

ADELPHA EROTIA EROTIA FORM "LERNA" (NYMPHALIDAE): EXPLORING A CORNER OF THE PUZZLE

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ABSTRACT. The larvae and pupa of *Adelpha erotia erotia* "lerna" are described and figured, and it is concluded that the taxon belongs to the *A. mesentina* species-group. *Cecropia longipes* is reported as the larval food plant. Relationships among the six *A. mesentina* group species are explored.

Additional key words: life history, Panama, Bombacaceae, Cecropiaceae, Malvaceae, Urticaceae

INTRODUCTION

The immature stages of any group of Lepidoptera, and the affiliations among their larval food plants, can provide valuable insights into species identities and alliances, and they can prove especially valuable in helping untangle a perplexing group, such as the speciose Neotropical genus *Adelpha* Hübner.

Adelpha dorsal wing patterns are confusing, and that has led to numerous misidentifications in widely consulted works, and hence to increasing confusion. Thus, for more than a century, *Adelpha* defied attempts to sort out its more than 350 published taxa, though the best did try (Godman & Salvin 1879–1901, Fruhstorfer 1907, Forbes unpublished manuscript). But difficulties of identification are now largely behind us, thanks to the recent revision of *Adelpha* by Willmott (2003b), who has taken us a giant leap forward in our understanding of this bewildering group. After evaluating all available type material and all published names, Willmott concluded that *Adelpha* comprises 85 species and 209 taxa. His detailed descriptions and color photographs make it possible at last to identify virtually any specimen with near certainty.

The task remains, to devise a satisfying classification for the group, one that reflects natural relationships. A major obstacle to understanding relationships within *Adelpha* is that the dorsal wing patterns are deceptive; species of similar appearance are not necessarily closely related, and closely related species do not necessarily resemble each other.

There is substantial evidence that dorsal wing patterns are mimetic, perhaps through Müllerian mimicry based on difficulty of capture (Mallet & Singer 1987, Srygley 1994) or through Batesian mimicry (Aiello 1984, Prudic et al. 2002). Though ventral wing patterns do provide some reliable characters useful in species identification, they also are subject to some variation directly resulting from selection on the dorsal wing pattern (Willmott personal communication). Like many

other limenitidine genera, *Adelpha* is extremely homogeneous morphologically, both in wing pattern and genitalia, thus providing few reliable characters for phylogenetic analysis. Character systems other than adult morphology thus are essential for achieving a better understanding of *Adelpha* evolution and extant species relationships. The time is ripe for a molecular study of *Adelpha*. As well, the immatures and food plants offer a wealth of taxonomic information, but detailed and reliable knowledge of them is available for only about 25% of known *Adelpha* species (Müller 1886, Moss 1933, Aiello 1984, 1991, Otero & Aiello 1996, Freitas et al. 2001, Willmott 2003b, & references therein). For that reason, it is important for all who possess new information on *Adelpha* biology, to publish it. Even a small bit of new information can provide a valuable clue to species relationships, or offer support for or against suspected ones, and thus also shed light on the reliability of other characters. Here, I present information about the larvae, pupa, and larval food plant of *Adelpha e. erotia* form "lerna" (Hewitson, 1847), in the Republic of Panama, and point out possible alliances within the *A. mesentina* group, to which it belongs.

MATERIALS AND METHODS

Thirteen individuals were collected, 11 as larvae (representing various stadia) and two as pupae, on the dates, at the localities (all in Panama), under the lot numbers, and by the collectors listed in the appendix. Of these 13 individuals, one was preserved as a larva, five died as larvae and were preserved, one was preserved as a pupa, and six were reared to adults. Preservations were made by bringing the larva or pupa to a boil in distilled water, then dropping it into 80% ethanol. Adults were frozen, then pinned and spread.

Reared individuals were housed in petri dishes until fourth or early fifth stadium, then transferred to small cages fashioned from petri dishes and window

screening, and placed in Ziploc® bags with folded, moistened paper towel strips to regulate humidity. Pupae were suspended in the same type of cages, by taping their support silk to the covers. All reared individuals were maintained in an air-conditioned lab. Behaviors were observed and recorded daily (with few exceptions), and shed head capsules and pupal exuviae were collected and mounted.

Lot numbers for reared individuals consist of the year plus a sequential number. When more than one individual was reared, an individual number (#) is appended. Thus "lot 2000-20 #2" refers to individual #2 of the 20th lot for the year 2000. These numbers appear on the labels of all reared specimens and their associated parts, and correspond to numbers on daily data forms maintained by Aiello at the Smithsonian Tropical Research Institute (STRI), Republic of Panama. All material relating to these rearings, including plant vouchers, is at STRI.

The first individual reared (lot 1996-24) was identified by Keith Willmott, from a photograph showing dorsal and ventral views of the adult (Fig. 1), and is alluded to on page 174 of his *Adelpha* revision (Willmott 2003b).

First instar setal terminology follows Stehr (1987).



FIG. 1. *Adelpha erotia erotia* "lerna" adult, dorsal (left), ventral (right), lot 1996-24.

Head chalazae positions—second instar on—do not correspond to first instar setal positions, thus, chalaza and scoli terminology (Fig. 2 top) was devised and developed by Aiello and Willmott over the course of previous publications (Aiello 1984, Willmott 2003b) and in correspondence between us during the writing of this paper.

Plant classification follows Stevens (2001 onwards). Note that Bombacaceae, Malvaceae, Sterculiaceae, Tiliaceae, and several other families are now combined as the Malvaceae, and that Cecropiaceae is included in

the Urticaceae.

RESULTS

All 11 larvae were found on *Cecropia longipes* Pittier, 1917 (Urticaceae) (plant vouchers Aiello 1588, 1612), in Parque Natural Metropolitano (PNM), on the Pacific side of the isthmus. Though *C. peltata* L., 1759, is more common in PNM, no evidence of *Adelpha* was found on it, and one larva (lot 2000-11) to which *C. peltata* was offered, ate some, then produced liquid fecula and died the next day. On the Atlantic side of the isthmus, *C. insignis* Liebm., 1851, the only *Cecropia* accessible from the Fort Sherman canopy crane, yielded no *Adelpha*. Though *C. obtusifolia* Bertol., 1840, is present in PNM, and, *C. longipes*, *C. obtusifolia*, and *C. peltata* are found at Fort Sherman, they were outside the areas accessible from the canopy cranes, and thus could not be searched.

Egg. Not seen.

First Instar. Head brown, with setae set in beige or gray pinacula in positions MD1, P1, P2, L1, AF1, AF2, F1, C1, A1, S1, S2, S3, SS1, and SS2, and with 3 setae on each half of labrum. Body pale greenish brown, with beige pinacula and bands of tiny beige spots that resemble pinacula but lack setae.

Second Instar. Head brown, densely dappled with pale, broadly conical chalazae—each with a terminal seta—representing three size groups. The principal chalazae—largest and plumpest—are arranged in four series—7 posterior, 4 medial, 2 anterior, 1 parafrontal. Among these, m1 and a1 are the most prominent. The spaces among the principals are filled by a few medium-sized and many small chalazae. The longest setae are found on the smallest chalazae, located on the lower portion of the head. All plain setae—i.e., set in pinacula—are confined to the mouthparts. Body yellow ocher above, brown on the sides, with short, yellow ocher scoli and gray chalazae and pinacula.

Third Instar. Head upper fourth, dark brown, with ocher chalazae; lower three-fourths gray, with small salmon-colored chalazae and still smaller gray ones; principal chalazae arranged in four series—7 posterior, 4 medial, 3 anterior, 1 parafrontal (minute or absent); the bases of the largest lumpy due to minute chalazae. Body pale ocher to salmon-brown dorsally, and dark gray to dark brown laterally, those ground colors mostly obscured by densely set, gray pinacula and chalazae; scoli stubby, ocher to salmon-brown, arranged as sub-dorsal and supra-spiracular on T2, T3, and A2-A7, and as only sub-dorsal on A8 and A10; spiracles dark brown, almost black.

Fourth Instar. Head now pale, with brown pits and numerous tiny chalazae surrounding the principal chalazae—otherwise similar in form and arrangement to the third instar. Body like third instar, but with a more pronounced 2-toned appearance, i.e., the sides of the thorax much darker than the rest of the body.

Fifth Instar (Figs 2 top left, top middle, and bottom; and 4 bottom left). Head cream-color to pale beige, with flat-bottomed pits of the same color, numerous setae set in minute chalazae, brown-marked frons, and dark brown mandibles; chalazae white, with conspicuous black-tips, and arranged in four series: 7 posterior, 6 medial, 4 anterior (a1 and a3 larger than a2 and a4), and 1 parafrontal. Body with thorax yellow ocher, mottled with red dorsally, chestnut brown laterally; abdomen yellow ocher with red mottling dorsally, cream-color laterally; simple, widely spaced setae arranged as several rings per body segment; chalazae white, ranging from tiny to long; subdorsal scoli (dorsal of Stehr 1987) (on T2–A8) large (except tiny on A1), white, with several tiers of black-tipped, black-based branches; supraspiracular scoli (on T2–A7) similar to subdorsals, but tiny and 2 or 3 branched; subspiracular scoli pale, tiny, grading from sessile and forked on anterior segments, to subsessile and 3–4 branched on

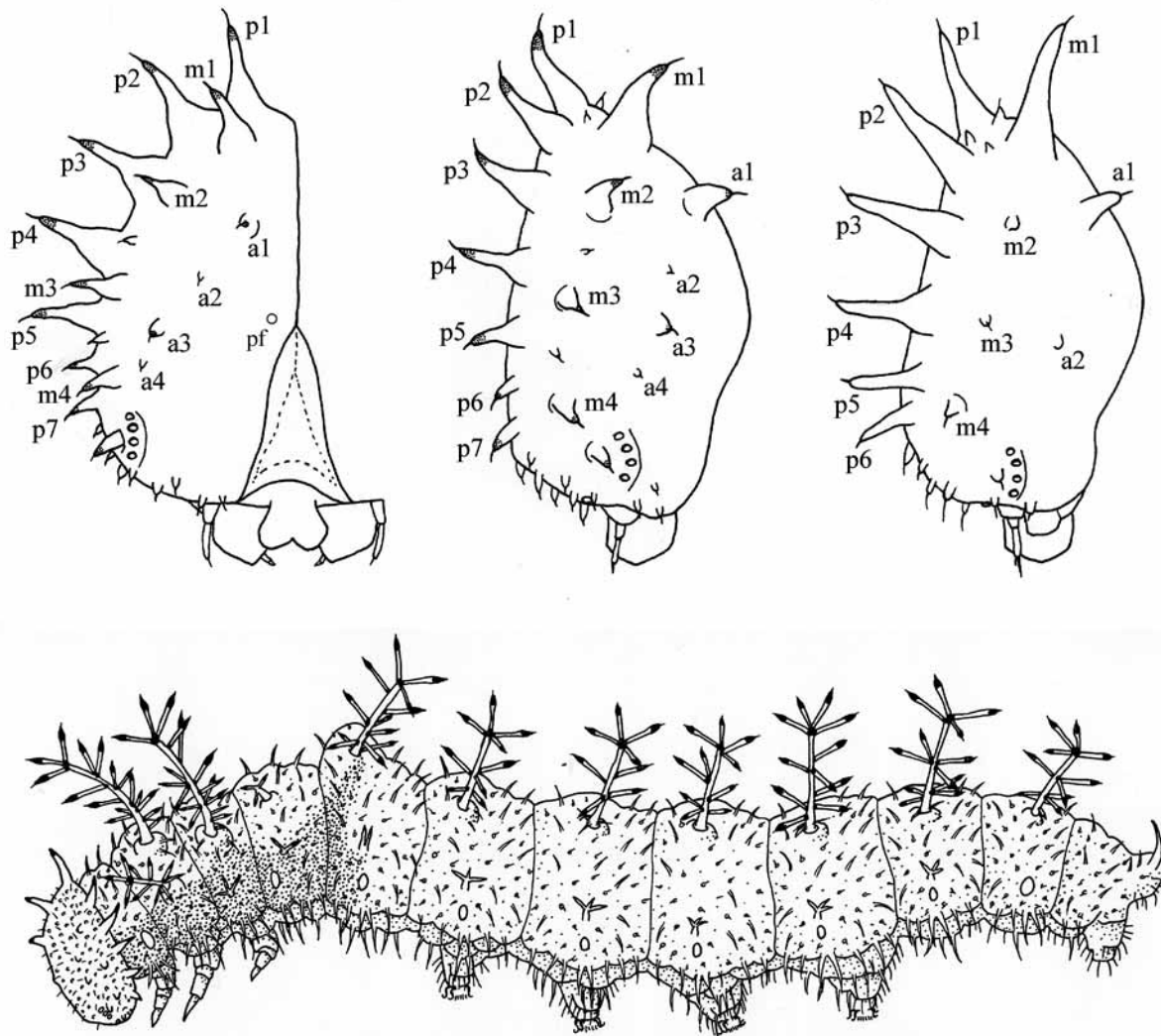


FIG. 2 Top, fifth instar head capsules: *Adelpha erotia erotia* "lerna" (lot 2000-29 #1) front view (left) and lateral view (middle); *Adelpha serpa celerio* (lot 1984-10 #2), lateral view (right); bottom, fifth instar habitus: *Adelpha e. erotia* "lerna," (lot 2000-29 #3). Chalazae: a = anterior, m = medial, p = posterior, pf = parafrontal.

posterior segments; caudal scoli simple, anteriorly curved; spiracles pinkish beige with dark brown borders.

A beautiful larva, whose white scoli with black tips and joints, and numerous white chalazae viewed against the yellow body give it a frosted appearance (Fig. 4 bottom left).

In mature larvae, abdominal segment 2 has a large, rounded, middorsal hump that corresponds to the huge A2 hook of the impending pupa.

Larval behavior. First instars constructed fecula and silk rods anchored to the leaf lobe margin, i.e., they were not leaf vein extensions, and rested head outward on them between feeding bouts and during molting. These rods were lengthened gradually, until they reached several times the body length of the larva. Second through fourth instars added tiny leaf bits to the base of their fecal rods, and continued to rest on them as before. First through third instar feeding damage was characterized by tiny holes all over the leaf, and fourth and fifth instars ate whole leaf. Following the molt to the final stadium, larvae abandoned their fecal rods entirely, and when disturbed assumed a head down, T1–A2 arched, A7–A10 up position.

Pupa (Fig. 3). Entirely dark bronzy brown except for an area of

shimmering gold reflection on the dorsum of the thorax, from the inner curve of a T2 middorsal projection through the inner curve of a A2 middorsal hook. The A2 middorsal hook huge, fairly straight, with a wider, slightly curved apex, far surpassing the bluntly rounded tip of the T2 middorsal projection, and reaching almost to head level. Head "horns" small, rounded, very similar to, but narrower than those of *A. lycorias melanthe* (Bates, 1864). Pupation silk chestnut brown. Both field-collected pupae, were found suspended beneath leaves.

Development and eclosion times. See appendix.

POSITION WITHIN ADELPHA

The 2-toned, uniform-scoli larva and the "huge hook" pupa of *A. erotia erotia* "lerna" indicate that this taxon belongs to the *A. mesentina* group (Aiello 1984), which, so far comprises six species as outlined by Willmott (2003b, as *phylaca* group) [=group II of Aiello (1984, 1991)], and includes *A. mesentina* (Cramer, 1777), the

type species of the genus. The final instars of the four *A. mesentina* group taxa reared in Panama (Fig. 4) also share similar head morphology; they have 7 posterior and 4 anterior chalazae, whereas most *Adelpha* have 6 and 2 respectively (see Key). Neither preserved larvae nor head capsules of the two Brazilian species were available for examination.

Willmott (2003a, 2003b) tentatively includes *A. pollina* Fruhstorfer, 1915 in the *mesentina* group, though he suspects that it is misplaced there. In his revision (Willmott, 2003b) he places *Adelpha hesterbergi* Willmott & Hall, 1999 in the *A. capucinus* group, whereas in his cladograms (Willmott 2003a) it appears loosely allied with the *mesentina* group (as "*phylaca* group"), but is not commented on in the text. The immature stages and larval food plant(s) are unknown for either taxon, and their logical affiliations remain to be discovered.

Final stadium larvae of *A. e. erotia* "lerna" and *A. lycorias melanthe* share a number of characteristics not reported for other *Adelpha* species; both have a frosted appearance due to the contrasting dark tips and branch bases of their pale scoli and to the numerous tiny chalazae that further ornament the body; and in both, the A2 subdorsal scoli terminates in a whorl of subequal branches.

By contrast, final instar *A. phylaca pseudoaethalia* Hall, 1938 and *A. messana messana* (C. & R. Felder, 1867) have uniformly brownish scoli and chalazae, set among plain setae; and one of the terminal branches of the A2 subdorsal scoli is elongate and upwardly inclined. They also share a dark, elliptical, lateral patch across the junction of abdominal segments 4 and 5, a feature not present in either *A. e. erotia* "lerna" or *A. lycorias melanthe*.

Moss (1933) does not comment on larval scoli form or color pattern in *A. mesentina* or *A. thesprotia* (C. & R. Felder, 1867), but does note that the two were "...so similar...in larva and pupa that no special observations were made." However, his illustrations are sufficiently clear to show that the larvae of those two species share the relatively unornamented body and dark contrasting elliptical spot with *A. phylaca pseudoaethalia* and *A. m. messana*.

The pupa of *A. e. erotia* "lerna" is distinctive in having the A2 "hook" nearly straight, and surpassing the T2 projection, whereas in each of the other five *A. mesentina* group species (Fig. 4 shows the four Panamanian species) it is curved and directed towards the tip of the T2 projection, with which it forms a nearly closed circle. In *A. e. erotia* "lerna," the T2 projection is short and broadly rounded, whereas in the other five taxa it is drawn out to a rounded point.

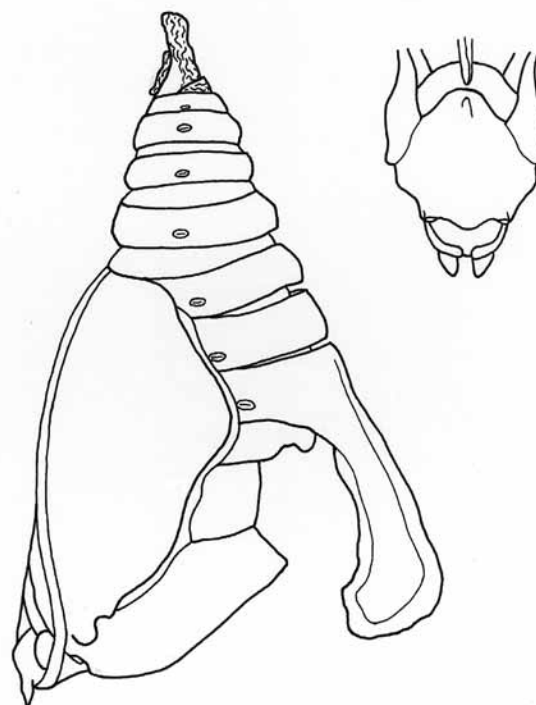


FIG. 3. *Adelpha erotia erotia* "lerna" pupa, lateral habitus and dorsal head and thorax (lot 1996-24).

Those unique features aside, the pupae of *A. e. erotia* "lerna" and *A. lycorias melanthe* resemble one another, and differ from *A. phylaca pseudoaethalia* and *A. m. messana* in having the A2 "hook" apex slightly widened and truncate, instead of tapering to a rounded tip; and the "head horns" small and rounded, instead of outwardly curved points, or, as in *A. mesentina* and *A. thesprotia*, outwardly curved and leaf-like (Moss 1933). Though the illustrations in Moss (1933) are sufficiently detailed to comment on some characteristics of the latter two taxa, examination of preserved pupae or exuviae would be necessary to verify the form of the A2 "hook."

Combining published information on the group (Müller 1886, Moss 1933, Aiello 1984, 1991) and the present report, we now have descriptions of the larvae and pupae of at least one subspecies for each of the six, well-accepted members of the *A. mesentina* group. Based on those descriptions, *A. e. erotia* "lerna" and *A. lycorias melanthe* appear to form a subgroup, and the other four taxa another. Within the second subgroup, and based upon the form of the pupal "head horns," *A. phylaca pseudoaethalia* appears to pair with *A. m. messana*, and *A. mesentina* with *A. thesprotia*.

The intra-group relationships suggested by the immature stages of the *mesentina* group are rather

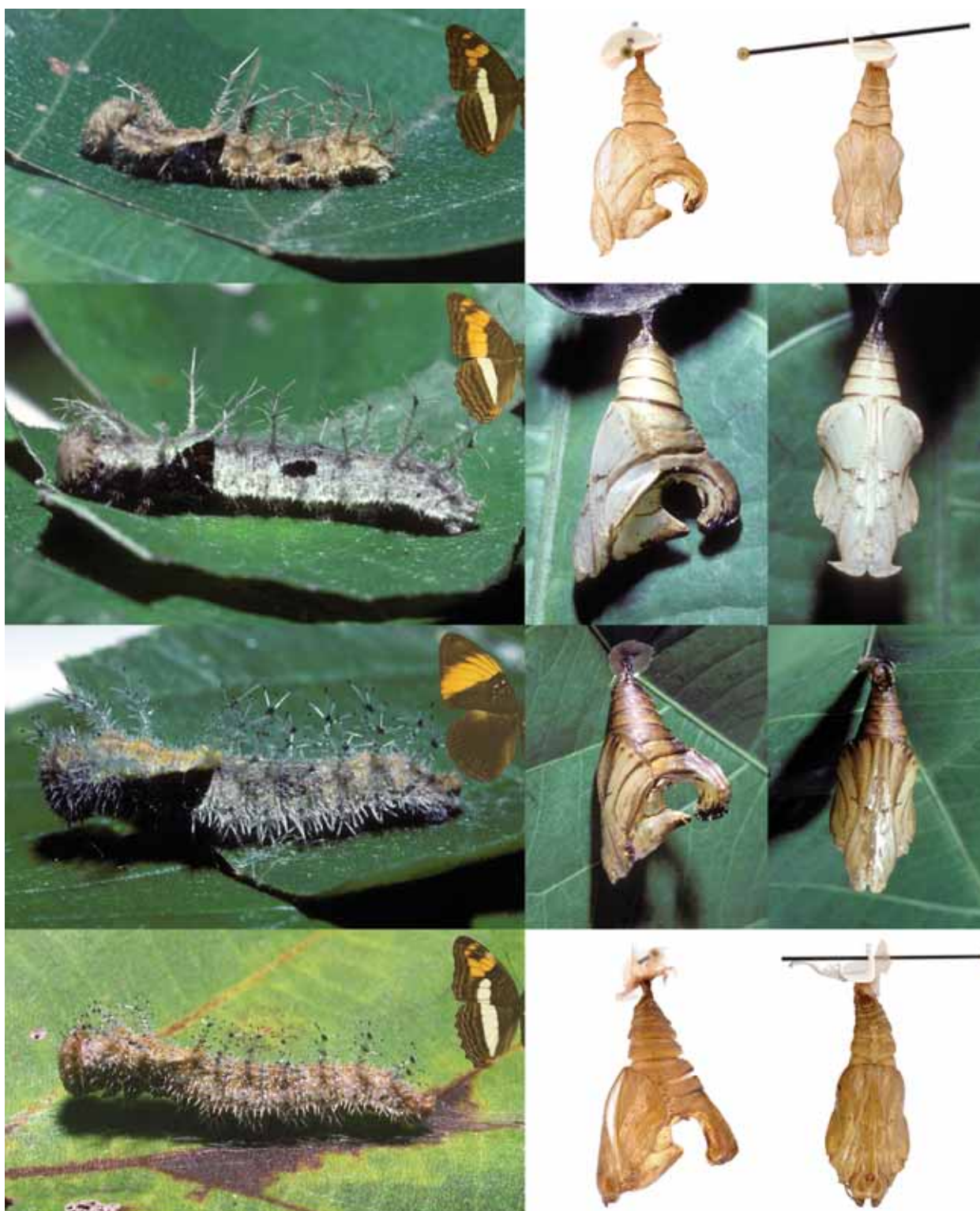


FIG. 4. Top row: *Adelpha messana messana* final instar, adult, pupal exuviae (lateral, ventral) (all lot 1989-22 #2); Second row: *A. phylaca pseudoaethalia* final instar, adult, pupa (lateral, ventral) (all lot 1983-78); Third row: *A. lycorias melanthe* final instar, adult, pupa (lateral, ventral) (all 1983-8 #3); Bottom row: *A. e. erotia "lerna"* final instar and adult (lot 2000-20 #5), pupal exuviae (lateral, ventral) (lot 1996-24).

TABLE 1. Larval food plant genera and families reported for *Adelpha phylaca* Group taxa, for specimens with identifications verified. Plant classification follows Stevens (2001 onwards). Divisions reflect possible species affinities.

ADELPHA TAXON	ORDER ROSALES		ORDER MALVALES	REFERENCE
	Ulmaceae	Urticaceae	Malvaceae	
<i>A. lycorias melanthe</i>	<i>Trema</i>			Aiello 1984 (lot 83-8), as <i>melanthe</i> ; Aiello lot 03-14
<i>A. lycorias lycorias</i>		<i>Cecropia</i>		Müller 1886, as <i>isis</i>
<i>A. lycorias lycorias</i>		<i>Coussapoa</i>		Müller 1886, as <i>isis</i>
<i>A. lycorias lycorias</i>		<i>Pourouma</i>		Müller 1886, as <i>isis</i>
<i>A. erotia erotia "lerna"</i>		<i>Cecropia</i>		Aiello lots 98-45, 00-20, 02-29
<i>A. mesentina</i>		<i>Pourouma</i>		Moss 1933
<i>A. thesprotia</i>		<i>Pourouma</i>	<i>Bombax</i>	Moss 1933, as <i>delphicola</i>
<i>A. phylaca pseudoaethalia</i>		<i>Cecropia</i>		Aiello 1984 (lots 81-70, 82-39, 82-40, 83- 78), as <i>phylaca aethalia</i> ; Aiello lot 00-27
<i>A. messana messana</i>			<i>Luehea</i>	Aiello 1990 (lot 89-22), as <i>ixia leucas</i>

different from those obtained by the cladistic analysis of Willmott (2003a), which relies strongly on adult characters. It is to be hoped that molecular studies will provide both a clearer concept of intra-group relationships and an assessment of the relative importance of immature and adult character sets.

LARVAL FOOD PLANTS OF THE ADELPHA MESENTINA GROUP

Though three plant families have been reported for members of the *A. mesentina* group (Table 1), the Urticaceae clearly dominate these records, and at least one member of each of the three *A. mesentina* group species-pairs has been reported on that plant family. The dominance of Urticaceae may prove greater once additional records (DeVries 1986, 1987; Janzen & Hallwachs 2004) of *A. lycorias melanthe* and *A. m. messana* on *Cecropia* are verified by Keith Willmott. Within the Rosales, as outlined by Stevens (2001

onward), Urticaceae (including *Cecropia*) and Ulmaceae, together with Cannabaceae and Moraceae, form a well-supported clade. Furthermore, within the Malvaceae, which comprise 9 subfamilies, the two that concern us here, Malvoideae and Bombacoideae, form their own well-supported clade. Thus, the *A. mesentina* group taxa are restricted to two small plant clades.

Two of the three plant families just discussed, have been reported as larval hosts in another *Adelpha* group, the *A. serpa* group: *A. celerio* on *Ochroma* (Malvaceae) (lot 1982-41) and *Cecropia* (Coley lot 15 in Aiello 1984); and an unidentified *Adelpha* taxon on *Heliocarpus* (Malvaceae) (lots 1982-75, 1983-68, 1985-122). Whether larval host plant switches and expansions have played an important role in *Adelpha* speciation cannot be determined until we have clearer knowledge of species relationships within *Adelpha*, and more complete information on host plant associations throughout the ranges of *Adelpha* taxa.

KEY TO PANAMANIAN ADELPHA MESENTINA-GROUP SPECIES BASED ON LARVAE AND PUPAE

p = posterior, m = medial, a = anterior

- 1a. Larva head with 6 posterior chalazae, 4 medial chalazae (in *serpa*-Group m1 is long and slender, and m2-m4 are low, rounded bumps), and 2 anterior chalazae (see fig. 2); frons bordered by a stripe of smooth relatively pit-less cuticle; body usually with A2 subdorsal scolus noticeably different in form and/or size from rest; thorax not significantly different in color or pattern from rest of body; pupa A2 dorsal projection not massive and not forming a circle with or surpassing the T2 dorsal projection
- 1b. Larva head with 7 posterior chalazae, 4 medial chalazae plus 2 or 3 tiny intercalated extras (sometimes not well aligned), and 4 anterior chalazae; pit-less stripe absent or poorly defined; main body scoli fairly uniform in shape and size; sides of thorax conspicuously darker than rest of body; pupa with a huge A2 dorsal hook that curves inward, nearly touching and forming a circle with the T2 dorsal projection, or nearly straight and surpassing the T2 projection

non-mesentina groups

2

- 2a. Larva head chalazae tipped with black or dark brown; body main scoli pale, with black or brown branch tips and bases; body also clothed with densely set, short, pale chalazae; all the above combine to give the larva a frosted appearance; head extra medial chalazae conspicuous and usually well aligned with principals, forming fairly uniform line; terminal branches of body A2 scolus similar to each other in length and inclination; abdomen without dark lateral patches; pupa head horns small and rounded.

3

2b. Larva head and body scoli not dark-tipped, though larger branch junctions of main body scoli may be darkish; body also with short chalazae, but these not densely set, except perhaps laterally; head extra medial chalazae minute or small and often not well-aligned with principals; one terminal branch of body A2 subdorsal scoli noticeably longer than rest, and tilted upward; abdominal segment 5 with well-defined, dark brown lateral patch; pupa head horns outwardly curved, small, rounded or acute points, or outwardly curved and leaf-like. **4**

3a. Larva head chalazae slender conical, with somewhat rounded, conspicuously black tips; pits indistinct, same pale color as surrounding cuticle; pupa A2 dorsal hook nearly straight, and surpassing the T2 dorsal projection; T2 dorsal projection short and broadly rounded

***A. erotia erotia* "lerna"**

3b. Larva head chalazae slender tapered, the larger ones with acute, dark tips; pits well-defined, a few darker than surrounding cuticle; pupa A2 dorsal hook curving inward to form nearly closed circle with T2 dorsal projection; T2 dorsal projection drawn out to a rounded point

A. lycorias melanthae

4a. Pupa head horns outwardly curved, small, rounded or acute points **5**

4b. The larvae of *A. mesentina* and *A. thesprotia* have not been examined, but if they key to this couplet, then pupa head horns outwardly curved and leaf-like separates them from the two species keyed in couplet 5 ***A. mesentina* and *A. thesprotia***

5a. Larva head with 3 extra medial chalazae nearly same size as principals, one each between m1/m2, m2/m3, and m3/m4, but not well aligned with them, resulting in a ragged line; pupa head horns very small, outwardly curved, rounded points ***A. messana messana***

5b. Larva head with 2 tiny, extra medial chalazae, one each between m2/m3 and m3/m4, usually well aligned with principals; pupa head horns outwardly curved, pointed and leaf-like ***A. phylaca pseudaeathalia***

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