

Full Issue

Source: The Journal of the Lepidopterists' Society, 67(3)

Published By: The Lepidopterists' Society

URL: <https://doi.org/10.18473/lepi.v67i3.a15>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, 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 Complete 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 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.

Volume 67 Number 3

2013

ISSN 0024-0966

Journal of the Lepidopterists' Society



Published quarterly by The Lepidopterists' Society

THE LEPIDOPTERISTS' SOCIETY

EXECUTIVE COUNCIL

TODD GILLIGAN, President

ANDREW WARREN, Immediate Past President

ASTRID CALDAS, Vice President

JEFFREY MARCUS, Vice President

ANDREW NEILD, Vice President

MICHAEL E. TOLIVER, Secretary

KELLY M. RICHERS, Treasurer

CHARLES V. COVELL, JR.

DAVID JAMES

HARRY PAVULAAN

Members at large:

JOHN CALHOUN

ROBERT DIRIG

WAYNE WEHLING

MICHAEL M. COLLINS

KENELM W. PHILIP

JENNIFER ZASPEL

EDITORIAL BOARD

JOHN W. BROWN (*Chair*)

MICHAEL E. TOLIVER (*Member, at large*)

KEITH SUMMERVILLE (*Journal*)

LAWRENCE F. GALL (*Memoirs*)

JAMES ADAMS (*News*)

JOHN A. SNYDER (*Website*)

HONORARY LIFE MEMBERS OF THE SOCIETY

LINCOLN P. BROWER (1990), RONALD W. HODGES (2004) CHARLES V. COVELL, JR. (2009), DON R. DAVIS (2009), JACKIE MILLER (2010), JERRY POWELL (2010), CARL COOK (2011), PAUL R. EHRLICH (2011), RUDI MATTONI (2011), MOGENS C. ("Mo") NIELSEN (2011), PAUL OPLER (2012)

The object of The Lepidopterists' Society, which was formed in May 1947 and formally constituted in December 1950, is "to promote the science of lepidopterology in all its branches, . . . to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

Membership in the Society is open to all persons interested in the study of Lepidoptera. All members receive the *Journal* and the *News of The Lepidopterists' Society*. Prospective members should send to the Treasurer full dues for the current year, together with their full name, address, and special lepidopterological interests. The additional cost for members outside the U.S. is to cover mailing costs. In odd-numbered years the Society publishes a Membership Directory, with addresses, a geographical index, and a subject index of special interests.

Active members—annual dues \$45.00 in U.S. (\$50.00 in Canada & Mexico; \$55 elsewhere)

Affiliate members—annual dues \$10.00 worldwide

Student members—annual dues \$20.00 in U.S. (\$25.00 in Canada & Mexico; \$30 elsewhere)

Sustaining members—annual dues \$60.00 in U.S. (\$65.00 in Canada & Mexico; \$70 elsewhere)

Life members—single sum \$1,800.00

Institutional subscriptions—annual \$60.00 (\$65.00 in Canada & Mexico; \$70 elsewhere)

Airmail postage for the *News* \$15.00, \$30.00 outside North America (U.S., Canada, Mexico)

Send remittances, payable to *The Lepidopterists' Society*, to: Kelly M. Richers, Treasurer, 9417 Carvalho Court, Bakersfield, CA 93311-1846; and address changes, claims for missing or damaged issues, and back issue orders to: Julian P. Donahue, 735 Rome Dr., Los Angeles, CA 90065-4040, e-mail: julian@lepsoc.net. For information about the Society, contact: Michael E. Toliver, Division of Math & Sciences, Eureka College, 300 E. College Ave., Eureka, IL 61530-1500, e-mail: mikel@eureka.edu. To order back issues of the *Memoirs*, write for availability and prices to Kenneth R. Bliss, 2438 Falcon Drive, Round Rock, TX 78681-2755, e-mail: krlbliss@gmail.com.

Journal of The Lepidopterists' Society (ISSN 0024-0966) is published quarterly by The Lepidopterists' Society, c/o Julian P. Donahue, Asst. Treasurer, 735 Rome Dr., Los Angeles, CA 90065-4040. Periodicals postage paid at Los Angeles, CA and at additional mailing offices. POSTMASTER: Send address changes to The Lepidopterists' Society, 735 Rome Dr., Los Angeles, CA 90065-4040.

<http://www.lepsoc.org/>
<https://www.facebook.com/lepsoc>

Cover Illustration: *Isanthrene perbosci* (Guérin-Meneville, 1844), is a Mexican-Central American day flying moth (Erebidae: Arctiinae: Arctiini: Euchromiina) that can be eventually captured at night attracted to lights. It lives in temperate and tropical wet forests in Mexico. Specimens from Yucatan and Quintana Roo are known and mentioned herein by Hernández-Baz et al. 2013. The illustrated specimen belongs to the Scientific Collection SEMARNAT/CITES/CP-0026-VER/05 in Xalapa, Veracruz, Mexico. Picture: Fernando Hernández-Baz.

CTENUCHINA AND EUCHROMIINA (LEPIDOPTERA: EREBIDAE: ARCTIINAE) OF THREE BIOLOGICAL RESEARCH STATIONS OF MÉXICO'S ECOSUR

FERNANDO HERNÁNDEZ-BAZ

Facultad de Biología-Xalapa, Universidad Veracruzana. Circuito Gonzalo Aguirre Beltrán s/n. C.P.91000. Zona Universitaria. Xalapa, Veracruz, México. PhD student CITRO-Universidad Veracruzana. e-mail: fhermandez@uv.mx ; ferhbm@yahoo.com.mx

MIGUEL A. MORÓN

Red de Biodiversidad y Sistemática, Instituto de Ecología, A.C., Apdo. Postal 63, Xalapa, 91000 Veracruz, México.
E mail: miguel.moron@inecol.edu.mx

EDUARDO CHAMÉ-VÁZQUEZ

El Colegio de la Frontera Sur, Unidad Tapachula, Carretera Antiguo Aeropuerto Km 2.5. 30700, Tapachula, Chiapas, México.
E-mail: echame@ecosur.mx

AND

JORGE M. GONZÁLEZ

California State University, Fresno, Department of Plant Sciences, Fresno, CA 93740-8033 (Research Associate, McGuire Center for Lepidoptera & Biodiversity); e-mail: gonzalez.jorge.m@gmail.com

ABSTRACT. Two hundred and seventy one adult specimens representing 58 species in the subtribes Ctenuchina and Euchromiina (Arctiinae) were found at the entomological collections of ECOSUR (Southern Border College). The collections are based at three research stations: San Cristóbal de las Casas and Tapachula, located in the state of Chiapas, and Chetumal, in the state of Quintana Roo. They respectively contained 191 specimens representing 49 species, 54 specimens representing 15 species, and 26 specimens representing 6 species. The species *Correbidia fana* (Druce, 1900) was found within the collections and as far as we know this is a first record for Mexico.

Additional key words: Biogeography, Ecology, scientific collection, Taxonomy, wasp moths, Biological conservation

El Colegio de la Frontera Sur (ECOSUR) (the Southern Frontier College) was founded in 1994 on the remains of the Centro de Investigaciones Ecológicas del Sureste (CIES) (Southeastern Center for Ecological Research), which had started its activities 20 years prior in 1974. ECOSUR's objective is to do original research that might contribute to the sustainable development along the southern border of Mexico, Central America, and the Caribbean. The institution is comprised of five research stations, three of which contain entomological collections. The first is located at the San Cristobal de Las Casas station in the northern mountains of Chiapas (N16°42'05" W92°36'45"), the second is located at the Tapachula station near the border with Guatemala (N14°52'56" W92°11'45"), and the third is at the Chetumal station at the border with Belize (N18°32'13" W88°17'46"). Insect collecting also started in 1994 with the general purpose of establishing an inventory of insects of ecogeographic and taxonomic importance from Mexico's southeast region.

Commonly known as tiger moths, the Arctiinae is a monophyletic group characterized by two

synapomorphies: the presence of dorsal, eversible pheromone glands in females, and the presence of sound producing, metathoracic tymbal organs in both sexes (although secondarily reduced or lost in some groups) (Kitching & Rawlins 1998). Long considered a family within the Noctuoidea, the Arctiinae was also previously treated as a subfamily of Noctuidae (Lafontaine & Fibiger 2006). Phylogenetic relationships supported by molecular data and re-evaluation of morphological data have shifted the Arctiinae to subfamily within the Erebidae (Lafontaine & Schmidt 2010). The group contains about 11,000 species from around the world, including about 6,000 Neotropical species, with 658 reported from Mexico (Watson & Goodger 1986; Hernández-Baz 2009, 2010, 2012a).

Additionally, the Ctenuchinae was once considered a subfamily, and even a family as part of the Syntomidae (Hampson 1898; Zerny 1912; Draudt 1917; and others) but many authors merged it into the Arctiinae as the tribe Ctenuchini. However, Lafontaine & Schmidt (2010) keeps the subtribes Euchromiina and Ctenuchina in the tribe Arctiini.



FIG. 1. Male, *Correbidia fana* (Druce, 1900). First record for Mexico. Specimen deposited at the Entomology Collection ECO-SC-E, in San Cristobal de las Casas, Chiapas, Mexico. Photo: F. Hernández-Baz.

The Euchromiina and Ctenuchina include notable mimics of wasps and are sometimes referred to as “wasp moths.” They are represented by approximately 2,400 Neotropical species, but only 240 of them are known from Mexico (Heppner 1991; Hernández-Baz 2009, 2012a). The Euchromiina and Ctenuchina sub tribes are supported by two synapomorphies: loss of tympanal pocket V and an enlarged tympanal hood (Simmons & Weller 2006)

Euchromiina comprises 112 species from México (Hernández-Baz 2009, 2012a). The males of several species have subabdominal pouches, highly modified second and third abdominal sternites that store woolly scales called flocculent (Barth 1953; Weller et al. 2000). These abdominal modifications are unique to the subtribe as currently defined (Weller et al. 2009). Wing veins have also important characteristics, $Sc+R_1$ are absent in the hind wing. The vein M_2 is rudimentary or lacking and it is frequently represented by a vein that looks like a line formed by scales. Cu_1 and Cu_2 are very close to each other or even fused.

Ctenuchina comprises 128 species from Mexico (Hernández-Baz 2009, 2012a). It contains several dayflying species in genera such as *Dinia*, *Saurita*, and *Cyanopepla*, among others. M_2 is present in the hind wing; Cu_1 and Cu_2 are widely separated except in the genus *Horama* (Kitching & Rawlins 1999; Jacobson & Weller 2002; Teston & Corseuil 2003; Hernández-Baz & Bailey 2006, Hernández-Baz 2012a).

The main aim of this work is to present the inventory of the wasp moths (Arctiini: Ctenuchina, Euchromiina) deposited in the three insect collections owned by ECOSUR and located at the research units of San Cristóbal de las Casas, Tapachula and Chetumal. A checklist and discussion about comparative richness of the group in Southeast Mexico are provided.

MATERIALS AND METHODS

We have reviewed all curatorial information found with the specimens of Ctenuchina and Euchromiina (Arctiinae) deposited in the entomological collections of ECOSUR at San Cristóbal de las Casas (ECO-SC-E), Tapachula (ECO-TAP-E) and Chetumal (ECO-CH-E). Specimen data was entered and analyzed in an Excel (Microsoft Corp.) spreadsheet.

Even though we have studied Kitching & Rawlins (1999), Jacobson & Weller (2002) and Lafontaine & Fibiger (2006), we follow Lafontaine and Schmidt (2010) for supra-generic classification of the reported specimens. The genera were identified following Hampson (1898, 1914), although Watson et al. (1980), Watson & Goodger (1986) and Cerda (2008) were used for comparison purposes. For species identification, we followed Draudt (1917), Dietz & Duckworth (1976), Dietz (1994), and Hernández-Baz (1992, 2011). The original descriptions of every species were studied and compared with each specimen found in the ECOSUR collections. They were also compared with identified specimens contained in the Lepidoptera Collection SEMARNAT/CITES/CP-0026-VER/05 in Xalapa, Veracruz. The distribution of specimens was also compared with the “Polilla” database at the above mentioned collection in Xalapa. A faunistic list indicating abundance of specimens of each species in every studied insect collection is presented. Genera and species for every subtribe are presented alphabetically.

RESULTS AND DISCUSSION

The species list for the three insect collections belonging to three research units of ECOSUR was developed from a total of 271 specimens across the three collections. Specimens represented 58 taxa that were distributed in the sub-tribes Ctenuchina, with 16 genera and 26 species, and Euchromiina, with 19 genera and 32 species (Table 1). The specimens deposited in the above mentioned collections were mainly collected from their adjacent regions; however there are cases in which specimens were collected from outside the area of influence of the cited research units, as in the case of ECO-SC-E which has a lot of material from the state of Tamaulipas. The larger number of species was found at San Cristobal de las Casas with 49 and 191 specimens, followed by that of Chetumal with 15 species and 54 specimens and Tapachula with six species and 26 specimens. When comparing the abundance of specimens in each collection, it was found that the one at San Cristobal de las Casas research station (USC) represented the 84.5% of the total found, while the one at Chetumal research station (UCH) was

25.8% and the Tapachula research station (UTAP) represented only 10.3%. Specimen information was integrated to the “Polilla” database of the project “Inventario de las palomillas Ctenuchinae (Insecta: Lepidoptera: Noctuidae: Arctiinae) de la República Mexicana” (inventory of the Ctenuchinae moths of the Mexican Republic). Project Key: 22314200531-UV, at Universidad Veracruzana, Xalapa, Veracruz, Mexico.

A comparative analysis of richness of species as deposited in each of the studied collections with the total number of known species at the national level (Hernández-Baz 1992, 2011, 2012a) indicates that ECO-SC-E, with its 49 species, has 16% of the species known in Mexico, while ECO-CH-E has 5% and ECO-TAP-E has only 2% (Table 2). Two hundred species of wasp moths have been recorded in the state of Chiapas (Hernández-Baz 2012b). When comparing this number of species of wasp moths found at the ECOSUR collections from that state we notice that ECO-SC-E has a representation 24.5% while ECO-TAP-E has only a very low 3%. Hernández-Baz (2011) documented 25 species of wasp moths for the state of Quintana Roo, but we only found 15 of those species in the ECO-CH-E collection. This means that the Quintana Roo Research station's collection currently contains 60% of what is known for that state.

We have to acknowledge that all faunistic inventories are biased depending on the person who collects the specimens (Jiménez-Valverde & Hortal 2003) which is possibly why the Ctenuchina and Euchromiina deposited in institutional collections in Mexico are not well represented, since no more than 60 species have been found among them (Hernández-Baz 2012a; Hernández-Baz & Coates 2011). A similar situation is found in Guatemala (Hernández-Baz & Bailey 2007). The species we present herein possibly show a regional fauna bias, since most collected material comes from around the area of influence of the three ECOSUR's research stations.

ECOSUR's collections have specimens belonging to 58 species of Ctenuchina and Euchromiina while only 36 species have been found in North America (Lafontaine & Schmith 2010). When comparing with several faunistic studies we have found that ECOSUR collections contain 24 % of the 240 species known from México (Hernández-Baz 2012a) and 27 % of the 216 cited from Guatemala (Hernández-Baz & Bailey, 2006; Hernández et al., 2008). If we take into consideration the biogeographic, ecological and climatic similarities between Chiapas and Guatemala, we can see that there is a high possibility that the collections ECO-SC-E and ECO-TAP-E could be increased to accumulate up to 200 species of wasp moths by doing a systematic

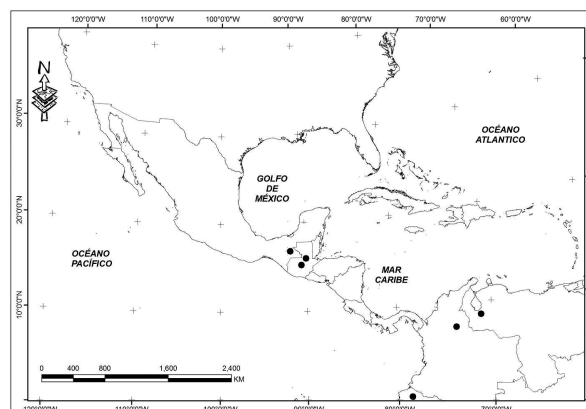


FIG. 2. Distribution of *Correbidia fana* (Druce, 1900) in the Americas. From: “Polilla” data Base, annex to the Lepidoptera collection SEMARNAT/CITES/CP-026-VER/05. The black dots represent the area where the known/reported collecting sites are found.

sampling of the ecosystems of the tropical evergreen mountainous forest and the cloud forests of Chiapas. Similarly, the ECO-CH-E could increase the actual number of species up to 150 thanks to the a) close proximity of Southwest Quintana Roo with Belize, a country with over 78 species within the Ctenuchina + Euchromiina (Barnes 2000), and b) the semi-evergreen seasonal forest mainly, and to a lesser extent the evergreen mountainous regions, which cover most of Quintana Roo (Valdéz-Hernández & Islebe 2011) and provide excellent conditions for the development of a larger diversity of moths.

Even though many wasp moths are known from Mexico, their reported distribution is highly fragmented which is also a characteristic of the group for most of the Americas. Thus, the knowledge about the group is far from complete. We are also certain that species are still to be described and some of the new, undescribed species are likely cryptic within already collected museum material around the world. It is necessary to continue efforts to collect and report the distribution and natural history since most of the hosts and life histories of this interesting group of moths are not described or known, even though some efforts have been done somewhere else (i.e., Dan Janzen and his group have studied life cycles of some species from Costa Rica).

This work is part of a larger project to study the Ctenuchina and Euchromiina from México and the Americas. This project will focus on five lines of research during the next few years: a) To do a faunistic inventory of the wasp moths of the Americas; b) To study the life cycles and trophic relations of each wasp

TABLE 1. Taxa and number of specimens of wasp moths of the subtribes Ctenuchina and Euchromiina (Erebidae: Arctiinae: Arctiini) in the insect collections at three research stations of ECOSUR (USC = San Cristóbal de las Casas; UCH = Chetumal; UTAP = Tapachula). First Record for México = FRM)

		ECOSUR's Research Stations		
		USC	UCH	UTAP
Erebidae: Arctiinae: Arctiini: Ctenuchina				
1	<i>Aclytia heber</i> (Cramer, 1780)	2		
2	<i>Aclytia punctata</i> (Butler, 1876)	5		
3	<i>Aclytia ventralis</i> (Guérin-Ménéville, 1849)	1		
4	<i>Agyrta dux</i> (Walker, 1854)	1	4	
5	<i>Belemnia inaurata</i> (Zulzer, 1776)		2	
6	<i>Correbia affinis</i> (Druce 1884)	2		
7	<i>Correbia lycoides</i> (Walker, 1854)	1		
8	<i>Correbia undulata</i> (Druce, 1884)	1		
9	<i>Correbidia fana</i> (Druce, 1900)	1		
10	<i>Correbidia elegans</i> (Druce, 1884)	1		
11	<i>Correbidia germana</i> (Rothschild, 1912)	2		
12	<i>Cyanopepla bella</i> (Guérin-Ménéville, 1844)	2		
13	<i>Delphyre rubricincta</i> (Hampson 1898)		1	
14	<i>Dinia eagrus</i> (Cramer, 1779)	4		1
15	<i>Episcepsis inornata</i> (Walker, 1856)	1		
16	<i>Epidesma oceola</i> (Dyar, 1910)	1		
17	<i>Eucereon erythrolepsis</i> (Dyar, 1910)	1		
18	<i>Eucereon pseudarchias</i> (Hampson, 1898)	1		
19	<i>Eucereon rosina</i> (Walker, 1854)		3	
20	<i>Eucereon tripunctatum</i> (Druce, 1884)	2		
21	<i>Heliura rhodophila</i> (Walker, 1854)		1	
22	<i>Horama plumipes</i> (Drury, 1773)	1	1	
23	<i>Horama panthalon</i> (Fabricius, 1793)		9	
24	<i>Ixylasia schausi</i> (Druce 1896)	2		
25	<i>Nelphe relegatum</i> (Schaus, 1911)		1	
26	<i>Sciopsyche tropica</i> (Walker, 1854)	1		

TABLE 1. (continued)

		ECOSUR's Research Stations		
	Erebidae: Arctiinae: Arctiini: Euchromiina	USC	UCH	UTAP
27	<i>Apeplopoda mecrida</i> (Druce, 1889)	3		
28	<i>Apeplopoda ochracea</i> (Felder, 1894)	2		
29	<i>Andrenimorpha ethodaea</i> (Druce, 1889)		4	
30	<i>Cosmosoma auge</i> (Linnaeus, 1767)	4		
31	<i>Cosmosoma braconoides</i> (Walker, 1854)	7		
32	<i>Cosmosoma caecum</i> (Hampson 1898)	7		
33	<i>Cosmosoma festiva</i> (Walker, 1854)	6	8	
34	<i>Cosmosoma impar</i> (Walker, 1854)	4		
35	<i>Cosmosoma impudica</i> (Schaus, 1911)	8		13
36	<i>Chrostosoma sectinota</i> (Hampson 1898)	2		
37	<i>Cosmosoma stilbosticta</i> (Butler, 1876)	6		
38	<i>Cosmosoma teuthras cingulatum</i> (Butler, 1876)	22	4	7
39	<i>Cosmosoma xanthostictum</i> (Hampson, 1898)	2		
40	<i>Chrysocale principalis</i> (Walker, 1865)	1		
41	<i>Dycladia correbioides</i> (Felder, 1874)	6		
42	<i>Homoeocera gigantea</i> (Druce, 1884)	18		2
43	<i>Homoeocera rodriguezi</i> (Druce, 1890)	1		
44	<i>Isanthrene cajetani</i> (Rothschild, 1911)	1		2
45	<i>Isanthrene perbosci</i> (Guérin-Menéville, 1844)		3	
46	<i>Leucotmemis nexa</i> (Herrich-Schäffer, 1854)	4	2	
47	<i>Loxophlebia imitata</i> (Druce, 1884)		5	
48	<i>Macrocneme chrysitis</i> (Guérin-Menéville, 1844)	13		
49	<i>Nyridela xanthocera</i> (Walker, 1856)	5		
50	<i>Pheia albisigna</i> (Walker, 1854)	2		
51	<i>Phoenicoprocta mexicana</i> (Walker, 1865)	2		
52	<i>Pseudohyaleucerea vulnerata vulnerata</i> (Butler, 1875)	2		
53	<i>Psilopleura vittata</i> (Walker, 1865)	6		
54	<i>Psoloptera basilfulva</i> (Schaus, 1894)	7		
55	<i>Scena potentia</i> (Druce, 1894)	9		
56	<i>Sphecosoma felderi</i> (Druce, 1883)	2		
57	<i>Syntomeida epilais epilais</i> (Walker, 1854)	2	6	1
58	<i>Syntomeida melanthus albifasciata</i> (Butler, 1876)	4		
Total Number of specimens = 271		191	54	26

TABLE 2. Species richness of Ctenuchina and Euchromiina (Erebidae: Arctiinae: Arctiini) in Chiapas and Quintana Roo, México, based on ECOSUR's entomological collections (USC = San Cristóbal de las Casas; UCH = Chetumal; UTAP = Tapachula)

Collection	Number of Taxa found	Richness (expressed in absolute numbers and %) México (°°)		Richness (absolute numbers and %) Chiapas (°°°)		Richness (absolute numbers and %) Quintana Roo (°°°°)	
		Total	%	Total	%	Total	%
USC	49	240	20.4	200	24.5	--	--
UTAP	6	240	2.5	200	3.0	--	--
UCH	15	240	6.3	--	--	25	60.0
Total	58(°)	240	24.0	--	--	--	--

(°) Total number of taxa is not the sum of the column since several species were found in multiple collections. This total was obtained from Table 1. (°°) According to Hernández-Baz (1992, 2009, 2010); (°°°) According to Hernández-Baz (2012), (°°°°) According to Hernández-Baz (2011).

moth species; c) to know their biogeographic distribution patterns; d) to determine the endemic species in each country, in each continental region and their habitat; and finally e) to propose a strategy for conservation based on the analysis of their vulnerability according to the criteria of the International Union for Conservation of Nature red list of threatened species.

The list that follows, presents the material examined highlighting the specific localities where every species was found in the states of Chiapas and Quintana Roo. The information for each species is presented as it appears on the labels of each insect. Ctenuchina and Euchromiina from the Insect Collections at ECOSUR are identified as: San Cristóbal de las Casas (ECO-SC-E); Chetumal (ECO-CH-E) and Tapachula (ECO-TAP-E).

LIST OF FAUNA

The next list loosely follows Vargas et al. (1996) and includes all available label information for each specimen in the three Insect Collections of ECOSUR.

Erebidae: Arctiinae: Arctiini: Ctenuchina
(26 species)

***Aclytia heber* (Cramer, 1780).** 1 ♂, Mexico, Jalisco, de la Huerta, Ejido San Mateo, 6-IX-1993, E. Gálvez. N. Barajas y E. Rodríguez, Light trap, ECO-SC-E; 1 ♂, Chiapas, Maravilla Tenejapa, Ejido Loma bonita, N16°11'24" W91°18'28", 241m, 4-IX-2002, L. Martín, Light trap, ECO-SC-E.

***Aclytia punctata* (Butler, 1876).** 2 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido Loma Bonita, N16°11'38" W91°18'35", 283m, 1-IX-2002, L. Martín, black & white light trap, ECO-SC-E; 1 ♂, 1 ♀,

Maravilla Tenejapa, Ejido Loma Bonita, N16°12'04" W91°80'05", 369m, 30-VIII-2002, L. Martín, black & white light trap, ECO-SC-E; 1 ♂, Res. Bios. "Montes Azules", Chajul, UNAM. 30-IV-1992, J. León, ECO-SC-E.

***Aclytia ventralis* (Guérin-Ménéville, 1849).** 1 ♂, Mexico, Chiapas, Ocozocuatla, Reserva "el Ocote" 9km SW Cuauhtemoc, 11-VII-1994, O. Gómez, ECO-SC-E.

***Agyrta dux* (Walker, 1854).** 1 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido Loma bonita, N16°11'19" W91°18'25", 241m, 31-VIII-2002, J. León, day flying moth, ECO-SC-E; 1 ♂, Campeche, Calakmul, Nuevo Becal, 23-VIII-1997, S. Uc, ligh trap, ECO-CH-E; 1 ♂, Calakmul, Entrada a Papagayo, 19-IX-1999, S. Uc, ECO-CH-E; 1 ♂, Calakmul: Calakmul, Dos naciones rural, 31-VIII-1999, S. Uc, ligh trap, ECO-CH-E; 1 ♀, Calakmul, Calakmul, Zona arqueológica 1, 18-III-2007, C. Pozo, ligh trap, ECO-CH-E.

***Belemnia inaurata* (Zulzer, 1776).** 1 ♂, Mexico, Campeche, Calakmul, Dos Naciones, 13-VIII-2002, E. May, ECO-CH-E; 1 ♀, Quintana Roo, Solidaridad, Jardín Botánico, Puerto Morelos, 3-VIII-2001, E. May, ECO-CH-E.

***Correbia affinis* (Druce 1884).** 1 ♂, 1 ♀, Mexico, Chiapas: Villa Flores, Reserva de Biosfera "La Sepultura", Ejido Sierra Morena, N16°09'32" W93°35'27", 1185m, 17-VII-2003, A. Molina, black & white light trap, ECO-SC-E; 1 ♂, Ocozocuatla, Res "El Ocote", Las Palmas, 8-VIII-1994, B. Gómez, ECO-SC-E.

***Correbia lycoides* (Walker, 1854).** 1 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido Loma bonita, N16°11'38" W91°18'35", 283m, 1-X-2002, F. Pérez-Espinoza & L. Morfín, black & white light trap, ECO-SC-E.

***Correbia undulada* (Druce, 1884).** 1 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido Loma bonita, N16°11'38" W19°18'35", 283m, 1-X-2002, F. Pérez-Espinoza & L. Morfín, black & white light trap, ECO-SC-E.

***Correbidia fana* (Druce, 1900)** (Fig. 1). 1 ♂, Mexico, Chiapas, Miguel Ángel Albino Corzo, Reserva "El Triunfo" Maravilla Tenejapa, N15°39'42" W92°48'57", 2020m, 16-XI-2001, J. León & M. Girón, light trap, ECO-SC-E. As far as we know this species is reported herein for the first time in Mexico.

***Correbidia elegans* (Druce, 1884).** 1 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido Loma bonita, Reser. "El Triunfo" Maravilla Tenejapa, N16°11'38" W19°18'35", 283m, 1-X-2002, F. Pérez-Espinoza & L. Martín, black & white light trap, ECO-SC-E.

***Correbidia germana* (Rothschild, 1912).** 2 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido Loma bonita, Reser. "El Triunfo" Maravilla Tenejapa, N16°12'07" O91°18'04", 380m, 28-VIII-2002, F. Pérez-Espinoza, black & white light trap, collecting time: 22:30, ECO-SC-E.

***Cyanopepla bella* (Guérin-Ménéville, 1844).** 1 ♂, Mexico, Chiapas, Tapalapa, 6 km NW Tapalapa, 14-III-1994, O. Gómez, day flying moth, ECO-SC-E; 1 ♂, Mexico, Chiapas, Tributaria, close to "cinco lagos", 21-II-1994, O. Gómez, day flying moth, ECO-SC-E.

***Delphyre rubricincta* (Hampson, 1898).** 1 ♂, Mexico, Calakmul, Dos Lagunas, 14-XI-2006, E. May, light trap, ECO-CH-E.

***Dinia eagrus* (Cramer, 1779).** 1 ♂, Mexico, Chiapas, Villa Corzo, Reserva "La Sepultura", Ejido Sierra Morena, 19-VII-2005, G. Ramírez-Cedillo, day flying moth, ECO-SC-E; 1 ♀, Tuxtla, Predio San Fco. Terán, 3-X-1974, A. Zacarías, day flying moth, ECO-SC-E; Ocosingo, Ejido Loma bonita, 3-IV-1982, A. Zacarías, 1 ♀, day flying moth, ECO-SC-E; Huehuetán, N15°00'38"-O92°24'07", 34m, 3-X-1985, W. Rosa, 1 ♂, light trap, ECO-TAP-E; 1 ♂, Jalisco, de la Huerta, Ejido Zapata, 9-IX-1993, E. Gálvez & N. Barajas, day flying moth, ECO-SC-E.

***Episcepsis inornata* (Walker, 1856).** 1 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido Loma bonita, N16°11'38" W91°18'35", 283m, 8-IV-2002, L. Martín, ECO-SC-E.

***Epidesma oceola* (Dyar, 1910).** 1 ♂, Mexico: Chiapas: Reserva de Biosfera. "Montes azules", Chajul, 30-IV-1992, A. Zacarias, ECO-SC-E.

***Eucereon erythrolepsis* (Dyar, 1910).** 1 ♀, Mexico, Tamaulipas, Reserva de Biosfera "El Cielo", 18-VII-2006, J. Luna Cozar, ECO-SC-E.

Eucereon pseudarchias (Hampson, 1898). 1 ♂, Mexico, Chiapas, Reserva de Biosfera "Montes azules", Chajul,

11-VIII-1991, H. Chacón, ECO-SC-E.

***Eucereon rosina* (Walker, 1854).** 1 ♂, Mexico, Quintana Roo, Othón P. Blanco, Chetumal, alrededores de ECOSUR, 14-VI-2007, J.L. Salinas, light trap, ECO-CH-E; 1 ♀, Othón P. Blanco, Álvaro Obregón Nuevo, 16-III-2008, E. Domínguez, light trap, ECO-CH-E; 1 ♀, idem, 23-XII-2008, ECO-CH-E.

***Eucereon tripunctatum* (Druce, 1884).** 1 ♂, 1 ♀, Mexico, Tamaulipas, Gómez Farias. Reserva de Biosfera "El Cielo", Rancho el cielo, N23°06'02" W99°12'46", 18-VIII-2006, miss-Barrera, black & white light trap, ECO-SC-E.

***Heliura rhodophila* (Walker, 1854).** 1 ♂, Mexico: Campeche: Calakmul: Zoh Laguna, 23-VII-2007, E. Leyequien, light trap, ECO-CH-E.

***Horama plumipes* (Drury, 1773).** 1 ♂, Mexico, Quintana Roo, Lázaro Cárdenas, Reserva "El Eden", 13-X-1995, O. Gómez, black & white light trap, ECO-SC-E; 1 ♂, 1 ♀, Quintana Roo, Solidaridad, Jardín Botánico Puerto Morelos, 30-VII-2001, E. May, light trap, ECO-CH-E; 1 ♂, Othón P. Blanco, Álvaro Obregón Nuevo, 1-XI-2008, E. Domínguez, light trap, ECO-CH-E.

***Horama panthalon* (Fabricius, 1793).** 1 ♂, Mexico, Quintana Roo, Solidaridad, Jardín Botánico Puerto Morelos, 10-VIII-2001, E. May, light trap, ECO-CH-E; 1 ♂, idem, 31-VIII-2001, E. May, ECO-CH-E; 1 ♀, idem, 7-VIII-2001, E. May; 1 ♀, idem, 3-VIII-2001, E. May, ECO-CH-E; 1 ♂, idem, 8-VIII-2001, E. May, ECO-CH-E; 2 ♂, idem, 31-VII-2001, E. May, ECO-CH-E.

***Ixylasia schausi* (Druce 1896).** 1 ♂, Mexico, Chiapas, Coapilla, 20-VIII-2008, Irma D. & Miss-B, black light trap, ECO-SC-E.; 1 ♀, Ocozocautla, Reserva "El Ocote", 18-VII-1994, O. Gómez-N., black light trap, ECO-SC-E.

***Nelphe relegatum* (Schaus, 1911).** 1 ♂, Mexico, Quintana Roo, Othón P. Blanco, Álvaro Obregón: 23-XII-2008, E. Domínguez, light trap, ECO-CH-E.

***Sciopsyche tropica* (Walker, 1854).** 1 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ej. Loma Bonita, N16°11'16" W91°18'24", 241m, 27-VIII-2002, J. León-C, black and white light trap, ECO-SC-E.

Erebidae: Arctiinae: Arctiini: Euchromiina
(32 species)

***Apeplopora mecrida* (Druce, 1889).** 1 ♂, Mexico, Chiapas, Ángel Albino Corzo, Reserva "El Triunfo": Road to Mapastepec, N15°39'82" W92°48'62", 2180m, 19-XI-2001, A. Molina & Lind, black and white light trap, ECO-SC-E; 2 ♀, idem, 18-XI-2001, ECO-SC-E.

***Apeplopora ochracea* (Felder, 1894).** 1 ♂, México, Chiapas, Ángel Albino Corzo, Reserva "El Triunfo":

Camino a Mapastepec, N15°39'82" W92°48'62", 2180m, 19-XI-2001, A. Molina & Lind, black and white light trap, ECO-SC-E.

Andrenimorpha ethodaea (Druce, 1889). 1 ♂, México, Campeche, Calakmul, Dos lagunas, 11-VIII-2006, A. Xool, black and white light trap, ECO-CH-E; 1 ♂, Quintana Roo, Othón P. Blanco, Álvaro Obregón, 1-XI-2008, E. Domínguez, light trap, ECO-CH-E; 1 ♀, Othón P. Blanco: Chetumal: alrededores de ECOSUR, 13-VI-2007, N. Salas, light trap, ECO-CH-E; 1 ♂, idem, 14-VI-2007, E. May, ECO-CH-E; 1 ♂, idem, 22-II-2008, N. Salas; 1 ♂, idem, 22-II-2008, B. Prado, ECO-CH-E.

Cosmosoma auge (Linnaeus, 1767). 2 ♂, Mexico, Chiapas, Ángel Albino Corzo, Reserva "El Triunfo", N15°39'42" W92°48'53", 2020m, 18-XI-2001, A. Molina, light trap, ECO-SC-E; 1 ♀, Ocozocuatla, Reserva "El Ocote", 14 km, Norte Ejido Cuauhtemoc, 14-VIII-1994, O. Gómez, light trap, ECO-SC-E; 1 ♂, Ocosingo, Playón de la Gloria, 26-VI-2008, U. Caballero, light trap, ECO-SC-E.

Cosmosoma braconoides (Walker, 1854). 1 ♂, 3 ♀, Mexico: Chiapas: Ocosingo: Lacanjá Chansayab, 22-VIII-2008, U. Caballero, P., light trap, ECO-SC-E; 2 ♂, Maravilla Tenejapa, Ej. Loma Bonita, N16°11'19" W91°18'25", 241m, 28-V-2002, U. Caballero, light trap, ECO-SC-E; 1 ♀, idem, 9-X-2002, ECO-SC-E.

Cosmosoma caecum (Hampson 1898). 2 ♂, Mexico, Chiapas, Maravilla Tenejapa: Ejido Loma bonita, N16°11'19" W91°18'25", 241m, 28-V-2002, J. León, ECO-SC-E; 1 ♂ 1 ♀, Ocozocuatla, Reserva "El Ocote", Ejido Nueva providencia, 10-II-1995, Gómez, light trap, ECO-SC-E; Maravilla Tenejapa, Ejido Loma Bonita, N16°11'24" W91°18'28", 241m, 4-IX-2002, light trap, J. León, ECO-SC-E; 1 ♂, Ocosingo, Lacanjá Chansayab, 22-VIII-2008, Irma-D, Miss-B, light trap, ECO-SC-E; 2 ♂, idem 22-VIII-2008, U. Caballero, ECO-SC-E.

Cosmosoma festiva (Walker, 1854). 1 ♂ 3 ♀, México, Campeche, Calakmul, Calakmul, 22-XI-2008, J. León, light trap, ECO-SC-E; 1 ♂, Chiapas, Maravilla Tenejapa, Ejido loma bonita, N.16°11'32" W91°18'34", 235m, 8-IV-2002, F. Pérez, light trap, ECO-SC-E; 3 ♂, San Fernando, Vicente Guerrero, 21-IX-2001, J. León, ECO-SC-E; 1 ♀, idem, 22-XI-2008, J. León, ECO-SC-E; 1 ♂, Campeche, Calakmul, Dos Lagunas Sur, 12-XI-2006, R. Plantaz, light trap, ECO-CH-E; 1 ♂, Quintana Roo, Othón P. Blanco, Chetumal, alrededores de ECOSUR, 13-VI-2007, M. Bálcazar, light trap, ECO-CH-E; 1 ♀, Othón P. Blanco, Álvaro Obregón Nuevo, 6-VII-2008, E. Domínguez, light trap, ECO-CH-E; 1 ♀, idem, 5-VII-2008, ECO-CH-E; 1 ♂, idem, 27-IX-2008, ECO-CH-E; 1 ♂, idem, 1-II-2009, ECO-CH-E; 1 ♂, Yucatán, Oxkutzcab, Reserva Kinuc, 27-II-2008, E. Domínguez, light trap, ECO-CH-E; 1 ♂, idem, 28-II-

2008, ECO-CH-E.

Cosmosoma impar (Walker, 1854). 2 ♀, Mexico, Chiapas, Ocosingo, Lacanjá Chansayab, 22-VIII-2008, Irma-D & Miss-B, light trap, ECO-SC-E; 2 ♂, idem, 22-VIII-2008, J. León, ECO-SC-E; 2 ♂, idem, 28-VIII-2008, U. Caballero, ECO-SC-E.

Cosmosoma impudica (Schaus, 1911). 2 ♀, Mexico, Chiapas, Ángel Albino Corzo, Reserva "El Triunfo", N15°39'42" W92°48'53", 2020m, 19-XI-2008, A. Molina-Linda, light trap, ECO-SC-E; 3 ♂, idem, 3-VIII-2008, J.A. Arreola, ECO-SC-E; 1 ♀, idem, 29-IV-1997, L. Solis-P., ECO-SC-E; 2 ♂, idem, 16-V-2009, J. León, ECO-SC-E; 1 ♂, Cacahoatán, Camino Azteza volcán Tacaná, N15°05'59" W92°08'16", 1700m, 13-VI-2009, C. Magaña, Bosque Mesófilo, light trap, ECO-TAP-E; 8 ♂, 3 ♀, Ángel Albino Corzo, Reserva Biosfera "El Triunfo", N15°39'24" W92°48'30", 1998m, 2-VII-2008, J. Macias, light trap, ECO-TAP-E; 1 ♂, idem, 7-VII-2003, B. Gómez, ECO-TAP-E.

Cosmosoma sectinota (Hampson, 1898). 1 ♀, Mexico, Chiapas, Coapilla, 20-VIII-2008, Irma D. & Miss-B, light trap, ECO-SC-E; 1 ♂, Tapalapa, 6 km Noreste de Tapalapa, 12-III-1994, O. Gómez, ECO-SC-E.

Cosmosoma stilbosticta (Butler, 1876): 2 ♂ 1 ♀, Mexico, Chiapas, Lacanjá Chansayab, 23-VIII-2008, J. León, ECO-SC-E; 1 ♂, Chiapas, Playón de la Gloria, 26-VI-2008, J. León, light trap, ECO-SC-E; 1 ♀, Maravilla Teneja, Ejido loma bonita, N16°11'24" W91°18'28", 241m, 4-IX-2002, F. Pérez-Espinoza, ECO-SC-E; 1 ♂, Maravilla Teneja, Ejido loma bonita, N16°11'38" W91°18'35", 283m, 11-IV-2002, L. Martin, ECO-SC-E.

Cosmosoma teuthras cingulatum (Butler, 1876): 2 ♀, Mexico, Campeche, Calakmul, Calakmul, 22-XI-2008, J. León, light trap, ECO-SC-E; 2 ♂, mismos datos, 22-X-2008, ECO-SC-E; 1 ♂, Calakmul, Dos Lagunas, 14-II-2006, N. Salas, light trap, ECO-CH-E; 5 ♂, Chiapas: Coapilla, 21-VIII-2008, J. León, light trap, ECO-SC-E; 3 ♂, idem, 20-VIII-2008, J. León, ECO-SC-E; 4 ♀, Ocosingo, Lacanjá Chansayab, 22-VIII-2008, J. León, light trap, ECO-SC-E; 3 ♂, San Fernando, Vicente Guerrero, 22-IX-2001, J. León, light trap, ECO-SC-E; 1 ♀, Ángel Albino Corzo, Reserva "El Triunfo", 2014m, 17-XI-2001, J. León, light trap, ECO-SC-E; 1 ♂, Maravilla Tenejapa, Ejido loma bonita, N.16°12'01"-W91°18'27", 370m, 2-VI-2002, F. Pérez, light trap, ECO-SC-E; 1 ♂, Chiapas, Tuxtla Chico, Campo Exp. Rosário Izapa, N.14°58'29" W92°09'18", 443m, 14-VI-1997, L. Jiménez, light trap, ECO-TAP-E; 1 ♂, idem, C. Cadena, ECO-TAP-E; 1 ♂, idem, 21-V-1999, A. Trejo, ECO-TAP-E; 1 ♂, Tuxtla Chico, 1ª Sección medio monte, N14°52'43" W92°12'52", 160m, 6-VI-1997, A. Dávila, light trap, ECO-TAP-E; 1 ♀, Unión Juárez, N15°03'45" W92°04'50", 1319m, 21-V-1999, V. Castillejos, light trap,

ECO-TAP-E; 1 ♂, Tapachula, Parque Ecológico, N14°53'08" W92°17'32", 122m, 1-V-2005, A. Niño, light trap, ECO-TAP-E; 2 ♀, Quintana Roo, Lázaro Cárdenas, Reserva Biosfera "El Eden", 13-X-1995, O. Gómez, light trap, ECO-SC-E; 1 ♂, idem, 13-IX-1995, ECO-SC-E; 1 ♂, idem, 22-IX-1995, ECO-SC-E; 1 ♂, Othón P. Blanco, Chetumal, 13-II-2007, N. Salas, light trap, ECO-CH-E.

Cosmosoma xanthostictum (Hampson, 1898). 2 ♂, Mexico, Chiapas, Ocosingo, Lacanjá Chansayab, 22-VIII-2008, Irma D, light trap, ECO-SC-E.

Chrysocale principalis (Walker, 1865). 1 ♂, Mexico, Chiapas, Berriozabal: 8km norte de Berriozabal, 15-IX-1992, R. Jones, ECO-SC-E.

Dycladia correbioides (Felder, 1874). 1 ♂, Mexico, Chiapas, Coapilla, 20-VIII-2008, U. Caballero, light trap, ECO-SC-E.; 1 ♂ 1 ♀, Angel Albino Corzo, reserva "El Triunfo", N. 15°39'42" W92°48'53", 2020m, 16-XI-2001, J. León, H. Linda, M. Girón, light trap, ECO-SC-E; 1 ♀, idem, 19-XI-2001, A. Molina, ECO-SC-E; 1 ♀, San Fernando, Vicente Guerrero, 22-IX-2001, J. León, trampa de luz, ECO-SC-E; 1 ♂, Tamaulipas, Gomes Farias, Reserva de Biosfera "El Cielo", N.23°06'02" W99°12'46", 18-VII-2006, Miss Barrera, ECO-SC-E.

Homoeocera gigantea (Druce, 1884). 1 ♂, 1 ♀, Mexico, Chiapas, Tapalapa, 6 km Nw Tapalapa, 12-III-1994, O. Gómez, ECO-SC-E; Albino Corzo, Reserva "El Trinunfo", 2020m, 18-X-1997, A. Morón-R. 1 ♂, UV light trap, ECO-SC-E; 1 ♀, idem, 25-II-1998, O. Gómez, ECO-SC-E; 1 ♀, idem, 24-II-1998, O. Gómez, ECO-SC-E; 1 ♀, 1 ♂, idem, 19-XI-2001, A. Molina, ECO-SC-E; 1 ♀, idem, 18-XI-2001, A. Molina, ECO-SC-E; 1 ♂, idem, 29-IV-1997, L. Solís, ECO-SC-E; 3 ♂, idem, 16-V-2009, J. León, ECO-SC-E; 1 ♀, idem, mismos datos 22-V-2008, J. León, ECO-SC-E; 1 ♂, idem, 22-V-2008, J. A. Arreola ECO-SC-E; 1 ♂, idem, 18-X-1997, O. Gómez ECO-SC-E; 1 ♂, idem, 29-II-1997, O. Gómez, ECO-SC-E; 1 ♂, Coapilla, 21-VII-2008, Irma D, y Miss B., ECO-SC-E; 1 ♂, idem, 20-VII-2008, J. León, ECO-SC-E; 1 ♂, Ángel Albino Corzo, El Triunfo, N.15°39'24" W92°48'30", 1998m, 14-V-2005, H. Gallardo, light trap, ECO-TAP-E; 1 ♂, idem, 2-VII-1998, J. Macías, ECO-TAP-E.

Homoeocera rodriguezi (Druce, 1890). 1 ♂, Mexico, Chiapas, Coapilla, 21-VIII-2008, U. Caballero, light trap, ECO-SC-E.

Isanthrene cajetani (Rothschild, 1911). 1 ♂, Mexico, Chiapas, Ángel Albino Corzo, Reserva "El Triunfo", 18-X-1997, O. Gómez, light trap, ECO-SC-E; 1 ♂, Ángel Albino Corzo, Finca Prusia, N15°42'51" W92°47'39", 1051m, 29-VI-1998, J. Macías, light trap, ECO-TAP-E; 1 ♂, Huehuetán, N15°00'38" W92°24'07", 34m, 7-II-1986, W. Rosa, light trap, ECO-TAP-E.

Isanthrene perbosci (Guérin-Ménéville, 1844). 1 ♀, Mexico, Quintana Roo, Othón P. Blanco, Chetumal, 2-

II-2008, N. Salas, light trap, ECO-CH-E; 1 ♂, Yucatán, Oxtutzcab, Reserva Kinuc, 20-VIII-2008, light trap, ECO-CH-E.

Leucotmemis nexa (Herrich-Schäffer, [1854]). 1 ♂, Mexico, Chiapas, Ocosingo, Playón de la gloria, 26-VI-2008, L.D., light trap, ECO-SC-E; 1 ♀, Ocosingo, Lacanjá chansayab, 22-VIII-2008, U. Caballero, ECO-SC-E; 1 ♂, Coapilla, 20-VIII-2008, U. Caballero, ECO-SC-E; 1 ♂, Quintana Roo, Othón P. Blanco, Estero Franco, 19-IX-1991, E. Escobedo, ECO-SC-E; 1 ♂ 1 ♀, Othón P. Blanco, Álvaro Obregón, Nuevo, 23-XII-2008, E. Domínguez, light trap, ECO-CH-E.

Loxophlebia imitata (Druce, 1884). 1 ♀, Mexico, Quintana Roo, Othón P. Blanco, Chetumal: alrededores del ECOSUR, 14-VI-2007, M. Bálcazar, light trap, ECO-CH-E; 1 ♂, idem, 14-VI-2007, N. Salas, ECO-CH-E; 1 ♂, idem, 22-II-2008, N. Salas, ECO-CH-E; 1 ♀, Othón P. Blanco, Álvaro Obregón Nuevo, 5-VII-2008, E. Domínguez, light trap, ECO-CH-E; 1 ♂, idem, 27-IX-2008, ECO-CH-E.

Macrocneme chrysitis (Guérin-Ménéville, 1844). 2 ♀, Mexico, Chiapas, Tenejapa, Ejido Loma bonita, N16°11'19" W91°18'25", 241m, 28-V-2002, L. Martín, ECO-SC-E; 1 ♂, idem, 28-V-2002, J. León, ECO-SC-E; 1 ♂, idem, 7-X-2002, J. León, ECO-SC-E; 1 ♂, idem, 8-IV-2002, F. Pérez, ECO-SC-E; 1 ♀, idem, 8-IV-2002, L. Martín, ECO-SC-E; 3 ♂, Coapilla, 26-V-2008, Irma-D y Miss-B, light trap, ECO-SC-E; 3 ♀, Reserva "Montes Azules", 4-VII-1992, J. León, light trap, ECO-SC-E; 2 ♂, Ocosingo, Playón de la Gloria, 26-V-2008, J. León, light trap, ECO-SC-E; 2 ♂ 3 ♀, Tamaulipas, Gómez Farias, Reserva biosfera "el cielo", Rancho "el cielo", N23°06'02" W99°12'46", 18-VII-2006, J. León, ECO-SC-E.

Nyridela xanthocera (Walker, 1856). 1 ♂, 1 ♀, Mexico, Chiapas, Coapilla, 21-VIII-2008, J. León-C, light trap, ECO-SC-E; 1 ♂, idem, 21-VIII-2008, Irma D., ECO-SC-E; mismos datos 20-VIII-2008, U. Caballero, ECO-SC-E; 1 ♂, México, Chiapas, Coapilla, 20-VIII-2008, U. Caballero, light trap, ECO-SC-E.

Pheia albisigna (Walker, 1854). 1 ♂, Mexico, Chiapas, Villa Flores, Reserva Biosfera "La Sepultura", Ejido Sierra Morena casa ejidal, N.16°69'32" W93°35'27", 1185m, 17-VII-2003, A. Molina, light trap, ECO-SC-E; 1 ♀, Ocosingo, Playa de la Gloria, 26-VI-2008, U. Caballero, light trap, ECO-SC-E.

Phoenicoprocta mexicana (Walker, 1865). 1 ♂, Mexico, Chiapas, Coapilla, 20-VII-2008, J. León-C, light trap, ECO-SC-E; 1 ♀, idem, 27-V-2008, J. León, ECO-SC-E.

Pseudohyaleucerea vulnerata vulnerata (Butler, 1875). 1 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido loma bonita, N.16°12'03" W91°18'40", 231, 1-IX-2002, J. León, light trap, ECO-SC-E; 1 ♂, Ocosingo, Lacanjá

Chansayab, 22-VIII-2008, U. Caballero, light trap, ECO-SC-E

Psilopleura vittata (Walker, 1865). 1 ♂, 1 ♀, Mexico, Tamaulipas, Gómez Farias, Reserva de Biosfera "El Cielo", N.23°06'02" W99°12'46", 18-VII-2006, I.D. Miss Barrera, ECO-SC-E; 1 ♂, idem, 18-VIII-2006, I.D. Miss-Barrera, ECO-SC-E; 1 ♀, idem, 19-VII-2006, J. León, ECO-SC-E; 1 ♀, idem, 18-VII-2006, J. León, ECO-SC-E; 1 ♂ 1 ♀, Chiapas, Maravilla Tenejapa, Ejido loma bonita, N.16°11'23" W91°18'34", 236m, 8-IV-2002, J. León, ECO-SC-E.

Psoloptera basifulva (Schaus, 1894). 2 ♂, Mexico, Chiapas, Maravilla Tenejapa, Ejido loma bonita, N.16°11'32" W91°18'34", 235m, 2-IX-2002, F. Pérez, ECO-SC-E; 1 ♀, idem, 241m, 9-X-2002, J. León, ECO-SC-E; 1 ♀, idem, 283m, 1-IX-2002, F. Pérez, ECO-SC-E; 1 ♀, idem, 380m, 28-VIII-2002, F. Pérez, ECO-SC-E; 1 ♂, idem, 369m, 31-V-2002, J. León, ECO-SC-E; 1 ♂, idem, 235m, 2-IX-2002, F. Pérez, ECO-SC-E.

Scena potentia (Druce, 1894). 1 ♂, 1 ♀, Mexico, Chiapas, Coapilla, 21-VIII-2008, U. Caballero, ECO-SC-E; 1 ♂, idem, 21-VIII-2008, J. León, ECO-SC-E; 1 ♂, idem, 21-VIII-2008, Irma D, ECO-SC-E; 1 ♂, idem, 20-VIII-2008, U. Caballero, ECO-SC-E; 1 ♀, idem, 20-VIII-2008, J. León, ECO-SC-E; 1 ♀, idem, 20-VIII-2008, Irma D, ECO-SC-E; 1 ♂, 1 ♀, Albino Corzo, Reserva Biosfera "El Triunfo", 16-V-2009, J. León, ECO-SC-E; 1 ♂, idem, 3-VIII-2008, J. León, ECO-SC-E; 1 ♂, 1 ♀, Ocosingo, Playón de la Gloria, 26-VI-2008, J. León, ECO-SC-E.

Sphecosoma felderi (Druce, 1883). 1 ♂, Mexico, Chiapas, Coapilla, 20-VIII-2008, Irma I, light trap, ECO-SC-E; 1 ♂, idem, 20-VIII-2008, U. Caballero, ECO-SC-E.

Syntomeida epilais epilais (Walker, 1854). 1 ♂, Mexico, Campeche, Calakmul, Calakmul, 6-VI-1997, S. Uc, light trap, ECO-CH-E; 1 ♂, Calakmul, Dos Lagunas, 12-II-2006, E. May, light trap, ECO-CH-E; 1 ♂, Chiapas, Maravilla Tenejapa, Ej. Loma Bonita, N16°11'24" W91°18'28", 241m, 27-V-2002, J. León, light trap, ECO-SC-E; 1 ♀, Quintana Roo, Isla Cozumel, Fiesta Americana Hotel, 20-IX-1996, O. Gómez, light trap, ECO-SC-E; 1 ♀, idem, 10-III-1997, P. Beutelspacher, ECO-SC-E; 1 ♀, Solidaridad, Jardín Botánico, Puerto Morelos, 6-VII-2002, E. May, light trap, ECO-CH-E; 2 ♂, Othón P. Blanco: Álvaro Obregón Nuevo, 2-II-2009, E. Domínguez, light trap, ECO-CH-E.

Syntomeida melanthus albifasciata (Butler, 1876). 1 ♂, Mexico, Tamaulipas, Gómez Farias, Reserva Biosfera "El Cielo", N23°06'02" W99°12'46", 19-VII-2006, J. León, light trap, ECO-SC-E; 1 ♂, 2 ♀, idem, 18-VII-2006, J. León, ECO-SC-E.

Among all the reported species *Correbidia fana* (Druce) (Ctenuchina) (Figure 1) is known from the cloud forests of Merida, Venezuela, the high regions of Río Negro, Colombia, and the central region of Ecuador, in South America, but it has been also reported in the mountainous regions of Baja and Alta Verapaz, Guatemala, in Central America (Druce, 1900; Hampson, 1914; Draudt, 1917, Hernández-Baz et. al, 2008). It is now reported from the cloud forests in the South of Chiapas and it constitutes a first report of the species in Mexico (Figure 2).

ACKNOWLEDGEMENTS

The first author thanks CONACyT, México for financial support (scholarship code: 223961) and CITRO of Universidad Veracruzana, Xalapa, Mexico, for general support through his graduate studies. We are greatly indebted to Carmen Pozo de la Tijera (ECO-CH-E), and Jorge León Cortéz (ECO-SC-E) for allowing us to study all specimens held at the ECOSUR biological stations/collections under their care. Thanks also go to S.B. Vinson (Texas A & M University) for comments and suggestions to the manuscript, and Andrew Warren (McGuire Center for Lepidoptera & Biodiversity) for suggestions to one of the first drafts. Our deepest gratitude is extended to the editor, two anonymous reviewers and to Robert W. Matthews (University of Georgia) whose thoughtful and enlightening comments/corrections help us improve the final manuscript.

LITERATURE CITED

- BARNES, M. J. C. 2000. Moths of Belize. An illustrated catalogue of the larger moths of Belize. <http://www.mbarnes.force9.co.uk/belize-moths/belizehome.htm>. Revised 20 July 2012.
- BARTH, R. 1953. Órgãos odoríferos masculinos de algumas Syntomidae Brasileiras (=Ctenuchidae; Lepidoptera). Memórias do Instituto Oswaldo Cruz 51: 227–237.
- CERDA, J. 2008. Euchromiini de Guyane Française. Lepidoptera: Arctiidae, Arctiinae. Author, Matoury, French Guiana. 176 pp.
- DIETZ IV, R. E., 1994. Systematics and biology of the genus *Macrocname* Hübner (Lepidoptera: Ctenuchinae). Univ. Calif. Pub. Entomol. 113: 1–121.
- DIETZ IV, R. E. & W.R. DUCKWORTH, 1976. A review of the genus *Horama* Hübner and reestablishment of the genus *Poliopastea* Hampson (Lepidoptera: Ctenuchinae). Smithsonian Contributions to Zoology No. 215, Smithsonian Institution Press. Washington D.C., pp 1–53.
- DRAUDT, M. 1917. Syntomidae, pp. 33–230. In A. Seitz A. (ed.) Die Gross-Schmetterlinge der Erde. II. Abteilung: Die Gross-Schmetterlinge des Amerikanischen Faunengebietes, 6 Band, Die Amerikanischen Spinner und Schwärmer. Alfred Kernen, Stuttgart.
- DRUCE, H. 1900. Description of some new species of Heterocera from Tropical South America. Ann. Mag. Nat. Hist. 7: 64–67.
- HAMPSON, G. F. 1898. Catalogue of the Syntomidae in the Collection of the British Museum. British Museum Natural History, London. 559 pp.
- HAMPSON, G. F. 1914. Catalogue of the Lepidoptera Phaleana in the British Museum. Supplement. Vol. I. 387p.
- HEPPNER, J. B. 1991. Faunal regions and the diversity of Lepidoptera. Trop. Lepid. 2 (Supplement 1): 1–85.
- HERNÁNDEZ-BAZ, F. 1992. Catálogo de los Ctenuchidae (Insecta: Lepidoptera: Heterocera) de México. Boletín Sociedad Mexicana de Lepidopterología, A.C., Nueva Serie 2:19–47.
- , 2009. Mariposas Arctiidae. Pp. 109–112, + appendix VI, pp. 409–410. In G. Ceballos, R. List, G. Garduño, C. R. López, M. J. Muñozcano-Quintana, E. Collado, & J. E. San Román (comp.).

- La diversidad biológica del estado de México. Estudio de Estado. Conabio & Gobierno del Estado de México.
- , 2011. Palomillas nocturnas Arctiidae, pp. 197–201. *In* C. Pozo (ed.) Riqueza Biológica de Quintana Roo. Un análisis para su conservación. Tomo 2. Colegio de la Frontera Sur, Conabio, Gobierno del Estado de Quintana Roo, México.
- , 2012A. Las polillas avispa de México (Lepidoptera: Erebiidae: Arctiinae: Ctenuchina y Euchromiina): Biogeografía y Conservación. Universidad Veracruzana. Tesis Doctoral. 341p.
- , 2012B. Mariposas tigre (Arctiidae) de Chiapas, pp. 602–605 *In* Gobierno del estado de Chiapas (ed.). La Biodiversidad de Chiapas. México: Comisión Nacional para el Conocimiento y uso de Biodiversidad y Gobierno del estado de Chiapas. (in press)
- HERNÁNDEZ-BAZ, F. & A. C. BAILEY. 2006. Los ctenuchinae (Insecta: Lepidoptera: Arctiidae) de la República de Guatemala: Una síntesis preliminar, pp. 403–413. *In* E. Cano (ed.). La Biodiversidad de Guatemala. Universidad del Valle de Guatemala, CONCYT, Guatemala.
- , 2007. Los Ctenuchinae (Lepidoptera: Arctiidae) de la colección de artrópodos de la Universidad del Valle, Guatemala, Guatemala. *Dugesiana* 14(2): 99–106.
- HERNÁNDEZ-BAZ, F. & R. COATES. 2011. The wasp moths (Lepidoptera: Noctuidae: Arctiinae) deposited in the entomological collection of the Los Tuxtlas Tropical Biology Station, Veracruz, Mexico. *Dugesiana* 18(1): 31–34.
- HERNÁNDEZ-BAZ, F., A. C. BAILEY & J. MONZÓN. 2008. Notes on some Ctenuchinae dry season (Lepidoptera: Arctiidae) from a cloud forest and pine-oak forest in Guatemala, Middle America. *Dugesiana* 15(2): 87–89.
- JACOBSON, N.L. & S.J. WELLER. 2002. A cladistic study of the Arctiidae (Lepidoptera) by using characters of immatures and adults. Lanham, Maryland: Thomas Say Publications in Entomology, Entomological Society of America. 98 p.
- JIMÉNEZ-VALVERDE, A. & J. HORTAL. 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Revista Ibérica de Aracnología, sección Boletín* 8:151–161.
- KITCHING, I.J. & J.E. RAWLINS. 1999. The Noctuoidea, pp. 355–401. *In* Kristensen, N.P. (ed.) *Lepidoptera, moths and butterflies*. Handbook of Zoology. Volume IV. Arthropoda: Insecta. Part 35. Volume I. Evolution, Systematics and biogeography. Berlin and New York: Walter de Gruyter.
- LAFONTAINE, J.D. & M. FIBINGER. 2006. Revised higher classification of the Noctuoidea (Lepidoptera). *Canad. Entomol.* 138: 610–635.
- LAFONTAINE, J.D. & B.C. SCHMIDT. 2010. Annotated check list of the Noctuoidea (Insecta, Lepidoptera) of North America north of Mexico. *ZooKeys* 40: 1–239. doi:10.3897/zookeys.40.414
- SIMMONS, R. B. & S. J. WELLER. 2006. Review of the Sphecosoma genus group using adult morphology (Lepidoptera: Arctiidae). *Entomol. Soc. Amer. Monogr.* 108p
- TESTON, J.A. & E. CORSEUIL. 2003. Arctiinae (Lepidoptera: Arctiidae) o correntes no rio grande do soul, Brasil. Parte 3, Ctenuchini e Euchromiini. *Biociencias* 2(1): 81–90.
- VALDÉZ-HERNÁNDEZ, M. & G.A. ISLEBE. 2011. Tipos de vegetación de Quintana Roo. Pp. 32–36. *In*: C. Pozo (ed.) Riqueza biológica de Quintana Roo. Un análisis para su conservación, Tomo 2. Colegio de la Frontera Sur, CONABIO, Gobierno del estado de Quintana Roo: México.
- VARGAS, F., I.A. LUIS M., J. LLORENTE B. & A.D. WARREN. 1996. Butterflies of the State of Jalisco, Mexico. *J. Lepid. Soc.* 50: 97–135.
- WATSON, A., D.S. FLETCHER & W. B. NYE. 1980. The generic names of moths of the World. The Natural History Museum, London. 229 p.
- WATSON, A. & D.T. GOODGER. 1986. Catalogue of the Neotropical tiger-moths. *Occasional Papers on Systematic Entomology (British Museum Natural History)* 1:1–71p.
- WELLER, S. J., R. B. SIMMONS, R. BOADA, & W. E. CONNER. 2000. Abdominal modifications occurring in wasp mimics of the ctenuchine-euchromiine clade (Lepidoptera: Arctiidae). *Ann. Entomol. Soc. Amer.* 93: 920–928.
- WELLER, S., M. DACOSTA, R. SIMMONS, K. DITTMAR & M. WHITING. 2009. Evolution and taxonomic confusion in Arctiidae, pp. 11–30. *In* Conner, W. E. (ed) *Tiger moths and woolly bears*. 303p.
- ZERNY, H. 1912. Family Syntomidae, *In* *Lepidopterorum Catalogus*, W. Junk (ed.) Berlin, Germany, part 7, 1–179.

Received for publication 15 May 2012; revised and accepted for publication 1 August 2012.

Journal of the Lepidopterists' Society
67(3), 2013, 156–160

THE DESCRIPTION OF *PLATPHALONIA MAGDALENAE* (TORTRICIDAE, TORTRICINAE, EULIINI, COCHYLINA) FOUND NECTARING DIURNALLY ON *CENTROMADIA PUNGENS* (ASTERACEAE) IN THE CENTRAL VALLEY OF CALIFORNIA ALONG WITH A LIST OF SPECIES OF *PLATPHALONIA*

ERIC H. METZLER

Michigan State University, Adjunct Curator of Lepidoptera, Research Collaborator U.S.N.M. Natural History,
P.O. Box 45, Alamogordo, New Mexico 88311-0045, USA; email: metzler@msu.edu

AND

VALERIU ALBU

23032 Oak Meadow Ln., Friant, California 93626, USA; email: valalbu@netptc.net

ABSTRACT. *Platphalonia* Razowski, 2011 (Tortricidae, Tortricinae, Euliini, Cochylina) was proposed for *Saphenista mystica* Razowski & Becker, 1983 (type species) and several species previously assigned to *Platphalonia* Razowski, 1985. However, with the exception of the type species, none of the other purported congeners have been listed. We formally transfer 16 species to *Platphalonia*, resulting in the following new combinations: *P. albertae* (Razowski, 1997), *P. assector* (Razowski, 1967), *P. californica* (Razowski, 1986), *P. campicolana* (Walsingham, 1879), *P. dangi* (Razowski, 1997), *P. decrepita* (Razowski & Becker, 2002), *P. dubia* (Razowski & Becker, 1983), *P. fusifera* (Meyrick, 1912), *P. galbana* (Meyrick, 1917), *P. lavana* (Busck, 1907), *Platphalonia luxata* (Razowski & Becker, 1986), *P. mendora* (Clarke, 1968), *P. ochraceana* (Razowski, 1967), *P. paranae* (Razowski & Becker, 1983), *P. plicana* (Walsingham, 1884), and *P. sublimis* (Meyrick, 1917). We describe *Platphalonia magdalenae* Metzler & Albu, **new species**, from a series of specimens that were discovered nectaring on *Centromedia* (= *Hemizonia*) *pungens* (Hook. & Arn.) Greene ssp. *pungens* (Asteraceae) during the day-time on 2 May 2011 in Tulare County, in the Central Valley of California. Adults and male and female genitalia of *P. magdalenae* are illustrated.

Additional key words: *Platphalonia magdalenae*, Tulare County, California native plants, *Platphalonia*, *Phalonia*

Based on the type species of *Platphalonia* Razowski, 1985 (i.e., *Phalonia felix* Walsingham, 1895), Razowski (2011) synonymized that genus with *Phalonia* Le Marchand, 1933 (Tortricidae, Tortricinae, Euliini, Cochylina). He concomitantly proposed *Platphalonia* Razowski, 2011 for *Saphenista mystica* Razowski & Becker, 1983 (type species) and the remaining species of *Platphalonia* (i.e., all species formerly included in *Platphalonia*, except its type species). In his description of *Platphalonia*, Razowski stated that 29 unnamed species are transferrable to *Platphalonia*, but he did not list them.

In 2011 Valeriu Albu collected a series of a previously unknown species of Cochylina found nectaring during the day in the Central Valley of California. Razowski (in litt. 2012) concurred that the new species from California's Central Valley belonged in the genus *Platphalonia*. Because there was no list of North American species of *Platphalonia*, there was no way to properly diagnose the new taxon.

The purposes of this paper are to transfer 16 species to *Platphalonia* and to describe a new species of *Platphalonia* from California's Central Valley.

MATERIALS AND METHODS

The classification Euliini, Cochylina comes from Regier et al. (2012). Józef Razowski from the Polish

Academy of Sciences, Krakow, (in litt., 2012) provided a list of species that he referred to *Platphalonia*. We carefully compared published illustrations of male and female genitalia of species from the list to published illustrations of the type species, *Platphalonia mystica*. We examined the male and female genitalia of all other species listed in *Platphalonia* in Brown (2005), and we made similar examinations of all species described in *Platphalonia* subsequent to Brown (2005).

Valeriu Albu collected a series of 21 specimens of an undescribed species of *Platphalonia* nectaring on *Centromedia* (= *Hemizonia*) *pungens* (Hook. & Arn.) Greene ssp. *pungens* (common spikeweed) (Asteraceae) during the day in Tulare County, California. The moths were common on the flower blossoms. He sent the specimens to Eric Metzler for study.

Identification was made by comparing the specimens to published illustrations of adults and genitalia. Photographs of adults were sent to Kevin Tuck (The Natural History Museum, London) who opined that the Tulare County species is different from *P. plicana* (Walsingham, 1884), to which the male genitalia structures bear some resemblance. Photographs of the adults and male genitalia were sent to Józef Razowski who confirmed that the species was undescribed.

Genitalia were dissected following procedures outlined in Hardwick (1950), Lafontaine (2004), and

Pogue (2002). Abdomens were removed from the moths, wetted in 95% ethanol, and soaked in 10% KOH for 1 hour at 50°C. Genitalia were dissected in water, dehydrated in 100% ethanol, cleared in oil of cloves, rinsed in xylene, and slide mounted in Canada balsam. The genitalia were stained with Chlorazol Black in water and/or Safranin O in 95% ethanol. Many authorities (e.g. Hardwick 1950, Lafontaine 2004, Pogue 2002) presented techniques for dissection and examination of genitalia. Not all authors agree on each technique and each author offered unique ideas. Over time Metzler assembled a collection of techniques from the several sources, not all of which can be found in any one source, yet when taken together the techniques provide an overview that makes the task of dissection and slide preparation easier for Metzler to accomplish.

Terminology for elements of wing pattern follows Horak (1991). Terminology for morphology and genital structures follows Horak (1991) and Razowski (1970, 2008). Forewing length was measured to the nearest 0.1 mm, from the base to the apex excluding fringe, using a stereo-microscope with reticle.

Specimens cited in this paper are deposited in the following collections:

- VA Valeriu Albu, Friant, CA
- MSU Albert J. Cook Arthropod Research Collection,
Department of Entomology, Michigan State
University, East Lansing, MI
- UCB University of California Berkeley, Berkeley, CA
- USNM US National Museum of Natural History (Smith-
sonian Institution), Washington, DC

RESULTS

We transfer 16 species to *Platphalonia*.

Platphalonia Razowski, 2011

Type species: *Saphenista mystica* Razowski & Becker, 1983 by original designation.

Platphalonia albertae (Razowski, 1997)
[*Platphalonidia*] comb. n.

Platphalonia assector (Razowski, 1967) [*Cochylis*]
comb. n.

Platphalonia californica (Razowski, 1986)
[*Platphalonidia*] comb. n.

Platphalonia campicolana (Walsingham, 1879)
[*Cochylis*] comb. n.

Platphalonia dangi (Razowski, 1997)
[*Platphalonidia*] comb. n.

Platphalonia decrepita (Razowski & Becker, 2002)
[*Platphalonidia*] comb. n.

Platphalonia dubia (Razowski & Becker, 1983)
[*Saphenista*] comb. n.

Platphalonia fusifera (Meyrick, 1912) [*Phtheochroa*]
comb. n.

Platphalonia galbanea (Merick, 1917) [*Phalonia*]
comb. n.

Platphalonia lavana (Busck, 1907) [*Phalonia*] comb.
n.

Platphalonia luxata (Razowski & Becker, 1986)
[*Platphalonidia*] comb. n.

Platphalonia mendora (Clarke, 1968) [*Cochylis*]
comb. n.

Platphalonia ochraceana (Razowski, 1967)
[*Cochylis*] comb. n.

Platphalonia paranae (Razowski & Becker, 1983)
[*Saphenista*] comb. n.

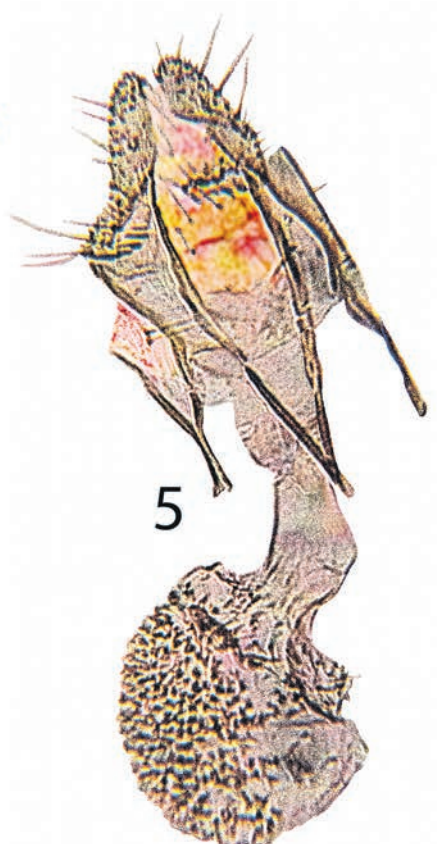
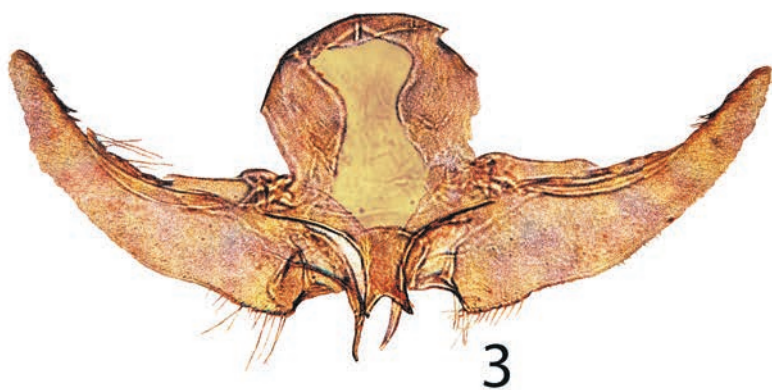
Platphalonia plicana (Walsingham, 1884)
[*Conchylis*] comb. n.

Platphalonia sublimis (Meyrick, 1917) [*Phalonia*]
comb. n.

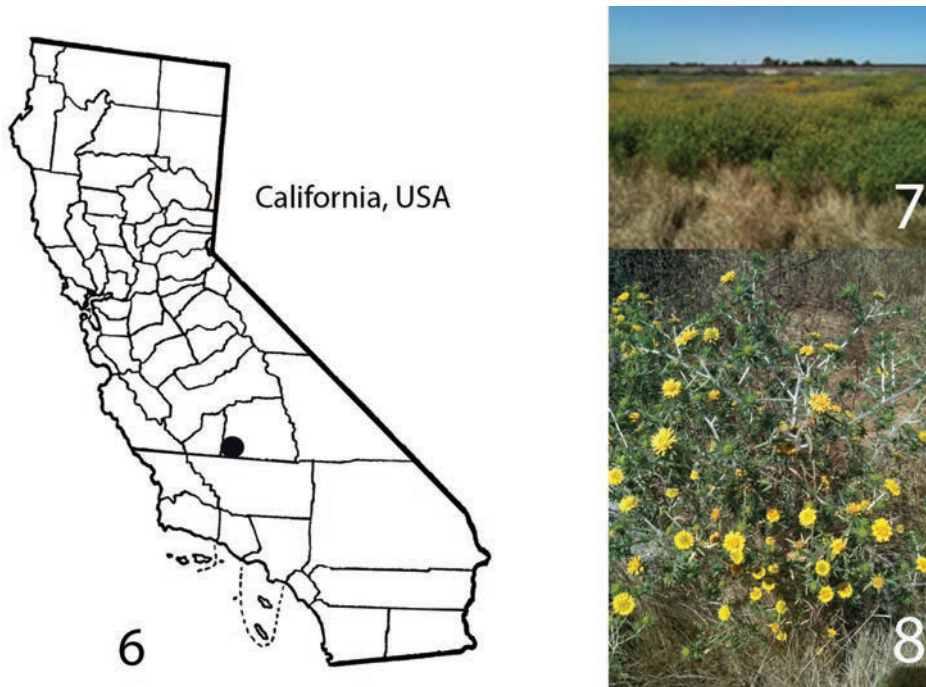
***Platphalonia magdalenae* Metzler & Albu, new species**

(Figs 1–6)

Diagnosis. *Platphalonia magdalenae* is a small tan moth with a pale reddish-brown transverse fascia. The diagnostic features are the tan ground color, the slightly reflective nature of the fore wing scales, the curved reddish-brown postmedial fascia that extends from the inner margin to the costa, and the brownish-gray hind wings. As is typical with many species of *Cochylina*, the generic assignment of *P. magdalenae* cannot be determined from the external appearance of the adult moth. Superficially, *P. magdalenae* might be confused with several species, in several genera, of *Cochylina*. An examination of the male genitalia is required for positive assignment to a genus. Within the genus *Platphalonia*, the only other described species from California is *P. campicolana* (Walsingham, 1879). The fore wing of *P. campicolana* is cream-white, the reddish fascia extends from the inner margin to mid-wing, the postmedian fascia does not reach the costa, and the fringe is black. The fore wing of *P. magdalenae* is tan and the fringe is not black. *Platphalonia albertae*, *P. californica*, *P. dangi*, *P. lavana*, *P. luxata*, *P. parvimaculana*, and *P. plicana*, also occur in the Nearctic Ecozone. The width of the mesal process of the transtilla narrows subapically in *P. albertae*; whereas in *P. magdalenae* it is not narrowed subapically. The acutely pointed apices of the bifurcate terminus of the mesal process of the transtilla are distinctly pointed laterally in *P. californica*; whereas in *P. magdalenae* are not pointed laterally. The fore wing of *P. dangi* is dirty-white with an oblique dark colored fascia extending from just before the apex to outer margin 2/3 from the tornus; the fore wing of *P. magdalenae* is tan without an oblique dark fascia. The ground color of the fore wing of *P. lavana* is dirty-white, the fore wing has an excurved subterminal gray fascia extending from just



FIGS. 1–5. *Platphalonia* adults and genitalia. 1, *P. magdalenae* male holotype. 2, *P. magdalenae* female paratype. 3, *P. magdalenae* male paratype genitalia. 4, *P. magdalenae* male paratype aedeagus. 5, *P. magdalenae* female paratype genitalia.



FIGS. 6–8. Distribution map and habitat of *Platphalonia magdalenae*. **6**, Distribution map for *P. magdalenae*. **7**, Habitat picture of type locality of *P. magdalenae*. **8**, *Centromadia pungens* ssp. *pungens*.

before the apex to the tornus, and the fringe is black; in contrast, the ground color of the fore wing of *P. magdalenae* is tan without a subterminal fascia, and the fringe is concolorous. The ductus bursae of *P. luxata* is ringed with sclerotization at the junction with the corpus bursae; the ductus bursae of *P. magdalenae* is encircled with linear rugosities at the junction with the corpus bursae. The ground color of the fore wing of *P. plicana* is dirty-white, the subterminal area contains a patch of contrasting dark-brown scales, the terminal line is black, the fringe is contrastingly dark brown, and the hind wing is gray; the fore wing of *P. magdalenae* is tan, there is no patch of dark-brown scales in the subterminal area, the terminal line and fringe are not contrastingly dark, and the hind wing is dark fuscous.

Description. **Adult male** (Fig. 1). *Head*: Front smooth, tan, with scattered tan-tipped orange scales; vertex pale-tan, with scattered dark-tan scales, smooth, posterior margin with scales erect. Labial palpus porrect, segments 1 and 2 mixed with tan and chamois-colored scales, lateral and mesal surfaces with scales appressed, dorsal and ventral surfaces weakly tufted, segment 3 directed anteriorly, with light tan, appressed scales. Antenna with dorsal surface scaled, tan, ventral surface naked with setae numerous, length = width of antennal segment. *Thorax*: Dorsum tan and chamois-color, smoothly scaled; underside with scales appressed, shining white and silver. Fore-leg femur with scales appressed, dorsal surface tan, with scattered brown and orange scales, ventral surface dirty-white, scales of tibia, femur and tarsi appressed, dorsal surface tan, scattered brown scales, ventral surface dirty-white. Mid-leg scales appressed, femur dirty-white, tibia, femur, and tarsi dorsal surface tan, scattered light-brown scales, ventral surface dirty-white. Hind-leg scales appressed, dirty-white. Forewing length 3.9–5.5 mm, mean 4.7 mm, $n = 18$. Upper surface of forewing reflective white (appears tan), anterior one half of basal 1/3

narrowly salmon, basal 1/3 of costa dark brown, distal 2/3 of costa tan; posterior one half of basal area chamois color; subbasal fascia angled outward from inner margin, chamois color; postmedial fascia angled outward from inner margin, bent at cell towards costa, pale horn color; at costa mixed with brown and salmon, brown scales at bend; subterminal fascia angled from cell to just before apex, pale horn color, subterminal area below apex with small patch of brown scales; fringe pale horn color mixed with salmon and brown scales; underside inner margin reflective white scales, area over cell brown-tipped reflective white scales, basal one half of costa brown, outer one half salmon; fringe reflective white. Hindwing with tan-gray tipped reflective white scales, base lighter, inner angle darker, fringe concolorous, reflective; underside reflective white, tan-gray tipped scales numerous, inconspicuous; fringe concolorous. *Abdomen*: Dorsum scales appressed, reflective silver-tan; underside scales appressed, mixed tan and pale gray. *Genitalia* (Fig. 3) with tegumen wide, prominent, apex flattened, suture mesially; uncus absent; socii appressed, membranous, broad, lightly sclerotized apically; transtilla robust, directed ventrally, mesally bent, mesal process drawn out, apex robust, bifurcate, each arm drawn to a blunt point, apex with tiny teeth laterally; juxta broad, elliptical; saccus obscure; valva simple, elongate, curved dorsally, with scattered setae apically, costa sclerotized; saccular region not produced, weakly sclerotized, with scattered setae; phallus (Fig. 4) longer than wide, gradually narrowing apically, bent 30° at 1/3 length; cornuti poorly defined, obscure, lightly sclerotized.

Adult female (Fig. 2). *Head and thorax*: Essential as described for male. Forewing length 5.0–5.3 mm, mean 5.1 mm, $n = 3$. Hindwing with frenulum of one, two, or three bristles, asymmetrical. *Abdomen*: *Genitalia* (Fig. 5) with papilla analis membranous, narrow, setose; posterior apophysis extending to anterior margin of 8th segment; anterior apophysis divided basally, extending to anterior end of ductus bursae; antrum weakly sclerotized; ductus bursae lightly sclerotized posteriorly, mesally membranous, anteriorly sclerotized, fluted and widening at junction with corpus bursae; corpus bursae short, round, membranous, densely covered with spicules in patches; signa absent.

Holotype. Adult male, pinned with labels as follows: "Legit Val Albu, Tulare Co/California, Rt. 43 @ Allensworth, 2 V 2011"

"HOLOTYPE USNM *Platphalonia magdalenae* Metzler & Albu" [red handwritten label] (USNM).

Paratypes. 20 ♂, 3 ♀: same data as Holotype. Depositories: VA, MSU, UCB, USNM.

Systematics. This new species is placed in the genus *Platphalonia* based on comparison of the female genitalia with the holotype of *Saphenista mystica* Razowski & Becker, 1983, which is the type species of *Platphalonia*. Our analysis was confirmed by Józef Razowski (in litt., 2012).

Etymology. The species is named after Magdalena Albu, who, as the wife of the second author, lovingly and dutifully followed and helped with his entomological excesses. The name is in the genitive case.

Distribution and biology. The diurnal nectaring behavior of adult *Cochylina* is unusual, and we call attention to it here with the idea that the behavior could be present, and as yet unobserved, in other species of *Cochylina*.

Platphalonia magdalenae occurs in the Central Valley of California. Its distribution outside Tulare County is unknown. Nothing is known about its life history, however, an association with *Centromadia pungens* ssp. *pungens* is reasonably inferred.

The adults of *P. magdalenae* were collected in early May. The habitat is in the intensively farmed Central Valley, along California State Route 43, in the vicinity of Allensworth, CA at 60 m elevation (Fig. 7). The plant upon which the adults were found, *Centromadia pungens* ssp. *pungens* (Fig. 8), is found in the U.S. from Washington south through Oregon, California, Nevada, and southern Arizona (USDA 2012). The plant is not recorded from Canada, and the Mexican distribution is unknown. The plant's distribution in California (Baldwin et al. 2012) is extensive at lower elevations, from the Sierra Nevada foothills to the coast. It is not recorded from the eastern deserts of the state. In Tulare County it occurs abundantly in disturbed areas, along roads and rail road tracks. It has a long blooming period, from April to September.

Remarks. Some specimens are slightly darker. They have scattered dark-brown scales on the head, the palpi, and an increased number of dark-brown scales on the legs.

DISCUSSION

Our study examined the published illustrations of the genitalia of the 24 species included in *Platphalonia* (Brown 2005), the list of species provided by Józef Razowski (in litt. 2012), and all species described in the genus *Platphalonia* subsequent to Brown (2005). We were able to confirm the congeneric status of 16 species which we transferred to *Platphalonia*. We transferred species where the genitalia were in agreement with the type species *Platphalonia mystica*. Razowski (2011) indicated that 29 species are referable to *Platphalonia*. This paper is not a revision of the genus *Platphalonia*,

and we do not resolve the correct generic assignments of the remaining 13 species because such an endeavor falls outside the scope of this paper.

The many species of *Cochylina*, even within a single genus, e.g. *Aethes* Billberg, 1820, often have forewing patterns that are incongruous. Several references (e.g. Horak 1991, Razowski 1970, 2008) illustrate the variety of forewing patterns of *Cochylina*. We reference Horak (1991) in this paper because her illustration on page 6 has wing pattern elements, sub-basal and postmedial fascia, represented in *P. magdalenae*.

ACKNOWLEDGMENTS

We thank Joanna Clines, Forest Botanist at the Sierra National Forest in North Fork, CA for identifying the plant upon which the moths were found nectaring and for providing useful information about it. We especially thank Kevin Tuck of the Natural History Museum in London and Józef Razowski of the Polish Academy of Sciences in Kraków for their rapid and detailed replies to our requests for information. We appreciate the assistance of Jerry A. Powell and John W. Brown with advice on how to broach the taxonomy of *Platphalonia*. We thank Jason J. Dombroskie and two anonymous reviewers for reading the paper and offering constructive suggestions.

LITERATURE CITED

- BALDWIN, B. G., H. G. DOUGLAS, D. J. KEIL, R. PATTERSON, & T. J. ROSARTI. 2012. The Jepson Manual: Vascular Plants of California, Second Edition. University of California Press, Berkeley, California. 1,600 pp.
- BROWN, J. W. 2005. World Catalogue of Insects Volume 5 Tortricidae (Lepidoptera). Apollo Books, Stenstrup, Denmark. 741 pp.
- HARDWICK, D. F. 1950. Preparation of slide mounts of lepidopterous genitalia. *Canad. Entomol.* 82:231–235.
- HORAK, M. 1991. Chapter 1 Morphology, phylogeny and systematics, 1.1 Morphology. pp. 1–22. In Van Der Geest, L. P. S. & H. H. Evenhuis. (eds.). *World Crop Pests, 5. Tortricid Pests Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam.
- LAFontaine, J. D. 2004. The Moths of North America Including Greenland, Fascicle 27.1, Noctuoidea Noctuidae (part) Noctuidae (part - Agrotini). The Wedge Entomological Research Foundation, Washington, DC. 385 pp.
- POGUE, M. G. 2002. A World revision of the genus *Spodoptera* Guenée (Lepidoptera: Noctuidae). *Mem. Amer. Ent. Soc.* 43:1–202.
- RAZOWSKI, J. 1970. *Microlepidoptera Palaearctica dritter Band Cochylidae*. Verlag Georg Fromme & Co. Wien, Germany. 2 volumes. 528 pp.
- . 2008. *Tortricidae of the Palaearctic Region Volume 1*. Frantisek Slamka, Bratislava, Slovakia. 152 pp.
- . 2011. Diagnoses and remarks on genera of Tortricidae, 2: *Cochylini* (Lepidoptera: Tortricidae). *SHILAP Revta. Lepid.* 39:397–414.
- REGIER, J. C., J. W. BROWN, C. MITTER, J. BAIXERAS, S. CHO, M. P. CUMMINGS, & A. ZWICK. 2012. A molecular phylogeny for the leaf-roller moths (Lepidoptera: Tortricidae) and its implications for classification and life history evolution. *PLoS ONE* 7(4): e35574.
- USDA. 2012. United States Department of Agriculture Natural Resources Conservation Service Plants Profile. Available from: <http://plants.usda.gov/java/profile?symbol=CEPUP6> (Accessed 19 April 2012).

Submitted for publication on 11 June 2012; revised and accepted 13 September 2012.

HIDING BEHIND GAUDY LOOKS, A NEW CENTRAL AMERICAN SPECIES OF *PHAREAS* (HESPERIIDAE: EUDAMINAE)

NICK V. GRISHIN

Howard Hughes Medical Institute and Departments of Biophysics and Biochemistry, University of Texas Southwestern Medical Center, 5323 Harry Hines Blvd, Dallas, TX, USA 75390-9050; email: grishin@chop.swmed.edu

DANIEL H. JANZEN

Department of Biology, University of Pennsylvania, Philadelphia, PA 19104; email: djanzen@sas.upenn.edu

AND

WINNIE HALLWACHS

Department of Biology, University of Pennsylvania, Philadelphia, PA 19104; email: whallwac@sas.upenn.edu

ABSTRACT. A new species of *Phareas* is described from Costa Rica and Panama. *Phareas burnsi* Grishin, **sp. nov.** differs from its South American sister species, *Phareas coeleste* Westwood, 1852, by wing patterns, which were quantified and revealed two clusters with a profound hiatus between them; male secondary sexual characters on hindwing; female genitalia, mostly in the depth of distal notch on lamella postvaginalis; and mitochondrial DNA sequences showing about 4.5% divergence in the COI barcode. Unexpectedly large individual variation in the shape of the *Phareas* male genitalic valvae is illustrated.

Additional key words: Area de Conservación Guanacaste, biodiversity, caterpillars, cryptic species, skipper butterflies

A question of what constitutes a species and how to define boundaries between species is in the core of biological sciences. Insects, and butterflies in particular, are valuable model organisms to address such problems due to their easily observed diversity of shapes and patterns. Recent advances in molecular techniques enable researchers to add molecules into the mix of characters used in delineation of species. Comparisons of short, 654 nucleotide sequences of mitochondrial DNA encoding the C-terminal segment of cytochrome oxidase subunit 1 (COI), dubbed DNA barcodes, were able to flush out a number of unsuspected cryptic species in many groups of organisms, but in particular in the Eudaminae, a subfamily of skipper butterflies (Hesperiidae) (Janzen et al. 2011). When combined with traditionally used characters such as wing patterns and genitalia, DNA barcodes have been shown to be a useful taxonomic tool for detecting cryptic species, as well as for straight identification of them (Janzen et al. 2009).

Species differ in their ranges and variability. Some Eudaminae are known from both Americas and maintain constant phenotypes and barcodes throughout, e.g. *Urbanus dorantes dorantes* (Stoll 1790) has been recorded from USA to Argentina, and barcode sequences are identical in specimens from Arizona and Paraguay, as may be seen from the BOLD database (www.boldsystems.org, Ratnasingham & Hebert 2007).

Others have more limited distributions and elevated diversity in barcodes, e.g. *Astraptes fulgerator* (Walch 1775) group taxa, which all look very similar and may not even be consistently separable by any adult characters except their DNA barcodes; they are, however, readily separable by the combination of their caterpillar color patterns and food plants (Hebert et al. 2004). There are all imaginable cases in between these two extremes. Thus, Central and South American skippers that look similar may in fact be distinct biological species and should be carefully examined. Many neotropical skippers have been described from South American specimens, mostly from Suriname and Brazil (e.g. Cramer 1775–1780, Westwood 1852), thus leaving their Central American and North American sibling species without names.

Here, we analyze one of the most beautiful or gaudy skippers, depending on your viewpoint. The well-known neotropical *Phareas coeleste* Westwood, 1852 displays a white smiley face on its metallic blue forewing and an astonishingly different ventral hindwing that is orange bordered with black shining purple. Armed with a dozen Central American specimens reared from Area de Conservación Guanacaste (Costa Rica) and backed up by the analysis of wing shapes and patterns, genitalia and barcodes, we conclude that the Costa Rican and Panamanian populations are an undescribed species, distinct from South American *P. coeleste*.

MATERIALS AND METHODS

Adult specimens used in this study are in the following collections: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); Museum für Naturkunde, Berlin, Germany (ZMHB); and Natural History Museum, London, UK (BMNH). Standard entomological techniques were used for dissection (Robbins 1991), i.e. the adult abdomen was soaked for 24 hours in 10% KOH at room temperature, dissected and subsequently stored in a small glycerol vial pinned under the specimen. Genitalia and wing venation terminology follow Klots (1970) and Comstock (1918), respectively. Length measurements are in metric units and were made from photographs of specimens taken with a scale and magnified on a computer screen. Photographs of whole specimens were taken with Nikon D200 camera through a 105mm f/2.8G AF-S VR Micro-Nikkor lens; genitalia were photographed through a microscope. DNA sequences were downloaded from GenBank <http://www.genbank.gov/>, aligned by hand since insertions or deletions were absent, and analyzed using the Phylogeny.fr server at <http://www.phylogeny.fr/> with default parameters (Dereeper et al. 2008). The majority of these DNA barcodes have been reported in Janzen et al. (2011) and photos and collateral data of the reared Costa Rican specimens are available from the on-line database (Janzen & Hallwachs 2012) for the caterpillar inventory of Area de Conservación Guanacaste (ACG) and the BOLD database (Ratnasingham & Hebert 2007), to confirm identifications.

RESULTS AND DISCUSSION

Mass rearing and collecting of ACG moths, butterflies and their caterpillars (Janzen et al. 2011) has produced rich datasets of specimens and their DNA barcode sequences. Many of these species are very rare in collections made from net-caught or trap-caught free-flying adults. A number of common South American species were recorded from Costa Rica, or sizable Central American series of them were obtained for the first time. These allow meaningful comparison and analysis. Close inspection of large series of specimens and their DNA barcodes often leads to the discovery of cryptic sibling species hiding within series of named well-known, brightly colored and uniquely recognizable phenotypes (Janzen et al. 2009: 20–21).

Phareas coeleste described by indication (illustration only, text followed a couple of months later) by Westwood (1852) from a single female (Figs. 5, 21) is unmistakable in its appearance. In fact, it is so unique and distinctive, that no synonyms have been coined for

it by subsequent researchers, not considering misspellings, and it has been mostly residing in a monotypic genus (either *Phareas* Westwood, 1852, or its junior objective synonym *Grynopsis* Watson, 1893). *Phareas coeleste* is widespread in South America, and recorded from Colombia to Bolivia and Brazil (Evans 1952). A series of several dozen South American specimens is curated in the Natural History Museum, London (BMNH), but there are no specimens north of Colombia. Very few collections house *Phareas* sp. from Costa Rica and Panama. Not counting ACG reared material, there are four Panamanian specimens (1 male and 3 females, curated as *P. coeleste*) in USNM and one Costa Rican specimen in Ichiro Nakamura collection. These numbers are so few, and the looks of *Phareas* are so inimitable that it might be hard to imagine that there is a species different from *P. coeleste* in this genus.

Rearing caterpillars by the ACG inventory produced a series of this skipper, totaling 12 adult specimens, which were compared to Panamanian and South American specimens. Interesting wing shape and pattern similarities to Panamanian specimens, and differences from South American specimens prompted further investigation, which, being supported by morphometric analysis of wing patterns and comparison of DNA barcodes and genitalia, led to the conclusion that Central American specimens represented a species very similar to, but consistently distinct from *P. coeleste*. This undescribed species is named here.

***Phareas burnsi* Grishin, new species**

(Figs. 1–4, 9–12, 17–20, 25–28, 33 part, 34a–c, 35a–k, 36a–d,i–q, 37a–r, 38 part)

Description: *Female* (n=11, Figs. 1–4, 17–20) – holotype forewing length 28 mm (paratypes 27 to 29 mm); wings broad and rounded, forewing termen slightly convex, hindwing almost elliptical in shape, with a broad but shallow lobe in the posterior half from just before vein M_3 to tornus, termen scalloped at veins antieriad of the lobe; dorsal forewing metallic dark teal blue with purple gloss at the base and apex, six white partly opaque spots: discal cell spot quadrate, slightly smaller than Cu_1 – Cu_2 cell, almost pentagonal spot near the base of Cu_1 , elongated oval, medially constrained spot by the tornus in Cu_2 –2A cell, elongated rhomboid-shaped spot from the base of M_3 vein to the middle of Cu_1 vein, a triplet of smaller subapical spots in R_5 – M_1 , M_1 – M_2 and M_2 – M_3 cells, central spot offset distad, and a doublet of aligned small spots in R_3 – R_4 and R_4 – R_5 cells; dorsal hindwing monochrome metallic dark teal blue with purple sheen; ventral forewing darker shade of blue than dorsal side, brown-gray by the base, basal half of Cu_2 –2A cell and 2A cell, slightly overscaled with orange near the base towards costa, dorsal pattern of spots repeated; ventral hindwing orange with broad dark purple blue marginal band narrowing from costa to the middle of Cu_1 – Cu_2 cell, stair-step edges of the band along veins $Sc+R_1$, R_s , and M_1 within basal 1/3 of these cells, edge continuous posteriad, bleeding blue scales into orange areas, dark scales along and posteriad of vein 2A and marginally along veins Cu_1 and Cu_2 , at the base of humeral lobe dark area diffuse, not forming a defined spot; fringes dark brown above and below, forewing with some white scales between the veins above, and longer narrow

areas of white scales below, hindwing with three white areas between veins Sc+R₁, R₅, M₁ and M₂, a speckle of dark scales next to M₂ and some white scales below along the margin between veins within the lobe; head dark-brown above, ridges of pale scales near palpi and near collar, white spots above and behind the eyes, below white, narrowly dark brown posteriad of white cheeks, collar dark-brown, eyes brown, palpi with the third segment stout and spatulate, placed near the outer edge of the second segment, palpi brown with patches of pale scales above, white centrally below and on the sides; antennae dark brown, near the club pale orange laterally posteriad and ventrally half-ringed with pale orange along distal segment edges, nudum paler brown, 22–25 segments (n=5); thorax dark brown above, orange below; legs mostly orange with darker scales dorsally, more at the bases, hind tibiae with 1 pair of spurs; abdomen dark-brown above, cream to pale orange centrally below. *Female genitalia* (Fig. 36a–d, i–q): lamella postvaginalis broader than long, distal margin with a central deep triangular notch, almost straight, very slightly concave on both sides of the notch, lamella bulged anteriorly of the notch, the notch as deep as the anterioposterior bulge length; lamella antevaginalis very narrow, fully sclerotized, margin undulated; antrum sclerotized, matching the notch length in diameter; ductus with corpus bursae about 2.5 times sterigma width.

Male (n=6, Figs. 9–12, 25–28, 34a–c) – forewing lengths 26 to 28 mm, similar to female, nudum comprised of 22–24 segments (n=5), but with costal fold on forewing for about half of its length and a shallow fold along 2A vein for most of its length on hindwing, scales inside the fold brown, concolorous with the background, tufts of dark hair-like scales along the sides of 2A hindwing fold and inside it, and on sides of abdomen; white spot in Cu₁–2A more elongated basad, its basal end reaches the level of the middle of the Cu₁–Cu₂ white spot. Pecten on hindleg tarsus, concolorous with leg scales. *Male genitalia* (Fig. 35a–k): tegumen a bit longer than wide, rounded; uncus slightly shorter than tegumen, undivided, beak-like, terminally bifid in lateral view, with 2 small side lobules; gnathos widely separated from uncus, prominently sculptured; saccus triangular in ventral view, as long as wide; valva without processes and projections, cucullus bending inwards dorsad and expanding into a broad tooth directed anteriodorsad and a lobe directed posteriad, the lobe mostly short, equal to the tooth in length, but longer in some specimens, cucullus abnormally underdeveloped in one specimen (Fig. 35k, voucher code 05-SRNP-30469); aedeagus slightly longer than tegumen together with uncus, but shorter than valva, with a row of medium-sized (length about equal to aedeagus diameter) cornuti.

Barcode sequence of the holotype: GenBank accession GU149831, 658 bp:

```
AACTTTATATTTTATTTTGGAAATTTGAGCTGGAATATTAGG
TACTTCATTAAGATTACTAATTCGAACAGAAATGGGAACCCCA
GGATCTTTAATTTGGAGATGACCAAAATTTATAATCAATTTGTAAC
AGCTCATGCTTTTATTATTATTTTATAGTTATACCTATTATATA
ATTGGAGGATTTGGAATTTGACTTGTTCCCTTAATATTAGGTC
CCCCGATATAGCCTTCCCACGAATAAACAACATAAGTTTTTG
ATTACTACCCCATCATTAACCTTTATTAATTTCTAGAAGATTGT
AGAAATGGTGACAGGAATCGGATGAACAGTATATCCCCCTTTA
TCAGCAAACATTGCACACCAAGGATCATCTGTAGATTTAGCAA
TTTTCTCTTTACATTTAGCAGGAATTTTCATCTATTTTAGGAGCT
ATTAATTTTATTAACAATTTATTAATATACGAATTAGAAATTTAT
CCTTTGATCAAAATCTTTATTTGTTTGAGCAGTAGGAATTACA
GCATTATTACTTCTTCTATCTCTCCAGTTTTAGCTGGAGCTAT
TACTATATTACTTACTGATCGAAATTTAAATACATCATTCTTTGA
TCCAGCAGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
```

Types: *Holotype* female has the following labels: white printed & hand-printed - / Voucher: D.H.Janzen & W.Hallwachs / DB: <http://janzen.sas.upenn.edu> / Area de Conservación Guanacaste, / COSTA RICA. / 05-SRNP-30644 /; yellow printed - / LEGS AWAY / FOR DNA /; red printed - /HOLOTYPE ♀ / *Phareas burnsi* / Grishin /. *Holotype* data: Costa Rica: Guanacaste Province, Area de Conservación Guanacaste, Sector Pitilla, Pasmompa, 11.01926° - 85.40997°, 440m, collected on 14-II-2005 as first instar feeding on buds and young leaves of a sapling of the rain forest tree *Ormosia coccinea* (Fabaceae) by the parataxonomist Manuel Ríos, caterpillar

prepupal date: 16-III-2005, adult eclosion date: 07-IV-2005. Paratypes: 6♂♂ and 10♀♀. **Costa Rica:** 1♀ Limón Prov., Tortuguero, 2 km N of the village, 10-V-2005; Guanacaste Prov., Area de Conservación Guanacaste, Sector Pitilla: 1♂1♀ Pasmompa, 11.01926° -85.40997°, 440m, reared in 1999, food plant *O. coccinea*, voucher codes 99-CALI-790 and 99-CALI-787, respectively; 1♂ Pasmompa, 11.01926° -85.40997°, 440m, collected on 05-II-2005 as antepenultimate instar, adult eclosed on 27-III-2005, food plant *O. coccinea*, voucher code 05-SRNP-30469; 1♂ Pasmompa, 11.01926° -85.40997°, 440m, collected on 05-II-2005 as instar before antepenultimate, adult eclosed on 20-III-2005, food plant *O. coccinea*, voucher code 05-SRNP-30577; 2♂♂ Estacion Pitilla, 10.98931° -85.42581°, 675m, reared in 1999, voucher codes 02-SRNP-35231 and 02-SRNP-35232; 1♀ Pasmompa, 11.01926° -85.40997°, 440m, collected on 14-II-2005 as penultimate instar, adult eclosed on 17-III-2005, food plant *O. coccinea*, voucher code 05-SRNP-30643; 1♀ Pasmompa, 11.01926° -85.40997°, 440m, collected on 05-II-2005 as last instar, adult eclosed on 10-III-2005, food plant *O. coccinea*, voucher code 05-SRNP-30576; 1♀ Pasmompa, 11.01926° -85.40997°, 440m, collected on 14-II-2005 as first instar, adult eclosed on 31-III-2005, food plant *O. coccinea*, voucher code 05-SRNP-30642; 1♀ Sendero Evangelista, 10.98680° -85.42083°, 660m, collected on 27-III-2004 as last instar, adult eclosed on 24-IV-2004, food plant *O. panamensis*, voucher code 04-SRNP-31520; 1♀ Sendero Cuestona, 10.99455° -85.41461°, 640m, collected on 09-XI-2004 as last instar, adult eclosed on 12-XII-2004, food plant *O. coccinea*, voucher code 04-SRNP-56226. **Panama:** 1♂ Canal Zone, Summit, 2-V-1964, genitalia NVG120207-05; 1♀ Canal Zone, Gamboa, X-1968; 1♀ Canal Zone, Gamboa, 9° 07'N 79° 41'W, 28-X-1978, leg. G. B. Small, genitalia NVG120207-06; 1♀ Darién Province, Cerro Pirre, ca. 0m, 15-IV-1976, leg. G. B. Small. Additional data for ACG specimens (voucher codes with -SRNP-) are at <http://janzen.sas.upenn.edu/caterpillars/database.lasso> (Janzen & Hallwachs 2012).

Deposition of types: Holotype is in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Two paratypes are deposited in the Natural History Museum, London, UK (BMNH) (02-SRNP-35231 & 05-SRNP-30642), two paratypes are deposited in the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL (MGCL) (02-SRNP-35232 & 04-SRNP-56226), one paratype from Costa Rica: Limón Province is in the Ichiro Nakamura collection, and all other paratypes remain in USNM.

Type locality: COSTA RICA: Guanacaste Province, Area de Conservación Guanacaste, Sector Pitilla, Pasmompa, 11.01926° -85.40997°, 440m.

Etymology: *Phareas burnsi* is named in honor of Dr. John M. Burns, Curator of Lepidoptera (emeritus) Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, who has identified and curated over 17,000 reared and DNA barcoded ACG inventory specimens of Hesperidae in which this species and these specimens are embedded. John's extraordinary skill of combining science with poetry to craft a flowing prose of entertaining taxonomic texts ("entertaining" and "taxonomic" could be sympatric!) remains unmatched and can hardly, if ever, be repeated. His meticulous attention to details, keen eye for the differences and hard, diligent work are behind a myriad of exciting discoveries about skippers, their genitalia and evolution, many of which are yet to come. The name is a masculine noun in the genitive case.

Distribution and phenology: Currently, the species is known from Costa Rica and Panama. In Costa Rica, it has been collected in May and reared to eclose in March, April and December (Janzen & Hallwachs 2012). In Panama, collection dates are from April, May and October.

Diagnosis: The new species belongs to *Phareas* as defined by Evans (1952) because: (a) it possesses palpi with the third segment being stout and spatulate and positioned near the outer edge of the second segment, not in the center of it; (b) antennae are bent at the



FIGS. 1-32. Adults. 1-16. dorsal views and 17-32. ventral views of the same specimens. 1-4, 17-20. *P. burnsi* ♀♀, 9-12, 25-28. *P. burnsi* ♂♂; 5-8, 21-24. *P. coeleste* ♀♀, 13-16, 29-32. *P. coeleste* ♂♂; 1, 17 & 5, 21. are holotypes of *P. burnsi* (voucher code 05-SRNP-30644, data in text) & *P. coeleste* (Brazil: Pará, Hewitson coll., specimen number BMNH(E) #808437), respectively; 2-4, 18-20, 9-12, 25-28. paratypes. All specimens in USNM collection, except as indicated in brackets, and except *P. coeleste* holotype (5, 21.) which is in BMNH; copyright of its photos: Trustees of the Natural History Museum, London; used with permission. Voucher codes for Costa Rica, ACG paratypes: 2, 18. 04-SRNP-56226 [MGCL]; 3, 19. 05-SRNP-30576; 9, 25. 05-SRNP-30577; 10, 26. 02-SRNP-35232 [MGCL]; 11, 27. 05-SRNP-30469; data in text. Data for others: 4, 20. Panama: Canal Zone, Gamboa, X-1968; 6, 22. Guyana: Acarai Mountains, Sipu River, 1° 21.3'N 58° 57.4'W 2000-2500' (4-10)-XI-2000, leg. S. Fratello et al. USNM ENT 00179859; 7, 23. Peru: near Iquitos, 23-I-1932;



FIGS. 1-32 (continued from previous page). 8, 24. Ecuador: Sucumbíos, ridge between Río Ushaue and Río Puchuchoa, km. 4 Lumbaquí - La Bonita rd., 0° 05'N 77° 17'W, 850m, [12-14]-III-2004, leg. I. Aldas; **12, 28.** Panama: Canal Zone, Summit, 2-V-1964, genitalia NVG120207-05 (genitalia Fig. 35g); **13, 29.** Brazil: Pará, Belem, IV-1960, leg. J. Kesselring, genitalia NVG120207-18; **14, 30.** French Guiana: St. Jean, Maroni, IV-1904, collection Wm. Schaus (genitalia Figs 35t); **15, 31.** Venezuela: T. F. Amaz. Cerro de la Neblina Basecamp, 0° 50'N 66° 10'W, 140m, 26-I-1985, at black light on bank of Río Baria, leg. P. J. & P. M. Spangler, R. A. Faitoute & W. E. Steiner; **16, 32.** Colombia: Caquetá Department, Florencia, 1300', 22-I-1971, leg. S. S. Nicolay (genitalia Fig. 35q). F to the right of the tornal lobe indicates mirror image (left-right inverted). Labels for primary type specimens (**1, 5, 17, 21**) are shown near each specimen. Species names for each row, general locations and sexes are shown. All images are to scale except labels of *P. burnsi* holotype, which are 0.75 times the scale (reduced).

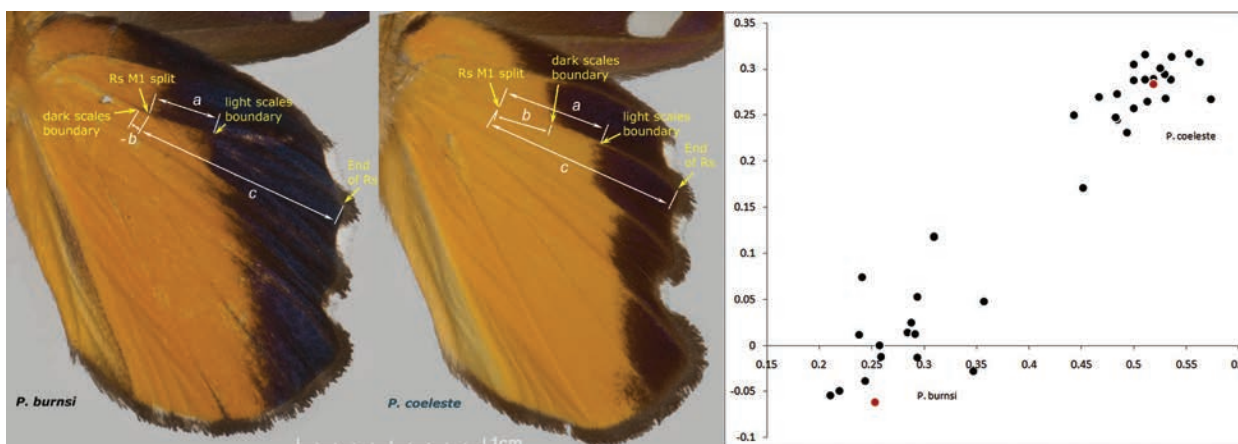


FIG. 33. Measurements used to distinguish *P. burnsi* and *P. coeleste*. Hindwings ventrals of *P. burnsi* holotype (left) and *P. coeleste* holotype (right) are shown. Distances measured are: **a** – between the split of Rs and M_1 veins and the boundary of light scales in Rs – M_1 cell along Rs vein; **b** – between the split of Rs and M_1 veins and the boundary of dark scales in Sc+ R_1 – Rs cell along Rs vein; **c** – between the split of Rs and M_1 veins and the distal end of Rs vein. Negative values of **b** correspond to dark scales intruding basally of the Rs and M_1 split. **Morphometric differences** between *P. burnsi* (lower left cluster of points) and *P. coeleste* (upper right cluster of points) are shown on the graph. Horizontal axis is the ratio **a/c** of the distance between the split of Rs and M_1 veins and the boundary of light scales in Rs – M_1 cell along Rs vein (**a**) to the distance between the split of Rs and M_1 veins and the distal end of Rs vein (**c**) on hindwing ventral side. Vertical axis is the ratio **b/c** of the distance between the split of Rs and M_1 veins and the boundary of dark scales in Sc+ R_1 – Rs cell along Rs vein (**b**) to the distance between the split of Rs and M_1 veins and the distal end of Rs vein (**c**) on hindwing ventral side. Points corresponding to holotypes of both taxa are shown in red.

beginning of the nudum with 22–25 segments, not after the nudum; (c) distance between forewing veins Cu_1 and M_3 at the origin is about twice the distance between veins M_3 and M_2 , not equal to it; (d) hindwing lobed from vein M_3 to the tornus; (e) hind tibiae with 1 pair of spurs, not 2; (f) males with a fold along hindwing vein 2A surrounded by tufts of dark long hair-like scales and short tufts on both sides of abdomen. In all these and other characters the new species is very close to South American *P. coeleste* and is reasonably considered to be its Central American counterpart; however, there is no way to know, with the data in hand, which is the ancestor of which, or neither. The following characters consistently set *P. burnsi* n. sp. apart: 1) the marginal dark band on the ventral hindwing is broader, as quantified on Figs. 33, and is more diffuse along the inner edge with dark scales bleeding into the orange area; while the stair-step scalloping breaks at the veins of *P. coeleste* are noticeable in cells near the costa, the inner edge of the dark band is straighter, not wavy towards tornus (Figs. 17–32); 2) the hindwing is rounder, less elongated and the tornal lobe, while similarly broad, is shallower and less developed (Figs. 1–32); 3) *P. coeleste* has a prominent patch of dark scales, some of which are hair-like, at the base near and on the humeral lobe on the ventral hindwing, but in *P. burnsi* it is reduced to a diffuse patch of dark scales and does not stand out (Figs. 17–32); 4) the fold along the vein 2A on dorsal hindwing in males is less developed in *P. burnsi* than in *P. coeleste*, covered with brownish

scales concolorous with the background and anal fold scales, but not prominently cream-colored as in *P. coeleste* (Fig. 34, however, when the fold is closed, its pale, cream colors may not be clearly visible in *P. coeleste*, e.g. in Fig 13, fold is open on the left wing and is closed on the right wing, fold is closed in Fig. 14, fully open in Fig. 15, and partly open (basad) in Fig. 16; additionally, a tuft of darker hair-like scales inside the fold may obscure its pale lining), tufts of hair-like scales around 2A hindwing vein seem to be darker colored in *P. burnsi* than in *P. coeleste* (Fig. 34); 5) the central notch in the lamella postvaginalis is deeper, about equal to the anteriorodorsal length of the bulge anterior of the notch, but is only about half of the bulge length in *P. coeleste* (Fig. 36); 6) the DNA barcode sequence differs from *P. coeleste* by about 4.5% (Fig. 38). Interestingly, morphological and wing pattern characters 1–3 are similarly expressed in both sexes, making unambiguous association of sexes possible in the absence of barcode data, and female genitalia offer a more consistent separation between the two species than do the male genitalia, which are very variable in the shape of cucullus (Fig. 35).

Immatures and food plants: All ACG caterpillars of *P. burnsi* (Fig. 37a–m) have usually been found feeding on buds and very young, flimsy and expanding leaves in the crowns of 1–3 m tall saplings of *Ormosia coccinea* (Aubl.) Jacks. (Fabaceae), with the single exception being a caterpillar feeding on the very young foliage of *O. panamensis* Benth. The habitat of these

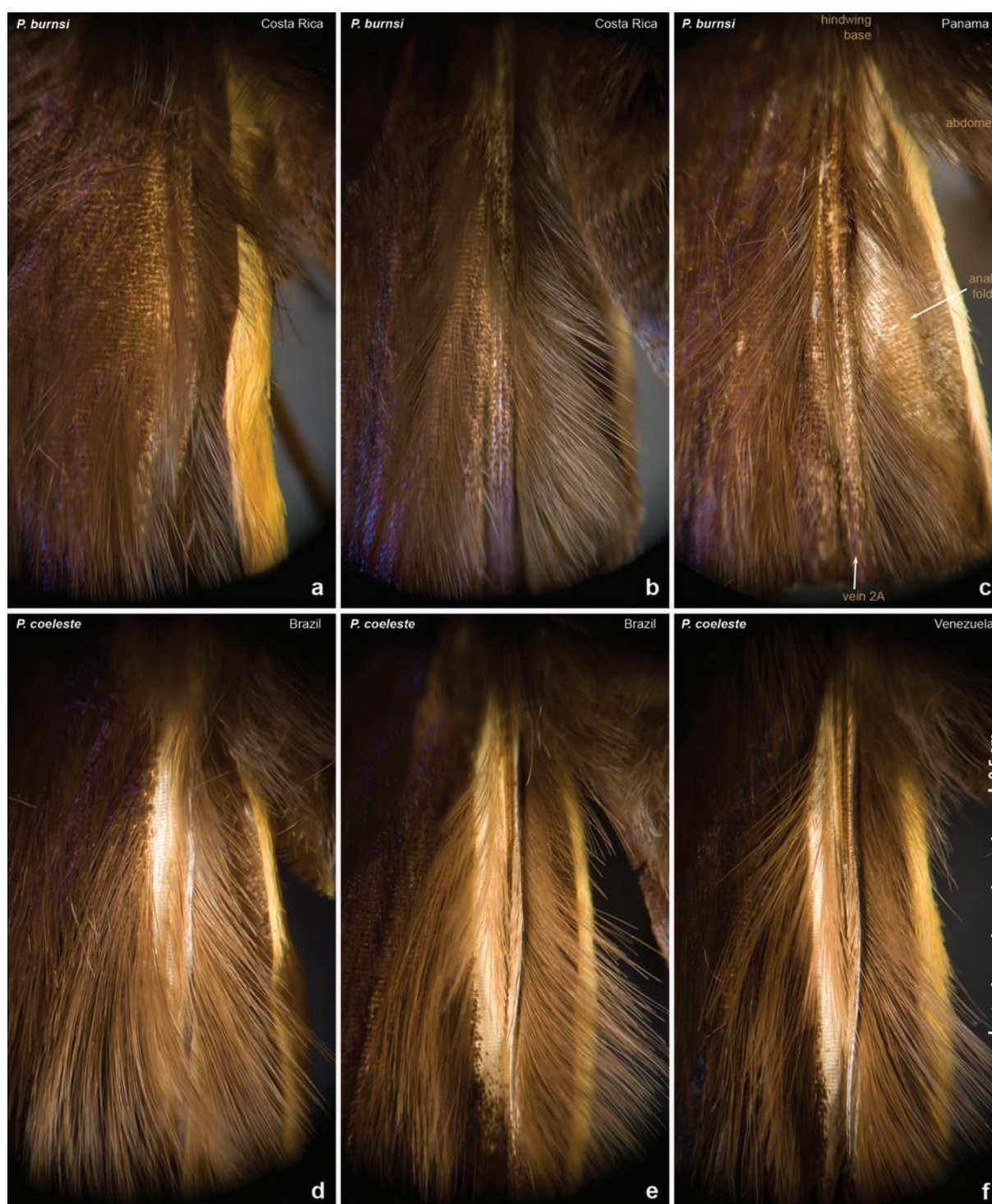


FIG. 34. Dorsal view of left hindwing area around vein 2A in males. a–c. *P. burnsi* paratypes, **d–f.** *P. coeleste*. Base of hindwing is above, tornus below (but is out of view). Part of abdomen base is visible in the right upper corner. Yellow area in **a.** by the anal margin is a part of ventral surface of anal fold that it bent over. All specimens in USNM collection, except as indicated in brackets. **a.**, **b.** Costa Rica: ACG, voucher codes 02-SRNP-35231 [BMNH] (genitalia Figs. 35i) and 02-SRNP-35232 [MGCL] (wings Figs. 10, 26), respectively; **c.** Panama: Canal Zone, Summit, 2-V-1964, genitalia NVG120207-05 (wings Figs. 12, 28, genitalia Fig. 35g); **d.** Brazil: Pará, Belem, V-1962; **e.** Brazil: Rondônia, 62km S Ariquemes, Fazenda Rancho Grande, 10° 32'S 62° 48'W, 165m, 29-IX - 10-XI-1991, leg. B. P. Harris (genitalia Fig. 35v); **f.** Venezuela: T. F. Amaz. Cerro de la Neblina Basecamp, 0° 50'N 66° 10'W, 140m, 26-I-1985, at black light on bank of Rio Baria, leg. P. J. & P. M. Spangler, R. A. Faitoute & W. E. Steiner (wings Figs. 15, 31). All images are to scale.

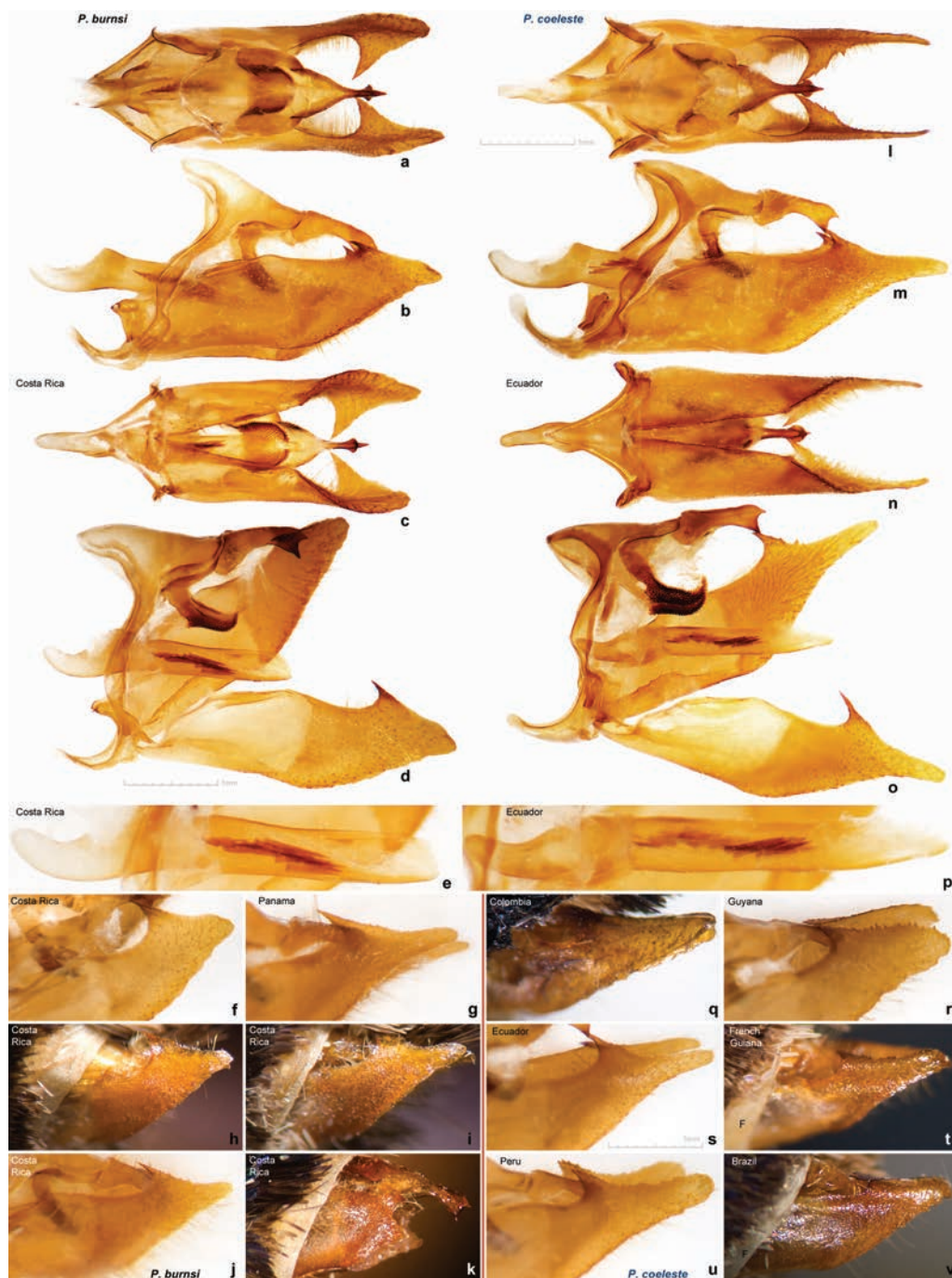


FIG. 35. Male genitalia. a–k. *P. burnsi*; l–v. *P. coeleste*. a–d, l–o. complete genital capsule; e, p. enlarged right lateral view of penis; f–k, q–v. lateral view of distal parts, mostly valvae, h, i, k, q, t, v. photographed in situ. Views: a, l. dorsal; b, d, m, o. right lateral, in d, o. valvae are pushed apart; c, n. ventral. All specimens in USNM collection, except as indicated in brackets. Specimen data: a–f. Costa Rica: ACG, voucher code 05-SRNP-30577, genitalia NVG120513-05; g. Panama: Canal Zone, Summit, 2-V-1964, genitalia NVG120207-05 (specimen Figs. 12, 28); h. Costa Rica: ACG, voucher code 02-SRNP-35323; i. Costa Rica: ACG, voucher code 02-SRNP-35231 [BMNH]; j. Costa Rica: ACG, voucher code 99-CALI-790, genitalia NVG120207-07; k. Costa Rica: ACG, voucher code 05-SRNP-30469; l–p, s. Ecuador: Esmeraldas, El Durango, km. 40, Lita-San Lorenzo Rd., 1° 02'45"N 78° 38'06"W, 300m, {25,27}-VIII-2002, J.P.W. Hall & M.A. Solis, genitalia NVG120513-04; q. Colombia: Caquetá Department, Florencia, 1300', 22-I-1971, leg. S. S. Nicolay (specimen Figs. 16, 32.); r. Guyana: Mazaruni-Potaro, Kaieteur Falls, 5° 14'N 59° 33'W, 200–450m, 26-XII-1989 - 1-I-1990, leg. S. Fratello, genitalia NVG120207-08; t. French Guiana: St. Jean, Maroni, IV-1904, collection Wm. Schaus (specimen Figs. 14, 30); u. Peru: Tingo Maria, VIII-1979, genitalia NVG120513-03; v. Brazil: Rondônia, 62km S Ariquemes, Fazenda Rancho Grande, 10° 32'S 62° 48'W, 165m, 29-IX - 10-XI-1991, leg. B. P. Harris. F indicates mirror image (left–right inverted). All images are to scale except e. and p., which are 1.7 and 1.5 times the scale (enlarged) respectively.

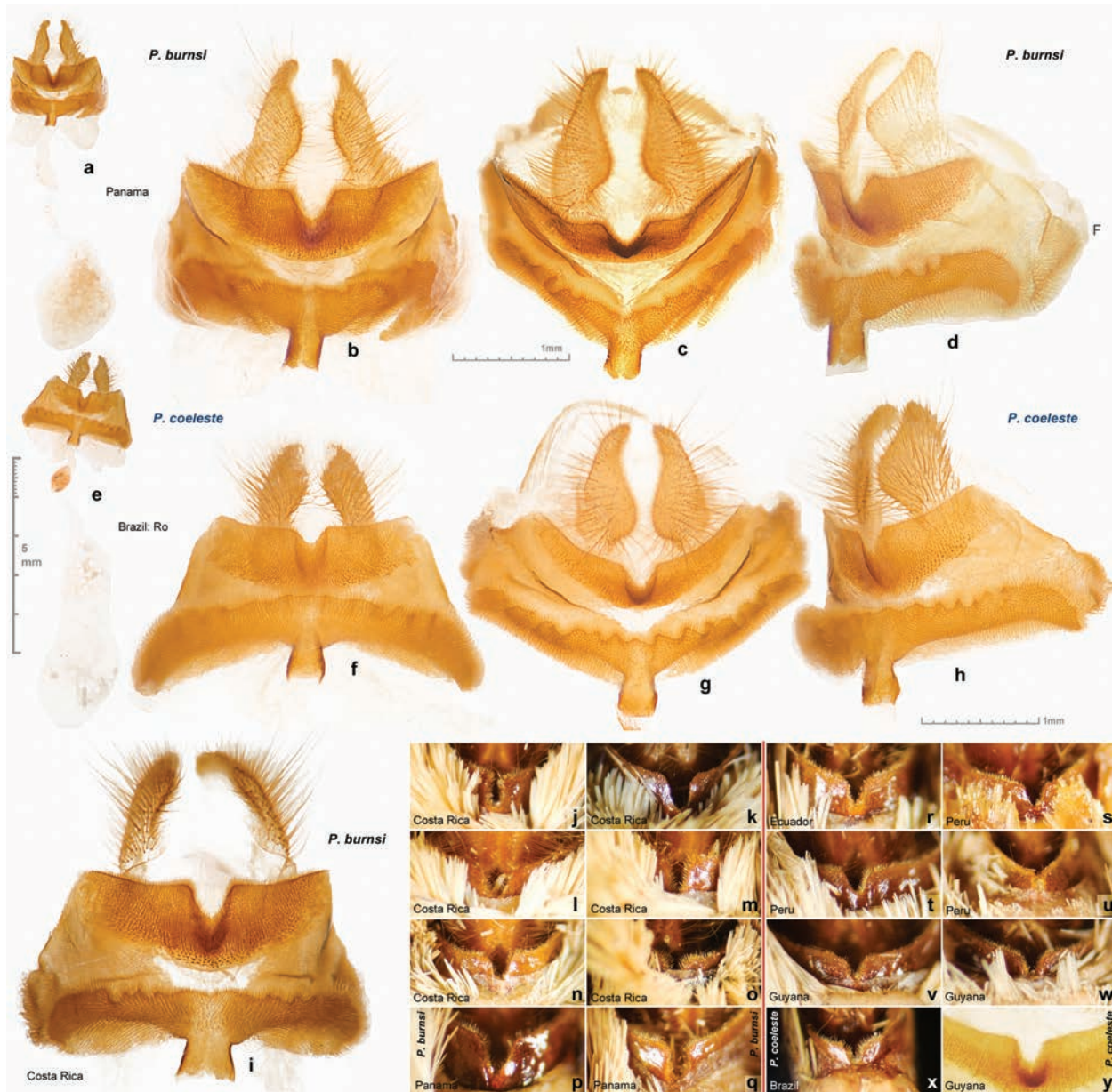


FIG. 36. Female genitalia. a–d, i–q. *P. burnsi*; e–h, r–y. *P. coeleste*. a, e. complete genitalia, b–d, f–i. enlarged sterigma and ovipositor lobes, j–y. median part of lamella postvaginalis, j–x, y. photographed in situ. All specimens in USNM collection, except as indicated in brackets. All images are to scale, except a. and e., which are smaller and the scale for them is indicated on the left. a–d. paratype, Panama: Canal Zone, Gamboa, 9° 07'N 79° 41'W, 28-X-1978, leg. G. B. Small, genitalia NVG120207-06; e–h. Brazil: Rondônia, vic. Caucalandia, 10° 32'S 62° 48'W, 160–350m 22-X-1991, leg. J. Kemner, genitalia NVG120207-19; i, k–q. paratypes, j. holotype, i–o. Costa Rica, ACG, voucher codes: i. 05-SRNP-30642, genitalia NVG120513-01 [BMNH]; j. 05-SRNP-30644; k. 05-SRNP-30576; l. 04-SRNP-56226 [MGCL]; m. 05-SRNP-30643; n. 04-SRNP-31520; o. 99-CALI-787; data in text. Data for others: p. Panama: Darién Province, Cerro Pirre, ca. 0m, 15-IV-1976, leg. G. B. Small; q. Panama: Canal Zone, Gamboa, X-1968; r. Ecuador: Sucumbíos, ridge between Río Ushaue and Río Puchuchoa, km. 4 Lumbaquí - La Bonita rd., 0° 05'N 77° 17'W, 850m, [12-14]-III-2004, leg. I. Aldas; s. Peru: Loreto Province, Río Amazonas, 200m, Explorama Inn, 25mi E Iquitos; 9-12 & 17-21-IX-1990, leg. R. Leuschner; t. Peru: Huanaco Department, Upper Huallaga Valley, X-1990; u. Peru: near Iquitos, 23-I-1932; v. Guyana: Acarai Mountains, Sipu River, 1° 21.3'N 58° 57.4'W 2000–2500' [4-10]-XI-2000, leg. S. Fratello et al. USNM ENT 00179859; w. Guyana: Mazaruni-Potaro, Kaieteur Falls, 5° 14'N 59° 33'W, 200–450m, 18-XII - 25-XII-1989, leg. S. Fratello; x. Brazil, J. C. Hopfinger Collection 1962; y. Guyana, Omai, genitalia NVG120513-02. F indicates mirror image (left–right inverted).



FIG. 37. *Phareas* immatures. **a–r** *P. burnsi* - Costa Rica: ACG; **s, t** *P. coeleste* - French Guiana: Galion. **a–m, s** caterpillars: **a–l, s** last instar, **j–m** penultimate instar. **o–r, t** pupae. Voucher codes for *P. burnsi* immatures: **a–c** 95-SRNP-576; **d–i** 01-SRNP-9030; **j–n** 04-SRNP-31795; **o** 95-SRNP-577; **p–r** 04-SRNP-31800. The lengths of caterpillars 01-SRNP-9030, 04-SRNP-31795, and *P. coeleste* are 48, 50, and 42mm, respectively. All *P. burnsi* immatures shown did not produce adults and were either parasitized or died of disease. For instance, in addition to white spots, white *Winthemia* Wood28 (Tachinidae) eggs are glued to the cuticle of the last two segments of the caterpillar in **e** and **i**; the diseased and dead pupa in **o** is dark with little pattern, the other pupal images are normal in coloration, except that one wing case of the pupa shown on **p** is darker than the rest of the pupa, possibly due to disease. *P. coeleste* immatures **s** and **t** photographed on 29-IV-1991 and 9-V-1991 respectively, eclosed on 22-V-1991; F indicates mirror image (left-right inverted). Photographs of *P. coeleste* are by Christian Brévignon.

species of *Ormosia* Jacks. is natural and anthropogenic rain forest margins at intermediate elevations (400–700 m). This degree of specialization needs to be considered in an ecosystem containing at least 4,000 species of plants, more than 2,000 species of which have been surveyed for caterpillars feeding on them. Considering that more than 350 species of Hesperidae caterpillars (ca. 102,000 specimens) have been found by the rain forest portion of the ACG caterpillar inventory, we feel comfortable viewing *P. burnsi* as highly specialized to feed on very young *Ormosia* foliage. Whether or not the caterpillars also occur in the new foliage of the crowns of 20–40 m tall adult *Ormosia* remains to be seen.

The newly hatched caterpillar takes about 30 days to develop into a prepupa, which is at the fast end of the Hesperidae development process for such a large skipper caterpillar. Other skipper species of similar high body weight often use as much as twice as long for caterpillar development; however, they generally feed on mature foliage as well as very young foliage, while *P. burnsi* unambiguously prefers very young foliage (whose chemical defenses may be poorly developed, and nutrient content high). It folds a leaf over itself and lightly silks the two portions together. When the nest is ripped open, as a bird might do, instead of retreating or vacating the nest, it turns its head toward the opening and thrusts it out at the intruder, rendering its “face” (Fig. 37c,f,h) part of a very large array of ACG caterpillar species with face-like color patterns on wings, and on caterpillar and pupal heads. The selective force generating these false eyes could be that of small birds, and perhaps some mammals, in that it fits a general pattern that suggests a snake or other predator from which the caterpillar predator does best if it flees (Janzen et al. 2010). Pupae (Fig. 37o–r) are cream-colored with black stripes and spots, and possess an unusually expanded and rounded compartment on the head anterioventrad and between glazed eye-pieces (Mosher 1916).

Interestingly, both caterpillar and pupa of *P. coeleste* (Fig. 37s–t) show apparent differences from *P. burnsi* (Fig. 37a–r), however it remains unclear if these differences hold in a series larger than one individual. A single caterpillar of *P. coeleste* from French Guiana, found as an ultimate instar, was reared by Christian Brévignon (unpublished). Prominent white spots of *P. burnsi* caterpillar are either missing or residual in *P. coeleste* caterpillar. However, the yellow “headlights” on the head are similar, and behavior of disturbed caterpillar pointing the “face” at intruder is similar as well (C. Brévignon, pers. comm.). The shape and pattern of protruding compartment on the head seem to differ in pupae (Fig. 37r,t), being more rounded and

with the dark lateral stripe being further from its distal end in *P. coeleste*.

DISCUSSION

The monotypic genus *Phareas* was proposed by Westwood (1852) for *P. coeleste*, newly described from a single female. This genus (or its synonym *Grynopsis*) has been used for *P. coeleste* by most authors (Mielke 2005) who stress the uniqueness of this skipper. *Phareas coeleste* is set far apart from many other skippers not only by the metallic-blue white spotted, and orange with black and white dorsal and ventral wing patterns and peculiar hindwing shape with a very wide tornal lobe, but also by male secondary sexual characters on the hindwing and abdomen, consisting of a fold along the vein 2A surrounded by tufts of long scales and smaller tufts on the abdomen. This uniqueness masks potential existence of other species with similar appearance. It is hard to suspect diversity when the prototype South American species is very different from all other skippers.

The paucity of specimens in collections is another obstacle to assessing intraspecific variation. *Phareas coeleste* is widely distributed in South America. Large series of it exist in collections worldwide, and it is commonly observed in the field in South America by butterfly watchers and photographers. In contrast, *P. burnsi* is known only from Costa Rica and Panama, is exceedingly rare in collections (e.g. there were none in the Natural History Museum, London) and we have never seen an adult in the wild in ACG. Without the special barcoding, ecological and morphological attention that the ACG specimens receive, it is not likely that this species would have been noticed, at least not any time soon. A small series of four specimens from Panama in the USNM collection, which look like *P. coeleste* and were curated among it, were apparently insufficient to notice phenotypic differences. Only with a series of a dozen ACG specimens did meaningful analysis of variation become possible, and consistent differences in the width of the ventral hindwing black band were detected. DNA barcoding did not reveal *P. burnsi* because the ACG inventory had no barcoded South American specimens with which to compare it. To assess statistical significance of these apparent differences, they were quantified (Fig. 33) in all 16 *P. burnsi* specimens and a similar size sample of *P. coeleste* specimens, together with the holotype, from all parts the range, including Colombia, Ecuador, Peru, Guyana, British Guiana and Brazil. The analysis resulted in two well-separated clusters of points with a definitive hiatus between them. Costa Rican and Panamanian specimens formed one cluster, and all South American specimens,

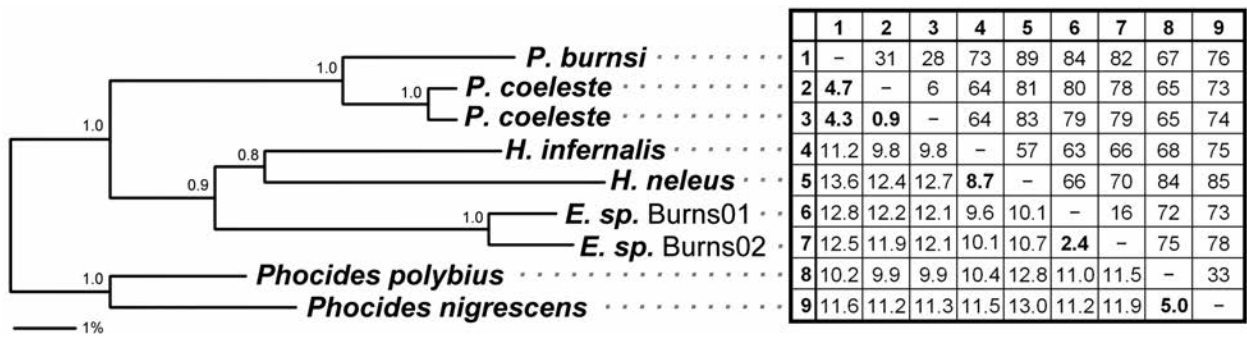


FIG. 38. DNA-derived data. Distance tree obtained with BioNJ method (www.phylogeny.fr; Dereeper et al. 2008) is shown on the left and distance matrix is shown on the right. Bootstrap support values are shown by each node in the tree. The scale bar corresponds to about 1% difference. All specimens are from Costa Rica, Area de Conservación Guanacaste, unless stated otherwise. ACG voucher codes where available (with -SRNP-, Janzen & Hallwachs 2012) and GenBank accessions (two letters followed by 6 digits, <http://genbank.gov>) for each of the nine sequences are: **1.** *Phareas burnsi* holotype – 05-SRNP-30644, GU149831; **2.** *P. coeleste* – Peru: San Martin, Juanjui, -7.1° -76.44°, 280m, 25-X-2003, F. Koenig, JF851944; **3.** *P. coeleste* – French Guiana: Nouragues Research Station, 4.09831° -52.6804°, 300m, 25-I-2010, leg. C. Lopez-Vaamonde, HQ989371; **4.** *Hyalothyrus infernalis* (Möschler, 1877) – French Guiana: Nouragues Research Station, 4.09831° -52.6804°, 300m, 16-I-2010, leg. C. Lopez-Vaamonde, HQ989294; **5.** *H. neleus* (Linnaeus, 1758) – 00-SRNP-2796, JF752878; **6.** *Entheus* Burns01 – 05-SRNP-30012, DQ292436; **7.** *Entheus* Burns02 – 05-SRNP-31934, GU150401; **8.** *Phocides polybius* lilea (Reakirt, [1867]) – 05-SRNP-45012, GU150688; **9.** *Phocides nigrescens* E. Bell, 1938 – 04-SRNP-23796, GU161792. The two *Entheus* species are currently undescribed and bear the interim names of “Burns01” and “Burns02” as in Janzen et al. (2011). Percent difference and the number of different nucleotides are shown below and above the diagonal in the distance matrix, respectively. For congeners, percent difference values are shown in bold font.

including a specimen from Colombia, formed another cluster. Assuming Gaussian distribution of points in each morphometric cluster from Fig. 33, out of ten million *Phareas* specimens, only one is expected to cross from one cluster to the next and thus be identified incorrectly (P-value $9.76 \cdot 10^{-8}$). This statistic gives high confidence in reliability of wing pattern characters in telling *P. burnsi* and *P. coeleste* apart, though once it was realized that there are two species, DNA barcodes reliably distinguish them as well (see below).

Analysis of genitalia revealed interesting differences among females and unexpectedly large variability in male genitalia. As stated in the diagnosis, the depth of the notch in lamella postvaginalis seems to distinguish the two species (Fig. 36). This difference might be noticeable *in situ* upon brushing the scales off the end of the abdomen. While it is not possible to relate the depth of the notch to the length of the bulge anterior to the notch without full dissection, because the bulge is covered by the last sternite (Fig. 36), a simple measurement of the notch depth is usually sufficient. Despite differences in sizes of these specimens, for 10 females of *P. burnsi* and 9 females of *P. coeleste*, the notch was less than 0.24mm deep in *P. coeleste* (Mean: 0.196mm, SD: 0.025mm), and more than 0.24mm deep in *P. burnsi* (Mean: 0.287mm, SD: 0.036mm). While some measurements in pairs of species are close to each other and thus using them might not offer reliable separation for a large *P. coeleste* (with possibly larger notch) and a smaller *P. burnsi* (with expectedly smaller

notch), they are indicative of potential female genitalic differences between the two species. Due to these differences in females, variability of male genitalia, definitive sex associations of reared *P. burnsi* specimens backed up not only by phenotypic characters (1 to 3 in the diagnosis above), but also by identical barcodes, female specimen was chosen as the holotype of *P. burnsi*. While mostly male specimens are selected as holotypes nowadays, we decided that a choice of a female is particularly fitting in this case to facilitate comparisons with *P. coeleste*, largely because *P. coeleste* holotype (by monotypy) is also a female.

Male genitalia, on the contrary, revealed a wide array of phenotypes. When a single typical individual is taken to illustrate genitalia (Fig. 35a–e, l–o) the most noticeable difference is in length and shape of the distal portion of valvae (cucullus). The distal part of the cucullus is shorter and broader in the *P. burnsi* specimen (Fig. 35a–e), while being longer and narrower in the *P. coeleste* specimen (Fig. 35l–o). Although this general trend seems to hold up in many specimens (Fig. 35), there are interesting exceptions. Even for reared ACG specimens, variation in cucullus is appreciable (e.g. Fig. 35hi), and one specimen had highly aberrant genitalia (Fig. 35k) with an underdeveloped cucullus reduced to a doublet of small terminal projections. All ACG specimens possess 100% identical barcodes and we have no cause to think that they are anything but a single species. Interestingly, one *P. coeleste* specimen from Guyana had an unexpectedly broad cucullus (Fig.

35r), and one *P. burnsi* specimen from Panama had a longer and narrower cucullus (Fig. 35g). We suggest that these levels of differences in cucullus shape are intraspecific individual variation. We hypothesize that the distal end of the cucullus is not fully formed in a pupa, but expands upon eclosion. Conversely, it is also conceivable that male genitalic variation may reflect additional cryptic species to be discovered, but many more specimens, dissections and DNA sequences would be required to support such a view. Careful examination of other characters in genitalia failed to reveal differences beyond those expected from individual variation. It is interesting that in some HesperIIDae, like *Phareas*, female genitalia might show more taxonomically useful differences than male genitalia.

DNA barcodes are available for nine ACG *P. burnsi* specimens and they are all identical in sequence. DNA barcodes are available for two *P. coeleste* specimens, one from Peru, the other one from French Guiana, and they show 0.9% difference between the two (Fig. 38), but 4.3% and 4.7% difference from *P. burnsi*. Differences within 1% in specimens from distant localities are expected as intraspecific variation, however barcode differences of as little as 0.2% are known between morphologically and ecologically different (but very similar) HesperIIDae (Burns et al. 2007). Importantly, we are not aware of any HesperIIDae species showing 4.5% barcode difference within a species. Such a difference is highly indicative of an interspecific divergence, consistent with morphological differentiation in wing shapes, patterns and genitalia. Interestingly, this 4.5% difference is significantly larger than the 2.4% difference between the two undescribed *Entheus* species from ACG (Fig. 38), which are sympatric and distinct in their biology (Janzen et al. 2011).

Although 654 base pairs of barcode sequence are usually too few for statistically sound phylogenetic inference, which also could be hindered by hybridization and introgression (Zakharov et al. 2009), we observe confident bootstrap statistics close to 1 for all nodes in a NJ tree of selected taxa that were viewed as being evolutionarily close to *Phareas* (Evans 1952) (Fig. 38). Also, other phylogenetic methods offered by phylogeny.fr web-server (Dereeper et al. 2008), such as PhyML, MrBayes and TNT produce the same tree (data not shown), increasing our confidence in the results. The three genera, in addition to *Phareas*, selected for the tree were *Hyalothyrs* Mabille, 1878, *Entheus* Hübner, [1819] and *Phocides* Hübner, [1819]. *Hyalothyrs* and *Entheus* are the genera placed next to *Phareas* in Evans (1952) key and are expected to be evolutionarily closest to it. *Phocides* Hübner, [1819] was

taken as a genus from the same “Group B.” of Evans (1952), but with different palpi and suggested to be close to *Nascus* E. Watson, 1893 in a comprehensive phylogenetic analysis (Warren et al. 2008, 2009). Thus, *Phocides* seemed to be a reasonable choice for an outgroup for the tree. In the Evans key, which frequently reflects phylogenetic arrangements, *Phareas* is grouped with *Hyalothyrs* by the ratio of distances between origins of certain forewing veins, and *Entheus* is set apart. In the barcode tree, *Hyalothyrs* and *Entheus* are sister taxa, but *Phareas* is positioned away from both of them, and it is closer to *Phocides* by DNA distance (Fig. 38). While the closeness of *Hyalothyrs* and *Entheus* is not particularly surprising, especially taking into account closeness of female wing patterns between certain species of these genera (images in Warren et al. 2013) coupled with synapomorphic similarities in palpi and antennae (Evans 1952), smaller than expected distances between *Phareas* and *Phocides* are interesting and require further analysis. It is possible that peculiar palpi shared by certain genera in the Evans’ “Group B” are synapomorphic, and *Phareas* is a true member of the group, but its pupa (Fig. 37o–r) appears very different from any of the other ACG species of HesperIIDae in the Evans’ “Group B”, with a protruding compartment on the head, and is superficially more similar to such genera as *Nicephellus* Austin, 2008 and *Dyscophellus* Godman & Salvin, 1893 than to *Entheus* and *Phocides* (Janzen & Hallwachs 2012, Warren et al. 2013). Clearly, more data are needed to assess the phylogenetic position of *Phareas*.

In summary, consistency of differences in wing shapes and patterns, female and to lesser extent male genitalia and DNA barcodes strongly argue for *P. burnsi* being a distinct biological species, which is a Central American relative of the widespread and more common South American *P. coeleste*. In wing patterns, *P. burnsi* can be most easily distinguished from *P. coeleste* by a broader and more diffuse dark marginal band on the ventral hindwing. Careful analysis of Central American specimens of other species described from South America may similarly lead to further discoveries of undescribed species.

ACKNOWLEDGEMENTS

We are grateful to Robert K. Robbins, John M. Burns and Brian Harris (National Museum of Natural History, Smithsonian Institution, Washington DC), Wolfram Mey (Museum für Naturkunde, Berlin, Germany), David Lees and Blanca Huertas (Natural History Museum, London, UK), for granting access to the collections under their care and stimulating discussions; Bernard Hermier for many enlightening discussions, critical reading of the manuscript and numerous suggestions; Christian Brévignon for his records and photographs of *P. coeleste* immatures and kind permission to use them in this work; Andy War-

ren and Ichiro Nakamura for providing information about the Limón Province Costa Rican specimen and encouragement; Ernst Brockmann for DNA barcode of *P. coeleste* and discussions; and anonymous reviewers for helpful comments, corrections and edits. The study has been supported by U.S. National Science Foundation grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, 0515699, and grants from the Wege Foundation, International Conservation Fund of Canada, Jessie B. Cox Charitable Trust, Blue Moon Fund, Guanacaste Dry Forest Conservation Fund, Area de Conservación Guanacaste, and University of Pennsylvania (DHJ).

LITERATURE CITED

- BURNS, J.M., JANZEN, D.H., HAJIBABAEI, M., HALLWACHS, W., & P.D.N. HEBERT. 2007. DNA barcodes of closely related (but morphologically and ecologically distinct) species of skipper butterflies (Hesperiidae) can differ by only one to three nucleotides. *J. Lepid. Soc.* 61: 138–153.
- COMSTOCK, J. H. 1918. The wings of insects. The Comstock Publishing Company, Ithaca. xviii+430 pp., 10 pls.
- CRAMER, P. 1775–1780. De uitlandische Kapellen voorkomende in de drie Waereld-Deelen Asia, Africa en America. Papillons exotiques des trois parties du monde l'Asie, l'Afrique et l'Amérique. Amsterdam, S. J. Baalde; Utrecht, Barthélemy Wild and J. Van Schoonhoven & Comp. 4 Volumes.
- DEREEPER, A., V. GUIGNON, G. BLANC, S. AUDIC, S. BUFFET, F. CHEVENET, J. F. DUFAYARD, S. GUINDON, V. LEFORT, M. LESCOT, J. M. CLAVERIE, & O. GASCUEL. 2008. Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nucleic Acids Research* 36(Web Server issue): W465–W469.
- EVANS, W. H. 1952. A catalogue of the American Hesperidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part II (Groups B, C, D) Pyrginae. Section I. London, British Museum (Natural History). v + 178 pp., pls. 10–25.
- HEBERT, P. D. N., PENTON, E. H., BURNS, J. M., JANZEN, D. H. & W. HALLWACHS. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proc. Nat. Acad. Sci.* 101: 14812–14817.
- JANZEN, D. H. & W. HALLWACHS. 2012. Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservación Guanacaste (ACG), northwestern Costa Rica <<http://janzen.sas.upenn.edu>>.
- JANZEN, D. H., W. HALLWACHS & J. M. BURNS. 2010. A tropical horde of counterfeit predator eyes. *Proc. Nat. Acad. Sci.* 107: 11659–11665.
- JANZEN D. H., W. HALLWACHS, J. M. BURNS, M. HAJIBABAEI, C. BERTRAND & P. D. N. HEBERT. 2011. Reading the Complex Skipper Butterfly Fauna of One Tropical Place. *PLoS ONE* 6: e19874.
- JANZEN D. H., W. HALLWACHS, P. BLANDIN, J. M. BURNS, J.-M. CADIOU, I. A. CHACÓN, T. DAPKEY, A. R. DEANS, M. E. EPSTEIN, B. ESPINOZA, J. G. FRANCLEMONT, W. A. HABER, M. HAJIBABAEI, J. P. W. HALL, P. D. N. HEBERT, I. D. GAULD, D. J. HARVEY, A. HAUSMANN, I. KITCHING, J. D. LAFONTAINE, J.-F. LANDRY, C. LEMAIRE, J. Y. MILLER, J. S. MILLER, L. D. MILLER, S. E. MILLER, J. J. MONTERO, E. G. MUNROE, S. RAB GREEN, S. RATNASINGHAM, J. E. RAWLINS, R. K. ROBBINS, J. J. RODRIGUEZ, R. ROUGERIE, M. J. SHARKEY, M. A. SMITH, M. A. SOLIS, J. B. SULLIVAN, P. THIAUCOURT, D. B. WAHL, S. J. WELLER, J. B. WHITFIELD, K. R. WILLMOTT, D. M. WOOD, N. E. WOODLEY & J. J. WILSON. 2009. Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. *Mol. Ecol. Res.* 9 (Supplement 1): 1–26.
- KLOTS, A. B. 1970. Lepidoptera, pp. 115–130. *In* Tuxen S. L. (ed.), *Taxonomist's glossary of genitalia in insects*. Munksgaard, Copenhagen.
- MIELKE, O. H. H. 2005. Catalogue of the American Hesperioidea: Hesperidae (Lepidoptera). Sociedade Brasileira de Zoologia, Curitiba, Paraná, Brazil, xiii + 1536 pp.
- MOSHER, E. 1916. A classification of the Lepidoptera based on characters of the pupa. *Bull. Illinois State Lab. Nat. Hist.* 12: 17–159.
- RATNASINGHAM, S. & P. D. N. HEBERT. 2007. BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Mol. Ecol. Not.* 7: 355–364.
- ROBBINS, R. K. 1991. Evolution, comparative morphology, and identification of the Eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). *Smith. Contr. Zoo.* #498, 64 pp.
- WARREN, A. D., K. J. DAVIS, E. M. STANGELAND, J. P. PELHAM & N. V. GRISHIN. 2013. Illustrated Lists of American Butterflies. [20-VII-2013] <<http://www.butterfliesofamerica.com>>.
- WARREN, A. D., J. R. OGAWA & A. V. Z. BROWER. 2008. Phylogenetic relationships of subfamilies and circumscription of tribes in the family Hesperidae (Lepidoptera: Hesperioidea). *Cladistics* 24: 642–676, 2 figs., 5 tabs.
- WARREN, A. D., J. R. OGAWA & A. V. Z. BROWER. 2009. Revised classification of the family Hesperidae (Lepidoptera: Hesperioidea) based on combined molecular and morphological data. *System. Entomol.* 34: 467–523, 4 figs., 1 tab.
- WESTWOOD, J. O. 1852. *In*: Doubleday, E., The genera of diurnal Lepidoptera: comprising their generic characters, a notice of their habits and transformations, and a catalogue of the species of each genus. London, Longman, Brown, Green & Longmans. 2, pl. 78, fig. 4 (d).
- ZAKHAROV E. V., N. F. LOBO, C. NOWAK & J. J. HELLMANN. 2009. Introgression as a likely cause of mtDNA paralogy in two allopatric skippers (Lepidoptera: Hesperidae). *Heredity* 102: 590–599.

Submitted for publication 24 October 2012; revised and accepted 6 December 2012.

TWO NEW SPECIES OF *PHANETA* (TORTRICIDAE)
FROM SOUTHERN CALIFORNIA,
WITH REVIEWS OF TEN SIMILAR SPECIES

DONALD J. WRIGHT

3349 Morrison Ave., Cincinnati, Ohio 45220-1430, USA, e-mail: wrightdj@fuse.net

ABSTRACT. *Phaneta kramerana* and *Phaneta donahuei*, new species, are described from southern California. Ten congeners that might be confused with the new taxa based on forewing appearance are reviewed: *Phaneta tenuiana* (Walsingham), *Phaneta nepotinana* (Heinrich), *Phaneta fertoriana* (Heinrich), *Phaneta subminimana* (Heinrich), *Phaneta complicana* (McDunnough), *Phaneta migratana* (Heinrich), *Phaneta alatana* (McDunnough), *Phaneta cinereolineana* (Heinrich), *Phaneta crassana* (McDunnough), and *Phaneta spectana* (McDunnough). Adults and genitalia are illustrated for each species.

Additional key words: Olethreutinae, Eucosmini, western North America

The primary purpose of this paper is to make names available for two new species of *Phaneta* Stephens from southern California. The new taxa are small nondescript brownish-gray moths that might be mistaken for several named western *Phaneta* based on forewing appearance but which are readily distinguished by genitalic characters. The similar looking congeners can themselves be difficult to identify due to a scarcity of diagnostic forewing markings, a fair amount of intraspecific variation, and a lack of information on the female genitalia. Ten species are reviewed here: *Phaneta tenuiana* (Walsingham), *Phaneta nepotinana* (Heinrich), *Phaneta fertoriana* (Heinrich), *Phaneta subminimana* (Heinrich), *Phaneta complicana* (McDunnough), *Phaneta migratana* (Heinrich), *Phaneta alatana* (McDunnough), *Phaneta cinereolineana* (Heinrich), *Phaneta crassana* (McDunnough), and *Phaneta spectana* (McDunnough). Three others, *Phaneta indagatricana* (Heinrich), *Phaneta misturana* (Heinrich), and *Phaneta latens* (Heinrich), were recently reviewed by Wright (2010). The new species are placed in *Phaneta* for lack of a costal fold on the male forewing.

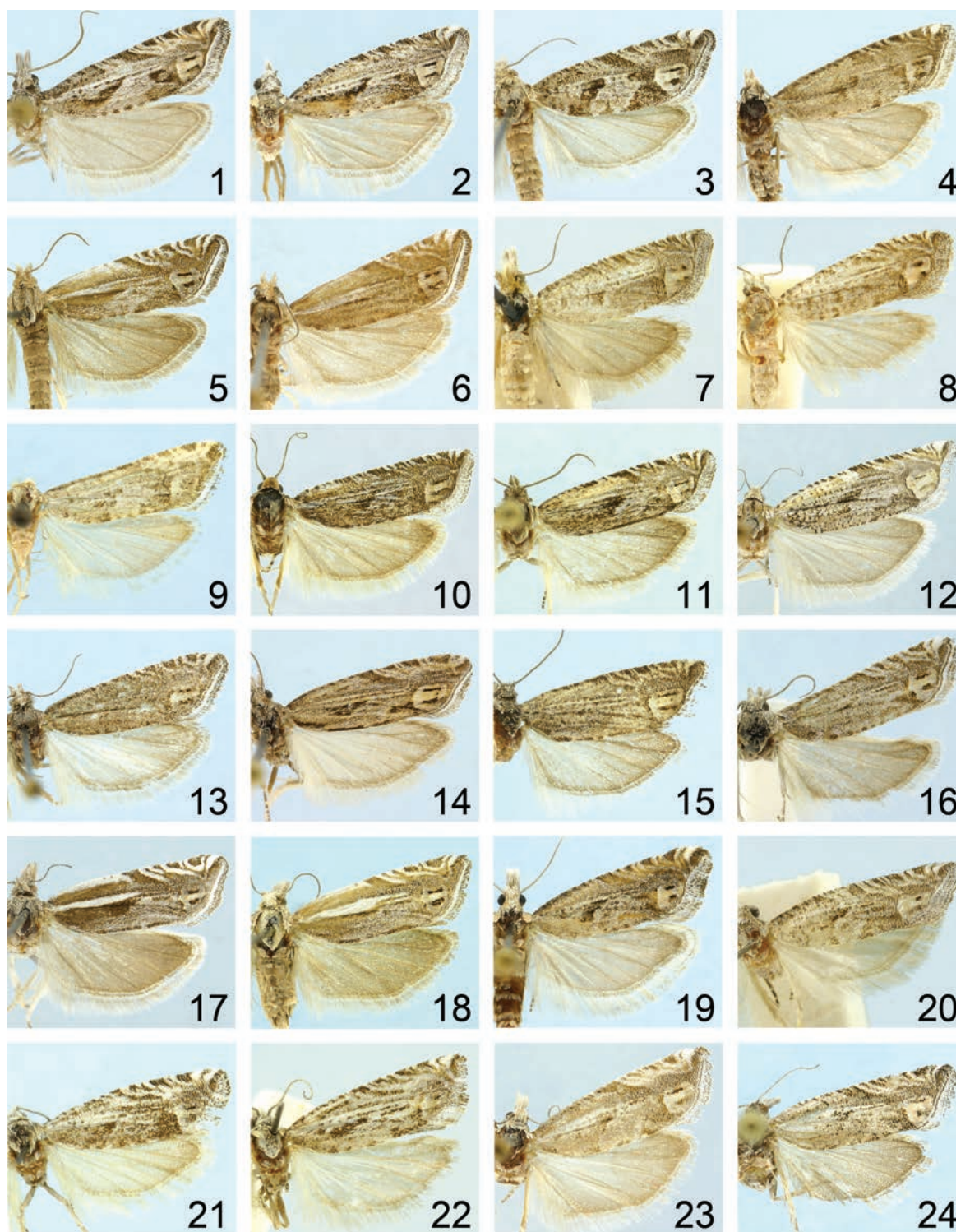
MATERIALS AND METHODS

I examined 376 adult specimens and 121 associated genitalia preparations from the following institutional and private collections: V. Albu, Friant, California; American Museum of Natural History, New York (AMNH); George J. Balogh, Portage, Michigan; Canadian National Collection, Ottawa (CNC); Lawrence L. Crabtree, Bieber, California; Essig Museum of Entomology, UC Berkeley (EME); The Natural History Museum of Los Angeles County, Los Angeles (LACM); John S. Nordin, Laramie, Wyoming; Strickland Museum, University of Alberta, Edmonton

(UASM); United States Museum of Natural History, Washington D.C. (USNM); and Donald J. Wright (DJW).

Adults were examined with a Leica MZ95 stereomicroscope equipped with an ocular micrometer, genitalia with a Leica DME compound microscope. Images of adults were edited in Adobe Photoshop CS5, and line and stipple drawings were made with the aid of a Ken-A-Vision X1000-1 microprojector. Morphological terminology follows Gilligan et al. (2008). Aspect ratio (AR) is defined as forewing length (FWL) divided by medial forewing width, valval neck ratio (NR) as minimum neck width divided by valval width near the saccular corner, and saccular angle (SA) as the angle-like projection on the ventral margin of the valva where the sacculus meets the neck (see Wright 2011). These statistics are reported as the average of several such measurements. The term clasper refers here to a small portion of the medial surface of the valva located at the distal margin of the basal excavation. In *Phaneta* its form varies from an elongate tongue-like projection (sometimes called a pulvinus) to a variably raised tab-like projection, and its surface is usually covered with stiff setae. An estimate of the number of cornuti in the male vesica was obtained by counting sockets. The symbol “≈” stands for “approximately equal to,” and *n* signifies the number of observations supporting a particular statement.

I examined the primary types of the species treated here except for that of *P. tenuiana*. In that case my determinations are based on photographs taken by Obraztsov sixty years ago of the adult and genitalia of a specimen he chose as the lectotype. His selection was never published, so for the sake of nomenclatorial stability that designation is made below.



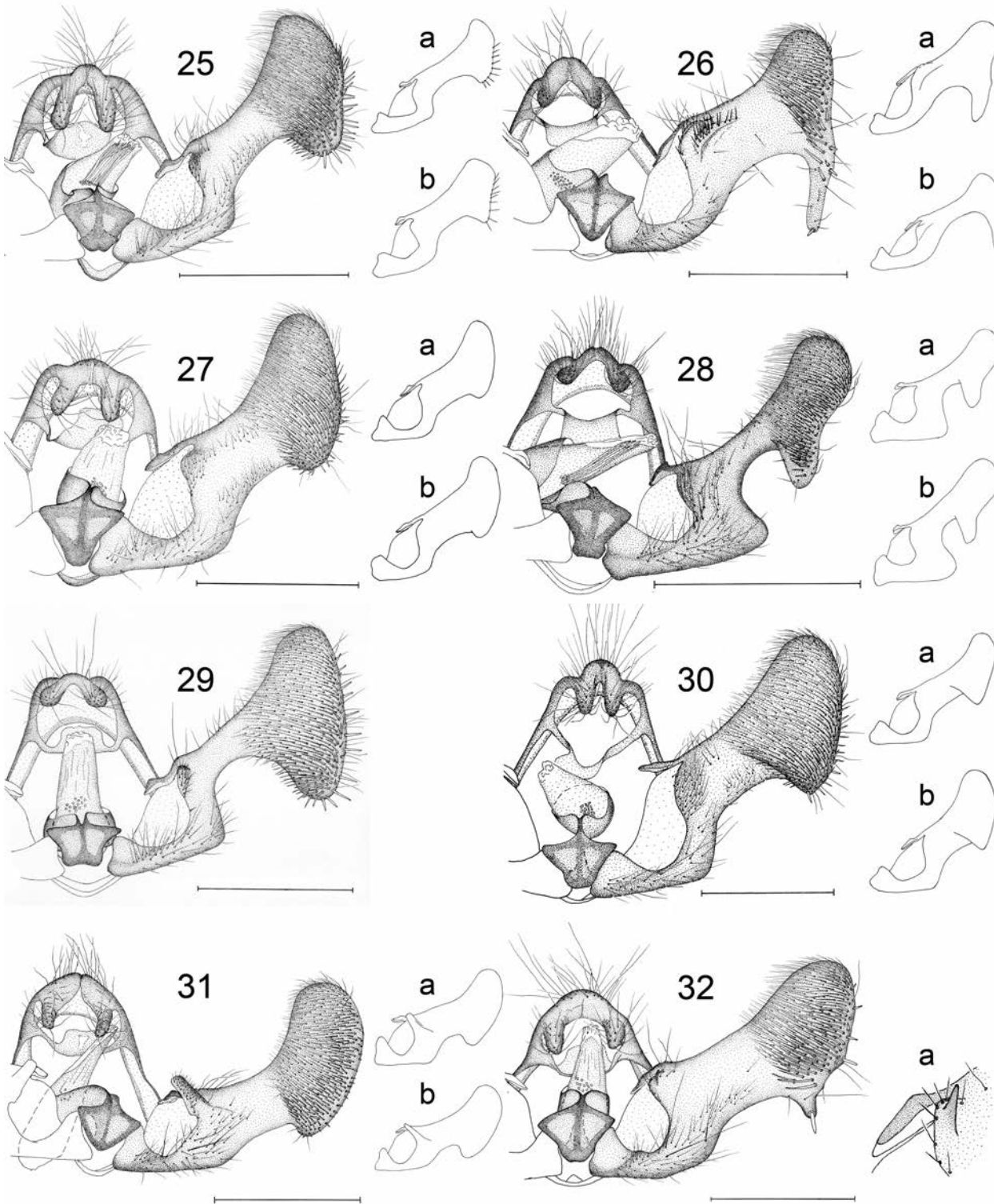
FIGS. 1–24. 1–2, *P. tenuiana*. 1. ♂ Grand Co., Colorado. 2. ♂ Esmeralda Co., Nevada. 3–4, *P. nepotinana*. 3. ♂ Summerland, British Columbia. 4. ♂ Routt Co., Colorado. 5–6, *P. fertoriana*. 5. ♂ Peachland, British Columbia. 6. ♂ Hardy W.C., South Dakota. 7–8, *P. subminimana*, ♀, ♀ San Diego Co., California. 9, *P. complicana*, ♂ holotype. 10–12, *P. migratana*. 10. ♂ Deschutes Co., Oregon. 11. ♂ Albany Co., Wyoming. 12. ♀ Alamosa Co., Colorado. 13–14, *P. alatana*. 13. ♂ holotype. 14. ♂ San Diego Co., California. 15–16, *P. cinereolineana*. 15. ♂ holotype. 16. ♂ Lost River Bandlands, Alberta. 17–18, *P. crassana*. 17. ♂ Osoyoos, British Columbia. 18. ♀ Lethbridge, Alberta. 19–20, *P. spectana*. 19. ♂ Slope Co., North Dakota. 20. ♂ White Pine Co., Nevada. 21–22, *P. krammerana*. 21. ♀ holotype. 22. ♀, San Bernardino Co., California. 23–24, *P. donahuei*. 23. ♂ Kern Co., California. 24. ♂ Inyo Co., California.

SPECIES ACCOUNTS

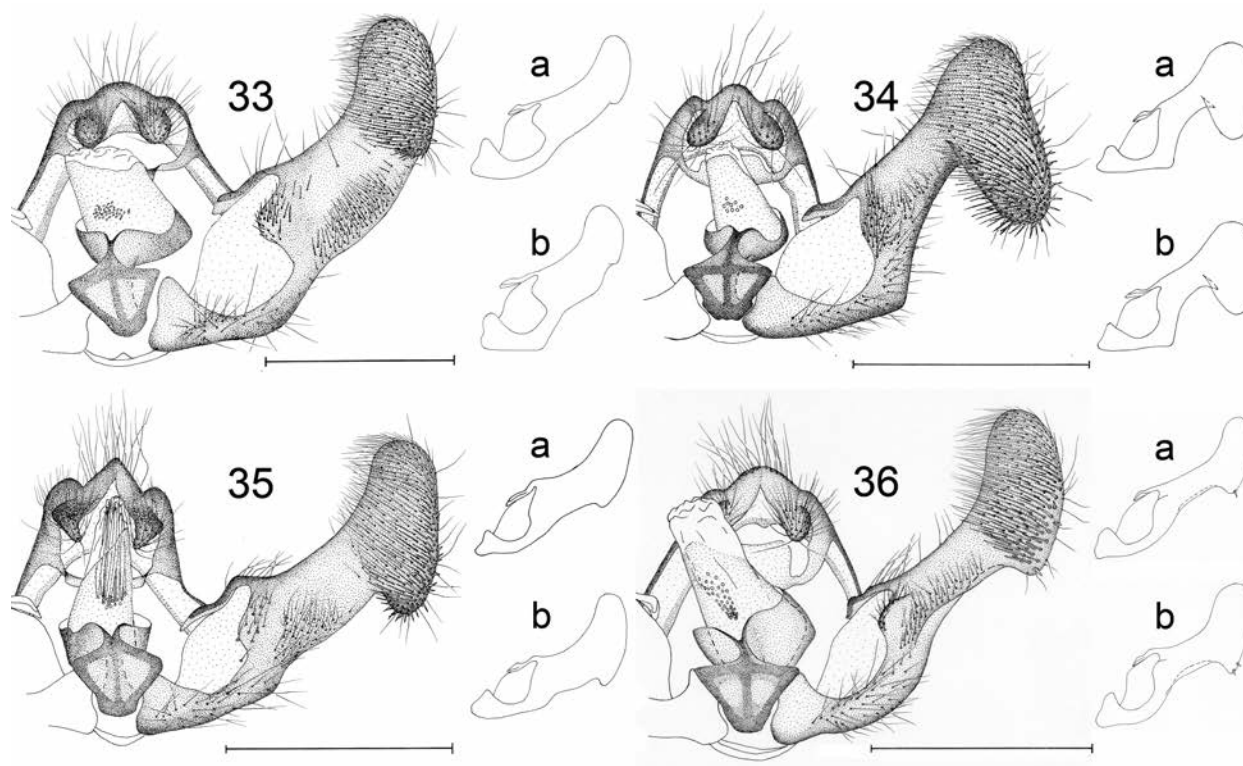
Phaneta tenuiana (Walsingham)
(Figs. 1–2, 25, 37, 45)*Semasia tenuiana* Walsingham 1879:59.*Thiodia tenuiana*: Fernald [1903]:462; Heinrich 1923:54; McDunnough 1939:44.*Eucosma tenuiana*: Barnes and McDunnough 1917:172.*Phaneta tenuiana*: Powell 1983:33; Brown 2005:496.**Lectotype** (here designated): ♂, California, Siskiyou County, Sheep Rock, Walsingham, 3 September 1871, slide 11584, BMNH(E) #819942, BMNH.**Syntype**: ♀, same data as lectotype, slide 11548, BMNH.**Description.** *Head.* Frons white; vertex with medial scales white, lateral scales mostly gray with white apices; labial palpus elongate, with medial surface grayish white, lateral surface gray, long scales on second segment concealing third segment; antenna concolorous with vertex. *Thorax.* Dorsal surface grayish; fore- and mid-legs with anterior surfaces blackish gray to brownish gray, posterior surfaces grayish; hind-legs pale brownish gray; tarsi with conspicuous white annulations. Forewing (Figs. 1, 2): ♂ FWL 7.0–9.4 mm (mean = 8.3, n = 78), AR = 3.42; ♀ FWL 7.4–8.4 mm (mean = 7.8, n = 14), AR = 3.23; costa straight to weakly arched; apex acute; termen straight to weakly concave; dorsal surface with blackish-brown markings and grayish-white interfascial areas; subbasal fascia represented by small costal dash and outwardly oblique dash from A_{1+2} to cubitus, the latter adjoined by an irregular orange-brown to grayish-brown patch extending along inner margin to base of wing; median fascia consisting of a blackish-brown bar from mid-costa to radius and a semi-rectangular mark on inner margin bordering proximal edge of ocellus; subbasal and median fasciae interrupted in cell by whitish diffuse longitudinal streak from base to ocellus; ocellus with whitish central field crossed by two prominent blackish-brown dashes and bordered proximally and distally by fawn to grayish-white lustrous bars; costal strigulae from median fascia to apex white, divided, and sharply separated by blackish-brown costal marks; termen with thin white line from tornus to apex; fringe scales white with black to gray cross-marks. Hindwing pale gray brown. *Abdomen.* Male genitalia (Fig. 25) (n = 13): Uncus moderately developed, clearly differentiated from dorsolateral shoulders of tegumen; socii fingerlike; phallus moderately tapering distally; vesica with 14–24 deciduous cornuti; valva with costal margin concave, NR = 0.51, SA obtuse (mean = 107°), clasper tablike and weakly raised; cucullus with apex somewhat angular, anal angle well developed; distal margin of cucullus with bend at two-thirds distance from anal angle to apex and 8–10 moderately stout setae evenly distributed from anal angle to bend. Female genitalia (Figs. 37, 45) (n = 4): Papillae anales laterally facing and moderately setose; lamella postvaginalis rectangular, width $\approx 2 \times$ length, with microspinulate central trough weakly depressed; lamella antevaginalis ringlike; sternum 7 with lateral projections pointed and posterior edge emarginated to length of sterigma; anterolateral corners of sterigma fused with sternum 7; ductus bursae with sclerotized ring at juncture with ductus seminalis; corpus bursae with two signa of distinctly different size.**Distribution and biology.** I examined 114 specimens (100 ♂, 14 ♀) from Arizona, California, Colorado, Nevada, Oregon, Utah, Washington, and Wyoming. Capture dates range from 25 August to 17 October. Several of the California specimens were collected in association with *Haplopappus* (Asteraceae).*Phaneta nepotinana* (Heinrich)

(Figs. 3, 4, 26, 38, 46)

Thiodia nepotinana Heinrich 1923:263; McDunnough 1939:44.*Phaneta nepotinana*: Powell 1983:33; Brown 2005:494.**Holotype**: ♂, Utah, [Juab Co.], Eureka, T. Spalding, 30 May 1911, slide 72771, USNM.**Paratypes**: UTAH. [Juab Co.], Eureka, T. Spalding, 30 May 1911, (5 ♂, slide 70034; 1 ♀, slide DJW 2611) USNM; [Tooele Co.], Stockton, T. Spalding, 24 May 1904, (1 ♂, slide CH 13 June 1922) AMNH. NEVADA. [Washoe Co.], Verdi, A. H. Vachell, 1–10 June, (2 ♂, slide 70036) USNM, (3 ♂; 1 ♀, slide DJW 2671) AMNH; CALIFORNIA. Inyo [Inyo] Co., Olancho, 16–23 June, (1 ♂, slide 70035) USNM. This accounts for 14 of the 15 paratypes mentioned by Heinrich (1923). He reported two females from Eureka, Utah; I found only one. However, the AMNH has a ♂ from Eureka, Utah dated 2 June 1911 that was not mentioned by Heinrich but does bear his handwritten paratype label.**Description.** *Head.* Frons white to brownish gray; vertex with medial scales white, lateral scales mostly gray brown with white apices; labial palpus with medial surface grayish white, lateral surface white toward base, with long gray-brown scales on second segment concealing third segment; antenna gray brown dorsally, white laterally; scape with ventral surface white, dorsal surface brownish gray. *Thorax.* Dorsal surface brownish gray to blackish gray; legs with anterior surfaces brownish gray to blackish gray, posterior surfaces pale tan; mid-leg with white mark at mid-tibia; tarsi with white annulations. Forewing (Figs. 3, 4): ♂ FWL 4.3–7.8 mm (mean = 6.7, n = 42), AR = 3.24; ♀ FWL 4.5–6.4 mm (mean = 5.8, n = 7), AR = 3.17; costa nearly straight; apex acute; termen straight to weakly concave; dorsal surface with fascial markings blackish brown, interfascial areas usually grayish white, sometimes suffused with gray brown; subbasal fascia chevron shaped, usually interrupted by thin whitish streak on radius; median fascia complete (Fig. 3) to barely discernible (Fig. 4), always represented by blackish-brown bar at mid-costa and variably expressed blackish-brown patch on inner margin adjacent to proximal edge of ocellus; ocellus edged proximally and distally by fawn to grayish-white lustrous bars, with proximal margin thinly edged with black; central field of ocellus whitish, crossed by two blackish dashes; costal strigulae from median fascia to apex white, divided, and sharply delimited by blackish-brown marks; scales along termen white with black cross-marks that form a thin black line from tornus to apex, the line flanked proximally and distally by thin and broader white lines, respectively; outer fringe scales gray brown with white apices. Hindwing pale gray brown. *Abdomen.* Male genitalia (Fig. 26) (n = 15): Uncus semi-circular, weakly divided medially, clearly differentiated from dorsolateral shoulders of tegumen; socii short and stubby; phallus cylindrical; vesica with 23–41 deciduous cornuti; valva with costal margin weakly concave, NR = 0.54, saccular corner broadly rounded, SA obtuse but ill defined; clasper consisting of two ridges lined with stiff setae, one bending parallel to costal edge of valva from margin of basal excavation to base of neck, the second parallel to first and displaced slightly toward ventral margin of neck; cucullus with apex evenly rounded, distal margin nearly straight, occasionally with shallow concave inflection or weak convex protrusion, ventral angle developed into long narrow finger-like projection; setae on medial surface of cucullus hairlike toward apex, coarse and less densely distributed toward base of ventral projection, sparse and stubby on ventral projection. Female genitalia (Figs. 38, 46) (n = 5): Papillae anales laterally facing and moderately setose; sterigma (Fig. 46)



FIGS. 25–32. Male genitalia. **25.** *P. tenuiana*, slides DJW1009, USNM70040, 70039. **26.** *P. nepotinana*, slides DJW2165, 2610, USNM70032. **27.** *P. fertoriana*, slides DJW882, 2217, 2216. **28.** *P. subminimana*, slides DJW2635, 2637, USNM70080. **29.** *P. complicana*, slide TOR981 (holotype). **30.** *P. migratana*, slides USNM72770 (holotype), DJW2146, 281. **31.** *P. alatana*, slides DJW2115, 2618, USNM87883. **32.** *P. cinereolineana*, slide DJW2266. Scale bar = 0.5 mm.



FIGS. 33–36. Male genitalia. **33.** *P. crassana*, slides USNM70041, DJW2651, USNM70042. **34.** *P. spectana*, slides DJW2619, 2213, 1092. **35.** *P. kramerana*, slides DJW2108, JAP234, DJW2632. **36.** *P. donahuei*, slides DJW3062, 3063, 2796. Scale bar = 0.5 mm.

ovately ringlike, microspinulate on posterior margin, fused with sternum 7 along lateral and anterior margins; sternum 7 with posterior edge emarginated beyond length of sterigma and with pair of outwardly projecting crescent shaped flaps, one on each lateral section, the two aligned with anterior margin of ostium; ductus bursae with irregularly shaped sclerotized ring at juncture with ductus seminalis, the latter located near ostium; corpus bursae with two signa of nearly equal size.

Distribution and biology. I examined 66 specimens (59 ♂, 7 ♀) from California, Colorado, Idaho, Nevada, Utah, Washington, and Wyoming collected between mid-February and mid-July. Six specimens in the USNM (5 from Asotin, Co., Washington, 1 from Jerome Co., Idaho) were reared by O. O. Filmore from *Artemisia tridentata* (Asteraceae).

Remarks. At the USNM there are a few male specimens from southern California with an unusually narrow valval neck (Fig. 26b). I tentatively determined them as *P. nepotinana* but did not include them in the statistics reported above.

Phaneta fertoriana (Heinrich)

(Figs. 5, 6, 27, 39, 47)

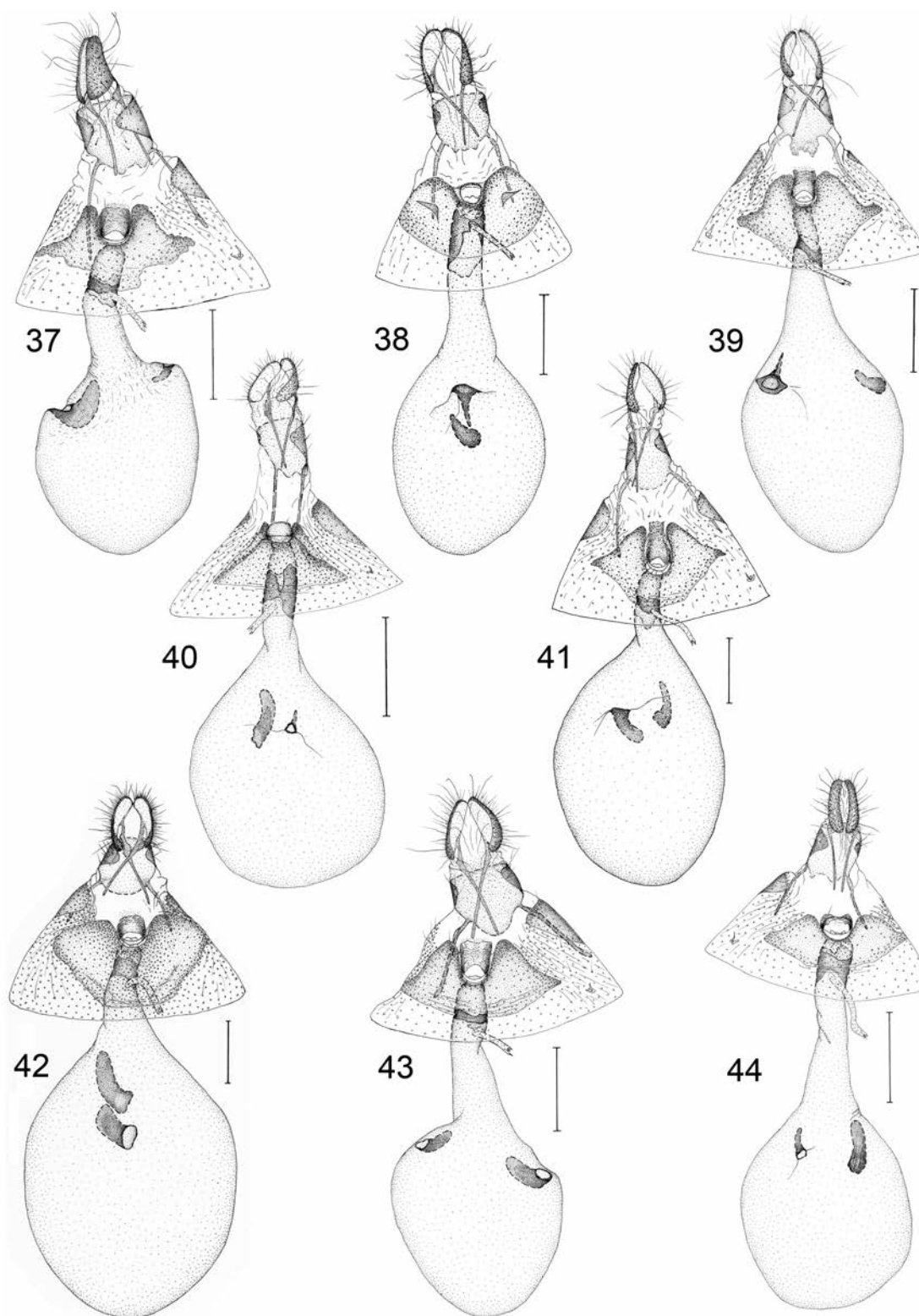
Thiodia fertoriana Heinrich 1923:264; McDunnough 1939:44.

Phaneta fertoriana: Powell 1983:33; Brown 2005:493.

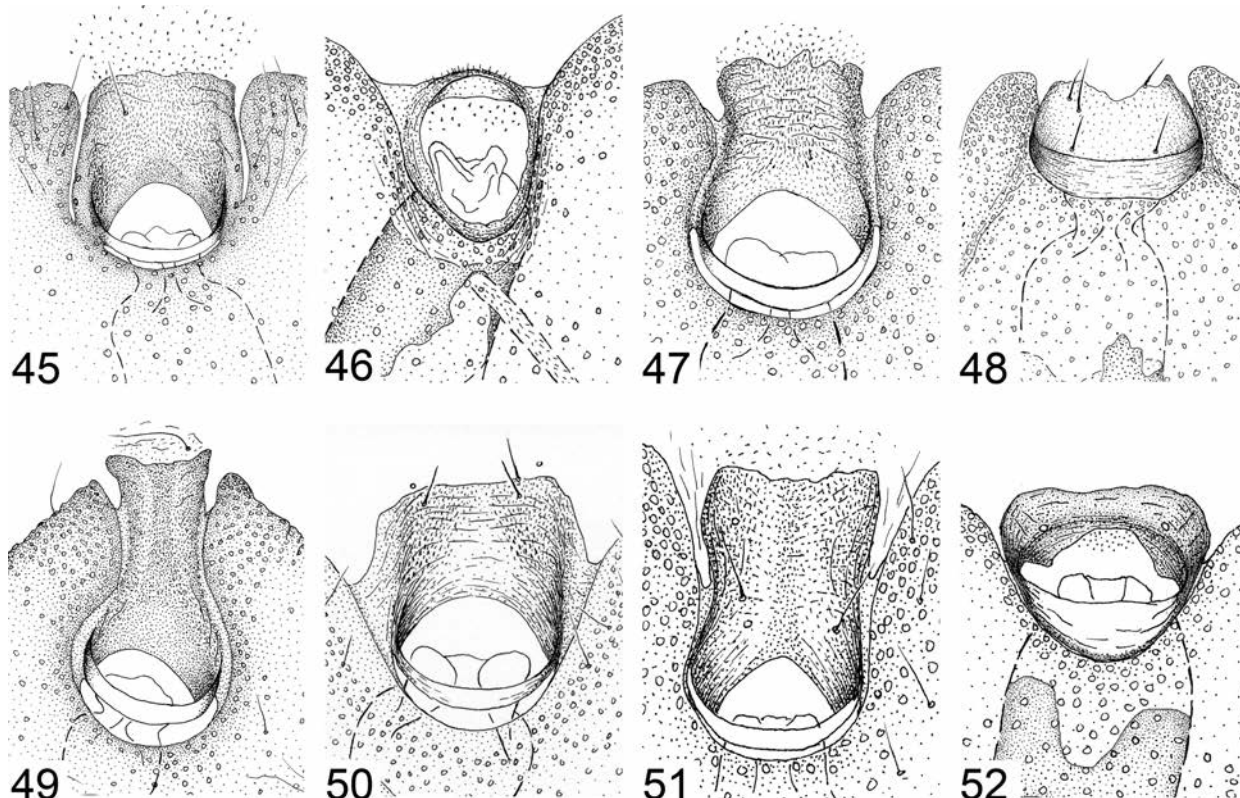
Holotype: ♂, Canada, British Columbia, Goldstream, 24 May 1903, slide 72767, USNM.

Paratypes: same location as holotype, 10 May 1903 (1 ♀, slide DJW 2214) USNM, (1 ♀) AMNH. Heinrich (1923) reported 10/5/03 as the collection date for all three type specimens, but the pin label on the holotype reads 24/5/03, which admits only one interpretation (24 May 1903). Both paratypes are labeled 10/5/03, which I presume is to be interpreted as 10 May 1903.

Description. *Head.* Frons white; vertex gray brown, sometimes with obscure whitish medial line; labial palpus with first segment white, medial surface of second segment white shading to gray brown at margins, lateral surface mostly gray brown; antenna gray brown dorsally, whitish laterally. *Thorax.* Dorsal surface gray brown; legs with anterior surfaces brown, posterior surfaces tan; tarsi with pale



FIGS. 37–44. Female genitalia. 37. *P. tenuiana*, slide DJW1937. 38. *P. nepotinana*, slide DJW2611. 39. *P. fetoriana*, slide DJW2215. 40. *P. subminimana*, slide DJW2636. 41. *P. migratana*, slide DJW2253. 42. *P. crassana*, slide DJW3071. 43. *P. spectana*, slide DJW2628. 44. *P. kramerana*, slide DJW2145. Scale bar = 0.5 mm.



FIGS. 45–52. Sterigmata. **45.** *P. tenuiana*, slide DJW2211. **46.** *P. nepotinana*, slide DJW2157. **47.** *P. fetoriana*, slide DJW2215. **48.** *P. subminimana*, slide DJW2634. **49.** *P. migratana*, slide DJW2202. **50.** *P. crassana*, slide DJW3076. **51.** *P. spectana*, slide DJW2018. **52.** *P. kramerana*, slide DJW2167.

annulations. Forewing (Figs. 5, 6): ♂ FWL 6.3–8.3 mm (mean = 7.5, $n = 22$), AR = 3.28; ♀ FWL 5.4–8.0 mm (mean = 6.8, $n = 9$), AR = 3.20; costa nearly straight; apex acute; termen straight; dorsal surface brownish, with dark brown markings, a diffuse whitish streak along costa from base to median fascia, and sometimes an indistinct whitish streak along cubitus from base to mid-wing; cubital streak usually edged posteriorly with blackish-brown line and sometimes anteriorly by yellow-brown band from base to median fascia; subbasal fascia obscure to undetectable; median fascia complete but often fading toward inner margin; ocellus bordered proximally and distally by lustrous gray bars, with white to pale brown central field crossed by two prominent black dashes; costal strigulae from median fascia to apex white, divided, and delimited by brown marks; termen with thin black line from tornus to apex, followed distally by prominent white line; fringe scales brown to blackish brown with white apices. Hindwing gray brown. *Abdomen.* Male genitalia (Fig. 27) ($n = 16$): Uncus convex, weakly developed, weakly differentiated from dorsolateral shoulders of tegumen; socii short and fingerlike; phallus moderately tapering distally; vesica with 18–31 deciduous cornuti; valva with costal margin concave, NR = 0.65, SA obtuse (mean = 109°), clasper tablike and weakly raised; cucullus with apex evenly rounded, distal margin convex, ventral angle weakly developed, medial surface densely setose, margins lacking spiniform setae. Female genitalia (Figs. 39, 47) ($n = 4$): Papillae anales laterally facing and moderately setose; lamella postvaginalis rectangular, width $\approx$ length, with microspinulate central trough weakly depressed; lamella antevaginalis ringlike; sternum 7 with posterior edge emarginated nearly to length of sterigma and fused with lateral margins of lamella postvaginalis, lateral projections pointed; ductus bursae with sclerotized ring at juncture with ductus seminalis; corpus bursae with two signa, one somewhat larger than the other.

Distribution and biology. I examined 54 specimens (38 ♂, 16 ♀) from British Columbia, Manitoba, Arizona, California, New Mexico, South Dakota, Oregon, and Wyoming. Adults fly from late March to mid-July.

Phaneta subminimana (Heinrich)

(Figs. 7, 8, 28, 40, 48)

Thiodia subminimana Heinrich 1923:61;

McDunnough 1939:45.

Phaneta subminimana: Powell 1983:34; Brown 2005:496.

Holotype: ♂, California, [San Diego Co.], San Diego, 1–7 August, slide 72776, USNM.

Paratypes: California, [San Diego Co.], San Diego, (5 ♂, slides 70080, DJW 2635) USNM, (2 ♂) AMNH, 1–7 August (1 ♂) USNM, 16–23 August (3 ♂, slide DJW 2637) USNM; W. S. Wright, 22 July 1908 (1 ♂) AMNH, 8 August 1908 (2 ♂) USNM, AMNH.

Description. *Head.* Frons whitish; vertex whitish shading to pale brown laterally; labial palpus largely whitish; second segment with brown mark on lateral surface and long brownish scales concealing third segment; antenna whitish with thin brown line along dorsal surface. *Thorax.* Dorsal surface pale brown; legs with anterior surfaces tan, posterior surfaces whitish; tarsi with white annulations. Forewing

(Figs. 7, 8): ♂ FWL 5.0–7.0 mm (mean = 5.9, $n = 11$), AR = 3.14; ♀ FWL 5.4–7.1 mm (mean = 6.2, $n = 15$), AR = 3.03; costa weakly arched; apex acute; termen straight; interfascial areas of dorsal surface whitish with pale brown suffusion and brown transverse reticulations; fascial markings brown; subbasal fascia reduced to small mark on CuP; median fascia represented by short bar at mid-costa and diffuse mark on inner margin adjacent to proximal edge of ocellus; cell with diffuse whitish band interrupting subbasal and median fasciae; ocellus edged proximally and distally by white to pale gray lustrous bars; central field of ocellus white to pale brown, crossed by two blackish streaks, the latter sometimes reduced to two small dots; costal strigulae whitish, delimited by short brown dashes; fringe scales whitish with brown cross-marks. Hindwing gray brown. *Abdomen*. Male genitalia (Fig. 28) ($n = 4$): Uncus moderately developed, weakly divided medially by shallow indentation, clearly differentiated from dorsolateral shoulders of tegumen; socii short and stubby; phallus strongly tapering distally; vesica with 8–12 deciduous cornuti; valva with costal margin concave, NR = 0.32, SA acute (mean = 64°) with rounded vertex, clasper reduced to band of moderately stiff setae along margin of basal excavation; cucullus elongate, tapering from broadly rounded apex to narrowly rounded anal angle, with distal margin concavely indented, basoventral margin weakly overlapping ventral margin of neck, medial surface densely setose, margins lacking spiniform setae. Female genitalia (Figs. 40, 48) ($n = 4$): Papillae anales laterally facing and moderately setose; tergum 8 densely covered with minute hairlike setae; sterigma ovate, with lamella postvaginalis very weakly developed, lamella antevaginalis ringlike; sternum 7 semi-triangular, with a pair of ridges extending more or less parallel to lateral margins from anterolateral corners of sterigma to anterolateral vertices; posterior “vertex” of sternum 7 emarginated to length of sterigma and fused with lamella antevaginalis; ductus bursae with sclerotized ring at juncture with ductus seminalis; corpus bursae with two signa of distinctly different size.

Distribution and biology. I examined 26 specimens (11 ♂, 15 ♀) from San Diego and Monterey Counties, California with capture dates ranging from mid-July to mid-September.

Phaneta complicana (McDunnough)
(Figs. 9, 29)

Thiodia complicana McDunnough 1925:16;
McDunnough 1939:44.

Phaneta complicana: Powell 1983:33; Brown 2005:493.

Holotype: ♂, British Columbia, Osoyoos, C. B. Garrett, 19 May 1923, slide TOR-981, CNC.

Description. *Head*. Missing. *Thorax*. Dorsal surface tan; legs tan, with anterior surfaces darker; tarsi with whitish annulations. Forewing (Fig. 9): ♂ FWL 7.4 mm, AR = 3.36, $n = 1$; costa nearly straight; apex acute; termen straight; dorsal surface with brown markings and whitish interfascial areas, the latter somewhat suffused with pale brown; subbasal fascia indicated by outwardly oblique dark shade from inner margin to mid-cell; median fascia complete, outwardly oblique from mid-costa to ocellus, continuing to inner margin along proximal edge of ocellus; ocellus obscure, with broad white bar on proximal margin and narrow lustrous white bar on distal margin; central field of ocellus brownish with a few blackish scales; veins anterior to ocellus accentuated by pale brownish lines; costal strigulae from median fascia to apex whitish, well defined; fringe scales white with gray-brown cross-marks, the latter aligned to produce prominent white band along termen from tornus to apex followed distally by a narrow blackish line. Hindwing pale gray brown. *Abdomen*. Male genitalia (Fig. 29) ($n = 1$): Uncus reduced, rounded, weakly differentiated from dorsolateral shoulders of tegumen; socii short and

stubby; phallus moderately tapering distally; vesica with 16 deciduous cornuti; valva with costal margin weakly concave, NR = 0.31, SA = 95° , clasper raised, moundlike; cucullus nearly symmetric about horizontal center line, with apex and anal angle strongly developed and evenly rounded, distal margin weakly convex, medial surface densely setose; distal margin of cucullus with series of spiniform setae evenly distributed from anal angle nearly to apex. Female genitalia unknown.

Distribution and biology. This species is known only from the holotype.

Phaneta migratana (Heinrich)
(Figs. 10–12, 30, 41, 49)

Thiodia migratana Heinrich 1923:53; McDunnough 1939:44.

Phaneta migratana: Powell 1983:33; Brown 2005:494

Holotype: ♂, California, Inyo Co., Olancha, 24–30 April, slide 72770, USNM.

Paratype: ♀, same data as holotype, slide DJW 2253, USNM.

Description. *Head*. Frons grayish white to pale brown; vertex scales white to pale yellow, shading to gray brown at apices; labial palpus with first segment white, second segment white, shading to gray distally, with gray mark on lateral surface, third segment gray; antenna concolorous with vertex. *Thorax*. Dorsal surface brown to gray, often with some yellow-brown suffusion; legs white to gray brown; tarsi blackish brown with white annulations. Forewing: ♂ FWL 6.4–9.9 mm (mean = 8.3, $n = 35$), AR = 3.35; ♀ FWL 8.0–9.8 mm (mean = 8.3, $n = 7$), AR = 3.14; costa nearly straight; apex acute; termen straight to weakly concave; dorsal surface with blackish-brown markings and grayish interfascial areas, the latter usually suffused with pale brown; most specimens with yellowish-brown to orange-brown subcostal band from base to median fascia; subbasal fascia reduced to irregularly shaped mark on cubitus; median fascia represented by outwardly oblique bar at mid-costa; ocellus with proximal and distal margins edged by lustrous fawn to pearl-gray bars, whitish central field crossed by two blackish dashes; costal margin white with numerous interruptions by blackish dashes associated with costal strigulae; fringe scales white with blackish cross-bars. Hindwing gray brown. *Abdomen*. Male genitalia (Fig. 30) ($n = 14$): Uncus well developed, clearly differentiated from dorsolateral shoulders of tegumen, sometimes with distal margin medially indented; socii short, fingerlike; phallus moderately tapering distally, usually with protuberance on ventral surface (not shown in illustration); vesica with 17–31 deciduous cornuti; valva with costal margin weakly concave, dorsal and ventral margins of neck nearly parallel, NR = 0.56, SA obtuse (mean = 118°), clasper represented by patch of stiff setae; cucullus with apex rounded, distal margin straight to weakly convex, anal angle moderately developed, basoventral margin overlapping ventral one-half of neck. Female genitalia (Figs. 41, 49) ($n = 3$): Papillae anales laterally facing and moderately setose; lamella postvaginalis elongate, length $\approx 2 \times$ width, with lateral margins weakly concave, shallow central trough microspinulate; lamella antevaginalis ringlike; posterior edge of sternum 7 emarginated to full length of sterigma and fused with lateral margins of lamella postvaginalis; sternum 7 with strongly produced, sharply pointed, lateral projections; ductus bursae with sclerotized ring posterior to juncture with ductus seminalis; corpus bursae with two signa of nearly equal size.

Distribution and biology. I examined 42 specimens (35 m, 7 f) from California, Colorado, Nevada, Oregon, Utah, and Wyoming. Capture dates range from late March in southern California to late June in Colorado.

Phaneta alatana (McDunnough)
(Figs. 13, 14, 31)

Thiodia alatana McDunnough 1938:100;
McDunnough 1939:44.

Phaneta alatana: Powell 1983:33; Brown 2005:492.

Discussion. Until recently this species was known only from the holotype (Fig. 13), which was collected in desert-like habitat along the Okanogan River in southern British Columbia. Its most distinctive feature is a long tongue-like clasper on the margin of the basal emargination of the valva (Fig. 31). In the late 1990's a series of moths with similar genitalia was collected by N. Bloomfield during a survey of the Lepidoptera of Marine Corps Air Station Miramar, San Diego County, California (Brown and Bash 2000). I am tentatively determining these San Diego specimens as *P. alatana*. McDunnough's (1938, fig. 4) illustration of the male genitalia of *P. alatana* shows a narrower neck and a more weakly produced anal angle than is depicted in Fig. 31, but these differences are due largely to the genitalia being excessively tilted on the slide. The cucullus in Fig. 31 is a little less elongate than in the holotype. Figures 13 & 14 illustrate differences in forewing appearance, the San Diego specimens having more strongly expressed markings. Lacking additional material with which to evaluate these characters, I am attributing the differences to intraspecific variation. The description below of the forewing maculation relies heavily on the San Diego specimens.

Holotype: (Fig. 13) ♂, British Columbia, Osoyoos, Kreuger Mt., A. N. Gartrell, 9 May 1936, slide TOR-948, CNC.

Description. *Head.* Frons whitish; vertex gray brown with diffuse whitish medial line; labial palpus with medial surface and ventral edge whitish, lateral surface and dorsal edge gray brown; antenna gray brown with whitish scaling on lateral surfaces. *Thorax.* Dorsal surface gray brown; fore- and mid-legs gray brown with white mark at mid-tibia; hind-legs pale brown; tarsi with white annulations. Forewing (Figs. 13, 14): ♂ FWL 6.6–8.1 mm (mean = 7.4, n = 13), AR = 3.50; costal margin weakly arched; apex acute, termen straight to weakly concave; dorsal surface grayish brown with brown to blackish-brown markings; subbasal fascia reduced to dark mark between A_{1+2} and cubitus; median fascia represented by outwardly oblique bar arising at mid-costa; basal two-thirds of wing with fine longitudinal streaking, including a pale line along cubitus from base nearly to ocellus, a black line on CuP, and a pale line along A_{1+2} from base to tornus; inner margin with thin black edging that expands into a wider blackish mark near base; ocellus bordered proximally and distally with lustrous pale gray bars; central field of ocellus white to pale orange, crossed by two prominent black dashes; anterior margin of ocellus bordered by longitudinal brown band connecting median fascia to apex; costal strigulae gray brown to whitish; termen with thin white line from tornus to apex followed distally by thin black line and wider white line; outer fringe scales white with black to gray-brown cross-marks. Hindwing grayish white basally, shading to gray brown at margins. *Abdomen.* Male genitalia (Fig. 31) (n = 4): Uncus broad, not differentiated from dorsolateral shoulders of tegumen, with

medial line of division on ventral surface; socii short, fingerlike, somewhat wider toward base; phallus elongate, tapering distally; vesica with 8–14 deciduous cornuti; valva with costal margin concave, NR = 0.62, SA obtuse (mean = 123°), clasper long, tongue-like, projecting obliquely outward from medial surface of valva; cucullus with apex rounded, distal margin convex of nearly uniform curvature, anal angle acute and weakly developed, medial surface densely setose. Female genitalia unknown.

Distribution and biology. This species is known from Osoyoos, British Columbia and San Diego, California. Adults fly in early May at the former locality, from mid-January to early March at the latter.

Phaneta cinereolineana (Heinrich)
(Figs. 15, 16, 32)

Thiodia cinereolineana Heinrich 1923:52;
McDunnough 1939:44.

Phaneta cinereolineana: Powell 1983:33; Brown 2005:492.

Holotype: (Fig. 15) ♂, Utah, [Juab County], Eureka, T. Spalding, 21 April 1910, slide 72762, USNM.

Description. *Head.* Frons whitish; vertex scales pale brown basally, grading to white distally; labial palpus with medial surface whitish, lateral surface largely pale brown; antenna with thin brown line along dorsal surface and whitish lateral surfaces. *Thorax.* Dorsal surface gray brown; fore- and mid-legs with anterior surfaces brown, posterior surfaces whitish; hind-legs whitish; tarsi with alternating brown and whitish annulations. Forewing (Figs. 15, 16): ♂ FWL 6.5–6.7 mm (mean = 6.5, n = 3), AR = 3.29; costa straight to weakly arched; apex acute; termen weakly concave; dorsal surface grayish brown with dark brown markings; subbasal fascia not expressed; median fascia represented by indistinct outwardly oblique bar at mid-costa; proximal two-thirds of wing with fine longitudinal streaking, including thin brown line from base to tornus along CuP; ocellus edged proximally and distally by lustrous gray to beige bars, with whitish central field crossed by two blackish dashes; costal strigulae pale brown to whitish, more clearly defined from median fascia to apex; termen with thin white line from tornus to apex, followed distally by thin brown line and wider white line; fringe scales whitish with gray-brown cross-marks. Hindwing gray brown. *Abdomen.* Male genitalia (Fig. 32) (n = 3): Uncus broad, uniformly rounded, and barely differentiated from dorsolateral shoulders of tegumen; socii short and fingerlike; phallus moderately tapering distally; vesica with 11–13 deciduous cornuti (n = 3); valva with costal margin concave, NR = 0.62 (n = 3), SA obtuse (mean = 116°) (n = 3), clasper tablike with variably developed bladlike projection perpendicular to surface (Fig. 32a); cucullus with apex rounded, distal margin convex, anal angle developed into narrow projection with one spiniform seta at apex, medial surface densely setose; distal margin of cucullus with three to five spiniform setae that are noticeably stouter than adjacent setae on medial surface. Female genitalia unknown.

Distribution and biology. In addition to the holotype I examined two males in the CNC from Lost River badlands, 10 km south of Onefour, in the southeast corner of Alberta, collected by J.-F. Landry on 22 May 1982, and one male in the LACM from Scodie Meadow, Tulare Co., California, collected by J. P. Donahue on 25 May 1976.

Phaneta crassana (McDunnough)
(Figs. 17, 18, 33, 42, 50)

Thiodia crassana McDunnough 1938:99, Fig. 6;
McDunnough 1939:44.

Phaneta crassana: Powell 1983:33; Brown 2005:493.

Holotype: ♂, British Columbia, Kreuger Mt., Osoyoos, A. N. Gartrell, 9 May 1936, slide TOR-989, CNC.

Paratypes: BRITISH COLUMBIA: Kreuger Mt., Osoyoos, A. N. Gartrell, 9 May 1936 (1 ♂, slide 70041; 1 ♀, abdomen missing) USNM, (2 ♀, slide DJW 3071, abdomen missing) CNC, 12 May 1936 (1 ♂) CNC; Shingle Creek Road, Keremeos, A. N. Gartrell, 12 May 1936 (1 ♂) CNC; Shingle Creek, Penticton, A. N. Gartrell, 16 May 1936 (1 ♂) CNC; Brent's Lake, Penticton, A. N. Gartrell, 30 May 1935 (1 ♀) CNC. The paratype data are taken from pin labels and does not always agree in date/sex with that reported by McDunnough.

Description. *Head.* Frons whitish; vertex gray brown; labial palpus gray brown with white scaling on ventral margins of first and second segments; antenna with lateral surfaces white, dorsal surface brown. *Thorax.* Dorsal surface gray brown; legs whitish with anterior surfaces shading to pale gray brown; tarsi darker with whitish annulations. Forewing (Figs. 17, 18): ♂ FWL 7.1–8.4 mm (mean = 7.7, n = 4), AR = 3.44; ♀ FWL 7.1–8.9 mm (mean = 7.7, n = 5), AR = 3.23; costa nearly straight; apex acute; termen straight; dorsal surface gray brown with two prominent white streaks, one along costa, the other along cubitus, both extending from base to median fascia; subbasal fascia not expressed; median fascia represented by prominent dark bar at mid-costa; area between costal and cubital streaks usually with orange-brown tint; posterior margin of cubital streak edged with blackish brown; ocellus bordered proximally and distally by lustrous gray bars, with white central field crossed by two black dashes; ocellus bordered anteriorly by band of white-tipped gray-brown scales extending from median fascia to termen; costal strigulae from median fascia to apex white and sharply defined; termen with conspicuous white line from tornus to apex; fringe scales white with brown to blackish-brown cross-marks. Hindwing gray brown. *Abdomen.* Male genitalia (Fig. 33) (n = 6): Uncus moderately developed, clearly differentiated from dorsolateral shoulders of tegumen; socii short and stubby; phallus short, cylindrical; vesica with 34–43 deciduous cornuti; valva with costal margin concave, neck elongate with ventral margin weakly convex, NR = 0.56, SA obtuse (mean = 137°), clasper tablike; cucullus with apex rounded, distal margin convex, anal angle weakly produced; valval neck with elongate patch of setae on ventral one-half of medial surface; medial surface of cucullus densely setose. Female genitalia (Figs. 42, 50) (n = 2): Papillae anales laterally facing and moderately setose; lamella postvaginalis semi-rectangular, width ≈ 2 × length, with central trough weakly depressed and lateral ridges microspinulate; lamella antevaginalis ringlike, separated from sternum 7 by narrow band of membrane; posterior edge of sternum 7 emarginated to length of sterigma and fused with lateral margins of lamella postvaginalis; ductus bursae with sclerotized ring posterior to juncture with ductus seminalis; corpus bursae with two signa of nearly equal size.

Distribution and biology. I examined 15 specimens (9 ♂, 6 ♀) from southern British Columbia, southern Alberta, and central Nevada. Capture dates range from 9 May to 30 May.

Phaneta spectana (McDunnough)
(Figs. 19, 20, 34, 43, 51)

Thiodia spectana McDunnough 1938:100;
McDunnough 1939:44.

Phaneta spectana: Powell 1983:33; Brown 2005:496.

Holotype: ♂, Alberta, Edmonton, K. Bowman, 31 August 1930, slide TOR-1062, CNC.

Paratypes: same location & collector as holotype, 1 September 1936, (1 ♂) CNC, (1 ♂) USNM, (1 ♂) UASM.

Description. *Head.* Frons whitish; vertex pale gray brown; labial palpus with medial surface whitish, lateral surface pale gray brown; antenna whitish laterally, with dorsal surface gray brown. *Thorax.* Dorsal surface gray brown; legs gray brown anteriorly, whitish posteriorly, with whitish tarsal annulations. Forewing (Figs. 19, 20): costa weakly arched; apex acute; termen weakly concave; ♂ FWL 5.5–7.4 mm (mean = 6.6, n = 18), AR = 3.33; ♀ FWL 5.9–6.5 (mean = 6.1, n = 3), AR = 3.05; dorsal surface gray brown with pale orange-brown highlights and a thin white line on cubitus from base to subbasal fascia; subbasal fascia reduced to dark brown mark on cubitus and associated dark marks on costa and inner margin; median fascia represented by outwardly oblique bar from mid-costa to ocellus, connecting along proximal edge of ocellus to weakly expressed dark mark on inner margin; ocellus edged proximally and distally by lustrous gray bars, with orange-brown central field crossed by two black dashes; costal strigulae from median fascia to apex white, delimited by brown triangular marks, divided by orange-brown striae; fringe scales white with blackish-gray cross-marks. Hindwing brownish gray. *Abdomen.* Male genitalia (Fig. 34) (n = 6): Uncus moderately developed, apex rounded; dorsolateral shoulders of tegumen somewhat hunched; socii short, fingerlike; phallus moderately tapering distally; vesica with 6–12 deciduous cornuti; valva with costal margin very weakly concave, neck long, tapering distally, emargination of ventral margin semi-triangular, NR = 0.46, saccular corner sharply angulate, SA obtuse (mean = 112°), clasper represented by patch of stiff setae; cucullus with apex and anal angle rounded of nearly equal radius, distal margin nearly straight, basoventral margin overlapping ventral one-third of neck, medial surface densely setose. Female genitalia (Figs. 43, 51) (n = 2): Papillae anales laterally facing, moderately setose; lamella postvaginalis semi-rectangular, length ≈ width, microspinulate, with central trough weakly depressed; lamella antevaginalis ringlike; sternum 7 with posterior edge emarginated to length of sterigma, separated from lamella antevaginalis by narrow strip of membrane, but fused with anterior one-half of lateral margins of sterigma; lateral projections of sternum 7 sharply acute; ductus bursae with narrow sclerotized band posterior to juncture with ductus seminalis; corpus bursae with two signa of slightly different size.

Distribution and biology. I examined 30 specimens (27 ♂, 3 ♀) from Alberta, Iowa, Montana, Nevada, North Dakota, and South Dakota. Adults fly from the end of August to late September.

Phaneta kramerana, new species
(Figs. 21, 22, 35, 44, 52)

Diagnosis. The only other gray-brown Nearctic *Phaneta* with convex curvature of the ventral margin of the valval neck is *P. crassana*, which differs from *P. kramerana* in the shapes of the cucullus, uncus, and socii (Figs. 35 & 33) and in forewing appearance (Figs.

17, 18, 21, 22). The male genitalia of *P. kramerana* are most similar to those of *Phaneta mayelisana* Blanchard, a much larger whitish species with distinctly different forewing maculation (Blanchard 1979, figs. 1, 6). The female genitalia somewhat resemble those of *P. nepotinana* in that the sterigma is greatly reduced and the ductus seminalis arises relatively close to the ostium, but the flap-like structures on sternum 7 in *P. nepotinana* are not present in *P. kramerana*.

Description. *Head.* Frons and vertex white; labial palpus white with brownish-gray shading on lateral surface of second segment; antenna white with gray-brown dorsal streak. *Thorax.* Dorsal surface whitish, variably suffused with pale brown; legs pale brownish gray to whitish; tarsi with white annulations. Forewing (Figs. 21, 22): ♂ FWL 5.8–6.5 mm (mean = 6.1, $n = 4$), AR = 3.25; ♀ FWL 5.3–5.6 mm (mean = 5.5, $n = 4$), AR = 3.11; costal margin weakly arched; apex acute; termen weakly convex; dorsal surface white from cubitus to costa, with gray-brown to blackish-brown markings and some longitudinal brown streaking; region from CuA_2 to inner margin strongly suffused with gray brown; subbasal fascia variably expressed as dark mark between A_{1+2} and cubitus; median fascia a thin dash at mid-costa; ocellus with lustrous pale gray bars marking proximal and distal margins and two blackish longitudinal dashes on white to pale brown central field; fringe with patch of white scales (terminal strigula) at M_1 , otherwise white with black to gray-brown cross-marks. Hindwing whitish to pale gray brown. *Abdomen.* Male genitalia (Fig. 35) ($n = 4$): Uncus semi-triangular; dorsolateral shoulders of tegumen hunched; socii fingerlike, with distal one-half angling medially and tapering to apex; phallus moderately tapering distally; vesica with 16–23 deciduous cornuti; valva with costal margin concave, neck elongate, of uniform width, with convex ventral margin nearly parallel to costal margin, NR = 0.72, SA obtuse (mean = 141°), clasper represented by patch of stiff setae; cucullus with apex rounded, distal margin convex to nearly straight, anal angle weakly developed with rounded vertex, medial surface densely setose. Female genitalia (Figs. 44, 52) ($n = 3$): Papillae anales ventrolaterally facing, moderately setose; lamella postvaginalis weakly developed, bandlike, with posterior margin sometimes indented medially; lamella antevaginalis ringlike, rather wide at anterior margin of ostium; posterior edge of sternum 7 emarginated to length of sterigma and fused with lamella antevaginalis; ductus bursae with sclerotized band posterior to juncture with ductus seminalis, the latter located relatively near ostium; corpus bursae with two signa, one considerably larger than the other.

Holotype: (Fig. 21) ♀, California, San Bernardino County, Kramer Hills, J. A. Powell, 19 April 1958, slide DJW 2109, EME.

Paratypes: CALIFORNIA, same data as holotype (3 ♂, slides JAP 234, DJW 2108, 2632; 2 ♀, slide DJW 2145) EME; Inyo Co., Olancho, 1–7 May (1 ♀, slide DJW 2167) USNM; Los Angeles Co., April (1 ♂, slide DJW 3098) USNM.

Etymology. The specific epithet refers to the name of the type locality, Kramer Hills.

Distribution and biology. Seven of the eight types were collected in May and June at two sites along US Highway 395 in southern California: the Kramer Hills, located approximately 14 miles west of Hinkley, and Olancho, some 100 miles farther north.

Phaneta donahuei, new species

(Figs. 23, 24, 36)

Diagnosis. This moth was illustrated but not described by Wright (2011, fig. 33). It is distinguished from the other brownish-gray *Phaneta* considered here by valval shape (Figs. 25–36). There is some similarity in male genitalia among *P. donahuei*, *Phaneta labiata* Wright, and *Phaneta latens* (Heinrich), but in the latter two species the cucullus has a much more strongly developed anal angle and a basoventral margin that overlaps the ventral margin of the neck (Fig. 36, Wright 2010: figs. 55 & 57). Moreover, *P. donahuei* has a ridgelike clasper and a ridge along the ventral margin of the medial surface of the neck, neither of which occurs in the other two species.

Description. *Head.* Frons white; vertex whitish, tinted with tan; labial palpus white with tan suffusion on lateral surface of second segment; antenna concolorous with vertex. *Thorax.* Scales on dorsal surface pale brownish gray with white apices; fore- and mid-legs with anterior surfaces pale brown, posterior surfaces whitish, obscure white mark at mid-tibia; hind-legs mostly whitish; tarsi with whitish annulations. Forewing (Figs. 23, 24): ♂ FWL 6.8–7.9 mm (mean = 7.3, $n = 12$), AR = 3.17; costal margin weakly arched near base; apex acute; termen straight; dorsal surface pale brown with dark brown markings, the interfascial areas usually suffused with white; subbasal fascia reduced to diffuse mark on cubitus; median fascia consisting of outwardly oblique bar from mid-costa to ocellus and a variably expressed semi-triangular mark extending along proximal edge of ocellus from inner margin to cubitus; cell with diffuse whitish streak from base to median fascia; ocellus with lustrous gray to fawn bars along proximal and distal margins, white central field crossed by two blackish dashes; anterior margin of ocellus bordered by brown band connecting median fascia to mid-termen, extending from there to apex; costal strigulae white, particularly well-defined from median fascia to apex; fringe scales white with blackish-brown cross-marks, the marks aligned to form a thin white terminal line followed distally in turn by a thinner black line and a wider white line. Hindwing pale grayish brown. *Abdomen.* Male genitalia (Fig. 36) ($n = 8$): Uncus broad-based, distally rounded, clearly differentiated from dorsolateral shoulders of tegumen; socii short and stubby; phallus somewhat cylindrical; vesica with 31–41 deciduous cornuti; valva with costal margin concave, neck elongate with ventral margin of medial surface ridgelike, NR = 0.41, saccular corner broadly rounded, SA obtuse but ill-defined, clasper ridgelike; cucullus with apex evenly rounded, distal margin convex to nearly straight, anal angle acute and moderately produced, setation of medial surface coarse; anal angle with one stout stubby seta at vertex; medial surface of neck with elongate patch of setae along ventral margin. Female genitalia unknown.

Holotype: ♂, California, Kern County, Piute Mountains, Rancheria Creek, T29S R33E Sec. 23, 4350 ft., J. P. & K. E. Donahue, 1–3 June 1973, slide DJW 2796, LACM.

Paratypes: CALIFORNIA. Same data as holotype (4 ♂, slides DJW 2794, 3062, 3063) LACM; Kern County, Walker Pass, V. & M. Albu, 18 May 2006 (2 ♂, slides DJW 2615, 3087) DJW; Inyo County, Lone Pine, V. & M. Albu, 15 May 2009 (1 ♂, slide DJW 3086) DJW, Olancho, 8–15 June (1 ♂, slide 70079) USNM; San Bernardino County, Grace Vy. Ranch near Onyx

Summit, 2475m, Powell & Sperling, 26–27 June 1998 (1 ♂, slide 6519) EME, 2 km S. Wildhorse Spring, San Bernardino Mountains, 2450m, J. A. Powell, 26 June 1998 (1 ♂, slide 6518) EME; San Bernardino Mountains, 6200 ft., J. Grinnell, 19 June 1907 (1 ♂, slide DJW 3107), USNM.

Etymology. This species is named after Julian P. Donahue, one of the collectors of the series of five specimens from which the holotype was selected.

Distribution and biology. *Phaneta donahuei* is known from three California counties: Inyo, Kern, and San Bernardino. Adults were collected between mid-May and late June. The type locality is approximately thirty miles east of Bakersfield, California.

Remark. The paratype from Olancho, California is the specimen that was incorrectly illustrated by Heinrich (1923, fig. 131) as *Phaneta minimana* (see Wright 2010).

ACKNOWLEDGEMENTS

I thank J. W. Brown, J. P. Donahue, D. Grimaldi, J.-F. Landry, J. A. Powell, and F. Sperling for the loan of specimens. Val Albu, George Balogh, Lawrence Crabtree, and John Nordin provided additional specimens, and Kevin Tuck supplied label data on the syntypes of *P. tenuiana*. Two anonymous reviewers contributed helpful comments on the manuscript.

LITERATURE CITED

- BARNES, W. & J. McDUNNOUGH. 1917. Checklist of the Lepidoptera of Boreal America. Herald Press, Decatur, Illinois. 392 pp.
- BLANCHARD, A. 1979. Five new species of the tribe Eucosmini (Tortricidae). J. Lepid. Soc. 33:209–215.
- BROWN, J. W. 2005. Tortricidae (Lepidoptera) In World Catalogue of Insects 5:1–741.
- BROWN, J. W. & K. BASH. 2000. The Lepidoptera of Marine Corps Air Station Miramar: calculating faunal similarity among sampling sites and estimating total species richness. J. Res. Lepid. 36:45–78.
- FERNALD, C. H. [1903]. In Dyar, H. G., A list of North American Lepidoptera, U.S. Nat. Mus. Bull. 52:1–723.
- GILLIGAN, T. M., D. J. WRIGHT & L. D. GIBSON. 2008. Olethreutine moths of the Midwestern United States. An Identification Guide. Ohio Biological Survey Bulletin New Series. Vol. XVI, No. 2. vii + 334 p.
- HEINRICH, C. 1923. Revision of the North American moths of the subfamily Eucosminae of the family Olethreutidae. U.S. Nat. Mus. Bull. 123:1–298.
- MCDUNNOUGH, J. 1925. New Canadian Lepidoptera with notes. Can. Entomol. 57:11–23.
- . 1938. Some apparently new Eucosmidae (Lepid.). Can. Entomol. 70:90–100.
- . 1939. Check List of the Lepidoptera of Canada and the United States of America. Part II Microlepidoptera. Mem. South. Calif. Acad. Sci. 2:3–171.
- POWELL, J. A. 1983. Tortricidae, pp. 31–41. In Hodges, R. W. et al. (eds.), Check list of the Lepidoptera of America north of Mexico. E. W. Classey & Wedge Entomol. Res. Foundation. London, England.
- WALSINGHAM, T. DEGRAY, SIXTH EARL. 1879. Illustrations of typical specimens of Lepidoptera Heterocera in the collection of the British Museum, Part IV. North American Tortricidae. 88pp. + 17 Pls. Dept. of Zoology, British Museum, London.
- WRIGHT, D. J. 2010. Nine new species of *Phaneta* Stephens (Tortricidae) from western North America, with reviews of ten related species. J. Lepid. Soc. 64:117–138.
- . 2011. Review of the *Eucosma pulveratana* (Walsingham) species group, with descriptions of eight new species (Tortricidae). J. Lepid. Soc. 65:101–118.

Submitted for publication 12 September 2012; revised and accepted 30 October 2012.

LONGEVITY AND INDIVIDUAL ACTIVITY OF THE YUCCA MOTH, *TEGETICULA MACULATA*
EXTRANEAE (PRODOXIDAE), BASED ON MARK-RELEASE MONITORING

JERRY A. POWELL

Essig Museum of Entomology, University of California, Berkeley, CA; powellj@berkeley.edu

ABSTRACT. The life history and pollination biology of *Tegeticula maculata* (Riley), the sole pollinator of *Hesperoyucca whipplei* (Agavaceae), have been studied extensively, but individual moth longevity and plant-to-plant movements have remained poorly known. I recorded activity by capture, mark-release, and recapture of adult moths over a 12-day period at two sites near San Diego, California. Moths lived 2–10 days at room temperatures, and, in the field, marked *Tegeticula* lived 2–9 days between captures. In total, 51 of 145 (35%) marked and released moths were sighted on one or more subsequent days (33% of males, 37% of females). Males tended to stay in one or two adjacent inflorescences: 18 of 29 (62%) recaptures were recorded at the same plant as previous release, whereas females usually relocated to another plant on a following day: 24 of 29 (83%) were found on plants distant (> 2m, avg. 53 m) from the preceding capture. The results help confirm long-held assumptions that cross pollination of yuccas is provided through purposeful behavior by yucca moths moving from plant to plant.

Additional key words: Pollination, Agavaceae, Incurvarioidea, moth longevity

Members of the genus *Tegeticula* (Lepidoptera: Incurvarioidea, Prodoxidae) represent perhaps the most widely acclaimed classic example of plant-insect mutualism. Employing uniquely specialized maxillae of the mouthparts, the female moth gathers pollen, moves to another yucca where she oviposits into a floral ovary, then purposefully transfers pollen to the floral stigma. The resultant larvae feed on the seeds; each consumes only a small number, so many seeds are left intact. This symbiotic interaction was first observed by the botanist George Engelmann (1872) at the Missouri Botanical Garden. C.V. Riley, then the State Entomologist for Missouri, carried out extensive studies on yucca moths (Riley 1872, 1881, 1892, 1893) and used the wonderful story to help promote the importance of insects in pollination when he became Chief of the Entomology Division of the U.S. Department of Agriculture as first entomologist in the USDA and founder of the American Association of Economic Entomologists.

This story of biological coevolution has been repeated in floras and biology and entomology text books, often almost unchanged from Riley's accounts, even becoming increasingly simplified (e.g., Trelease in Riley 1892, Jepson 1951, Webber, 1953), but in reality the relationships have been discovered to be much more complex. Included are species acting as "cheaters" in the system, which are not modified for pollen transfer, fly later, and oviposit into young seed capsules (Addicott et al. 1990). Olle Pellmyr and his students, in a series of elegant studies based on molecular and morphological evidence, demonstrated that cheater species are independently derived at least three times (Pellmyr et al. 1996). Ultimately, Pellmyr (1999) described a complex of 13 *Tegeticula* species in the western U.S. among

populations formerly treated as *T. yuccasella* Riley, including two cheater species and 10 pollinators newly named.

Hesperoyucca (formerly *Yucca*) *whipplei* (Torrey) (Agavaceae) in California and Baja California (Fig. 1) harbors a distinctive pollinator, *Tegeticula maculata* (Riley), which was first collected by H. K. Morrison in Kern County in 1880. The typical moth in Sierra Nevada populations is white with evenly spaced black dots on the forewing distally (Fig. 2); there is a coastal phenotype (*apicella* Dyar) with apical, black blotch, that occurs from the Santa Monica Mountains northward; and south of the Transverse Ranges the moths' scaling is black (*T. m. extranea* H. Edwards; Fig. 3). Within *T. maculata*, Segreaves and Pellmyr (2001) defined three distinct lineages based on cytochrome oxidase1 mtDNA sequences, one represented by the northernmost population in the Sierra Nevada (Kaweah, Tulare Co.); a second includes Kern (typical) and coastal (*apicella*) populations; and the third clade consists of the black southern California populations (*extranea*) plus a slate gray race in Baja California Norte. The last is a southern geographic isolate, located approximately equally distant from *extranea* at the Mexican border as the latter is from the northern race in Tulare Co. Diurnal activity and black scaling may be thermoregulatory adaptations in response to early spring (February– March) flowering of *H. whipplei*, when nocturnal temperatures may deter moth activity.

Yucca moth activity. Describing the pollination process of *Tegeticula yuccasella*, Riley (1892) stated, "After collecting the pollen . . . she usually runs about or flies to another plant; I have often noticed that oviposition as a rule is accomplished in some other

flower than that from which the pollen was gathered.” There has been a general assumption this is the typical behavior of all *Tegeticula*.

For *Hesperoyucca whipplei*, Wimber (1958) made extensive observations of *T. maculata* behavior at the Rancho Santa Ana Botanic Garden, and found the moths active all day; dusk seemed to be the busiest time. She observed variation in female behavior, pollen collection, and searching for a suitable flower in which to oviposit. Consistently, upon withdrawal of the ovipositor, the female proceeded immediately to ascend the style to brush pollen over the stigma, then returned to oviposit in another groove of the same ovary, or more frequently, proceeded to another flower. Moths sometimes omitted the oviposition; one female consistently did so but pollinated many flowers, and one female was observed ovipositing and pollinating one day and replenishing her pollen load in the same inflorescence the following day. Wimber also carried out experiments with artificial pollination of *H. whipplei* and found that self-pollination generally is not as effective as cross-pollination. Aker and Udovic (1981) performed similar experiments at two localities in San Diego County, bagging individual branches of three inflorescences. Their results (0, 35, 0% capsules matured) supported Wimber's conclusion that *H. whipplei* is self-incompatible to a considerable extent. Because some other yuccas have been shown to be self incompatible, many authors have taken it for granted that the pollen-laden yucca moths regularly fly between separate plants, thus ensuring cross pollination. Powell & Mackie (1966) conducted studies of the interrelationships between *H. whipplei* and its moth guild. They described larval feeding habits, host partitioning, observed pollen collection, oviposition, and pollination.

Subsequently, Aker and Udovic carried out detailed studies of *Tegeticula maculata* and *H. whipplei*, including oviposition, pollination, and regulation of fruit numbers (Aker & Udovic 1981, Udovic 1981, Udovic & Aker 1981, Aker 1982,). They provided confirmation of Riley's reports on *T. yuccasella*; no female was seen ovipositing in the same inflorescence from which she collected pollen. They observed individuals of *T. maculata* in natural populations in Riverside and San Diego counties and concluded that females consistently disperse to another plant immediately after collecting pollen. In at least 9 of 12 instances the females crawled to branch tips, rested briefly, and then flew off. These flights were high, well above the surrounding vegetation, as are the yucca inflorescences, in a straight line, relatively long distances (i.e., “tens of meters”), often ignoring other yucca inflorescences closer by (Aker & Udovic 1981). None of these authors, however,

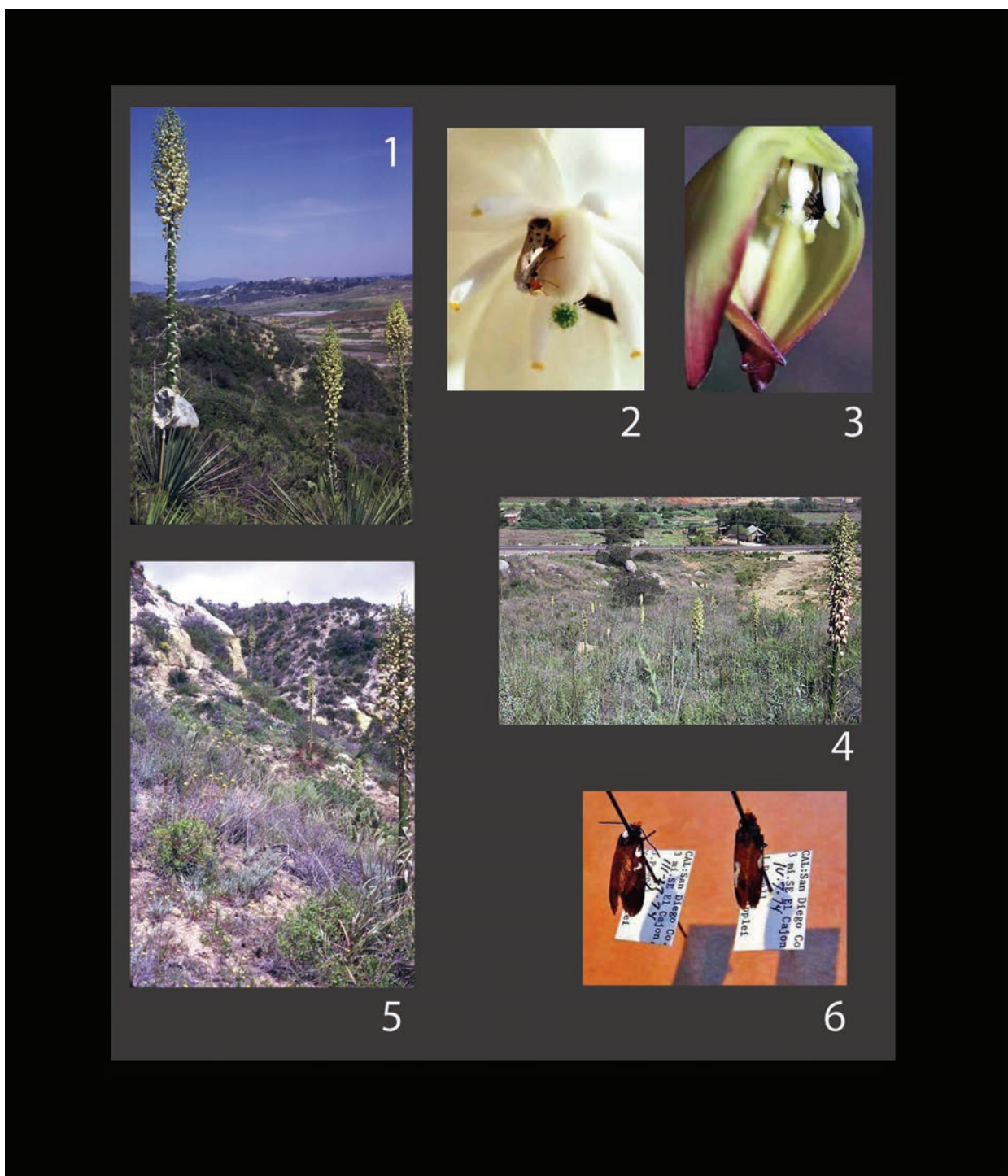
documented longevity and individual moth movements among plants subsequent to the initial flight following pollen collection; i.e., if and when females carried pollen from one plant to another.

In 1972, during the first 10 days of flowering by *Yucca schottii* in southern Arizona, I attempted a mark-release-recapture study to monitor individuals in a population of *Tegeticula* (later named *T. maderae* Pellmyr, 1999) and a member of its sister genus, *Parategeticula pollenifera* Davis, at Cave Creek in the Chiricahua Mountains (Powell 1984). However, too few marked individuals were recovered to yield meaningful results; in 32 hours observation time during daily examination of 50 panicles, I found only 38 individual *Tegeticula*. I marked and released 24 (12♂, 12♀), and only 2 males were sighted on subsequent nights, one after 52 hours on the same plant where it had been released, and the other in an inflorescence 15 m from its release site after 3 and 4 days. *Parategeticula* outnumbered its *Tegeticula* competitor by 4:1 at Cave Creek, but although I released 99 marked *Parategeticula*, only 3 males were recovered, each in its original inflorescence, after 8, 8, and 24 hours. At the same time I caged two pairs each of marked and unmarked *Parategeticula*, and they survived only 2–4 days. I doubted that all the pollinator moths regularly dispersed long distances and concluded they were short lived, perhaps only 1–4 days (Powell 1984).

Despite minimal results in Arizona, in 1974 I elected to attempt a mark-release study of *Tegeticula maculata* in southern California, reasoning that monitoring should be more efficient because moths of this race are diurnal and black, more easily observed in the white flowers than are adults of the *T. yuccasella* complex. Goals of this study were to provide data on longevity of individuals, determine if females regularly move from plant to plant, and investigate differences between the sexes in daily movements.

METHODS

Study sites. Observations were conducted concurrently at two sites in San Diego Co., California: **A**) an inland locality off Jamacha Road, ca. 6 km SE of El Cajon. This was a gently sloping area of sparse chaparral vegetation that had been disturbed by recent construction of access roads to new home sites, building of which had not commenced (Fig. 4); and **B**) a coastal bluff at Manchester Road just east of Highway I-5. This was a steep sandstone slope supporting dense chaparral, and many of the yucca in bloom were difficult to access (Fig. 5). They were separated by about 43 airline km, with intervening urban development for many decades, industrial and agricultural plots, and the Miramar Naval Air Station, a region that included colonies of the yucca.



FIGS. 1–6. **1**, Upper Left, *Hesperoyucca whipplei* in bloom near Manchester Road (Study Site A), San Diego Co., California. Each inflorescence develops flowers during a period of 3–4 weeks or more. The net in foreground is 2.5 feet in height. **2**, female *tegeticula m. maculata*, typical form, in oviposition posture, head downward in pendant flower of *Hesperoyucca whipplei*, Tulare Co., Calif. **3**, female *T. maculata extranea* in oviposition posture in flower of *H. whipplei*, petals cut away, in San Diego Co., Calif. **4**, view down-slope at the El Cajon Study Site A, with *Hesperoyucca* coming into bloom. **5**, View across the steep bluff near Manchester Road, Study Site B. **6**, Pinned specimens bearing white markings employed to distinguish individuals of *T. Maculata extranea*, captured on the first day of observations at Site A.

These two yucca populations had extensive colonies of *Hesperoyucca whipplei* flowering in similar density.

Site A included an observation area about 150 × 90 m, defined by a two-lane county road along its lower margin and by paved cul-de-sac roads along its northern and western border. Additional habitat with yucca occurred <20 m away, so moths readily could fly to plants outside the monitored area. By March 27, 15 yuccas had begun blooming, including one nearly finished, and others in bud stage began flowering during subsequent days. A total of 70 *Hesperoyucca* bloomed in Site A during the 12-day study period.

At Site B the observation area was arbitrarily defined within a much larger area supporting an enormous colony of *Hesperoyucca*, an estimated 150–200 plants in bloom across a wide sandstone cliff and its subtending talus slope. The study site was defined by two parallel ridges perpendicular to the slope, by the sandstone cliff on the north, and a graded road and agricultural field on the lower, south border. Thus defined, site B was similar in area to Site A, ca. 150 × 80 m in right angle area, but most of the flowering yuccas were concentrated in a central zone ca. 80 × 60 m, with scattered clusters of plants to the east and west. In total, 43 inflorescences were sufficiently accessible to enable daily sampling, including two in late bloom at study onset, March 28, and three newly flowering on the last observation day, April 7.

Daily monitoring. I visited one or both sites daily during a 12-day period: at site A from March 27 to April 7 (except March 31 and April 3); and at site B from March 29 to April 7 (except March 30 and April 3 and 6). Hence there were 9 and 6 days at the two sites respectively during which individually marked moths could be recovered. Typically, the inland San Diego area is warm early in the day, while at the coast fog persists until late morning or later. I visited Jamacha Road (A) for 2–3 hours starting ca. 1100 PDT, then drove to Manchester Road (B) for afternoon observations but not after 1800 PDT. Each inflorescence was numbered, mapped, and monitored daily as thoroughly as feasible for change in flowering sequence and for moth activity. At site A, I employed a 3-foot stepladder to access inflorescences on taller stalks, whereas at site B the steep terrain did not permit use of a stepladder, but taller inflorescences usually were reachable, at least by net, from the steep slope above the plant.

Each *Tegeticula* was captured into a plastic vial or netted, and its sex, time, pollen load, and yucca plant number recorded. New specimens were marked, and all the data and other observations were tape recorded. After marking, I attempted to reintroduce each moth into a flower in the same inflorescence where it had been

captured. Nonetheless, about 14% of males and 25% of females flew off upon release, usually to nearby plants and were recaptured.

Marking technique. The southern California race of *Tegeticula maculata* has black forewing and thoracic scaling (Fig. 3). Therefore, marking individuals with felt-tipped pen, a technique favored by butterfly population biologists, was not feasible. Instead, I employed white Liquid Paper® typewriter correction fluid. I immobilized the captured specimen between layers of netting, without attempting to hold it by grasping with fingers or forceps; thus positioned, I applied 1, 2, or 3 small, white spots to left or right FW, either anteriorly or posteriorly, and/or on the prothorax (e.g., Fig. 6). I tape-recorded the Liquid Paper spot patterns and each evening reproduced them graphically on paper for field reference on subsequent days. After day 5 at Site A, with 47 moths marked, I began adding a red dot by felt-tipped marker to one of the white marks, on newly assigned moths #48–67, and later a green dot on #68–100. At Site B fewer *Tegeticula* were marked, and a red dot was added to moths #28–45. I assumed there was no chance that an individually marked moth would migrate 43 km to be found at the other site and did not try to maintain separate patterns or colors for individual moths at the two sites.

At the onset of study, I captured 6 *Tegeticula* (5♂, 1♀) and marked 3 with white spots of Liquid Paper to test its permanency and possible effects on longevity. These were confined in a small terrarium at household temperatures with a water source, although *Tegeticula* are not known to feed.

RESULTS

Abundance. There is enormous variation in relative abundance of *Tegeticula maculata* among different populations of *Hesperoyucca* and from year to year (Powell & Mackie 1966, Aker & Udovic 1981). Coastal *Hesperoyucca* are solitary—each plant dies after flowering once—and the number of inflorescences developing in a colony in any given year appears to be correlated with winter and spring rainfall. By contrast, desert populations consist of caespitose plants, vegetative clumps of many rosettes. As a result, hundreds of flowering stalks develop every year in a given colony, but the prodoxid moths are rare, in contrast to fewer inflorescences and more numerous *Tegeticula* in coastal solitary plant populations (Powell and Mackie 1966).

During the present study, in ca. 42.5 hr field observation time, I recorded 195 sighting events of *T. maculata* at Site A, including original capture and sighting of the same individuals on subsequent days, and 69 at Site B. This low frequency is in marked contrast to

TABLE 1. *Tegeticula maculata*: Movements by individual moths (site A = Jamacha Rd.; site B = Manchester Rd.)

Moths marked	Site	Moths resighted	Total resight events	Resight at same/ adjacent plant	Resight at distant plant
49 ♂	A	15 (31%)	29	18 (62%)	11 (38%)
20 ♂	B	8 (40%)	14	7 (50%)	7 (50%)
51 ♀	A	21 (41%)	30	5 (17%)	25 (83%)
25 ♀	B	7 (28%)	10	5 (50%)	5 (50%)
TOTAL					
69 ♂♂		23	43	25 (58%)	18 (42%)
76 ♀♀		28	40	10 (25%)	30 (75%)

my experience with some other populations of *T. maculata*, where several could be observed at any given inflorescence, including many females engaged in oviposition. My total number of sightings was meager compared to daily numbers recorded by Aker and Udovic (1981) in the Santa Rosa Mountains, Riverside Co., Calif. (i.e., daily peaks of 400–500+), but I monitored approximately the same number of inflorescences (ca. 113) as did Aker and Udovic (1981) at two sites in 6-day intervals during 1979. The abundance of *T. maculata* observed during my study (30–40/day) cannot be compared on an individuals per hour basis because the capture, marking, release, and recording appreciably slowed the process.

Recapture success. At Jamacha Road (A), 100 *Tegeticula* (49♂, 51♀) were successfully marked and released; 36 of them were sighted on at least one subsequent day. Of the marked moths released, 15 males (31%) and 21 females (41%) were recovered, and a total of 95 recaptures were recorded for the 36 moths (Table 1). Among those recovered, 4 males and 8 females were seen only on the following day. Moreover, 3♂, 8♀ (30%) were recorded on the last day, 4 of those (1♂, 3♀) only on the last two days of observation, so might well have been encountered again had the study continued. At Manchester Road (site B), 45 *T. maculata* were marked and released, 15 of which were sighted on one or more subsequent days. These included 8 males (40% and 7 females (28%) and 24 total recapture events (Table 1).

Mating, pollen collection, and oviposition. Considering the time devoted to field observations during the 10-day study, I encountered relatively few instances of mating and oviposition and none of pollen collection. Mating was observed only twice, both at Site A: 1) on March 29, 1430 PDT, female #22, which carried no visible pollen load, with male #11, which had been marked the previous day. 2) March 30 at ca. 1330, neither male nor female had been previously marked.

The latter female was recaptured without pollen at 1210 on April 1 >110 m from the inflorescence where mating occurred two days previously. Females engaged in oviposition were recorded on 8 occasions, all but one at Site A, at various times, 1150 to 1645 PDT; 5 times (62%) between 1430 and 1520. All 5 carried pollen.

Longevity. Confined *Tegeticula* lived 2 to 10 days (avg. 5.5); unmarked individuals lived 5, 5, and 10 days, while marked specimens lived 2, 3, and 8 days; two were observed perched on cotton water wick but were not seen feeding. This trial suggested that the Liquid Paper applied to wings or thorax had minor adverse affect on longevity and indicated the markings were permanent for the duration of my study.

In the field, recaptured *T. maculata* that were marked during the first 4 days, March 27–30, provided the best estimate of longevity. At site A, recaptured males that were released March 27–30 (n = 7) lived 4–8 days (avg. 6.3), and females (n = 8) were recorded during 2–10 day spans (avg. 5.6). These are first to last dates observed, inclusive, and represent the minimum number of days individuals lived. Some may have eluded notice one or more days prior to first capture and/or after the last sighting. Moths marked and recaptured after March 30, with successively fewer observation days following marking, averaged shorter recapture spans. Statistical analyses of male-female relative abundance and longevity are subject to sampling error because males were active, easily seen moving from flower to flower, whereas females spent much of the time engaged in oviposition or resting deep in the flowers (Fig. 3). Moreover, temperatures were usually much lower and moth activity reduced at Site B.

Male movements. Males patrolled ceaselessly from one flower into another, not taking flight unless disturbed by the observer. They displayed a tendency to remain in the same or an adjacent (<2 m distant) inflorescence over several days—At site A, 15 marked

TABLE 2. *Tegeticula maculata*: ♂♂ movement documented by recapture (El Cajon site A)
 + = 1st mark-release; ● = same or adjacent yucca; ○ = distant yucca; – = no observation

Day:	1	2	3	4	5	6	7	8	9	10	11	12
Moth #												
4	+	●		○	–			–				
7		+	●	●,○	–		○	–				
11		+	●,○		–		●	–				
12			+	●	–	●	●	–	○			
25				+	–	●		–		○		
28				+	–		○	–	●			
30				+	–	○		–			○	
39					–	+	●	–				
41					–	+	●	–				
43					–	+	●	–				
54					–		+	–		●		
57					–			–	+	○	●	
64					–			–	+	●		
69					–			–		+	●	○
93					–			–			+	●

TABLE 3. *Tegeticula maculata*: ♀♀ movement documented by recapture (El Cajon site A)
 + = 1st mark-release; ● = same or adjacent yucca; ○ = distant yucca

Day:	1	2	3	4	5	6	7	8	9	10	11	12
Moth #												
5	+	○										
13			+						○		○	
17			+			○						
18			+	●								
19			+									○
22			+				○		○	○		
29				+		○	○					
32				+		○			○			
34						+	○		○			
35						+			○			
36						+,○						
37						+	●					
42						+	●					
47						+			○		○	●
73										+		○
77										+		○
82										+	○	
88											+	○
92											+	○
96											+	○,○
100											+	●

males were recovered 29 times, 18 (62%) in the same inflorescence as the preceding record, and 11 (38%) on more distant plants (Table 2). On average, the latter moved long distances (2–98 m, avg. 49 m).

Nine individual moths recorded on 3 or more dates were sighted 12 times in the same or 2 adjacent inflorescences. Male #12 was seen on the same plant on 4 dates spanning 5 days (Table 2). Three males flew off upon first release on March 30, and each was recovered on April 2 or 3, two from distant plants (25, 58 m), and one had returned to the original inflorescence of capture.

Female movements. Females at Site A. recorded two or more times usually had relocated to another plant each time (Tables 1, 3). Only 5 of 29 (17%) marked females were found in the previous inflorescence on a following day, a highly significant contrast to males ($\chi^2 = 10.942$, $df = 1$; $p = 0.0009$).

One female (#47) was found on the same plant 2 and 3 days after having flown from its original yucca upon release. Female #22 was observed on 4 different yucca plants over a 7-day period. Four females flew off upon first release, and all four were recovered in different plants on one or 2 later dates, 12–32 m distant (Tables 1, 3). Of the 21 marked females recorded again 29 times, 24 (83%) were recovered in different plants than the preceding capture, only 5 in the same inflorescence (Table 3). On average, females moved long distances (15–115 m, avg. 53.5 m), and their net average movement distance was 44.2 m, reflecting the more prevalent plant to plant movements by females.

Recaptures at Manchester Rd. (B) (14♂, 10♀) were too few to be significant, and equal numbers of each sex were recorded at the plant of preceding capture and at distant plants (Table 1). Overall, combined data from the two sites were 58% of 43 male recaptures had remained in the release inflorescences, whereas only 25% of 40 recaptured females had done so; 75% moved to a distant inflorescence, and the difference from males is highly significant ($\chi^2 = 8.023$, $df = 1$; $p = 0.0046$).

DISCUSSION

The 4–10 days life span recorded in the field was longer than expected, based on reports for *Tegeticula yuccasella* and my experience with mark-release of *T. maderae* on *Yucca schottii* (Powell 1984). Rau (1945) studied *Yucca filamentosa*–*T. yuccasella* relationships during several seasons at Kirkwood, MO. He found males lived 2–3 days, females 3–5 days in the laboratory. That lifespan has been quoted by subsequent authors (Marr et al. 2000 based on Kingsolver 1984, Dodd and Linhart 1994), but

evidently there has not been a study of yucca moth longevity in the field comparable to this one.

Marr et al. (2000) used fluorescent dyes to test the prediction that yucca moths primarily perform out-cross pollination. They dusted different color dyes on the anthers of newly opened flowers of *Yucca filamentosa* at five sites in Ohio and Tennessee, then subjected all inflorescences within each local population to ultraviolet light later the same night. Although transfers occurred up to 50 m radius from the source plant, they found pollen was moved primarily among flowers within an inflorescence or between plants in close proximity; e. g., 80% of transfers occurred within 8 m and 50% of pollen collections were followed by oviposition and pollination on the same plant. This contrasts markedly to the behavioral sequence of *T. maculata* on *H. whipplei* observed by Aker and Udovic (1981) and indicated by results of the present study.

Based on DNA analysis of Agavaceae and related plants, Bogler et al. (1995) concluded that *Yucca sens. lat.* is polyphyletic, with *Hesperaloë* a sister to *Hesperoyucca* after divergence from the *Yucca* lineage. They suggested the yucca–yucca moth association therefore must have originated at least twice. The parsimony is based on characteristics of the Agavaceae. The conclusion that the yucca moth association must have evolved two or more times is not believable. The Bogler et al. proposal would require ignoring the numerous evolutionary steps during origin and development of the maxillary tentacles, together with correlated female moth behavior, which are without homologous development throughout Lepidoptera worldwide.

There are minor differences in pollination behavior between the *Tegeticula maculata*–*Hesperoyucca* association and those exhibited by other *Tegeticula* species and their host yuccas.

These involve differences in the plant; because the pollen of *Hesperoyucca* is glutinous, the female *T. maculata* drags several pollinia into a sticky ball that is carried in the same manner as the granulated pollen masses by other *Tegeticula*. *T. maculata* then scrapes the pollen across the capitate stigma of *H. whipplei*, contrasted with other *Tegeticula*, pushing it into the open stigmatic duct characteristic of other yuccas. The origin of the maxillary tentacles, their morphology, musculature, nervous system cues, and the elaborate female moth behavior are fundamentally the same and provide a uniquely derived character complex. Another evolutionary origin other than that indicated by the plants must have been the foundation of the complex. For example, during early radiation of Agavaceae,

ancestral *Parategeticula* may have adapted to seed feeding, although their oviposition occurs externally on the inflorescence stems (Davis 1967, Powell 1984). Adaptation to pollinating by a *Parategeticula* ancestor, which is effective in absence of *Tegeticula* (Powell 1984), may have developed later. Oviposition into the ovaries presumably evolved early in the *Tegeticula sens. lat.* lineage prior to the *Hesperoyucca* + *Hesperaloë* split. Bogler et al. (1995) presumed yucca-yucca moth symbiosis probably arose when one of the seed-feeding prodoxid moths, precursor to the *Tegeticula* + *Parategeticula* lineage, evolved the ability to purposefully pollinate the plant upon which its larvae fed. They proposed two possible origins:

Scenario 1) yucca moth pollination evolved in the ancestor of *H. whipplei* + *Hesperaloë* and *Yucca* prior to evolution of the floral specialization of *Yucca sens. str.* The yucca moth pollination syndrome subsequently could have been lost from the *Hesperaloë* lineage and retained in *H. whipplei* without development of stylar and stigmatic specialization now seen in the *Yucca sens. str.* complex—i.e. distinctly recessed stigma, clavate and often bent filaments, outward pollen presentation, little or no nectar, and nocturnal blooming, all of which would have been developed later in the *Yucca sens. str.* clade. This scenario retains a single origin of yucca moth pollination and requires loss of dependence by *Hesperaloë* and associated morphological features of an early yucca association. *Hesperaloë* are arid habitat plants of the Chihuahuan Desert having tubular corollas. They are pollinated by hummingbirds (Pellmyr and Augenstein 1997) and possibly hawk moths, bees and bats, in horticultural situations, but not by prodoxid moths (Bogler et al. 1995).

In **Scenario 2)** Ancestors of *Hesperaloë* + *Hesperoyucca whipplei*, and *Yucca* had a presumably general zoophilous pollination system, which was retained by the *H. whipplei* + *Hesperaloë* clade, whereas the ancestors of *Yucca sens. str.* became adapted to yucca moth pollination. Selection to reduce the costs of resource-based pollination (small anthers loss of nectar production, perhaps recessed stigma) led to dependence on *Yucca* seen now. They suggest that a secondary yucca with mutualism apparently arose when an ancestor of *Hesperoyucca whipplei* was colonized by a yucca moth as a pollinator. Reduction/loss of nectar production and elaboration of the large, cup-shaped white flowers would have resulted as convergent features evolved with increased dependency on yucca moths as pollinators. Other features would have been retained from a previous pollination system. Bolger et al. favor this

scenario because it is more parsimonious than the single-origin hypothesis, and later authors have accepted this alternative (e.g. Smith et al. 2008).

Bogler et al.'s first scenario seems more plausible, requiring multiple losses in the *Hesperaloë* lineage but not a repeat origin of the yucca/yucca moth complex, in which several otherwise uniquely derived features would need to have evolved a second time: development of novel, movable, paired appendages on the base of the maxillae and their musculature; development of cues from the brain to direct purposeful collection of pollen and transfer of it to the stigma; oviposition into the immature yucca ovary. An alternative, more parsimonious scenario would be early origins of the yucca-moth association (e.g. during the Paleocene (Pellmyr and Leebens-Mack 1999), followed by separation of the *Hesperaloë* + *Tegeticula maculata* lineage. Later success of *Hesperaloë* would have been dependent upon evolving plant characteristics for attraction of pollinators, with concurrent loss of characteristics favorable to and dependent on yucca moths.

The phylogenetic relationships derived by Pellmyr et al. (2008), with the *T. maculata* lineage sister to the rest of the *Tegeticula*, best represent our current understanding of the pollinator genera but do not entirely reflect the phylogeny of Agavaceae. Certainly we do not have all pieces of the puzzle because there is a 20-million year discord between the age of *Yucca* (6–10 Myr) (Smith et al. 2008) and best estimates for the age of the pollinators (32–40 Myr) (Pellmyr and Leebens-Mack 1999).

CONCLUSIONS

Results of the present study support the beliefs by Riley in the 19th Century and numerous subsequent biologists for *Tegeticula* in general and *T. maculata* in particular: females mate prior to or following pollen collection, leave the pollen source and fly to distant plants (e.g. 20–100 m) for oviposition and purposeful pollen transfer. On subsequent days, each female usually moves to a different plant, whereas males in search of mates often remain in one or two adjacent inflorescences day after day. Individual moths live longer than had been supposed, up to at least 9–10 days. Despite their conspicuous black color in the white flowers, no predator activity has been recorded. Their color may be a thermoregulatory adaptation favoring diurnal activity in early spring when temperatures are low contrasted with warm evenings prevalent in habitats occupied by other species of *Tegeticula*.

ACKNOWLEDGMENTS

Peter Oboyski, UC Berkeley, assisted with formatting the tables and statistical assessment. Suggestions by two anonymous reviewers improved clarity and expanded the content and focus of the discussion.

LITERATURE CITED

- ADDICOTT, J. F., J. BRONSTEIN, AND F. KJELLBERG. 1990. In Gilbert, F. (ed.) Genetics, Evolution, and Coordination of Insect Life Cycles: 143–161; Springer-Verlag.
- AKER, C. L. 1982. Spatial and temporal dispersion patterns of pollinators and their relationship to the flowering strategy of *Yucca whipplei* (Agavaceae). *Oecologia* 54: 243–252.
- AKER, C. L. AND D. UDOVIC. 1981. Oviposition and pollination behavior of the yucca moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relation to the reproductive biology of *Yucca whipplei* (Agavaceae). *Oecologia* 49: 96–101.
- BOGLER, D. J., J. L. NEFF, AND B. B. SIMPSON. 1995. Multiple origins of the yucca-yucca moth association. *Proc. Natl. Acad. Sci.* 92: 6864–6867.
- DAVIS, D. R. 1967. A revision of the moths of the Subfamily Prodoxinae (Lepidoptera: Incurvariidae). *Bull.* 255, Smithsonian Inst., U. S. Natl. Museum; 170 pp.
- DODD, R. J. AND Y. B. LINHART. 1994. Reproductive consequences of interactions between *Yucca glauca* (Agavaceae) and *Tegeticula yuccasella* (Lepidoptera) in Colorado. *Amer. J. Botany* 81: 815–825.
- ENGELMAN, G. 1872. The flower of *Yucca* and its fertilization. *Bull. Torrey Bot. Club* 3: 33.
- JEPSON, W. L. 1951. A Manual of the Flowering Plants of California. U. Calif. Press, Berkeley and Los Angeles; 1238 pp.
- KINGSOLVER, R. W. 1984. Population biology of a mutualistic association: *Yucca glauca* and *Tetgeticula yuccasella*. Ph. D. Dissertation; Univ. Kansas.
- MARR, D. L., J. LEEBENS-MACK, L. ELMS, AND O. PELLMYR. 2000. Pollen dispersal in *Yucca filamentosa* (Agavaceae): the paradox of self-pollination behavior by *Tegeticula yuccasella* (Prodoxidae). *Amer. J. Botany* 87: 670–677.
- PELLMYR, O. 1999. Systematic revision of the yucca moths in the *Tegeticula yuccasella* complex (Lepidoptera: Prodoxidae) north of Mexico. *Syst. Entomol.* 24: 243–271.
- PELLMYR, O. AND E. J. AUGENSTEIN. 1997. Pollination biology of *Hesperaloe parviflora*. *Southwest Naturalist* 42: 182–187.
- PELLMYR, O., M. BALCÁZAR-LARA, K. A. SEGRAVES, D. M. ALTHOFF, AND R. J. LITTLEFIELD. 2008. Phylogeny of the pollinating yucca moths, with revision of Mexican species (*Tegeticula* and *Parategeticula*; Lepidoptera, Prodoxidae) *Zool. J. Linn. Soc.* 152: 297–314.
- PELLMYR, O. AND J. LEEBENS-MACK. 1999. Forty million years of mutualism: Evidence for Eocene origin of the yucca-yucca moth association. *Proc. Natl. Acad. Sci.* 96: 9178–9183.
- PELLMYR, O. AND J. N. THOMPSON. 1992. Multiple occurrences of mutualism in the yucca moth lineage. *Proc. Natl. Acad. Sci. USA* 89: 2927–2929.
- PELLMYR, O., J. N. THOMPSON, AND C. J. HUTH. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* 380: 155–156.
- POWELL, J. A. 1984. Biological interrelationships of moths and *Yucca schottii* (Lepidoptera: Incurvariidae, Cochylidae, Blastobasidae). U. Calif. Publ. Entomol. 100: 93 pp., 49 figs.
- POWELL, J. A. AND R. A. MACKIE. 1966. Biological interrelationships of moths and *Yucca whipplei* (Lepidoptera: Gelechiidae, Blastobasidae, Prodoxidae). U. Calif. Publ. Entomol. 42: 146, 6 pl.
- RAU, P. 1945. The yucca plant, *Yucca filamentosa*, and the yucca moth, *Tegeticula (Pronuba) yuccasella* Riley: An ecologico-behavior study. *Annals Missouri Bot. Garden* 32: 373–394.
- RILEY, C. V. 1872. Insects shaped by the needs of flowers. In Anonymous, Report Amer. Assoc. Advance. Sci., Dubuque Iowa, 1872 Meeting. *Nature* 6: 444.
- RILEY, C. V. 1881. Further notes on the pollination of yucca and on *Pronuba* and *Prodoxus*. *Proc. Amer. Assoc. Advance. Sci.*, 1880: 617–639.
- RILEY, C. V. 1892. The yucca moth and yucca pollination. *Third Ann. Rept. Mo. Bot. Garden*: 99–159.
- RILEY, C. V. 1893. Further notes on yucca insects and yucca pollination. *Proc. Biol. Soc. Washington* 8: 41–54.
- SEAGRAVES, K. A. AND O. PELLMYR. 2001. Phylogeography of the yucca moth *Tegeticula maculata*: the role of historical biogeography in reconciling high genetic structure with limited speciation. *Molecular Ecol.* 10: 1247–1253.
- SMITH, C. I., O. PELLMYR, D. M. ALTHOFF, M. BALCÁZAR-LARA, J. LEEBENS-MACK AND K. A. SEGRAVES. 2008. Pattern and timing of diversification in *Yucca* (Agavaceae): specialized pollination does not escalate rates of diversification. *Proc. Royal Soc. B* 275: 249–258.
- UDOVIC, D. 1981. Determinants of fruit set in *Yucca whipplei*: reproductive expenditure vs. pollinator availability. *Oecologia* 48: 389–399.
- UDOVIC, D. AND C. L. AKER. 1981. Fruit abortion and the regulation of fruit number in *Yucca whipplei*. *Oecologia* 49: 245–248.
- WEBBER, J. M. 1953. Yuccas of the Southwest. U. S. Dept. Agric., Agric. Monograph 17; 93 pp., 71 pl.
- WIMBER, D. R. 1958. Pollination of *Yucca whipplei* Torr. M. S. Thesis, Claremont Graduate School, Claremont, Calif. [unpublished].

Submitted for publication 29 October 2012; revised and accepted 15 May 2013.

Journal of the Lepidopterists' Society
67(3), 2013, 196–205

LIFE HISTORY TRAITS AND REARING TECHNIQUES FOR FALL WEBWORMS (*HYPHANTRIA CUNEA* DRURY) IN COLORADO

KATRINA J. LOEWY*, AMY L. FLANSBURG§, KYLEE GRENIS§,
MACKENZIE K. KJELDGAARD§, JENNIFER MCCARTY§, LILY MONTESANO§,
JENNIFER VERNICK§ AND SHANNON M. MURPHY

University of Denver Department of Biological Sciences, 2190 East Iliff Ave., Denver, CO 80208, USA

*Email: kjloewy@gmail.com

ABSTRACT. The fall webworm (*Hyphantria cunea* Drury) is a moth species native to North America and an invasive pest in Europe and Asia. *Hyphantria cunea* larvae are noted generalists, and have been recorded feeding on dozens of plant families worldwide. There appear to be at least two forms of *H. cunea* that are distinguished by the larval head capsule color: black or red. Most previous accounts of *H. cunea* in the literature focus on the black-headed form. The three goals of the research we present here are to 1) detail successful rearing techniques for the red-headed form of *H. cunea*, 2) describe life history traits of red-headed *H. cunea* in Colorado and 3) test whether female pupal mass predicts potential fecundity for *H. cunea* as well as other lepidopteran species. Our data are compiled from two years of rearing experiments in the lab. In addition, we compare measures of life history traits from our research with those of other collections of *H. cunea* from Asia, Europe, Canada, and other regions of the United States to enable a better comparison between the black-headed and red-headed forms of *H. cunea*.

Additional key words: Arctiidae, Erebidae, fitness, life history, potential fecundity

The fall webworm (*Hyphantria cunea* Drury) is a moth species native to North America and an invasive pest in Europe and Asia (Tadić 1963, Yang et al. 2008). The gregarious larvae spin extensive webs for protection (Ito 1977) and thermoregulation (Morris and Fulton 1970, Rehnberg 2002, 2006), usually on the outer branches of deciduous trees. *Hyphantria cunea* are noted generalists and have been recorded feeding on dozens of plant families worldwide (Warren and Tadić 1970). Their preferred hosts are deciduous, woody plants, but larvae have been observed on herbaceous plants like *Clematis* (Swain 1936) and even gymnosperms (Oliver 1964).

The taxonomic status of *H. cunea* is unclear. There are at least two genetically distinct ‘races’ or forms of *H. cunea* in North America (Jaenike & Selander 1980) capable of interbreeding to produce fertile offspring (Oliver 1964, Masaki & Ito 1977). Morphologically, the only distinguishing feature is larval coloration: a black-headed form and a red or orange-headed form. The two larval forms are also behaviorally distinct as fifth instar larvae; black-headed *H. cunea* leave the web during the ultimate instar and become solitary (Szalay-Marzso 1972), whereas red-headed *H. cunea* are reported to cluster within the communal web until pupation (Oliver 1964). Masaki and Ito (1977) noted a third form with a mottled head native to North America. Because red and mottled-headed larvae create a much thicker web that spreads to the crook of

the host tree, similar to the behavior of tent caterpillars, they are sometimes referred to collectively as *Malacosoma*-type *H. cunea* (Masaki & Ito 1977). We do not distinguish between red and mottled-headed *H. cunea*, both of which may exist in Colorado, and refer to the *H. cunea* form that we study as red-headed. Within North America, the black-headed form is primarily in the east and northeast, whereas the red-headed form is mostly in the south and west, with large areas of sympatry (Masaki 1977). Voltinism is graded geographically; *H. cunea* populations in the northeastern United States and Canada are univoltine, and populations in the Gulf States and Mexico have been observed with four or more generations per year (Masaki 1977). Where red and black-headed forms co-occur in the mid-Atlantic, they are phenologically distinct, with a univoltine red-headed generation emerging between two black-headed generations (Masaki 1977). Host selection also differs between the two forms, however, there is some overlap (Oliver 1964).

Several researchers have published rearing techniques for *H. cunea* on both natural host plants and artificial media (Jasič & Macko 1961, Yearian et al. 1966, Morris & Fulton 1970,) as well as studies of larval fitness on natural host plants (Jasič & Macko 1961, Morris & Fulton 1970, Greenblatt 1978, Gomi et al. 2005, Mason et al. 2011). However, all of these studies have focused on the black-headed form, which is the only form present in Europe and Asia, and there are very few studies on the red-headed form (but see Oliver 1964, Masaki & Ito 1977). For this paper we had

*Corresponding Author

§Authors contributed equally to this research and are listed in alphabetical order

three objectives. Our first objective was to provide the first published account of successful rearing techniques for red-headed *H. cunea*. Our second objective was to measure and report life history traits of *H. cunea* in Colorado and to compare them with other published accounts. Our third objective was to test whether female pupal mass predicts fecundity, and thus lifetime fitness, for *H. cunea* as well as other lepidopteran species.

MATERIALS AND METHODS

Objective 1 – Rearing techniques for red-headed *H. cunea*

Larval collection. The red-headed form of *H. cunea* is widespread in North America; in Colorado, researchers and hobbyists have recorded the moths in 15 counties (Ferguson et al. 2000). We collected wild larvae from multiple field sites near the cities of Boulder (Boulder County, 40.090013, -105.359962), Fort Collins (Larimer County, 40.5852602, -105.084423), and Idledale (Jefferson County, 39.746944, -105.210833) in Colorado (Fig. 1). The conspicuous webs were visible along roads and waterways, and we most commonly found webs in canyons dominated by deciduous woody plants and on the plains abutting the foothills. We collected larval *H. cunea* from July 21 through September 21 of 2010, after which webs that we searched were empty. Webs were distributed at heights greater than one meter from the ground on the outer branches of woody shrubs and trees. When webs were out of reach of hand clippers, we used an extendable tree pruner (4.9m Jameson poles, Marvin pruner head, Sherrill Tree, Greensboro, North Carolina) to remove the inhabited branch. After cutting down a web, we placed 12 larvae into a 0.5L clear plastic container (Fabri-Kal, Kalamazoo, Michigan) provisioned with a wet filter paper disc (7.5 cm diameter; VWR, West Chester, Pennsylvania) and a sprig of the natal host, and replaced the web within the branches of the tree of origin. We kept the containers cool and transported them to the laboratory on the same day.

Rearing larvae in the laboratory. We successfully reared both wild-caught *H. cunea* larvae in 2010 and *H. cunea* larvae hatched from eggs in 2011 (see subsections below on ‘Mating adult moths’ and ‘Oviposition, eggs and early instar larvae’) in ambient conditions in our laboratory at the University of Denver in Denver, Colorado. Depending on size, we reared larvae individually or in groups of up to six individuals in the same type of clear plastic containers that we used to collect them from the field. Large larvae were housed individually and small larvae were housed in

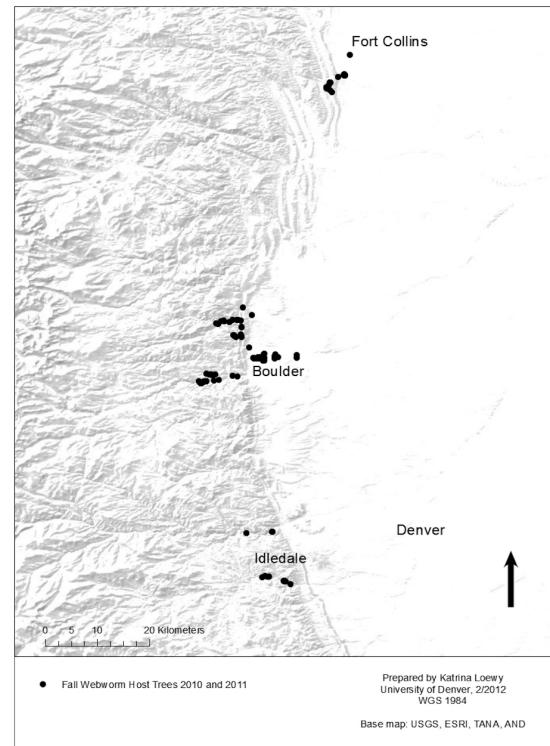


FIG. 1. Map of observed *Hyphantria cunea* webs along the Colorado Front Range during the summers of 2010 and 2011. Each dot represents the location of a host tree. Dots are allowed to overlap. The directional arrow points north.

groups, with group size decreasing as they grew larger. Early instar larvae are naturally aggregative feeders and it has been shown previously that group sizes of four to eight black-headed *H. cunea* hatchlings are necessary for establishment and survival, while later instars develop faster with less crowding (Watanabe & Umeya 1968). We stored the plastic containers with *H. cunea* larvae at room temperature on shelves with exposure to ambient light from outside a nearby window.

We collected fresh host plant branches from our field sites biweekly and stored them in 49.2L plastic bags (Tall Kitchen Bags, Safeway, Pleasanton, CA) in a walk-in growth chamber (Kysor-Sherer, Marshall, MI) set at 4–10°C. For each larval container, we replaced old food plants with fresh foliage and removed frass biweekly. In 2010, we reared larvae on 5 host plant species: chokecherry (*Prunus virginiana*, n = 183), crabapple (*Malus* sp., n = 40), Lombardy poplar (*Populus nigra*, n = 20), narrowleaf cottonwood (*Populus angustifolia*, n = 167), and thinleaf alder (*Alnus tenuifolia*, n = 20); although larvae were reared on all of these host plants, any single larva was reared for the entirety of its development on the single host plant species upon

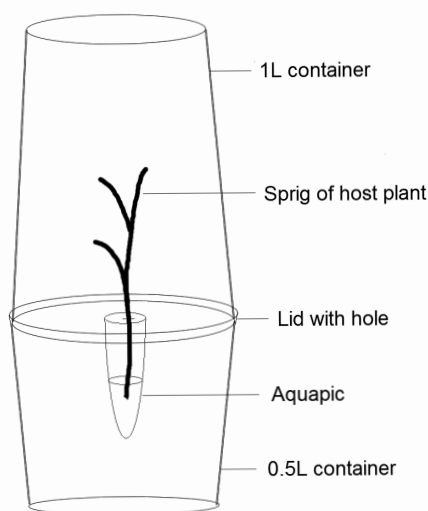


FIG. 2. Diagram of rearing chamber configuration used to rear *Hyphantria cunea* larvae in environmental chambers.

which it was discovered. During feeding, we used a spray bottle filled with tap water to remoisten the filter paper, which helped to keep the host plant material fresh and to increase ambient humidity, a function performed by the web in wild populations (Morris & Fulton 1970). When larvae reached the prepupa stage, we suspended maintenance, as pupating larvae experience higher mortality when disturbed (Morris & Fulton 1970).

Rearing larvae in growth chambers. In 2011, we moved a subset of 400 20-day-old, lab-reared larvae from the lab to environmental growth chambers (Percival Scientific, Pery, IA) set to a diurnal cycle calculated to mimic average field temperatures in Boulder, CO on August 15, 2011 (L14:D10 and 27°C:19.5°C). Individual larvae were housed in an inverted 1L plastic container (Fabri-Kal, Kalamazoo, Michigan) with a sprig of host plant from one of four plant species (chokecherry, crabapple, narrowleaf cottonwood and thinleaf alder); we divided the 400 larvae equally among the host plants such that there were 100 larvae reared on each host. The plant had a fresh water supply provided by an aquapic (7.6 cm recycled water tubes, Afloral.com, Jamestown, NY). We replaced sprigs of host plant and refilled aquapics with water biweekly. The aquapic was placed in a 1.5 cm diameter hole in the lid so that when closed, the host plant and larva were enclosed in the 1L plastic container (Fig. 2). The inverted 1L container was then placed on an upright 0.5 L container so that the entire

apparatus could stand alone. Condensation built up quickly inside the containers, and it was especially important to remove standing water from containers with later instars, because too much water can prevent successful splitting and shedding of the final larval skin (Morris & Fulton 1970, Loewy, pers. obs.). We checked containers daily to record any larvae that had reached the prepupa or pupal stage.

Pupae. We removed hardened pupae, most of which had entered diapause, from their containers and cleaned them of debris and frass. We placed each individual pupa into a new 0.5 L plastic container that contained 2–3 cm of moist sphagnum peat (Ferti-lome peat moss, Cheek Garden Products, Austin, TX). We overwintered the containers with peat and pupae in environmental growth chambers (L0:D24 and 4 °C) for seven months, starting in early November. Morris and Fulton (1970) suggested a minimum chilling period of 6 months at 1.7 degrees C, and a maximum of 8 months, after which survival rate decreased sharply. We moistened the peat with tap water by misting the containers every two to three months to maintain ambient humidity.

Adult emergence. In the beginning of June, we cleared pupal containers of peat, misted the pupae, and placed a moistened filter paper disc under each pupa in its container. Then we returned the containers to the environmental growth chambers set to a diurnal cycle calculated to mimic average field temperatures in Boulder, CO on June 8, 2011 (L15:D9 and 23°C:16°C). We recorded newly-emerged adults daily, and definitively determined their sex. Male moths have pectinate antennae and tend to have smaller abdomens, while female moths have filamentous antennae and

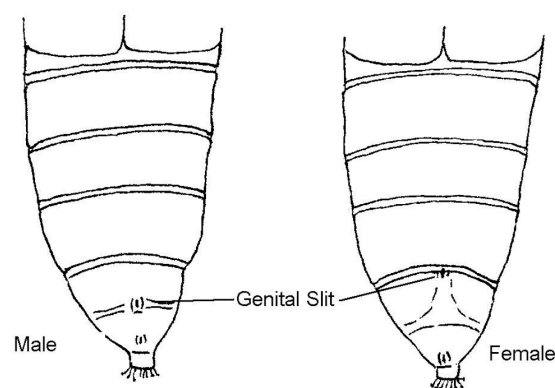


FIG. 3. Diagram of pupal sex differences in *Hyphantria cunea*, with the ventral surface of a male pupa on the left and a female pupa on the right. On female pupae, the genital slit is located on the anterior edge of the fourth abdominal segment posterior to the wing covers. On male pupae, the genital slit is located on the posterior edge of the same segment. The genital slit of both sexes sometimes appears to transect two segments.

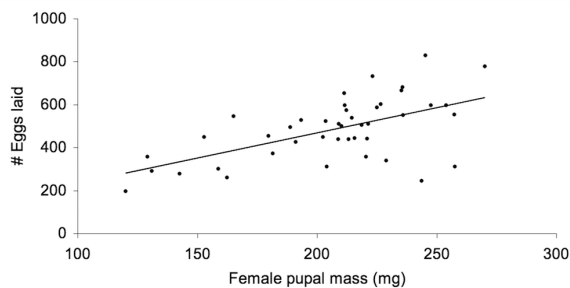


FIG. 4. The relationship between female fecundity, measured by eggs laid per female, and female pupal mass ($y = 2.353x - 1.8343$; $N = 43$ females, $R^2 = 0.34$, $t = 4.59$, $P < 0.0001$) for red-headed *Hyphantria cunea* in Colorado.

larger abdomens, at times with greenish eggs visible within.

Mating adult moths. On the day of emergence, we placed a single female and one to three males into a plastic shoebox (34.6 cm × 21 cm × 12.4 cm, Sterilite Corp., Townsend, MA) lined with wax paper that served as a mating chamber, taking care that none of the females were paired with a male sibling from the same natal web to avoid potential inbreeding depression in our colony. Jaenike and Selander (1980) confirmed that black-headed larvae within a single web are full-sibs, and we assumed the same of the red-headed form. Putting the mating chambers in an environmental growth chamber with its stark transition between light and dark did not facilitate mating behavior. However, when we moved the mating chamber into the lab and exposed it to natural light, mating took place within two days. Hidaka (1977) found that mating flight is likely cued by the dim light of dawn or dusk in black-headed *H. cunea*. We did not record the precise timing of mating behavior in the lab, although we only discovered mated pairs, still in coitus, in the mornings.

Oviposition, eggs and early instar larvae. A day after copulation, we removed males from the mating chamber so that they would not disturb the ovipositing female; females were left to oviposit in the shoebox mating chamber. Oviposition began 1–3 days after mating was observed. With rare exceptions, females laid their eggs on the wax paper-lined walls of the mating chamber, rather than the floor or lid. Females slowly swung their abdomens back and forth, creating row after row of eggs, usually in a single layer. When undisturbed, most females laid all eggs in a single batch and often died with their wings covering the egg mass, a behavior also observed in wild populations by Swain (1936).

We removed egg masses from the mating chamber by cutting the wax paper around them with a X-acto

knife. We kept eggs on the wax paper until hatching to avoid breakage and placed the egg masses in a new 0.5 L plastic deli container with a moist cotton ball. We kept most of the containers in the lab under ambient conditions, and moved eight into the growth chamber at 26°C. We labeled containers with information about the eggs' maternal and paternal lineage and the date that they were laid. As long as the cotton ball was moist, humidity within the container was sufficient to allow hatching. Head capsules became visible, turning the eggs dark, a day before the larvae hatched.

Once larvae began to eclose, we removed the moist cotton ball and replaced it with a moist filter paper disc. We also placed a sprig of host plant into the container. We found that if we tried to move neonate larvae to a host plant leaf with a fine paintbrush, they suffered higher mortality than neonates we allowed to locate the leaf on their own. We placed fresh leaves in the container biweekly. To minimize disturbance of delicate early instar larvae, we only removed old leaves if they started to get moldy. We misted containers lightly while introducing the fresh host plant. As the larvae grew, we divided them into smaller groups and moved them to new containers to minimize the frequency with which food needed to be replaced and make individual identification easier.

Objective 2 – Life history traits of red-headed *H. cunea* in Colorado

To better understand the life history of red-headed *H. cunea* in Colorado, in 2011 we recorded the timing of life events for larvae reared in the lab for the entirety of their development, including the dates of oviposition, eclosion, and pupation so that we could calculate total larval development time. For ease of comparison with the results from other studies, larval development times are only included for larvae that completed their development in the environmental growth chambers, not in the lab. After overwintering, we also recorded the number of days that passed from when the pupae were first exposed to spring conditions in the environmental chambers to adult emergence. For adult females, we recorded the number of days that passed from mating to the onset of oviposition.

Pupae deplete their fat stores over time, so we weighed all pupae exactly 30 days after pupation (to the nearest 0.01 mg; Mettler-Toledo XP6, Columbus, Ohio). We determined the sex of each individual by viewing the pupae under a dissecting microscope and noting the location of the genital slit (Fig. 3), similar to methods reported by Villiard (1975) and Carter and Feeny (1985). We confirmed our sex determinations after the moths emerged as adults the following spring.

Objective 3 – Pupal mass as a predictor of potential fecundity and lifetime fitness in Lepidoptera

To quantify fecundity for red-headed *H. cunea*, we photographed egg masses using the macro setting on a Cannon PowerShot SD780 IS and uploaded the pictures to a computer for counting in Paint (Microsoft, Redmond, WA). For greatest accuracy, we dotted each egg with the pencil tool and kept track of the number with a tally counter. We also reviewed the literature for other studies that have investigated the relationship between female pupal mass and fecundity. We performed keyword searches on Web of Science and Google Scholar using various combinations of the following terms: fecundity, fitness, Lepidoptera, lifetime fitness, pupa^{*} mass and realized fitness. We then limited the results to studies that ran a regression of female pupal mass by potential fecundity. Following Awmack and Leather (2002), potential fecundity is a measure of the number of eggs an insect produces, while realized fecundity refers to the number of offspring produced.

Statistical analyses. We analyzed our results with T test and regression using JMP Pro 9.0.0 (SAS Institute Inc., Cary, NC). All means are reported $\pm$ 1 standard error.

RESULTS

Survival. We found that our rearing technique for fall webworm was quite successful. When larvae were reared on a high-quality host plant such as chokecherry ($n=100$), we found that 98% of the larvae successfully pupated and 74% successfully completed their development to the adult stage. Survival was lower for larvae collected from the field or reared on lower quality host plants, but this was due to mortality related to parasitism and host plant quality, rather than our rearing technique.

Sex determination. For our analyses, we identified morphological differences between male and female *H. cunea* pupae. Of the 129 pupae that we determined to be female, 125 emerged as female moths. Of the 141 pupae that we determined to be male, 139 emerged as male moths. Thus, we were able to successfully identify 99% of male pupae as males and 97% of female pupae as females. Our ability to distinguish males from females in the pupal stage allowed us to investigate whether male and female larvae differ in developmental life history traits without excluding individuals that did not reach adulthood.

Development time. We found that all eggs from a single egg mass hatched on the same day and the mean development time was 13.9 ± 0.2 days ($N=44$ egg

masses, range=10–16 days) in the population kept in ambient lab conditions, and 11.6 ± 0.6 days ($N=7$ egg masses, range=9–13 days) in the population kept in an environmental chamber set at 26°C. After the eggs hatched, we found that mean larval development time was 42.1 ± 0.2 days ($N=332$, range=35–62 days) in the environmental chamber (L14:D10 and 27°C:19.5°C).

We found that female larvae took longer to develop than male larvae by 0.3 days, but the difference was not significant ($t=0.9$, $P=0.36$). Females took 42.2 ± 0.3 days ($N=167$, range=36–53 days) to develop while males took 41.8 ± 0.3 days ($N=155$, range=35–62 days).

After pupae were removed from the overwintering chamber, we found that it took 26.8 ± 0.5 days for adults to emerge ($N=264$, range=17–52 days); of the 300 pupae that we overwintered in growth chambers from 2010–2011, 88% emerged. Females took longer to emerge than males by 1.8 days ($t=1.93$, $P=0.055$). Females emerged 27.7 ± 0.7 days ($N=125$, range=17–52 days) after removal from cold storage, while adult males emerged 25.9 ± 0.6 days ($N=139$, range=17–44 days) after removal from the cold.

Pupal mass. As in most Lepidoptera, female pupae were significantly larger than males ($t=13$, $P<0.0001$). The mean mass for male pupae was 185.66 mg (± 1.9 , $N=155$, range=127.78–286.00 mg), while the mean mass for female pupae was 223.25 mg (± 2.19 , $N=167$, range=143.58–300.52 mg), which is 120% heavier than male pupae.

Adult female fecundity. An average of 2.2 ± 0.2 days elapsed from when female *H. cunea* were mated until they began to lay eggs ($N=45$, range=1–5 days). Females laid an average of 484.2 ± 22.4 eggs ($N=43$, range=34–830 eggs). We found a significant positive relationship between a female's pupal mass and the number of eggs that she laid during her lifetime ($R^2=0.34$, $t=4.59$, $n=43$, $P<0.0001$); for every additional mg of pupal mass, a female laid an additional 2.35 eggs (Fig. 4). Our literature review demonstrated that there is a significant, positive relationship between pupal mass and potential female fecundity for the majority of lepidopteran species for which this relationship has been investigated (Table 1).

DISCUSSION

Here we report natural history for the red-headed form of *H. cunea* for the first time; previously, all detailed published accounts of *H. cunea* natural history have focused on the black-headed form. To our knowledge, this is also the first account of successful rearing techniques for red-headed *H. cunea*. Our results suggest that much of the phenology of red-headed *H. cunea* differs from that of the black-headed

form; red-headed eggs took longer to hatch and larvae took longer to develop than those in studies of the black-headed form. Additionally, red-headed pupae were heavier than black-headed pupae.

Comparison of *H. cunea* life history traits among studies is complicated because different studies have used a variety of different host plants and temperatures for rearing caterpillars. Furthermore, voltinism differs among populations with anywhere from one to more than four generations per year; *H. cunea* in Colorado has a single generation each year (pers. obs.), but black-headed populations in Maryland are bivoltine while populations in southwestern Japan are trivoltine (Gomi & Takeda 1996, Mason et al. 2011). Despite these complications, we compared our results with those of other studies to better understand how life histories may differ between red-headed and black-headed *H. cunea*. At several life stages, red-headed *H. cunea* took longer to develop than the black-headed form. European, Asian, and North American measurements of embryonic development time (the time from oviposition to hatching) for black-headed *H. cunea* range from ~7 days at 27°C to ~23 days at 16°C (Jasič & Macko 1961, Yearian et al. 1966, Szalay-Marzso 1972, Gomi et al. 2005). We found that red-headed *H. cunea* eggs incubated at 26 °C took 11.6 days to hatch, which is longer than in any study of black-headed *H. cunea* eggs incubated at that temperature. Red-headed *H. cunea* larvae took longer to develop than black-headed *H. cunea* larvae in similar studies; published development times for black-headed *H. cunea* larvae range from 17–47 days depending on which host plants were used as food, the temperature at which the larvae were reared, and the sex of the larva (Jasič & Macko 1961, Yearian et al. 1966, Morris & Fulton 1970, Gomi et al. 2005). The red-headed larvae we studied took 40–70% longer to develop compared with black-headed larvae in other studies. Furthermore, Jasič and Macko (1961) recorded shorter larval development times for males than for female black-headed *H. cunea*, with 1–2 days difference between the sexes. Notably, males and females in our study both took about 42 days to develop from egg hatch to pupation, with mean male development time shorter than mean female development time by only a fraction of a day.

The pupae of female red-headed *H. cunea* tend to be much larger than the female pupae of the black-headed form studied by Jasič and Macko (1961), Morris and Fulton (1970), and Gomi et al. (2005). One complicating factor when comparing pupal masses across studies is that there is a positive relationship between rearing temperature and pupal mass such that even on the same host plant, larvae develop into

heavier pupae when reared at higher temperatures (Jasič & Macko 1961). Despite the use of a different host plant, white mulberry (*Morus alba* L.), Jasič and Macko (1961) reared black-headed *H. cunea* at a similar temperature to the temperatures we used to rear red-headed *H. cunea*, differing only by about 1–2 degrees. Jasič and Macko (1961) recorded a mean pupal mass for black-headed *H. cunea* that was 24% lower than the mean pupal mass we recorded for red-headed *H. cunea*, despite rearing the larvae at a mean temperature 2.1 degrees higher than that of our study.

Intraspecific variation in insect body mass is often correlated with lifetime fitness (Slansky & Scriber 1985, Honěk 1993). Two studies have previously found a positive correlation between pupal mass and potential fecundity for *H. cunea* (Jasič & Macko 1961, Morris & Fulton 1970), but both of these studies focused only on the black-headed form. Our results demonstrate that pupal mass may be used as a predictor of potential fecundity for the red-headed form of *H. cunea* as well. Furthermore, our results support and add to the limited but growing body of literature that demonstrates a positive relationship between body size and lifetime fitness for Lepidoptera. In a thorough review of the literature, we were able to find studies for 21 lepidopteran species that investigated the relationship between female pupal mass and potential fecundity (Table 1). For 19 of these 21 species, a significant, positive relationship exists between pupal mass and female fecundity (Table 1); for the two limacodid species, the relationship was still positive, but not significant. Thus, for all of the lepidopteran species studied to date, females that gain more mass as larvae are able to produce more eggs as adults. The magnitude of the effect size may depend on the feeding behaviors of adult female moths; the mass gained as larvae may be even more critical to lifetime fitness for species that do not feed as adults (Jervis et al. 2005).

Our data on the natural history of red-headed *H. cunea*, combined with genetic and molecular analyses (Jaenike & Selander 1980, McIntee & Nordin 1983) and behavioral observations (Oliver 1964), suggest that red-headed and black-headed *H. cunea* may be two distinct species or subspecies. To better understand natural history and behavioral differences between the two forms of *H. cunea*, there needs to be consistency among studies to allow for meaningful comparisons among populations of these two host forms. Previous studies have all used different rearing temperatures and diets that reflect the local climate and habitat of the focal *H. cunea* population, but this makes it difficult to compare natural history traits for the two forms across their geographic range. In Colorado, we find only the

TABLE 1. Compilation of data that examines the relationship between female pupal mass and potential fecundity from studies of other Lepidoptera gathered from the literature. The slope represents the increase in the number of eggs per mg of additional pupal mass. Depending on the study, the number of eggs could refer to eggs laid, dissected out, matured, or any combination of the three. If a variable was not reported, it is noted as NR. Other values given in the table are the correlation coefficient r (all correlation coefficients are significant unless noted 'ns' for not significant) and the number of groups or individuals in the study (n).

Family	Species	Slope	r	n	Source
Erebidae	<i>Hyphantria cunea</i>	4.8	0.64	71	Jasič and Macko (1961)
	(black head)	4.4	0.68	86	
		4.7	0.70	20	
		3.8	0.49	167	
		3.8	0.89	30	Morris and Fulton (1970)
	<i>Hyphantria cunea</i>	2.35	0.58	43	Loewy et al. (this study)
	(red head)				
	<i>Orgyia antiqua</i>	1.12	0.93	39	Tammaru et al. (2002)
	<i>Orgyia leucostigma</i>	1.29	0.89	187	Tammaru et al. (2002)
	<i>Orgyia vetusta</i>	NR	0.69	32	Harrison and Karban (1986)
Geometridae	<i>Operophtera brumata</i>	10.5	0.92	91	Roland and Myers (1987)
		9.14	0.96	41	
	<i>Epirrita autumnata</i>	2.31	NR	296	Heisswolf et al. (2009)
Lasiocampidae	<i>Malacosoma disstria</i>	0.45°	0.89	12	Lorimer (1979)
		0.45°	0.82	12	
		0.45°	0.71	12	
		0.45°	0.6(ns)	9	
		0.45°	0.89	13	
		0.59°	0.81	13	
		0.59°	0.95	11	
		0.59°	0.92	14	
		0.59°	0.82	15	
	<i>Streblote panda</i>	0.09	0.73	55	Calvo and Molina (2005)

TABLE 1. Continued from previous page

Family	Species	Slope	r	n	Source
Limacodidae	<i>Acharia stimulea</i>	0.24	0.57(ns)	11	Murphy et al. (2011)
	<i>Euclea delphinii</i>	0.27	0.32(ns)	23	Murphy et al. (2011)
Noctuidae	<i>Mythimna convecta</i>	7.02	0.7	NR	Smith (1986)
	<i>Mythimna pallens</i>	4.36	0.61	14	Hill and Hirai (1986)
		2.29	0.57	13	
		6.05	0.83	21	
		1.97	0.53	15	
	<i>Mythimna separata</i>	6.24	0.9	10	Hill and Hirai (1986)
		7.99	0.92	20	
		2.46	0.39	29	
		3.43	0.51	28	
	<i>Sesamia nonagrioides</i>	5.73	0.49	50	Fantinou et al. (2008)
	<i>Spodoptera exigua</i>	11.2	0.73	NR	Tisdale and Sappington
		12.5	0.60	NR	(2001)
		16.8	0.81	NR	
Plutellidae	<i>Plutella xylostella</i>	28.0	0.78	15	Sarfraz et al. (2011)
Saturniidae	<i>Antheraea polyphemus</i>	0.05	0.88	26	Miller et al. (1982)
	<i>Callosamia promethea</i>	0.14	0.99	25	Miller et al. (1983)
Tortricidae	<i>Choristoneura confictana</i>	2.09	0.2(ns)	20	Evenden et al. (2006)
		4.36	0.81	13	
		-4.7	0.3(ns)	7	
		4.07	0.65	22	
		5.37	0.73	16	
		1.91	0.5(ns)	6	
	<i>Choristoneura fumiferana</i>	1.1	0.4(ns)	42	Lorimer and Bauer (1983)
		1.9	0.78	40	
	<i>Cnephasia jactatana</i>	35.7	0.62	175	Jiménez-Pérez and Wang (2004)

*Slopes were obtained by combining nine separate broods of *Malacosoma disstria* into two geographic groups

red-headed form, but in some areas of North America the black-headed and red-headed forms are sympatric, which would allow for more direct comparisons between the two forms. Investigations into ecological, phenotypic and genetic differences among black-headed and red-headed populations of *H. cunea* across the entire geographic range, both where the forms are sympatric and allopatric, would be a fruitful area of future research.

ACKNOWLEDGEMENTS

This research was supported by the University of Denver through the generous support of the Undergraduate Research Center with separate awards to Amy Flansburg, MacKenzie Kjeldgaard and Jennifer Vernick. We would like to thank Boulder County Open Space, City of Boulder Open Space and Mountain Parks, Fort Collins Natural Areas, and Jefferson County Open Space for granting research permits and their support of our research. We thank Tim McGowan for his help with field and lab work. We also thank members of the University of Denver Ecology reading group as well as Martin Quigley, Tom Quinn, John Lill and an anonymous reviewer for helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

- AWMACK, C. S. AND S. R. LEATHER. 2002. Host plant quality and fecundity in herbivorous insects. *Ann. Rev. Entomol.* 47:817–844.
- CALVO, D. AND J. M. MOLINA. 2005. Fecundity-body size relationship and other reproductive aspects of *Streblote panda* (Lepidoptera: Lasiocampidae). *Ann. Entomol. Soc. Amer.* 98:191–196.
- CARTER, M. AND P. FEENY. 1985. Techniques for maintaining a culture of the black swallowtail butterfly *Papilio polyxenes asterius* Stoll (Papilionidae). *J. Lepid. Soc.* 39:125–133.
- EVDENDEN, M. L., M. S. LOPEZ, AND B. A. KEDDIE. 2006. Body size, age, and disease influence female reproductive performance in *Choristoneura conflictana* (Lepidoptera: Tortricidae). *Ann. Entomol. Soc. Amer.* 99:837–844.
- FANTINOU, A. A., D. C. PERDIKIS, AND N. STAMOGIANNIS. 2008. Effect of larval crowding on the life history traits of *Sesamia nonagrioides* (Lepidoptera: Noctuidae). *Eur. J. Entomol.* 105:625–630.
- FERGUSON, D. C., P. A. OPLER, M. J. SMITH, AND J. P. DONAHUE. 2000. Distribution of Arctiidae of Western North America. Moths of Western North America. C.P. Gillette Museum of Arthropod Diversity, Colorado State Univ., Fort Collins.
- GOMI, T., M. HIROCHIKA, M. NAGASAKA, H. HAGIHARA, AND T. FUKUDA. 2005. Effects of the diet on the life-history traits in a trivoltine Kobe population of *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae). *Appl. Entomol. Zool.* 40:475–482.
- GOMI, T. AND M. TAKEDA. 1996. Changes in life-history traits in the fall webworm within half a century of introduction to Japan. *Function. Ecol.* 10:384–389.
- GREENBLATT, J. A. 1978. Larval feeding preferences and inducibility in the fall webworm, *Hyphantria cunea*. *Ann. Entomol. Soc. America* 71:605–606.
- HEISSWOLF, A., T. KLEMOLA, T. ANDERSSON, AND K. RUOHMÄKI. 2009. Shifting body weight-fecundity relationship in a capital breeder: maternal effects on egg numbers of the autumnal moth under field conditions. *Bul. Entomol. Res.* 99:73–81.
- HIDAKA, T. 1977. Mating behavior, pp. 81–100. *In* T. Hidaka, editor. *Adaptation and Speciation in the Fall Webworm*. Kodansha, Tokyo.
- HILL, M. G. AND K. HIRAI. 1986. Adult responses to larval rearing density in *Mythimna separata* and *Mythimna pallens* (Lepidoptera: Noctuidae). *Appl. Entomol. Zool.* 21:191–202.
- HONÉK, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66:483–492.
- ITO, Y. 1977. Birth and death, pp. 101–128. *In* T. Hidaka, editor. *Adaptation and Speciation in the Fall Webworm*. Kodansha, Tokyo.
- JAENIKE, J. AND R. K. SELANDER. 1980. On the question of host races in the fall webworm, *Hyphantria cunea*. *Entomol. Exper. Appl.* 27:31–37.
- JASIČ, J. AND V. MACKO. 1961. Some results of experimental study of fall webworm (*Hyphantria cunea* Drury) (Lepidoptera: Arctiidae) ecology. Publishing Office of the Slovak Academy of Science, Bratislava.
- JERVIS, M. A., C. L. BOGGS, AND P. N. FERNS. 2005. Egg maturation strategy and its associated trade-offs: a synthesis focusing on Lepidoptera. *Ecol. Entomol.* 30:359–375.
- JIMÉNEZ-PÉREZ, A. AND Q. WANG. 2004. Effect of body weight on reproductive performance in *Cnephasia jactatana* (Lepidoptera: Tortricidae). *J. Insect Behav.* 17:511–522.
- LORIMER, N. 1979. Patterns of variation in some quantitative characters of *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *Ann. Entomol. Soc. Amer.* 72:275–280.
- LORIMER, N. AND L. S. BAUER. 1983. Spruce budworm weight and fecundity: means, frequency distributions, and correlations for two populations (Lepidoptera: Tortricidae). *Great Lakes Entomol.* 16:153–156.
- MASAKI, S. 1977. Past and future, pp. 129–148. *In* T. Hidaka, editor. *Adaptation and Speciation in the Fall Webworm*. Kodansha, Tokyo.
- MASAKI, S. AND Y. ITO. 1977. Speciation, pp. 149–172. *In* T. Hidaka, editor. *Adaptation and Speciation in the Fall Webworm*. Kodansha, Tokyo.
- MASON, P. A., S. R. WILKES, J. T. LILL, AND M. S. SINGER. 2011. Abundance trumps quality: bi-trophic performance and parasitism risk fail to explain host use in the fall webworm. *Oikos* 120:1509–1518.
- MCINTEE, E. E. AND G. L. NORDIN. 1983. Electrophoretic comparison of two types of fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae), occurring in central Kentucky. *J. Kansas Entomol. Soc.* 56:190–198.
- MILLER, T. A., W. J. COOPER, AND J. W. HIGHFILL. 1982. Relationships between pupal size and egg-production in reared female *Antheraea polyphemus* (Lepidoptera: Saturniidae). *Ann. Entomol. Soc. Amer.* 75:107–108.
- MILLER, T. A., W. J. COOPER, AND J. W. HIGHFILL. 1983. Egg production in female *Callosamia promethea* (Lepidoptera: Saturniidae) as a function of pupal size and adult longevity. *Ann. Entomol. Soc. Amer.* 76:668–670.
- MORRIS, R. F. AND W. C. FULTON. 1970. Models for development and survival of *Hyphantria cunea*. *Mem. Entomol. Soc. Can.* 70:1–312.
- MURPHY, S. M., J. T. LILL, AND M. E. EPSTEIN. 2011. Natural history of Limacodid moths (Zygaenoidea) in the environs of Washington, D.C. *J. Lepid. Soc.* 65:137–152.
- OLIVER, A. D. 1964. A behavioral study of two races of the fall webworm, *Hyphantria cunea*, (Lepidoptera: Arctiidae) in Louisiana. *Ann. Entomol. Soc. Amer.* 57:192–194.
- REHNBERG, B. G. 2002. Heat retention by webs of the fall webworm *Hyphantria cunea* (Lepidoptera : Arctiidae): infrared warming and forced convective cooling. *J. Therm. Biol.* 27:525–530.
- REHNBERG, B. G. 2006. Temperature profiles inside webs of the fall webworm, *Hyphantria cunea* (Lepidoptera : Arctiidae): Influence of weather, compass orientation, and time of day. *J. Therm. Biol.* 31:274–279.
- ROLAND, J. AND J. H. MYERS. 1987. Improved insect performance from host-plant defoliation: winter moth on oak and apple. *Ecol. Entomol.* 12:409–414.
- SARFRAZ, R. M., L. M. DOSDALL, A. B. KEDDIE, AND J. H. MYERS. 2011. Larval survival, host plant preferences and developmental responses of the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) on wild brassicaceous species. *Entomol. Sci.* 14:20–30.
- SLANSKY, F. AND J. M. SCRIBER. 1985. Food consumption and utilization, pp. 87–163. *In* G. A. Kerkut and L. I. Gilbert, editors.

- Comprehensive Insect Physiology Biochemistry and Pharmacology. Pergamon Press, New York.
- SMITH, A. M. 1986. Fecundity and survival of the common armyworm, *Mythimna convecta*: Effects of temperature and larval nutrition. Entomol. Exper. Appl. 42:31–37.
- SWAIN, R. B. 1936. The biological control of the fall webworm in Colorado. Colorado State College, Fort Collins.
- SZALAY-MARZSO, L. 1972. Biology and control of the fall webworm (*Hyphantria cunea* Drury) in the Middle- and East European countries. Bulletin OEPP. EPPO Bulletin 1:23–35.
- TADIĆ, M. D. 1963. Natural enemies of fall webworm (*Hyphantria Cunea* Dr.) in North America. Entomophaga 8:245–252.
- TAMMARU, T., T. ESPERK, AND I. CASTELLANOS. 2002. No evidence for costs of being large in females of *Orgyia* spp. (Lepidoptera, Lymantriidae): larger is always better. Oecologia 133:430–438.
- TISDALE, R. A. AND T. W. SAPPINGTON. 2001. Realized and potential fecundity, egg fertility, and longevity of laboratory-reared female beet armyworm (Lepidoptera: Noctuidae) under different adult diet regimes. Ann. Entomol. Soc. Amer. 94:415–419.
- VILLARD, P. 1975. Moths and how to rear them. Dover Publications, Inc., New York.
- WARREN, L. O. AND M. TADIĆ. 1970. The fall webworm (*Hyphantria cunea*). Ark. Agri. Exper. Stat. Bull. 1–106.
- WATANABE, M. AND K. UMEYA. 1968. Biology of *Hyphantria cunea* (Lepidoptera: Arctiidae) in Japan IV: Effects of group size on survival and growth of larvae *Platanus acerifolia* D. Res. Bull. Plant Protect. Serv. Japan 6:1–6.
- YANG, Z. Q., X. Y. WANG, J. R. WEI, H. R. QU, AND X. R. QIAO. 2008. Survey of the native insect natural enemies of *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) in China. Bull. Entomol. Res. 98:293–302.
- YEARIAN, W. C., K. L. GILBERT, AND L. O. WARREN. 1966. Rearing the fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) on a wheat germ medium. J. Kansas Entomol. Soc. 39:495–499.

Submitted for publication 3 July 2012; revised and accepted 7 December 2012.

Journal of the Lepidopterists' Society
67(3), 2013, 206–220

THE DODGE FAMILY: AN ENDURING TRADITION OF ENTOMOLOGY

JOHN V. CALHOUN

977 Wicks Drive, Palm Harbor, Florida 34684, email: bretcall1@verizon.net
Research Associate, McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History,
University of Florida, Gainesville, FL

ABSTRACT. The brothers Edgar A. Dodge and George M. Dodge studied insects during the late 19th and early 20th centuries. They corresponded and exchanged countless specimens with many prominent entomologists. Their younger brother, Charles F. Dodge, collected insects to a lesser extent. The Dodes obtained specimens primarily where they resided in Illinois, Nebraska, Missouri, and California. Edgar's son, Ralph E. Dodge, collected moths, mostly in Nebraska and California. Detailed biographical information is provided for these members of the Dodge family, as well as for John P. Strohbeen, who collected Lepidoptera with Edgar in California. Their photographs are presented for the first time. George described 17 taxa of Lepidoptera and Orthoptera, which are summarized with remarks about related type specimens. Also listed are seven entomological patronyms that honor Edgar and George.

Additional key words: Charles Francis Dodge, Edgar Addison Dodge, George Marshall Dodge, Ralph Edgar Dodge, John Peter Strohbeen, type specimens

The entomological literature is filled with references to the name “Dodge”, especially in association with the insects of Illinois, Nebraska, Missouri, and California. Brothers George M. Dodge (1846–1912) and Edgar A. Dodge (1853–1933) supplied insect specimens and information to scores of leading entomologists, including William Barnes, Ernest L. Bell, Foster H. Benjamin, John A. Comstock, William H. Edwards, Jeane D. Gunder, Samuel Henshaw, Theodore L. Mead, Herbert K. Morrison, Samuel H. Scudder, F. H. Herman Strecker, Edward P. Van Duzee, and Roswell C. Williams. Edgar had an early influence on the 20th century lepidopterist, James W. (“Bill”) Tilden who was an authority on California butterflies (Smith 1990). Edgar's son, Ralph E. Dodge (1892–1925) shared his father's interest and collected moths for many years. Charles F. Dodge (1862–1936), youngest brother of George and Edgar, also studied insects, but to a lesser degree.

Edgar and George sold and exchanged countless insect specimens. They placed advertisements in a number of entomological periodicals, even some published outside North America. Articles and observations by the Dodge brothers appeared in a variety of journals and bulletins, including the *American Entomologist and Botanist*, *American Gardening*, the *Auk*, the *Canadian Entomologist*, *Entomological News*, *Gleanings of Bee Culture*, *Insect Life*, *Lepidoptera*, and the *Lepidopterist*. A prodigious author, George described 17 taxa of Lepidoptera and Orthoptera. Specimens collected by George and Edgar contributed to the descriptions of many additional insects, some of which bear the name *dodgei* in tribute. Van Duzee (1921) recognized Edgar for his “efficient work in the cause of entomology” and “courteous assistance to

students of insects whose paths of effort are fortunate enough to meet his.” Edgar was also interested in ornithology and horticulture (Widmann 1908, E. Dodge 1897).

Despite their numerous contributions, biographical information about the Dodes was sorely lacking. Their dates of birth and death were obscure and their photographs were never published. Even their names were incorrectly cited in the literature, such as Edwards' (1887–1897) erroneous allusion to “Edward A. Dodge.” Van Duzee (1933) and Ewan & Ewan (1981) published brief biographical notes about Edgar. George received very little notice, despite being more widely published. A few brief remarks about George and Edgar were offered by Meiners (1949), dos Passos (1951), and Irwin (1972). Charles was completely overlooked entomologically, though details of his personal life were published by Baldwin & Baldwin (1932). A few remarks about Ralph's entomological work were offered by Van Duzee (1925).

The Dodes lived in five different states, but the timing of their moves was poorly understood (e.g. Brown & Miller 1980). In addition, the tendency of the family to live in towns with state's names has resulted in persistent confusion about the localities where George and Edgar collected insects (McDunnough 1950, Metzler 1987). To better appreciate the Dodes and their entomological contributions, I offer a long-overdue glimpse into the lives of these devoted naturalists.

METHODS

Over 100 letters and postcards from George M. Dodge and Edgar A. Dodge, dated 1870–1932, were located and examined. The recipients, and the



FIGS. 1–7. **1**, (L–R), George M. Dodge, Edgar A. Dodge, and Charles F. Dodge in 1892. **2**, Charles, ca. 1890. **3**, Edgar in 1901, with his wife and daughter. **4**, George, 1910. **5**, Ralph E. Dodge, 1919. **6**, labels from Dodge specimens. Top: replacement label of C. P. Whitney (female syntype of *H. pawnee*, Glencoe, Nebraska, 9 July 1873, PMNH); Bottom: original G. M. Dodge label (female topotype of *H. pawnee*, Dodge Co., Nebraska, 1880; CAS). **7**, John P. Strohbeen, ca. 1960.

repositories of their correspondence, are as follows: Foster H. Benjamin (among the manuscripts of William Barnes, National Archives, Kansas City, Missouri; NAKC), Joseph P. B. Henshaw and his older brother, Samuel Henshaw (Ernst Mayr Library, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MCZ), Theodore L. Mead (Archives and Special Collections, Olin Library, Rollins College, Winter Park, Florida; RC, and McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, Florida; MGCL), Samuel H. Scudder (Lyman Library, Museum of Science, Boston, Massachusetts; BMS), F. H. Herman Strecker (Research Library, Field Museum of Natural History, Chicago, Illinois; FMNH), and Edward P. Van Duzee (Library of the California Academy of Sciences, San Francisco, California; CAS). Also examined were copies of letters that Benjamin, Mead, and Van Duzee sent in response to George and Edgar. Correspondence is cited by date (day.month.year) and repository (as abbreviated above).

Also consulted were a variety of additional sources, including federal and state census records, state death indexes, gazetteers, city directories, military and voter registries, society membership lists, and local historical essays. I obtained digital images of the Dodge's

Lepidoptera collection catalog, which was bequeathed to CAS with Edgar's insect collection. Finally, I received valuable information and photographs from members of the Dodge and Angle families. This includes an unpublished genealogical manuscript, edited by Charles F. Dodge and his daughter, Catharine D. Angle.

Current insect nomenclature is consistent with Pelham (2008), Eades et al. (2012), and Gall & Hawks (2010). Information on the disposition of type specimens was obtained from Pelham (2008), Eades et al. (2012), online museum databases, and personal communications with museum staff.

RESULTS

Early history. Seven days after his 25th birthday, George Marshall Dodge shared aspects of his early life in a letter to 19 year old T. L. Mead (23.viii.1870 RC):

I was born of poor but honest parents in Augusta, Maine, A.D. 1846 in the month of August, the 16th day. In '47 we moved to Waldo County, Me [Maine], and in '54 moved to Illinois and established ourselves in the northern part of Bureau Co. where we still remain. We are farmers and I help 'carry on' the homestead and shall remain here a year or two longer. In the mean time I have preserved much of

my youthful habits and appearance, and shall not write myself [a] man until I can produce a fair crop of whiskers. I have two brothers aged 17 and 8.

George's birthplace in Augusta, Maine was situated adjacent to a large home which was later purchased by the famous Maine legislator James G. Blaine (1830–1893) (Dodge & Angle [1926]). Since 1920 the Blaine house has served as the Maine Governor's residence.

Edgar Addison Dodge was born in Burnham, Waldo County, Maine on 11 April 1853. Charles Francis Dodge was born on 27 August 1862 in Bureau County, Illinois (Dodge & Angle [1926]). The father of the three brothers was George Addison Dodge (1819–1895), a farmer who also worked as a merchant tailor and later as a surveyor (Dodge & Angle [1926]). He served as a Selectman in the town of Burnham, Maine during the 1850s and represented Burnham in the 1854 Maine State Legislature (Dodge & Angle [1926], Sanborn 2012). The brothers' mother, Caroline Elizabeth Marshall (1819–1892), taught school in Maine for several years, an avocation shared by several other members of her family (Baldwin & Baldwin 1932, Dodge & Angle [1926]). As the eldest brother, George benefited from his mother's experience as an educator. George and Edgar also were skilled farmers, whereas Charles broke this tradition and pursued a career in business. Family and friends fondly referred to Edgar as "Ed" or "Eddy" and Charles as "Charlie". This branch of the Dodge family was descended from William Dodge, who arrived in Salem, Massachusetts in 1629 from Cheshire, England. He was a farmer who became very active in public affairs in Salem (J. Dodge 1894).

The Dodge brothers (Fig. 1) were distant cousins of two other entomologists. Charles Richards Dodge (1847–1918) was a researcher of plant fibers who published numerous articles and observations related to entomology. He served as an Assistant in Entomology under the first federal entomologist, Townend Glover, at the U. S. Department of Agriculture (Howard 1930). Frank Waldo Dodge (1875–1958) was a postal carrier in Melrose, Massachusetts who collected insects, especially aquatic beetles. He was very active in the Cambridge Entomological Club and served as its treasurer from 1913 to 1916 (Matthews 1974). Another entomologist, Harold Rodney Dodge (1913–1973), was possibly related to the brothers, but his family lineage is not well known. He was an economic entomologist who specialized in Diptera (Denmark 1973).

Illinois. In 1854, the Dodge family moved from Maine to Bureau County, Illinois. They lived temporarily with other former Maine residents, the

Haynes family (Dodge & Angle [1926]). Shortly after their arrival, Edgar and his father contracted Asiatic cholera, which killed the entire Haynes family within a short time. After a few days, Edgar was "left lying on a bed as dead" but later recovered. His father also recovered, but was too weak to work until at least November of that year and never fully regained his strength (Dodge & Angle [1926]). In December 1854, George A. Dodge purchased 32 ha (80 ac) of land for \$1,600, comprising the northeastern one-eighth of Section 19 of Ohio Township, Bureau County, Illinois (Warner & Beers 1875). Also purchased was 4.1 ha (10 ac) of woodland in an area known as "Heatoon's Grove" (Dodge & Angle [1926]). Their farm was located 3.2 km (2 mi) southwest of the town of Ohio, which was named after the state of Ohio (Callery 2009). Sewell C. Dodge, the brothers' uncle, later moved to Illinois and purchased 65 ha (160 ac) immediately to the north (Warner & Beers 1875; Dodge & Angle [1926]). The nearest railroad station was in the town of Princeton, 19 km (12 mi) to the south (17.xii.1870 RC). The family cultivated various crops (such as corn) and grew garden flowers from seeds sent by family members in Maine. They also raised cattle, chickens, and turkeys (Dodge & Angle [1926]). Following in his mother's footsteps, George M. Dodge passed the teacher's examination in 1868 and later worked as a teacher during the winter months, traversing bad roads to reach the school (Dodge & Angle [1926]; 17.xii.1870, 16.i.1872 RC).

George M. Dodge vividly recalled his life in Illinois. "When we first came here," he wrote, "wolves, rattlesnakes and deer were our nearest neighbors and called early and often. I have lain awake many a night listening to the howling Coyotes. Our nearest neighbor was a mile away then and thousands of acres of treeless prairie, unbroken by the plough, lay around us" (23.viii.1870 RC). As George grew older he no longer appreciated the isolation on the prairie: "I suppose it wouldn't seem so pleasant to me now. Man is a gregarious animal and I expect solitude isn't good for him" (ibid.). A portion of a letter from Caroline Dodge, describing fires on the Illinois prairies, was published in 1857 in the *Piscataquis Observer*, a Maine newspaper. When the Dodes first arrived in Illinois, Native Americans still lived in the vicinity, a fact that unnerved Caroline (Dodge & Angle [1926]).

In June of 1870, the young New York entomologist T. L. Mead wrote a letter to a potential correspondent by the name of "Marshall Dodge," asking if he wanted to exchange insects (16.vi.1870 RC). This of course was George M. Dodge, who responded that he collected "chiefly moths and butterflies with an occasional beetle" (28.vi.1870 RC). George admitted that his collection

was “yet quite small,” adding, “I am but a beginner and although an enthusiast in the pursuit of insects need information on almost every point connected with the ‘business’ if I may call it.” He did not know the names of the local species, but was confident that he would “remedy that difficulty, if possible” (ibid.).

The Dodge brothers seriously began to study entomology during the summer of 1870, when George advised Mead, “You must excuse the meagerness of my collection on the grounds that as this is my first year in the business, I have but little more than got fairly initiated” (17.xii.1870 MGCL). George proposed to Mead that they “keep up a social correspondence on this theme and at the last of the season, having found what we lack, and the other one can supply, that we exchange” (28.vi.1870 MGCL). This would become the model by which he and his brother, Edgar, would exchange specimens with other entomologists for years to come. George recalled the “exclamations” expressed by his brothers when they received their first box of butterflies from Mead (23.viii.1870 RC).

Entomology had long been “a ruling passion,” of the brothers, but they “never before attempted to become acquainted with the scientific names or to make a regular collection” (23.i.1871 RC). During their first year of their correspondence, Mead offered advice to George on how to properly mount specimens, fold specimen envelopes, and rear perfect specimens. Despite Mead’s input, the brothers initially had trouble rearing some Lepidoptera (29.viii.1872 RC), a problem they quickly remedied. Mead also urged George to contact J. P. B. Henshaw, a Massachusetts naturalist who collected beetles. When George did not have time to personally collect Lepidoptera, his brothers would obtain the specimens and George would mount them in the evenings (20.v.1871 RC).

The friendship between George and Mead quickly grew. In May 1872, Mead took the train to Illinois and visited George for two weeks: “The Dodges welcomed me cordially & endeavor to make things as agreeable as possible.” He described the family as “plain western farmer folk, keep no servants & eat in the kitchen, but they are well read & the boys are enthusiastic entomologists.” Mead considered the brothers to be “quite expert to entomological matters” and he complimented George on his “fine collection” (6.v.1872, 13.vii.1873 RC). Mead encouraged the brothers to contact other entomologists and suggested that they send preserved butterfly eggs to the lepidopterist William H. Edwards, who was then completing the first volume of his seminal book *The Butterflies of North America* (Edwards 1868–1872) (28.v.1872, 28.ix.1873 RC). Edwards corresponded with the Dodges for many

years and cited some of their observations in his publications.

Early on, George and Edgar were primarily interested in local butterflies, which they exchanged for colorful exotic species suitable for “exhibition” (5.iv.80 FMNH). Despite their desire for showy specimens, they did not ignore the smaller species, including skippers (Hesperiidae). Edgar collected some unfamiliar skippers in June of 1872, upon the “grassy slopes of the high rolling prairie that forms the divide between the Illinois and Rock Rivers.” George soon after described them as a new species, *Hesperia illinois* (G. Dodge 1872c). This was George’s first published description. “If every describer of a new species would do it as clearly and distinctly as you have done,” Mead told Dodge, “the Halcyon days of entomology would have fairly commenced” (22.xii.1872 RC). Unfortunately, George quickly discovered that this new skipper was described a few years earlier as *Hesperia acanootus* Scudder, which in turn was a synonym of *Hesperia bimacula* Grote & Robinson (= *Euphyes bimacula*) (Calhoun in press). Dodge (1873) published a retraction, blaming himself for re-describing a known species “with injudicious haste.” Two weeks after Edgar discovered *E. bimacula* in Bureau County, the brothers found the Poweshiek skipper (*Oarisma poweshiek* (Parker)) abundantly at the same locality (Dodge 1872c). Their few surviving specimens of *O. poweshiek* remain the only known examples of this rare species from Illinois (Bouseman et al. 2006).

During the early 1870s, George began rearing Lepidoptera and published some of his observations (G. Dodge 1870, 1872b). The brothers also became very interested in moths of the genus *Catocala* (Noctuidae). In addition to Lepidoptera, George was curious about a wide variety of insects and arthropods, even mites (G. Dodge 1872a). He was fond of grasshoppers and was “considerably interested” in Coleoptera. He started exchanging beetles with J. P. B. Henshaw and had numerous species in his collection (10.iii.1873 MCZ). Although George sometimes claimed that he “never could get up much enthusiasm” over beetles (14.xi.1875 RC), he continued to collect them for many years, especially those of the family Cicindelidae (Van Duzee 1926). He wished to someday visit the Rocky Mountains of Colorado, Montana and Wyoming. “I had much rather take a trip through them than go sightseeing in Europe,” he wrote (26.vi.1871 RC). He presumed that the Rockies would hold “quite as much enchantment” as the Alps.

Nebraska. In 1869, the brother’s father, George A. Dodge, purchased property near Glencoe, Dodge County, Nebraska (Dodge and Angle [1926]). During

the autumn of 1871, George M. Dodge traveled to Nebraska where he bought land in the same area (26.vi.1871 RC). On a later map of Dodge County (Olge & Co. 1902), his property is shown as comprising the entire northern half of Section 3 of Pleasant Valley Township. It encompassed over 127 ha (314 ac) and was situated between present-day County Roads 6 and 8, south of State Road 91. Almost the entire town of Snyder is now located within a small portion of George's property. It is unclear, however, if George acquired a separate parcel or simply added to the property owned by his father. He described his land as consisting of "some very pretty high rolling prairie," which was "better adapted to farming than the rolling prairies of Illinois and Iowa" (26.vi.1871 RC). In early 1873, George spent time at Glencoe in anticipation of the family relocating to the area. They moved on the first day of August that year, riding the train to North Bend, Nebraska, and completing the journey by farm wagon (G. Dodge 1882a, 1882b, Dodge & Angle [1926]). "I have not got into my own house yet but we will soon begin to build," George wrote shortly after their arrival (17.viii.1873 MCZ). Burdened with farm chores in Nebraska, George especially disliked harvesting corn, an occupation he described as "practical on paper but is really eminently prosaic" (14.xi.1875 RC). Charles later surmised that if the family had not moved to Nebraska, all three brothers would have been consigned to tenant farming in Illinois for the rest of their lives (Dodge & Angle [1926]).

Dodge County, Nebraska was named in honor of Augustus Caesar Dodge (1812–1883), a United States Senator from Iowa who was descended from a different branch of the Dodge family. Glencoe was situated about 6.4 km (4 mi) southeast of the town of Dodge and 22.5 km (14 mi) north of the Union Pacific railroad line (2.i.1888 BMS). The town of Dodge first appeared on maps during the mid-1880s and took its name from George A. Dodge, a prominent local citizen and father of Charles, Edgar, and George (Fairclough 1960).

Edgar married his first cousin, Ida May Dodge (1865–1953), on 4 July 1885. Possibly during this time, Edgar purchased three parcels of land totaling nearly 162 ha (400 ac) in Sections 1, 2, and 11 of Pleasant Valley Township, Dodge County, between present-day County Roads 8 and 12 (Ogle & Co. 1902). Like his father had done in Maine, George became active in state politics and society affairs. He served on the 1879 Nebraska State Legislature and on the advisory board of the Nebraska State Horticultural Society during the 1880s (Barnard & Allen 1887, G. Brown 1879).

After moving to Nebraska, George spent a great deal of time studying the migratory habits of the now-extinct

Rocky Mountain Locust (*Melanoplus spretus* (Walsh)) (G. Dodge 1875b). Acknowledging that he gave more attention to this species than to "all other insects put together" (Packard 1877), George unwittingly documented the last major swarms of the species. Undaunted by his earlier misadventure with *H. illinois*, George described *Hesperia pawnee*, which he found "upon the rolling prairie" around Glencoe (G. Dodge 1874a). "I'm afraid you won't think it a very pretty name," George explained to Mead, "but I gave it on account of the region having been the old hunting ground of the Pawnee Indians, who still are seen at times along the line of the U. P. [Union Pacific R.R.] in this county" (9.iv.1874 RC). George described *pawnee* only after consulting with the New Hampshire naturalist Charles P. Whitney (1838–1928), who took specimens to Boston in order to compare them with skippers in the collection of S. H. Scudder (26.xii.1873 RC). Though George had little faith that *pawnee* was new to science, Scudder "pronounced it a new species" (9.xii.1873 RC). In jest, or as an act of outright extortion, Scudder agreed not to publish his own description of the species if George sent him duplicate specimens (23.iv.1874 BMS). At least one of the specimens that Scudder received from Dodge in April 1874 is preserved at MCZ (see Type Specimens below). Today, *pawnee* is recognized as a subspecies of *Hesperia leonardus* Harris.

George and Edgar often wrote to their correspondents about the Lepidoptera of Illinois and Nebraska, thus many of their observations were subsequently published (e.g. Packard 1876, Edwards 1880, 1887–1897, Scudder 1888–1889, Forbes 1889, Taylor 1889). They continued to cultivate their interest in *Catocala* moths, rearing larvae and employing sugar baits to attract adults (G. Dodge 1874b; 28.iv.1880, 8.x.1881 FMNH). Based on specimens collected by the brothers in Illinois and Nebraska, George described *Catocala whitneyi*, *C. nebraskae*, and *C. nebraskae* form *somnus* (G. Dodge 1874c, 1875a, 1881). "I take great interest in *Catocalas*," George wrote in 1875, "and shall always be on the alert to exchange for new species in that genus" (14.xi.1875 RC). He publicized his desire to provide insects of any order in exchange for *Catocala* and other species of Lepidoptera. Edgar, on the other hand, still preferred butterflies (Cassino 1877).

In addition to Lepidoptera, George described nine taxa of grasshoppers that he found in Dodge County, Nebraska and published remarks about several other species (G. Dodge 1876a, 1876b, 1877, 1878). He also became interested in flies, particularly horseflies (Diptera, Tabanidae), and his specimens from Nebraska resulted in the description of *Tabanus dodgei* (= *Anacimas dodgei*) by C. P. Whitney, in whose honor

George had previously described *Catocala whitneyi*. It should be noted that Charles Richards Dodge collected insects in Nebraska during the 1870s, hence a few literature references cite specimens from “Mr. Dodge” (e.g. Thomas 1876) that do not pertain to the Dodge brothers.

By the year 1880, extreme weather in the Midwest had impacted the insect fauna of Nebraska. George remarked that during the previous seven years Lepidoptera “fairly swarmed,” but they had become more scarce each year: “now it barely pays to collect at all” (15.x.[1880] FMNH). Possibly compelled to find new fields to explore, George traveled that summer on the Union Pacific railway line as far west as Ogden, Utah, evidently collecting some insects along the way (2.i.1888 BMS). Meanwhile, Edgar wrote of his desire to spend three months collecting insects in the Black Hills of South Dakota, with the hope of selling the specimens “very cheap” (i.1880 BMS, i.1880 FMNH). Not able to make this trip, he lamented, “I feel pretty blue about it as I had hoped to get many rare specimens in that vicinity” (29.vi.1880 FMNH).

In 1881, the imported cabbage butterfly, *Pieris rapae* (L), made its first appearance around Glencoe, when Edgar observed, “I caught one early this spring, the first living ex[ample] I ever saw.” Only a few months later, he mentioned that local gardens were “covered with the butterflies” (22.x.1881 FMNH). George later published some observations of this species (G. Dodge 1882a, 1882b). Scudder (1888–1889) cited the abundance of *P. rapae* in Fremont, Nebraska in 1881, which included one of the only known published references to Charles F. Dodge in an entomological context. Scudder did not correspond directly with Charles, however, but received this information from George (2.i.1888 BMS).

During the 1880s, Edgar continued to collect Lepidoptera and Coleoptera, and also developed an interest in apiculture (E. Dodge 1888). He sold “a good many” more insect specimens than he exchanged (ii.1882 FMNH). In July 1882, Edgar traveled to Colorado, where he collected insects primarily in the vicinities of Boulder, Idaho Springs, and Manitou. He also collected on Pike’s Peak. He boasted that he returned with as many as 900 specimens of butterflies, hoping to “sell enough to partly cover expenses of the trip” (17.i.1883 FMNH). Later that year, Edgar and other family members nursed George through a serious illness (ibid.).

The brothers became acquainted with several influential entomologists during this period. In August 1884, Charles V. Riley, then serving as entomologist to the U.S. Department of Agriculture, visited George at Glencoe and discussed the extensive damage in the

region caused by the elm sawfly (*Cimbex americana* Leach; Hymenoptera) (Riley 1884). Edgar met Lawrence Bruner, who later became a professor at the University of Nebraska. Edgar later recalled that he and Bruner “used to collect together sometimes” (20.vi.[1919] CAS).

Probably to attend school, Charles moved as a youth to the larger town of Fremont, the county seat of Dodge County, where he boarded with the family of George Stanley. Charles was described in 1887 as “a boon chum” and a “right jolly good boy” (Hayes 2002). About the year 1890, Charles was photographed as a rising young businessman (Fig. 2). That year, Charles apparently took a trip to Florida and was on board a steamer ship that burned on its way down the St. Johns River en route to the city of Sanford, killing four passengers on board (Anonymous 1890). On 10 May 1893, he married Eva Clarendon (1869–1929), with whom he had four children; Catharine (often misspelled “Catherine”) Elizabeth Dodge (1896–1973), Margaret Dodge (1898–1919), and Caroline Dodge (1908–1957), as well as an infant who died shortly after birth in 1894. Charles was an avid reader and often read to his family in the evenings; his favorite book was Don Quixote. From the 1880s through the early 1900s, he worked in real estate and insurance and was a cashier at the Farmers’ and Merchants’ National Bank in Fremont, where he later rose to the position of President (Anonymous 1913, Buss & Osterman 1921, Baldwin & Baldwin 1932). Among the bank’s first board of directors in 1884 was Charles’ father, George A. Dodge (Buss & Osterman 1921). Charles was elected in 1914 as the President of the Security Savings Bank in Fremont and served for many years as the President of the affiliated Fremont National Bank (Anonymous 1914; Buss & Osterman 1921). He was a member of the Society of the Sons of the American Revolution and his home, located at 1219 Park Avenue in Fremont, was figured by Lucas ([1914]). In addition to his home in Fremont, Charles owned nearly 129 ha (318 ac) of land, comprising the entire western half of Section 1 of Pleasant Valley Township, Dodge County, Nebraska (Ogle & Co. 1902). This property abutted two of Edgar’s properties and was near the large parcel owned by George. Two years after the death of his wife Eva, Charles married Nona S. Turner (1877–1959) (Baldwin & Baldwin 1932). He died as a respected member of the Fremont community on 20 November 1936 at the age of 74 and was buried in Ridge Cemetery in Fremont. Although Charles appears to have studied insects into the early 20th century (Barnes & McDunnough 1918b), his interest evidently waned later in life. His insect collection, in two large cabinets, was

inherited by his oldest daughter Catharine. Decimated by insect pests by the time of her death in 1973, the collection was discarded.

Missouri. In late 1888 or early 1889, the Dodge family (except for Charles) moved to Louisiana, Pike Co., Missouri, a town named after an early resident of the region (Williams 1913). That portion of Missouri invoked memories of their home back in Maine (Dodge & Angle [1926]). During this period, Edgar and his wife had two children, Ralph Edgar Dodge (1892–1925) and Alice May Dodge (1896–1989). In 1892, the three brothers gathered in Freemont, Nebraska for a cabinet card portrait (Fig. 1), which portrays George at the age of 46, Edgar at 39 and Charles at 30.

The brothers' parents died within five years of their arrival in Missouri. Edgar and his family continued to live with George, who owned 110 ha (272 ac) of land on the southeast side of town, about 0.40 km (0.25 mi) south of the present-day intersection of S. 30th Street and Noix Creek (Ogle & Co. 1899). Edgar owned 4.9 ha (12 ac) just west across the road from George's large property. In 1901, Edgar and his family (minus Ralph) posed for family portrait (Fig. 3). Edgar was 48 years of age.

For some time after arriving in Missouri, George had little time for natural history studies (10.xii.1892 BMS). Toward the end of the century, he and Edgar became increasingly busy with farming, including owning and operating the Hillview Poultry Farm, specializing in breeding barred Plymouth Rock chickens (11.ii.1900). After a number of years of entomological inactivity, George and Edgar resumed collecting in 1899. Confirming that their interest was "again aroused" ([1900] FMNH), this inaugurated another productive phase for the two brothers, who continued studying *Catocala* moths and published several papers on the subject (G. Dodge 1900a, Dodge & Dodge 1904). They reared many species of *Catocala* and George advertised eggs for sale and exchange. George described *Catocala titania* from specimens which he and Edgar collected at Louisiana, Missouri in 1899 (G. Dodge 1900b). This pursuit of *Catocala* probably was reinforced by the enthusiastic Missouri collector Robert R. Rowley (1854–1935), a teacher and paleontologist who lived in the same town (Meiners 1949). Rowley (1908a, 1909) and Rowley & Berry (1910, 1913, 1914) included many of the Dodge's observations of *Catocala*. Rowley (1908b) also described a Paleozoic crinoid (*Platycrinus dodgei*) and a Paleozoic brachiopod (*Crania dodgei*) in honor of Edgar, his "valued friend and co-worker."

With Edgar's assistance, George continued to study flies and publish notes on various species (G. Dodge

1893, 1899). By this time, George's natural history pursuits had expanded even to include nematodes (G. Dodge 1890). He continued to collect grasshoppers, admitting in 1892, "I have by no means lost interest in that family" (10.xii.1892 BMS). During the spring of 1902, George traveled to Texas and collected insects around the towns of Higgins, Ingram, Kerrville, and Llano. Fulfilling a lifelong dream, he also visited Colorado during June and July of that year, where he collected insects at several locations, including Denver, South Park, and Mt. Audubon. Specimens collected by Edgar and George in Colorado and Missouri contributed to the descriptions of several new fly taxa by Whitney (1904).

Never having lost his fundamental interest in butterflies, George published notes on the hoary edge skipper (*Achalarus lyciades* (Geyer)) and described a form of the American painted lady (*Vanessa virginiensis* (Drury)) from one of his own specimens (G. Dodge 1898, 1900c). He also described the skipper *Nisoniades llano* (= *Gesta invisus* (Butler & Druce)) from a specimen he collected in Llano County, Texas (G. Dodge 1903). This was the last taxon that George described during his lifetime.

California. During the first few years of the 20th century, the soil which Edgar and George had long cultivated in Missouri became unworkable "solid Portland cement" (Dodge & Angle [1926]). They decided to retire in 1909 and relocate to Santa Cruz, California. Stories about their uncle, William Dodge, who had previously lived in California, possibly prompted this decision. Edgar first lived at 552 Bay Street, but he soon moved to 546 Bay Street, into a house built in 1888 on several hectares of land at the northeast corner of Bay and King Streets (the house still stands, now as 1512 Bay St.). Calling it his "farm," he resided on this property for the remainder of his life, though he later sold off a portion (28.viii.1925 CAS). He continued his entomological studies, including rearing Lepidoptera and illustrating early stages. He kept his insect collection in a building that had previously been used as a barn (v.1919 CAS). A very talented artist, Edgar sometimes sent life-sized sketches of his captures to other entomologist for identification (ii.1882 FNMH). Two of his drawings were published by Hiser & Hiser (1918).

George never married. Although the 1910 federal census listed him as a real estate agent in Santa Cruz, his voter registration that year indicated that he was retired, which is consistent with family history (Dodge & Angle [1926]). He lived at 164 Wilkes Circle, less than a mile from Edgar, where he had a German boarder by the name of Constantine Boettger. It does

not appear that George was entomologically active after moving to California, possibly because of declining health. A worn photograph of George in California is preserved at CAS (Fig. 4). Inscribed, “George M. Dodge, Santa Cruz, Cal 1910,” it portrays the intrepid naturalist at the age of 64. He died two years later in Santa Cruz on 25 February 1912 and was buried at Odd Fellows Cemetery (currently Oakwood Memorial Park) in that city. Edgar later donated George’s collections of 165 horseflies and 478 cicindelid beetles to CAS (Van Duzee 1919, 1926). The former were largely collected “in the days when eastern Nebraska and Kansas was mostly virgin prairie” (13.viii.[1925] CAS). George’s Lepidoptera specimens were retained by Edgar.

Edgar often collected insects in the vicinity of his home, where he discovered a new skipper which Bell (1927) described as *Pamphila juba* race *dodgei* (now recognized as *Hesperia columbia dodgei*). He and another collector, John P. Strohbeen, first encountered these skippers in 1926 within vacant lots around the King Street section of Santa Cruz, an area now heavily developed. Not surprisingly, that population was extirpated by 1950 (Martin 1950). An article about the discovery of this skipper appeared in the local Santa Cruz newspaper, in which it was announced, “It is with great pleasure that this new race of butterflies is named for E. A. Dodge, who with Mr. Strohbeen spend their leisure time in gathering all forms of insect life” (Anonymous 1927). During the early 1920s, Edgar was still defending his late brother’s description of *H. pawnee* as a species separate from *Hesperia ottoe* W. H. Edwards (12.i.1921 CAS). Despite his best efforts, Barnes & Benjamin (1926) and other authors considered them to be synonymous. George and Edgar were ultimately vindicated, as *pawnee* and *ottoe* are now recognized as members of distinct species.

In addition to Hesperiidae, Edgar became “quite interested” in geometrid moths ([x.1919] CAS), though his curiosity in this group wavered over the years: “I have never been much interested in these as I liked the Noct [Noctuidae] better” (28.vii.1926 NAKC). He eventually grew frustrated with the many varieties of moths that he found. “I have about concluded that a collection of moths is [too] much for me,” Edgar confessed, adding, “I may have to let some other fellow attend to things in that line” (27.?.[1922] CAS). Despite his waning interest in other types of moths, his obsession with *Catocala* remained strong. He argued that if he knew anything, “it is the *Catocalae*” (8.ix.1920 CAS). He published short notes about *Catocala* that he and George had previously found in Nebraska and Missouri (E. Dodge 1919, 1925). In 1914, Edgar visited

Nebraska where he collected *Catocala* with his old friends (E. Dodge 1919). Edgar continued to collect other California insects, including Hymenoptera and Diptera, and his specimens were mentioned by a numerous authors (e.g. Malloch 1914, Van Duzee 1926, Middlekauff 1950, 1960, Hurd 1955, Alexander 1967, Perkins 1973, MacNiell 1964). So many specimens of the Dodge’s were in circulation by the 1920s that the Illinois Lepidopterist William Barnes obtained some through secondary sources (10.vi.1926 NAKC).

During the 1920s, Edgar desired to sell most of his remaining land in Pleasant Township, Dodge County, Nebraska. He accomplished this with the help of his brother Charles and Herman H. Holsten, a fellow bank president who owned several properties around the town of Dodge (Dodge & Angle [1926]). Plat maps of Dodge County indicate that Edgar retained ownership of 65 ha (160 ac), which transferred to his wife, Ida, after his death. Ida had family in Nebraska and this connection probably convinced Edgar to retain land there.

Through Barton W. Everman, then Director of CAS, Edgar became acquainted in 1919 with E. P. Van Duzee, an entomologist who had recently become the curator of the museum (10.i.1919, 20.vi.[1919] CAS). Edgar and Van Duzee quickly developed a close friendship. Not long after becoming acquainted with Van Duzee, Edgar wrote, “I should not be surprised if the museum did not fall heir to my collection some day when I am through with them” (19.iv.1919 CAS). Beginning in 1919, Edgar donated batches of his specimens to CAS. For many years, Edgar and Van Duzee corresponded, visited one another, and collected insects together. Edgar reassured Van Duzee that he was “always glad to have a fellow collector to hunt with” (16.vi.1919 CAS). Following one early collecting trip with Van Duzee, Edgar contracted a severe illness, possibly a reaction to poison oak, which temporarily affected his eyesight (ibid.). Unable to afford his own copy of *The Moth Book* (Holland 1903), Edgar repeatedly borrowed a copy from Van Duzee, who was never inconvenienced to help his friend, mailing it back and forth without complaint.

Edgar was an expert naturalist, but he did not care for fishing. An unpleasant fishing trip with his son forever turned him against this leisurely pursuit. Ralph was an expert fisherman and thought his father would enjoy an outing. “About the first thing I was foolish enough to do was to fall in the creek,” Edgar wrote. “I started back to the car for any clothes and got lost in the chaparral and wandered about for thirty six hours before I found a friendly Italian and got back to civilization.” This effectively resolved Edgar’s dilemma:

"Ralph has said nothing since about making a fisherman of Dad" ([v.1919] CAS).

In 1922, Edgar suffered "something in the nature of a stroke." As a result, he did not recognize his family and could "walk but little" (14.vii.[1922] CAS). He also "got moths and everything else badly mixed," thus he temporarily quit working with insects until his health improved ([v.1926] NAKC). In 1930, he complained that he had "serious heart trouble" and his doctor advised him to discontinue collecting insects or climbing the stairs to his "bug house". Refusing to stifle his passion, Edgar declared, "I shall however continue to climb the stairs and if it kills me I shall die in a good cause" (6.v.1930 CAS). Edgar died three years later on 22 March 1933 at the age of 79 and was buried at Odd Fellows Cemetery (currently Santa Cruz Memorial Park) in Santa Cruz.

As he had proposed many years earlier, Edgar bequeathed his remaining insects to CAS. Three days after Edgar's death, Van Duzee contacted Ida Dodge to arrange for the transport of her husband's collection. "I will run down there at any time with one days notice and attend to packing up the specimens," he assured Ida. Grateful for the gift, Van Duzee added, "It certainly was very kind and thoughtful in Mr. Dodge to wish his material placed in this collection but I am sure there is not a place where they would be of so much service to future entomologists as they will be here" (25.iii.1933 CAS). Accession records at CAS indicate that over 7,600 specimens, mostly Lepidoptera, were ultimately obtained from Edgar. The Dodge's employed distinctive triangular labels (Fig. 6, bottom), which are helpful in recognizing Dodge specimens at CAS. These large labels were often replaced by others who obtained their specimens. For example, those from the C. P. Whitney collection at the Peabody Museum of Natural History (Yale University, New Haven, Connecticut; PMNH) bear smaller replacement labels in Whitney's hand (Fig. 6, top).

In the CAS archives is a 100-page "Day Book" ledger that evidently accompanied the transfer of Edgar's insect collection to the museum after his death in 1933. Written in pencil in Edgar's hand is the inscription, "*List of the collection of G. M. and E. A. Dodge, with notes, names of the food plants, where from localities, etc. - from 1869 - to - 1916,*" to which is added, "*Continued by E. A. Dodge to 1930.*" Another notation reads, "*This book should go with the collection. Contains lists of all insects in the collection.*" This ledger consists primarily of a list of Lepidoptera species with running tallies that record the number of specimens in their collection and brief references to localities (e.g. "Ill." and "Neb."). Species collected by

the Dodge's are often accompanied by "G. M. Dodge," "E. A. Dodge," or simply "Dodge." Hostplants are listed for many species, especially *Catocala* moths, many of which were "bred by Dodge." This catalog follows the arrangement and nomenclature of the *Check List of the Lepidoptera of Boreal America* by Barnes & McDunnough (1917). Because George died prior to the publication of this checklist, Edgar is entirely responsible for the creation of the catalog, which he probably began during the 1920s. Tipped into the ledger are a few photographs and several original letters, mostly regarding taxa named in honor of Edgar. Also included is a list by Edgar of the butterflies that he collected in Santa Cruz and a tally of the specimens in the collection of J. P. Strohbeen. Unfortunately, there are no records of who received their specimens via exchange or sale. Names of other collectors appear next to some entries, presumably identifying the sources of those specimens. Because George's specimens were clearly combined with those of Edgar, it is likely that some published references to Edgar's specimens at CAS (e.g. MacNeill 1964) are attributable to George. Many unattributed specimens listed by Burns (1964) from Nebraska, Missouri and California were undoubtedly collected by both Edgar and George.

In addition to specimens from George, some of the insects donated by Edgar to CAS were collected by Edgar's son, Ralph E. Dodge. Born in Louisiana, Missouri on 13 April 1892, Ralph shared his father's interest in insects. His moth collecting activities were mentioned by Rowley (1908a, 1909) and personal advertisements indicate that Ralph also collected bird eggs, Native American artifacts, shells, and stamps. He supposedly had one of the largest private collections of Native American artifacts in California ([x.1919] CAS) and some of his objects were listed by Moorehead (1917). Ralph published a few natural history notes in various journals and bulletins (e.g. R. Dodge 1914a, 1914b).

Around 1912, Ralph briefly relocated to Nickerson, Dodge County, Nebraska, where he collected *Catocala* moths (Rowley & Berry 1913). Probably in 1915, the year he joined the Cooper Ornithological Club (Hollywood, California), Ralph returned to Santa Cruz. He briefly worked in banking before becoming an automobile garage owner. In 1917, he described himself on his military draft registration as "physically able," tall and slender, with brown hair and brown eyes. He enlisted in the army the following year with the expectation of serving in the First World War: "I look forward to taking up my relic collecting with a great deal of pleasure as soon as the war is over" (Anonymous 1918). He served in France during the last part of the

war. A photograph of Ralph, taken in New York upon his return from Europe in 1919, portrays a war-weary doughboy at the age of 27 (Fig. 5).

After the war, Ralph co-owned an automobile garage and dealership, selling Hupmobile, Marmon, and Nash models. He remained active in natural history and presented a paper on the birds that he had observed in France during the war (Chambers 1919). He and his father continued to sugar for moths in the vicinity of Santa Cruz (14.x.1920 CAS). In 1922 Ralph moved to Exeter, Tulare County, California, where he bought an "orange orchard" and also grew olives (vi.1922, 8.xi.1922 CAS). For several months he lived alone on his property along Rural Delivery 9 (Box 468). Assuming this solitude would be short-lived, Edgar predicted, "I have an idea he expects to export one of the Santa Cruz maidens before many days to help him out on his ranch" (27.[vii].1922 CAS). Only two months later, on 10 September 1922, Ralph married Cordelia M. Blewett (1891–1941), an accountant from Santa Cruz. They had one child, Marshall Blewett Dodge (1923–1945). Ralph collected moths in the vicinity of his ranch in the San Joaquin Valley and sent many of the specimens to his father. In 1922, Ralph traveled to San Francisco where he met E. P. Van Duzee (17.ix.1922 CAS).

In early May 1925, Ralph lacerated his toe while working on his tractor and developed "blood poisoning" (presumably septicemia). He visited his parents in Santa Cruz a few days after the accident, but his condition worsened and he did not recover (13.viii.[1925] CAS). Tragically, he died in a Santa Cruz hospital on 14 May 1925 at the age of 33. He was buried at Odd Fellows Cemetery (currently Santa Cruz Memorial Park) in Santa Cruz, where his father would be interred less than a decade later. Referring to Ralph's last entomological project, Edgar wrote, "He was interested in the moths and at the time of his death he was making a local collection at Exeter for a farm advisor or fruit specialist for the valley" (*ibid.*).

Not only did Edgar suffer the loss of a son, he also lost a collecting companion and entomological heir. "If Ralph had lived he would have taken over my collection," he remarked (2.vi.1926 NAKC). Van Duzee (1925) announced Ralph's death in a brief notice, in which he lamented, "Our Western entomologists will feel that their branch of science has sustained a serious loss in the death of young Mr. Dodge." The following year, Edgar donated 211 moths to CAS that Ralph had collected in Exeter (Van Duzee 1926). Ralph's Native American artifacts were loaned to the "Los Angeles Park Museum" (now the Natural History Museum of Los Angeles County; Los Angeles, California; LACM).

It was hoped that Ralph's son, Marshall, would someday "want to carry on this line of work" (13.viii.[1925] CAS, 2.vi.1926 NAKC), but Marshall was later found to suffer from mental disabilities and reportedly committed suicide in 1945 at the age of 22. Ralph's artifact collection was acquired in 1930 by the amateur archaeologist Harry H. Bergman, who in 1920 had married Ralph's sister, Alice. Ralph's artifacts formed the basis of Bergman's Museum of Natural History, which opened to the public in 1930 near Aguanga, California. The museum was closed in 1993 and its collections sold. Many of Ralph's artifacts were available for sale on the Internet just a few years ago. Bergman's museum reportedly also possessed a collection of butterflies and moths (Karr 1968), perhaps including old specimens from Ralph and his father, Edgar.

Edgar's daughter, Alice, undoubtedly also enjoyed an appreciation of insects. Hoping to "find out something about them," she sent Edgar some hemipteran specimens which she had found in the vicinity of her home in the Imperial Valley of California, (vi.1922 CAS). Edgar collected Lepidoptera during his visits to her ranch in Riverside County (14.vii.[1922] CAS). In 1926, Alice joined her parents and the Strohbeens on an insect collecting trip to Truckee and Lake Tahoe, California (2.vii.1926 NAKC). Fond of painting water color portraits of flowers, Alice's interest in natural history is also indicated by her marriage to H. H. Bergman, who claimed that she accompanied him on all of his collecting expeditions (Karr 1968). She died on 3 July 1989 at the age of 93 and was buried in Radec Cemetery, Radec, California.

John P. Strohbeen. Edgar's field companion in California, John P. Strohbeen, also had broad interests in natural history, especially entomology, conchology, and botany. In his later years, Edgar collaborated with Strohbeen in the study of the Lepidoptera of Santa Cruz County (E. Dodge 1920, Van Duzee 1933). As Edgar aged, Strohbeen's assistance became more valuable. Being the younger of the two, Strohbeen did most of the collecting, while Edgar mounted the specimens ([v.1926] NAKC). Little has been published about Strohbeen, thus I take this opportunity to more fully introduce him to the entomological community. The following account is taken from a variety of public records and a brief biographical memo preserved in the archives of the Museum of Art and History in Santa Cruz.

The eldest of seven children, John Peter Strohbeen (Fig. 7) was born on 18 April 1884 in Remsen, Iowa, where he worked as a dry goods clerk during his teens. In 1904, he moved to Santa Cruz, California, where he

was employed as a grocery clerk, then as a clerk and driver for the dry goods retailer Bias & Company. In 1913 he married Carolyn Hertz (1887–1973), a department store clerk. Five years later, Strohbeen went to work for the Pacific Telephone and Telegraph Company as a repairman, electrician, and installer. In 1918, he described himself on his military draft card as 1.8 m (6 ft.) in height, medium build, with gray eyes and blond hair. He worked for P.T. & T. until his retirement in 1946, after which he was able to commit more time to his natural history studies. He was a prolific collector and traveled throughout much of California in search of specimens. Edgar referred to Strohbeen's zealous field methods as "wholesale collecting" (2.xi.1919 CAS). Strohbeen yearned to take a trip to South America in search of *Morpho* butterflies ("these big ones look good to John"), but I have found no evidence that he ever took such a trip. Strohbeen sometimes worked with other naturalists on various projects outside entomology (e.g. Sorenson et al. 1955). As with Edgar Dodge, Strohbeen was an early source of encouragement to the California lepidopterist J. W. Tilden (Smith 1990).

During a collecting trip in Santa Cruz in 1923, Strohbeen collected some butterfly specimens which he sent to Edgar. Many years later, Edgar forwarded a few to the San Francisco entomologist Robert F. Sternitzky, who described them as a new subspecies, *Parnassius clodius strohbeeni* (Sternitzky 1945). Coincidentally, Gunder (1932) previously described an aberration of this taxon as *dodgei* in honor of Strohbeen's old friend, Edgar Dodge. Regrettably, *P. c. strohbeeni* was last seen in 1958 and is believed to be extinct (Garth & Tilden 1986).

Shortly after the death of Edgar in 1933, Strohbeen and his wife moved to 315 King Street, a few doors down from the new residence of Edgar's widow, Ida. Some years later, Strohbeen purchased all but a small portion of Edgar's remaining land in Santa Cruz. He moved onto this property around 1945 and resided there for the next thirty years at 1135 King Street. He died at the age of 92 on 10 August 1976 at a convalescent hospital in Arroyo Grande, California, and was buried at Santa Cruz Memorial Park in Santa Cruz. His natural history specimens are deposited in various museums, including CAS, LACM, the National Museum of Natural History (Washington, D.C.; USNM), and the Santa Cruz Museum of Natural History (Santa Cruz, California). His collection of photographs of the 1906 San Francisco earthquake and fire are preserved by the California Historical Society.

Type specimens. Some of G. M. Dodge's type specimens were destroyed in a fire around 1905. Based

on information from Edgar, Beutenmüller (1907, 1908) stated that the types of *Catocala whitneyi* were destroyed by fire and that all but one specimen from the type series of *C. titania* met the same fate. Referring to the types of *titania*, Edgar indicated in his ledger that this taxon was described from an adult specimen which had been reared from a larva "beaten from young trees." He also stated that two other specimens of *titania* were taken that season "and about 25 more the next season," all of which were lost in the fire. In 1914, Edgar recalled, "The types of *Nebraskae* and *Whitneyi* also *Somnus* were destroyed by fire a number of years ago" (14.xi.1914 NAKC). The brothers evidently sent a few syntypes to correspondents before the fire. A surviving name-bearing type of *titania*, for many years in the possession of William Barnes and figured in Barnes & McDunnough (1918a), was designated as lectotype by Gall & Hawks (2010). Leussler (1921) claimed that a "type" of *Hesperia pawnee* also was lost in a fire, but this contradicts the comments of Edgar, who claimed that only a box of *Catocala* had burned, but it "unfortunately contained all our types" (29.xii.1920 CAS).

George and Edgar sold and exchanged many specimens, including those they considered to represent "types" (see G. Dodge 1872c). In addition, their use of the term "type" was loosely defined and included specimens of "typical" appearance. It is therefore important to scrutinize some alleged "types" that are currently preserved in museums. For example, Van Duzee (1919) stated that Edgar had donated male and female specimens of *H. pawnee* to CAS, both of which he identified as "the types" from Nebraska. These specimens, however, are similarly labeled and the female was collected in 1880 (Fig. 6, bottom); much too late to be included in the type series of a taxon described in 1874. This discrepancy was later noted by E. P. Van Duzee, who ultimately dismissed them as primary types. In a letter to Edgar, Van Duzee asserted that they "evidently are topotypes having been taken at the same locality." He recalled that Edgar previously indicated that the specimens were "from a series carefully compared with the type" by Edgar and George, "so there could be little if any chance of their not belonging to this species" (25.i.1921 CAS). Despite the date on the female, CAS considers both specimens to represent syntypes (CAS 2012). Presumably valid syntypes of *H. pawnee* are deposited in the Carnegie Museum of Natural History (Pittsburg, Pennsylvania; CMNH), MCZ, and PMNH. Male and female "paratypes" of *pawnee* were figured by Holland (1931, Pl. 52, figs. 30, 31) from specimens in CMNH, but only the male is from Nebraska (where the entire type series

originated). The female was collected in Montana.

A “type” of *C. whitneyi*, labeled 11 July with no locality, is deposited in CAS, but all *Catocala* types in the possession of the Dodge brothers were supposedly destroyed by fire before they moved to California. Because the type series of *whitneyi* was from Illinois, but George lived in Nebraska when he described this species, the “type” in CAS most likely was collected in Nebraska and does not represent a name-bearing type. Another alleged “type” of *whitneyi* is deposited in The Natural History Museum, London (BMNH) (Metzler 1987), but George informed William Beutenmüller that this specimen (ex. A. R. Grote collection) was not from the type series (Beutenmüller 1907).

Although some of George’s type specimens are lost, others are merely misplaced, unrecognized, or overlooked. For example, Pelham (2008) stated that the holotype of *Nisoniades llano* was lost in the San Francisco fire of 1906, yet that event took place three years before George and Edgar moved to California. This holotype, collected by George in Llano, Texas on 17 April 1902, was found in the CAS general collection. Likewise, the whereabouts of the holotype of *Pyrameis huntera* var. *fulvia* was unknown for many years (Pelham 2008). It was figured by John A. Comstock (1927), whose collection is deposited in LACM. A brief search of that collection revealed that Comstock had retained the specimen. Although Gatrell (1999) designated a neotype for *Hesperia illinois* Dodge, at least three syntypes were found to exist in the American Museum of Natural History (New York, New York; AMNH), The Academy of Natural Sciences (Philadelphia, Pennsylvania; ANSP) (see F. Brown 1974), and PMNH. Other Dodge type specimens surely await discovery.

Many of the Dodge’s specimens serve as name-bearing types of insects that were described by other authors. A few of these, however, are routinely overlooked because of misunderstandings about their origin. McDunnough (1950) dismissed a purported type of the moth *Agrotis personata* Morrison (= *Euxoa detersa* (Walker); Noctuidae), which was collected by George Dodge in Illinois, because it is labeled “Ohio.” McDunnough apparently was unaware that George lived and collected around the town of Ohio, Illinois. Some types were received from other collectors, but were wrongly credited to the Dodge’s. For example, Edwards (1879) stated that four syntypes of the butterfly *Argynnis hippolyta* (= *Speyeria zerene hippolyta* (W. H. Edwards)) were “received from Mr. G. M. Dodge and taken in Oregon.” Subsequent authors (e.g. Barnes & McDunnough 1916; F. Brown 1965; Dornfeld 1980) interpreted this to mean that the

specimens were collected by George Dodge. However, Elwes (1889) explained that the specimens had been received by George from Orson B. Johnson (1849–1917), a pioneer resident collector of Oregon and Washington. The entry for this taxon in Edgar’s ledger (CAS) supports this contention, reading, “Oregon, Johnson.” In a letter to Herman Strecker, Edgar recalled that they had received “about 20 ♂♂ and 1 ♀” of *hippolyta* from Johnson (8.1881 FMNH).

Taxa described by G. M. Dodge. Listed below are the insect taxa described by George M. Dodge, arranged chronologically by Order, in their original nomenclatural combination, with current synonymy, type locality, and known locations of recognized type specimens. Information regarding Orthoptera is from Eades et al. (2012).

LEPIDOPTERA

1. *Hesperia illinois* G. Dodge, 1872 (= *Euphyes bimacula illinois*; Hesperidae). TL: Bureau Co., Illinois (neotype from Grundy Co., Illinois). Invalid neotype at MGCL (see Calhoun in press); syntypes at AMNH, ANSP and PMNH. Topotypes at CAS. A lectotype will be designated (Calhoun in press).
2. *Hesperia pawnee* G. Dodge, 1874 (= *Hesperia leonardus pawnee*; Hesperidae). TL: Glencoe, Dodge Co., Nebraska. Syntypes at MCZ, PMNH, and CMNH. Topotypes at CAS.
3. *Catocala whitneyi* G. Dodge, 1874. (Noctuidae). TL: Ohio, Bureau Co., Illinois. Syntypes purportedly destroyed. “Type” at CAS is likely from Nebraska and thus not a syntype.
4. *Catocala nebraskae* G. Dodge, 1875 (= *Catocala luciana* Strecker, 1874; Noctuidae). TL: Glencoe, Dodge Co., Nebraska. Lectotype at USNM. This specimen was apparently sent to W. Barnes before a fire claimed George’s other *Catocala* types.
5. *Catocala nebraskae* var. *somnus* G. Dodge, 1881 (= *Catocala luciana* Strecker, 1874; Noctuidae). TL: Glencoe, Dodge Co., Nebraska. Location of type(s) unknown; purportedly destroyed.
6. *Pyrameis huntera* var. *fulvia* G. Dodge, 1900 (= *Vanessa virginiensis* (Drury, 1773); Nymphalidae). TL: Louisiana, Pike Co., Missouri. Holotype at LACM.
7. *Catocala titania* G. Dodge, 1900 (= *Catocala alabamiae* Grote, 1875; Noctuidae). TL: Louisiana, Missouri. Lectotype at USNM. This specimen was apparently sent to W. Barnes before a fire claimed George’s other *Catocala* types.
8. *Nisoniades llano* G. Dodge, 1903 (= *Gesta invisus* (Butler & Druce, 1872); Hesperidae). TL: Llano, Llano Co., Texas. Holotype at CAS.

ORNITHOPTERA

1. *Pezotettix junius* G. Dodge, 1876 (= *Melanoplus borealis* (Fieber, 1853); Acrididae). TL: Glencoe, Dodge Co., Nebraska. Lectotype at USNM.
2. *Pezotettix autumnalis* G. Dodge, 1876 (= *Phoetaliotes nebrascensis* (Thomas, 1872); Acrididae). TL: Glencoe, Dodge Co., Nebraska. Possible syntype at USNM.
3. *Pezotettix alba* G. Dodge, 1876 (= *Hypochlora alba*; Acrididae). TL: Glencoe, Dodge Co., Nebraska. Syntype at ANSP.
4. *Caloptenus lurida* G. Dodge, 1876 (= *Melanoplus keeleri luridus*; Acrididae). TL: Dodge Co., Nebraska. Syntypes at ANSP and USNM.
5. *Caloptenus regalis* G. Dodge, 1876 (= *Melanoplus regalis*; Acrididae). TL: Glencoe, Dodge Co., Nebraska. Location of type(s) unknown.
6. *Caloptenus angustipennis* G. Dodge, 1877 (= *Melanoplus angustipennis*; Acrididae). TL: Banks of Elkhorn River, Dodge Co., Nebraska. Location of types unknown.
7. *Caloptenus volucris* G. Dodge, 1877 (Acrididae). TL: Glencoe, Dodge Co., Nebraska. Location of type(s) unknown.
8. *Caloptenus plumbum* G. Dodge, 1877 (Acrididae). TL: Glencoe, Dodge Co., Nebraska. Location of types unknown.
9. *Pezotettix abditum* G. Dodge, 1877 (= *Melanoplus dawsoni* (Scudder, 1875); Acrididae). TL: Glencoe, Dodge Co., Nebraska. Syntype in ANSP.

Patronyms. Listed below are patronyms of insects which honor the Dodge brothers, arranged chronologically by Order, in their original nomenclatural combination, with current synonymy and honoree name.

DIPTERA

1. *Tabanus dodgei* Whitney, 1879 (= *Anacimas dodgei*; Tabanidae). G. M. Dodge.

LEPIDOPTERA

1. *Mamestra dodgei*, Morrison, 1875 (= *Lacinipolia lorea* (Guenée, 1852); Noctuidae). G. M. Dodge.
2. *Pamphila juba* race *dodgei* Bell, 1927 (= *Hesperia colorado dodgei*; Hesperidae). E. A. Dodge.
3. *Euptoieta claudia dodgei*, ♀ nov. tr. form Gunder, 1927 (= *Euptoieta claudia*; Nymphalidae). E. A. Dodge.
4. *Everes amyntula* tr. f. *dodgei* Gunder, 1927 (= *Cupido a. amyntula*; Lycaenidae). E. A. Dodge.
5. *Argynnis dodgei* Gunder, 1931 (= *Speyeria hesperis dodgei*; Nymphalidae). E. A. Dodge.

6. *Parnassius clodius* tr. f. *dodgei* Gunder, 1932 (= *Parnassius clodius strohbeeni* Sternitzky, 1945; Papilionidae). E. A. Dodge.

ACKNOWLEDGEMENTS

Members of the Dodge family, especially Norman Dodge, offered valuable genealogical assistance regarding the Dodge family. Carol Angle, Catherine Angle, and Monica Angle generously shared photographs and documents related to the Dodge brothers, including an unpublished manuscript previously owned by Charles' daughter, Catharine, who married Edward E. D. Angle. Jacqueline Y. Miller & Andrew D. Warren (MCGL) and Wenxian Zhang & Darla Moore (RC) kindly permitted access to the manuscript collections under their care. Darla Moore also hosted my visit to RC. Pamela J. Anderson (NAKC), Danielle Castronovo & Kelly Jensen (Library, CAS), Armand Esai (FMNH), Vincent F. Lee (Dept. of Entomology, CAS), Violetta Wolf (BMS), and Robert Young & Dana Fisher (MCZ) supplied numerous images and copies of correspondence. Marla Novo (Museum of Art and History, Santa Cruz, California) sent biographical information about J. P. Strohbeen and permitted me to publish his image. James H. Boone (FMNH), Rodney Eastwood (MCZ), Suzanne R. Green & Andrew A. Johnston (AMNH), Donald J. Harvey (USNM), Vincent F. Lee & Norman D. Penny (CAS), John E. Rawlins (CMNH), Jason D. Weintraub (ANSP), and Weiping Xie (LACM) answered questions and searched for specimens. Ken Lyons (McHenry Library, Univ. of California Santa Cruz) supplied scans from the Santa Cruz News. Julie Thompson made available the photographs of E. A. Dodge and his family, including Ralph. I thank Megan MacKenzie of Santa Cruz Memorial Park for confirming cemetery records. Finally, I am grateful to James R. Wiker, and an anonymous reviewer for reading drafts of the manuscript.

LITERATURE CITED

- ALEXANDER, C. P. 1967. The crane flies of California. Bull. Calif. Ins. Surv. 8:1–269.
- ANONYMOUS. 1890. Burned to the water's edge: the steamer H. B. Plant destroyed—four lives probably lost. New York Times. 30 Ap.
- . 1913. New banks and changes. Nebraska. Comm. West 24:30.
- . 1914. New banks and changes. Nebraska. Comm. West 26:28.
- . 1918. [Ralph E. Dodge joins the Army]. Arch. Bull. 9:59–60.
- . 1927. Rare butterfly is given classification. Santa Cruz News. 35:1.
- BALDWIN, S. M. & R. M. BALDWIN. 1932. Nebraskana: biographical sketches of Nebraska men and women of achievement who have been awarded life membership in the Nebraskana Society. Baldwin Co., Hebron, Nebraska. 1374 pp.
- BARNARD, S. & J. T. ALLEN (eds.). 1887. Annual report of the Nebraska State Horticultural Society. 1885. State Jour. Co., Lincoln, Nebraska. 150 pp.
- BARNES, W. & F. H. BENJAMIN. 1926. Check list of the diurnal Lepidoptera of boreal America. Bull. So. Calif. Acad. Sci. 25:3–27.
- BARNES, W. & J. McDUNNOUGH. 1916. Notes on North American diurnal Lepidoptera. Contrib. Nat. Hist. Lepid. North Amer. 3:53–156, 11 pls.
- . 1917. Check list of the Lepidoptera of boreal America. Herald Pr., Decatur, Illinois. viii+392 pp.
- . 1918a. Illustrations of the North American species of the genus *Catocala*. Mem. Amer. Mus. Nat. Hist. 3:1–47, 22 pls.
- . 1918b. Life histories of North America species of the genus *Catocala*. Bull. Amer. Mus. Nat. Hist. 38:147–177.
- BELL, E. L. 1927. Description of a new race of *Pamphila juba* Scudder (Lepidoptera—Rhopalocera—Hesperidae). J. New York Entomol. Soc. 35:175–176.
- BEUTENMÜLLER, W. 1907. Notes on and description of new forms of *Catocala*. Bull. Amer. Mus. Nat. Hist. 23:145–151.

- . 1908. Description of a new *Catocala*. Entomol. News 19:54–55.
- BOUSEMAN, J. K. J. G. STERNBURG, & J. R. WIKER. 2006. Field guide to the skipper butterflies of Illinois. Illinois Nat. Hist. Surv. Man. 11. Champaign, Illinois. viii+200 pp.
- BROWN, F. M. 1965. The types of the nymphalid butterflies described by William Henry Edwards. Part I. Argynninae. Trans. Amer. Entomol. Soc. 91:233–350.
- . 1974. The types of butterflies in the Academy of Natural Sciences, Philadelphia, Pennsylvania. Proc. Acad. Nat. Sci. Phil. 126:51–54.
- BROWN, F. M. & L. D. MILLER. 1980. The types of the hesperiid butterflies named by William Henry Edwards. Part II, Hesperidae: Hesperinae, section II. Trans. Amer. Entomol. Soc. 106:43–88.
- BROWN, G. A. (ed.). 1879. Manual of the legislature of the State of Nebraska for the year 1879. State printer, Lincoln, Nebraska. 175 pp.
- BURNS, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. Univ. Calif. Publ. Entomol. 37:i–iv, 1–214, 1 pl.
- BUSS, W. H. & T. T. OSTERMAN. 1921. History of Dodge and Washington Counties, Nebraska and their people. Amer. Hist. Soc., Chicago, Illinois. iv+455 pp.
- CALHOUN, J. V. in press. *Hesperia illinois* Dodge (Hesperiidae): an invalid neotype and the designation of a lectotype. J. Lepid. Soc.
- CALLERY, E. 2009. Place names of Illinois. Univ. Illinois Pr., Champaign, Illinois. xxvii+425 pp.
- CAS [California Academy of Sciences]. 2012. Types collection database. Webpage: <http://research.calacademy.org/redirect?url=http://researcharchive.calacademy.org/research/entomology/typesDB/default.asp>.
- CASSINO, S. E. 1877. The naturalists' directory, containing the names of naturalists, chemists, physicists, & meteorologists, arranged alphabetically, with an index arranged according to departments. Naturalists Agency, Salem, Massachusetts.
- CHAMBERS, W. L. 1919. Minutes of Cooper Club meetings. Southern Division. Condor 21:242.
- COMSTOCK, J. A., Jr. 1927. Butterflies of California. A popular guide to a knowledge of the butterflies of California, embracing all of the 477 species and varieties at present recorded for the state. The author, Los Angeles, California. 334 pp., 63 pls.
- DENMARK, H. A. 1973. Harold Rodney Dodge (1913–1973). Florida Entomol. 56:300–304.
- DODGE, C. F. & C. D. ANGLE (eds.). [1926]. [Marshall family history]. Unpubl. typescript. 64 pp.
- DODGE, E. A. 1888. Wire-screening a portico to keep out mice, etc. Glean. Bee Cult. 16:100.
- . 1897. [comments about *Begonia* disease]. Amer. Garden. 18:553.
- . 1919. *Catocala* notes. Lepid. 3:54.
- . 1920. The early stages of *Syneda dinergens*. Lepidopterist 3:117–118.
- . 1925. Notes on the life history of *Catocala whitneyi* (Dodge) (Lepid.: Noctuidae). Entomol. News 36:267–268.
- DODGE, G. M. 1870. The antiopa butterfly. Amer. Entomol. Bot. 2:371–372.
- . 1872a. [Mites on beetles]. Our young folks 8:188.
- . 1872b. An error corrected. Can. Entomol. 4:198–199.
- . 1872c. A new hesperian. Can. Entomol. 4:217–218.
- . 1873. *Hesperia illinois* identical with *Hesp. acanoetus*, Scud. Can. Entomol. 5:60.
- . 1874a. *Hesperia pawnee* n. sp. Can. Entomol. 6:44–45.
- . 1874b. Notes on collecting Lepidoptera. Can. Entomol. 6:114–115.
- . 1874c. *Catocala whitneyi*, n. sp. Can. Entomol. 6:125–126.
- . 1875a. *Catocala nebraskae*, Dodge. Can. Entomol. 7:2.
- . 1875b. Notes on *Caloptenus spretus*. Can. Entomol. 7:133–135.
- . 1876a. New species of Acridini from Nebraska. Can. Entomol. 8:9–12.
- . 1876b. Notes on the variation in color of *Oedipoda corallipes* and *Oedipoda cincta*. Can. Entomol. 8:101–102.
- . 1877. New species of *Orthoptera*. Can. Entomol. 9:111–113.
- . 1878. Variations in the wing expanse of *Pezotettix*. Can. Entomol. 10:103–105.
- . 1881. On a variety of *Catocala nebraskae*, Dodge. Can. Entomol. 13:40.
- . 1882a. The cabbage butterfly, *Pieris rapae*, in Nebraska. Ann. Rpt. Entomol. Soc. Ontario 13:30–31.
- . 1882b. *Pieris rapae* in Nebraska. Can. Entomol. 14(2):39–40.
- . 1890. Root knot on apple trees. Ins. Life 2(10):315.
- . 1893. A peculiar gad-fly. Ins. Life 6(1):34.
- . 1898. Food of *Eudamus lycidas*. Entomol. News 9(4):89.
- . 1899. Concerning flies. Colman's. Rural World (14 September).
- . 1900a. List of catocalae taken at Louisiana, Missouri. Entomol. News 11(3):433.
- . 1900b. *Catocala titania* n. sp. Entomol. News 11(5):472.
- . 1900c. *Pyrameis huntera*, n. var. *fulvia*. Can. Entomol. 32(3):92.
- . 1903. A new butterfly from Texas. Can. Entomol. 35(3):78.
- DODGE, G. M. & E. A. DODGE. 1901. Notes on the early stages of *Catocala*. Can. Entomol. 33(7):221–226, (11):298–300.
- . 1904. Notes on the early stages of *Catocala*. Can. Entomol. 36(4):115–117.
- DODGE, J. T. 1894. Genealogy of the Dodge family of Essex County, Mass: 1629–1894. Printed for the author, Madison, Wisconsin. v+448 pp.
- DODGE, R. E. 1914a. California shell mounds. Archaeol. Bull. 4(5):114–116.
- . 1914b. [Discovery of old village site]. Archaeol. Bull. 5(3):51–52.
- DORNFELD, E. J. 1980. The butterflies of Oregon. Timber Pr., Forest Grove, Oregon. xiv+276 pp.
- DOS PASSOS, C. F. (ed.). 1951. The entomological reminiscences of William Henry Edwards. J. New York Entomol. Soc. 59(3):129–186.
- EADES, D. C., D. OTTE, M. M. CIGLIANO & H. BRAUN. 2012. Orthoptera Species File Online. Webpage. Version 2.0/4.1. <http://Orthoptera.SpeciesFile.org>.
- EDWARDS, W. H. 1879. Descriptions of new species of North American butterflies; also, notes upon certain species. Can. Entomol. 11(5):81–89.
- . 1880. On certain species of *Satyrus*. Can. Entomol. 12(2):21–32, (3):51–55, (5):90–94, (6):109–115.
- . 1887–1897. The butterflies of North America [with coloured drawings and descriptions]. Vol. 3. Houghton, Mifflin & Co., Boston, Massachusetts and New York, New York. [8]+430 pp., [51] pls.
- ELWES, H. J. 1889. A revision of the genus *Argynnis*. Trans. Entomol. Soc. London 1889(4):535–575.
- EWAN, J. & N. D. EWAN. 1981. Biographical dictionary of Rocky Mountain naturalists: a guide to the writings and collections of botanists, zoologists, geologists, artists and photographers 1682–1932. Bohn, Scheltema & Holkema, Utrecht, Netherlands. xvi+253 pp.
- FAIRCLOUGH, G. T. (ed.). 1960. Nebraska place-names. Univ. Nebraska Pr., Lincoln, Nebraska. xi+228 pp.
- FORBES, S. A. (ed.). 1889. Report of the state entomologist on the noxious and beneficial insects of the State of Illinois. 15:i–vi, 1–115.
- GALL, L. F. & D. C. HAWKS. 2010. Systematics of moths in the genus *Catocala* (Lepidoptera, Erebidae) IV. Nomenclatural stabilization of the Nearctic fauna, with a revised synonymic check list. ZooKeys 39:37–83.
- GARTH, J. S. & J. W. TILDEN. 1986. California butterflies. Univ. California Pr., Berkeley, California. xvi+246 pp., 24 pls.
- GATRELLE, R. R. 1999. Three new Hesperioidea [sic] (Hesperiinae) from South Carolina; new subspecies of *Euphyes bimacula*, *Poanes aaroni*, and *Hesperia attalus*. Taxon. Rpt. 1(10):1–13.
- GUNDER, J. D. 1932. A few new butterflies (Lepidoptera, Rhopalocera). Pan-Pacific Entomol. 8(3):123–127.
- HAYES, K. J. 2002. An American cycling odyssey, 1887. Univ. Nebraska Pr., Lincoln, Nebraska. x+200 pp.

- HISER, O. F. & J. S.. HISER. 1918. Life history of *Catocala nuptialis*. Lepidopterist 2(9-10):66-69.
- HOLLAND, W. J. 1903. The moth book. A popular guide to a knowledge of the moths of North America. Doubleday, Page & Co., New York, New York. xxiv+479 pp., 48 pls.
- . 1931. The butterfly book. New and thoroughly revised edition. A popular and scientific manual, describing and depicting all the butterflies of the United States and Canada. Doubleday & Co., Garden City, New York. xii+424 pp., 77 pls.
- HOWARD, L. O. 1930. A history of applied entomology (somewhat anecdotal). Smith. Misc. Coll. 84:i-viii, 1-564.
- HURD, P. D., Jr. 1955. The carpenter bees of California (Hymenoptera: Apoidea). Bull. Calif. Ins. Surv. 4(2):35-72.
- KARR, H. 1968. Museum by the side of the road. Desert Mag. 31:14-15.
- IRWIN, R. R. 1972. A brief history of lepidopterology in Illinois. Trans. Illinois St. Acad. Sci. 65(3-4):45-49.
- LEUSSLER, R. A. 1921. *Pamphila ottoe* Edw. and *pawnee* Dodge, with descriptions of a new form (Lep. Rhop.). Entomol. News 32(7):206-207.
- LUCAS, C. A. [1914]. Fremont pictured. C. A. Lucas and J. Martin, Fremont, Nebraska [108] pp.
- MACNEILL, C. D. 1964. The skippers of the genus *Hesperia* in western North America with special reference to California (Lepidoptera: Hesperidae). Univ. Calif. Publ. Entomol. 35:i-iv, 1-221, 8 pls.
- MALLOCH, J. R. 1914. American black flies or buffalo gnats. U.S. Dept. Agric. Tech. Ser. 26:1-70, 6 pls.
- MARTIN, L. M. 1950. Field season summary. California. Lepid. News 4(8-9):86-89.
- MATTHEWS, J. R. 1974. History of the Cambridge Entomological Club. Psyche 81(1):3-37.
- MCDUNNOUGH, J. H. 1950. Species of *Euxoa* of eastern North America, with particular reference to genitalic characters (Lepidoptera, Phalaenidae). Bull. Amer. Mus. Nat. Hist. 95:355-408.
- MEINERS, E. P. 1949. A brief history of lepidopterology in Missouri. Lepid. News 3(4-5):52-53.
- METZLER, E. H. 1987. The type locality of *Catocala whitneyi* and reports of the species in Ohio. J. Lepid. Soc. 41(4):212-213.
- MIDDLEKAUFF, W. W. 1950. The horse flies and deer flies of California (Diptera - Tabanidae). Bull. Univ. Calif. Ins. Surv. 1(1):1-21.
- . 1960. The siricid wood wasps of California. Bull. Univ. Calif. Ins. Surv. 6(4):59-77.
- MOOREHEAD, W. K. (ed.). 1917. Stone ornaments used by Indians in the United States and Canada, being a description of certain charm stones, gorgets, tubes, bird stones and problematical forms. The Andover Pr., Andover, Massachusetts. 448 pp.
- OGLE, G. A. & Co. (firm). 1899. Standard atlas of Pike County Missouri: including a plat book of the villages, cities and townships of the county. G. A. Ogle & Co., Chicago, Illinois. xxii+88 pp.
- . 1902. Standard atlas of Dodge County Nebraska: in including a plat book of the villages, cities and townships of the county. G. A. Ogle & Co., Chicago, Illinois. xxii+77 pp.
- PACKARD, A. S., Jr. 1876. A monograph of the geometrid moths or Phalaenidae of the United States. Rpt. U.S. Geol. Surv. Terr. 10:i-iv, 1-607, 13 pls.
- . 1877. The injurious insects of the west. A report on the Rocky Mountain locust, and other insects now injuring, or likely to injure, field and garden crops in the western states and territories, pp. 590-815. In Hayden, F. V. (ed.), ninth annual report of the United States Geological and Geographical Survey of the territories, embracing Colorado and parts of adjacent territories: being a report of progress of the exploration for the year 1875. Govt. Printing Office, Washington, D.C.
- PELHAM, J. P. 2008. Catalogue of the butterflies of the United States and Canada, with a complete bibliography of the descriptive and systematic literature. J. Res. Lepid. 40:i-xiv, 1-658 pp.
- PERKINS, E. M., JR. 1973. Revision of the *Boloria epithore* complex, with description of two new subspecies (Nymphalidae). Bull. Allyn Mus. 11:1-23.
- RILEY, C. V. 1884. Report of the Entomologist, pp. 285-418. In Loring, G. B. (ed.), report of the Commissioner of Agriculture for the year 1884. Govt. Pr. Off., Washington, D.C.
- ROWLEY, R. R. 1908a. Notes on *Catocala*. Entomol. News 19(3):115-120.
- . 1908b. The geology of Pike County. Rpt. Mo. Bur. Geol. Mines 8(2nd Ser.):i-xiv, 1-122.
- . 1909. Another season with *Catocalae*. Entomol. News 20(3):127-135.
- ROWLEY, R. R. & L. BERRY. 1910. Notes on the life stages of *catocalae*; a summer's record and incidental mention of other Lepidoptera. Entomol. News 21(10):441-455.
- . 1913. Last year's work with *Catocalae* and other Lepidoptera. Entomol. News 24(5):197-205.
- . 1914. 1913 as a *Catocala* year (Lepid.). Entomol. News 25(4):157-167.
- SANBORN, J. B. 2012. History of the town of Burnham. Webpage. <http://familytreemaker.genealogy.com/users/b/e/n/Yojean-A-Benson/FILE/0005page.html>.
- SCUDDER S. H. 1888-1899. The butterflies of the eastern United States and Canada with special reference to New England. 2 vols. Author, Cambridge, Massachusetts. 1858 pp., 89 pls.
- SMITH, A. C. 1990. James Wilson Tilden (1904-1988): a remembrance. J. Lepid. Soc. 44(1):45-55.
- SORENSEN, A., STROHBEEN, J. P. & H. P. WHELCHER. 1955. Molluscan predators and their prey. Ann. Rpt. Amer. Malacol. Union (for 1955):34.
- STERNITZKY, R. F. 1945. A new race of *Parnassius clodius* Men. Proc. New England Zool. Club 23:81-82.
- TAYLOR, W. E. 1889. Preliminary catalogue of and notes on Nebraska butterflies. Amer. Nat. 23(275):1024-1030.
- THOMAS, C. 1876. Notes on the saltatorial Orthoptera of the Rocky Mountain regions. Ann. Rpt. U.S. Geol. Surv. Terr. 5:423-466.
- VAN DUZEE, E. P. 1919. Department of entomology. Proc. Calif. Acad. Sci. 9(14-15):380-383.
- . 1921. Characters of some new species of North American hemipterous insects, with one new genus. Proc. Calif. Acad. Sci. 11(10):111-134.
- . 1925. [Death of Ralph E. Dodge]. Pan-Pacific Entomol. 2:48.
- . 1926. Department of entomology. Proc. Calif. Acad. Sci. 14(19-20):538-539.
- . 1933. Edgar A. Dodge. Pan-Pacific Entomol. 9(9):52.
- WARNER & BEERS (firm). 1875. Atlas of Bureau County and the state of Illinois: to which is added an atlas of the United States, maps of the hemispheres, etc., etc. etc. Warner & Beers, Chicago, Illinois. 89 pp.
- WHITNEY, C. P. 1904. Descriptions of some new species of Tabanidae. Can. Entomol. 36(7):205-207.
- WIDMANN, O. 1908. Another Clark's crow taken in Missouri. Auk 25(2):222.
- WILLIAMS, W. (ed.). 1913. A history of northeast Missouri. Vol. 1. Lewis Publ. Co., Chicago, Illinois & New York, New York. xxix+682 pp.

Submitted for publication 18 October 2012; revised and accepted 2 January 2013.

Journal of the Lepidopterists' Society
67(3), 2013, 221–224

EUSELASIA HYGENIUS OCCULTA (RIODININAE): FIRST REPORT OF FEEDING ON *PSIDIUM*
GUAJAVA (MYRTACEAE) IN MINAS GERAIS STATE, BRAZIL

JOSÉ COLA ZANUNCIO

Departamento de Biologia Animal, Universidade Federal de Viçosa, 36571-000, Viçosa, Minas Gerais State, Brazil, E-mail: zanuncio@ufv.br

MARCUS ALVARENGA SOARES

Departamento de Agronomia, Universidade Federal dos Vales do Jequitinhonha e Mucuri, 39100-000, Diamantina, Minas Gerais State, Brazil, E-mail: marcussoares@yahoo.com.br

TERESINHA VINHA ZANUNCIO

Departamento de Biologia Animal, Universidade Federal de Viçosa, 36571-000, Viçosa, Minas Gerais State, Brazil, E-mail: tvzanuncio@ufv.br

OLAF HERMANN HENDRIK MIELKE

Departamento de Zoologia, Universidade Federal do Paraná, 19020, Curitiba, Paraná State, Brazil, E-mail: omhesp@ufpr.br

FRANCISCO DE SOUSA RAMALHO

Unidade de Controle Biológico, Embrapa Algodão, Av. Osvaldo Cruz, 1143, CEP 58107-720, Campina Grande, Paraíba State, Brazil, E-mail: framalho@cnpa.embrapa.br

SEBASTIÃO LOURENÇO DE ASSIS JÚNIOR

Unidade de Controle Biológico, Embrapa Algodão, Av. Osvaldo Cruz, 1143, CEP 58107-720, Campina Grande, Paraíba State, Brazil, E-mail: assisjr_ento@yahoo.com.br

AND

CARLOS FREDERICO WILCKEN

Departamento de Produção Vegetal, Universidade Estadual Paulista Júlio de Mesquita Filho, 18603-970 Botucatu, São Paulo State, Brazil; cwilcken@uol.com.br

ABSTRACT: Insect defoliators of native Myrtaceae in Brazil are important because of potential outbreaks in reforestation of exotic *Eucalyptus* spp. The objective of this study was to identify a lepidopteran defoliator of *Psidium guajava* (Myrtaceae) found at the Federal University of Viçosa in Viçosa, Minas Gerais, Brazil. Insects were identified as *Euselasia hygenius occulta* Stichel 1919 (Lepidoptera: Riodininae). Larvae of this insect are gregarious and feed, rest, molt, and pupate synchronously. This species exhibits processionary behavior during its five instars. Caterpillars are yellow in the first instar and dark brown in the last one with six longitudinal white stripes, two on the back, and two on each side. Head of caterpillars is orange in color and the body has multiple setae per segment. Adults of this species have sexual dimorphism with females having a pale gray dorsal tinge, a darker gray ventral coloration and a 2.5 cm wingspan. Males are dark gray ventrally and black dorsally with a 2.7 cm wingspan. The head of both sexes has a "V" shape when viewed from the front. *Euselasia hygenius occulta* should be included in monitoring programs of *P. guajava* pests, its native host, and also on those of *Eucalyptus* spp. due to the apparent palatability of these nonnative plants.

Additional key words: Caterpillars, *Eucalyptus*, Lepidoptera

Native Myrtaceae in Brazil are damaged by defoliating caterpillars, which can migrate to important crops such as exotic *Eucalyptus* spp. (Zanuncio et al. 1993, Oliveira et al. 2000). Lepidoptera defoliators of *Eucalyptus* species in Brazil include native moth species such as *Eupseudosoma aberrans* (Schaus 1905) and

Eupseudosoma involuta (Sepp 1855) (Lepidoptera: Erebididae), *Automeris* sp. (Walker) and *Eacles imperialis* (Walker 1856) (Lepidoptera: Saturniidae), *Oxydia vesulia* (Cramer 1779), *Sabulodes caberata* (Guenée 1857) and *Thyrintina arnobia* (Stoll 1782) (Lepidoptera: Geometridae) (Zanuncio et al. 1998, Soares et al. 2009a).

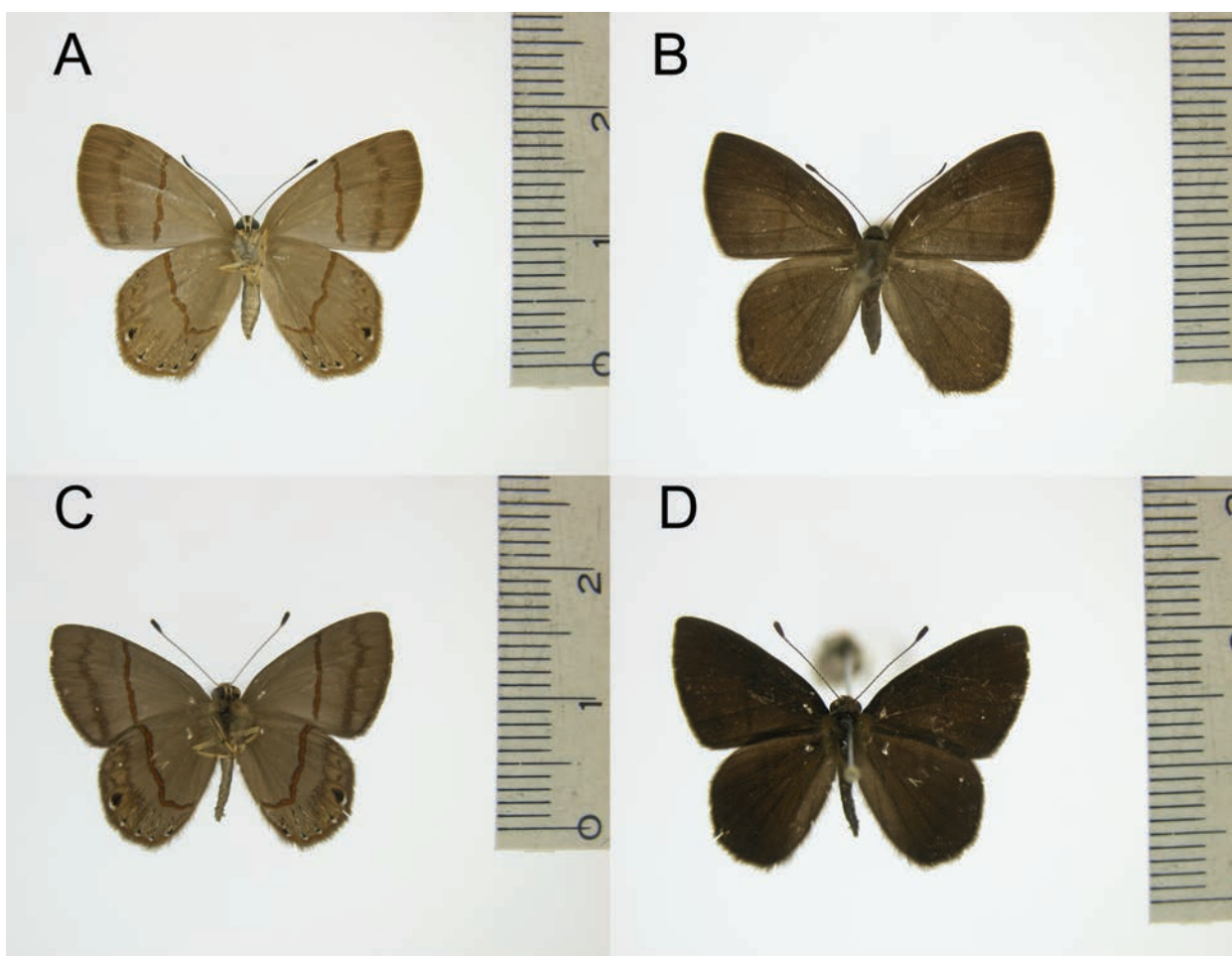


FIG. 1. *Euselasia hygenius occulta* (Lepidoptera: Riodininae); Ventral view of female (A); dorsal view of female (B); ventral view of male (C); dorsal view of male (D). Viçosa, Minas Gerais State, Brazil.

Insects can expand their host plant range onto nonnative agricultural plants that have been introduced as reported for tropical crops such as cocoa (*Theobroma cacao*), sugarcane (*Saccharum officinarum*), tomato (*Solanum lycopersicum*) (Leite et al. 2001) and eucalyptus (*Eucalyptus* spp.) (Strong 1974, Oliveira et al. 2005, Soares et al. 2009b). Caterpillars of the genus *Euselasia* spp. feed on *Eucalyptus* spp. and on *Eugenia pitanga*, *Eugenia uniflora*, *Psidium grandifolium* and *Psidium guajava* (Myrtaceae), their natural hosts (Silva et al. 1968). *Euselasia eucerus* (Hewitson 1982) (Lepidoptera: Riodininae), reported as *Euselasia apisaon*, was collected in an *Eucalyptus* sp. plantation in the Vale do Rio Doce and Zona da Mata regions of Minas Gerais State, Brazil (Zanuncio et al. 2009). Eggs of *Euselasia apisaon* (Dahman 1823) (Lepidoptera: Riodininae) were collected in plantations of *Eucalyptus grandis* (Myrtaceae) in Belo Oriente, Minas Gerais State, Brazil (Murta et al. 2008). *Euselasia mys lara* (Stichel 1919)

(Lepidoptera: Riodininae) was reported feeding on plants of *P. guajava* in Viçosa, Minas Gerais State, Brazil. The inclusion of this species in monitoring programs of *Eucalyptus* spp. was recommended due to the phylogenetic proximity of these host plants (Soares et al. 2009b).

A basic understanding of host plant diet breadth is critical to understanding population dynamics of native lepidopterans and for modeling the probability that a species of Lepidoptera might extend its feeding to an exotic plant species (Murta et al. 2008, Zanuncio et al. 2009). The objective of this study was to identify a Lepidoptera feeding on *P. guajava* at the Federal University of Viçosa in Viçosa, Minas Gerais State, Brazil.

First instar caterpillars of a lepidopteran were observed on the underside of *P. guajava* leaves in August 2009 at the campus of the Federal University of Viçosa in Viçosa, Minas Gerais State, Brazil (South Latitude of 20° 45'14" and West Longitude of 42°

52'55" and altitude of 648 meters). Leaves of *P. guajava* with caterpillars were detached from the plant, packed in plastic containers and taken to the Laboratory of Biological Control of Insects of the Institute of Biotechnology Applied to Agriculture (BIOAGRO) where they were kept at $25 \pm 2^\circ \text{C}$, $70 \pm 5\%$ relative humidity and photoperiod of 12 hours. These leaves were changed daily until adult emergence. Adults were killed in a killing chamber, wrapped in an entomological blanket and sent to Dr. Olaf Hermann Hendrik Mielke of the Federal University of Paraná in Curitiba, Paraná State, Brazil for identification.

Insects were identified as *Euselasia hygenius occulta* Stichel 1919 (Lepidoptera: Riodininae). Its larvae are gregarious and feed, rest, molt, and pupate synchronously. This species has five instars with processionary behavior throughout its development. Caterpillars range in color from yellow during early instars to dark brown at the final instars with six longitudinal white stripes, two on the back, and two on each side. The head is orange and strongly sclerotized and caterpillars have many setae dorsally on all segments. Adults of this species exhibit sexual dimorphism. Females are pale gray dorsally and gray ventrally, abdomen prominent and 2.5 cm wingspan wings. Males are dark gray ventrally and dorsally black with 2.7 cm (Fig. 1). Adults of both sexes show a "V" at the front view of the head.

This species had been cited in monitoring programs in tropical forests and savanna areas with traps, but without its host plants being specifically identified (Emery et al. 2006, Bonfanti et al. 2009). Thus, this is the first report of *E. hygenius occulta* feeding on *P. guajava* anywhere. Aside from the observations here, the habitat and host plants of different species of the genus *Euselasia* spp. are poorly known (Callaghan et al. 2007).

Immature stages of *E. hygenius occulta* present morphology and behavior similar to those of other species of this genus such as *Euselasia chrysippe* (Bates 1866) and *Euselasia bettina* (Hewitson 1869) (Lepidoptera: Riodininae), but with shorter larva stadium and apparent absence of the sixth instar stage (Nishida 2010).

Euselasia hygenius occulta adults differ from other species such as *E. hygenius* by its sexual dimorphism (Zanuncio et al. 1995). Adults of the latter species do not show dimorphism. In both male and females the front and rear wings are black dorsally. *Euselasia eucerus*, reported as *E. apisaon*, also shows sexual dimorphism, but the dorsal surface of male wings has red brick color with dark edges on both pairs. Females of this species are dark gray and sometimes exhibit

three pairs of white circular spots in the middle of the forewing (Zanuncio et al. 1990). *Euselasia mys lara* has accentuated sexual dimorphism. The dorsal of both pairs of wings of males are black with dark red spots, that begin near the chest and radiate to the edge of wings. These spots are absent in females. Males of *E. mys lara* have an average wingspan of 3.0 cm and females 2.6 cm (Soares et al. 2009b).

The abundance of species of *Euselasia* spp. in Brazil and reports of *E. eucerus* feeding on *Eucalyptus* spp. plants show that other species of this butterfly genus could also damage this plant as a result of selection pressure in extensive forest plantation areas (Soares et al. 2009b). This is important because other Lepidoptera such as *T. arnobia*, the main defoliator of *Eucalyptus* spp. in Brazil (Oliveira et al. 2005, Soares et al. 2009a,c) has often being reported causing economic damage in this culture. *Euselasia hygenius occulta* should be included in monitoring programs of *P. guajava* pests and *Eucalyptus* spp. due to its potential migration to plants of this last genus.

ACKNOWLEDGEMENTS

To "Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES)" and "Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG)" for scholarships and funding this research.

LITERATURE CITED

- BONFANTI, D., R. A. DI MARE & R. GIOVENARDI. 2009. Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) from two forest fragments in northern Rio Grande do Sul, Brazil. Check List – J. Species Lists and Distrib. 5:819-829.
- CALLAGHAN, C. J., J. LLORENTE-BOUSQUETS & A. LUIS-MARTINEZ. 2007. Descriptions of four new Mexican riodinids (Lepidoptera: Riodinidae). Zootaxa 1660:33-43.
- EMERY, E. O., K. S. BROWN JR. & C. E. G. PINHEIRO. 2006. As borboletas (Lepidoptera, Papilionoidea) do Distrito Federal, Brasil. Rev. Bras. Entomol. 50:85-92.
- LEITE, G. M. P. P. CANO, R. N. C. GUEDES & J. C. ZANUNCIO. 2001. Role of plant age in the resistance of *Lycopersicon hirsutum* f. *glabratum* to the tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae). Sci. Hortic. 89: 103-113.
- MURTA, A. F., F. T. O. KER, D. B. COSTA, M. M. ESPÍRITO-SANTO & M. L. FARIA. 2008. Efeitos de remanescentes de Mata Atlântica no controle biológico de *Euselasia apisaon* (Dahman) (Lepidoptera: Riodinidae) por *Trichogramma maxacalii* (Voegelé e Pointel) (Hymenoptera: Trichogrammatidae). Neot. Entomol. 37:229-232.
- NISHIDA, K. 2010. Description of the immature stages and life history of *Euselasia* (Lepidoptera: Riodinidae) on *Miconia* (Melastomataceae) in Costa Rica. Zootaxa. 2466:1-74.
- OLIVEIRA, H. N., J. C. ZANUNCIO, D. PRATISSOLI & I. CRUZ. 2000. Parasitism rate and viability of *Trichogramma maxacalii* (Hym.: Trichogrammatidae) parasitoid of the *Eucalyptus* defoliator *Euselasia apisaon* (Lep.: Riodinidae), on eggs of *Anagasta kuehniella* (Lep.: Pyralidae). For. Ecol. Manage. 130:1-6.
- , J. C. ZANUNCIO, E. P. PEDRUZZI & M. C. ESPINDULA. 2005. Rearing of *Thyrintina arnobia* (Lepidoptera: Geometridae) on guava and *Eucalyptus* in laboratory. Braz. Arch. Biol. Technol. 48:801-806.

- SILVA, A. G. D. A., C. R. GONÇALVES, D. M. GALVÃO, A. J. L. GONÇALVES, J. GOMES, M. N. SILVA, L. SIMONI. 1968. Quarto catálogo dos insetos que vivem nas plantas do Brasil, seus parasitas e predadores, v.2, n.1, Laboratório Central de Patologia Vegetal, Rio de Janeiro. 622pp.
- SOARES, M. A., J. C. ZANUNCIO, G. L. D. LEITE, E. D. WERMELINGER & J. E. SERRÃO. 2009a. Does *Thyrinteina arnobia* (Lepidoptera: Geometridae) use different defense behaviours against predators? J. Plant Dis. Protect. 116:30-33.
- , T. V. ZANUNCIO, J. C. ZANUNCIO, O. H. H. MIELKE & J. E. SERRÃO. 2009b. *Euselasia mys lara* (Stichel, 1919) (Lepidoptera: Riodinidae) a potential pest on *Eucalyptus* in Brazil? J. Res. Lepid. 41:76-83.
- , C. TORRES-GUTIERREZ, J. C. ZANUNCIO, A. R. P. PEDROSA & A. S. LORENZON. 2009c. Superparasitismo de *Palmistichus elaeisis* (Hymenoptera: Eulophidae) y comportamiento de defensa de dos hospederos. Rev. Col. Entomol. 35:62-65.
- STRONG, D. R. 1974. Rapid asymptotic species accumulation in phytophagous insect communities: The pests of cacao. Science 185:1064-1066.
- ZANUNCIO, J. C., J. B. ALVES, G. P. SANTOS & W. O. CAMPOS. 1993. Levantamento e flutuação populacional de lepidópteros associados à eucaliptocultura: VI- Região de Belo Oriente, Minas Gerais. Pesq. Agropecu. Bras. 28:1121-1127.
- ZANUNCIO, T. V., J. C. ZANUNCIO, J. B. TORRES & A. J. LARANJEIRO. 1995. Biologia de *Euselasia hygenius* (Lepidoptera: Riodinidae) e seu consumo foliar em *Eucalyptus urophylla*. Rev. Bras. Entomol. 39:487-492.
- ZANUNCIO, T. V., J. C. ZANUNCIO, M. M. M. MIRANDA & A. G. B. MEDEIROS. 1998. Effect of plantation age on diversity and population fluctuation of Lepidoptera collected in *Eucalyptus* plantations in Brazil. For. Ecol. Manage. 108:91-98.
- ZANUNCIO, J. C., J. F. GARCIA, G. P. SANTOS, T. V. ZANUNCIO & E. C. NASCIMENTO. 1990. Biologia e consumo foliar de lagartas de *Euselasia apisaon* (Dalman, 1823) (Lepidoptera: Riodinidae) em *Eucalyptus* spp. Rev. Árv. 14:45-54.
- , J. B. TORRES, C. A. Z. SEDIYAMA, F. F. PEREIRA, P. L. PASTORI, E. D. WERMELINGER & F. S. RAMALHO. 2009. Mortality of the defoliator *Euselasia eucerus* (Lepidoptera: Riodinidae) by biotic factors in an *Eucalyptus urophylla* plantation in Minas Gerais State, Brazil. An. Acad. Bras. Ciên. 81:61-66.

Submitted for publication 17 August 2012; revised and accepted 13 March 2013.

USE OF A NATIVE AND AN EXOTIC MALVACEAE BY THE LITTLE KNOWN SKIPPER *PYRGUS BOCCHORIS TRISIGNATUS* (MABILLE) (HESPERIIDAE) IN NORTHERN CHILE**Additional key words:** Folivorous, Naturalized, *Malva nicaeensis*, *Tarasa operculata*

Many butterflies are highly specialized in their use of host plants. Some are monophagous (Brückmann et al. 2011); at least at a local scale (Jordano et al. 1990, Vargas 2012). Despite this tendency towards specialization, however, oviposition by native butterflies on exotic plants, and the subsequent successful larval development, has been documented many times within the New World fauna and is probably a global phenomenon (Shapiro 2006). These host range shifts have been remarkably well studied in California, USA, where alien hosts are very important for the maintenance of the native butterfly fauna in both urban and suburban environments (Shapiro 2002, Graves & Shapiro 2003). Recently, Jahner et al. (2011) have shown that the use of exotic hosts is predicted by geographic range and native diet breadth, although the former is a stronger predictor.

Examples of associations among native butterflies and exotic plants have also been mentioned for the South American fauna (Shapiro 2006), including Chile (Shapiro 1997). For the Chilean butterfly fauna, the use of some exotic Malvaceae by the native *Vanessa carye* (Hübner, 1812) (Nymphalidae) is well known (Herrera 1987). This butterfly-host plant system is regularly used for teaching purposes at different levels of local educational programs. Moreover, the ability of *V. carye* to develop on exotic mallows is probably one of the reasons for its widespread occurrence in disturbed habitats in Chile, especially in urban and agricultural environments.

Pyrgus bocchoris (Hewitson, 1874) is a Neotropical skipper with three subspecies currently recognized along its geographic range (Mielke 2005), although some controversy exists concerning the synonymies (Shapiro 1991). *Pyrgus bocchoris trisignatus* (Mabille, 1875) is a little known skipper described from Valparaíso, Chile. Its geographic range along this country embraces a very long, narrow strip of about 2,000 km length, from the northern coastal desert south to the type locality (Herrera et al. 1957). However, Peña and Ugarte (1996) indicated that this skipper reaches the Bío Bío Region, increasing by about 500 km its range southward. Furthermore, its presence has been also reported in Peru (Herrera 1972, Warren et al. 2012).

In the northernmost part of Chile, *P. b. trisignatus* has been collected from near sea level, in the valleys of the coastal desert, up to the highlands of the Andes, exceeding 3,500 m. A number of environments are present along this elevational gradient, each

characterized by a typical fauna and flora (Luebert & Plischoff 2006). This skipper is one of the more frequently observed butterflies in many of these situations, including relatively pristine areas and also highly modified agricultural lands. Shapiro (1991) indicated that a Chilean representative of *P. bocchoris* (i.e.: *trisignatus*) is associated with weedy mallows (Malvaceae), but nothing more was published thereafter dealing with the field biology of this skipper. Thus, the objective of this paper is to document two Malvaceae host plants for *P. b. trisignatus* based on field collections performed in northern Chile.

In October 2008, some HesperIIDae larvae were collected on leaves of the exotic mallow *Malva nicaeensis* All. (Malvaceae) in the Azapa valley, located in the coastal desert of the Arica Province, near sea level. These larvae were brought to the lab in plastic vials with absorbent paper on the bottom. Leaves were changed daily until feeding was completed. Pupation occurred among fragments of leaves or absorbent paper. Nine adults were obtained in November 2008. Seven additional adults were reared from *M. nicaeensis* at the same locality from October 2011.

Between September 2011 and April 2012 additional skipper larvae were collected on leaves of the native *Tarasa operculata* (Cav.) Krapov. (Malvaceae) in the Cardones valley, located in the Precordillera of Arica Province, at about 2,000 m. Sixteen adults of *P. b. trisignatus* were obtained in the lab following the same procedures mentioned above.

Use of Malvaceae by *P. b. trisignatus* is consistent with the host plant relationships previously reported for this group of New World *Pyrgus*, Hübner, 1819 (Robinson et al. 2010), including the Neotropical representatives (Shapiro 1991, 2009). Exotic *Malva* L. species, including *M. nicaeensis*, are used as host plants by at least five species of native butterflies in California, including *Vanessa annabella* Field, the sister-species of the South American *V. carye*, *Pyrgus communis* (Grote) and its sibling species *P. albescens* Ploetz (Graves & Shapiro 2003).

The Azapa valley is a highly disturbed habitat, where much of the native vegetation has been eliminated by intensive agricultural practices. This is also the case for most of the coastal valleys of the northern Chilean Atacama Desert. Under these conditions, the presence of native Malvaceae is extremely low. Contrastingly, weedy

mallows, as *M. nicaeensis*, are abundant. Moreover, in highly disturbed areas of Arica Province, at least two Gracillariidae micro-moths have also colonized exotic host plants: *Acrocercops serrigera serrigera* Meyrick, 1915 is associated with *M. nicaeensis* and the native *Waltheria ovata* Cav. (Malvaceae) (Vargas et al. 2013), while *Angelabella tecomae* Vargas & Parra, 2005 has been reared from the introduced tree *Tecoma stans* (L.) in addition to the native *Tecoma fulva* (Cav.) D. Don (Bignoniaceae) (Vargas 2010).

The Cardones valley is a relatively pristine place, where agricultural activities are not performed. One of the representatives of the native flora of this locality is *T. operculata*, which occurs frequently in many habitats throughout the Precordillera of the Parinacota Province, where exotic mallows are more or less restricted to small villages in which little agriculture is conducted.

The host plant relationships here recorded for *P. b. trisignatus* suggest that the abundance levels of this skipper in relatively pristine habitats of northern Chile are dependent on the populations of the native *T. operculata*, as was observed in Cardones valley, while in highly human modified environments the populations are dependent on the presence of the exotic *M. nicaeensis*, as detected in the Azapa valley. Thus, it constitutes another example of the importance of an alien plant for the maintenance of populations of a native butterfly in disturbed areas (Shapiro 2002).

In the future it would be interesting to survey for additional native or exotic Malvaceae as possible host plants for *P. b. trisignatus* in other localities throughout its complete Chilean range. It is hoped that other native Malvaceae will be associated in different pristine locals, while exotic mallows would be the larval substrate in disturbed landscapes.

Voucher specimens will be deposited in the "Museo Nacional de Historia Natural" (MNNC), Santiago, Chile, and in the "Colección Entomológica de la Universidad de Tarapacá" (IDEA), Arica, Chile.

Material examined. CHILE, Arica. Five ♂ and four ♀ Azapa, Arica, Chile, November 2008, H.A. Vargas coll., reared from *Malva nicaeensis*, October 2008; four ♂ and three ♀ Azapa, Arica, Chile, October 2011, H.A. Vargas coll., reared from *Malva nicaeensis*, September 2011; nine ♂ and three ♀ Cardones, Arica, Chile, October 2011, H.A. Vargas coll., reared from *Tarasa operculata*, September 2011; three ♂ and one ♀ Cardones, Arica, Chile, April 2012, H.A. Vargas coll., reared from *Tarasa operculata*, March 2012.

ACKNOWLEDGEMENTS

The author would like to thank Dr. Arthur M. Shapiro and the anonymous referee for useful comments and suggestions on a

preliminary version. Financial support was obtained from project DIEXA-UTA 9711-12, from Universidad de Tarapacá.

LITERATURE CITED

- BRÜCKMANN, S. V., J. KRAUSS, C. VAN ACHTERBERG & I. STEFFAN-DEWENTER. 2011. The impact of habitat fragmentation on trophic interactions of the monophagous butterfly *Polyommatus coridon*. J. Insect. Conserv. 15: 707–714.
- GRAVES, S. D. & A. M. SHAPIRO. 2003. Exotics as host plants of the California butterfly fauna. Biol. Conserv. 110: 413–433.
- HERRERA, J. 1972. Mariposas comunes a Chile y Perú (Lepidoptera, Rhopalocera). Rev. Peru Entomol. 15: 72–74.
- . 1987. Biología de *Cynthia carye* Hübnér, 1812, especie críptica de *C. annabella* Field, 1971 (Lepidoptera: Nymphalidae). Acta Ent. Chilena 14: 65–116.
- , M. ETCHEVERRY & C. HOCHLEITNER. 1957. Los Pyrginae de Chile (Lepidoptera, Hesperidae). Rev. Chil. Ent. 5: 143–182.
- JAHNER, J. P., M. B. BONILLA, K. J. BADIĆ, A. M. SHAPIRO & L. M. FORISTER. 2011. Use of exotic hosts by Lepidoptera: widespread species colonize more novel hosts. Evolution 65: 2719–2724.
- JORDANO, D. J., FERNÁNDEZ HAEGUER, J. RODRÍGUEZ GONZÁLEZ. 1990. The life-history of *Tomares ballus* (Fabricius, 1787) (Lepidoptera: Lycaenidae): phenology and host plant use in southern Spain. J. Res. Lepid. 28: 112–122.
- LUEBERT, F. & P. PLISCOFF. 2006. Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago, Chile. 316 pp.
- MIELKE, O. H. H. 2005. Catalogue of the American Hesperoidea: Hesperidae (Lepidoptera). Sociedade Brasileira de Zoologia, Curitiba, Brazil. xiii + 1536 pp.
- PEÑA, L. E. & A. J. UGARTE. 1996. Las mariposas de Chile. Editorial Universitaria, Santiago, Chile. 359 pp.
- ROBINSON, G. S., P. R. ACKERY, I. J. KICHING, G. W. BECCALONI & L. M. HERNÁNDEZ. 2010. HOSTS – A database of the World's lepidopteran hostplants. Natural History Museum, London. Available from: <http://www.nhm.ac.uk/hosts> (accessed: 26 September 2012).
- SHAPIRO, A. M. 1991. Convergent evolution in Western North American and Patagonian skippers (Hesperidae). J. Res. Lepid. 30: 162–174.
- . 1997. Impactos antropogénicos sobre la fauna de mariposas (Lepidoptera: Rhopalocera) de Patagonia Austral y Tierra del Fuego. Anales Inst. Patagonia Ser. Cs. Nat. (Chile) 25: 117–126.
- . 2002. The Californian urban butterfly fauna is dependent on alien plants. Divers. Distrib. 8: 31–40.
- . 2006. Use of an exotic weed as an oviposition substrate of the high-Andean pierid *Phulia nymphaula*. J. Lepid. Soc. 60: 103–104.
- . 2009. The Neo-Riparian butterfly fauna of western Argentina. J. Res. Lepid. 41: 24–30.
- VARGAS, H. A. 2010. *Angelabella tecomae* (Lepidoptera: Gracillariidae): an exotic hostplant in northern Chile and first record from Peru. Rev. Colomb. Entomol. 36: 340–341.
- . 2012. First host plant record for *Teriocolias zelia andina* Forbes (Lepidoptera: Pieridae) and evidence for local specialization. Neotrop. Entomol. 41: 524–525.
- , M. VARGAS-ORTIZ, W. HUANCA-MAMANI, D. BOBADILLA. 2013. First Record of *Acrocercops serrigera serrigera* Meyrick (Lepidoptera: Gracillariidae) from Chile. Neotrop. Entomol. 42: 112–114. DOI 10.1007/s13744-012-0089-x
- WARREN, A. D., K. J. DAVIS, E. M. STANGELAND, J. P. PELHAM & N. V. GRISHIN. 2012. Illustrated list of American butterflies. Available from: <http://www.butterfliesofamerica.com/> (accessed: 25 September 2012).

HÉCTOR A. VARGAS, *Departamento de Recursos Ambientales, Facultad de Ciencias Agronómicas, Universidad de Tarapacá, Casilla 6-D, Arica, Chile; email: havargas@uta.cl*

Submitted 4 October 2012; revised and accepted for publication 21 November 2012.

OVERCROWDING LEADS TO LETHAL OVIPOSITION MISTAKES IN THE BALTIMORE
CHECKERSPOT, *EUPHYDRYAS PHAETON* DRURY (NYMPHALIDAE)**Additional key words:** *Asclepias syriaca*, Milkweed, *Plantago lanceolata*, Plantain, population explosion

Errors in oviposition choice have the potential to expand host plant range or, alternatively, result in death of offspring hatching from eggs laid on inappropriate host plant species (Chew 1977, Larsson and Ekblom 1995). *Euphydryas phaeton* Drury (Nymphalidae), the Baltimore Checkerspot, has relatively recently expanded its oviposition range to include the introduced plant species, Narrow-leaved or Ribwort Plantain, *Plantago lanceolata* L. (Plantaginaceae) (Stamp 1979, Bowers et al. 1992). *Plantago lanceolata* has proven to be a suitable host plant and populations of *E. phaeton* in certain parts of the Northeast are flourishing on this host (Bowers et al. 1992, Bowers, pers. obs.; 4th of July butterfly count Rhode Island/Tiverton circle, 2012). *Plantago lanceolata* was introduced into North America approximately 200 years ago (Cavers et al. 1980) and a variety of native lepidopterans (including both specialist and generalist taxa) have incorporated this species into their diet (Robinson et al. 2002). The primary native oviposition host plant for *E. phaeton* is Turtlehead, *Chelone glabra* L. (Plantaginaceae), a species that is found in wetlands and is becoming less common as wetlands are disappearing. *Aureolaria flava* (L.) Farw. (Orobanchaceae) is used as an oviposition plant for populations designated as the subspecies *E. phaeton ozarkae* (Masters 1968) in the Midwest.

Euphydryas phaeton is a specialist on plants that contain iridoid glycosides (Bowers 1980, Bowers et al. 1992) and the incorporation of *P. lanceolata* as an oviposition plant is likely due, at least in part, to the similarity in the iridoid glycoside profiles of *P. lanceolata* and *C. glabra* (Bowers et al. 1992). Iridoid glycosides are bitter compounds found in plants in more than 50 families (Jensen 1991). Both Turtlehead and Ribwort Plantain contain the same two iridoid glycosides, aucubin and catalpol (Bowers et al. 1992). All host plant species on which Baltimore Checkerspot larvae feed contain iridoid glycosides (Bowers 1980, Bowers et al. 1992) and these insects have the ability to sequester these compounds, rendering them unpalatable to many of their natural enemies (Bowers 1980, Bowers and Farley 1990). While *E. phaeton* populations on Turtlehead are typically relatively small and localized, populations on Ribwort Plantain may become quite large. For example, in a survey of a *P. lanceolata*-feeding population in southeastern Massachusetts in the early

1990's, counts of post-diapause larvae at two different sites estimated thousands to tens of thousands of individuals (Bowers, pers. obs.).

A more recent survey of adults from a population on June 19, 2010, in Bristol, Rhode Island, in a field of approximately seven acres, revealed a population estimate of over 3,200 individuals of *E. phaeton*. Counts of adults from 2009 had shown similarly high numbers (E. Marks, pers. obs.). This population uses *P. lanceolata* for both oviposition and larval feeding, and at the time of the survey, although old flowering stalks of *P. lanceolata* were observed, all plants that we found had been eaten down to the ground. On the day of the survey, both adult males and females were observed and late instars and unclosed pupae were common. Larvae had dispersed out of the field, through the woods (approximately 8–10 meters), apparently in search of food, and were seen in large numbers on the side of the road. The only other potential host plant observed at this site was *Nuttallanthus* (formerly *Linaria*) *canadensis* (L.) D.A. Sutton (Plantaginaceae), which also contains iridoid glycosides (Mizouchi et al. 2011); however, this is not a preferred host plant (Bowers, pers. obs.). No *Plantago major*, another potential host plant, was observed at this site.

Large numbers of adults were observed nectaring on Common Milkweed, *Asclepias syriaca* L. (Asclepiadaceae) present in the field. To our surprise, we also found several egg masses of *E. phaeton* on this plant (Fig. 1)! *Asclepias syriaca*, like other milkweeds, contains a very different group of chemical compounds, cardiac glycosides (Malcolm 1991). These compounds are responsible for the unpalatability of the Monarch, *Danaus plexippus* L. (Nymphalidae) and the latex produced by milkweeds is rich in these compounds and deterrent and toxic to a variety of herbivores (Malcolm 1991). Although extensive searches were not made, no egg masses were observed on other plant species.

A search of 157 ramets of *A. syriaca* over 30 cm in height revealed 19 *E. phaeton* egg masses or their remains occurring on 15 individual plants, four plants had two egg masses. In some cases, egg masses were next to each other on the same leaf; in others they were on different leaves (Fig. 1A, B, D). On three individual ramets, larvae had moved from their egg masses to the top of the plant and were starting to make webs (Fig

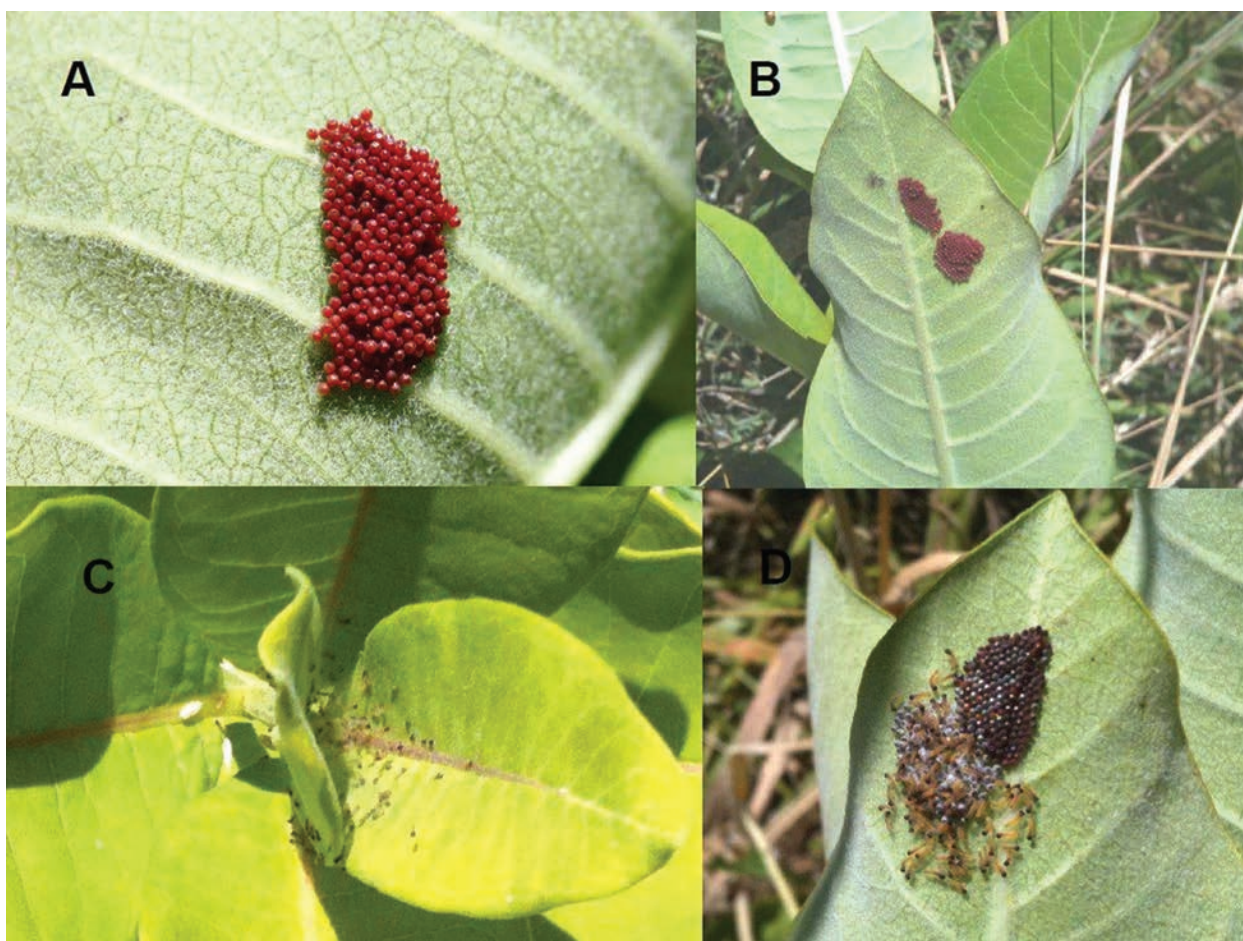


FIG. 1. **A.** Single egg mass of *E. phaeton* on *A. syriaca* leaf. **B.** Two *E. phaeton* egg masses on *A. syriaca* leaf. **C.** Newly hatched *E. phaeton* larvae that had left the site of their egg mass and moved to the top of the *A. syriaca* ramet. **D.** A mass of newly hatched *E. phaeton* larvae next to an unhatched egg mass on *A. syriaca*.

1C), typical behavior for newly hatched *E. phaeton* larvae. In one of these, most larvae were dead. In at least two other cases, empty egg cases were observed and there were many dead and no living larvae. Given the cardiac glycoside and latex content of this milkweed, it is highly unlikely that any larvae would survive and a later visit provided no evidence of successful larval establishment.

The obvious question is, why did *E. phaeton* females oviposit on a completely unsuitable host plant? There are several contributing factors to this oviposition mistake. First, the appropriate oviposition plant, *Plantago lanceolata*, was unavailable, since the post-diapause larvae had decimated these individuals, eating them down to the ground. Second, *Asclepias syriaca* was one of the most common nectar sources in this population and adults were abundant on the flowers during our survey; thus females would frequently encounter this plant. Third, although females unable to find suitable oviposition plants are likely to disperse, this

field was surrounded by unsuitable habitat (forest) that discouraged dispersal. Finally, this milkweed has a growth form quite similar to the native host plant, Turtlehead; although the chemical cues would be quite different. As a result, females searching for a suitable oviposition site could make such an oviposition error, which will be lethal for their offspring. Thus overcrowding and decimation of the suitable host plant species, *P. lanceolata*, by post-diapause larvae led to inappropriate oviposition choices by female *E. phaeton*.

ACKNOWLEDGEMENTS

We especially thank Eugenia Marks for introducing us to this *E. phaeton* population and for help in the field, Hugh Willoby and Eric Lopresti for help in the field and Eric Lopresti for the photograph in Figure 1A. We appreciate Brown University for allowing us access to this site.

LITERATURE CITED

- BOWERS, M.D. 1980. Unpalatability as a defense strategy of *Euphydryas phaeton* (Lepidoptera: Nymphalidae). *Evolution* 34:586–600.

- BOWERS, M.D. & S.D. FARLEY. 1990. The behaviour of gray jays (*Perisoreus canadensis*) towards palatable and unpalatable Lepidoptera. *An. Behav.* 39:699–705.
- BOWERS, M.D., N.E. STAMP, & S.K. COLLINGE. 1992. Early stage of host range expansion in a specialist insect, *Euphydryas phaeton* (Nymphalidae). *Ecology* 73:526–536.
- CAVERS, P. B., I. J. BASSETT, & C. W. CROMPTON. 1980. The biology of Canadian weeds .47. *Plantago lanceolata* L. *Can. J. Plant Sci.* 60:1269–1282.
- CHEW, F. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. *Evolution* 31:568–579.
- JENSEN, S. 1991. Plant iridoids, their biosynthesis and distribution in angiosperms, pp. 133–158. *In* Harborne, J.B. and Tomas-Barberan, F.A. (eds.), *Ecological chemistry and biochemistry of plant terpenoids*. Clarendon Press, Oxford, U.K.
- LARSSON, S. & B. EKBOM. 1995. Oviposition mistakes in herbivorous insects: confusion or a step towards a new host plant? *Oikos* 72:155–160.
- MALCOLM, S.B. 1991. Cardenolide-mediated interactions between plants and herbivores, pp. 251–296. *In* Rosenthal, G.A. and Berenbaum, M.R. (eds.), *Herbivores: Their interactions with secondary plant metabolites*. 2nd ed. Academic Press, New York, USA.
- MASTERS, J.H. 1968. *Euphydryas phaeton* in the Ozarks. *Entomol. News* 79:85–91.
- MIZUOCHI, K., T. TANAKA, I. KOUNO, T. F. UJIOKA, Y. YOSHIMURA K. ISHIMARU. 2011. New iridoid diesters of glucopyranose from *Linaria canadensis* (L.) Dum. *J. Nat. Med.* 65:172–175.
- ROBINSON, G.S., P.R. ACKERY, I.J. KITHCING, G.W. BECCALONI, AND L.M. HERNANDEZ. 2002. *Hostplants of the Moth and Butterfly Caterpillars of America North of Mexico*. Gainesville: The American Entomological Institute.
- STAMP, N.E. 1979. New oviposition plant for *Euphydryas phaeton* (Nymphalidae). *J. Lepid. Soc.* 33:203–204.
- M. DEANE BOWERS (corresponding author), *Museum of Natural History and Department of Ecology and Evolutionary Biology, UCB 334, University of Colorado, Boulder Colorado 80309, USA* (deane.bowers@colorado.edu); JOHANNA SCHMITT, *Department of Ecology and Evolutionary Biology, Brown University, Providence RI 02901*

Received for publication 28 August 2012; revised and accepted 20 September 2012.

Journal of the Lepidopterists' Society
67(3), 2013, 230

SATURNIIDAE MUNDI: SATURNIID MOTHS OF THE WORLD, PART II, by Bernard d'Abrera. 182 pages; text in English; 10.5 × 14 inches, hardbound; ISBN: 978-0-947352-24-7; US\$340.00; Hill House Publishers, Melbourne & London. Publication date: October 2012.

A large book depicting hundreds of color images of African Saturniidae has recently been published. Bernard d'Abrera's Part II of *Saturniidae Mundi* has finally appeared, after Part I was published in 1995 and Part III in 1998. However, d'Abrera published several more butterfly books between these, so the delay is not because he was idle or slow. In this volume, we find the African saturniids, as well as the genera *Salassa* (tropical Asia) and *Antheraea* (Asian and American), the Hemileucinae that were missing from Part I, such as the genera *Cerodirphia*, *Polythysana*, *Ormiscodes*, *Dirphia*, *Periphoba*, *Meroleuca*, *Molippa*, and a few more. The generally large and colorful *Argema* and *Epiphora* were treated in Part III with their nearest relatives, but all other African genera are in Part II. The book is the same large format as d'Abrera's other volumes on butterflies and larger moths with flawless life-size images against a light background. Photographs of several lepidopterists, primarily Saturniidae specialists, are provided in an early section. Additionally, there are eleven photographs showing habitats in tropical America and Africa, plus a series of photographs showing *Opodiphthera eucalypti* from egg to mature larva, and then an excellent sequence of the emergence from its cocoon to a fully expanded adult, revealing d'Abrera's skill at photographing *living* Lepidoptera.

Anyone using this book will be able to put a species name on most African saturniid specimens, or assign them to the correct genus. That said, most of the Afro-tropical saturniid fauna is in taxonomic disarray, meaning most of the genera need to be revised or defined, and as a result, the book inevitably contains some misspellings, incorrect citations of authorships, a small number of misidentified figures, and taxonomic errors. In spite of this, the book will remain an important reference for the African Saturniidae and the genera *Antheraea* and *Salassa* long into the future. D'Abrera's figures of type specimens are valuable for helping formulate taxonomic hypotheses for species and names of which I have no material to study. Further, d'Abrera is the first author to appreciate the significance of artificial selection and artificial dispersal for sericulture when dealing with the taxonomy of *Antheraea*.

The author has not minced words in his assessment of the work by some amateurs who own (i.e., self-publish) and operate synonym factories. He has synonymized or ignored many of these names, and I concur with his taxonomic decisions in this regard. In other cases he is more conservative by questioning the validity of certain genera and species, where I would have synonymized them. D'Abrera provides detailed discussions of his taxonomic and scientific viewpoints, and I would like to focus briefly on his views about the mtDNA-barcoding technique, which has unfortunately been misused and misinterpreted by some lepidopterists that are eager to name new species, or by others who cannot consider the biology of moths outside the blinders called the biological species concept. I share d'Abrera's disdain for this situation, and I was glad to see that he quoted me on page 118 when I wrote to him about this: The misuse of this methodology is "the betrayal of Linnaeus' vision to bring clarity to the natural world." In recent years, a few amateurs have proposed and self-published several hundreds of names for what they believe to be real species of Saturniidae, and qualified taxonomists will have a huge mess to clean up in future revisions. Genetics and reproductive biology aside, their writings are also an affront to the International Code of Zoological Nomenclature. These amateurs were apparently given no guidance or accountability on how to use the data, and they obviously have a minimal understanding of systematics.

Bernard d'Abrera is not only one of the most prolific publishers on Lepidoptera of our time, but he stands unique (as far as I know) in presenting engaging narratives for readers who consider themselves to be critical thinkers. He was formally trained in the history and philosophy of science, and as such, attempts to hold science accountable to the rules of philosophy. Whether one agrees or disagrees with his views, d'Abrera actually challenges his readers to think.

Saturniidae Mundi, Part II is a significant and valuable resource for those who study Saturniidae, and will be a sheer pleasure to use by all who collect and rear saturniids. I highly recommend this book, and I hope many copies will be purchased by libraries.

RICHARD S. PEIGLER, *Department of Biology, University of the Incarnate Word, 4301 Broadway, San Antonio, Texas 78209-6397; and Research Associate, McGuire Center for Lepidoptera & Biodiversity, Gainesville, Florida; peigler@uiwtx.edu*

Journal of the Lepidopterists' Society
67(3), 2013, 231

LIFE HISTORIES OF CASCADIA BUTTERFLIES. 2011 by David G. James & David Nunnallee. 447pp. Publisher: Oregon State University Press, Corvallis. Price: US \$35. ISBN 978-0-87071-626-3.

The great American satirist George Carlin (1937-2008) once observed, "The caterpillar does all the work, but the butterfly gets all the publicity." Carlin was decidedly not an entomologist, but his maxim is a nice philosophical summary of the book, *Life histories of Cascadia butterflies*. The work hearkens back to a time when exploring and clearly illustrating the natural history of butterfly early stages, host plants, predators, defenses, diapause, and migration pointed to the future scientific understanding of butterflies and their evolution. William Henry Edwards, Samuel Scudder and colleagues understood caterpillars and dedicated fieldwork, and they all would have been excited by *Life histories of Cascadia butterflies*. The book illuminates what naturalists dream about; the secret lives of insects that abound in nature.

All of the photographic portraits in this field guide are alive with vibrant detail and information, and they demonstrate both the dedicated naturalist's understanding of the subject and the craft of photography. The well-wrought chapters and species accounts are concise models of how to convey

information. There are few, if any, shrill diatribes about species names or political fluff. This book is about butterfly life histories, and it does an admirable job. The text not only informs, it poses questions that point to future directions of discovery and research. What is more, readers of this field guide are encouraged to solve problems by making their own field observations, and getting them published; an excellent example of educational science. True, the coverage is restricted to a small geographic area, but the butterfly species treated in the book occur in a much wider area. Not just another pretty butterfly book—*Life histories of Cascadia butterflies* is a unique contribution to the American butterfly fauna that will likely inspire the next generation of butterfly naturalists.

Congratulations to the authors for making public an exceptionally informative work and providing hopeful evidence that butterfly field guides are undergoing a sea change. There is little I can add except to assert that everyone should own a copy of *Life histories of Cascadia butterflies* and use it to gain a better understanding of butterflies and their place in nature. Get to work.

P. J. DEVRIES, *Department of Biological Sciences, University of New Orleans, New Orleans, LA 70148, email: pdevries@uno.edu*

Journal of the Lepidopterists' Society
67(3), 2013, 231–232

BUTTERFLIES & OTHER INSECTS. MY ENDURING IMPRESSIONS, by Phillip R. Ackery, 193pp., ISBN 978-09564692-2-9, size approximately A4, cardback, published by Forrest Text, Cardigan, Wales, in association with the Natural History Museum, London; 2012; cost approximately £40 sterling (US\$61).

Prior to his retirement in 2006, Phil Ackery was employed for over four decades in the Entomology Department of the Natural History Museum (formerly the British Museum (Natural History)), primarily associated with the butterfly collections. His many achievements include the (joint) award of the Karl Jordan medal in 1989, presented in Albuquerque. Unlike so many of his peers, Phil was not a butterfly nerd (his word, not mine!) in his early years, taking no interest in insects until the age of 18. But by the time of his retirement his knowledge of the “BM” butterfly collections was unrivalled, as visitors during his time as the Museum’s “butterfly man” will testify.

The book consists of three main parts: “An insect vocation”, “Butterflies and moths”, and “An insect miscellany”. The first begins with Linnaeus and his students, discusses the ‘mystery’ and metamorphosis of taxonomic names, novelist and entomologist Vladimir Nabokov and his butterflies, ‘great’ private collections, butterfly hunters historical and modern, and the circumstances of some odd butterfly fakes and fixers—the last including an account of the destruction of the Linnaean “Piltdown butterfly” *Papilio ecclipsis* by Edward Gray, in an uncharacteristic display of emotion that may have represented “probably the only positive action [he made] in an otherwise undistinguished museum career”. The second contains a potted history of research, liberally sprinkled with anecdotes, on the subject of Phil’s main research interests – milkweed, apollo and birdwing butterflies – and other Lepidoptera interests including hawkmoths, silkworms and the famous story of Ford, Kettlewell and ‘industrial melanism’ in the Peppered Moth. Finally, a diverse selection of miscellany skips from forensic entomology to honey production, bubonic plague in the 14th century, and creepy-crawlies generally. Scattered throughout the book are almost 70 full page plates, largely colour, mostly butterflies or their early stages, taken from some of the

most historically significant works published from the early 18th century to modern times, reproduced from the unparalleled library collections of the NHM. Many have informative annotations. Sadly, some of the plates look a little ‘faded’, lacking the sharpness and bright colours of the originals.

The book is well researched and full of anecdotes, making it a comfortable place to meander at your leisure. Two things make this book a real pleasure: firstly the uncomplicated, unpretentious, and relaxed style; secondly the author’s knack for plucking the most apt and amusing anecdotes from the ramblings of denizens of a bygone age and skilfully weaving them, in a personal and highly readable style, into an engaging series of connected stories. The book brings people to life, in all their glorious eccentricity, from a combination of the author’s experience and a literature which at its worst can be dry as dust. Researching the content has clearly given Phil Ackery a great deal of pleasure. Reading it has provided the same for the reviewer—this is one of very few books that can and should be picked up regularly during a lifetime. The diverse content, with the author’s sharp perception combined with dry delivery, will invariably raise a smile.

I noticed no obvious errors and have no complaints of substance, although a scarcity of direct reference to cited sources becomes mildly frustrating. I also believe the unremarkable title belies a content that is stuffed full of Life and dry humour, and it defeats me why such an expensive (and it is rather expensive) book is produced in a card cover. It deserves to be in hard back.

It is depressing to think that the “characters”—in the best sense—inhabiting the pages of this book are ghosts from an age that can never be recovered or be repeated. We live in an age of modern molecular researchers, tied to their microscopes, many of whom have never got their boots muddy or slept under the stars with the mosquitoes (there are some notable exceptions). Notwithstanding the minor issues noted above, this must be regarded as a prominent contribution to the history of western entomology over several centuries.

Buy it now—you really won’t be disappointed.

JOHN TENNENT, *Oxfordshire, England, e-mail:*
johntennent@hotmail.co.uk

Journal of the Lepidopterists' Society
67(3), 2013, 234–239

WILLIAM E. MILLER

(1930–2013)

William E. Miller was curious about what made the natural world tick, particularly when it came to Lepidoptera. Although he lived much of his life in the North, he never lost the warm, southern charm acquired from his birthplace in Texas and early years in Louisiana. This tall, thin gentleman with beard and jaunty beret was a fixture on the St. Paul Campus at the University of Minnesota. Spring on campus brought him the pleasures of seeing the magnolia trees in full bloom. Little did the students in the Student Center nearby know that this emeritus professor had once sung in a barbershop quartet!

Bill's academic career began at Louisiana State University where he obtained his B.S. in Zoology in 1950. He then migrated north to study, receiving both his M.Sc. in 1951 and his Ph.D. in 1955 at The Ohio State University under the guidance of his major professor Alvah Peterson, who is best known for his seminal two-volume work *Larvae of Insects*. Bill enjoyed the rural setting of the Wooster Campus while working on his dissertation research titled *The biology*

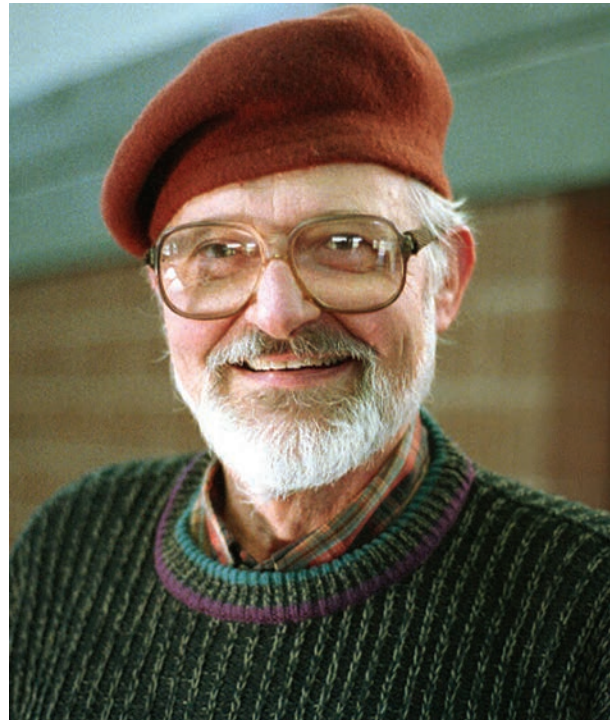
and control of the European pine shoot moth. He was a research assistant at the Ohio Agricultural Experiment Station in Wooster until 1954, when he joined the U.S. Army Division of Communicable Diseases at the Walter Reed Army Institute of Research.

A fellowship from the West German Government (1957–1958) at the Forest Zoology Institute of Göttingen University, Hann. Münden coincided with Dr. Miller's appointment as Project Leader at the Lake States Forest Experiment Station in East Lansing, Michigan (1956–1964) on the campus of Michigan State University. Upon his return state-side, he worked at the experiment station while obtaining a second M.Sc. in Forestry from Michigan State (1961).

Dr. Miller was a Project Leader at the North Central Forest Experiment Station on the St. Paul campus of the University of Minnesota from 1964 until he retired in 1982. He became an adjunct (and later emeritus) professor in the Department of Entomology, Fisheries and Wildlife (now the Department of Entomology) in 1976, where he generously contributed to teaching,



October 1971



May 2005

mentoring of graduate students, and departmental service for more than 20 years. Bill was reserved but influential to the intellectual and social fabric of the department. He was a major professor and favorite mentor of graduate students even after his “official” retirement. His thoughtful and positive encouragement was not limited to students, as he mentored faculty as well. Many a faculty member sought his advice on everything from statistical analyses to balancing the demands of a personal life with work. Bill was a favorite editor of manuscript drafts, leaving his carefully penned comments, which were rigorous, thorough, and never harsh, in green ink. For many years, he taught a special course on Lepidoptera he titled *Lepidopterology*, which included a potpourri of information such as atypical examples of strange biologies, life histories undergirded by his copious knowledge of evolution, and systematics of this prolific insect order. When Bill stepped away from daily university activities in the early 2000s due to health issues, he remained active in his research and contributions to the Minnesota Department of Entomology.

During his career, Dr. Miller authored 137 publications, including several monographs; his complete bibliography follows this article. In the realm of systematics, Bill was a specialist on the Tortricidae, subfamily Olethreutinae. He described many new taxa (2 genera and 43 species), proposed new synonymies, and elucidated features of their life histories, becoming recognized as an authority on the North American members of this difficult group. His in-depth knowledge of systematics dovetailed nicely with his work responsibilities in the U.S. Forest Service, particularly for economic pests such as the European pine shoot moth, a species he published on extensively. Bill was especially interested in documenting or describing tortricid species that were introduced into North America, and many of his publications focused on these taxa. He also had an interest in documenting the “true” distribution of Holarctic species, many of which were considered different species in the Palearctic and Nearctic regions. His interest in past North American tortricid workers resulted in detailed catalogs of the species described by J. B. Clemens and C. H. Fernald, which became foundations for stabilizing the names proposed by these two early lepidopterists. Dr. Miller’s vast knowledge of Olethreutinae was partially summarized in his monograph *Guide To the Olethreutine Moths of Midland North America* (1987), a publication that greatly influenced many of the current Olethreutinae experts in North America. However, Bill did not limit

his studies to tortricids. In his ecological work on Lepidoptera he researched and published on a diversity of topics such as body size and its relation to geography and altitude, the correlation between adult feeding and oviposition, the diversity and life-histories of gall-forming Lepidoptera, and many others. His research explored and documented the interplay of systematics, ecology, evolution, and behavior in an experimental framework.

Dr. Miller was an avid reader, and he enjoyed fleshing out information from the literature by reanalyzing published data. For example, in his work on the population dynamics of Lepidoptera, he and his graduate student used published data on populations of multiple species from the same locality over at least a seven-year period to find that their fluctuations were often correlated. In more recent years, Bill compiled various literature sources of day-degree data and reanalyzed them using a more accurate analytical method that had been previously published but largely ignored. Just before his death, he worked to exhumate and correct Professor Alexander Hodson’s data set that detailed the past 51 years of spring development by woody plants on the St. Paul campus, and to make this data available to phenology researchers through the University of Minnesota’s Digital Conservancy.

As an academic advisor and experienced editor, Dr. Miller stressed the importance of writing every day and challenged students to make the most of their creative faculties. He did this by example with his 1978 publication of *The facile mind: an annotated bibliography for enhancing creativity and problem solving*. Some of his other favorite topics included the use of multiple induction in hypothesis testing and various ideas on how to explain low probability events.

Bill was a dedicated member of the Lepidopterists’ Society. Among his contributions to the Society was his service on the Executive Council. He served as editor of the Society’s journal from 1985 to 1988, an important period of time where he was able to steer the journal back on track in his collected and methodical way. His thoughtful approach to giving critical but kind reviews and his organized system for keeping manuscripts moving served as a model for subsequent editors of the Journal. Bill became a life member of the Society and served as editor of the Society’s *Memoirs* for over a decade, which culminated in an all-consuming effort to complete David Winter’s *Basic Techniques for Observing and Studying Moths & Butterflies* in 2000. Bill put a number of his own projects on hold in order to complete this important manual and ensure the book was published. Thankfully, he was able to complete many of his postponed projects. The last paper for

which he read galleys was published just prior to his death in the March 11, 2013 issue of the Journal of the Lepidopterists' Society and another is in press.

Bill encouraged students and young professionals to go to the Lepidopterists' Society annual meetings, which he himself was able to attend for many decades uninterrupted. Bill would often converse with students and new members, taking an interest in their passion for Lepidoptera and making them feel welcome to the Society he loved. For all of these reasons and more, he received one of the Society's highest honors, the William D. Winter Service Award, at the 2007 meeting in Bakersfield, California.

In the last couple of years of his life, Bill continued to be a presence in the Department of Entomology as often as his health permitted and worked on his manuscripts from home and at his beloved cabin in Ely, Minnesota. His wife Jocelyn persuaded him to substitute his habitual walk with a car ride from their home in a nearby neighborhood. Bill is survived by Jocelyn M. Muggli, his wife of 35 years, and his six adult children. We were privileged and thankful to have the talents, contributions, and scholarly spirit of William E. Miller in the service of entomology and lepidopterology for over six decades. His legacy will live on in his publications, students, and friends.

BIBLIOGRAPHY

- MILLER, W. E. 1953. Biological notes of five hymenopterous parasites of pine bud and stem moth in Ohio. *Ohio J. Sci.* 53: 59–63.
- MILLER, W. E. & R. B. NEISWANDER. 1955. Biology and control of the European pine shoot moth. *Ohio Ag. Exper. Stat. Res. Bull.* 760, 31 pp.
- MILLER, W. E. 1955. Biology of *Anacampsis innocuella* (Zeller), a leafroller on aspen. *J. Econ. Entomol.* 48: 622–623.
- MILLER, W. E. 1955. Notes on the life cycles of three parasites of the pitch twig moth. *Ohio J. Sci.* 55: 317–319.
- MILLER, W. E. 1956. The pitch twig moth and its occurrence in Ohio. *Ohio Ag. Exper. Stat. Res. Bull.* 79, 24 pp.
- MILLER, W. E. 1958. Control of the European pine shoot moth with concentrated DDT sprays. *U.S. Dept. Ag. Lake States For. Exp. Stat. Tech. Note* 543, 2 pp.
- MILLER, W. E. 1958. Ecological notes on the pine midges *Retinodiplosis resinicola* (Osten Sacken) and *R. inopis* (Osten Sacken) in Southern Ohio (Diptera, Itonididae). *Ohio J. Sci.* 58: 231–235.
- MILLER, W. E. & S. A. ALTMANN. 1958. Ecological observations on the Virginia pitch-nodule moth, *Petrova wenzeli* (Kearfott), including a note on its nomenclature. *Ohio J. Sci.* 58: 273–281.
- MILLER, W. E. & D. L. HAYNES. 1958. Timing DDT sprays in the spring for European pine shoot moth control. *U.S. Dept. Ag. Lake States For. Exp. Stat. Tech.* 542, 2 pp.
- MILLER, W. E. 1959. A unique new North American species of pine-cone-feeding *Laspeyresia* related to *L. ingens* Heinrich (Lepidoptera, Olethreutidae). *Florida Entomol.* 42: 131–134.
- MILLER, W. E. 1959. Natural history notes on the goldenrod ball gall fly, *Eurosta solidaginis* (Fitch), and on its parasites *Eurytoma obtusiventris* Gahan and *E. gigantea*. *J. Tenn. Acad. Sci.* 34: 246–251.
- MILLER, W. E. 1959. *Petrova houseri*, a new pitch-nodule moth from eastern North America. *Ohio J. Sci.* 59: 230–232.
- MILLER, W. E. 1959. Preliminary study of European pine shoot moth parasitism in Lower Michigan. *J. Econ. Entomol.* 52: 768–769.
- MILLER, W. E. 1959. Spread of forest Lepidoptera. *Proceedings of the 14th Annual Meeting of the N. Cen. Bran. Entomol. Soc. Amer.* 14: 11. [abstract]
- MILLER, W. E. & R. B. NEISWANDER. 1959. The pitch pine tip moth and its occurrence in Ohio. *Ohio Ag. Exper. Stat. Res. Bull.* 840, 23 pp.
- MILLER, W. E. & H. J. HEIKKENEN. 1959. The relative susceptibility of eight pine species to European pine shoot moth attack in Michigan. *J. Forest.* 57: 912–914.
- MILLER, W. E. 1960. A new pine tip moth (Olethreutidae) from the Gulf of Mexico region. *J. Lepid. Soc.* 14: 231–236.
- MILLER, W. E. 1960. Discovery in Michigan of *Orgilus obscurator* (Nees), a foreign parasite of the European pine shoot moth. *J. Econ. Entomol.* 53: 318.
- HEIKKENEN, H. J. & W. E. MILLER. 1960. European pine shoot moth damage as related to red pine growth. *U.S. Dept. Ag., Lake States For. Exp. Stat. Tech. Note* 83, 12 pp.
- MILLER, W. E. & J. L. AREND. 1960. European pine shoot moth damage reduced to sheared Christmas trees. *U.S. Dept. Ag., Lake States For. Exp. Stat. Tech. Note* 592, 2 pp.
- MILLER, W. E. 1960. The European pine shoot moth: relationship between proportion of trees infested and number of insects per tree. *J. Forest.* 58: 647–648.
- MILLER, W. E. 1960. Unusual occurrence of the Virginia pitch-nodule moth, *Petrova wenzeli* (Kearfott) in Canada (Lepidoptera: Olethreutidae). *Can. Entomol.* 92: 879.
- MILLER, W. E. & D. L. HAYNES. 1961. Experiments with concentrated DDT sprays for European pine shoot moth suppression in forest plantations. *J. Econ. Entomol.* 54: 1014–1018.
- MILLER, W. E. 1962. Differential population levels of the European pine shoot moth, *Rhyacionia buoliana*, between Europe and North America. *Ann. Entomol. Soc. Amer.* 55: 672–675.
- TALERICO, R. L., H. J. HEIKKENEN & W. E. MILLER. 1963. Growth of red pine trees after chemical suppression of the European pine shoot moth. *Can. Entomol.* 95: 522–524.
- MILLER, W. E. & C. H. SCHALLAU. 1963. Problems in identifying old European pine shoot moth damage. *J. Forest.* 61: 677–678.
- MILLER, W. E. 1963. The goldenrod gall moth *Gnorimoschema gal-laesolidaginis* (Riley) and its parasites in Ohio. *Ohio J. Sci.* 63: 65–75.
- MILLER, W. E. 1963. The shortleaf pitch-blister moth, *Petrova houseri* Miller. *Ohio J. Sci.* 63: 297–301.
- MILLER, W. E. & L. F. WILSON. 1964. Composition and diagnosis of the pine tip moth infestations in the Southeast. *J. Econ. Entomol.* 57: 722–726.
- MILLER, W. E. 1965. Number of branchlets on red pine in young plantations. *For. Sci.* 11: 42–49.
- MILLER, W. E. 1965. Pine tip moths in Central America. *Turrialba* 15: 58.
- MILLER, W. E. 1965. Protecting Christmas tree plantations. *J. Forest.* 63: 849–852.
- MILLER, W. E. 1966. A new species of moth destructive to pine cones in Mexico (Tortricidae). *J. Lepid. Soc.* 20: 251–253.
- SCHALLAU, C. H. & W. E. MILLER. 1966. Intercept site-index equations for red pine damaged by European pine shoot moth. *J. Forest.* 64: 538–540.
- MILLER, W. E. 1966. Spiders in old insect galls on goldenrod. *Ohio J. Sci.* 66: 618–619.
- MILLER, W. E., L. F. WILSON & R. B. BUCHMAN. 1967. Relative infestation of European pine shoot moth on interplanted ponderosa and red pines in Michigan. *J. Forest.* 65: 818–819.
- MILLER, W. E. 1967. Taxonomic review of the *Rhyacionia frustrana* group of pine-tip moths, with description of a new species (Olethreutidae). *Can. Entomol.* 99: 590–596.
- MILLER, W. E. 1967. The European pine shoot moth: ecology and control in the Lake States. *For. Sci. Mon.* 14, 72 pp.
- POINTING, P. J. & W. E. MILLER. 1967. European pine shoot moth *Rhyacionia buoliana* (Schiff.), pp. 163–166. *In* Davidson, A. G.

- & R. M. Prentice (eds.), Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. Department of Forestry and Rural Development, Ottawa, Canada, no. 1180.
- WILSON, L. F. & W. E. MILLER. 1968. How to control European pine shoot moth and pine root collar weevil. U.S. Dept. Ag. For. Serv. North Central Forest Exp. Stat., 6 pp.
- MILLER, W. E. & A. H. TAYLOR. 1968. How to control red pine cone beetle. U.S. Dept. Ag. For. Serv. North Cen. For. Exp. Stat., 5 pp.
- MILLER, W. E., A. R. HASTINGS & V. M. CAROLIN. 1970. European pine shoot moth. U.S. Dept. Ag. For. Serv. North. Area State Priv. Forest. Forest Insect & Disease Leaflet 59.
- MILLER, W. E. 1970. Fernald types of North American Olethreutinae (Lepidoptera: Tortricidae). Proc. Entomol. Soc. Wash. 72: 288–294.
- MILLER, W. E. 1971. Annual variation in starting date of spring feeding by the European pine shoot moth in a Michigan planting. Michigan Entomol. 4: 28–31.
- MILLER, W. E. 1971. Identity of *Phaneta refusana* (Walker) with a description of a new species (Tortricidae). J. Lepid. Soc. 25: 284–287.
- ADDY, N. D., H. O. BATZER, W. J. MATTSON & W. E. MILLER. 1971. Impact of insects on multiple-use values of North Central forests. U.S. Department of Agriculture, Forest Service, North Central Forest Exp. Stat., Research Paper NC-57, 8 pp.
- MILLER, W. E. 1972. Insect interlude in Michigan dune fixation. J. Forest. 70: 387.
- MILLER, W. E. 1973. Clemens types of Olethreutinae (Lepidoptera, Tortricidae). Trans. Amer. Entomol. Soc. 99: 205–234.
- MILLER, W. E. 1973. Insects as related to wood and nut production. U.S. Dept. Ag. Forest Serv. Gen. Tech. Report NC-4, 114 pp.
- MILLER, W. E. 1973. Two previously unrecognized scientific names for the strawberry leafroller (Lepidoptera: Tortricidae). Ann. Entomol. Soc. Amer. 66: 553–554.
- MILLER, W. E. 1974. Identities of taxonomically confused moths of the *Eucosma agricola* group and description of a new species (Lepidoptera: Tortricidae). Ann. Entomol. Soc. Amer. 67: 601–604.
- MILLER, W. E. 1976. Biology and taxonomy of three gall forming species of *Epiblema* (Olethreutidae). J. Lepid. Soc. 30: 50–58.
- MILLER, W. E. 1977. A new species of *Laspeyresia* from Michigan (Lepidoptera: Olethreutidae). Great Lakes Entomol. 9: 171–172.
- MILLER, W. E. 1977. Two new species of *Petrova* moths from pine in Southeast Asia (Tortricidae: Olethreutinae). J. Lepid. Soc. 31: 135–138.
- MILLER, W. E. 1977. Uniform genitalia among wing color morphs of olethreutid moths. J. Lepid. Soc. 31: 118.
- MILLER, W. E. 1977. Weights of *Polia grandis* pupae reared at two constant temperatures (Lepidoptera: Noctuidae). Great Lakes Entomol. 10: 47–49.
- MILLER, W. E. 1977. Wing measure as a size index in Lepidoptera: the family Olethreutidae. Ann. Entomol. Soc. Amer. 70: 253–256.
- MILLER, W. E., R. F. WAMBACH & R. A. ANFANG. 1978. Effect of past European pine shoot moth infestations on volume yield of pole-sized red pine. For. Sci. 24: 543–550.
- MILLER, W. E. 1978. *Larisa subsolana*, a new genus and species of moth from eastern North America (Olethreutidae). J. Lepid. Soc. 32: 256–260.
- POWELL, J. A. & W. E. MILLER. 1978. Nearctic pine tip moths of the genus *Rhyacionia*: Biosystematic Review (Lepidoptera: Tortricidae, Olethreutinae). Forest Service, U.S. Department of Agriculture, Agriculture Handbook No. 514, 51 pp.
- MILLER, W. E. 1978. *Petrova* pitch-blistar moths of North America and Europe: two new species and synopsis (Olethreutidae). Ann. Entomol. Soc. Amer. 71: 329–340.
- MILLER, W. E. 1978. The facile mind: an annotated bibliography for enhancing creativity and problem-solving. U.S. Dept. Ag. For. Serv. North Central Forest Exp. Stat., 13 pp.
- MILLER, W. E., K. J. KESSLER, J. H. OHMAN & J. T. ESCHLE. 1978. Timber quality of northern hardwood regrowth in the Lake States. For. Sci. 24: 247–259.
- MILLER, W. E. 1978. Use of prescribed burning in seed production areas to control red pine cone beetle. Environ. Entomol. 7: 698–702.
- MILLER, W. E. 1979. Fire as an insect management tool. Bull. Entomol. Soc. Amer. 25: 137–140.
- MILLER, W. E. 1979. Identity corrections for two North American *Apotomis* moths (Tortricidae: Olethreutinae). Great Lakes Entomol. 12: 115–118.
- MILLER, W. E. 1979. Prior name for a *Petrova* pine moth (Tortricidae). J. Lepid. Soc. 33: 204.
- MILLER, W. E. 1979. The genus *Olethreutes*: identity corrections and description of a new species (Lepidoptera: Tortricidae: Olethreutinae). Ann. Entomol. Soc. Amer. 72: 232–236.
- MUGGLI, J. M. & W. E. MILLER. 1980. Instar head widths, individual biomass, and development rate of forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae), at two densities in the laboratory. Great Lakes Entomol. 13: 207–209.
- MILLER, W. E. 1981. Composition of goldenrod (*Solidago*: Compositae) populations by species in the Upper Midwest. J. Minn. Acad. Sci. 47: 15–17.
- MILLER, W. E. 1982. *Grapholita delineana* (Walker), a Eurasian hemp moth, discovered in North America. Ann. Entomol. Soc. Amer. 75: 184–186.
- MILLER, W. E. 1983. Decomposition rates of aspen bole and branch litter. For. Sci. 29: 351–356.
- MILLER, W. E. 1983. *Eucosmomorpha albersana* (Hübner), a Palaearctic species, collected in North America (Tortricidae, Grapholitini). J. Lepid. Soc. 37: 88–89.
- MILLER, W. E. 1983. Genus *Phaneta*: new synonymies and a new species (Lepidoptera: Tortricidae). Ann. Entomol. Soc. Amer. 76: 98–103.
- MILLER, W. E. 1983. Nearctic *Endothenia* species: a new synonymy, a misidentification, and a revised status (Lepidoptera: Tortricidae). Great Lakes Entomol. 16: 5–12.
- MILLER, W. E. 1983. New synonymies in Nearctic *Dichrorampha* (Lepidoptera: Tortricidae). Proc. Entomol. Soc. Wash. 85: 727–733.
- BROWN, R. L. & W. E. MILLER. 1983. Valid names of the spruce seed moth and a related *Cydia* species (Lepidoptera: Tortricidae). Ann. Entomol. Soc. Amer. 76: 110–111.
- MILLER, W. E. & M. G. POGUE. 1984. Ragweed borer (Lepidoptera: Tortricidae: Eucosmini): taxonomic implications of an allometric analysis of adult characters. Ann. Entomol. Soc. Amer. 77: 227–231.
- MILLER, W. E. 1984. Review of Dear Lord Rothschild: birds, butterflies, and history, by Miriam Rothschild. Univ. Minn. Dept. Entomol. News.
- MILLER, W. E. 1985. Comments on the proposed conservation of *Laspeyresia* Hübner, 1825. Z.N. (S.) 2421. Bull. Zool. Nomen. 42: 8–10.
- MILLER, W. E. 1985. Nearctic *Epiblema*: a new synonymy, a revised identity, and two new species (Lepidoptera: Tortricidae). Great Lakes Entomol. 18: 33–38.
- MILLER, W. E. 1985. Nearctic *Eucosma* (Lepidoptera: Tortricidae) four new species and three new synonymies. Ann. Entomol. Soc. Amer. 78: 240–247.
- MILLER, W. E. 1985. Nearctic *Olethreutes*: five new synonymies, two revised statuses, and notes (Lepidoptera: Tortricidae). Proc. Entomol. Soc. Wash. 87: 408–417.
- MILLER, W. E. 1985. Nearctic *Rhyacionia* pine tip moths: a revised identity and a new species (Lepidoptera: Tortricidae). Great Lakes Entomol. 18: 119–122.
- MILLER, W. E. 1985. *Pammene perstructana* (Walker) (Lepidoptera: Tortricidae) identified after more than a century. Great Lakes Entomologist 18: 145–147.
- MILLER, W. E. 1985. Review of Forest entomology: ecology and management, by R. N. Coulson and J. A. Witter. For. Sci. 31: 517–518.

- MILLER, W. E. 1986. *Epinotia nisella*: an unrecorded host and mode of feeding (Lepidoptera: Tortricidae). Great Lakes Entomol. 19: 205–207.
- MILLER, W. E. 1986. New species of the genus *Cydia* that attack seeds of Mexican conifers (Lepidoptera: Tortricidae), pp. 5–7. In Cibrián-Tovar, D., B. H. Ebel, H. O. Yates & J. T. Mendez-Montiel (eds.), *Insectos de conos y semillas de las coníferas de México/Cone and seed insects of the Mexican conifers*. U.S. Department of Agriculture, Southeastern Forest Experiment Station (Asheville, N.C.)/Universidad Autónoma Chapingo, SE-40.
- MILLER, W. E. & M. E. EPSTEIN. 1986. Synchronous population fluctuations among moth species (Lepidoptera). Environ. Entomol. 15: 443–447.
- MILLER, W. E. 1986. The species of *Pseudexentera* (Tortricidae). J. Lepid. Soc. 40: 218–237.
- MILLER, W. E. 1987. A new species of *Gretchena* (Tortricidae) injurious to planted Neotropical walnut J. Lepid. Soc. 41: 151–153.
- MILLER, W. E. 1987. Change in nutritional quality of detached aspen and willow foliage used as insect food in the laboratory. Great Lakes Entomol. 20: 41–45.
- MILLER, W. E. 1987. Guide to the Olethreutine moths of midland North America (Tortricidae). U.S. Dept. Ag. For. Serv. Ag. Hand. 660, 104 pp.
- MILLER, W. E. 1987. Spruce budworm (Lepidoptera: Tortricidae): role of adult imbibing in reproduction. Environ. Entomol. 16: 1292–1295.
- MILLER, W. E. 1988. European corn borer reproduction: effects of honey in imbibed water. J. Lepid. Soc. 42: 138–143.
- MILLER, W. E. 1988. Two new species of *Rhyacionia* pine moths from Mexico (Tortricidae: Olethreutinae). J. Lepid. Soc. 42: 236–239.
- MILLER, W. E. 1989. Reproductive enhancement by adult feeding: effects of honeydew in imbibed water on spruce budworm. J. Lepid. Soc. 43: 167–177.
- MILLER, W. E. 1990. A new species of *Sonia* from eastern North America (Tortricidae). J. Lepid. Soc. 44: 88–90.
- MILLER, W. E. 1990. Body size and diet quality in the genus *Cydia* (Tortricidae). J. Lepid. Soc. 44: 113–142.
- MILLER, W. E. 1990. Differences between Nearctic *Pammene perstructana* and its most similar Palearctic relatives (Tortricidae). J. Lepid. Soc. 44: 288–289.
- MILLER, W. E. 1991. Body size in North American Lepidoptera as related to geography. J. Lepid. Soc. 45: 158–168.
- GRANT, G. G., B. PENDREL, K. N. SLESSOR, M. Z. MENG & W. E. MILLER. 1991. Identification of sex pheromone components for two lepidopteran defoliators, the oak olethreutid leafroller, *Pseudexentera spoiliana* (Clemens), and the aspen leafroller, *Pseudexentera oregonana* (Walsingham). Can. Entomol. 123: 1209–1218.
- MILLER, W. E. 1991. Positive relation between body size and altitude of capture site in tortricid moths (Tortricidae). J. Lepid. Soc. 45: 66–67.
- MILLER, W. E. 1993. Review of: Systematics of the *Chrysoxena* group of genera (Lepidoptera: Tortricidae: Euliini). Ann. Entomol. Soc. Amer. 86: 216–217.
- MILLER, W. E. 1993. Review of: Tortricid Pests: their biology, natural enemies and control. Ann. Entomol. Soc. Amer. 39: 45–46.
- GIBSON, L. D. & W. E. MILLER. 1994. Two new synonymies in Nearctic *Eucosma* (Tortricidae: Olethreutinae). J. Lepid. Soc. 48: 69–71.
- MILLER, W. E. 1995. Beringian Tortricidae: a new synonymy in *Epiblema* and a recount of Holarctic species. J. Lepid. Soc. 49: 250–252.
- MILLER, W. E. 1995. *Jerapowellia burnorum*, a new genus and species of moth from the southwestern United States (Tortricidae: Olethreutinae). J. Lepid. Soc. 49: 24–30.
- GRANT, G. G. & W. E. MILLER. 1995. Larval images on lepidopteran wings—an unrecognized defense mechanism? Amer. Entomol. 41: 44–48.
- BATZER, H. O., M. P. MARTIN, W. J. MATTSO & W. E. MILLER. 1995. The forest tent caterpillar in aspen strands: distribution and density estimation of four life stages in four vegetation strata. For. Sci. 41: 99–121.
- MILLER, W. E. 1996. Population behavior and adult feeding capability in Lepidoptera. Environ. Entomol. 25: 213–226.
- MILLER, W. E. 1997. Body weight as related to wing measure in hawkmoths (Sphingidae). J. Lepid. Soc. 51: 91–92.
- MILLER, W. E. 1997. Diversity and evolution of tongue length in hawkmoths (Sphingidae). J. Lepid. Soc. 51: 9–31.
- MILLER, W. E. 1997. Intoxicated lepidopterans: how is their fitness affected, and why do they tipple? J. Lepid. Soc. 51: 277–287.
- SABOURIN, M., R. J. PRIEST & W. E. MILLER. 1997. Nearctic *Acleris*: resurrection of *A. stadiana* and a revised identity for *A. semianula* (Lepidoptera: Tortricidae). Great Lakes Entomol. 30: 71–78.
- JALAVA, J. & W. E. MILLER. 1998. Boreal Olethreutini 1 (Lepidoptera: Tortricidae): new synonymies and Holarctic records. Entomol. Fennica 9: 137–142.
- MILLER, W. E. & B. K. NAYAK. 1998. The body size-altitude correlation in Lepidoptera: new findings from tropical *Antheraea* silk moths (Saturniidae). Bull. Indian Acad. Seric. 2: 16–20.
- MILLER, W. E. 1999. A new synonymy in *Dichrorampha* that reveals an overlooked immigrant record for North America (Tortricidae). J. Lepid. Soc. 53: 74–75.
- MILLER, W. E. 2000. A comparative taxonomic-natural history study of eight Nearctic species of *Gnorimoschema* that induce stem galls on Asteraceae, including descriptions of three new species (Lepidoptera: Gelechiidae). Entomol. Soc. Amer., Thomas Say Pub. Entomol., 80 pp.
- MILLER, W. E. & J. JALAVA. 2000. Boreal Olethreutini 2 (Tortricidae): wing and genitalia illustrations, a new synonymy and a new Holarctic addition. J. Lepid. Soc. 54: 47–51.
- MILLER, W. E., R. L. BROWN & K. R. TUCK. 2000. Taxonomic clarification of *Notocelia rosaecolana* (Doubleday) and *N. trimaculana* (Haworth) (Tortricidae). J. Lepid. Soc. 54: 111–115.
- MILLER, W. E. 2001. A new species of *Eucosmomorpha* from North America (Tortricidae). J. Lepid. Soc. 55: 81–84.
- MILLER, W. E. & E. H. LA GASA. 2001. First report of *Gypsonoma aceriana* (Duponchel) (Lepidoptera: Tortricidae), an Old World poplar pest, in North America. Proc. Entomol. Soc. Wash. 103: 1020–1022.
- SABOURIN, M., W. E. MILLER & P. T. DANG. 2002. *Hedya salicella* (L.), a Palearctic species, collected in North America (Tortricidae). J. Lepid. Soc. 56: 172–173.
- SABOURIN, M., W. E. MILLER, E. H. METZLER & J. T. VARGO. 2002. Revised identities and new species of *Aethes* from Midwestern North America (Tortricidae). J. Lepid. Soc. 56: 216–233.
- GRANT, G. G., P. DE GROOT, D. LANGEVIN, S. A. KATOVICH, K. N. SLESSOR & W. E. MILLER. 2002. Sex attractants and seasonal flight patterns for three *Eucosma* (Lepidoptera: Tortricidae) species sympatric in eastern pine seed orchards and plantations. Can. Entomol. 134: 391–401.
- ROBERTS, M. A. & W. E. MILLER. 2003. First report of the Palearctic *Dichrorampha acuminatana* (Lienig & Zeller) in North America (Tortricidae). J. Lepid. Soc. 57: 152–153.
- COOKE, B. J., W. E. MILLER & J. ROLAND. 2003. Survivorship bias in tree-ring reconstructions of forest tent caterpillar outbreaks using trembling aspen. Tree-Ring Res. 59: 29–36.
- MILLER, W. E. 2004. Host breadth and voltinism in gall-inducing Lepidoptera. J. Lepid. Soc. 58: 44–47.
- MILLER, W. E. 2005. Gall-inducing Lepidoptera, pp. 431–466. In Raman, A., C. W. Schaefer & T. M. Withers (eds.), *Biology, ecology, and evolution of gall-inducing arthropods*, Volume 2. Science Publishers Inc., Enfield, NH, USA.
- MILLER, W. E. 2005. Extrinsic effects on fecundity-maternal weight relations in capital-breeding Lepidoptera. J. Lepid. Soc. 59: 143–160.
- MILLER, W. E. 2005. Reproductive bulk in capital-breeding Lepidoptera. J. Lepid. Soc. 59: 229–233.
- MILLER, W. E. 2006. Forest tent caterpillar mating, oviposition, and adult congregation at town lights during a northern Minnesota outbreak. J. Lepid. Soc. 60: 156–160.

- SULLIVAN, J. B. & W. E. MILLER. 2007. Intraspecific body size variation in macrolepidoptera as related to altitude of capture site and seasonal generation. *J. Lepid. Soc.* 61: 72–77.
- MILLER, W. E. 2011. Temperature-dependent development in capital-breeding Lepidoptera. *J. Lepid. Soc.* 65: 227–248.
- MILLER, W. E. 2013. Smallness and bigness: relation of underlying cell size and number to lepidopteran body size. *J. Lepid. Soc.* 67: 67–69.
- MILLER, W. E. (in press) Phenotypic correlates of genome size in Lepidoptera. *J. Lepid. Soc.*

MARC E. EPSTEIN *Plant Pest Diagnostics Branch, California Department of Food and Agriculture, 3294 Meadowview Road, Sacramento, CA 95832, email: marc.epstein@cdfa.ca.gov;* SUSAN J. WELLER *Department of Entomology, 219 Hodson Hall, 1980 Folwell Ave., University of Minnesota, St. Paul, MN 55108 and The Bell Museum of Natural History, 10 Church Street SE, Minneapolis, MN 55455, email:*

welle008@umn.edu; ROGER D. MOON *Department of Entomology, 219 Hodson Hall, 1980 Folwell Ave., University of Minnesota, St. Paul, MN 55108, email: rdmoon@umn.edu;* WILLIAM D. HUTCHISON *Department of Entomology, 219 Hodson Hall, 1980 Folwell Ave., University of Minnesota, St. Paul, MN 55108 email: hutch002@umn.edu;* WILLIAM J. MATTSON *Institute for Applied Ecosystem Studies, Northern Research Station, USDA Forest Service, Rhinelander, WI 54501, email: wjmattson@gmail.com;* IAN V. MACRAE *University of Minnesota, Northwest Research and Outreach Center, 2900 University Ave., Crookston, MN 5671, imacrae@umn.edu;* AND TODD M. GILLIGAN *Colorado State University, BSPM, 1177 Campus Delivery, Fort Collins, CO 80523, email: tgilliga@gmail.com.*

EDITORIAL STAFF OF THE *JOURNAL*

KEITH S. SUMMERVILLE, Editor
Department of Environmental Science and Policy
Drake University
2507 University Ave., 131 Olin Hall
Des Moines, Iowa 50311-4505
ksummerville@drake.edu

PEG TOLIVER, Layout Editor
Natural Imprints | 706 Lake Road
Eureka, Illinois 61530-1654
naturimp@mtco.com

Associate Editors:

GERARDO LAMAS (*Peru*), KENELM W. PHILIP (*USA*), ROBERT K. ROBBINS (*USA*), FELIX SPERLING (*Canada*),
DAVID L. WAGNER (*USA*), CHRISTER WIKLUND (*Sweden*), CARLA PENZ (*USA*), ANDREW WARREN (*USA*)

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, General Notes, Technical Comments, Book Reviews, and Obituaries. Obituaries must be authorized by the president of the society.

Send *Journal* submissions electronically to: ksummerville@drake.edu or to the editor at the above address. Contributors should feel free to recommend one or two reviewers upon submission of their manuscript. Short manuscripts concerning new state records, book reviews, new book releases, current events and notices should be sent to the *News*, James Adams, School of Sciences and Math, 650 College Dr., Dalton State College, Dalton, GA 30720-3778, e-mail: jadams@daltonstate.edu.

Before submitting manuscripts or electronic files, consult instructions on the Society's web site at <http://www.lepsoc.org/>.

Authors should provide an electronic copy of the manuscript in a standard PC or Macintosh-based word processing format.

Abstract: Include an informative abstract for Articles, Profiles, and Technical Comments.

Additional key words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Write with precision, clarity and economy, and use the active voice and the first person whenever appropriate. Make title explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Use metric units for measurements, and a 24-h clock (0930 h, not 9:30 AM) to express time. Underline only where *italics* are intended.

Literature cited: References to Articles, Profiles, General Notes, and Technical Comments should be given as Sheppard (1959) or (Sheppard 1959, 1961a,b) and listed alphabetically under the heading Literature Cited, in plain text (**do not capitalize author names**) and without underlining as follows:

Sheppard, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.

—— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. *Adv. Genet.* 10:165–216.

Illustrations: Electronic submissions are expected. Initial submissions may be low-resolution *.jpg format, but final illustrations should be *.tif format with image layers flattened, saved at a resolution of at least 350 ppi (137 pixels per cm), sent on a CD. Illustrate only half of symmetrical objects such as adults with wings spread, unless whole illustration is crucial. Bear in mind that your illustrations will be sized to fit a *Journal* page (plan to make lettering sufficiently large) and that the figure legend will appear at the bottom of the page (*Journal* page: 16.5 cm width, 22.5 cm height). One-column illustrations should be 1000 pixels wide; two-column illustrations should be 2200 pixels wide. Figures, both line drawings and photographs, should be numbered consecutively in Arabic numerals; do not use "plate." Type figure legends double-spaced at the end of the manuscript following Literature Cited. Use a separate paragraph for each legend. Color illustrations are encouraged; contact editor or consult our web site for submission requirements and cost.

Tables: Number tables consecutively in Arabic numerals. Label them in plain text (e.g., Table 1.) and use a concise and informative heading. Type each table on a separate sheet and place after the Literature Cited section, with the approximate desired position indicated in the text. Avoid vertical lines and vertical writing.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting the identity of organisms can be found. Kinds of reports that require vouchers include descriptions of new taxa, life histories, host associations, immature morphology, and some experimental studies.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes will be charged to authors at the rate of \$3.00 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are \$50 per *Journal* page. For authors without institutional support, page charges are \$25 per *Journal* page. For authors who are not members of the Society, page charges are \$75 per *Journal* page. Authors unable to pay page charges for any reason should apply to the editor at the time of submission for a reduced rate. Authors of Book Reviews and Obituaries are exempt from page charges.

Correspondence: Address all matters relating to the *Journal* to the editor. Address book reviews directly to the *News* editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

CTENUCHINA AND EUCHROMIINA (LEPIDOPTERA: EREBIDAE: ARCTIINAE) OF THREE BIOLOGICAL RESEARCH STATIONS OF MÉXICO'S ECOSUR <i>Fernando Hernández-Baz, Miguel A. Morón, Eduardo Chamé-Vázquez and Jorge M. González</i> -----	145
THE DESCRIPTION OF <i>PLATPHALONIA MAGDALENAE</i> (TORTRICIDAE, TORTRICINAE, EULIINI, COCHYLINA) FOUND NECTARING DIURNALLY ON <i>CENTROMADIA PUNGENS</i> (ASTERACEAE) IN THE CENTRAL VALLEY OF CALIFORNIA ALONG WITH A LIST OF SPECIES OF <i>PLATPHALONIA</i> <i>Eric H. Metzler and Valeriu Albu</i> -----	156
HIDING BEHIND GAUDY LOOKS, A NEW CENTRAL AMERICAN SPECIES OF <i>PHAREAS</i> (HESPERIIDAE: EUDAMINAE) <i>Nick V. Grishin, Daniel H. Janzen and Winnie Hallwachs</i> -----	161
TWO NEW SPECIES OF <i>PHANETA</i> (TORTRICIDAE) FROM SOUTHERN CALIFORNIA, WITH REVIEWS OF TEN SIMILAR SPECIES <i>Donald J. Wright</i> -----	175
LONGEVITY AND INDIVIDUAL ACTIVITY OF THE YUCCA MOTH, <i>TEGETICULA MACULATA EXTRANEA</i> (PRODOXIDAE), BASED ON MARK-RELEASE MONITORING <i>Jerry A. Powell</i> -----	187
LIFE HISTORY TRAITS AND REARING TECHNIQUES FOR FALL WEBWORMS (<i>HYPHANTRIA CUNEA</i> DRURY) IN COLORADO <i>Katrina J. Loewy, Amy L. Flansburg, Kylee Grenis, Mackenzie K. Kjeldgaard, Jennifer McCarty, Lily Montesano, Jennifer Vernick and Shannon M. Murphy</i> -----	196
THE DODGE FAMILY: AN ENDURING TRADITION OF ENTOMOLOGY <i>John V. Calhoun</i> -----	206
<i>EUSELASIA HYGENIUS OCCULTA</i> (RIODININAE): FIRST REPORT OF FEEDING ON <i>PSIDIUM GUAJAVA</i> (MYRTACEAE) IN MINAS GERAIS STATE, BRAZIL <i>José Cola Zanuncio, Marcus Alvarenga Soares, Teresinha Vinha Zanuncio, Olaf Hermann Hendrik Mielke, Francisco de Souza Ramalho, and Carlos Frederico Wilcken</i> -----	221
GENERAL NOTES	
USE OF A NATIVE AND AN EXOTIC MALVACEAE BY THE LITTLE KNOWN SKIPPER <i>PYRGUS BOCCHORIS TRISIGNATUS</i> (MABILLE) (HESPERIIDAE) IN NORTHERN CHILE <i>Héctor A. Vargas</i> -----	225
OVERCROWDING LEADS TO LETHAL OVIPOSITION MISTAKES IN THE BALTIMORE CHECKERSPOT, <i>EUPHYDRYAS PHAETON</i> DRURY (NYMPHALIDAE) <i>M. Deane Bowers and Johanna Schmitt</i> -----	227
BOOK REVIEWS	
SATURNIIDAE MUNDI: SATURNIID MOTHS OF THE WORLD, PART II, BY Bernard d'Abbrera. <i>Richard S. Peigler</i> -----	230
LIFE HISTORIES OF CASCADIA BUTTERFLIES BY David G. James & David Nunnallee. <i>P. J. DeVries</i> --	231
BUTTERFLIES & OTHER INSECTS. MY ENDURING IMPRESSIONS, BY Phillip R. Ackery. <i>John Tennent</i> ---	231
TRIBUTE — WILLIAM E. MILLER (1930–2013) -----	234