Zebra Swallowtail *Protographium marcellus* (Cramer) (Insecta: Lepidoptera: Papilionidae)[1]

Donald W. Hall and Jerry F. Butler[2]

Introduction

The zebra swallowtail, *Protographium marcellus* (Cramer), is our only native US kite swallowtail (tribe Leptocircini [=Graphiini]) (Opler and Krizek 1984). It is one of our most beautiful swallowtails (Figures 1 and 2).

Figure 1. Zebra swallowtail, *Protographium marcellus* (Cramer), with wings spread.
Credits: Jerry F. Butler, UF/IFAS

Figure 2. Zebra swallowtail, *Protographium marcellus* (Cramer), with wings closed.
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Synonymy

The zebra swallowtail was originally grouped with the other butterflies in the genus Papilio and named *Papilio ajax* by Linnaeus (1758). It has also been placed in the following genera:

- *Iphiclides* Hübner
- *Graphium* Scopoli
- *Protesilaus* Swainson
- *Cosmodesmus* Haase

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2. Donald W. Hall, professor emeritus; and Jerry F. Butler, professor emeritus, Entomology and Nematology Department; UF/IFAS Extension, Gainesville, FL 32611.

- *Eurytides* Hübner
- *Neographium* Möhn
- *Protographium* Munroe

For many years the zebra swallowtail was known by the genus name *Eurytides,* until Möhn (2002) moved it from *Eurytides* to the genus *Neographium* and most recently, Lamas (2004) moved it to the genus *Protographium*. The name *Protographium* is now being used in recent taxonomic journal papers (e.g., Allio et al. 2020; Condamine et al. 2018), but *Eurytides* is still used by some field guides and butterfly books (e.g., Evans 2008; Glassberg 2017).

Distribution

The zebra swallowtail is widely distributed from southern New England west to eastern Kansas and south to Texas and Florida (Figure 3).

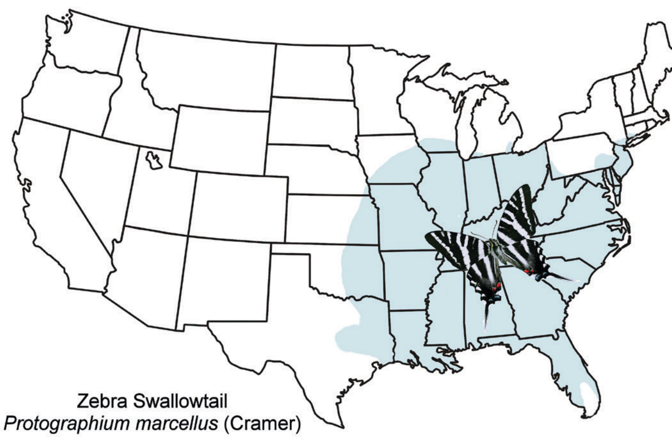

Figure 3. General distribution map for the zebra swallowtail, *Protographium marcellus* (Cramer).

Description

Adults

The wingspread of adults is 2.5 to 4 inches (64 to 104 mm) (Opler and Malikul 1992). The upper surface of the wings is white with black stripes. The hindwings have very long tails. The lower surface of the wings is similar, except there is a red stripe running through the middle of the hind wing. Zebra swallowtails exhibit seasonal polymorphism. Early spring specimens are lighter in color, smaller, and have shorter tails (Scott 1986). There are also transitional forms. Mather (1970) detailed descriptions of the color forms. For lists of the names that have been used for the seasonal and transitional forms, see Tyler et al. (1994) or Heppner (2007). Unlike most of our other native swallowtails, zebra swallowtails are not involved in a mimicry complex. Males have a patch of elongated sex-pheromone-producing scent scales (androconia) in the anal folds (Figure 4) of the hind wings (Scott 1986, Simonsen et al. 2012).

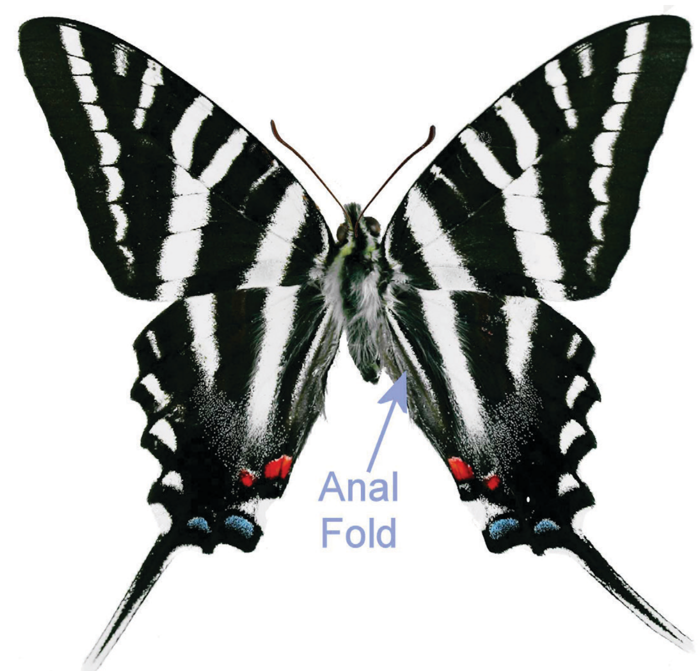

Figure 4. Male zebra swallowtail, *Protographium marcellus* (Cramer) showing anal fold.
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Eggs

Eggs are pale green (Figure 5).

Figure 5. Egg of zebra swallowtail, *Protographium marcellus* (Cramer).
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Larvae

For detailed descriptions of the larval instars, see Edwards (1862–1897) and Scudder (1889). Early instar larvae (first and second instars) are dull gray (Figure 6).

Middle instar larvae (Figure 7) are dark colored with transverse black, yellow, and white bands.

Fifth (last) instar larvae (Figure 8) are green with broad blue, black, and yellow transverse bands between the thorax and abdomen usually, yellow bands between abdominal segments, and numerous fine transverse black lines on thorax and abdomen. However, larvae exhibit color polymorphism, and some fifth instars are dark colored. The osmeterium is yellow (Figure 9).

Figure 6. Early instar larva of *Protographium marcellus* (Cramer).
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Figure 7. Middle instar larva of *Protographium marcellus* (Cramer).
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Figure 8. Last instar larva of zebra swallowtail, *Protographium marcellus* (Cramer).
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Figure 9. Last instar larva of zebra swallowtail, *Protographium marcellus* (Cramer), with osmeterium extruded.
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Pupae

Pupae are dimorphic (green or brown) with light lines simulating a leaf-like texture and are supported with a silken girdle (Figures 10 and 11).

Figure 10. Green pupa of the zebra swallowtail, *Protographium marcellus* (Cramer).
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Figure 11. Brown pupa of the zebra swallowtail, *Protographium marcellus* (Cramer).
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Life Cycle

There are two flights in the North and many flights in Florida from March to December. Males patrol for females in the vicinity of host plants, and females frequently may be observed ovipositing on host foliage. Adults seek nectar at a variety of flowers, but the adult proboscis is shorter than those of other swallowtails. Therefore, zebra swallowtails cannot reach the nectar of long tubular flowers (Opler and Krizek 1984). Male swallowtails also obtain moisture and minerals (primarily sodium) from mud, a behavior known as "puddling" (Figure 12) (Cech and Tudor 2005; Minno and Minno 1999; Otis et al. 2006). While puddling is primarily a behavior of males, females have also been observed puddling (Berger and Lederhouse 1985).

Figure 12. Male zebra swallowtail, *Protographium marcellus* (Cramer), feeding at moist sand for moisture and minerals.
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Females select young plants or plants with young leaves for oviposition (Damman and Feeny 1988). They respond strongly to host volatiles (as yet unidentified) that enhance landing rates and are then stimulated to oviposit by the contact oviposition stimulant 3-caffeoyl-muco-quinic acid (Haribal and Feeny 1998). Eggs are laid singly near the tips of young leaves (Wagner 2005) on which larvae prefer to feed. Larvae will also feed on flowers when available (Damman and Feeny 1988) (Figure 13). Larvae are highly cannibalistic (Klots 1951; Minno and Minno 1999; Wagner 2005).

The requirement for new leaves may limit reproduction of *Protographium marcellus* in summer and fall: however, production of new leaves during this period is often stimulated by defoliation of the host plant by larvae of the pyralid moth, *Omphalocera munroei* Martin (Figures 14 and 15) (Damman 1989). Therefore, late season abundance of *Protographium marcellus* may be dependent on the abundance of *Omphalocera munroei*. *Omphalocera munroei* larvae live in nests constructed by silking leaves together (Figure 16). The nests sometimes extend down stems as tubular structures. The outer layers of the silk nests are covered with frass (fecal pellets) (Figure 15) that may repel potential predators.

Figure 13. Young larva of zebra swallowtail, *Protographium marcellus* (Cramer), in slimleaf pawpaw, *Asimina angustifolia* Raf., flower.
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Figure 14. *Omphalocera munroei* Martin (Pyralidae) full-grown larva removed from nest.
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Figure 15. Larval nest of *Omphalocera munroei* Martin (Pyralidae) covered with frass (fecal pellets). Note growth of new foliage stimulated by *Omphalocera munroei* defoliation.
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Figure 16. Common pawpaw, *Asimina triloba* (L.) Dunal (Annonaceae), a larval host for the zebra swallowtail, *Protographium marcellus* (Cramer).
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Full-grown larvae evacuate the gut and begin to wander in search of a pupation site around midday (West and Hazel 1985). Larvae usually pupate on the undersides of either living or dead leaves of the host plant. Pupae formed on living leaves are usually green, while those formed on dead (brown) leaves are usually brown (West and Hazel 1985; West and Hazel 1996). The brown pupa in Figure 11 resulted from a larva that was placed in a container containing only dead leaves and brown twigs immediately after it voided the gut and began to wander. Short photoperiod produces diapausing pupae that hibernate (Hazel and West 1983). However, some pupae of each flight overwinter (Scott 1986). Diapausing pupae are usually brown (Scott 1986) and are camouflaged on the dead leaves during the winter.

Natural Enemies and Defenses

Zebra swallowtail eggs are occasionally parasitized by *Trichogramma* (Trichogrammatidae) wasps (Sime 2005). Larvae are parasitized by tachinid flies (Sime 2005) and the ichneumonid wasps *Itopletis conquisitor* Say and *Trogus pennator* (Fabricius) (Krombein et al. 1979).

The larval osmeterium (Figure 9) is coated with the strongly smelling chemicals isobutyric and 2-methyl butyric acids (Eisner et al. 1970). When disturbed, larvae extrude the osmeterium and smear the offender with the chemicals.

At the same time the osmeterium is extruded, larvae regurgitate gut fluids. These fluids may become mixed with the osmeterial fluids, and Eisner et al. (2005) suggested that the effectiveness of the mixture may be enhanced by toxic compounds from the host plant contained in the regurgitated fluids. The larval host plants contain toxic acetogenins that would certainly be contained in the regurgitated fluids and are also sequestered by larvae and persist in the tissues and wings of adults (Martin et al. 1999). Some of these acetogenins have insecticidal activity against some insects (McGlaughlin 2008). It is unknown whether they offer any protection against parasitoids.

Osmeterial fluids have been shown to be an effective defense against small ants and spiders but not against most other predators or against the ichneumonid parasitoid of papilionids, *Trogus pennator* (Fabricius), which does not trigger extrusion of the osmeterium with its attacks (Damman 1986).

Larvae may thrash (Cech and Tudor 2005) or drop off the host plant when disturbed by a predator (Damman 1986). Older larvae sometimes hide in leaf litter at the base of the plant when not feeding (Damman 1986; Minno et al. 2005). The resemblance of the pupae to leaves provides protection from predators (Eisner et al. 2005).

Hosts

The larval host plants are *Asimina* species (pawpaws) (Annonaceae). Throughout most of the range of the zebra swallowtail common pawpaw, *Asimina triloba* (L.) Dunal (Figure 16), is the only host. In the Deep South, other Asimina species are utilized (Minno et al. 2005), including smallflower pawpaw, *Asimina parviflora* (Michx.) Dunal (Figure 17); slimleaf pawpaw, *Asimina angustifolia* Raf. (Figure 18); woolly pawpaw, *Asimina incana* (W. Bartram) Exell (Figure 19); dwarf pawpaw, *Asimina pygmea* (W. Bartram) Dunal (Figure 20); four petal pawpaw, *Asimina tetramera* Small, netted pawpaw, *Asimina reticulata* Shuttlew. ex Chapm., pretty false pawpaw, *Asimina pulchella* (Small) Rehder and Dayton, and Rugel's false pawpaw, *Asimina rugelii* B.L. Rob. Plant names are from Wunderlin et al. (2019).

Figure 17. Smallflower pawpaw, *Asimina parviflora* (Michx.) Dunal (Annonaceae), a larval host for the zebra swallowtail, *Protographium marcellus* (Cramer).
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Figure 18. Slimleaf pawpaw, *Asimina angustifolia* Raf. (Annonaceae), a larval host for the zebra swallowtail, *Protographium marcellus* (Cramer).
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Figure 19. Woolly pawpaw, *Asimina incana* (W. Bartram) Exell (Annonaceae), a larval host for the zebra swallowtail, *Protographium marcellus* (Cramer).
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Figure 20. Dwarf pawpaw, *Asimina pygmea* (W.Bartram) Dunal (Annonaceae), a larval host for the zebra swallowtail, *Protographium marcellus* (Cramer).
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