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ABERRANT COLOR PATTERNS IN THE *PAPILIO* AND AN UPDATE ON THE SEMI-MELANIC "*FLETCHERI*" VARIANTS, INCLUDING FEMALES (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT. Specimens resembling the male melanic aberration called "*fletcheri*" have been reported since the 1800's, primarily from *Papilio canadensis* populations across northern USA and Canada. These records have generally exhibited similar but very distinctive wing color patterns on the upper and undersides, especially the orange and blue on the hindwings. This paper reviews the 120-year history of "*fletcheri*"-type records and presents a number of new records, including some from *P. glaucus* and one from *P. rutulus*. Other female variants are also figured and compared since "*fletcheri*" phenotypes have historically almost always been males. We report on the first known female specimen of "*fletcheri*" from Vermont and discuss another female *fletcheri* phenotype captured in eastern Washington (also in 2008). It remains unclear whether interspecific introgression between *P. canadensis*, *P. glaucus*, and *P. rutulus* plays any role in generating these rare phenotypes, but *fletcheri* specimens are all from areas near the hybrid zone. Natural environmental conditions may play some role in causing this phenotype, especially since none have been generated under lab conditions.

Additional key words: aberrant mosaics, wing color variants, bilateral gynandromorphs, *Papilio glaucus*, *P. rutulus*, semi-melanics, Nearctic, female *fletcheri*.

Melanic male aberrants of *Papilio canadensis* Rothschild and Jordan have been reported at least since the 1880's when Fletcher (1889) described a very distinctive form collected from the Collins Inlet on Georgian Bay, 18 miles east of Killarney, Ontario in Canada. The similarities in subsequent captures were noted (Table 1) and the name *Papilio turnus* ab. *fletcheri* was suggested (Kemp 1900). While apparently no new reports were made for the next 60 years, a series of at least 12 letters and papers featuring discussion of the "*fletcheri*" form appeared during the period from 1960–1983 (see Table 1; Scriber & Lintereur 1983). While most of the reported specimens are from geographic areas now known to be in the range of *P. canadensis*, there are some putative "*fletcheri*" phenotypes from *P. glaucus* (Table 1). There has apparently been no successful rearing of offspring from a "*fletcheri*" parent (of either sex) and we still lack genetic studies of this form. Here we report our attempts to obtain offspring from "*fletcheri*" male parent and describe nine new male "*fletcheri*" (including *P. glaucus* and *P. rutulus* population sources) and female aberrants that could represent a form of "*fletcheri*".

METHODS AND RESULTS

New specimens of "*fletcheri*" from three different *Papilio* species. We report the capture and present figures of two "*fletcheri*" from northern Wisconsin (Sawyer and Oconto Counties; Figs. 1–3) and two from northern Michigan (Presque Isle and Cheboygan Counties, Figs. 4–5). The male from Cheboygan County (Fig. 5) was hand-paired to virgin females upon return to the lab in an attempt to see if this trait was dominant and whether it would occur in daughters as well as sons. However, we were unsuccessful at obtaining offspring from either pairing. On 31 May 1991 we hand-paired this male to a virgin *P. canadensis* female. While copulation lasted 49 minutes, no eggs were laid. A second pairing of this male was made to a lab-reared virgin *P. glaucus* female. Copulation lasted 51 minutes and eggs were laid on tulip tree (*Liriodendron tulipifera* L., Magnoliaceae), white ash (*Fraxinus americana* L., Oleaceae) sassafras (*Sassafras albidum* (Nutt.) Nees, Lauraceae) and black cherry (*Prunus serotina* Ehrh., Rosaceae), but none were fertile.

Field collections in eastern New York state and southwestern Vermont yielded five male "*fletcheri*"

types (during the period 1982–1999; Figs. 6–10; Table 1). These Vermont specimens all appear to be from areas that historically were *P. canadensis* while the New York specimen (Fig. 10) looks much more like *P. glaucus*, based on the inner black band width of the hindwing cell (Luebke *et al*. 1988; Scriber 2002). Cambridge, New York is a site that we have observed for two decades and recently, during the last two to three years, a second flight of *P. glaucus* has been observed. The Vermont populations of *P. canadensis* in adjacent southwest Vermont (Bennington County) have shown some evidence of extensive genetic introgression from *P. glaucus*, possibly from longer growing seasons (degree day thermal accumulations) during the mid-1990s (Scriber & Gage 1995; Scriber *et al*. 2008). This delayed "false second generation" flight in mid-July is much more hybrid-like than the May–June individuals and may represent the prototype (incipient species) or early stage of the mountain swallowtail, *P. appalachiensis* (Pavulaan & Wright 2002), which appears to be a recombinant (homoploid) hybrid species, unique genetically but sharing a delayed flight and many hybrid-like traits (Scriber & Ording 2005; Scriber *et al*. 2008). The late-June specimen (Fig. 10) appears to reflect these intermediate wing traits, while the early June and May specimens from the same Battenkill River Valley populations (Fig. 6–9; Table 1) do not.

Other specimens with *"fletcheri"* wings. A *"fletcheri"* type *P. rutulus* was collected in Lincoln County, Wyoming on 28 June 1973 (Fig. 11). Once again, we are not certain about the degree of introgression (if any) from other species such as *P. canadensis* and *P. glaucus*, although *P. eurymedon* and *P. multicaudatus* (see Scriber *et al*. 1990, 1995) do not appear to be involved here (see also field collected interspecific hybrids described in Guppy & Shepard 2001).

A *P. glaucus "fletcheri"* type was collected in Frederick County, MD on 29 July 1978 by Joseph Zeligs (Table 1; Fig. 12). It is very much *glaucus*-like in wing morphometrics and near to the *glaucus-canadensis* hybrid zone further inland in the Pennsylvania/West Virginia Appalachian Mountains (Scriber 1990).

In 2008, before acceptance/revision of this manuscript, we were fortunate in obtaining a female *"fletcheri"* phenotype from Bennington County, Vermont (captured by H. R. 27 May 2008; Fig. 21). Also, a female *fletcheri* (possibly *P. rutulus*) from eastern Washington, near the Canadian border, was figured in a web site (dorsal view: http://www.insectnet.com/dcforum/User_files/485349cd202d92a7.jpg; ventral view: http://www.insectnet.com/dcforum/User_files/485349dc48c9c1e6.jpg). This Washington state specimen was also captured in 2008 on 1 June, by Robert Goodmiller, and this female looks almost identical to the one we figure here. These two specimens are the only clear examples of female *"fletcheri"* phenotypes.

Discussion

These melanic male *"fletcheri"* types (clearly distinguishable from color mosaics and gynandromorphs) are apparently inherited independently of the (Y-linked, X-modified) melanic polymorphism that characterizes females of the *Papilio glaucus* and *Papilio alexiares* species (Clarke & Sheppard 1962; Scriber *et al*. 1996). In rearing more than 15,000 different families (offspring of a single female) of the *P. glaucus* group (producing approximately 80,000–100,000 adults) we have never seen a *"fletcheri"* type emerge. We report here that the *"fletcheri"* type is found in the natural populations of the western tiger swallowtail, *P. rutulus*, from Wyoming, as well as New England, Michigan, Wisconsin and Canada populations of *P. canadensis* (Figs. 1 and 2). Before the revision of this paper in 2008, we had not confirmed that female *"fletcheri"* exist, but some literature records suggest it is likely (Table 1; Brewer 1977; Drees 1977). However, from the photo and discussion, the individual depicted in Brewer (1977) from Virginia may be a semi-melanic gynandromorph (not a pure female). The semi-melanic female reported by Miller (1990; Table 1) may also represent a different "dark cells" type (Scriber & Evans 1988a and see discussion below; Fig. 13a). The female melanic reported by Drees (1978) was not figured. Therefore, we report here, officially, that *"fletcheri"* coloration does exist in females.

Another superficially similar dorsal wing melanism, called "dark cells", reported only from females of *P. glaucus* occurs as black blotches throughout the dorsal surface of forewings, especially distally (Figs. 13). This melanic aberration is heritable, appearing in 29 of 38 daughters of two sibling pairs from a "dark cell" type mother (Scriber & Evans 1988b).

Melanic wing patterns (bilaterally symmetrical) in female tiger swallowtails from the Great Lakes hybrid zone of *P. canadensis* and *P. glaucus* (Scriber 1996a) have also been described (Scriber 1990). These distinctive patterns have the black band virtually completely filling the anal cell of the hindwing, but otherwise appear to have near-normal, tiger-striped patterns with "vein smearing" of dark scales. Some additional suffusion of dark scales appears to widen the black tiger stripes. Both specimens described came from different mothers with normal wing coloration

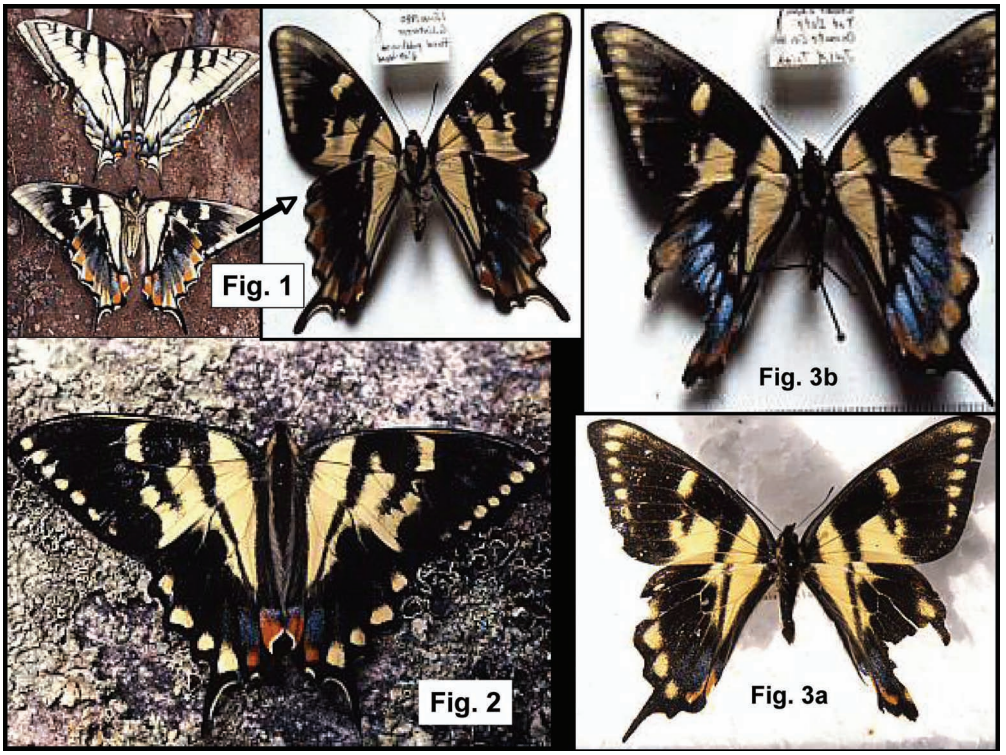


FIG. 1-3. **(1)** Ventral view of male "*fletcheri*" phenotype *P. canadensis* from Sawyer Co., WI near Pigeon Lake, shown with a normal male (Greg Lintereur captured 2 June 1980). **(2)** Dorsal view of "*fletcheri*" specimen (of Fig. 1). **(3a,b)** Dorsal (a) and ventral (b) view of male "*fletcheri*" phenotype *P. canadensis* (Joel Trick captured 6 June 1980 in Oconto, Co., WI).

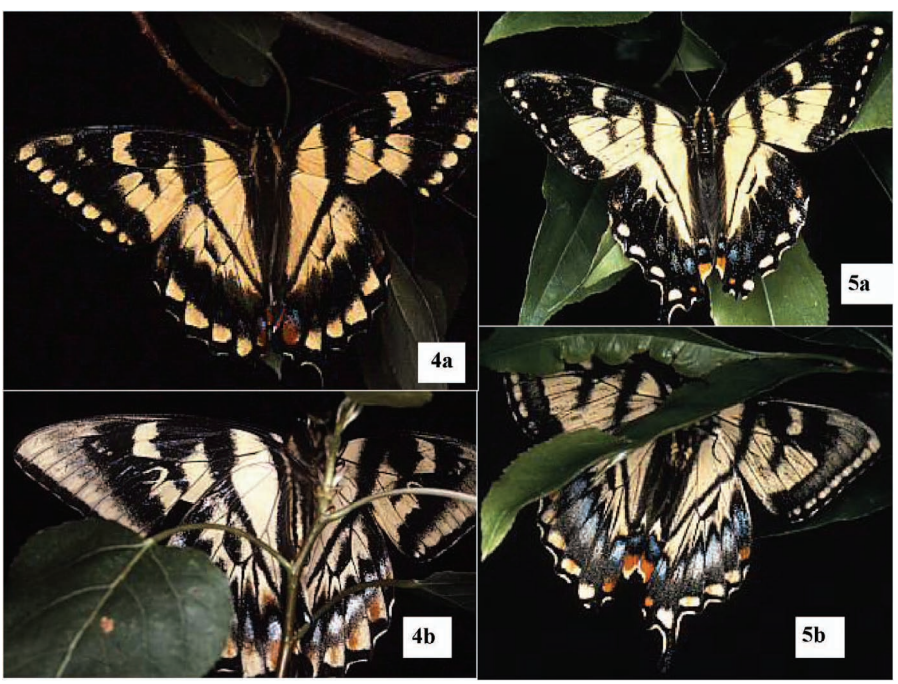


FIG. 4-5. **(4a,b)** Dorsal/ventral view of male "fletcheri" from Presque Isle Co., MI (27 May 1991, Jim Keller). **(5a,b)**. Dorsal/ventral view of male "*fletcheri*" from Cheboygan Co., MI (June 1992, J. M. Scriber).

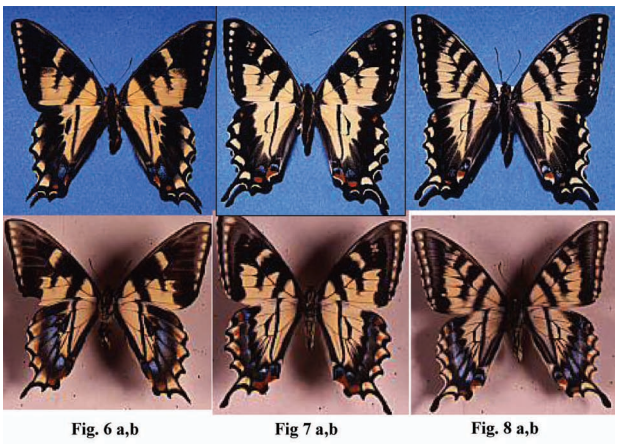


FIG. 6–8. Dorsal and ventral views of "*fletcheri*" types collected by H. Romack, all in southwestern Vermont (Bennington Co.). **(6)** 26 May 1982 male *P. canadensis*. (**7**) 12 June 1983 male *canadensis*. (**8**) 6 May 1995 male canadensis.

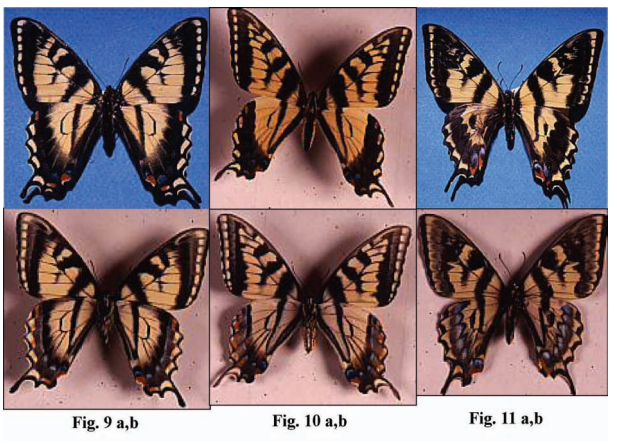


FIG. 9–10. Dorsal and ventral views of "fletcheri" types collected by H. Romack, all in southwestern Vermont (Bennington Co.). (**9**) 6 June 1995 male canadensis. **(10)** A male *P. canadensis "fletcheri"* from Washington Co. (26 June 1999, Cambridge) NY. (**11**) A male *P. rutulus "fletcheri"* from Lincoln Co., Wyoming 28 June 1983.

patterns (Fig. 14; Scriber 1990). Here we figure two recent specimens from northern Michigan that appear to have similar patterns, again only seen in the females, not in their male siblings.

Another melanic aberration found, to our knowledge, only in males has the inner third of the wings (dorsal and ventral, forewings and hindwings) melanic, with a light to heavy (solid) "dusted" appearance (Fig. 15; Scriber & Evans 1987). Except that the aberration occurred in males, it might be considered as a variant on the continuum of "intermediate" between the female polymorphism of normal yellow tiger striped or dark form. Such completely dusted-looking intermediates (Figs. 16 & 17) are common in females (usually only in offspring from dark form mothers; Edwards 1884; Scriber *et al*. 1996) and may be induced by rearing at higher temperatures. Similar melanism on the proximal 1/3 of wings of females has also been described (Clark 1932; Clark & Clark 1951) and may in fact represent incomplete expression of the Y-linked melanic female form (due to only partial suppression by an X-factor; Scriber *et al*. 1996) or due to environmental factors (e.g. high temperatures; Ritland 1986). It is interesting that the males carrying this inner wing melanism trait were also suspected to be carriers of the Y-linked melanism trait previously believed found only in females (Scriber & Evans 1987).

Variations of melanism (dark cells, "sooty", intermediates, and semi-melanics), as shown in Figs 13–17, may be the result of multiple enzyme activities which regulate underlying synthetic pathways for melanization via a single Y(=W)-linked (female) genetic factor (Clark & Sheppard 1962; Scriber *et al*. 1996; Koch *et al*. 2000; Ffrench-Constant & Koch 2003). Other hypotheses, such as broadening of the dark pattern elements, have been proposed as a model of melanism in *P. glaucus* (Nijout 1991). However, these recent molecular studies of the biochemistry of the enzymes dopa decarboxylase show that it affects both of the two major scale color pigments, papiliochrome (yellow) and melanin (black) and that the melanization occurs later in the formerly yellow area. The single major sex-linked gene (the Y-linked black or b+ gene) and a modifying gene (the X-linked suppressor, s+; Scriber *et al*. 1996), that interact in the hybrid zone with suppression of the dark potential, are compatible with

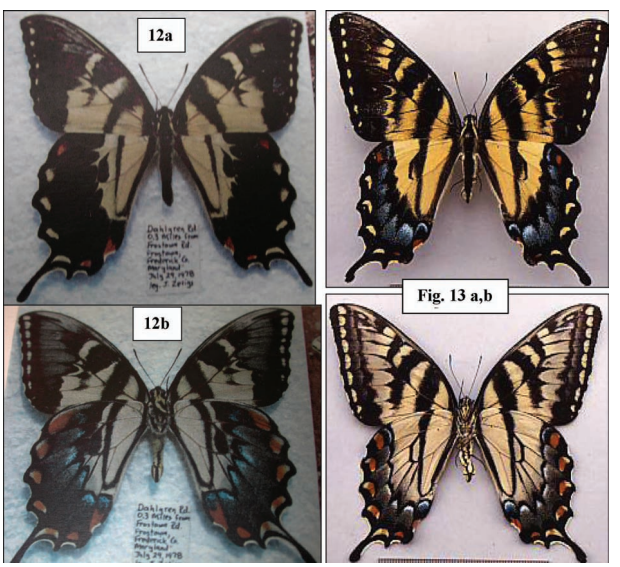
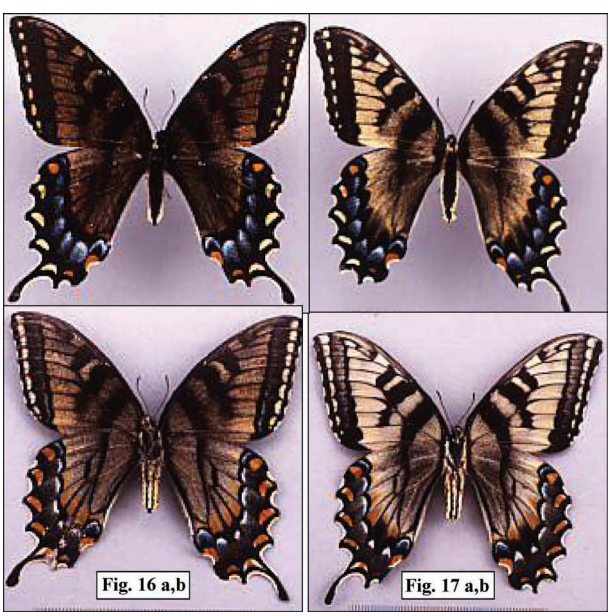


FIG. 12–13. **(12)** Dorsal and ventral views of "*fletcheri*" type male *Papilio glaucus* from Frederick Co. Maryland (captured 29 July 1978 by J. Zeligs, pers. comm. to JMS). **(13)** Dorsal/ventral views of the "dark cells" female expressed trait (Scriber & Evans 1988a).

FIG. 14. **(14)** Dorsal **(a)**/ventral **(b)** views of 2 "vein-smeared" females emerged in August 1997 reared from 2 mothers caught in Chippewa Co., MI. These phenotypes have been reared from four different females of Chippewa Co. (family #12229, 12230, 12235, 12236) and from wild female from Cheboygan Co. **(15)** Dorsal/ventral view of male melanic with dusted inner wings only (Scriber & Evans 1987).



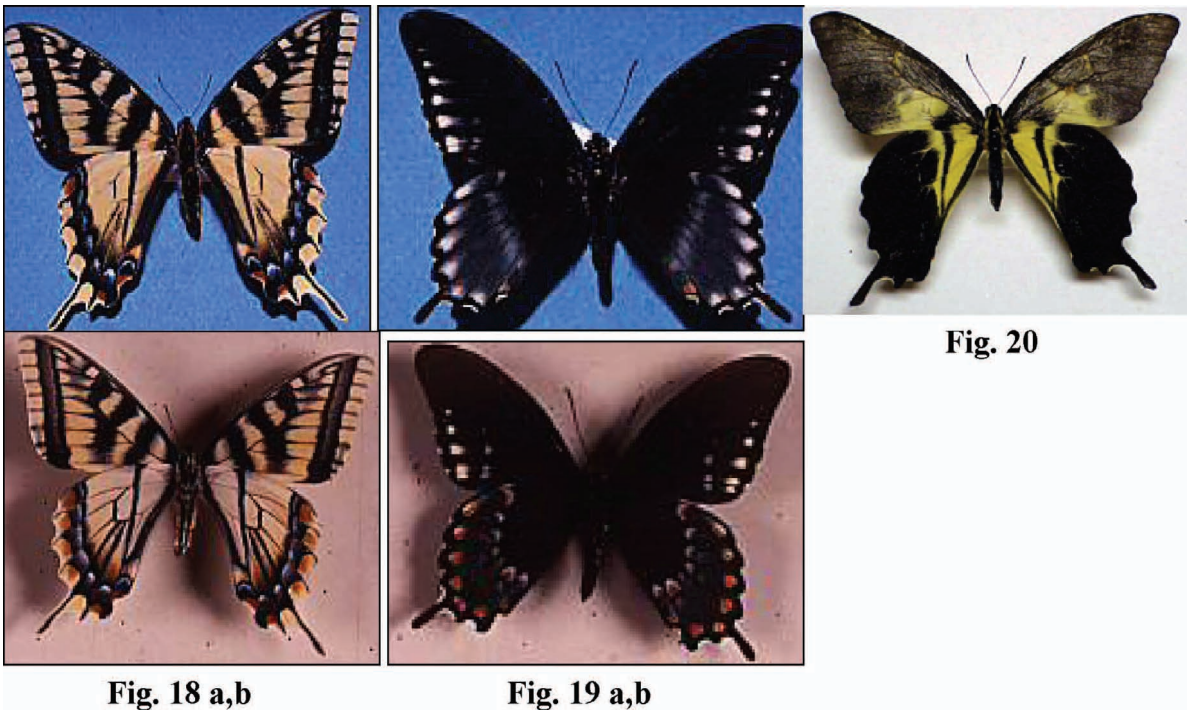
FIGS 16 & 17. Dorsal/ventral views of two sibling females showing "intermediate" dark morph coloration family #1396 of a Texas dark female x *P. canadensis* male from Marquette Co., Wisconsin, in the hybrid zone (Scriber et al. 1996).

the biochemical results described by Koch *et al*. (1998). However, except for the tendency to produce intermediate lightly dusted dark females at warmer temperatures (for females with the b+ gene; Ritland 1986), the reasons for aberrant melanic patterns remain basically unknown, although they appear genetically based since they are passed to some offspring (sometimes including males; Scriber & Evans 1987, 1988a). For example, odd-segregating dark daughters (2/3 of the individuals) in two different families (one *P. canadensis* female, and the other a yellow *P. glaucus* female) that were sired by a single "sooty" male (as Fig. 15) cannot be explained by any genetic patterns known to date (Scriber *et al*. 1996). Normally only the heterogametic lepidopteran females [XY (=ZW)] would have the Y-linked b+ gene for black. However, the remote possibility exists that a piece of the Y-chromosome (with the b+ black gene) broke off and translocated to another autosome without losing its expression potential, explaining the odd results of Scriber & Evans (1987). A similar case of chromosomal translocation was described for moths by Marec *et al*. (2001).

In contrast, the "*fletcheri*", believed to be a stable low-level polymorphism of *P. canadensis*, has now been

TABLE 1. Literature records of the *Papilio* semi-melanic aberration putatively of the type called "*fletcheri*".

Collecting Location	Date/Year	Collector	Reference
Collins Inlet on Georgian Bay, 18 miles east of Killarney,ONT	(July 1888) (male,*P. canadensis*)	Robert Mackenzie	Fletcher 1889
Orillia, Ontario	(male, *P.c.*)	C.E. Grant	Grant 1896
Elizabeth, NJ	July 1899 (male, ?)	A. Ronke	Kemp 1900
Forest County, WI	16 June 1958 (male, *P.c.*)	Louis Allen	Ebner 1960
Gorge Creek/Hwy #11, north of Nipigon, Ontario	27 June 1961 (male, *P.c.*)	E.M.S. (?)	Sicher 1962
Brown's Mill, Fairfax Couty, VA	August 1976 (female P. *glaucus*, gynandromorph?)	Richard H. Smith	Brewer 1977
Penland, NC	August 1975 (male, *P. glaucus*)	R. Peter Rosier	Rosier 1977
Source ?	18 ?? (*P. glaucus*)	Herman F. Strecker	Walsten 1977
Brighton, MI	May 1977 (sex?, *P.g./P.c.*)	Marc W. Grocoff	Grocoff 1977
Salem, VA	August 1975 (sex?/*P. glaucus*)	Fred Eichleman	Eichleman 1977
Clothier, WV	24 August 1972 (female, *P. glaucus*)	Tom Allen	Drees 1978
Markham, Ontario, Canada	June 1978 (sex?/*P.c.*)	John Johnstone	Johnstone 1978
Great Smoky Mountains Little Pigeon River, Sevier Co. TN	2 August 1979 (*P.g./P.c.*?)	Mecky Furr	Brewer 1980
Source?	Reports seeing *fletcheri* type in *P. eurymedon* but not *rutulus*	Art Shapiro	Shapiro 1981
Frederick County, MD	24 July 1978 (male, *P.g.*)	Joseph D. Zeligs	(pers. corresp.)(Fig. 12)
Pigeon Lake, WI, (Sawyer County, WI)	2 June 1980 (male *P.c.*)	Greg Lintereur	Scriber and Lintereur 1983, (Fig. 1)
Green Bay, Oconto County, WI	6 June 1980 (male *P.c.*)	Joel Trick	Scriber and Lintereur 1983 (Fig. 4)
Bethel Park, PA	Summer 1990 (female *P. glaucus*)	Monica Miller	Miller 1990
Presque Isle County, MI	27 May 1991 (male *P.c.*)	Jim Keller	Scriber *et al*. 1995, (Fig. 5)
Cheboygan County, MI	June 1992 (male *P.c.*)	Mark Scriber	Scriber *et al*. 1995
Southwest VT	26 May 1982 (male *P.c.*)	Howard Romack	Fig. 6
Southwest VT	12 June 1983 (male *P.c.*)	Howard Romack	Fig. 7
Southwest VT	6 May 1995 (male *P.c.*)	Howard Romack	Fig. 8
Southwest VT	6 June 1995 (male *P.c.*)	Howard Romack	Fig. 9
Cambridge, NY, (Washington County)	26 June 1999 (male *P.c.*)	Howard Romack	Fig. 10
Lincoln County, WY	28 June 1973 (male *P. rutulus*)	P. Grey	Fig. 11
Gunnison Co. Colorado	2004 2 male *P. rutulus*	Matthew Garhart	(Clark 2006)
Bennington Co. Vermont	2008 female	Howard Romack	Fig. 13
Eastern Washington	2008 female	Robert Goodmiller	http://www.insectnet.com/dcforum/User_files/485349dc48c9c1e6.jpg



FIGS. 18-20. Dorsal/ventral view of aberrant *P. canadensis* female from Ontario, Canada (5 June 1995) with submarginal wing cell coloration elongated. **(19).** *P. troilus* from Glenns Falls (8 July 1987; Warren Co., NY); submarginal wing cell coloration elongated (as with Fig. 18). **(20).** Potential "*fletcheri*" type (courtesy of David and Marc Perlman).

shown to also occur in *P. glaucus* and *P. rutulus*. In addition to our observation, two male specimens of "*fletcheri*"-like individuals were found in *P. rutulus* from Gunnison County, Colorado by Mathew Garhart in 2004 (Clark 2006). This suggests the possibility of a common evolutionary origin of this polymorphic development color pathway in wings many millions of years ago in a common ancestor of the tiger swallowtail butterflies. Alternatively, it may reflect recent or historical hybridization of *P. canadensis* with *P. glaucus* and *P. rutulus* (Guppy & Shepard, 2001; but see Sperling 1993).

We are not sure if interspecific hybridization between *P. glaucus* and *P. canadensis* played any role in the enhanced rate of expression of the "*fletcheri*" type wing patterns at the Battenkill River Valley between Vermont and New York (or elsewhere). However, the "*fletcheri*" specimen from Frederick Co., MD (Fig. 12; Zelig, pers comm.) was captured at the end of July (a late flight) and may represent a specimen of *P. appalachiensis* (which may be a hybrid species and is known to fly in that county of Maryland; Pavulaan & Wright 2002). This raises the possibility that *glaucus-canadensis* hybridization may have been involved (Scriber *et al.* 2008) as may be the case in the late June specimen (Fig. 10) from New York, near Vermont. Similarly, the area of Washington that produced a female "*fletcheri*" in 2008 is also near areas with suspected hybrids between *P. canadensis* and *P. rutulus* (Guppy & Shepard 2001; but see Sperling 1993).

While we are not really certain that hybrid introgression has anything directly to do with causing the "*fletcheri*" phenotype, it is still worthwhile pointing out the fact that all examples of this phenotype are in areas where hybridization is known to occur. Natural environmental conditions may play some major role in causing this phenotype, especially since none have been

FIG. 21. Female fletcheri **a)** dorsal **b)** ventral; Vermont, Bennington County, Kelly Stand Road. 27 May 2008 (HR).

generated under controlled lab conditions for many thousands of individuals.

Other non-*fletcheri* type aberrants. We also have observed some additional aberrant color patterns in specimens from Canada, New York, and Vermont. The submarginal cell color elongation in *P. canadensis* (Fig. 18) and *P. troilus* (Fig. 19) look similar to the *P. troilus* aberration called "*radiatus*" by Clark (1932) (see also *P. troilus* specimen collected by Raymond Thomas 12 April 2006 from Fremont, Missouri; Clark 2006). Another odd individual image was sent by David Perlman (Fig. 20), which may or may not be a "*fletcheri*".

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