Notes on the Life Cycle and Natural History of Butterflies of El Salvador III A.—*Temenis laothöe liberia* Fabricius (Nymphalidae-Catonephelinae)

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Abstract: For the first time a complete description, including photographs, of the life cycle of *Temenis laothöe liberia* Fabricius is presented, as well as a record of the foodplants in Central America. Behavior during early and adult stages is described and compared with behavior of closely related species. The findings are discussed with relation to the possibility that this species is protected against predators as a result of the poisonous properties of its foodplants.

This is the third article of a series dealing with what my sons and I have found in relation to the life cycles and natural history of the local butterflies belonging to the Catonephelinae, a group of the Nymphalidae. Another series has been presented elsewhere describing the life cycle with notes on the natural history of some of the local Charaxinae. The purpose of these articles is to present information on tropical butterflies, mostly of the family Nymphalidae, of which there is only exiguous knowledge in the literature. The papers will provide the experts with new elements that hopefully will help them in the sorely needed revision of the Nymphalidae, which are grouped by many authors on the basis of the broad characteristic that both adult sexes have the prothoracic legs much atrophied. Similarly, the actual Papilionidae and Pieridae were grouped not long ago under one family, Papilionidae, on the bases that adults of both sexes have six ambulatory legs and the pupae are secured not only by the cremaster but also by a girdle (Holland 1914). Simultaneous with the presentation of the articles, complete series of preserved specimens of the early stages of the species described have been sent to museums where they are available to students of those groups.

Our greatest difficulty has been the actual determination of the species because we are dependent on old publications (Seitz 1924), which, although they represent a formidable step in the knowledge of tropical American fauna and

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therefore deserve due credit, refer to many species by names that have since been changed. To overcome this handicap, Drs. Alexander B. Klots and Frederick H. Rindge of the American Museum of Natural History have made the determination of the species mentioned in this article. For future verifications of identifications, specimens have been placed in the museum.

When describing the life cycle of *Prepona omphale octavia* Frühstorfer (Muyshondt 1973a), a short description of the country is included, with pertinent information regarding its climatic conditions, altitudes, and vegetation, to familiarize the reader with the habitats of the species described.

The adults of *Temenis laothöe liberia* Fabricius, like its close relative *Epiphile adrasta adrasta* Hewitson, favor wooded ravines and creeks in the vicinity of coffee plantations. The ravines and creeks harbor the remains of the wild flora of El Salvador, consisting of second-growth plant communities where the wild vines used as food by the larvae are quite abundant. This species ranges from about 500 to 1500 m. altitude.

Shortly after our finding, in 1970, the eggs of *Epiphile adrasta adrasta* (Muyshondt 1973c), we found on the same plant other eggs resembling them so much that we expected the new ones to belong to a closely related species. After a time we obtained from these eggs orange-colored butterflies, later determined as *Temenis laothöe liberia*, thus confirming our expectations.

The eggs collected at that time and the larvae that hatched from them were kept until pupation in transparent plastic bags under ambient lighting and temperature conditions. The pupae were transferred to a wooden box with wide openings covered by mosquito netting and maintained until the adults emerged. Photographs were taken of every stage and records of developmental time and measurements were kept. Specimens of early stages were preserved in alcohol and have been sent to the American Museum of Natural History, New York City.

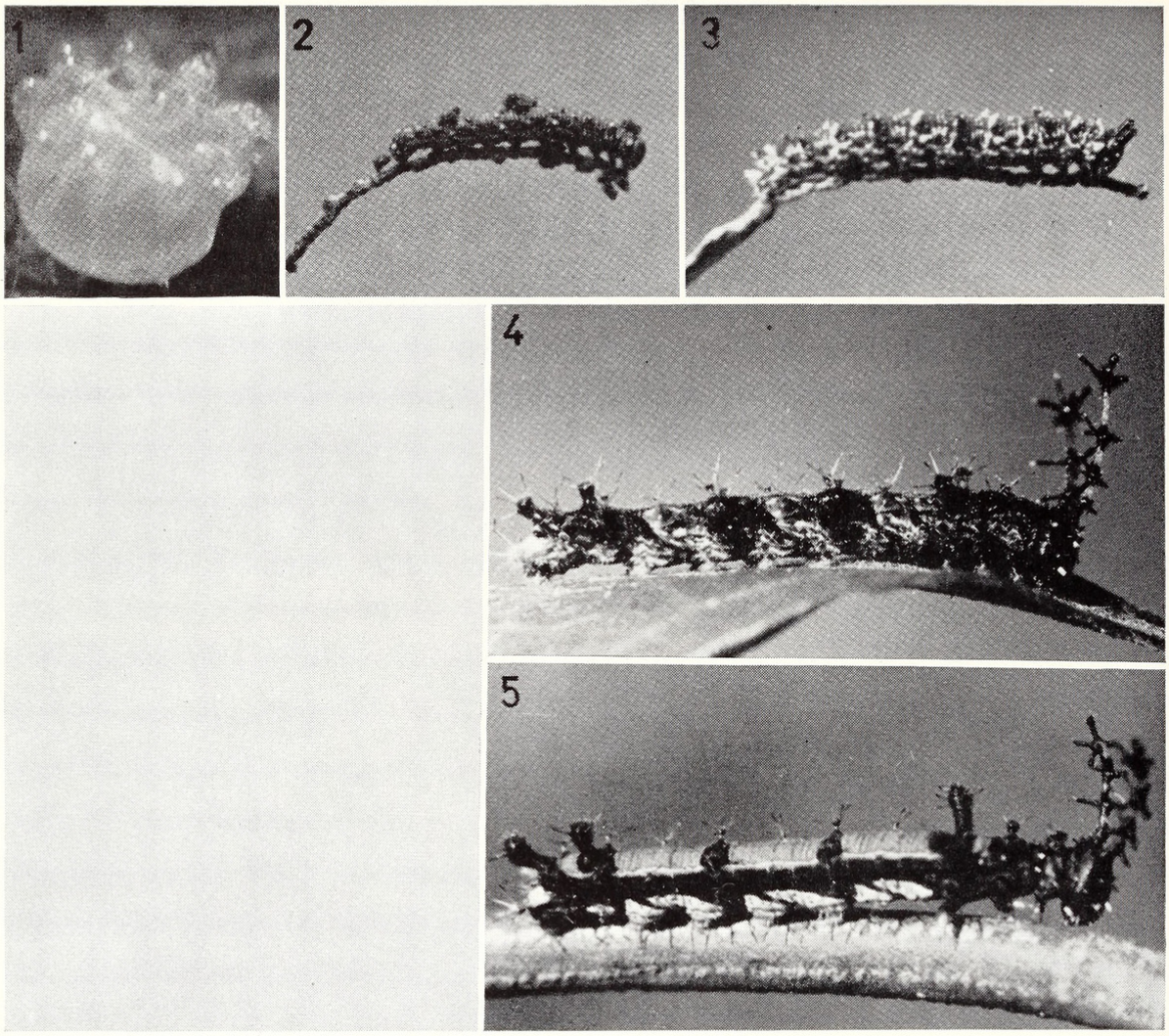
Since that occasion we have reared this species from egg to adult a number of times, during different months of the year, obtaining about the same results.

LIFE CYCLE STAGES

Egg. White, truncated, cone-shaped. Surrounding the micropylar zone, there are nine thick prominences, from which inconspicuous white ribs originate that reach the base of the egg. It measures about 1 mm. longitudinally and laterally at widest point. The eggs hatch in 5 days.

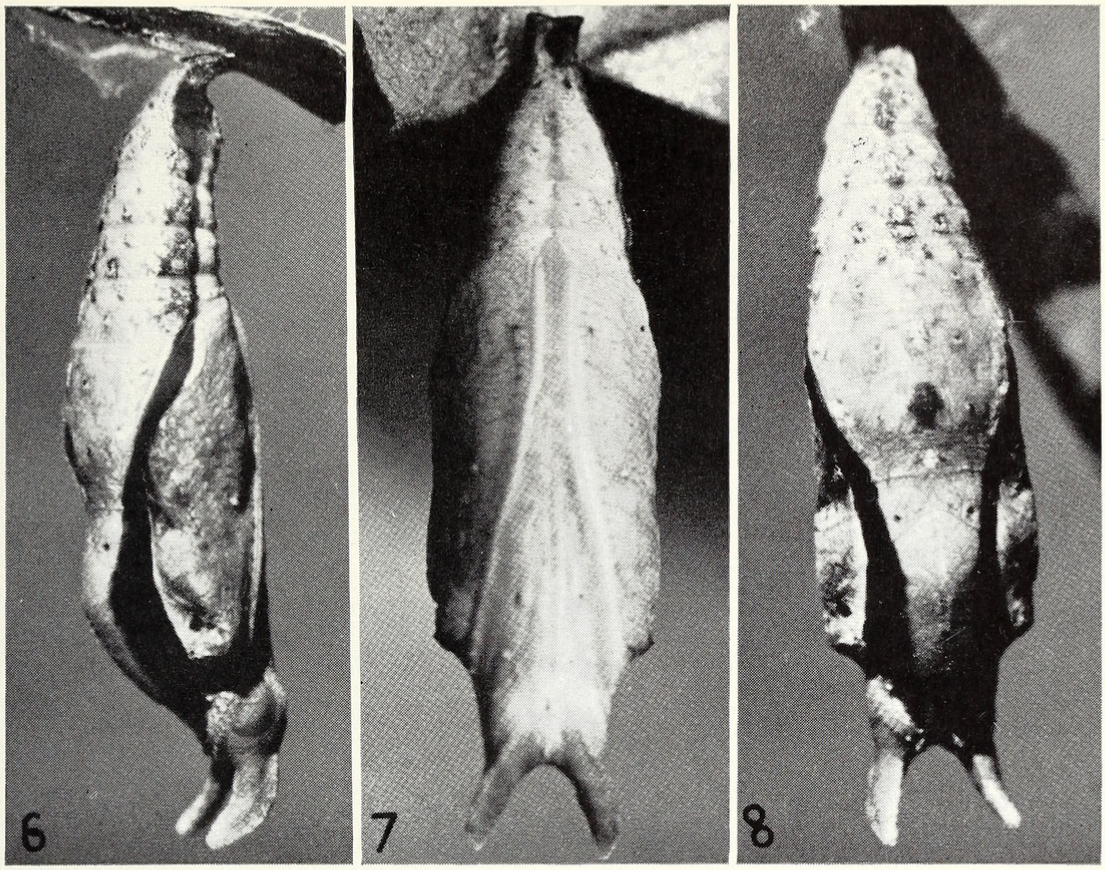
First instar larva. Head dark brown, naked, roundish. Body naked, about the same width as head, dark brown mottled with lighter tiny tubercules. About 1.8 mm. long upon emerging and 4 mm. when ready to moult in 6 days.

Second instar larva. Head dark brown with thick and short horns at apex of epicrania. Horns and sides of head with tiny spines of lighter color. Body brown with transversal rows of short forked spines, the rows being alternately dark brown and light brown in the segments. Measures about 7 mm. when ready to moult in 3 to 6 days.



FIGS. 1 to 5. *Temenis laothöe liberia.* Fabricius. 1. Egg, about 1 mm. 2. First instar larva, about 3.8 mm. Notice frass pellets stuck to the body. 3. Second instar larva, about 6 mm. 4. Fourth instar larva, about 1.5 cm. 5. Fifth instar larva, about 3 cm. Notice enlarged spines on third thoracic segment and 7th and 8th abdominal segments.

Third instar larva. Head very dark brown with long slender horns at apex of epicrania. The horns bear three transversal rows of spines, one basad, one at the middle, and the last at the tip. Spines scattered on the head, mostly at sides. Body very dark brown with longer forked spines, brown basally, light brown distally. The spines are located in the following order, as seen laterally: on first thoracic segment (T-1), two simple spines on the shield, one forked spine supraspiracularly, and one simple spine subspiracularly. On T-2 and T-3, one prominent forked spine subdorsally, one smaller forked spine supraspiracularly, and one simple spine subspiracularly. On first abdominal segment (A-1), one forked spine subdorsally, one forked spine subspiracularly. From A-2 to A-6, one forked spine subdorsally, one forked spine supraspiracularly, one forked spine subspiracularly, and one simple spine supraventrally. On A-7 and A-8, one prominent forked spine at meson, one forked spine subdorsally, one forked spine supraspiracularly, and one forked spine subspiracularly. On A-9, one forked spine directed caudad supraspiracularly. Measures 1.1 cm. before moulting in 4 to 7 days.



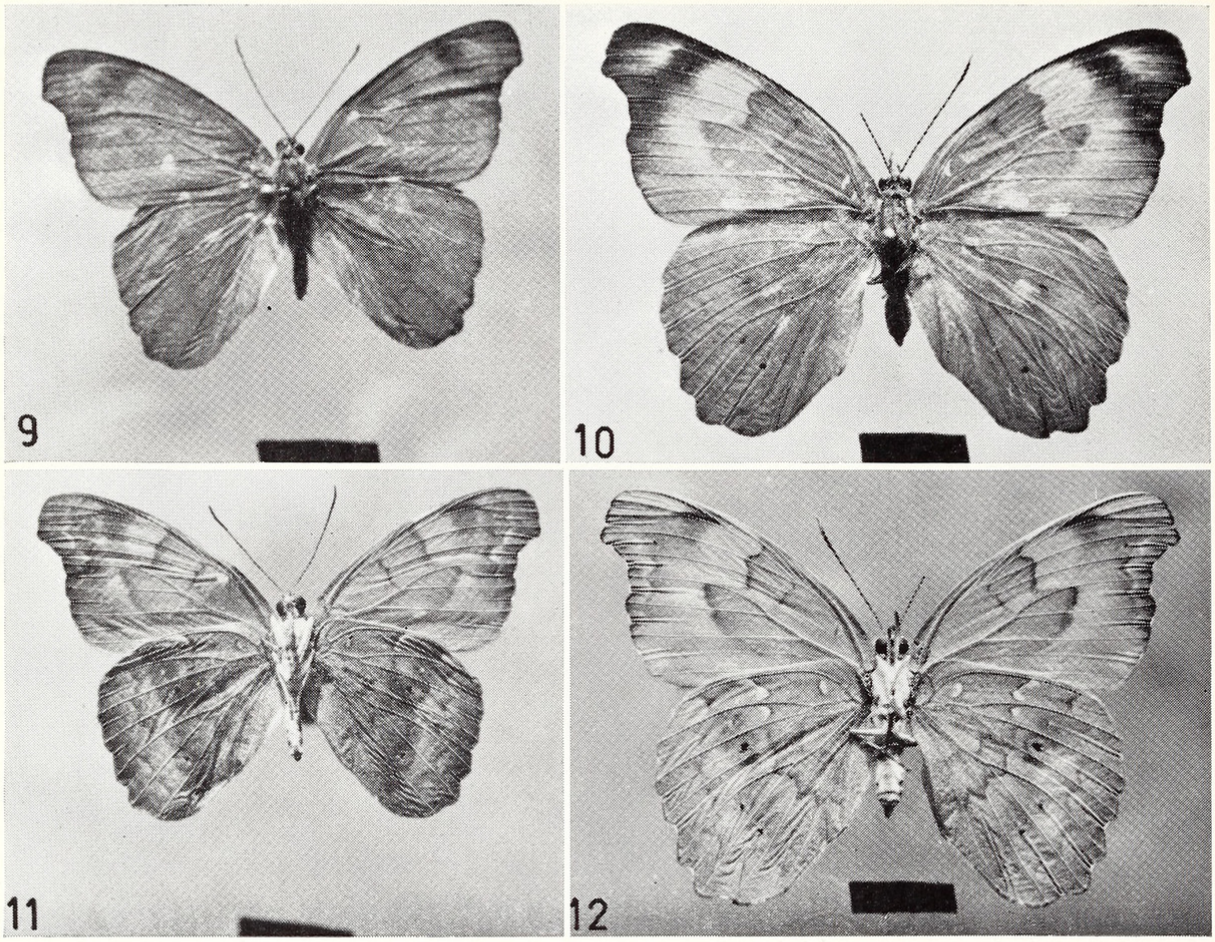
FIGS. 6 to 8. *Temenis laothöe liberia.* 6. Pupa lateral aspect. 7. Pupa ventral aspect. 8. Pupa dorsal aspect.

Fourth instar larva. Head as in third instar with longer horns, slightly incurvated posterad, with lighter color between rosettes of spines. The apical rosette has the spines blunted and swollen at the tip. Spines at sides of head long and slender; spines on frons short, stubby, and whitish. Body lighter brown than in third instar, with segments alternately brown and light brown (A-2, A-4, and A-6). Subdorsal spines on T-3 and the median spine on A-7 and A-8 swollen and clubbed with a crown of fine spines around the tip. Some spines have a metallic blue pinaculum. Measures 1.8 cm. before moulting in 5 to 6 days.

Fifth instar larva. Head as in fourth instar but with longer, thicker horns whose shafts are covered by visible but minute sharp tubercules between the rosettes of spines. Body shows a drastic change of color: It is now mostly green from A-1 caudad, with a longitudinal dark brown band spiracularly, originating from dark brown thoracic segments, terminating around A-8. From this band arise several dorsal transversal stripes on A-3, A-5, and A-7, and diagonal infiltrations into ventral area, the stripes and infiltrations of the same dark brown color. Subdorsal spines on T-3 and median spines on A-7 and A-8 long and greatly thickened and clubbed, covered by tiny sharp tubercules, with a crown of spines distally. It grows to about 3 cm. in 5 to 8 days.

Prepupa. No color changes, but the larva shortens and thickens considerably. Lasts one day.

Pupa. Long and slender. Abdomen thickens gradually from flat cremaster to wingcases which are the widest and thickest point laterally and dorsoventrally, then tapers gradually to bifid head, which terminates in two prolongations flat and slightly incurved dorsad.



FIGS. 9 to 12. *Temenis laothöe liberia*. 9. Male, dorsal aspect. 10. Female, dorsal aspect. 11. Male, ventral aspect. 12. Female, ventral aspect. Black bar 1 cm.

General color light green with dark green lining dorsally along wingcases and along the cephalic prolongations. Sparse brown spots along abdominal meson and spiracular zone. Measures about 2.5 cm. long, 0.8 cm. laterally and dorsoventrally, at widest point. Duration nine days.

Adults. Very little sexual dimorphism in this species. Both sexes have the same shape and about the same color. Forewing with a projecting angle at apex of front wings, followed by a concavity to vein M3, then a slight convexity to tornus; inner margin straight. Hind wing rounded with sinuose outer margin and a fold at inner margin.

Wings dorsally orange of various shades, darker at apex of front wings, more so in females. Wings ventrally dull orange of various shades, with some inconspicuous "eyes" in the hindwings, again more noticeable in females. Body orange dorsally, whitish ventrally; eyes brown, proboscis orange, as well as the antennae, which show whitish rings between segments. The females are noticeably larger than males: 5.4 cm. in females, 4 cm. in males between apex of spread front wings.

Total developmental time for this species varies from 38 to 48 days, that of females being slightly longer than of males.

NATURAL HISTORY

The females of *Temenis laothöe liberia* oviposit, usually from 1000 to 1500 hrs, on various wild vines of the Sapindaceae family, belonging to the genera

Paullinia, *Serjania*, *Urvillea* and *Cardiospermum*, with a definite preference for *Paullinia fuscescens* H.B.K.

Paullinia fuscescens is a scandent plant with biternate, winged-petiolated, lustrous, glabrate, and persistent leaves composed of sparsely serrate-dentate leaflets, from 3 to 7 cm. long. The inflorescence is axilar, pedunculate, with small whitish flowers that produce reddish, three-angled, thick-skinned capsules that open when mature, revealing up to three black seeds, half covered by a spongy, white arillum.

Many vines belonging to the Sapindaceae are used in the tropics by the natives to stun fish in streams and lakes. They are known locally under the common name of "barbasco." Wells (1857) gives a description of a fishing party in Honduras, which poured a decoction of a Sapindaceae vine (possibly a *Paullinia*) into the stream of Almendares River in Olancho. Standley (1923) says about *Paullinia*: "The crushed plants of various species of *Paullinia* and related genera are often thrown in streams to stupefy fish." And he says about *Serjania* (alternate foodplant for *Temenis l. liberia*): "All the species are believed to possess narcotic poisonous properties of varying intensity, and some of them are employed for stupefying fish." Standley and Calderon (1941) say about *Paullinia fuscescens*: "Los tallos estrupados son puestos en el agua como un estupefaciente para entorpecer los peces." ("The crushed stems are placed in water as a narcotic to anesthetize the fish.")

The females of *T. laothöe liberia* oviposit their eggs on the underside of mature leaves of the foodplants, one on each leaf, not in clusters. When two or more eggs are found on the same leaf, more than one female has oviposited.

Recently emerged larvae eat the top of the eggshell and at times parts of the walls but always leave at least a recognizable portion of the eggshell. Soon after emerging the larvae move to the edge or the tip of the leaf, nibble around the end of a vein, and affix to the bared vein pellets of frass stuck with silk, until the vein seems to project beyond the leaf limits. To do this, the larvae bend the body until they can grab with their months the pellet as it is expelled from the anus and proceed to place it on the bared vein. At times they affix the pellets to their own body. First and second instar larvae stay on the bared vein most of the time, often holding to it with only the prolegs, the anterior part of the body slightly raised. They leave their resting place only to feed, usually at dawn or at dusk. From third instar stage on, the larvae abandon their vein and stay on tops of leaves, at times with the anterior part of the body raised; they adopt two typical attitudes, one S-shaped, the other straight, but in both cases the head is bent forward so that the horns are parallel to the leaf surface. When crawling to another place, larvae move their heads from side to side, laying footholds of silk with the spinnerets on the leaves. When prodded with a sharp object the larvae strike viciously with their horns, a behavior which also occurs when two larvae meet on the same leaf. At time of pupation, the

larvae weave a silken mat over or under a leaf or a twig and affix their anal prolegs thereon. The larvae shorten and thicken considerably. In the process they expel an amount of liquid mixed with excrements to clean their digestive tract. The larvae do not hang as most do, but keep parallel to the supporting surface.

The pupae are usually hidden among the abundant leaves of their foodplant, but some of them are found over the uppermost leaves. Due to the flat surface of their cremaster they practically "stand" on the supporting surface. When disturbed they wriggle or move vigorously in an accordion-like manner, producing an audible creaking sound that is similar to the one emitted by cerambicid beetles.

Adults emerge from the pupa shell rapidly and find an appropriate place from which to hang until their wings are rigid, meanwhile ejecting a reddish-brown meconium. The adults of *T. laothöe liberia* dwell on treetops, returning to the ground to feed on fermenting fruits or vertebrate excrements. Females are often seen flying at lower levels in search of the foodplant for the purpose of ovipositing. Males show a marked territorial-defense behavior. Recently emerged females we have dissected did not have eggs in their abdomen.

We have reared this species a number of times during the rainy and part of the dry season (June to February) and up to the present never have found any cases of parasitism.

DISCUSSION

Seitz (1914) describes the larva and the pupa of the genus *Temenis* Hübner as follows: "The larvae are green with a cordiform head bearing two long horns furnished with rosettes of accessory spines; the dorsal spines are reduced in number, somewhat irregular, those on the 3rd. and 11th. segment thickened in the shape of a clavola; the pupa is green with fine red markings and two points on the head." Unfortunately, no mention of the foodplant is made.

The genus *Temenis*, if judged by the close morphological similarities existent in the respective early stages, is very closely related to the genera *Catonephele, Epiphile, Pseudonica, Pyrrhogyra,* and, according to Ebert (1969), to the genera *Cybdelis* and *Myscelia*, which he groups under the Catonephelinae. This group on the other hand seems to be very closely related to Ebert's grouping of Callicorinae (which comprises the genera *Callicore, Diaethria, Paulogramma,* to which we add *Catagramma*). Seitz calls the Catonephelinae, Group G.: Epicaliidi and the Callicorinae; Group H: Catagrammidi. Some modern authors lump the two groups, with other genera not so closely related (*Mestra, Hamadryas, Biblis*), under the tribe Ergolini (Ehrlich and Ehrlich, 1961) or under the subfamily Ergolinae (Klots, 1960), but they warn that the present status of the classification within the Nymphalidae is confused and the groupings in many instances are arbitrary. We use Ebert's system because it seems more in

accordance with reality, based on what modern authors state (Ford, 1945; Brower, Brower, and Collins, 1963; Crane, 1957), that morphological and behavioral characteristics in the early stages are as important as wing venation and structure of the genitalia in the adults for accurately establishing the phylogenetic relationship of the genera. Comparing the photographs and descriptions of the early stages and behavior in our presentation of *Catonephele numilia esite* Felder and of *Epiphile adrasta adrasta* (Muyshondt, 1973b and c), the reason for preferring Ebert's classification is evident, as will also be our opinion regarding the close affinity of the Catonephelinae with the Callicorinae when the future article on *Diaethria astala* Guérin will be presented.

T. laothöe liberia, like most Catonephelinae and Callicorinae, feed exclusively during the larval stage on plants belonging to the Sapindaceae. The only exceptions found so far are *Catonephele numilia esite* and *C. nyctimus* Westwood, which feed on Euphorbiaceae; but Röber (1915) says: "According to Müller the following is to be said [referring to the genus *Myscelia*], about the early stages: Foodplant of *M. orsis* is *Daleschampia triphylla* Lam" (*Daleschampia* is another Euphorbiaceae), and about *Callicore meridionalis*: "The larva lives on *Trema micrantha* Dell." *Trema micrantha* (an Ulmaceae) abounds in El Salvador in the same localities as the Sapindaceae, but so far no Callicorinae have been found there, so this may be a case of misidentification of the plant or an instance when a larva ready to pupate was collected on that plant by Müller after it had abandoned a Sapindaceae vine.

T. laothöe liberia prefers *Paullinia fuscescens* but also uses several species of the genera *Serjania, Urvillea*, and *Cardiospermum*. Most, if not all, of these plants are reputed to contain noxious substances; therefore, it would be expected than an animal feeding on them would accumulate in its body sufficient poisonous material to cause it to be avoided by predators. It is generally accepted that Lepidoptera protected by toxic components of their food plants have evolved gaudy and showy warning coloration in all stages combined with fluttery flight of the adults. In this way, they avoid automatic rush attacks by predators. Contradictory to this, the larvae of *T. laothöe liberia* seem to depend on crypsis for their survival. First and second instars remain motionless through the day on their prolonged vein, looking very much like remnants of leaf tissue on it. They move away from the vein only to feed at dawn or at dusk, minimizing the chances of being perceived. During the subsequent stadia the larvae favor the upper surface of the leaves where the third and fourth instar larvae, owing to their dark brown color, can be taken for bird excrement, mostly when they assume the S attitude. The fifth instar larvae are hard to notice because their shape is concealed by the cryptical combination of green and dark brown colors. The pupae also have an effective camouflaging combination of different shades of green to dissolve their contours among the shady leaves.

Conversely this species seems to be losing the mechanical defense against predators that the horns armed with sharp accessory spines provide *Catonephele numilia esite*, because in *T. laothöe liberia* the accessory spines are found to be thick and blunt. This alteration may indicate an evolutionary deterioration of mechanical defenses as a result of the defensive superiority of unpalatability from the noxious components of their foodplant. The orange coloration of the adults also points in this direction: instead of the flash-and-hide effect related species derive from their brilliant dorsal colors contrasted with the dull brown of their underwings (*C. n. esite, C. nyctimus, Epiphile a. adrasta*, etc.), *Temenis laothöe liberia* (and *Pseudonica flavilla canthara* Doubleday) are orange all over, making them very conspicuous against the green background of the leaves. But it is true that their flight is still faster than the species traditionally considered distasteful (*Danaus plexippus, Heliconius petiveranus, Battus polydamas*, etc.). Another characteristic this species has lost is the puzzling sexual dimorphism other Catonephelinae (*C. numilia, C. nyctimus,* and *E. adrasta*) exhibit, even if the benefit that dimorphism represents in their case is not clear, as neither sex imitates any of the local protected species, thus eliminating the logical explanation of a Müllerian mimicry.

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