Pipevine Swallowtail, Blue Swallowtail *Battus philenor* (Linnaeus 1771) (Insecta: Lepidoptera: Papilionidae: Papilioninae: Troidini)[1]

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Introduction

The pipevine swallowtail, *Battus philenor* (L.), is one of our most beautiful swallowtails. It is also known as the blue swallowtail (e.g., Howe 1988, Iftner et al. 1992). Its life cycle was beautifully illustrated during the 18th century by John Abbot (Smith 1797) (Figure 1).

Figure 1. Life cycle of the pipevine swallowtail, *Battus philenor* (L.). Credits: John Abbot (From Smith 1797). (For aesthetic reasons, the color temperature of the image was adjusted to compensate for yellowing of the manuscript due to age)

Nomenclature

The pipevine swallowtail was originally described by Linnaeus (1771) and placed in the genus *Papilio* with the other swallowtails. It was later moved to the genus *Battus* (Scopoli 1777). The name "*Battus*" is from Battus I, founder of the ancient Greek colony Cyrenaica and its capital, Cyrene, in Africa. The specific epithet is from the Greek word "philenor" which means fond of husband or conjugal (Opler and Krizek 1984).

Larvae of the pipevine swallowtail and those of the other swallowtails belonging to the tribe Troidini feed on plants in the genus *Aristolochia* and are commonly referred to as the *Aristolochia* swallowtails.

For synonymy, see the excerpt from Pelham (2008) at the Butterflies of America web page on *Battus philenor* (Accessed December 23, 2016).

Distribution

The US distribution of the pipevine swallowtail extends from southern Connecticut south to central Florida and west to Arizona with an isolated population in northern California (Figure 2). The pipevine swallowtail is also found northward to southeastern Ontario, Canada and southward

to southern Mexico (Cech and Tudor 2005, Opler and Malikul 1998, Scott 1986).
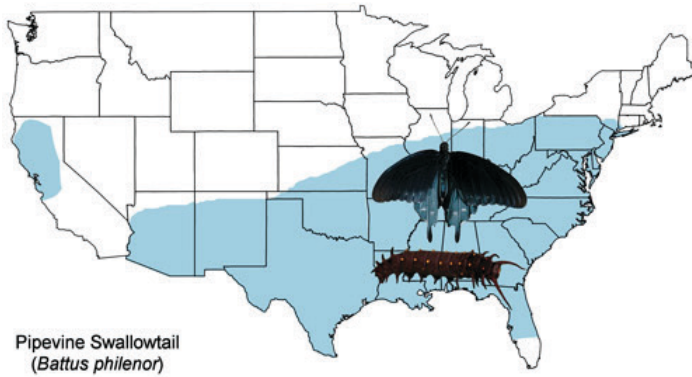

Figure 2. Pipevine swallowtail, *Battus philenor* (L.)
Credits: US distribution map

Published distribution maps (e.g., Brock and Kaufman 2003, Scott 1986, Moth Photographers Group, *Battus philenor* species page, Butterflies and Moths of North America) differ due to records of adult "strays" and to planting of larval host plants as ornamentals (Iftner et al. 1992, Layberry et al. 1998) outside their native ranges. For example, the only documented records for *Battus philenor* larvae in Ontario are from *Aristolochia macrophylla* vines planted as ornamentals (Layberry et al. 1998).

Description
Adults

The wingspread is 2 3/4–5 1/8 in. (72–132 mm) (Opler and Malikul 1992). The dorsal surfaces of the wings of males are mostly black with blue or blue-green iridescence on the hind wings (Figure 3). The dorsal aspect of the hindwings of females (Figure 4) has duller iridescence than that of males. There are light marginal and sub-marginal spots on both forewings and hindwings. The ventral hind wings of both sexes have blue iridescence and a row of seven bright orange sub-marginal spots (Figures 4 and 5). There is a row of white spots on the lateral aspect of the abdomen (Figure 5).

California specimens are smaller, with hairy bodies. Their larvae also have shorter thoracic filaments than those of eastern specimens. The California population also differs from eastern populations in some aspects of biology (Sims and Shapiro 1983b) and may represent a different subspecies, *Battus philenor hirsuta* (Sourakov and Daniels 2002). According to Field (1938, p. 200), individuals of the spring generation in Kansas resemble those from California populations.

Figure 3. Adult male pipevine swallowtail, *Battus philenor* (L.), dorsal view showing brilliant iridescence.
Credits: Donald W. Hall, UF/IFAS

Figure 4. Adult female pipevine swallowtail, *Battus philenor* (L.), dorsal (left) and ventral (right) views.
Credits: Donald W. Hall, UF/IFAS

Figure 5. Newly-emerged adult male pipevine swallowtail, *Battus philenor* (L.), with wings folded showing undersides of the wings and white spots on abdomen.
Credits: Donald W. Hall, UF/IFAS

Eggs

The eggs are reddish-orange (Figure 6) in contrast to those of the related Polydamas swallowtail, *Battus polydamas* (L.), which are yellow or yellowish-orange. The eggs of all *Aristolochia* (troidine) swallowtails are partially covered by a hard, nutritious secretion that is usually laid down in

vertical bands (Comstock and Grimshawe 1935, Tyler et al. 1994). There are numerous relatively large droplets on the bands. The secretion is produced by a large gland that lies above the female's ovipositor duct (Tyler et al. 1994).

Figure 6. Eggs of the pipevine swallowtail, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

Larvae

Full-grown larvae are approximately 50 mm (about 2 in.) in length (Minno et al. 2005, Stehr 1987, Wagner 2005).

First instar larvae have numerous short orange tubercles—each with a single seta (Figure 7). Second instars have longer tubules—each bearing multiple setae (Figure 8). The tubercles of third and fourth instars are proportionately longer, and the exoskeleton takes on a slightly glossy appearance (Figure 9).
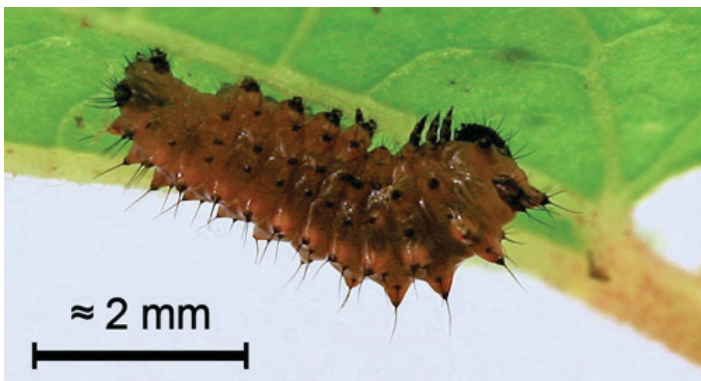

Figure 7. First instar larva of the pipevine swallowtail, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

Full-grown larvae are typically dark brown to black with sub-dorsal and lateral rows of bright orange tubercles (Figure 10), but some are red (Figure 11). In western Texas and southern Arizona, the red form predominates under conditions of higher temperature (above about 30°C) (Nice and Fordyce 2006, Nielsen and Papaj 2015, Papaj and Newsome 2005). The factor(s) responsible for red larvae in the eastern US has not been investigated. The red larva

in Figure 11 was photographed in Gainesville, Florida on July 29, 2016, during the heat of the summer.

Figure 8. Second instar larva of the pipevine swallowtail, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

Figure 9. Third instar larva of the pipevine swallowtail, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

Figure 10. Full-grown dark larva of the pipevine swallowtail, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

Figure 11. Full-grown red larva of the pipevine swallowtail, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

Lateral tubercles on the thorax and abdominal segments 2, 7, 8, and 9 of larvae are modified into elongated filaments. The filaments on the prothorax are particularly long (Scott 1986, Minno et al. 2005, Stehr 1987). Full-grown larvae are covered with fine hairs that give them a velvety appearance (Howe 1975).

The sex of larvae of all ages can be determined by the structure of sex-specific pits on the ventral surface of the 8th and 9th abdominal segments (Underwood 1994).

Pupae

Pupae may be either green or brown (Figure 12). Unlike pupae of other swallowtails, the sides of the bodies of *Battus* pupae are widened into lateral flanges. In the lateral views of pupae shown in Figure 12, the lateral flanges appear as bluish-purple ridges along the anterior half of the abdomen.

Figure 12. Green pupa and brown pupa of the pipevine swallowtail, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

Host Plants

Larval Host Plants

Pipevine swallowtail larvae feed on plants belonging to the genus *Aristolochia* in the family Aristolochiaceae (Cech and Tudor 2005, Minno et al. 2005, Opler and Krizek 1984, Scott 1986). Reports in the literature (e.g., Arnett 2000, Howe 1975, Robinson et al. undated, Schull 1987, Tyler 1975) of larvae feeding on wild ginger, *Asarum canadense* L. (Aristolochiaceae), knotweed, *Polygonum* (Polygonaceae), and morning glories, *Ipomoea* (Convolvulaceae), are probably erroneous (Heitzman and Heitzman 1987, Opler and Krizek 1984, Scott 1986) and likely due to misidentification of the host plant by Blatchley (1896) in the case of *Asarum* (see Weintraub 1995) and to wandering larvae for the other plant species.

Aristolochia species are commonly known as pipevines or Dutchman's pipes because the flowers of some species are shaped like tobacco pipes (Figure 13). They are also known as birthworts ("wort" is Old English for herbaceous plant) because of their historical use in child birth. The name *Aristolochia* is derived from the Greek roots *aristos* (best) and *lochia* (delivery or child birth) (Crosswhite and Crosswhite 1985, Flora of North America undated). All Aristolochiaceae are believed to contain pharmacologically active aristolochic acids (Chen and Zhu 1987).

Figure 13. Unopened flower of woolly pipevine, *Aristolochia tomentosa* Sims, and tobacco pipe graphic showing the similarity of shapes.
Credits: Flower bud, Donald W. Hall, UF/IFAS; Tobacco pipe graphic, PNG Clip Art (graphic modified and pasted into photograph by Donald W. Hall, UF/IFAS)

Although they are now officially banned in many countries, *Aristolochia*-derived herbal products or parts of the plants themselves are still used in many areas of the world for various conditions including snake bite, gastrointestinal problems, respiratory problems, wounds, infectious diseases, and fever (Austin 2004, Chen & Zhu 1987, Duke 2001, Schaneberg et al. 2002).

Virginia snakeroot, *Aristolochia serpentaria* L., has been used for many medical applications (Austin 2004, Duke 2001, Heinrich et al. 2009, Moerman 1998), and preparations made from it are still for sale online. An extract of the southwestern pipevine, *Aristolochia watsonii* Wooton and Standl., was the main ingredient in the snakeroot oil sold by traveling "snakeroot doctors" at medicine shows in the Old West during the 19th century (Crosswhite and Crosswhite 1985). Aristolochic acids in the products have been implicated as causative agents of renal toxicity and also may be carcinogenic (Heinrich et al. 2009, Schaneberg et al. 2002).

Aristolochia serpentaria L., ranges from central Florida northward in much of the eastern United States. In the Southeast, it has broad-leaved and narrow-leaved forms

(Figures 14, 15, and 16). The broad-leaved form is more common in richer mesic forests while the narrow-leaved form is more common in drier, sandy areas (Allard 2002, D.W. Hall personal observation).
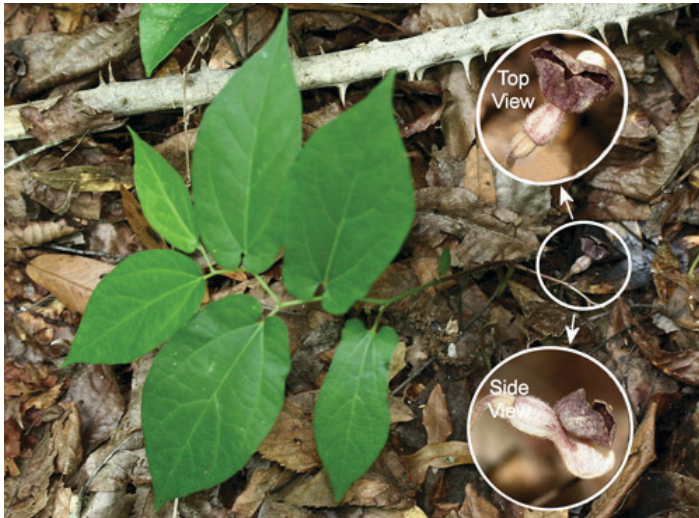

Figure 14. Virginia snakeroot, *Aristolochia serpentaria* L. (broad-leaved form), a host of the pipevine swallowtail caterpillar, *Battus philenor* (L.), with flower.
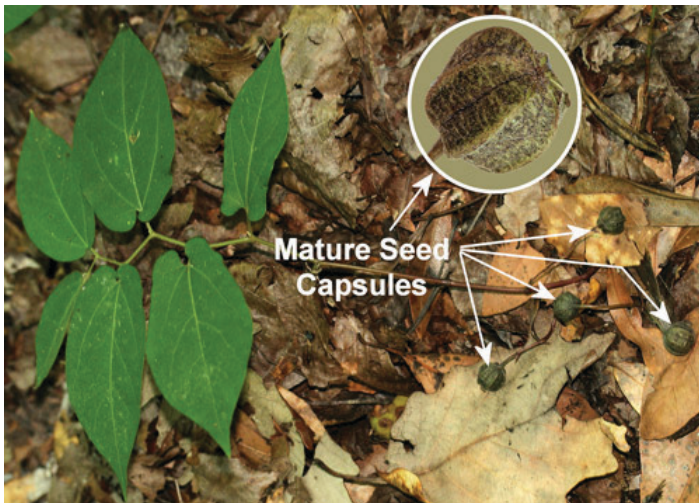Credits: Donald W. Hall, UF/IFAS

Figure 15. Virginia snakeroot, *Aristolochia serpentaria* L. (broad-leaved form), a host of the pipevine swallowtail caterpillar, *Battus philenor* (L.), with seed capsules.
Credits: Donald W. Hall, UF/IFAS

Aristolochia serpentaria L. and *Aristolochia macrophylla* Lam. (Figure 17) have been assayed for aristolochic acid, and both species were determined to contain significant quantities of aristolochic acid I (Schaneberg et al. 2002). Because of their toxicity and distastefulness, the aristolochic acids play a major role in the biology of pipevine swallowtails.

Figure 16. Virginia snakeroot, *Aristolochia serpentaria* L. (narrow-leaved form), a host of the pipevine swallowtail caterpillar, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS
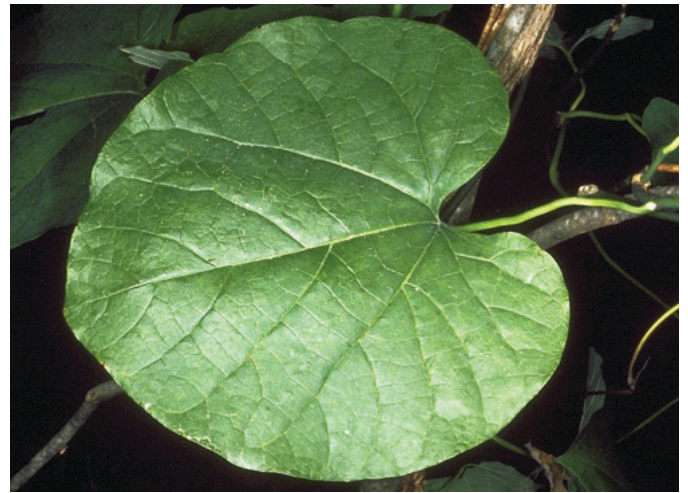
Figure 17. Pipevine, *Aristolochia macrophylla* Lam. (synonym, *Aristolochia durior* Hill) a host of the pipevine swallowtail caterpillar, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

All of our native species of *Aristolochia* within the range of the pipevine swallowtail are documented larval hosts (for distribution maps see their respective USDA Plants Database species pages—links below):

- Virginia snakeroot, *Aristolochia serpentaria* L. (Figures 14, 15, and 16) USDA Plants Database species page.
- Pipevine, *Aristolochia macrophylla* Lam. (synonym, *Aristolochia durior* Hill) (Figure 17) USDA Plants Database species page.
- Woolly Dutchman's pipe, *Aristolochia tomentosa* Sims. (Figure 18) USDA Plants Database species page.

Figure 18. Woolly Dutchman's pipe, *Aristolochia tomentosa* Sims., a host of the pipevine swallowtail caterpillar, *Battus philenor* (L.), leaf (left), unopened flower (middle), opened flower (right).
Credits: Donald W. Hall, UF/IFAS

- Texas Dutchman's pipe, *Aristolochia reticulata* Jacq. USDA Plants Database species page.

- Watson's Dutchman's pipe, *Aristolochia watsonii* Wooton and Standl. USDA Plants Database species page.

- California Dutchman's pipe, *Aristolochia californica* Torr. USDA Plants Database species page.

Various exotic *Aristolochia* species are planted as ornamentals because of their unusual and sometimes beautiful flowers. Some of these may be too toxic (or too distasteful) for pipevine swallowtail larvae and may be "death traps" for the larvae. Elegant Dutchman's pipe or calico flower, *Aristolochia elegans* Mast (synonym, *Aristolochia littoralis* Parodi) (Figure 19), is attractive to female pipevine swallowtails for oviposition, but larvae usually do not survive on it (Kendall 1964, Scott 1986, Tyler 1975). Kendall (1964) suggested that *Aristolochia elegans* is probably only distasteful and not toxic to *Battus philenor* larvae and that the larvae probably die due to starvation because of their refusal to eat it. Therefore, planting of *Aristolochia elegans* and other exotic pipevines is not recommended where *Battus philenor* (L.) occurs (central Florida and northward).

Figure 19. Elegant Dutchman's pipe or calico flower, *Aristolochia elegans* M.T. Mast [synonym: *Aristolochia littoralis* Parodi], a cultured exotic which is a death trap for the pipevine swallowtail caterpillar, *Battus philenor* (L.).
Credits: Donald W. Hall, UF/IFAS

Seed Dispersal

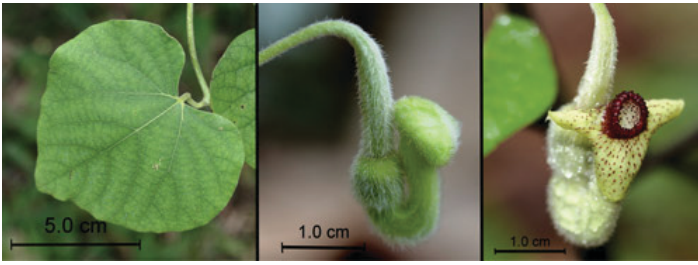*Aristolochia tomentosa* and *Aristolochia macrophylla* are tall vines (Pfeifer 1966) with flattened seeds. Their seeds are probably dispersed by wind and possibly also by animals and flowing water. Two Russian *Aristolochia* vines with similar seeds that grow in similar habitats have been shown to be primarily dispersed by wind and water and to a lesser extent by birds (Nechaev and Nakonechnaya 2009).

Aristolochia serpentaria is a small herb. Its seeds have an attached oil body (elaiosome), and the seeds are dispersed by ants (myrmecochory) that collect the seeds for the edible elaiosomes (D.W. Hall, personal observation, Osorio 2010) (Figure 20).

Figure 20. Myrmecochory (ant dispersal) of Virginia snake root, *Aristolochia serpentaria* L., seed by trap-jaw ant, *Odontomachus brunneus* (Patton): a) dehisced (opened) seed capsule showing seeds with attached oil bodies (elaiosomes); b) trap-jaw ant, *Odontomachus brunneus* (Patton), removing seed from capsule; c) trap-jaw ant, *Odontomachus brunneus* (Patton), carrying seed by the elaiosome.
Credits: Donald W. Hall, UF/IFAS

Both *Aristolochia serpentaria* and *Aristolochia reticulata* are small herbs, and their flowers (and seeds) are usually formed near the bases of the plants, usually underground or at least under leaf litter. Rausher and Feeny (1980) suggested that this may be an adaptation to protect the flowers and seeds from predation by *Battus philenor* caterpillars. However, it may also be an adaptation for dispersal of the seeds by ants. The mechanism of dispersal of seeds for *Aristolochia reticulata* is unknown but likely also involves ants.

Pollination
INSECT POLLINATION

Aristolochia species have fascinating pollination biologies (Proctor et al. 1996). When the flowers first open, the stigmas are receptive, but the anthers are not releasing pollen—a phenomenon known as protogyny (from the Greek roots "proto" [first] and "gyne" [female]). During the first day of bloom, the flowers are attractive to flies (usually small flies—often, but not always, scuttle flies in

the family Phoridae [Hall & Brown 1993]) which enter the flowers carrying pollen from another flower. The flies are then prevented from leaving by the presence of downward projecting guard hairs or tiny spines and slippery surfaces in the tube of the flower (Proctor et al. 1996, Zomlefer 1994) (Figures 21, 22, and 23).
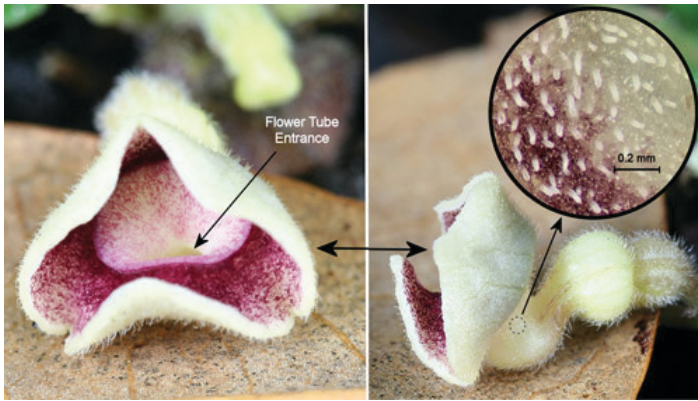

Figure 21. Virginia snakeroot, *Aristolochia serpentaria* L., flower: front view (left), side view (right), and inside of tube with slippery surface and small downward pointing hairs (inset).
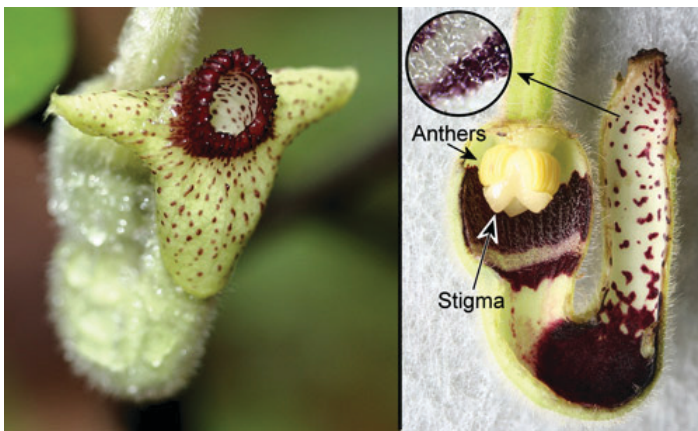Credits: Donald W. Hall, UF/IFAS

Figure 22. Woolly pipevine, *Aristolochia tomentosa* Sims, flower (left) and longitudinal section (right) showing inside of tube with slippery surface and small downward pointing spines (inset).
Credits: Donald W. Hall, UF/IFAS

On the second day (after pollination), the stigmas become non-receptive, and the anthers dehisce (open) dusting the flies with pollen. The guard hairs in the flower tubes wither, and in some species (e.g., *Aristolochia gigantea* Mart. and Zucc.) the flowers also droop into a more horizontal position (Burgess et al. 2004) releasing the flies that are now carrying the new pollen.

CLEISTOGAMY

In addition to its open (chasmogamous) insect-pollinated flowers, *Aristolochia serpentaria* also has flowers that never open (cleistogamous) and are self-pollinated (Ahles 1959, Pfeifer 1966). The terms chasmogamous and cleistogamous are from Greek roots ("chasma" [open or gaping], "cleist,"

[closed], and "gam," [marriage]) (Borror 1960). Cleistogamy is actually a common phenomenon in angiosperms (flowering plants). It is known from at least 693 species in 228 genera and 50 families (Culley and Klooster 2007).
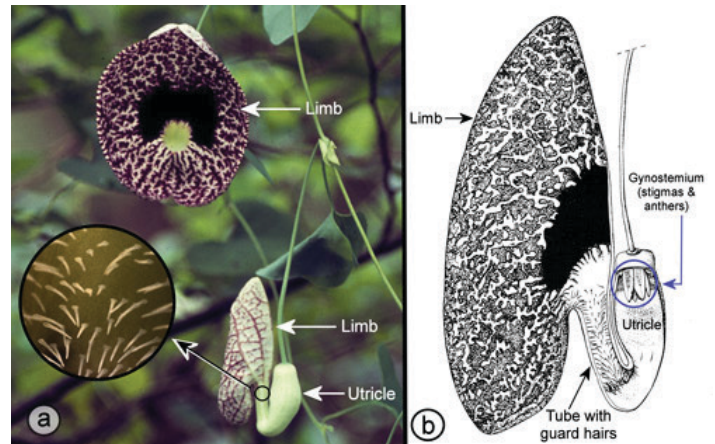

Figure 23. Elegant pipevine, *Aristolochia elegans* M.T. Mast (synonym: *Aristolochia littoralis* Parodi): a) flowers in front and side view orientations and downward pointing guard hairs (inset); b) drawing of longitudinal section of flower showing inside of tube with downward pointing guard hairs.
Credits: Donald W. Hall, UF/IFAS

The cleistogamous flowers of *Aristolochia serpentaria* (Figures 16 and 24) and their resultant seed capsules (Figure 24) are little more than half the size of the chasmogamous flowers and their seed capsules (Figures 14 and 15). Also, the cleistogamous flowers do not have the characteristic "tobacco pipe" shape as they do not trap insects for pollination. Both cleistogamous and chasmogamous flowers often occur on the same plant. In contrast to the chasmogamous flowers, the cleistogamous flowers are often formed later in the season in some species (Mondal 2016) and higher on the plant (Figure 24) where those of *Aristolochia serpentaria* are more susceptible to being eaten by *Battus philenor* larvae.
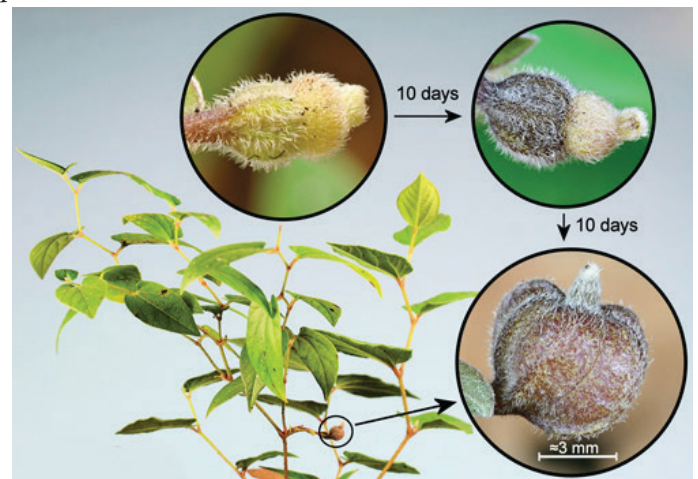

Figure 24. Virginia snakeroot, *Aristolochia serpentaria* L., plant with insets showing sequential stages of development of cleistogamous flower to mature seed capsule.
Credits: Donald W. Hall, UF/IFAS

NECTAR HOST PLANTS

There are many plants that are valuable as nectar sources for butterflies. Pink and purple flowers (e.g., phlox [*Phlox* species], ironweed [*Vernonia* species], and thistles [*Cirsium* species]) are particularly attractive to pipevine swallowtails (Scott 1986). Minno and Minno (1999) have extensive lists of both native and exotic nectar plants for butterflies. When possible, native plants should be planted as nectar sources rather than exotics that have the potential to be invasive.

Most states have native plant societies that are valuable sources of information on native plants, and many also hold native plant sales. For a list and contact information for native plant societies, see the American Horticultural Society's website. For Florida and the Deep South, the Florida Wildflowers Growers Cooperative is an excellent source of information and also has wildflower seeds for purchase.

To maximize butterfly populations in yards, both caterpillar hosts and nectar plants for adults should be planted.

Life Cycle

There are three or more generations in the Deep South (Gulf of Mexico area and peninsular Florida) and two generations northward (Cech and Tudor 2005, Glassberg et al. 2000, Howe 1975).

Males suck moisture from mud to obtain nutrients (particularly sodium) and attraction to the mud appears to be enhanced by the presence of other males (Otis et al. 2006). Males transfer some of the sodium to the female in the spermatophore as a nuptial gift during mating (Otis et al. 2006).

Mating

Males patrol host plants and flyways to locate females (Lederhouse 1995). Courtship flights are slow with the male hovering above the female (Cech and Tudor 2005). *Battus* males have androconia (scent scales) hidden in a fold of the inner margin on the upper surface of the hind wing (Field 1938) (Figure 25). The scales are fluted—possibly to increase surface area for release of pheromone (Miller 1987, Racheli and Oliverio 1993). When courting, *Battus* males are reported to "helicopter" around the females while fanning the androconial chemicals over them (Tyler et al. 1994, p. 53). However, West (1983) reported an observation of mating of *Battus philenor* without fanning of the wings. He also described a method for hand-pairing them in captivity.

Figure 25. Pipevine swallowtail, *Battus philenor* (L.), male showing iridescent scales (left inset) and androconia (right inset).
Credits: Donald W. Hall, UF/IFAS; Lyle J. Buss assisted with the photograph of androconia

The brilliant iridescent blue on the dorsal surface of the hind wings of males is believed to serve as a sexual signal for recognition and possibly for assessment of male quality by females (Rutowski et al. 2010, Rutowski and Rajyaguru 2013). For a general review of the functions of iridescence in animals, see Doucet and Meadows (2009).

Oviposition

Females search for larval host plants based on leaf shape (Allard and Papaj 1996, Rausher 1978). Plants with new leaf buds are more attractive for oviposition (Papaj 1986b). If females detect either eggs or larvae on a plant they avoid ovipositing on it (Rausher 1979).

Females will also investigate non-host plants with leaves shaped like those of the local host plants. In Florida, they frequently visit young *Smilax* (Smilacaceae) vines that resemble *Aristolochia serpentaria* (Feeny 1991). Papaj (1986a) observed a female examine a *Smilax laurifolia* L. plant repeatedly before finally depositing an egg on it. However, when he transferred larvae to *Smilax*, they all died. Oviposition mistakes by Lepidoptera are not uncommon. In fact, long-tailed skippers (*Urbanus proteus* [L.]) will oviposit on *Aristolochia tomentosa*, but the larvae are only able to survive on it during the early instars (Figure 26) and die before reaching maturity (Marc Minno [personal communication], D.W. Hall [personal observation]).

Aristolochic acids I and II, the inositols D-(+)-pinitol and sequoyitol, and a monogalactosyl diglyceride (all isolated from *Aristolochia macrophylla*) were demonstrated to serve as synergistic contact oviposition stimulants for *Battus*

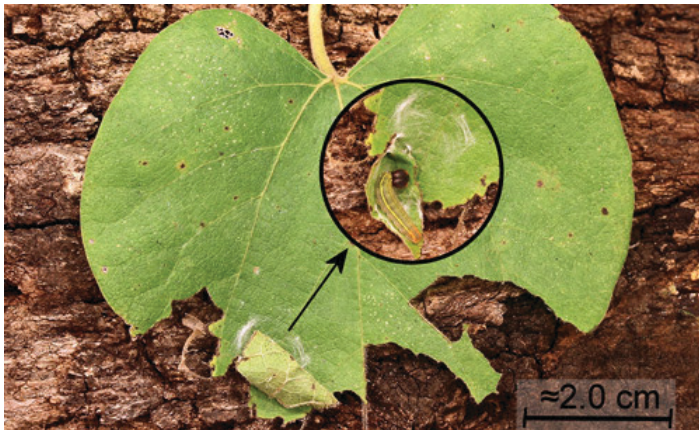*philenor* (Sachdev-Gupta et al. 1993). None of the chemicals by themselves had significant activity.

Figure 26. Early instar long-tailed skipper (*Urbanus proteus* [L.]) leaf shelter on woolly pipevine, Aristolochia tomentosa Sims. Inset: leaf shelter opened to show larva.
Credits: Donald W. Hall, UF/IFAS

Eggs are laid on young foliage or on stems at the bases of leaves—either singly or in small groups on small vines or in larger groups on large vines (Allen 1997. Minno et al. 2005). Young larvae are gregarious, but older larvae are solitary (Allen 1997, Scott 1986).

In Lepidoptera eggs, a small quantity of yolk remains trapped between two of the embryonic membranes (amniotic and serosa) (Barbier and Chauvin 1976) that remain inside the egg shells (chorions) after hatching. Soon after hatching, larvae eat the egg shells (Figure 27), and the residual yolk serves as their first meal (Richards and Davies 1977). Larvae also eat their exuviae after molting to conserve nutrients (Figure 28).
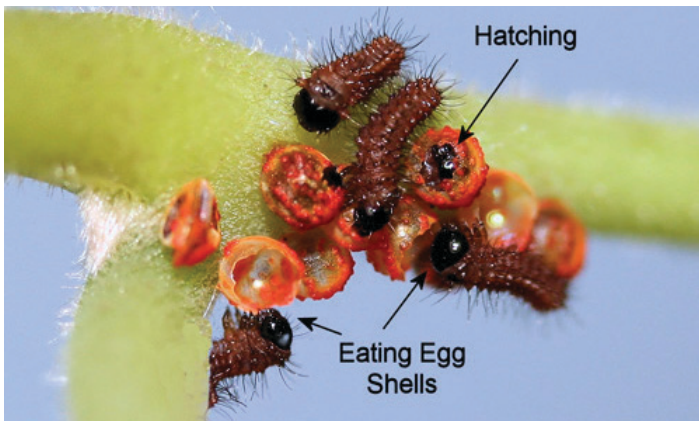

Figure 27. Pipevine swallowtail, *Battus philenor* (L.), newly-emerged first instar larvae eating egg shells (chorions).
Credits: Donald W. Hall, UF/IFAS

Battus larvae commonly defoliate their host plants (Tyler et al. 1994) and need to wander in search of new plants. The elongated thoracic filaments of larvae have only tactile sensors and no chemosensory structures. These filaments and the lateral stemmata (eyes) appear to merely help larvae

locate vertical objects, which must then be identified as host or non-host by the antennae and mouthparts (Kandori et al. 2015). Wandering larvae may find new host plants by detection of plant volatiles. *Aristolochia* volatiles have been shown to be attractive to larvae of *Battus polydamas* (Pinto et al. 2009).

Figure 28. Pipevine swallowtail, *Battus philenor* (L.), last instar larva eating its exuviae.
Credits: Donald W. Hall, UF/IFAS

When full-grown, larvae (prepupae) wander off the host plant to find a pupation site. Pupation occurs well off the ground—usually on tree trunks or on cliff faces in the Appalachians (West and Hazel 1979). Larvae rarely pupate on green substrates (Hazel 1995). Before pupation they spin a silk girdle for support and a silk pad which they grasp with their terminal prolegs (Figure 29). After splitting the old larval exoskeleton and wriggling free, the new pupa hooks the cremaster at the tip of its abdomen into the silk pad (Figure 29).

Figure 29. Pipevine swallowtail, *Battus philenor* (L.), prepupa beginning pupation. Note the silk girdle.
Credits: Donald W. Hall, UF/IFAS

Figure 30. Pipevine swallowtail, *Battus philenor* (L.), prepupa molting to pupal stage. Note the successive positions of the shed larval head capsule (arrows).
Credits: Donald W. Hall, UF/IFAS

Brown pupae predominate (Hazel and West 1979, West and Hazel 1979). Pupal color is partially influenced by the texture of the pupation substrate but not by the photoperiod during the larval stage (Hazel and West 1979). Short larval photoperiod induces pupal diapause (Hazel and West 1983).

Shortly before emergence of adults, the patterns of the wings and body show through the pupal exoskeleton (Figure 31a). The adult emerges through a series of cleavage lines: a mid-dorsal cleavage line on top of the thorax, lines between the head and thorax, and lines between the thorax and wings (Scott 1986) (Figure 31b–d). After emergence, the adult rests near the old pupal case (Figure 31e) while expanding the wings and joining the two halves of the proboscis (tongue) together. During this time, it also voids droplets of the red, liquid, pupal waste products (meconium) (Figure 31e [inset]).
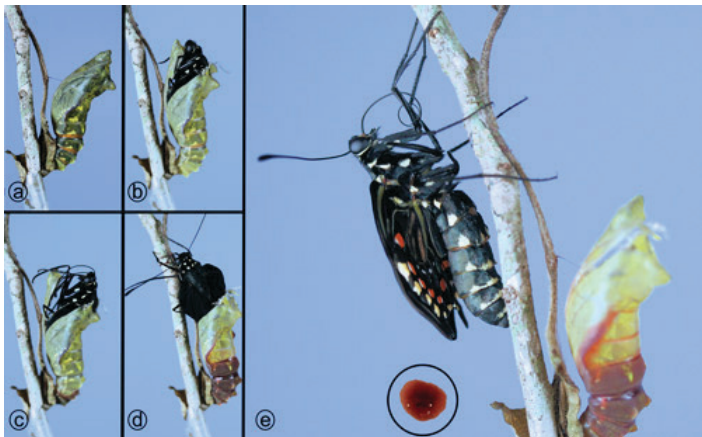

Figure 31. Pipevine swallowtail, *Battus philenor* L., stages in emergence of adult from pupal stage. Inset: droplet of pupal waste product (meconium).
Credits: Donald W. Hall, UF/IFAS

Natural Enemies

Stamp (1986) observed a third instar coccinellid larva (*Hippodamia convergens* Guerin-Meneville) feeding on a second instar pipevine swallowtail larva.

Records of parasitoids from *Battus philenor* are rare. However, there are records of at least one tachinid fly (*Compsilura concinnata* (Meigen)) (Arnaud 1978, p. 601) and two ichneumonid wasps (*Theronia atalantae* (Poda) and *Apechthis annulicornis* (Cresson)) (Sime 2000). Sims and Shapiro (1983a) reported the pupal parasitoid *Brachymeria ovata* (Say) (Hymenoptera: Chalcididae) from California *Battus philenor* and also noted significant mortality to pupae from a "disease" of unknown causes—possibly fungus.

Howe (1988) reported many species of birds eating *Battus philenor* larvae with "relish." *Anolis* lizards will also eat the larvae (Odendaal et al. 1987).

Defenses
Sequestered Aristolochic Acids

Battus philenor larvae sequester aristolochic acids from their host plants and the acids are passed on to the pupae, adults, and ultimately to eggs of the next generation (Dimarco et al. 2012, Dimarco and Fordyce 2013, Sime et al. 2000). The aristolochic acids are reported to render larvae, pupae, and adults unpalatable to some birds. Adults have tough bodies that allow them to survive being tasted (Scott 1986).

Contradictory reports on the palatability of larvae to birds may be due to differences in the ability of some populations (families) of *Battus philenor* to sequester aristolochic acids (Dimarco et al. 2012). Also, lower aristolochic acid concentrations in some *Aristolochia* species or variations in concentrations between individuals of the same species may explain the contradictions.

The chemical defenses appear to be effective against some parasitoids. The ichneumonid wasp *Trogus pennator* (Fabricius), which normally parasitizes papilionid larvae, rejected Battus philenor larvae after examining them with their antennae (Sime 2002).

Osmeteria

All United States swallowtail larvae have forked, eversible, horn-like organs behind the head known as osmeteria (singular, osmeterium). The osmeteria of *Battus philenor* larvae are bright yellow in all larval instars. Fifth instar *Papilio* species secrete isobutyric and 2-methyl butyric acids from their osmeteria (Ômura et al. 2006). The chemical makeup of the osmeterial secretion of fifth instar *Battus philenor* is unknown. However, the secretion of fourth and fifth instar larvae of the closely-related *Battus polydamus* reared on *Aristolochia elegans* is composed of the two sesquiterpenes: β-selinine and selin-11-en-4α-ol

(Eisner et al. 1971). These compounds were not found in the host plant in detectable amounts and are assumed to be synthesized by the larvae instead of being sequestered (Eisner et al. 1971).

The osmeterial repellent of *Papilio* species is effective against ants (Eisner and Meinwald 1965), but Berenbaum et al. (1992) reported that soldier bugs (Hemiptera: Pentatomidae) could attack and eat swallowtail larvae (*Papilio* species) without evoking extrusion of the osmeteria.

Aposematism (warning coloration or appearance)

The orange color on the ventral surface of the wings and the blue iridescence on both ventral and dorsal surfaces have been demonstrated to function as aposematic coloration against attack by vertebrate predators (Pegram et al. 2013, Pegram et al. 2015, Pegram and Rutowski 2014, Pegram and Rutowski 2016).

Mimicry
Batesian Mimicry

Batesian mimicry is a type of mimicry in which an edible species (the mimic) gains protection through its resemblance to a poisonous or distasteful species (the model). *Battus philenor* is believed to be the distasteful, aposematic model for the following edible swallowtail and brushfoot butterfly Batesian mimics (Brower 1958, Brower and Brower 1968, Poulton 1909):

Swallowtail butterfly mimics of *Battus philenor*:

Spicebush swallowtail (*Pterourus* [formerly *Papilio*] *troilus*) (Linnaeus)), (Papilionidae)

Eastern black swallowtail (*Papilio polyxenes* Fabricius), (Papilionidae)

Tiger swallowtail, (*Pterourus* [formerly *Papilio*] *glaucus* Linnaeus), (Papilionidae)—only the dark morph female is mimetic.

Brushfoot butterfly mimics of *Battus philenor*:

Red-spotted purple (*Limenitis arthemis astyanax* (Drury)) (Nymphalidae)

Diana fritillary (*Speyeria diana* (Cramer)) (Nymphalidae)—only the female is mimetic.

Female spicebush and black swallowtails have blue on the dorsal surface of the hind wings and appear to be more convincing mimics than males when viewed dorsally. Male spicebush swallowtails have light green and those of black swallowtails have a lot of yellow and very little blue dorsally on the hind wings. However, males of these species have orange spots on the ventral surface of the hind wings and are probably mimetic when the wings are closed. Under experimental conditions, male and female black swallowtails were equally protected when their ventral sides were presented to captive blue jays, but males were eaten more frequently than females when their dorsal sides were presented (Codella and Lederhouse 1989).

For additional photographs of these mimetic butterflies, see their respective species pages at the Butterflies of America web site (Warren et al. 2016).

Müllerian Mimicry

Müllerian mimicry is a type of mimicry in which two or more species are similar in appearance and are mutually distasteful or dangerous. Therefore, each species acts simultaneously as a model and a mimic and gains protection from the resemblance. Scott (1986, p.73) suggested that *Battus philenor* larvae and certain millipedes may be Müllerian mimics. Some millipedes are dark colored like *Battus philenor* larvae and release hydrogen cyanide when threatened (Eisner 2003, Eisner et al. 2005).

Acknowledgements

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