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Cover Illustration: Images from the study of leaf-mining Gracillariidae from *Schinus terebinthifolius*. Clockwise from top left: *Caloptilia schinusifolia* Davis and Wheeler, *Leurocephala schinusae* Davis and Mc Kay (photos by Patricia Gentili), leafmine of *L. schinusae* on *S. terebinthifolius* in Argentina, Cocoon of *L. schinusae* with last (5th) instar larva (photos by Fernando Mc Kay). See article starting on page 61.

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BIOLOGY AND SYSTEMATICS OF THE LEAFMINING GRACILLARIIDAE OF BRAZILIAN PEPPER TREE, *SCHINUS TEREBINTHIFOLIUS RADDI*, WITH DESCRIPTIONS OF A NEW GENUS AND FOUR NEW SPECIES)

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ABSTRACT. Recent surveys in southern Florida, USA, Brazil and Argentina, for biological control agents to assist in the control of the invasive Brazilian peppertree, have discovered several previously unknown species of plant mining Lepidoptera of the family Gracillariidae. Morphological descriptions with summaries of their biology for the following four new species and one new genus are presented: *Caloptilia schinusifolia* Davis and Wheeler, from Brazil and possibly Argentina; *Eucosmophora schinusivora* Davis and Wheeler, from Argentina and Brazil; *Leurocephala schinusae* Davis and Mc Kay, new genus and species, from Argentina and Brazil; and *Marmara habecki* Davis, new species, from Florida, USA. The larvae of all four species exhibit a hypermetamorphic development consisting of early instar sapfeeding and later instar tissue feeding stages typical for members of Gracillariidae. Larvae of *M. habecki* were also observed to possess an additional nonfeeding, transitional instar prior to the final instar as is typical for the genus (Wagner *et al*. 2000). Larvae of the new genus *Leurocephala* were discovered to undergo an intermediate, nearly apodal tissue feeding stage between the sapfeeding and final tissue feeding instars. Unique specimens representing an additional three species of Gracillariidae also have been reared from this tree in Argentina or Brazil, but these could not be identified because of inadequate material. COI barcodes were obtained for *Marmara habecki*, *M. smilacisella*, and an undescribed *Marmara* from Brazil. Each species was separated by a minimum barcode divergence of > 4.5% (Fig. 111).

Additional key words: Adult and larval morphology, larval biology, Anacardiaceae, biological control, *Astronium balansae*, *Caloptilia coruscans*, leaf mining, hypermetamorphosis, *Lithrea molleoides*, *Morella faya*, parasitoid, *Schinus fasciculatus*, *Schinus lentiscifolius*, *Schinus weinmannifolius*, Smilacaceae, *Smilax*, stem mining.

Brazilian peppertree (*Schinus terebinthifolius* Raddi, Anacardiaceae) is a Neotropical species whose native range extends along the Atlantic coast of Brazil and Uruguay, west to northeastern Argentina and adjacent Paraguay (Barkley 1944, 1957; Mc Kay unpublished data; Fig. 1). This species has been introduced to many countries around the world as an ornamental (Morton 1978; Panetta & McKee 1997). In

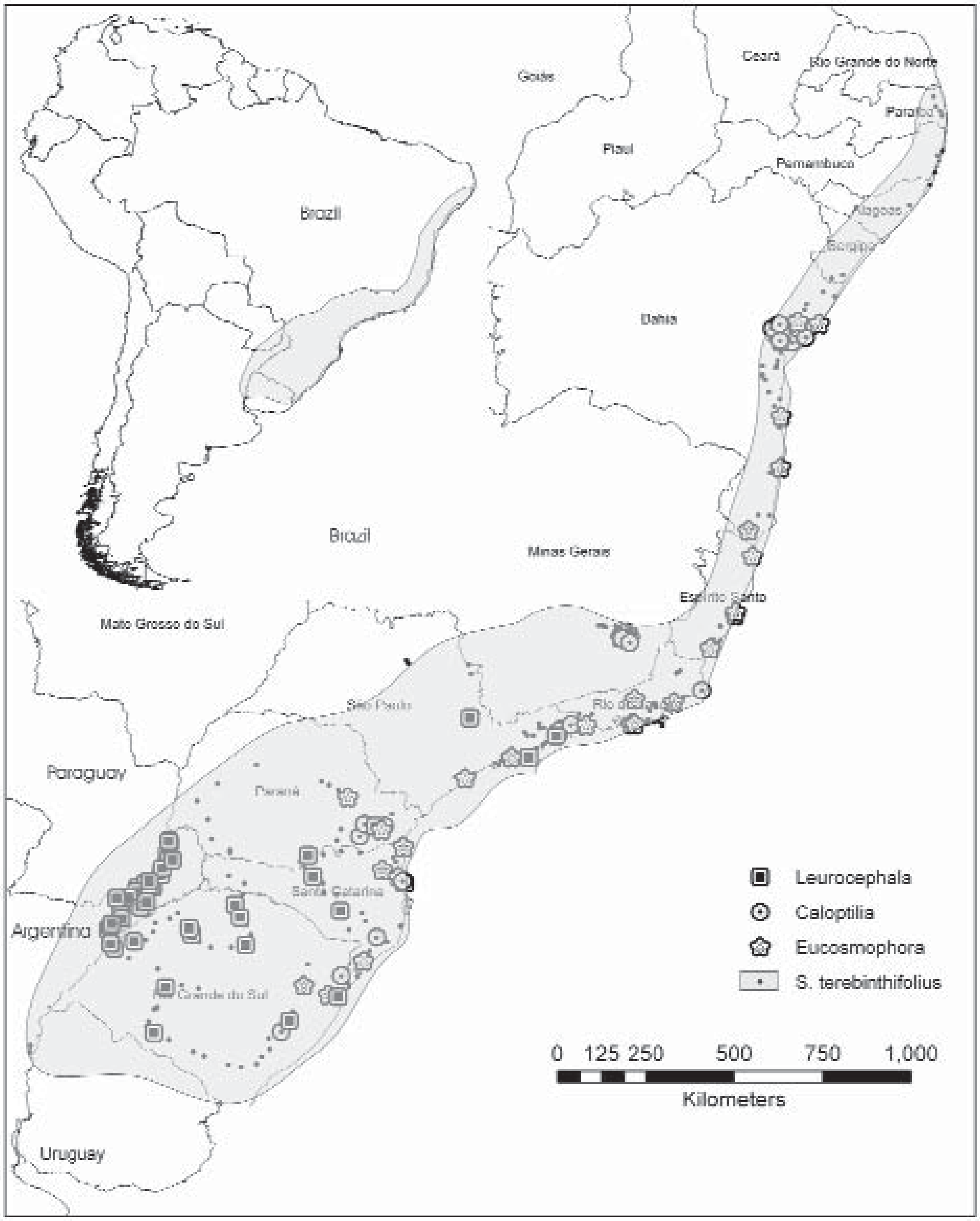


FIG. 1. Distribution of the host *Schinus terebinthifolius* in South America and its gracillariid leafminers: *Caloptilia schinusifolia*, *Eucosmophora schinusivora*, and *Leurocephala schinusae*.

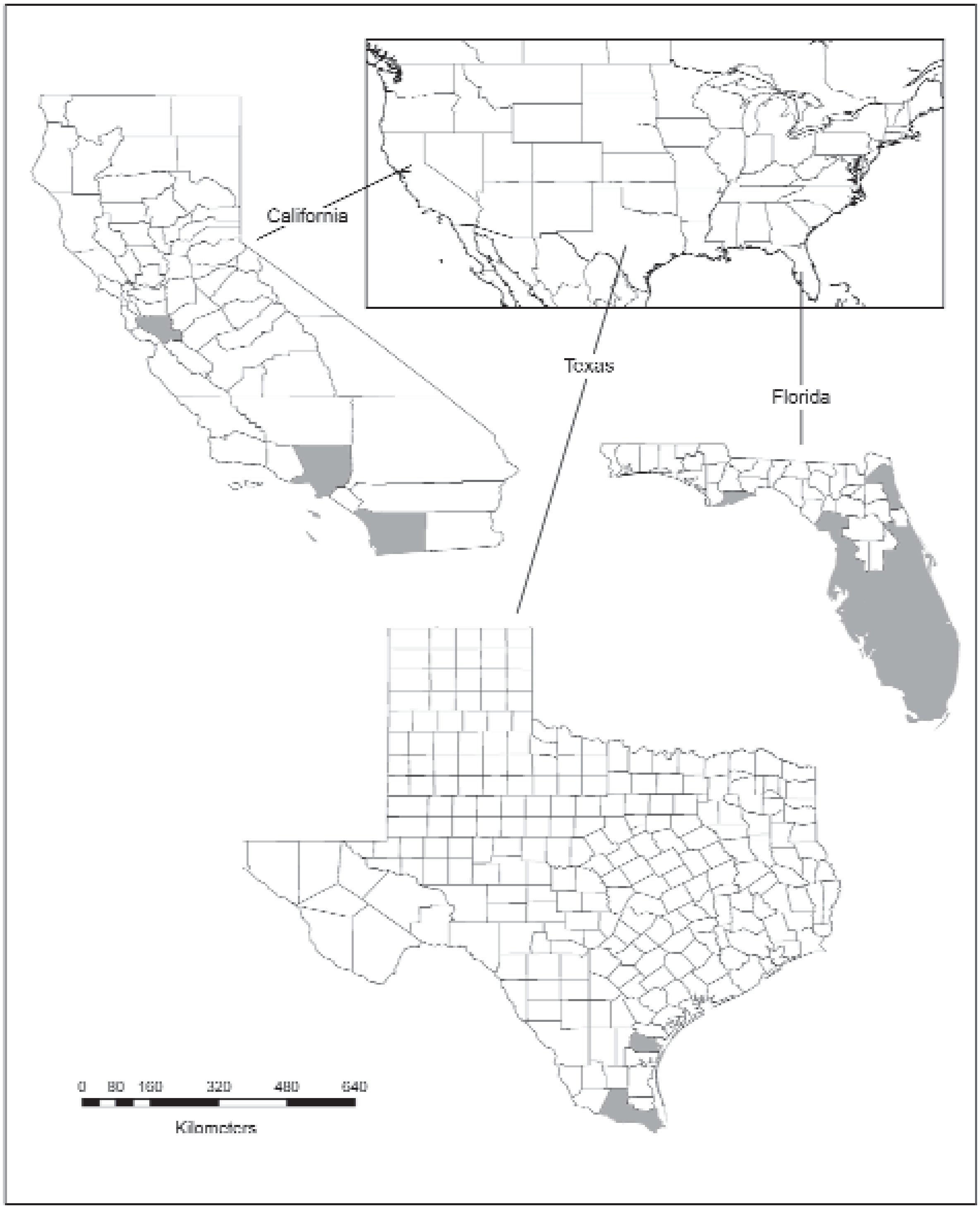


FIG. 2. Distribution of *Schinus terebinthifolius* in the United States showing counties (shaded) where it has been collected (from Wunderlin & Hansen 2008).

its exotic range, especially in Florida, the tree decreases the biodiversity of infested natural areas by aggressively invading a variety of coastal and upland habitats (Mytinger & Williamson 1987; Gann et al. 2001). Currently, in the USA, *S. terebinthifolius* is considered an invasive species in Florida, California, Texas, Hawaii, Puerto Rico and the Virgin Islands (Randall 2000; HSASC 2001; FLEPPC 2009; USDA-NRCS 2009). In Florida, where infestations of *S. terebinthifolius* are estimated to occupy over 283,400 ha (Wunderlin & Hansen 2008; Fig. 2), the species is a prohibited plant and a noxious weed. *Schinus terebinthifolius* constitutes not only a threat to natural areas but also to agriculture and cattle production (Morton 1978; Ewel 1986; Yoshioka & Markin 1991). Allelopathic compounds are known to be produced that suppress the growth of neighboring plant species (Gogue et al. 1974; Morgan & Overholt 2005). *Schinus terebinthifolius* is also suspected of causing allergic reactions and respiratory illnesses in sensitive humans from volatiles released by the leaves, flowers, and fruit (Morton 1978). Conservation organizations consider *S. terebinthifolius* a high-priority target due to its already widespread occurrence and great potential to expand its range (Randall 1993).

Biological control of *S. terebinthifolius* began in the 1950s and resulted in the release in Hawaii of three insect species: a gall-forming caterpillar, *Crasimorpha infuscata* Hodges (Lepidoptera: Gelechiidae), a defoliating caterpillar, *Episimus utilis* Zimmerman (Lepidoptera: Tortricidae), and a seed-feeding beetle, *Lithraeus atronotatus* (Pic) (Coleoptera: Bruchidae) (Davis & Krauss 1962; Krauss 1962, 1963; Hight et al. 2002). Only the last two species established in Hawaii, but are exerting negligible control of the weed population (Hight et al. 2002). A previously unidentified species of *Caloptilia*, herein confirmed to be *C. coruscans* Wlsm., was introduced into the island of Hawaii in 1991 (Markin 2001) to control the invasive Firetree, *Morella* (=*Myrica*) *faya* (Aiton). By 1994 the moth had become established in Hawaii Volcanoes National Park and adjacent areas. It is not known if this *Caloptilia* is also feeding on *Schinus* in Hawaii.

In Florida, exploration for biological control agents of *S. terebinthifolius* occurred in the 1980s and 1990s. These studies, mostly literature reviews of Brazilian work, listed at least 200 species of insects associated with the plant in its native range (d'Arújo et al. 1968; Bennett et al. 1990; Bennett & Habeck 1991). Included in these studies were the reports by Krauss (1962, 1963) wherein he listed a species of "*Gracillaria*" (= *Caloptilia*) mining leaves of *S. terebinthifolius* in Salvador and Bahia and a species of *Parornix* mining leaves in Sao Paulo. Three insects were selected for further studies in Florida: the leaf-feeding sawfly *Heteroperreyia hubrichi* Malaise (Hymenoptera: Pergidae), the sap-feeding thrips *Pseudophilothrips ichini* Hood (Thysanoptera: Phlaeothripidae), and the defoliating caterpillar *E. unguiculus* (= *utilis*) (Medal et al. 1999; Hight et al. 2002; Martin et al. 2004).

To date, none of these biological control candidates has been released in Florida. However, the continuous spread of *S. terebinthifolius* motivated the search for additional natural enemies against this weed in northern Argentina, an area that had not been surveyed and the most likely center of origin of the genus *Schinus* (Barkley 1944; Muñoz 2000). The results of these surveys indicate that Argentine *S. terebinthifolius* populations harbored natural enemies not previously reported (Mc Kay et al. 2009). Among these, several blotch leaf miners (Lepidoptera: Gracillariidae) were selected for further studies.

Four species of Gracillariidae belonging to four separate genera, all reared from *S. terebinthifolius*, are described in this report: *Caloptilia schinusifolia* Davis and Wheeler, new species, from Brazil; *Eucosmophora schinusivora* Davis and Wheeler, new species, from Argentina and Brazil; *Leurocephala schinus*ae Davis and Mc Kay, new genus and species, from Argentina and Brazil; and *Marmara habecki* Davis, new species, from Florida, USA. Unique specimens representing an additional three species of Gracillariinae have also been collected from *S. terebinthifolius* in Brazil, but these could not be identified because of their poor physical condition. Interestingly, one of these is a stem mining *Marmara* closely related to *Marmara habecki*, currently known only from southern Florida, USA. As discussed under the latter species in this report, sequence divergence of their CO1 barcode region of nearly 12% indicates that these two *Marmara* represent distinct species.

METHODS AND MATERIALS

Genitalic dissections were cleared by heating in hot 10% KOH for ~ 30 minutes, and subsequently cleaned and stained with either 2% chlorazol black E or mercurochrome solutions. All genitalic illustrations were drawn from dissections temporarily stored in glycerin, which were later permanently embedded in Canada balsam. Genitalic terminology follows Klots (1970). Samples of alcohol-preserved larvae and pupae were gently washed in 409® detergent, then dried in a critical point drier, sputter coated with 20–25 gold palladium 60:40 alloy, and photographed with an Amray 1810 scanning electron microscope.

Field Collections. Argentina. Field collections of these leaf mining insects were part of larger biological control surveys searching for arthropods and diseases associated with *S. terebinthifolius* in its native range. Collections began in 2004 and continued through 2009 and were conducted throughout the Argentina range of the host in Misiones, Corrientes, and Entre Rios provinces (Fig. 1). These surveys were conducted 4–6 times per year.

Field Collections. Brazil. In Brazil surveys began in 2005 and continued through February 2010. The host plant is reported to occur (JBRJ 2009; NYBG 2009; Tropicos 2009) mostly along the Atlantic coast from Recife, Pernambuco (S 8.05°) south to Bagé, Rio Grande do Sul (S 31.33°), then west to northeastern Argentina and eastern Paraguay. Our surveys ranged from Natal, Rio Grande do Norte (S 5.79°), to Pelotas, Rio Grande do Sul (S 31.76°) at the northern and the southern extremes of the host plant range, respectively (Fig. 1). Additionally, these surveys extended west from the coast until the host plants disappeared. In Bahia this occurred near Feira de Santana and in Minas Gerais this species ranged west to Belo Horizonte then south to western Rio Grande do Sul. These surveys were conducted 2–3 times each year, generally lasted 14 days, and usually included three collectors (e.g., GSW, FM, and MDV). All three leaf blotch miner species *L. schinusae*, *E. schinusivora*, and *C. schinusifolia* were common, and were discovered in this Brazilian range during the first year of the project (2005). Insect collections during all trips were conducted under the IBAMA export licenses: 07BR001027/DF; 08BR002120/DF; 09BR003939/DF; 10BR004731/DF.

Results

Field Collections. Field surveys conducted in Argentina (Mc Kay et al. 2009) and Brazil indicate that *L. schinusae*, *E. schinusivora* and *C. schinusifolia* were almost always collected on *S. terebinthifolius*. Larvae of *Leurocephala schinus*ae (on leaves of *S. terebinthifolius*) and *Eucosmophora schinusivora* (on leaves of *Lithrea molleoides*) were first discovered in Argentina in 2004 and 2008, respectively. Leaf mines similar to those of *L. schinusae* also have been found on *S. weinmannifolius*, *S. lentiscifolius*, *S. fasciculatus*, and *Astronium balansae*, but adults have not been reared. Likewise, mines similar to *E. schinusivora* were found on *S. weinmannifolius* and *Astronium balansae*, but no adults were reared. *Caloptilia schinusifolia* has not been reared in Argentina, although leaves with folded tips have been observed there, as also noted below.

Although data were not collected on insect densities, the species *L. schinusae* was seasonally abundant in northeastern Argentina and southern Brazil during the austral winter and spring from June to November; this species was difficult to find during the remainder of the year. No seasonality was noticed for *E. schinusivora* or *C. schinusifolia*.

Distribution. Leaflets of *S. terebinthifolius* infested with blotch mines of *L. schinusae* were found at several sites in the northeastern provinces of Argentina (Corrientes and Misiones; Fig. 1). In Brazil this species was collected from sites as far north as near Salvador, BA (S 12.33°) south to Santana Do Livramento, Rio Grande do Sul (S 30.85°). *Eucosmophora schinusivora* generally had a more northern distribution and was collected near Salvador, Bahia (S 12.32°) south to near Porto Alegre, Rio Grande do Sul (S 29.88°). In Argentina this species was only found near Santa Ana, Misiones Province on *L. molleoides*, its other known natural host. *Caloptilia schinusifolia* had a similar broad range from near Salvador, Bahia (S 12.35°) south to near Porto Alegre, Rio Grande do Sul (S 30.83°). *Caloptilia* mine damage with folded leaf tips were also found on *Lithrea molleoides*, *Schinus weinmannifolius*, and *S. lentiscifolius* in Argentina, but no adults were reared for species confirmation.

Natural enemies. Several parasitoids emerged from *Leurocephala schinus*ae blotch mines in Argentina from species assigned to Orgilinae (Braconidae) and Brachycyrtinae (Ichneumonidae) and *Isdromas* spp. (Cryptinae: Phygadeuontini). In Brazil parasitism of *L. schinusae* occurred from *Lymeon* sp. (Ichneumonidae: Cryptinae), *Acrolyta* n. sp., *Isdromas* (3 species), and *Pimpla croceiventris* (Cresson) (Ichneumonidae: Pimplinae). Parasitoids belonging to Braconidae included three species of *Orgilus* (Orgilinae), *Pholeteser* sp. (Microgastrinae) and several Chalcidoidea (undetermined species). Parasitism by these Ichneumonidæ and Braconidae species reached its highest level (40%) during a collection in July 2008.

DNA Sequencing. Unidentified species of Braconidae and Ichneumonidae and Chalcidoidea have been recovered in Brazil from larval rearings of *Caloptilia schinusifolia* and *Eucosmophora schinusivora* respectively. In Florida a single parasitoid of Chalcidoidea emerged from the pupa of *Marmara habecki*. Sequences were produced at the Biodiversity Institute of Ontario, University of Guelph, Canada. DNA was extracted from legs, entire bodies of adult moths, or entire larvae using a QIAGEN DNeasy Tissue Kit. Primers LepF1 and LepR1 (Herbert et al. 2004) were used to obtain a 658 base pair fragment of

CO1 with a standard thermocycling regime (Hajibabaei et al. 2006). Sequences are available at the National Center for Biotechnology Information GenBank database and at the Barcode of Life Database (BOLD). Neighbor-joining (NJ) trees were generated from nucleotide sequences as implemented in BOLD (Ratnasingham & Hebert 2007). Phylogenetic and molecular evolutionary analyses were conducted using Molecular Evolutionary Genetics Analysis (MEGA) version 4 (Tamura et al. 2007).

The acronyms used in this study for institutions in which specimens are deposited are as follows:

BMNH The Natural History Museum (formerly the British Museum (Natural History)), London, United Kingdom.
HAD Hawaii Department of Agriculture, Honolulu, HI, USA
MACN Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.
MGCL McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, FL., USA.
UPZB Federal University of Paraná, Department of Zoology, Curitiba, Paraná, Brazil
USNM Collections of the former United States National Museum, now deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Species summaries

Caloptilia schinusifolia Davis and Wheeler, new species

Figs. 1, 3, 9–10, 22–25.

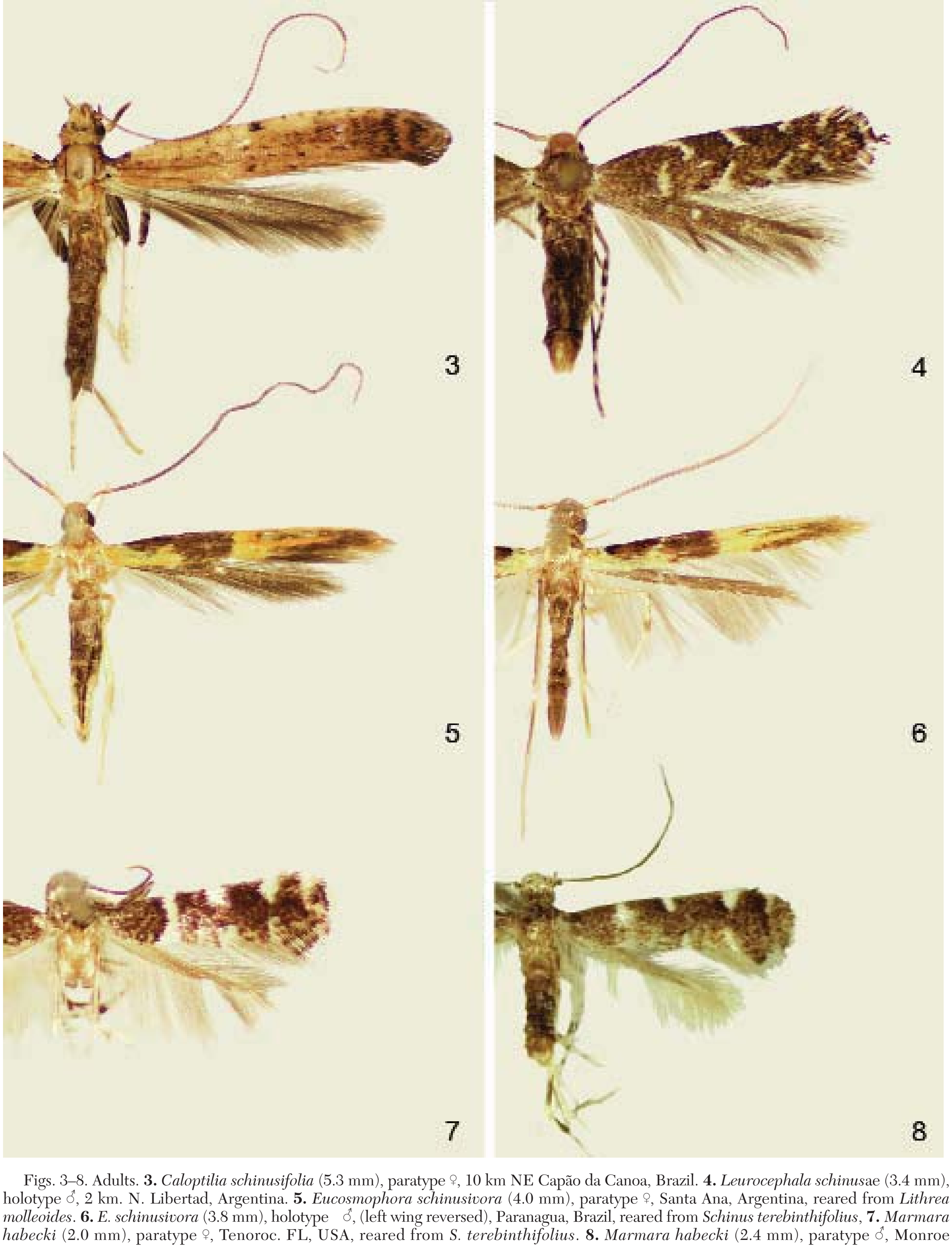
Diagnosis. *Caloptilia schinusifolia* differs from the only other two congeneric species known to feed on *Schinus* in distribution, wing pattern and male genitalic characters. The forewing of *Caloptilia schinusifolia* is predominantly medium brown with small patches of fuscous scales sparsely scattered over most of the forewing and along the costa, and generally possesses a less iridescent wing color than that of *C. coruscans* (Wlsm.). The forewing of *C. rhoifoliella* (Cham.) is a much darker brown to fuscous, with usually a slender suffusion of white along the costal margin which is lacking in the other two species. The basal half of the male valva of *schinusifolia* is more slender (< half the maximum width across the cucullus) than in either *rhoifoliella* or *coruscans* (~ equal in width), and the vinculum of *schinusifolia* is proportionately longer and more slender (< 0.7 the length of valve in the other two species). *Caloptilia coruscans* occurs widely through the southern Palearctic region (De Prins & De Prins, 2010) and Hawaii. *Caloptilia rhoifoliella* is known only from North America and Bermuda.

Description. Adult (Fig.3). *Head*: Frons smooth, shiny light brown to bronze, with a lateral pair of partially raised tufts of dark brown to fuscous scales arising from rim of eye below antenna and directed medially; scales of tufts sometimes tipped with paler brown; vertex smooth, light brown to nearly white; occipital tufts prominent, light brown. Antenna with a single row of slender scales encircling each flagellomere; scales mostly dark brown, with bases lighter brown; scape dark brown, usually paler ventrally. Maxillary palpus mostly fuscous laterally, cream to light brown mesally and dorsally on segment II. Labial palpus smooth, mostly whitish cream to light brown over segments I and II, becoming fuscous near apex of II and most of III; extreme apex and a portion of mesal surface of III cream to light brown. *Thorax:* Mostly dark brown dorsally, sharply light cream ventrally; tegula dark brown becoming fuscous anteriorly. Forewing: length 5.0–5.5mm; mostly brown with a small basal patch of fuscous to black of costal scales adjoining tegula; small patches of fuscous scales sparsely scattered over most of forewing and along costa, becoming more concentrated near apex where they form a pair of fuscous transverse bands narrowly separated by brown; a moderately large, fuscous scale patch midway along costa; fringe around apex and along hind margin uniformly dark gray. Hindwing uniformly dark gray. Foreleg with coxa mostly whitish cream with suffusion of brown laterally and fuscous at apex; femora and tibiae of all legs fuscous faintly banded with cream to light brown; tarsomeres white on fore and midlegs, more cream on hindleg, and faintly tipped with fuscous on all legs. *Abdomen:* Sharply demarcated from dark fuscous dorsally to mostly cream ventrally with a few fuscous scales scattered ventrally. Male with 2 pairs of coremata of ~ equal lengths present on segments VII and VIII; caudal margin of tergum VII with a slender, rounded lobe; tergum VIII T-shaped, very slender, abruptly expanded caudally.

Male genitalia (Figs. 22, 23). Tegumen weakly sclerotized; attenuate caudally. Vinculum-saccus relatively long and slender, equaling tegumen in length. Valva simple, lacking ridges or processes, with costal and hind margins evenly curved, gradually widening to smoothly rounded cucullus; maximum width of cucullus nearly 2× that of base of valve. Aedeagus a slender tube ~ 1.3× length of vinculum-saccus, with a slender spinose process projecting from one edge of apex; cornuti consisting of an elongate, tightly and obliquely compressed row of ~ 9–11 slender spines in distal half of aedeagus; phallobase narrowly inflated, ~ 1.25× length of aedeagus.

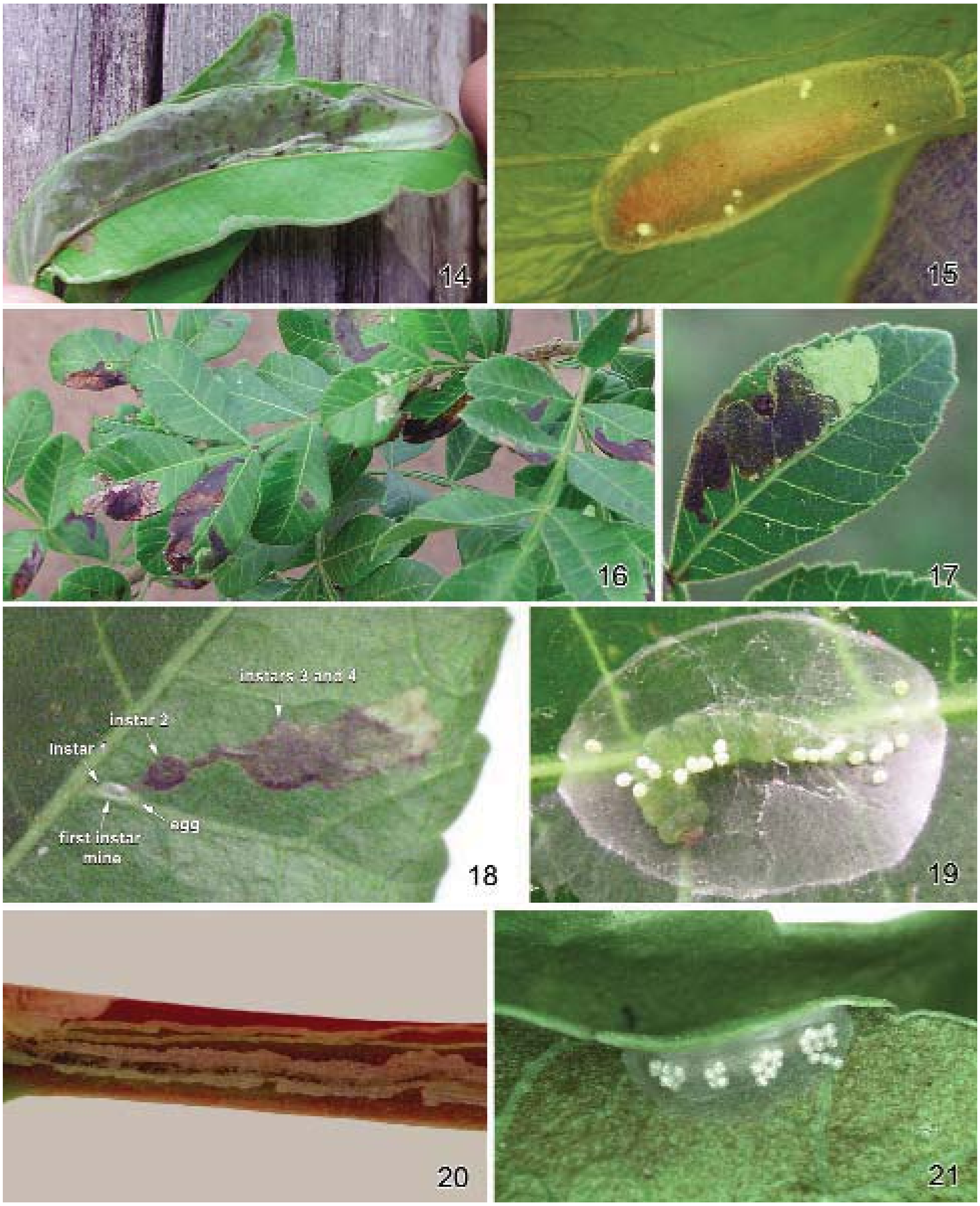
Female genitalia (Figs. 24, 25). Anterior and posterior apophyses ~ equal in length, with similar broad bases. Ostium broad, width ~ 2/3 the length of anterior apophysis; antrum moderately enlarged, narrowing to junction with ductus seminalis; length of antrum to junction ~ equal to length of anterior apophysis. Ductus bursae extremely long, ~ 10× the length of anterior apophysis, narrow, membranous, and abruptly enlarging at termination with corpus bursae. Corpus bursae oblong-elliptical, with finely wrinkled, membranous walls; length ~ 3.25× length of anterior apophysis; signa a symmetrical pair of slender spines ~ equal to anterior apophysis in length, each with a truncate, spatulate, basal end which projects exteriorly beyond wall of corpus bursae.

Larval biology (Figs. 9–10). Early instars of *Caloptilia schinusifolia* form a serpentine mine that begins along the mid-vein and continues along the leaflet margin. Mid-sized larvae emerge from this mine and feed under a narrow fold of the leaflet edge. Late instars roll the tips of the leaflet and feed externally skeletonizing the lower surface of the leaflets. When

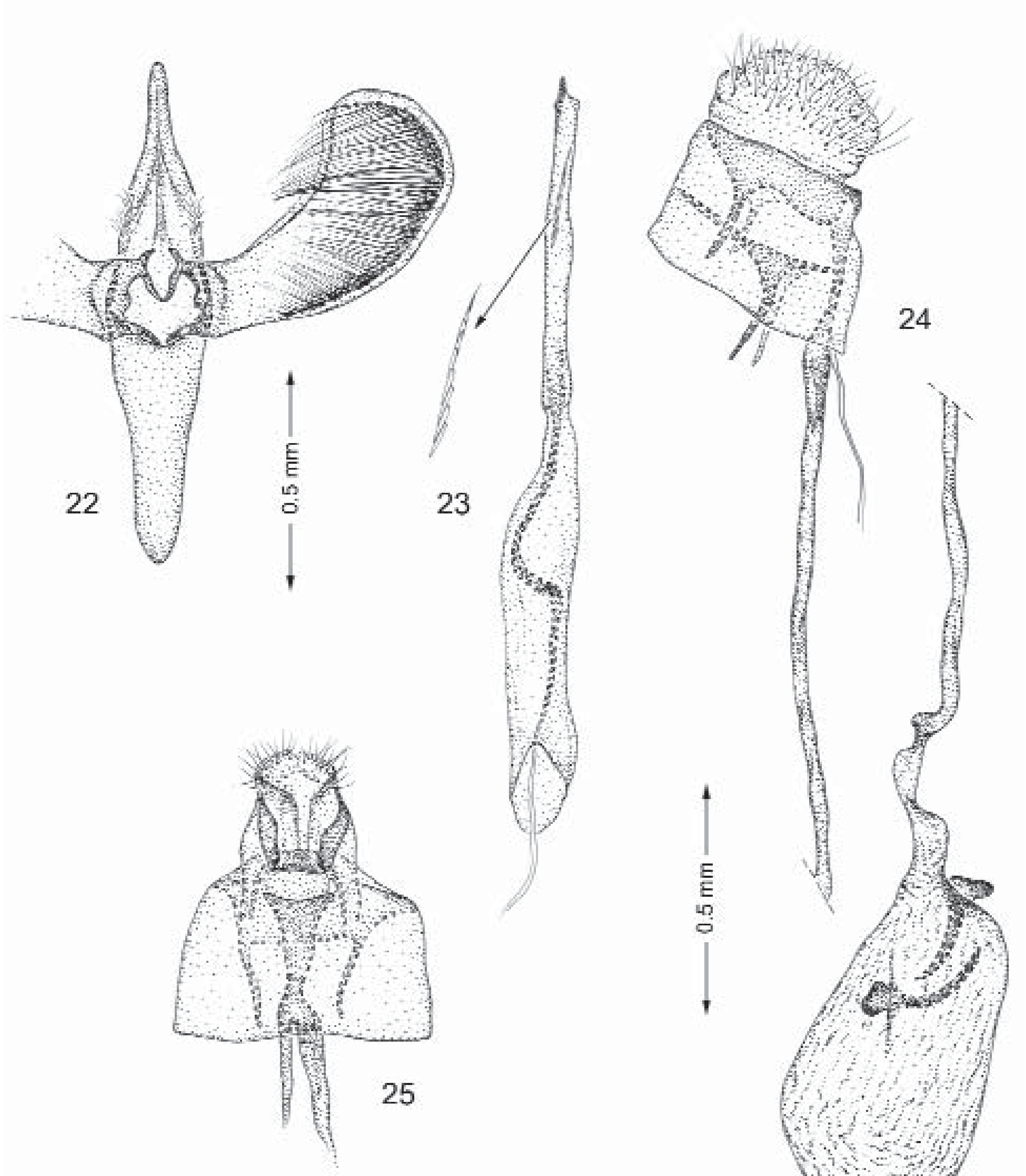


Figs. 3–8. Adults. **3.** *Caloptilia schinusifolia* (5.3 mm), paratype ♀, 10 km NE Capão da Canoa, Brazil. **4.** *Leurocephala schinus*ae (3.4 mm), holotype ♂, 2 km. N. Libertad, Argentina. **5.** *Eucosmophora schinusivora* (4.0 mm), paratype ♀, Santa Ana, Argentina, reared from *Lithrea molleoides*. **6.** *E. schinusivora* (3.8 mm), holotype ♂, (left wing reversed), Paranagua, Brazil, reared from *Schinus terebinthifolius*, **7.** *Marmara habecki* (2.0 mm), paratype ♀, Tenoroc. FL, USA, reared from *S. terebinthifolius*. **8.** *Marmara habecki* (2.4 mm), paratype ♂, Monroe Station, FL, USA, reared from *Schinus* sp. (Forewing length in parentheses).

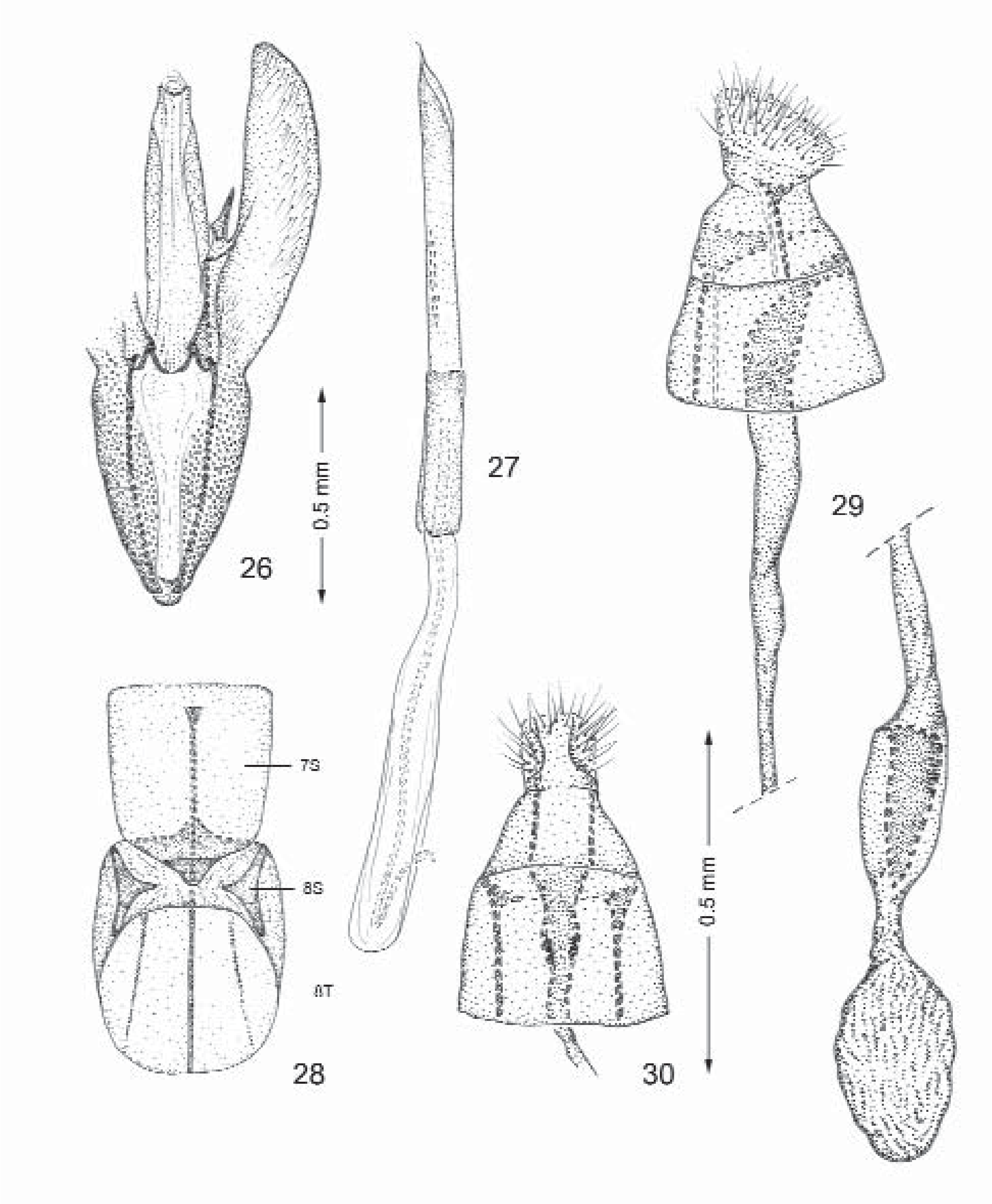
FIGS. 9–13. Larval host damage and cocoons. **9**. Leaf curling by late instar larvae of *Caloptilia schinusifolia* on *Lithrea brasiliensis*; Lapa, Paraná, Brazil. **10.** Leaf curling and cocoons (arrow) of *C. schinusifolia* on *Schinus terebinthifolius*; 1.6 km S of Caraguatatuba, Sao Paulo State, Brazil, Nov 6, 2009. **11**. Leaf mines of *Eucosmophora schinusivora* on *S.terebinthifolius*; Macaé, RJ, Brazil, July 2008. **12.** Leaf mines of *E. schinusivora* on *S. terebinthifolius*; Macaé, RJ, Brazil. **13.** Detail of leaf mine of *E. schinusivora* on *S. terebinthifolius*; Macaé, RJ, Brazil.



FIGS. 14–21. Larval damage and cocoons. **14.** Leaf mine of *Eucosmophora schinusivora* on *Lithrea molleoides*; Argentina. **15.** Cocoon of *E. schinusivora* with 7 exterior bubbles on *L. molleoides*; Argentina. **16.** Larval damage on *Schinus terebinthifolius* by *Leurocephala schinus*ae; near Libertad, Argentina, July 17, 2007. **17.** Leaf mine of *L. schinusae* on *S. terebinthifolius*; near Libertad, Argentina. **18.** Leaf mine of *L. schinusae* on *S. terebinthifolius* showing approximate location of sequential immature stages and collected head capsules; near Libertad, Argentina. **19.** Cocoon with last (5th) instar larva inside; note linear arrangement of bubbles. **20.** Stem mine of *Marmara habecki* on *S. terebinthifolius*; Ft Lauderdale, FL, USA. **21**. Cocoon of *M. habecki* on *S. terebinthifolius* with 4 groups of bubbles; Ft Lauderdale, FL, USA.



FIGS. 22–25. *Caloptilia schinusifolia*, genitalia. **22.** Male, ventral view. **23.** Aedeagus. **24.** Female, lateral view. **25.** Female, ventral view. (Scale lengths indicated).



FIGS. 26–30. *Eucosmophora schinusivora*, genitalia and postabdomen. **26.** Male, ventral view. **27.** Aedeagus. **28.** Male postabdominal segments 7–8, ventral view. **29.** Female, lateral view. **30.** Female, ventral view. (Scale lengths as indicated).

development is complete, larvae emerge from the rolled leaflet and pupate on the lower side of the leaf in a prepared short crevice covered with silk. No bubbles were attached to the pupal cocoon.

Hosts. Anacardiaceae: *Schinus terebinthifolius* Raddi and *Lithrea molleoides* (Vell.) Engl. Mines similar to *C. schinusifolia* were also found on *Schinus lentiscifolius* March. and *Schinus weinmannifolius* Engl., but no adults were reared.

Parasitoids. Unidentified species of Braconidae (Cheloninae possibly *Phanerotoma* sp.) and Chalcidoidea have been recovered from larval rearings of *C. schinusifolia*.

Types. Holotype - ♂; BRAZIL: Rio de Janeiro: Maricá, S22.90270, W42.82358, 7 m: 15 Jul 2008, S22.90270, W42.82358 RJ 44, Wheeler & Mc Kay, emerged from [leaf tip fold] on leaves of *S. terebinthifolius*, (UPZB). Paratypes (7♂, 5♀) - BRAZIL: Bahia: 11 km NE Salvador, S12.96176, W38.40338, 2 m: 1♂, 1♀, 2 Apr 2008, Wheeler, perimeter leaf miner, BAH37, ♀ slide USNM 34031. Paraná: Paranagua, Rio Guaraguacu: Sambaqui: 19 Oct 1992, 1♂, adult 30 Oct 1992, slide USNM 34152; 2♂, adult 31 Oct 1992; 1♀, pupa 27 Oct 1992, adult 2 Nov 1992; Host: *Schinus terebinthifolius*, F.D. Bennett, J.H. Pedrosa Macedo, C. Wickler, M.D. Vitorino, ♀ slide USNM 33920. Paraná: 36 mi W. Curitiba, S25.47520; W49.60064: 1♂, 3 Feb 2009, ARO5, Wheeler & Mc Kay, tip folding leaves *S. terebinthifolius*. Rio Grande do Sul: 10 km NE Capão da: Canoa, S29.68000, W49.99180: 1♂, 2♀, 11 Feb 2009, RS52, Wheeler & Mc Kay. Santa Catarina: 20 mi. E. Canomhas, S26.18269, W50.20403: 1♂, 13 Feb 2009, SC33, Wheeler & McKay, tip folding leaves *S. terebinthifolius*, slide USNM 34097. (Paratypes deposited in MGCL, UPZB, USNM.)

Flight period. Adults have been collected in February, April, July, and October.

Distribution (Fig. 1). This species has been collected from mostly coastal areas from Bahia Province, Brazil south to Rio Grande do Sul. It has also been observed in Misiones Province (northeastern Argentina).

Etymology. The species name is derived from the generic name of the plant host (*Schinus*) and the Latin *folium* (leaf).

Discussion. At least two species of *Caloptilia* have been reported previously as mining the leaves of *Schinus*: *Caloptilia coruscans* Wlsm. (= *C. schinella* Wlsm.) and C. *rhoifoliella* (Cham.) (Robinson, et al. 2007; De Prins & De Prins 2010). *Caloptilia coruscans* occurs from southern Europe to North Africa and on several associated Atlantic islands (e.g., Azores, Canary Islands), where it has been reared from three genera of Anacardiaceae (including *Schinus molle* L.) and *Morella faya* (Aiton) of the Myricaceae. Several names are now considered synonyms of *C. coruscans*, including *C. schinella* (Wlsm.), *C. terebinthiella* Chrétien, *C. instincta* Meyr., and *C. ferruginipennis* Turati, (Triberti 1985; De Prins & De Prins 2010). *Caloptilia rhoifoliella* occurs across much of the United States where it mines the leaves of *Rhus* and *Toxicodendron*, and in Bermuda where it has been reported feeding on *Schinus terebinthifolius* (Ferguson et al. 1991; Robinson et al. 2007).

Caloptilia schinusifolia differs from both of the foregoing species in wing pattern and male genital characters. The forewing of *schinusifolia* is predominantly medium brown with a less iridescent color than that of *coruscans*, as described and figured by Walsingham (1908). The forewing of *rhoifoliella* is generally much darker brown to fuscous, with usually a slender suffusion of white along the costal margin which is lacking in the other two species. The basal half of the male valvae of *schinusifolia* is more slender (< half the maximum width across the cucullus) than in either *rhoifoliella* or *coruscans* (~ equal in width), and the vinculum of *schinusifolia* is proportionately longer and more slender (< 0.7 the length of valve in latter two species). The male genitalia from the type series of *C. coruscans* has not been figured, but that of the junior synonym, *C. schinella*, was illustrated by Klimesch (1970).

Only one other species of *Caloptilia*, *C. pastranai* Bourquin, has been reported from southern South America within the maximum range of either *Schinus terebinthifolius* or *Lithrea molleoides*. *Caloptilia aeolastis* (Meyrick), *C. hexameris* (Meyrick), *C. pneumatica* (Meyrick), and *C. semiclausa* (Meyrick) were described from Brazil, but are known to occur only along the Amazon River well north of the range of *Caloptilia schinusifolia*, and none of the foregoing *Caloptilia* are similar to *C. schinusifolia* in forewing pattern. *Caloptilia pastranai* is known to feed only on *Scutia buxifolia* Reiss (Rhamnaceae) in Buenos Aires Province, Argentina. The body and forewings of this species are considerably darker than that of *C. schinusifolia*.

A previously unidentified species of *Caloptilia*, "*Caloptilia* species, near *schinella* Walsingham", was introduced into the island of Hawaii in 1991 (Markin 2001) to control the invasive Firetree, *Morella* (=*Myrica*) *faya* (Aiton). By 1994 the moth had become established in Hawaii Volcanoes National Park and adjacent areas. Specimens of this introduced species originating from a laboratory colony imported from the Azores Islands, Portugal were borrowed for examination by DRD from the Hawaii Department of Agriculture. This examination confirmed that the Hawaiian species (originating from the Azores) agreed with *C. coruscans* and was distinct from *C. schinusifolia*. The Azores specimens also agreed in wing pattern and male genitalia with specimens in the collections of the USNM, which had been collected in the Canary and Medeira Islands and reared from *Schinus* molle L. and *Myrica faya*. Currently no rearings of *Caloptilia* have been reported from *Schinus terebinthifolius* in Hawaii.

Eucosmophora schinusivora Davis and Wheeler, new species

Figs. 1, 5–6, 11–15, 26–30.

Diagnosis. *Eucosmophora schinusivora* is the only species of *Eucosmophora* known to feed on a member of the Anacardiaceae. The male genitalia of *Eucosmophora schinusivora* agree with those of the *sideroxylonella* species group (Davis & Wagner 2005) in possessing a costal lobe on the male valve, and with the *dives* species group in the absence of scale tufts on the seventh sternite. The female genitalia of *E. schinusivora* differ from those of both groups in lacking signa and in possessing an enlarged, pocket-like sclerotization within the ductus bursae (Fig. 29). The forewing pattern of *schinusivora* is also unique in possessing a pair of dark fuscous, longitudinal fascia that converge before the apex of the wing (Figs. 5–6).

Description. Adult (Figs. 5–6). *Head:* Frons smooth, pale gold, gradually becoming gray to shiny black over vertex to occiput; collar a narrow band of pale golden white. Antenna slightly exceeding length of forewing; scape smooth, elongate, ~ equal to width of frons, pale gold to light orange; apex of scape with a distinct dorsal tuft of pale golden scales, slightly suffused with fuscous at apex along posterior margin; base of antenna bent slightly ventrad at pedicel; pedicel and basal 2–3 flagellomeres sometimes with light orange luster; remainder or usually all of flagellum lustrous dark gray; each flagellomere completely encircled by a single, dense row of slender scales. Maxillary palpus smooth, pale gold, sometimes with a slight orange luster. Labial palpus smooth, similar to frons and maxillary palpi in color. *Thorax:* Dorsum light orange; light orange beneath wing and tegula but mostly silver to gold ventrally; tegula shiny black. Forewing: length 3.5–4.2mm; ~ equally covered by light orange and dark fuscous to black scales as follow: basal half of forewing dark fuscous along costa, extending completely across wing just before middle; basal third of hind margin light orange with a sinuate medial edge separated from dark fuscous costal margin by an oblique patch of silvery scales; apical half of wing mostly orange except for a pair of elongate, shiny, dark fuscous fascia along the subcostal area and hind margin that converge before entirely fuscous apex; fringe around apex pale gray becoming fuscous toward hind margin. Hindwing uniformly dark fuscous. Fore and midlegs mostly pale golden cream with fuscous banding on dorsum of tibia; hindleg mostly pale golden cream; fuscous laterally on femur, tibia and first tarsomere. Abdomen (Fig. 28): Fuscous to black dorsally and laterally on A3–5; golden cream ventrally. Sternum 7 of male abruptly narrowing caudally to broadly triangular, rounded apex without setal brush. Eighth sternites consisting of a small pair of widely divided, triangular sclerites ~ 0.4 × the length of main body of tergum 8. Tergum 8 with slender median rod extending nearly to anterior margin of sternum 7; anterior apex of rod slightly enlarged.

Male genitalia (Figs. 26–27). Valva slender with mostly straight costal margin and evenly curved saccular margin, gradually narrowing to a rounded apex; a small, acute process arising from basal third of costa. Aedeagus a slender, nearly smooth, elongate cylinder; a series of ~ 20 minute spines arranged subdorsally near middle in 2 irregular rows; apex of aedeagus asymmetrical, with a relatively large, acute, terminal process from dorsal side.

Female genitalia (Figs. 29–30). Antrum mostly membranous. Ductus bursae elongate; walls covered internally with minute, circular spicules, gradually becoming larger and more dense around sclerotized, U-shaped internal pocket just before enlargement of corpus bursae; walls of corpus bursae membranous; signum absent.

Larval biology (Figs. 11–15). The eggs are oval shaped, nearly transparent, milky-white. Eggs are deposited generally on the upper leaf surface adjacent to a secondary vein. After hatching, the first instar forms a broad leaf blotch. In high densities 3–5 larvae may form blotches on the same leaflet that merge to form a single large blotch which covers most of the leaflet. Leaf damage seems to induce premature leaf drop in the field.

Cocoon (Fig. 15). Pupae are covered with silk, located on leaves on the ground, and are usually on the lower leaf surface. The silk is covered with frothy bubbles, generally six in number, bright white, and arranged around the perimeter of the cocoon. Pupation occurs usually in a constructed leaf groove or occasionally under a folded leaf edge.

Hosts. Anacardiaceae: *Schinus terebinthifolius* Raddi and *Lithrea molleoides* (Vell.) Engl. Mines similar to that of *Eucosmophora schinusivora* were also found on *Schinus longifolius* (Lindl.) Speg., *Schinus weinmannifolius* Engl. and *Astronium balansae* Engl., but no adults were reared.

Parasitoids. Unidentified parasitoids of Ichneumonidae and Chalcidoidea have been reared from this species collected in Brazil.

Types. *Holotype*: ♂- BRAZIL: Paraná: Paranagua, Rio Guaraguacu, , Sambaqui, 19 Oct 1992, adult 13 Nov 1992, Host: *Schinus terebinthifolius*, F.D. Bennett, J.H. Pedrosa Macedo, C. Wickler, M.D. Vitorino, digital image captured USNM, (MACN). Paratypes (21 ♂, 15 ♀) : ARGENTINA: Misiones Prov: Santa Ana: 4 ♂, 3 ♀, 4 Apr 2008, leaf mining larva feeding on *Lithrea molleoides*, Mc Kay & Oleiro, slides USNM 33966♂, 33967, 34032♀. BRAZIL: Paraná: Same data as holotype: 1 ♂, 19 Oct 1992; 1 ♂, adult 29 Oct 1992; 1 ♂, adult 29 Oct 1992; 1 ♂, adult 7 Nov 1992; 1 ♂, adult 8 Nov 1992; 2 ♂, 9 Nov 1992; 1 ♀, pupa 27 Oct 1992, adult 10 Nov 1992, slide USNM 33917; 1 ♂, adult 12 Nov 1992, slide USNM 33918. Rio de Janeiro: 41 km SE Campos: 1 ♂, 1 ♀, 9 Apr 2008, Wheeler. coll. As larvae, globules random on silk. Rio Grande do Sul: 5 km N N. Hamburgo: 1 ♀, 9 Apr 2008, Wheeler & Mc Kay, RS1, emerged from leafmines on *Schinus terebinthifolius*; Lagoa Itapeva: 1 ♂, 9 Jul 2008, Wheeler & Mc Kay, RS5, emerged from leafmines on *Schinus terebinthifolius*, slide USNM 34025♂. Santa Catarina: 5 km S. Itajai, S26.92026 W48.64137: 3 ♂, 2 ♀, 8 Feb 2010, Wheeler & Mc Kay, SC40, reared from leaves of *Schinus terebinthifolius*. 11 km N Sombrio: 2 ♀, 10 Jul 2008, Wheeler & Mc Kay, SC4, reared from leafmines on *Schinus terebinthifolius*, 2 ♂, 4 ♀, 11 Feb 2009, Wheeler & Mc Kay, SC4, reared from leafmines on *Schinus terebinthifolius* (Paratypes deposited in MACN, MGCL, UPZB, and USNM).

Flight period. Adult emergences have been reported in February, April, July, October, and November.

Distribution (Fig. 1). This species has been collected in Misiones Province (northeastern Argentina). In Brazil, this species has been commonly collected from Salvador, Bahia, south to Porto Alegre, Rio Grande do Sul.

Etymology. The species name is derived from the generic name of the plant host (*Schinus*) and the Latin *voro* (eat, devour).

Discussion. The Neotropical genus *Eucosmophora* was revised recently by Davis & Wagner (2005), and generic diagnoses of the larval, pupal, and adult stages are provided in that study. *Eucosmophora* was found to consist of two morphologically distinct groups, each possibly restricted to feeding on a single plant family. The Fabaceae- mining *dives* group containing possibly 5 species, was partially characterized by males lacking a costal lobe on the valva, seventh abdominal sternite without caudal scale tufts, and females bearing a pair of spinulose signa in the corpus bursae. The *sideroxylonella* group included 11 species, 3 of which are known to be leafminers on Sapotaceae. The males of this group possess a small costal lobe on the valva similar to *E. schinusivora* (Fig. 26), as well as a caudal scale tuft on the seventh abdominal sternite; the paired signa of the females are long, often laciniate, and prominently serrate to spinose. Males of *Eucosmophora schinusivora* agree with those of the *sideroxylonella* group in possessing the costal lobe on the male valve, and with the *dives* group in the absence of scale tufts on the seventh sternite. The female genitalia of *E. schinusivora* differ from those of both groups in lacking signa and in possessing an enlarged, pocket-like sclerotization within the ductus bursae (Fig. 29). The forewing pattern of *schinusivora* is also unique in possessing a pair of dark fuscous, longitudinal fascia that converge before the apex of the wing (Figs. 5–6). It is also notable that no *Eucosmophora* had been reared previously from Anacardiaceae.

Leurocephala Davis and Mc Kay, new genus

Figs. 1, 4, 31–43.

Type species. *Leurocephala schinus*ae Davis and Mc Kay, new species

Description. Adult (Fig. 4). Small moths with forewing length 3.1–3.5 mm. *Head* (Figs. 31–32): Vestiture entirely smooth; scales tightly appressed, slender, with apices broader, slightly rounded. Eye relatively large, round; vertical diameter equal to minimum interocular distance across frons. Antenna filiform, long, ~ equal to forewing in length, smoothly scaled; a single annulus of long, slender scales completely encircling each flagellomere; scape elongate, ~ 4.8x length of pedicel. Labrum trilobed, pilifers well developed, triangular. Mandible absent. Haustellum naked, elongate, ~ 2.2x length of labial palpus. Maxillary palpus short, smoothly scaled, 4-segmented; ratio of segments from base: ~1.0: 2.1:1.0:2.7. Labial palpus smoothly scaled, moderately long and drooping; ratio of segments from base: ~1.0:2.4:0.8. *Thorax:* Smoothly scaled. Forewing (Fig. 33) lanceolate, L/W index ~ 5.0; R 5-branched; all veins arising separate from cell except with Rs3, Rs4, and M1 either connate at their bases or with Rs4 and M1 stalked; discal cell ~ 0.4x length of forewing; 1A + 2A completely fused, well developed, extending more than half the length of hind margin. Hindwing extremely slender, L/W index ~ 7.0; M1 shortly stalked to M2+3; cell open between M and Cu; CuP present but weak; male frenulum a single stout bristle; female with frenulum divided at extreme base, then fused for nearly its entire length and appearing as a single stout bristle. Legs with tibial spur pattern 0-2-4; epiphysis absent. Abdomen (Figs. 40–41): Male with segments VII–VIII complex and greatly reduced except for enlarged tergum VIII; VII reduced to a very narrow, nearly complete, sclerotized ring, with lateral juncture of VII tergum and sternum barely discernible; segment VIII with a weakly sclerotized, elongate, hoodlike tergum (Fig. 41) overlapping tegumen (tergum IX); sternum VIII greatly reduced, extending as a narrow ventral ring from indistinct lateral junction with anteriolateral angle of tergum VIII; lateral portions of sternum VIII slightly broaden and bearing a pair of elongate hair pencils (coremata); a second, immediately anterior pair of hair pencils arising from distal apex of an elongate, mostly membranous, everted, tubular lobe arising in membrane between sterna VII and VIII, with a slender, supporting rodlike sclerite extending the length of lobe. Female postabdominal segments unmodified; corethrogyne absent.

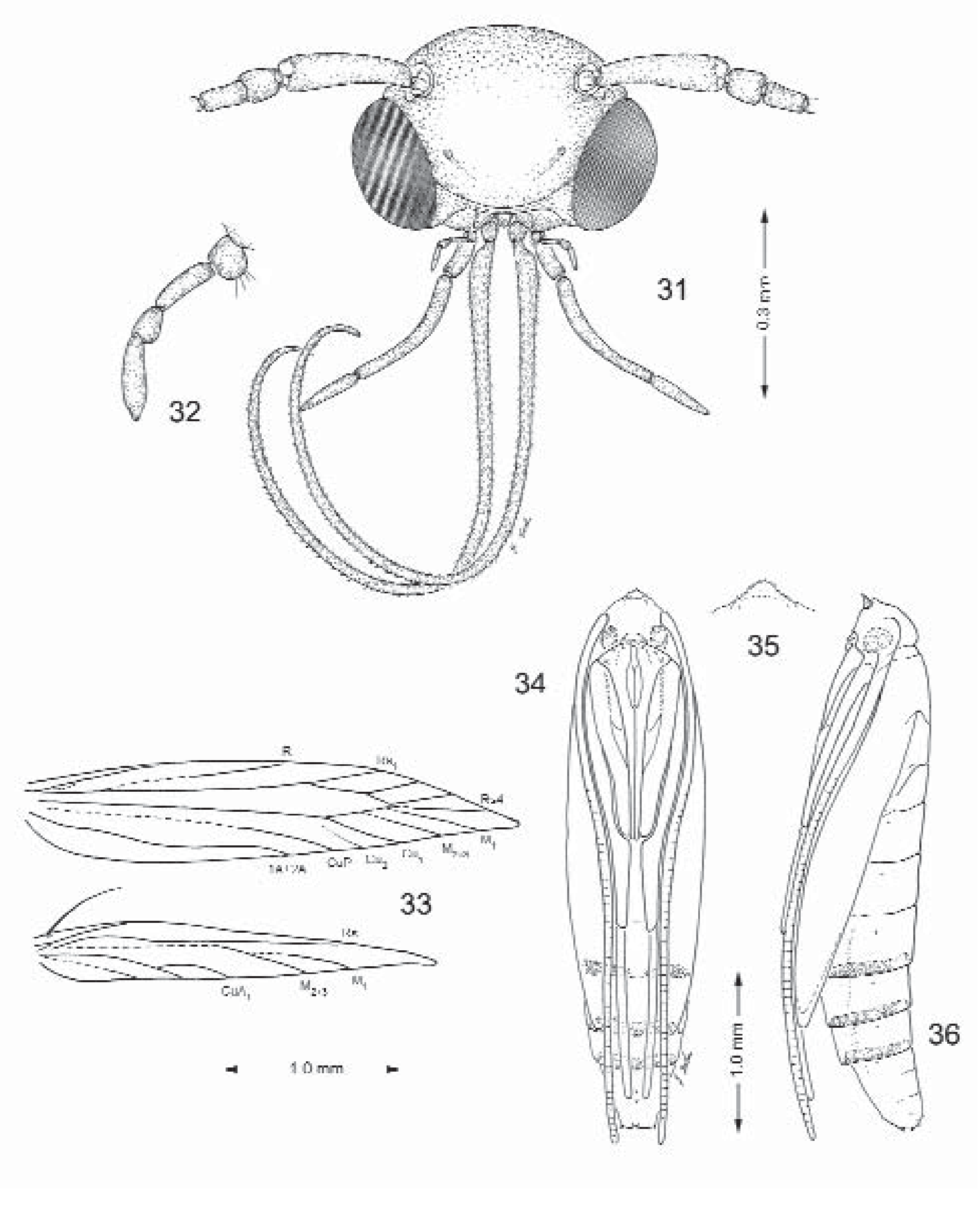
Male genitalia (Figs. 37–39). Uncus absent. Tegumen relatively broad, hood-shaped, partially membranous, with a shallow apical notch. A pair of short, rounded, membranous lobes arising ventrally from mostly membranous area beneath tegumen, possibly representing rudimentary gnathos. Vinculum short, broadly V-shaped, extending laterally along base of valva; sacculus only slightly developed, length equal to less than half the length of vinculum. Valva broad at base, with sharply defined saccular lobe, abruptly narrowing to truncate, slightly flared apex; costal margin relatively straight. Base of valvae joined by a strongly arched, moderately sclerotized transtilla. Juxta a small, dorsally concave, lightly sclerotized plate firmly attached to middle of aedeagus. Aedeagus (Fig. 39) sinuate, relatively short; length ~ equal to length of valva; basal half of aedeagus tapering cephalad beyond entry point of ductus ejaculatorius.

Female genitalia (Figs. 42–43). Anterior and posterior apophyses short, of similar lengths; posterior apophysis broader at base. Ostium forming a broad chamber with lateral extensions, opening on caudal margin of sternum VII. Ductus bursae short, slightly thickened, abruptly expanding to elongate, elliptical corpus bursae. Ductus seminalis connected immediately anterior to junction of ductus bursae and corpus bursae. Walls of corpus bursae membranous, appearing externally wrinkled, with a single ovoid lenticular signum near middle, possessing a relatively long slender spine projecting anteriorly into corpus bursae.

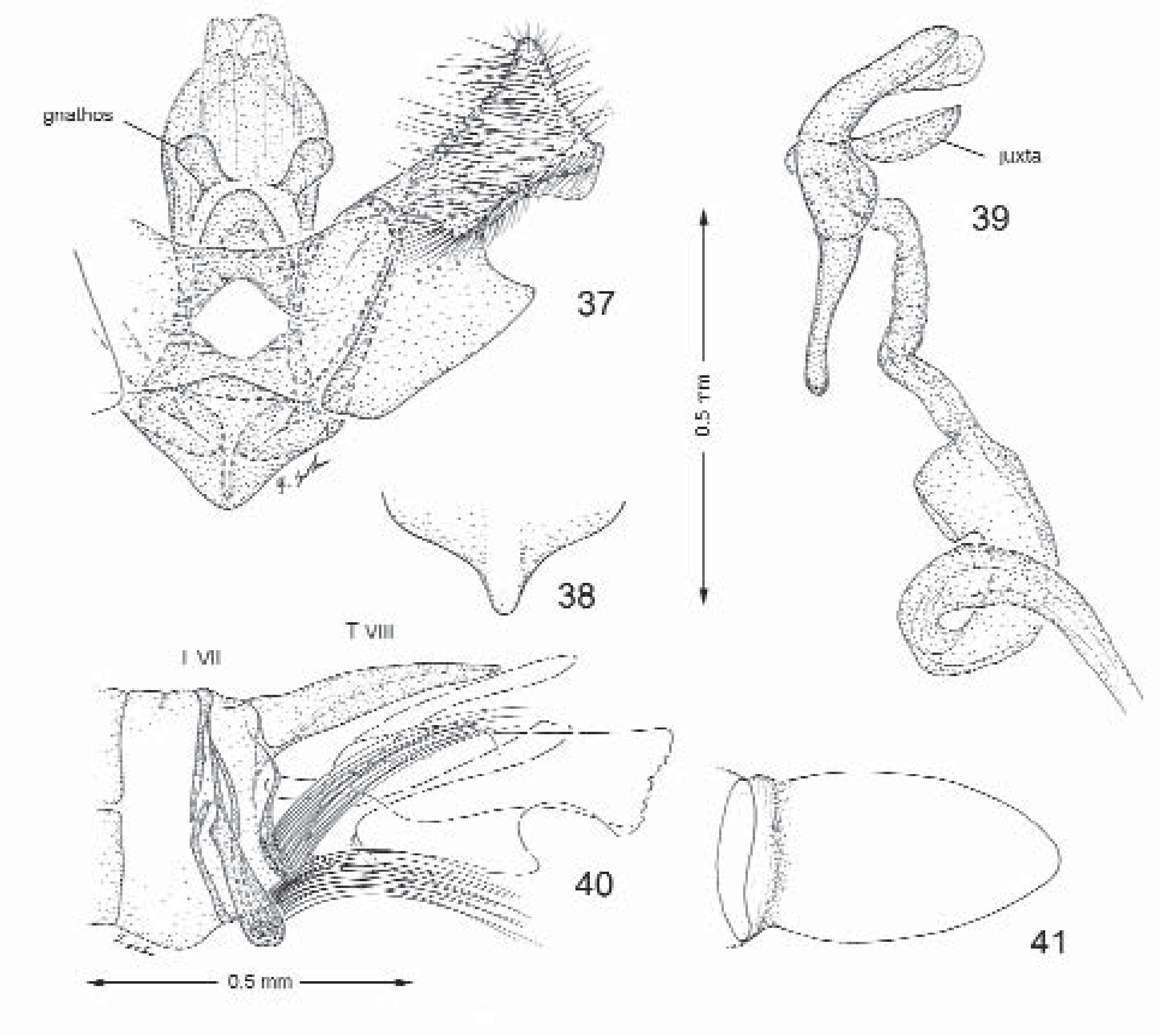
Etymology. The generic name is derived from the Greek *leuros* (smooth, polished) and *kephale* (head), in reference to the entirely smooth-scaled head of the adult.

Discussion. Several morphological characteristics place this genus within the subfamily Gracillariinae, including a smoothly scaled head, 4-segmented maxillary palpus, hindwing with base of Rs arched toward Sc, 2 pairs of coremata in male, pupation outside of mine, and resting posture of the adult with the anterior portion of body raised at ~ 45° angle. *Leurocephala* differs from all known genera in several features, particularly by the presence of paired gnathal lobes in the male genitalia and the anterior extension of aedeagus beyond entry point of the ductus ejaculatorius. In addition, the development of three distinct larval forms similar to that in *Leurocephala* has been observed in only a few other genera of Gracillariidae. The three distinct developmental stages include an apodal, first instar sapfeeding form, a mostly apodal tissue feeding form, and a last instar tissue feeding form with relatively well developed legs and prolegs.

Leurocephala shows some similarity to the American genus *Neurostrota* in fore- and hindwing venation, in



FIGS. 31–36. *Leurocephala schinus*ae, adult and pupal morphology. **31.** Head, anterior view. **32.** Maxillary palpus. **33.** Wing venation. **34.** Pupa, ventral view. **35.** Detail of frontal ridge (cocoon cutter). **36.** Pupa, lateral view. (Scale lengths as indicated).



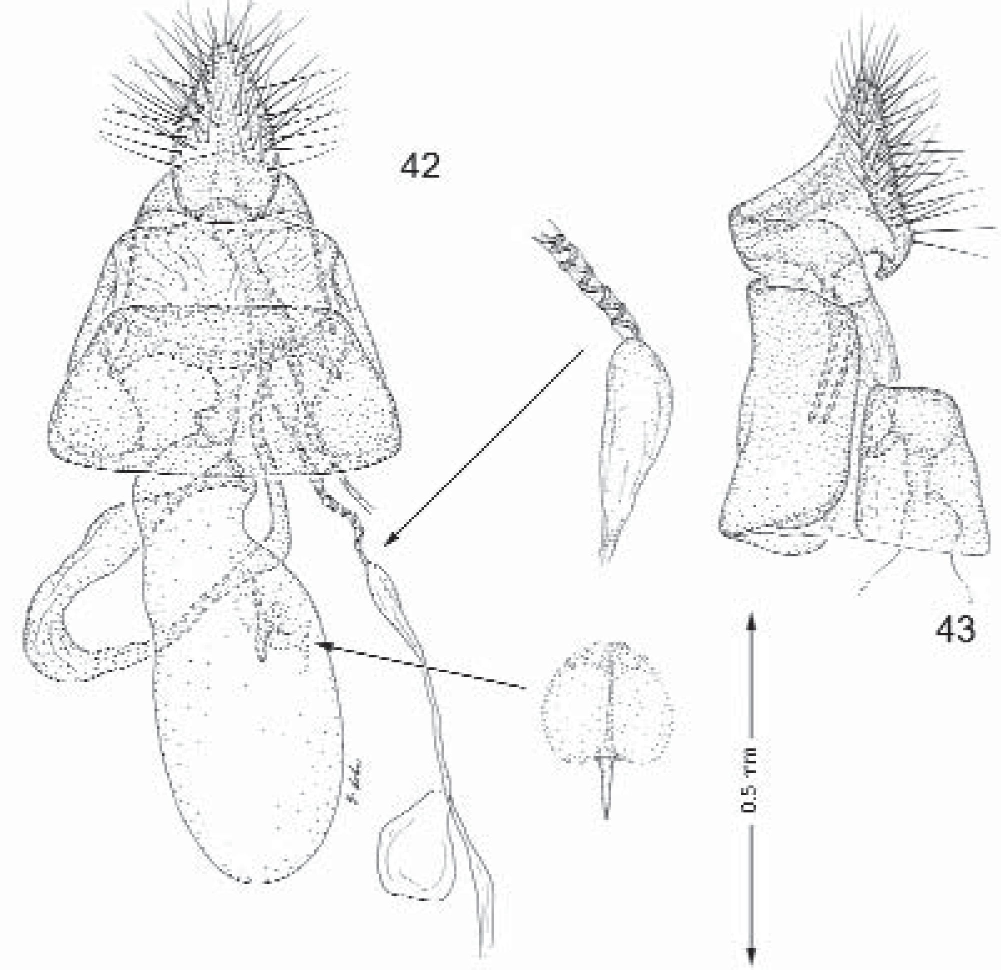
Figs. 37–41. *Leurocephala schinus*ae, male genitalia and postabdomen. **37.** Genitalia, ventral view. **38.** Variation of anterior margin of vinculum. **39.** Aedeagus; J = juxta. **40.** Postabdominal segments 7–8 with coremata, lateral view. **41.** Tergum 8, ventral view. (Scale lengths as indicated).

the development of a broad saccular lobe on the male valva, a greatly enlarged tergum 8 in the male abdomen, and in the larval excretion of numerous bubbles over the surface of the cocoon. Larval bubble excretion also occurs in several other gracillariid genera, including *Eucosmophora* and *Marmara*, as noted herein. Molecular analysis now nearing completion on the genera of Gracillariidae by Akito Kawahara (2010) place *Leurocephala* within the *Parectopa* group of Gracillariinae near the genera *Liocrobyla*, *Micrurapteryx*, and *Parectopa.*

Leurocephala schinusae Davis and Mc Kay, new species

Figs. 1, 4, 16–19, 31–106.

Diagnosis. As discussed under the genus, *Leurocephala schinus*ae differs from all known genera and species of Gracillariidae in several features, particularly by the presence of paired gnathal lobes in the male genitalia and the anterior extension of the aedeagus beyond the entry point of the ductus ejaculatorius, and, in part, by the development of three distinct larval forms. The intermediate (transitional) form differs from all other known Gracillariidae in



FIGS. 42–43. *Leurocephala schinus*ae, female genitalia. **42.** Ventral view, with enlargements of spermatheca and signum. **43.** Lateral view. (Scale lengths as indicated).

possessing three instars with a unique, enlarged spinneret and well developed mandibles of the tissue-feeding type.

Description. Adult (Fig. 4). *Head:* Frons mostly white, becoming slightly more bronzy brown caudally from vertex. Antenna dark bronzy fuscous; scape with a slender white, longitudinal streak dorsally which gradually fade to flagellomeres 1–2; venter of scape and basal flagellomeres white, gradually becoming more light brown distally. Maxillary palpus white. Labial palpus mostly silvery white, dark fuscous laterally and at apex of segment 2. *Thorax:* Mostly fuscous dorsally with scales brown basally gradually becoming more fuscous over distal half; white ventrally; tegula dark fuscous. Forewing: length 3.1–3.5mm; mostly fuscous, scale bases slightly paler; usually with 4 oblique white striae of variable width equally spaced along costa and a similar number of nearly opposite white striae along hind margin; fringe around apex fuscous banded with lighter gray; a small apical tuft of 3–6 fuscous scales projecting beyond fringe; fringe along hind margin uniformly fuscous. Hindwing uniformly fuscous. Legs mostly fuscous dorsally, white ventrally; tibiae and tarsi strongly banded with white and fuscous. Abdomen (Figs. 40–41): Fuscous dorsally, mostly white ventrally with oblique segmental bands of fuscous laterally. Coremata from segment VIII of male white. Postabdominal segments as described for genus.

Male genitalia (Figs. 37–39). As described for genus.

Female genitalia (Figs. 42–43). As described for genus.

Egg (Figs. 44–45, Table 1). Glued to upperside (adaxial) leaf surface of host, often adjacent to either main or secondary vein. Generally oval to nearly round in outline, relatively depressed, with center slightly raised; length ~ 0.40 – 0.48 mm; width 0.33 to 0.44 mm. Chorion of dorsal surface finely reticulated.

Larva (Figs. 46–98, Table 1). Hypermetamorphic, with three distinct larval forms: 1) First instar, apodal, sapfeeding stage with flattened (depressed) mandibles and rudimentary spinneret. 2) Instars

TABLE 1. Egg and larval head capsule widths of *Leurocephala schinusae* on *Schinus terebinthifolius.*

		Egg and head capsule widths (mm)	
Life stage	***N***	**Mean ± SD**	**Range**
Egg	10	0.39 ± 0.04	0.33-0.44
L I	10	0.14 ± 0.01	0.13-0.14
L II	10	0.14 ± 0.01	0.13-0.14
L III	10	0.21 ± 0.01	0.2-0.22
L IV	10	0.35 ± 0.02	0.32-0.39
L V	10	0.43 ± 0.02	0.4-0.46

2–4 more cylindrical, nearly apodal, tissue feeding, with stouter, more opposable mandibles; broad, stout spinneret with a greatly enlarged, flared aperture. 3) Last (5th) tissue feeding instar with a more cylindrical body, stout, opposable mandibles; spinneret fully developed "normal", more slender; fully developed thoracic legs, and 3 + 1 pairs of abdominal prolegs. Head capsule widths of each instar are provided in Table 1. Among the 10 larvae sampled each for instars 1 and 2, no significant differences were observed between the width of their heads. The morphology of their mouthparts, particularly the spinneret, was distinctly different as described below.

Sap-feeding Instar (Figs. 46–55). First instar ~ 0.85 – 1.0mm in length, with relatively depressed head and body modified for sap-feeding in subepidermal tissue of leaves. *Head:* Most setae reduced to absent. Stemmata absent. Antenna with 3rd segment relatively shorter but with similar sensillae compared with that of later instars. Labrum (Figs. 46–47) generally similar to later instars in outline, moderately bilobed with a median, apical depression; setae greatly reduced, indistinct. Mandibles depressed (Fig. 49), with 3 acute and 1 blunt teeth. Labium (Figs. 50–51) relatively broad and flat, projecting slightly beyond labrum, with anterior margin broadly rounded; spinneret greatly reduced, with only a minute, flush opening at apical-ventral margin of labium; labial palpi vestigial, reduced to a pair of closely appressed, slender setae (Fig. 51). Body: Relatively depressed; white except for brownish tergal and dorsal plates, with pronotal plate and abdominal tergal plates 1–7 the largest in size; tergal plates of meso- and metathorax reduced. Legs, prolegs, and crochets absent. Paired dorsal and ventral ambulatory callosities present on all thoracic segments and abdominal segments 1–8.

Apodal tissue feeding Instars (Figs. 56–71). Instars 2–4 with more cylindrical body and head, and larva feeding deeper into mesophyll tissue than first instar and beginning blotch mine; maximum length of 4th instar larva ~ 4 mm. *Head:* Moderately depressed. Chaetotaxy similar to 5th instar. Labrum identical to that of last instar, with 4 pairs of setae. Stemmata relatively flat, poorly defined, with only stemmata 4 (near S1) and 1 (near S2, Figs. 63–64) evident. Antenna and maxilla similar to that of last instar, with segments proportionally equal in length. Mandible similar to last instar, with 5 teeth. Labium with 2-segmented labial palpus; length of basal segment ~ 2x its width; with 2 elongate setae, longest ~ twice the length of shorter seta. Spinneret (Figs. 60, 67) extremely broad and stout, triangular shape, terminating in a flared, fimbriate rim that encloses the aperture of the spinneret in a shallow depression. Body: white except for brownish tergal and dorsal plates. Pronotum a large, brown, rectangular plate; plates reduced in size and nearly colorless on meso- and metanotum; only subventral pinaculum of prothorax brown. Prosternum similar to pronotum; meso- and metasterna with small, dark brown plates. Dorsum of abdominal segments 1–9 with brownish plates slightly smaller than corresponding ventral plates; plates slightly decreasing in size caudally, except A9 tergal plate larger, broader; dark brown, oval plates present on sterna of A1–10; plate of sterna 9 broader. Most setae reduced, with L1 the longest. Thoracic legs (Figs. 69, 71) vestigial, unsegmented, bearing 2–3 short setae and a terminal, rudimentary pretarsal unguis. Prolegs, and crochets absent. Paired dorsal and ventral ambulatory callosities present on all thoracic segments and abdominal segments 1–8.

Tissue-feeding Last Instar (Figs. 72–98). Fifth instar more typical caterpillar form with cylindrical body, feeding on mesophyll tissue of leaf and enlarging full depth blotch mine; maximum length to 5.5 mm; width to 0.8 mm. Body color light green. Head brown; maximum width 0.46 mm; relatively dorsoventrally flattened Fig. 77) with mouthparts fully developed; dorsal area around seta P1 minutely spinose, broadly triangular in outline (Figs. 72, 93); epicranial notch deeply formed as in previous instars and generally similar to that of *Parectopa* except more broadly separated at junction, U-shaped. Frons elongate, extending to epicranial notch and about half the length of head capsule; ecdysial line terminating at lateral margins of epicranial notch. Chaetotaxy relatively well developed; all three MD setae present. P1 well separated from ecdysial line. P2 reduced, widely separated from P1, arising nearer to A3. Six stemmata, arranged in 3 groups: stemmata 1 and 2 together anterior to A3; stemmata 3–5 in an oblique line between A1 and SS2; stemma 6 situated immediately ventrad to S2. Antenna 3-segmented, with sensilla as shown (Figs. 74–75). Labrum with 4 pairs of setae; M2 and L1 lost; epipharyngeal spines and epipharyngeal sclerite not observed. Mandible (Fig. 98) with 5 moderately large cusps; median 3 cusps the longest; both lateral seta present. Maxilla as shown in Fig. 79. Spinneret (Figs.80–81) relatively short, slender; apex rounded, densely covered with minute, blunt papillae ventral to minute aperture. Labial palpi (Fig. 80) with basal segment ~ 4x length of smaller apical segment and bearing short subapical sensillum; apical segment bearing elongate apical sensillum, exceeding length of basal segment. Body: Pale green at maturity. Pronotum relatively large, pale brown, smooth. XD1 and 2 short, arising near ventral margin of pronotum. Ambulatory callosities present dorsolaterally on T1–3. L group bisetose on T1–3. SV bisetose on T1, unisetose on T2–3 (Fig. 92). Sternal plate large, wrinkled. Legs moderately well developed; claw with large axial spine (Fig. 86); coxae widely separated. *Abdomen:* Dorsal plates indistinct, smooth. Paired dorsal and ventral ambulatory callosities present on A1–7. Both D setae present on A9. L unisetose on A1–10. SV group trisetose on A1–10. Prolegs present on A3–5 and A10; crochets arranged in a staggered caudal row of ~ 12 hooks on A3–5 (Fig. 85); A10 with crochets reduced to 2 hooks (Figs. 88, 89). Chaetotaxy of A10 as shown in Figs. 88, 90–91, 95; SD1 and SD2 bisetose.

Pupa (Figs. 34–36, 99–106). Length to 4 mm and width 0.9 mm; brown to fuscous ventrally, white to light brown dorsally with dark brown intersegmental rings over abdomen. Frontal process (cocoon cutter) a low, broad, triangular, mostly transverse ridge bearing numerous minute teeth in scattered rows, with medial 3 teeth the largest; (Fig. 100). Antenna long, extending slightly beyond end of abdomen. Labial palpi extending about 1/3 the length of proleg. Proboscis as long as proleg. Forewings narrow, well separated, extending to abdominal segment A6. Prolegs to A2; midlegs to A4; and hindlegs to A8 or 9+10. D1, SD1, and L1 present on A1–6; only D1 present on A7–8. Dorsum of abdomen minutely and densely spinose, without prominent rows of spines (Fig. 102). Sternum of A7 relatively smooth, without accessory cremaster. Cremaster consisting of a ring of four pairs of small slightly curved spines, with those on dorsum closely set and slightly enlarged (Figs. 103–106).

Cocoon (Fig. 19). Oval in general outline; ~ 6–6.5 mm long, 2.5–3.5 mm wide. Surface flat, adorned with average of 16 (± 2.8; n=22; range 9–20), pearly-white, minute, compartmentalized bubbles, arranged either in an approximate line along longitudinal axis or peripherally around edge of cocoon. These bubbles were discharged from the anus at intervals of approximately 10 minutes by the mature larvae and attached through a slit in the cocoon.

Larval Biology (Figs. 16–19). The first instar larva bores into the plant epidermis and makes a short mine (length = 0.93 ± 0.08 mm; mean ± SD; n=21) parallel to the leaf vein. After this initial slender mine, the mine of later instars turns 90° and continues forming an increasingly broader blotch mine in the leaf blade. The initial two thirds of a fully developed blotch mine are dark brown and the most distal third is light green. One fully developed mine may remove up to 40% of the leaflet photosynthetic tissue. Occasionally two, but generally one blotch is found per leaflet. Mature larvae leave the blotch through a slit in the light colored part and spin a silk cocoon on the adaxial surface of the leaves.

Hosts. Anacardiaceae: *Schinus terebinthifolius* Raddi and *Schinus longifolius* (Lind.) Speg. Mines similar to that of *Leurocephala schinus*ae were also found on *Astronium balansae* Engl.; *Schinus fasciculatus* (Griseb.) *Schinus lentiscifolius* March., *S. longifolius* (Lindl.) Speg. and *Schinus weinmannifolius* Engl., but no adults were reared.

Parasitoids. In Argentina the following parasitoids emerged from *L. schinusae* blotch mines: Braconidae (Orgilinae); Ichneumonidae (Brachycyrtinae) and *Isdromas* sp. (Cryptinae: Phygadeuontini). In Brazil parasitism occurred from Braconidae *Orgilus* sp (Orgilinae), *Pholeteser* sp. (Microgastrinae) and several Chalcidoidea (undetermined species), Ichneumonidae *Lymeon* sp. (Cryptinae), *Acrolyta* n.sp., 2 species of *Isdromas* (including the same as those from Argentina, as well as a third species), and *Pimpla croceiventris* (Cresson) (Pimplinae).

Types. *Holotype*: ♂; ARGENTINA: Misiones Province; Road 12; 2 km N Libertad, 2 Aug 2006, Mc Kay & Oleiro, leaf blotch miner collected as larva on *Schinus terebinthifolius*, GPS: 394; Digital image captured USNM, (MACN). Paratypes (27 ♂, 19 ♀): ARGENTINA: Buenos Aires Province: Hurlingham: July 2007, 3 larvae, [23 larvae], host: *Schinus terebinthifolius*, DRD SEM, slide 33913; Corrientes Prov: Santo Tomé: 1 ♀, 16 Jul 2007, Mc Kay & Oleiro, *Schinus terebinthifolius*, slide 33909; Road 14, km 728: 2 pupae, 16 Jul 2007, Mc Kay & Oleiro, collected as leaf miner larva on *Schinus terebinthifolius*; Road 94, 13 km NE Santo Tomé: 4 larva, 21 Sep 2007, Mc Kay & Oleiro, host: *Schinus terebinthifolius*, SEM slides 33912, 34092. Misiones Prov: 26 km N Capiovi: 1 ♂, 26 Mar 2006, Mc Kay & Wheeler, leaf blotcher collected as larva on *Schinus terebinthifolius*, GPS: 016; Road 12: 24 km N Capiovi: 2 ♂, 2 June 2005, Mc Kay & Oleiro, emerged from mines on leaves of *Schinus terebinthifolius*, GPS: 6; Road 12: 26 km N Capiovi: 5 larvae, 6 Jun 2007, Mc Kay & Oleiro, leaf miner on *Schinus terebinthifolius*, SEM slide USNM 34100; Road 12, 2 km N. Libertad: 3 pupae, 20 Jul 2007, SEM slide 33911; 1 ♂, 1 ♀, 2 Aug 2006, reared ex larva blotch miner on *Schinus terebinthifolius*, Mc Kay & Oleiro; Road 14, km 909: 2 ♂, 3 Aug 2006, Mc Kay & Oleiro, slide USNM 33910; Road 14, near Cerro Azul: 3 larvae, 5 Jun 2007, Mc Kay & Oleiro, leaf miner on *Schinus terebinthifolius*, slide USNM 33931; Road 17, 4 km W 9 de Julio: 8 ♂, 5 ♀, 3 Aug 2006, Mc Kay & Oleiro, slides USNM 33655, 33696, 33908; Road 17, 14 km W 9 de Julio: 2 ♂, 3 Aug 2006, Mc Kay & Oleiro, slide USNM 33699; Road 103, 14 km W Oberá: 1 ♂, 15 Oct 2005, Gandolfo & Mc Kay, leaf blotcher collected as larva on *Schinus terebinthifolius*, GPS: 58. Road 103, 16 km W Oberá: 1 larva, 5 Jun 2007, Mc Kay & Oleiro, leaf miner on *Schinus terebinthifolius*. BRAZIL: Parana: Curitiba Zoo: 1 ♂, 2–7 May 1991, *Schinus terebinthifolius*, D. Habeck; 1 ♂, 9 Oct 1992, pupa 17 Oct 1992, adult 31 Oct 1992, host: *Schinus terebinthifolius*, F.D. Bennett, J.H. Pedrosa Macedo, C. Wikler, M.D. Vitorino. Rio de Janeiro: 41 km SE Campos, S22.07491, W41.15992, RJ 28, 11 m: 3 ♂, 6 ♀, 9 Apr 2008, Wheeler, slides USNM 34022, 34026, collected as pupae, globules on silk perimeter. 13 km NW Cabo Frio, S22.82407 / W42.12493, RJ 51, 4 m, 11 Jul 2008, Wheeler; 2 ♀, 3 Feb 2010, RJ51, host: *Schinus terebinthifolius*, globules on silk perimeter, Wheeler & Mc Kay, slide USNM 34217. Santa Catarina Province: 14 km N Imbituba, S28.10610 / W48.66161, 7 m, 3 , 10 Jul 2008, Wheeler & Mc Kay. Santa Catarina: 14 km N. Imbituba, S28.10610, W48.66161, 7 m: 1 ♂, 2 ♀, 10 Jul 2008, SC7, reared from leafminer on *Schinus terebinthifolius*, Wheeler and Mc Kay, slide USNM 34087; Itapoa, S26.08309, W 48.61151, 12 m: 2 ♂, 12 Jul 2008, SC14, Wheeler and Mc Kay, reared from leafminer on *Schinus terebinthifolius*. Sao Paulo: Alomberi [probably Alambari]: 2 ♀, No. 48, 52, 17 Sep 1987, pupa 21 Sep 1987, adult 2 Oct 1987; No 50, 1 ♂, 17 Sep 1987, pupa, 29 Sep 1987, adult 9 Oct 1987, Host: *Schinus terebinthifolius*, L. Crestana, USNM slide 33916. PARAGUAY: Coronel: 7 km W Coronel: 1 ♂, 17 Sep 2004, reared from leaf mines on *Schinus terebinthifolius*, Gandolfo and Mc Kay, slide USNM 33195. (Paratypes deposited in MACN, UPZB, and USNM).

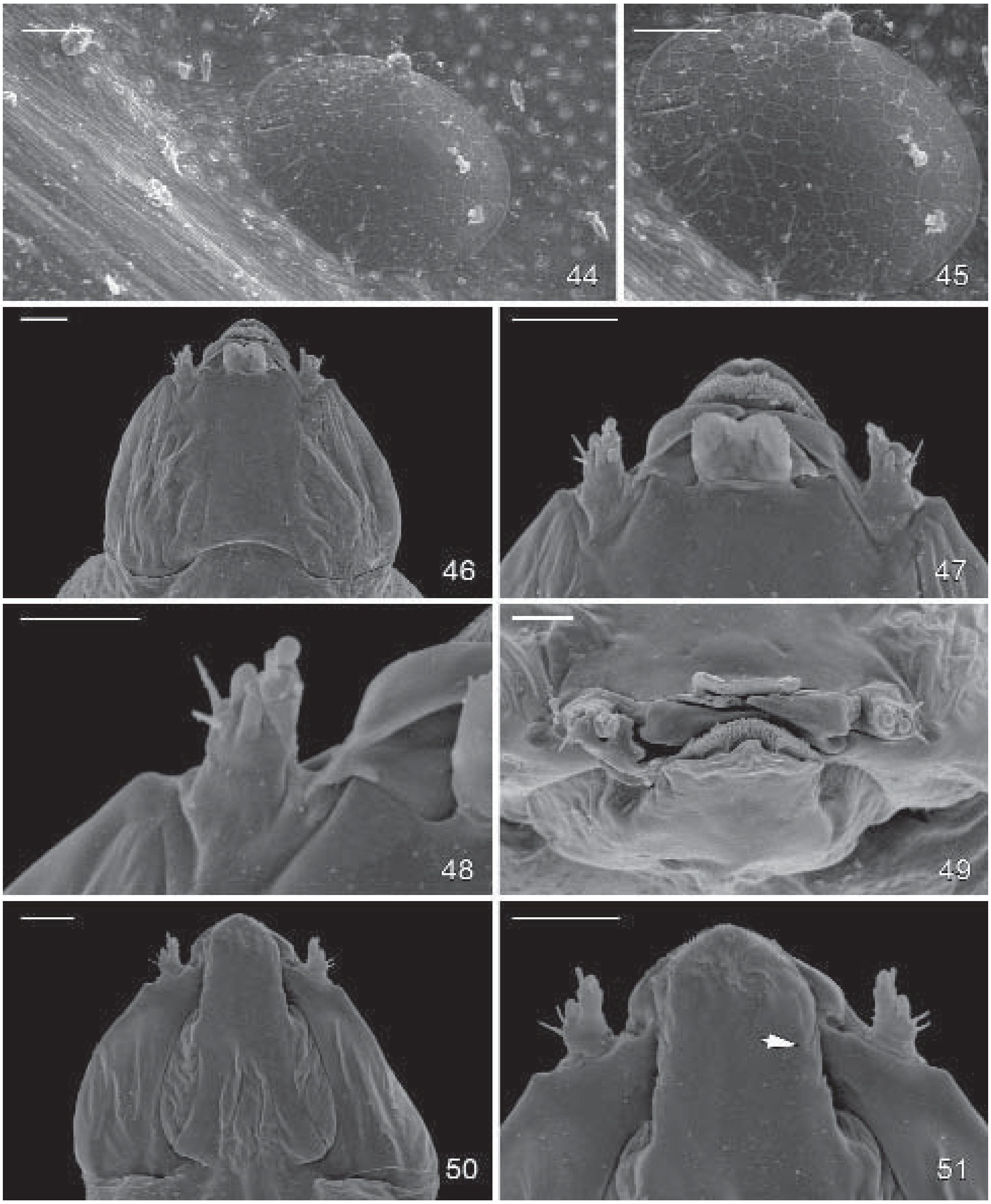
Flight period. Active mines were present year-round, the highest numbers were found during the Austral winter (June-August).

Distribution (Fig. 1). Leaflets of *S. terebinthifolius* infested with blotch mines of *L. schinusae* were found at several localities in northeastern Argentina (Corrientes and Misiones Provinces) and at one site in Paraguay. In Brazil this species was collected near Macae, Rio de Janeiro south to Porto Alegre, Rio Grande do Sul.

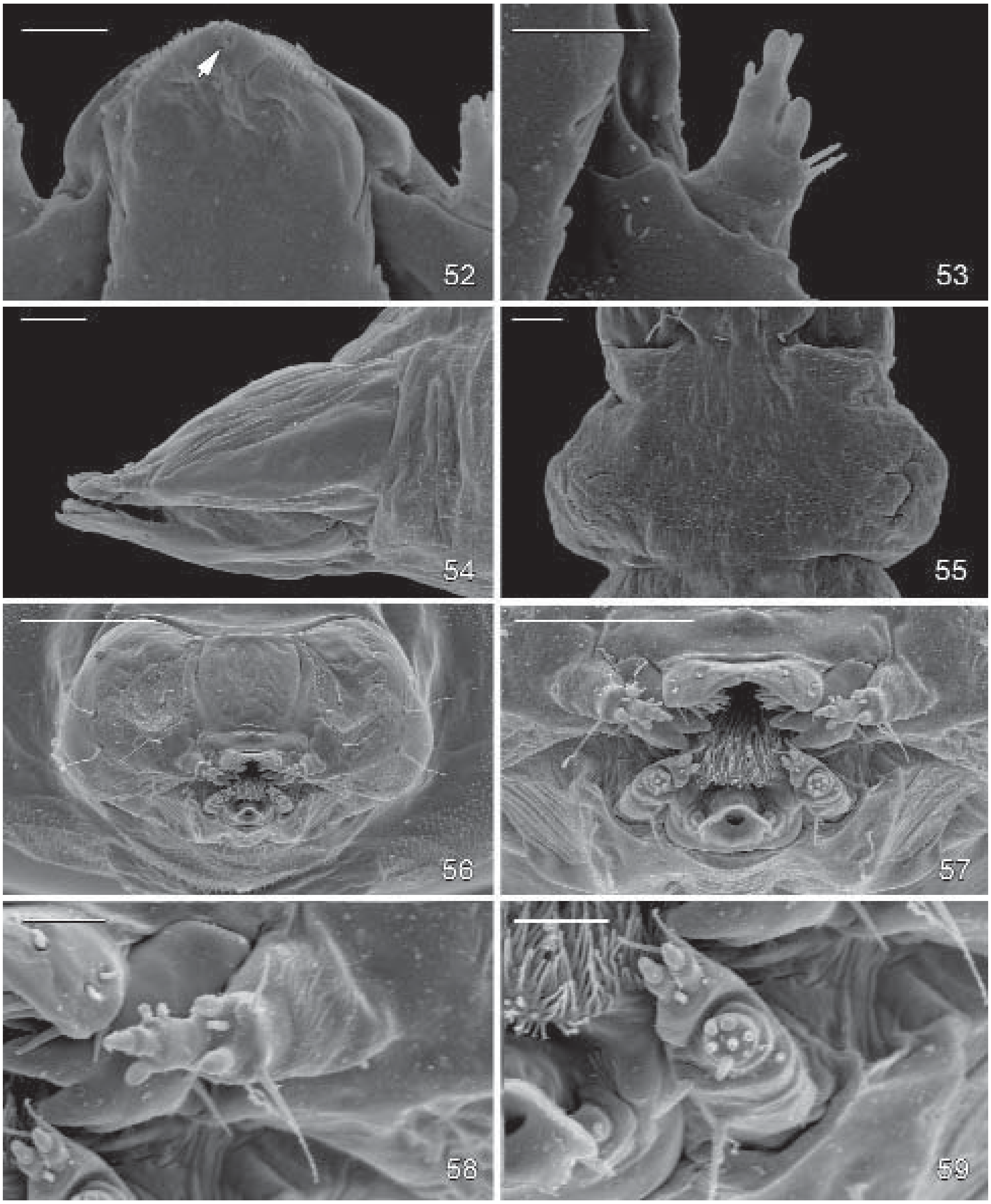
Etymology. The species name is derived from the generic name of the host plant (*Schinus*), with the addition of the genitive suffix (-ae).

Discussion. Other than *Leurocephala*, only a few gracillariid genera have been reported undergoing an additional intermediate larval stage between the sap-feeding and tissue-feeding forms. Intermediate larval forms have been observed in *Chrysaster* and *Dendrorycter* (Kumata 1978), *Marmara* (DeGryse 1916; Fitzgerald & Simeone 1971; Wagner et al. 2000); and *Neurobathra strigifinitella* (Clemens), (Heinrich & DeGryse 1915). In *Chrysaster*, *Dendrorycter*, and *Marmara* the transitional instar is a nonfeeding, penultimate instar, and in *N. strigifinitella* it appears as a tissue-feeding, third instar. The intermediate larval form in *L. schinusae* is believed to comprise the second to fourth, tissue-feeding instars (Table 1).

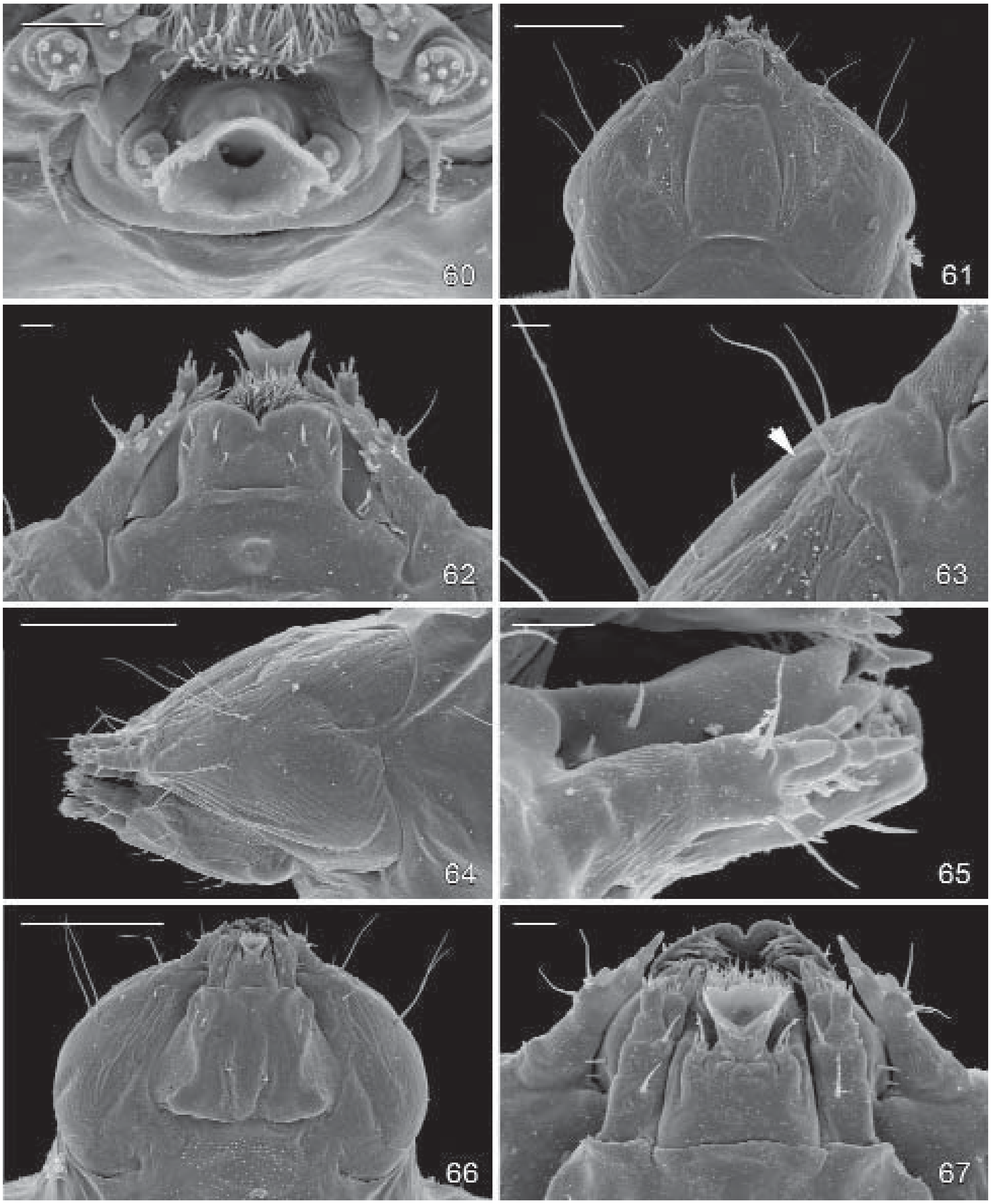
Biological studies were conducted on *Leurocephala schinus*ae at the USDA-ARS South American Biological Control Laboratory (SABCL), Hurlingham, Buenos Aires, Argentina between 2006 and 2008. Cultures of *L. schinusae* were established at the laboratory from leaf mines collected on *Schinus*



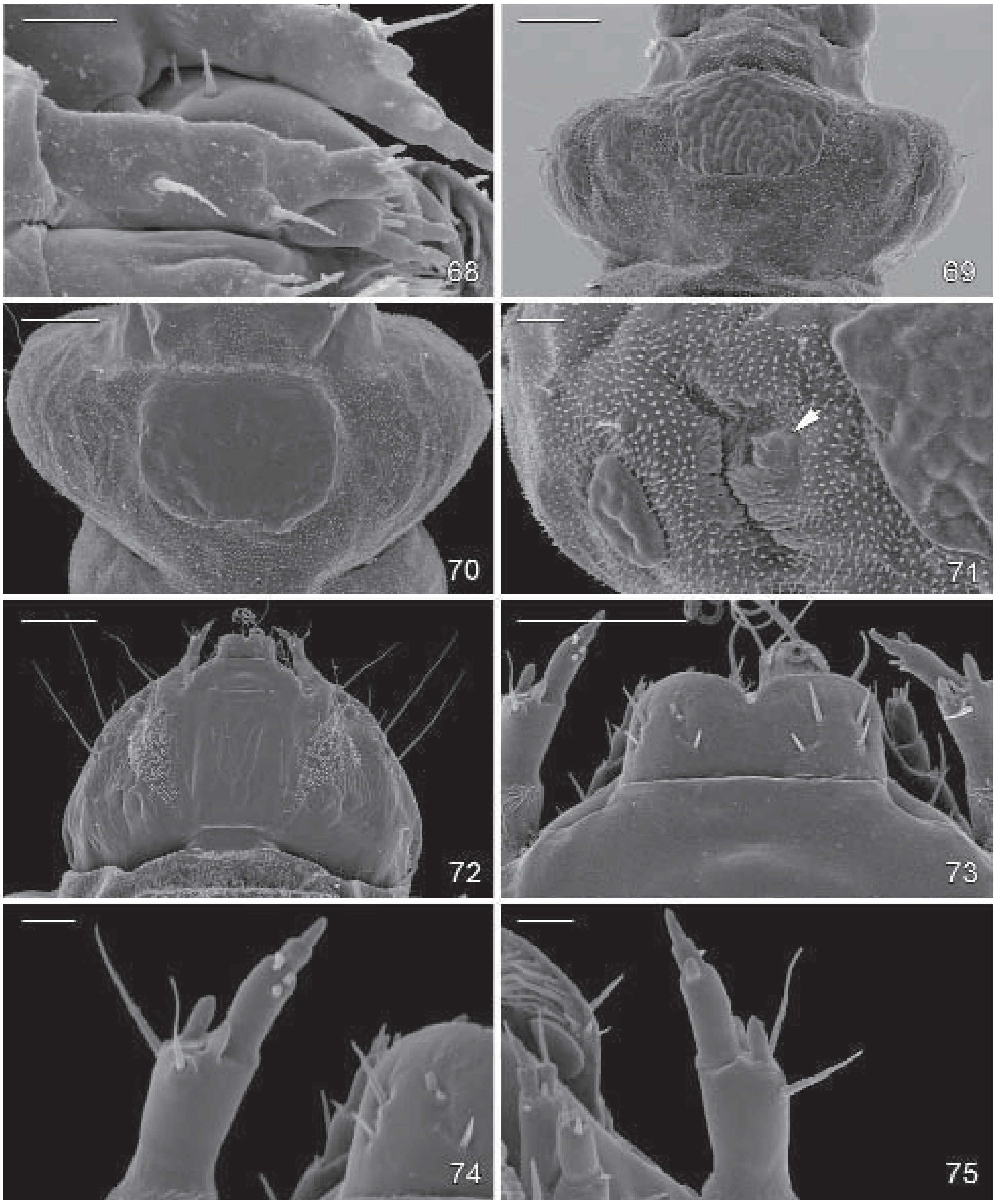
FIGS. 44–51. *Leurocephala schinus*ae, Egg and sapfeeding larva. **44.** Egg adjacent to midvein (100µ). **45.** Detail of egg (100µ). **46.** Head, dorsal view (20µ). **47.** Dorsal view of antennae and mouthparts (20µ). **48.** Dorsal view of antennae (10µ). **49.** Anterior view of mouthparts (20µ). **50.** Head, ventral view (20µ). **51.** Ventral view of antenna and labium; vestigial labial palpus shown by arrow (20µ). (Length of scale bar in parentheses).



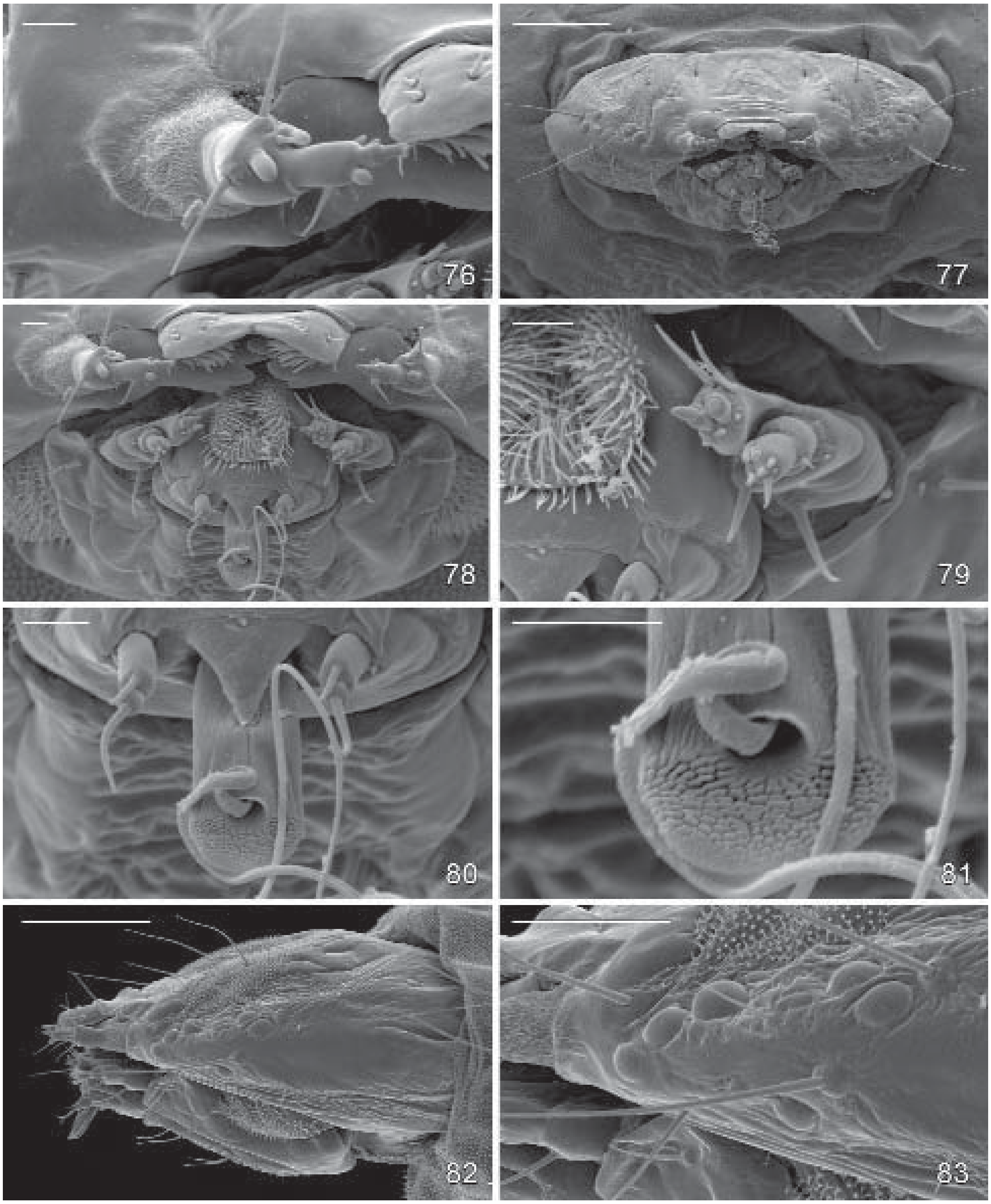
FIGS. 52–59. *Leurocephala schinus*ae, sapfeeding larva (Figs. 52–55) and penultimate instar, apodal tissue feeding larva (Figs. 56–59). **52.** Ventral view of labium, spinneret (arrow), and labial palpi (10µ). **53.** Ventral view of antennae (10µ). **54.** Head, lateral view (20µ). **55.** Ventral view of prothorax with paired callosities (20µ). **56.** Dorsal- anterior view of head (100µ). **57.** Detail of mouthparts in Fig. 54 (50µ). **58.** Antenna, lateral view (10µ). **59.** Maxilla, anterior view (10µ). (Length of scale bar in parentheses).



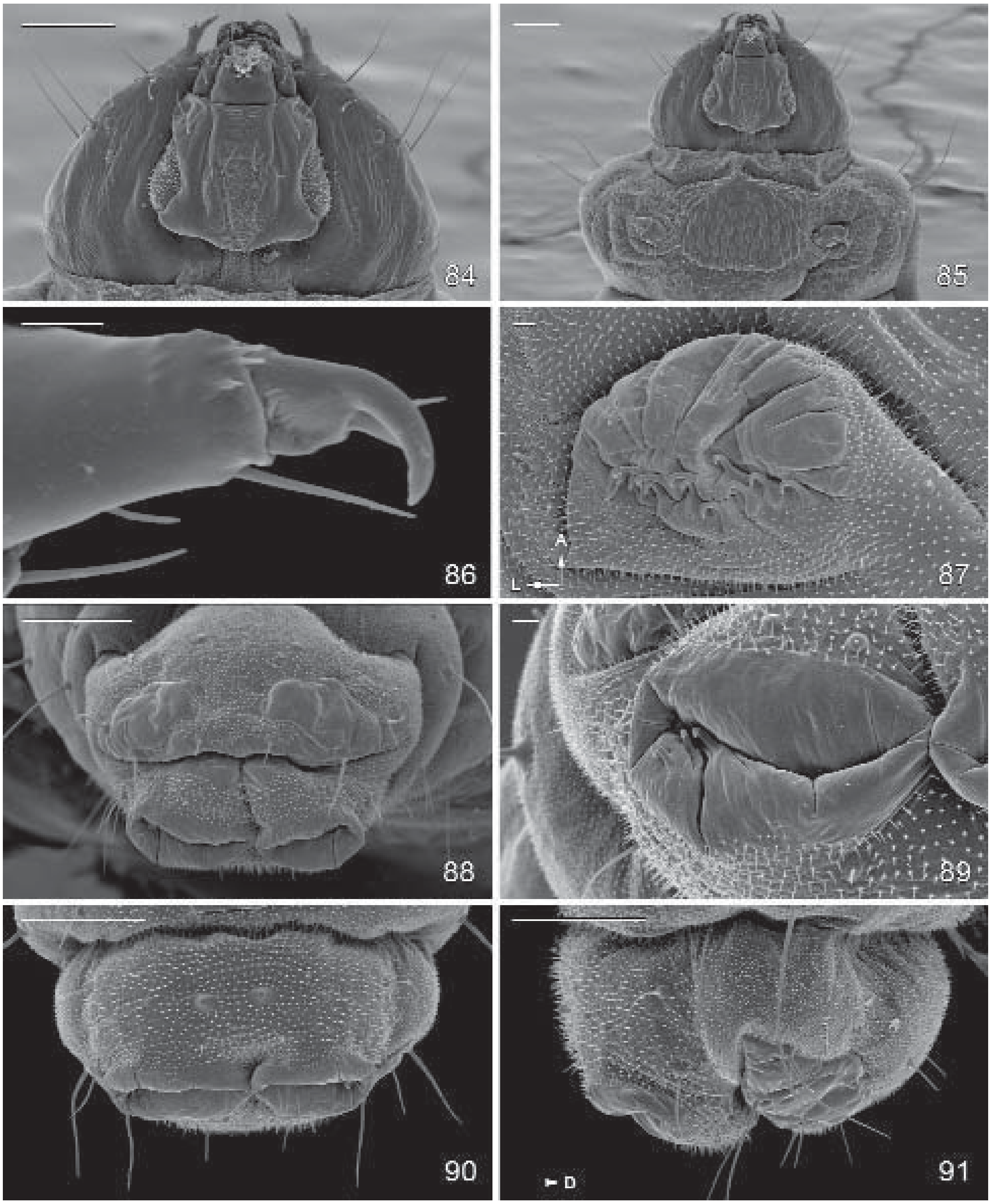
FIGS. 60–67. *Leurocephala schinusae*, penultimate instar, apodal tissue feeding larva. **60.** Spinneret, anterior view (10µ). **61.** Head, dorsal view (100µ). **62.** Dorsal view of antennae and mouthparts (10µ). **63.** Stemmata (arrow), dorsal view (10µ). **64.** Head, lateral view (100µ). **65.** Antenna, lateral view (10µ). **66.** Head, ventral view (100µ). **67.** Detail of mouthparts in Fig. 66 (10µ). (Length of scale bar in parentheses).



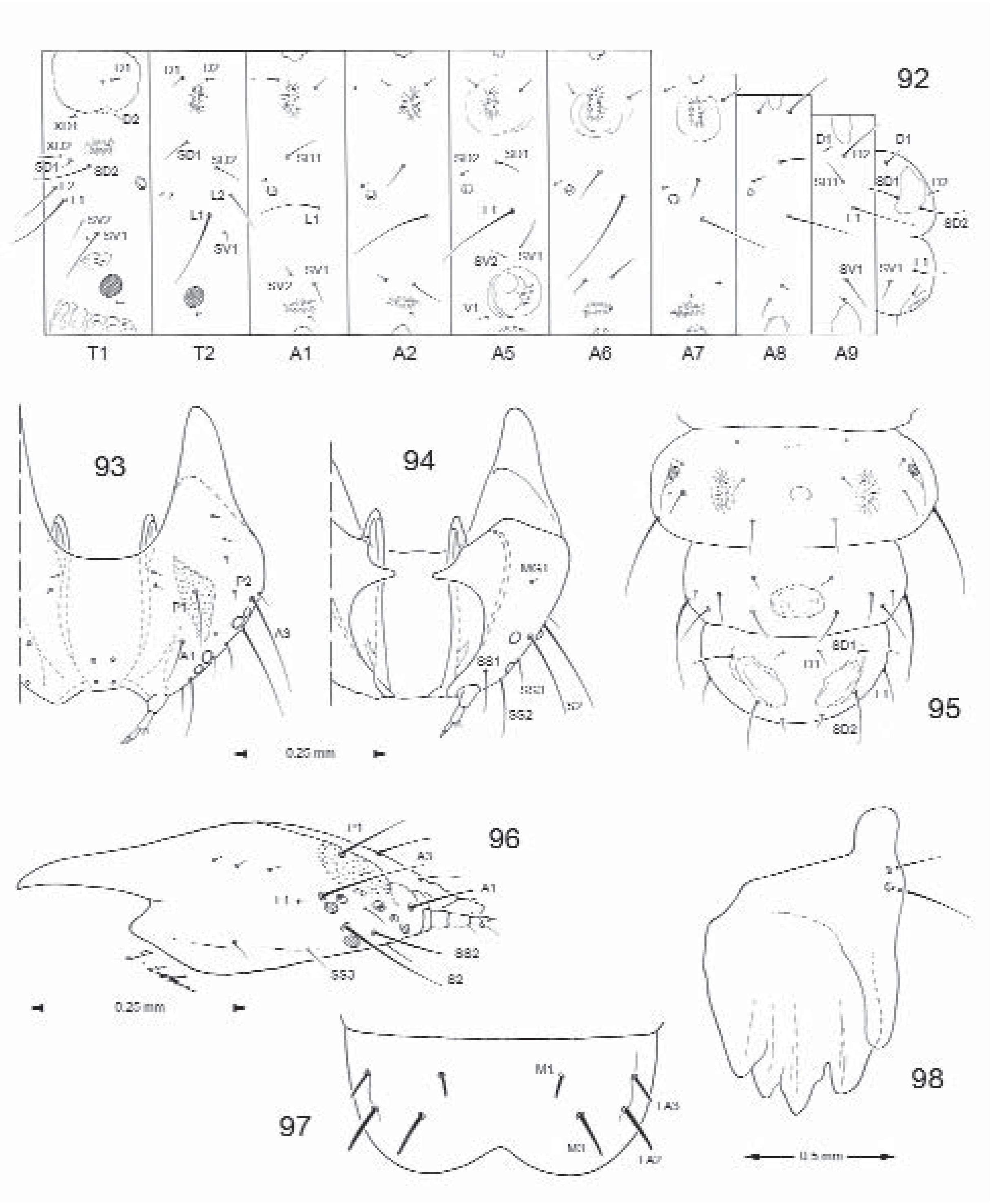
FIGS. 68–75. *Leurocephala schinusae*, penultimate instar, apodal tissue feeding larva (Figs. 68–71) and last instar, tissue feeding larvae (Figs. 72–75). **68.** Maxilla, ventral view (10μ). **69.** Prothorax, ventral view (100μ). **70.** Prothorax, dorsal view (100μ). **71.** Detail of prothorax (Fig. 69) showing rudimentary leg (arrow, 10μ). **72.** Head of last instar larva, dorsal view (100μ). **73.** Dorsal view of antennae and mouthparts (50μ). **74.** Antenna, dorsal view (10μ). **75.** Antenna, ventral view (10μ). (Length of scale bar in parentheses).



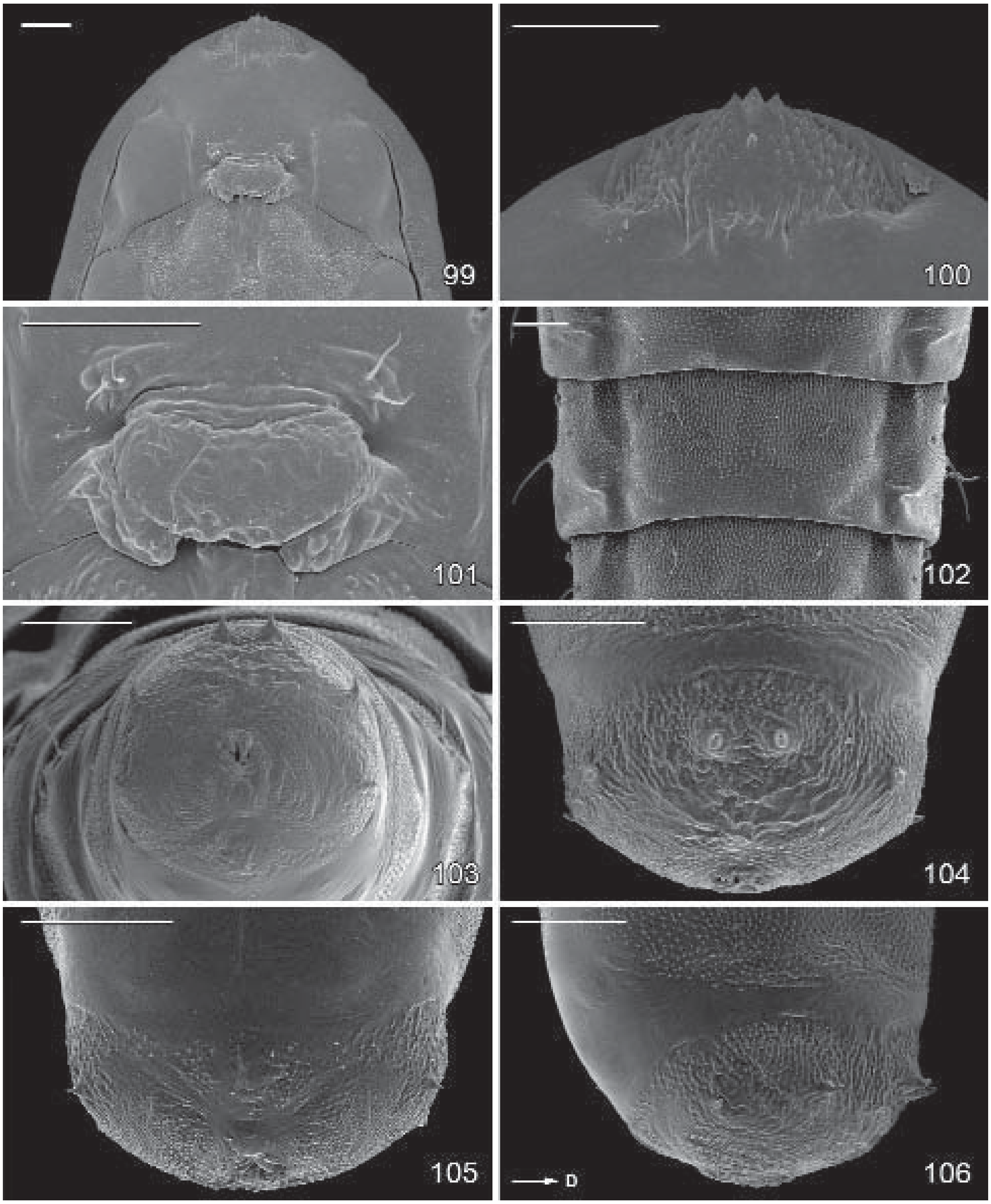
FIGS. 76–83. *Leurocephala schinus*ae, last instar tissue feeding larva. **76.** Antenna, anterior view (10μ). **77.** Head, anterior view (100μ). **78.** Mouthparts, anterior view (10 μ). **79.** Detail of left maxilla in Fig. 78 (10μ). **80.** Detail of spinneret (with silk) and labial palpi in Fig. 78 (10μ). **81.** Apex of spinneret (10μ). **82.** Head, lateral view (100μ). **83.** Detail of stemmata in Fig. 82 (50μ). (Length of scale bar in parentheses).



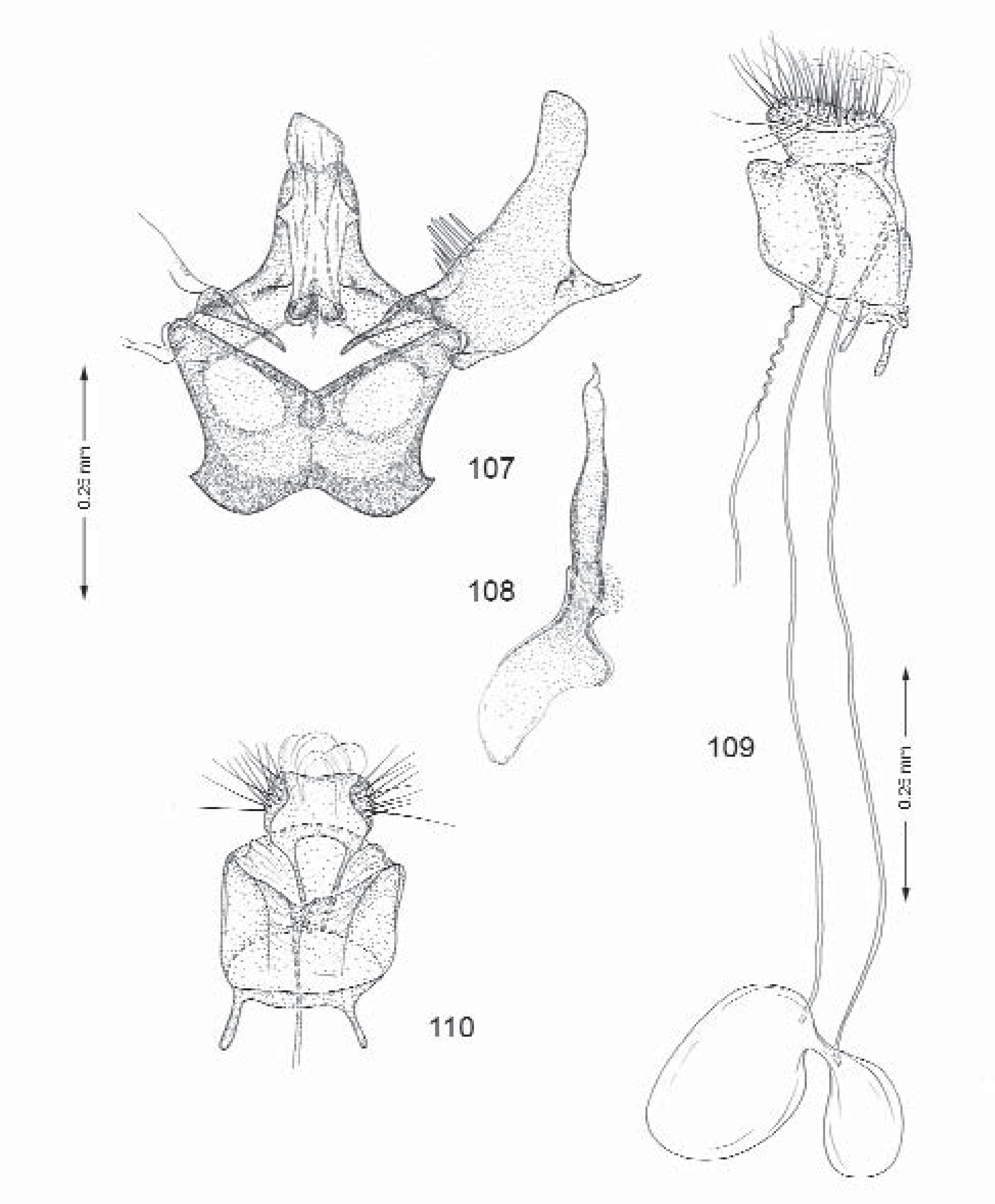
FIGS. 84–91. *Leurocephala schinus*ae, last instar tissue feeding larva. **84.** Head, ventral view (100µ). **85.** Head and prothorax, ventral view (100µ). **86.** Thoracic leg (10µ). **87**. Abdominal proleg, A5, A=anterior, L=lateral (10µ). **88.** Abdominal segment 10, dorsocaudal view (100µ). **89.** Anal proleg A10 (10µ). **90.** Abdominal segment 10, ventral view (100µ). **91.** Abdominal segment 10, lateral view, D= dorsal (100µ). (Length of scale bar in parentheses).



FIGS. 92–98. *Leurocephala schinusae*, chaetotaxy of last instar tissue feeding larva. **92.** Lateral schematic of prothorax, mesothorax, and abdominal segments 1, 2, 5–10. **93.** Head, dorsal view. **94.** Head, ventral view. **95.** Dorsal view of abdominal segments 8–10. **96.** Head, lateral view. **97.** Labrum, dorsal view. **98.** Mandible. (Scale lengths indicated).



FIGS. 99–106. *Leurocephala schinus*ae, pupa. **99.** Head, ventral view (100µ). **100.** Head, apex of Fig. 99. **101.** Detail of labrum of Fig. 99 (100µ). **102.** Abdominal terga A6–7 (100µ). **103.** Caudal end of abdomen, dorsal side up (100µ). **104.** Dorsal view of Fig. 101, A10 (100µ). **105.** Ventral view of Fig. 104 (100µ). **106.** Lateral view of Fig. 104 (100µ), D=dorsal. (Length of scale bar in parentheses).



FIGS. 107–110. *Marmara habecki*, genitalia. **107.** Male, ventral view. **108.** Aedeagus. **109.** Female, lateral view. **110.** Ventral view of Fig. 109. (Scale lengths indicated).

terebinthifolius plants growing on the shoulders of secondary roads of north-eastern Argentina. Rearing experiments were conducted in a walk-in chamber under controlled environmental conditions (25±1°C; 60±5% RH; 14-10 L:D). Twenty newly emerged adults were confined inside insect rearing sleeves (20 cm in diameter by 60 cm in length) wrapped around branches of potted *S. terebinthifolius* plants. A piece of cotton soaked in water-sucrose solution tied with a wire and hung from the upper access hole of the sleeve constituted the adults' food source. Adults were held for 24h to synchronize oviposition. Measurements were collected on egg incubation time, larval and pupal stage duration. The duration of the different life stages was: 5 days for eggs (mean ± SD = 5 ± 0; n = 5), 11–14 days for larvae (mean ± SD = 12 ± 1.1; n = 19), and 9–11 days for pupae (mean ± SD = 10 ± 1.5; n = 19).

Results of field surveys conducted in Argentina (Mc Kay unpublished data) and Brazil indicate a preference for *Schinus* species. However, host specificity tests currently underway at the quarantine facility of the USDA/ARS/IPRL in Ft Lauderdale, reveal that *L. schinusae* lays eggs and the larvae complete development on native North American Anacardiaceae (*Rhus* species). Consequently, the host range has been determined too broad to be considered as a biocontrol agent against Brazilian peppertree in the United States. (Wheeler unpublished data).

Marmara habecki Davis, new species

Figs. 7–8, 20–21, 107–111.

Diagnosis. The forewing patterns of *Marmara habecki* and *M. smilacisella* (Chambers) are essentially identical, with both subject to slight variation. The morphology of their male valvae is also similar in possessing a large, slightly curved saccular spine and a prominent comb of 4–5 spines arising near the base of the costal margin. The genitalia of the two species differ slightly with the curvature of the lateral margin of the vinculum more concave and the laterocaudal angle slightly flared in *habecki*, compared to being more convex and the angle more rounded in *M. smilacisella*. The larva of *M. habecki* is a stem miner on *Schinus terebinthifolius*, whereas that of *M. smilacisella* has been reared only from the leaves of *Smilax* (Smilacaceae). The most significant difference between the two species is indicated by their different CO1 barcode sequences (Fig. 111) which show a divergence of over 5.6 %.

Adult (Figs. 7–8). *Head:* Frons and vertex smooth, silvery white, irrorated with brown-tipped scales; collar grayish fuscous. Antenna ~ 0.8x length of forewing; scape fuscous, with pecten consisting of ~ 10–13 slender, fuscous, piliform scales; pedicel mostly white, with fuscous apical margin; flagellum smoothly scaled, uniformly fuscous, each flagellomere encircled by a single row of slender scales. Maxillary palpus dark fuscous. Labial palpus mostly white, dark fuscous laterally and at apices of segments 2 and 3. *Thorax:* Fuscous dorsally; paler, mostly white ventrally; tegula dark fuscous. Forewing: length 1.8–2.5mm; mostly dark fuscous to black with slight bluish luster, usually with 3 short, triangular, white striae of variable size equally spaced along costa and 3 similar, nearly opposite, white striae along hind margin; basal most striae sometimes fused to form a transverse band; a slender, white costal stria present near subapex at base of fuscous fringe; apex of wing white; terminal fringe with grayish bases to dark-tipped scales. Hindwing uniformly gray. Legs mostly white, strongly banded with dark fuscous at joints. *Abdomen*. Dark fuscous dorsally, except for white scales around T7; partially white ventrally with oblique segmental bands of fuscous laterally at anterior margins of each segment. Male with a pair of coremata consisting of a loose cluster of long, white piliform scales arising ventral-laterally from elongate pockets of eighth segment.

Male genitalia (Figs. 107–108). Uncus absent. Tegumen abruptly constricted to narrow apical half; apex slightly bilobed, with a shallow apical depression. Vinculum broad, with lateral margins curved inwards then flaring slightly outwards at broad, shallowly bilobed anterior margin. Valva with a prominent row of ~ 4–5 large spines arising near basal third of costal margin and 3–4 smaller spines basal to larger spines; apical half (cucullus) relatively narrow, basally expanding slightly to prominent, elongate saccular lobe bearing a single apical spine; a moderately long, slender triangular lobe projecting mesally from base of saccular lobe. Aedeagus slender, slightly sinuate, with acute apex; total length ~ 1.3x length of valva; phallobase well developed, usually directed more toward right side of genital capsule, ~ half the aedeagus in length, with hood evenly curved dorsad and with a distinct swelling near junction with of aedeagus.

Female genitalia (Figs. 109–110). Anterior and posterior apophyses short, with posterior apophyses ~ 1.5 × length of anterior pair. Ostium a simple opening on caudal margin of sternum VII. Ductus bursae a very long and slender tube ~ 10 × length of posterior apophyses, terminating on smaller chamber of bilobed corpus bursae. Corpus bursae consisting of two oval chambers connected by a constricted, short passage of variable length. Ductus seminalis similar to ductus bursae in length and diameter, terminating on larger chamber of corpus bursae. Walls of corpus bursae membranous; signum absent.

Hosts. Anacardiaceae: *Schinus terebinthifolius* Raddi.

Parasitoids. In Florida a single parasitoid emerged from the pupa of *M. habecki*, possibly *Copidosoma* sp. Encyrtidae, (Chalcidoidea).

Larval biology (Fig. 20). Larva a stem miner on *Schinus terebinthifolius*. Larvae from Florida (Fig. 20) were observed to mine along the stems a total distance of nearly 70 cm. The width of the stem mines varied from 0.26–2.15 mm. Stem mines of another undescribed species, as indicated by divergent CO1 sequences (Fig.111), were also discovered on *S. terebinthifolius* in Brazil.

Cocoon (Fig. 21). Cocoons were formed in crevices among dried leaves (in rearing culture) indicating that the larva leaves the mine to pupate. The surface of the cocoon is covered by approximately

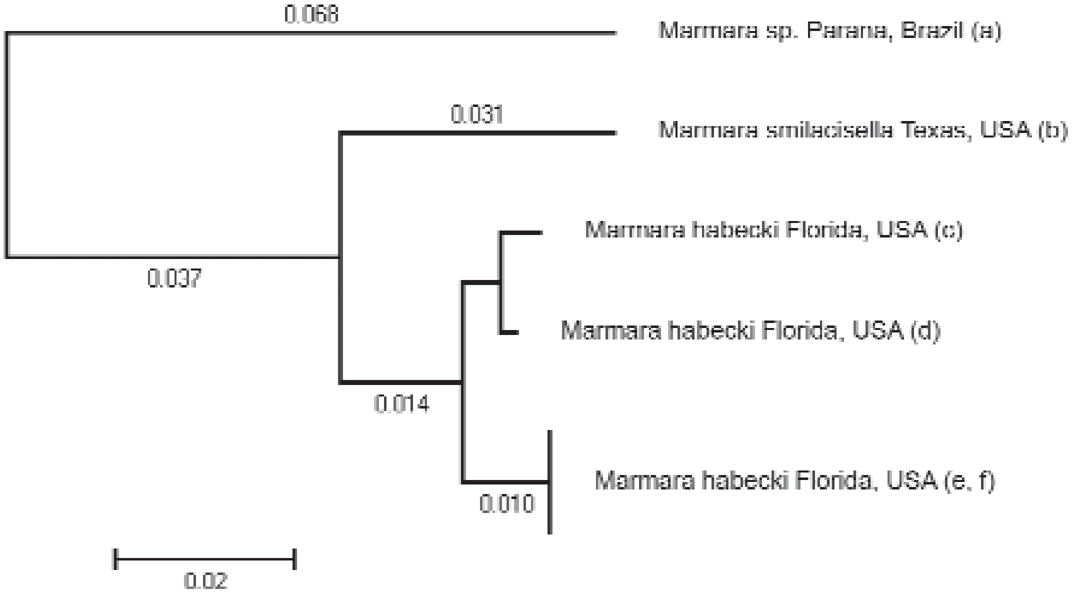


FIG. 111. Sequence distance tree of *Marmara* derived from 6 samples among 3 species based upon neighbor-joining analysis with Kimura 2-parameter model. The analysis shows significant CO1 divergences among the North American *Marmara smilacisella* reared from *Smilax* (b), the apparently undescribed *Marmara* reared from *Schinus terebinthifolius* in Brazil (a), as well as *Marmara habecki* mostly reared from *Schinus* in Florida, USA (c–f). Sequence lengths are shown on main branches. Pertinent specimen data including source of tissue samples for each specimen are: (a) Brazil: Parana: 13 km W Curitiba, larva, host: *Schinus terebinthifolius*; (b) USA: Texas: Harris Co: Houston, adult legs, host: *Smilax* sp.; (c) USA: Florida: Pinellas Co: Fort Desoto Park, adult legs, host: *Schinus* sp.,; (d) USA: Florida: Polk Co: entire moth, Lake Alfred, from *Marmara gulosa* pheromone trap; (e, f) USA: Florida: Broward Co: Fort Lauderdale, larvae, host: *Schinus terebinthifolius*.

30–40 small, silvery, frothy bubbles often arranged in 3–4 smaller clusters of ~ 10–12 bubbles each.

Types. *Holotype*: ♂; USA: FLORIDA: Broward Co: Fort Lauderdale: 13 Aug 2008, Dyer & Wheeler, reared from stem of *Schinus terebinthifolius*, (USNM). Paratypes (7 ♂, 7 ♀): USA: FLORIDA: Alachua Co: Edgecliff: 1 ♂, 21 May 1994, adult 5 Jul 1994, DHH rearing, Host: *Schinus* sp., D. Habeck. Collier Co: 1 ♂, em. 2009, Host: *Schinus terebinthifolius*, stem miner, slide USNM 34188. Monroe Station, HWY. 41: 1♂, 13 Dec 1989, pupa 16 Dec 1989, adult 8 Jan 1990, DHH rearing #A-5373, Host: *Schinus* sp., berries, J. Gilmore, J. DeNicole, Digital image captured USNM. Lee Co: Ft. Myers: 2 ♂, 14 Sep 1998, adult 1 Oct, Host *Schinus* sp., DHH rearing #A-4542b, D. Habeck, F. Bennett, DRD slide 3731. Monroe Co: Key West: 22 Jul 1991, adult 9 Aug, 1991, F. Bennett, DHH rearing #A-6008, Host: *Schinus* sp., berries & foliage, DRD slide 4491, Digital image captured USNM; 1 ♂, 22 Jul 1991, adult 12 Aug 1991, 1 ♀, 22 July 1991, pupa 2 Aug 1991, adult 9 Aug, 1991, F. Bennett, DHH rearing #A-6008, Host: *Schinus* sp., berries & foliage. Pinellas Co: Ft. Desoto Park: 24 Jan 1989, 1 ♀, adult 10 Feb 1989; 1 ♀, pupa 30 Jan 1989, adult 9 Feb 1989; 1 ♀, pupa 31 Jan 1989, adult 16 Feb 1989, DHH rearing #A-4702c, slide USNM 33926; 1 ♀, pupa 3 Feb 1989, adult 16 Feb 1989, DHH rearing #A-4702c, slide USNM 33919; 1 ♀, pupa 2 Feb 1989, adult 14 Feb 1989; 1 ♂, 4 Feb 1989, adult 20 Feb 1989, DHH rearing #A-4726a, Host: *Schinus* sp., leaves & berries W. Klerks, F. Bennett. Polk Co: Tenoroc: 1 ♀, 13 Jan 1994, adult 1 Feb 1994, D. Habeck, DHH rearing #A-6818, Host: *Schinus terebinthifolius*, slide USNM 34058. (Paratypes deposited in MGCL and USNM).

Other specimens examined: USA: FLORIDA: Polk Co: Lake Alfred: 2 ♂, 25 Sep 2007, L. Stelinski, N-40 Citrus Peelminer, USNM slide 34146; 2 ♂, Jun 2008, W. L. Meyer, Citrus sp. Pheromone trap. USNM slides 34123.34124, 2 adults (sex?), BOLD ID: RDOPO096-09, BOLD ID: RDOPO097-09, (USNM).

Flight period. Adult emergences have been reported in Florida from January to mid October with most emergences occurring in February.

Distribution. In Florida this species has been reared on *Schinus terebinthifolius* from Alachua County in northern Florida south to the Florida Keys. Larval mines of an unidentified *Marmara* have been found on stems of *S. terebinthifolius* in Brazil and Argentina, but only a single adult female from near Macae, RJ, Brazil has been reared.

Etymology. This species is named in honor of Dr. Dale Habeck (deceased 17 May 2010) who first reared many of the specimens studied in this report.

Discussion. The genus *Marmara* is known to occur only in the New World where 23 species have been described, 19 of these from North America north of Mexico (De Prins & De Prins 2010). The Neotropical leafmining fauna, however, is largely unknown (Guillén et al. 2001).

Adults of *M. habecki* are nearly inseparable morphologically from *M. smilacisella*. As noted in the diagnoses, slight differences have been observed in the shape of the male vinculum, with that of *habecki* possessing more concave lateral margins and more flared anterocaudal angles. Distinct differences in their larval biologies are probably significant, although polyphagy and variation between a leaf mining and stem mining habit have been reported in at least one other *Marmara*, *M. gulosa* (Guillén et al. 2001). Because of these uncertainties, attempts were made to obtain CO1 barcode sequences from the few most recently collected populations available of *M. habecki* and *M. smilacisella*, as well as of an unidentified stem mining *Marmara* discovered on *S. terebinthifolius* in Argentina and Brazil. Of the 10 specimens submitted, 4 could not be sequenced. The 6 specimens that were (for the entire 658 bp segment) revealed three distinct groups, each separated by a minimum divergence of 4.5% or more (Fig. 111). Although only a single female was reared from the Brazilian stem mines, CO1 sequence divergence of nearly 12% between the Brazil and Florida populations strongly suggest that these represent distinct species. Because females often provide inadequate morphological diagnostics in this genus, males need to be reared from the Brazilian populations, and more specimens in general need to be sequenced to verify these conclusions.

During a recent survey for *Marmara* pests of Citrus in southern Florida using sticky traps baited with the sex pheromone of the citrus peelminer, *Marmara gulosa* Guillén and Davis from California (W. Meyer in litt.), numerous adult *M. habecki* were collected. These adults were very similar to the adults of *habecki* reared from *Schinus* stem mines in their CO1 barcode sequences and male genitalia but were not included in the type series because of their poor physical condition.

Although most of Habeck's rearing labels variously state "berries", "berries & foliage", or "leaves & berries", it is apparent from Habeck's rearing records, graciously provided by D. Mathews Lott, that most of the moths were reared from the stems of *Schinus terebinthifolius*. This is particularly evident in records A4542b, A4702c, A4726a, A6008, and A6818.

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FIRST DESCRIPTION OF A FEMALE OF *ANTHERAEA MEISTERI* BRECHLIN AND NOTES ON SOME PRE-IMAGINES OF THREE RECENTLY DESCRIBED SPECIES OF SATURNIIDAE (LEPIDOPTERA) FROM THE TROPICAL MOIST FORESTS OF THE ANDAMAN ISLANDS

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ABSTRACT. Between the years 2001 and 2002 four species of Saturniidae were added to the fauna of the Andaman Islands. *Antheraea* (*Antheraea*) *insularis* was raised from a subspecies to a full species (Brechlin & Kitching 2001) and three new species, *A.* (*Antheraea*) *meisteri*, *A.* (*Antheraeopsis*) *rudloffi* and *A.* (*Antheraea*) *cernyi* were described by Brechlin (2001). With these additions the total number of saturniids known from these islands rose from six to ten. While the pre-imagines and the larval food plants of six of these species were discovered and studied since the 1990s (Veenakumari *et al*. 1992, 1996, 2005; Prashanth Mohanraj *et al*.1993, 1998; Prashanth Mohanraj & Veenakumari 2002), we describe and figure some pre-imaginal stages of the three recently described saturniid species (*A. meisteri*, *A. insularis* and *A. rudloffi*), report on the natural host plants of *A. meisteri* and *A. rudloffi*, and describe the female of *A. meisteri*.

Additional key words: *Antheraea meisteri, Antheraea insularis, Antheraea rudloffi*

The Andamans and Nicobars form the northern extremity of the island arc extending from New Guinea through the Lesser and Greater Sunda Islands (Indonesia). Politically a part of India, these islands are home to some of the least disturbed forests of the country. The Saturniidae were among the earliest groups of insects to be collected and studied from the forests of these islands since the British colonized them in the mid nineteenth century. Nevertheless it is clear that the saturniids of these islands are still not fully known as is evidenced by the discovery of a number of new species in the early twenty first century. It is also intriguing that not a single saturniid is known from the Nicobar Islands where the forests are even less disturbed than those of the Andamans and are floristically more similar to the southeast Asian islands which harbor a very rich and varied fauna of Saturniidae (Holloway 1987; Nassig et al. 1996a, b). The immature stages and life histories of the Andaman saturniids were also unknown until the closing decade of the twentieth century. The Saturniidae play a definitive role in nutrient turnover, as the largest Lepidoptera, voraciously feeding on the foliage of different species of native trees. The saturniid fauna of the Andaman and Nicobar islands remains to be studied in all its varied aspects.

Only six species of Saturniidae (described between 1877 and 1914) were known to occur in the Andaman islands (Moore 1877; Jordan 1911; Watson 1911; Peigler 1989) until Brechlin & Kitching (2001) elevated *Antheraea* (*Antheraea*) *insularis* from a subspecies of *A.* (*Antheraea*) *frithi* to a full species and Brechlin (2002) described three new species—*A.* (*Antheraea*) *meisteri*, *A.* (*Antheraeopsis*) *rudloffi* and *A.* (*Antheraea*) *cernyi*—from the Andaman islands. A second species of *Cricula* was mentioned but not described by Watson (1913) from the Andaman Islands but no specimen of this species is known to exist in any museum (Nassig 1990, personal communication). The total number of saturniids now known to occur in the Andamans is ten, and all are endemic to these islands. Until the 1990s all the Andaman saturniids were known from adult specimens only. The pre-imagines of the 6 species originally known from these islands were described and illustrated in color between the years 1992 and 2005 (Veenakumari et al. 1992, 1996, 2005; Prashanth Mohanraj et al. 1993, 1998; Prashanth Mohanraj & Veenakumari 2002).

The species described by Brechlin & Kitching (2001) and Brechlin (2002) are known only from adult specimens. The pre-imaginal stages of these species are not known. We describe and figure some pre-imagines of three of these new species viz., *A. meisteri*, *A. insularis* and *A. rudloffi* and report the natural host plants of *A. meisteri* and *A. rudloffi*. We also figure and describe the female of *A. meisteri* for the first time.

To overcome the problems in the systematics of the genus *Antheraea*, Nassig (1991) proposed the utilization of characters from the life history and the pre-imaginal morphology of these species. He stressed that this would entail the rearing of each species collected in their respective areas of distribution. On this basis he proposed the tentative division of the large subgenus *Antheraea* (*Antheraea*) into four species groups. Subsequent studies (Nassig 1996b) have established the validity of these suggestions, though the phylogeny of the group remains to be worked out.

Materials and Methods

Light traps were employed for collecting adults, while immature stages were collected by searching probable host plants. The collection sites and the mode of collection of each species are summarized in Table 1.

When adult females were collected they were brought to the laboratory and maintained in cages for oviposition. The eggs were then incubated under ambient conditions for hatching and the larvae reared on their respective host plants when known. When the food plants were not known, a number of probable host plants were provided to the larvae and the accepted plant(s) were subsequently provided until they pupated. The rearing methods were otherwise identical to those detailed in Prashanth Mohanraj & Veenakumari (2002).

A. meisteri was collected by looking for fecal pellets on the ground beneath the possible food plants. Fecal droppings of a large lepidopterous caterpillar were first noticed at the base of a *Hopea odorata* (Dipterocarpaceae) tree as the shrubbery beneath it had been cleared and burnt. This tree was situated on a hill about 52m above mean sea level at Garacharma, S. Andaman (Fig. 3d). Some droppings were large and quite fresh indicating the presence of large larvae in the tree.

Since it was not possible for anyone to climb the tree, we used a 50m length of fishing line and a 5mm diameter nylon rope as well as a catapult and a penicillin bottle packed with soil. One end of the fishing line was secured around the neck of the weighted penicillin bottle, while the other end was tied to the nylon rope. The penicillin bottle was then shot over a desired branch of the tree with the catapult. Once the bottle came within reach, it was pulled to draw the nylon rope over the branch. The two free ends of the nylon rope were brought together and 6 or 7 people pulled it (Fig. 3e), until the branch broke and fell to the ground. Each fallen branch was scoured for eggs, larvae or pupae. None were found on the branches brought down on the first two days. Fresh fecal droppings however were visible every day. On the third day, 5 August 2000, we successfully brought down late instar larvae of *Antheraea meisteri* from a branch about 25m above ground level. This time, unlike in earlier instances when branches were brought down (Prashanth Mohanraj & Veenakumari 2002), some larvae were crushed to death by the falling branches (Fig. 1g).

The larvae of *A. meisteri* were reared on the leaves of *Hopea odorata* Roxb. (Dipterocarpaceae) in plastic cages following methods described earlier (Veenakumari et al. 1992, 1996; Prashanth Mohanraj et al. 1993, 1998; Prashanth Mohanraj & Veenakumari, 2002). Four days after collection, they pupated.

Results and Discussion

Months and localities of occurrence. Adults of *A. insularis* were earlier collected in the months of March and November from South Andaman (Brechlin & Kitching 2001). We have found adults in all the months between December and March at Bloomsdale, S. Andaman. We collected all the adults in a light trap in which some of the females laid eggs.

Table 1. Collection localities, mode and stage of collection of the three new species of Antheraea from the Andaman islands.

Species	Locality	Mode of collection	Stage of insect collected
A. meisteri	Garacharma, S. Andaman	Visual search	Larvae
	Mt. Harriet, S. Andaman	Insect net	Adult
A. rudloffi	Mt. Harriet, S. Andaman	Visual search	Larvae
	Wimberleygunj, S. Andaman	Visual search	Larvae
A. insularis	Bloomsdale, S. Andaman	Light trap	Adult; Eggs

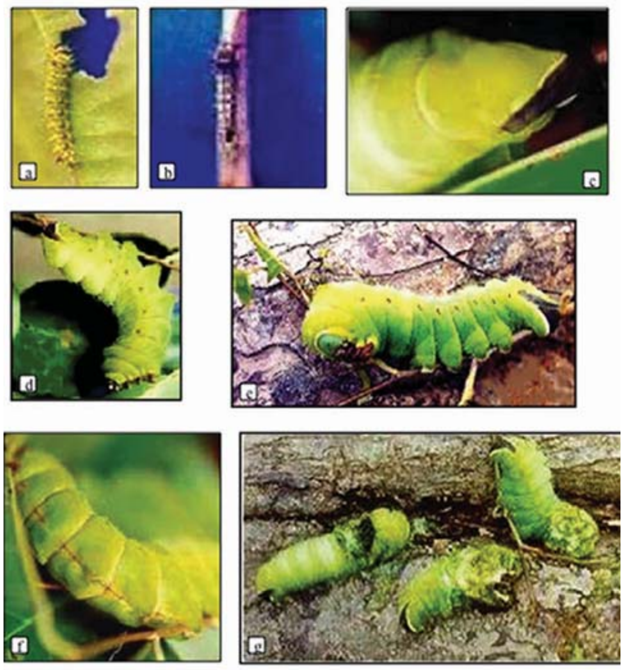

FIG. 1. (upper left column)*Antheraea (Antheraea) insularis* **(a)** first instar larva; *Antheraea (Antheraea) meisteri* **(b)** first instar larva, **(c)** dorsal view of anal segment of fifth instar, **(d)** fifth instar larva, **(e)** fifth instar larva collected from a branch broken by the 'rope method', **(f)** ventral surface of fifth instar larva, **(g)** larvae damaged as a consequence of hitting the ground when the branch was brought down.

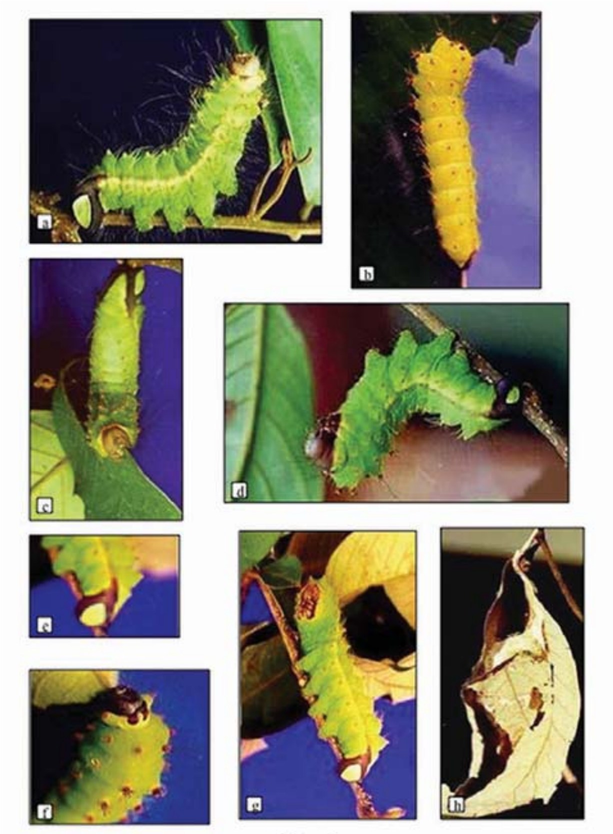

FIG. 2. (lower left column) *Antheraea (Antheraeopsis) rudloffi* **(a)** fifth instar larva, **(b, c)** dorsal views of fourth instar larva, **(d)** fourth instar larva, **(e)** triangle on anal proleg of fourth instar, **(f)** close-up of head, prothoracic shield and dorsal thoracic scoli, **(g)** head and lateral view of fourth instar larva, **(h)** cocoon.

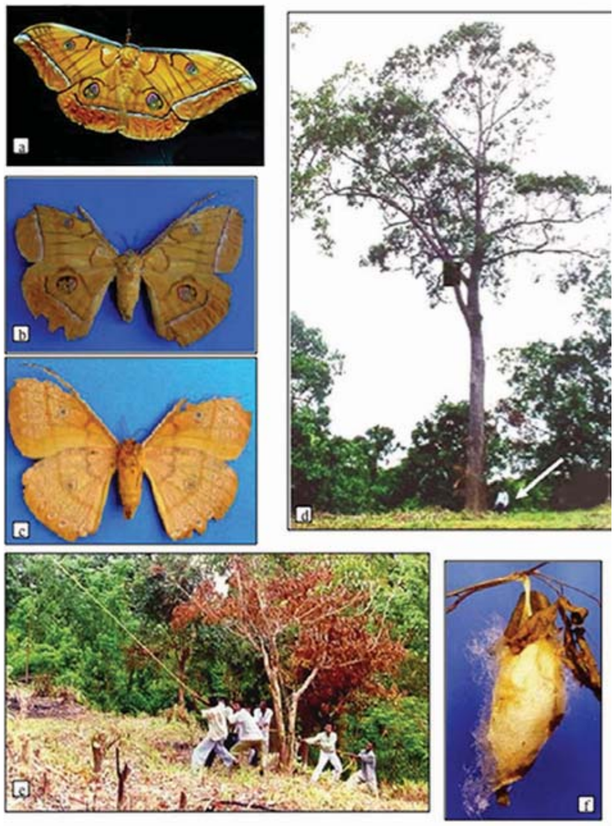

FIG. 3. (below right column) *Antheraea (Antheraea) meisteri* **(a)** freshly emerged female, **(b)** dorsal and **(c)** ventral surfaces of pinned specimen. All photographs are of the same female. The wings are frayed in the latter photographs because the virgin female seen in (a) was placed in a wire-mesh cage in a futile attempt to attract males. **(d)** *Hopea odorata* (note relative sizes of man- indicated by arrow- and tree) – the tree from which larvae of *A. meisteri* were collected. **(e)** Field assistants tugging at the nylon rope to bring down a branch suspected to harbor larvae of *A. meisteri*. **(f)** Cocoon of *A. meisteri.*

The first adult specimens of the nominotype of *A. meisteri* were collected in August from Little Andaman (Brechlin 2002). We collected the larvae of this species in August, but from Garacharma in S. Andaman. One adult female was also collected on Mount Harriet on 1 August 1993. This is the second species of Saturniidae reported from Little Andaman (we failed to collect it from this island), the other being *A. andamana* (Prashanth Mohanraj & Veenakumari 2002). The type locality is misspelled as 'Huck' Bay instead of Hut Bay in Brechlin 2002.

Adults of *A. rudloffi* were collected from South Andaman in the months of August and November (Brechlin 2002). We collected adults from Mt. Harriet and Wimberleygunj, South Andaman in the months of March, August and December.

Larval descriptions: (i) *Antheraea (Antheraeopsis) rudloffi* Brechlin 2002. Like the other members of this subgenus, *A. rudloffi* feeds on Lauraceae and has crimson markings. The larvae of this species have prominent burnished, gold markings, which have not been reported in the larvae known in other species in this subgenus (Nassig et al. 1996b). Nevertheless the late instars of *A. rudloffi* have the typical supra-spiracular line characteristic of the genus and the yellow-green "patch" on the anal proleg (akin to the "patch" seen in the Attacini), which is unique to the subgenus *Antheraea* (*Antheraeopsis*). Prior to molting the larvae hang limp and bend sideways (as though infected by a nucleopolyhedrosis virus). When excreting, the larva detaches its anal prolegs from the twig, bends the anal end sideways, extrudes the fecal pellet and then resumes its original position. The morphologies of the fourth and fifth instars of *A. rudloffi* are described below.

***Antheraea rudloffi* fourth instar (Figs. 2b, c, d, g).** Six larvae of *A. rudloffi* were collected in May and August, about 15 feet above the ground on, *Litsea kurzii* King ex Hook f. (Lauraceae), a small understory tree growing along the roadside, in Mount Harriet National Park, South Andaman.

The head is a dull chocolate brown. There is a distinct, prominent chocolate brown band between the head and the prothoracic shield. The prothoracic shield is yellowish with the dorsal scoli being terminally crimson and black basally. The legs are chocolate brown with yellow bases. The prolegs are green with a black band. The crochets are brown.

The spiracles are black in the center surrounded by a crimson border. As the instar matures the spiracle on A8 turns fully yellow. The supra-spiracular line is maroon above and yellow below. The dorsal scoli, with the exception of those on the prothorax are crimson terminally and a combination of black and burnished gold basally. The supra-spiracular scoli are bright crimson with golden yellow setae. Subspiracular scoli are crimson with black setae. Dorsal scoli on A8 are fused and crimson without any golden color. All setae above the spiracular line are golden yellow. The ventral surface is deep green. The supra-anal triangle is small and bluish-green. The triangle on the anal clasper is yellow-green with a black border that is widest at the apex. A faint, but distinct, grey band runs diagonally from the supra-spiracular line to the (imaginary) line joining the supra-spiracular scoli on abdominal segments 1 to 8. The spiracles lie on these diagonals.

Fifth instar (Fig. 2a). The head is very light brown. The legs are brown and are set in a brown ring. The prolegs are light green and of a different shade from the yellow-green of the rest of the body. There are raised black spots on the prolegs with black setae, which are positioned lower on the anal prolegs. The crochets are brown.

The supra-anal triangle, as well as those on the anal claspers, is more yellowish than the rest of the body. The triangles on the anal claspers (Fig. 2e) have a thin, distinct black inner border, which in turn is surrounded by a broad brown grey band. The spiracles are yellow and enclosed in a reddish-brown band. The supra-spiracular line is bicolored; pinkish brown above and yellow below. The dorsal scoli have the shining, metallic, golden basal spot, while the inner basal surface is reddish brown. The subdorsal and the subspiracular scoli are reddish brown below and terminally yellow. All scoli are tipped with black setae. The setae on the surface of the body are long and yellow.

This instar measures 5.7 to 6.9 cm (mean = 6.4cm; n=4) long and pupates in 13 to 14 days (mean = 13.5 days; n=2).

Pupal period. Pupation takes place in a stalked cocoon constructed between leaves (Fig. 2h). The pupal period lasted for 272 days (n=1).

Adults. While adult moths were collected from their natural habitat in March 1997, and December 1998, the laboratory reared individual emerged in June 1999.

(ii) *Antheraea (Antheraea) insularis* (Watson 1914). Four adults were collected between December and March 1997–1998, in a light trap set up at Bloomsdale, South Andaman. The light trap was placed in the center of a rice field, which had a disturbed forest all along one border. The moths laid between 9 and 20 eggs in the light trap. The eggs were 0.6 cm in length and hatched in 9 days. Since the host plant of this species is not known in the Andaman Islands, we provided the newly hatched larvae with leaves of *Dipterocarpus* spp. and *Ficus* spp. The larvae fed minimally on these leaves and died. We therefore describe only the first instar larvae of this species.

A. insularis and *A. andamana* are the only two species of Andaman saturniids belonging to the *frithi* subgroup of the *paphia/frithi* species-group. *A. insularis* failed to feed on Dipterocarpaceae and on Moraceae, though *Ficus* spp. belonging to the latter family are the food plants of *A. andamana* (Prashanth Mohanraj & Veenakumari 2002). Stone (1991) reports Euphorbiaceae and Lauraceae in addition to Dipterocarpaceae as other recorded food plants of *A. frithi*. Future studies will have to test plants from these families as possible food of the larvae of *A. insularis*.

The first instar larva of *A. insularis* as described below is yellow with a black head, prothoracic or cervical shield and anal plate as expected in the species subgroup (*frithi* of *paphia/frithi*) to which this taxon belongs.

First instar (Fig. 1a). This larva measures 0.6cm in length at eclosure and is pale yellow in color. The head is glossy brown; the labrum is brown, but the clypeus is white. The prothoracic shield is glossy black while the anal plate is black.

The legs are brownish – black with deep brown claws and brown crochets. The prolegs are pale yellow with a broad grey band on the outer surface and a row of long, golden, inward curving setae. The anal prolegs have a grayish-black, triangular patch on the outer surface. Crochets are brown in color.

The dorsal scoli on the metathorax and on abdominal segment VIII are black in color, all the rest are pale yellow. The setae on the abdominal scoli are golden-yellow basally and deep brown or black terminally. The setae on the thoracic scoli are black except for a few white ones on the dorsal prothoracic scoli. The spiracular scolus on the prothorax has the largest number of terminal setae, numbering from 20–22. The dorsal and subdorsal abdominal scoli have one terminal, centrally located, seta surrounded by a circle of 4 to 6 setae —while the subspiracular scoli on the abdomen have two centrally located terminal setae surrounded by a circle of 7 setae. The pale brown to whitish spiracles are located in a row of irregular brown to black markings along the spiracular line.

(iii) *Antheraea (Antheraea) meisteri* Brechlin 2002. *A. meisteri* occurs in the *helferi* species-group. It has been found to feed on *Hopea odorata*, a species of Dipterocarpaceae. This is unlike the other species in this group, which are known to feed on Fagaceae, Sapindaceae and Betulaceae. On the other hand, three species of *Antheraea* belonging to the *paphia–frithi* species-group are the only saturniids known to feed on dipterocarps. This could perhaps be one character linking the *paphia/frithi* and *helferi* species groups as sister groups. A further difference is that this is the first report of a species of *Hopea* being used as a larval food plant by *Antheraea*. All other dipterocarp-feeding *Antheraea* utilize *Shorea* spp. only. *Shorea* does not occur in the Andaman Islands. The only two genera of dipterocarps that occur here are *Dipterocarpus* and *Hopea*. Interestingly no dipterocarp is found in the Nicobars. If *A. meisteri* occurs there its larvae will have to utilize a food plant belonging to a different family.

Though food plant utilization by the larvae may indicate that it be placed in the *paphia–frithi* species-group, the green head of the final instar and the yellow color of the cocoon indicate its similarity to the other members in the *helferi* group.

The first and fifth instar larvae as well as the cocoon and the female of this species are described.

First instar (Fig. 1b). The head is the color of honey or golden brown with whitish setae. The maxillae are whitish – grey, the maxillary palps pale brown, the clypeus and labrum whitish, and the labial palps brown. The prothoracic shield is broad, dull yellow-brown.

The dorsal scoli are black on the metathorax and abdominal segment VIII; all other scoli are transparent yellow. Long, brown-black setae arise from the dorsal scoli while setae on all other scoli are white or pale yellow. The area behind the line joining the dorsal scoli on the metathorax is black and extends onto abdominal segment I, where it tapers to a point on the imaginary line joining the dorsal scoli, thus forming a black triangle with its base on the metathorax and apex on the first abdominal segment. There is a broad black band anterior to the dorsal scoli on abdominal segment VIII. The latero-ventral tubercles on the thorax are small, yellow and papilla-like.

There are three lines on abdominal segments I to VII: a broad, brown mid-dorsal line or band between the dorsal tubercles; a brown line between the dorsal and lateral tubercles and a black line between the subdorsal and lateral tubercles.

The lateral prothoracic scoli are the largest of all the scoli. These are bulbous apically and yellow along the basal two-thirds. On the bulbs are situated the setae. The central setae are pale yellow while those on the periphery are brownish black. Dorsal and subdorsal scoli on prothorax are in contact with each other while on all other segments they are separated. The setae on these scoli are long with 2 setae being brown and the remaining pale yellow.

The legs are deep glossy brown basally and pale yellow terminally with brownish black claws. The prolegs are yellow with brown crochets. The spiracles are deep yellow. Transverse brown bands occur on the mesothorax, one of which is anterior and the other posterior to the tubercular line.

The anal shield is pale brown in the center and yellow along the periphery. The anal prolegs have a dark basal patch.

The ventral surface is dirty white to yellow.

Fifth instar (Figs. 1d, e, f). The overall color of the larva is yellow green. The ventral surface is green with a distinct mid-ventral magenta stripe running along the length of the larval abdomen but broken in the spaces between each pair of prolegs, including the space between the anal prolegs.

The head including the frons is apple green and of a shade different from the rest of the body. The labrum is light brown, and the mandibles deep brown. The antennae arise from cream/off-white bases, which are of the same color as the prothoracic band. This is a cream band along the anterior margin of the green prothoracic shield, which is distinctly visible even when the larva stands in its contracted 'S' shaped posture.

All spiracles are deep brown with longitudinal yellow centers bordered by pale yellow halos along their outer margins. Small blue spots with brown setae set in them are present below the spiracles on the first five abdominal segments. A very small, indistinct blue spot is also present on the sixth abdominal segment. In line with these spots, two blue spots are present on the pro- and mesothorax.

The legs are deep burnt brown. The crochets are also deep brown. The prolegs are green with a cream to yellow band above the crochets. The anal claspers have a deep burnt chocolate brown basal and cream band bordering the inner margin.

There are six to eight whitish setae along the anterior margins of the dorsal surface of abdominal segments I to VIII, all of which are directed forwards or towards the anterior end of the larva. The 'supra-spiracular line' is not a separate line but formed by the meeting of the margins of the upper dark green region and the lower light green region and extends from abdominal segments II to VIII.

When the larva assumes its contracted 'S' shaped stance, a pinkish band separates each segment from its neighboring segment except between the pro- and meso-thoracic segments where this band is absent.

Cocoon (Fig. 3f). The larvae pupate in stalked cocoons between leaves. The freshly spun cocoon is pure white in color and later turns golden yellow.

Pupal period: The pupal period in our lone female lasted 20 days.

Oviposition. A virgin female laid 33 eggs in the night within 24 hours after emergence. It laid 141 eggs in 4 days.

Forty eight hours after emergence we placed the female moth in a cage in the field on two consecutive nights close to the *Hopea odorata* tree from which the larvae had been collected. No male moths were attracted to this female.

Adult female. Allotype ♀ (Figs. 3a, b, c). South Andaman island, Garacharma 52m above m.s.l., 28.viii.2000; coll. K. Veenakumari and Prashanth Mohanraj; in coll. National Bureau of Agriculturally Important Insects, Bangalore, India

Additional material: South Andaman island, 1 ♀, damaged, no date; 1 ♀, Garacharma, South Andaman, 1.viii.1993 in coll. R.S. Peigler, Texas A & M University, USA.

Description of adult female. Antennae 17mm long; forewing length 82mm (n=2); Forewing ocelli (11-12mm long and 9mm wide; n=2) tear-drop shaped with hyaline center (3mm diameter, n=2); hind wing length 13mm (n=1) with larger tear-drop shaped ocellus (13mm long and 11mm wide inclusive of eyelid; n=1); hind wing with very small hyaline center; eyelid 3mm long with large prominent yellow center An eyelid of this kind with the yellow center or iris is characteristic of this species.

Wings and abdomen ochre on upper surface; median line faint; antemedian line reddish brown; post median line absent; submarginal line is double colored on both wings, thickly edged with white along the outer margin.

We stress that the female of *A. meisteri* has the distinguishing black 'eyelid' on the hind wing ocellus and exhibits the 'pronounced venation' seen in some forms of *A. helferi* (Nassig 1996a). This, together with the pre-imaginal characters mentioned above, indicates that this does belong to the *helferi* species-group, lending credence to the conclusions of Brechlin (2002).

To conclude, our observations corroborate Brechlin & Kitching's (2001) and Brechlin's (2002) placement of *A. insularis* and *A. meisteri* in the *paphia/frithi* and *helferi* species groups (respectively) of the subgenus *Antheraea* (*Antheraea*). It also substantiates the placement of *A. rudloffi* in the subgenus *Antheraea* (*Antheraeopsis*). It is however important that these species are reared on their natural host plants and their complete life histories studied. It would be ideal if detailed studies on pre-imaginal morphologies along the lines of the study by Rougerie & Estradel (2007) are undertaken for all the saturniids of the Andaman and Nicobar islands.

Of the ten species of saturniids known from the Andaman Islands, five belong to the genus *Antheraea* thus making it the most speciose genus of this family on these islands. Two species of *Antheraea*, viz., *Antheraea andamana* and *A. meisteri*, are the only saturniids on these islands with ranges extending beyond the island of South Andaman. The fact that saturniids have not been collected from even the proximate islands of North and Middle Andaman, which together with South Andaman constitute the Great Andaman (all three of which were one island during periods of sea level lowering in the Pleistocene), clearly indicates the inadequate attempts at collection and the likelihood of the existence of hitherto unknown species in the forests of these islands. Being close to Sumatra and the rest of the SE Asian region, which are rich in saturniids, it is very surprising that so far none have been collected from any of the Nicobar Islands. Increased efforts to look for and collect these moths will reveal the presence of many more novelties on these islands.

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REVIEW OF THE *EUCOSMA PULVERATANA* (WALSINGHAM) SPECIES GROUP, WITH DESCRIPTIONS OF EIGHT NEW SPECIES (TORTRICIDAE)

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ABSTRACT. *Eucosma pulveratana* (Walsingham) is reviewed along with its closest congeners, *E. suadana* Heinrich, *E. mirosignata* Heinrich, *E. consobrinana* Heinrich and *E. aeana* McDunnough. Eight new species are described that are similar to *E. pulveratana* in forewing pattern and genitalia: *E. coconana*, *E. costastriata*, *E. floridensis*, *E. mojaveana*, *E. navajoensis*, *E. parapulveratana*, *E. seamansi*, and *E. sepiana*. *Eucosma aeana* is recognized as a junior synonym of *E. suadana*. Adults and genitalia of each species are illustrated.

Additional key words: Olethreutinae, Eucosmini, *consobrinana*, *suadana*, *mirosignata*

Walsingham (1879) described *Paedisca pulveratana* from four specimens he collected at San Francisco, California in 1871. The species now resides in *Eucosma* Hübner, having been transferred there by Fernald [1903]. During the past one hundred and thirty years, specimens of similar forewing pattern and genitalia have accumulated in North American collections, and only four additional names have been proposed to accommodate them: *E. consobrinana* (Heinrich 1923), *E. suadana* (Heinrich 1923), *E. mirosignata* (Heinrich 1929), and *E. aeana* (McDunnough 1942). This material includes perhaps a dozen unrecognized species, some represented by only a few specimens. The present paper reviews the current members of the group, interprets *E. aeana* as a synonym of *E. suadana*, and provides descriptions and illustrations for eight new species. Three additional species are illustrated that are probably new but are not described for lack of sufficient material.

MATERIALS AND METHODS

This study is based on the examination of 643 adult specimens (387 ♂, 256 ♀) and 208 genitalia preparations deposited in the following institutional and private collections: American Museum of Natural History, New York (AMNH); The Natural History Museum, London (BMNH); Canadian National Collection, Ottawa, Ontario (CNC); Colorado State University, Fort Collins, Colorado (CSU); Donald J. Wright (DJW); Essig Museum of Entomology, UC Berkeley (EME); George J. Balogh, Portage, Michigan (GJB); John S. Nordin, Laramie, Wyoming (JSN); Mississippi Entomological Museum, Mississippi State University (MEM); Museum of Comparative Zoology, Harvard University (MCZ); Todd M. Gilligan, Loveland, Colorado (TMG); and United States Museum of Natural History, Washington DC (USNM).

Forewing length (FWL), the distance from base to apex including fringe, and aspect ratio (AR), defined as FWL divided by medial forewing width, are used as indications of specimen size and forewing geometry, respectively. The former is reported to the nearest one tenth of a millimeter, the later as the average of several such values rounded to two decimal places. Measurements were made with a Leica M-Z95 stereomicroscope equipped with an ocular micrometer. Saccular angle (SA) refers to the angle formed by linear approximations to the ventral margin of the sacculus and the adjacent margin of the neck (Fig. 1b) and was measured to the nearest degree with a protractor on a projected image of the valva. The SA concept is inherently imprecise, being dependent on the choice of approximating lines, but it has some taxonomic utility in the group of species considered here. The number of observations supporting a particular statistic is indicated by n. Adult images and genitalia drawings were edited in Adobe Photoshop CS. Several were flipped horizontally, so that what appears to be a right wing or valva in the illustration is in fact the left such item on the insect. Morphological terminology follows Gilligan et al. (2008).

For stability of nomenclature, a lectotype is designated for *E. pulveratana* based on an unpublished selection made by Obraztsov approximately fifty years ago. I examined that specimen.

GROUP CHARACTERS

This section defines the *pulveratana* group by discussing characters shared by most, if not all, of its members. It serves as a basis for the descriptions in the subsequent species accounts, thus avoiding an excessive amount of repetition and allowing each account to focus on exceptions and/or variations peculiar to the species at hand.

Forewing (Fig. 1a). The forewing pattern includes two prominent marks on the dorsum, referred to here as the subbasal and pretornal marks, and a less conspicuous postmedian band. The subbasal mark

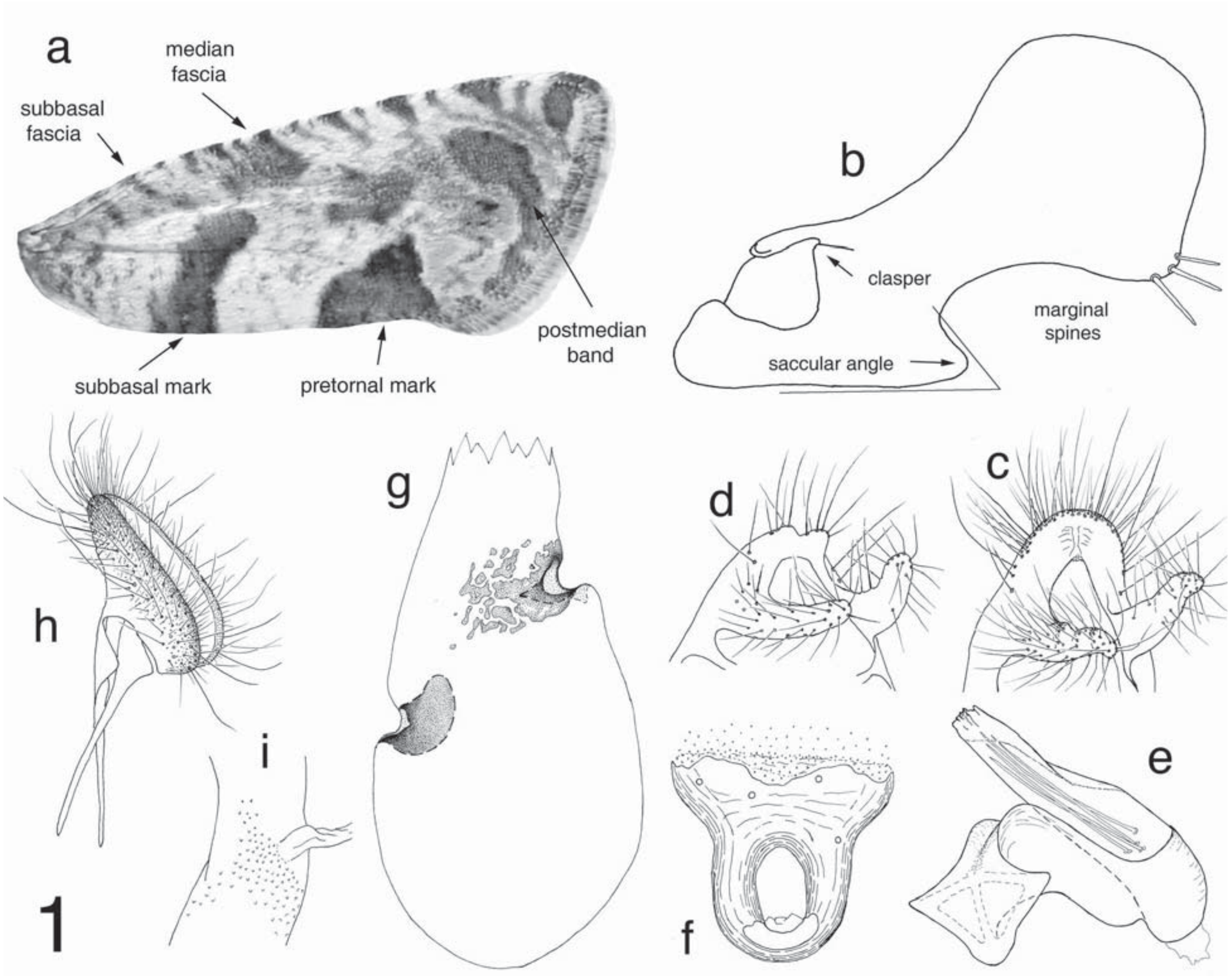


FIG. 1. *Eucosma pulveratana* group characters. a, forewing pattern, *E. suadana*. b, valva, *E.* pulveratana. c, d, uncus and socii, *E. mirosignata*, *E. parapulveratana*. e, phallus, anellus, caulis, and juxta, *E. consobrinana*. f, sterigma, *E. pulveratana*. g, signa and corpus bursae, *E. consobrinana*. h, papillae anales, *E. costastriata*. i, microspinules in ductus bursae, *E. mirosignata*.

tends to be narrow and elongate, extending obliquely from the dorsum nearly to the radius. In some instances there is an associated mark on the costa, which, if connected to the anterior extremity of the subbasal mark, would complete a chevron-shaped subbasal fascia. The pretornal mark is semitriangular, with its distal margin bordering the ocellus. Most variable of the forewing markings is the postmedian band, which frequently is interrupted near the costa and often blends with a patch of dark scales anterior to the ocellus. All the species have conspicuous costal strigulae delimited by dark costal marks of essentially two types, striate and triangulate. In a few species thin striae predominate from base to apex, but usually the proximal one-half of the costa is striate, and the distal one-half has a more or less even mix of striate and semitriangular marks. Often the two patterns are separated at mid-costa by a dark shade interpreted here as a remnant of a median fascia. The ocellus is inconspicuous and bordered basally and distally by lustrous transverse bars. Its central field is concolorous with the interfascial areas and is often marked by blackish longitudinal dashes.

Hindwing. In all members of the group the hindwing is uniformly grayish brown, often with a little darker edging along the margins of the membrane and somewhat lighter fringe.

Male genitalia (Fig. 1b–e). The uncus is dorsally setose and poorly differentiated from the dorsolateral shoulders of the tegumen. Usually it is weakly developed and divided into two convex lobes by a shallow medial indentation (Fig. 1d), but in two species it is strongly produced and semicircular (Fig. 1c). The fingerlike socii are broad basally and taper distally, with the apex narrowly rounded. All species in the group have an elongate phallus (Fig. 1e). Its ventral surface is sclerotized, its anterior extremity is closely surrounded by the anellus, and the vesica contains up to eight deciduous cornuti. The correspondingly elongate caulis has a posterodorsal surface in the form of a trough of V-shaped cross-section. Valval characteristics (Fig. 1b) include: costa concave; distal margin convex except for occasional shallow concave inflection near anal angle; anal angle moderately developed and rounded, measuring ca. 90°; ventral margin of neck broadly emarginated, producing a prominent saccular angle; medial surface with raised setose clasper at basal margin; cucullus with several spines, referred to here as marginal spines, on ventral one-half of distal margin and with medial surface densely setose, the setae arranged in something of a starburst pattern emanating from the midpoint of the distal margin. The marginal spines are positioned on the edge rather than the medial surface of the cucullus. In typical slide-mounted genitalia, their sockets are seen in lateral aspect and appear rectangular, whereas setal sockets on the medial surface have a circular appearance.

Female genitalia (Fig. 1f–i). The papillae anales (Fig. 1h) are laterally facing and moderately setose. The lamella postvaginalis (Fig. 1f) is well developed, with posterolateral corners flared, lateral margins usually concave, and posterior margin variably indented medially. The lamella antevaginalis is ring-like, with medial portion partially membranous. Sternum VII has strongly sclerotized lateral margins and a weakly sclerotized medial area (Figs. 51–62). Its posterior edge is concavely emarginated to approximately one-half the length of the sterigma and is separated from the sterigma by a band of membrane. In most members of the group there are two inwardly projecting invaginations of the intersegmental membrane between sterna VI and VII (e.g. Fig. 52), referred to as pockets. In all but two species there is some sclerotization of the ductus bursae between the juncture with the ductus seminalis and the constriction anterior to the ostium (e.g. Fig. 51), and in all cases there is a patch of microspinules near that juncture on the interior surface of the ductus bursae (Fig. 1i). The corpus bursae (Fig. 1g) contains two signa of unequal size, the larger located on the ventral surface at mid-bursa, the smaller on the dorsal surface nearer the juncture with the ductus bursae. Often there is some sclerotization of the membrane adjacent to the smaller signum. In some species it takes the form of a broad plate extending laterally from the signum (Fig. 1g), in others a small patch at the base of the signum (e.g. Fig. 51), and in all cases as microspinules on the interior surface of the membrane and/or sclerotized patch surrounding the signum.

Discussion. Most species in the *pulveratana* group exhibit considerable intraspecific variation. In particular, specimen size (as measured by FWL) frequently varies by up to 2 mm and occasionally by as much as 4 mm. Figure 2 shows the range of values for each species and the amount of interspecific overlap, the taxa being ordered according to increasing average FWL.

In the male genitalia, the number of marginal spines on the cucullus varies not only from specimen to specimen in a given species but from valva to valva in a single specimen. Despite interspecific overlap, most species tend to have many spines (more than 5) versus few (less than 5). Similarly, intraspecific variation in the saccular angle can be considerable from specimen to specimen (as much as 45°) and from one valva to the other. Nevertheless, SA does allow a rough sorting of the species into three categories: acute, obtuse, or approximately 90°.

In females, the form of the sclerotization surrounding the smaller signum appears to be relatively constant within species. Sterigma shape is not (Figs. 63–74). The length of the membranous portion of the lamella antevaginalis as compared to ostium width tends to be stable within species and is useful in segregating taxa according to <, >, and ≈ (nearly equal to). The ostium is generally ovate to elongate. In a few instances the ostium in combination with the unsclerotized portion of the lamella antevaginalis presents a distinctive key-hole shape.

A summary of the data relating to selected genitalic characters is presented in Table 1. It is apparent from Figure 2 and Table 1 that interspecific differences in specimen size and/or genitalia are often subtle and frequently not discrete. Consequently, many of the diagnoses below rely heavily on forewing appearance and geographic distribution.

SPECIES ACCOUNTS

Eucosma pulveratana (Walsingham)
(Figs. 1b, f, 3–7, 39, 51, 63, 75)

Paedisca pulveratana Walsingham 1879:45.

Eucosma pulveratana: Fernald [1903]:457; Barnes and McDunnough 1917:170; Heinrich 1923:128, fig. 238; McDunnough 1939:47; Powell 1983:35; Brown 2005:326.

Types. Lectotype here designated (Fig. 3): ♂, California, San Francisco, Walsingham, 16 May 1871, genitalia slide 11527, BMNH. Paralectotypes: same data as lectotype (3 ♂, BMNH).

Description. *Head*: Frons pale brown to creamy white, vertex pale brown; labial palpus concolorous with vertex, with medial surface shading to creamy white toward base and along dorsal margin, third segment concealed by long scales on second segment; antenna pale brown.

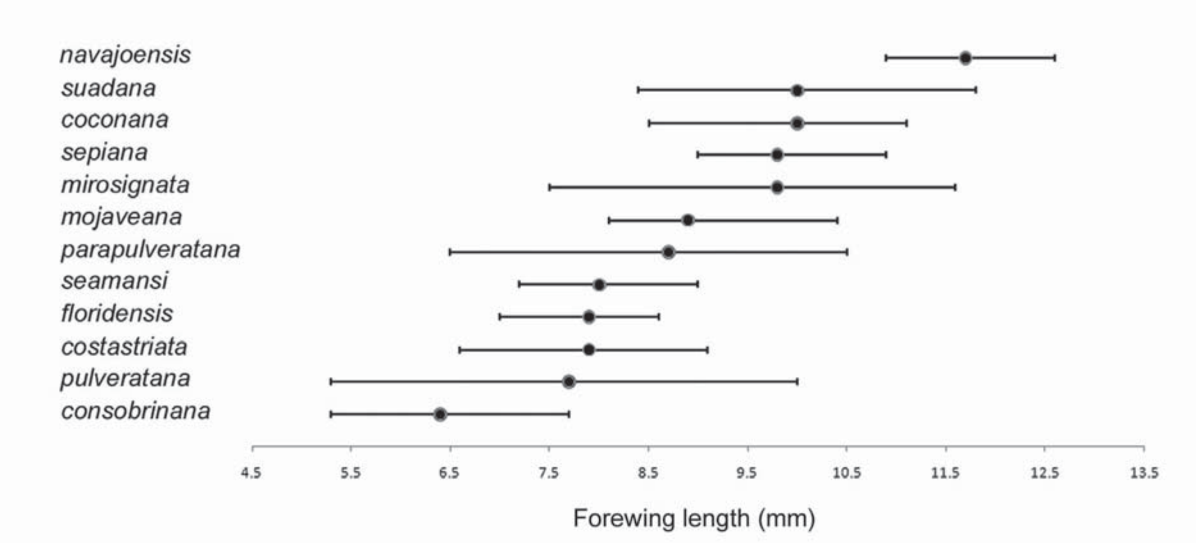


FIG. 2. Comparative FWL data.

TABLE 1. Comparative data on selected genitalia characters.

Species	♂ genitalia				♀ genitalia			
	uncus	average SA	average # of marginal spines	cornuti	pockets	sclerotization on ductus bursae	sclerotization of membrane near posterior signum	width of membrane of lam. antevag. vs. width of ostium
coconana	divided	79	5.7	2-4	none	yes	small	<
consobrinana	divided	69	3.0	4-6	deep	yes	broad	≈
costastriata	divided	32	4.4	6-8	shallow	yes	spinulate	<
floridensis	divided	46	2.7	4-6	moderate	yes	spinulate	<
mirosignata	semicircular	122	6.3	2-8	deep	no	broad	>
mojaveana	semicircular	136	2.6	2-5	shallow	no	broad	>
navajoensis	divided	66	4.6	6-8	shallow	yes	spinulate	>
parapulveratana	divided	51	6.2	3-7	shallow	yes	spinulate	<
pulveratana	divided	55	3.8	1-7	none	yes	small	≈
seamansi	divided	62	5.8	1-5	moderate	yes	spinulate	<
sepiana	divided	59	4.6	2-6	none	yes	spinulate	≈
suadana	divided	66	5.9	2-5	none	yes	spinulate	≈

Thorax: Dorsal surface concolorous with head; ventral surface creamy white; legs with anterior surfaces pale brown, posterior surfaces creamy white; distal extremities of tarsomeres ringed with pale tan. *Forewing* (Figs. 3–7): ♂ FWL 6.0–10.0 mm (mean = 8.1, n = 88), AR = 3.09; ♀ FWL 5.3–9.0 mm (mean = 7.2, n = 62), AR = 3.03; markings dark brown; interfascial areas creamy white with extensive fine brown reticulations; postmedian band weakly defined, concolorous with apical spot and with scaling anterior to ocellus; fringe scales brown with paler apices; costal markings striate, intermixed with triangulate marks from mid-costa to apex; strigulae obscure on proximal one-half of costa, more clearly defined from mid-costa to apex.

Male genitalia (Fig. 39) (n = 34): Uncus with medial indentation; vesica with 2–7 deciduous cornuti; saccular angle acute (37°–76°, mean = 55°); cucullus usually with 2–5 marginal spines, occasionally with 6 or 7. *Female genitalia* (Fig. 51, 63) (n = 27): Ostium and membranous portion of lamella antevaginalis of nearly equal width; membrane between sterna VI and VII with pockets lacking or barely discernable; sclerotization of ductus bursae extending from ductus seminalis to constriction near ostium; base of posterior signum usually expanded into small sclerotized patch on membrane, infrequently with patch obsolete.

Distribution and biology. I examined 229 specimens (140 ♂, 89 ♀) from 12 counties in California (Yuba to San Diego); from Apache, Cochise and Coconino counties in Arizona; and from Catron, Cibola, Grant, Lincoln, Luna, McKinley and Otero counties in New Mexico (Fig. 75). Capture dates range from early March to November. In southern California the records cluster in April and May and again in September and October, suggesting the occurrence of two primary flights.

Remarks. *Eucosma pulveratana* has been a catch-all taxon, and I believe the treatment presented here still fits that description to some extent. The California specimens, which tend to be homogenous in forewing appearance and genitalia, compare favorably with the lectotype. Arizona and New Mexico populations treated here as *pulveratana* exhibit greater variation in size, coloration, and genitalia (Figs. 5–7). These latter specimens may well represent two or more sibling species, but intergradations with the California material renders diagnosis of additional species problematic based on the methods utilized here.

Eucosma consobrinana Heinrich
(Figs. 1e, g, 8–12, 40, 52, 64, 77)

Eucosma consobrinana Heinrich 1923:128, fig. 242; McDunnough 1939:47; Powell 1983:35; Brown 2005:318.

Types. Holotype: ♂, South Dakota, [Union Co.], Elk Point, C. N. Ainslie, August 1913, genitalia slide 72845, USNM. Paratypes.

SOUTH DAKOTA: Same data as holotype, (2 ♂, USNM; 2 ♂, AMNH; 2 ♀, USNM, genitalia slides DJW 2273, USNM 70485). IOWA: [Woodbury Co.], Sioux City, C. N. Ainslie, August 1913 (2 ♀, USNM, genitalia slide DJW 2272; 1 ♀, AMNH).

Description. *Head*: Frons pale tan; scales of vertex pale grayish brown basally, with whitish-tan tips; labial palpus with medial surface whitish tan, lateral surface grayish brown, third segment concealed by long scales on second segment; antenna concolorous with vertex.

Thorax: Dorsal surface concolorous with head; ventral surface whitish tan; legs with anterior surfaces brown, posterior surfaces whitish tan; distal extremities of tarsomeres with whitish-tan annulations. *Forewing* (Figs. 8–12): ♂ FWL 5.3–7.7 mm (mean = 6.4, n = 35), AR = 2.98; ♀ FWL 5.5–7.3 mm (mean = 6.4, n = 23), AR = 2.85; markings brown to blackish brown, interfascial areas whitish tan to pale gray, with fine brown to brownish-gray reticulations; median fascia represented by rectangular mark at mid-costa; fringe scales whitish tan with gray-brown to blackish-brown subapical cross-markings; costal strigulae usually well defined from median fascia to apex, obscure from base to mid-costa.

Male genitalia (Fig. 40) (n = 14): Uncus with medial indentation; vesica with 4–6 deciduous cornuti; saccular angle acute (60°–87°, mean = 69°), with vertex rounded; cucullus usually with 2 or 3 marginal spines, occasionally with 4. *Female genitalia* (Figs. 52, 64) (n = 15): Ostium and membranous portion of lamella antevaginalis of approximately equal width; membrane between sterna VI and VII with well developed pockets; sclerotization of ductus bursae not reaching ductus seminalis; posterior signum located medially on broad sclerotized plate, the latter often somewhat fragmented and frequently with ridge emanating laterally from signum.

Distribution and biology. The 64 specimens examined (36 ♂, 28 ♀) document a range extending roughly from the Mississippi River to the eastern slope of the Rocky Mountains and from South Dakota to southern Texas and Mississippi (Fig. 77). In Texas there appear to be two primary flights, March–April and September–November. Most Midwest records are from August.

Remarks. This moth is most similar in forewing appearance and genitalia to *E. pulveratana* but is generally smaller (mean FWL ≈ 6.4 vs. 7.6 mm). The ranges of the two species appear to be disjunct but are nearly contiguous in New Mexico. Females of *consobrinana* are distinguished from those of *pulveratana* by the breadth of the sclerotized patch on the corpus bursae and the presence of well developed pockets in the membrane between sterna VI and VII. The male genitalia of the two species are very similar, and intraspecific variation in both species renders diagnosis on that basis unreliable.

Eucosma suadana Heinrich

(Figs. 1a, 13–14, 41, 53, 65, 75))

Eucosma suadana Heinrich 1923:130, fig. 243; McDunnough 1939:48; Powell 1983:35; Brown 2005:327.

Eucosma aeana McDunnough 1942:68; Powell 1983:35; Brown 2005:314, **new synonymy**.

Discussion. The description of *E. aeana* was based on a single male from Fillmore, Utah. The specimen is somewhat worn, but in forewing pattern and coloration it is an excellent match to the types of *E. suadana*. McDunnough (1942) recognized the similarity of the two species but relied on subtle differences in genitalia (saccular angle less sharp, ventral emargination of the neck more broad, cucullus more circular) to separate *aeana* from *suadana*. My investigations indicate that these are not diagnostic differences but represent intraspecific variation in *suadana*; hence the proposed synonymy.

Types. *Eucosma suadana*. Holotype: ♂, Utah, [Utah Co.], Vineyard, Tom Spalding, 10 July 1912, genitalia slide 72802, USNM. Paratypes: same locality and collector as holotype, 6 July 1912 (1 ♀, AMNH), 8 July 1912 (1 ♂, USNM; 1 ♀, AMNH), 10 July 1912 (2 ♀, genitalia slide 70499, USNM), 14 July 1912 (1 ♂, USNM). *Eucosma aeana*. Holotype: ♂, Utah, [Millard Co.], Fillmore, D. H. Bishoff, 10 August 1940, genitalia slide 90, CNC.

Description. *Head*: Frons and vertex white; labial palpus white, with some grayish-brown shading on lateral surface of second segment; antenna white.

Thorax: Dorsal surface whitish, with some grayish-brown shading; ventral surface white; fore- and mid-legs with brown to blackish-brown anterior surfaces, whitish posterior surfaces, and whitish annulations at mid-tibia, distal end of tibia, and distal extremity of each tarsomere. *Forewing* (Figs. 13–14): ♂ FWL 8.6–11.8 mm (mean = 10.3, n = 21), AR = 3.06; ♀ FWL 8.4–10.2 mm (mean = 9.4, n = 12), AR = 2.91; markings brown to blackish-brown; interfascial areas whitish, variably reticulated with pale brown; subbasal and pretornal marks strongly contrasting with interfascial areas; median fascia represented by dark mark at mid-costa; postmedian band strongly expressed, usually complete but sometimes interrupted by white scaling near costa; lustrous bars bordering ocellus gray to fawn; fringe scales grayish-brown with white apices; striate costal markings interspersed with larger triangulate markings from median fascia to apex.

Male genitalia (Fig. 41) (n = 7): Uncus weakly divided; vesica with 2–5 deciduous cornuti; saccular angle acute (54°–78°, mean = 66°); cucullus with 5–7 marginal spines. *Female genitalia* (Fig. 53, 65) (n = 7): Width of membranous portion of lamella antevaginalis equal to or a little larger than width of ostium; pockets in membrane between sterna VI and VII lacking to barely discernable; sclerotization of ductus bursae extending from juncture with ductus seminalis to constriction near ostium; corpus bursae with membrane near small signum microspinulate.

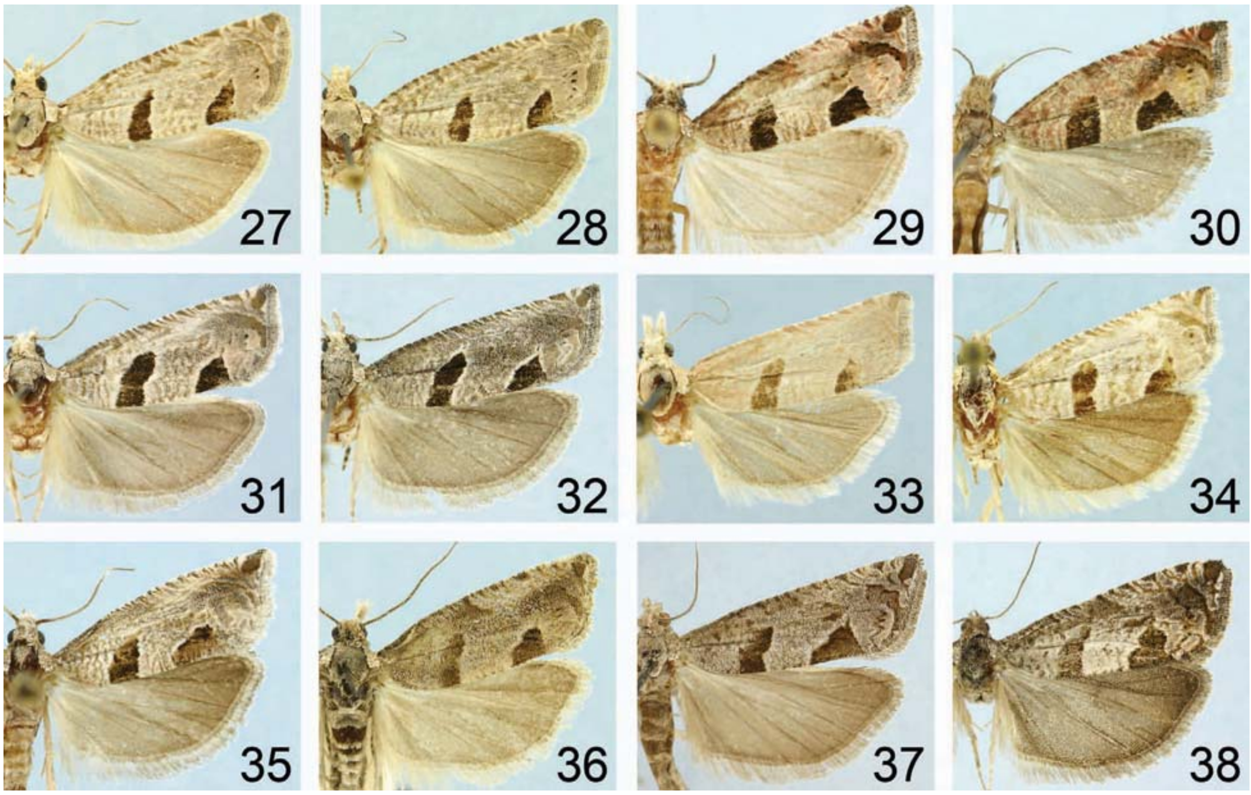
Distribution and biology. I examined 34 specimens (22 ♂, 12 ♀) collected at elevations between 4500 and 9000 feet in Nevada, Utah and Wyoming (Fig. 75). Capture dates range from 8 June to 10 August, the vast majority of records being from July.

***Eucosma seamansi*, new species**

(Figs. 17–18, 42, 54, 66, 77)

Diagnosis. *Eucosma seamansi* is similar in appearance to *E. suadana* but is smaller (mean FWL ≈ 8.0 vs. 10.0 mm) and darker (head and interfascial areas of forewing more strongly suffused with brownish gray). In *E. seamansi* the median fascia extends from costa to cubitus and is connected to the post median band by a patch of dark scaling anterior to the ocellus. The male genitalia of the two species are essentially indistinguishable. Females of *E. seamansi* have well developed pockets in the membrane between sterna VI

FIGS. 3-26. **3–7,** *E. pulveratana*. **3,** ♂ lectotype. **4,** ♂ Santa Cruz Island., California. **5,** ♀ White Mountains, Arizona. **6,** ♂ Grant Co., New Mexico. **7,** ♀ Coconino Co., Arizona. **8–12,** *E. consobrinana*. **8,** ♂ Monona Co., Iowa. **9,** ♀ Otero Co., Colorado. **10,** ♀ Cheyenne Co., Colorado. **11,** ♀ Colfax Co., New Mexico. **12,** ♂ Oktibbeha Co., Mississippi. **13–14,** *E. suadana*, ♂,♀ Albany Co., Wyoming. **15–16,** *E. coconana*, ♂,♂ Coconino Co., Arizona. **17–18,** *E. seamansi*. **17,** holotype. **18,** ♂ Pocahontas Co., Iowa. **19–20,** *E. sepiana*. **19,** holotype. **20,** Bear Lake Co., Idaho. **21,** ♂ *E. pulveratana* group nr. *sepiana*, Elko Co., Nevada. **22-26,** *E. parapulveratana*. **22,** ♂ Morton Co., Kansas. **23,** ♂ Albany Co., Wyoming. **24,** ♂ holotype. **25,** ♂ Albany Co., Wyoming. **26,** ♂ Coconino Co., Arizona.



FIGS. 27–38. **27–28,** *E. navajoensis*. **27,** holotype. **28,** San Juan Co., Utah. **29–30,** *E. floridensis*. **29,** holotype. **30,** ♀ Highlands Co., Florida. **31–32,** *E. mirosignata*. **31,** ♂ Jeff Davis Co., Texas. **32,** ♂ Eddy Co., New Mexico. **33–34,** *E. mojaveana*. **33,** holotype. **34,** ♀ Riverside Co., California. **35,** *E. costastriata*, holotype. **36,** ♂ *E. pulveratana* group, Ventura Co., California. **37,** ♂ *E. pulveratana* group, Teller Co., Colorado. **38,** ♂ *E. pulveratana* group, Albany Co., Wyoming.

and VII, those of *E. suadana* do not. The ranges of the two species are disjunct; *E. seamansi* is a resident of the Great Plains, from southern Canada to Iowa, *E. suadana* of the central Rocky Mountain and Great Basin regions.

Description. *Head*: Frons tan to pale grayish brown; vertex grayish brown; labial palpus with medial surface whitish, lateral surface grayish brown; antenna a shade darker than vertex.

Thorax: Dorsal surface grayish brown; ventral surface pale tan; legs gray brown to tan with paler tarsal annulations. *Forewing* (Figs. 17–18): ♂ FWL 7.5–9.0 mm (mean = 8.0, n = 5), AR = 2.90; ♀ FWL 7.2–9.0 mm (mean = 8.0, n = 9), AR = 2.78; markings brown to blackish brown; interfascial areas white to pale grayish brown, usually with gray-brown reticulations; median fascia represented by oblique rectangular mark extending from mid-costa to cubitus; postmedian band sharply expressed and connected to median fascia by patch of grayish-brown scales anterior to ocellus; lustrous gray bars bordering ocellus thinly edged with white; scales along termen blackish brown with white apices; fringe scales paler with white apices; costal markings alternating striate and triangulate from median fascia to apex.

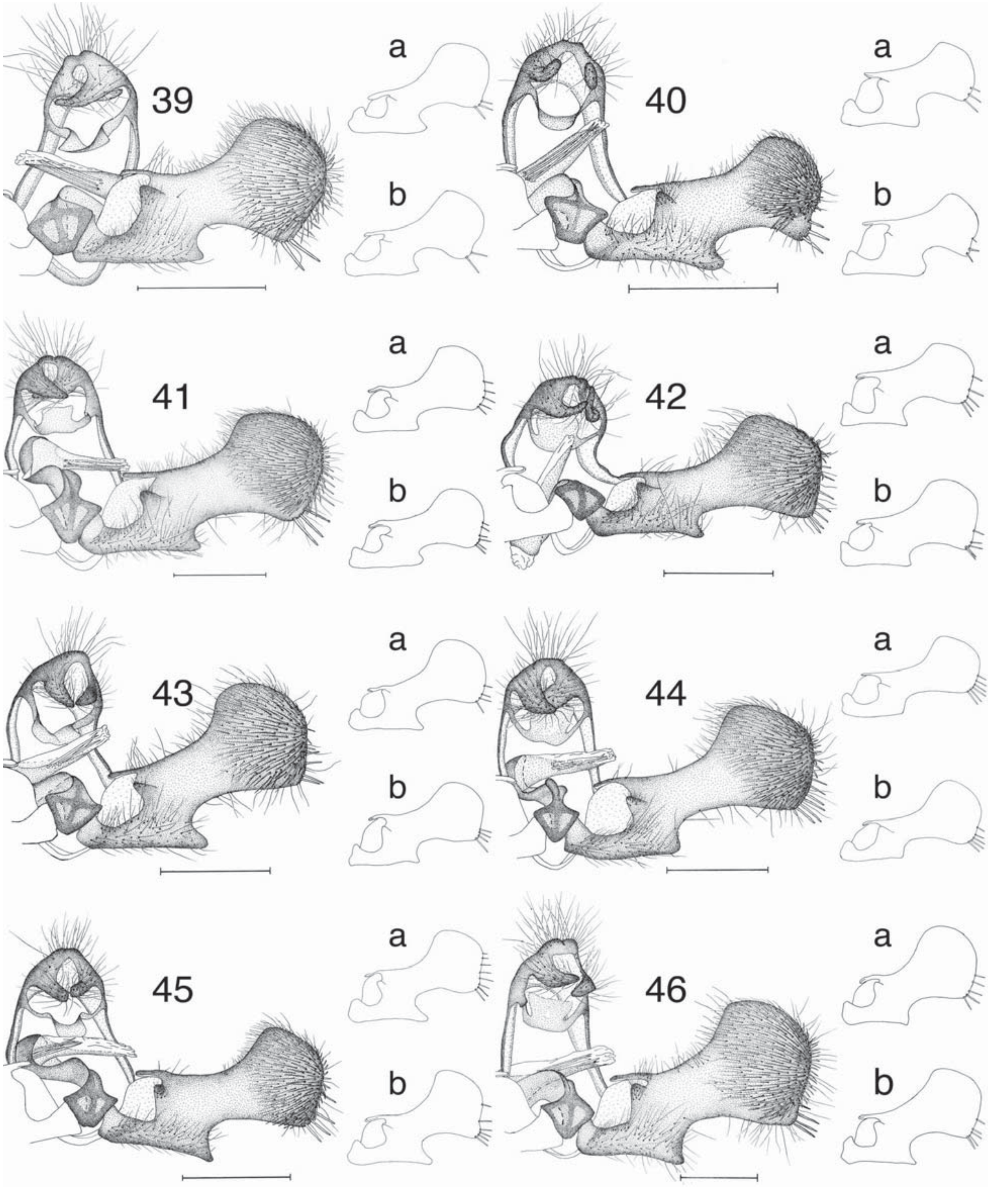
Male genitalia (Fig. 42) (n = 5): Uncus medially indented; vesica with 1–5 deciduous cornuti; ventral margin of sacculus weakly concave; saccular angle acute (53°–72°, mean = 62°); cucullus with 5–7 marginal spines. *Female genitalia* (Fig. 54, 66) (n = 4): Width of membranous portion of lamella antevaginalis less than width of ostium; membrane between sterna VI and VII with distinct pockets; sclerotization of ductus bursae extending from juncture with ductus seminalis to constriction near ostium; corpus bursae with membrane near posterior signum microspinulate.

Holotype (Fig. 17). ♂, Canada, Alberta, Lethbridge, H. L. Seamans, 13 July 1928, genitalia slide DJW 2081, CNC.

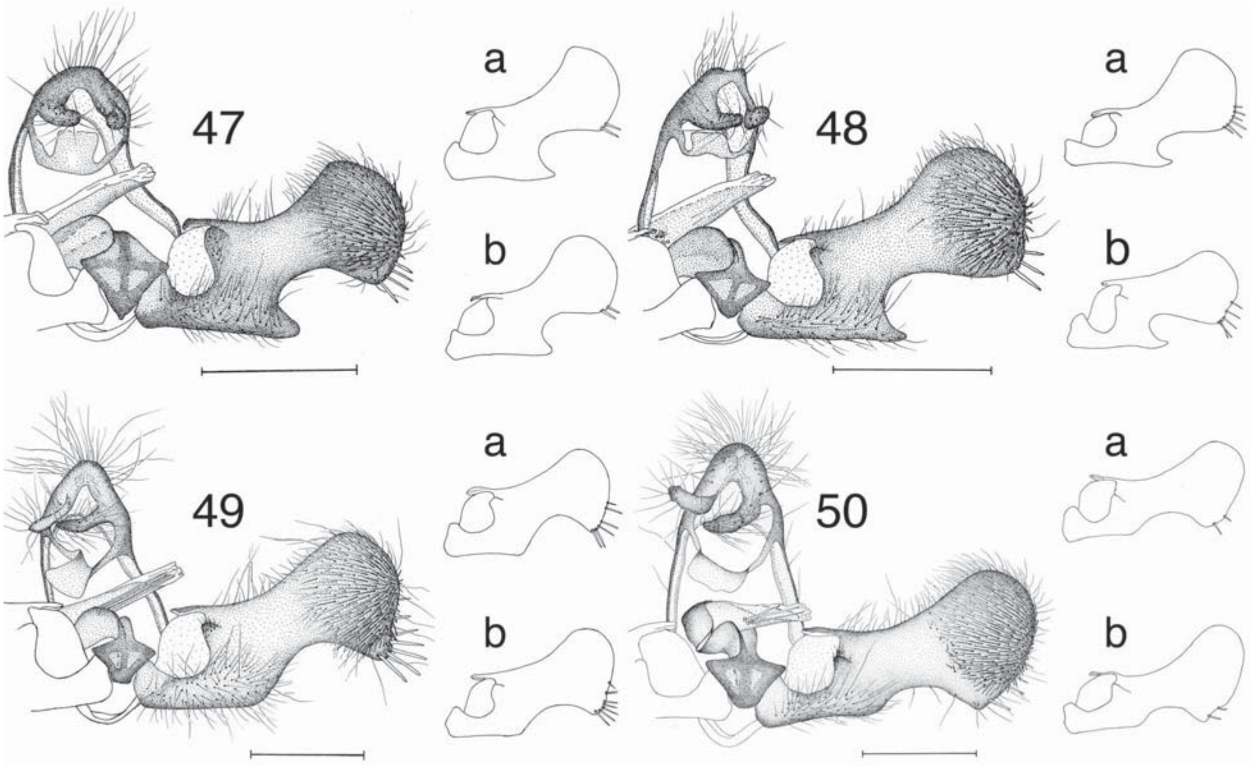
Paratypes. CANADA. Same location and collector as holotype, 7 June 1920 (1 ♀, genitalia slide DJW 2316), 29 June 1922 (1 ♂, genitalia slide DJW 2315), 4 July 1922 (1 ♂, genitalia slide DJW 2330; 3 ♀, genitalia slide DJW 2313), 12 July 1922 (1 ♂, genitalia slide CNC 136; 2 ♀, genitalia slide DJW 2080), 13 July 1928 (1 ♂, genitalia slide DJW 2081); Manitoba, Aweme, N. Criddle, 16 July 1923 (1 ♀); R. D. Bird, 25 August 1924 (1 ♀). IOWA. Pocahontas Co., Kalsow Prairie, D. J. Wright, 18 June 1992 (1 ♂, genitalia slide DJW 2082); [Johnson Co.], Iowa City, C. N. Ainslie, 23 August (1 ♀). Paratype depositories: CNC, DJW, USNM.

Etymology. This species is named after Howard L. Seamans, the head of the Dominion Entomological Laboratory at Lethbridge, Alberta from 1921 to 1938 and the collector of most of the specimens in the type series.

Distribution and biology. I examined 14 specimens (5 ♂, 9 ♀), documenting a range from southeastern Alberta to southeastern Manitoba and south to Iowa (Fig. 77). Adult capture dates range from 6 June to 25 August.



FIGS. 39–46. Male genitalia. **39,** *E. pulveratana*, slides DJW 1256, USNM 70490, JAP 4224. **40,** *E. consobrinana*, slides DJW 133, 314, USNM 90211. **41,** *E. suadana*, slides DJW 2069, 2079, 2070. **42,** *E. seamansi*, slides DJW 2081, 2330, 2082. **43,** *E. sepiana*, slides DJW 2306, 2307, 764. **44,** *E. coconana*, slides DJW 2325, 2325, 2322. **45,** *E. parapulveratana*, slides DJW 1040, 829, 1190. **46,** *E. navajoensis*, slides DJW 2296, 1075, 2298. Scale bar = 0.5 mm.



FIGS. 47–50. Male genitalia. **47,** *E. floridensis*, slides DJW 2310, 2309, 1161. **48,** *E. costastriata*, slides DJW 2294, 253, 350. **49,** *E. mirosignata*, slides DJW 2222, 2223, 1258. **50,** *E. mojaveana*, slides DJW 1131, 1851, 2285. Scale bar = 0.5 mm.

***Eucosma sepiana*, new species**

(Figs. 19–20, 43, 55, 67, 75)

Diagnosis. *Eucosma sepiana* is similar in size and genitalia to the sympatric *E. suadana* but is distinguished from that species and from other members of the *pulveratana* group by color (Figs. 19–20): interfascial areas pale yellow brown, markings a darker shade of the same color. *Eucosma mojaveana* (described below) is somewhat similar in appearance (Fig. 33) but is easily separated from *E. sepiana* by genitalia (Figs. 43 vs. 50 & 55 vs. 62).

Description. *Head*: Frons and vertex creamy white, the latter often with pale yellowish-brown tints; labial palpus with medial surface creamy white, lateral surface pale yellowish brown; antenna a shade browner than vertex.

Thorax: Dorsal surface yellowish brown; ventral surface creamy white; legs gray brown with paler tarsal annulations. *Forewing* (Figs. 19–20): ♂ FWL 9.0–10.9 mm (mean = 9.8, n = 22), AR = 3.02; ♀ FWL 9.2–10.6 mm (mean = 9.8, n = 4), AR = 2.83; interfascial areas creamy white to pale yellowish brown, sometimes with fine brown reticulations; subbasal and pretornal marks yellowish brown, often thinly edged with blackish brown; postmedian band yellowish brown and variable in expression; lustrous bars bordering ocellus pale gray; fringe scales pale yellowish brown with creamy white apices; costal markings striate, with interspersed triangular marks from mid-costa to apex.

Male genitalia (Fig. 43) (n = 8): Uncus with dorsal margin straight to weakly indented; vesica with 2–6 deciduous cornuti; saccular angle acute (45°–70°, mean = 59°), with vertex rounded; cucullus with 3–8 marginal spines. *Female genitalia* (Figs. 55, 67) (n = 4): Width of membranous portion of lamella antevaginalis approximately equal to ostium width; membrane between sterna VI and VII lacking pockets; sclerotization of ductus bursae extending from ductus seminalis to constriction anterior to ostium; surface of corpus bursae near smaller signum microspinulate.

Holotype (Fig. 19). ♂, Utah, [Juab Co.], Eureka, Tom Spalding, 16 August 1911, genitalia slide USNM 95243, USNM.

Paratypes. IDAHO: Bear Lake Co., along FS 405, 2 mi. E. Danish Flat, 3 mi. W. Lanark Rd., 7150 ft., 42°17.730' N, 111°30.144' W, T. M. & J. M. Gilligan, 17 August 2004 (2 ♂, genitalia slide DJW 2307); Oneida Co., Curlew NG, 4 mi. ENE of Holbrook, 1 August 2001, D. J. Wright, (1 ♂, genitalia slide DJW 764). UTAH: [Juab Co.], Eureka, Tom Spalding, 30 August 1911 (1 ♂, genitalia slide DJW 2306). WASHINGTON: [Walla Walla Co.], Walla Walla, H. R. Lanchester, 27 August 1953 (1 ♂; 1 ♀, genitalia slide DJW 2302); [Whitman Co.,], Pullman, C. V. Piper, 11 July 1898 (1 ♀, genitalia slide USNM 95244), 10 August 1898 (1 ♀, genitalia slide USNM 70650), 18 September 1898 (1 ♂); [Whitman Co.], Pullman, T. C. Clarke, 27 July 1930 (1 ♂, genitalia slide USNM 70500, wing slide USNM 70501); [Whitman Co.], Kamiack Butte, J. F. Clarke, 4 August 1930 (1 ♂). WYOMING: [Teton Co.], Moran [Junction?], G. H. & J. L. Sperry, 19 July 1938 (3 ♂, genitalia slide DJW 2304), 24 July 1938 (3 ♂, genitalia slide DJW 2308), 25 July 1938 (2 ♂), 29 July 1938 (1 ♂), 30 July 1938 (3 ♂), 11 August 1939 (1 ♂). Paratype depositories: CNC, DJW, TMG, USNM.

Etymology. The specific epithet refers to the distinctive forewing color.

Distribution and biology. The type series consists of 26 specimens (22 ♂, 4 ♀) from Idaho, Utah, Washington, and Wyoming (Fig. 75). Adults fly from mid-July to early September, and capture sites vary in elevation from approximately 950 feet at Walla Walla, Washington to 7150 feet in Bear Lake Co., Idaho.

Remarks. Two paratypes from Pullman, Washington collected by C. V. Piper were treated by Kearfott (1907) as cotypes of *Eucosma palousana*, a name interpreted by Wright (2008) as a synonym of *Eucosma biquadrana* (Walsingham).

I examined ten male specimens from the AMNH, CNC, and USNM that have darker brown forewing coloration (Fig. 21) but otherwise seem indistinguishable from *E. sepiana*. They were collected in Colorado, Montana, Nevada and New Mexico at elevations of 7500 to 10,000 feet and are a little larger than the *sepiana* paratypes (mean FWL = 10.6 vs. 9.8 mm).

Eucosma coconana, new species

(Figs. 15–16, 44, 56, 68, 75)

Diagnosis. *Eucosma coconana* is similar in size to *E. suadana*, *E. sepiana*, and *E. mirosignata* (treated below). It lacks the whitish interfascial areas of *E. suadana* and the yellow-brown coloration of *E. sepiana*. It is distinguished from *E. mirosignata* by both forewing appearance (Figs. 15–16 vs. 31–32) and genitalia (Figs. 44 vs. 49 & 56 vs. 61). The SA is usually close to 90°, a feature that distinguishes *E. coconana* from all other members of the group except two possibly unnamed species discussed but not described in the remarks at the end of the paper. *Eucosma coconana* seems to be restricted to the vicinity of Flagstaff, Arizona.

Description. *Head*: Frons pale tan; vertex scales pale tan basally, grayish brown distally; labial palpus with medial surface and dorsal edge pale tan, lateral surface grayish brown; antenna concolorous with vertex.

Thorax: Dorsal surface grayish brown; ventral surface pale tan; fore- and mid-leg with brown anterior surfaces, tan posterior surfaces, and tan annulations at mid-tibia, distal end of tibia, and distal extremity of each tarsomere; hind-leg mostly tan, with tarsomeres somewhat darker and distally ringed with tan. *Forewing* (Figs. 15–16): ♂ FWL 8.5–11.1 mm (mean = 10.1, n = 41), AR = 3.02; ♀ FWL 9.0–10.4 mm (mean = 9.8, n = 6), AR = 2.85; subbasal and pretornal marks blackish-brown; interfascial areas white to tan, heavily reticulated with brown and/or gray, producing a rather dark forewing appearance; median fascia represented by rectangular mark at mid-costa; postmedian band brown to gray, edged with black; lustrous bars bordering ocellus gray; central field of ocellus crossed by three black dashes; scales along termen blackish brown with white apices; fringe scales paler with tan apices; costal markings blackish brown, with striate and triangulate marks interspersed from median fascia to apex, the striae often thinly edged with orange brown.

Male genitalia (Fig. 44) (n = 6): Uncus with dorsal margin straight to weakly indented; vesica with 2–4 deciduous cornuti; saccular angle acute to slightly obtuse (68°–94°, mean = 79°), with broadly rounded vertex; cucullus with 4–7 marginal spines. *Female genitalia* (Figs. 56, 68) (n = 5): width of membranous portion of lamella antevaginalis less than width of ostium; membrane between sterna VI and VII lacking pockets; sclerotization of ductus bursae extending from juncture with ductus seminalis to constriction near ostium; posterior signum with flared base, often extending into narrow sclerotized ring/patch on membrane, with surrounding area microspinulate.

Holotype. ♂, Arizona, Coconino Co., Fort Valley, 7.5 mi. NW Flagstaff, 7350 ft., J. G. Franclemont, 22 July 1964, USNM.

Paratypes. ARIZONA: same location as holotype, R. W. Hodges, 20 June 1961 (1 ♂), 21 June 1961 (1 ♂), 25 June 1961 (1 ♂), 26 June 1961 (1 ♂), 28 June 1961 (1 ♂, genitalia slide DJW 2322; 1 ♀, genitalia side DJW 2323), 3 July 1961 (1 ♂), 6 July 1961 (1 ♀, genitalia side DJW 2367), 7 July 1961 (1 ♂; genitalia slide USNM 70510), 10 July 1961 (1 ♂), 17 July 1961 (1 ♂), 21 July 1961 (1 ♂), 29 July 1961 (1 ♂; 2 ♀, genitalia slide USNM 70512), 30 July 1961 (1 ♂), 7 August 1961 (1 ♂), 9 August 1961 (1 ♂), 11 August 1961 (1 ♂), 22 August 1961 (1 ♀, genitalia slide DJW 2321), 26 August 1961 (1 ♂), 9 September 1961 (1 ♂); J. G. Franclemont, 16 June 1964 (1 ♂), 19 June 1964 (1 ♀, genitalia slide DJW 2324), 26 June 1964 (1 ♂), 28 June 1964 (2 ♂), 29 June 1964 (1 ♂), 1 July 1964 (1 ♂, genitalia slide DJW 2364), 2 July 1964 (1 ♂), 4 July 1964 (1 ♂), 7 July 1964 (4 ♂), 10 July 1964 (3 ♂, genitalia slides DJW 2365, 2366), 13 July 1964 (3 ♂), 14 July 1964 (2 ♂, genitalia slide DJW 2325), 22 July 1964 (1 ♂); Coconino Co., 7 mi. NW Flagstaff, Ft. Valley Exp. For., 7000 ft., H. F. Hsu, J. Powell and M. Prentice, 22–24 July 1989 (4 ♂); Coconino Co., W. Fork Oak Creek, 19 rd. miles SW Flagstaff, 6500 ft., J. A. Powell and F. A. Sperling, 16 July 1995 (1 ♂). Paratype depositories: EME, USNM.

Etymology. The specific epithet derives from the word Coconino, the name of both the County and the National Forest in which the type series was collected.

Distribution and biology. I examined 55 specimens (49 ♂, 6 ♀), all from the vicinity of Flagstaff, Arizona (Fig. 75). Adults have been captured from mid-June to early September, but two-thirds of the records are from July.

Eucosma parapulveratana, new species

(Figs. 1d, 22–26, 45, 57, 69, 76)

Diagnosis. *Eucosma parapulveratana* is recognized by the following combination of characters: forewing elongate (AR = 3.17); interfascial areas uniformly pale and weakly reticulated; cucullus with numerous marginal spines (usually 5 or more); saccular angle acute and strongly produced, with narrowly rounded vertex; width of membranous portion of lamella antevaginalis distinctly smaller than width of ostium; membrane between sterna VI and VII with shallow pockets; surface of corpus bursae near posterior signum microspinulate.

Description. *Head*: Frons creamy white; vertex creamy white to tan; labial palpus with medial surface creamy white, lateral surface pale gray brown; antenna gray brown.

Thorax: Dorsal surface pale tan to gray brown; ventral surface creamy white, sometimes shaded with gray; legs with gray-brown anterior surfaces, creamy white posterior surfaces, and whitish annular markings at mid tibia, distal end of tibia, and distal end of each tarsomere. *Forewing* (Figs. 22–26): ♂ FWL 7.8–9.9 mm (mean = 8.7, n = 27), AR = 3.24; ♀ FWL 6.5–10.5 mm (mean = 8.7, n = 41), AR = 3.13; interfascial areas pale gray to tan, variably suffused with white, and weakly reticulated with brown; subbasal and pretornal marks brown to blackish brown, often edged with black; postmedian band blackish brown, thin, and frequently interrupted near costa; lustrous bars bordering ocellus gray; fringe concolorous with interfascial areas, often darker at apex and at terminal end of postmedian band; costa with striate and triangulate marks from mid-costa to apex.

Male genitalia (Fig. 45) (n = 12): Uncus with dorsal margin straight to weakly indented; vesica with 3–7 deciduous cornuti; saccular angle acute (36°-64°, mean = 51°), with vertex narrowly rounded; cucullus usually with 5–8 marginal spines, occasionally with 4 or 9. *Female genitalia* (Figs. 57, 69) (n = 10): Width of membranous portion of lamella antevaginalis approximately one-half width of ostium; membrane between sterna VI and VII with shallow pockets; sclerotization of ductus bursae extending from ductus seminalis nearly to constriction anterior to ostium; corpus bursae with membrane near smaller signum microspinulate.

Holotype (Fig. 24). ♂, Kansas, Morton Co., Cimarron R. & Hwy 51, G. J. Balogh, 25 September 1999, USNM.

Paratypes. COLORADO: Cheyenne Co., Wild Horse Post Office, Hwy 287, 4453 ft., 38°49.60' N, 103°00.60' W, T. M. Gilligan & C. E. Harp, 15 September 2007 (1 ♂; 4 ♀); El Paso Co., Fountain Valley School, 5800 ft., F. M. Brown, 20 June 1958 (1 ♀); Larimer Co., 2 mi. W of Mishawaka on St. Rt. 14, 6300 ft., D. J. Wright, 12 July 1993 (1 ♂, genitalia slide DJW 92); vic. Fort Collins, A. B. Klots, 17 August 1935 (1 ♂); Morgan Co., 3.5 mi. W. of Co. Rd. 19 on Co. Rd. I, 4610 ft., D. J. Wright, 28 July 1995 (1 ♂, genitalia slide DJW 1040); Otero Co., Vogel Canyon Picnic Area, 15 mi. S of La Junta, 4340 ft., 37°46'13" N, 103°30'46" W, D. J. Wright, 18 August 1997 (1 ♂; 2 ♀, genitalia slide DJW 2289); Washington Co., Eastern Colo. Res. Ctr., 16 mi. N Akron, E. Buckner & P. Opler, 19 June 1994 (1 ♂, genitalia slide DJW 270); Weld Co., Pawnee NG, T8N R64W S3, D. J. Wright, 8 August 2004 (1 ♂; 1 ♀); 9 mi. S & 3 mi. W of Fort Morgan by S26 & S27, T2N R58W, T. S. Dickel, 15 August 1992 (1 ♀); 2.5 mi. NE of Roggen on Co. Rd. 386, 4664 ft., 40°11.75' N, 104°20.36' W, C. Harp, 25–26 August 2007 (1 ♂; 2 ♀); Pawnee Nat'l Grassland, Jct. CR-96 & CR-61, 4969 ft., 40°41'00.2" N, 104°24'38.7" W, T. M. Gilligan & P. A. Opler, 31 August 2007 (1 ♂; 2 ♀); Pawnee Nat'l Grassland, Jct. CR-96 & CR-61, 5030 ft., 40°40'58.2" N, 104°24'25.1" W, T. M. Gilligan & P. A. Opler, 31 August 2007 (8 ♀). KANSAS: Morton Co., Cimarron NG, 7.5 mi. N Elkhart, 3414 ft., 37°07.2' N, 101°53.7' W, D. J. Wright, 2 August 1999 (2 ♀, genitalia slide DJW 2290), 25 August 2000 (2 ♀), 26 August 2000 (1 ♂, genitalia slide DJW 2300); Cimarron R. & Hwy 51, G. J. Balogh, 25 September 1999 (2 ♂; 2 ♀, genitalia slide DJW 1261). TEXAS: Cottle Co., Matador WMA, E. C. Knudson, 17 May 1985 (1 ♂, genitalia slide DJW 1263); Hemphill Co., Canadian, A. & M. E. Blanchard, 29 May 1970 (1 ♀, genitalia slide USNM 90403), 2 June 1970 (2 ♂, genitalia slides USNM 90384, 90404); Potter Co., Lake Meredith NRA, Plum Creek, E. C. Knudson, 23 June 1985 (1 ♀, genitalia slide DJW 1265). WYOMING: Albany Co., T15N R73W S1, 2217 Sky View Lane, 7468 ft., J. S. Nordin, 1 July 2002 (1 ♀), 2 July 2005 (1 ♀), 21 July 2004 (1 ♂), 30 July 2001 (1 ♂, genitalia slide DJW 829), 30 July 2006 (1 ♀, genitalia slide DJW 2288); T15N R73W S1, C. D. Ferris, 18 July 2002 (1 ♀, genitalia slide DJW 1038); T15N R75W S29, W side Gelatt Lake, 7250 ft., J. S. Nordin, 9 July 2007 (1 ♀, genitalia slide DJW 1875), 12 July 2004 (1 ♂), 18 July 2005 (1 ♂), 21 July 2004 (2 ♂, genitalia slide DJW 1190; 1 ♀, genitalia slide DJW 1191). Paratype depositories: AMNH, BMNH, CNC, CSU, DJW, EME, GJB, TMG, MEM, USNM.

Etymology. The prefix para, Greek for near, reflects the long history of confusion regarding this species and *E. pulveratana*.

Distribution and biology. I examined 78 specimens (37 ♂, 41 ♀), mostly from the high plains of eastern Colorado, eastern Wyoming, far western Kansas, and the panhandle of Texas (Fig. 76). This count includes some mottled looking specimens (Fig. 26) from Coconino County, Arizona that agree in other respects with typical *E. parapulveratana* but are not designated as paratypes. Adult capture dates range from 20 June to 25 September.

Eucosma navajoensis new species

(Figs. 27–28, 46, 58, 70, 76)

Diagnosis. This is the largest of the species treated here. It is distinguished by size (mean FWL ≈ 11.7 mm) and by the uniformly pale grayish-fawn color of the forewing (Figs. 27–28). In females, the membranous portion of the lamella antevaginalis is distinctly wider than the ostium (Fig. 70). All known specimens are from the southeastern corner of Utah.

Description. *Head*: Frons creamy white; vertex beige; labial palpus with medial surface creamy white, lateral surface beige; antenna concolorous with apex.

Thorax: Dorsal surface beige; ventral surface creamy white; legs with anterior surfaces beige, posterior surfaces creamy white, with ring of creamy-white scales at distal end of tibia, distal end of each tarsomere, and at middle of fore- and mid-tibia. *Forewing* (Figs. 27–28): ♂ FWL 10.9-12.4 mm (mean = 11.6, n = 7), AR = 3.02; ♀ FWL 11.0-12.6 mm (mean = 11.8, n = 4), AR = 2.84; interfascial areas creamy white, heavily reticulated with beige; subbasal and pretornal marks blackish brown; postmedian band narrow, inconspicuous, and largely concolorous with scales anterior to ocellus; lustrous bars bordering ocellus pale fawn; fringe scales beige with creamy-white tips; costal markings alternating striate and triangulate from mid-costa to apex.

Male genitalia (Fig. 46) (n = 4): Uncus weakly divided medially; vesica with 6–8 deciduous cornuti; saccular angle acute (43°–84°, mean = 66°); cucullus with 3–6 marginal spines. *Female genitalia* (Figs. 58, 70) (n = 4): Membranous portion of lamella antevaginalis broader than ostium; membrane between sterna VI and VII with shallow pockets; ductus bursae with sclerotization extending from ductus seminalis nearly to constriction anterior to ostium; membrane of corpus bursae microspinulate near smaller signum.

Holotype (Fig. 27). ♂, Utah, San Juan Co., Comb Ridge west of Bluff, G. J. Balogh, 26 September 2003, genitalia slide DJW 1075, USNM.

Paratypes. UTAH. San Juan Co., Valley of the Gods Rd., 0.5 mi. N. of Hwy 163, G. J. Balogh, 19 September 2000 (1 ♂; 3 ♀, genitalia slides DJW 2297, 2299, 2301), 21 September 2000 (1 ♂, genitalia slide DJW 2298); Comb Ridge west of Bluff, G. J. Balogh, 26 September 2003 (3 ♂, genitalia slides DJW 2077, 2296), 27 September 2003 (1 ♀, genitalia slide DJW 1163). Paratype depositories: DJW, EME, GJB, USNM.

Etymology. The specific epithet refers to the Navajo Indians, whose tribal lands are located just south of the type locality.

Distribution and biology. This species is known from 11 specimens (7 ♂, 4 ♀) collected in September in San Juan County, Utah (Fig. 76) at an elevation of approximately 4500 feet.

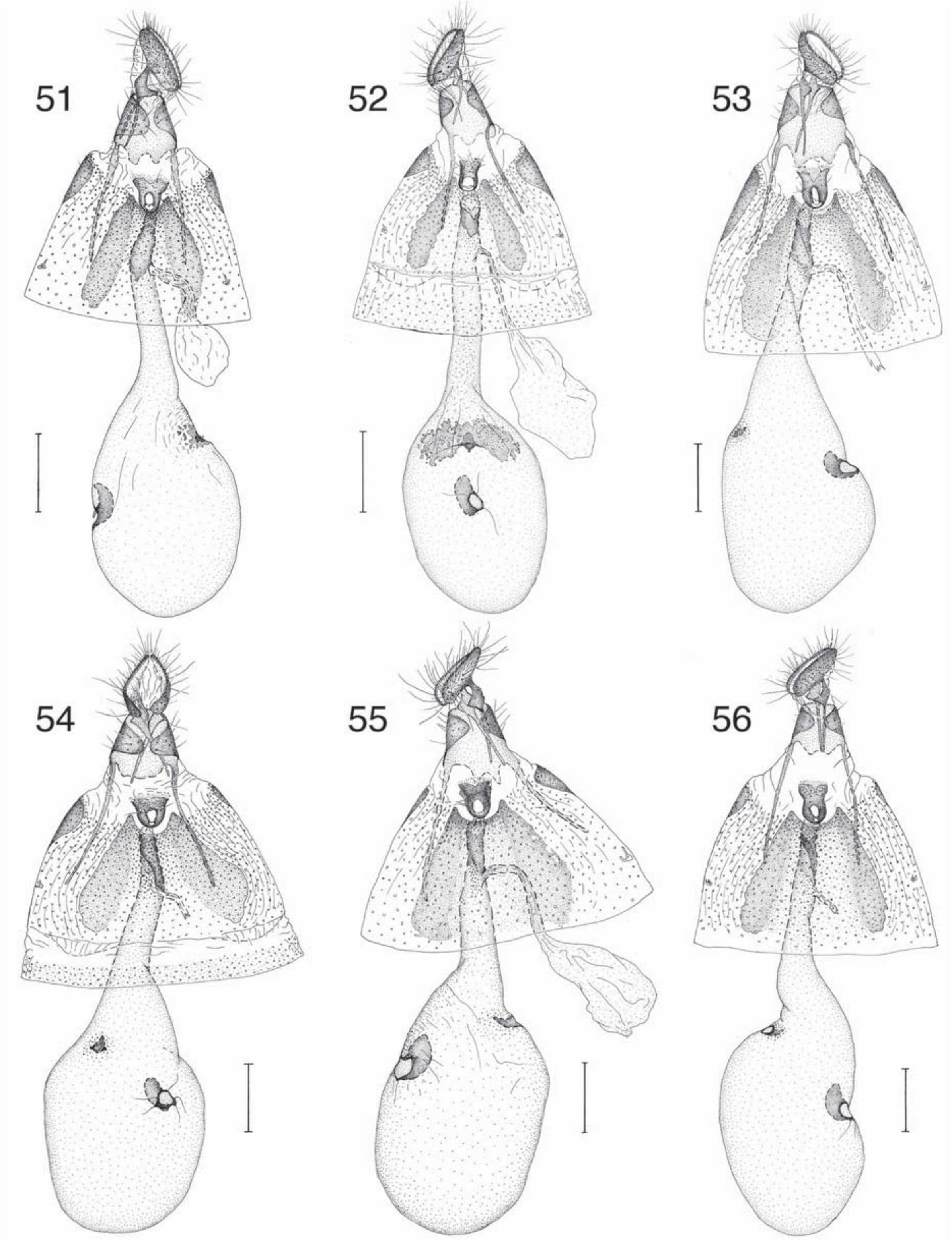
Eucosma floridensis, new species

(Figs. 29–30, 47, 59, 71)

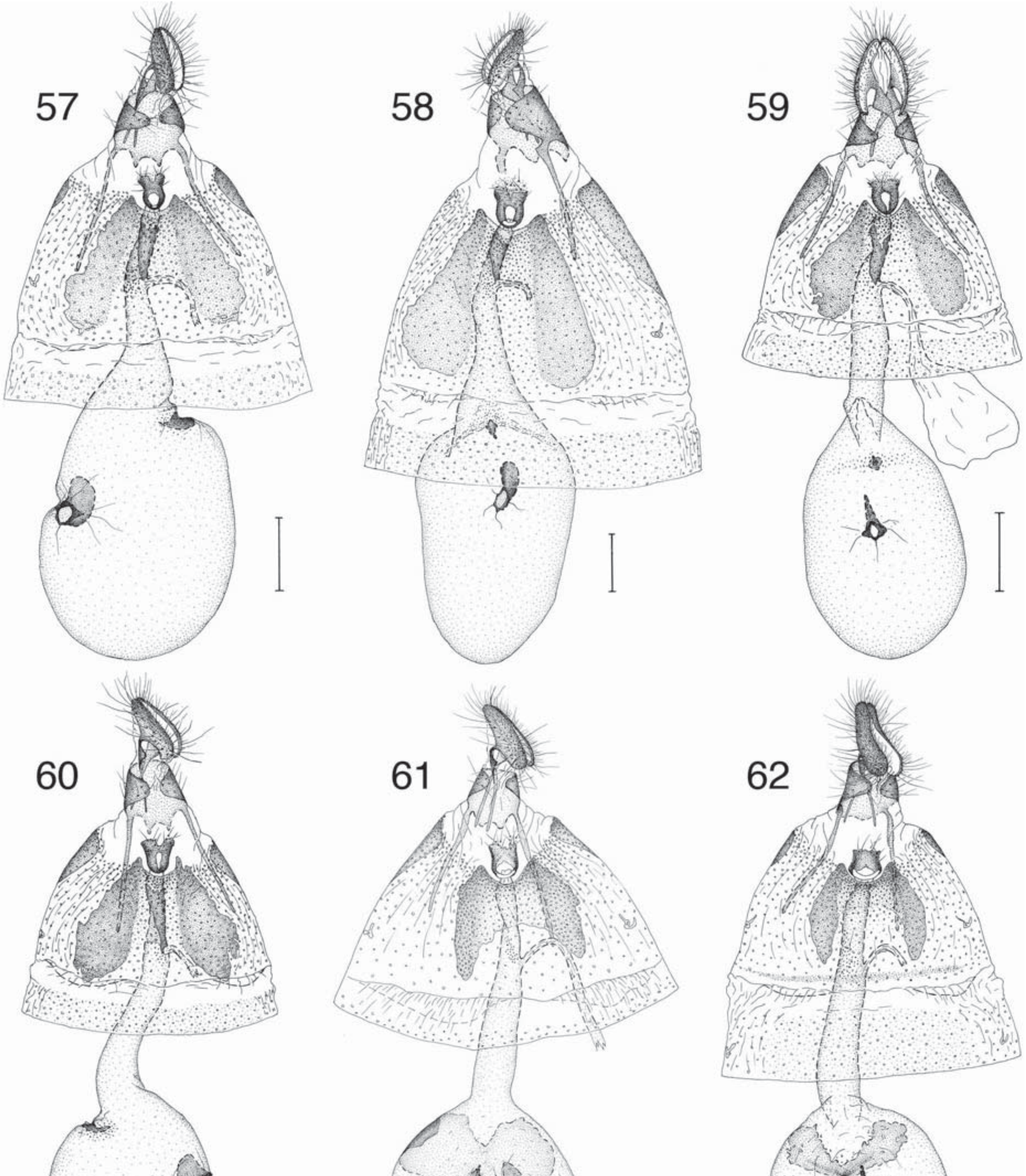
Diagnosis. *Eucosma floridensis* appears to be the only member of the *E. pulveratana* group that has been recorded from Florida. It is distinguished by the wine-red color of the postmedian band and the pinkish tint to the distal one-half of the forewing.

Description. *Head*: Frons white; vertex brownish gray to creamy white, sometimes with pale reddish-brown tints; labial palpus with medial surface white, lateral surface brownish gray, shading to white basally; antenna gray to brownish gray.

Thorax: Dorsal surface brownish gray tinted with reddish brown; ventral surface whitish; fore- and mid-legs with gray-brown anterior surfaces, whitish posterior surfaces, and whitish markings at mid-tibia, distal end of tibia, and distal ends of tarsomeres; hind-legs whitish, with proximal ends of tarsomeres darker. *Forewing* (Figs. 29–30): ♂ FWL 7.0–8.6 mm (mean = 7.9, n = 5), AR = 2.99; ♀ FWL 7.6 mm (n = 1), AR = 3.17; interfascial areas pale gray brown, variably suffused



FIGS. 51–56. Female genitalia. **51,** *E. pulveratana*, slide DJW 1257. **52,** *E. consobrinana*, slide DJW 2275. **53,** *E. suadana*, slide DJW 2072. **54,** *E. seamansi*, slide DJW 2313. **55,** *E. sepiana*, USNM 95244. **56,** *E. coconana*, slide DJW 2321. Scale bar = 0.5 mm.



FIGS. 57–62. Female genitalia. **57,** *E. parapulveratana*, slide DJW 2288. **58,** *E. navajoensis*, slide DJW 2299. **59,** *E. floridensis*, slide DJW 2311. **60,** *E. costastriata*, slide DJW 2293. **61,** *E. mirosignata*, slide DJW 1264. **62,** *E. mojaveana*, slide DJW 2287. Scale bar = 0.5 mm.

with white and pale reddish brown; subbasal and pretornal marks blackish brown with white edging; postmedian band reddish brown, with some black and gray scaling; lustrous bars bordering ocellus gray; fringe scales blackish gray to reddish gray, with white apices; costal markings mostly striate.

Male genitalia (Fig. 47) (n = 3): Uncus with dorsal margin straight to medially indented; vesica with 4–6 deciduous cornuti; saccular angle acute (38°–56°, mean = 46°), with rounded vertex; cucullus with 2–4 marginal spines. *Female genitalia* (Fig. 59, 71) (n = 1): Width of membranous portion of lamella antevaginalis less than width of ostium; membrane between sterna VI and VII with pockets; sclerotization of ductus bursae extending from ductus seminalis nearly to constriction anterior to ostium; corpus bursae microspinulate near smaller signum.

Holotype. ♂, Florida, Highlands Co., Archbold Biol[ogical] Sta[tion], Lake Placid, D. C. Ferguson, 17 February 1985, USNM.

Paratypes. FLORIDA: same data as holotype (1 ♂, genitalia slide DJW 2309); Highlands Co., Archbold Biol. Sta., S. W. Frost, 22 January 1967 (1 ♂, genitalia slide DJW 1161), 30 January 1964 (1 ♂); Highlands Hammock St. Pk. Cpgd., George J. Balogh, 1 October 1985 (1 ♂, genitalia slide DJW 2310), 15 November 1987 (1 ♀, genitalia slide DJW 2311). Paratype depositories: DJW, MCZ, USNM.

Etymology. The name refers to the state of Florida.

Distribution and biology. The six specimens (5 ♂, 1 ♀) in the type series are from Highlands Co., Florida and were captured between 1 October and 17 February.

Eucosma costastriata **new species**

(Figs. 1h, 35, 48, 60, 72, 77)

Diagnosis. This species is similar in forewing appearance to *E. mirosignata* (discussed below) but is smaller (mean FWL ≈ 7.9 vs. 9.8 mm) and has distinctly different genitalia (Figs. 48 vs. 49 & 60 vs. 61). The SA is sharply acute (mean ≈ 32°) and the dorsal margin of the uncus is medially indented vs. obtuse (mean ≈ 122°) and semicircular, respectively, in *E. mirosignata*. Females of the two species differ in the sclerotization of both the ductus bursae (present in *E. costastriata*, absent in *E. mirosignata*) and the membrane surrounding the smaller signum (microspinules in *E. costastriata*, a broad plate in *E. mirosignata*). Present data suggest that the ranges of the two species are disjunct (Figs. 77 & 76), but both occur in Texas.

Description. *Head*: Frons pale tan to creamy white; vertex grayish brown; labial palpus with medial surface creamy white, lateral surface grayish brown; antenna concolorous with vertex.

Thorax: Scales on dorsal surface gray brown with white apices; ventral surface tan to creamy white; fore- and mid-legs with anterior surfaces gray-brown, posterior surfaces whitish, and with white annular markings at mid-tibia, distal end of tibia, and distal end of each tarsomere; hind-leg pale tan with lighter tarsal annulations. *Forewing* (Fig. 35): ♂ FWL 6.6–9.1 mm (mean = 7.7, n = 13), AR = 3.02; ♀ FWL 6.8–8.8 mm (mean = 8.0, n = 15), AR = 3.03; interfascial areas pale tan to creamy white, extensively reticulated with gray brown; subbasal and pretornal marks dark brown; postmedian band thin and inconspicuous, often interrupted by whitish subcostal streak; ocellus with lustrous bars gray to fawn and with central field often lacking dark dashes; fringe scales with white tips and pale-brown to blackish-brown medial cross-markings; costal markings striate from base to apex.

Male genitalia (Fig. 48) (n = 8): Uncus weakly divided medially; vesica with 6–8 deciduous cornuti; saccular angle acute (21°–45°, mean = 32°), often weakly falcate; cucullus usually with 4–5 marginal spines, occasionally with 3 or 6. *Female genitalia* (Figs. 60, 72) (n = 5): Membranous portion of lamella antevaginalis shorter than ostium width; membrane between sterna VI and VII with shallow pockets; sclerotization of ductus bursae extending from ductus seminalis nearly to constriction anterior to ostium; corpus bursae microspinulate near small signum.

Holotype (Fig. 35). ♂, Nebraska, Cherry Co., Valentine NWR, Hackberry Lake, R. W. Hodges, 30 June 1983, USNM.

Paratypes. COLORADO: Cheyenne Co., Wild Horse Post Office, 38° 49.60' N, 103°00.60' W, 4453 ft., T. M Gilligan, 11 August 2009 (1 ♂); [El Paso Co.], Colorado Springs, Fountain Valley School, 12–19 July 1932 (1 ♂, genitalia slide ABK 21-XII-32); vic. Colorado Springs, 17 August 1937 (1 ♀); Lincoln Co., Hugo, hospital on Shell St., 5040 ft., T. M. Gilligan, 11 August 2009 (1 ♂; 2 ♀, genitalia slide DJW 2393); Morgan Co., Muir Springs Pk. & Rec. Area, 3 mi. W. Fort Morgan, 4320 ft., T. S. Dickel, 1 August 1992 (1 ♂; 5 ♀, genitalia slide DJW 2293); Morgan Co., 9 mi. S. Ft. Morgan, 3 mi. W. Co. Rd. 19, D. J. Wright, 6 September 2000 (2 ♀); Weld Co., Rd. 386, 1 mi. W Deerfield, Buckner & Opler, 2 September 1994 (1 ♀); Yuma Co., Bonny Reservoir SRA, 0.7 mi. E. of US 385 on Co. Rd. 3, 3720 ft., D. J. Wright, 5 August 1996 (1 ♂, genitalia slide DJW 253). ILLINOIS: Cook Co., Bartel wetland, R. Panzer, 5 September 2002 (1 ♂, genitalia slide DJW 2294). INDIANA: Lake Co., Du Pont Savanna, R. Panzer, 3 August 1999 (1 ♀, genitalia DJW 2295). IOWA: Muscatine Co., Big Sand Mound S. of Muscatine, G. J. Balogh, 11 September 1993 (2 ♂, genitalia slide DJW 350). KANSAS: Morton Co., Cimarron NG, D. J. Wright, 26 August 2000 (1 ♀). MICHIGAN: Allegan Co., T2N R15W S1, G. J. Balogh, 25 July 1992 (1 ♂, genitalia slide DJW 2292), T3N R14 W S31, G. J. Balogh, 25 July 1992 (1 ♂). MONTANA: Carter Co., Medicine Rocks St. Pk., G. J. Balogh, 4 September 2002 (2 ♂; 2 ♀, genitalia slides DJW 1037, 2392), 5 September 2002 (1 ♂, genitalia slide DJW 2076). WISCONSIN: Oneida Co., Lake Katherine, H. M. Bower, 9 August 1961 (1 ♀), 13 August 1961 (1 ♂). Paratype depositories: AMNH, CNC, CSU, DJW, EME, MEM, TMG, USNM.

Etymology. The specific epithet refers to the fine striate markings along the costal margin of the forewing.

Distribution and biology. This moth appears to be restricted to the Great Plains. The 36 specimens (18 ♂, 18 ♀) that I examined document a range extending from southwestern Michigan to eastern Montana, south to Texas and northern Indiana (Fig. 77). Adult flight occurs from early July to mid-September, but most records are from August and September.

Remark. Miller (1987) illustrated as *E. pulveratana* a specimen from Wisconsin that I have included above among the paratypes of *E. costastriata*.

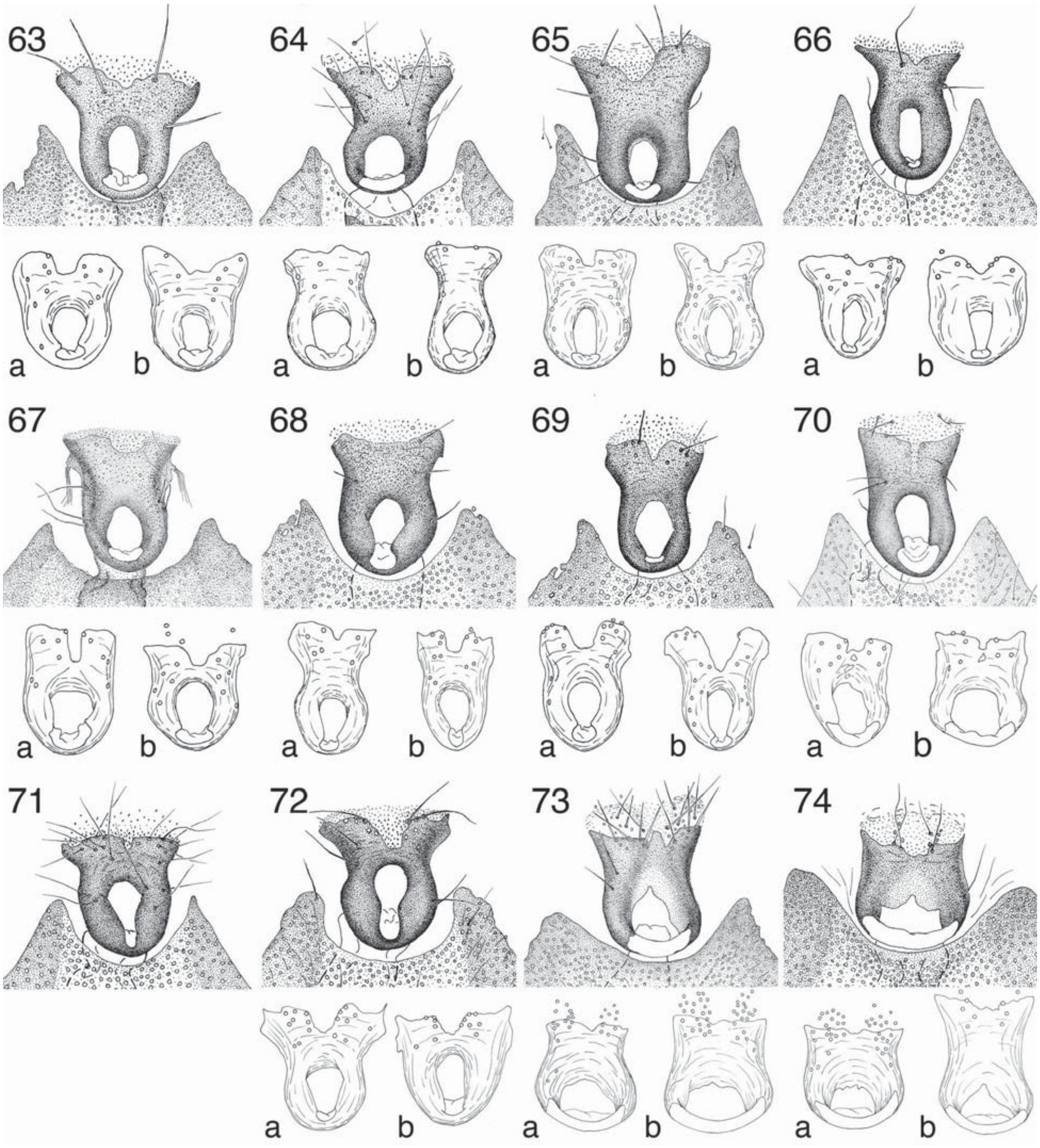
Eucosma mirosignata Heinrich

(Figs. 1c, i, 31–32, 49, 61, 73, 76)

Eucosma mirosignata Heinrich 1929:11, fig. 10; McDunnough 1939:47; Powell 1983:35.

Eucosma microsignata: Brown 2005:324, misspelling.

Types. Holotype: ♂, Arizona, Pima Co., Baboquivari Mts., O. C. Poling, 15–30 Oct 1924, genitalia slide 70483, USNM. Paratypes. ARIZONA: Same locality and collector as holotype, 15–30 April 1924 (1 ♀, AMNH), 1–15 May 1924 (2 ♀, USNM, genitalia slide DJW 1259), 15–30 May 1924 (1 ♀, USNM, genitalia slide DJW 1260), 15–30 July 1924 (1 ♀), 27–31 July 1923 (1 ♀, AMNH), 15–30 August 1923 (1 ♀, USNM; 2 ♀, CNC), 1–15 September 1923 (3 ♀, USNM, genitalia slide 70484), 15–30 November 1924 (1 ♀, USNM). CALIFORNIA: (1 ♀, AMNH); San Bernardino Co., Loma Linda, 24–31 August (1 ♀), 16–23 October (1 ♀); San Diego, [San Diego Co.], K. R. Coolidge, 4 August 1920 (1 ♀). [This accounts for 18 of the 20 paratypes mentioned by Heinrich (1929)].



FIGS. 63–74. Sterigmata. **63,** *E. pulveratana*, slides DJW 1257, USNM 70491, DJW 2073. **64,** *E. consobrinana*, slides USNM 70485, DJW 2272, USNM 90477. **65,** *E. suadana*, slides DJW 1188, 1212, 2278. **66,** *E. seamansi*, slides DJW 2080, 2314, 2316. **67,** *E. sepiana*, slides USNM 95244, DJW 2302, USNM 70650. **68,** *E. coconana*, slides DJW 2323. USNM 70512, DJW 2324. **69,** *E. parapulveratana*, slides DJW 1875, 1191, 2289. **70,** *E. navajoensis*, slides DJW 1163, 2297, 2301. **71,** *E. floridensis*, slide DJW 2311. **72,** *E. costastriata*, slides DJW 1037, 2392, 2393. **73,** *E. mirosignata*, slides DJW 1850, 1260, 1854. **74,** *E. mojaveana*, slides DJW 2286, 2382, 1160.

FIG. 75–77. Geographic distribution of species.

Description. *Head*: Frons white; vertex scales predominantly white, shading to gray brown basally; labial palpus with medial surface white, scales of lateral surface pale brown with white tips; antenna concolorous with vertex.

Thorax: Scales on dorsal surface gray brown with white apices; ventral surface whitish; legs gray brown with white annular markings at mid tibia, distal end of tibia, and distal end of each tarsomere. *Forewing* (Figs. 31–32): ♂ FWL 7.5–11.6 mm (mean = 9.6, n = 27), AR = 3.14; ♀ FWL 8.9–11.2 mm (mean = 10.0, n = 23), AR = 2.95; interfascial areas pale brownish gray, variably reticulated with white; subbasal and pretornal marks blackish brown and prominently edged with white; postmedian band pale brown and inconspicuous, often interrupted by white subcostal streak; lustrous bars bordering ocellus pale fawn to gray; fringe scales with brown to blackish-brown medial cross-markings and white apices; costal markings striate from base to apex.

Male genitalia (Fig. 49) (n = 7): Uncus well developed, with apex rounded; vesica with 2–8 deciduous cornuti; saccular angle obtuse (112°–134°, mean = 122°), with vertex broadly rounded; anal angle acute; cucullus with 5–8 marginal spines. *Female genitalia* (Figs. 61, 73) (n = 9): Lamella postvaginalis with shallow medial trough and with lateral margins weakly concave; membranous portion of lamella antevaginalis broader than ostium; membrane between sterna VI and VII with well developed pockets; ductus bursae lacking sclerotization; sclerotized patch on membrane of corpus bursae moderate to large, constricted medially; smaller signum variable in size, sometimes nearly obsolete.

Distribution and biology. This species seems to be restricted to the desert region of southwestern United States bordering Mexico. I examined 71 specimens (34 ♂, 37 ♀) from southern Arizona, southern California, southern New Mexico, and west Texas (Fig. 76). Adults fly from 24 March to 15 November, but the largest concentrations of records are in April and September.

Remarks. This moth might be confused with *E. costastriata* based on forewing appearance, but the two species are easily separated by genitalia. Differences are discussed in the diagnosis section for *E. costastriata*.

Eucosma mojaveana new species

(Figs. 33–34, 50, 62, 74, 76)

Diagnosis. This species is closest to *mirosignata*, the only other member of the *pulveratana* group with a large apically rounded uncus and an obtuse saccular angle. The two differ in forewing color, *mirosignata* being gray to brownish gray with blackish-brown markings, *mojaveana* creamy white to salmon with orange-brown markings. In *E. mojaveana*, the cucullus has 2–4 marginal spines, and the width of the valva narrows gradually from base to saccular angle; in *E. mirosignata* there are 4–8 marginal spines, and the costal and ventral margins of the basal portion of the valva are parallel.

Description. *Head*: Frons creamy white; vertex and labial palpi creamy white with some pale fawn shading; antenna concolorous with vertex.

Thorax: Dorsal surface pale fawn; ventral surface creamy white; legs creamy white to pale fawn, with white ring at distal extremity of each tarsomere. *Forewing* (Figs. 33–34): ♂ FWL 8.1–8.9 mm (mean = 8.5, n = 11), AR = 2.88; ♀ FWL 8.3–10.4 mm (mean = 9.6, n = 6), AR = 2.89; interfascial areas creamy white, with pale fawn reticulations; subbasal and pretornal marks orange brown; postmedian band pale orange brown, inconspicuous, and usually interrupted by white scaling near costa; lustrous bars bordering ocellus fawn to pearly gray; fringe scales white with brown medial cross-markings; costal markings mostly striate from base to apex.

Male genitalia (Fig. 50) (n = 4): Uncus well developed, with apex rounded; vesica with 2–5 deciduous cornuti; valva narrowing from base to distal end of sacculus; saccular angle obtuse (127°–146°, mean = 136°), with broadly rounded vertex; cucullus with 2–4 marginal spines and with apex semicircular. *Female genitalia* (Figs. 62, 74) (n = 4): Lamella postvaginalis with shallow central trough and with lateral margins straight to weakly concave; lamella antevaginalis almost entirely membranous; membrane between sterna VI and VII with pockets; ductus bursae lacking sclerotization; sclerotized plate on surface of corpus bursae broad, often disintegrating toward lateral extremities, sometimes with thickened ridge emanating laterally from signum.

Holotype (Fig. 33). ♀, California, San Bernardino Co., Afton Road, 23 mi SW Baker, Kitayama, Cave & Chemsak, 23 April 1977, genitalia slide DJW 2287, EME.

Paratypes. ARIZONA: En route Dewey to Salome, 1–7 May (1 ♂); Mohave Co., 8–15 June (1 ♀, genitalia slide DJW 2286); Beaver Dam Canyon, G. J. Balogh, 28 September 2000 (1 ♂, genitalia slide DJW 1131). CALIFORNIA: Imperial Co., Ocotillo, P. A. Opler, 5 October 1967 (1 ♂, genitalia slide DJW 2285); Painted Gorge, E. C. Johnson, 18 April 1950 (1 ♀); [Riverside Co.], Palm Springs, Chino Canyon, E. C. Johnson, 19 April 1950 (1 ♂, genitalia slide DJW 1851); San Bernardino Co., 10 mi. NE Earp, D. D. Linsdale, 17 April 1964 (1 ♂); 10 mi. N Earp, J. R. Powers, 22 April 1960 (6 ♂, genitalia slide DJW 2284), 23 April 1960 (1 ♂; 1 ♀); J. F. Lawrence, 22 April 1960 (1 ♀, genitalia slide DJW 1160). Paratype depositories: CNC, DJW, EME, USNM.

Etymology. The specific epithet refers to the Mojave Desert.

Distribution and biology. The type series consists of 18 specimens (12 ♂, 6 ♀) from southern California and northwestern Arizona (Fig. 76). Most were collected in April, but there is one record each from late September and early October.

REMARKS

Figures 36–38 illustrate moths in the *pulveratana* group which very likely represent three additional unnamed species but which are not described here for lack of sufficient material. The first (Fig. 36) is known from three male specimens collected by A. J. Slater and J. A. Powell on 24 April 1966 at the mouth of the Ventura River in Ventura Co., California. It is a medium sized member of the group (mean FWL = 8.3 mm) with a distinctive olive-brown forewing color. The male genitalia are similar to those of *E. coconana*, with SA ≈ 90°. Figure 37 depicts one of several male specimens acquired by various collectors in July at ca. 8500 ft. in Teller Co., Colorado. These moths are nearly as large as *E. navajoensis* but have a darker and narrower forewing. In male genitalia they resemble *E. suadana*. Finally, Figure 38 is representative of a population of rather melanic-looking members of the *pulveratana* group collected by J. S. Nordin in late June and throughout July at Gelatt Lake in Albany Co., Wyoming. In size they are similar to *E. suadana*, but the male genitalia are closer to those of *E. coconana*, with SA ≈ 90°. A few females have been collected at this location, but they are smaller than the males (mean FWL = 9.2 vs. 10.6 mm) and may not be conspecific with the males.

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THE ROLE OF ENVIRONMENTAL FACTORS IN THE NORTHEASTERN RANGE EXPANSION OF *PAPILIO CRESPHONTES* CRAMER (PAPILIONIDAE)

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ABSTRACT. The Giant Swallowtail butterfly, *Papilio cresphontes* Cramer (Papilionidae), has been reported in New York State for nearly 150 years. In recent years there has been an unexplained increase in *P. cresphontes* occurrences along the northeastern periphery of its geographical range. This study examined historical records to describe the movement of *P. cresphontes* populations into New York State and adjacent Ontario. Climate data and field studies were used to identify environmental factors that may influence the range expansion, which was found to correspond with an absence of September frosts beginning in 2001. Field studies indicated that some *P. cresphontes* larvae were capable of withstanding multiple frosts and descended to pupate normally into late October in the range expansion area. Although the larvae may have adapted to endure cooler temperatures to some degree, the effects of warming temperatures on other factors such as natural enemies and larval host plant quality in autumn may influence the spread of *P. cresphontes* populations at least as much as larval frost tolerance.

Additional key words: Butterfly range expansion, climate change, biogeography

In 1864 the first record of a Giant Swallowtail (*Papilio cresphontes* Cramer, Papilionidae) was documented for the state of New York (Scudder 1889; Lintner 1893; Comstock & Comstock 1929), but over the last century sightings of this butterfly have been extremely scarce until the past nine years (New York State Butterfly Records 2001–2005; Dirig 2008, 2009). Indeed, over the past decade *P. cresphontes* has become increasingly abundant in central New York State and appears to be expanding along the northeastern boundary of its range. The causes and characteristics of this recent increase in geographical distribution and population density of *P. cresphontes* are currently unknown.

This paper provides some of the first field data on the presence and survival of *P. cresphontes* in central New York, and the influence of environmental factors on the range expansion of this butterfly. We followed a *P. cresphontes* larval field population to pupation, assessing their ability to overwinter in the area and their vulnerability to natural enemies. Weather records were used to examine climatic impacts on larval populations, and literature and historical records revealed distribution and occurrence reports of *P. cresphontes*. These data suggest that what shapes the geographical distribution of *P. cresphontes* may not just be host plant abundance, available habitat, or freeze-induced mortality as previously emphasized (Scudder 1889; Wild 1939; Tyler et al. 1994; Hughes 2000; Dennis et al. 2005; Hellman et al. 2008), but may well include the effect of climate on host plant condition and abundance of parasitoids.

METHODS

Field studies. The main field site for this autumn 2008 study was Cornell University's Eames Memorial Natural Area, part of Mud Creek Swamp, located near Freeville, New York, approximately 20 km northeast of Ithaca. The area covers 11 ha and was selected based on previous sightings of *P. cresphontes*, an abundance of the local host plant (*Zanthoxylum americanum* Mill., Rutaceae), and prior evidence of larval populations. In October and November, foliage of *Z. americanum* was searched for the presence of *P. cresphontes* larvae and pupae. Each tree with one or more larvae was marked with flagging tape, and trees with larvae were revisited later for pupal searches.

After winter passed, marked *Z. americanum* were thoroughly checked for pupae. Because *P. cresphontes* larvae generally pupate within 5 m of their host plant (West & Hazel 1996), all vegetation within a 5 m radius of the host plant was exhaustively checked for pupae. This was used as a standardized searching method. Cadavers of *P. cresphontes* collected from the site were inspected for evidence of predation, parasitoids or other sources of mortality by Dr. Ann Hajek at Cornell University.

Distribution studies. Occurrence reports of *P. cresphontes* in the region were compiled from annual Season Summaries in News of the Lepidopterists' Society (1947–2008) and New York State Butterfly Records (2001–2005). Ontario occurrence reports were gathered from Season Summaries in News of the Lepidopterists' Society (1970–2008) as well as summaries published by the Toronto Entomologists' Association between 1977 and 2002. Many occurrence records were documented by the same person at each town or county, suggesting there was consistency in the reports and sampling efforts. Although it is impossible to completely disregard an increase in sampling, *P. cresphontes* is such a large, conspicuous, and somewhat rare butterfly that it is expected to be reported if it occurred in any numbers. The information gathered from these reports was used to create graphs and a map tracking the movement of *P. cresphontes* into New York. A one-tailed two-sample unequal variance *t*-test was run to examine the differences in number of *P. cresphontes* occurrences over time, and means were derived from annual occurrences.

Weather data. To determine if climate change had an impact on *P. cresphontes* populations, New York weather records from 1980–2008 were obtained from the Northeast Regional Climate Center (NRCC 2009). Only frosts from the Ithaca, New York weather station were used in data analysis. Every frost event, i.e., temperature occurrence of 0° C or colder, between the months of September and November (the time period when larvae can still be found feeding on host plants) was noted. A two-tailed two-sample unequal variance *t*-test was run to compare frost incidences to *P. cresphontes* occurrences. The occurrences of below-freezing temperatures in autumn 2008 were also compared with the amount of time *P. cresphontes* larvae continued to feed on *Z. americanum*, despite the frigid temperatures. Finally a two-tailed Fisher's exact test was used to examine the association between butterfly occurrences and frost absence. Means were calculated based on annual frost reports for September–November and September only.

RESULTS

Historical records. The season summaries and occurrence reports of *P. cresphontes* in New York showed no official sightings between 1947 and 2000 (there are scarce previous reports of *P. cresphontes* in the state from older historical records, and informal reports support that this species was rare or nonexistent in central New York at least during the 1960's; A. Shapiro, pers. comm.). Beginning in 2001, there was a rapid increase in *P. cresphontes* reports (Fig. 1). There is a significant difference between past (1947–2000) and recent (2001–2008) butterfly occurrences (P = 0.036, DF = 61, past occurrences $\bar{x}$ = 0.0, SE = 0.0; recent occurrences $\bar{x}$ = 6.38, SE = 3.01). Based on recent sightings, it appears that the butterfly populations are moving both north and east through New York (Fig. 2A).

According to the season summaries and sighting reports from Ontario, the first post-1970 observation of *P. cresphontes* was made in 1974. Reports were much more common from 1975–2008 in Ontario than they were in New York. A significant difference is observed between past (1970–2000) and recent (2001–2008) reported *P. cresphontes* occurrences in Ontario, with a much higher number of occurrences during recent years (P = 0.007, DF = 38, past occurrences $\bar{x}$ = 13.65, SE = 2.40; recent occurrences $\bar{x}$ = 99.75, SE = 53.78; see Fig. 1). We recognize a boom and bust pattern during 2005–2008, preceded by no occurrence reports in 2004 and very few in 2002–2003. Multiple Ontario sightings described groups of tens of members, and a 2005 sighting reported 306 *P. cresphontes* adults in one large meadow on Pelee Island in Essex County.

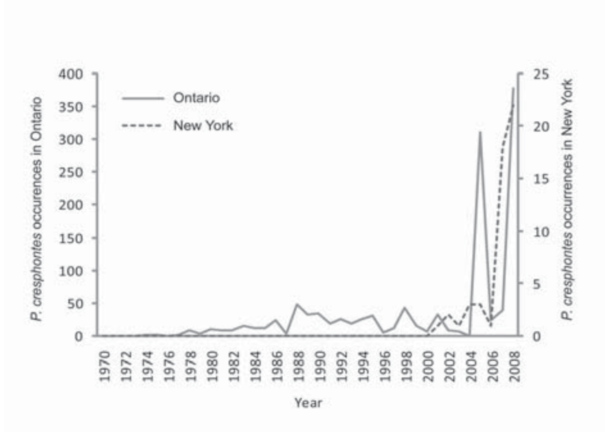

FIG. 1. Combined occurrence reports (larvae and adults) of *P. crephontes* in Ontario and New York State, 1970–2008.

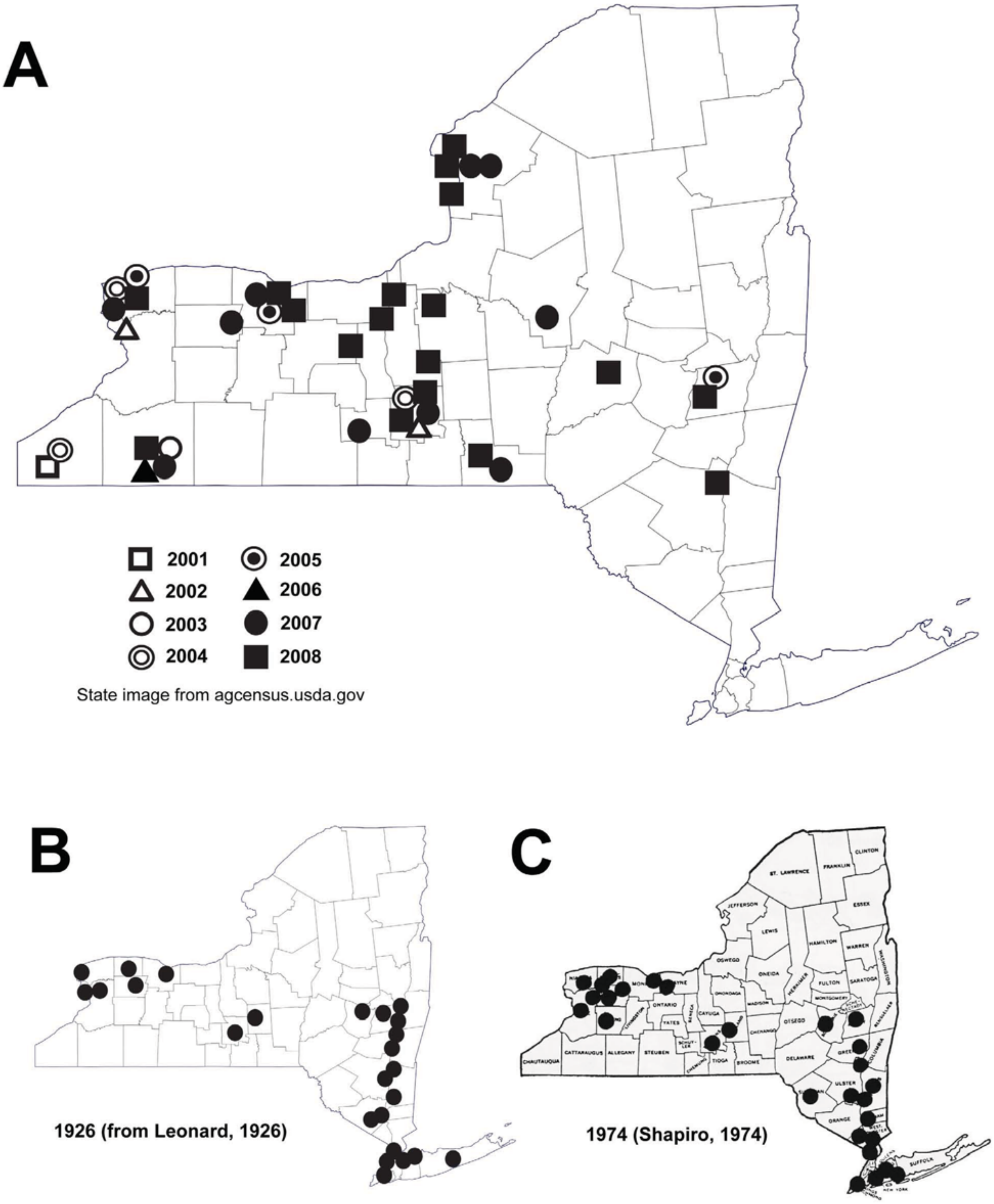

FIG. 2. Recent versus historical distribution of *P. cresphontes* sightings in New York State.

Fall Temperatures. Ithaca frost records from September through November during 1980–2008 showed no statistically significant difference between the total numbers of past (1980–2000) and recent (2001–2008) frost occurrences (P = 0.127, DF = 28, past occurrences $\bar{x}$ = 26.0, SE = 0.976; recent occurrences $\bar{x}$ = 22.5, SE = 1.880). However, no frosts were reported during the month of September in Ithaca after 2000. This also holds true for most of the 33 locations in New York where other sightings occurred. There is a significant difference between past and recent September frost occurrences, with frosts more common prior to 2001 (P < 0.001, DF = 28; past occurrences $\bar{x}$ = 0.857, SE = 0.199; recent occurrences $\bar{x}$= 0.0, SE = 0.0). The Fisher's exact test shows a significant relationship between the absence of September frosts and the presence of *P. cresphontes* (P = 0.0089; Fig. 3). All frost data in general showed the least number of frosts in September and the most in November.

Larval survival. Twelve *P. cresphontes* larvae of various instars were found at the Eames field site on 3 October 2008, on five different *Z. americanum* plants. The larvae were monitored over the course of four weeks, during which time there were multiple gaps where the air temperature fell below freezing for several hours each time. All 12 larvae survived the first frost of the season (7 October, minimum temperature; -1.2° C, 6 hours (h) frost duration). Larvae surviving the remaining frosts endured minimum temperatures of -2.7° C, -3.9° C, -0.4° C, -2.5° C, -3.1° C, and -0.9° C, with temperatures below freezing for 6 h, 10 h, 10 h, 10 h, 8 h, and 3 h, respectively. Evidence of mortality was not seen until 19 October, with further mortality observed on 26 October (Table 1). Six larval cadavers were found at the site, the majority of them hanging from the host plant. According to laboratory examination, the cause of mortality of one specimen appeared to be predation. It had a large hole in the dorsum through the body, yet looked very healthy with a gut full of food. The other larvae contained no recognizable evidence of the cause of mortality.

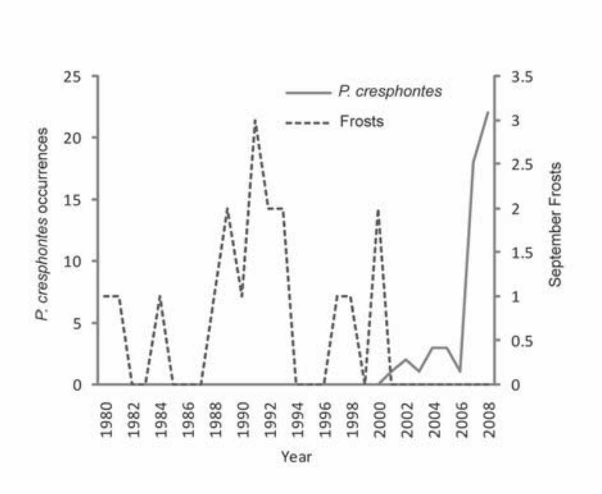

FIG. 3. Occurrence reports of *P. cresphontes* in New York State (1980-2008), compared to September frost records for Ithaca.

The Eames field site was revisited on 28 March 2009, to search for pupae. Only one *P. cresphontes* specimen was found. It appeared to be a dead pre-pupa; it was partially decomposed, with the head capsule present but split in half. The cadaver was propped in a silken girdle, indicating that this was a pupation attempt. A large cavity was found in the center of the pre-pupa, likely from a parasitoid that exited the larval host.

TABLE 1. Number of *P. cresphontes* larvae over time on five *Z. americanum* host plants at Eames Memorial Natural Area near Ithaca, New York. Larval instars are indicated by the instar number followed by "*i*", preceded (outside of parenthesis) by the number of larvae found at that instar. Frosts (NRCC 2009) were recorded on 7, 18, 19, 20, 21, 23, and 24 October.

	Plant #1		Plant #2		Plant #3		Plant #4		Plant #5	
Date	Living	Dead	Living	Dead	Living	Dead	Living	Dead	Living	Dead
3 Oct 08	1(5*i*)	0	3(3*i*) 2(5*i*)	0	1(3*i*) 1(5*i*)	0	1(3*i*) 1(4*i*) 1(5*i*)	0	1(5*i*)	0
11 Oct 08	1(5*i*)	0	3(3*i*) 2(5*i*)	0	1(3*i*) 1(5*i*)	0	1(3*i*) 1(4*i*) 1(5*i*)	0	1(5*i*)	0
19 Oct 08	1(5*i*)	0	3(3*i*)	2	0	0	2(5*i*)	1	1(5*i*)	0
26 Oct 08	0	0	0	1	0	0	2(5*i*)	1	0	1

DISCUSSION

Larval frost tolerance. The results from the field data indicate *P. cresphontes* larvae are capable of withstanding multiple frosts (as low as -3.9° C) and temperatures below freezing for up to 10 hours. The minimum lethal temperature for *P. cresphontes* larvae is undetermined. Evidence confirming that larvae can endure not one but several frosts contradicts a previous hypothesis about *P. cresphontes* by Scudder (1889) stating that "frosts must here [Massachusetts] as elsewhere kill off the belated caterpillars". He also suggested the progeny of later larval broods would be unable to grow to maturity due to frosts. Hanks (1988) described the lack of giant swallowtail butterfly observations in Ontario later in the season as a probable indication the adult population was killed by cold temperatures.

It is common to link freezing temperatures with insect mortality. In other insect larvae, such as the beetle *Oncideres pustulatus* LeConte (Cerambycidae), freezing was responsible for high mortality rates that likely limit its northern distribution in Texas (Rice 1986). There are several published examples, however, where lepidopterans and other insects (in particular larvae) have been capable of withstanding temperatures below freezing (Sømme 1986; Bale 1991; Storey & Storey 1996; Brown et al. 2004; Ross 2008). Observations by Hine (1908) concerning the effects of freezing on the Cattail borer moth (*Bellura obliqua* Walker, Noctuidae) indicate successful and complete recovery by larvae from multiple freezes ranging from -19 to -28° C. Based on field observations with *P. cresphontes* in October 2008, it is possible this species has recently adapted to endure cold temperatures on the northern periphery of its range.

Frosts affect host plant quality. Although frost data from Ithaca for the past 29 years do not reveal significant changes in the number of frosts each fall, they do indicate a higher frequency of September frosts before the *P. cresphontes* boom. After 2000, no September frosts were recorded. Perhaps *Z. americanum* plants had been previously affected by early frosts before the 21st century enough to starve late larval populations of *P. cresphontes*, or slow their growth rate and in turn increase the likelihood of attacks by natural enemies. If early frosts had a significant impact on plant populations, then they likely had an impact on the herbivores dependent upon those plants.

That climate affects larval populations through poor host quality is supported by other research. The unavailability of fresh food for larvae during late autumn and early winter is one suggestion why subtropical, southern butterflies do not expand into more northern environments (Ross 2008). The caterpillars become so severely weakened by starvation that they die of metabolic failure or prolonged exposure to predators. During a follow-up visit to the field site in late October, the *Z. americanum* host plants were nearly bare and had dropped most of their leaves. Nevertheless, there were still two fifth-instars continuing to feed on the remaining poor-quality leaves. There is a connection made between chill effects, larval growth rate, and vulnerability to predators, the latter two comprising the slower-growth/higher-mortality hypothesis (Feeny 1976; Clancy & Price 1987; Fordyce & Shapiro 2003). Cooler temperatures inhibit the growth rate of larvae, which in turn leads to a greater likelihood of encountering a predator or other natural enemy. This hypothesis coincides well with our field results from the cadavers. With evidence of both parasitism and a predator assault, it seems logical to suspect that natural enemies are affecting the survivorship of *P. cresphontes* larvae in central New York.

Range expansion. Previous hypotheses that butterfly ranges are limited by host distribution (Tyler et al. 1994; Hughes 2000; Dennis et al. 2005) are contradicted by the results. *Z. americanum* is widely distributed throughout the eastern half of North America (USDA Plant Database 2009), and climate likely plays a greater role in range expansion than host plant availability. Other butterfly populations show evidence of distribution shifts due to temperature changes in their natural area (Parmesan et al. 1999). *Papilio zelicaon* Lucas (Papilionidae) and *Erynnis propertius* Scudder (Hesperiidae) may increase at their range edge with warming (Hellmann et al. 2008), and warmer winters drive range expansion in the sachem skipper *Atalopedes campestris* Boisduval (Hesperiidae) (Crozier 2004). Larger fluctuations in butterfly populations are seen in more northern than southern ranges, and temperature most likely has the largest influence on butterflies during late larval and pupal development (Dennis 1993). Co-variations between sites and species further indicate climate could be a major source of population fluctuations. Boom and bust patterns, such as the pattern in Ontario from 2005–2008, are common at geographic range margins where populations expand in warm years but retract during cool years (Thomas et al. 1998). Shapiro (1974) considered *P. cresphontes* likely a breeding resident in western New York and breeding sporadically in the Hudson Valley, and Klots (1951) mentions that this species is sporadic northward. This is a pattern consistent with most species at the northern edge of their range.

Although data support a strong correlation between lack of September frosts and an increase in *P. cresphontes* occurrences, we can only present a plausible causal hypothesis that the decrease in autumn frosts could be responsible for the increase in occurrences. Other environmental variables may contribute to the range expansion in this species, therefore we emphasize that this correlation does not equal causation. There are two instances of three consecutive years without September frosts prior to 2000, yet no sightings were made following these intervals, which further suggests other factors besides (or in addition to) lack of September frosts have contributed to the increase in occurrences and range expansion.

Given the map created using occurrence reports, a distributional shift north and east into New York State is recognized. The individuals observed most recently in central New York may have traveled eastward from the Rochester and Niagara Falls regions, or perhaps crossed into New York from Ontario (assuming higher densities of the species exist in Ontario, as depicted in the occurrence reports). When a historical distribution map (data from Leonard 1926) for *P. cresphontes* is compared to the map created by Shapiro in 1974, the distributions are quite similar (Fig. 2B and 2C). The similarity between the two maps is likely a result of no new records found during the intervening period, and no distinction is made in Shapiro's map between historic and current records. There does not appear to be any significant increase in the range, although the possibility of a decrease prior to 1974 is not excluded. This leads us to believe that population shifts by *P. cresphontes* were rare in New York State between 1926 and 1974, and provides further evidence that colonization and range expansion by this species is a recent phenomenon that requires close monitoring.

Based on field and historical data, an assumption can be made that populations of *P. cresphontes* will continue to appear in central New York and possibly increase in numbers, given the recent trend in heightened occurrences. Their distribution is predicted to expand in a northern and eastern direction toward appropriate habitats where the larval host plant is available, but cooler temperatures and natural enemies may slow the growth of certain populations. Over the course of the past century, *P. cresphontes* larvae may have adapted to endure cooler temperatures, thus allowing the opportunity for the advancement of populations beyond the limits of their previous geographical range. It is unclear why this adaptation would be happening now since the species has such a long history in North America. Further studies investigating the progression of *P. cresphontes* populations through New York will be helpful in connecting factors such as climate change, anthropogenic influences, and natural enemies to fluctuations in butterfly distribution ranges. Details following this movement will present valuable information regarding distributional shifts, not merely in butterflies, but in other organisms that may expand their ranges and colonize this region in future years.

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ON THE ANOMALOUS ALTITUDINAL DISTRIBUTION OF WEST HIMALAYAN TROIDINI AND PAPILIONINI (PAPILIONIDAE)

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ABSTRACT. The altitudinal distribution of those Papilioninae species that occur in both eastern and western parts of the Himalayan range is compared. Ten species were found to ascend with the latitude, one descends as latitude increases and fourteen are almost unaffected by latitude. The presence of a suitable larval host plant appears to be one of the decisive factors governing altitudinal distribution of these species. In four Papilioninae species, the same subspecies has exclusively colonized entirely different habitats in different parts of the Himalaya.

Additional key words: *Atrophaneura, Byasa, Graphium, Meandrusa, Pachliopta, Papilio, Troides*

The Himalayan range extends in a great arc from northwest to southeast, across the northern boundary of the Indian subcontinent. The eastern part of the range is several degrees of latitude south of the western part. The southernmost part of the range is nearly 27 degrees North latitude and 90 degrees East longitude in West Bengal, India, while the northernmost part of the range is around 34 degrees North latitude and 75 degrees East longitude in Jammu and Kashmir, India. The western half of the range has a drier, more temperate climate than the eastern half, with greater Palearctic affinities, both in plants (Polunin & Stainton 1984) and butterflies (Evans 1932). Both the tree line and the snow line are lower in the western Himalaya than in the east (Polunin & Stainton 1984) and plant species that occur along the entire length of the range generally grow at lower elevation in the west than in the east (Brandis 1875).

57 (+/- 1) species of Papilioninae are known from the Himalaya east of Sikkim. Of these, 27 species have been recorded from the Himalaya west of Nepal.

In the present study, the altitudinal distribution of the Papilioninae fauna found west of Nepal has been compared with that of the same species in the eastern Himalaya.

Atrophaneura varuna White, *Papilio alcmenor* C. & R. Felder and *Papilio helenus* L. have not been reported from the western Himalaya for nearly a century since Hannyngton (1910) and are therefore excluded from the discussion. However, it is worthy of note that Hannyngton recorded *alcmenor* up to 2100 m elevation while in the eastern Himalaya it is known from 300 m (Arora & Mondal 1981) to 1800 m (Talbot 1939).

MATERIALS AND METHODS

The altitudinal distributions of the Papilioninae species were obtained from three sources: the first, published literature; the second, unpublished notes compiled by my father, the late Fred Smetacek Sr. in Nainital district of the Kumaon Himalaya west of Nepal between 1949 and 1986 and the third, my own observations, mainly in the W. Himalaya, comprising specimens, field notes and the results of breeding experiments compiled since 1980.

The altitudinal distribution of the plant species mentioned was obtained from published botanical works. In all cases, the extreme altitude was taken, since these plants occur at different elevations in different localities. For example, since *Zanthoxylum armatum* DC (Rutaceae) ascends as high as 2100 m in Kumaon (Osmaston 1927) but to 2500 m further west in Kullu (Dhaliwal & Sharma 1999), I used 2500 m as the maximum elevation for the plant in the western Himalaya.

RESULTS

The altitudinal distribution of the Leptocircini (8 species common to both halves of the Himalaya) was found to be practically identical in both areas. Of these, only subgenus *Pazala* Moore of *Graphium* Scopoli containing two or three species and *Meandrusa* Moore are restricted to a montane habitat. There is some confusion regarding the taxonomic position of Himalayan members of *Pazala*, so suffice it to say that they occupy a belt between 1600 m and 2600 m along the entire range, with stragglers descending to 900 m (de Nicéville 1894; Wynter-Blyth 1957) and ascending to 3300 m (Ebert 1966). In the western Himalaya, two species are found, namely *Graphium* (*Pazala*) *eurous caschmirensis* Rothschild and *Graphium* (*Pazala*) *mandarinus garhwalica* Katayama. Although there is a record for a member of the genus ("*Papilio glycerion* Westwood" = *G. (P.) eurous vide* Racheli & Cotton 2009)) being bred on *Persea odoratissima* (Nees) Kosterm. (Lauraceae) in Mussoorie, W. Himalaya

(Robson 1895), I have only found *G. (P.) eurous* larvae on *Persea duthiei* (King ex Hook. f.) Kosterm. and *Neolitsea umbrosa* (Nees) Gamble (both Lauraceae), and both butterfly species entirely absent in areas where only *P. odoratissima* occurs in the Western Himalaya.

The remaining members of the tribe belong to *Graphium* (*Graphium*) Scopoli and are low elevation butterflies that inhabit the plains adjoining the hills and low outer ranges, with two species, *G. cloanthus* Westwood and *G. sarpedon* L. ascending to 2750 m even in the main range (Wynter-Blyth 1957). Recently, Singh (2006) discovered what appears to be an isolated population of *Meandrusa lachinus* Fruhstorfer in a moist temperate forest below the tree line in the Kedarnath Musk Deer Reserve in the Garhwal Himalaya, India. The type locality of the nominate subspecies is Darjeeling, West Bengal, India and Lachen-Lachung, Sikkim, India (Racheli & Cotton 2009), both in the eastern Himalaya, which are more or less at the same elevation as the Kedarnath Musk Deer Reserve in Garhwal.

The Palearctic *Papilio machaon* L. occurs in the Himalaya as far east as Sikkim (Gaonkar 1999). It is the only member of the subfamily that is found at higher elevation in the east than in the west. In the extreme west in Kashmir, it descends to 600 m, but is not found below 2450 m in Sikkim (Wynter-Blyth 1957). This distribution pattern is in keeping with classical views on the subject. It feeds on various umbellifers.

Papilio agestor Gray occurs throughout the range in a belt between 1200 m and 2600 m elevation, occasionally ascending to 2750 m in the western Himalaya (Wynter-Blyth 1957). It has been bred on *Persea odoratissima* (by Fred Smetacek Sr.) and *Persea duthei* (King ex Hook.f.) Kosterm. (Lauraceae) (mihi) in the western Himalaya.

Four species, *Pachliopta aristolochiae* Fabricius, *Papilio polytes* L., *Papilio demoleus* L. and *Chilasa clytia* L. are widespread on the Gangetic plain, which adjoins the Himalayan foothills. They are common along the entire length of the outer Himalaya, ascending to 1500 m with stragglers at 2250 m (Wynter-Blyth 1957; mihi).

The remaining ten species, comprising members of Troidini and Papilionini, were found to ascend with the latitude, occurring at low elevation in the eastern Himalaya and at higher elevation in the west (Table 1).

Concerning the larval host plants in the Himalaya, *Zanthoxylum armatum* is a known host plant of *Papilio bianor* Cramer and *Papilio protenor* Cramer. It grows between 610 m and 915 m in the eastern Himalaya and hills of N.E. India (Hooker 1872) and between 900 m and 2100 m in the Kumaon Himalaya west of Nepal (Osmaston 1927). Further west in Kullu, it ascends to 2500 m (Dhaliwal & Sharma 1999). *Limonia acidissima* L. (Rutaceae) is also a known host plant of *P. bianor.* This butterfly does not appear to use this plant in the western Himalaya, where it grows from the plains to 900 m (Osmaston 1927), but has been bred on it and probably uses it routinely in the eastern Himalaya, where the plant grows to 1200 m (Hooker 1872).

Bailey (1951) reported *Papilio arcturus* Westwood feeding on *Skimmia* Thunberg (Rutaceae) in the Kathmandu valley, Nepal. Recently, the eastern and western populations of Himalayan *Skimmia* have both been raised to species rank. The east Himalayan *S. laureola* Sieb. & Zucc. grows between 1500 m and ?3350 m (Brandis 1875), while the west Himalayan *S. anquetilia* Taylor & Airy Shaw grows between 2100 m (Osmaston 1927) and 3350 m (Brandis 1875; Osmaston 1927 gives 3200 m). These are nearly exactly the altitudinal limits given by Wynter-Blyth (1957) for *arcturus* in the respective areas, although the butterfly has not actually been bred on *S. anquetilia* in the western Himalaya so far.

Papilio paris L. has been bred on *Euodia roxburghiana* Bentham (Rutaceae). This plant does not occur in the west Himalaya although the butterfly does. In the hills of northeast India, this plant ascends to 1200 m (Hooker 1872). The larval host plant in the west Himalaya is still unknown, although Robinson et al. (2001) report a wide variety of rutaceous larval host plants from the eastern Himalaya, notably several species of *Zanthoxylum*, including *Z. armatum*, and *Citrus* L..

The Troidini are believed to be primarily *Aristolochia* L. feeders. Neither of the 2 known west Himalayan members of this plant genus has been reported from below 1950 m (Osmaston 1927; Gupta 1968). *Byasa dasarada* and *B. polyeuctes* Doubleday have been bred by Michael Green on Aristolochiaceae at Chamba in Himachal Pradesh, India (in litt. to Fred Smetacek Sr.). However, no botanical works record any Aristolochiaceae from Himachal Pradesh except Hooker (1885), who included a specimen of *Aristolochia punjabensis* Lace from there in the supplementary section of his work and Dhaliwal & Sharma (1999) who did not find the plant in Kullu but included it on the basis of Hooker (1885) with the observation "origin doubtful". *B. dasarada* and *B. polyeuctes* are known from Kullu and even further west in Kashmir and Pakistan, while *B. latreillei* Donovan has been reported from as far west as Afghanistan (Bozano 2010) so they probably feed on the only known *Aristolochia* in that area, *A. punjabensis*.

TABLE 1. Comparative altitudinal distribution of some Papilioninae in the Western and Eastern Himalaya.

Species	Minimum Elevation (m)		Maximum Elevation (m)		Remarks
	W. Himalaya	E. Himalaya	W. Himalaya	E. Himalaya	
P. janaka	2000 (1)	900 (8)	2500 (1)	1525 (4)	W. Himalayan LFP unknown.
P. protenor	900 (6)	100 (2)	2600 (8)	900 (7)	LFP: Z. *armatum;* Z. *acanthopodium.*
P. bianor	900 (6)	200 (2)	2250 (8)	1500 (8)	LFP: Z. *armatum.*
P. paris	1200 (1)	50 (2)	2100 (8)	1525 (2)	W. Himalayan LFP unknown.
P. arcturus	2250 (5)	900 (4)	3350 (8)	2750 (4)	W. Himalayan LFP unknown.
T. aeacus	1750 (1)	50 (2)	2700 (1)	1000 (2)	E. Himalayan low elevation LFP unknown.
A. aidoneus	1200 (1)	100 (2)	2400 (1)	1500 (2)	E. Himalayan low elevation LFP unknown.
B. dasarada	1700 (1)	150 (2)	2750 (8)	2400 (7)	E. Himalayan low elevation LFP unknown.
B. polyeuctes	1700 (1)	150 (8)	3600 (3)	3050 (2)	E. Himalayan low elevation LFP unknown.
B. latreillei	2100 (8)	1600 (2)	2750 (8)	2730 (7)	E. Himalayan low elevation LFP unknown.

1) pers. obs., 2) Arora & Mondal (1981), 3) Bang Haas (1933), 4) de Nicéville (1894), 5) de Rhé Philipe (1931), 6) Peile (1937), 7) Talbot (1939), 8) Wynter-Blyth (1957)

TABLE 2. Comparative altitudinal distribution of known and probable larval host plants of Papilioninae in the Western and Eastern Himalaya.

Species	Minimum Elevation (m)		Maximum Elevation (m)	
	W. Himalaya	E. Himalaya	W. Himalaya	E. Himalaya
Aristolochia dilatata N.E. Brown	2000 (5)		2600 (1)	
Aristolochia punjabensis Lace	1950 (1)		2250 (1)	
Aristolochia platanifolia Duchart		900 (6)		1800 (6)
Aristolochia saccata Wallich		300 (6)		1220 (6)
Aristolochia cathcartii Hooker		600 (6)		900 (6)
Aristolochia tagala Cham.	Cultivated on plains adjoining Himalaya	600 (6)	?400	1500 (6)
Aristolochia griffithii Hooker		1800 (7)		2900 (7)
Aristolochia indica L.	? on plains adjoining Himalaya	on plains adjoining Himalaya (6)		?200
Zanthoxylum armatum DC	900 (1)	600 (2)	2500 (3)	900 (2)
Skimmia anquetilia Tay & Shaw	2100 (1)		3200 (1)	
Skimmia laureola Sieb. & Zucc.		1500 (4)		?3350 (4)
Euodia roxburghiana Bentham		on plains adjoining Himalaya (2)		1200 (2)

1) Osmaston (1927), 2) Hooker (1872), 3) Dhaliwal & Sharma (1999), 4) Brandis (1875), 5) Gupta (1968), 6) Hooker (1885), 7) Polunin & Stainton (1984)

G. Flutsch (pers. comm.) found a *Troides* Hübner larva on *Aristolochia dilatata* N.E. Brown at 2400 m in the Binsar Wildlife Sanctuary in Almora district, Uttarakhand state in the west Himalaya. Since *T. aeacus* C. & R. Felder is the only *Troides* in the area, it is reasonable to assume that it was a *T. aeacus* larva.

I have found *T. aeacus* to be selective in the forests it inhabits. I bred it on *A dilatata* in the western Himalaya, feeding the larvae leaves only. However, Igarashi (1966) noted the predilection of the larvae for leaf stalks and stems, eventually consuming more stems and leafstalks than leaves in the later larval instars. I found final instar larvae of *T. aeacus* consuming the seed pods of *A dilatata* and must note that the individuals bred by me only on a diet of leaves emerged rather stunted. Having examined numerous plants of *A. dilatata* in different forests, I was struck by the fact that *T. aeacus* only occurs in forests where mature, seed bearing plants of *A. dilatata* grow, unlike the members of *Atrophaneura* Reakirt and *Byasa* Moore, that willingly lay eggs on and complete their life cycles on what may best be described as seasonal plants of *A. dilatata*, with up to 20 leaves during the summer months from April to June and a spurt of growth during the wet summer season from late June to September. Such plants, growing in dry upland locations, do not bear seed pods while plants growing near perennial water have stems up to 5 inches in circumference with hundreds of leaves and dozens of seed pods. Such plants support populations of *T. aeacus*.

The only resident, low elevation Troidine in the west Himalaya is *Pachliopta aristolochiae* Fabricius, whose larval host plant in the area is unknown. Seitz (vide Sevastopulo 1973) includes Piperaceae among the known larval hosts of this butterfly. Robinson et al. (2001) overlooked this latter record but report *Dioscorea wallichii* (Dioscoreaceae) as a larval host plant as reported by Beeson (1941). Certainly, *Dioscorea* is a common plant in the western Himalaya and might account for this butterfly's abundance at suitable seasons.

As an experiment, ten potted plants of *Aristolochia dilatata* were brought down from 2400m and placed in a garden at Bhimtal in the Western Himalaya at 1500m from July 2010 to June 2011. During this period, although at least 50 female *Pachliopta aristolochiae* flew past these pots and investigated nearby plants for flowers and larval host plants, none of these butterflies either investigated the *A. dilatata* plants nor oviposited on them. This shows that *A. dilatata* is not likely a larval host plant of *Pachliopta aristolochiae* and this factor perhaps limits its altitudinal distribution in the western Himalaya .In other parts of India and S.E. Asia, it has been reported to feed on at least 15 species of Aristolochiaceae (Robinson et al. 2001). It undoubtedly feeds on cultivated *Aristolochia tagala* Cham. plants at the foot of the hills, but this plant is not part of the original flora of the area, although the butterfly appears to have been present before the introduction of this plant. Therefore, it must feed on some other, wild, plant in the area.

In the eastern Himalaya, six species of *Aristolochia* occur (Hooker 1885; Polunin & Stainton 1984). Only one occurs in the temperate zone between 1800 and 2900 m (Polunin & Stainton 1984). The remainder occurs from low elevation to 900 m (2 species), 1200 m (1 species); 1500 m (1 species) and 1800 m (1 species). The 2 west Himalayan *Aristolochia* species do not occur in the east Himalaya (Table 2).

The larval host plants of *Byasa latreillei* and *Papilio janaka* Moore in the west Himalaya are unknown, although Igarashi (1966) bred them on *Aristolochia griffithii* Hook.f. & Thoms. *ex* Duchartre and *Zanthoxylum alatum* (=*Zanthoxylum armatum* DC) respectively in Nepal. *A. giffithii* does not occur in the western Himalaya and *P. janaka* does not appear to feed on *Z. armatum* in the western Himalaya. Rather, it appears to be restricted to patches of *Zanthoxylum acanthopodium* DC, although it has not actually been bred on this plant so far.

The altitudes assigned to species in Table 1 are for populations. Stragglers of the following species have been recorded at lower elevation in the western Himalaya: *T aeacus* (1200 m: *mihi*); *B. latreillei* (1500 m: Fred Smetacek's unpublished notes); *B. polyeuctes*: 1200 m: *mihi*); *B. dasarada* (1500 m: *mihi*); *P. protenor*, *P. bianor* and *P. paris* (all at 660 m: Roonwal et al. 1956; Singh & Bhandari 2003). Howarth & Povolny (1973) described *B. latreillei afghana* on the basis of two males recorded from 580 m elevation in Jalalabad, Afghanistan. These are the only two specimens known.

DISCUSSION AND CONCLUSION

It is generally accepted that on a north–south axis, temperate zone species tend to occur at higher elevation towards the Equator, while tropical forms tend to be found at lower elevation as we progress towards the poles.

In butterflies, montane species tend to occur in altitudinal belts. Such species are not generally found above or below their chosen altitudinal limits, although stragglers are occasionally encountered. Factors restricting the altitudinal distribution of species are not wholly understood. Among the factors believed to influence altitudinal distribution are the thermal tolerance of the butterfly, wing color and presence of the larval host plant.

Table 3. Papilioninae with a pan-Himalayan distribution.

Species	Western Subspecies	Eastern Subspecies
Leptocircini		
1.*Graphium* (*Pazala*) *eurous* Leech	*caschmirensis* Rothschild	*sikkimica* Heron
2. *Graphium* (*Pazala*) *mandarinus* Oberthur	*garhwalica* Katyama	*paphus* de Niceville
3. *Graphium* (*Pathysa*) *nomius* Esper	*nomius* Esper	*nomius* Esper
4. *Graphium* (*Graphium*) *doson* C.&R. Felder	*axion* C.&R. Felder	*axion* C.&R. Felder
5. *Graphium* (*Graphium*) *agamemnon* Linnaeus	*agamemnon* Linnaeus	*agamemnon* Linnaeus
6. *Graphium* (*Graphium*) *sarpedon* Linnaeus	*sarpedon* Linnaeus	*sarpedon* Linnaeus
7. *Graphium* (*Graphium*) *cloanthus* Westwood	*cloanthus* Westwood	*cloanthus* Westwood
8. *Meandrusa lachinus* Fruhstorfer	*lachinus* Fruhstorfer	*lachinus* Fruhstorfer
Papilionini		
9. *Papilio agestor* Gray	*govindra* Moore	*agestor* Gray
10. *Papilio clytia* Linnaeus	*clytia* Linnaeus	*clytia* Linnaeus
11. *Papilio janaka* Moore	*janaka* Moore	*janaka* Moore
12. *Papilio alcmenor* C.&R. Felder	*alcmenor* C.&R. Felder	*alcmenor* C.&R. Felder
13. *Papilio protenor* Cramer	*protenor* Cramer	*euprotenor* Fruhstorfer
14. *Papilio bianor* Cramer	*polyctor* Boisduval	*ganesa* Moore
15. *Papilio paris* Linnaeus	*decorosa* Fruhstorfer	*decorosa* Fruhstorfer
16. *Papilio arcturus* Westwood	*arius* Rothschild	*arcturus* WEstwood
17. *Papilio helenus* Linnaeus	*helenus* Linnaeus	*helenus* Linnaeus
18. *Papilio polytes* Linnaeus	*romulus* Cramer	*romulus* Cramer
19. *Papilio demoleus* Linnaeus	*demoleus* Linnaeus	*demoleus* Linnaeus
20. *Papilio machaon* Linnaeus	*asiatica* Menetries	*sikkimica* Heron
Troidini		
21. *Pachliopta aristolochiae* Fabricius	*aristolochiae* Fabricius	*aristolochiae* Fabricius
22. *Troides aeacus* C.&R. Felder	*aeacus* C.&R. Felder	*aeacus* C. &R. Felder
23. *Atrophaneura aidoneus* Doubleday	*aidoneus* Doubleday	*aidoneus* Doubleday
24. *Atrophaneura varuna* White	*astorion* Westwood	*astorion* Westwood
25. *Byasa dasarada* Moore	*ravana* Moore	*dasarada* Moore
26. *Byasa polyeuctes* Doubleday	*letincius* Fruhstorfer	*letincius* Fruhstorfer
27. *Byasa latreillei* Donovan	*latreillei* Donovan	*latreillei* Donovan

Table 4. Papilioninae that do not exhibit anomalous altitudinal distribution in the Himalaya.

Species	Minimum Elevation (m)	Maximum Elevation (m)
Leptocircini		
Graphium eurous	1800 (1)	2900 (1)
Graphium mandarinus	W. Himalaya:2200 (1); E. Himalaya: 900 (3)	2500 (1)
Graphium nomius	Plains adjoining Himalaya (1)	900 (4)
Graphium doson	Plains adjoining Himalaya (2)	848 (2)
Graphium agamemnon	Plains adjoining Himalaya (1)	1500 (1)
Graphium sarpedon	100 (2)	2750 (4)
Graphium cloanthus	227 (2)	2750 (4)
Meandrusa lachinus	1524 (4)	2133 (4)
Papilionini		
Papilio agestor	1524 (2)	2424 (4)
Papilio clytia	Plains adjoining Himalaya (4)	2750 (4)
Papilio polytes	Plains adjoining Himalaya (4)	1601 (2)
Papilio demoleus	Plains adjoining Hmalaya (1)	2133 (4)
Papilio machaon	609 in west (Kashmir); 2438 in east (Sikkim) (4)	4876 (4)
Troidini		
Pachliopta aristolochiae	Plains adjoining Himalaya (1)	1500 (1)

1) pers. obs., 2) Arora & Mondal (1981), 3) de Nicéville (1894), 4) Wynter-Blyth (1957)

There seems to be a strong positive correlation between the altitudinal belt occupied by the various Papilionidae and their larval host plants in the west Himalaya.

While Ferris (1974) drew attention to the fact that different subspecies of a butterfly can occur in widely disparate habitats, in the case of *Troides aeacus aeacus* in the Himalaya, the same subspecies occurs in widely disparate habitats at either end of the mountain range. In the west, it is found in temperate and higher elevation subtropical forests and never in the tropical zone below 1000 m elevation, while in the east it occurs mainly in tropical forests at low elevation. Igarashi (1966) reported that in the Central Himalaya in Nepal, the species mainly inhabits lowland forests but occasionally was seen up to 3000 m elevation. *Byasa dasarada, Atrophaneura aidoneus, Papilio janaka* and *Papilio paris* also occur at low elevation in the east and higher elevation in the west.

In the case of *T. aeacus*, the presence of a suitable larval host plant appears to be the decisive factor governing its distribution. However, this is not necessarily the case with other birdwing butterflies. The Papuan *Ornithoptera priamus* L. and *O. goliath* Oberthur have been bred on *Aristolochia tagala* Cham. in Papua New Guinea (Borch & Schmid 1973; Straatman & Schmid 1975). This plant also occurs naturally in S. India, Sri Lanka and the E. Himalaya, where these butterflies do not occur.

In the case of *Zanthoxylum armatum* feeders such as *P. bianor* and *P. protenor* and *Skimmia*-feeding *P. arcturus*, the similarity in the altitudinal distribution of the butterflies and the plants is too striking to be ignored (Tables 3 & 4). Interestingly, *P. protenor* also feeds on *Zanthoxylum acanthopodium* in the western Himalaya and so occurs at higher elevation than *P. bianor*, which appears not to feed on this plant and is therefore found at lower elevation, as high as *Zanthoxylum armatum* occurs.

De Rhé Philipe (1931) and Wynter-Blyth (1957) noted the absence of *B. dasarada* and *B. polyeuctes* from the area around Shimla (=Simla) in the western Himalayan state of Himachal Pradesh, although both species are ubiquitous at suitable altitudes east, west and north of Shimla. Wynter-Blyth (1957) suggested that it was only a temporary phase and that both populations would eventually re-establish themselves and become common again. However, Collett (1921) did not find any Aristolochiaceae in the area around Shimla, which probably accounts for the absence of these butterflies from that area.

Besides the ten Papilionidae species mentioned in this paper, at least eight satyrine species and three nymphalines also ascend with the latitude on the Himalaya while one danaine and three satyrines exhibit the reverse tendency (Wynter-Blyth 1957). Unfortunately, very little is known about the larval host plants of the satyrines.

From the above, it is evident that a butterfly subspecies does not necessarily occur in the same type of habitat throughout its range; that a butterfly species' altitudinal distribution can increase with the latitude when, in the classical view, the opposite should be the case; and that the presence of a larval host plant can decisively influence the altitudinal distribution of a butterfly.

These observations in turn suggest that some butterflies possess a hitherto unsuspected ability to adapt to different climatic conditions; that such adaptation does not necessarily express itself in the colors or patterns on the wings in the form of melanism or otherwise; that Himalayan Troidini and Papilionini are generally only found more or less in the altitudinal belt of their larval host plants; that two major factors governing a butterfly's distribution are the presence or absence of a suitable larval host plant and the butterfly's ability or inability to adapt to the ***plant's*** habitat.

This still leaves unresolved the question why some plant species ascend with the latitude on the Himalaya, but that is beyond the scope of this paper. However, Hooker (1849) while referring to this phenomenon noted that the same tendency is exhibited in some plant groups in the high southern and Antarctic latitudes. In fact, he stressed the fact that the snowline ascends with the latitude in the Himalaya from 14,000 feet (4267 m) (in the eastern Himalaya) south of the Brahmaputra river in latitude 27 degrees N to 20,000 feet (6096 m) at the north western extremity of the range beyond the Sutlej river in latitude 36 and 37 degrees N. He pointed out that on the Himalaya, the range of tropical forms is extended upward to greater elevation and temperate forms descend to lower elevation, of which Rosaceae and Ericaceae are good examples. However, there is no accepted explanation why this happens.

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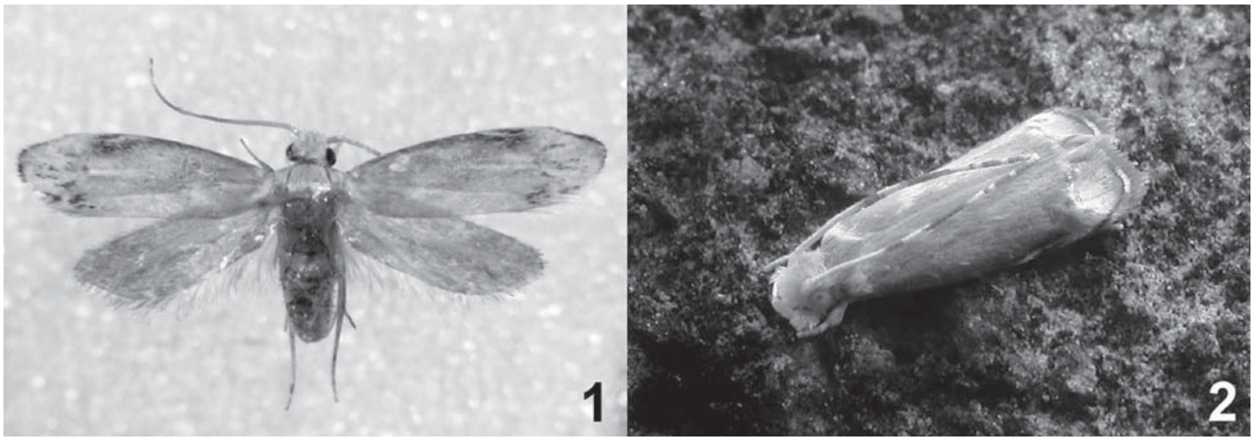
BEHAVIOR OF THE HAWAIIAN DANCING MOTH, *DRYADAULA TERPSICHORELLA* (TINEIDAE: DRYADAULINAE)

The Hawaiian Dancing Moth, *Dryadaula terpsichorella* (Busck, 1910) (Figs. 1, 2) is an invasive tineid first collected in Hawaii around 1900 (Busck 1910; Swezey 1909; Zimmerman 1978). The origin of the moth is unknown, but it has been recorded from Fiji (Meyrick 1920), Rapa Island (Clarke 1971), French Polynesia, Samoa, and Central America (Zimmerman 1978). It was recently discovered in California (Powell 1999) and Florida (Heppner & Davis 2008). In Hawaii, it was recorded from the islands of Hawaii, Maui, Molokai, Oahu (Zimmerman 1978) and is likely also on Kauai. All known larval hosts for *D. terpsichorella* in Hawaii are the dead leaves of monocots, including banana (*Musa*, Musaceae), pineapple (*Ananas*, Bromeliaceae), screw-pine (*Pandanus*, Pandanaceae) and sugarcane (*Saccharum officinarum*, Poaceae) (Swezey 1909). Zimmerman (1978) reported ferns and *Costus spicatus* (Costaceae) as possible hosts, but these records have not been confirmed.

Dryadaula terpsichorella is peculiar because the adult rapidly "dances" on the upper (adaxial) surface of leaves (e.g., Powell 1999; Swezey 1909; Zimmerman 1978). While this moth has been reported to dance, neither its behavior nor that of any other dancing tineid has been described in detail. We provide the first description of the dancing pattern of *D. terpsichorella* and present videos of its behavior. We also synthesize the published hypotheses on dancing in microlepidoptera, and postulate that the behavior is a strategy allowing the moth to simultaneously forage and avoid predation.

Sixteen adults of *D. terpsichorella* were observed on the islands of Hawaii and Oahu during August – December 2010. Dancing was observed on *Gardenia bringhamii* (Rutaceae) and *Alpinia* sp. (Zingiberaceae) at the University of Hawaii Lyon Arboretum in Manoa, and on *Chrysophyllum oliviforme* (Sapotaceae) at Pupukea-Paumalu Forest Reserve on Oahu. All specimens were collected after observations of dancing were recorded. We took video footage of seven individuals using a Nikon Coolpix 4500 digital camera during August 3–7 2010. Two QuickTime® video files of *D. terpsichorella* recorded by the first author are available as supplementary material and can be downloaded from the Rubinoff Lab website: http://www.ctahr.hawaii.edu/rubinoffd/. Specimens collected are deposited in the University of Hawaii Insect Museum, Honolulu, HI.

The dancing movement of *D. terpsichorella* (Fig. 3; Supplementary Movie 1, 2) is smooth and rapid with frequent concentrated areas of spinning. The movement is similar to the dancing behavior found in Gelechioidea (Forbes 1923; Kawahara & Adamski 2006; Koster 2010; Morrison 1968; Nishida 2007; Plant 1980; Robinson 1988), but differs significantly from the jerky movements of the choreutid genus *Brenthia* (Aiello & Becker 2004; Rota & Wagner 2006). Moths of *D. terpsichorella* danced on the adaxial surface of leaves by shifting their legs back and forth and ran both sideways and, at times, rapidly forward, covering most of the adaxial leaf surface (Fig. 3). Compared to the dancing movement of *Beltheca oni* Kawahara & Adamski, the



FIGS. 1, 2. *Dryadaula terpsichorella* (Busck). 1) Pinned male, collected 07-viii-2010, UH Manoa Botanical Garden, Honolulu, Hawaii; A. Kawahara and K. Nishida leg. 2) Adult resting on shaded side of a concrete seawall in downtown Hilo, Hilo, Hawaii: photo K. Nishida. Scale bar = 1 mm.

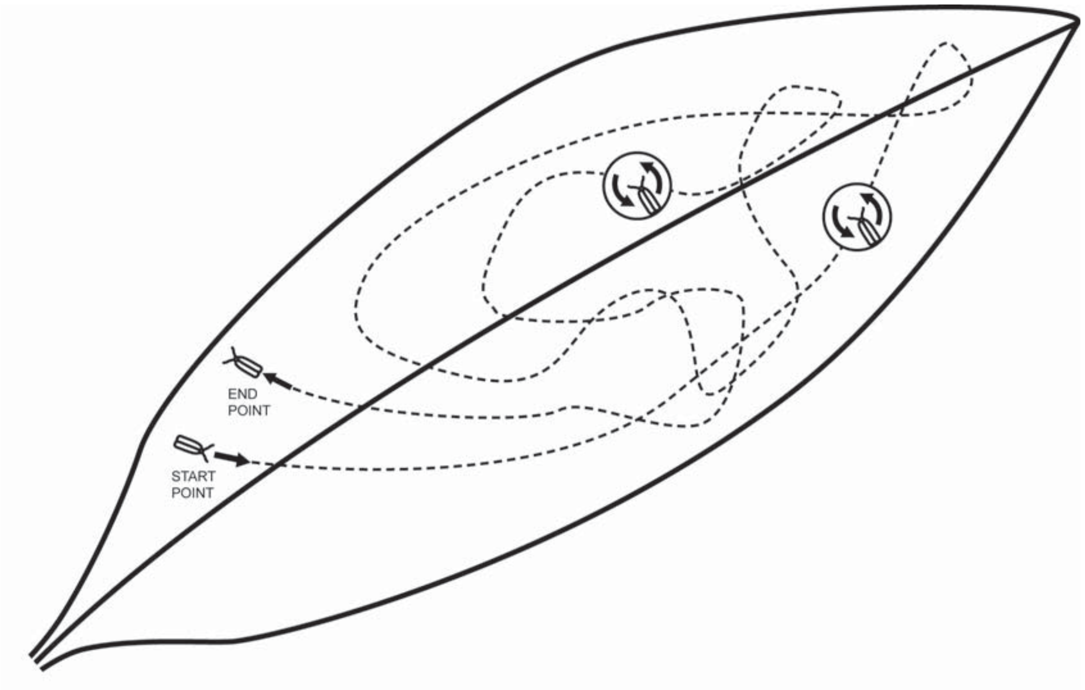


FIG. 3. Illustration of a typical dancing path of *D. terpsichorella* (Busck). Circles indicate areas where the moth spins (and pivots) while running sideways around a particular point on the leaf.

dancing movement was more linear. While *B. oni* appears to be more active in direct sunlight (Kawahara & Adamski 2006), *D. terpsichorella* was most active in shaded microhabitats. When the wind was strong, moths would stop dancing and rest. Moths occasionally ran to the abaxial surface of a leaf and rested or flew to another plant and continued to dance. In four cases we observed two individuals on the same leaf. In two of the four cases, the individuals were both male and in the other two cases there was one male and one female. No mating was observed, nor did we find any mated pairs on the leaves. In all cases, the behavior of moths did not change when they were in close proximity. Dancing behavior was most commonly observed on broad-leaved plants with smooth surfaces, as was observed in the gelechiid, *Beltheca oni* in Costa Rica (Kawahara & Adamski 2006). The average time of dancing was 45.3 seconds (± 22.7 seconds; n = 12).

The purpose of the dancing behavior seen in *D. terpsichorella* and other dancing microlepidoptera remains unknown. Two hypotheses have been proposed, which we here call the "mate search" and "aggregation" hypotheses. Morrison (1968) observed *Dryadaula pactolia* Meyrick dancing and hypothesized that dancing is a behavior associated with mating. Initial observations of *B. oni* also suggested that dancing might be associated with mating (Kawahara & Adamski 2006). Under this "mate search" hypothesis, we would expect greater dancing at times when a moth is in close proximity with the opposite sex, and the behavior should change when a male and female are in close proximity. We did not observe any change in behavior of *D. terpsichorella* during the few instances of observing a male and female on the same leaf. In both *D. terpsichorella* and previously in *Beltheca oni* (Kawahara & Adamski 2006), we rarely observed two moths circling on one leaf together.

Davis & Sinev (2008) proposed an alternative explanation that we here call the "aggregation hypothesis". They described the dancing behavior of *Cosmopterix victor* Stringer and wrote, "dancing behavior … can be a special adaptation of monophagous and strictly oligophagous forms providing the aggregation of adults on the host plants for mating and subsequent oviposition. It allows uniting of two different life activities, the searching for a sexual partner and the searching for appropriate host plant, which leads to the economy of energy and to the success of reproduction" (p. 208). They believed that adult moths dance primarily on the surface of their hosts, attracting additional individuals for mating which leads to eventual oviposition. Under their hypothesis, moths would be expected to spend more time on their host than on a non-host and engage in greater dancing activity on their host. From our observations of *D. terpsichorella*, dancing occurrence is equally common on monocots known to be larval hosts and those that are not.

Given our observations, we hypothesize that this type of rapid dancing behavior in microlepidoptera is neither associated with mate searching nor an aggregatory behavior that is used to attract mates to their larval host plant. Instead, we hypothesize that this type of dancing is associated with foraging and a defense against predatory arthropods such as salticid jumping spiders that attack small insects on leaves. This "foraging" hypothesis, first mentioned briefly in Kawahara & Adamski (2006) and later by Koster (2010) is supported by the fact that the moth makes very concentrated circles at particular areas on the leaf. In *Beltheca oni*, moths were seen drinking from a drop of water while dancing, and the proboscis is extended while the moth runs across the leaf surface (A. Y. Kawahara & K. Nishida, unpublished). By moving swiftly and running in concentrated circles with an extended proboscis, the moth can search for nutrients on the leaf surface and at the same time avoid potential attack by predators that use a fixed search image for hunting. However, we could not measure the composition or quantity of nutrients on the leaf nor were we able to determine whether nutrient availability was the primary factor that triggered the moth's movement from one leaf to another. Thus, additional field observations are clearly necessary to test our hypothesis. We hope that our ongoing ecological experiments and additional observations will expand on this initial report.

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REPRODUCTIVE BEHAVIOR OF *SPEYERIA DIANA* (NYMPHALIDAE) IN ARKANSAS

The Literature Cited section of the above-named paper from issue 65(1), 2011, 51–53 was updated, corrected and resubmitted by the authors.

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