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ADELPHA (NYMPHALIDAE): DECEPTION ON THE WING*

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INTRODUCTION

For the past century, lepidopterists have puzzled over the genus *Adelpha* Hübner, in an attempt to discover the secret character or combination of characters which might lead to a satisfying classification of the 100 or more butterfly species included in this large neotropical group. Several approaches have been tried (Godman & Salvin, 1884, 1901; Fruhstorfer, 1907; Forbes, unpublished manuscript): wing pattern (both upperside and lowerside), wing venation, genitalia, and various combinations of these. If one attempts to coordinate all the information available, the result is a hopeless tangle. As a result, the most obvious set of characters (wing pattern) traditionally has been used in classification; other character groups (genitalia, larvae, pupae) which appear to confuse the situation have been largely ignored. A new strategy is needed, one which would both evaluate the reliability of the different groups of characters already surveyed, and search anew for overlooked sources of information. It was the purpose of my research to review what is known of the immature stages of *Adelpha* species and, based upon that information plus my own observations made in Panama between 1978 and the present, to make speculations regarding species relationships.

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History of Classification

The first attempt at classification within *Adelpha* was made by Godman & Salvin (1884, 1901) with their revision of the 32 species reported from Central America. At that time some 70 species were known for the genus. In their treatment, Godman & Salvin discuss *Adelpha* and its relationship to *Limenitis* and note that several species *(bredowi, populi, camilla, lorquini)* are difficult to assign to either genus. Distribution of such characters as eye pubescence, venational differences, variation in proportions of male leg segments, and peculiarities of male genitalia within *Adelpha-Limenitis* is surveyed. Classification of the 32 species begins with isolation of *A. bredowi* (eyes smooth in front) from all others (eyes hairy in front) and continues by arranging the other 31 species using gross features of wing pattern. The result is eleven groups, six of which are represented by single species.

With Fruhstorfer (1907) came the first and only published revision of the entire genus *Adelpha.* The 90 species treated are assigned to two main groups based upon the length of the forewing discal cell; short = *Adelpha* group, elongate = *Heterochroa* group. Upon this division, Fruhstorfer comments, "Anatomically there are also two series [male genitalia with or without clunicula] of species distinguishable. They, however, do not agree with those based upon the structure [discal cell length]." The linear arrangement of species within the largest group (*Heterochroa* with 82 species) reflects presumed relationships based upon wing pattern features.

Fruhstorfer touches upon but does not pursue the possibility of a closer than realized alliance between New and Old World groups. In his introduction he notes that the male clasping organs of *Adelpha* "...approach those of the [Old World] genus *Pantoporia (Athyma)* in such a way that...it would be quite impossible to ascertain where organs or photes [sic] of them belong to, which are not denominated." Concerning the male valves, he further observes, "...there exist also nearly square ones with 2 or 3 small acicular teeth (resembling a *Limenitis [Moduza] procris* from India and Ceylon)."

Fruhstorfer's revision included a number of misidentifications, which presumably were corrected by Hall (1938) following examination of the original material.

At the time of his death (1968) W. T. M. Forbes had made a good deal of progress on a revision of *Adelpha,* and his manuscript is in

the Archives of the Museum of Comparative Zoology, Harvard University. About half of this manuscript is in a nearly illegible hand; half is typewritten. The typed portion includes part of an introduction, notes on each species, a key (based upon wing pattern) to species and species groups, and descriptions of four new species. Included also are more than 70 genitalic illustrations (inside of right valve) by Howarth. Forbes had analyzed these latter and was in the process of constructing a key to genitalia. His two approaches, of wing pattern and genitalia, yielded different species groupings, and it is not clear whether he favored one of these, or intended to use a combination of the two in his final classification.

Of the immature stages of *Adelpha,* very little has been said, and what has been said has been largely ignored for the simple reason that this new information appears to confuse matters rather than clarify them.[1] Forbes (uncompleted manuscript) had read Moss's (1933) paper on *Adelpha* larvae and pupae, and had examined several pupal skins of *Adelpha* and Old World Limenitini in the collections of the British Museum (Natural History) when he commented, "The larvae and pupae are highly varied and unless a high percent are misdetermined, show characters wholly incongruent with adult structures and patterns."

The fact that, within *Adelpha,* the study of adult characters results in species-alignments different from those obtained by consideration of the immature stages and/or genitalia, suggests that at least one set of characters is unreliable or perhaps even deliberately deceptive.

Immature Stages

Due to taxonomic confusion within *Adelpha,* it is impossible to know how many species actually are represented by the 34 or so life history accounts published for this genus. My estimate is that at least 24 species are illustrated (including illustrations in this paper) as final instar larva, or pupa, or both, many of these by more than one author. Most accounts, whether illustrated or not, include a foodplant record.

[1]This author has located only four publications (Moss, 1933; Müller, 1886; Young, 1974; Comstock & Vasquez, 1960) which figure any immature stages of *Adelpha;* several publications present descriptions only.

In the present paper, all illustrated reports are reviewed to see whether it is possible to distinguish natural species groups within the genus *Adelpha.*

Oviposition

Judging from the few scattered reports (Table 1) of oviposition in the Limenitidini, eggs are laid singly and are usually placed at the tips of leaves. While many accounts do not specify whether placement is on the upper or lower surface, the majority that do specify, report upper surface oviposition.

Adelpha iphicla females alight upon a leaf and walk backwards while searching for the desired oviposition site with the tip of the abdomen; the egg is then placed and the butterfly takes flight before her next oviposition, which may be on the same leaf. In the case of lower surface oviposition, the female merely bends her abdomen around the edge of the leaf and touches its tip to the leaf.

Among the six species of *Adelpha* whose eggs were collected in Panama, four (Table 1) place their eggs along damaged portions of leaves, especially on jagged points, as well as at the leaf tip, and one of these *(A. iphicla)* is about as likely to lay eggs along an intact leaf margin as at the tip. As well, a female *A. iphicla* may return to the same leaf several times and place as many as four eggs on one leaf, often on its undersurface.

Eggs

Eggs of the seven *Adelpha* species (*basiloides, cocala, cytherea, marcia, iphicla, melanthe, phylaca aethalia,* and *salmoneus*) examined by this author, were all similarly sculptured (figure 1) with pits (hexagonal due to packing) and seta-like projections (one from each junction of three pits). This same sculpture type is figured for *Limenitis* by both [2]Scudder (1889) and Eltringham (1923).

Young's (1974) description of the egg of *Adelpha leucophthalma* as having the seta-like projections "aris[ing] from the facets," is doubtful.

Also doubtful is the account by Comstock and Vazquez (1960) which describes and illustrates the egg of *A. celerio* as having convex rather then concave hexagons. Such an error is easily made, as these

[2]As *Basilarchia.*

Table 1. Placement of egg on leaf by various members of the Limenitidini (Nymphalidae)

BUTTERFLY SPECIES	EGG PLACE-MENT	REFERENCE
Adelpha basiloides Bates	T↓, D↓	Aiello
Adelpha celerio diademata Fruh.	T	Comstock & Vazquez (1960, pg. 407)
Adelpha cocala Cr.	T↓, (D↓)	Aiello
Adelpha cytherea (?)	↑	Müller (1886, pg. 484)
Adelpha iphicla L.	T↓(↑), M↓(↑)	Aiello
Adelpha iphicla	↑	Müller (1886, pg. 484)
Adelpha isis Dru.	T↓, D↓	Müller (1886, pg. 481)
Adelpha leucophthalma tegeata Fruh.	D↓	Young (1974, fig. 2)
Adelpha melanthe Bates	D↓	Aiello
Adelpha phylaca aethalia Feld.	T↓	Aiello
Adelpha plesaure	T↓	Müller (1886, pg. 484)
Adelpha salmoneus Butl.	T↓, (D↓)	Aiello
Adelpha serpa	T↓	Müller (1886, pg. 484)
Adelpha syma Godt.	T	Hoffmann (1937, pg. 212)
Athyma nefte Cr. (as *Parathyma nefte* Cr.)	T↓, (M↑)	Morrell (1954, pg. 160)
Athyma opalina Kollar	↑	Robson (1894, pg. 338)
Lasippa tiga Moore (as *Neptis heliodore* Fruh.)	T	Morrell (1954, pg. 160)
Limenitis archippus (as *Basilarchia archippus)*	T↑	Scudder (1889, fig. 16)
Limenitis lorquini burrisonii Maynard	T	Dornfeld (1980, pg. 61)
Moduza procris Cr.	T	Morrell (1954, pg. 157)
Neptis nata Moore	T	Morrell (1954, pg. 162)

T = leaf tip (tooth, in case of *A syma*), M = leaf margin (intact), D = damaged portion of leaf, ↓ = upper surface of leaf, ↑ = lower surface of leaf, ( ) = less commonly

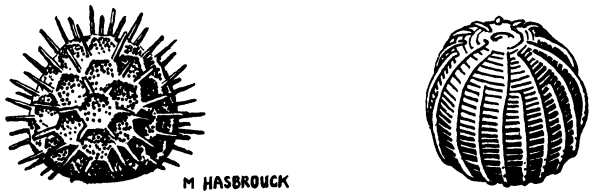

Figure 1. Eggs of *Adelpha* (left) and *Doxocopa* (right).

eggs can present an optical illusion, however, an edge view of a partly eaten egg shell shows clearly that the hexagons are indeed pits.

Comstock and Vazquez (1960) also describe and figure a differently sculptured egg, which they call *A. iphicla* with the reservation that it might actually be an egg of [3]*Doxocopa.* Because their larvae died soon after hatching, the authors never knew that they had indeed been fooled by the ovipositing *Doxocopa* female, a mimic of *Adelpha.* My own rearing of *Doxocopa laure* (LOT 83-6) was from two eggs with pattern (figure 1) identical to that in figure 33 of their paper. My reared *Adelpha iphicla* were from eggs patterned as those of all the other *Adelpha* species examined so far. Possibly this egg sculpture pattern will be found throughout the Limenitini and may prove useful in defining tribal limits.

Development Time

Oviposition was observed only for *Adelpha iphicla,* and each of the three fresh eggs collected required 5 days development before the first instars emerged. Of five other species collected as eggs, of unknown age, three had longer minimum egg-development times than did *A. iphicla: A. basiloides* (LOT 82-65), one egg hatched after 6 days; *A. cytherea* (LOT 83-3), one egg hatched after 7 days; and *A. salmoneus* (LOT 83-14), two eggs hatched after 6 days.

Because individuals were collected at various stages of development, total time from hatching to eclosion could be determined for only a few individuals of ten species. In spite of the fact that the resulting data (Table 2) is not uniform, it is clear that development time is variable, and often more so within a species than between species. The extreme example of wide variation is in *A. basiloides* which has a longer development time than other species, and which sometimes passes through six instars instead of the usual five. Five 6-instar individuals of *A. basiloides* were encountered, and these were from four separate rearing lots, each of which included 5-instar individuals as well. Each of these lots was collected on *Amaioua corymbosa;* larvae collected on *Alibertia edulis* and *Bertiera guianensis* did not produce extra instars. In spite of the additional instar, 6-instar individuals did not require longer development times

[3]As *Chlorripe.*

than 5-instar individuals, however, larvae on *Amaioua,* regardless of number of instars, were slower to develop (41–48 days) than were larvae on *Alibertia* or *Bertiera* (32–44 days).

LARVAE

Miles Moss reared twelve species of *Adelpha* from Pará, Brasil, and illustrated (1933) the final instar larva and the pupa for each of them. In spite of the lack of detail in his illustrations and descriptions, and the fact that his scheme for numbering body segments omits abdominal segment-9, his little paper remains the masterpiece on *Adelpha* immatures. It was Moss who realized (page 15) that:

> "...systematists,...by a careful examination of certain hitherto unsuspected points of likeness or dissimilarity between the species in their early stages, may perhaps be led to modify the existing order and grouping of the butterflies of this difficult genus. It is just possible that a few unexpectedly close relationships may thus be established, while others at present confused, or regarded as near of kin, may be found to be more distantly related than was supposed."

He concluded that *A. cytherea,* and *pseudococala* are closely related, also *delphicola* and *mesentina,* and *serpa* and *paraëna*. My analysis of published illustrations and live material lends support to Moss's groupings and adds several more.

FIRST INSTAR LARVAE

First instar larvae, of all species which I have seen, appear identical in form, and are some shade of brown or grey. The head bears setae, but none of the ^{4}chalazae of later instars; pale bumps on the body are found where the future ^{4}scoli will be, and the body is covered with tiny pale spots each centered with a minute seta. After their first meal, larvae take on the green color of their foodplant, although the head remains brown.

SECOND INSTAR LARVAE

From the second instar on, the head is ornamented with chalazae which give it a spiny appearance. The face has numerous round,

Table 2. Duration (in days) of larval instars and pupal stage for twelve *Adelpha* species.

Species	Instar 1	2	3	4	5	6	Pupa	Total Time 1–Adult
basiloides (5-instar)	4–7	3–8	3–6	4–10	6–14	–	8–11	39–48
	[10]	[15]	[17]	[21]	[18]		[20]	[9]
basiloides (6-instar)	m6	6–7	4–7	3–(4)	3–6	7–11	8–11	48
	[1]	[4]	[5]	[5]	[5]	[5]	[5]	[1]
celerio	–	–	m3	8	11	–	10	–
			[1]	[1]	[1]		[1]	
cocala	4, 5	3–5	4–5	4–(6)	7–13	–	8–11	35, 39
	[2]	[4]	[5]	[8]	[7]	–	[7]	[2]
cytherea	4	3, 4	3, 4	(3), 10	(6)–10	–	7, (9)	28
	[1]	[2]	[2]	[3]	[4]	–	[4]	[1]
iphicla	(4), 7	(3)–7	(3)–6	1–7	4–10	–	7–10	29
	[4]	[11]	[23]	[24]	[32]	–	[27]	[3]
isis (in Müller, 1886)	5	6	4	5	9	–	13	42
	[1]	[1]	[1]	[1]	[1]	–	[1]	[1]
justina	m4	4	3, 4	3, 4	4–6	–	6–9	m30
	[2]	[2]	[3]	[3]	[3]	–	[4]	[1]

Table 2. (Continued) Duration (in days) of larval instars and pupal stage for twelve *Adelpha* species.

Species	Instar 1	2	3	4	5	6	Pupa	Total Time 1–Adult
leucophthalma	–	6 [1]	4 [3]	4, 5 [3]	6–(7) [4]	–	9 [3]	–
melanthe	m5 [1]	m4 [2]	4 [1]	4 [1]	10 [1]	–	10 [1]	m37 [1]
nr. *paraëna*	–	–	–	7 [2]	12, 13 [2]	–	10 [2]	
phylaca aethalia	m4 [1]	m4 [2]	3, 7 [2]	6, (7) [6]	7–9 [8]	–	8–11 [7]	m41 [1]
salmoneus	(4), 5 [3]	3–5 [4]	4–6 [5]	3–(5) [6]	6–12 [6]	–	9, 10 [4]	32, 35 [2]

Unless otherwise noted, the above data was collected in Panamá by the author.
[ ] = n
( ) = commonest number of days in cases of strong bias towards one end of range; otherwise, ranges are normal curves.
m = minimum number of days in cases where full time for an instar is not known.

flatbottomed pits which first appear in small numbers in instar two, three, or four depending upon the species. These may be the same color as the rest of the head capsule or may be a contrasting color. Facial stripes appear in the fourth instar of some species as well.

The body now bears stubby scoli (each with 3–5 radiating apical spines). These scoli are arranged in three rows (subdorsal, supraspiracular, and subspiracular), thus, each body segment has three pairs of scoli. The subdorsal scoli on thoracic segments 2 & 3 and abdominal segments 2, 7, & 8 are very slightly larger than the others, but all are similar in form.

Beginning with the second instar there are color and pattern changes in some species, but most are fairly uniformly colored (brown, green, or black) and have paler scoli and tiny spots, much as the first instar. In *Adelpha basiloides,* the larval color depends upon the foodplant; larvae are light brown or reddish brown on *Amaioua,* and dark brown on *Alibertia* and *Bertiera.*

THIRD AND FOURTH INSTAR LARVAE

From instar three on, the face is framed by two distinct rings of chalazae, and body scoli show further development, especially those scoli which will be the largest or most distinctive in the final instar. By late fourth instar, body scoli have become swollen at the bases due to developing final instar scoli inside. In these two instars, the scolus spines are pale, and as before, the body is speckled with tiny pale spots.

A dorsal, paler patch ("saddle") appears in the third or fourth instar of many species. In *A. salmoneus* and *cytherea* the "saddle" is faint and extends from abdominal segment 2 or 3 through segment 6. *A. cocala* and *leucophthalma* may have a "saddle" on abdominal segments 5–6. *A. justina* is pale dorsally from thoracic segment 2 through abdominal segment 8. *A. basiloides,* nr. *paraëna,* and *celerio* have a triangular "saddle" with its base on the posterior portion of abdominal segment 4, and its apex at mid abdominal segment 6. In the latter two species the "saddle" is poorly defined; in *A. basiloides* it is sharply demarcated.

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[4]Terminology of Peterson (1962). CHALAZAE(AE): a distinctly elevated cone-shaped area, bearing 1–3 simple setae; (SCOLUS(I): an elongated projection, bearing 4 or more setae or spines.

FINAL INSTAR LARVAE

Final instar larvae (Figures 4 & 5) of all species studied have several things in common. The head (Figure 2) has a spiny appearance owing to the numerous chalazae which frame the face. These seem to be fairly constant in number and position (Figure 3) and to vary from species to species mainly in their relative size. *A. iphicla* for example has a relatively smooth face because it lacks several of the chalazae found in other species. *A. phylaca* and especially *melanthe* are the spiniest in appearance due to numerous additional setae. Color and pattern also vary: *A. celerio* has a striped face, *A. basiloides* and *A. cocala* patterned ones. The pits of *A. cytherea* are darker than the rest of the face; the head of *A. salmoneus* is reddish and constrasts strongly with its green body.

Each body segment bears three pairs of scoli (subdorsal, supraspiracular, and subspiracular); there are no dorsal scoli. While the scoli are variable in form and length, in all species studied, those of the prothorax and abdomen-1 are either very short or are reduced to a few spines. Usually the longest are the subdorsal scoli of meso- and meta-thorax and abdomen-2, -7 & -8, and the supraspiracular scoli of the meso-thorax. In many species the subdorsal scoli of abdomen-2 are the most distinctive in form and often are curved backwards.

Body scoli are diverse but the various forms can be grouped into two main types: those which are terete (round in cross-section), and those which are flattened.

The terete scolus, in its simplest form, is a short stalk with 3–5 spines radiating star-like from its apex (e.g., [5]scoli A3–6 of *A. celerio, cytherea, salmoneus,* and *justina*). More complex scoli are slender and longer with spines at intervals along their full length, and either with one to a few ascending spines towards the apex (thoracic scoli of many species, e.g., *A. phylaca, melanthe, cocala, basiloides, cytherea, justina, salmoneus*), or with 3–5 radiating apical spines (e.g., scoli of A3–6 in *A. phylaca, melanthe*). Scoli also may be short and thick with a dense covering of spines (e.g., A2 of *A. cocala, leucophthalma, basiloides*), or be club-shaped and more sparsely spined (e.g., A8 of *basiloides*).

[5]Throughout the remainder of this paper, "scolus(i)" refers to the subdorsal set unless otherwise noted; T = thorax, thoracic segment; A = abdomen, abdominal segment.

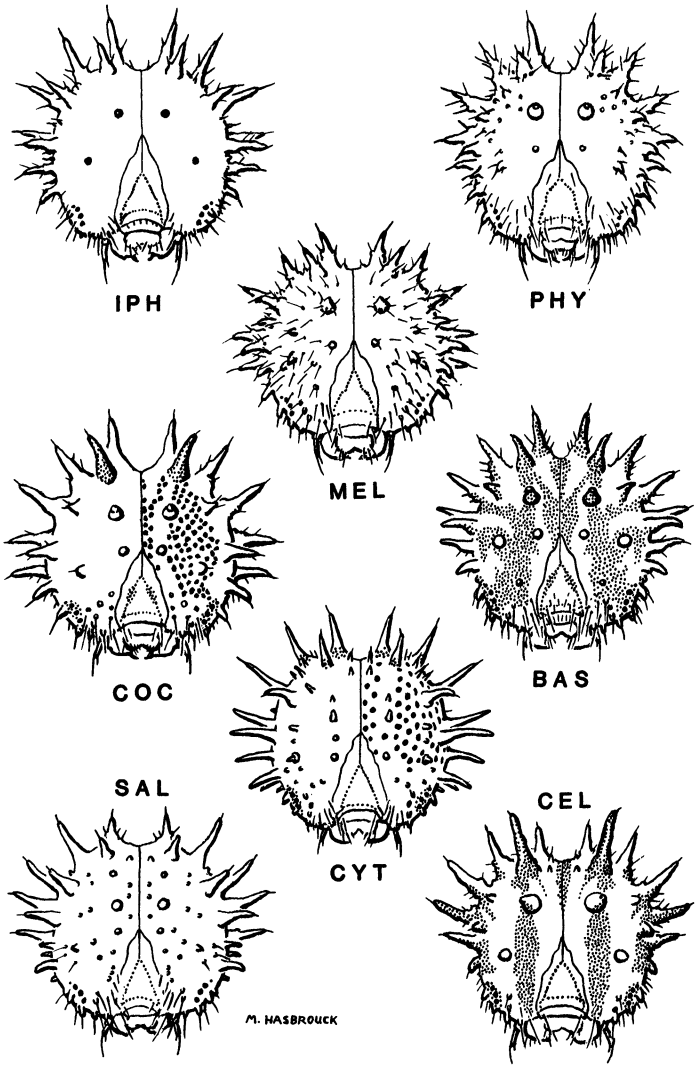

Figure 2. Faces of final instar larvae of *Adelpha* species reared in Panamá: BAS = *basiloides*, CEL = *celerio*, COC = *cocala*, CYT = *cytherea marcia*, IPH = *iphicla*, MEL = *melanthe*, PHY = *phylaca aethalia*, SAL = *salmoneus*.

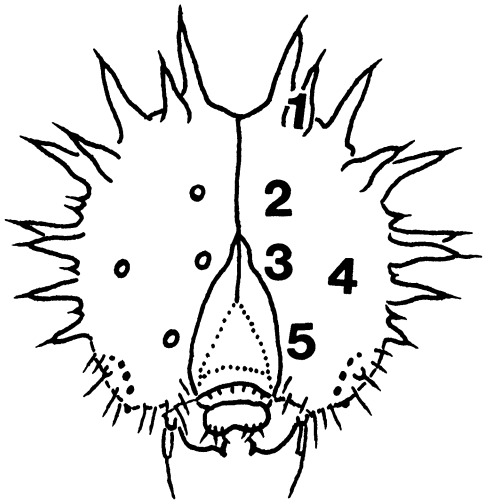

Figure 3. Location of head chalazae 1–5, referred to in text.

Flattened scoli have a plumose or leaf-like appearance (e.g., *A. celerio, serpa, paraëna*) which is due not only to the arrangement of spines in two opposite rows along the scolus, but also to the flattening and widening of those spines which may take on spatulate, elliptical, or lanceolate forms, and may be so crowded that they overlap one another. In the case of extremely condensed scoli, the spines appear to fuse with one another (see *A. serpa* in Müller, 1886).

Larval Behavior

Upon hatching, a larva eats some or all of its egg shell and then feeds on the leaf tip leaving the midrib intact. Larvae rest out on the midribs which they have exposed, and eventually extend them by addition of fecal pellets held in place with silk. Most larvae fashion several such supports during each instar, often using lateral veins instead of the midrib. When not feeding, *Adelpha* larvae rest out on their supports, facing away from the leaf; molting takes place on the support as well. After they molt to the final instar, larvae abandon their supports and thereafter rest on the upper surface of a leaf.

In addition to the above behavior, typical of many nymphalid butterfly species, first through fourth instar *Adelpha* larvae engage in an odd practice not known for other New World butterflies; they accumulate their fecal pellets, fastening them in place with silk, to form a mass which either surrounds the base of the support or is suspended beneath it. This mass may include bits of leaf in *A. iphicla,* or consist of more leaf than feces in *A. phylaca* and *melanthe.* The work of *A. basiloides* is the most distinctive because, in addition to the mass just described, this species consistently constructs a small, usually curved, larva-form mass on the leaf surface, several mm away from either the leaf edge or the usual mass. Upon viewing this artistry, one cannot help imagining that it serves as a decoy larva to discourage would-be predators. A single reared individual of *A. iphicla* also engaged in this behavior, but excepting that, I have observed it only in *A. basiloides.*

Resting larvae position their bodies in one of several ways:

(1) Straight Position (figures 4 & 5). Larvae in any instar may use this position, and typically when out on their supports they rest this way.

(2) Front-Curved Position, as shown in Young (1974, fig. 2. B, C). In this position, the larva grasps its support with the prolegs only, and raises and curves its anterior portion (head through A2) so that the head is somewhat inclined, and the toracic scoli are directed forwards. Larvae about to molt use this position; the second instar in Young's (1974, fig. 2C) photograph has a swollen pro-thorax and is probably preparing to molt to third instar. Final instar larvae of *A. justina* use a raised but uncurved version of this position instead of the usual final instar stance, described next.

(3) Front-Arched-Rear-Up Position. This position is typical of final instar larvae but occurs in earlier instars as well. Involved are the raising and arching of the anterior portion of the body (head through A2), plus elevation of the posterior portion (A7–10). In addition, the thoracic scoli are directed forwards, and those of A2 are held backwards. In this position, the face and the area at the top of the arch (T3 through A2) are parallel to each other and to the substrate. This and the next position are assumed when the larva is disturbed.

(4) Curled Position. The larva curls to one side into a "C" or "J" shape on the upper surface of the leaf; the rear portion (A7–10) may or may not be elevated. *A. celerio* often rests in this position,

and when it does, the scoli on the outside of the curve stick out all around and the animal resembles a bit of moss. Moss (1933) reported the same behavior and appearance for *A. thesprotia.*

FOODPLANTS

At first inspection, it would appear that larvae of *Adelpha* butterflies are not very particular about their foodplant selection. Indeed, some 56 plant species, representing 42 genera and 16 families have been reported as larval foodplants of *Adelpha.* Moreover, many *Adelpha* species are known to be polyphagous: *A. melanthe, delphicola,* and *isis* have each been reared on three plant genera, *A. celerio* on four, and *A. cocala* and *iphicla* each on eight. *Cecropia* (Cecropiaceae), *Sabicea* (Rubiaceae), and *Vitex* (Verbenaceae) are each attacked by five different species of *Adelpha.*

However, when larval foodplants are grouped by the butterfly species which feed upon them (Table 3), a pattern does emerge: *Adelpha* species fall nicely into two main feeding groups: (1) Rubiaceous feeders, and (2) Non-rubiaceous feeders.

With the following three exceptions, butterfly species that feed upon members of the Rubiaceae have not been reported on plants outside that family. *A. boreas tizona* was reared on both Rubiaceae and Ericaceae (Marquis and DeVries, unpublished); *A. cocala,* reared on seven members of the Rubiaceae, also has been reported on *Emmotum* of the Icacinaceae (Moss, 1933); *A. syma,* on Rubiaceae and Rosaceae. The record of *A. iphicla iphicleola* on *Celtis* (Ulmaceae) (Comstock and Vazquez, 1960) is in error; their butterfly was actually *Doxocopa,* misidentified as *Adelpha.*

It is interesting to note that the rubiaceous genera, utilized as foodplants by *Adelpha,* belong to at least seven of the 18 tribes outlined for the Rubiaceae by Kirkbride (1982).

Several non-rubiaceous feeders do show wide foodplant preferences, the extreme examples being: *A. melanthe* which feeds on three plant genera representing three families, and *A. celerio* which feeds on five genera in four families. The only common bond among the foodplants of these two butterflies seems to be that all are scabrous- or pubescent-leaved, second-growth trees. Some plants attract a more specialized group of feeders: *Vitex* (Verbenaceae) is attacked by *A. abia, calliphane, epizygis,* and *jordani,* which have not been reported on any other plants. *A. naxia ipiphilca,* also

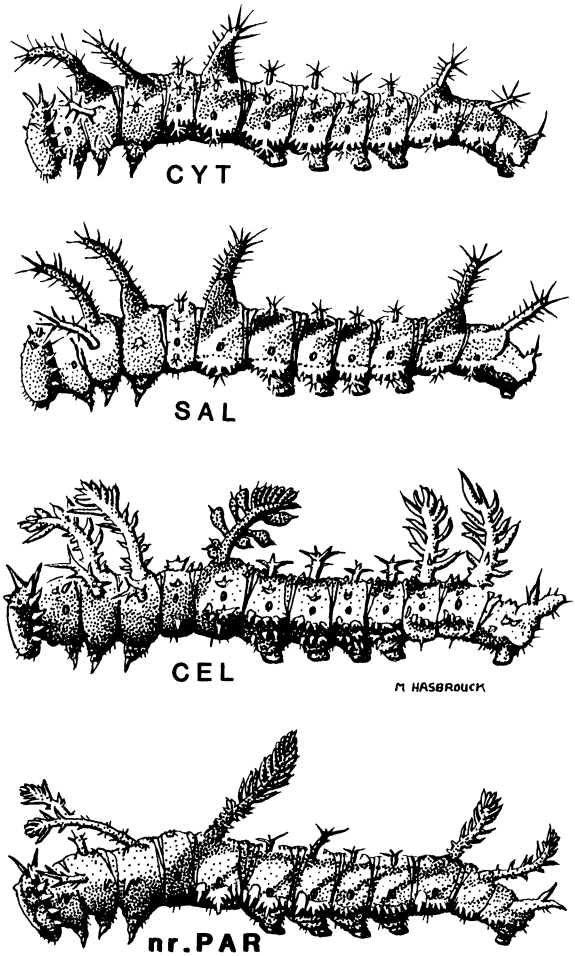

Figure 4. Final instar larvae of *Adelpha* species reared in Panamá: abbreviations are the same as in Figure 2 except that CEL = nr. CEL; in addition nr. PAR = near *paraëna*.

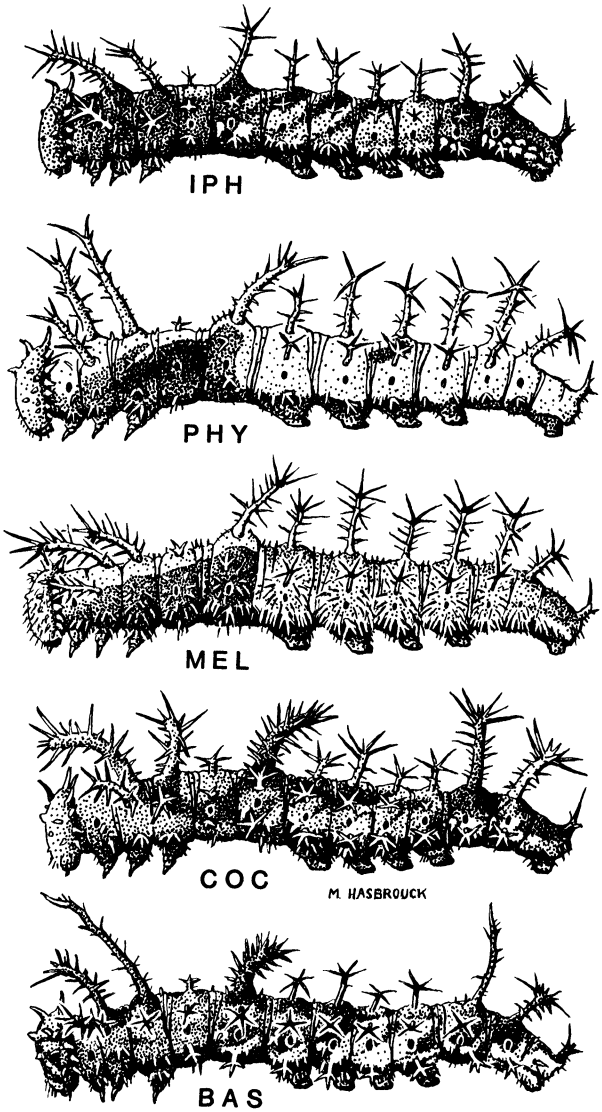

Figure 4. (Continued)

Table 3. Larval foodplants reported for *Adelpha* species, arranged alphabetically by butterfly species.

ADELPHA SPECIES/ FOODPLANT	PLANT FAMILY	LOCALITY	REFERENCE
ABIA			
Vitex sp.	Verbenaceae	Brasil	Müller (1886)
BASILEA			
Calycophyllum sp.	Rubiaceae	Cuba	Dewitz (1879)
BASILOIDES			
Alibertia edulis	Rubiaceae	Panamá	Aiello LOTS 79-121, 80-38, 81-17, 81-42, 81-49, 83-16, 83-42
Amaioua corymbosa	Rubiaceae	Panamá	Aiello LOTS 82-59, 82-65, 82-70, 82-72, 83-42
Bertiera guianensis	Rubiaceae	Panamá	Aiello LOTS 82-64, 82-73, 83-87
Ixora nicaraguensis	Rubiaceae	Panamá	Mallet in DeVries (unpub)
BOETIA OBERTHURI			
Luehea seemannii	Tiliaceae	Costa Rica	Mallet in DeVries (unpub)
BOREAS TIZONA			
Satyria sp.	Ericaceae	Costa Rica	Marquis in DeVries (unpub)
Chomelia bispinosa	Rubiaceae	Costa Rica	DeVries (unpub)
BREDOWI CALIFORNICA			
Quercus chrysolepis	Fagaceae	California	Orsak (1977)
Quercus spp. (especially *chrysolepis*	Fagaceae	California	Howe (1975)
Quercus spp.	Fagaceae	California	Dornfeld (1980)
BREDOWI EULALIA			
Quercus spp.	Fagaceae	Mexico, US	Ferris & Brown (1980)
CALLIPHANE			
Vitex montevidensis	Verbenaceae	Brasil	cited in Lima (1968)
CALLIPHICLEA			
Ilex paraguariensis	Aquifoliaceae	Paraguay	Jorgensen (1921)
CELERIO			
Cecropia peltata	Cecropiaceae	Panamá	Coley LOT 15
Miconia argentea	Melasto-mataceae	Costa Rica	Mallet in DeVries (unpub)
Ochroma pyramidale	Bombacaceae	Panamá	Aiello LOT 82-41
Ochroma pyramidale	Bombacaceae	Panamá	Coley LOT 22
Urera sp.	Urticaceae	Costa Rica	DeVries (unpub)

Table 3. (continued)

ADELPHA SPECIES/ FOODPLANT	PLANT FAMILY	LOCALITY	REFERENCE
CELERIO DIADEMATA			
Conostegia xalapensis	Melasto-mataceae	Mexico	Comstock & Vazquez (1960)
Miconia sp.	Melasto-mataceae	Mexico	Comstock & Vazquez (1960)
nr. CELERIO			
Heliocarpus popayanensis	Tiliaceae	Panamá	Aiello LOTS 82-75, 83-68
COCALA			
Calycophyllum candidissimum	Rubiaceae	Panamá	Aiello LOT 81-44
Calycophyllum candidissimum	Rubiaceae	Costa Rica	Janzen 81-SRNP-740 in DeVries (unpub)
Chomelia psilocarpa	Rubiaceae	Panamá	Aiello LOT 81-14
Emmotum nitens?	Icacinaceae	Brasil	Moss (1933)
Malanea sp.	Rubiaceae	Brasil	Moss (1933)
Pentagonia macrophylla	Rubiaceae	Costa Rica	DeVries (unpub)
Psychotria sp.	Rubiaceae	Costa Rica	Marquis in DeVries (unpub)
Uncaria tomentosa	Rubiaceae	Panamá	Aiello LOT 81-54
Warscewiczia coccinea	Rubiaceae	Panamá	Aiello LOT 82-66, 82-71, 82-74
CRETON			
Quercus?	Fagaceae	Mexico	Miller & Miller (1970)
CYTHEREA			
Sabicea aspera	Rubiaceae	Brasil	Moss (1933)
CYTHEREA MARCIA			
Sabicea panamensis	Rubiaceae	Panamá	Aiello LOT 83-129
Sabicea villosa	Rubiaceae	Panamá	Aiello LOTS 82-26 83-3
Sabicea villosa	Rubiaceae	Costa Rica	DeVries (unpub)
DELPHICOLA			
Bombax munguba	Bombacaceae	Brasil	Moss (1933)
Cecropia sp.	Cecropiaceae	Brasil	Moss (1933)
Pourouma sp.	Cecropiaceae	Brasil	Moss (1933)
DEMIALBA			
Rondeletia sp.	Rubiaceae	Costa Rica	Haber in DeVries (unpub)
DONYSA			
Quercus?	Fagaceae	Mexico	Miller & Miller (1970)

Table 3. (continued)

ADELPHA SPECIES/ FOODPLANT	PLANT FAMILY	LOCALITY	REFERENCE
EPIZYGIS			
Vitex montevidensis	Verbenaceae	Brasil	cited in Lima (1968)
EROTIA			
Tetrapteris sp.	Malpighi-aceae	Brasil	Müller (1886)
FESSONIA			
Randia echinocarpa	Rubiaceae	Costa Rica	Janzen 79-SRNP-216 in DeVries (unpub)
Randia learstenii	Rubiaceae	Costa Rica	Janzen 79-SRNP-725 in DeVries (unpub)
IPHICLA			
Antirrhoea trichantha	Rubiaceae	Panamá	Aiello LOTS 81-25, 82-27, 83-41
Alseis blackiana	Rubiaceae	Panamá	Aiello LOTS 82-36, 82-56, 82-63, 82-69
Bathysa sp. nr. *barbinervis*	Rubiaceae	Brasil	Müller (1886)
Calycophyllum candidissimum	Rubiaceae	Panamá	Aiello LOTS 81-34, 81-78
Calycophyllum candidissimum	Rubiaceae	Cuba	Riley (1975)
Gonzalea spicata	Rubiaceae	W.I.	Barcant (1970)
Gonzalea spicata	Rubiaceae	W.I.	Riley (1975)
Isertia haenkeana	Rubiaceae	Panamá	Aiello LOT 81-16
Rondeletia panamensis	Rubiaceae	Panamá	Aiello LOTS 83-101, 83-111
Uncaria (as *Ourouparia*) *guianensis*	Rubiaceae	Brasil	Moss (1933)
Uncaria tomentosa	Rubiaceae	Panamá	Aiello LOTS 81-46, 81-51
IPHICLA EPHESA (as *ephicla ephesa*)			
Bathysa sp.	Rubiaceae	Brasil	cited in Lima (1968)
IPHICLA IPHICLEOLA			
Calycophyllum candidissimum	Rubiaceae	Costa Rica	Janzen 79-SRNP-135 in DeVries (unpub)
IPHICLA IPHICLEOLA (*Doxocopa* misidentified as *Adelpha*)			
Celtis sp.	Ulmaceae	Mexico	Comstock & Vazquez (1960)

Table 3. (continued)

ADELPHA SPECIES/ FOODPLANT	PLANT FAMILY	LOCALITY	REFERENCE
ISIS			
Cecropia pachystachia	Cecropiaceae	Brasil	cited in Lima (1968)
Cecropia pachystachia	Cecropiaceae	Brasil	Müller (1886)
Coussapoa schottii	Cecropiaceae	Brasil	cited in Lima (1968)
Coussapoa schottii	Cecropiaceae	Brasil	Müller (1886)
Pourouma acutiflora	Cecropiaceae	Brasil	cited in Lima (1968)
Pourouma acutiflora	Cecropiaceae	Brasil	Müller (1886)
JORDANI			
Vitex triflora	Verbenaceae	Brasil	Moss (1933)
JUSTINA JUSTINA			
Alternate-leaved plant	?	Panamá	Aiello 83-23, 83-67
LARA	Cecropiaceae	Trinidad	M. J. W. Cock (pers. comm.)
LEUCOPHTHALMA			
Pentagonia wendlandia	Rubiaceae	Costa Rica	Young (1974)
Undetermined	Rubiaceae	Panamá	Aiello LOTS 83-22, 83-24, 83-25
Undetermined	Rubiaceae	Costa Rica	DeVries (unpub)
MELANTHE			
Cecropia sp.	Cecropiaceae	Costa Rica	DeVries (unpub)
Trema micrantha	Ulmaceae	Panamá	Aiello LOT 83-8
Trema micrantha	Ulmaceae	Costa Rica	DeVries (unpub)
Urera sp.	Urticaceae	Costa Rica	DeVries (unpub)
MELONA			
Malanea sp.	Rubiaceae	Brasil	Moss (1933)
MESENTINA			
Pourouma sp.	Cecropiaceae	Brasil	Moss (1933)
MYTHRA			
Bathysa sp. nr. *barbinervis*	Rubiaceae	Brasil	Müller (1886)
NAXIA IPIPHILCA			
Piper areanum	Piperaceae	Costa Rica	Marquis in DeVries (unpub)
Vitex cooperi	Verbenaceae	Costa Rica	DeVries (unpub)
PARAENA			
Isertia longiflora	Rubiaceae	Brasil	Moss (1933)
Remijia amazonica	Rubiaceae	Brasil	Moss (1933)

Table 3. (continued)

ADELPHA SPECIES/ FOODPLANT	PLANT FAMILY	LOCALITY	REFERENCE
nr. PARAÈNA			
Combretum decandrum	Combretaceae	Panamá	Aiello LOT 82-55
PHLIASSA			
Alibertia edulis	Rubiaceae	Brasil	Moss (1933)
Bertiera guianensis	Rubiaceae	Brasil	Moss (1933)
PHYLACA AETHALIA			
Cecropia obtusifolia	Cecropiaceae	Panamá	Aiello LOTS 82-39, 82-68, 82-76, 83-78
Cecropia peltata	Cecropiaceae	Panamá	Aiello LOT 81-70
Cecropia peltata	Cecropiaceae	Panamá	Coley LOT 5
Cecropia sp.	Cecropiaceae	Panamá	Aiello LOT 82-40
PLESAURE			
Bathysa? sp.	Rubiaceae	Brasil	Müller (1886)
PSEUDOCOCALA			
Sabicea aspera	Rubiaceae	Brasil	Moss (1933)
PSEUDOCOCALA? (as nr. *cocala*)			
Sabicea sp.	Rubiaceae	Brasil	Müller (1886)
SALMONEUS			
Sabicea panamensis	Rubiaceae	Panamá	Aiello LOTS 82-37, 83-14
SERPA			
Miconia minutiflora	Melastomataceae	Brasil	Moss (1933)
Misc. spp.	Melastomataceae	Brasil	Müller (1886)
SERPA HYAS			
Ilex paraguariensis	Aquifoliaceae	Barsil	cited in Lima (1968)
SOPHAX (= *zalmona zalmona*)			
SYMA			
Rubus fructicosus	Rosaceae	Brasil	Müller (1886)
Rubus?sp. ("bramble")	Rosaceae	Brasil	Jones & Moore (1882–3)
Cephalanthus sarandi	Rubiaceae	Brasil	cited in Lima (1968)
THESPROTIA?			
Alternate-leaved climber	?	Brasil	Moss (1933)
TRACTA			
Undetermined	Rubiaceae	Costa Rica	Haber, Chacon in DeVries (unpub)
ZALMONA ZALMONA (as *sophax*)			
Sabiceae aspera	Rubiaceae	Costa Rica	DeVries (unpub)

reared on *Vitex,* has been found on only one other plant species (*Piper,* Piperaceae).

PUPA

Adelpha pupae (Figures 5 & 6) are diverse in form, yet have several features in common:

(1) The body is slender and tapers towards the cremaster, so that the posterior wing margins protrude and appear as keels.

(2) Segments T2 and A2 are expanded dorsally to form two projections of varying shape and size.

The thoracic projection is the smaller of the two and may be pointed and directed posteriorly (*A. salmoneus, cytherea, iphicla, justina*), or pointed and oriented almost perpendicularly to the body (*A. melanthe, phylaca aethalia*), or it may be reduced to a slight hump (*A. celerio*), or smooth curve (*A. basiloides*).

The abdominal projection is the larger and more variable of the two. It may be short, pointed, and directed anteriorly (*A. basiloides, justina*), a bit larger and curved anteriorly (*A. iphicla, celerio, cytherea, cocala*), even larger and directed posteriorly (*A. salmoneus*), or it may be a huge laterally flattened hook (*A. melanthe, phylaca aethalia*).

(3) The head usually has a pair of apical projections ("horns") of varying shape and size. These may be long, slender, and slightly curved (*A. celerio*), sickle-shaped and recurved to the sides (*A.*

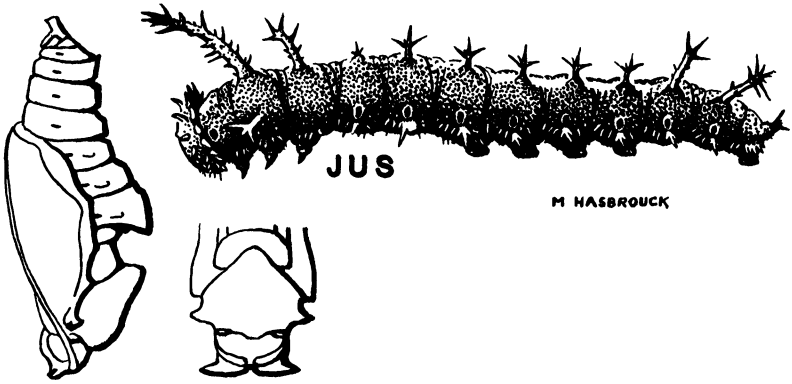

Figure 5. Final instar larva and pupa of *Adelpha justina justina,* (JUS) reared in Panamá.

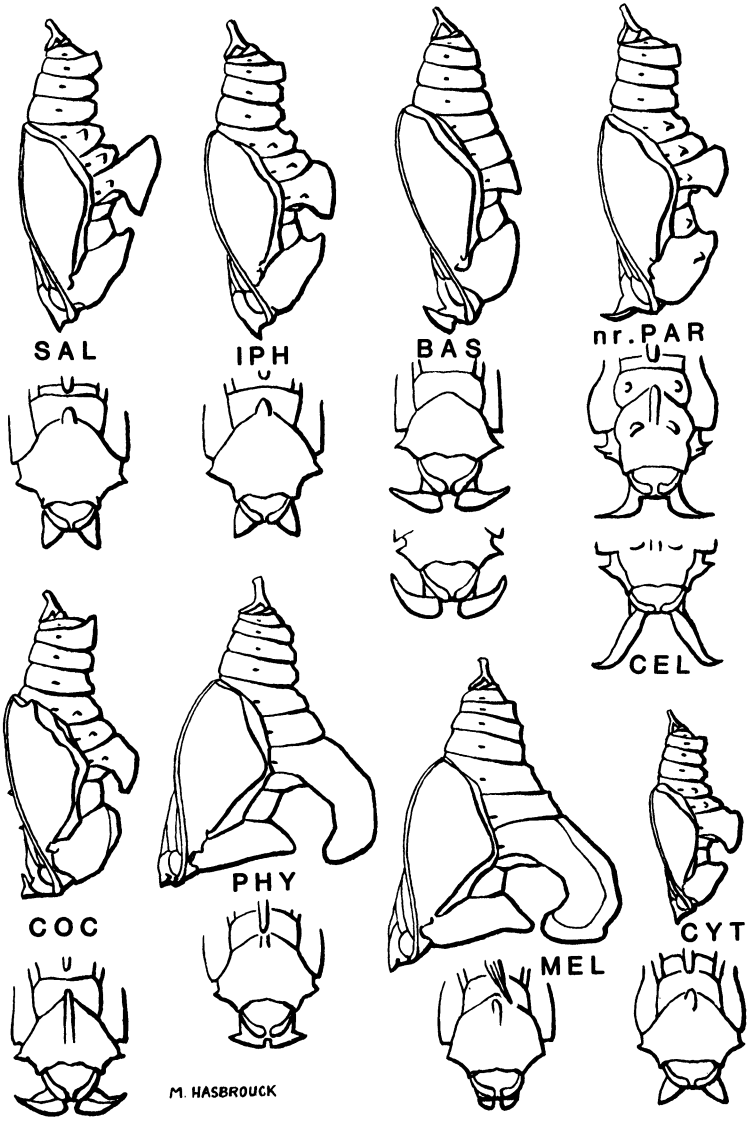

Figure 6. Pupae of *Adelpha* species reared in Panamá: abbreviations are the same as in Figures 2 & 4; CEL = *celario*.

basiloides), shaped like tiny asymmetrical leaves (*A. cocala, leucophthalma*), small and triangular, like cat ears (*A. iphicla, cytherea, salmoneus*), smaller triangles which are bent to the sides (*A. justina, phylaca aethalia*), or they may be reduced to two tiny rounded projections (*A. melanthe*).

(4) Pupal color varies from pearly white, through straw-color, brown, green, copper, or shimmering gold or silver. Whatever its color, an *Adelpha* pupa gives the impressing that it is empty or diseased. The pearly white pupa of *A. basiloides* is especially deceptive; it appears more to be an abandoned skin than a solid object. The shimmering silver pupae of *A. celerio* and nr. *paraëna* have black sutures and both give the impression that they are transparent with black lines showing through from the other side. As far as I know, the only other instance of a totally silver pupa occurs in *Mechanitis* of the Ithomiidae. The pupa of *A. salmoneus* is coppery brown and resembles a dead or diseased individual.

ADELPHA SPECIES GROUPS

In exploring for possible correlations between pupal and larval types, I began with species whose pupae have a large flat hook-like projection from the dorsum of A2. As it turned out, all have similar larvae, foodplants, and adult male genitalia, yet, the adult wing patterns are diverse. Further analysis revealed several other species groups that show similar correlations. Based upon this work, I have come to the conclusion that the genus *Adelpha* comprises five to seven natural groups, and possibly more. The only set of characters that doesn't hold together within these groups is adult wing pattern.

Some twenty species, for which adequate illustrations are available, are included in the classification which follows, and several others whose immatures were described only, are discussed.

The outline and discussion of *Adelpha* species groups includes brief final instar descriptions for species reared by me in Panamá, as well as comments upon previously published accounts of other species belonging to these groups. The MAJOR CHARACTERISTICS listed at the beginning of each group do not function as a key, rather, they represent defining characters for those groups, except as noted in parentheses. FOODPLANTS may host more than one butterfly group: members of GROUPS I and II have been reared on plants from

a number of families, GROUP III on Verbenaceae, and the remaining GROUPS (IV–VII) on Rubiaceae.

At this stage of our knowledge, an attempt to work out a phylogeny within *Adelpha* would be premature indeed; more information on life histories of *Adelpha* and its relatives (especially Old World genera) would be necessary to such an undertaking.

*KEY TO *ADELPHA* SPECIES GROUPS BASED UPON FINAL INSTAR LARVAE, PUPAE, AND FOODPLANTS

A. LARVA: body scoli, especially scolus of A2, flattened and feather-like; face with dark stripes. PUPA: shimmering silver with slender, very slightly twisted horns. FOODPLANTS: non-rubiaceous. (*A. celerio,* sp. nr. *celerio, serpa, paraëna*)

A. LARVA: body scoli not flattened or feather-like; face patterned or plain, but not striped. PUPA: perhaps with some metallic portions, but not totally metallic; head horns, various ... B

B. LARVA: scoli of A2–8 of similar form, although those of A2, and/or 7 & 8 may be longests. FOODPLANTS: non-rubiaceous C

C. LARVA: pale grey or pale brown with sides of thorax through A2 much darker than rest of body; scolus of A2 long. PUPA: with huge, hook-like dorsal projection from A2; head horns various..... .....(*A. phylaca aethalia, melanthe, isis, mesentina, delphicola,* (?)*calliphiclea,* (?)*abyla*)

C. LARVA: dark, or not patterned as above; scolus of A2 short. PUPA: hangs tilted with ventral side superior; head horns short points bent sharply to sides..... .....(*A. justina, jordani*)

B. LARVA: scolus of A2 different in form from scoli of A3–6 (in *A. iphicla* the difference is merely the swelling at base of A2 scolus) FOODPLANTS: rubiaceous..... D

D. LARVA: scoli of T2 or 3, and A2 & 7 swollen at base; (in *A. iphicla,* T2 & A2 only); face not patterned; head chalaza-1 not darker than others (don't known for *A. pseudococala*). PUPA: horns small, triangular "cat-ears" ..... E

*The reader should bear in mind that in all *Adelpha* species, the scoli of T1 and A2 are tiny.

E. LARVA: scoli of A2 conical, close together, and with fewer spines at base; scoli of A3–6 very short ..... (*A. cytherea, salmoneus, pseudococala*)

E. LARVA: scolus of A2 not conical, similar to other scoli except for its swollen base; scoli of A3–6 of moderate length; face smoother than other species due to reduction or loss of most chalazae ..... (*A. iphicla*)

D. LARVA: body scoli about same thickness at middle as at base; scolus of A2 strongly arched towards the posterior, thick and densely spined; face patterned; head chalaza-1 dark, and chalazae-3 & 4 pale compared to rest of face. PUPA: head horns curved or recurved to sides ..... F

F. LARVA: scoli of T3 and A7 long, slender, and tapered to sharp point; scoli of A7 & 8 differ in form from each other (that of A8 club-shaped). PUPA: head horns sickle-shaped ..... (*A. basiloides, phliassa*)

F. LARVA: body scoli not tapered to sharp point; scoli of A7 & 8 similar in form. PUPA: head horns like tiny asymmetrical leaves ..... (*A. cocala, leucophthalma*)

GROUP I

MAJOR CHARACTERISTICS:

(1) Larval body scoli flattened;
(2) Larva with face striped;
(3) Larval head chalaza-1 dark (also true of GROUPS VI & VII);
(4) Larvae assume a curled resting position;
(5) Pupa shimmering silver,
(6) Valves of male genitalia without clunicula;

FOODPLANTS: Aquifoliaceae, Bombacaceae, Cecropiaceae, Combretaceae, Melastomataceae, Rubiaceae, Urticaceae.

Two larval types have been observed within this group:

A. Final instar larvae with A2 scolus broad, curved posteriorly, and with median spines spreading ..... nr. *celerio, serpa.*

A. Final instar larvae with A2 scolus longer, slender, straight (although directed posteriorly), and with median spines ascending ..... *celerio, paraëna*

Pupae vary only slightly, the more apparent differences being in the length, and degree of curvature of the head horns, and in the shape of the dorsal projections on T2 and A2. Head horn shape and size do not appear to correlate with the two larval types seen so far, and perhaps varies even within a species.

celerio, Panamá (Aiello, Coley)

Larvae are dark, mostly black above and green laterally, with pinkish lateral spots on A2–4, 7 & 8; scoli on thorax and A7 & 8 are pale, while that of A2 is black; subspiracular scoli A2–4 are mixed pale lime and bright green. A black subspiracular stripe passes along the thorax and turns sharply upward across A1 and fuses with the dark scolus of A2. A few days before pupation the pinkish lateral marks change to green, as do the scoli of T3 and A7 & 8; the scolus of A2 remains dark. Just prior to pupation larvae fade to a dirty yellow. Larvae rest in the curled position with the posterior end elevated and the white undersurface of A8 & 9 exposed, and in this configuration resemble a bit of fallen moss and lichen mingled.

Pupal head horns are long, and slightly curved near their tips. Adults resemble *iphicla* in wing pattern.

nr. *celerio,* Panamá (Aiello)

A larva resembling *celerio* produced, but with the A2 scolus short and broad, a pupa that had short head horns and appeared identical to my nr. *paraëna.*

Unfortunately the pupa died and its identity remains a mystery.

celerio diademata, Mexico (Comstock & Velazquez, 1960)

The illustrations of this larva and its pupa indicate membership in GROUP I; the larva is clearly of the *celerio* type having long narrow scoli, even on A2. The pupa closely resembles that of the *celerio* reared by me in Panamá; the head horns are long and slightly curved just before their tips.

The authors report that their larva faded to yellow just before pupation.

paraëna, Brasil (Moss, 1933)

From its illustration, the larva of this species is of the slender scolus type. Moss noted that it was brighter green than *serpa* and had none of the orange spines. The record of Rubiaceae for *paraëna* is unique for this group.

nr. *paraëna,* Panamá (Aiello)

In pattern, this larva is very similar to *A. celerio,* but is paler above, being mottled brown and black, with a white dorsal patch joining A6 & 7. The scoli are brown, that of A2 being the darkest; subspiracular scoli A2–4 are pink. The larva turned yellowish just prior to pupation.

The pupal head horns are shorter than those of *celerio,* and curve outward at about their midpoint.

Adults resemble *celerio* so closely that I did not realize they were different species until rearing them, and doubtless they are mingled in many collections.

serpa, Brasil (Moss, 1933)

The larva of *serpa* has the scolus of A2 shorter and denser than the other major scoli, and I take it to be of the same general type as *celerio.* Moss described the scolus of A2 (segment 6 in his system) as being bushy and dark green, and the other major scoli as ochreous (orange). His larva rested with the anterior portion turned, and resembled a bird dropping.

serpa, Brasil (Müller, 1886)

Müller's illustrations of *serpa* show the larval face, and a scolus from A2. The face is clearly striped, and the scolus is short, thick, and has flattened spines overlapping each other; each of these conditions of the scolus is more extreme than in nr. *celerio.*

Group II

MAJOR CHARACTERISTICS:

(1) Larva pale, with sides of thorax through A2 darker than rest of body;
(2) Pupa with huge, laterally flattened, hook-like projection from dorsum of A2;
(3) Pupal head horns diverse: leaf-shaped, bent triangular, rounded;

(4) Valves of male genitalia armed with row of teeth beginning at apex and extending along lower edge; clunicula broad;

FOODPLANTS: Aquifoliaceae, Bombacaceae, Cecropiaceae, Ulmaceae, Urticaceae.

abyla, Jamaica (Swainson, 1901)

There are several things in Swainson's description that lead me to place *abyla* tentatively with GROUP II. "On first segments are two brown horns with sharp points bending over the head; from this to the end of the third segment is silvery grey; then two tiny horns bending backward." "The [pupa] shape is very curious, resembling the pictures of 'Punch,' long nose and all." It appears that larval segments T1 and A1 were overlooked, probably because of their small size and tiny scoli. The silver area would then be bounded by scoli of T2 and A2, suggesting the two-toned larva of GROUP II. The pupal description may be in reference to the long abdominal hook of GROUP II, or it may be an overreaction to the shorter dorsal projection of a species in some other group (*iphicla* perhaps). Unfortunately, no foodplant is mentioned.

calliphiclea, Paraguay (Jorgenson, 1921)

Jorgensen's description of the pupa as having the abdomen prolonged toward the thorax, forming a large hook, induces me to place *calliphiclea* in GROUP II: "El torax arriba con una carena alta como el abdomen en el dorso este ultimo hacia el torax prolongado, formando un gran gancho." In addition, the non-rubiaceous foodplant (*Ilex*) is consistent with this group.

Each of the five species remaining, possess characteristics 1 & 2 above, and there is no doubt in my mind that they are all close relatives. Pupal head horn shape may have taxonomic value within the group but that cannot be determined until a larger number of species has been reared.

delphicola, Brasil (Moss, 1933)

The pupal head horns curve to the sides and resemble tiny asymmetrical leaves; the hook on dorsal A2 is rounded at the tip.

isis, Brasil (Müller, 1886).

Müller's illustration of the pupa is a lateral view so the head horn shape does not show, however, it is stated in the text that

the horns are small points bent to the sides. The hook on A2 is enlarged slightly at the tip much as in *melanthe.*

melanthe, Panama (Aiello)

The larva is grey (darker above) excepting the dorsal thorax through A2, which is dirty yellow, and the sides of that same area, which are dark brown. The scoli are grey with black spine bases and apices. The larva has a frosted appearance partly due to its patterned scoli, but mostly because the entire body is densely clothed with short thick grey setae. It is the only *Adelpha* species so far that has rounded pupal head horns. The hook on A2 is slightly expanded at the tip.

Adults of *melanthe* look like large *salmoneus* but the undersurface is quite different.

mesentina, Brasil (Moss, 1933)

From Moss's illustrations, *mesentina* and *delphicola* larvae are similar, and no doubt these two species are close relatives. As a result of their close resemblance, Moss did not realize that he had two species until the adults emerged. If his illustrations are accurate, then *mesentina* has a less rounded pupal hook than *delphicola,* but the head horns are nearly the same.

phylaca aethalia, Panamá (Aiello, Coley)

The larva is greenish or pinkish grey, and speckled with darker grey (especially on the dorsum); the sides of the thorax through A2 are dark brown, and some individuals have a dark brown oval on each side of A5, just below the scolus. Pupal head horns are short triangles bent to the sides.

Adults are very close look-alikes of *cocala.*

GROUP III

MAJOR CHARACTERISTICS:

(1) Larval scoli A2–6 all similar and short;
(2) Pupa tilted so that ventral side is superior (at least in *justina*);
(3) Pupal head horns small triangles bent to sides (also occurs in GROUP II);
(4) Valves of male genitalia unarmed (also true of GROUP IV);

FOODPLANTS: Verbenaceae.

The most interesting thing about this group is the fact that the scolus of A2 is just the same as those of A3–6. Both species, thus far included, rest in the front-curved position, as shown in Moss's illustration of *jordani*. Also in both, the pupal dorsal A2 projection is a short point, directed anteriorly, and the T2 projection is smaller.

This and GROUP IV have similar genitalia, but feed on different foodplant groups. I see them as close but distinct relatives.

jordani, Brasil (Moss, 1933)

The larva is dull green with black-spined, orange scoli; the pupa is white with black spots.

justina, Panamá (Aiello & Small)

Early final instar larvae are dark brown (lighter dorsally) with paler scoli (black at tips of those on T2 and A7 & 8), but later change to black and white checkered with transverse orange bands joining members of scolus pairs (A2–8).

The straw-colored pupa has a dorsal metallic sheen, from head through A1, and lacks the prominent spotting of *jordani*.

Adults of *justina* closely resemble *leucophthalma* and the two can be found flying together.

GROUP IV

MAJOR CHARACTERISTICS:

(1) Larva with scoli of A2 conical, close together, and with fewer spines at base;
(2) Larval face with chalazae reduced in size;
(3) Pupal head horns of this and Group V, are small, triangular "cat-ears;"
(4) Valves of male genitalia unarmed (also true of GROUP III);

FOODPLANTS: *Sabicea* (Rubiaceae).

nr. *cocala,* Brasil (Müller, 1886)

The larva illustrated does not at all resemble that of *cocala,* so I guess Müller's label "bei *cocala*" to have been based upon adult appearance. Like *cytherea,* this larva shows the conical scolus of A2, the thick based scoli of T2, and A7, and the very short scoli of A3–6. As well, Müller's larva fed on *Sabicea.*

cytherea, Brasil (Moss, 1933)

Of this larva, Moss commented, "Now in two shades of brown, on the stem or near flower-head easily mistaken for a part of the plant...."

cytherea marcia, Panamá (Aiello)

The larva is patterned dark and light brown; with dark brown, oblique lateral stripes, which cross segments A3–8. A thin white subspiracular line expands into a lime-green mark on A7–9.

The pupa is straw-color but takes on a silver or gold sheen at certain angles.

pseudococala, Brasil (Moss, 1933)

Moss states merely that the larva of this species is identical to *cytherea,* although larger and greener at the ends.

The pupal abdominal projection is directed towards the posterior as in *salmoneus.*

salmoneus, Panamá (Aiello)

The dark brown second through fourth instar larvae, with their grey, oblique, lateral stripes, are well camouflaged amongst the dark, pale-veined, young leaves of their foodplant. Fourth and fifth instars have red-brown heads.

Early final instar larvae are brownish green, and become greener with age. By late final instar, larvae are bright yellow-green; the dorsal area of A4 & 5 is pale purple-brown; A4 & 5 each bear a dark lateral purple mark; the head is red-brown; scoli of T2 & 3, and A2 & 7 are brown-purple, while that of A8 is still green.

The pupa is bronze with dorsal gold, and has an A2 projection that is prolonged more towards the posterior end than the anterior.

GROUP V

MAJOR CHARACTERISTICS:

(1) Larval scoli of T2 and A2 swollen at base, otherwise, all body scoli usually similar in form;

(2) Pupal head horns of this and GROUP IV, are small, triangular "cat-ears";

(3) Larval head uniformly dark, and face smooth except for usual pits, and two pairs of reduced chalazae (nos. 2 & 4);

(4) Valves of male genitalia armed with apical row of teeth which extend to outside of valve;

FOODPLANTS: *Antirrhoea, Alseis, Bathysa, Calycophyllum, Gonzalea, Isertia, Rondeletia, Uncaria* (Rubiaceae).

iphicla, Panamá (Aiello)

The color of *iphicla* larvae varies from dark grey, through golden brown, and red-brown, to almost black, regardless of the foodplant eaten. The head is always smooth (by *Adelpha* standards) and also varies, from yellow-brown with black punctations to uniform dark brown or black. Final instar larvae show the most pattern (especially light-colored individuals): dark, oblique lateral stripes on A2–5, which terminate part way up the bases of the scoli, and often but not always, white lateral marks on A2, 7 & 8.

The pupa varies from waxy white to straw-color or pale brown, and often is partly or entirely burnished gold or silver, especially on dorsal T1 & 3, and A1. Almost always there is a small silver diamond located on the base of each mesothoracic leg.

iphicla, Brasil (Moss, 1933)

Moss described *iphicla* larvae as "very similar to *cytherea,* the two species evidently being closely related, as is also shown by the pupae."

GROUPS IV and V may be related; the "cat-eared" pupae, and oblique-striped larvae of both, seem to hint at that. As well, both groups of larvae display varying degrees of reduction of head chalaze, and swelling of certain scoli bases. However, the genitalia of the two groups are different, and, in *iphicla* the scoli on A3–6 are longer and the face smoother than in Group IV. And so, for the moment they will be kept separate, but near to each other.

GROUP VI & VII

MAJOR CHARACTERISTICS:

(1) Larva with scolus of A2 arched towards the posterior, thick, and densely spined;
(2) Larval face patterned;
(3) Larval head chalza-1 dark (also true of GROUP I);

(4) Valves of male genitalia armed with apical row of 2–6 fairly uniform teeth;
(5) Larval head chalazae 3 & 4 pale, and contrasting with face.

FOODPLANTS: Rubiaceae.

These two groups are very closely related and perhaps will be merged when more is known of their larval and pupal diversity. For now they are placed apart on account of the specialized scoli in *basiloides,* and differences in the form of the pupal head horns.

GROUP VI

ADDITIONAL CHARACTERISTICS:

(5) Larval scoli of T3 and A7 long, slender, and tapered to sharp point;
(6) Larval scolus of A8 club-shaped;
(7) Larval face pattern, independent of pits;
(8) Pupal head horns sickle-shaped;

FOODPLANTS: *Alibertia, Amaioua, Bertiera, Ixora* (all Rubiaceae).

basiloides, Panamá (Aiello)

Larvae are mottled black and brown, and are paler towards the posterior end. The dark and pale portions intersect obliquely along a line beginning at the subspiracular scolus of A4, and terminating dorsally at the beginning of segment A7. The dorsal dark portion thus comes to a point at the beginning of A7. As larvae approach pupation, they may become tinged with rose or green, especially at scoli bases, and laterally on A4–6.

The pupa is pearly white with black tiped head horns, and appears empty. Head horns vary somewhat in length and degree of curvature, even among larvae collected on the same plant. Both extremes are illustrated (Figure 6).

phliassa, Brasil (Moss, 1933)

Comparing my observations of *basiloides* with Moss's description and illustrations of *phliassa,* it appears that the two are extremely close relatives.

plesaure, Brasil (Müller, 1886)

The pupa illustrated appears identical to those of *phliassa* and *basiloides.* Hall (1938) feels that *plesaure* and *phliassa* are one and the same species.

GROUP VII

ADDITIONAL CHARACTERISTICS:

(4) Larval face pattern due to dark pits against a paler face;
(5) Pupal head horns shaped like tiny asymmetrical leaves (also occurs in GROUP II);

FOODPLANTS: *Calycophyllum, Chomelia, Malanea, Pentagonia, Psychotria, Uncaria, Warscewiczia* (all Rubiaceae).

cocala, Panamá (Aiello)

Early fifth instars are crypticaly patterned with golden brown and black; later the pattern remains but the colors become moss-green, black, and cream, and a pinkish grey and black area appears on dorsal A3–6, plus a broad, oblique, lateral pinkish or yellowish stripe across A4 and 5 together. Some individuals have a subspiracular lime-green mark on each of A7 & 8.

The pupa is dark green.

cocala, Brasil (Moss, 1933)

The curved, thick scoli of A2 show clearly in Moss's illustration, but his larvae had more than one lateral oblique stripe. The pupae appear nearly identical.

His record of *Emmotum* (Icacinaceae) as a foodplant, in addition to *Malanea* (Rubiaceae) is odd, and is the only reported deviation, by *cocala,* from Rubiaceae.

leucophthalma leucophthalma, Panamá (Aiello & Small)

The larva of *leucophthalma* is apparently indistinguishable from that of *cocala* (G. Small, personal communication) and the two species must be closely related.

The pupa also is very similar to *cocala,* but differs in being brown or copper-color, and in having the abdominal projection rather square, the thoracic projection more pointed, and the head horns farther appart at their bases.

leucophthalma leucophthalma (as *l. tegeata*), Costa Rica (Young, 1974)

The observations by Young are consistent with those of Gordon Small and myself.

SPECIES EXCLUDED FROM THIS CLASSIFICATION

erotia, Brasil (Müller, 1886)

An isolated scolus, figured by Müller and labelled *erotia,* would

place that species in GROUP I, but I would like to see more evidence. In addition, the *erotia* wing-undersurface pattern does not have the sharply stamped appearance typical of GROUP I, and it is possible that the butterly was misidentified.

iphicla iphicleola, Mexico (Comstock & Vazquez, 1960)
This record was in error; the authors misidentified *Doxocopa* as *Adelpha.*

melona, Brasil (Moss, 1933)
The larval description and illustrations in Moss do not give sufficient detail to place this species, although from the pupa it belongs in GROUP VII.

thesprotia, Brasil (Moss, 1933)
The larval description and illustration in Moss do not give sufficient detail to place this species, although I suspect that it may represent an eighth group. As well, there is a good deal of disagreement concerning the identity of Moss's *thesprotia;* Forbes (unpublished) believed that Moss actually had *nea*, a species which on the basis of genitalia probably belongs to GROUP I. Moss's statement that the larva rested in a curled position (typical of GROUP I), lends support to Forbe's suspicion. However, from what can be seen of the scoli in Moss's illustration, they are all similar in size and form, are not flat, and the pupa looks more like those of GROUP VIII.

Significance of Adult Wing Pattern

When adult specimens of *Adelpha* are sorted into the species groups just outlined, the result is a jumble of wing pattern types that would make any biologist wince, this author included. However, it would seem even less natural to split groups that are based upon the presumably more conservative characters of the immatures. I prefer to think that in *Adelpha,* wing pattern not only does not reflect species relationships, but instead may be intended to deceive. One might expect adult wing characters to be the most specialized and difficult to interpret; adults move about with ease and interact with each other and with other butterfly species, as well as with potential predators, while in most cases the immature stages must contend, in

a less active way, with predators and parasites alone. An explanation of *Adelpha's* wing pattern madness, might be that this genus is comprised of several groups, of various affinities, which together form a large mimicry complex, perhaps based upon members whose larvae feed on alkaloid-bearing plants (e.g., Rubiaceae). Possible examples are found among the unrealted look-alikes reared by me in Panamá (Figure 7): *phylaca aethalia* (non-rubiaceous feeder (NR)) closely resembles *cocala* (rubiaceous feeder (R)); *justina* (NR) resembles *leucophthalma* (R); *melanthe* (NR) is larger than, but very similar in pattern to *salmoneous* (R); and *celerio* and nr. *paraëna* (both NR) are very similar in pattern to *iphicla* and *basiloides* (both R). The idea is intriguing, but must be labelled "pure speculation" until data on palatability of *Adelpha* butterflies is available. In its defense, however, I would like to point out that there are several examples of *Adelpha* look-alikes in uncontestably unrelated butterflies. *Nymula velabrum* (Riodinidae), whose wing pattern closely resembles that of *A. iphicla,* and several other *Nymula* species that are look-alikes of other *Adelpha* types, all depart from the basic wing pattern of their genus. Female *Doxocopa laure* and *pavon* (Nymphalidae) resemble *A. iphicla,* while female *D. clothilda* are even more convincing look-alikes of *A. salmoneus.* Male *Doxocopa clothilda* and *pavon* differ from the females of their species, and do not resemble *Adelpha,* while the male of *D. laure* has an *Adelpha*-like wing pattern with overlying purple iridescence. *Pyrrhogyra hypsenor* (Nymphalidae) is similar in appearance to *Adelpha* species that have broad white bands, and has fooled at least one lepidopterist (Muyshondt, 1974).

Old World Relatives

The few published accounts of life histories for Old World Limenitidinae provide intriguing glimpses into the trove of information awaiting the attention of lepidopterists. Many larval and pupal forms, similar to those of *Adelpha,* occur among Old World genera, and in addition, many utilize the same foodplant genera as *Adelpha* and display similar larval behavior. Life history studies, that compare Old and New World groups, are essential to our understanding of generic limits and relationships within this subfamily.

[6]Morrell (1954) gives a fascinating account of larval behavior in several Malayan genera of the tribes Limenitidini *(Athyma, Moduza, Pandita)*, and [7]Neptini *(Lasippa, Neptis, Phaedyma)*. Except for *Neptis leucoporos*, the larvae, of the butterflies he observed, expose the midrib, or a secondary leaf vein, by feeding around it (just as *Adelpha* does); young larvae rest out on these slender supports. Like *Adelpha* also, *Athyma, Moduza,* and *Pandita* accumulate their feces to form a mass at the base of the support vein; Neptini do not.

Judging from Morrell's illustrations, the larva of *Moduza* resembles a combination of *Adelpha cocala* and *basiloides*, especially in having short thick scoli on A2; its pupa is remarkably like *A. cocala* or *leucophthalma*, but with slightly stalked head horns; the host plants are mainly Rubiaceae *(Mussaenda, Nauclea, Timonias, Uncaria, Wendlandia)*, with one record on Oleaceae *(Olea)*.

The larvae of *Athyma kanwa* feeds on *Uncaria*, and is described by Morrell (1960) as "brown with delicate green branched spines, and resembles a growth of moss on a decaying patch of leaf;" the pupa (illustrated in Morrell, 1954) is silver with long head horns and to me looks for all the world like a pupa of *Adelpha celerio*.

In form, *Athyma nefte* larvae (Morrell, 1954) are reminiscent of a very plump *Adelpha iphicla* larva, and have been reported on *Glochidion* (Euphorbiaceae) and *Mussaenda* (Rubiaceae); the pupa is "golden brown in colour, with two dorsal plates of brilliant metallic gold," and from what can be determined from its picture, it looks like the pupa of *Adelpha iphicla* or *cytherea*, but with an exagerated A2 projection, and like those species it appears to have short pointed head horns.

Pandita sinope is described by Morrell (1954) as having a larva similar to that of *Athyma nefte* in color and general appearance; the illustration of the pupa is also similar to *A. nefte*, but has a less

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[6]According to Corbet and Pendlebury (1978), five of the seven names used by Morrell (1954) should be amended: his *Neptis columella* = *Phaedyma columella; Neptis heliodore* = *Lasippa tiga; Neptis nata* = *Neptis leucoporos; Parathyma kanawa* = *Athyma kanwa; Parathyma nefte* = *Athyma nefte*. His *Moduza procris* and *Pandita sinope* remain unchanged.

[7]Neptini is defined by Eliot (1969) to include *Aldania, Lasippa, Neptis, Pantoporia,* and *Phaedyma*.

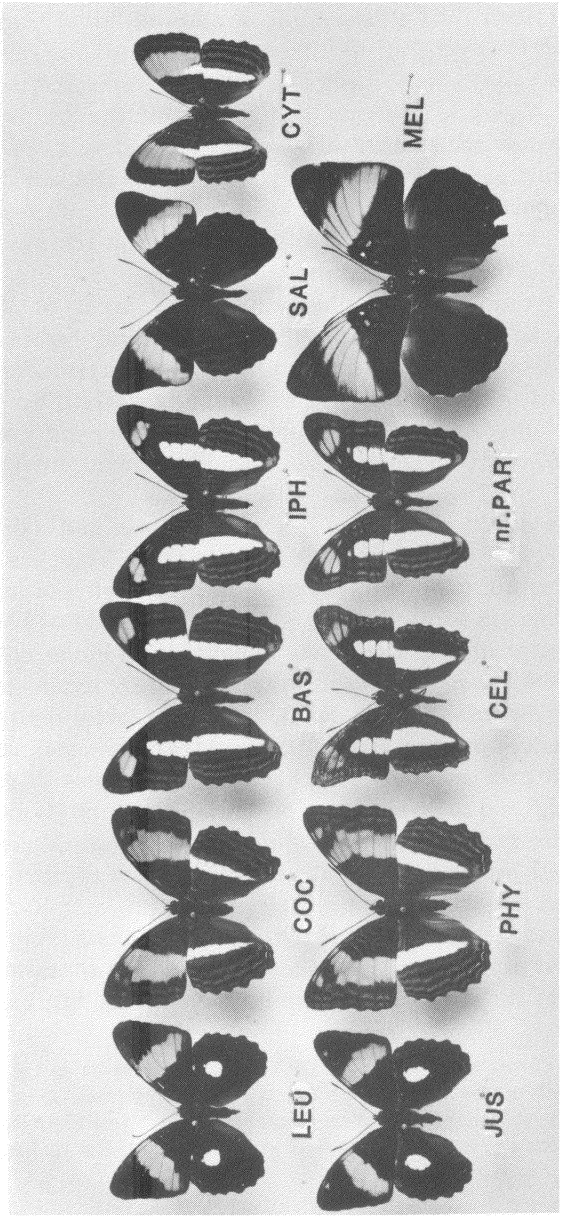

Figure 7a. Upper and lower surfaces of adult Adelpha species reared in Panamá: BAS = *basiloides*, CEL = *celerio*, COC = *cocala*, CYT = *cytherea marcia*, IPH = *iphicla*, JUS = *justina*, LEU = *leucophthalma*, MEL = *melanthe*, nr. PAR = *near paraëna*, PHY = *phylaca aethalia*, SAL = *salmoneus*. Species in the upper row are rubiaceous feeders as larvae, whereas larvae of those in the lower row feed on various non-rubiaceous plants.

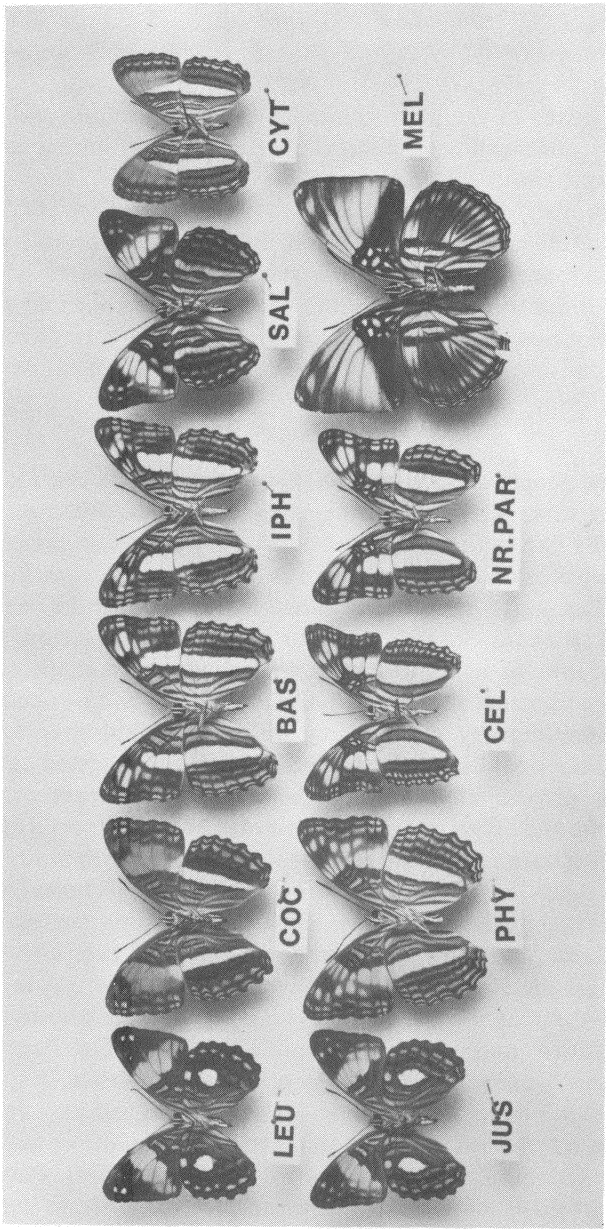

Figure 7b. Lower surfaces of adult *Adelpha* species reared in Panamá. Abbreviations as in figure 7a.

exagerated A2 projection and thus appears almost identical to pupae of *Adelpha iphicla* and *cytherea*. Larvae of *P. sinope* feed on *Uncaria* (Rubiaceae).

The valves of the male genitalia in *Pandita sinope* and *Athyma nefte* are unarmed, have cluniculae, and look very similar to those of *Adelpha* GROUPS III & IV.

A number of other life history accounts for Old World Limenitidini have been published, but it is not the intent of this paper to report them in detail. Instead, I merely wish to point out a few of the intriguing similarities that exist between Old and New World groups, in hope of prompting other workers to investigate this promising group.

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Literature Cited

Aiello, A.
(Unpub) Insect Rearing Records (mainly for Lepidoptera). Each year is in a separate notebook; lot numbers used in the present paper refer to pages in these notebooks.

Barcant, M.
1970. Butterflies of Trinidad and Tobago. 314 pp.; Collins. London.

Coley, L.
(Unpub) L. Coley has reared a number of Lepidoptera on *Ochroma* and *Cecropia*. Numbers given are her identification numbers.

Comstock, J. A. and L. Vázquez G.
1960.
(1961) Estudios de los ciclos biológicos en Lepidópteros Mexicanos. an inst biol mexico **31**: 349–488.

Corbet, A. S., and H. M. Pendlebury
1978. The Butterflies of the Malay Peninsula. 3rd edition revised by J. N. Eliot. xiv + 578 pp., 35 pl., 438 figs. Malayan Nature Society.

DeVries, P. J.
(Unpub) List of host plants of butterflies of Costa Rica, compiled from his own data plus that of a dozen other workers. The last compilation was prepared during early 1982.

Dewitz, H.
1879. Naturgeschichte Cubanischer Schmetterlinge. In: Zeitschrift für die gesammten Naturwissenschaften. Bd. **52**: 166–167.

Dornfeld, E. J.
1980. The Butterflies of Oregon. xiv + 276 pp.; Timber Press. Forest Grove, Oregon.

Eliot, J. N.
1969. An analysis of the Eurasian and Australian Neptini (Lepidoptera: Nymphalidae). 155 pp., 3 pl., 101 text-figs. Supplement 15 to bull brit mus.

Eltringham, H.
1923. Butterfly Lore. 180 pp.; Oxford, at the Claredon Press.

Ferris, C. D., and F. Martin Brown (editors)
1980. Butterflies of the Rocky Mountain States. xviii + 442 pp.; University of Oklahoma Press. Norman.

Fruhstorfer, H.
1907. *Adelpha*. pp. 510–533 + pls. 106–110a. In: seitz, A. The Macrolepidoptera of the World. Div. II, Vol. **5**, viii + 1139 pp.

Godman, F. D., and O. Salvin
1879–
1901. Biologia Centrali-Americana. Insecta. Lepidoptera-Rhopalcera. Vol. I, xlv + 487 pp. (1879–1901); Vol. II, 782 pp. (1887–1901).

HALL, A.
1938. On the types of *Adelpha* (Lep., Nymphalidae) in the Collection of the British Museum. ENTOMOLOGIST **71**: 184–187, 208–211, 232–235, 257–259, 284–285.

HAYWARD, K. J.
1950. Las especies y formas Argentinas del género *Adelpha*. ACTA ZOOL LILLOANA **9**: 375–393.

HOFFMANN, F.
1937. Beiträge zur Naturgeschichte brasilianischer Schmetterlinge. II. ENTOMOLOGISCH ZEITSCRIFT **51**: 212–213, 231–232.

HOWE, W. H.
1975. The Butterflies of North America. xiii + 633 pp., 97 color plates containing 2093 illus. and 32 text figs. Doubleday & Company, Inc. Garden City, New York.

JONES, E. D., AND F. MOORE
1883. Metamorphoses of Brazilian Lepidoptera from San Paulo, Brazil. Second Series. PROC LIT PHILOS SOC LIVERPOOL **37**: 229–259.

JORGENSEN, P.
1921. Sobre algunos nuevos enemigos de la yerba-mate, *Ilex paraguariensis*. REV SOC CIENTIFICA PARAGUAY 1(1): 27–30.

KIRKBRIDE, A. C. G.
1982. A preliminary phylogeny for the neotropical Rubiaceae. PL SYST EVOL **141**: 115–122.

MILLER, L. D., AND J. Y. MILLER
1970. Notes on two rare Mexican *Adelpha* and related Central American species (Nymphalidae). J LEP SOC **24**(4): 292–297.

MORRELL, R.
1954. Notes on the larval habits of a group of nymphalid butterflies. MALAYAN NAT J **8**: 157–164.
1960. Common Malayan Butterflies. Malayan Nature Handbooks. xii + 64 pp., 20 pls. Longman. London.

MOSS, A. M.
1933. Some generalizations on *Adelpha*, a neotropical genus of nymphalid butterflies of the group Limenitidi. NOV ZOOL **39**: 12–20 + pls. 1 & 2.

MÜLLER, W.
1886. Südamerikanische Nymphalidenraupen, versuch eines natürlichen Systems der Nymphaliden. ZOOL JAHRB, ZEIT SYST, GEOGR BIOL THIERE **1**: 417–678 + pl. 12–15.

MUYSHONDT, A.
1974. Notes on the life cycle and natural history of butterflies of El Salvador. V. A. *Pyrrhogyra hypsenor* (Nymphalidae-Catonephelinae). J NY ENT SOC **82**(3): 163–172.

ORSAK, L. J.
1977. The Butterflies of Orange County, California. xii + 349 pp.; University of California, Irvine. Center for Pathobiology MISC PUBL No. 3; Museum of Systematic Biology RES SER No. 4.

PETERSON, A.
1962. Larvae of Insects: An Introduction to Nearctic Species. Part I. Lepidoptera and Plant Infesting Hymenoptera. Columbus, Ohio.

RILEY, N. D.
1975. A Field Guide to the Butterflies of the West Indies. 224 pp. + 338 color illus.; Collins. London.

SCUDDER, S. H.
1889. Butterflies their Structure, Changes and Life-histories with special reference to American Forms. viii + 322 pp.; Henry Holt & Co. New York.

SILVA, A. G. D'A. E., C. R. GONCALVES, D. M. GALVAO, A. J. L. GONCALVES, J. GOMES, M. DO N. SILVA, AND L. DE. SIMONI.
1967–
1968. Quartro Catalogo dos insetos que vivem nas plantas do Brasil, sues parasitos e predadores. parte I (2 vol., 906 pp.) & parte II (2 vol., 887 pp.). Ministerio da Agricultura. Rio de Janeiro, GB, Brasil.

SMALL, G.
(Unpub) List of Panamanian Butterflies. This list is based upon twenty years of observations in Panamá.

SWAINSON, E. M.
1901. Notes on lepidopterous larvae from Jamaica, B.W.I. J NY ENT SOC **9**: 77–82.

YOUNG, A. M.
1974. Notes on the natural history of a rare *Adelpha* butterfly (Lepidoptera: Nymphalidae) in Costa Rica high country. J NY ENT SOC **82**(4): 235–244.