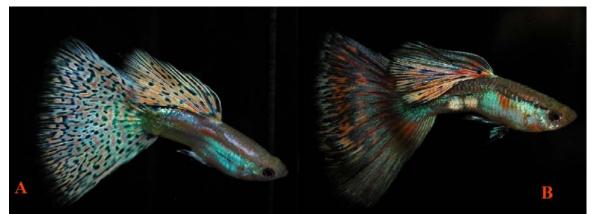
Fig 10. (A) Half Black (*NiII*) Red Delta expressing Pb modified ornaments (*Pb/pb*). (B) 191

Half Black (*Nill*) Red Delta (*pb/pb*), photos courtesy of Bryan Chin and Cheng-Hsien Yang. 192 Note the darker red replacing lighter orange-red by Pb through xanthophore removal.

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194 Peduncle and topline expresses increased iridophores in Pb, and dorsal shows reduction of 195 xanthophores revealing violet-blue iridophores (arrow).

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Fig 11. (A) Red Multi-Color (*Pb/pb*) Delta expressing Pb modified ornaments. Note the 198 199 change of orange body spots to pinkish-purple from xanthophore removal, while darker red is unaffected with Pb. (B) Red Multi-Color Delta (*pb/pb*), photos courtesy of Bryan Chin. 200 201



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Fig 12. (A) Purple Multi-Color (*Pb/Pb*). (B) Red Multi-Color Deltas expressing Pb modified ornaments (*Pb/Pb*), photos courtesy of Bryan Chin. Note the erythrophores show partial Pb modification in both males' finnage and the violet coloration in the fish to the left. Genes other than Pb are responsible for some of these differences. Some orange spots are modified to pinkish-purple. Pb reduces sex-linked xanthophores in dorsal and caudal, revealing white leucophores (*Le*) in finnage. There is a slight increase in violet-blue structural color in body.

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Fig 13. (A) Purple Multi-Color Delta (*Pb/Pb*). (B) Red Multi-Color Deltas expressing Pb
modified ornaments (*Pb/Pb*), photos courtesy of Bryan Chin. Again, additional genes are
involved here. Orange spots are modified to pinkish-purple. Pb reduces sex-linked
xanthophores in dorsal and caudal, revealing white leucophores (*Le*) in finnage. There is a
slight increase in violet-blue structural color in body.

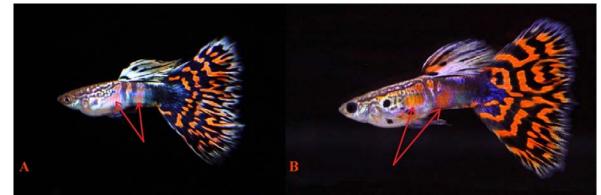
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Fig 14. (A) Purple Multi-Color (*Pb/Pb*). (B) Red Multi-Color Deltas expressing Pb modified ornaments (*Pb/Pb*), photos courtesy of Bryan Chin. Orange spots are modified to pinkish-

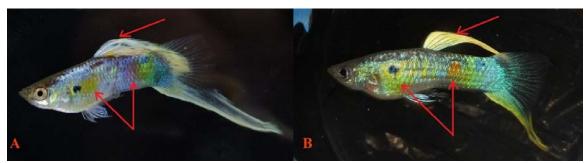
- 221 purple, and increased violet-blue iridophores (arrows). Some anterior Metal Gold (Mg)
- remains over blue iridophores and in the VEG peduncle spot. 222
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Fig 15. (A) Red Mosaic Delta (*Pb/Pb or Pb/pb*) expressing Pb modified ornaments. (B) 226 Red Mosaic Delta (*pb/pb*), photos courtesy of Kevin and Karen Yang. Pb converts lighter 227 carotenoid orange to pinkish-purple on the body (arrows), but the effect on the darker 228 pteridine red in caudal fin is less pronounced. Pb reduces sex-linked xanthophores in dorsal and caudal, revealing white leucophores (Le) in finnage. There is a slight increase in violet-229 230 blue structural color in body.

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233 Fig 16. (A) Vienna Lowersword expressing Pb modified ornaments (Pb/Pb). (B) Vienna Lowersword (*pb/pb*). Green coloration is the product of yellow xanthophores over blue 234 iridophores. Note that when Pb reduces the yellow, it reduces green as well. Posterior 235 236 orange spots are modified to pinkish-purple (arrows). There is increased expression of 237 violet-blue iridophores while collected sex-linked xanthophores are removed and clustered 238 Metal Gold (Mg) are only reduced by Pb (arrow).

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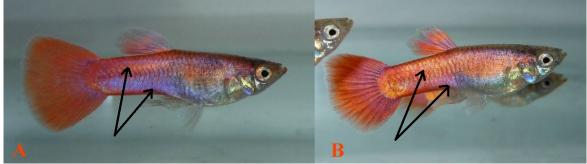
- Fig 17. (A): Coral Red (Co) Doublesword expressing Pb modified ornaments (Pb/Pb or 241
- *Pb/pb*). **(B)** Coral Red (*Co*) Doublesword (*pb/pb*), photos courtesy of Krisztián Medveczki 242
- 243 and Gary Lee. Note how Pb changes orange to deep red. Pb removes sex-linked
- 244 xanthophores in the dorsal and caudal, leaving only white leucophores (Le), as no sex-

246 there is proliferation of iridophores in the body. Sex-linked collected yellow pigment is

247 removed from both caudal and dorsal (arrow). There is a heavy increase in violet-blue

248 structural color in body, but not finnage, as Pb modification of erythrophores is minimal.

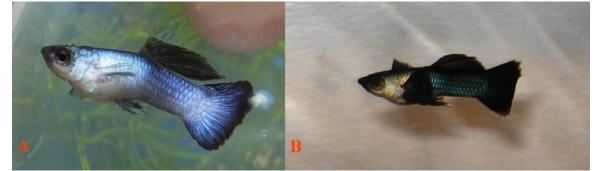
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Fig 18. (A) Magenta (M) Delta expressing Pb modified ornaments (Pb/pb). (B) Magenta (M) Delta (pb/pb), photos courtesy of Krisztián Medveczki. Note how Pb converts orange to 252 red by reduction of xanthophores (arrows) and deepens and expands the violet-blue 253 254 iridophore coloration. Orange spots are modified to pinkish-purple, and increased 255 expression of violet-blue iridophores by xanthophore reduction (arrows).

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258 Fig 19. (A) Purple Panda Moscow (Mw + pp) Roundtail expressing Pb modified ornaments

(*Pb/Pb*). (B) Panda Moscow (Mw + pp) Roundtail (pb/pb). Green is replaced by purple 259 with Pb, by removal of xanthophores with increased expression of violet-blue iridophores. 260

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Phenotypic expression of Pb and non-Pb modification in 262 Albino (aa) 263



264 Fig 20. (A) Full Red Albino (aa) Delta expressing Pb modified ornaments (Pb/pb). (B) Full 265 Red Albino (aa) Delta (pb/pb), photos courtesy of 曾皇傑 Tseng Huang Chieh. 266

268 xanthophore removal, with proliferation of violet-blue iridophores visibly modified to

269 pinkish-purple (arrows).

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Fig 21. (A) Albino (aa) Delta expressing Pb modified ornaments (*Pb/Pb or Pb/pb*), photo
courtesy of Benson Liu. (B) Albino (aa) Lowersword (*pb/pb*). Melanophores are removed by
Albino, though dendritic pattern remains. Posterior orange spots are modified to pinkishpurple, with increased expression of violet-blue iridophores.

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# Phenotypic expression of Pb and non-Pb modification in Blond (*bb*)



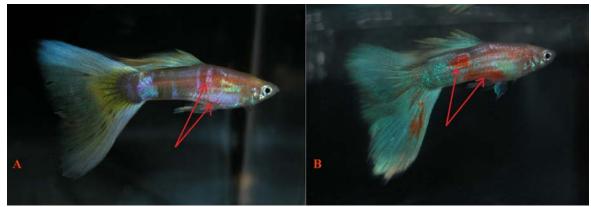
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Fig 22. (A) Blond (bb) Red Delta expressing Pb modified ornaments (Pb/pb or Pb/Pb). (B)
Blond (bb) Red Delta (pb/pb), photos courtesy of Bryan Chin and 黃啟閔 Kiddo Huang.
Removal of xanthophores and a proliferation of violet-blue iridophores modifies orange to a
darker red and spots are modified to pinkish-purple (arrows).



Fig 23. Blond (*b*) Red Multi-Color Delta expressing Pb modified ornaments (*Pb/pb*), photo
 courtesy of Bryan Chin. Blond reduces melanophore size. Posterior orange is converted to
 pinkish-purple by Pb (arrows), with increased expression of violet-blue iridophore structural
 color. Pb reduces sex-linked xanthophores in dorsal and caudal, revealing white
 leucophores (*Le*) in finnage.

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**Fig 24.** (A) Blond (*bb*) Multi-Color Delta expressing Pb modified ornaments (*Pb/pb*).

Heterozygous Pb converts some orange spots over Zebrinus (Ze) to pinkish-purple (arrows) with increased purple violet iridophores, some anterior orange remains. Pb reduces sex-

296 linked xanthophores in dorsal and caudal fins, revealing white leucophores (*Le*) in finnage.

297 There is a slight increase in violet-blue structural color in body. **(B)** Blond (*bb*) Multi-Color

298 Delta (*pb/pb*), photos courtesy of Bryan Chin. Blond reduces melanophore size. There is no 299 modification to orange spotting ornaments (arrows) comprised of xantho-erythrophores.

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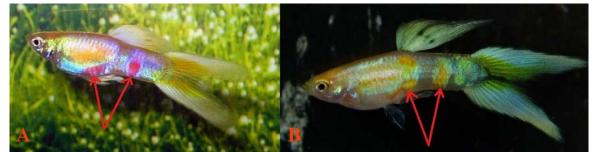
Fig 25. (A) Blond (bb) Vienna Lowersword expressing Pb modified ornaments (Pb/Pb).
(B) Blond (bb) Vienna Lowersword (pb/pb). Blond reduces melanophore size. Orange is converted to pinkish-purple by xanthophore removal (arrows), green is almost eliminated by Pb.



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**Fig 26. (A)** Blond (*bb*) Schimmelpennig Platinum (*Sc*) Delta expressing Pb modified ornaments (*Pb/Pb*). **(B)** Blond (*bb*) Schimmelpennig Platinum (*Sc*) Delta (*pb/pb*), photos courtesy of Bryan Chin. Blond reduces melanophore size. Orange is converted to pinkishpurple by xanthophore removal (arrows), green is eliminated by Pb. Pb reduces sex-linked xanthophores in dorsal and caudal fins, revealing white leucophores (*Le*) in finnage. Metal Gold (*Mg*) remains in body and finnage. There is a slight increase in violet-blue structural color in body.

313 color in b 314



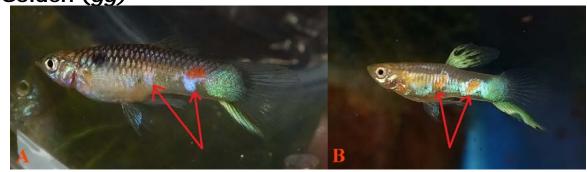
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Fig 27. (A) Blond (*bb*) Schimmelpennig Platinum (*Sc*) Doublesword expressing Pb modified
ornaments (*Pb/Pb*). (B) Blond (*bb*) Schimmelpennig Platinum (*Sc*) Doublesword (*pb/pb*).
Blond reduces melanophore size. Orange is converted to pinkish-purple by xanthophore
removal (arrows), green is eliminated by Pb. Note that the large platinum shoulder area,
comprised of clustered Metal Gold (*Mg*) xanthophores, is still present in homozygous Pb. Pb
reduces sex-linked xanthophores in dorsal and caudal, revealing white leucophores (*Le*) in
finnage. There is a slight increase in violet-blue structural color in body.

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# 324 Phenotypic expression of Pb and non-Pb modification in

325 Golden (gg)



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Figure 28. (A) Golden (gg) Vienna Lowersword expressing Pb modified ornaments
 (Pb/Pb). (B) Golden (gg) Vienna Lowersword (pb/pb). Melanophores are reduced and

collected by Golden. Orange is converted to pinkish-purple by Pb by xanthophore removal
 (arrows), pale blue is deepened to violet, green is reduced. Pb reduces sex-linked
 xanthophores in dorsal and caudal, revealing white leucophores (*Le*) in finnage. Metal Gold
 (*Mg*) remains in body and finnage. Slight increase in violet-blue structural color in body.

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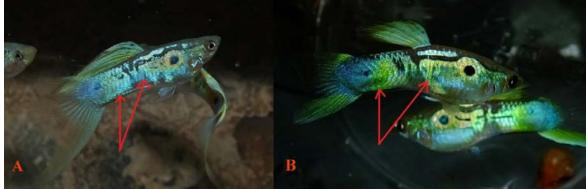


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**Fig 29. (A)** Golden (*gg*) Purple Panda Moscow (Mw + pp) Roundtail expressing Pb modified ornaments (*Pb/Pb*). **(B)** Golden (*gg*) Panda Moscow (Mw + pp) Roundtail (*pb/pb*). Green is replaced by purple with Pb, through xanthophore removal and proliferation of violet-blue iridophores (arrow). Reduction in melanophore numbers, especially ectopic, reduces dark peduncle coloration (arrow).

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# Phenotypic expression of Pb and non-Pb modification in Asian Blau (*Ab*)



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Fig 30. (A) Asian Blau (Ab) Vienna Lowersword expressing Pb modified ornaments (Pb/Pb.
(B) Asian Blau (Ab) Vienna Lowerswords (pb/pb). Orange is converted to pinkish-purple by
Pb xanthophore removal (arrows). Erythrophores are further removed by Ab revealing

- 347 modified violet-blue iridophores (arrows).
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Fig 31. (A) Asian Blau (*Ab*) Ivory (*ii*); i.e. Lavender Coral Red (*Co*) Doublesword
expressing Pb modified ornaments (*Pb/Pb or Pb/pb*), photo courtesy of Taketoshi Sue.
Orange is converted to pinkish-purple by Pb. Asian Blau removes orange and Ivory
removes yellow-orange revealing modified violet-blue iridophores and white leucophores.
(B) Asian Blau (*Ab*) Coral Red (*Co, pb/pb*). Doublesword Orange converted to pinkishpurple by Pb, and removed by Ab revealing underlying leucophores and modified

356 iridophores.

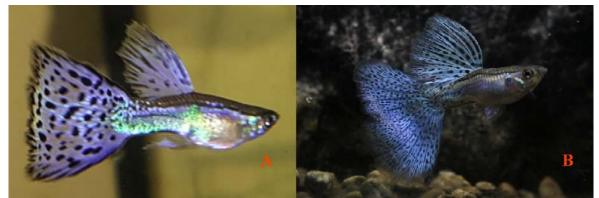
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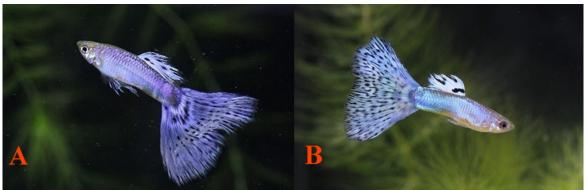
**Fig 32. (A)** Asian Blau (*Ab*) Ivory (*ii*); i.e. Lavender Grass Delta expressing Pb modified ornaments (*Pb/pb*). Orange converted to pinkish-purple by Pb. Asian Blau removes orange and Ivory removes yellow-orange revealing modified violet-blue iridophores and white leucophores. **(B)** Red Grass Delta expressing orange ornaments (*pb/pb*). Orange converted to pinkish-purple by Pb, photos courtesy of Taketoshi Sue. **(C)** Pink Grass Delta expressing Pb modified ornaments (*Pb/pb*). Orange converted to pinkish-purple by Pb, photo courtesy of Gyula Pasaréti.

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Figure 33. (A) Asian Blau (Ab) Purple Grass Delta expressing Pb modified ornaments
(Pb/pb). Orange converted to pinkish-purple by Pb. Asian Blau removes orange revealing
modified violet-blue iridophores. Photo courtesy of Leanne Shore. (B) Asian Blau (Ab) Blue
Grass Delta (pb/pb). Orange converted to pinkish-purple by Pb. Asian Blau removes
orange revealing modified blue iridophores. Photo courtesy of Kevin Yao.



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Figure 34. (A) Asian Blau (Ab) Ivory (i); i.e. Lavender Coral Red (Co) Grass Delta
expressing Pb modified ornaments (Pb/pb). Orange converted to pinkish-purple by Pb.
Asian Blau removes orange and Ivory removes yellow-orange revealing modified violet-blue
iridophores and white leucophores. (B) Asian Blau (Ab) Coral Red (Co) Blue Grass Delta
(pb/pb). Orange is converted to pinkish-purple by Pb. Asian Blau removes orange
revealing modified blue iridophores and minimal Metal Gold (Mg). Photos courtesy of
Taketoshi Sue.

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Fig 35. Top: Asian Blau (*Ab*) Albino (*aa*) Ivory (*il*); i.e. Albino Lavender Grass Delta
expressing Pb modified ornaments (*Pb/Pb or Pb/pb*). Albino removes melanophores.
Orange converted to pinkish-purple by Pb. Asian Blau removes orange and Ivory removes
yellow-orange revealing modified violet-blue iridophores. Bottom: Asian Blau (*Ab*) Albino
(*aa*); i.e. Albino Blue Grass Delta. Albino (*aa*) removes melanophores. Asian Blau (Ab)
removes orange revealing modified blue iridophores and Metal Gold (*Mg*). Photos courtesy
of Taketoshi Sue.

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Fige 36. (A) Asian Blau (Ab) Blond (bb) Vienna Lowersword expressing Pb modified
 ornaments (Pb/Pb). (B) Asian Blau (Ab) Blond (bb) Vienna Lowersword (Pb/pb). Blond

reduces melanophores. Orange converted to pinkish-purple by Pb, by xanthophore removal(arrows). Asian Blau removes orange revealing modified light violet-blue iridophores.

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# 397 **Discussion and Conclusions**

The genes kita, kitla, csf1ra, and csf1rb have been identified in Guppies (Kottler 2013; 2015).

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Kita is a required precursor gene in the development of early forming motile melanophores (kita-dependent) in Guppies. Kita is not required for development of genetically distinct late forming, possibly non-motile, melanophores (kita-independent). Together, they produce the reticulated scale pattern found in both sexes; wild and domestic.

Csf1ra is a required precursor gene (colony-stimulating factor 1 receptor) in the development and formation of xantho-erythrophores. In Guppies csf1ra is not required in development of late forming, possibly non-motile, melanophores (kita-independent). Together, they contribute to non-defective ornaments of wild-type males.

Interactions between late forming melanophores in conjunction with xantho erythrophores affect Domestic Guppy strain ornaments in both sexes. Thus, functional kita
 and csf1ra are found in non-defective ornaments of Domestic strains in both sexes.

Purple body removes certain classes of yellow-orange-red color pigment over silver iridophores or white leucophores. Dark red pteridine color pigment does not seem to be modified by Purple Body in fins lacking an underlying silver iridophore or white leucophore pattern. Modification by Pb seems limited predominantly to wild-type orange color pigmented xantho-erythrophores; i.e. those which also contain yellow-orange carotenoids in addition to red pteridines, over an iridophore pattern. Heterozygous Purple Body (*Pb/pb*) alters orange spots in select regions of the body and in finnage to "pinkish-purple".

Heterozygous Pb does not appear to greatly reduce visible structural yellow color pigment cells over white leucophore or reflective clustered yellow cells in body and finnage. A slight increase in visibility of violet and blue iridophores is often found. Homozygous Pb expression results in a further removal of xantho-erythrophores, in conjunction with both increased populations and/or greater visibility of modified melanophores and naturally occurring violet and blue iridophores. Pb/Pb plus an unidentified additional genetic component is required for production of the all-purple phenotype.

When Pb is combined with any of the autosomal or sex-linked mutants well known to breeders, Albino (*aa*), Blond (*bb*), Golden (*gg*), and Asian Blau (*Ab*), further combined effects occur. The modifications of each of these genes on "wild-type" grey and resulting co-expressions with the Purple Body (*Pb*) gene are briefly discussed as follows:

431

#### 432 Autosomal Genes With References

Albino (aa). Recessive. Also known as Real Red Eye Albino (RREA) or (Type B). There is 433 434 an inability to produce black melanophores in the body and finnage. It eliminates all classes 435 of melanophores; dendritic, corolla and punctate. Therefore melanin is absent as well. 436 Albino is epistatic to both the Blond and Golden genes; thus mutant alleles of each may be 437 found in the albino genotype (e.g., aa Bb, aa bb, aa Gg, aa gg, etc.). In Albino, the result when combined with Pb is similar to that with Blond, except that the melanin is completely 438 439 absent and the colors appear even paler (except when a different pigment cell is over 440 expressed as in full red). Red can appear deepened and "darker" when Pb is present.

Blond (*bb*). Recessive. It has been identified as a defective gene mutation in adenylate
(adenylyl) cyclase 5 (adcy5; ac5), and mapped to Linkage Group (LG) 2 (Kottler et al.
2015). It is also known to pedigree breeders as IFGA Gold, Asian Gold, European Blond.
This mutation produces a near normal number of black melanophores of all types; Dendritic,

445 Corolla and Punctate. However, the size of each is greatly reduced and the structure 446 modified as compared to "wild-type" grey. According to published results Blond is not 447 linked to Golden. This gene should be viewed not as a suppressor of melanophores, but 448 rather one that alters melanophore size and shape.

When Pb is combined with homozygous blond (*bb*), a violet-blue sheen co-expresses with often paler and less intense xantho-erythrophores, resulting from the reduction in melanophore size. The reflective qualities of xantho-erythrophores in Blond are determined by the composition of underlying structural colors (iridophores are more reflective and leucophores are less reflective) and angles at which crystalline platelets reside.

454 Golden (gg). Recessive. The Golden gene is a defective ortholog of kita (Kottler et al. 455 2013). Kita has been mapped on Guppy autosomal LG 4 (Tripathi et al. 2008). It is also 456 known to pedigree breeders as European Gold, IFGA Bronze or Asian Tiger. This gene produces a reduced amount of black melanophores (approximately 50%) of all types; 457 458 dendritic, corolla and punctate. However, the size of dendritic and corolla melanophores is 459 greatly increased and the collection of corolla melanophores is concentrated into "clumps" or "islands" of melanophores along the scale edges. 460 Males and females lack skin 461 melanophores at birth, but they develop with maturity. Scale edging will become lighter with a higher inbreeding co-efficient; i.e. long-term Golden x Golden breeding's. This 462 463 suggests that there are non-allelic modifier genes affecting the Golden phenotype.

According to published results Golden and Blond are in different linkage groups and assumedly different chromosomes and thus *can not* be alleles of each other or linked to each other. This gene should be viewed as a suppressor of melanophore population numbers.

- In Pb plus Golden (*gg*), the effect is similar to Blond, except that melanophores are
   present at higher frequencies and with a modified distribution. As a result, the colors while
   paler than in grey are not as pale as in Blond.
- 471

472 Asian Blau (Ab). Incompletely Dominant. Also known to pedigree breeders as (r2) Europe 473 and (Rr) Asia. [Note: The use of lower case "r" violates the accepted genetic use of 474 symbols since this is not a recessive gene, this usage came about prior to identification of 475 Ab as a second erythrophore defect.] In heterozygous condition red color pigment is 476 removed, while collected yellow color pigment and clustered Metal Gold (Mg) is little 477 This produces an iridophore based phenotype. Snakeskin patterns degrade in affected. 478 both heterozygous and homozygous expression, as a result of disruption of melanophore 479 structure or melanin content. The Purple (Violet) sheen found above the lateral line of both 480 males and females is removed.

In homozygous condition certain black melanophores are removed along with red and yellow color pigments. In homozygous condition finnage may be reduced in size, but the genes are still present in the genotype for normal finnage. An outcross of homozygous Ab will produce the expected finnage in F<sub>1</sub> offspring. [**Note:** As there are distinct types of red color pigment (carotenoid and pteridine) present in both body and finnage, removal may not be complete, as in a red "Old Fashioned" shoulder stripe. A very faint "red shoulder stripe" is sometimes visible.]

The result when Asian Blau is combined with Pb can range from highly reflective violetblue to non-reflective violet-blue in combination with additional genes that remove and/or reduce iridophores or alter angles of crystalline platelets.

491

**European Blau** (*r* or *r1*); also (*eb*). Recessive. Both csf1ra and csf1rb genes have been identified in Guppies, and are the result of an ancestral genome duplication event that produced four copies of each gene rather than two. (The guppy is an ancestral tetraploid.) In many fish species one or the other pair of some genes has been lost to reduce the total gene dosage back to a "diploid level" of two rather than four copies. In some other cases, the two genes diverge from each other and assume different functions. The European Blau gene is a defective ortholog of csf1ra. Expression levels of csf1rb were not upregulated to compensate for the deficiency in csf1ra (Kottler et al., 2013), which suggests that Csf1ra and Csf1rb have functionally diverged from each other in the guppy. Csf1ra has been mapped on Guppy autosomal LG 10 (Tripathi et al. 2008).

502 European Blau is also known as Dunkel in Asia. Csf1ra activity is required for the 503 dispersal or differentiation of male-specific xanthophores (Kottler et al, 2013). In 504 homozygous condition it is epistatic to wild type genes for red and yellow; major red and 505 yellow color pigments are removed from the body. Certain red color pigments may be 506 present in finnage, and to a lesser degree in the body. Reflective gualities are reduced. 507 Ecotopic melanophores may be removed, while basal level melanophores such as are 508 found in Half Black (NIII) are only slightly reduced. "The salient feature of the csf1ra 509 mutant males was the absence of all orange traits, with concomitant severe changes in 510 black ornaments" (Kottler et al, 2013). Snakeskin patterns degrade in homozygous 511 expression. The purple (violet) sheen found above the lateral line of both males and 512 females is removed. There is minimal finnage reduction.

513

#### 514 Additional Autosomal Genes Referred To

**Pink** (*p*, Luckman 1990; Förster 1993; *pi* Kempkes 2007) Recessive. Removal of orange erythrophores in body resulting in a "yellow-orange" cast in finnage. Homozygous reduction of NiII melanophores and increase in MBAG. Removes blue iridophores. Reduces size of finnage. Pb modification: Orange spotting is converted to pinkish-purple. Collected yellow pigment cells are removed, but not Clustered Mg. Body color may be modified to violetblue.

521

Ivory (*I*, Tsutsui, Y 1997) Autosomal Dominant. Heterozygous suppression of
erythrophores (red color). Homozygous suppression of xantho-erythrophores (yellow-red
color), with reduction in fin size. Possible differences in melanophore modifications in
heterozygous vs homozygous states. Resulting in a "white" appearance. II (homozygous),
Ii (heterozygous) and ii (non-Ivory). Pb modification: Previous orange spotting is removed
by Ivory. Underlying iridophores and leucophores converted to light pinkish-purple.

528

529 Magenta (*M*, undescribed) Autosomal Dominant. Proliferation of red color pigment when 530 present and an increase of violet-blue iridophore structural color. Converts yellow color 531 pigment cells (xanthophores) to red erythophores), though Metal Gold (Mg) may remain. 532 Concentrates black melanophores. There is a reduction in fin size. Pb modification: Orange 533 spotting is converted to pinkish-purple. Collected yellow pigment cells are removed, but not 534 Clustered Mg.. Converts orange to red and deepens violet blue coloration. 535

**Zebrinus** (*Ze*, Winge 1927) Autosomal Dominant. Color Character; Barred pattern of vertical stripes on the peduncle, viz. 2-5, generally 3 dark pigment stripes. Effect resembles that of Tigrinus gene, but is as a rule more pronounced. ZeZe (homozygous), Zeze (heterozygous) and zeze (non-Zebrinus). Pb modification: No direct effect on barring pattern. Overlaying orange spotting is converted to pinkish-purple. Collected yellow pigment cells are removed, but not Clustered Mg.

542

#### 543 Major Sex-linked Traits Referenced

544 **Coral Red** (*Co, undescribed*) Y-linked. Red color pigment shoulder pattern. Linked in 545 complex with Ds. Probably a Full Body modifier. It originated out of Vienna Emerald Green 546 Ds. Pb modification: Proliferation of violet structural color. Orange spotting is converted to 547 pinkish-purple. Collected yellow pigment cells are removed, but not clustered Mg. 548 549 Grass (Gra, Tsutsui, Y. 1997; Iwaski, N. 1989) X and/or Y-linked dominant. The Grass phenotype is a highly variable random "fine dot" circular melanophore pattern in finnage. 550 551 Primarily limited to caudal ornamentation, with limited dorsal influence. Often associated with "Nike Melanophore Stripe" body pattern. Variegation shape is dependent upon in-552 553 breeding co-efficient. Color pigments can be added. "Glass Grass" genotype is similar to Multi with a translucent background and color pigments. "Grass Grass" genotype is often 554 555 linked in complex with sex-linked xantho-erythrophore color pigment spots. Pb 556 Modification: Some orange spotting is converted to pinkish-purple. Collected yellow 557 pigment cells are removed, but not Clustered Mg. Xanthophore removal may reveal white 558 leucophores if present.

559

560 **Moscow Blau Additional Gene** (*MBAG*, *undescribed*) X-linked dominant. Half body pattern 561 expressing motile black mediating moderate & translucent melanin development over entire 562 body area posterior to dorsal fin, and in caudal peduncle. Other posterior peduncle color 563 patterns may be nearly or wholly obscured. Early Russian MBAG strains, in addition to NiII, 564 may have been identified as "Tuxedo; i.e. HalfBlack" (Pg. 58, Iwasaki 1989). Pb 565 modification: Orange spotting is converted to pinkish-purple. Collected yellow pigment cells 566 are removed, but not Clustered Mg. Peduncle may take on violet-blue reflective coloration.

567 Mosaic (Mo, Khoo and Phang 1999b) X-linked dominant. The Mosaic phenotype is a highly 568 variable random "large spot" crescent shaped melanophore pattern in finnage. Primarily limited to caudal ornamentation, with limited dorsal influence. 569 Variegation shape is 570 dependent upon in-breeding co-efficient. Normally associated with erythrophore color 571 pigment (carotenoid and/or pteridine). Pb modification: Some orange spotting in the body 572 is converted to pinkish-purple. Collected yellow pigment cells are removed, but not 573 Clustered Mg. Xanthophore removal may reveal white leucophores if present. Dark Red 574 Caudal pigment is generally not modified.

575 **Multi** (--, *undescribed*) X-linked dominant. The Multi phenotype is a highly variable random 576 "fine dot" circular melanophore pattern in finnage. Primarily limited to caudal 577 ornamentation, with limited dorsal influence. Variegation shape is dependent upon in-578 breeding co-efficient. Color pigments can be added. Not linked with erythrophore color 579 pigment (carotenoid and/or pteridine) spots. This must be added through outcrossing. 580 Little or no effect on existing body color or pattern. Pb modification: Some orange spotting 581 in the body is converted to pinkish-purple. Collected yellow pigment cells are removed, but not Clustered Mg. Xanthophore removal may reveal white leucophores if present. Dark Red 582 583 Caudal pigment is generally not modified.

584

Moscow (*Mw*, Kempkes 2007) Y-linked. Blue iridophore shoulder pattern. Likely a Full
 Body modifier. Color variation with addition or removal of xantho-erythrophores. Pb
 modification: Orange spotting is converted to pinkish-purple. Collected yellow pigment cells
 are removed, but not Clustered Mg. Body color is modified to violet-blue.

590 **Variegation** (*Var*, Khoo and Phang 1999). (See Grass, Mosaic, Multi) X and / or Y-linked 591 dominant gene. Inheritance of variegated tail patterns appears to be determined by a 592 single locus on the X and Y chromosomes.

The gene study of Variegation focused on variable random "large spot" shaped melanophore pattern in the caudal, though specimens exhibited similar dorsal pattern. Variegation shape is dependent upon in-breeding co-efficient. Color pigments (xanthoerythrophores) were not linked. Pb modification: Some orange spotting in the body is converted to pinkish-purple. Collected yellow pigment cells are removed, but not Clustered Mg. Xanthophore removal may reveal white leucophores if present. Dark Red Caudal pigment is generally not modified.

#### 600

Nigrocaudautus (*NiI*, Nybelin 1947 and NiII, Dzwillo 1959) X and/or Y-linked dominant
 gene. Full body modifier, epistatic to many other genes in outcrosses. Pb modification:
 Orange spotting is converted to pinkish-purple. Collected yellow pigment cells are removed,
 but not Clustered Mg.

605

611

**Schimmelpennig Platinum** (*Sc*); **Buxeus** (Kempkes 2007). Y-linked dominant gene. Silver-Blue iridophore shoulder pattern with Metal Gold (*Mg*) overlay. Probably a Full Body modifier. Linked in complex with Ds. Originated out of Vienna Emerald Green Ds. Pb modification: Orange spotting is converted to pinkish-purple. Collected yellow pigment cells are removed, but not Clustered Mg.

## 612 SUMMARY

The newly described gene Purple Body and prior described genes Albino, Blond, Golden, Asian Blau, and European Blau each limits or otherwise reduces the normal expression of chromatophores found in "wild-type" Grey. When they are combined together and with other frequently used color genes, new phenotypes are produced which are useful to Pedigree Guppy Breeders and Commercial Farmers alike. Their basic effects are of interest to geneticists, biochemists and molecular biologists.

619

# 620 Photo Imaging

Photos by author(s) were taken with a Fujifilm FinePix HS25EXR; settings Macro, AF: 621 center, Auto Focus: continuous, varying Exposure Compensation, Image Size 16:9, Image 622 623 Quality: Fine, ISO: 200, Film Simulation: Astia/Soft, White Balance: 0, Tone: STD, Dynamic 624 Range: 200, Sharpness: STD, Noise Reduction: High, Intelligent Sharpness: On. Lens: Fujinon 30x Optical Zoom. Flash: External mounted EF-42 Slave Flash; settings at EV: 0.0, 625 35mm, PR1/1, Flash: -2/3. Photos cropped or brightness adjusted when needed with 626 627 Microsoft Office 2010 Picture Manager and Adobe Photoshop CS5. All photos by author(s), 628 unless otherwise noted.

629

# 630 Ethics Statement

- 631
- No specimens were euthanized or harmed in this study.
- 632

# 633 Competing Interests and Funding

The authors declare that they have no competing interests. Senior author is a member of the Editorial Board for Poeciliid Research; International Journal of the Bioflux Society, and requested non-affiliated independent peer review volunteers.

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# 640 Notes

This publication is number three (3) of four (4) by Bias and Squire in the study of Purple Body (*Pb*) in *Poecilia reticulata*:

- 643
- The Cellular Expression and Genetics of an Established Polymorphism in *Poecilia reticulata*; "Purple Body, (*Pb*)" is an Autosomal Dominant Gene,
- 646 2. The Cellular Expression and Genetics of Purple Body (*Pb*) in *Poecilia reticulata*, and its
   647 Interactions with Asian Blau (*Ab*) and Blond (*bb*) under Reflected and Transmitted Light,
- 648 3. The Cellular Expression and Genetics of Purple Body (*Pb*) in the Ocular Media of the 649 Guppy *Poecilia reticulata*,

- 4. The Phenotypic Expression of Purple Body (*Pb*) in Domestic Guppy Strains of *Poecilia reticulata.*
- 652

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658

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