NOTES ON THE LIFE CYCLE AND NATURAL HISTORY OF BUTTERFLIES OF EL SALVADOR. VI. *ANAEA* (*MEMPHIS*) *PITHYUSA* (NYMPHALIDAE)

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It is evident in modern literature (e.g., Rydon, 1971; Comstock, 1961) that what little is known about the early stages of many Neotropical Charaxinae appears mostly in very old publications as descriptions with illustrations of varying quality. Unfortunately many of them are not much use to taxonomists. This paucity of life-history data has caused some confusion in the placing of genera within tribes and subtribes. My sons and I hope that our contribution will help the experts reach a consensus. We follow Comstock's (1961) nomenclature in this paper as in our previous five papers on the local Charaxinae.

Eggs and larvae of *Anaea* (*Memphis*) *pithyusa* R. Felder were first collected in 1967. These were reared in transparent plastic bags containing leaves of the foodplant, which were replaced every third day. Pupae were transferred to a box covered with mosquito netting until the adults emerged. The bags and box were kept in our insectary under ambient light and temperature conditions. Photographs were taken and records of measurements and time elapsed for each stage were kept. Specimens of the immature stages were preserved in alcohol and sent to the Allyn Museum of Entomology, Sarasota, Florida.

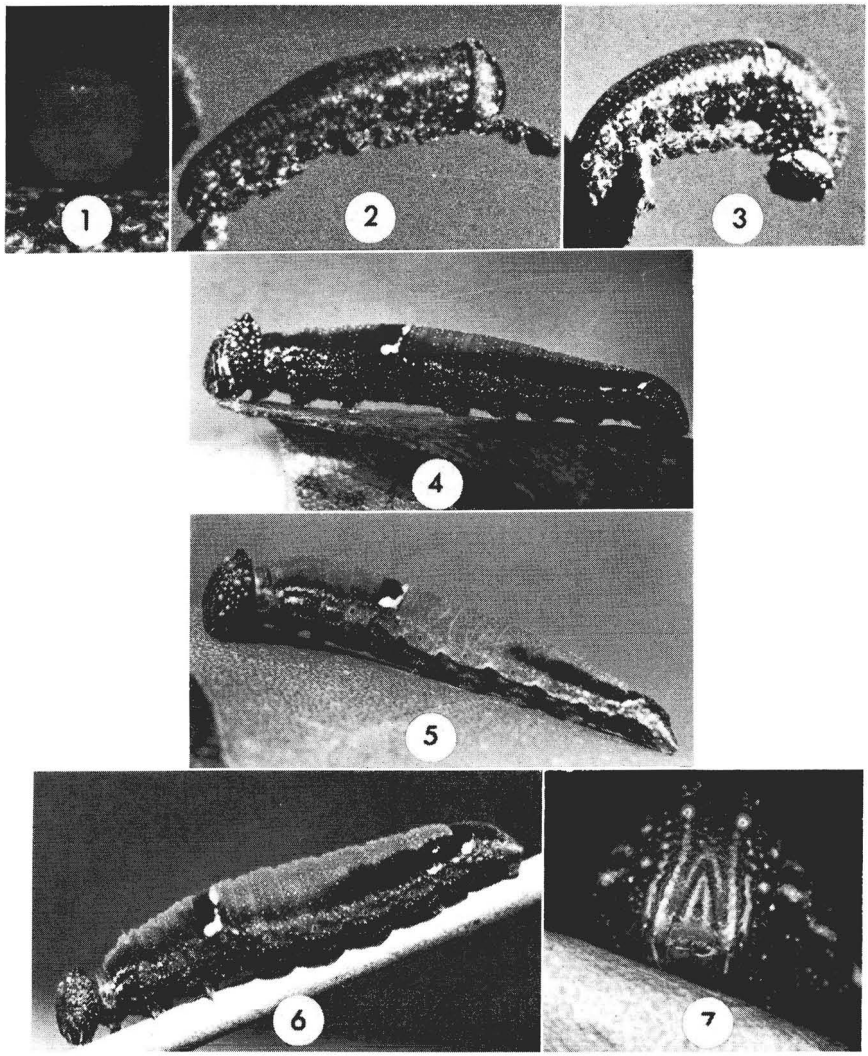
Life Cycle Stages

Egg (Fig. 1). Transluscent light green, almost spherical with flattened base and depression at micropylar zone. No sculpturing visible under 10× magnification. Diameter about 1.0 mm. Hatch in 5 days.

First instar larva (Fig. 2). Head brown, hemispherical, naked, slightly thicker than body. Body greenish brown, naked, with annulets between segments. Body wedge-shaped on hatching, thickening around first abdominal segments after feeding. Measures 2.5 mm in length when recently hatched, growing to 5.0 mm before molting in 5–7 days.

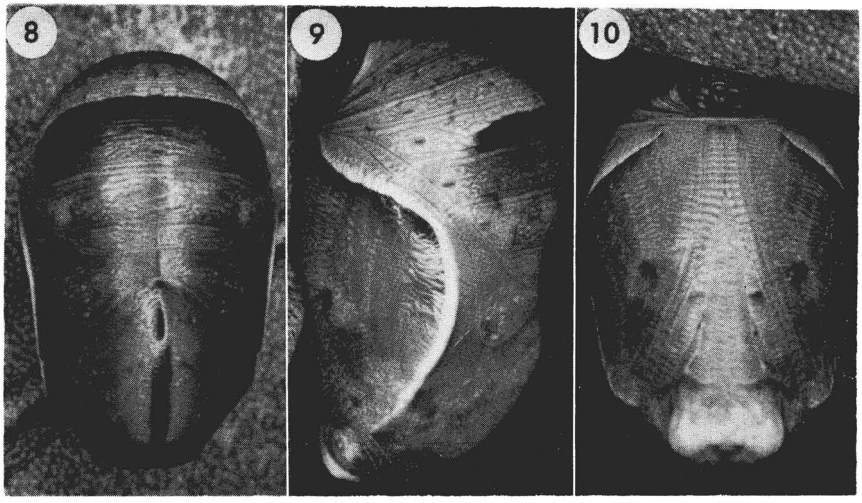
Second instar larva (Fig. 3). Head thicker than thoracic segments, brown with lighter tubercles and short black horns on epicranial apices. Body green or brownish green with faint black "saddle" across second abdominal segment. "Saddle" ends laterally by a whitish dot. Caudal segments with blackish tinge dorsally. Entire body spattered with tiny light brown spots. Grows to 7.0–9.0 mm in 3–5 days.

Third instar larva (Fig. 4). Groundcolor of head black with many yellowish tubercles, mostly around the stubby and knobbed black horns. Yellowish lines bordering frontal and adfrontal sutures, forming triangles, plus another two lines:



Figs. 1–7. *Anaea* (*Memphis*) *pithyusa*. 1, Egg, width about 1.0 mm; 2, first instar larva, length about 2.5 mm; 3, second instar larva, length about 4.0 mm; 4, third instar larva, length 15.0 mm; 5, fourth instar larva, length 26.0 mm; 6, fifth instar larva, 40.0 mm; 7, fifth instar larva, head, frontal view.

one descending from base of horns to side of mandible and a second line, shorter and parallel to the first, ending at antennal base. Body green or brownish green with many lighter spots, and a dark brown or blackish zone, variable in size, along subdorsal area of thoracic segments. Black "saddle" across second abdominal segment lined posteriorly by a white streak. Caudal segments show a variable black zone similar to second instar. First and second abdominal segments thicker than



Figs. 8–10. *Anaea* (*Memphis*) *pithyusa*. Pupa: 8, dorsal view; 9, lateral view; 10, ventral view.

the rest, body tapering caudad. Spiracles black, prothoracic much larger than the others; those on the second and eighth abdominal segments being slightly higher than the rest. Grows to 15.0–17.0 mm in 4–6 days.

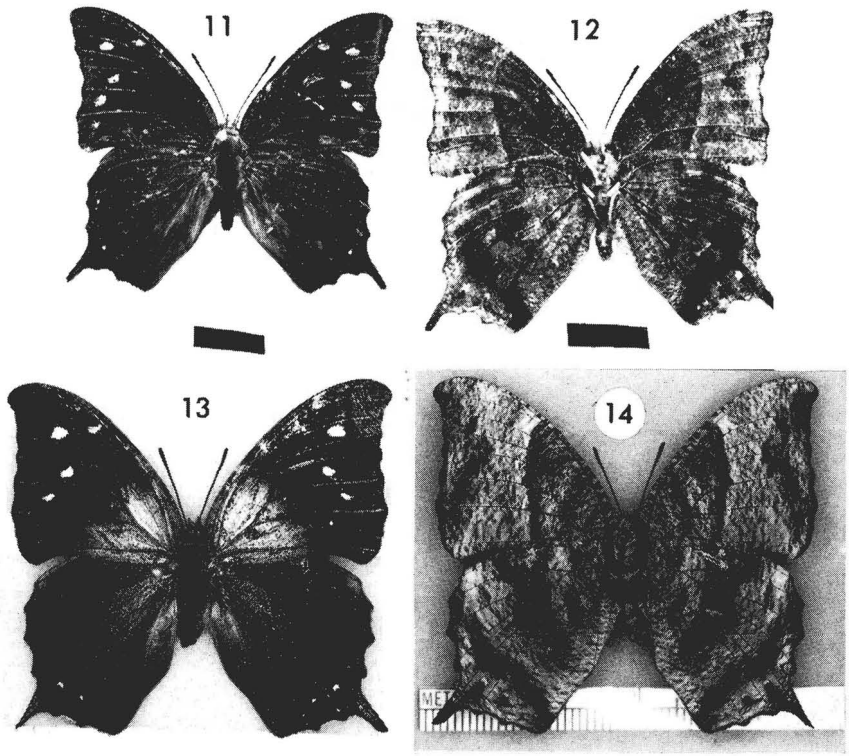
Fourth instar larva (Fig. 5). Head as in third instar, but horns thicker, tubercles more prominent, some of them orange tinged. Body as before, thicker than head at first abdominal segments. Grows to 23.0–28.0 mm in 5–6 days.

Fifth instar larva (Figs. 6, 7). Head as before, looking smaller due to thickness of body. First thoracic segment narrow, forming a "neck". Color of body varies from green to brownish green, with dark markings as in third instar. Grows to 34.0–40.0 mm in 10–12 days.

Prepupa. Body shortens and takes dark purplish tinge. Stays so for one day.

Pupa (Figs. 8–10). Cremaster black, the rest purplish brown, with a darker band of variable intensity dorsally across fifth abdominal segment. Abdomen incurved ventrally, very short from cremaster to ventral limit of wing cases, rounded dorsally, curving inward to thorax. Thorax slightly keeled dorsally, ending smoothly at head. Semicircular row of 4 tubercles present midway along ventral edge of wing covers. Measures 15.0–17.0 mm long, 10.0 mm laterally and dorsoventrally. Adult emerges in 8–12 days.

Adults (Figs. 11–14). Shape and color variable, both in males and females. Forewing apex variably acuminate or not, outer margin sinuose and concave, tornus acute; inner margin sickle-shaped. Hindwing with convex inner margin, sinuose outer margin with variably long, thick tail located at vein M-3, anal angle not pronounced and inner margin almost straight. Dorsal groundcolor dull black with pronounced greenish to bluish reflection basally in males, more so in front wings; light blue in females. Usually 4 blue spots on forewing subapically and along outer margin, conspicuous or completely absent. Hindwing usually shows a small blue spot near the base of the tail and a row of half-moon shaped light blue spots along outer margin. Ventrally both sexes present a combination of different shades of brown, at times almost black, at times light brown. Body short and thick, more so in females. Antennae black.



Figs. 11–14. *Anaea* (*Memphis*) *pithyusa*. 11, Male, dorsal view (black bar = 1 cm); 12, male, ventral view; 13, female, dorsal view; 14, female, ventral view.

Natural History

Eggs and larvae of *Anaea pithyusa* are found all year on mature leaves of two local species of *Croton* (Euphorbiaceae): *C. reflexifolius* HBK and *C. niveus* Jacquin. The most common is *C. reflexifolius* which is used to fence coffee plantations to form wind breakers. Both plant species are known locally under the same vernacular name, "Copalchí," and both are very appreciated in popular medicine as tonics and febrifuges. The leaves and bark are very aromatic and bitter. The plants are perennial and grow to about six meters.

The ovipositing female flies swiftly to a group of Copalchí, circles a tree several times more slowly, and finally alights under a mature leaf. One egg is then deposited about at the middle of the leaf, after which the female resumes flying around. The female repeats the process several times before moving away. The small greenish eggs are very hard to spot against the green of the leaves.

The tiny larva completely consumes the egg shell upon hatching and does not feed further for about one day. When ready to feed, the larva proceeds to the edge of the leaf, usually to the tip. Here it constructs a resting perch by nibbling around a vein until it is exposed, affixing frass to it with silk. This perch is used through the first, second and third instars. Once the fourth instar is reached, the perch is abandoned and the larva wanders about the plant until another leaf is chosen. There the larva makes a funnel by rolling an edge of the leaf and tying it to the leaf surface with silk. The funnel is then lined with silk. This refuge is used by the larva when not feeding. The massive head of the larva effectively blocks the wider end of the funnel, and the excreta is expelled out the narrow end. When the feeding larva goes back to its funnel, it positions the caudal end of the body at the wide entrance and crawls backwards until the head plugs the entrance.

The larva produces a pungent but not disagreeable odor when molested, probably from an eversible gland located between the head and the prothoracic legs. If this defense method does not work and a larva is compressed, it regurgitates a green liquid.

When the larva is ready to pupate, as indicated by a change of color, it abandons the funnel and wanders about the plant until a suitable location is chosen. This is usually the inner side of a mature leaf hanging vertically, but sometimes a twig is chosen. A silk pad then is woven, where the anal prolegs are affixed. The larva stays there, curled sideways—not hanging, until pupation. Before becoming a pupa, the larva clears the digestive tract by expelling green liquid mixed with frass through the anus.

The dark purplish brown pupa is passive and seldom reacts when touched and then only by a very slight lateral swing. Prior to adult emergence, the pupa turns black.

The emerging adult breaks the dorsal meson of the thorax and forces down the head and antennal covers, making a fast exit. Hanging from the pupal shell, it starts expanding the wings while ejecting a reddish meconium. The process takes about 15 minutes.

Adults favor wooded areas with neighboring open land. Males are seen resting with folded wings on tree tops, where they exhibit a strong territorial behavior, rushing at any passing butterfly. Both males and females come to the ground to feed on decaying fruits and vertebrate feces. We have never seen males courting females. This may be done high up in the trees.

The species is much affected by parasites from the egg through the pupal stage. Many eggs in the field turn black and give forth tiny

chalcidoids (up to six per egg). During the larval stage, tachinid larvae kill the host and abandon the shriveled body to pupate. We have obtained an unbelievably large adult tachinid from the rather small pupa of the species. It was determined by Dr. C. W. Sabrosky of the USDA as "*Archytas* sp., probably a new species."

We noticed a marked reduction in the number of larvae in the field during the peak of the dry season (February–April). This cannot be attributed to the lack of food, as would be the case with species feeding on annual weeds or deciduous trees because the foodplants of *A. pithyusa* are perennials with leaves showing little loss of succulency. Perhaps the heavy winds which usually blow during the dry season dislodge the eggs from the leaves by rubbing the leaf surfaces together. This may be facilitated by the heavy layer of dust deposited on the leaf surfaces by the wind, hindering the effective attachment of the eggs.

The adults of the species, in addition to a noticeable sexual dimorphism based mostly on color differences, show a confusing assortment of wing shape and color variations.

Discussion

As far as we know this is the first published, illustrated description of the complete life cycle of *Anaea pithyusa*.

This species shares its foodplants with *Anaea* (*Memphis*) *eurypyle confusa* Hall (Muyshondt, 1974a), one of the reddish *Anaea*. Larvae of the two species can often be collected simultaneously from the same tree. Even so, there is no apparent interaction between the larva of the two species, due perhaps to the rather sedentary behavior of both species and the profusion of leaves on the trees.

The eggs of *A. pithyusa* cannot be distinguished from the eggs of *A. eurypyle*. In fact, they are also similar to the eggs of *A.* (*Consul*) *fabius* (Cramer) (Muyshondt, 1974b), *A.* (*C.*) *electra* (Westwood), and *A.* (*Memphis*) *morvus boisduvali* W. P. Comstock (Muyshondt, 1975), which are found on other plants. First instar larvae also look very much the same in all these species and have similar behaviors, but the color of *A. pithyusa* is markedly green, while *A. eurypyle* is brownish. As the larvae progress into subsequent stadia the differences become more evident: head shape and head and body color make identification easy. The differences between all these species reach a maximum at the pupal stage, both in shape and color. Based on these differences, we dare to disagree with Comstock (1961), who groups both *A. pithyusa* and *A. eurypyle* under the subgenus *Memphis*. We do not agree with the placing of these species with *A.* (*M.*) *morvus* (Fabricius). There is a

drastic larval and pupal discrepancy between *A. morvus* and these two species indicating a greater phylogenetic distance between them. We think that within Comstock's conception of *Anaea* the local species form five distinct groups as follows: *A.* (*Zaretis*) *itys* (Cramer) and *A.* (*Siderone*) *marthesia* (Cramer) forming one group, *A.* (*C.*) *fabius* and *A.* (*C.*) *electra* a second, *A.* (*M.*) *eurypyle* a third, *A. pithyusa* a fourth, and finally *A.* (*M.*) *morvus* a fifth.

It is a pity we have been unable to find the foodplants of the few other species found in this country to complete our observations, and thence support our claim. But we do have partial evidence regarding *A. morvus,* as A. Muyshondt, Jr. collected a larva in Panama very much like it, on a tree (Euphorbiaceae) resembling *Croton* sp. This larva produced a typical *morvus* pupa. Unfortunately the pupa died before forming an identifiable adult, but the undeniable resemblance of the larva and pupa to our local *morvus* would seem sufficient to prove they correspond to the same group. In addition, two illustrations in Rydon (1971) of the larvae of *A.* (*M.*) *porphyrio* (Bates) (= *leonida* (Cramer) according to Comstock, 1961) and *A.* (*M.*) *morvus* resemble ours of a *A. morvus boisduvali* (Muyshondt, 1975) fifth instar larva. Rydon (1971) illustrates the larva of *Anaea phidile* Geyer, and this larva conforms to our *eurypyle.* There must be others resembling our *pithyusa.* An invitation is made to other workers in Central and South America to present their findings on the early stages of species belonging to the genus *Anaea* (*sensu lato*).

We adopted Comstock's (1961) nomenclature from the start of the series, so for the sake of clarity we maintain it, despite our recent acquaintance with the work of Rydon (1971). Rydon has presented a systematic revision of the Charaxidae (with family status) which separates Comstock's subgenera *Zaretis, Siderone* and *Coenophlebia* from the rest of *Anaea* and places them into the subfamily Zaretidinae with full generic status. He similarly places the subgenera *Hypna, Anaea, Polygrapha, Consul* and *Memphis* in the subfamily Anaeinae as full genera. Rydon also resurrects *Cymatogramma* from synonymy with *Memphis* and describes the genus *Fountainea* as new. He splits Anaeinae into the following tribes: Hypnini, Anaeini, Consulini, Cymatogrammini, Polygraphini, Fountaineini and Memphidini. *Anaea* (*Consul*) *fabius* and *A.* (*C.*) *electra* are placed in the Consulini, *A.* (*Memphis*) *eurypyle* in Fountaineini, *A.* (*M.*) *pithyusa* in Cymatogrammini and *A.* (*M.*) *morvus* in Memphidini. Rydon warns that as the early stages of more species become better known, some of the species now placed in *Memphis* may be shown to belong elsewhere.

Funnel formation by fourth instar larvae is found in all species listed above under the Anaeinae. *A.* (*Z.*) *itys* and *A.* (*S.*) *marthesia* larvae do not make leaf funnels. The funnels of *A.* (*M.*) *pithyusa*, *A.* (*M.*) *eurypyle*, *A.* (*C.*) *fabius*, *A.* (*C.*) *electra* and *A.* (*M.*) *morvus* are located at the tip or the sides of a leaf. It has been assumed (Rydon, 1971) that the funnel is used as protection against the heat or sunlight, but in our experience it seems to be a protective device against predation, as these species make funnels even if maintained continuously in the shade in our insectary. Only some parasitized or diseased individuals fail to make funnels.

The habit of making resting perches with frass pellets exhibited by the species mentioned is shared not only by the other Charaxinae we have studied, but by a host of other Nymphalidae (*sensu lato*) as well, including Catonephelinae, Coloburinae, Apaturinae, Biblinae, Callicorinae, Hamadryadinae (except *Hamadryas amphinome* (L.) which has evolved gregarious habits during the larval stage), Limenitinae (except the genus *Dynamine* which we doubt belongs to the group) and Marpesiinae (nomenclature according to Ebert, 1969). This common factor may prove of value in establishing phylogenetic relationships.

Adults of *A.* (*M.*) *pithyusa*, *A.* (*M.*) *eurypyle*, and *A.* (*M.*) *morvus* have similar rapid flight habits. *A.* (*C.*) *fabius* and *A.* (*C.*) *electra* fly much more slowly.

The defense mechanisms of *A. pithyusa* against predation, based on crypsis and chemical deterrents, do not protect the early stages against parasitism. This seems to support our contention, expressed in our papers dealing with *Pseudonica flavilla canthara* Doubleday (Muyshondt, 1973 (1974)) and *Pyrrhogyra hypsenor* Godman & Salvin (Muyshondt, 1974c), that species chemically protected against predation by the noxious components of the foodplants may be preferred by dipterous and hymenopterous parasites because of the increased survival of the host, thus increasing the survival of the parasites.

Anaea pithyusa is one of the local Charaxinae most frequently reared by us, and the adults are extremely variable. This indicates a single species with marked polymorphism, or two species with very similar early stages and identical foodplants. These species might interbreed in nature, producing hybrids of intermediate shape and color. In order to clarify the situation seven adults reared *ex ova* were sent to the American Museum of Natural History, representing the two extremes and several intermediate forms. The specimens with no blue subapical spots or with the spots much reduced were determined as *A. pithyusa*. Specimens with larger blue subapical spots were determined as *A.* (*M.*)

perenna Godman and Salvin. S. Steinhauser (pers. comm.) stated once that in his experience, it was very difficult, if at all possible, to tell *pithyusa* from *perenna* by examination of male genitalia. On the basis of the similar morphological and behavioral characteristics of the early stages and the use of the same foodplant, plus the determination made at the American Museum of Natural History, we dare to suggest the two species are only one, with a host of different morphs. If that is the case, the name with priority would then be *A. pithyusa.*

ACKNOWLEDGMENTS

We are obliged to Dr. A. H. B. Rydon for kindly supplying a copy of "The Systematics of the Charaxidae" and the valuable information made available in his correspondence, and to Dr. F. H. Rindge from the American Museum of Natural History for the determination of the species. We also thank Dr. C. W. Sabrosky of the USDA for determining the tachinid parasites, S. Steinhouser for sharing with us his personal observations on the species, and Dr. G. L. Godfrey and Mr. M. Toliver for revising the manuscript and making constructive criticisms.

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