

Description of *Apatelodes audubonin*. sp. from Texas (Bombycoidea: Apatelodidae), with a Query as to Whether Apatelodid Larvae are Batesian Mimics

Author: Wagner, David L.

Source: The Journal of the Lepidopterists' Society, 68(3) : 211-217

Published By: The Lepidopterists' Society

URL: <https://doi.org/10.18473/lepi.v68i3.a9>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

DESCRIPTION OF *APATELODES AUDUBONI* **N. SP.** FROM TEXAS (BOMBYCOIDEA:
APATELODIDAE), WITH A QUERY AS TO WHETHER APATELODID LARVAE ARE
BATESIAN MIMICS

DAVID L. WAGNER

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043, USA,
email: david.wagner@uconn.edu

AND

EDWARD C. KNUDSON

8517 Burkhart Road, Houston, Texas, USA, email: eknudson@earthlink.net

ABSTRACT. *Apateledes auduboni* **n. sp.** is described from Cameron County in the lower Rio Grande Valley of Texas. Male and female genitalia and the larval stage are figured. Larvae *A. auduboni* **n. sp.** were recovered from lime pricklyash, *Zanthoxylum fagara* (Rutaceae). We discuss evidence suggesting that the larva's bright coloration and conspicuous diurnal behaviors as well as those of other apatelodid larvae are consistent with the hypothesis that *Apateledes* and perhaps other apatelodids are Batesian mimics of arctiines and megalopygids.

Additional key words: *Zanthoxylum fagara*, Sabal Palm Refuge, larval mimicry, warning coloration

The Apatelodidae are a largely tropical New World family of Bombycoidea containing more than 150 species (Lemaire and Minet 1998). Only a half dozen species are found north of the Mexican border and only one of these occurs northward to Canada (Franclemont 1973, 1983; Covell 2005). The nominate genus *Apateledes* contains much of the subfamily's diversity with more than 50 described species and many new species (sorted as such) existing in collections. Only two *Apateledes* are recognized as occurring in the United States north of Mexico (Franclemont 1973, 1983; Powell & Opler 2009): *A. torrefacta* (J. E. Smith, 1797) and *A. pudefacta* Dyar, 1904. The former is a widespread moth found across much of eastern North America (Covell 2005), while the latter is principally a Mexican species that reaches its northernmost limit in southeastern Arizona (Franclemont 1973). Here we report on a third, undescribed, *Apateledes* from the lower Rio Grande Valley of Texas: *A. auduboni*. We describe the adult, provide photographs of the middle and late instars, make brief observations on the species' natural history, and conclude with a discussion of the possible adaptive significance of the larva's conspicuous bright pink-red, white, and black coloration, as well as that of other apatelodids.

METHODS AND MATERIALS

In the Sabal Palm Refuge, Southmost, Cameron Co., Texas, where most of our paratypes were collected, DLW, Henning von Schmeling, and colleagues spent over 20 person-hours beating a wide taxonomic range

of plants and examining vegetation by eye for caterpillars in 2006, 2007, 2008, and 2013. An extensive array of plants was sampled during each visit as part of a general caterpillar survey. Any plant species that lent itself to beating (trees, shrubs, forbs, and bunch grasses > 20 cm in height) was likely to be sampled three or more times on each visit. Larvae of *A. auduboni* were collected from *Zanthoxylum fagara* on 20 October 2006 (DLW Lot: 2006K7) and 19 October 2007 (DLW Lot: 2006K71). The larval description is based on larval images (deposited at the University of Connecticut); no larvae were preserved because of the need to successfully rear at least one individual to the adult stage. Genitalia were prepared and mounted according to Lafontaine (2004) except that the preparations were mounted in euparal. COI sequences were generated by the Barcodes of Life Project. Adult specimens, including genitalic preparations, were deposited in the collections listed below.

CNC Canadian National Collection, Ottawa, Ontario, Canada.

ECK Collection of Edward C. Knudson, Houston, Texas, USA.

TAMU Texas A & M University, College Station, Texas, USA.

UCMS University of Connecticut, Storrs, Connecticut, USA.

USNM United States National Museum, Washington D. C., USA.

RESULTS

Apatelodes auduboni new species

Figures 1–12

Diagnosis: Adults average smaller than many members of the genus with wingspans usually under 39 mm in males. The outer margin of male forewing is more rounded and the subapical cavity shallower than those of many *Apatelodes* (Figs. 1, 2). The reddish flush in the hindwing and small, divided brown subbasal spot (above inner margin of FW) will distinguish *A. auduboni* from other Neotropical *Apatelodes*. Superficially adults resemble those of *A. batina* Dyar, 1912 (TL Guerrero), *A. gladys* Dyar, 1918 (TL Veracruz), and *A. torrefacta* (TL United States), but the degree to which the subbasal spot is broken (into a small upper spot and usually larger, oblique, lower spot) is diagnostic. The ground color of both *A. gladys* and *A. torrefacta* averages lighter, tending to pale to mouse gray, but gray-brown in *A. auduboni*. The postmedial line in *A. batina* and *A. gladys* is straight—not scalloped as in the new species. The male genitalia of *A. auduboni* are similar to those of *A. torrefacta* (Franclemont 1973: 18) but the uncus is proportionately larger and the caudal margin is straight between the laterally projecting lobes (Fig. 4), not concave as in *A. torrefacta*; the paired knobs on the juxta of *A. auduboni* are smaller and more wart-like than those of *A. torrefacta*.

Description: Male. *Head:* Mostly brown, concolorous, but sometimes with tan or frosted scales over vertex. Distal segment of labial palpus obovate, brown with tan scales common over mesal face (often concealed), reaching above midpoint of compound eye in living moth. *Thorax:* Dorsum of thorax gray-brown with narrow ridge of dark reddish brown scales. Procoxa brown, concolorous with palpus and frons; distal segments of leg pale brown to tan, irrorated with contrasting, dark brown scales. Middle and hindlegs pale tan-brown and irrorated with dark brown scales. *Wings* (Figs. 1, 2):

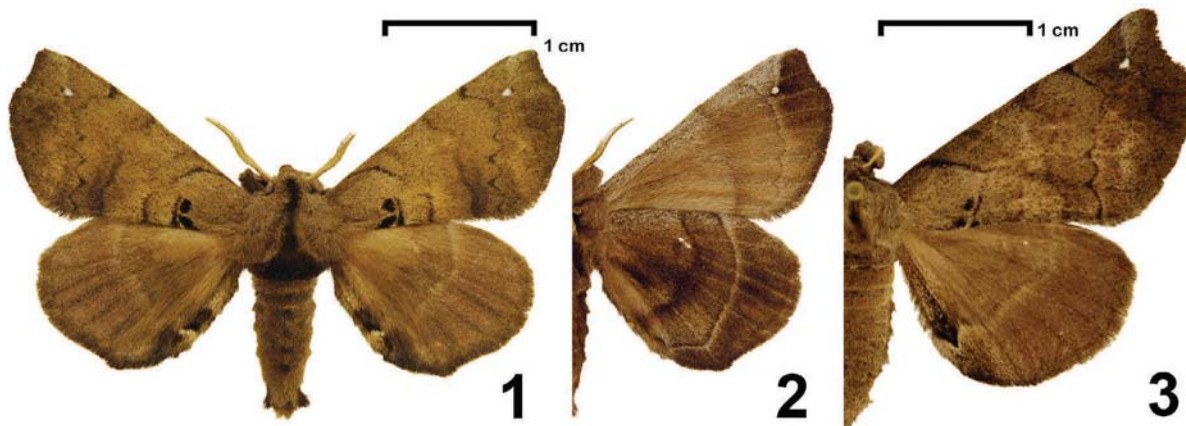
Forewing: length 17–18 mm (n=37). Ground color gray- to chocolate-brown. Upper arm of antemedial line abruptly bent basad at cell; lower portion almost perpendicular to inner margin and often separated from upper arm. Dark brown subbasal spot along inner margin broken into small upper spot and usually larger oblique spot edged with few white scales along inner margin (of wing). Medial line weakly expressed, sometimes doubled. Postmedial line scalloped especially from M₁ to inner margin (subtornus), although sometimes vague or absent. Subapical white spot small and triangular. Underside of forewing (Fig. 2) with white line connecting costa to subapical spot, and wing proximal to line with patch of whitish scales along costa. Hindwing dingy brown with reddish flush; ill-defined medial line of pale scales; dark scales confined to dark spot along anal margin—this spot edged with white scales that join medial line. *Abdomen:* Dorsum of A1 deep chocolate brown; remainder of abdomen essentially same color as hindwings with slight rose tint; weakly developed middorsal tufts; A8 with small lateral tufts that project away from body. *Genitalia* (Figs. 4, 5): Valve tongue-like, parallel-sided, with rounded apex; strongly sclerotized horn from base and weakly differentiated sacculus; uncus extending caudad past valves, almost flipper-shaped apically; two “gnathal” warts; tegumen with lateral digitate lobe (that extends toward juxta in Fig. 4); juxta with medial, dorso-proximally projecting lobes; saccus extended as a rounded cone. Aedeagus (Fig. 5) with a cone-shaped anterior diverticulum and laterocaudal projections drawn into horns; vesica tubular, about 2x length of phallobase.

Female (Fig. 3): As in male, except forewing length 19–20 mm (n=3). *Genitalia* (Fig. 6): Papillae anales elongate triangular, roughly twice as long as wide, bearing long setae subequal to width of papillae anales. Bursa ovoid with signum divided into two spindled-shaped plates; ductus bursae about 2x length of bursa; ductus seminalis entering ductus bursae near strongly sclerotized sterigma, which is rounded posteriorad.

Holotype male (Fig. 1): TEXAS: Cameron Co., Southmost, Audubon Sabal Palm Refuge [25°51'2.62"N, 97°25'1.59"W], 9 December, 1998, E. C. Knudson, 15 W blacklight. CNC male genitalic slide 14492. Deposited at TAMU, College Station, TX.

Paratypes: 36 males and 3 females.

Texas, Cameron County: Brownsville, 27.IX.1988 (1 ♂), ECK, at light. Sabal Palm Grove: (as “ASPGS, Brownsville”), 26.X.1986 (1 ♂), ECK, at light; 27.IX.1988 (13 ♂, 1 ♀), CNC female genitalic slide 14493), ECK, at light; 6.X.1994 (5 ♂), C. Bordelon, at light; 16.X.1995 (1 ♂), ECK and C. Bordelon, at light; 21.X.1995 (1 ♂, 1 ♀), ECK and C. Bordelon, at light; 10-11.X.1996 (4 ♂), ECK and C. Bordelon, at light; 12.X.2004 (3 ♂), C. Bordelon, at light; 16.X.2005 (2 ♂) (Barcodes of Life Project 00081909) ECK and C. Bordelon, at light; no date (1 ♀), ECK, at light; larva on *Zanthoxylum fagara*, 19.X.2007,



FIGS. 1–3. *Apatelodes auduboni* n. sp. (1) Holotype male, dorsal. (2) Holotype male, ventral. (3) Female.



FIGS. 4–6. *Apatelodes auduboni* n. sp. genitalia. (4) Male. (5) Aedeagus. (6) Female. Scale bar equals 1 mm.

emerged 2.IV.2008 (1 ♂), Henning von Schmeling and DLW (Barcodes of Life Project 00081910). Santa Maria National Wildlife Refuge: 10.III.1999 (3 ♂), ECK, at light. Southmost: 27-X-1986 (1 ♂), ECK, at light. Paratypes deposited in CNC, ECK, TAMU, UCMS, and USNM.

Larva: Last instar (n=8) (Figs. 11, 12): Head ruddy red-brown and essentially unpatterned; clypeus and basal antennal segment cream (Fig. 12). Labrum with V-shaped cleft extending halfway to clypeus. Trunk densely covered with abundant black, white, and pinkish red secondary setae with series of elongate middorsal tufts from T2 to A8 (Fig. 11). Middorsal tuft over T2 longest, black (but apically whitened), curving anteriorly; tufts over T3 and A8 nearly as long, black with white apical setae; those over A1 and A7 about 2/3 as long, with that over A1 mostly black and that over A7 mostly white; intervening tufts subequal, less than 1/2 height those over T3 and A8 and colored as follows: A2 pinkish red to orange or tan, A3–A4 black, A5 white, A6 black. Subdorsal and lateral areas with numerous pinkish red setae on T2–A3, A5, A6, and A7. Venter of thoracic segments dark; contrasting with pale midventer of abdominal segments. Prolegs black apically (not reddened as in some *Apatelodes*). Caudal end with long, wispy trailing setae.

Middle to penultimate instars often with more yellow or white setae and reduced pinkish red subdorsal and lateral setae; middorsal tufts over (A1), A4, A5, and A7 mostly white (Figs. 9, 10). Early instars with tangle of gray-black setae over thorax that makes anterior portion of body appear swollen; bright red setae over A3 (Figs. 7, 8).

Distribution: So far known only from the Audubon Sabal Palm Sanctuary and Santa Maria National Wildlife Refuge in Cameron County, Texas, but undoubtedly ranging southward into Mexico (see below).

Barcodes: Two specimens of *A. auduboni* from the Sabal Palm Refuge (Barcodes of Life Project 00081909 and 00081910) and the two other North American *Apatelodes* species, *A. torrefacta* (n=7) and *A. pudefacta*. (n=3), were barcoded. In a Kimura 2P neighbor-joining tree, all three species formed distinct (monophyletic) clusters, with *Apatelodes auduboni* clustering as the sister to the two Nearctic species (Fig. 13). See also Discussion.

Etymology: This species is dedicated to the early French-American ornithologist, naturalist, and painter John James Audubon, and the Sabal Palm Sanctuary in Southmost, Texas named in his honor.

DISCUSSION

To confirm that *A. auduboni* had not been described previously we went through the *Apatelodes* holdings in the USNM, which contains the most important collection of New World *Apatelodidae*, as well as a great number of *Apatelodes* types—the family was a favorite of two early USNM workers, Harrison G. Dyar and William Schaus. We located one specimen in the United States National Museum that closely approached *Apatelodes auduboni* in appearance. The moth, bearing a single label “Chilpancingo” [Mexico], is significantly larger and differs in enough minor traits not to be included in the type series. Interestingly, the single specimen was placed in its own unit tray in the vicinity of other undescribed apatelodid species, perhaps by Dyar or Schaus, suggesting that a moth close to and perhaps conspecific with *A. auduboni* was thought to represent a new species by one or more workers at the USNM. We also examined the *Apatelodes* holdings at the American Museum of Natural History, reviewed Druce’s (1893a) treatment of the genus in *Biologia Centrali-Americana*, and worked through other important taxonomic treatments of the genus (e.g., Dyar 1912, 1918; Schaus 1939) in our efforts to determine if *A. auduboni* was in fact undescribed.

We also compared the barcodes of the new species (Barcodes of Life Project 00081909 and 00081910)



Figs. 7–12. *Apatelodes auduboni* n. sp. larva. (7, 8) Early instars, approximately 8–13 mm. (9, 10) Middle to penultimate instars. (11) Last instar. (12) Last instar, head.

with those of 234 Central and North American *Apatelodes* individuals representing about 26 species-level taxa (tree not shown). Our specimens clustered together. Their sister was a specimen of *A. pandara*¹ Druce (1893b) [DHJ02|07-SRNP-103174|655 bp] from Guanacaste, Costa Rica; it differed by an uncorrected distance of about 0.7%. *A. auduboni* differs from Costa Rican *A. pandara* in numerous ways: *A. pandara* has straight antemedial, medial, and postmedial lines that are absent in *A. auduboni*. The subbasal spot along the inner margin is large and undivided in *A. pandara*, and always divided into two small spots in *A. auduboni*. In

A. pandara the hindwings are heavily suffused with dark brown scales; in *A. auduboni* dark scales are confined to a spot along the anal margin, and the hindwings have a pinkish cast. Given the number and magnitude of the differences in the two species, we are surprised that the two taxa differ by only 0.7% (uncorrected distances) in a neighbor-joining tree.

With the exception of the widespread North American polyphage, *A. torrefacta*, which has been recorded from more than 10 hostplant families (Wagner 2005, DLW unpublished data; Robinson et al. 2014), little published information exists on the life

¹ Costa Rican *A. pandara* has not yet been compared with Druce's (1893b) type at the British Museum of Natural History.

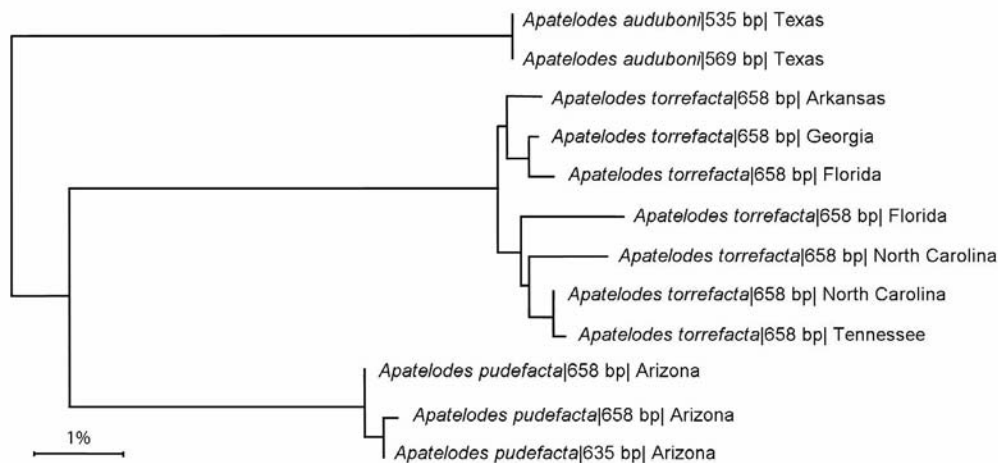


FIG. 13. Kimura 2P neighbor-joining tree for 12 *Apatelodes* specimens representing the three known North American species.

histories of *Apatelodes*. The eight larvae of *A. auduboni* that we found all came from *Zanthoxylum* (L.) Sarg (lime pricklyash or colima) (Rutaceae) growing in the Audubon Palm Sanctuary. Seth Patterson (personal communication), the current Sanctuary manager, reports seeing the caterpillar most commonly on lime pricklyash, although he posted one image of the caterpillar on *Salix* (<http://bugguide.net/node/view/859153>) (but evidence of feeding was not observed). *Apatelodes pudefacta* is a somewhat generalized composite feeder in southern Arizona. In addition to various species of *Viguiera*, a favored hostplant, larvae have been found on *Ambrosia*, *Baccharis*, *Brickellia*, and *Helianthus* (Franclemont 1973; DLW unpublished data); and at least in later instars, larvae wander onto and feed on many other hosts such as *Aralia* and *Garrya* (DLW unpublished data).

The solitary larva of *A. auduboni*, boldly marked in rose, black, and white, appears to be warningly colored. Such is the case for many other apatelodids (e.g., see <http://janzen.sas.upenn.edu/caterpillars/database.lasso> for images of apatelodid caterpillars from Costa Rica). Moreover, apatelodid caterpillars sometimes perch on upper leaf surfaces and are conspicuous enough in habit to be found readily during the day simply by scanning foliage. To the best of our knowledge, *Apatelodes* are not known to be distasteful. Dyer (1995) scored both polar and non-polar extracts from a Costa Rican apatelodid (*Tarchon felderi*) as palatable. Likewise, no apatelodids are known to cause erucism (Diaz 2005; Hossler 2010). Hence, the evolutionary

raison d'être for their signaling coloration remains unexplained. Undoubtedly, long, dense setae are a deterrent for many natural enemies, including numerous invertebrate predators: e.g., ants, wasps, and many parasitoids. Lee Dyer (personal communication) has pictures of a bala ant (*Paraponera clavata*) with wads of *Tarchon* setae all about its mandibles, which the ant spent much time removing—whether the hairs are sticky or simply become physically interdigitated once free of the caterpillar's body is not known. Yet, it seems unlikely that most insectivorous vertebrates would be thwarted by apatelodid hairs if they were not distasteful, urticating, barbed, sharp, or some other way provided appreciable chemical or mechanical protection. Furthermore, it is not obvious why a hairy caterpillar that is not chemically protected would be brightly colored with red—shouldn't it be enough to be hairy and at least somewhat cryptic as is the case with hairy pterophorids, nolidids, acronictine noctuids, and pantheine noctuids? Additionally, Noel McFarland pointed out to us that pupation in apatelodids takes place below ground in a cell, and not in a hair-embellished cocoon as is commonly the case with protected arctiines and lymantriines (Wagner 2008 and Ferguson 1978, respectively). Such is suggestive that the larval hairs of *Apatelodes* by themselves provide little chemical or physical protection for pupae (or larvae). In contrast, arctiine caterpillars—well known for their distastefulness both as larvae and pupae (Bowers 2008; Hartmann 2008) and for their hairs being able to cause erucism, even after they are shed from the body (Frazer 1965; Rothschild 1985; Ken

Strothkamp unpublished data)—weave their setae into the walls of their cocoons or, in those arctiine lineages with aposematic pupae, construct a see-through cocoon above ground that displays the pupa (Wagner 2008). Finally, there is a common tendency for unpalatable (and aposematic) caterpillars to occur in clusters (Tullberg 1988)—yet North American apatelodids and those that we have encountered over the course of more than two dozen visits to forests of Costa Rica and Ecuador have been solitary.

Given the above, we speculate that apatelodid caterpillars are mimetic of other protected hairy Lepidoptera, and in particular the larvae of tussock-bearing phaeopterine (tussocks) and ctenuchine (wasp moths) arctiines and megalopygids². Members of both arctiine groups are known to be unpalatable and/or cause erucism (Bowers 2008). In the tropics, some apatelodids appear to be mimics of megalopygids (see examples posted at: <http://janzen.sas.upenn.edu/>)—a group widely known for their painful stings (Stehr 1987; Epstein et al. 1998; Wagner 2005; Hossler 2010). Until it is shown that the apatelodid caterpillars are unpalatable, e.g., simply by virtue of being “hairy” or for other reasons, it is our guess that the caterpillars of *A. auduboni* and other apatelodids are generalized Batesian mimics. But whatever the evolutionary basis for their signaling coloration—be it Batesian mimicry, Mullerian mimicry, aposematism, or otherwise—studies are needed to quantify the payoffs (and costs) of their flamboyant vestiture and behavior.

ACKNOWLEDGEMENTS

Henning von Schmeling spent many hours beating vegetation and searching for caterpillars of this moth (and other species) in October 2006, 2007, and 2008. Our thanks to Noel McFarland who pointed out that the pupation site of *Apelodes* spp. (below ground) is peculiar for a hairy caterpillar. Jimmy Paz and Seth Patterson assisted with permits and helped with logistics at the Palm Sanctuary. Don Lafontaine and Jocelyn Gill made the genitalic dissections and supplied the genitalic images that appear here. Don Lafontaine, Dan Janzen, Winnie Hallwachs, and Chris Schmidt helped with the barcoding of our specimens and shared other sequences from their databases. The foundation for many of barcodes used in this study were provide by Dan Janzen and Winnie Hallwachs's ongoing inventory of the caterpillars, their parasitoids, and their food plants of Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica (<http://janzen.sas.upenn.edu>). Andrea Farr and Amy Fernald prepared Figs. 1-12; Jocelyn Gill prepared Fig. 13. A draft of the manuscript was reviewed by April Rodd and Annette Evans. Anonymous reviewers made numerous helpful suggestions. Partial financial support for the work came from the U.S. Department of Agriculture, Forest Services, Forest Health Technology Enterprise Team, cooperative agreement number 01-CA-11244225-215 and a State Wildlife

Grant from the Connecticut Department of Environmental Protection.

LITERATURE CITED

- BATES, H. W. 1865. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. Trans. Linn. Soc. Lond. 23: 495-566.
- BERENBAUM, M. 1995. Aposematism and mimicry in caterpillars. J. Lepid. Soc. 49: 386-396.
- BOWERS, M. D. 2008. Chemical defenses in woolly bears: Sequestration and efficacy against predators and parasitoids, pp. 83-101. In W. E. Conner (ed.), *Tiger Moths and Woolly Bears: Behavior, Ecology, and Evolution of the Arctiidae*. Oxford University Press, Oxford, United Kingdom.
- COVELL, C. V., Jr. 2005. A Field Guide to the Moths of Eastern North America. 2nd Ed. Virginia Museum of Natural History, Martinsville, Virginia. 496 p.
- DEVRIES, P. J. 1994. Patterns of butterfly diversity and promising topics in natural history and ecology, pp. 187-194. In L. A. McDade & K. S. Bawa (eds.), *La Selva. Ecology and Natural History of a Neotropical Rainforest*. Univ. Chicago Press, Chicago.
- DIAZ, J. 2005. The evolving global epidemiology, syndromic classification of caterpillar envenoming. Amer. J. Trop. Med. Hygiene 72: 347-357.
- DRUCE, H. 1893a. Apatelodidae, pp. 437-438. In H. Druce (ed.), *Insecta. Lepidoptera-Heterocera. Biologia Centrali-Americana. Volume II*, R.H. Porter, London.
- DRUCE, H. 1893b. Descriptions of new species of Lepidoptera-Heterocera from Central and South America. Proc. Zool. Soc Lond. 1893: 280-310.
- DYAR, H. G. 1904. New species of North American Lepidoptera and a new limacodid larva. J. N. Y. Entomol. Soc. 12: 42.
- DYAR, H. G. 1912. Descriptions of new species and genera of Lepidoptera, chiefly from Mexico. Proc. Natl. Mus. 42: 39-106.
- DYAR, H. G. 1918. New moths from Mexico and Cuba (Lepidoptera). Insecutor Inscitiae Menstruus 6: 130-140.
- DYER, L. A. 1995. Tasty generalists and nasty specialists? A comparative study of antipredator mechanisms in tropical lepidopteran larvae. Ecology 76: 1483-1496.
- EPSTEIN, M. E., H. GEERTSEMA, C. M. NAUMANN, & G. M. TARMANN. 1998. The Zygaenoidea, pp. 159-180. In N. P. Kristensen (ed.), *Lepidoptera, Moths and Butterflies. Volume 1: Evolution, Systematics, and Biogeography. Handbook for Zoology. Volume IV. Arthropoda: Insecta*, Walter de Gruyter, Berlin, Germany.
- FERGUSON, D. C. 1978. Lymantriidae, Noctuoidea. In R. B. Dominick et al. (eds.), *The Moths of America North of Mexico. Fasc. 22.2. Wedge Entomological Foundation*, Washington DC. 110 p.
- FRANCLEMONT, J. G. 1973. Mimallonoidea (Mimallonidae) and Bombycoidea (Apatelodidae, Bombycidae, Lasiocampidae). In R. B. Dominick et al. (eds.), *The Moths of America North of Mexico. Fasc. 20.1. E.W. Classey Ltd. and Richard B. Dominick Publ.* London, United Kingdom. 86 p.
- FRANCLEMONT, J. G. 1983. Apatelodidae, p. 107. In R.W. Hodges et al. (eds.), *Check List of the Lepidoptera of America North of Mexico*, E.W. Classey Ltd. and The Wedge Entomological Research Foundation, Cambridge Univ. Press, Cambridge, United Kingdom.
- FRAZER, J. F. D. 1965. The cause of urtication produced by larval hairs of *Arctia carya* (L.) (Lepidoptera: Arctiidae). Proc. Royal Entomol. Soc. Lond. (Series A). 40: 96-100.
- HARTMANN, T. 2008. Pytrolizidine alkaloids: The successful adoption of a plant chemical defense, pp. 55-81. In W. E. Conner (ed.), *Tiger Moths and Woolly Bears: Behavior, Ecology, and Evolution of the Arctiidae*. Oxford University Press, Oxford, United Kingdom.

² Batesian mimicry in larval lepidopterans has been reported for a variety of macrolepidopteran taxa (DeVries 1994; Berenbaum 1995; Wagner 2005: 328, 333; Wagner et al. 2011: 78, 283; Willmott et al. 2011), but cases are infrequent relative to its prevalence in adult Lepidoptera, where the phenomenon of mimicry was first proposed and studied (Bates 1865).

- HOSSLER, E. W. 2010. Caterpillars and moths: Parts I & II. Dermatologic manifestations of encounters with Lepidoptera. *J. Amer. Acad. Dermatol.* 62.1 (1–28); doi: 10.1016/j.jaad.2009.08.060.
- JANZEN, D. H. & W. HALLWACHS. 2014. Caterpillar, pupae, butterflies, and moths of the Area de Conservación Guanacaste. (<http://janzen.sas.upenn.edu/index.html>) (accessed Jan 2014).
- LAFONTAINE, J. D. 2004. Noctuoidea. Noctuidae (Part), Noctuinae (Part—Noctuini). In R. B. Dominick et al. (eds.), *The Moths of America North of Mexico*. Fasc. 27.1, Wedge Entomological Research Foundation, Washington, DC. 385 p.
- LEMAIRE, C. & J. MINET. 1998. The Bombycoidea and their relatives, pp. 321–353. In N. P. Kristensen, (ed.), *Lepidoptera, Moths and Butterflies*. Volume 1: Evolution, Systematics, and Biogeography. Handbook for Zoology. Volume IV. Arthropoda: Insecta, Walter de Gruyter, Berlin, Germany.
- POWELL, J. A. & P. OPLER. 2009. *Moths of Western North America*. University of California Press, Berkeley, California. 383 p.
- ROBINSON, G. S., P. R. ACKERY, I. J. KITCHING, G. W. BECCALONI, & L. M. HERNÁNDEZ. 2014. HOSTS - a database of the hostplants of the world's Lepidoptera. <http://www.nhm.ac.uk/research-curation/projects/hostplants/> (accessed Jan. 2014).
- ROTHSCHILD, M. 1985. British aposematic Lepidoptera, pp. 9–62. In J. Heath and A. M. Emmet (eds.), *The Moths and Butterflies of Great Britain and Ireland*, Part 2. Harley Books, Colchester, United Kingdom.
- SCHAUS, W. 1939. New species of moths of the families Notodontidae and Bombycidae in the United States National Museum. *Proc. US Nat. Mus.* 86: 543–561.
- SMITH, J. E. 1797. Pp. 151–152, pl. 76. In J. E. Smith & J. Abbot, *The Natural History of the Rarer Lepidopterous Insects of Georgia. Including Their Systematic Characters, the Particulars of Their Several Metamorphoses, and the Plants on Which They Feed. Collected from the Observations of Mr. John Abbot, Many Years Resident in that Country*. Vol. 2. J. Edwards, Cadell & Davies, and J. White, London, United Kingdom.
- STEHF, F. S. 1987. Megalopygidae, pp. 454–456. In F. W. Stehr (ed.), *Immature Insects*. Kendall Hunt, Dubuque, Iowa.
- TULLBERG, B. 1988. Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. *Evolution* 42: 299–317.
- WAGNER, D. L. 2005. *Caterpillars of Eastern North America: A Guide to Identification and Natural History*. Princeton University Press, Princeton, New Jersey. 512 p.
- WAGNER, D. L. 2008. The immature stages: structure, function, behavior, and ecology, pp. 31–53. In W. E. Conner (ed.), *Tiger Moths and Woolly Bears: Behavior, Ecology, and Evolution of the Arctiidae*. Oxford University Press, United Kingdom.
- WAGNER, D. L., D. F. SCHWEITZER, J. B. SULLIVAN, & R. C. REARDON. 2011. *Owlet Caterpillars of Eastern North America*. Princeton University Press, Princeton, New Jersey. 576 p.
- WILLMOTT, K. R., M. ELIAS, & A. SOURAKOV. 2011. Two possible caterpillar mimicry complexes in Neotropical danaine butterflies (Lepidoptera: Nymphalidae). *Ann. Entomol. Soc. Amer.* 104: 1108–1118.

Submitted for publication 9 November 2009, revised and accepted 2 March 2014.