

OBSERVATIONS ON *PAPILIO ARISTODEMUS PONCEANUS*  
(PAPILIONIDAE)

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*Papilio aristodemus ponceanus* Schaus is a swallowtail which few Lepidopterists have seen alive. As the North American population of a polytypic Antillean species, it is limited to tropical hardwood hammocks in southern Florida. Before the extensive land clearing which accompanied settlement, its range may have extended from a southwestern limit near Marathon in the Florida Keys, into peninsular Florida as far north of Miami as soil character and climatic fluctuations would permit these hammocks to flourish. Today its range is greatly reduced.

The life history was described by Grimshawe (1940) who also illustrated some of the early stages. The accompanying figures will supplement her photographs.

During late spring of 1970, I made observations which can be added to those of Grimshawe. I spent the first week of June in the habitat of *P. a. ponceanus* at times of day varying from dawn to just before sunset. During this time I watched about 35 *ponceanus*. Nearly half of these were caught in order to determine sex and condition, but almost all were set free. Except for a female released and then recaptured an hour later and a mile away, it is not possible to say how many individuals these sightings might represent.

Circumstances did not permit the rigorous survey with marked specimens and large sampling which would have made these notes more objective. Nevertheless I offer this tentative account because *ponceanus* is on the verge of extinction. Collectors hunt it down while developers are destroying its habitat (Kimball 1965, Klots 1951). As I hope to show, over-protective conservation practices can endanger it further.

Published dates for *ponceanus* (Henderson 1945a, 1945b, 1946) extend mostly from April to June. Although the finding of two larvae in their third instar on June 5 (discussed below) indicates that parents had been on the wing in mid-May, the main 1970 flight seemed to have started with the heavy rains which culminated in Hurricane Alma near the end of May. Local newspapers claimed that this had been the wettest May in years. And when I arrived on the afternoon of June 2, residents told me about the unusually heavy and continuous rains which had stopped just the night before. The weather stayed mostly fair until the 5th, when it rained heavily late in the afternoon and intermittently through the

night. Between these two rains *ponceanus* was locally in fresh condition and not rare, whereas the usually common butterflies were scarce and worn. After the rain on the 5th, the few *ponceanus* I could find were all shabby, and ordinarily abundant species such as *Nathalis iole* Boisduval, *Junonia coenia* (Hübner) and *Danaus gilippus berenice* (Cramer) first appeared as freshly-emerged singletons.

**Adults.** *Ponceanus* usually flew in brushy hammocks. The earliest any were seen was just before 9 AM (Eastern Daylight Time) on two bright days, in each instance a female visiting the blossoms of Cheese Shrub (*Morinda Roioe* L.) at the eastern edges of hammocks. The latest observation was at 5 PM, a freshly-emerged female hovering low over Cheese Shrub blossoms at the sunlit west edge of open hammock. On June 2, 1970, sunrise in the Miami area was at 6:29 AM (E.D.T.) and sunset was at 8:08 PM.

Before the hottest part of the day, which was from 1 to 2 PM, both sexes were within the hammocks, fluttering in diffused light about a foot above the ground at blossoms of Guava (*Psidium guajava* Raddi). Guava was abundant within the hammocks whereas Cheese Shrub grew commonly at the edges of hammocks or out in the open. Those *ponceanus* seen at flowers within hammocks were invariably visiting Guava, while at the edges of hammocks or out in the open they were visiting only Cheese Shrub when they were on flowers at all.

On bright days the butterflies flew higher during the hot afternoon. Males patrolled the tree tops at a height of 10 feet or more, sometimes descending into open spaces to investigate any other *ponceanus*. However, no combats were observed nor was it possible to see whether individual males kept to flyways above the forest canopy. During the heat of the day I rarely saw a male descend from the canopy to feed at flowers.

At 10 o'clock on a hazy morning after a drizzle, I found a male of *Papilio cresphontes cresphontes* Cramer and a male *ponceanus* along an open trail. After a short encounter the *ponceanus* veered into the woods while the *cresphontes* settled on a shrub to bask. Three other *cresphontes* were found in open places near midday; all were males visiting various flowers in bright sunlight.

Regardless of how fresh they were otherwise, many *ponceanus* males had one or both hind wings torn more or less cleanly at a 90° angle to the anal margin, often with the tails intact. No females were found damaged in this way. Such mutilation may be evidence of bird attack, although no specimen bore a v-shaped beak mark. Although none of the four male *cresphontes* had torn wings, one was missing a tail which apparently had

been pulled out from its root. The tails of *resphontes* are spatulate, marked above and below with a conspicuous yellow spot; *ponceanus* tails are slender and dark. It is possible that the conspicuous *resphontes* tails might offer marginal survival advantage by distracting the attention of birds from the body of the insect or from graspable parts of the wings. Male *ponceanus* seemed to fly just as strongly as male *resphontes* when out in the open. I could not distinguish the two species by flight alone.

A *ponceanus* male and a *resphontes* male of about the same size were roughly compared for wing strength by measuring the diameter of each wing vein with a micrometer at a point  $\frac{1}{4}$ " from the outer margin. The averages were then taken. The average reading for the *ponceanus* male was .0165" while the *resphontes* average was only .0150". A female of each species similarly compared showed less discrepancy. They both averaged .0185". Though the *ponceanus* male might seem to be the more robust insect, other things being equal, it is worth mention that the pointed shape of *resphontes* wings increases the rigidity of wing surface relative to vein diameter. From the standpoint of total mass that must be kept in motion to maintain a given speed, to say nothing of maneuverability, the pointed *resphontes* wings seem to be more efficient than the blunt *ponceanus* wings.

In an attempt to see how important wing pattern or color might be in species recognition, I looked at a pair of *resphontes* and a pair of *ponceanus* under long-wave ultraviolet light. The bulb used was a General Electric 8 watt BLB, which I hoped would approximate the wavelength by which these insects perceive pattern or color. Under ultraviolet illumination the relation of light spots to dark background on the upperside of both species was similar to the relation visible in daylight. The undersides of the *resphontes* pair also looked much as they do in daylight. However, the undersides of the *ponceanus* pair differed strikingly from *resphontes*. The wide orange-brown band on the hind wings which is so characteristic of *ponceanus* (but which tends to vanish in Antillean *aristodemus* populations) was invisible under ultraviolet light. Furthermore, the yellow underside ground color was nearly obliterated. Except for the blue lunules on the hind wings, the entire underside of the *ponceanus* pair appeared a deep violet brown. For this reason I suspect that *resphontes* and *ponceanus* can distinguish each other in flight better than a Lepidopterist can.

Living males of *ponceanus* smell strongly of sweet lemon with a suggestion of vanilla, while a freshly-emerged female had no perceptible scent. A living male *resphontes* caught in the same place at the same

time, had a faint odor which is best described as acrid. These scents fade soon after death.

At 10:15 AM in a dimly-lit trail through brushy hammock I saw a female and two male *ponceanus* visiting flowers at opposite ends of a Guava tangle. The fresher of the two males eventually approached this slightly worn female while she was still feeding. He hovered over her. She then settled on the ground with wings flattened and vibrating, raising her abdomen. The male fluttered on the ground behind and then rose over her before flying away. In contrast, during part of a *creosphontes* courtship witnessed at 3 PM on a bright day in May 1966, the pair flew straight up until they were hovering about 30 feet above nearly bare ground. Their nuptial flight was interrupted by a bird which darted up out of nearby mangroves to attack one of the butterflies from a "five o'clock" position. The *creosphontes* evaded this attack by an easy dip sideways while its would-be mate fled.

Female *ponceanus* behaved differently from males. The few times they were seen along the edges of hammocks their sex could seldom be determined unless they were captured. But when flying within hammocks in search of Torchwood, *Amyris elemifera* L., the larval foodplant, they fluttered slowly about 6 feet from the ground, with the axis of the body at about 45° from horizontal.

**Oviposition.** Several *ponceanus* females at the outer edges of hammocks were seen to investigate shrubs of Wild Lime, *Zanthoxylum Fagara* (L.), a common larval foodplant of *creosphontes* in southern Florida. These females all flew lower than usual, at about 4 feet. One female (12:30 PM) flew 12 feet out of her straight course to pass near one of these shrubs. Two others were seen hovering around Wild Lime at 12:45 PM and 1 PM. Since Wild Lime flowers are small and inconspicuously located in the axils, I assumed that the *ponceanus* females were seeking nectar. But none of these shrubs proved to be in bloom.

On June 5 at 1 PM I followed a female as she fluttered through an overgrown trail in a way that I had learned to associate with oviposition. With wings vibrating closely together over her back, she perched for an instant on a young shoot of Wild Lime at a height of 6 feet and laid an egg on the leaf tip. I took this egg home to New York with me. The larva which it produced is illustrated in the figures. It is also the basis of some of the observations recounted below.

As will be apparent, this unexpected use of Wild Lime as a larval foodplant offers a clue to the way in which *ponceanus* is adapted to its habitat. Both Torchwood (the previously-recorded larval foodplant) and Wild Lime are pioneering shrubs in whose shade sprout other hard-

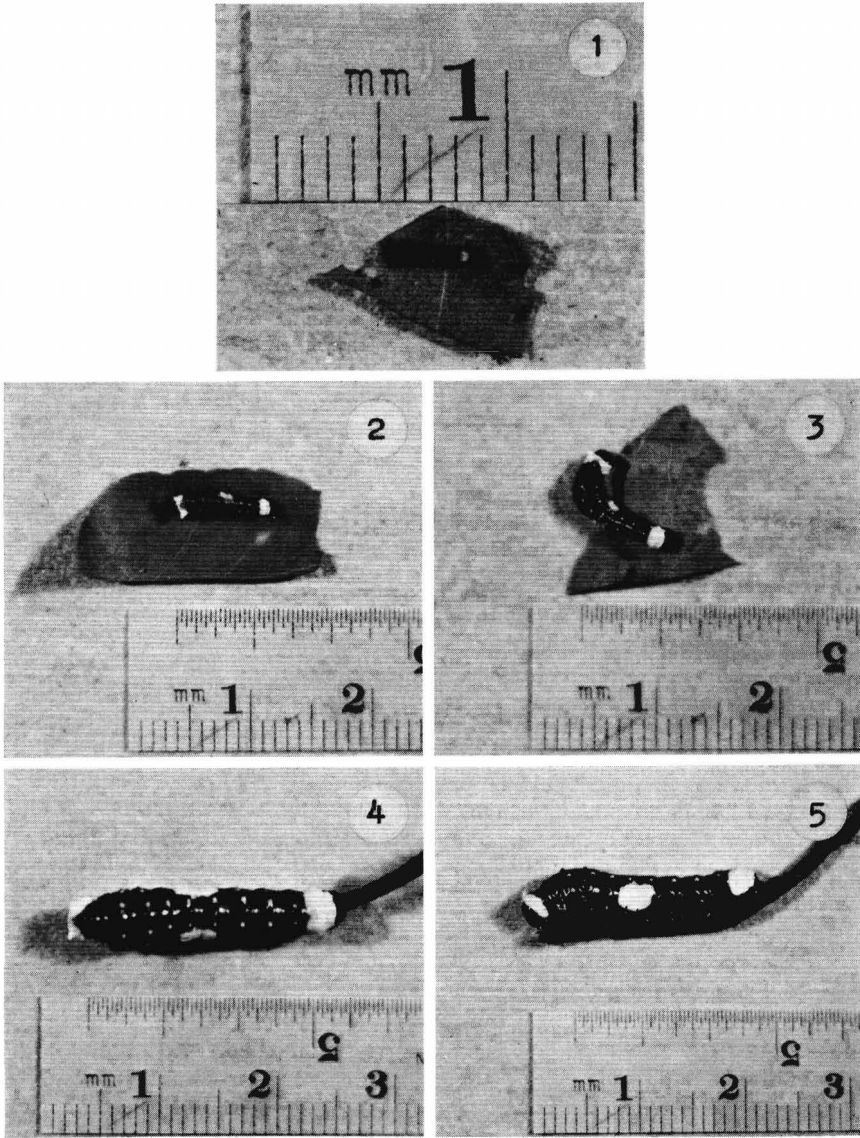
wood seedlings which can eventually grow up to hammock. Therefore both grow abundantly at the edges of advancing hammocks but are scarcer within the hammock itself, where they must struggle for light. Wild Lime seems to need more sunlight than Torchwood. It often grows completely exposed among low herbs, and conversely it is scarce in even fairly open hammock. At the borders of hammocks both plants are usually densely-foliated shrubs up to 8 feet tall, but inside hammocks they are slender trees over 15 feet tall, with fewer leaves. Presumably this change to an arboreal habit is partly an adaptation to keep them from having to struggle against their own shade in addition to the shade of overtopping vegetation.

Most of the Torchwood and Wild Lime and the *ponceanus* associated with them occurred in moderately shady hammock on rather bare limestone pitted with sinkholes. Torchwood but not Wild Lime was nearly as abundant in a still shadier habitat, proliferating on rich humus, but only one *ponceanus* was seen there. This was a female found at 12:30 PM flying higher than usual at about 15 feet within diffused sunlight just below the forest canopy. In the shadiest place of all, a dense mature hammock into which little light penetrated, no Torchwood and no *ponceanus* were seen.

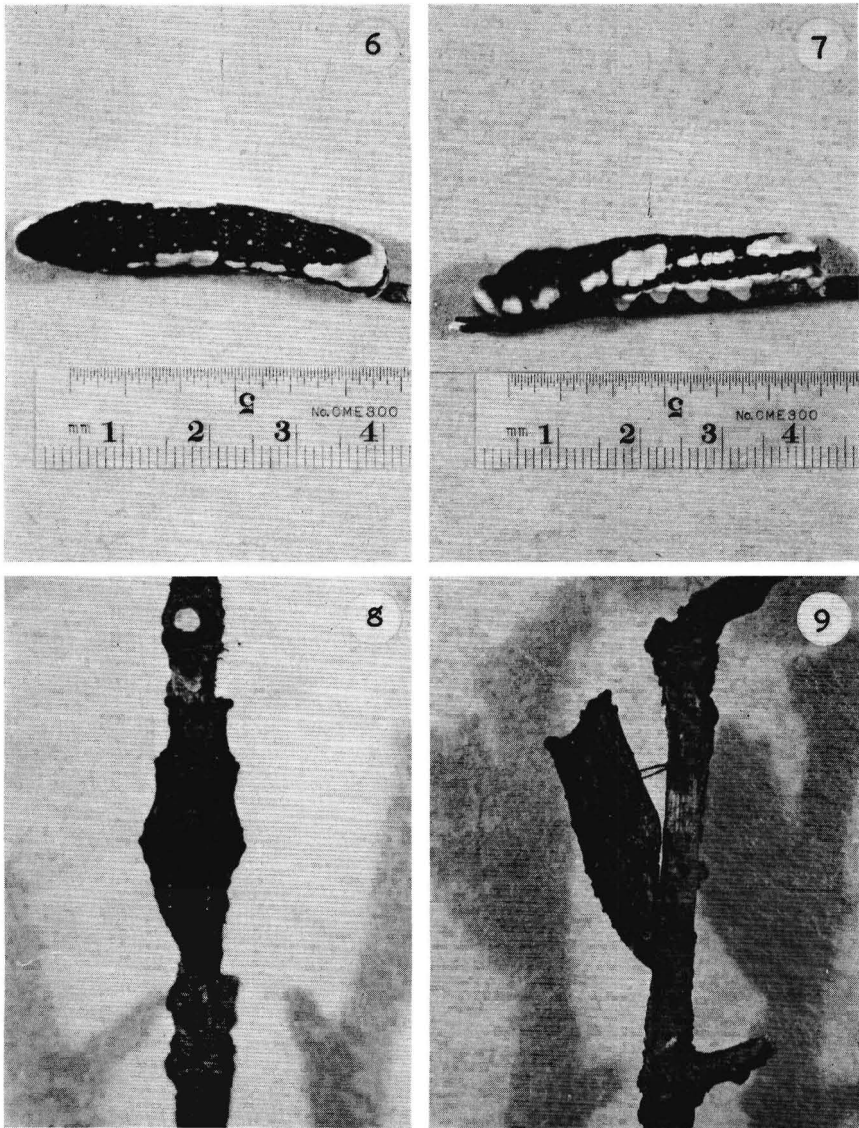
In contrast to the preference for partial shade shown by female *ponceanus*, three female *crsphontes* were seen laying eggs on Wild Lime growing on a similar limestone formation (11 AM in October, 1968). Each *crsphontes* was completely exposed in bright sunlight, ovipositing at a height of about 5 feet.

**Eggs and Larvae.** After learning to recognize *ponceanus* females in search of the larval foodplants I was able to find eggs and larvae. It 11 AM on June 5, I followed a female to a spindly Torchwood tree growing in the shade. She laid an egg on one of its new leaves. There were two other eggs and eight larvae in various stages of development, even two larvae in their third instar, on this one tree. On Torchwood trees in similar situations I found other eggs and larvae but fewer of them. Eggs were always on top of young leaves (but not always the youngest leaves) and once on the rachis. Larvae were invariably on top of the youngest and tenderest leaves, the new growth brought out by the spring rains. Even the two third-instar larvae were feeding on young shoots and refused older growth when it was offered.

No larvae were found on the few Wild Lime trees within the hammock, nor on the numerous Torchwood and Wild Lime shrubs exposed to direct sunlight along the edges of hammocks. Three *Papilio* eggs were found in sunlight at a height of 3 feet on a Torchwood shrub growing half ex-



Figs. 1-5. *Papilio aristodemus ponceanus* Schaus. 1, First-instar larva, dorsal aspect; 2, second-instar larva, dorsal aspect; 3, third-instar larva, dorsal aspect; 4, fourth-instar larva, dorsal aspect; 5, fourth-instar larva, lateral aspect.



Figs. 6-9. *Papilio aristodemus ponceanus* Schaus. 6, Fifth-instar larva, dorsal aspect; 7, fifth-instar larva, lateral aspect; 8, pupa, dorsal aspect; 9, pupa, lateral aspect.

posed along a trail. They did not produce detectable embryos. No *ponceanus* eggs or larvae were found lower than 3 feet or higher than 7 feet from the ground.

First- and third-instar larvae which had been feeding on Torchwood unhesitatingly accepted the youngest leaves of Wild Lime, and so did my newly-hatched larva which had not yet eaten. This larva was later transferred to potted Torchwood which I had brought back to New York with it. When the larva was in its second instar I ran out of young Torchwood shoots and had to give it slightly older leaves. It refused them. Thinking that perhaps the waxy integument of an older leaf made it too tough for food, I scraped the leaf edges with a razor blade, but the larva still would not eat. Finally I gave this larva young shoots of Prickly Ash, *Zanthoxylum americanum* Mill. from New Jersey. Prickly Ash, the preferred larval foodplant of *creosphontes* in the Northeast, grows in rocky places (limestone ledges in New Jersey, sandstone outcroppings in Illinois) much as the related *ponceanus* hostplants occur on well-drained limestone in Florida.

Prickly Ash lacks the waxy covering of its subtropical relatives. Even its mature leaves are tender. However, its youngest leaves are thick and hairy, unlike the young shoots of Torchwood and Wild Lime. The hungry *ponceanus* larva nibbled at the youngest growth of Prickly Ash but seemed to have trouble eating the thick edges of these leaves despite their tenderness. It reluctantly accepted leaves of intermediate age but fed so seldom that its second instar lasted 7 days instead of 5. As the larva matured it ate any Prickly Ash leaves offered, without apparent preference for younger ones. It was reared to the pupal stage on this substitute foodplant.

When kept at 80° F., about 5° lower than the average daytime temperature of its natural habitat, the *ponceanus* larva was remarkably irritable. Confined in a vial, it would jerk its head backward if the vial was jarred even slightly. If the vial was picked up, the larva shook its head from side to side. Though newly-hatched wild larvae and my own reared larva would protrude their white osmateria (producing an unpleasant smell) when I even touched the leaves on which they rested, my larva as it matured into its fourth and fifth instars became reluctant to do so even when prodded. At the same time it gradually abandoned its habit of resting on top of leaves. Instead it clung to twigs below the leaves when it was not actually feeding. Nearly mature *creosphontes* larvae found on Prickly Ash in northern Illinois, rested in a similar position.

Grimshawe noted the curious thirst of *ponceanus* larvae in all instars.



In Florida, when I temporarily confined young wild larvae at 85° F. with nearly saturated humidity, I never saw them drink. And when I reared my larva in New York under similar conditions it apparently did not drink during its earlier instars. But when in its fifth instar it was transferred to a roomy plastic box and kept at 80° F. with relative humidity which varied from 60% to 70%, it would seek out and quickly drink water droplets which I had scattered to keep the foodplant fresh.

#### Summary and Discussion

*Papilio aristodemus ponceanus* is found most often in old disturbed places which are growing up to hammock. Feeding of larvae and adults, courtship and oviposition occur in these second-growth hammocks, indicating that *ponceanus* is a forest insect. The sympatric *P. cresphontes* feeds and reproduces in open places.

*Ponceanus* seems highly sensitive to moisture. It may emerge in numbers only after heavy or prolonged rains have ended the dry season and brought out new growth on its host plants. A twenty-year summary of South Florida weather records (Butson 1962) showed little change in relative humidity between dry and rainy seasons. In the shelter of hammocks, where there is usually no noticeable wind, the relative humidity would be even more stable. However, Butson pointed out that the first month of a rainy season usually has double the rainfall of the preceding dry month. The beginning of the rainy season in South Florida varies from late April to late June, the same months as the flight period of *ponceanus*.

The ability of pupae to remain dormant for longer than a year as noted by Grimshawe, may be a mechanism to synchronize adult emergence with the beginning of the rainy season which in turn produces abundant new growth for the larvae. In an exceptionally dry spring, emergence could be delayed or suppressed. It is possible that pupae respond to light intensity as well, for *ponceanus* does not emerge throughout the rainy season as Antillean *aristodemus* populations apparently do.

The habitat of *ponceanus* is more or less continuous except where man has destroyed it. But feeding adults disperse widely. Their distribution seems related to the freshness of Guava blossoms, the preferred adult foodplant within hammocks at the time of my observations. Adults would not be found at the same Guava patches for more than a day. However, one patch of Cheese Shrub blooming in the open attracted a male a day for three days. The short duration of Guava blossoms may aid the reproductive dispersal of *ponceanus*.

In contrast with the fluid distribution of feeding adults, the eggs and

larvae were distributed very narrowly. The single Torchwood tree which yielded eight larvae in various stages of development seems to indicate that it or its situation was especially attractive to several ovipositing females. This contention seems supported by the fact that other Torchwood trees of the same size growing in similar conditions, generally had larvae on them.

Young larvae will accept other foodplants rather than eat any but the tenderest leaves of the "right" foodplant. They will feed on at least two other Rutaceous plants besides Torchwood, the primary hostplant. Oviposition on one of these, Wild Lime, occurs in nature. Of course ready acceptance of Wild Lime does not necessarily mean that most larvae will thrive on this diet and mature into adults capable of reproducing. Nevertheless, the assured behavior of the female which oviposited on a Wild Lime tree growing in the shade, as compared with the hesitation of the three females seen around Wild Lime shrubs growing in the open, suggests that specific habitat might be a stronger stimulus to oviposition than specific foodplant. The fact that *ponceanus* females are only stragglers in open places and that Wild Lime is only a straggler in shady places makes it unlikely that oviposition on this secondary hostplant is frequent.

It is remarkable that the shady habitat of *ponceanus* is not the most favorable place for its primary hostplant either. As the price of reproductive isolation *ponceanus* lives out of step with both Wild Lime and Torchwood. Both are constantly being shaded out of hammocks, each at its own rate, by normal plant succession.

The mechanisms which maintain environmental separation between *ponceanus* and *crephontes* are not fully understood. An initial hurdle of reproductive isolation may be environmental separation of virgin females which are feeding. Fertilized female *ponceanus* may have a genetically controlled preference for partial shade when ovipositing. As for males, there seems to be a tension zone at the edges of hammocks, characterized by occasional combat between cruising males of *ponceanus* and *crephontes*.

In the mottled light of its habitat *ponceanus* may benefit from a pattern resemblance to *Heliconius charithonius tuckeri* Comstock & Brown. I was sometimes unsure whether a yellow-streaked butterfly vanishing into the edge of a hammock was a rare swallowtail or merely a common heliconian. When I saw such a butterfly from behind, foreshortening increased the resemblance.

It is well known that the wing patterns of *H. c. tuckeri* and *P. crephontes* are "hard edged" while that of *P. a. ponceanus* is suffused. Pattern suffusion is a reputed characteristic of tropical mimetic butterflies

(Corbet & Pendlebury 1956), perhaps indicating that the need for close resemblance to a model is reduced by the preference for shady habitats which such mimics often show. I have already mentioned the "agreeable" scent of *ponceanus* males and the "disagreeable" scent of a male *creosphontes* from the same place. Further investigation could determine whether it is more than coincidence that some *creosphontes* hostplants belonging to the genera *Ruta*, *Dictamnus* and *Ptelea* have been responsible for photosensitive dermatitis in mammals (Muenscher 1951). My few dried Torchwood specimens have more and larger resin dots on young leaves from a completely exposed plant than on young leaves from a plant which grew in partial shade. It is conceivable not only that South Florida *creosphontes* might be protected by an irritant substance in some native *Rutaceae*, but also that shade-grown Torchwood and Wild Lime might be deficient in that irritant.

Putting conjecture aside, there is reason to believe that *Papilio aristodemus ponceanus* must continuously colonize new places partially deforested by storm or fire, which temporarily are in a state of regrowth suited to its habits. The extremes of heedless real-estate development and over-protective maintenance of mature hammocks both threaten to disrupt the natural cycle of renewal on which its survival depends.

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