Bilateral Differentiation of Color and Morphology in the Larval and Pupal Stages of *Papilio Glaucus* (Lepidoptera: Papilionidae)

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BILATERAL DIFFERENTIATION OF COLOR AND MORPHOLOGY IN THE LARVAL AND PUPAL STAGES OF *PAPILIO GLAUCUS* (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT

A sharply delineated, bilateral differentiation of color patterns and morphology were observed in a final (5th) instar larva of a subspecies backcross of a female *Papilio glaucus glaucus* with a hybrid male (*P. g. glaucus* x *P. g. canadensis*). Color and morphological differences were detectable in the pupa as well. In addition, a bilateral size difference was evident in both the pupa and the resulting adult butterfly. Such observations within a single living individual attest to the bilateral independence (also evident in perfect gynandromorphs) and general flexibility of the developmental control in this species of Lepidoptera.

A number of abnormalities have been observed during our laboratory interspecific and intersubspecific hybridization and mass rearing of tiger swallowtail butterflies, *Papilio glaucus* L. We have previously described the occurrence of 39 intersexes (and/or color mosaics) and 3 perfect bilateral gynandromorphs in adult *Papilio glaucus* (Scriber and Evans 1988). In none of these cases did we observe abnormal larvae, nor do we know of the occurrence of bilateral color and/or morphological differentiation in any other larvae or pupae of this species. Such differential bilateral development has been described for larvae of the silkworm, *Bombyx mori* (Tazima 1964). However, larval mosaics may generally be even less frequently noticed and reported than the rare mosaic adults. Here we describe a bilaterally differentiated larva which resulted in a bilaterally distinct pupa and adult *Papilio glaucus*.

MATERIALS AND METHODS

The bilaterally differentiated larva described below is from our general rearing and hand-pairing procedures. While these methods have been described in detail (Scriber et al. 1989), a brief summary is provided here.

Oviposition by adult females is induced by placing each field-captured or lab-paired individual into its own clear plastic box (approx. 10 cm deep x 15 cm x 30 cm) with a moist paper towel and selected foodplant leaves. Heat and light are produced by an incandescent bulb placed at a distance of approximately 0.3 – 0.5 m from the plastic boxes. Larvae were reared to pupation on foodplant leaves supported in water-filled plastic vials under controlled environmental conditions (18:6 photo-/scotophase at 25°C). Pupae were placed into cylindrical screen cages (15 cm diam-

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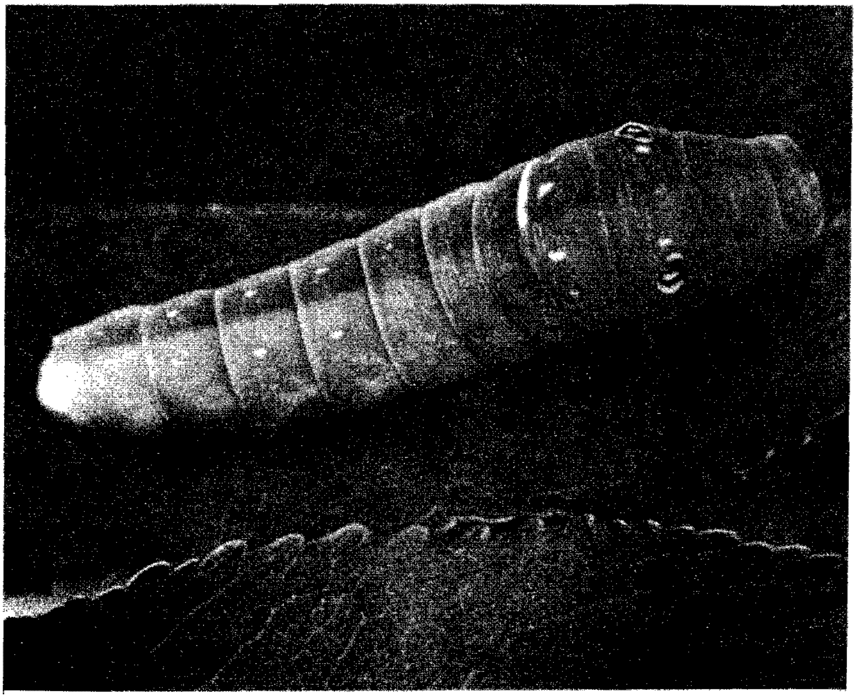

Figure 1. A bilateral asymmetrical larva (color and morphology) of a subspecies backcross of the eastern tiger swallowtail, *P. g. glaucus*, and the Canadian tiger swallowtail *P. g. canadensis*.

eter x 12 cm height) under larval rearing conditions to permit development and eclosion as adults.

The dark *Papilio glaucus glaucus* mother of pairing #4188 that produced this brood with the bilateral individual was from a Champaign County, Illinois dark mother (provided by May Berenbaum). The 4188 brood father was a hybrid male produced by a pairing of a reared dark female *P. g. glaucus* of a brood from Adams County, Ohio (original collection by Mark Evans and Jeff Thorne) and a male *P. g. canadensis* from Taylor County, Wisconsin.

RESULTS

The left half of this final instar *Papilio glaucus* larva was dark green (normal) and the right half was a bleached lime or yellowish-green color (Fig. 1). In addition, the superanal tubercles were prominent and yellow on the right half (as in many *P. g. canadensis*), compared to the reduced size on the left side (normal *glaucus*-like). The yellow band on the dorsal thorax was prominent on the left half, but not on the right. Otherwise no major differences were noted.

The resulting pupa was bilaterally asymmetrical as well (Fig. 2). The resulting adult (Fig. 3) eclosed with the right side smaller than the left and with minor

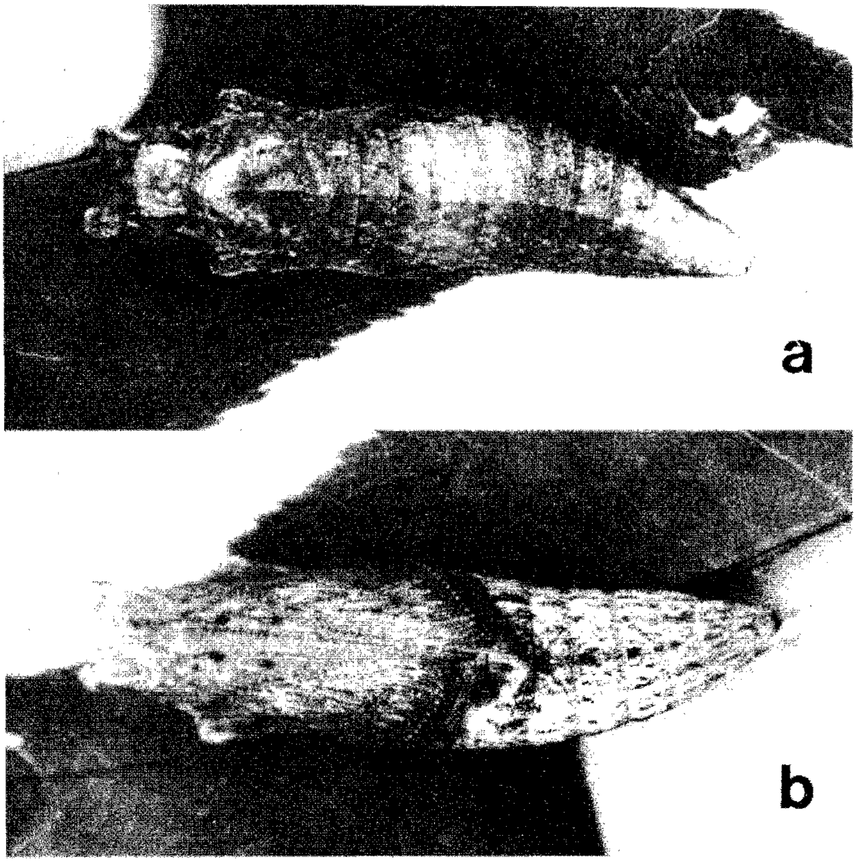

Figure 2. The dorsal (a) and ventral (b) views of the pupal stage of the same individual (Fig. 1) illustrating the bilateral asymmetry in color and morphology.

morphological differences (in the hind wings especially). The adult appears to be a fairly typical *P. g. glaucus* male (Fig. 3) without obvious evidence of sexual mosaicism or gynandromorphism.

In addition to the bilateral individual, brood 4188 produced one dark morph female and 3 male siblings. These adults all appeared normal in wing pattern. A total of 53 eggs were produced (43 of these were sterile) by the mother of pairing 4188. Seven larvae were reared on wild black cherry to pupation (2 pupae died). Two eggs were fertile but failed to eclose, and one neonate larva died before pupation.

DISCUSSION

This backcross (#4188) that produced this bilaterally distinct individual was also part of a study of the linkage relationships of diapause regulation, color suppres-

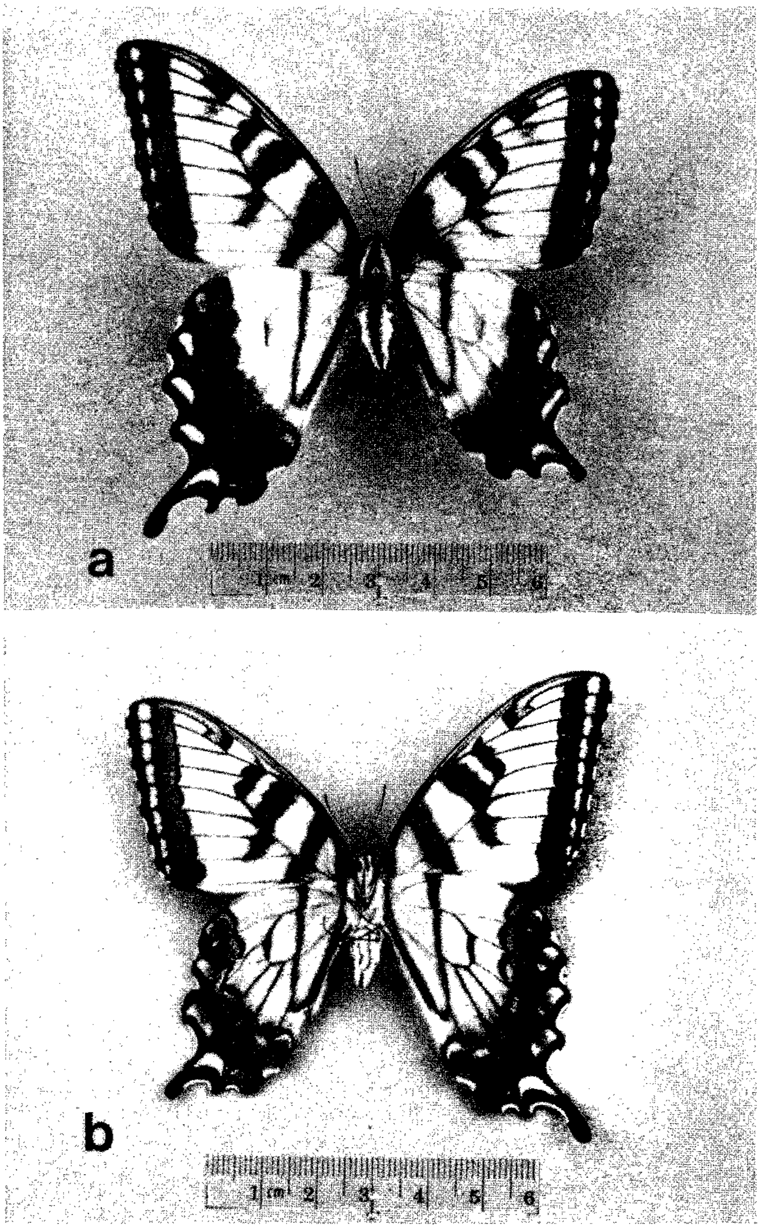

Figure 3. The dorsal (a) and ventral (b) views of the adult male reared from the same individual as in Figs. 1 and 2.

sion, and allozymes on the sex chromosome of *Papilio glaucus* (Hagen and Scriber 1989). Morphological and color differences exist between the two subspecies (*P. g. glaucus* and *P. g. canadensis*; see Luebke et al.1988). However, it is not clear that this individual is necessarily reflecting subspecific traits in its two halves. This individual is, however, one of a brood that appears to have had recombination of sex-linked (X-chromosome) alleles (Hagen and Scriber 1989). Developmental incompatibilities in *P. g. glaucus* are sometimes introduced from *P. g. canadensis* genes (see Rockey et al. 1987, Scriber and Evans 1986, 1988, Hagen and Scriber 1989) and may have been involved with this bilateral larva.

Developmental processes producing mosaic individuals may result from monozygotic fertilization or dizygotic fertilization. Unlike many other animals, insects have embryos of dizygotic origin which can have 2 cell populations fairly easily brought together into a developmental unity (Tazima 1964), resulting in mosaicism (rather than twinning). Several types of mosaics have been described, and it has been noted that the vast majority are bilateral mosaics with contrasting characters manifested on both sides of the body divided by the median long axis (Tazima 1964). While such bilaterally differentiated larvae, pupae, and adults may not necessarily be extremely rare, we have, in our *Papilio* rearing efforts over the last decade, handled more than 100,000 larvae and never noticed any others like this one.

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