

Full Issue

Source: The Journal of the Lepidopterists' Society, 68(1)

Published By: The Lepidopterists' Society

URL: <https://doi.org/10.18473/lepi.v68i1.a14>

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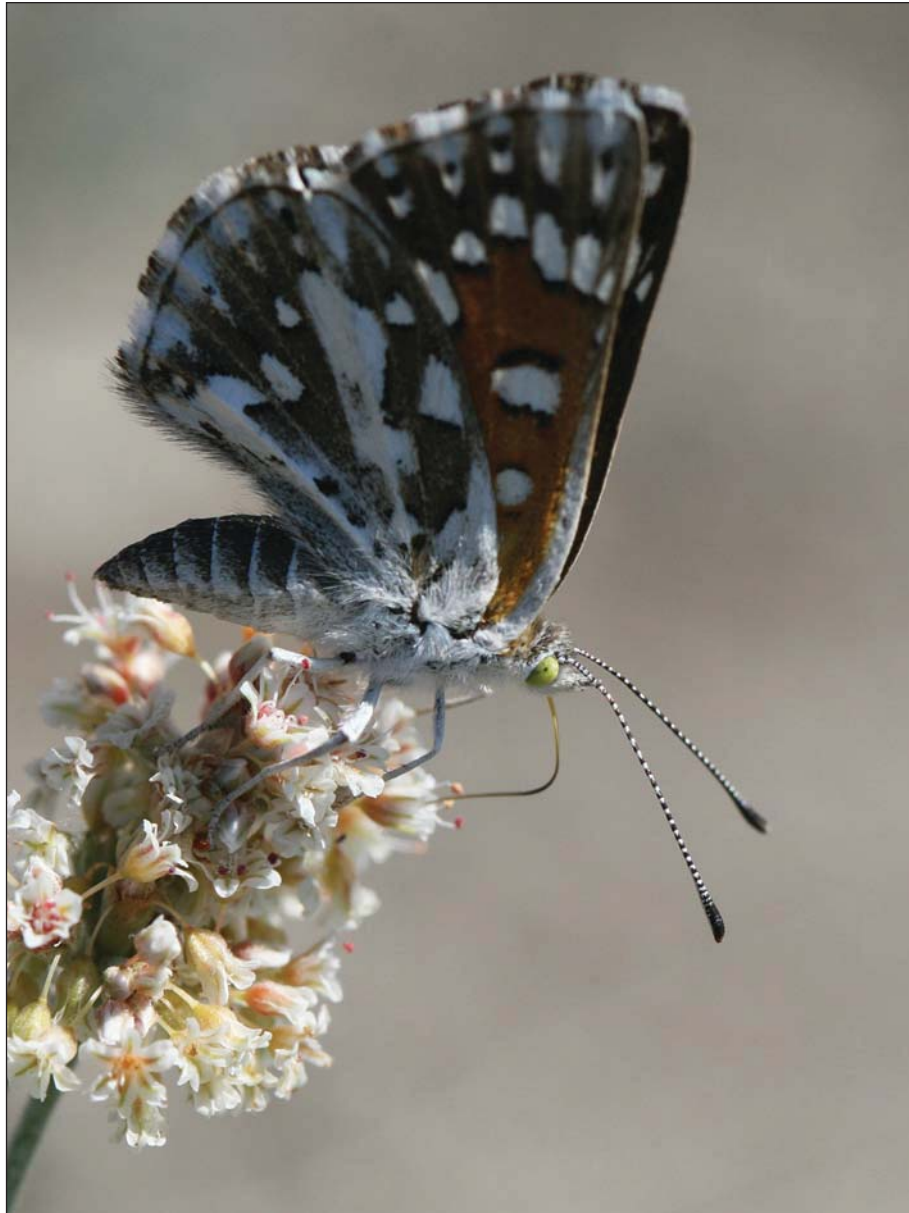
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Volume 68 Number 1
2014
ISSN 0024-0966

Journal of the Lepidopterists' Society



Published quarterly by The Lepidopterists' Society

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

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Cover Illustration: Mormon metalmark (Riodinidae: *Apodemia mormo*) nectaring on its host plant, *Eriogonum pauciflorum* in Grasslands National Park, Saskatchewan. This is the only metalmark that occurs in Canada, where it is listed as threatened in SK and endangered in BC. In its northern range, *A. mormo* has a short flight season, and can be found flying in mid-August in badlands. Photo credit is Johane Janelle (of Val Marie, SK). See article on page 54.

REVIEW OF *AESIOCOPA* ZELLER, 1877, WITH THE DESCRIPTIONS OF TWO NEW SPECIES
(TORTRICIDAE: SPARGANOTHINI)

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ABSTRACT. The formerly monotypic genus *Aesiocopa* Zeller, 1877 is reviewed. Three species are included: *A. vacivana* Zeller, 1877 (type species) from Panama and Costa Rica; *A. necrofolia* Brown & Phillips, new species, from Mexico, Nicaragua, and Costa Rica; and *A. grandis* Brown, new species, from Costa Rica. The genus is recorded sparingly from Mexico to Panama. Although *A. vacivana* and *A. grandis* are known from only a handful of specimens, *A. necrofolia* has been reared from larvae numerous times in Costa Rica and from 15 different plant families: Asteraceae, Euphorbiaceae, Fabaceae, Hernandiaceae, Icacinaceae, Lauraceae, Magnoliaceae, Myrsinaceae, Myrtaceae, Piperaceae, Rubiaceae, Salicaceae, Sapindaceae, Smilacaceae, and Urticaceae. The abundance of rearing records suggests that the species is polyphagous, and the paucity of field-collected adults suggests that it may not be avidly attracted to light. The same may be true for its congeners.

Additional key words: Costa Rica, host plants, Mexico, new species, Panama

Sparganothini are among the most well-defined tribes in the family Tortricidae on the basis of both morphology and life history features (Powell 1986, Powell & Brown 2011). The tribe includes about 240 described species in 18 genera nearly restricted to the New World. Outside the Western Hemisphere, there are five species of *Sparganothis* Hübner, [1825] in the Palearctic region; two species of *Cenopsis* Zeller, 1875 in the Palearctic region; and two species of *Lambertiodes* Diakonoff, 1959 in the Oriental Region. Over the past decade or so our knowledge of the group has increased faster than that of any other tortricid tribe, with systematic revisions of *Sparganothis* Powell and Lambert, 1986 and relatives by Landry and Powell (2001); *Amorbia* Clemens, 1860 by Phillips-Rodriguez and Powell (2007); *Sparganothoides* Powell and Lambert, 1986 by Kruse and Powell (2009); and *Amorbimorpha* Kruse, 2011 by Kruse (2011); and a review of the entire North American (north of Mexico) fauna by Powell and Brown (2012). Although a stable generic-level classification has emerged for the North American members, many described species from the Neotropics still defy confident generic assignment, and a large portion of the fauna remains undescribed. Faunal surveys and rearing projects in the latter region, including those by Janzen and Hallwachs of Area de Conservación Guanacaste in northwestern Costa Rica (Janzen & Hallwachs 2012); the ALAS Project in Heredia Province, Costa Rica (ALAS 2012); efforts by Wojtusiak in Ecuador (e.g., Razowski & Wojtusiak 2006, 2008, 2010); and various other field work, have continued to reveal an array of undescribed sparganothine taxa. The purpose of this contribution is to review the formerly monotypic *Aesiocopa* Zeller, 1877, describe two new species in that genus, and

modify the description of the genus based on the new species.

MATERIALS AND METHODS

Dissection methods follow those presented in Brown and Powell (1991). Images of adults and genitalia were captured using a Canon EOS 40D digital SLR (Canon U.S.A., Lake Success, NY) mounted on a Visionary Digital BK Lab System (Visionary Digital, Palmyra, VA). Terminology for genitalia structures and forewing pattern elements follows Powell and Brown (2012). The phallus of all dissected male genitalia was examined using a compound microscope to determine the presence/absence of cornuti and/or their associated sockets or scars.

Larvae were collected during an ongoing survey of the Lepidoptera of Area de Conservación Guanacaste (ACG) in northwestern Costa Rica (Janzen & Hallwachs 2012). Caterpillars discovered in the field were taken to “rearing barns” where they were placed in plastic bags with cuttings of the host upon which they are discovered. As adult moths emerged, they were dispatched, pinned, and labeled. Each specimen received a unique voucher number in the form of YY-SRNP-XXXX (e.g., 09-SRNP-15328), where the prefix is the last two digits of the year (e.g., 2009), “SRNP” refers to the project “call letters” assigned in 1977 (when the project site was referred to as Santa Rosa National Park), and the suffix is a unique number assigned within the year.

The following depositories are abbreviated in the text: American Museum of Natural History, New York, New York, U.S.A. (AMNH); The Natural History Museum, London, U.K. (BMNH); Essig Museum of Entomology, University of California, Berkeley, California, U.S.A.

(EME); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A. (LACM); Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (MNHU); and National Museum of Natural History, Washington, D.C., U.S.A. (USNM). Other abbreviations used in the text are as follows: em = emerged; GS = genitalia slide; P.N. = Parque Nacional; r.f. = reared from; TL = type locality.

Co-authorship of *Aesiocopa necrofolia*, n. sp., is shared with Eugenie Phillips-Rodriguez who discovered this new taxon and recognized that it was distinct from *Amorbia*.

RESULTS AND DISCUSSION

Aesiocopa belongs to a group of genera within Sparganothini that are characterized by a long crescent- or ribbon-shaped signum in the corpus bursae of the female genitalia that likely represents a synapomorphy for a clade. Genera that share this character state are *Aesiocopa* Zeller, 1877, *Amorbia* Clemens, 1860, *Amorbimorpha* Kruse, 2011, *Coelostathma* Clemens, 1860, *Lambertiodes* Diakonoff, 1959, *Paramorbia* Powell & Lambert, 1986, *Rhynchophyllus* Meyrick, 1932, *Sparganopseustis* Powell & Lambert, 1986, *Sparganothina* Powell, 1986, and *Sparganothoides* Lambert & Powell, 1986. The presence of secondary arms of the socii divide the group—they are present in *Aesiocopa*, *Amorbimorpha*, *Sparganopseustis*, and *Sparganothoides*, and absent in *Amorbia*, *Coelostathma*, *Lambertiodes*, *Paramorbia*, and *Sparganothina*. The male of *Rhynchophyllus* is unknown.

AESIOCOPA Zeller, 1877

Type species: *Aesiocopa vacivana* Zeller, 1877, by monotypy.

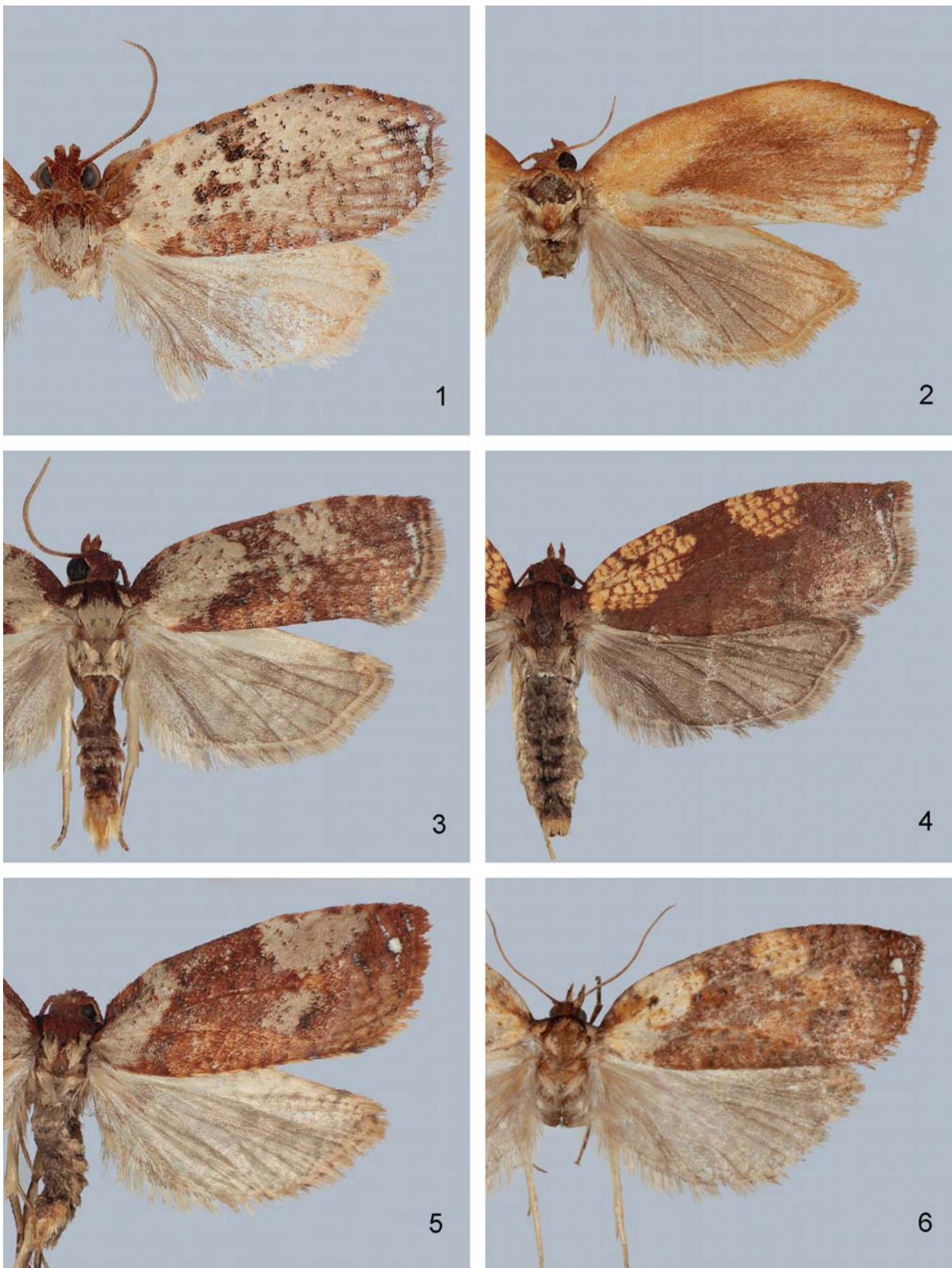
Aesiocopa was described by Zeller (1877) to accommodate the single species *A. vacivana* Zeller, known only from the holotype female from Chiriquí, Panama. Walsingham (1914) illustrated the female and discussed three specimens (1♂, 2♀) collected at Bugaba, Chiriquí, Panama. A small series of males from Costa Rica (INBio) appears to match Walsingham's description of the male, and two new species from Costa Rica appear to be congeneric with the type species. Based on these three species, the genus is redescribed below.

Diagnosis. *Aesiocopa* can be distinguished from all other sparganothine genera by facies alone. With the exception of the female of *A. vacivana*, the forewing pattern is somewhat reminiscent of a necrotic leaf—

mostly pale to dark brown with an ovoid pale region basally (orange or ochreous in the female and grayish tan in the male), with a similarly colored, semicircular patch (in the female) or blotch (in the male) just beyond mid-costa. There is a variably developed row of small bluish or silvery white dots in the subterminal region in both sexes. In the forewing of *A. vacivana* the distal 0.3 of the costa is angled downward at ca. 140° in both sexes; the costa is nearly evenly curved in the other two congeners. Adults of *Aesiocopa* are about the same size as those of *Amorbimorpha* Kruse, but sexual dimorphism is much more pronounced in the former (Figs. 1–6). Females are conspicuously larger than males and have conspicuously to subtly different forewing maculation. The labial palpi in both sexes of *Aesiocopa* are shorter and less densely scaled than in all other described genera of Sparganothini (Figs. 7, 8). Both sexes have a large mid-dorsal pit on the second and third abdominal segments, as do many *Amorbia*, *Coelostathma*, and some *Sparganopseustis*. Both sexes of *Aesiocopa* have a small patch of modified scales in a shallow pouch laterally on the first abdominal segment that is unique to the genus.

The male genitalia of *Aesiocopa* possess well-developed secondary arms of the socius, the basal portion of which is entirely fused with the socii, so that the only evidence of the secondary arms is the distal part that projects beyond the anteriormost edge of the socii.

Description. *Head:* Frons with or without complex hood of scales; labial palpus relatively short, weakly upcurved, all segments combined 1.5–1.6 times horizontal diameter of compound eye; ocellus minute; antennal scaling in two bands per segment, sensory setae 0.6–0.8 times flagellomere width in male, short, unmodified in female. *Thorax:* Not smooth scaled throughout; legs unmodified. Forewing length 9.0–16.0 mm; costa angled downward at ca. 140° in distal 0.35 (i.e., *vacivana*) or nearly evenly curved throughout (i.e., *necrofolia*, *grandis*); male lacking forewing costal fold, but base of costa with scaling slightly more dense; no raised scales on forewing; R₄ and R₅ stalked in basal 0.25 in males, basal 0.16 in females; chorda absent, m-stem weak though cell. Hindwing with Rs and M₁ approximate at base, CuA₁ and M₃ connate, and M₂ and M₃ approximate at base; cubital hair pecten well developed in both sexes. *Abdomen:* Single rounded mid-dorsal pit on A2 and A3 in both sexes (Fig. 12). Weakly developed lateral pouch bearing specialized scales laterally on A1 of both sexes. Female lacking enlarged corethrogyne scaling. Male genitalia with uncus long, but not exceedingly slender as in most *Sparganothis* and *Coelostathma*; socius large, elongate, densely covered with scales, and with conspicuous secondary arm extending from anterior lobe of socius, with small patch of setae in distal portion; gnathos weakly developed with slender lateral arms and weak, slender mesal process; transtilla a short, broad, densely spined band; pulvinus weakly developed compared to other sparganothines; valva large, subrectangular, simple, only slightly narrowed distally, lacking subapical notch at distal termination of costa (that is characteristic of *Amorbia*); sclerotized basal portion of transtilla extending toward sacculus as a slender line of sclerotization; sacculus ill-defined, restricted to basal 0.6 of valva. Phallus relatively small, 0.4–0.8 length of valva, slightly bent at 0.65 distance from base; vesica with dense bundle of 15–20 aciculate, subbasally attached, deciduous cornuti. Female genitalia with papillae anales simple, large, unmodified;



FIGS 1–6. Adults of *Aesiocopa*. 1. *A. vacivana* (male). 2. *A. vacivana* (female). 3. *A. necrofolia* (male). 4. *A. necrofolia* (female). 5. *A. grandis* (male). 6. *A. grandis* (female).

apophyses simple, posteriores only slightly longer than anteriores; sterigma a simple lateral band, slightly narrowed laterally; ductus bursae slightly longer than corpus bursae, gradually broadened anteriorly; corpus bursae round-oblong, densely and finely punctate; signum a slender crescent-shaped band near middle of corpus bursae; a tiny, knoblike process externally on corpus bursae near signum.

Distribution and Biology. *Aesiocopa* is recorded from Mexico to Panama. The majority of specimens (71 of 88) of *Aesiocopa necrofolia* were collected as larvae, and most specimens (5 of 9) of *A. grandis* were retrieved from malaise traps. Hence, it is assumed that adults are only weakly attracted to lights. *Aesiocopa necrofolia* has been reared from 30 different species of vascular plants, encompassing 15 families, exhibiting polyphagy typical of most other genera of Sparganothini. The three known species of *Aesiocopa* appear to replace each other over an elevation gradient in Central America—*A. vacivana* is known from ca. 0–300 m; *A. necrofolia* has been recorded primarily from ca. 300–1000 m; and *A. grandis* is known only from ca. 1950–2500 m.

Aesiocopa vacivana Zeller, 1877

Figs. 1, 2, 9, 13

Tortrix (Aesiocopa) vacivana Zeller, 1877: 106.

Aesiocopa vacivana: Walsingham 1915: 207; Powell et al. 1995: 148; Brown 2005: 74.

Diagnosis. *Aesiocopa vacivana* is easily distinguished from all other Sparganothini by the shape of the forewing: angled downward at ca. 140° in the distal 0.3 of the costa in both sexes. In the female the forewing is primarily ochreous, whereas in the male it is mostly pale beige and gray, with an ill-defined, incomplete, brown, median fascia. The bright ochreous color of the female easily distinguishes it from congeners. Forewing maculation and pattern of the male are very similar to those of *A. necrofolia*, but the two are easily distinguished by forewing shape.

Description. Male (Fig. 1). *Head*: Vertex rust, frons cream; labial palpus short, upcurved, nearly appressed to frons, with moderately short, pale ochreous brown scales (i.e., not conspicuously expanded distally on segment II); antennal scaling pale orange brown. *Thorax*: Anterior 0.25 of nota, including tegula, pale rust, posterior 0.75 mostly cream-gray; without modified scaling on legs. Forewing length 10.0–11.0 mm (mean 10.5; n = 5); forewing costa angled downward at ca. 140° in distal 0.3; forewing ground color cream, with scattered small brown spots between veins in middle of wing and along veins in distal 0.3; basal 0.15 of costa and costo-apical region pale rust; faint, ill-defined, interrupted, brown median fascia from costa ca. 0.3–0.4 distance from base to apex, extending to dorsum ca. 0.15–0.25 distance from base to tornus; dorsum with faint, diffuse, pale rust patch from dorsal portion of median band, fading toward termen; row of round, pale bluish white dots along termen between veins; fringe cream at tornus, pale beige along termen. Hindwing pale ochreous, pale gray at base; fringe slightly paler. *Abdomen*: Cream. *Genitalia* (Fig. 9) with uncus rodlike, ca. as long as valva, from broadly rounded base; socius relatively slender with fine long scales, secondary arms arising from inner anterior portion of socius, moderately short, slightly dilated apically with patch of fine setae; transtilla bulbous mesially, slightly bilobed, densely covered with fine spines; valva simple, mostly parallel-sided, rounded apically, costa narrowly sclerotized to apex, sacculus sclerotized in basal 0.6; juxta a diamond-shaped plate; phallus ca. 0.85 length of valva, slightly swollen and curved near middle; vesica with 20–22 deciduous cornuti (represented by scars in genitalia preparations).

Female (Fig. 2). *Head*: Vertex pale orange brown, frons cream; labial palpus short, upcurved, nearly appressed to frons, with moderately short, ochreous, scales (i.e., not conspicuously expanded distally on segment II); antennal scaling pale orange brown. *Thorax*:

Anterior 0.25 of notum, including tegula, pale orange brown, posterior 0.75 cream. Forewing length 14.0 mm (n = 1); forewing costa angled downward at ca. 140° in distal 0.3; forewing ground color ochreous; broad area of pale orange brown in middle of wing, extending from dorsum ca. 0.15–0.75 distance from base to apex, through discal cell; row of 3–4 roundish white dots along termen between veins; fringe pale cream orange at tornus, slightly darker along termen. Hindwing pale cream orange. *Abdomen*: Genitalia (Fig. 13) essentially as described for genus (single preparation in poor condition).

Holotype ♀, Panama, Chiriquí, Ribbe (MNHU).

Additional Specimens Examined. COSTA RICA: Puntarenas: Estación Sirena, 0–100 m, P. N. Corcovado, Nov 1989 (1♂), Dec 1989 (1♀), Oct 1990 (1♂), May 1991 (1♂), Sep 1991 (1♂), G. Fonseca (INBio). Rancho Quemado, Peninsula de Osa, 200 m, Nov 1991 (1♂), F. A. Quesada (INBio). PANAMA: Bugaba, Chiriquí, 800–1500', [no date] (1♂, 2♀), G. C. Champion (BMNH, USNM).

Distribution and Biology. *Aesiocopa vacivana* is recorded only from southwestern Costa Rica and adjacent Panama. Nothing is known of the early stages.

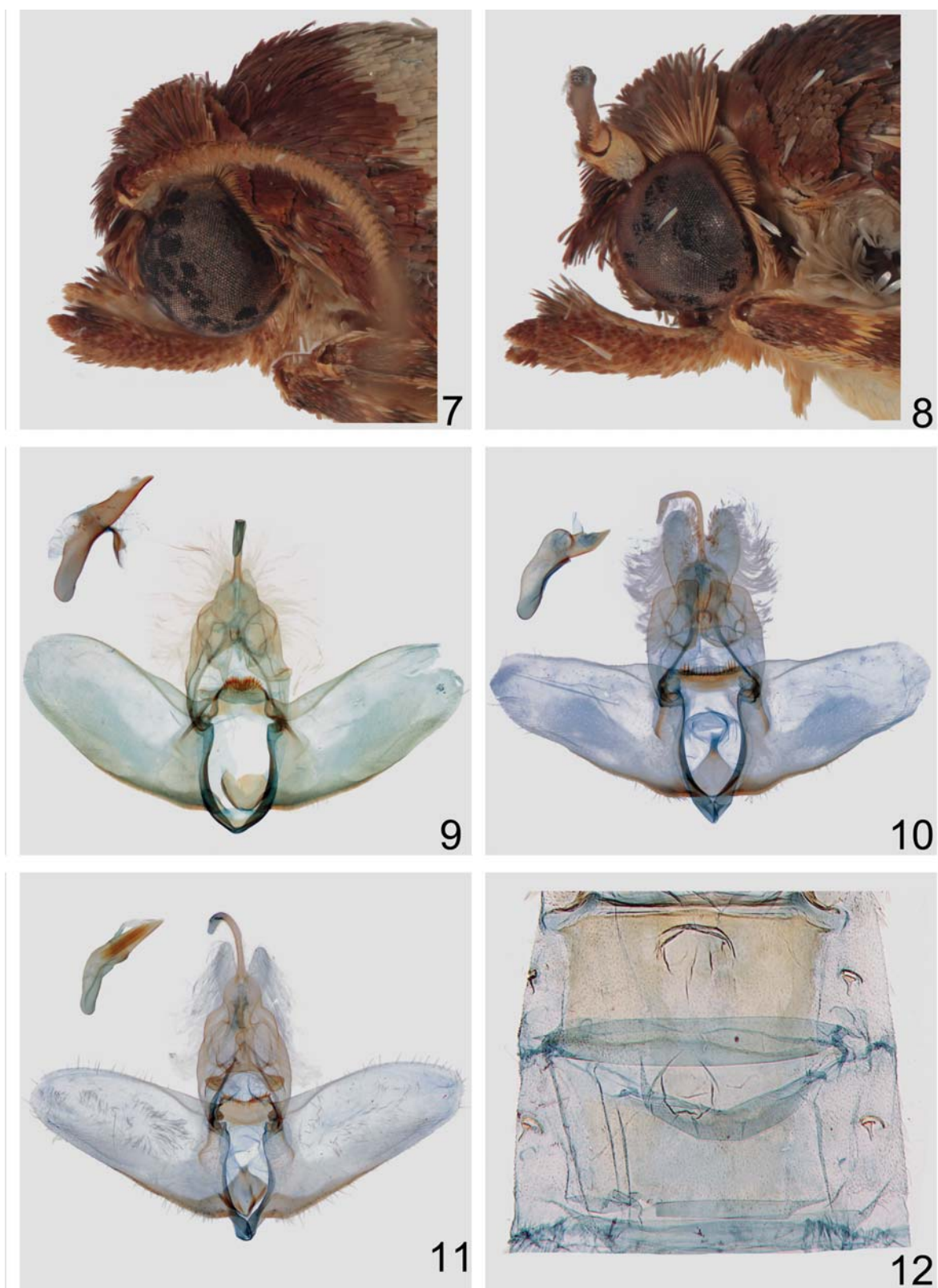
Remarks. Of the three known females, the genitalia slide is lost for the holotype (N. Obratsov slide 1964, B.19), the abdomen is lacking from another (USNM), and the preparation is rather poor for the last (BMNH slide 5344).

Aesiocopa necrofolia Brown and Phillips,
new species

Figs. 3, 4, 7, 8, 11, 12, 15

Diagnosis. Superficially, *A. necrofolia* is similar to the male of *A. vacivana* and both sexes of *A. grandis*. It can be distinguished from *A. vacivana* by the more uniformly rounded costa of the forewing (bent in the distal 0.3 in *A. vacivana*), and from *A. grandis* by its conspicuously smaller size (mean forewing length 9.9 vs 12.2 mm in males and 12.5 vs. 16.0 mm in females). Males have a narrow, slightly curved band of tiny pale bluish white dots paralleling the termen which in *P. grandis* is usually replaced by a single (or infrequently a second tiny), isolated silver-white dot near the termen subapically; and the scaling on the head of males is more complex in *P. necrofolia* than in either *P. grandis* or *A. vacivana*, with the frons scaling comprised of a shallow bowl-shaped ring beneath the overhanging scales of the vertex. The male genitalia of the three species are easily distinguished by the shapes of distal end of the socius and the transtilla, but the female genitalia are nearly identical.

Description. Male (Fig. 3). *Head*: Vertex dark rust, with smooth, ventrally-projecting tuft of scales, frons with a shallow bowl-like depression covered in smooth cream colored scales; labial palpus short, segment II nearly straight, with short, smooth, rust scales, segment III well exposed (Figs. 7, 8); antennal scaling rust. *Thorax*: Anterior 0.25 of nota, including tegula, dark rust, posterior 0.75 pale gray; without modified scaling on legs. Forewing length 9.0–10.0 mm (mean 9.9; n = 10); forewing costa nearly evenly curved throughout; forewing ground color pale reddish brown, isolating two broad patches of pale gray, one in basal portion of wing extending from basal 0.15 of dorsum to costa ca. 0.4 distance from base to apex, second less defined, near middle of costa, often with a small concolorous blotch immediately below; a conspicuous white dot in the terminal area subapically; fringe red-brown in apical 0.7 of termen, pale in



FIGS 7–12. Head, male genitalia, and dorsal pits of *Aesiocopa*. **7.** Head of *A. necrofolia* (male). **8.** Head of *A. necrofolia* (female). **9.** Male genitalia of *A. vacivana* (USNM slide 142,206). **10.** Male genitalia of *A. grandis* (USNM slide 142,026). **11.** Male genitalia of *A. necrofolia* (USNM slide 142,033). **12.** Dorsal pits of *A. necrofolia*.

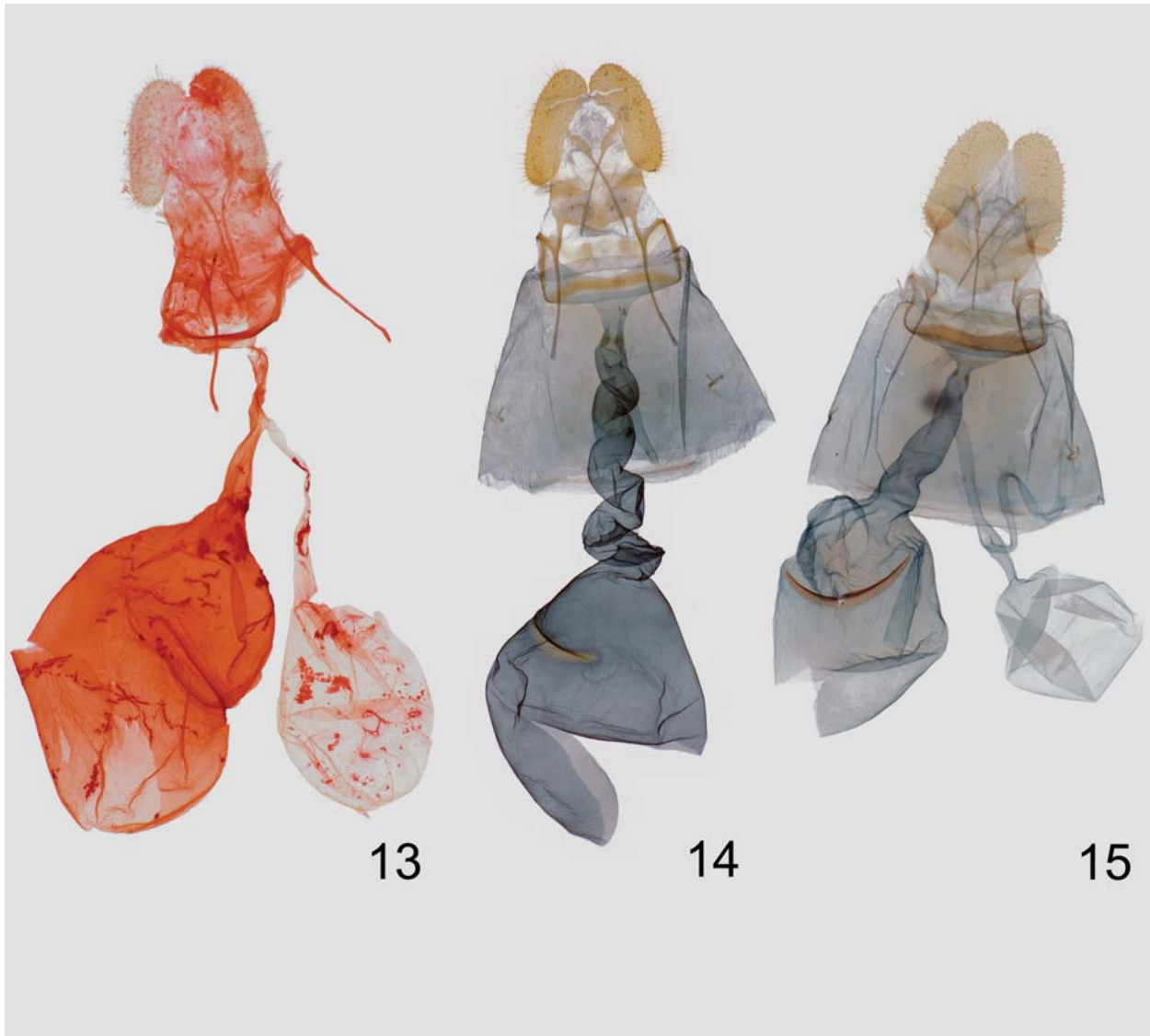
remainder (i.e. tomus). Hindwing gray-ocherous, weakly mottled with gray; fringe cream. *Abdomen*: Pale gray. Genitalia (Fig. 11) with uncus rodlike, ca. 0.75 as long as valva, from broadly rounded base; socius long, extending posteriorly nearly half length of uncus, relatively slender with fine long scales, secondary arms arising from inner anterior portion of socius, moderately short, slightly dilated and rounded apically with patch of fine setae; transtilla short, rectangular, slightly arched posteriorly, densely covered with fine spines; valva simple, somewhat parallel-sided, rounded apically, costa and sacculus sclerotized in basal 0.5; juxta a diamond-shaped plate; phallus ca. 0.7 length of valva, and curved near middle; vesica with 20–22 cornuti.

Female (Fig. 4). *Head*: Vertex dark rust, with tuft of ventrally-projecting scales, frons unmodified, pale brown; labial palpus short, segment II nearly straight, with short, smooth, rust scales, paler on inner surface, segment III well exposed; antennal scaling rust. *Thorax*: Dark rust, with a pair of cream sublateral patches on posterior 0.2; legs without modified scaling. Forewing length 12.0–14.0 mm (mean 12.6; n = 10); forewing costa nearly evenly curved throughout, apex weakly falcate; forewing ground color dark rust brown, isolating two broad patches of pale ocherous orange, reticulated with fine rust net-like pattern, one patch in basal 0.33 of wing, margined by ground color along dorsum, and second much smaller patch, semicircular, just apical of middle of costa; variably developed row of 6–8 tiny, narrow, contiguous, pale silver-white dashes along termen; fringe brown with narrow line of cream along inner edge. Hindwing pale gray brown; fringe slightly paler. *Abdomen*: Pale gray brown. Genitalia (Fig. 15) with papillae anales simple, large, unmodified; apophyses simple, posteriores only slightly longer than anteriores; sterigma a simple lateral band, slightly narrowed laterally; ductus bursae slightly longer than corpus bursae, gradually broadened anteriorly; corpus bursae round-oblong, densely and finely punctate; signum a slender crescent-shaped band near middle of corpus bursae.

Holotype ♂, Costa Rica, Guanacaste, Area de Conservación Guanacaste, Sector San Cristobal, Finca San Gabriel, 645 m, 10.87766N, -85.39343W, 26 Nov 2009, E. Araya, em: 26 Dec 2009, r.f. *Eugenia basilaris* (09-SRNP-6362) (USNM).

Paratypes (31♂, 48♀): COSTA RICA: Alajuela: Area Conservación Guanacaste: Sector Rincon Rain Forest, Sendero Parcelas, 375 m, 10.90777N, -85.29137W, 1 Feb 2003, M. Carmona, em: 16 Feb 2003 (1♀), r.f. *Myriocarpa longipes* (03-SRNP-10239); 25 May 2010, J. Perez, 11 Jun 2010 (1♂), r.f. *Calatola costaricensis* (10-SRNP-41930). Sector Rincon Rain Forest, Camino Río Francia, 410 m, 10.90425N, -85.28651W, 1 Aug 2000, F. Vargas, em: 18 Aug 2000 (1♀), r.f. *Piper auritum* (00-SRNP-14022). Sector Rincon Rain Forest, Flecha, 491 m, 10.94741N, -85.31501W, 7 Jul 2009, N. Castillo, em: 18 Jul 2009 (1♀), r.f. *Hernandia stenura* (09-SRNP-69456); 17 Sep 2009, N. Castillo, em: 29 Sep 2009 (1♂), r.f. *Hernandia stenura* (09-SRNP-80067); 31 Mar 2010, N. Castillo, em: 15 Apr 2010 (1♂), r.f. *Piper imperiale* (10-SRNP-69464). Sector Rincon Rain Forest, Camino Albergue Oscar, 560 m, 10.87741N, -85.32363W, 29 Dec 2011, E. Araya, em: 16 Jan 2012 (1♂), r.f. *Nectandra hihua* (11-SRNP-5229); 20 May 2010, G. Sihezlar, em: 18 Jun 2010 (1♂), r.f. *Acalypha diversifolia* (10-SRNP-2523); 16 May 2011, G. Sihezlar, em: 3 Jun 2011 (1♂), r.f. *Ardisia auriculata* (11-SRNP-1999). Sector Rincon Rain Forest, Selva, 410 m, 10.92291N, -85.3187709W, 6 Oct 2009, M. Catillo, em: 26 Oct 2009 (1♀), r.f. *Calatola costaricensis* (SRNP-80438). Sector Rincon Rain Forest, San Lucas, 320 m, 10.91847N, -85.30338W, 22 July 2012, A. Cordoba, 8 Aug 2012 (1♀), r.f. *Ardisia auriculata* (10-SRNP-42605). Sector Rincon Rain Forest, Sendero Rincon, 430 m, 10.8962N, -85.27769W, 31 Aug 2010, A. Cordoba, em: 18 Sep 2010 (1♂), r.f. *Calatola costaricensis* (10-SRNP-43105). Sector San Cristobal, Puente Palma, 460 m, 10.9163N, -85.37869W, 4 Sep 2009, C. Cano, em: 20 Sep 2009 (1♀), r.f. *Ardisia auriculata* (09-SRNP-4628); 4 Sep 2009, C. Cano, em: 7 Sep 2009 (1♂), r.f. *Ardisia auriculata* (09-SRNP-4629). Sector San Cristobal, Sendero Carmona, 670 m, 10.87621N, -85.38632W, 21 Jan 2003, G. Sihezlar, em: 10 Feb 2003 (1♀), r.f. *Piper enocladum* (03-SRNP-5129). Sector San Cristobal, Sendero Huerta, 527 m, 10.9305N, -85.37223W, 23 Jul 2007, E. Araya, em: 8 Aug 2007 (1♀), r.f. *Calatola costaricensis* (07-SRNP-3175); 29 Sep 2009, E. Araya, em: 19 Nov 2009 (1♀), r.f.

Hernandia stenura (09-SRNP-4978); 17 Sep 2006, G. Siheza, em: 5 Oct 2006 (1♀), r.f. *Calatola costaricensis* (06-SRNP-7618); 13 Apr 2009, O. Espinoza, em: 18 May 2009 (1♀), r.f. *Calatola costaricensis* (09-SRNP-1414), em: 29 Apr 2009 (1♂), (09-SRNP-1413); 28 Nov 2009, E. Araya, em: 15 Dec 2009 (1♂), r.f. *Calatola costaricensis* (09-SRNP-6443); 29 Sep 2009, E. Araya, em: 30 Sep 2009 (1♂), r.f. *Cupania juglandifolia* (09-SRNP-4979); 13 May 2009, G. Sihezlar, em: 26 May 2009 (1♂), r.f. *Calatola costaricensis* (09-SRNP-1924), em: 23 May 2009 (1♂) (09-SRNP-1925); 31 Oct 2011, C. Cano, em: 25 Nov 2011 (1♀), r.f. *Calatola costaricensis* (11-SRNP-4245), em: 26 Nov 2011 (1♂) (11-SRNP-4246); 9 Jan 2010, O. Espinoza, em: 12 Feb 2009 (1♀), r.f. *Lepidaploa tortuosa* (10-SRNP-282). Sector San Cristobal, Finca San Gabriel, 645 m, 10.87766N, -85.39343W, 11 Feb 2010, E. Araya, em: 6 Mar 2010 (1♀), r.f. *Ardisia calycosa* (10-SRNP-912); 26 Jan 2010, E. Araya, em: 1 Mar 2010 (1♀), r.f. *Ardisia auriculata* (10-SRNP-610); 1 Sep 2008, E. Araya, em: 19 Sep 2008 (1♂), r.f. *Ardisia compressa* (08-SRNP-5025); 13 Jul 2011, E. Araya, 4 Aug 2011 (1♀), r.f. *Hernandia stenura* (11-SRNP-2832); 13 Aug 2011, G. Sihezlar, em: 2 Sep 2011 (1♀), r.f. *Piper umbricola* (11-SRNP-3208). Sector San Cristobal, Sendero Perdido, 620 m, 10.8794N, -85.38607W, 27 Jul 2007, E. Ayara, em: 18 Aug 2007 (1♀), r.f. *Calatola costaricensis* (07-SRNP-3244). Sector Rincon Rain Forest, Quebrada Escondida, 420 m, 10.89928N, -85.27486W, 1 Feb 2010, J. Perez, em: 4 Mar 2010 (1♀), r.f. *Calatola costaricensis* (10-SRNP-40387); 26 Jan 2003, J. Perez, em: 9 Feb 2003 (1♀), r.f. *Calatola costaricensis* (03-SRNP-10191); 25 Nov 2009, A. Cordoba, em: 9 Dec 2009 (1♀), r.f. *Piper fimbriulatum* (09-SRNP-43300); 9 July 2009, A. Cordoba, em: 18 July 2009 (1♂), r.f. *Ardisia auriculata* (09-SRNP-41646); 9 Jul 2009, A. Cordoba, em: 29 July 2009 (1♂), r.f. *Ardisia auriculata* (09-SRNP-41653); 11 Nov 2011, J. Hernandez, em: 26 Nov 2011 (1♂), r.f. *Piper thomasi* (Piperaceae) (11-SRNP-44832); 10 Aug 2010, A. Cordoba, em: 29 Aug 2010 (1♂), r.f. *Calatola costaricensis* (10-SRNP-42830). Sector Rincon Rain Forest, Sendero Albergue Crater, 980 m, 10.84886N, -85.3281W, 14 Oct 2009, E. Araya, em: 7 Nov 2009 (1♀), r.f. *Ardisia compressa* (09-SRNP-5368), em: 5 Nov 2009 (1♂) (09-SRNP-5369); 23 Aug 2010, C. Cano, 12 Sep 2010 (1♀), r.f. *Ardisia calycosa* (10-SRNP-4761). Sector Rincon Rain Forest, Jacobo, 461 m, 10.94076N, -85.3177W, 25 Nov 2009, N. Castillo, em: 12 Dec 2009 (1♀), r.f. *Piper phytolaccaefolium* (09-SRNP-80714); 17 Jul 2009, N. Castillo, em: 25 Jul 2009 (1♀), r.f. *Vernonia patens* (09-SRNP-69542); 26 Aug 2009, N. Castillo, em: 16 Sept 2009 (1♀), r.f. *Inga* sp. (09-SRNP-69859); 18 Sep 2009, M. Castillo, em: 25 Sep 2009 (1♂), r.f. *Piper fimbriulatum* (09-SRNP-80110). Sector San Cristobal, Sendero Colegio, 520 m, 10.89296N, -85.3788W, 11 Oct 2006, G. Sihezlar, em: 27 Oct 2006 (1♀), r.f., *Ardisia auriculata* (06-SRNP-8402). Sector Rincon Rain Forest, Río Francia Arriba, 400 m, 10.89666N, -85.29003W, 23 Jun 2009, P. Calderon, em: 26 Jul 2009 (1♀), r.f. *Calatola costaricensis* (09-SRNP-41458); 25 Oct 2011, P. Umaña, em: 24 Nov 2011 (1♀), r.f. *Piper imperiale* (Piperaceae) (11-SRNP-44720); 27 Oct 2010, A. Cordoba, 23 Nov 2010 (1♀), r.f. *Ocotea cernua* (10-SRNP-43860); 27 Oct 2010, A. Cordoba, em: 1 Dec 2010 (1♂), r.f. *Ocotea cernua* (10-SRNP-43859). Cartago: Turrialba, 7–25 Feb 1965 (2♂), 1–6 Mar 1965 (4♂, 2♀), S. S. & W. D. Duckworth (USNM); 24–26 Jun 1974 (1♀), Harding & Donahue (LACM). Guanacaste: Sector Santa Rosa, Cafetal, 280 m, 10.85827N, -85.61089W, 29 Jun 2005, R. Franco, em: [date not given] (1♀), r.f. *Casearia nitida* (05-SRNP-1835). Sector Pitilla, Sendero Evangelista, 660 m, 10.98680N, -85.42083W, 8 Oct 2009, P. Rios, em: 1 Nov 2009 (1♀), r.f. *Calatola costaricensis* (09-SRNP-32674); 21 May 2004, J. Victor, em: 15 Jun 2004 (1♀), r.f. *Calatola costaricensis* (04-SRNP-32903). Sector Santa Rosa, Arboles Via, 305 m, 10.86081N, -85.60828W, 7 Jun 2010, D. Janzen, em: 29 Jun 2010 (1♀), r.f. *Alibertia edulis* (10-SRNP-129). Sector Pitilla, Sendero Naciente, 700 m, 10.98705N, -85.42816W, 2 Oct 2009, C. Moraga, em: 19 Oct 2009 (1♀), r.f. *Parathesis trichogyne* (09-SRNP-32633). Sector Pitilla, Sendero Laguna, 680 m, 10.98880N, -85.42336W, 4 Jan 2010, C. Moraga, em: 24 Jan 2010 (1♀), r.f. *Smilax mollis* (10-SRNP-30029). Sector Pitilla, Sendero Memos, 740 m, 10.98171N, -85.42785W, 12 May 2009, C. Moraga, em: 25 May 2009 (1♀), r.f. *Piper glabrescens* (09-SRNP-31591). Sector Cacao, Sendero Derrumbe, 1220 m, 10.92918N, -85.46426W, 12 Aug 1997, R.



FIGS 13–15. Female genitalia of *Aesiocopa*. **13.** *A. vacivana* (BMNH slide 5344). **14.** *A. grandis* (USNM slide 142,027). **15.** *A. necrofolia* (USNM slide 118,831).

Moraga, em: 4 Sep 1997 (1♀), r.f. *Piper* sp. (97-SRNP-1658). Sector San Cristobal, Sendero Corredor, 620 m, 10.87868N, -85.38963W, 25 Jun 2009, E. Araya, em: 17 July 2009 (1♀), r.f. *Ocotea tenera* (09-SRNP-2984); 26 Aug 2008, E. Araya, em: 15 Sep 2008 (1♂), r.f. *Ocotea whitei* (08-SRNP-4912). Sector San Cristobal, Río Blanco Abajo, 500 m, 10.90037N, -85.37254W, 16 Nov 2009, G. Sihezlar, em: 7 Dec 2009 (1♀), r.f. *Smilax vanilliodora* (09-SRNP-6046); 3 Dec 2009, C. Cano, em: 28 Dec 2009 (1♀), r.f. *Calatola costaricensis* (09-SRNP-6561). Sector San Cristobal, Tajo Angeles, 540 m, 10.86472N, -85.41531W, 17 May 2010, E. Araya, em: 12 Jun 2010 (1♂), r.f. *Talauma gloriensis* (10-SRNP-2491). Heredia: Estación Biología La Selva, 150 m, Jan 1998 (1♀), J. Powell (EME), 24–25 Feb 2004 (1♀), D. Wagner (INBio), 26 Feb 2004 (1♂), D. Wagner (INBio). Puntarenas: Estación Biología Las Alturas, 22–24 Jan 1993 (1♀), r.f. understory plant, J. Powell (EME). Limón: Haciendas La Suerte/Tapezco, 29 air km W Tortuguero, 40 m, 13031 Aug 1979, J. P. Donahue et al. (LACM). MEXICO: Veracruz: Estación Biología Los Tuxtlas, 1–9 Jul 1988 (1♀), J. Chemsak (EME).

Additional specimens examined. NICARAGUA: “Through D. Denning, Univ. Farm, St. Paul, Minn” (1♂) (USNM). COSTA RICA: Area de Conservación Guanacaste [no further data], reared from unknown food plant (3♂) (USNM).

Distribution and Biology. This species is recorded from Mexico to Costa Rica, from about 40 to 980 m, but primarily between 300–700 m. Field-collected larvae have been discovered and reared on the following plants in Area de Conservación Guanacaste: *Lepidaploa tortuosa* (Asteraceae) (n = 1), *Vernonia patens* (Asteraceae) (n = 1), *Acalypha diversifolia* (Euphorbiaceae) (n = 1), *Inga* sp. (Fabaceae) (n = 1), *Hernandia stenura* (Hernandiaceae) (n = 4), *Calatola costaricensis* (Icacinaceae) (n = 20), *Nectandra hihua* (Lauraceae) (n = 1), *Ocotea cernua* (n = 2) (Lauraceae), *Ocotea tenera* (n = 1), *Ocotea whitei* (n = 1), *Talauma gloriensis* (Magnoliaceae) (n = 1), *Ardisia auriculata* (Myrsinaceae) (n = 7), *Ardisia calycosa* (n = 2), *Ardisia compressa* (n = 2), *Parathesis trichogyne* (Myrsinaceae) (n = 1), *Eugenia basilaris* (Myrtaceae) (n = 1), *Piper* sp. (Piperaceae) (n = 1), *Piper auritum* (n = 1), *Piper cenocladum* (n = 1), *Piper*

fimbriatum (n = 2), *Piper glabrescens* (n = 1), *Piper imperiale* (n = 2), *Piper phytolaccaefolium* (n = 1), *Piper thomasi* (n = 1), *Piper umbricola* (n = 1), *Alibertia edulis* (Rubiaceae) (n = 1), *Casearia nitida* (Salicaceae) (n = 1), *Cupania juglandifolia* (Sapindaceae) (n = 1), *Smilax mollis* (Smilacaceae) (n = 1), *Smilax vanilliodora* (n = 1), and *Myriocarpa longipes* (Urticaceae) (n = 1). According to Janzen and Hallwachs (2012), the larva is pale translucent green with a pale head bearing a black genal band and black mandibles, and constructs a shelter between two leaves of the host.

Etymology. The specific epithet refers to the resemblance of the wing pattern to a necrotic leaf.

Aesiocopa grandis Brown, *new species*

Figs. 5, 6, 10, 14

Diagnosis. *Aesiocopa grandis* is superficially most similar to *A. necrofolia*, but the former has a conspicuously greater forewing length (mean 12.2 vs. 10.5 mm in males, 16.0 vs. 14.0 in mm females), and males have a more isolated silver-white dot subapically in the subterminal region; in *A. necrofolia* there is a narrow line of smaller and paler spots subterminally. In the male genitalia, the distal portion of the secondary arm of the socius is rectangular oar-shaped in *A. grandis*, whereas it is more rounded in *A. necrofolia*. The sterigma of the female genitalia of the two species is very similar, but based on limited dissections, the ductus bursae is coiled in *A. grandis* (n = 2) and nearly straight in *A. necrofolia* (n = 3). However, the latter feature may be an artifact of mating.

Description. Male (Fig. 5). *Head:* Vertex dark rust, with short, rough, ventrally-projecting tuft of scales, frons unmodified, covered in smooth grayish cream scales; labial palpus short, segment II nearly straight, with short, smooth, rust scales, segment III well exposed; antennal scaling rust. *Thorax:* Anterior 0.25 of nota, including tegula, dark rust, middle 0.5 with a pair of sublateral cream patches, posterior 0.25 rust; legs unmodified. Forewing length 12.0–13.0 mm (mean 12.2; n = 5); forewing costa nearly evenly curved throughout; forewing ground color rust brown, isolating two irregular patches of pale gray, one in basal 0.2 portion of wing, extending from dorsum to costa, narrowly border by rust along costa, second less defined, in distal 0.5 of wing, semicircular at costa, extending toward dorsum as a smaller, subrectangular blotch; roundish, silvery white dot subapically in subterminal area; fringe dark rust in apical 0.7 or termen, pale in lower 0.3 (tornus). Hindwing dirty white with faint pale grayish marbling; fringe concolorous with wing, but with ocherous hue. *Abdomen:* Pale brownish gray. Genitalia (Fig. 10) with uncus rodlike, ca. 0.75 as long as valva, from broadly rounded base; socius relatively slender with fine long scales, secondary arms arising from inner anterior portion of socius, moderately short, dilated apically into subrectangular, paddle-shaped processes bearing patch of fine setae; transtilla subrectangular mesially, densely covered with long slender spines; valva simple, broadest basally, slightly narrowed distally, rounded apically, costa and sacculus sclerotized in basal 0.75; juxta a diamond-shaped plate with slender terminal process for attachment of phallus; phallus ca. 0.75 length of valva, slightly swollen and curved near middle, with narrow rounded sclerite subdistally; vesica with 20–22 cornuti.

Female (Fig. 6). *Head:* Vertex pale brown with some rust scales rough, with ventrally-projecting tuft, frons unmodified, pale brown; labial palpus slightly longer than in male, segment II nearly straight, somewhat correct, with short, smooth, pale brown scales, paler on inner surface, segment III well exposed; antennal scaling pale brown. *Thorax:* Pale brown with paired sublateral patches of yellow ocherous

in posterior 0.75; without modified scaling on legs. Forewing length 16.0 mm (n = 2); forewing costa evenly curved throughout, apex weakly falcate; forewing ground color pale brown with tiny, evenly spaced, pale bluish white specks, particularly in apical region; pale ocherous patch in basal 0.33 of wing, margined by ground color in basal 0.25 of costa, with a small brown dot near middle; second ocherous patch near middle of costa small, faint, ill-defined; row of 4 tiny, subrectangular, pale bluish white dots in terminal region between R-veins; fringe rust, paler at tornus. Hindwing dirty white with faint, pale grayish brown mottling; fringe concolorous with wing. *Abdomen:* Genitalia (Fig. 14) with papillae anales simple, large, unmodified, mostly parallel-sided; apophyses simple, posteriores ca. as long as anteriores; sterigma a simple, narrow, transverse band, slightly concave mesially; ductus bursae slightly longer than corpus bursae, gradually and slightly broadened anteriorly, coiled ca. four revolutions; corpus bursae round-oblong, densely and finely punctate; signum a slender crescent-shaped band near middle of corpus bursae.

Holotype ♂, Costa Rica, Heredia, 6 km ENE Vara Blanca, 1950–2050 m, 12–21 Feb 2002, flight trap (INBio).

Paratypes (5♂, 2♀). COSTA RICA: Alajuela: Volcan Poás, 2350 m, 15 Dec 1982 (1♂), D. H. Janzen & W. Hallwachs (INBio). Cartago: Tuis, 2400', Coll. Wm. Schaus (1♂) (USNM). Heredia: 6 km ENE Vara Blanca, 1950–2050 m, 12–21 Feb 2002 (3♂), flight trap; 17 Mar 2002 (1♀) (INBio). Cerro Chompipe, Biol. Chompipe, 2100 m, 9 Oct 1991, J. F. Corrales (1♀) (INBio). San José: P.N. Cerrito, Llano Bonito, 2492 m, 20–21 Feb 2009 (1♂), K. Nishida (USNM).

ACKNOWLEDGMENTS

I thank Jack Longino, co-PI of the NSF-funded ALAS Project, Evergreen State College, Olympia, Washington, for the opportunity to conduct field work in Costa Rica and visit Instituto Biología de Biodiversidad (INBio) in Santo Domingo de Heredia, Costa Rica. I acknowledge Eugenie Phillips-Rodriguez, Jerry Powell, and James Kruse for discussions about Costa Rican Sparganothini; Phillips-Rodriguez provided access to the collection at INBio and Powell access to the collection at EME. I am especially grateful to Daniel Janzen and Winnie Hallwachs for making available for study reared specimens from Costa Rica. The illustrations were skillfully prepared by Taina Litvak and Gary Ouellette, USDA, Systematic Entomology Laboratory, National Museum of Natural History, Washington, DC. The project was completed with the support of the U.S. Department of Agriculture, an equal opportunity provider and employer. James Kruse and Eugenie Phillips-Rodriguez provided helpful reviews that increase the clarity and quality of the manuscript.

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Submitted for publication 25 January 2013; revised and accepted 2 April 2013.

Journal of the Lepidopterists' Society
68(1), 2014, 10–16

COMMUNAL ROOSTING IN *HELICONIUS* BUTTERFLIES (NYMPHALIDAE): ROOST RECRUITMENT, ESTABLISHMENT, FIDELITY, AND RESOURCE USE TRENDS BASED ON AGE AND SEX

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ABSTRACT. *Heliconius* passion-vine butterflies form communal roosts on a nightly basis as an anti-predatory defense. Although past studies have evaluated various components of this behavior, much remains unknown about many basic aspects of roost dynamics. To learn more about communal roosting I examined roost establishment, recruitment, roost-mate resource use, roosting participation in a population, and roost arrival, departure, and perch preferences in natural populations of *Heliconius erato petiverana* in Panama. My observations suggest that 1) younger butterflies are recruited more readily than older butterflies, 2) roosts are first established by a single butterfly roosting consecutively in the same location that later recruits butterflies, 3) males depart roosts earlier than females in the morning, 4) older butterflies tend to roost on the same perch in the same roost every night, 5) roost-mates share the same resource traplines, and 6) most butterflies in a population participate in roosts. These observations present an improved portrait of *Heliconius* roosting and raise several new questions about this behavior.

Additional key words: Aggregation, trapline, following behavior, butterfly memory, *Heliconius erato*

Since the late nineteenth century communal roosting in *Heliconius* Kluk (Nymphalidae) passion-vine butterflies has generated a great deal of scientific and popular interest (Edwards 1881). Many species from this genus assemble in communal roosts in which adults gather repeatedly in a particular location in their home range to roost for the night (Mallet 1986a), and a recent study determined this unique behavior provides predator deterrence through collective aposematism (Finkbeiner et al. 2012). Roost-mates are generally conspecifics, but occasionally include Müllerian co-mimics of other species (Mallet 1986a, Mallet & Gilbert 1995). *Heliconius* likely rely on memory to locate their roosts each night (Jones 1930, Turner 1975, Mallet 1986a), rather than pheromones or scent-marking which is commonly seen in other aggregating insects (Costa 2006). Many individuals stay loyal to their roost for several months and even until demise (pers. obs). It is proposed that communal roosting behavior in *Heliconius* is facilitated by unpalatability, slow reproductive rate (Erlich & Gilbert 1973), limited learned home range (Turner 1975, Mallet 1986b), and long lifespan due to pollen consumption (Gilbert 1972, Boggs et al. 1981).

A number of studies on roosting in *Heliconius* have evaluated the adaptive benefits, home range, spatial dynamics, roost assembly, fidelity, environmental elements, and origin of this behavior (Jones 1930, Turner 1975, Young & Thomason 1975, Young & Carolan 1976, Mallet 1980, Waller & Gilbert 1982, Mallet 1986a, Mallet & Gilbert 1995, Salcedo 2006, 2010a, 2011a, 2011b, Finkbeiner et al. 2012). Here I describe observations that address several key questions

about *Heliconius* roosting: 1) How are roosts established? 2) Do age and sex play a role in roost recruitment? 3) Are there trends in individual butterfly arrival, departure, or perch preference? 4) Do roosting butterflies share the same resources? 5) How many butterflies in a population participate in roosts? I addressed these questions through observations of natural roosts of *H. erato petiverana* Doubleday (Nymphalidae) in Panama in 2010.

MATERIALS AND METHODS

Field sites. All data were collected in Panama at the Smithsonian Tropical Research Institute Gamboa field station, located along the eastern side of the Panama Canal just north of the Chagres River, approximately 30 km north of Panama City. I chose this site based on the abundance and accessibility of *H. erato* butterflies and communal roosts. Data were collected from natural roosts during June through September of 2010 throughout the rainy season.

Age scoring and roost locating. Roosting and non-roosting *H. erato* butterflies collected in Gamboa were given unique numbers for identification using a Sharpie® permanent marker, with numbers written on the ventral side of the forewing pink band. Individuals were sexed and their ages were estimated based on wing wear (Erlich & Gilbert 1973, Karlsson 1987, Kemp 2000, Pinheiro 2009). I used a scale of 1–3 with (1) as young, (2) as middle-aged, and (3) as old. Although young butterflies sometimes have damaged wings and some older butterflies may have little wing damage, this method is generally reliable. To maintain consistency the same person scored all butterflies.

TABLE 1: Data representing frequencies of age and sex of butterflies from varying observations. Sample sizes differ since not all butterflies whose age was determined were successfully sexed. Significance values indicated by asterisks: ° $p < 0.05$, °° $p < 0.0001$ with corresponding pairs in bold.

Observation	Young	Mid–Old Age	Males	Females
Overall in population <i>n</i> =110 aged, <i>n</i> =82 sexed	41%	59%	44%	56%
Overall in roosts <i>n</i> =58 aged, <i>n</i> =57 sexed	52%	48%	46%	54%
Recruited Butterflies °° <i>n</i> =49 aged, <i>n</i> =29 sexed	84%	16%	52%	48%
Arrived to roost first <i>n</i> =97 arrivals by age <i>n</i> =93 arrivals by sex	55%	45%	46%	54%
Departed roost first ° <i>n</i> =54 departures by age <i>n</i> =48 departures by sex	54%	46%	65%	35%
Preferred same perch ° <i>n</i> =19 aged and sexed	26%	74%	58%	42%

I located roosts by following individual butterflies from foraging sites to their roosting locations in the late afternoon. These sites are usually within relatively close proximity due to the restricted home ranges of *Heliconius* (Mallet 1986b). Butterflies were captured and marked after departing their roosts in order to prevent them from associating the roost with danger (Young & Thomason 1975, Mallet et al. 1987). Identifying individual butterflies was important for detection of new roost recruits and monitoring roost fidelity.

Data collection. Here I follow the broader ecology literature in defining recruitment as the addition of new individuals to a population (Ricklefs 1979). Specifically, in the context of this study, recruitment refers to the addition of new individuals to a roost, and I refer to a recruit as a new roost-mate. In using the term recruitment it is worth noting that there is no implication that butterflies in established roosts are actively seeking out new roost-mates.

I evaluated roost establishment by monitoring single butterflies that roosted repeatedly in the same location. Individuals in existing roosts were noted nightly so recruitment could be monitored. Recruitment observations began one week after I located roosts to avoid counting existing roost members as recruits.

In order to look for trends based on individual, age, and sex, I made daily observations with binoculars during roost formation in the afternoon hours and during roost departures in the morning. Multiple roosts could be monitored by a single person in the morning

and evening given proximity of some roosts to one another (<15 m); also butterflies in roosts under forest cover convened at roosts at least 30 minutes earlier in the afternoon and departed approximately 30 minutes later in the morning compared to butterflies whose roosts were along the forest edge, where more ambient light is available during crepuscular hours. This made it possible to collect data from roosts in both types of light environments in the same day.

Roost-mate traplines—i.e. foraging routes defined as repeated sequential visits to a series of feeding locations (Gilbert 1975, Ohashi & Thomson 2009)—were determined by following individuals during foraging periods to determine whether roosting individuals share the same resources. I estimated the frequency of roosting butterflies in a population based on how many individuals marked in a single locality were found at roosts. Roost recruitment, arrival, departure, and perching location based on age and sex were analyzed using a Chi-squared test for given probabilities. Middle- and old-aged butterflies (wing wear score of 2 or 3) were pooled together and categorized as “older” individuals in the analyses. It is important to note that butterfly age was recorded the first time an individual was captured, and that some individuals were still observed in roosts later in the season. For data analysis, their ages remained as the initial age recorded, however the initial age recordings do not affect the results for recruitment data but may inflate the number of young butterflies in roosts throughout the season.

RESULTS

Roost recruitment and establishment. Nine *H. erato petiverana* roosts located in Gamboa were observed in this study. Recruitment frequency averaged 1.23 new butterflies per week ($SD = 0.92$, $n = 49$ recruits over the course of 10 weeks), but while some recruits stayed at the roost, many appeared for only one night. Recruitment likely depended on the number of established butterflies in the roost, and roosts on average contained 4.3 butterflies ($SD = 1.6$, $n = 233$ observations across nine natural roosts). On five occasions I observed a new recruit following an established roost member to the aggregation, suggesting that recruits find new roosts by following behavior (as speculated by Waller & Gilbert 1982).

Younger individuals were recruited more readily than older individuals. Of 49 roost recruits, 84% were young—their wings had bright colors and minimal damage, compared to middle-aged and old individuals whose wings were faded and tattered with apparent edge damage ($\chi^2 = 22.225$, d.f. = 1, $p < 0.0001$, $n = 49$ butterflies; Table 1). Within the *H. erato* butterfly population in Gamboa, only 41% were determined to be young (a total of 110 unique butterflies noted) providing support that the frequency of young roost recruits is independent of overall frequency of young butterflies in the population. I found, however, that there was no dominant age among all roosting butterflies ($\chi^2 = 0.069$, d.f. = 1, $p = 0.793$, $n = 58$ butterflies; Table 1).

The sex ratio of the recruits whose sex was determined was equal ($\chi^2 = 0.0345$, d.f. = 1, $p = 0.853$, $n = 29$ butterflies; Table 1), as was sex ratio of all butterflies observed in roosts whose sex was determined ($\chi^2 = 0.439$, d.f. = 1, $p = 0.508$, $n = 57$ butterflies; Table 1). With one exception, all roosting females observed were previously mated, as inferred from the characteristic anti-aphrodisiac odor that is present only after a female has mated (Gilbert 1976, Estrada et al. 2011). The next evening, however, the virgin female from the previous night had been mated. I observed a single mating event at a roost where a male from an established roost brought with himself, in copulation, a young female to the aggregation (Fig. 1). Copulation continued until nightfall and the female remained at the roost throughout the night but after departing in the morning she never returned to the roost. On three separate occasions a *Heliconius hecale* Fabricius (Nymphalidae) butterfly joined a roost for one night only, and I observed the same with a *Mechanitis* sp. Fabricius (Nymphalidae) butterfly. With respect to *Heliconius* mimicry, *H. hecale* and *Mechanitis* are members of the silvaniform 'tiger' mimicry ring, which has a

morphologically distinct wing pattern differing in appearance from the 'red' mimicry ring that *H. erato* belong to (Mallet & Gilbert 1995). Four different *H. erato* roosts had regular roost membership from hybrids between *H. erato hydara* Hewitson (Nymphalidae) and *H. erato petiverana* (Fig. 2). I also found libellulid and aeschnid dragonflies at *Heliconius* roosts multiple times, perching for the night on nearby twigs.

For one month, I monitored two solitary butterflies that chose to roost in the same location nightly. Eight days after one of these individuals had been roosting consistently in the same location, it was followed to the roost by a new butterfly. Nearly two weeks later there was a third butterfly recruited to the same roost. This suggests that roosts are established when new butterflies join single individuals that already roost consecutively in the same place. The other solitary individual observed continued to roost alone and did not gain any roost-mates.

Butterfly arrival and departure. Butterflies generally arrived at their roosting sites two hours before sunset, but individuals whose roosts were under forest cover arrived as early as three hours before sunset on cloudy days, which was often during the rainy season. In the early afternoon during a rain shower I observed two individuals at their roost at 2:00pm, more than four hours before sunset. They appeared to be using the roost as a retreat, unless low ambient light from the heavy rain clouds triggered early roosting behavior (Salcedo 2010a). Later they departed to forage once the rain stopped and returned to the roost again before dusk. In the mornings, butterflies generally left their roosts within an hour and a half after sunrise, but on cloudy mornings butterflies stayed at the roost up to two and a half hours past sunrise. On rainy mornings many butterflies did not leave their roosts at all.

Particular butterflies always arrived first to their roosts in the afternoon while other butterflies were repeatedly the last to leave in the mornings. There was no relationship between first roost arrival and age; middle-aged and old butterflies did not arrive to the roost earlier than younger butterflies ($\chi^2 = 0.835$, d.f. = 1, $p = 0.361$, $n = 97$ roost arrivals; Table 1). Roost arrival did not depend on sex either ($\chi^2 = 0.527$, d.f. = 1, $p = 0.468$, $n = 93$ roost arrivals; Table 1). I found no difference between first departing butterfly and age ($\chi^2 = 0.296$, d.f. = 1, $p = 0.586$, $n = 54$ roost departures; Table 1), however I found a trend between departing butterfly and sex: males tended to depart roosts first in the morning ($\chi^2 = 4.083$, d.f. = 1, $p = 0.0433$, $n = 48$ roost departures; Table 1).

Using observations from three roosts over the course of 54 nights, 61% of all roosting butterflies chose the



FIG. 1: Two mating *H. erato* butterflies at a communal roost. The male (labeled 5B upside-down) is on the left and the female is unmarked.

exact same perch to rest on each evening. There was no difference between perch choice and sex ($\chi^2 = 0.474$, d.f. = 1, $p = 0.491$, $n = 19$ butterflies; Table 1), although older butterflies were more likely to roost on the exact same perch, compared to young butterflies ($\chi^2 = 4.263$, d.f. = 1, $p = 0.039$, $n = 19$ butterflies; Table 1).

Roost-mate traplines. Trapline observations of butterflies from three neighboring roosts in a forest patch showed that butterflies shared the same resources, even if they were not all members of the same roost. They visited a series of *Lantana camara* Linnaeus (Verbenaceae) plants throughout Gamboa in the same order in the morning hours (Fig. 3), and by the afternoon they had reversed the trapline network to return to their roost for the night. None of these resources were visible from any of the three roosts.

It was common to find multiple roosts in visible range of each other (typically $\leq 15\text{m}$) in a given part of the home range. When individual *H. erato* were exercising pre-roosting behavior they often interacted with one another before dispersing to their preferred communal roosts. On multiple occasions I observed a butterfly from one roost following a butterfly to another roost, then eventually returning to its preferred roost before dark.

Roost participation and fidelity. Of 110 total marked *H. erato* in the Gamboa *Heliconius* population, I found at least 66 in roosts, providing evidence that, at minimum, over half of the butterflies within a population choose to participate in communal roosts. From the nine roosts used in this study, eight roosting butterflies (out of 66) moved between roosts. Most only

moved once and did not return to their previous roosts, however two individuals (during different evenings) moved between three different roosts that were in close proximity.

DISCUSSION

Roost recruitment and composition. Most of the *H. erato* butterflies within the Gamboa population participate in roosts, which supports the apparent adaptive benefits associated with communal roosting (Finkbeiner et al. 2012). Roost recruitment occurred regularly, and younger butterflies were recruited more often than older butterflies in a population, which was probably a result of older butterflies already being committed members of specific roosts. Even though the young:old ratio of roosting butterflies is close to equal, some individuals were recorded in roosts when they were recruited but aged over the course of the season. As was observed, roosts are likely established when a butterfly follows and roosts with a single butterfly that had been roosting consecutively in the same location, then eventually more individuals are recruited over time. Since I observed four roosts to have a *H. erato hydara* hybrid member, racial wing pattern differences may have little effect on recruitment, although Salcedo (2010a) suggested that altered wing patterns in *H. erato petiverana* interfere with roost formation.

My observation that dragonflies roost with *H. erato* butterflies is probably not a result of limited roost substrate, since many dry branches were available in these sites to support other aggregations or single roosting perches. Both dragonflies and damselflies have been documented to form communal roosts (Parr & Parr 1974, Miller 1989, Rehfeldt 1993, Switzer & Grether 2000). It could be possible that other insects in



FIG. 2: A *H. erato hydara*–*H. erato petiverana* hybrid roosting between two *H. erato petiverana* butterflies. The hybrid lacks the large yellow hindwing band.

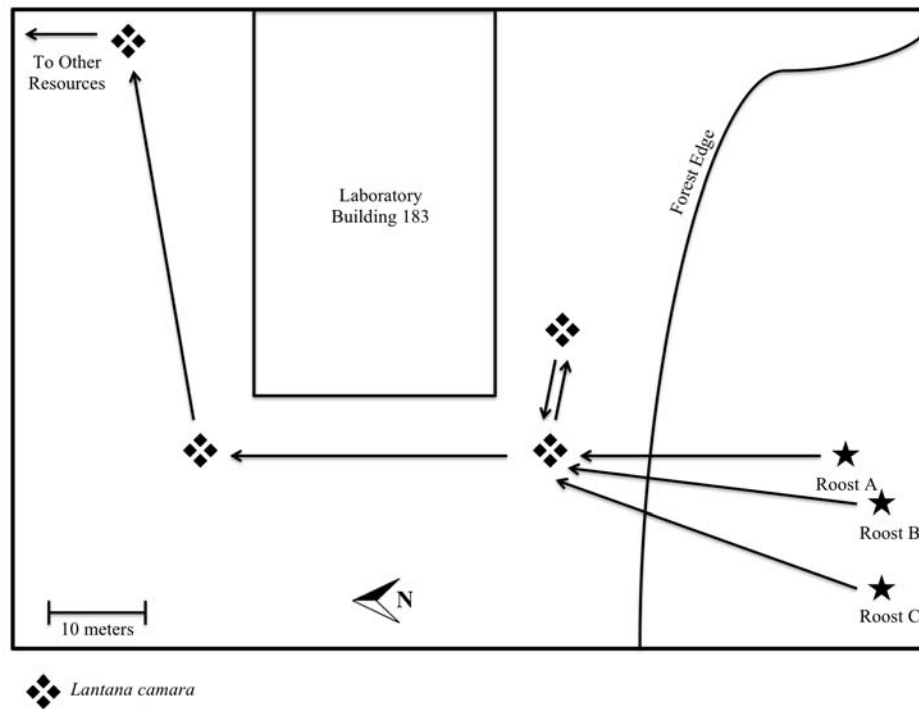


FIG. 3: Map of butterfly traplines from three neighboring roosts (A, B, C). Traplines are indicated by arrows and scaled according to distance measurements based on a Garmin GPS system. Traplines were reversed by butterflies upon return to the roosts in the afternoon. GPS coordinates for site: 9° 06' 58.26" N, 79° 41' 54.24" W.

in addition to *Heliconius* join the roosts as a strategy to avoid predation since *Heliconius* roosts are aposematic (Gamberale & Tullberg 1998, Finkbeiner et al. 2012). This possible commensalism should be investigated further since very little is known about the potential existence of “cheater” animals in aposematic aggregations. It is important to note that non-co-mimic *Heliconius* species have been seen roosting together (Mallet & Gilbert 1995, E. I. Deinert, pers. comm.) and *H. hecale* and *Mechanitis* species have been observed in *H. erato* roosts but with irregular attendance (pers. obs.), however these butterflies are chemically defended whereas dragonflies typically are not.

There appears to be no difference in roost sex ratio, suggesting the benefits of roosting have no relationship to mating, unlike other gregarious and roosting animals where this behavior may play a role in mate finding (Parrish & Edelstein-Keshet 1999, Blanco & Tella 2009, Bijleveld et al. 2010). The idea that *Heliconius* roosting behavior and mating behavior are un-related is further supported by my single mating observation where a non-established roost member was brought to the roost in copulation, but was never recruited later to the roost.

The fact that all observed roosting females were already mated indicates the females are unlikely to mate again (Gilbert 1976) so males would have no benefit from using roosts to locate mates. The only observed sex-related difference was that males depart roosts earlier than females in the morning. These early departures by males may be related to patrolling for unmated females or female pupae (Deinert et al. 1994, Estrada et al. 2010), although further work would be required to confirm this. In *Heliconius sara*, only females arrive to the roost with large pollen loads that are digested overnight which could affect early roost departure due to metabolic constraints (Salcedo 2010b), however in *H. erato* most individuals (both male and female) arrived to the roost in the afternoon without a pollen load. Thermoregulatory ability could also be an important factor determining which individuals are able to depart the roost first (Clench 1966), but this may not be as necessary in tropical climates as it is temperate climates. In other butterflies, males are able to fly at lower body temperatures (Gilchrist 1990), and smaller individuals (in particular males) have a heightened rate of heat exchange suggesting they would have greater control

over heat gain while basking (Kemp & Krockenberger 2004). In *H. erato*, males are sometimes slightly smaller than females so it is possible thermoregulation is associated with roost departure trends in this species.

Individuals prefer specific perch sites. I observed that older butterflies tend to prefer the same perch within the same roost every evening, thus implying individual butterflies are capable of remembering specific roosting locations. Such a precise spatial preference may be gained over time as a result of repeated visits to the roost (Salcedo 2006). There is little evidence that *Heliconius* use pheromones or scent-marking to locate their perches in the roost (Jones 1930, Mallet 1986a, Salcedo 2010a), and perch preference is likely based on memory and visual cues.

Roost members share resources. That butterflies from neighboring roosts share the same traplines strongly suggests following behavior occurs regularly in butterflies between flowering plants. Following between resources by *Heliconius* has been noted by Waller & Gilbert (1982) and Pinheiro (2009). There is no evidence that butterflies use the roosts as information-sharing centers (Mallet 1986a, Finkbeiner et al. 2012) in which individuals would learn the locations of foraging sites by following roost-mates during morning departures. The butterflies could, however, have the same traplines based on coincidence, but there were other flowering resources in the area and not all resources in the trapline were visible from one another, nor were any resources visible from either of the roosts. These results are consistent with Waller & Gilbert's (1982) findings that roosting *Heliconius charithonia* butterflies generally use the same pollen plants that are within close proximity to their roost. On the contrary, it is important to note that Mallet (1986a) observed that roosting *H. erato* butterflies have a predictable tendency to visit different flowers.

These results improve our understanding of communal roost dynamics in *Heliconius*. I conclude that age is strongly associated with roost recruitment and perch preference within a roost, suggesting young butterflies join roosts more willingly than older butterflies, while older butterflies have more precise roosting preferences. Earlier male departure from roosts could indicate either that females require more time at roosts in the morning before foraging, possibly due to thermoregulatory or metabolic constraints, or that males prefer an early start on searching for resources. These findings suggest that communal roosting behavior in *Heliconius* butterflies is somewhat unusual for insects since such trends are typically seen in roosting vertebrates rather than in gregarious insects.

ACKNOWLEDGEMENTS

Many thanks to Robert Reed for project guidance and manuscript suggestions; Kailen Mooney, Nancy Burley, Owen McMillan, James Mallet, Larry Gilbert, and Santiago Meneses for advice and comments on project design; Jasmine Velez and Talia Gustafson for field assistance; Adriana Briscoe, Kyle McCulloch, Aide Macias Muñoz, Arnaud Martin, Christian Salcedo, and an anonymous reviewer for manuscript feedback; The Smithsonian Tropical Research Institute (STRI) for use of field sites; La Autoridad Nacional del Ambiente (ANAM) for research permit approval; and my funding sources: Smithsonian Tropical Research Institute, the U.S. Department of Education GAANN; this material is based upon work supported by the National Science Foundation (NSF) Graduate Research Fellowship under Award No. DGE-0808392.

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Submitted for publication 15 March 2013; revised and accepted 16 August 2013.

ADDITIONAL NOTES ON THE HIMALAYAN GENUS *AULOCERA* BUTLER
(NYMPHALIDAE : SATYRINAE)

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ABSTRACT. All the four species i.e., *brahminus* Blanchard, *saraswati* Kollar, *padma* Kollar and *swaha* Kollar referable to the Himalayan genus *Aulocera* Butler have been re-examined. The structures of the male and female genitalia have been interpreted along with previously known characters. In spite of minor variation in the valva of the male genitalia of *saraswati* Kollar, all the four species are broadly congeneric and form a natural group in the Himalayan region.

Additional key words: Genitalia, brachia, angular appendices, signa, genital plate.

During the course of surveys undertaken in an ICAR (Indian Council of Agricultural Research) project, four species i.e., *Aulocera brahminus* (Blanchard), *A. saraswati* (Kollar), *A. padma* (Kollar) and *A. swaha* (Kollar) were collected from certain localities in Dhauladhar Range, Pir Panjal range, Greater Himalaya, and Shiwalik foot Hills. These localities fall within an altitudinal range varying from 1363 m to 2929 m. Based upon examination of various morphological characters, particularly the genitalia, it has been established that *Aulocera* Butler is a natural group, having its distribution only in the Himalayan region. Evans (1932), Talbot (1947) and Mani (1986) have given interspecific keys, but none has used the genitalic characters, which are otherwise quite consistent in different biological species. Accordingly, besides an updated key, an illustrated account of the genitalia and new distributional localities are presented here.

Key to species
Aulocera Butler

Common name: The Banded Satyrus

Aulocera Butler, 1867, Ent. mon. Mag. I 4 :121. Type –species by selection by Butler (Feb. 1868, Ent. mon. Mag. 4: 194) : *Satyryrus brahminus* Blanchard [1844], in Jacquemont, Voy. Inde 4 (Zool) : 22.

Type-species : *Satyryrus brahminus* Blanchard

1. Forewing upperside with band distinct.....2
- 1a. Forewing upperside with band indistinct.....3
2. Upperside dark brown, forewing upperside with white spot on inner side of subapical black spot present in male, band on forewing either bright yellow or white, hindwing upperside band enters cell; male genitalia with brachia arm like; female genitalia with central process of lamella antevaginalis bilobed.....*swaha* Kollar
- 2a. Upperside blackish, white spot on inner side of subapical black

spot on forewing upperside missing in male, band pure white, hindwing upperside band does not enter cell; male genitalia with brachia small, thumb-like; female genitalia with central process of lamella antevaginalis oval, posteriorly notched.....*padma* Kollar

3. Forewing upperside with white spots well separated and small, hindwing upperside band narrow, underside bronzy-brown with white striations; male genitalia with uncus long, slightly curved at distal end; female genitalia with central process of lamella antevaginalis long with trilobed distal end, signa smaller.....*brahminus* Blanchard
- 3a. Forewing upperside with white spots larger and narrowly spaced, hindwing upperside band broad, below very pale with numerous greyish-white striae; male genitalia with uncus very long, curved ventrally; female genitalia with central process of lamella antevaginalis reduced, deeply notched posteriorly, signa longer..... *saraswati* Kollar

Genitalic Descriptions

Aulocera swaha (Kollar)

Common name: The Common Satyr

Kollar, 1844, in Hugel's Kashmir 4(2): 444 (*Satyryrus*)

Male genitalia (Figs. 1–5). Uncus long, smaller than tegumen, more or less straight, distal end blunt, studded with small setae dorsally at proximal end; brachia arm-like, strongly sclerotized, twisted upwards, distal end dentate; tegumen broad dorsally, narrower ventrally, uniformly sclerotized; appendices angulares tooth-like with blunt distal end; vinculum almost equal in length to tegumen, slightly curved inwards, uniform in breadth except near saccus; saccus short, broad proximally, narrow distally; valva long, much broader in the middle than at both the ends, pilose, costa produced into a spine-like costal process, sacculus with ridge distally, sparsely setosed proximally and densely setosed distally, ampulla digitate distally and with wavy margin proximally, harpe cone-like with pointed distal end; juxta v-shaped; aedeagus long, tubular, suprazone

longer than subzone, coecum rounded in dorsal view, ductus ejaculatorius entering dorsally near proximal end.

Female genitalia (Fig. 6). Corpus bursae oblong, membranous; signa crescent-shaped, quite apart, lying longitudinally, moderately long, scobinate patches; ductus bursae less than corpus bursae, moderately sclerotized; ductus seminalis originate from ductus bursae near anterior end; central process of lamella antevaginalis bilobed, lateral lobes elongated, somewhat triangular plate present below central process; lamella postvaginalis with two ellipsoidal plates; apophysis anterioris wanting; apophysis posterioris moderately long, narrow, membranous; papilla analis oblong, pilose.

Length of forewing: Male: 28.0–34.0 mm (n = 30); Female: 30.0–36.0 mm (n = 26).

Material examined. Himachal Pradesh: 8♂, 9♀, 7.ix.1992, Narkanda, Shimla; 1♂, 18.ix.1991, Shimla; 9♂, 4♀, 17.ix.1992, Sangla, Kinnaur; 2♂, 3♀, 19.ix.1992, Kalpa, Kinnaur; 2♂, 5♀, 16.ix.1992, Nichar, Kinnaur; 2♂, 19.ix.1992, Bhabhanagar, Kinnaur; 2♂, 1♀, 13.ix.1992, Chowai, Kullu; 1♂, 25.ix.1994, Kalatop, Dalhousie. Jammu & Kashmir: 2♂, 4♀, 28.vii.1994, Patni Top; 1♂, 29.vii.1994, Kud, Patni Top.

Remarks: *Aulocera swaha* (Kollar), “as represented by its nominotype,” is quite common and extends throughout the length of the Himalaya and ascends almost to 3000 m (Marshall and de Niceville, 1883; Mani, 1986; Smith, 1993). As will be evident “from the above,” during the course of present studies a large, representative sample comprising fifty-six individuals (30♂, 26♀) was examined. Specimens were collected from localities falling within an altitudinal range varying between 1624 m and 2708 m. All specimens possess a conspicuous white discal band on both fore and hindwings except the forewing in 4–5 individuals among eight collected from Patnitop (2060 m) in the North Himalaya. According to Marshall and de Niceville (1883) ‘typical specimens of this variety are very distinct but gradations in tone of yellow tint are so gradual in intermediate localities that it is impossible to draw actual line of separation’. Fruhstorfer (1911) has referred to specimens with forewing bright yellow as garuna (different from the nominotype). This practice has also been followed by Evans (1932) and Talbot (1947), with a note that the habitat of this subspecies lies in the inner ranges from Kashmir to Kullu. However, in present surveys both types (white banded and yellow banded) have been collected from the same locality (Patni Top) in the northwestern Himalaya. Therefore, the naming of these two populations as different subspecies “appears to be unjustified.” In fact, this is simply a population variation because conspecificity of different individuals has been

confirmed through the examination of their male and female genitalia which form a precise lock and key arrangement (consistent character). With regard to sexual dimorphism, the brand is always present in the male of this species (not usually very obscure, Marshall and de Niceville, 1883), and is devoid of androconia. The androconia are always present in the remaining three species: *A. brahminus* Blanchard, *A. saraswati* Kollar and *A. padma* Kollar, presently studied. Evans (1932) and Talbot (1947) have separated this species on the basis of maculation of upper hindwing surfaces, in which the band narrows distinctly toward the inner margin and does not reach it except rarely in the females. It may be mentioned that this exception is also seen in two males where this band reaches the inner margin. The present study thus shows that this variable character should not be used as a key character, as it was applied by the above two workers.

Aulocera padma (Kollar)

Common name: The Great Satyr

Kollar, 1844, in Hugel's Kashmir 4(2): 445 (*Satyrus*)

Male genitalia (Figs. 7–11). Uncus beak-like, shorter than tegumen, beset with small setae on dorsal surface; brachia short, thumb-like, strongly sclerotized with dentate distal margin; tegumen broad dorsally, laterally compressed, narrow ventrally; appendices angulares reduced with distal margin straight; vinculum tapers from distal end to proximal end, longer than tegumen; uniformly sclerotized; saccus short, broad proximally, narrow and rounded apically; valva moderately long, pilose, broad in middle, costa produced into a straight, thin, strongly sclerotized, finger-like process, sacculus long, slightly curved dorsally, sparsely setosed, harpe digitate; juxta a rectangular plate, weakly sclerotized; aedeagus long, broader at distal end, subzone smaller, five pairs of small spines in the suprazone, coecum rounded, ductus entering dorsad.

Female genitalia (Fig. 12). Corpus bursae divided by a constriction into anterior small rounded structure and posterior large globular; signa quite apart, moderately long, lying in the posterior globular part, scobinate patches present; ductus bursae moderately long, curved in the middle, tapers towards posterior end; ductus seminalis enters into ductus bursae near corpus bursae; lamella antevaginalis with oval, posteriorly notched central process, lateral lobes leaf-like, below central process lies triangular plate; lamella postvaginalis wanting; apophysis anterioris missing; apophysis posterioris moderately long, narrow; papilla analis elliptical, fringed with setae.

Length of forewing: Male: 38.0–40.0 mm (n = 22); Female: 42.0 mm (n = 2).

Material examined. Himachal Pradesh: 8♂, 15.vi.1992, Chail, Shimla; 5♂, 13.vi.1996, Narkanda, Shimla; 2♂, 26.vi.1996, Dikadhar, Narkanda, Shimla; 2♂, 13.vi.1996, Kandyali, Narkanda, Shimla; 3♂, 1♀, 11.vi.1996, Phalgu, Narkanda, Shimla; 1♂, 14.vi.1996, Taklech, Rampur, Shimla; 1♀, 3.x.1993, Larji, Kullu; 1♂, 25.vii.1992, Rajgarh, Sirmaur.

Remarks: Out of all the four species, *A. padma* Kollar is the largest in the genus *Aulocera* Butler. The nominotype *A. padma padma* Kollar has been collected at an elevation ranging from 1408 m to 2708 m. The male population is much more abundant as compared to the female population (22♂, 2♀), and this record goes in accordance to Marshall and de Niceville (1883). The two females, one collected from Larji (Kullu) and the other from Phalgu (Shimla) show variations in the white-discal band on the upperside of the hindwings. The band is broad and scattered in the specimen collected from Larji and narrower in the other. However, the individuals were found conspecific on genitalic basis. The species *A. padma*, according to Evans (1932) and Talbot (1947) have eight subspecies i.e., *A. p. padma* Kollar, *A. p. burnetti* Evans, *A. p. grandis* Tytler, *A. p. loha* Dohery, *A. p. chumbica* Moore, *A. p. fulva* Evans, *A. p. japura* Tytler and *A. p. thawgawa* Tytler, of these *A. p. loha* has been upgraded to the level of full-fledged species by Smith (1993), who collected it from Nepal.

Aulocera brahminus (Blanchard)

Common name: The Narrow-Banded Satyr

Blanchard, 1844, In Jacquemont, Voy. Inde 4(Zool) : 22 (*Satyris*).

Male genitalia (Figs. 13–17). Uncus long, almost straight except slightly curved at distal end, sparsely setosed dorsally at base, shorter than tegumen; brachia small, less than half the length of uncus, slightly curved dorsally, narrow at base, broad distally; tegumen laterally compressed, dorsally narrow, strongly sclerotized; appendices angulares with conical distal end, broad at base; vinculum more than double the length of tegumen, strap-like, broader near saccus; saccus foot-like with rounded and narrow distal end; valva elongated, pilose, costa with elongated costal process, broad at base, sacculus with distal end rounded and fringed with short setae, ampulla and harpe well separated by deep groove, ampulla thumb-like with serrated distal end, harpe knife-like, studded with setae of equal size; juxta U-shaped; aedeagus longer, tubular, subzone smaller, distal end twisted upwards in lateral view, suprazone with six pairs of small spines, coecum rounded, ductus entering dorsad.

Female genitalia (Fig. 18). Corpus bursae elongated; signa comprising two, moderately long, parallel patches, situated in the middle, approximated, studded with minute teeth; ductus bursae smaller than corpus bursae, broader posteriorly, narrow towards corpus bursae; ductus seminalis entering ductus bursae near corpus bursae; lamella antevaginalis with central process well developed, posterior end with three lobes, lateral lobe with large, triangular plates, a rectangular, strongly sclerotized plate lies below central process; lamella postvaginalis wanting; apophysis anterioris missing; apophysis posterioris moderately long, spine-like, membranous, papilla analis oblong, fringed with setae.

Length of forewing: Male: 30.0–32.0 mm (n = 4); Female: 30.0 mm (n = 1).

Material examined. Himachal Pradesh: 4♂, 1♀, Dracha, Keylong, Lahoul and Spiti.

Remarks: Besides the nominotype, *Aulocera brahminus* (Blanchard) is represented by two subspecies: *A. b. dokwana* Evans extending from the Garhwal to Nepal Himalaya and *A. b. brahminoides* Moore in the East Himalaya. The range of the nominotype extends from Kashmir to Mossoorie/North-West to the Garhwal Himalaya (Evans, 1932; Talbot, 1947; Mani, 1986). Specifically speaking *Aulocera brahminus brahminus* (Blanchard) (= *scylla* Butler : *werang* Lang) has been reported from Kashmir (Goolmurg, now spelled as Gulmarg), Kullu, Koksar (Chandra Bhaga river), Keylong, Mandi and Pangi (Sach Pass) in the North-West Himalaya from 2121 m to 3939 m (Marshall and de Niceville, 1883). The species could not be collected from its old localities. The species has been collected from a new locality, Darcha (3400 m) which is about 32 Kms. ahead of Keylong in Lahoul. The inclusion of this species in Schedule II (Part II) of the Wildlife (Protection) Act, 1972 is supported on the basis of surveys. The steps need to be taken for its conservation, especially in Dracha and surrounding areas.

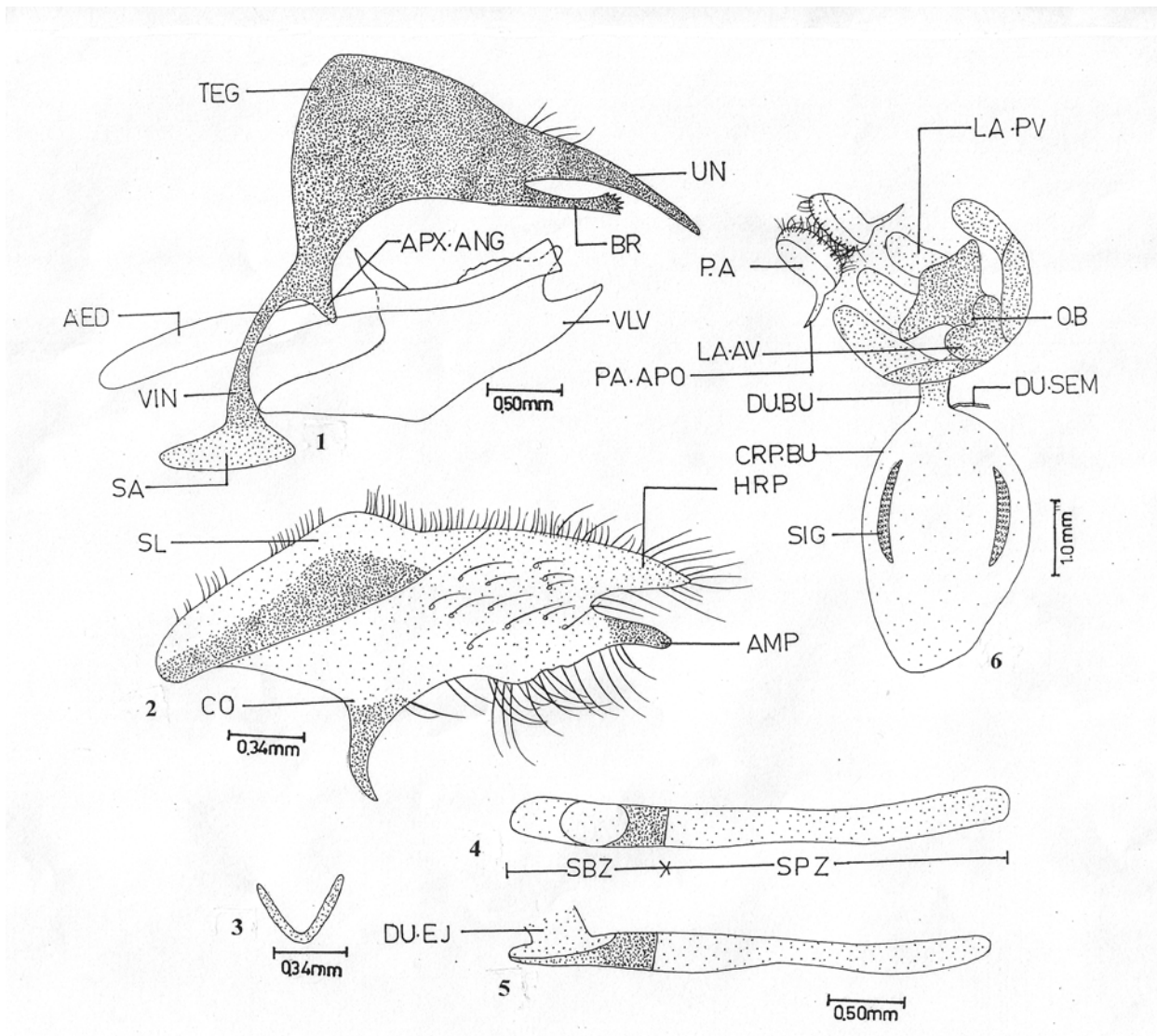
Two subspecific names i.e., *A. b. werang* Lang (Collected at Werang Pass, 3636 m, Lahoul; Patseo, 3333 m, Lahoul; Sach Pass 3939 m, Pangi; Goolmurg, 2727 m, Kashmir) and *A. b. scylla* Butler from Sylhet have already been considered as synonyms by Evans (1932).

Aulocera saraswati (Kollar)

Common name: The Striated Satyr

Kollar, 1844, in Hugel's Kashmir 4(2): 445 (*Satyris*)

Male genitalia (Figs. 19–24). Uncus long, proximal half broader, distal half narrower, curved ventrally, setae



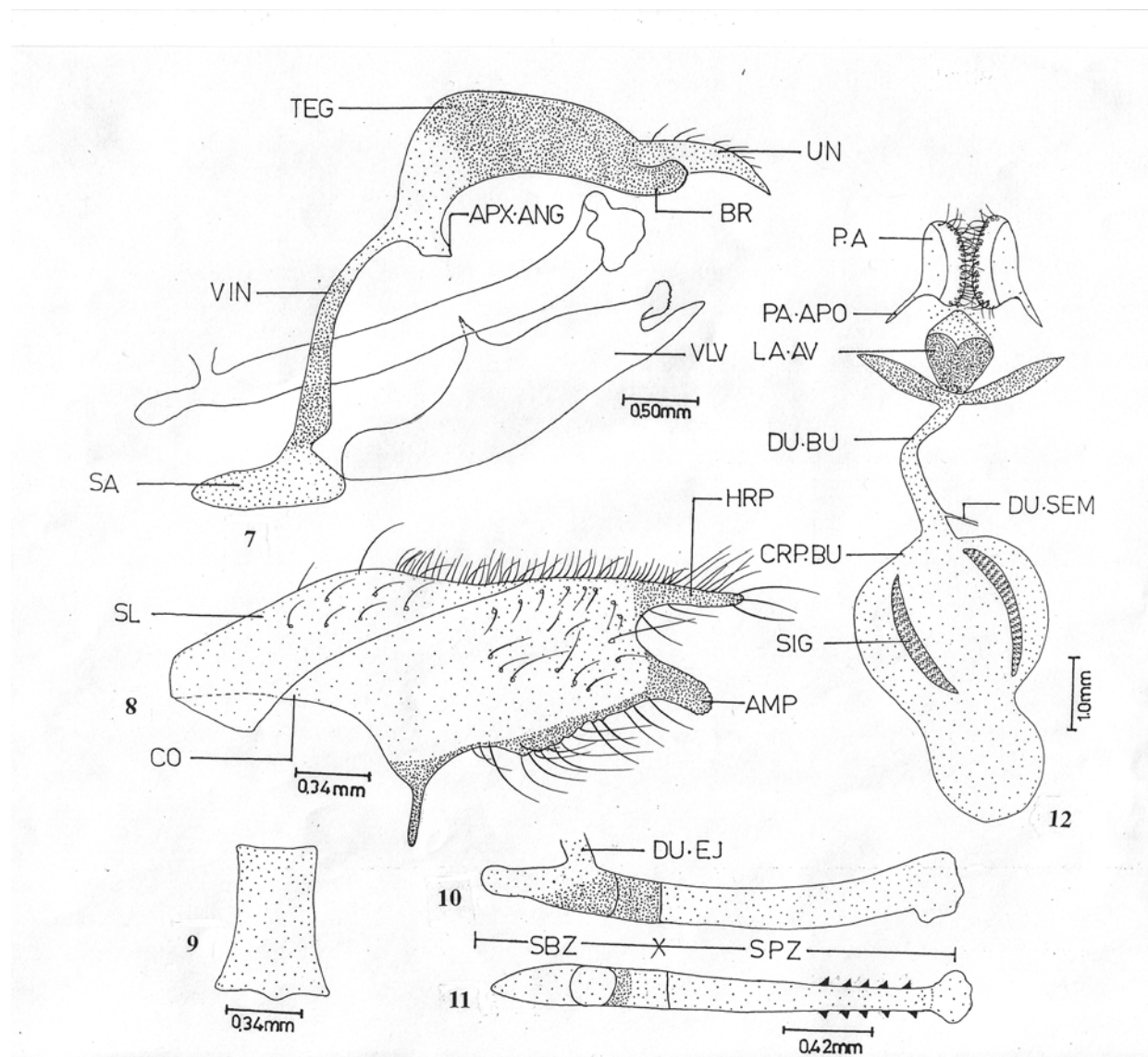
FIGS. 1–6. *Aulocera swaha* (Kollar): 1. Male genitalia (lateral view), 2. Valva (inner view), 3. Juxta, 4. Aedeagus (dorsal view), 5. Aedeagus (lateral view), 6. Female genitalia (Ventral view).

Abbreviations used in figures are: AED: Aedeagus, AMP: Ampulla, APX.ANG: Appendix angularis, BR: Brachium, CO: Costa, CRP.BU: Corpus bursae, DU.BU: Ductus bursae, DU.EJ.: Ductus ejaculatorius, DU.SEM: Ductus seminalis, HRP: Harpe, LA.AV: Lamella antevaginalis, LA.PV.: Lamella postvaginalis O.B.: Ostium Bursae, P.A.: Papilla analis, PA.APO: Apophysis posterioris, SA: Saccus, SBZ: Subzonal portion of aedeagus, SIG: Signum, SL: Sacculus, SPZ: Suprazonal portion of aedeagus, TEG: Tegumen, UN: Uncus, VIN: Vinculum, VLV: Valva.

absent; brachia slender, half the length of uncus, strongly sclerotized, distal end dentate; tegumen shorter than uncus, broad, hump-shaped, moderately sclerotized; appendices angulares small, spine-like, uniformly sclerotized; vinculum shorter than tegumen, uniform in breadth; saccus short, thumb-like, moderately sclerotized; valva moderately long, broad, pilose, costal process well developed, spine-like, sacculus slightly curved dorsally, setosed distally,

ampulla and harpe (Sibatani et.al, 1954) not properly developed, ampulla with distal end knob-like, well-sclerotized, harpe-stumpy, densely setosed; juxta oblong; aedeagus with distal half broader, subzone smaller, tubular, coecum with almost conical margin, ductus ejaculatorius entering dorsad.

Female genitalia (Fig. 25). Corpus bursae globular, membranous; signa moderately long, broader at middle than at ends, parallel, longitudinal patches beset with



FIGS. 7–12. *Aulocera padma* (Kollar): 7. Male genitalia (lateral view), 8. Valva (inner view), 9. Juxta, 10. Aedeagus (lateral view), 11. Aedeagus (dorsal view), 12. Female genitalia (Ventral view).

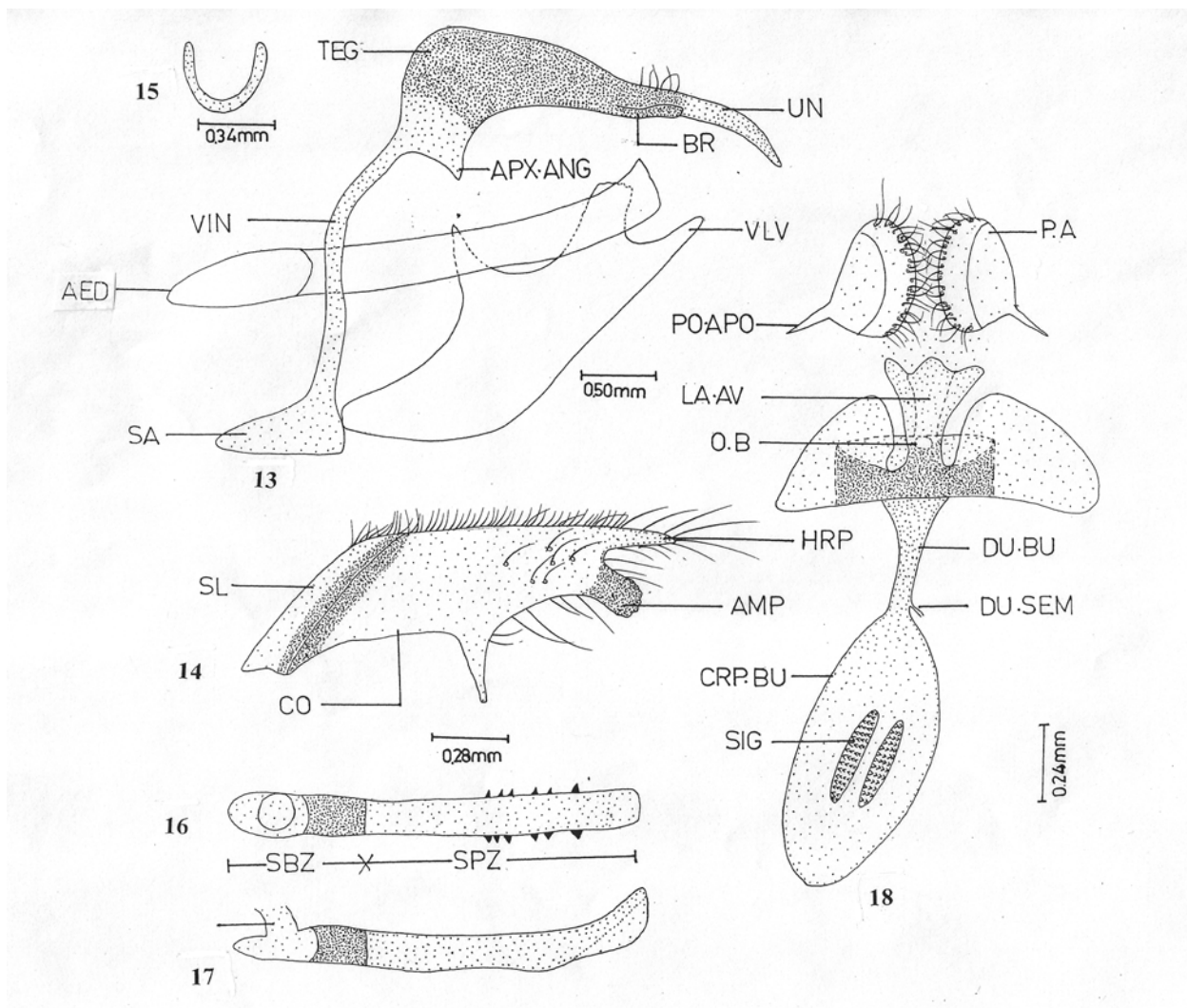
Abbreviations used in figures are: AED: Aedeagus, AMP: Ampulla, APX.ANG: Appendix angularis, BR: Brachium, CO: Costa, CRP.BU: Corpus bursae, DU.BU: Ductus bursae, DU.EJ.: Ductus ejaculatorius, DU.SEM: Ductus seminalis, HRP: Harpe, LA.AV: Lamella antevaginalis, LA.PV.: Lamella postvaginalis O.B.: Ostium Bursae, P.A.: Papilla analis, PO.APO: Apophysis posterioris, SA: Saccus, SBZ: Subzonal portion of aedeagus, SIG: Signum, SL: Sacculus, SPZ: Suprazonal portion of aedeagus, TEG: Tegumen, UN: Uncus, VIN: Vinculum, VLV: Valva.

minute teeth; ductus bursae short, membranous, broader anteriorly, narrow posteriorly; ductus seminalis entering ductus bursae near corpus bursae; central process of lamella antevaginalis deeply notched posteriorly into two small, slightly notched lobes distally, surrounded by a elliptical plate, below central process lies a finger-like projection; lamella-postvaginalis with two, parallel, elongated plates; apophysis anterioris missing; apophysis posterioris moderately long,

membranous, slightly curved; papilla analis oval, pilose.
Length of forewing: Male: 30.0–33.0 mm (n = 4); Female: 32.0–40.0 mm (n = 9).

Material examined. Himachal Pradesh: 1♀, 19.ix.1991, Shimla; 3♂, 5♀, 8.ix.1992, Kumarsain, Shimla; 1♀, 11.ix.1992, Duttanagar, Rampur, Shimla; 1♀, 12.ix.1992, Taklech, Rampur, Shimla; 1♂, 17.ix.1992, Sangla, Kinnaur; 1♀, 13.ix.1992, Chowai, Kullu.

Remarks: *Aulocera saraswati* (Kollar), a Himalayan species (Marshall and de Niceville, 1883; Wynter-Blyth, 1957) has been recorded from certain localities from



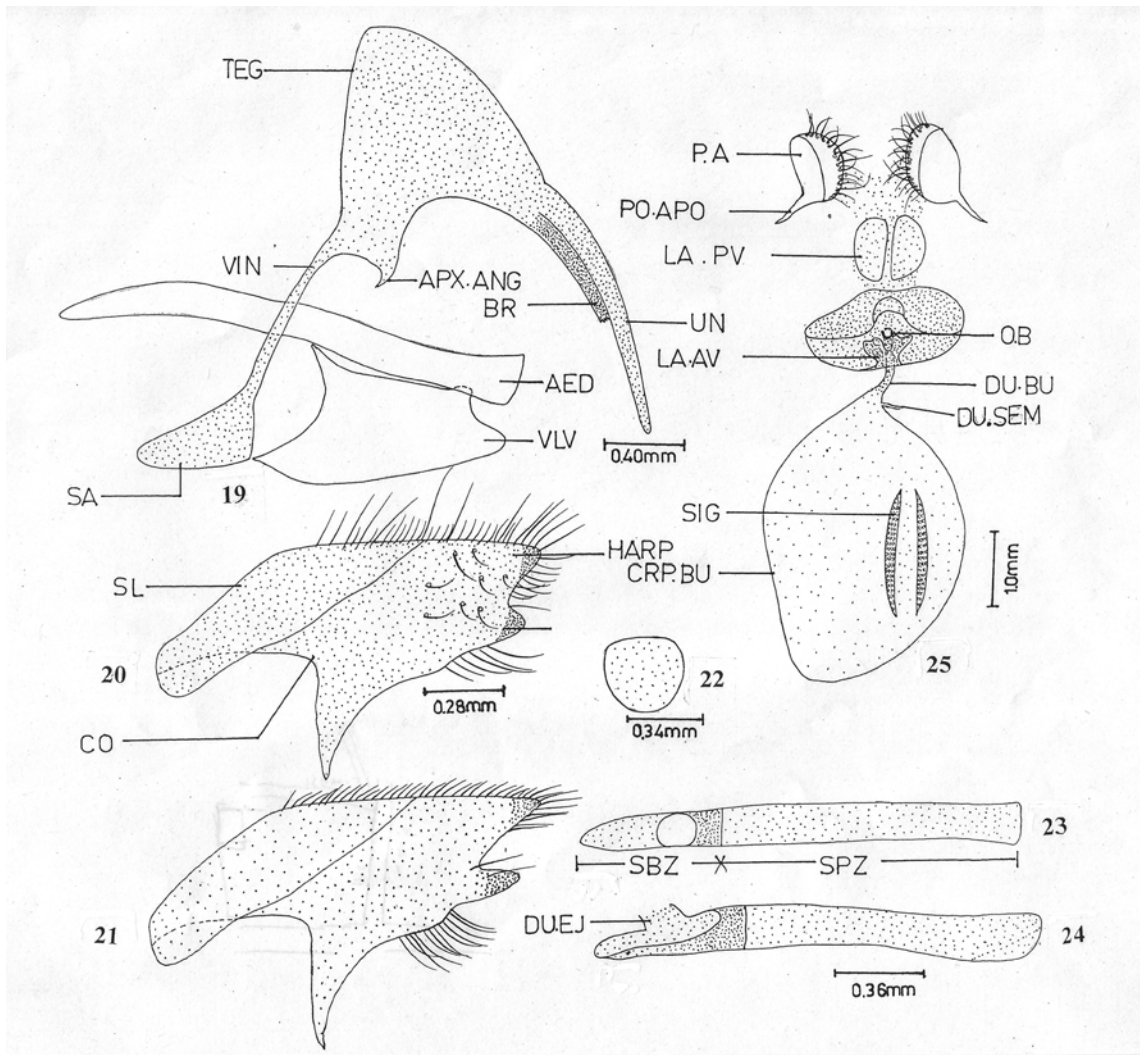
FIGS. 13-18. *Aulocera brahminus* (Blanchard): **13.** Male genitalia (lateral view), **14.** Valva (inner view), **15.** Juxta, **16.** Aedeagus (dorsal view), **17.** Aedeagus (lateral view), **18.** Female genitalia (Ventral view).

Abbreviations used in figures are: AED: Aedeagus, AMP: Ampulla, APX.ANG: Appendix angularis, BR: Brachium, CO: Costa, CRP.BU: Corpus bursae, DU.BU: Ductus bursae, DU.EJ.: Ductus ejaculatorius, DU.SEM: Ductus seminalis, HRP: Harpe, LA.AV: Lamella antevaginalis, LA.PV.: Lamella postvaginalis O.B.: Ostium Bursae, P.A.: Papilla analis, PO.APO: Apophysis posterioris, SA: Saccus, SBZ: Subzonal portion of aedeagus, SIG: Signum, SL: Sacculus, SPZ: Suprazonal portion of aedeagus, TEG: Tegumen, UN: Uncus, VIN: Vinculum, VLV: Valva.

Kashmir to Nepal (Bingham, 1905), Chitral to Sikkim (Evans, 1932; Talbot, 1947) and Nepal (Smith, 1993) by the respective workers. In spite of repeated intensive and extensive surveys, no topotype could be collected from Mussoorie in the month of June between 1992 to 1996, although it had been described as being quite common there by Mackinnon and de Niceville (1897). However, the species has been collected from some new localities such as Sangla (2680 m), Taklech (1600 m), Kumarsain (1485 m), Chowai (1800 m) and Rampur (924 m) although it could not be collected from its old

localities such as Shimla, Pangi, Kullu, Mussoorie or Kumaon. The collection data point out the shifting of the species to new breeding grounds, perhaps due to varied changes in the old localities.

Moreover, four males (three from Kumarsain and one from Sangla) vary from each other in respect of a white subapical speck on the innerside of black subapical ocellus on the upperside of the forewing (present in two males, absent in one male, developed in one male from Kumarsain). In view of these variations, all these males were dissected and found conspecific, excepting the one



FIGS. 19-25. *Aulocera saraswati* (Kollar): **19.** Male genitalia (lateral view), **20-21.** Valvae (inner view), **22.** Juxta, **23.** Aedeagus (dorsal view), **24.** Aedeagus (lateral view), **25.** Female genitalia (Ventral view).

Abbreviations used in figures are: AED: Aedeagus, AMP: Ampulla, APX.ANG: Appendix angularis, BR: Brachium, CO: Costa, CRP.BU: Corpus bursae, DU.BU: Ductus bursae, DU.EJ.: Ductus ejaculatorius, DU.SEM: Ductus seminalis, HRP: Harpe, LA.AV: Lamella antevaginalis, LA.PV: Lamella postvaginalis, O.B.: Ostium Bursae, P.A.: Papilla analis, PO.APO: Apophysis posterioris, SA: Saccus, SBZ: Subzonal portion of aedeagus, SIG: Signum, SL: Sacculus, SPZ: Suprazonal portion of aedeagus, TEG: Tegumen, UN: Uncus, VIN: Vinculum, VLV: Valva.

collected from Kumarsain, which shows some variation in the structure of the distal portion of the valva (Fig. 21). Goulson (1993), who studied such variations in the male genitalia of *Maniola jurtina* Linnaeus, has stated that they have no function to perform during copulation, and therefore appear to be a non-functional part of the valva. This characteristic has also been pointed out in another satyrid taxa (*Erebia* Dalman) by Lorkovic (1957). Rose and Sidhu (1996) have also discussed variations in the male genitalia of the type-species *Aricia agestis* (Denis and Schiffermuller). In

order to further confirm conspecificity of the variable males, their androconia have been examined. These are moderately long, with bottle-shaped bases, and their apical portion is very slender. Four females out of seven showing variations in the band on both the sides of the hindwing (three females with upperside band not in line, two females with band interrupted near the lower angle of cell on the underside) have been dissected and found to be conspecific. The ostial region in the female genitalia is also highly modified in this species.

Discussion: The present study re-establishes that the

genus *Aulocera* is represented by the above-mentioned four species and not by seven species as indicated by Marshall and de Niceville (1883) and Bingham (1905). Besides other morphological characters, Talbot (1947) specifically made an attempt to characterize this genus on the basis of the uncus in the male genitalia but failed to fully appreciate various genitalic characters, for example characterizing the brachia as “hooks” by him. Hemming (1967) has affirmed that *A. brahminus* Blanchard is the type-species of the genus, not *circe* (Fabricius). In view of the above, the present authors have examined both the external male and female genitalia of all four species. Evaluation of taxonomic characters shows that structures such as a slightly curved uncus and brachia are always present with variable length. There is a well pronounced gap between the tegumen and the uncus. The valvae are not only consistent in *A. saraswati* Kollar, *A. padma* Kollar, *A. swaha* Kollar but also conform to these structures in *A. brahminus brahminus* Blanchard, the type-species of the genus. The congeneric status of these species is also supported by the female genitalia because of the structures such as paired signa, small ductus bursae, complex genital plate and papillae anales. Maculation, wing-venation and genitalic structures all support the contention that *Aulocera* is a natural group having its distribution only in Himalayan localities. It also seems appropriate to mention here that Smith (1993) has considered *loha* Doherty as a full-fledged species rather than a subspecies of *padma* (Evans, 1932; Talbot, 1947).

ACKNOWLEDGEMENTS

The first author is thankful to Director, Dr. K. Venkataraman, Zoological Survey of India, Kolkata for all sorts of facilities and

encouragement. The authors are grateful to the Indian Council of Agricultural Research, New Delhi for funding.

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Submitted for publication 6 February 2013; revised and accepted 8 April 2013.

DEFINING *CLEPSIS PENETRALIS* RAZOWSKI (TORTRICIDAE) USING MORPHOLOGY AND MOLECULES: A WIDESPREAD BUT OVERLOOKED NORTH AMERICAN SPECIES

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ABSTRACT. The taxonomic status of *Clepsis penetralis* has remained enigmatic since its description in 1979. Using specimens collected or borrowed from across the U.S.A., we examined genitalic and wing characters as well as mitochondrial DNA sequence in order to distinguish *C. penetralis* from the similar congener *C. peritana*. The genomic integrity of the two species was strongly supported, and the mtDNA sequence data further suggest a potential additional new species from California. Examinations of collections across the country indicate that *C. penetralis* is a widespread species that has been widely overlooked.

Additional key words: Tortricinae, Archipini, Cytochrome Oxidase Subunit I (COI), mtDNA, systematics

In his comprehensive taxonomic revision of the genus *Clepsis* (Guenée), Razowski (1979) described *C. penetralis* from three localities in Utah. The status of this species has remained uncertain because the characters that best define it were lost from the only available female specimen, and because Razowski's illustration of them is unverifiable. He assigned *C. penetralis* to his Subgroup 1, which is defined primarily by having a "normally" developed ductus bursae (i.e. not spiralled and without a cestum).

Razowski compared the new species with *C. smicrotes* (Wlsm.), which was described from Guerrero, Mexico, but *C. penetralis* phenotypically more closely resembles the sympatric, widespread *C. peritana* (Clemens). The latter is a member of Razowski's Subgroup 2, species having a tightly coiled ductus bursae with a weakly sclerotized cestum along its length (Powell 1964, fig. 104; Razowski 1979, figs. 77–90). The female of *C. penetralis* illustrated by Razowski has the ductus bursae simple and uncoiled, lacking a cestum, and the corpus bursae lacking a signum.

A third species, *C. virescana* (Clemens), which is broadly sympatric in North America, is similar in forewing pattern but differs from the other two in possession of a costal fold in the male and by possession of an elongate, sclerotized antrum and well developed signum in the female (Powell 1964, fig. 100).

Razowski (1979) cited four males of *Clepsis penetralis*: the holotype from Logan, Cache Co., and three paratypes from Hooper, Weber Co. (for which four dates are listed), and one female from Johnson Pass, west of Clover, Tooele Co. Hence, association of

the sexes was equivocal. Unfortunately, the slide containing the female dissection has only the external sclerotized structures and a damaged abdominal pelt; examination under high magnification reveals no trace of the bursa copulatrix. As a result, the accuracy of the illustration cannot be verified, and we have been unable to locate another specimen possessing the peculiar combination of characters: forewing pattern with the dark markings and ground color resembling *C. peritana*, and the ductus bursae simple, gradually enlarged distally, resembling that of *C. virescana* but without the elongate antrum of that species.

In 1992 JAP obtained additional specimens that match the holotype of *C. penetralis* from Garfield Co. in southern Utah. Males and females are similar in forewing size, breadth, and color pattern, and this series has enabled definitive recognition of the species.

MATERIALS AND METHODS

Specimens. The specimens used in this study were provided by collaborators or were collected by the authors. The two outgroups were selected from related Archipine genera. Outgroup taxa from related genera were used from previously published work: *Argyrotaenia niscana* Kearfott from Santa Barbara County, CA (Landry et al. 1999); and *Choristoneura rosaceana* Harris from Ste. Agathe, Quebec (Sperling & Hickey 1994). Outgroups were chosen on the basis of presumed distant relationship but within the same tribe.

We attempted to obtain specimens from a diversity of sites across the ranges of ingroup species. Where possible, we sampled at least two specimens of each

species from each location to determine the extent of sequence divergence and to test species concepts. Specimens were collected using lights (ultraviolet, mercury vapor, or incandescent), searching foliage, or rearing from larvae collected in the field. Representative specimens were photographed using a Leica M16 Zoom Stereomicroscope with a Leica DSC 320 3MP digital camera using a DFC Twain 6.6.1 (2006) driver for Windows at the University of Alaska Museum. Images (Figs. 1–4) were manipulated in Photoshop. For molecular analyses, live specimens were either frozen at -20°C , -70°C , or dropped directly into 95–100% EtOH. Pinned museum specimens were used for the morphological portion of this study and to supplement the fresh specimens in the molecular portion when possible.

Specimens were identified initially by phenotype, specifically forewing pattern, prior to DNA extraction or dissection for slide preparation. The unused body parts of each specimen were preserved in a gelatin capsule for confirmation of identification, and these vouchers are deposited in the Essig Museum of Entomology (EME) or the National Museum of Natural History (NMNH).

Specimens examined of *Clepsia penetralis* Razowski (11 m, 9 f): CALIFORNIA: Whitney Trail (1 ♂), Tom's Place (1 ♀), Berkeley (1 ♀). COLORADO: Fort Collins (1 ♂). CONNECTICUT: Hampton (1 ♂). UTAH: Hooper (3 ♂), Bryce Jct. (3 ♂, 4 ♀), Ogden (1 ♂), Johnson Pass (1 ♀). VERMONT: Burlington (2 ♀). WASHINGTON: Brewster (1 ♂).

Specimens examined of *Clepsia peritana* (Clemens) (32 m, 22 f): ALASKA: Cantwell (1 ♂). CALIFORNIA: Albany (4 ♂), Bakersfield (3 ♂, 1 ♀), Berkeley (2 ♂, 8 ♀), Davis (2 ♂), Herbert Creek (1 ♀), Mission Gorge (1 ♀), Orinda (1 ♂), Pleasant Hill (2 ♂, 2 ♀), Richmond (1 ♂), San Lorenzo (4 ♂), Santa Cruz Island (1 ♀), Shafter (1 ♂), Walnut Creek (1 ♂, 1 ♀). CONNECTICUT: Hampton (4 ♂). MASSACHUSETTS: Sturbridge (1 ♀). MARYLAND: Laurel (2 ♂). MICHIGAN: no further info (1 ♀). TENNESSEE: Crosby (1 ♀). UTAH: Springdale (2 ♂). VIRGINIA: Alexandria (3 ♀). WISCONSIN: Lake Katherine (2 ♂, 1 ♀).

Eight specimens were selected for the molecular portion of this study: two *Clepsia penetralis* from Garfield Co., UT; two *C. peritana* from Berkeley, CA; three *C. peritana* from the Rutherford neighborhood, east of Fairfax City, VA, and one *C. peritana* from Putnam Co., IL.

Morphological techniques. Dissection methods follow those summarized in Brown & Powell (1991). Terminology for genital structures follows Horak (1984). Eighteen *C. penetralis* and ten *C. peritana* were also physically measured for forewing (FW) length and

FW width. Measurements were plotted on a scattergram (Fig. 5).

Molecular techniques. Total genomic DNA was extracted using a QIAamp DNA Mini Kit # 51306 (QIAGEN Inc., Valencia, CA, U.S.A.). Most amplified fragments were approximately 400–500 basepairs long. Amplifications were performed on an Ericomp TwinBlock EasyCycler using a hot start: Taq was added at the end of an initial denaturation at 94°C , followed by 35 cycles of 30 s at 94°C , 30 s at 45°C , 1 min at 72°C , and a subsequent 10 minute final extension at 72°C . For many of the older museum specimens, amplifications were performed on an MJ Research PTC200 using a hot start: Taq was added at the end of an initial denaturation at 94°C , followed by 10 repetitions of 30 s at 94°C , 30 s at 40°C and 40 s at 72°C , 10 repetitions of 30 s at 94°C , 30 s at 45°C and 40 s at 72°C , and 15 repetitions of 30 s at 94°C , 30 s at 50°C and 40 s at 72°C , and a subsequent 3-minute final extension.

PCR products were cleaned using a QIAquick PCR Purification Kit #28106 (QIAGEN Inc.). The PCR product was cycle sequenced with a Perkin-Elmer/ABI Dye Terminator Cycle Sequencing Kit with AmpliTaq FS (Perkin-Elmer/Applied Biosystems, Foster City, CA, U.S.A.) on an MJ Research PTC200 according to Perkin-Elmer's suggested thermal profile. The sequenced product was filtered through Sephadex-packed columns and dried. This product was resuspended and electrophoresed on an Applied Biosystems International 377 automated sequencer. All fragments were sequenced in both directions. Sequences were aligned manually to the sequence of *Drosophila yakuba* Burla (Clary & Wolstenholme 1985).

We chose an 816 basepair segment in the COI gene to compare 8 specimens from 2 species of *Clepsia*, and 1 specimen of each of the 2 outgroup species. This fragment corresponds to the second half of COI, between *Drosophila yakuba* basepair numbers 2184 and 3000. Sequence was obtained by PCR amplification using the end primers CI-J-2183: 5' CAA CAT TTA TTT TGA TTT TTT GG 3', CI-N-2659: 5' GAT AAT CCT GTA AAT AAA GG 3' and TL2-N-3014: 5' TCC AAT GCA CTA ATC TGC CAT ATT A 3'. *Choristoneura rosaceana* and *Argyrotaenia niscana* sequences are from other studies (Sperling & Hickey 1994; Landry et al. 1999).

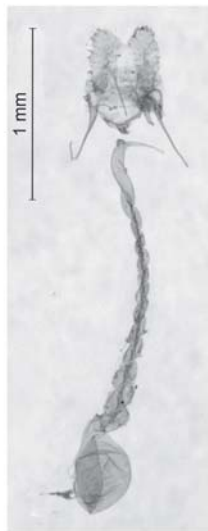
Phylogenetic analyses. Analyses using parsimony were carried out using PAUP 4.0b10 (Swofford 2002). Sequence alignments were done manually, and no indels were found relative to *Drosophila yakuba*. Variable nucleotide positions and morphological characters were treated as unordered characters with one state for each nucleotide or character. We employed



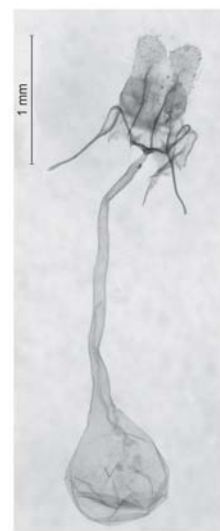
1.



2.



3.



4.

FIGS. 1–4. 1, Wing pattern photograph of *Clepsis peritana* (UT: Springdale, 19–20.VII.1993, J.A. Powell). 2, Wing pattern photograph of *Clepsis penetralis* (VT: Burlington, 25.VI.1987, D.L. Wagner). 3, Female genitalia photograph of *C. peritana* (VA: Alexandria, 17.VII.1991, slide JAP7329). Note the tightly twisted ductus bursae. 4, Female genitalia photograph of *C. penetralis* (UT: Bryce Jct. 28.VIII.1996, slide JAP7357). Note the slender, weakly twisted ductus bursae with faint cestral sclerotization.

some blackish or dark brown suffusion in the median transverse band and subapical costal spot, which usually are strongly contrasting with the tan ground color, appearing dark chocolate brown to the unaided eye (Fig. 1). In *C. penetralis* the forewing ground color tends to be paler, more yellowish tan; the markings are usually pale reddish brown, and if tinged with darker scaling, this tends to be restricted to the costal margin (Fig. 2).

Females of *C. penetralis* possess a slender weakly twisted ductus bursae with faint cestral sclerotization

(Fig. 4). If the original female was correctly associated, the illustration of the ductus bursae was poorly rendered or represents an attempt to reconstruct severely damaged structures that were lost prior to mounting. *Clepsis peritana* differs markedly, having a tightly coiled ductus bursae with central sclerotization (Fig. 3).

Differences in male genitalia between *C. peritana* and *C. penetralis* are subtle: the aedeagus is unevenly bent distally in *C. peritana* (Powell 1964, fig. 53) while it is evenly tapered in *C. penetralis* (Razowski 1979, fig.

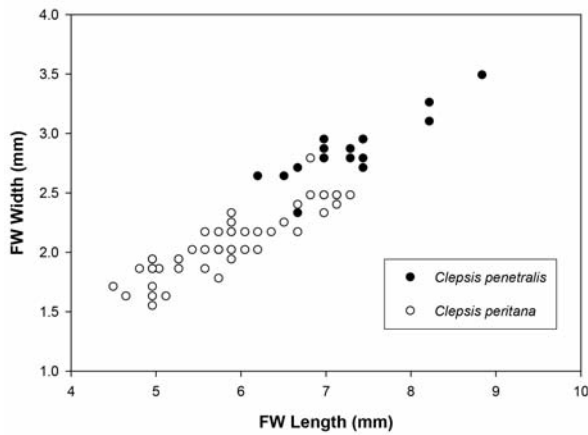


FIG. 5. Scattergram comparing forewing lengths and widths of adult male and female *Clepsis penetralis* [n=18] and *C. peritana* [n=49].

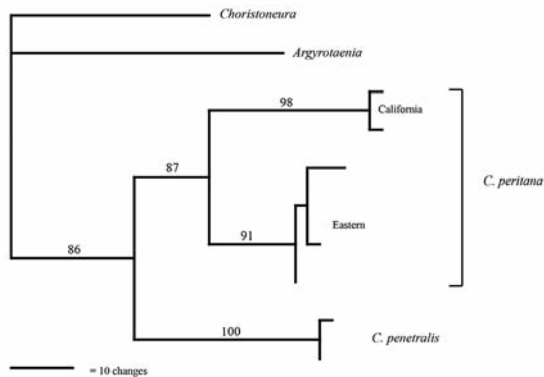


FIG. 6. Representative phylogram from five most parsimonious unrooted trees resulting from heuristic search of 74 molecular parsimony-informative characters from 8 ingroup mtDNA COI haplotypes (161 steps, CI = 0.876; RI = 0.851; RC = 0.745). Numbers at branch nodes indicate bootstrap values from the best Maximum Likelihood tree using GARLI 2.0 and Sumtrees 3.1.0. Only bootstrap values > 50% are shown.

23). Razowski also described two thin cornuti in the vesica of *C. penetralis*, but these have not been found in several dissections, so they may be deciduous. Razowski examined just one dissection of *C. penetralis*, from a paratype that was not returned to EME. We examined specimens mixed with *C. peritana* in the Essig Museum and University of Connecticut collections and discovered several additional females having the weakly coiled ductus bursae.

Adults of *C. penetralis* have forewing length of 6.2–8.8 mm, mean 7.5 mm [n=9] in males and 6.5–7.4 mm, avg. 7.0 mm [n=9] in females and are larger than those of *C. peritana* (FW length males: 4.5–6.4 mm, avg. 5.5 mm [n=27]; females 5.0–7.3 mm, avg. 6.4 mm [n=21]). *Clepsis penetralis* possesses a slightly broader forewing (avg. 1 mm broader), irrespective of sexual dimorphism in forewing length within and between populations (Fig. 5).

DISCUSSION

The utility of mitochondrial DNA sequence analyses in systematic studies at the species level has been demonstrated previously in studies involving the family Tortricidae (Sperling & Hickey 1994, Newcomb & Gleason 1998, Landry et al. 1999, Kruse 2000, Kruse & Sperling 2001, 2002). Mitochondrial genes provide a wealth of variation that may be particularly useful in generating phylogenetic trees of taxa where morphological differences are subtle (Sperling & Hickey 1994, Cognato et al. 1999, Kruse & Sperling 2001). However, mitochondrial DNA by itself represents only one linked, maternally inherited gene system, and may legitimately have different phylogenies or patterns of variation as the rest of the genome (Sperling & Roe 2009). Combined data sets that involve molecular, morphological, and/or ecological data in insects have led to better and more resolved knowledge of systematic relationships than have analyses of any single data set alone (Miller et al. 1997, Damgaard et al. 2000, Normark 2000, Skevington & Yeates 2000, Kruse & Sperling 2002).

In this study, the integrity of *C. penetralis* and *C. peritana* species concepts was strongly supported in morphological and molecular analyses. Support was found in molecular analyses to potentially describe a new species of *Clepsis* from California (specimens from TX and FL also seem to cluster with those from California, according to the BOLD database). Examinations of collections across the country indicate that *C. penetralis* is a widespread species that has been widely overlooked. According to our data, *Clepsis peritana* from Alaska tend to be as large as *C. penetralis* (male FW length 6.8 mm; n=1). A single female *C. peritana* from Michigan was also measured as quite large (FW length 7.1 mm; n=1). Therefore, confirmation via genitalic dissection is still recommended as some populations and/or some individuals are as large as *C. penetralis*.

ACKNOWLEDGEMENTS

We thank F.A.H. Sperling for review of this manuscript and use of his molecular lab for this study; D. Rubinoff and two anonymous

reviewers for helpful reviews and recommendations for improvement; J. Brown, D. Wagner and C. Ferris for acquisition of specimens and helpful insights. We thank the Essig Museum of Entomology (EME), National Museum of Natural History (NMNH), and University of Connecticut for the loan of specimens, and many others for allowing us to examine specimens during visits. M. San Jose conducted Maximum Likelihood analyses; C. Bickford photographed specimens; N. Lisuzzo manipulated photographs in Photoshop and prepared the photo plate. This project was made possible by an NSF-PEET grant to F.A.H. Sperling and J.A. Powell, and by California AES and NSERC grants to F.A.H. Sperling.

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Submitted for publication 21 March 2013; revised and accepted 1 June 2013.

EXPLOITATION OF FOOD BODIES ON *MACARANGA* MYRMECOPHYTES BY LARVAE OF A
LYCAENID SPECIES, *ARHOPALA ZYLDA* (LYCAENINAE)

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ABSTRACT. Larvae of *Arhopala zylde* (Lycaenidae) feed on food bodies (FBs) produced by two *Macaranga* (Euphorbiaceae) myrmecophytic species, *M. beccariana* and *M. hypoleuca*. We examined their feeding behavior in detail via field observations and rearing experiments in the field and laboratory. Larvae of *A. zylde* fed only on FBs and not leaves during the first through third instars; during the fourth (final) instar, they ate both FBs and leaves of the host plants. The larvae actively fed on FBs on young leaves, which were always attended by many plant symbiotic ants. These results suggested that *A. zylde* larvae depend entirely on FBs for food, except late in the final instar, and that the FB-feeding habit is associated with special traits that enable the larvae to evade ant aggression, which usually functions as an effective anti-herbivore defense for the host plants.

Additional key words: ant–plant interactions, Borneo, *Crematogaster* ants, larval growth, myrmecoxeny

Myrmecophytes are plants that have symbiotic associations with specific ant species, for which they provide nesting space, called domatia (Davidson & McKey 1993). In return, the symbiotic ants (plant-ants) protect them against herbivores, fungal pathogens, and plant competitors (reviewed by Heil & McKey 2003; Heil 2008). Some myrmecophytes also provide their plant-ants with cellular food bodies (FBs) on the plant surface at leaf tips, stipules, and/or stems (e.g., Janzen 1974; Rickson 1980; O'Dowd 1982; Heil et al. 1997). In addition, some non-myrmecophytic species provide FBs to attract ants to protect them (e.g., Webber et al. 2007; Paiva et al. 2009). FBs contain nutrients for the ants, such as lipids, carbohydrates, and proteins (Janzen 1974; Rickson 1976; Heil et al. 1998, 2004; Hatada et al. 2002). Usually plant-ants on myrmecophytes that produce FBs harvest the FBs as their main food and intensively protect newly-produced FBs (e.g., Rickson 1980; O'Dowd 1982; Fiala & Maschwitz 1990); herbivores that attempt to access the FBs would be aggressively attacked by the ants. Probably because of such anti-herbivore behavior, only a few non-ant FB-feeding insects have been recorded so far (e.g., Letourneau 1990; Jolivet 1996; Itino & Itioka 2001; Roux et al. 2011).

The paleotropical plant genus *Macaranga* Thou. (Euphorbiaceae) includes many myrmecophytic species that produce FBs for their plant-ants (Davidson & McKey 1993; Fiala et al. 1999; Davies et al. 2001). In some *Macaranga* myrmecophytic species, the relationship between the plants and ants are so obligate that neither can survive without the other, and the symbioses are maintained throughout most of both life cycles (Fiala & Maschwitz 1990; Heil et al. 2001). In such obligate partnerships, FBs are continuously patrolled and collected by the plant-ants (Fiala & Maschwitz 1990).

On the Malay Peninsula and Borneo, four *Arhopala* lycaenid species were recorded to feed on several *Macaranga* myrmecophytes that have obligate associations with their specific plant-ants (Maschwitz et al. 1984; Okubo et al. 2009). Of the four *Arhopala* species, only larvae of *Arhopala zylde* Corbet, 1941 feeds not only on leaves but also on FBs of two closely-related myrmecophytes, *M. beccariana* Merr. and *M. hypoleuca* (Reichb. f. & Zoll.) Müll. Arg. despite intensive defense for FBs by plant-ants. Larvae of *A. zylde* have myrmecoxenous traits; they can evade anti-herbivore defenses of the plant-ants without being attended by the ants and without providing honeydew

to tame them (Shimizu-kaya et al. 2013). The larval period comprises four instars. For additional details of *A. zylta* development, see Okubo et al. (2009).

The plant-ant of the both *M. beccariana* and *M. hypoleuca* is *Crematogaster decamera* Forel (Fiala et al. 1999; Itino et al. 2001). Plant seedlings are usually colonized by foundress queen ants when they reach approximately 10 cm in height (Murase et al. 2002) and start FB production at almost the same time (Fiala & Maschwitz 1992; Hatada et al. 2002). The leaves of both plant species are three-lobed, and FBs are produced on the abaxial surfaces of developing leaves along the veins and midrib (Fig. 1). Usually, the first, second, and sometimes third leaves from the plant apex bear such FBs. As leaves mature, they produce fewer FBs. Full-sized leaves bear very few FBs, even when they have not fully thickened (hereafter, we refer to these unhardened young leaves as “developed young leaves”).

Foundress plant-ant queens brood their workers inside the hollow stems. After the adult workers emerge, they constantly patrol the aboveground plant surfaces, especially leaves at the plant apex (Itioka et al. 2000). The ant colony grows with the host plant (Itino et al. 2001, Handa et al. 2013), but the ratio of ant-to-plant biomass peaks around the time the plant starts branching in *M. beccariana* (Handa et al. 2013), usually when the plant is 2.0–2.5 m tall. Thereafter, the plant-ant worker density on the host-plant surfaces decreases noticeably as the host plant grows (I. T. pers. obs.).

To our knowledge, *A. zylta* is the only known FB-feeding insect species that can feed on myrmecophyte FBs while the plant-ants are present. To better understand the ecology and evolution of this parasitism on myrmecophytism, the characteristics of FB-feeding by *A. zylta* larvae should be elucidated. In this report, we described the FB-feeding behavior of *A. zylta* with special reference to the degree to which the larvae depend on FBs. We observed larval behavior in the field and reared larvae in both the field and laboratory.

MATERIALS AND METHODS

Our study was conducted in the primary lowland mixed dipterocarp forest of Lambir Hills National Park, Sarawak, Malaysia (4°2'N, 113°50'E, 150–200 m asl), from 2006–2012. The main habitats of the two *Macaranga* species were riversides, forest gaps, and forest edges.

We randomly searched for *A. zylta* immatures on *Macaranga* saplings that were 0.5–4.0 m in height. We found 131 larvae and six pupae on approximately 130 saplings of *M. beccariana* and *M. hypoleuca* in the field. For 73 of those saplings, which together hosted 75 larvae and two pupae, we recorded the characteristics of

the saplings, such as height and number of leaves; the presence/absence of plant-ants; damage levels, including herbivory to leaves and non-herbivory damage due to tree-fall, litter-fall, and flooding; and the positions of the *A. zylta* larvae on the saplings. For the other saplings, with 56 larvae and four pupae, we recorded only the within-plant positions of the *A. zylta* larvae.

Three second- or third-instar (mid-instar) *A. zylta* larvae were reared in the field until the pupal stage to observe their feeding behavior and development times. These larvae were introduced onto randomly-selected *M. hypoleuca* saplings of about 1.5 m in height. These saplings were unbranched, colonized by plant-ants, and with almost no obvious herbivory damage. Each larva was placed onto the third apical leaf using forceps. After the introduction, we netted the sapling with mesh nylon (#9000 Honeyqueen: Toray Industries, Tokyo, Japan) to exclude other herbivores (Fig. 2). We checked the growth of each introduced larva daily and observed their behavior for 20–60 min at least twice a day. We observed the three larvae a total of 203 times.

In parallel, we reared three similar larvae by feeding them individually with fresh FB-bearing leaves of *M. hypoleuca* in plastic containers (9 × 15 × 7 cm) in the laboratory to estimate their FB consumption during the third and fourth instars. We transplanted *M. hypoleuca* seedlings that were at most 20 cm high and inhabited by plant-ants from the field into a nursery at the study site. These seedlings were cultivated to provide FBs for the laboratory-reared larvae. Larvae of the final instar were reared on FB-bearing and developed young leaves collected from a sapling of approximately 1.5–2.5 m in height in the field or the nursery. We removed all plant-ants from these leaves and inserted the ends of their petioles into wet floral-arrangement sponges (Aquafoam; Matsumura Kogei Co., Osaka, Japan) just before feeding them to the larvae. We replaced each leaf with a fresh one and checked larval growth daily.

To estimate the fresh weight of consumed FBs, we classified FBs into four size classes based on naked-eye assessments of diameter: < 0.2 mm, 0.2–0.4 mm, 0.4–0.5 mm, and > 0.5 mm. We collected 108–213 FBs of each class from seven fresh leaves of five randomly-selected saplings (approximately 1.5–2.5 m in height) in the field and measured the fresh weights of each class. Based on this data, we estimated the mean weight of FB in each class. During the laboratory rearing, we recorded the number of FBs of each size class on each leaf before and after providing them to the larvae. Using the previously estimated mean FB weights, we could thus estimate the fresh weight of FBs that each larva consumed in a day. To estimate the amount of FBs on



FIGS. 1–5. **1.** A new leaf on apical part of a sapling of *Macaranga beccariana* and a third-instar larva of *Arhopala zylde* which rested on the leaf. The leaf bore food bodies, pearl-like particles, on the abaxial side of leaf surface. **2.** A sapling of *Macaranga hypoleuca* enclosed by nylon mesh use to rear a larva of *Arhopala zylde*. **3.** A damaged leaf of *Macaranga beccariana* on which a pupa of *A. zylde* was found. **4.** A fourth-instar larva of *Arhopala zylde* reared on a sapling of *Macaranga hypoleuca*. It was resting along the midrib of a new leaf. **5.** A pupa of *Arhopala zylde* on a sapling of *Macaranga hypoleuca*. It pupated on the petiole of a new leaf after being reared in the field.

leaves of *A. zylida* host plants in the field, we measured the fresh weight of all FBs on the apical parts of each of five randomly-selected saplings of *M. hypoleuca* (approximately 1.5–2.5 m in height).

Each reared pupa was kept in a plastic container (4 × 6 × 1.5 cm) with moistened tissue in the laboratory until adult emergence. The adults have been kept as voucher specimens and deposited at the Forest Research Centre, Sarawak, Malaysia; Kyoto University Museum, Japan; or Tokyo University Museum, Japan.

RESULTS

Field observations. All 73 host plants for which we recorded characteristics were inhabited by plant-ants. There was no damage due to herbivores or accidental disturbances on 86.3% of those plants. There was virtually no leaf loss due to herbivore chewing on any host-plant leaves with either first-, second-, or third-instar larvae ($n = 52$) nor on some plants hosting fourth-instar larvae ($n = 7$). On host plants harboring the other fourth-instar larvae or pupae ($n = 14$), several holes, inferred to be caused by *A. zylida* larvae, were found on one or two apical leaves (Fig. 3). The larvae frequently rested on the abaxial sides of new FB-bearing leaves (Fig. 1), while all pupae were found on petioles of young leaves.

Developmental durations of third- and fourth-instar larvae and pupae. The third and fourth instars of the larvae reared in the field lasted 8 days ($n = 1$) and 20–29 days ($n = 3$), respectively, and the pupal period ranged from 12–19 days ($n = 3$). In the laboratory, the third- and fourth-instar periods of the larvae reared on ant-excluded leaves with FBs were 10–11 days ($n = 2$) and 17–31 days ($n = 3$), respectively, and the pupal period lasted 12–21 days ($n = 2$).

Larval behavior. In the mid-instar stages, larvae that were reared on saplings in the field spent most of their time on the abaxial sides of new leaves along the midrib or veins. Each larva usually remained stationary, but moved from lobe to lobe of the leaf at least once per day. All the larvae that were reared in the laboratory also rested still along the midrib or veins of the provided leaves, except when they ate FBs or leaves, although they moved around the leaves every few hours.

We confirmed at least four times that the larvae reared in the field ate FBs similarly to those in the laboratory. There were no chewing marks on other plant parts, such as leaves, stipules, or stems at mid-instar. Within 1–7 days after they reached the final instar, the larvae first began to eat the developed young leaves. At this time, FBs remained on the saplings. Leaf-feeding was observed only around sunset and at night. Except when they ate leaves, they rested along the midribs or

petioles of new leaves (Fig. 4). Both while stationary and while eating, the larvae were neither contacted nor attended by plant-ants on the saplings, even when the plant-ants walked nearby.

Larvae reared in the field ate leaves for a total of 7–11 days before pupation. During the first 3–7 days after initiating leaf feeding, the area of leaf loss to chewing increased daily. This period was followed by a 1–6 day break from leaf-feeding in which no new damage was observed. Then, the larvae resumed leaf-feeding, eating leaves daily until the prepupal stage, which entailed another break of 1–6 days. None of the larvae ate leaves for 1–3 days just before the prepupal stage. Each fourth-instar larva fed on two developed young leaves and consumed an area roughly equivalent to half of such a leaf. Whether they also ate FBs after they began to eating leaves is unknown. They pupated at the base of a petiole of a FB-bearing new leaf or a developed young leaf (Fig. 5).

Larvae reared in the laboratory were also observed to feed on FBs during the third and fourth instars. They preferred more developed FBs that were ≥ 0.4 mm in diameter and ate few small, undeveloped FBs. The fresh weight of FBs consumed per larva varied from day to day (Fig. 6), but was generally being less than the standing crop of FBs on the apical parts of the plant (3.5 ± 0.6 mg, $n = 5$). The average fresh weights of FBs consumed by a larva were 14.8 ± 1.1 mg ($n = 2$) and 22.6 ± 9.0 mg ($n = 3$) in the third and fourth instars, respectively. All three larvae ate only FBs during the initial 9–27 days after reaching the final instar, and they ate only developed young leaves during the 4–10 days just before becoming prepupae. Each larva consumed approximately half of a developed young leaf.

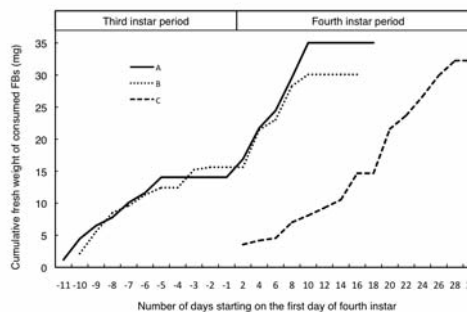


Fig. 6. Cumulative fresh weight of FBs consumed by each of the three *Arhopala zylida* larvae (A, B, C) reared in the laboratory during the third- and fourth- (final) instars. FB consumption of larvae A and B was estimated from the third instar until pupation, while it was estimated from the fourth instar through pupation for larva C. Fourth-instar estimates are plotted every 2 days.

DISCUSSION

Our results for both field- and laboratory-reared larvae strongly suggested that second- and third-instar *A. zylida* rely completely on FBs of their host-plant species for food and that fourth- (final-) instar larvae eat both FBs and young leaves. We inferred that first-instar larvae also rely entirely on FBs, because they were almost always found on FB-bearing leaves with virtually no leaf loss due to herbivore chewing when observed in the field.

In addition to ants, at least five insect species are known to feed on FBs produced by myrmecophytes (Letourneau 1990; Jolivet 1996; Itino & Itioka 2001; Roux et al. 2011), and Ozawa & Yano (2009) reported that a predatory mite species eats the FBs of a non-myrmecophytic species. However, these non-ant arthropods use FBs opportunistically or secondarily and only on plants that have not yet been colonized by ants or when the plant-ant colony declines dramatically due to accidental damage to the host plant. In comparison, the feeding behavior of *A. zylida* larvae is quite remarkable, both because their survival and growth are completely dependent on FBs and because they feed on FBs on intact myrmecophytes harboring active plant-ant colonies that seem able to protect the host plants against other herbivores. The lack of larval interference by plant-ants is probably strongly associated with myrmecoxeny, a peculiar system of evading plant-ants (Fiedler 1991; Pierce et al. 2002) in *A. zylida* (Shimizu-kaya et al. 2013). The other *Arhopala* species that use *Macaranga* myrmecophytes as host plants do not eat FBs or possess myrmecoxenous characteristics.

Our results also suggested that feeding on leaves was necessary to complete larval development and to pupate. Interestingly, larvae late in the final instar tend to shift abruptly from FB to leaf feeding and seem to eat no leaves before the shift. Nutritive components necessary for completing larval growth are presumed to be included in fresh leaves but not in FBs.

Considering that caterpillars tend to prefer nitrogen-rich plants (Pellissier et al. 2012) and that FBs on *M. beccariana* and *M. hypoleuca* are nitrogen rich (Rickson 1980; Hatada et al. 2002), the FBs seem to be an excellent food compared to foliage, so the larval growth rate of *A. zylida* was expected to be higher than that of other *Arhopala* species that eat leaves of other *Macaranga* myrmecophytes. However, contrary to expectation, *A. zylida*'s growth rate was much lower than that of other species (Okubo et al. 2009; U. S. pers. obs.) with a much longer duration especially of the final instar. There are a few plausible explanations. First, FBs may lack nutrients essential for larval growth, as

described above. The larval digestive system might also need time to the shift to its new diet during the final instar. Second, the costs of maintaining myrmecoxeny might prolong the growth period, even if FBs provide better nutrients. Of all the *Arhopala* species that feed specifically on *Macaranga* myrmecophytes, only *A. zylida* has a myrmecoxenous association with plant-ants (Shimizu-kaya et al. 2013). Third, *A. zylida* might experience a shortage of FBs throughout the larval period, thereby prolonging development. However, this hypothesis is refuted by our field observation that FBs of the preferred size were never exhausted by larval feeding. Further study is required to elucidate why the larval period is longer in *A. zylida* than in other congeneric species feeding on *Macaranga* myrmecophytes.

Leaf feeding during the final instar was different between larvae reared in the field and in the laboratory; intermittent leaf-feeding with a break was observed only in the field. Two factors could affect this difference. One is a possible reduction in plant chemical defenses under the laboratory conditions, in which the leaves had been cut from saplings. Secretory flow is eliminated when veins are cut, deactivating defensive secondary metabolites in some plant species (Dussourd & Denno 1991). If this were the case in our study, the cut leaves would be more suitable for larval growth than intact leaves in the field and allow the larvae in the laboratory to feed without breaks. Another possible explanation is ant attacks in the field. Because plant-ants of *Macaranga* myrmecophytes show aggressive behavior in response to host-plant volatiles released by leaf damage (Itioka et al. 2000, Inui & Itioka 2007), we can infer that leaf damage by chewing *A. zylida* larvae elicited ant attacks. To avoid or minimize these attacks, the larvae might need to suspend leaf feeding for a few days. Whether either or both factors caused the difference observed is a question to be addressed in future work.

ACKNOWLEDGEMENTS

This study was approved by the Forest Department of Sarawak. We are deeply grateful for the extensive help by Lucy Chong and Het Kaling (Sarawak Forestry Corporation) and Fatimah Mohammad, Paulus Anak Meleng, and Mohamad Nafri Ali (Forest Research Centre, Sarawak). We also thank Professors Tohru Nakashizuka (Tohoku University), Norio Yamamura (Doshisha University), and Shoko Sakai (Kyoto University) for their invaluable support. This study was financially supported by the Research Institute for Humanity and Nature, Japan, (project number D-04) and by Grant-in-Aids (no. 21255004 to T.I.) from the Japan Society for the Promotion of Science.

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Submitted for publication 27 April 2013; revised and accepted 11 June 2013.

ANNOTATED CATALOGUE WITH ILLUSTRATIONS OF MÉNÉTRIÉS' TYPES OF CTENUCHINA AND EUCHROMIINA (EREBIDAE, ARCTIINAE, ARCTIINI) DEPOSITED IN THE ZOOLOGICAL INSTITUTE OF THE RUSSIAN ACADEMY OF SCIENCES, ST. PETERSBURG, RUSSIA

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ABSTRACT. The types of *Ctenuchina* and *Euchromiina* that were described by E. Ménétriés, deposited at the Zoological Institute of the Russian Academy of Sciences of St. Petersburg, are catalogued. All but one of the types are of names described from Brazil and collected during the Langsdorff expedition; the only non-Brazilian type was collected in California, USA. **Lectotypes** are designated for the following names: *Laemocharis fasciatella*, *Charidea fastuosa*, *L. fulviventris*, *L. metallescens*, *L. ornata*, *Glaucoptis rubroscapus*, *G. vidua vidua* and *G. vidua spiracula*. The following **new combinations** are proposed: *Poecilosoma fasciatella*, **stat. rev.**, *Aethria ornata*, and *Xanthya metallescens*. Comments on each name are provided, as well as information on their current taxonomic status, illustrations of type specimens, and information about their conservation status.

Additional key words: Taxonomy, revalidated status, new combination, lectotype designation, Langsdorff expedition.

Édouard Ménétriés (1802–1861) was a French zoologist and linguist who was recommended by his professors Georges Cuvier and Pierre André Latreille (Komissarov 1994) to take part in the expedition to the interior of Brazil planned and commanded by Baron Georg Heinrich von Langsdorff (1774–1852), an amateur naturalist and Russian consul in Brazil (Komissarov 1994; Kryzhanovsky 2002).

The expedition was to the greatest extent financially supported by Tsar Alexander I, and was designed essentially for anthropological and scientific purposes, although political and commercial reasons also played an important role (Silva 1997). The expedition was divided in two parts, the first (1824–1825) included the exploration of the states of Rio de Janeiro and Minas Gerais, and the second (1826–1829) was done across the main rivers of the interior of the country, heading to Belém (Silva 1997). This is regarded as one of the most unsuccessful expeditions that took place in Brazil (Ihering 1902; Vanzolini 1996); some of the mishaps included the desertion of the illustrator Johann Moritz Rugendas, the suicide of the zoologist Christian Hasse, and the drowning of Aimé-Adrien Taunay (also an illustrator) in the Guaporé River (state of Mato Grosso). In addition to those misfortunes, Baron von Langsdorff acquired a serious mental illness that culminated in erasing all of his memories at the end of his life (Silva 1997).

Ménétriés participated only in the first part of the expedition, and apparently his contribution was not very satisfactory to Langsdorff (possibly because Ménétriés

had other interests besides collecting zoological material, which, in the eyes of the Baron, was leading to suboptimal sampling) (Vanzolini 1996; Silva 1997), and his relationship with the Baron worsened (Komissarov 1994; Silva 1997). During the expedition, Ménétriés organized anthropological and zoological annotations in diaries that are currently unpublished and kept in Moscow and St. Petersburg, respectively (Komissarov 1994).

The Lepidoptera material collected during the Langsdorff expedition was incorporated into the collection of the *Kunstkamera*, the cabinet of curiosities of the Tsar, where Ménétriés was hired as the curator shortly after his return to Russia in 1825 (Vanzolini 1997; Kryzhanovsky 2002). For this reason, the zoological material received more attention than other materials collected during the expedition, which were forgotten for a century, along with Langsdorff's diaries and other documentation produced during the expedition (Komissarov 1994). The zoological collection formed after the expedition is now part of the collection of the Zoological Institute of the Russian Academy of Sciences (ZIN).

This paper is an illustrated catalogue of the types of *Ctenuchina* and *Euchromiina* described by Ménétriés, along with taxonomic remarks when appropriate. Even though Ménétriés provided illustrations of all his American arctiines, it is unlikely that any author who worked on the taxonomy of the group visited the ZIN collection to inspect the type material. The types of all but one species were collected during the Langsdorff

expedition, and all of them were described in the family Zygaenidae, where most authors placed the Ctenuchina and Euchromiina at the time (Pinheiro & Duarte 2013).

MATERIALS AND METHODS

All the specimens examined from the Neotropical region are kept in small cardboard or wooden drawers; in most cases, there is a need for curatorial attention in identification, gathering specimens from the same species in the same drawer, separation of different subtribes, etc. (Fig. 1). Among the specimens are Ménétriés' types, Herrich-Schäffer's types described from the Kaden collection, and some other non-type specimens from various localities. Some specimens are unlabeled and many have only their putative names on the labels, without locality data.

Most of Ménétriés' types are identified based on a round gold label, and a green label that shows the type locality (Figs. 2; 4–9). The only exceptions are three specimens of *Charidea fastuosa* Ménétriés, 1857, for which the type status here advocated is explained in the remarks on this name. In some instances the number of potential types was not defined, due to the unfortunate practice (widely used in the past) of labelling only one of the specimens from the same locality, and placing the other one(s) below or beside the labelled one. In such cases, as stressed in the text, we decided to consider the unlabelled specimens also part of the type series if they were placed in the same drawer and below or beside the labelled one. This arrangement of the specimens was considered evidence of the composition of the type series, as allowed under article 72.4.1.1 (ICZN, 1999). In all cases, the original description was compared to the specimens to aid in the verification of their type status.

Some ambiguous type localities for birds described by Ménétriés have been discussed (Vanzolini 1996; Vasconcelos & Pacheco 2012). However, in the case of most moths treated here there are no doubts concerning type localities, for all the species described from Brazil belong to localities where the author is known to have collected (e.g., names described from “Brazil,” “interior of Brazil,” or “Minas Gerais”). The only exception is the material described as *Glaucoptis vidua* Ménétriés, 1857, and *G. vidua* var. *spiracula* Ménétriés, 1857, as explained below under these names.

The information from the original descriptions was compared with the respective label data. Additional information was added in square brackets when considered necessary. The names are given in alphabetical order by specific epithet. For each name, the original combination is given, as well as their current

placement, taxonomic notes and conservation status of the type(s). The labels are transcribed with a “/” to separate lines on the same label, and “;” to separate labels.

Lectotype designations are made to ensure stability of the names. Following recommendation 73F of the International Code of Zoological Nomenclature (ICZN, 1999), in the absence of evidence of monotypy, all the types found were considered to be syntypes, even if only one known specimen exists.

The acronyms used are as follows: (BMNH) Natural History Museum, London, England; (ZIN) Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; (ZMHB) Zoologische Museum der Humboldt Universität, Berlin, Germany; (ZMUC) Zoologisk Museum of the University of Copenhagen, Denmark. Dates of older literature follow Heppner (1982).

CATALOGUE

All the illustrations provided by Ménétriés (1857) match closely with his species. In spite of this, some taxonomic issues persist, as discussed case by case below.

fasciatella Ménétriés, 1857

(Figs. 2, 10–13)

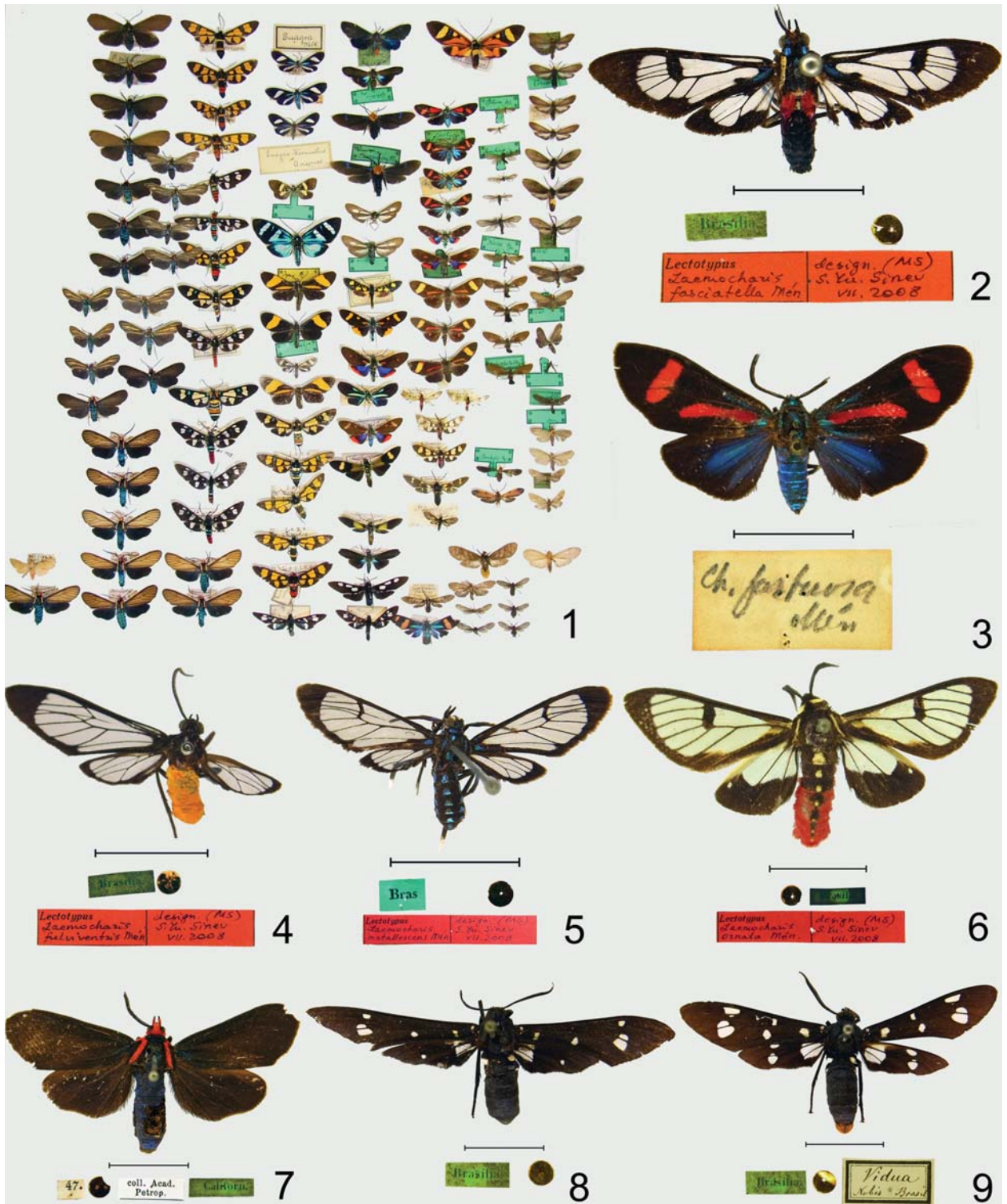
Laemocharis fasciatella Ménétriés, 1857: 140; pl. 14, fig. 4. **Lectotype hereby designated** male: BRAZIL [no further data]. With three labels: a round gold label; a green label with “Brasilia” printed; a red label “Lectotypus *Laemocharis fasciatella* Mén / design. (MS) S. Yu. Sinev vii.2008”.

Current combination. *Poecilosoma fasciatella* (Ménétriés) **comb. nov., stat. rev.**

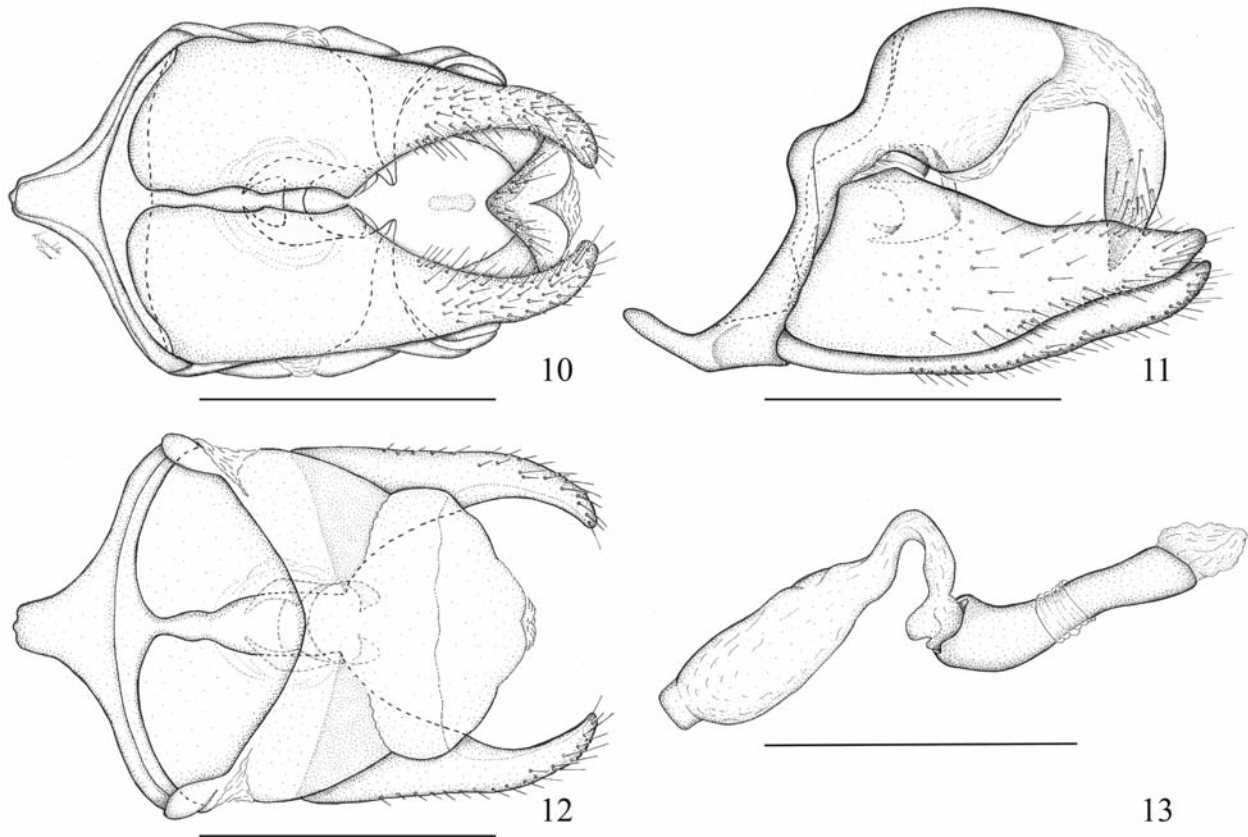
Condition of the lectotype. Both antennae broken, the left with the proximal portion still attached to the head. Right hindwing partly worn.

Remarks. This species was described from an unknown number of specimens, and only a single specimen was found. There is a label below the lectotype, on a different pin, with printed edges and “Fasciatella / Nobis Brasil” handwritten in ink, in what seems to be Ménétriés' handwriting (his handwriting is depicted in Horn & Kahle, 1935–1937, pl. 21, fig. 9). The lectotype corresponds reasonably well with the original illustration.

Ménétriés (1857) mentioned that this species resembles *Poecilosoma eone* (Hübner, 1831), the type species of *Agerocha* Hübner, 1831, which is a junior subjective synonym of *Poecilosoma* Hübner [1819]. In spite of this and with no evidence of having examined the type, Butler (1877: 34) synonymized *Laemocharis*



FIGS. 1–9. Arctiinae moths (Lepidoptera, Erebidae) deposited in the Zoological Institute of the Academy of Sciences of St. Petersburg. 1. Example of drawer with unsorted material (mostly unidentified) from Afrotropical, Indo-Malayan, Nearctic, and Neotropical regions. 2–9. Ménétries' type collection. 2. *Laemocharis fasciatella*; 3. *Charidea fastuosa* (lectotype); 4. *L. fulviventris*; 5. *L. metallescens*; 6. *L. ornata*; 7. *Glaucopsis rubroscapus*; 8. *G. vidua*; 9. *G. vidua spiracula*.

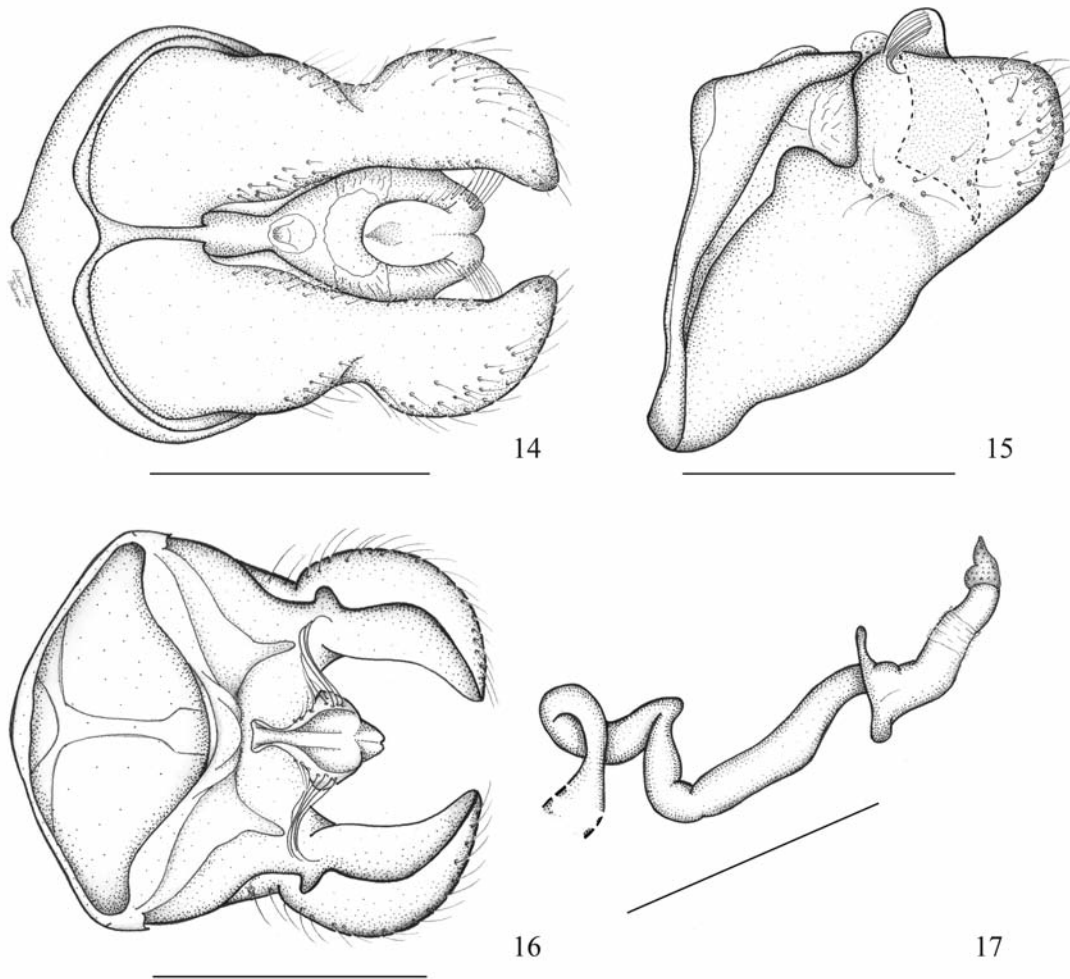


FIGS. 10–13. Male genitalia of *Poecilosoma fasciatella*. 10. Ventral view; 11. Lateral view; 12. Dorsal view; 13. Aedeagus. Scale bar: 1mm.

fasciatella under *Eunomia colombina* (Fabricius 1793), a species from the West Indies. This synonymy was followed by all subsequent authors (Kirby 1892: 146; Hampson 1898: 201; Zerny 1912: 60; Draudt 1915: 59), none of whom are believed to have seen the type.

Examination of the lectotype of *L. fasciatella* and the only known syntype of *E. colombina*, held at ZMUC, made it clear that they are not synonyms (*E. colombina* is correctly illustrated in color in Draudt, 1915: plate 12, row d, as *columbina*). *Laemocharis fasciatella* is indeed remarkably similar to the established concept of *Poecilosoma eone* (illustrated by Cerda 2008, fig. 83), but they are distinct species. As noted by Ménétrié in the original description, his type differs from the established concept of *P. eone* (whose type is probably lost, as is most of Hübner's collection) in the absence of whitish spots on the abdomen. However, this is probably a result of discoloration, given that fresh specimens of *L. fasciatella* have these spots. The male genitalia of *P. eone* was illustrated by Cerda (2008, figs. 89a–e), and is remarkably similar to that of *P. fasciatella* (Figs. 10–13), differing by the shorter valvae, longer saccus and wider coecum.

The transfer of *L. fasciatella* to *Poecilosoma* follows the current combination of *P. eone*. However, it is likely that neither of them belongs to this genus, given that characters of the male genitalia are quite different between *P. eone* and the type species of *Poecilosoma*, *P. chrysis* Hübner, 1823 (L. R. Pinheiro, personal observation). If this is indeed the case, *Agerocha* would need to be revalidated (as mentioned above, *P. eone* is the type species of *Agerocha*). According to a preliminary survey we made among various euchromiine genera, at least three other species seem very close to *P. eone* and *P. fasciatella*: *Saurita gracula* (Dognin 1911), and two others currently placed in *Chrostosoma* Hübner, [1819], *C. regia* (Schaus, 1894) and *C. bogotense* (Felder 1874). The last two appear in Draudt (1915) and Hampson (1898) as *Cosmosoma* Hübner, [1823], but because both authors placed the type species of *Chrostosoma*—*Sphinx evadnes* Cramer, 1781—in *Cosmosoma*, the former automatically became a senior subjective synonym of the latter (Julian Donahue, personal communication). This is why all the species that are treated here in *Chrostosoma* appear in previous catalogues as *Cosmosoma*.



FIGS. 14–17. Male genitalia of *Xanthyla metallescens*. 14. Ventral view; 15. Lateral view; 16. Dorsal view; 17. Aedeagus. Scale bar: 1mm.

fastuosa Ménétriés, 1857
(Fig. 3)

Charidea fastuosa Ménétriés, 1857: 143, pl. 14, fig. 8.

Lectotype hereby designated male: BRAZIL [no further data]. With one white label with the handwritten inscription “Ch. fastuosa Mén.” in pencil on the upper side, and “scintillans Am. M.” handwritten in ink on the underside. **Paralectotypes:** one male with a green “T” shaped label with “fastuosa Ménét.” handwritten in ink and another green label with the handwritten inscription “Ipanema / Beske” also in ink; one female, unlabelled.

Current combination. Junior subjective synonym of *Euchromia jucunda* Walker, 1854 (synonymized by Hampson 1898), a species currently placed in *Cyanopepla* Clemens, 1861.

Condition of the types. Lectotype. Wings rubbed. Left hindleg missing and right antenna broken. **Male paralectotype.** Wings slightly rubbed, right forewing

with minor damage on external margin. Female paralectotype. Left hindleg missing.

Remarks. *Charidea fastuosa* Ménétriés was described from an undetermined number of specimens. The three specimens here considered as part of the type series were arranged in a column in a drawer filled with specimens of many other species. The lectotype designated here was the second, with the other male above, and the female below, followed by a different species of *Cyanopepla*. Therefore we consider the other male and the female to be part of the type series. There was no round gold label with these specimens, but there is no question about their type status, given that the lectotype label data were clearly mentioned by the author in the original description. There was another box with specimens arranged under the name *Charidea scintillans* (no mention of the author’s name). These are *C. jucunda*, and not *C. scintillans* (Butler 1872) (a photograph of the type held at the BMNH was

examined by the first author), and are not considered part of the type series due to their placement in a different box, arranged under a different name.

Ménétriés (1857) compared his *C. fastuosa* with *C. fulgens* Herrich-Schäffer, 1854 (...). A syntype of the latter, deposited at the ZMHB, was consulted by the first author and is indeed a similar species, though it does not seem to be particularly closer to it than many other species of *Cyanopepla*. Hampson's synonymization of *C. fastuosa* under *E. jucunda* was followed by all subsequent authors. The holotype of the latter, held at the BMNH, was also examined by the first author, and the synonymy seems to be correct.

The name *scintillans* on the label of the lectotype cannot be a reference to *C. scintillans* (Butler), given the fact that the latter name was described 25 years later, unless the label had been added posteriorly. It is unknown to what the former name could refer.

There is a valid species in *Cyanopepla* that is a senior homonym of *C. fastuosa* Ménétriés—*C. fastuosa* (Walker 1854). The former is also a junior synonym of *C. jucunda* (see above), and for this reason no replacement name is required according to article 60.2.1 (ICZN 1999).

fulviventris Ménétriés, 1857
(Fig. 4)

Laemocharis fulviventris Ménétriés, 1857: 141, pl. 14, fig. 5. **Lectotype hereby designated male**, BRAZIL [no further data]. With three labels: a round gold label; a green label with "Brasilia" printed; a red label "Lectotypus *Laemocharis fulviventris* Mén. / design. (MS) S. Yu. Sinev vii.2008".

Current combination. Junior subjective synonym of *Glaucopsis (Ilipa) tengyra* Walker, 1854 (synonymized by Hampson 1898: 252), currently placed in *Chrostosoma* Hübner, [1819].

Condition of the lectotype. Right antenna and forewing missing, as well as some legs.

Remarks. *Laemocharis fulviventris* was described from an unspecified number of specimens, and only a single female was found. It was placed in *Ilipa* Walker, 1854 by Kirby (1892: 143). Hampson (1898: 252) considered *L. fulviventris* a junior subjective synonym of *Glaucopsis (Ilipa) tengyra* Walker, 1854, a species that he placed in *Cosmosoma* Hübner, [1823]. This treatment was followed by Zerny (1912: 75) and Draudt (1915: 82, pl. 14, row f).

The holotype of *C. tengyra*, deposited at the BMNH, was examined by the first author. Even though its abdomen and antennae are missing, it seems reasonable to regard the synonymy as correct.

ignicolor Ménétriés, 1857

Laemocharis ignicolor Ménétriés, 1857: 139, pl. 14, fig. 3. Lectotype male, BRAZIL [no further data]. With three labels: a round gold label; a green label with "Brasilia." printed; a red label "Lectotypus *Laemocharis ignicolor* Mén. / design. (MS) S. Yu. Sinev vii.2008".

Current combination. This name is currently considered a junior subjective synonym of *Erruca erythrarchos* (Walker 1854) (synonymized by Becker & Pinheiro 2009: 684).

Remarks. There is a label below the specimen on a different pin, with printed edges and "Ignicolor / Nobis Brasil" handwritten in ink.

This name was based on a composite glued specimen, with the head and thorax of *Erruca erythrarchos* and an abdomen of *Aethria haemorrhoidalis* (Stoll 1790), and is currently considered a synonym of *Erruca erythrarchos* Walker, 1854. For more information and an illustration, see Becker & Pinheiro (2009).

metallescens Ménétriés, 1857
(Figs. 5 and 14–17)

Laemocharis metallescens Ménétriés, 1857: 138, pl. 14, fig. 1. **Lectotype hereby designated female**, BRAZIL [no further data]. With three labels: a round gold label; a green label with "Bras." printed; a red label "Lectotypus *Laemocharis metallescens* Mén. / design. (MS) S. Yu. Sinev vii.2008".

Current combination. *Xanthhyda metallescens* (Ménétriés), **comb. nov.**

Condition of the lectotype. Both antennae missing.

Remarks. This species was believed to occur from Mexico to southeastern Brazil. However, Cerda (2008) determined that this distribution corresponds to the range of two distinct species, *X. metallescens*, whose type locality is in Atlantic Forest in eastern Brazil, and *X. chalcosticta* (Butler 1876), which occurs from Mexico and down at least to Pará, Brazil. This distinction is confirmed here, by the differences in the male genitalia (Figs. 14–17).

Xanthhyda metallescens is known to occur in the Brazilian states of Santa Catarina, Paraná, São Paulo, Rio de Janeiro, and Minas Gerais, in the Atlantic Forest and Cerrado biomes, and it is very similar in habitus to *Chrostosoma elegans* Butler, 1876. A full account of the misidentifications of *X. metallescens* may be found in Cerda (2008). This species is here transferred to *Xanthhyda* Hampson, 1920, which was revalidated by Cerda (2008), based on the overall similarity to its type species, plus the genital characters used by this author to

define the genus (mainly the outgrowths of the tegumen).

ornata Ménétriés, 1857
(Fig. 6)

Laemocharis ornata Ménétriés, 1857: 139, pl. 14, fig. 2.

Lectotype hereby designated male [BRAZIL], Minas Gerais [no further data]. With three labels: a round gold label; a green label with “Bras.” printed; a red label “Lectotypus / Laemocharis / ornata Mén. / design. (MS) / S. Yu. Sinev / VII.2008”.

Current combination. *Aethria ornata* (Ménétriés) **comb. nov.**

Condition of lectotype. Right forewing worn and both hindwings and most legs missing. Specimen not very well mounted.

Remarks. The species was described from an undetermined number of specimens, and only one was found. Below the specimen, on a different pin, there is another label, white with printed black edges, with “ornata/Nobis Brasil” handwritten. The lectotype corresponds quite well to the original illustration.

The reason for treating this species in *Aethria* Hübner, 1819, and not in *Mesolasia* Hampson, 1898, is because Hampson, mistakenly believing that *Sphinx leucaspis* Cramer, 1775, was the type of *Aethria*, designated *Sphinx haemorrhoidalis* Stoll, 1790 as the type species of *Mesolasia*, not realizing that this is also the type species of *Aethria* (designated by Kirby 1892). *Aethria ornata* seems to be congeneric with *A. haemorrhoidalis* (Stoll 1790), the type species of *Aethria* Hübner, 1819, but is probably more closely related to *A. melanobasis* (Druce 1897).

rubroscapus Ménétriés, 1857
(Fig. 7)

Glaucopis rubroscapus Ménétriés, 1857: 142, pl. 14, fig.

7. **Lectotype hereby designated**, male: [USA], California (Wosnesensky). With four labels: “47.”; a round gold label; a green label with “Californ.” printed; and a printed label “coll. Acad. Petrop.”.

Current combination. *Ctenucha rubroscapus* (Ménétriés).

Condition of the lectotype. Forelegs and right antenna missing. Abdomen partially eaten by museum pests, but genitalia seems to be intact.

Remarks. A single specimen was found, from a type series of unknown size. There is an additional white label with printed black edges on a different pin from the lectotype, below the specimen, with “rubroscapus/Nobis Californ.” handwritten.

The validity of the synonymies of *C. rubroscapus* has not been evaluated.

vidua Ménétriés, 1857
(Fig. 8)

Glaucopis vidua Ménétriés, 1857: 141, pl. 14, fig. 6.

Lectotype hereby designated female, BRAZIL [no further data]. With two labels: a round gold label, and a green label with “Brasilia” printed.

Current combination. This name is currently considered a junior subjective synonym of *Syntomeida syntomoides* (Boisduval 1836). Synonymized by Hampson (1898: 306).

Condition of type. Left antenna partly broken.

Remarks. Described from an unspecified number of specimens. With additional white label with printed black edges placed below the specimen, reading “vidua /Nobis Brasil” in handwriting. The specimen is likely mislabeled, as the species is not known to occur in Brazil, neither in any other country in South America (Hampson, 1898: 307).

Syntomeida syntomoides has many other synonyms, but their validity has not been evaluated here.

vidua var. *spiracula* Ménétriés, 1857
(Fig. 9)

Glaucopis vidua var. *spiracula* Ménétriés, 1857: 141.

Lectotype hereby designated male, BRAZIL [no further data]. With two labels: a round gold label, and a green label with “Brasilia” printed.

Current combination. See above under *vidua*.

Condition of type. Right antenna missing.

Remarks. Described from an unspecified number of specimens. Ménétriés (1857) mentioned that the specimen(s) that received this name came from the collection of a Mr. Becker in Paris. Although no label indicating this information was found, the round gold label and the location of the lectotype hereby designated, immediately below the lectotype of *Glaucopis vidua*, followed by the label saying “vidua Nobis Brasil”, are here considered evidence to support our hypothesis that the specimen here designated as a lectotype is in fact the same one received by Ménétriés from Mr. Becker.

According to article 45.6.4 of the ICZN (1999), this name is to be considered a subspecies, and the correct combination would be *Syntomeida syntomoides spiracula* (Ménétriés). The validity of this status remains to be evaluated, though it is likely that it is only an individual variation, as the wing pattern of this species shows some intraspecific differences in the size of the spots.

The discussion about the possible wrong type locality addressed in *Glaucopis vidua*, above, also applies here.

ACKNOWLEDGMENTS

The first author is most grateful to Sergey Sinev for providing access to the collection and facilities at ZIN, and to the staff of the Lepidoptera department of this institution for their support during her visit. This work could not have been completed without the kind assistance of Alessandro Giusti, Geoff Martin, and Martin Honey (BMNH), Wolfram Mey (ZMHB), and Niels Kristensen and Ole Karsholt (ZMUC). Our special gratitude to Julian Donahue for his very important and constant help. Janet Reid revised the manuscript, and Daniela Bená made the generic illustrations. We also thank Sergey Sinev, Vitor Becker, and anonymous reviewers for significant improvements in the manuscript. This research was funded by the Fundação de Amparo à Pesquisa do Estado de São Paulo (grants 2002/13898-0, 2009/11159-5, 2011/50225-3, and 2012/02444-0), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq grant 563332/2010-7 – SISBIOTA/ Rede Nacional de Pesquisa e Conservação de Lepidópteros), and Pró-Reitoria de Pesquisa da Universidade de São Paulo (Projeto 1). The second author has also been supported by a CNPq fellowship (process number 305905/2012-0).

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Submitted for publication 19 May 2013; revised and accepted 27 June 2013.

IMMATURE STAGES AND ECOLOGICAL CHARACTERISTICS OF *IDALUS LINEOSUS* WALKER
(EREBIDAE: ARCTIINAE)

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ABSTRACT. The caterpillars of *Idalus lineosus* Walker (Arctiinae) are external folivores that specialize in eating mature leaves of *Roupala montana* Aubl. (Proteaceae) in the cerrado (Brazilian savannah). The aim of this study was to present morphological and ecological characteristics of the immature stages of *I. lineosus*. We evaluated relative abundance, seasonal variation, and parasitized proportion of *I. lineosus* in various sites of the cerrado. The caterpillars are solitary, exhibit morphological variation between instars, and present varied color patterns in the last larval instar. The relative abundance of the caterpillar on the host plant varies seasonally and spatially in the cerrado sensu stricto reliefs of two soil types (oxysoil and rocky soil). The caterpillars were parasitized mainly by a gregarious Hymenoptera; multiparasitism was also registered, with interactions between *Apanteles* sp. and *Protapanteles* sp., and *Cidaphus* sp. with *Protapanteles* sp.

Additional key words: Caterpillar, cerrado, polymorphism, *Roupala montana*, tri-trophic interaction.

Arctiinae is currently considered a subfamily of Erebidae (Lafontaine & Schmidt 2010, Zahirí et al. 2010) and includes approximately 11,000 species worldwide (Scoble 1995). Of the 2,000 species of Arctiinae estimated to occur in Brazil (Brown Jr. & Freitas 1999), 723 have been recorded in the Cerrado biome (Brazilian savannahs) (Ferro et al. 2010).

The genus *Idalus* Walker, 1855, comprises approximately 60 species (Watson & Goodger 1986); of these, four species are considered *Idalus* sensu lato (*I. veneta* Dognin, 1901; *I. arrupta* Schaus, 1905; *I. flavibrunnea* Dognin, 1906; *I. lutescens* Rothschild, 1909). Thus, *I. lineosus* Walker 1869, is considered a true *Idalus* species and occurs throughout Central and South America (http://www.inra.fr/papillon/arct_guy/htm). In Brazil, *I. lineosus* occurs in forests (Teston et al. 2006, Ferro & Diniz 2007) and in open areas of vegetation, as found in the Cerrado (Bendicho-López et al. 2006, Ferro et al. 2010, Oliveira 2010). There are no publications that report the occurrence of *I. lineosus* in other biomes, such as Caatinga and Pantanal; however, we cannot exclude the possibility of its occurrence.

In Distrito Federal (DF) the caterpillars of *I. lineosus* are external leaf feeders on *Roupala montana* Aubl. (Proteaceae), with certain individuals feeding on their

inflorescences (Bendicho-López et al. 2006; the species *Idalus prop sublineata* presented by Bendicho-López et al. refers to the species *I. lineosus*, previously identified erroneously). Another species of this genus, *I. flavicostalis* Rothschild 1935, also feeds on this host plant (Bendicho-López et al. 2006).

Roupala montana is widely distributed in the Brazilian savannah, especially in the cerrado sensu stricto (Felfili & Abreu 1999), where it presents as shrubby or arboreal habit (Carvalho 2003), and in central Brazil, where *R. montana* ranges from 20 cm to 6 m in height (Oliveira 2010). This host plant may be considered evergreen because the old foliage persists on the tree until the emergence of new leaves (Franco 1998). To the best of our knowledge, the caterpillar of *I. lineosus* seems to specialize in feeding on this plant species (Diniz et al. 2001, Bendicho-López et al. 2006, Oliveira 2010).

Knowledge about the immature stages of Lepidoptera is important because it aggregates information on the biology and ecology of these organisms; it is also useful for their taxonomy and systematics (Beebe et al. 1960, Fleming 1960; Kaminski et al. 2002, Bizarro et al. 2003, Freitas & Brown Jr. 2004). Our study system comprised by *I. lineosus* and its host plant in a marked seasonal

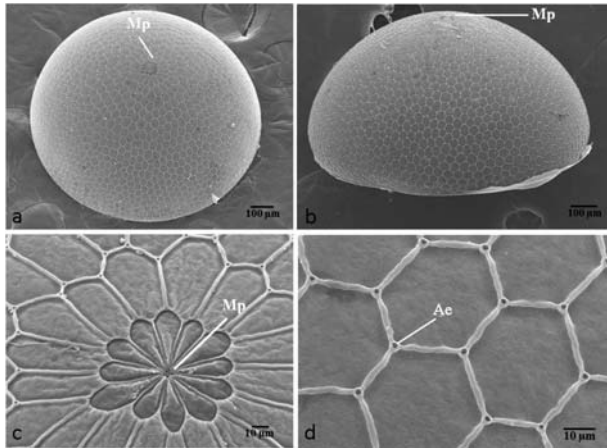


FIG. 1. Egg of *Idalus lineosus* in scanning electron microscopy. (a) Dorsolateral view; (b) lateral view; (c) micropylar area (Mp); (d) details of hexagonal cells and aeropyles (Ae).

biome, the central Brazilian cerrado, is useful for our investigation because the caterpillars of this moth species apparently consume only one species as a host plant, and this facilitates multiple comparisons, such as spatiotemporal studies. Furthermore, we can compare the relative abundance of this moth species between the two very marked climatic seasons. Thus, the objectives of this study were to characterize the immature stages of *I. lineosus*, to assess the relative abundance and seasonal variation of the caterpillars, and to verify the proportion of caterpillar parasitism of the different types of cerrado sensu stricto.

METHODS

Information on the immature stages of *I. lineosus* was obtained from three rounds of sampling at different time periods. In the three sampling methods described below, there was no duplication of any examined plants. All areas sampled are located in the Cerrado biome, which exhibits marked climatic seasonality with a dry season (May to September) and a rainy season (October to April).

In this work, we used three data sets. First, for morphological characterization, we searched for eggs, caterpillars, and pupae on the foliage of 500 plants of *R. montana* between May and June 2011 at Fazenda Água Limpa (FAL, $n = 100$) (altitude 1,117 m, 15°57'S, 47°55'W); Jardim Botânico de Brasília (JBB, $n = 100$) (altitude 1,118 m, 15°57'S, 47°55'W); and in the Ecological Reserve (RECOR, $n = 300$) (altitude 1,048 m, 15°56' S, 47°53' W). Second, the relative abundance of caterpillars *I. lineosus* on *R. montana* was accompanied by monthly searches on the foliage of 100 plants from May 2008 to April 2009 ($n = 1,200$ plants sampled), at Parque Estadual dos Pireneus (PESP), in Pirenópolis, state of Goiás (GO) (altitude 1,289 m, 15°48'S, 48°50'W), in the cerrado sensu stricto reliefs of the rocky soil. Finally, we compared the spatial relative abundance of *I. lineosus* caterpillars among sites by sampling caterpillars on 1,000 individuals of *R. montana* in May and June 2009 at each of the five cerrado sites: 1) PESP; 2) Parque Nacional Chapada dos Veadeiros

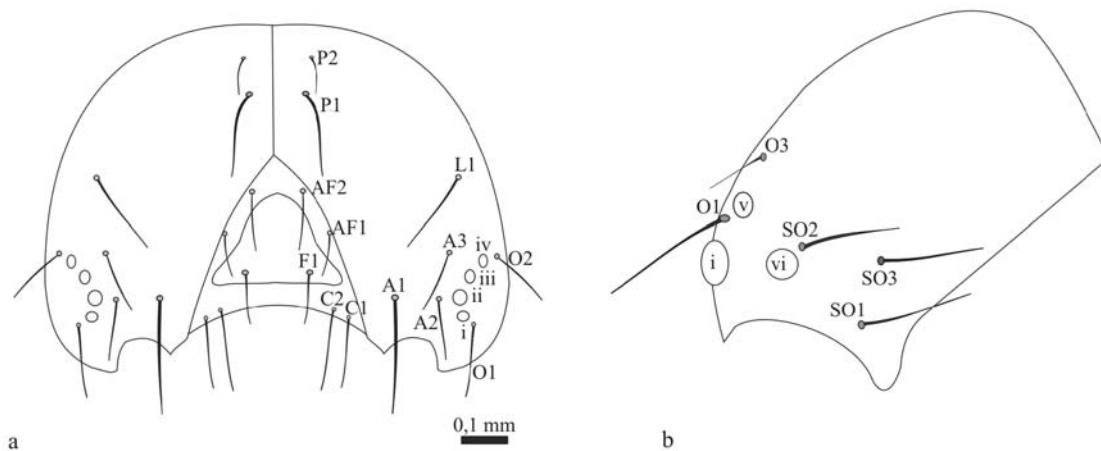


FIG. 2. Chaetotaxy of cephalic capsule of the first instar larvae of *Idalus lineosus*, (a) dorsal and (b) lateral views. Names of setae: A-anterior, AF-adfrontal, C-clypeal, F-frontal, L-lateral, O-stemmatal, SO-substemmatal; i-vi: stemmata. The small barbs on the setae and the presence of the microsetae and punctures were omitted.

(PNCV) in GO (altitude 1.034 m, 14°09'S, 47°47'W); 3) FAL; 4) JBB; and 5) Parque Nacional de Brasília (PNB) (altitude 1.085 m, 15°52'S, 47°49'W). FAL, JBB, and PNB are located in the state of DF. The study areas located in GO comprise a physiognomy cerrado sensu stricto developed in rocky soils (Felfili & Fagg 2007, Moura et al. 2007), while the other three locations comprise cerrado sensu stricto developed in oxisols (Ribeiro & Walter 2008).

All caterpillars found were individually reared in the laboratory in plastic pots protected by tulle fabric until the emergence of adults. Luminosity, humidity, and temperature were not controlled. Leaves of *R. montana*, with the petiole inserted into a small container with water to prevent drying, were added for food as needed. Two emerged adult females were kept in one cage in an attempt to obtain eggs. Observations of morphological aspects and measurements of immature stages were performed with a Leica® S8 APO stereomicroscope equipped with micrometer scale. Photographs were taken with a Canon® SX30IS digital camera.

Eggs were prepared for scanning electron microscopy (SEM), using Balzers® CPD 030 equipment for critical point drying. The eggs were then mounted on double-sided tape on a metal support and covered with gold in a Balzers® SCD 050 sputter coater. Specimens were examined in a JEOL® JSM 7001F microscope, and images were collected.

The terminology used for eggs follows Peterson (1963) and Dell'Erba et al. (2005); the general morphology of the immature stages, and the chaetotaxy of the head capsule follows Stehr (1987). Dead caterpillars were fixed in Kahle solution, and parasitoids were preserved in 70% alcohol and identified according to Wharton et al. (1997) and Gauld (1997). Species of Lepidoptera were identified by Vitor Becker, parasitoids by André R. Nascimento, and host plant species by the staff of the Herbário da Universidade de Brasília UB. Vouchers for all insect species were deposited in the entomological collection of the Department of Zoology, University of Brasília.

A circular analysis (Oriana version 4) (Kovach 2011) was used to verify the relative abundance of the caterpillars during 1 year of sampling (second data set), in which each month was converted into angles. January 2009 was chosen as 15°, and December 2008 was chosen as 345°. A Rayleigh test, available in version 4 of Oriana (Kovach 2011), was applied to determine whether the caterpillars had an aggregated or uniform temporal distribution.

A Chi-square test was used to assess spatial (PESP, PNCV, FAL, JBB, PNB) and temporal (dry season and

rainy season) differences in the proportion of caterpillars collected as well as in the proportion of parasitism by Hymenoptera between the rocky soil cerrado (GO) and the oxysoil cerrado (DF). The data used for analyses of the proportion of parasitism were lumped for all caterpillars reared from the three data sets. All analyses were performed with the statistical program R 2.12.4 (R Development Core Team, 2011).

RESULTS

General biology of immature stages

A total of 6,700 plants of *R. montana* were inspected, and 210 caterpillars of *I. lineosus* were collected. From these, only 54 of the reared (25.6%) caterpillars did not reach the adult stage, and of these 18.5% died from parasitism and the others (44 individuals) died from unknown reasons. All caterpillars were found solitary on leaves of *R. montana*. The detailed observation of larval development was performed with 25 caterpillars obtained from the first data set. The number of caterpillars followed in each instar (n) varied because they were collected in the field at different instar stages. From these, only five caterpillars emerged as adult.

No eggs were found in the field but instead were obtained by the oviposition of two females that emerged in the laboratory. The eggs were laid singly in the rearing pot (mean 68.5 ± 10.60 eggs from the two adult females) (Fig. 3a). These eggs failed to hatch because they were not fertilized.

Idalus lineosus presented six larval instars (Fig. 3b–g) and completed its development (from first larval instar to adult), on average, in 54 ± 5.6 days (n = 5). The first instar caterpillars remained on the abaxial leaf blade, but the last instar caterpillars occurred more often on the adaxial surface. No pupa was found in the field, but in the laboratory pupae occurred on the leaves or attached to the rearing pot.

Morphological traits of immature stages

Egg (Figs. 1, 3a): diameter 1.04 ± 0.03 mm; height 0.59 ± 0.02 (n = 10). Eggs are hemispherical, slightly flattened, with sculptured chorion and a yellowish color soon after oviposition.

First instar (Fig. 3b): body length 5 ± 0.07 (n = 5), cephalic capsule width 0.6 ± 0.11 (n = 5). Head, antennae, and stemmata whitish-yellow. Cephalic capsule with 17 pairs of long setae, as seen in most Lepidoptera. Head chaetotaxy (Fig. 2) conserved in all subsequent instars. Body tegument pale yellow with sparse orange pigmentation, with fine and pale setae arising from dorsal and lateral verrucae. Both thoracic legs and prolegs yellowish white. Development time 5–6 days.

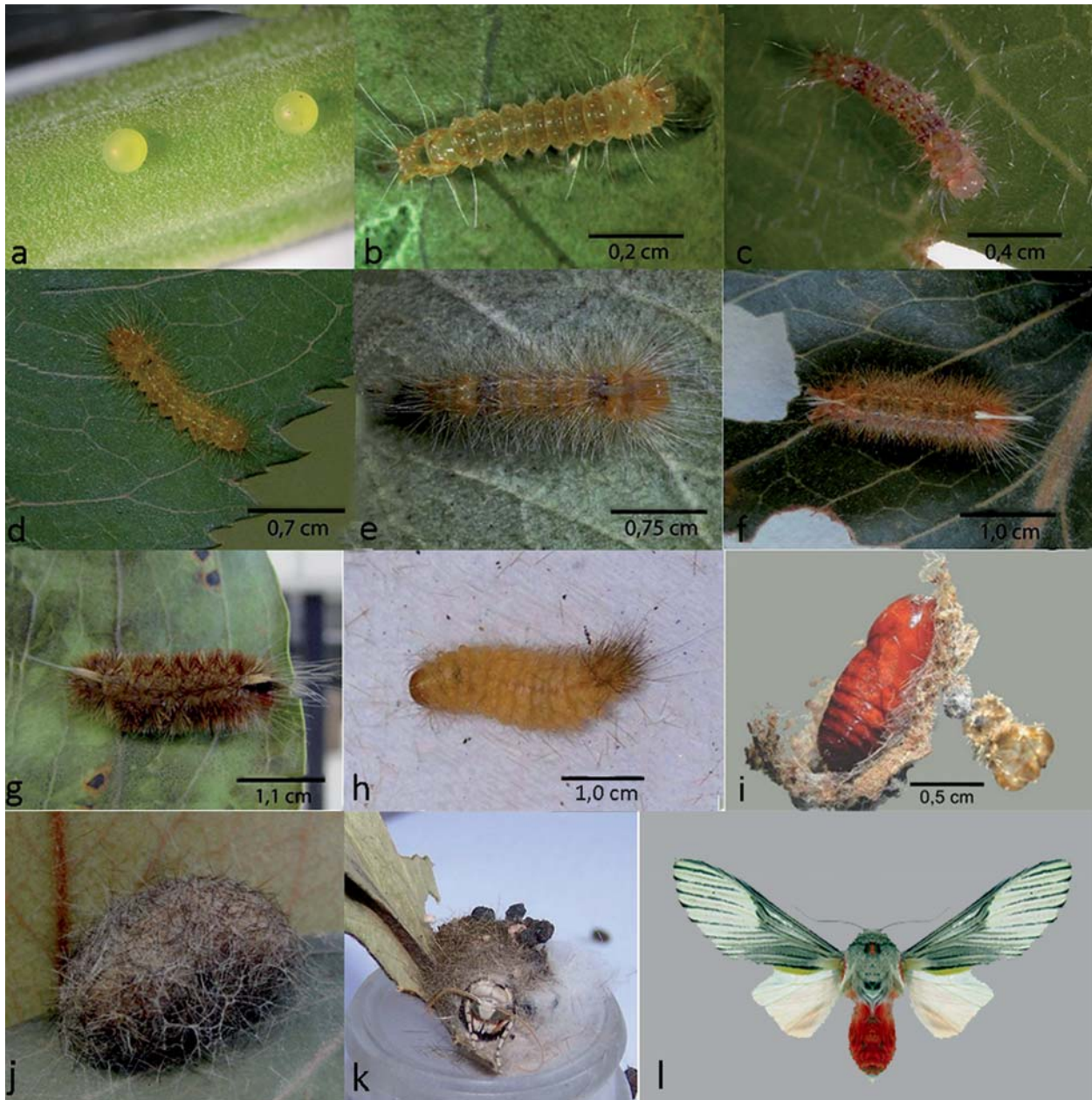


FIG. 3. Eggs, larval instars of *Idalus lineosus*, and pupa and adult of *I. lineosus*. (a) Eggs; (b) first instar; (c) second instar; (d) third instar; (e) fourth instar; (f) fifth instar; (g) sixth instar; (h) pre-pupa; (i) pupa; (j) pupal shelter; (k) adult emergence; (l) adult.

Second instar (Fig. 3c): body length 10.1 ± 0.15 ($n = 6$), cephalic capsule width 1.1 ± 0.04 ($n = 6$). Head and antennae as in the first instar. Stemmata darker than in the first instar. Body tegument pinkish with wine-colored dots all over the dorsal view, visibly darkest on abdominal segments A1 and A7. Setae larger and more densely distributed than in the first instar. Both thoracic legs and prolegs are pinkish. Development time 6–7 days.

Third instar (Fig. 3d): body length 13.1 ± 0.25 ($n =$

9), cephalic capsule width 1.4 ± 0.14 ($n = 9$). Head and antennae orange. Stemmata black. Body tegument orange, with two longitudinal light-orange stripes, and segments A1 and A7 slightly shadowed on the dorsal view. Presence of yellowish and some dark brown setae dorsally and laterally arranged. Setae are more elongated on segments A1, A2, A8, A9, and A10 than in the others. Both thoracic legs and prolegs are also orange. Development time 5–6 days.

Fourth instar (Fig. 3e): body length 16.3 ± 0.25



FIG. 4. Sixth instar caterpillar of *Idalus lineosus* showing variation in color of the setae. (a) whitish-yellow; (b) gray; (c) orange brown; (d) dark brown.

($n = 6$), cephalic capsule width 2.0 ± 0.14 ($n = 6$). Head, antennae, and stemmata as in the third instar. Body tegument orange brownish. Dark brownish pigmentation is evident on segments A1 and A7. Presence of tufts of white setae on dorsal view of segment A1. In the remaining segments, setae are similar to those of the previous instar. Both thoracic legs and prolegs orange. Development time 6–7 days.

Fifth instar (Fig. 3f): body length 19.4 ± 0.32 ($n = 5$), cephalic capsule width 2.4 ± 0.12 ($n = 5$). Head light brown, antennae white, stemmata dark brown. Body tegument orange brownish with two longitudinal, whitish, dorsal stripes. Presence of orange and dark brownish setae dorsally and laterally arranged. Setae arising from verrucae distributed around the body tegument, and the whitish tufts of setae become more apparent on segments A1 and A7. Lateral reddish verrucae are also present. Setae arising from A1, A2, A8, A9, and A10 are longer than those arising elsewhere. Both thoracic legs and prolegs as in the previous instar. Development time 7–8 days.

Sixth instar (Fig. 3g): body length 21.8 ± 0.21 ($n = 5$), cephalic capsule width 3.1 ± 0.23 ($n = 5$). Head pale brown, antennae white, and stemmata dark brown. Body tegument is greyish with setae displaying individual variations in coloration; setae may be whitish-yellow, gray, orange-brown, or dark brown (Fig. 4). In spite of the color variation of most setae, all caterpillars show whitish setae arising in tufts on segments A1 and A7. A1 also bears a distinct blackish tuft of setae. Setae arising from dorsal and lateral verrucae are disposed all over the tegument. White

setae arising from A1 and A2 segments are longer than those elsewhere. Both thoracic legs and prolegs orange. Development time 9–11 days.

Pre-pupa (Fig. 3h): mature sixth instar caterpillar exhibited reduced size and movement and lost almost all setae, which were used in constructing the pupal cocoon (Fig. 3j). Tegument becomes pale yellow, with setae restricted to the anterior and posterior ends.

Pupa (Fig. 3i): pupae (length 10.4 ± 0.15 ; $n = 5$) cylindrical, smooth, and dark brown. Development time 18 ± 2.7 days ($n = 5$). Attached to the pupal cocoon was a deposit of setae and feces discarded by the last larval instar (Fig. 3j). The emerged and mounted adults are illustrated in Figs. 3k–l.

Seasonal and spatial variation

For the second data set, we examined 1,200 plants in the PESP in 1 year and found 32 caterpillars of *I. lineosus*. The species showed an aggregated distribution in the dry season ($z = 25.88$, $p < 0.05$), and the peak of the relative abundance of the caterpillars occurred in May, with 21 individuals ($\mu = 137.28^\circ$, $sd_c = \pm 26.39^\circ$, mean = 135°) (Fig. 5).

For the third data set, we inspected 5,000 plants and collected 153 caterpillars. The relative abundance of caterpillars within each vegetation type did not differ significantly. However, the number of caterpillars was significantly higher ($Z = -9.10$, $Z1 = 0.26$, $Z2 = 0.67$, $p < 0.01$) in the oxysoil cerrado (DF sites) ($n = 121$) than in the rocky soil cerrado (GO sites) ($n = 32$). The probability of finding a caterpillar in a survey of 1,000 *R. montana* plants was similar in the three oxysoil

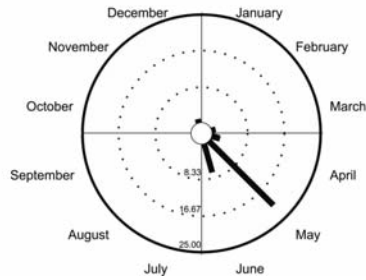


FIG. 5. Seasonal variation in caterpillar relative abundance of *Idalus lineosus* from May 2008 to April 2009, Parque Estadual dos Pireneus, Pirenópolis, Goiás. Angles and their corresponding months: 15° (January 2009), 45° (February 2009), 75° (March 2009), 105° (April 2009), 135° (May 2008), 165° (June 2008), 195° (July 2008), 225° (August 2008), 255° (September 2008), 285° (October 2008), 315° (November 2008), and 345° (December 2008).

cerrado sensu stricto sites ($p \leq 0.05$) (FAL 40 caterpillars, 26%; JBB 35 caterpillars, 22.9%; PNB 46 caterpillars, 30.1%) and was also similar between the two sites in the rocky soil cerrado sensu stricto (PNCV 13 caterpillars, 8.5%; PESP 19 caterpillars, 12.4%). However, this differed significantly if all sites were lumped together to compare oxysoil (DF) and rocky soil (GO) cerrados.

Parasitism

Parasitism was responsible for only 5% ($n = 10$ individuals) of the total caterpillars ($n = 210$) collected and reared in the laboratory for all periods and sites. Eight of the parasitized caterpillars were attacked by Hymenoptera (Braconidae and Ichneumonidae), and two were killed by dipterans (Tachinidae, Exoristinae). One species of the hymenopteran parasitoids belonging to *Protapanteles* (Braconidae: Microgastrinae), a gregarious species with 49.25 ± 15.9 individuals per host (Fig. 6b), was responsible for five of the caterpillar deaths (75%). The other species were *Apanteles* sp. (Braconidae: Microgastrinae) (Fig. 6c), *Cidaphus* sp. (Ichneumonidae: Mesochorinae), and *Pristomerus* sp. (Ichneumonidae: Cremastinae) (Fig. 6d). Multiparasitism occurred in three individuals of *I. lineosus*, with interactions between *Apanteles* sp. and *Protapanteles* sp. (two occurrences in the PESP), and *Cidaphus* sp. and *Protapanteles* sp. (one occurrence in PNCV).

For a comparative analysis of the proportions of parasitism, we used our third data set in the following five areas: PESP and PNCV (rocky soil cerrado) [GO]; FAL, JBB, and PNB (oxysoil cerrado) [DF], with equal samples and similar period by location ($n = 1,000$ censuses in *R. montana*). The caterpillars from the two

rocky soil cerrado areas ($n = 32$) showed a higher species richness of hymenopteran parasitoids ($n = 4$ species) and higher parasitism rates (18.75%). In oxysoil cerrado areas ($n = 121$ caterpillars collected), only one species of hymenopteran was found parasitizing *I. lineosus*, representing only 1.65% of the caterpillars collected. A Chi-square analysis revealed that the rates of parasitism differed significantly between areas of rocky soil cerrado sensu stricto (GO) and oxysoil cerrado sensu stricto (DF) ($\chi^2 = 11.68$, $p < 0.05$). The caterpillars collected in PESP (GO) had the highest parasitism rates (70% of the total parasitized caterpillars in the five areas). Parasitism differed significantly among areas ($\chi^2 = 7.52$, $p < 0.05$).

DISCUSSION

Despite the high sampling effort, we found no eggs on leaves during the field work. In the laboratory, only one egg was laid on the leaf of the host plant, and the remaining eggs were laid on the plastic pot walls. This suggests that oviposition may occur on another plant structure, such as the stem or outside of the host plant (see Bernays & Singer 2002). Similar biological characteristics have been found in another species, *Idalus agastus* Dyar 1910, which has a similar egg morphology and the same number of instars (see Carlos 2011). However, the development time of *I. lineosus* from larval first instar to adult was approximately 15 days shorter than that obtained for *I. agastus* and approximately 25 days longer than that obtained for *I. admirabilis* (Cramer 1777) (Santos et al. 2006; Carlos 2011). The caterpillar of the early instars remains on the abaxial leaf, and this may be a strategy to avoid dehydration because at this time of the year the cerrado has very low rainfall and relative humidity.

The larval morphological variation found among instars of *I. lineosus* is a common feature in the caterpillars of Arctiinae (Santos et al. 2006, Pereira et al. 2007, Rodríguez-Loeches & Barro 2008). As observed in other caterpillar species, certain characters may change during their development. These variations may include the color of the tegument; density, length, and color of the secondary setae; number of verrucae (Rab Green et al. 2011), and the arrangement of the setae (Rodríguez-Loeches & Barro 2008), and in many species of Arctiinae the first instars are completely different from the last instars (Rab Green et al. 2011).

The last larval instar of *I. lineosus* presented a phenotypic variation in color, a trait that has been described for other species of Arctiinae (Wagner 2005); this is considered a common event in lepidopteran (Greene 1996, Hazel 2002; Suzuki & Nijhout 2006, Noor et al. 2008, Yamasaki et al. 2009). Several

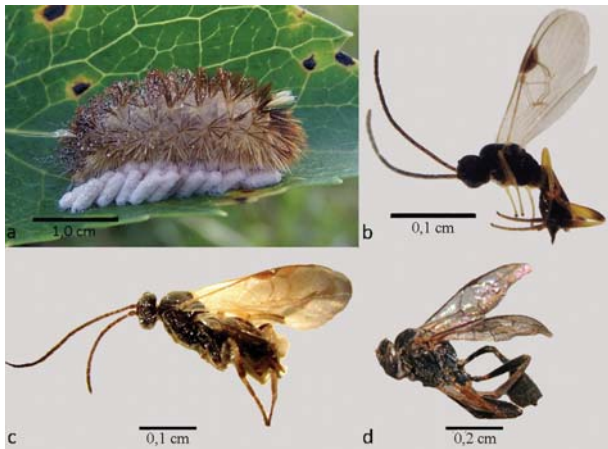


FIG. 6. (a) Parasitized sixth instar caterpillar of *Idalus lineosus*; (b) *Protapanteles* sp., the most frequent parasitoid of *I. lineosus* (Hymenoptera: Braconidae, Microgasterinae); (c) *Apanteles* sp.; (d) *Pristomerus* sp.

explanatory mechanisms for this phenomenon have been proposed. In many generalist caterpillar species, the color of the tegument varies due to the pigment present in the host plants (Greene 1989, Monteiro 1991, Ahmad 1992, Burghardt et al. 2001, Sandre et al. 2007a, Canfield et al. 2009). Other factors that may also influence this color variation include thermoregulation (Sandre et al. 2007b), seasonal hormonal regulation (Rountree & Nijhout 1995), and ontogenetic causes (Nylin et al. 2001, Grant 2007). For the *I. lineosus* caterpillars, the difference may be related to an ontogenetic process because it was found at sites with similar climate, in the same period of the year, and on a single host plant species. There appeared to be no relation to parasitism because it occurred in caterpillars of all colors, despite the proportion of parasitized caterpillars being low.

The aggregated temporal distribution of *I. lineosus* during the dry season confirms the expected pattern for caterpillars in the cerrado (Morais et al. 1999) and suggests that this species is univoltine. The convergence in the flowering times of the plants in the cerrado in the late dry season and early rainy season (Oliveira 2008) provides increased availability of food resources for adult Lepidoptera during this period. Therefore, the peak of caterpillar relative abundance in the dry season can ensure the occurrence of adults during a highly favorable period and in a probable “period free of enemies” (Morais et al. 1999).

In spite of the low overall proportion of parasitism of caterpillars, it is tempting to relate the higher proportion of parasitism and the lower abundance of caterpillars to the rocky soil cerrado. The higher proportion of hymenopteran attacks to caterpillars

compared to dipteran attacks is a common pattern in the cerrado (Scherrer et al. 1997, Pessoa-Queiroz 2008), and this pattern was found for parasitism in *I. lineosus*. In the present study, the most abundant parasitoid, *Protapanteles* sp. Ashmead 1898, described as an endoparasitoid of Lepidoptera (Whitfield et al. 2002, Yu et al. 2005, Pentead-Dias et al. 2011, Souza 2012), was recorded in *I. lineosus* for the first time.

Even in the case of a single caterpillar species consuming only one species of host plant, it is known that factors other than food availability affect the size of populations, e.g., interactions with natural enemies and climatic seasonality, as corroborated in this study. In addition, we present the first biological information on the immature stages of *I. lineosus*. This information is important for understanding tri-trophic interactions (plant–herbivore–parasitoid) in the cerrado. Further descriptions of life histories in many others species whose life histories are currently unknown, it will provide results to facilitate experimental studies and phylogenetic reconstructions.

ACKNOWLEDGMENTS

We thank Willer Bontempo for his help in collecting and rearing the caterpillars; Ingrid M.S. Gracielle and Márcia C.O. Rocha helped us in scanning electron micrographs in the microscopy laboratory of the University of Brasília. We thank University of Brasília, Fazenda Água Limpa and the Graduate Program in Ecology for permission to carry out the research and logistical support. Financial support was received from National Council for Scientific and Technological Development (CNPq), Federal District Foundation for Science and Research Supporting, all of which are in Brazil. CL was supported by fellowship from FAPDF (PRONEX), LB from CNPq, MN, NS and GF from Brazilian Agency for Improving University Education Capability (CAPES). I.R. Diniz is a CNPq fellow.

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Submitted for publication 7 February 2013; revised and accepted 28 August 2013.

MICROHABITAT USE IN A NORTHERN PERIPHERAL POPULATION OF *APODEMIA MORMO*:
FACTORS BEYOND THE HOST PLANT

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ABSTRACT. The Mormon metalmark (*Apodemia mormo*) is widely distributed throughout western North America. The species exists in two peripheral populations in Canada and is listed as threatened in Saskatchewan and endangered in British Columbia. In Saskatchewan, this butterfly relies on *Eriogonum pauciflorum* for larval food and as its primary nectar source; however, presence of its host plant is insufficient to define habitats actually utilized by the butterfly. We investigated microhabitat characteristics that might explain habitat use of *A. mormo* adults using 102 host plant quadrats in which the butterfly was occupied (present) or unoccupied (absent) in Grasslands National Park and the Val Marie Community Pasture, Saskatchewan. Linear discriminant analysis demonstrated significant differences between occupied and unoccupied quadrats. *Apodemia mormo* was found disproportionately in quadrats with a combination of the following variables: higher percent bare ground and soil pH, steeper slope, southerly to south-westerly aspect, lower elevation, and lower soil nitrogen. Our results show that habitat use by *A. mormo* butterflies is correlated with environmental factors that define, either directly or indirectly, the local probability of association with host populations.

Additional key words: *Apodemia mormo*, conservation, *Eriogonum pauciflorum*, Grasslands National Park, habitat selection

Understanding relationships between species and their habitats is a central aspect of ecology (Grinnell 1917; Elton 1927), and has particular significance for species deemed at risk as well as for populations at the extreme periphery of their ranges (Fraser 2000). According to evolutionary theory, individuals and necessary resources are expected to be more concentrated at the center of a species' range than at the periphery; therefore, gradual declines in abundance are often observed toward range edges (Brown 1984). However, given that resource abundance and associated population sizes are dynamic, these patterns vary. As recent range shifts to higher latitudes in some species are associated with climate change (e.g., Parmesan & Yohe 2003, Battisti et al. 2005), peripheral populations presently existing at higher latitudes in North America will likely become increasingly important for the persistence of many animal and plant taxa.

There are other ecological and evolutionary reasons for interest in peripheral populations. Although they are thought to be genetically impoverished relative to central populations, peripheral populations may also be more genetically distinct and freer to evolve and change (Mayr 1940, Noss 1994). Environmental variation clearly affects distribution, phenology, abundance, and diversity of populations (Crick & Sparks 1999; Roy & Sparks 2000, Parmesan & Yohe 2003), and such relationships may be more easily discerned in

populations near species range limits. Indeed, Rosenzweig (1991) suggested that it is crucial to investigate microhabitat characteristics of populations at range peripheries, where natural selection likely drives individuals to select the most advantageous microhabitats. This could have interesting consequences for understanding insect-host plant relationships, as under more extreme conditions microhabitat characteristics may be important constraints on host use. In more benign environments such constraints may be more difficult to discover.

Lepidopterans have long been used as model species for studies in ecology and evolutionary biology, and many species discriminate among habitats based on environmental variables in addition to presence of their host plants (Papaj & Rausher 1987, Lastra et al. 2006, Ashton et al. 2009). For example, soil nutrients affect habitat preferences of some butterfly species (Ehrlich 1965, Ravenscroft 1994, Prudic et al. 2005). Likewise, physical characteristics of grasslands, such as slope and aspect, may affect exposure to solar radiation and create a variety in thermal microenvironments that can affect larval growth and development, as has been shown in studies of the bay checkerspot butterfly (Murphy & Weiss 1988).

We investigated microhabitat characteristics for the disjunct northern peripheral prairie population of the Mormon metalmark (*Apodemia mormo* Felder &



FIG. 1. *Apodemia mormo* on *Eriogonum pauciflorum* in Grasslands National Park, Saskatchewan. (Photo credit: Johane Janelle of Val Marie, SK)

Felder 1859, Riodinidae) in southern Saskatchewan, Canada. *Apodemia mormo* is the only riodinid in Canada, and this prairie population is listed as threatened (COSEWIC 2003, SARA Public Registry). Our objective was to better understand microhabitat use of butterflies by comparing soils, vegetation, and topography between colonies of host plant habitats where the butterfly is present (occupied habitat) and colonies where it is absent (unoccupied habitat). Such higher understanding of this species, in turn, should contribute to greater efficiency in prioritizing particular local areas for conservation action.

MATERIALS & METHODS

Study sites. Grasslands National Park (GNP; 49° 15' N, 107° 09' W) was established in 1984 in the mixed grass prairie ecoregion of southern Saskatchewan. With long, cold winters and short, hot summers, GNP comprises upland and lowland grasslands that are interspersed with sparsely vegetated badland habitat. Approximately half of the 52,700 ha GNP includes badlands, which are eroded landscapes with distinct plant communities characterized by sparse vegetation (Michalsky & Ellis 1994).

Grasslands National Park is apportioned into the East and West Blocks. These two blocks are separated by approximately 40 km of privately owned pasture and farmland. The East Block includes much of Rock Creek and is surrounded by the Wood Mountain plateau while the West Block surrounds the Frenchman River valley southeast of the village of Val Marie (Saskatchewan Institute of Pedology 1992). The West Block contains a herd of plains bison (*Bison bison*) that graze the area at a density of one bison per 55 ha (W. Olson pers. com. 2012).

In addition to GNP, we studied butterfly habitat in the Val Marie Community Pasture (VMCP; 49° 41' N, 107° 92' W), a 40,649 ha area located several kilometers northwest of the park. The VMCP is stocked at a density of one cow-calf pair per 35 ha, and cattle graze from April until the end of October (T. Dyck pers. com. 2012). The VMCP contains several *A. mormo* colonies as well as large areas of host plant habitat where repeated surveys have not uncovered presence of the butterfly.

***Apodemia mormo* and host plant.** *Apodemia mormo* is a small butterfly of the principally neotropical family Riodinidae (Fig. 1). As the most wide-ranging riodinid in North America, it occurs from Mexico to Canada, throughout the western United States. Only two populations of *A. mormo* are found in southern Canada (Scott 1986, Layberry et al. 1998): the “mountain population” in the Similkameen River Valley in British Columbia, and the “prairie population” in Saskatchewan, which is the subject of this study (COSEWIC 2003, Pruss et al. 2008).

While *A. mormo* populations in the southern part of the species range may have multiple flight periods, the prairie population is strictly univoltine with adults generally emerging at the beginning of August and waning towards the end of the month (Arnold 1980; Peterson et al. 2010). However, depending on weather, the flight period of *A. mormo* can vary from mid-July into September (Henderson et al. 2008).

Branched umbrella plants (*Eriogonum pauciflorum* Polygonaceae) are the sole larval host plant and primary nectar source for *A. mormo* (Figure 1) and rabbitbrush (*Ericamerica nauseosa* Asteraceae) is a secondary nectar source. Females of the *A. mormo* prairie population have been recorded ovipositing in small crevices in the soil and on rocks near *E. pauciflorum*, on lichen growing on bare soil, and on the dead material at the base of *E. pauciflorum* (Wick et al. 2012).

Study design. Historically, presence of *A. mormo* in Saskatchewan has been documented through field surveys by Parks Canada, the Government of Saskatchewan, the University of Alberta, and Rev. R. Hooper. Locations of *E. pauciflorum* habitat without the butterfly have also been recorded (Parks Canada, unpublished data 2011). Using this historical information about presence of both imagos and larvae, we established 102 quadrats (5 m × 5 m) in areas where *E. pauciflorum* is present in the badlands of GNP and the VMCP in 2011. Roughly half (n=50) of these quadrats were in areas where *A. mormo* had previously been documented, or occupied habitat, with 33 in the West Block, 11 in the East Block and 5 in the VMCP. The remaining quadrats of unoccupied habitat were

randomly selected from *E. pauciflorum* locations where *A. mormo* had never been recorded, with 30 in the West Block, 9 in the East Block and 14 in the VMCP. Quadrats were visited from May to July of 2011 and a series of measurements were taken in each quadrat to characterize microhabitat.

Each quadrat was characterized with respect to several variables. Elevation, slope, and aspect were taken at the center of each quadrat, and one soil data based on one core taken from the center of each quadrat. The soil samples were dried and analyzed for total nitrogen content (TKN, mg/L; an indicator of soil fertility status), acidity (pH), and soil electrical conductivity (EC; a measurement of soil salinity) at the University of Alberta. We also measured soil penetrability on site using a penetrometer (g/cm; E280 Dayton Pocket Penetrometer). We characterized the biotic community in each quadrat by estimating percent bare ground, percent host plant cover, and percent cover of all vascular plant species. Grasses and sedges were difficult to reliably identify to species within the time-span of this study, so we estimated abundance of sedges and grasses as total grass cover.

Data Analysis. In order to discriminate between characteristics of occupied and unoccupied habitats, we ran a linear discriminant analysis (LDA) in the R package MASS (Venables & Ripley 2002, R Development Core Team 2009). Linear discriminant analysis is a classic parametric method of classification used with a categorical response variable. LDA aims to minimize variance within groups. It explains the variance between groups using a set of predictor variables and maximizes the ratio of between-class variance to within-class variance by defining the linear transformation, or discriminant function, that best fits the data. This method does not rely on the significance of any single predictor variable, but combines them to create a new linear transformation. In our study LDA models the data as two distributions: one each for occupied and unoccupied habitat. We used a Welch two sample t-test to test whether these two linear transformations (occupied vs. unoccupied) differed statistically from one another.

RESULTS

The average measurements of potential habitat predictors for quadrats occupied or unoccupied by *Apodemia mormo* are summarized in Tables 1 and 2. Table 1 shows that occupied sites had lower soil penetrability, lower available nitrogen, higher acidity, higher salinity, slightly higher bare ground, lower elevation, a more southerly or southwesterly aspect, and a steeper slope than unoccupied habitats. In particular,

on average, occupied habitats were more than 5 degrees steeper and 10 meters lower in elevation than unoccupied habitats.

The vegetation composition surveys were done from May to July, and therefore, there was high variability in which herbaceous flowering plants were present or in identifiable stages. Some of these plant species had a narrow phenological window and were absent from plots in one part of the sampling season, making the data of their presence or absence unreliable; such species were excluded from analyses. However, in addition to the host plant and *E. nauseosa*, creeping juniper, yellow umbrella plant, saltbush, prickly pear cactus, Colorado rubberweed, yellow sweet clover, wild rose and sage were all present throughout the summer and were included in candidate models used for selection of variables. In occupied habitats there was an average of 5.5% more host plant cover, 2% less grass/sedge cover, and 0.5% less yellow sweet clover cover.

The LDA results suggest that distributions of microhabitat traits differed between occupied and unoccupied habitats (Table 3; Figure 2). Table 3 shows the directionality of relationships with presence of the butterfly; for instance, there is a negative relationship with elevation, as more easily visualized in Figure 2. A Welch Two Sample T-test showed a significant difference (df: 122, $t=2.4$, $p=0.02$) between the distributions, indicating that *E. pauciflorum* habitat used by *A. mormo* adults differs from unoccupied habitat. Butterflies were more likely to be found in host plant habitat with lower elevation, a southerly to southwesterly aspect, lower available soil nitrogen, a steeper slope, higher % bare ground, and higher soil pH than those habitats without *A. mormo*.

DISCUSSION

Probability of finding *A. mormo* in quadrats with *E. pauciflorum* was affected by a combination of physical and biotic variables. Although host plant presence is a necessary predictor of butterfly presence, it is insufficient to fully characterize habitats occupied by *A. mormo*. In fact, the coefficients from the LDA show that, when factored in, several other variables were critical in distinguishing occupied and unoccupied habitats. *Apodemia mormo* was found disproportionately in *E. pauciflorum* habitat in low-lying areas, with steep slope, a southerly to southwesterly aspect, lower soil nitrogen, higher pH, and higher % bare ground.

Extent of local *E. pauciflorum* cover increased the probability of *A. mormo* presence. In fact, no other plant variables were identified as significant predictors

TABLE 1. Summary statistics averages (standard error of the mean) of habitat predictors at 102 microhabitat quadrats representing occupied (N=50) and unoccupied (N=52) sites by *Apodemia mormo* in southern Saskatchewan, Canada.

Variable	Unoccupied	Occupied	Difference in Means
Penetrability ^a	3.23 (0.199)	0.295 (0.188)	0.28
TKN mgL ^b	2.58 (0.248)	2.36 (0.136)	0.22
Soil acidity (pH)	5.86 (0.207)	5.96 (0.191)	-0.1
Soil salinity (EC) ^c	1055.3 (168.61)	1159.0 (198.08)	-103.7
Bare ground %	51.0 (3.02)	51.3 (3.10)	-0.3
Elevation (metres)	841.1 (5.91)	831.5 (6.34)	9.6
Aspect [°]	171.6 (13.62)	201.0 (15.12)	-29.4
Slope [°]	12.6 (1.22)	17.8 (1.75)	-5.2

^a Penetrability is a measure of the penetrability of the soil, a higher value implies a higher penetrability.

^b TKN is available soil nitrogen, an indicator of soil fertility status.

^c Soil electrical conductivity (EC) is a measurement of soil salinity.

[°] Compass degrees

TABLE 2. Plant survey in *Apodemia mormo* habitat results expressed as the average % cover for each species in occupied and unoccupied sites, in southern Saskatchewan, Canada.

Latin name	Common Name	Occupied %	Unoccupied %	Difference in %
<i>Eriogonum pauciflorum</i>	Branched umbrella plant	21.5	16.0	5.5
<i>Ericamerica nauseosa</i>	Rabbitbrush	6.4	5.1	1.3
<i>Juniperus horizontalis</i>	Creeping juniper	3.7	2.8	0.9
<i>Opuntia polyacantha</i>	Prickly pear cactus	0.5	0.9	-0.4
<i>Poaceae</i> & <i>Cyperaceae</i>	Grasses and sedges	5.4	7.4	-2.0
<i>Hymenoxys richardsonii</i>	Colorado rubberweed	0.1	1.1	-1.0
<i>Eriogonum flavum</i>	Yellow umbrella plant	0.7	0.6	0.1
<i>Artemisia sp.</i>	Sage	4.5	5.0	-0.5
<i>Atriplex nuttallii</i>	Saltbush	2.3	0.9	1.4
<i>Melilotus officinalis</i>	Yellow sweet clover ¹	0.1	0.6	-0.5
<i>Rosa sp.</i>	Wild rose	1.6	2.6	-1.0

¹ *M. officinalis* is an invasive species

of habitats occupied by *A. mormo*, including presence of the secondary nectar source, *E. nauseosa*. High host plant densities are likely crucial for developing larvae as they undertake several short distance migrations from one host plant to another during their late instar development (Peterson et al. 2010, Wick et al. 2012). Host plant density is also critical for other insect-plant systems. For example, density of host plant flowerheads, influenced the presence and abundance of the endangered large blue butterfly, *Maculinea teleius* in Europe (Batary et al. 2007).

Many other studies have also shown that microhabitat factors, in addition to host plant presence, affect habitat selection by insects. For example Thomas et al. (1986) demonstrated that the ideal habitat for the British silver spotted skipper (*Hesperia comma*) consisted of broken south-facing terrain with 45% host plant cover and 40% bare ground. In fact, the butterfly had apparently disappeared from sites after these habitat characteristics had been disturbed, suggesting strong ties between microhabitat characteristics and butterfly presence. Bonebrake et al. (2010) found that the relationship between oviposition behavior and offspring performance was context dependent, and that habitat heterogeneity was likely an important factor.

In a study on the Quino checkerspot butterfly (*Euphydryas editha quino*), presence was positively associated with microhabitat features such as vegetation composition and high solar insolation, in addition to presence of the host plant (Osborne & Redak 2000). Although in the current study we did not investigate how the microhabitat characteristics affect butterfly

TABLE 3. Coefficients of linear discriminants (Scores) included in the model explain the relationship of each variable with *Apodemia mormo* presence in host plant habitat.

Variable	Scores
Elevation	-0.0165
Aspect	0.0032
Available soil nitrogen	-6.7855
Slope	0.0823
% Bare ground	0.0043
pH	0.2059

biology, Osborne & Redak (2000) showed that high shade was associated with delayed emergence from diapause whereas low shade was associated with early emergence and accelerated development. Likewise, both Dobkin et al. (1987) and Weiss et al. (1988) reported that topographic heterogeneity, with respect to slope exposure in serpentine grasslands, contributed to the long-term persistence of populations of *E. editha*. This is likely because microclimate, which largely depends on microtopography, affects the phenology of larval host plants and adult nectar sources (Weiss et al. 1988). Microhabitat features of sites can also influence site preferences of insects by affecting microclimate, influencing lepidopteran thermoregulation and providing protection from predators (Quirt et al. 2006). Such results suggest that microtopography and microclimate effects on *A. mormo* could be further investigated to understand patterns of habitat use observed in the present study.

Presence of exotic plants influences habitat use in many butterfly species, mainly through competitive exclusion of host plants (Proctor & Woodwell 1975, Murphy & Ehrlich 1988, Murphy & Weiss 1988, Mattoni et al. 1997, Osborne & Redak 2000). In the current study, the only exotic species noted in *E. pauciflorum* habitat was *Melilotus officinalis* ((L.) Lam., Fabaceae). The occurrence of this species in host plant habitat was very low at an average of 0.1% cover in occupied vs. 0.6% cover in unoccupied habitats. We suspect two potential adverse effects of *M. officinalis* in *A. mormo* biology. Presence and abundance of this species may limit movement between host plants during larval dispersal and influence host plant selection during adult *A. mormo* dispersal, as there are large tracts of land that have been densely occupied by this exotic

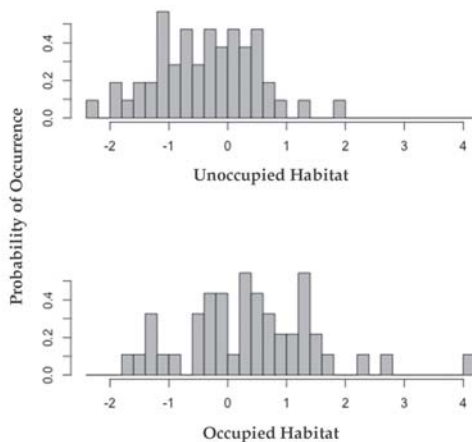


FIG. 2. Linear discriminant analysis shows the distribution “discriminants” of the two distributions, the first of which is “unoccupied” habitat and the second, which is “occupied”.

plant, some of them bordering small areas of *E. pauciflorum* habitat. Additional studies are needed to better understand the potential role of exotic plants during habitat selection by *A. mormo*.

The effects of grazing, either by bison or cattle, were not included in the final analyses used in this paper. Spatial autocorrelation among sites could not be separated from grazing categories, because grazing types and intensity were separated by several dozen kilometers. Continuing work may provide the opportunity to investigate the effects of grazing on *A. mormo* habitat choice and usage.

While the present study is specific to the Saskatchewan prairie population of *A. mormo*, new information presented may apply to the southern mountain population in British Columbia, as well as those in the northern portion of the species range in the United States. While the southern mountain population differs from the prairie population in climate and host plant (*Eriogonum niveum*), it is likely that this population may be under similar pressures and further work may reveal similar trends.

Conservation implications. In the face of global warming and other major environmental and land use changes, northern peripheral populations, such as those of *A. mormo* in southern Canada, will likely be important for the long-term persistence of many species (Hunter 1991, Fraser 2000). It is thus vital to understand the ecology and habitat requirements of these populations in order to effectively manage habitats to ensure that their survival is not negatively impacted by anthropogenic disturbance. The distribution of *A. mormo* in the prairie population is restricted in two ways: butterflies only occur in badland habitat and, in proximity of the larval host plant, *E. pauciflorum*. In addition, we have shown that other environmental characteristics influence butterfly occupancy in *E. pauciflorum* habitat. These additional factors should be considered in managing the occupied habitats in both GNP and VCMP. We suggest the following criteria be used to refine habitat designations for *A. mormo*: *E. pauciflorum* growing on soils with higher pH and low available nitrogen, on steep slopes that are south-west to south facing at lower than average elevation, in badland habitat with bare ground cover.

ACKNOWLEDGEMENTS

This research would not have been possible without the help of our field assistant, Heather Sauder, as well as indispensable assistance from the people of Val Marie, Saskatchewan and Grasslands National Park, and our colleagues at the University of Alberta. This project was funded by Parks Canada and the University of Alberta.

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Submitted for publication 5 June 2013; revised and accepted 9 September 2013.

HOW ENVIRONMENTAL CONDITIONS AND CHANGING LANDSCAPES INFLUENCE THE SURVIVAL AND REPRODUCTION OF A RARE BUTTERFLY, *PIERIS VIRGINIENSIS* (PIERIDAE)**Additional key words:** climate change, novel host use, *Alliaria petiolata*

Pieris virginiensis Edwards, the West Virginia White butterfly, is a rare, univoltine butterfly native to riparian areas of mature forests in North America, from Wisconsin to Vermont, and as far south as northern Georgia and Alabama (Finnell & Lehn 2007). *Pieris virginiensis* has been considered in decline due to forest disturbance via logging, fragmentation, deer grazing pressure, and plant invasion (Finnell & Lehn 2007). It is considered rare, but has not yet been evaluated by the International Union for Conservation of Nature's Red List, and there are no long-term studies of *P. virginiensis* populations to confirm anecdotal observations of continual decline (IUCN 2012). Although there are butterfly monitoring organizations, *P. virginiensis* is frequently overlooked as it flies early in the spring in forested areas, which are not major sources of butterfly diversity and are not often regularly monitored.

Pieris virginiensis primarily uses the spring ephemeral mustard, *Cardamine diphylla* as its larval host plant, but also occasionally uses *Arabis laevigata*, a spring ephemeral biennial mustard. Sparsely distributed, *A. laevigata* is not an ideal host, but it is the primary host of *P. virginiensis* in a site in Marengo, OH, where *C. diphylla* is rare. An alternative host, *C. concatenata*, can be used but is not preferred due to its small size and early senescence (Shuey & Peacock 1989).

Courant et al. (1994) and Porter (1994) observed *P. virginiensis* females ovipositing on *Alliaria petiolata*, an invasive, shade-tolerant biennial mustard that is most likely toxic to emerging offspring. Bowden (1971) had no larvae survive after consumption of *A. petiolata*, and Porter (1994) had moderate mortality of larvae before his experiment ceased at the second instar. Several chemical constituents of *A. petiolata* leaves have been shown to deter feeding and reduce survival of first and fourth instars of *P. oleracea*, although *P. oleracea* populations that have been exposed to *A. petiolata* for 60–100 generations may be adapting to its chemical arsenal (Renwick et al. 2001, Keeler & Chew 2008). If *A. petiolata* is similarly toxic to young *P. virginiensis* caterpillars, adults may be wasting eggs on the plant. If *A. petiolata* deters feeding in older *P. virginiensis* caterpillars, caterpillars searching for a new host plant

after consuming their previous host may starve before reaching an appropriate native food source (Cappuccino & Kareiva 1985, Porter 1994).

Shuey and Peacock (1989) examined a population of *P. virginiensis* reproducing entirely on the alternative hosts, *A. laevigata* and *C. concatenata*. The study site is surrounded by agricultural fields, adjacent to Alum Creek in Morrow Co., Ohio. They examined plants in three locations along a roughly 150 meter section of woodland; a ridge above a shale embankment, the shale embankment, and a riparian area. They found that of the two hosts, *A. laevigata* was strongly preferred, perhaps because *A. laevigata* senesces later, increasing time available for larval development. In addition, more eggs were laid on the south-facing shale embankment than in the other two locations, perhaps because higher temperatures there increased caterpillar development. However, these authors conducted their study before the conversion of nearby agricultural areas to fallow fields, a surge in the abundance of deer, and the introduction of *A. petiolata* to the region (Shuey & Peacock 1989, Porter 1994, Stinson et al. 2006, Finnell & Lehn 2007, Ripple et al. 2010). Each of these subsequent changes to the habitat may have influenced the survival and reproduction of this isolated population of *P. virginiensis*.

Deer, whose populations in Ohio have steadily increased, may negatively influence the presence or quality of nectar sources and host plants for this rare butterfly (Ripple et al. 2010). *Pieris virginiensis* adults feed on a variety of nectar sources, including members of Claytonia, Trillium and Viola, as well as on flowers of their larval host plants (Bess 2005). Increased deer browsing may change the plant community, and in turn, alter habitat quality for *P. virginiensis*, although the effects of deer on butterflies are complex and life-history dependent (Feber et al. 2001).

Introduction of the invasive *A. petiolata* may have also had profound effects at Shuey and Peacock's study site. Poor oviposition choices could severely reduce this site's population that, in 1988, had only 14.8 % of eggs survive to fourth instar even on its native hosts (Shuey & Peacock 1989). *Alliaria petiolata* may also host potential egg/caterpillar predators, such as spiders or predatory ants, reducing survival of *P. virginiensis* on a potentially

novel host. In addition, *A. petiolata* is known to negatively influence plants around it through direct competition and allelopathy, reducing the frequency or quality of nearby nectar or host plants (Stinson et al. 2006).

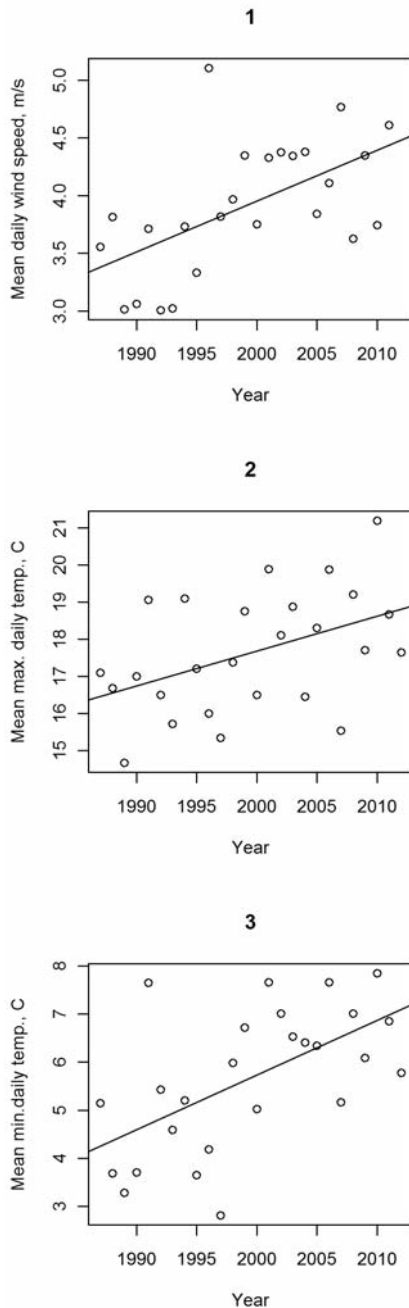


Fig. 1. FIGS. 1-3. (1) Mean daily wind speed (m/s) in April ($p < 0.01$); (2) mean daily maximum temperature (Celsius) in April ($p < 0.05$); and (3) mean daily minimum temperature (Celsius) in April ($p < 0.01$) at the Port Columbus International Airport weather station, Columbus, OH, 1987-2012, approximately 40 km. from the research location.

Finally, aberrant weather and long-term changing climatic conditions may influence *P. virginienis* populations. Although many butterfly species are expected to increase under warming temperatures, butterflies that have strict habitat requirements or exist at the edge of their range may be at risk for population reduction and eventual extinction (Forister & Shapiro 2003, Forister & Fordyce 2011). *Pieris virginienis* flies best in winds under 25 km/h and in temperatures between 19-30° Celsius (Cappuccino & Kareiva 1985, SD pers. obs.). To complicate matters, it is often the previous year's weather that has the most effect on butterfly population in the following year (Roy et al. 2001).

We investigated *P. virginienis* survival and reproduction over two field seasons (2011–2012) in a habitat which previously hosted a robust population of *P. virginienis*, to answer the following questions: Does successful reproduction occur at this location? Does *P. virginienis* differentially use *A. petiolata* and *A. laevigata*? How frequently does non-caterpillar damage (e.g. deer herbivory) occur to host plants? What is the frequency of potential predators on all possible host plants? Have climatic conditions relevant to suitable flying conditions changed over time at this site, and have aberrant weather patterns been noted?

Methods. The study site, in Morrow County, Ohio, is a privately owned forest fragment bordering Alum Creek adjacent to two fallow fields, which was originally surveyed by Shuey and Peacock (1989). On April 21, 2011, we surveyed the site and found 5 flying adult *P. virginienis* individuals, of which two were collected for identification and further study in the laboratory. This was the only occasion that we observed flying adults in 2011, but this confirmed that *P. virginienis* still persisted in this location.

In 2011, mimicking Shuey and Peacock (1989), we systematically searched for and tagged flowering stalks of both the native *A. laevigata* ($n=64$) and the invasive *A. petiolata* ($n=54$) on April 21, 2012, and returned twice to score plants (May 5 and May 11) for the presence of *P. virginienis* eggs or caterpillars, potential predators (ants, spiders), and herbivore damage (deer or other). We chose not to survey *C. concatenata* because it was a minor host in 1987. Plants were examined at the same ridge and shale embankment zones studied by Shuey and Peacock (1989), but were not systematically examined in the lowland-areas, as only one egg was found during their study in the lowland zone. Casual observations in the lowland zone revealed no eggs or caterpillars. During tagging and scoring events after the initial site visit, we searched visually for flying *P. virginienis* adults. We only conducted search events on

days appropriate for butterfly flight (temperature above 10° Celsius, wind speed under 25 km/hr) to maximize our chances of witnessing oviposition events.

In 2012, during a warmer spring than in 2011, flowering stalks of both the native, *A. laevigata* ($n = 113.6 \pm 26.85$ plants searched per visit) and the invasive, *A. petiolata* ($n = 95 \pm 34.53$ plants searched per visit) were tagged (March 30) and scored weekly (April 6, 13, 20, 27; May 4) using methods identical to 2011. In addition to these tagged plants, any unmarked plants found during repeated random searching were scored, but unmarked. During tagging and scoring events, we searched visually for flying *P. virginiensis* adults, but could confirm none, as the individuals seen may have been *P. rapae* adults.

The 2011–2012 scoring data were converted to presence/absence values and fit to one of several binomial regressions in R (R Development Core Team 2011). Year (2011 or 2012) and host plant (*Arabis* or *Alliaria*) were used as predictors for the presence or absence of deer damage, other herbivorous damage, and potential predators.

In 2011, the captured adult butterflies were kept together in a 0.216 m³ enclosure and allowed to feed from a 10% (v/v) sugar:water solution, and placed on a 16:8 hr light/dark cycle under fluorescent lights. These butterflies were given the choice of individual flowering *C. diphylla* (collected from Pennsylvania), *C. concatenata* (collected from Dayton, OH), or *A. petiolata* (collected from Dayton, OH) as oviposition substrate. We examined each plant daily for eggs until the butterflies died.

In 2011, emerging caterpillars ($n=4$) were allowed to hatch and feed on *C. diphylla*, *A. laevigata* (collected from Yellow Springs, OH), or *A. petiolata*. All four caterpillars were initially fed on *C. diphylla*, but were divided evenly and transferred to either *A. laevigata* or *A. petiolata* at the 4th instar for a no-choice survival test.

In addition to these field-collected variables, we examined weather data from the Port Columbus International Airport Weather Station (about 40 km from research location) to evaluate if there were any

trends in weather during the month of April (*P. virginiensis* flight season) between 1987, the year preceding the Shuey and Peacock (1989) study, and 2012. We analyzed climatic variables from 1987 to present using simple linear regression. All statistical analyses were completed in R 2.15 (R Development Core Team 2011).

2011 Results. Despite multiple visits to the study site, we recovered no *Pieris virginiensis* eggs, no caterpillars, and found little damage that could be attributed to caterpillar herbivory (Table 1). Furthermore, we witnessed no flying adults after April 21, 2011. In addition to these direct observations, indirect observations of host-plant conditions suggested no *Pieris*- related herbivory, although there was occasional incidence of leaf or stem damage from deer (*Arabis*: 5.47%, *Alliaria*: 4.63%) or other organisms (*Arabis*: 5.47%, *Alliaria*: 12.96%). Ants and spiders (*Arabis*: 4.69%, *Alliaria*: 17.5%) were observed on both study species.

When captured adult butterflies were given the choice between three potential host plants, all eleven eggs were oviposited on *A. petiolata*, the invasive mustard. These data were pooled, as the adult butterflies were not separated. The four surviving caterpillars readily consumed native mustard tissue, but those placed on *A. petiolata* only consumed a small amount of tissue, then would enter a quiescent state during which they refused to eat *A. petiolata*, but would resume eating when placed on *C. diphylla*.

2012 Results. In 2012, we began our search in March when unusually warm weather facilitated early plant and butterfly emergence. We found one egg on an *Arabis* plant, but saw no confirmed *P. virginiensis* butterflies, and occasionally witnessed *P. rapae* individuals flying through the woodlands. The egg was not removed for identification, and a week later, although there was minor herbivory to the *Arabis* plant where the egg was found, no larva was recovered (Table 1). In addition, there was one pierid caterpillar recovered, from a second-year (flowering) *Alliaria* individual, however, the caterpillar was small and we

TABLE 1. Number of eggs located on plants in Morrow Co., OH, in 1988 (Shuey and Peacock 1989), 2011, and 2012.

	<i>C. concatenata</i> ¹	<i>A. laevigata</i>	<i>A. petiolata</i>
1988	21 (n=68)	102 (n=52)	-
2011	-	0 (n=64)	0 (n=54)
2012	-	1 (n=114)	0 (n=81)

¹ Cardamine concatenata was not searched in 2011 and 2012 due to low incidence of egg deposition in 1988. Numbers are as follows: Eggs found (n=total plants searched).

were unable to confirm its identity as either *P. virginienensis* or *P. rapae*. The incidence of leaf or stem damage from deer (*Arabis*: 2.29%, *Alliaria*: 0.63%) or other organisms (*Arabis*: 8.27%, *Alliaria*: 3.58%), as well as ants and spiders (*Arabis*: 7.75%, *Alliaria*: 9.68%) was low on both study plant species.

Combined scoring for 2011 and 2012. The presence of deer damage was affected by both host plant species and year, with a model:

$$(1) \text{ Deer Damage} = -1.0529 * \text{Year} - 1.0066 * \text{Plant Species} - 2.7648 + \text{Error}$$

All factors in the model were significant, and it was more likely for us to find deer-browsed *Arabis* plants than *Alliaria* plants, and more deer damage in 2011 than 2012 ($p < 0.05$ for Year, Plant).

The presence of other herbivorous damage was predicted by host plant species, but not year, with *Arabis* having a higher incidence of damage being present ($p < 0.01$):

$$(2) \text{ Other Damage} = -0.6712 * \text{Plant Species} - 2.2026 + \text{Error}$$

Finally, predator presence could not be predicted by either host plant species or year.

Weather Analysis. Linear regressions across all years (1987–2012) indicated significant increases through time in average wind speed, maximum temperature, and minimum temperature in the month of April (Figures 1–3).

Discussion. In this study, we investigated the survival and reproductive success of *P. virginienensis* at a site in Ohio last evaluated in 1988 (Shuey & Peacock 1989). It is clear that at this site, *P. virginienensis* is not successfully using either a native host, *A. laevigata*, or an invasive host, *A. petiolata*. We found only one egg on over 150 plants repeatedly searched in two years at this location (Shuey and Peacock 1989). This suggests that *P. virginienensis* at this site may, in the near future, face local extinction.

It is possible that sometime in the intervening 24 years *P. virginienensis* may have attempted to shift to *A. petiolata*. In a scenario where *A. petiolata* was the only novel introduction to this location, we would perhaps conclude that *A. petiolata* had a detrimental effect, but the clear decline in this population could be due to any number of other factors, including changes in nectar source or host plant quality, deer damage, or climate. We found evidence of low to moderate damage from both deer and other sources, as well as a significant presence of potential predators (ants and spiders).

Although there were no differences in predator presence by host plant species, *A. laevigata* plants had a higher incidence of both deer browsing and other, non-caterpillar herbivory than *A. petiolata*.

We believe aberrant weather in 2011 and 2012 caused two recent years of failed *P. virginienensis* reproduction at this location. If it is too cool, wet, or windy, the univoltine *P. virginienensis* cannot fly or reproduce. These recent unusual weather patterns may soon become a chronic issue for this butterfly under predictions of global climate change. Evidence from other butterfly population studies indicates that although some butterflies benefit from warming global temperatures, others may suffer (Sparks & Yates 1997, Roy et al. 2001, Forister & Shapiro 2003). Severe weather could have particularly strong effects on butterfly populations at the edge of their acceptable weather ranges. Furthermore, butterflies with low population numbers are more at risk for local extinction events when faced with multiple “bad” years and the lack of carry-over pupae (Forister & Fordyce 2011).

Climate data demonstrate a linear increase in temperature and wind speed over the last 23 years that may have influenced these butterflies (Figures 1–3). Cappuccino and Kareiva (1985) showed that *P. virginienensis* has a difficult time flying in strong wind speeds, or in cool weather. Many days in an adult *P. virginienensis* lifespan were not ideal for flight in the 1980s, and although warming springs may provide more favorable flying weather, an increase in windiness may ameliorate any benefits of climate change for *P. virginienensis* (Cappuccino & Kareiva 1985, Doak et al. 2006). The spring of 2011 was remarkable for rainy, poor weather in Columbus, OH, with a record of 18.1 cm of precipitation in April. The spring of 2012 had excessively warm temperatures that facilitated early plant and butterfly emergence. As the probability of extreme or unusual climate events increases, we expect further disruptions in *P. virginienensis* populations across its range.

Alliaria petiolata may further contribute to *P. virginienensis* decline by serving as a population sink, however, despite the observations made by Courant et al. (1994) and Porter (1994), no one has yet determined how frequently this occurs and the risk it poses for *P. virginienensis*. Our limited lab data suggest that *P. virginienensis* adults will oviposit on *A. petiolata*, but caterpillars refuse to feed on *A. petiolata* in the fourth instar. While we are unable to confirm the role of *A. petiolata* in *P. virginienensis* decline at this site, we believe that severe or chronic weather anomalies, like the cool and wet spring of 2011 may negatively influence butterfly populations, as was seen in other studies. In

addition, selective herbivory of nectar and larval host plants by deer may directly and indirectly contribute to *P. virginiensis* decline. Future studies will include more observations at this location, as well as expansion into other locations to investigate the direct and indirect impacts of deer, predators, weather and climate patterns, and *A. petiolata* on the *P. virginiensis* life cycle.

ACKNOWLEDGEMENTS

The authors would like to thank Therese Poston for access to the study site; Liz Ervin for helping with fieldwork in 2012; Phipps Botany in Action and the Ohio Plant Biotechnology Consortium for funding this research.

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Submitted for publication 2 April 2013; revised and accepted 20 September 2013.

GENERAL NOTES

Journal of the Lepidopterists' Society
68(1), 2013, 65–66

OVIPOSITION ON A SHRUBBY DICOT BY *OCHLODES SYLVANOIDES* (BOISDUVAL)(HESPERIIDAE)

Additional key words: *Ceanothus cuneatus*, Buckbrush, Rhamnaceae, oviposition “mistake”

Most butterflies oviposit on their host plants; thus the first-instar larva does not need to forage actively. Some species that diapause as eggs avoid laying on plant parts that will senesce during the dormant period, and may instead lay on the ground or on litter near the growing point of the emergent host (Fordyce and Nice 2003). MacNeill (1964) described the seemingly anomalous oviposition behavior of the skipper *Hesperia lindseyi* (Holland) in Marin County, coastal northern California: eggs are laid on lichens on fence posts and trees and the larvae, which develop inside the shell but diapause, hatch in spring and drop to the ground to forage. Scott (1986) reports that eggs are laid “haphazardly” at one site and on annual lupine (Fabaceae) at another, localities not specified. I have seen *H. lindseyi* oviposit on apparently random dry litter at the soil surface in Colusa County, California. Scott also reports (echoing earlier anecdotes) that another skipper, *Polites sabuleti* (Boisduval), lays “on the host, on nearby dicotyledons, horsetail plants, soil, etc. (and on a sedge...which larvae refuse).” Different subspecies of *P. sabuleti* have very different life-cycles and may be uni-, bi-, or multivoltine; Scott does not differentiate among them in the oviposition records at the cited location.

On September 15, 2013 I saw a female *Ochlodes sylvanoides* (Boisduval) “disappear” into a clump of Buckbrush, *Ceanothus cuneatus* Nutt. (Rhamnaceae) on a serpentine “barren” at 1300m near the town of Washington, Nevada County, California in the foothills of the Sierra Nevada. Curious about what she might be doing, I observed her closely. Over a ten-minute period I saw her lay six eggs individually on twigs in the interior of this densely-branched shrub. She then flew to a nearby clump of *Ericameria* (Asteraceae) and began nectaring. This species is univoltine in late summer-

autumn at this site. There were dry bunchgrasses of several species growing less than a meter from the shrub.

All three of the skippers cited are presumed to feed on grasses (Poaceae) but as usual for grass-feeding butterflies, confirmed host records in the wild are rare. Supposedly, *P. sabuleti* overwinters as a part-grown larva and *O. sylvanoides* as a first-instar larva (both from Scott, 1992). If so, these records of strange oviposition substrates may be unrelated to winter egg dormancy. They could constitute an adaptation to “hide” the eggs from parasitoids that might key in on the larval host plant. In any case, there is a suggestion that grass-feeding skippers may frequently oviposit on non-host substrates, and this should serve as a warning to not take such oviposition “mistakes” as indicating actual or potential larval feeding without further study.

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Submitted for publication 17 September 2013; revised and accepted 18 October 2013.

THE BUTTERFLIES OF NORTH AMERICA BY W. H. EDWARDS: REVISED CITATIONS FOR THE FIRST VOLUME AND FOR THE *SYNOPSIS OF NORTH AMERICAN BUTTERFLIES*

Additional key words: publication, Samuel H. Scudder

Calhoun (2013) proposed detailed citations for the three-volume book *The Butterflies of North America* (*BNA*) and its related publications by William H. Edwards. However, I found it difficult to determine the actual publication schedule for the *Synopsis of North American Butterflies*, which was issued in parts in conjunction with the first volume of *BNA*. Because I did not have access to a complete copy of the first volume in wrappers as issued, I relied upon the summary by McHenry (1952) and other evidence for my proposed citation of the *Synopsis*.

Soon after the publication of Calhoun (2013), I was contacted by a lepidopterist who owns a copy of *BNA* with all the separate parts in their original wrappers bound into three volumes. It retains all pages and plates as issued. Moreover, this rare set was owned by the entomologist Samuel H. Scudder, who received the parts as they were published (Calhoun 2013). The book's owner (who prefers to remain anonymous for the purposes of this paper) generously provided photocopies of numerous pages for my review.

The first part of Scudder's copy of *BNA* bears an inscription reading "Mr. S. H. Scudder from the Author." Not in the hand of Edwards, this inscription was most likely written by a member of the American Entomological Society, who printed and mailed parts of the first volume of *BNA* from a room at The Academy of Natural Sciences in Philadelphia, Pennsylvania (ANSP) (Calhoun 2013). Scudder wrote the dates of receipt on the covers of most parts. He possibly did this for all parts of the book, but some of his notations may have been trimmed away when the volumes were bound. These dates provide a valuable record of publication of *BNA*, as Scudder lived in the same town (Cambridge, Massachusetts) as Riverside Press, the firm that printed and mailed parts of the second and third volumes.

The owner of this set of *BNA* acquired it in 1989 from the bookseller Wheldon & Wesley. Each volume bears a bookplate of the Boston Society of Natural History (BSNH), for whom Scudder served several positions, including president. The bookplate reads "S. H. Scudder Library / Gift of Samuel Hubbard Scudder / President of the Society 1880–1887 / June 22, 1903" (Fig. 1). Believing that his future was in jeopardy after developing symptoms of what we now recognize as Parkinson's Disease, Scudder donated his personal

library of nearly 10,000 books, offprints, and maps to BSNH before his death in 1911 (Allen 1904, Mayor 1919, Creed 1930). The specialized bookplate was created by BSNH a short time after the donation of Scudder's material in 1903 (Allen 1904). Written at the bottom of each bookplate in Scudder's copy of *BNA* is the notation "Replacing former copy" (Fig. 1), revealing that the BSNH subscription volumes were lost or removed from the society's library prior to 1903.

In 1946, the bulk of the library of the Boston Society of Natural History was sold to the Allan Hancock Foundation (Johnson 2004). The same year when the BSNH library was sold, the name of the society's museum was changed to the Boston Museum of Science (later, the Museum of Science, Boston; BMS) and the original museum building was sold to a clothier (Johnson 2004). The new museum opened five years later along the Charles River. The original BSNH building, at the corner of Berkeley and Boylston Streets, was recently refurbished to serve as a gallery of the luxury home furnishings company, Restoration Hardware.

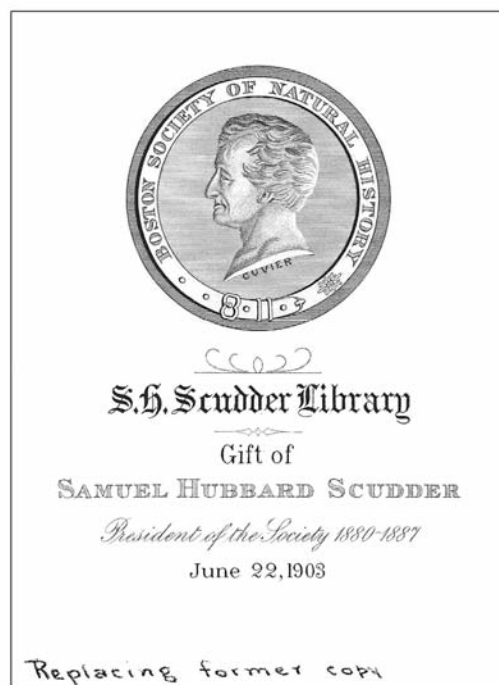


FIG. 1. Bookplate from Scudder's copy of *BNA*.

The books purchased in 1946 from BSNH are now deposited in the Doheny Memorial Library, University of Southern California (Los Angeles, California; USC). A copy of *BNA* is preserved at USC, but it was originally owned by the New York artist and lepidopterist Emily L. Morton (1841–1920), who was a correspondent of W. H. Edwards and collaborated with him on documenting the life history of the butterfly *Feniseca tarquinius* (F.) (Edwards 1886, Newcomb 1917). It was purchased by the Allan Hancock Foundation in 1943 (M. K. Hayes pers. comm.). The provenance of this copy supports the notion that the original BSNH subscription copy was removed from the society's library prior to 1903.

A number of books in the BSNH library were not sold in 1946 (Johnson 2004) and they presumably included Scudder's copy of *BNA*. The current owner of this copy possibly viewed it on display at the museum around 1970. No specific records about this copy of the book were found by BMS staff, but they noted that the museum previously sold books from its library. Some were purchased by the former Boston bookseller David L. O'Neal, who was in business from 1973 to 2001 (O'Neal 2013). O'Neal (pers. comm.) confirmed that he had obtained former BSNH books from the museum and Scudder's copy of *BNA* was possibly among them. Items from the Scudder library continue to circulate within the antiquarian book market. For example, I recently purchased a copy of Fernald (1888), which bears the "S. H. Scudder Library" bookplate.

Scudder's copy of *BNA* was acquired by the former bookseller Wheldon & Wesley just before they sold it in September 1989. Wheldon & Wesley was founded in 1921 in London, England, and ceased trading in 2004. The firm's records, dating back to about 1950, were purchased by private individuals and later donated to the Smithsonian Institution (Washington, D.C.), where they are now preserved in the Cullman Library. The records consist of index cards with handwritten information about every book bought and sold by the bookseller. Unfortunately, the record pertaining to Scudder's copy of *BNA* does not indicate where it had been acquired and mostly reflects the same information that appeared in the firm's published sales catalog (Wheldon & Wesley 1989). The brief catalog entry described the book as "Samuel Scudder's copy" and noted that the original part wrappers were "bound in place."

Scudder's copy of *BNA* affords the rare opportunity to more fully understand the publication sequence of the *Synopsis of North American Butterflies*, including all its revised pages. During this process, I discovered that several additional letterpress pages were reissued for the first volume, beyond those listed in Calhoun

(2013). I also recently became aware another important source of information regarding the dates of issue for the first volume.

Revised citation for the *Synopsis*. Although McHenry (1952) indicated that pages 51 and 52 of the *Synopsis* were issued with Part 10 of the first volume, I assumed this was in error. Edwards' notes for the *Synopsis*, which were published on these two pages, stated, "Pages 1 to 6, 10, 11 and 19, have been reprinted with corrections since their original issue." I therefore concluded that the replacement pages, which were not listed by McHenry (1952), were issued in Part 10 in September 1872, while the notes for the *Synopsis* were issued in the supplementary part of January 1873 (Calhoun 2013). Scudder's copy, however, reveals just the opposite. Included in the supplementary part of *BNA* was a group of pages preceded by a sheet reading "NOTE. The following pages are to be substituted for those previously issued." Twelve of these pages were related to the *Synopsis*.

Edwards referred to the replacement pages of the *Synopsis* before they were published, evidently because he originally planned to issue them in Part 10, the same in which his notes appeared. In a "Notice to Subscribers," mailed with Part 7, Edwards announced, "I have found myself unable to prevent some errors in the *Synopsis*, as on pages 5, 10 and 11. In these cases the pages will be reprinted and a corrected copy furnished to each subscriber on completion of the volume, with Part X." This did not occur, thus Edwards issued these pages in the subsequent supplement.

The following citation supersedes that given in Calhoun (2013) for the *Synopsis of North American Butterflies* as originally issued. It corrects the publication sequence of pages in Part 10 and the supplementary part.

[1869]–[1873]. *Synopsis of North American butterflies*. In: W. H. Edwards (1868–[1873]), *The Butterflies of North America* [with colored drawings and descriptions]. Philadelphia: American Entomological Society 1: (3) [1]–4 (Dec 1868 [May 1869]), (4) 5–6 (Apr [Sept] 1869), (5) 5–6 (replacements) (Dec 1869 [Apr 1870]), (6) 7–14 (Jun [Aug] 1870), (7) 15–22 (Jan [Mar] 1871), (8) 23–38 (Aug 1871), (10), 39–52 (Jul [Sep] 1872), (Suppl.) t.p., ii–v, [1]–6, 9–12, 19, 20 (all replacements) (1872 [Jan 1873]).

Revised citation for the first volume of *BNA*. The replacement pages that were issued in the supplementary part of January 1873 included new letterpress for five plates. These plates, the species treated, pages, and reasons for the new text are as follows: *Parnassius* I (*Parnassius clodius* Ménétriés

ssp.) ([19, 20]; updated discussion), *Argynnis* IV (*Speyeria nokomis* (Edwards)) ([73, 74]; updated description), *Argynnis* X (*Speyeria cybele leto* (Behr)) ([85, 86]; updated description and discussion), *Melitaea* I (*Euphydryas chalcedona* (Doubleday)) ([97, 98]; hostplants changed), and *Apatura* I (*Asterocampa celtis* (Boisduval & Le Conte)) ([135, 136]; name correction). I previously was aware only of the replacement pages for the *Argynnis* plates (Calhoun 2013).

Scudder's handwritten dates of receipt are visible on the covers of four parts of the first volume of his copy of *BNA*. All the dates are consistent with those given in Calhoun (2013): Part 1 (17 June 1868), Part 3 (13 May 1869), Part 5 (18 April 1870), Part 7 (24 March 1871). In addition to Scudder's notations, the Ewell Sale Stewart Library (ANSP) preserves a handwritten ledger entitled "Subscribers to Vol. 1," which records the names of the subscribers and their payments, as well as the dates of issue for most parts of this volume. This ledger was written by Ezra T. Cresson, Sr., who personally printed the first volume of *BNA* and handled its distribution (Calhoun 2013). The dates recorded by Cresson are as follows: Part 1 (not given), Part 2 (not given), Part 3 (8 May 1869), Part 4 (3 September 1869), Part 5 (7 April 1870), Part 6 (9 August 1870), Part 7 (6 March 1871), Part 8 (6 September 1871), Part 9 (19 February 1872), Part 10 (29 August 1872), Supplementary Part (13 January 1873).

Despite Cresson's records, Edwards noted that Part 8 was "out" by 25 August 1871 and John W. Weidemeyer reportedly received Part 9 by 13 February 1872 (Calhoun 2013). Cresson's ledger indicates that subscribers generally submitted payment after they received the parts, sometimes within days. The earliest payment received for Part 8 (excluding obvious pre-payments) was 11 September 1871, suggesting that Edwards' reference to 25 August was anecdotal, as he did not explicitly state that he had actually received the part by that date. The earliest payment for Part 9 was received on 23 January 1872, implying issuance during mid-January. Eighteen payments were received for this part during January and many more were received during early February.

Cresson's date of 29 August 1872 for Part 10 is reasonable, as Edwards received his own copy around 5 September (Calhoun 2013). This is consistent with the time required for mail to reach Coalburg, West Virginia, from Philadelphia. On the revised "Dates of Issue" page, which was created for copies of the first volume of *BNA* beginning with the 1874 reissue, Edwards attributed Part 10 to September. This suggests that he based this information on the dates when he personally

received the parts. Cresson most likely recorded the dates when he mailed the bulk of the parts, not the first copies.

The following citation supersedes that given in Calhoun (2013) for the first volume of *BNA* (Edwards 1868–[1873]) as originally issued. It incorporates the corrected dates of issue for Parts 8 and 10, as well as the additional replacement pages in the supplementary part.

1868–[1873]. *The butterflies of North America* [with colored drawings and descriptions]. Philadelphia: American Entomological Society 1: (1) ii, [63–76], pls. [20–24] (Apr [Jun] 1868), (2) [41–44, 77–80, 135–136], pls. [12, 13, 25, 26, 45] (Aug [Oct] 1868), (3) [81–84, 127, 128, 141–144, 149–152], pls. [27, 28, 41, 47, 49] (Dec 1868 [May 1869]), (4) [45–52, 85, 86, 129, 130, 145–148], pls. [14, 15, 29, 42, 48] (Apr [Sept] 1869), (5) [53, 54, 87, 88, 99, 100, 131, 132, 153–156], pls. [16, 30, 35, 43, 50] (Dec 1869 [Apr 1870]), (6) [37, 38, 55, 56, 89–92, 133, 134], pls. [10, 17, 31, 32, 44] (Jun [Aug] 1870), (7) [17–20, 39, 40, 57, 58, 97, 98, 137–140] pls. [4, 11, 18, 34, 46] (Jan [Mar] 1871), (8) [29–36, 93–96, 101–110], pls. [8, 9, 33, 36, 37] (Sept 1871), (9) [1–16, 111–120], pls. [1, 2, 3, 38, 39] (Dec 1871 [Jan 1872]), (10) [21–28, 59–62, 121–126], pls. [5, 6, 7, 19, 40] (Jul [Aug] 1872), (Suppl.) t.p, [ii], [4 pp.], [19, 20, 73, 74, 85, 86, 97, 98, 135, 136 (all replacements), 157–164], pls. [20, 23, 29 (all replacements) (1872 [Jan 1873]).

ACKNOWLEDGEMENTS

For kindly examining books, sending images, and other assistance, I thank Melinda K. Hayes and Rachelle B. Smith (Special Collections, USC), Richard James and Clare Flemming (Ewell Sale Stewart Library, ANSP), Leslie K. Overstreet (Cullman Library, Smithsonian Institution Libraries, Washington, D.C.), Claudia Rivers (Special Collections, University of El Paso Library, El Paso, Texas), and Violetta Wolf (BMS). David L. O'Neal (Oakland, California) confirmed his purchase of BSNH books. Mark Salvato and an anonymous reviewer provided helpful comments. Finally, I extend special thanks to the owner of Scudder's copy of *BNA*, who patiently answered my many questions, generously provided photocopies, and continues to selflessly promote a greater understanding of *BNA*.

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Submitted for publication 19 September 2013; revised and accepted 4 October 2013.

FIRST RECORD OF *ARICORIS CINERICIA* (STICHEL, 1910) (RIODINIDAE) FROM BRAZIL AND UPDATE ON ITS GEOGRAPHICAL DISTRIBUTION**Additional key words:** *Aricorina*, distribution map, grasslands, Nymphidiini, Pampa

Aricoris cinericia (Stichel, 1910) (Figs. 1-5) belongs to “*chilensis*” species group (sensu Hall & Harvey 2002) and all these species has its distribution restricted to austral South America, especially in open areas from Bolivia, Paraguay, Argentina and Uruguay (Hayward 1951, Hall & Harvey 2002, Callaghan & Soares 2001, Callaghan & Lamas 2004, Bentancur-Viglione 2009, Núñez-Bustos 2010, Núñez-Bustos & Volkmann 2011, Schweizer & Kay 1941, Siewert et al. in press.).

In the early 1970s, a species similar to *A. cinericia* was collected in Guarapuava municipality (51°27'29"W, 25°23'44"S), Paraná State, Brazil, by Hipólito Schneider and published by Dolibaina et al. (2011). However, a more detailed analysis revealed that the above species was not in fact *A. cinericia* (Siewert et al. in press), which continues then unrecorded in Brazil.

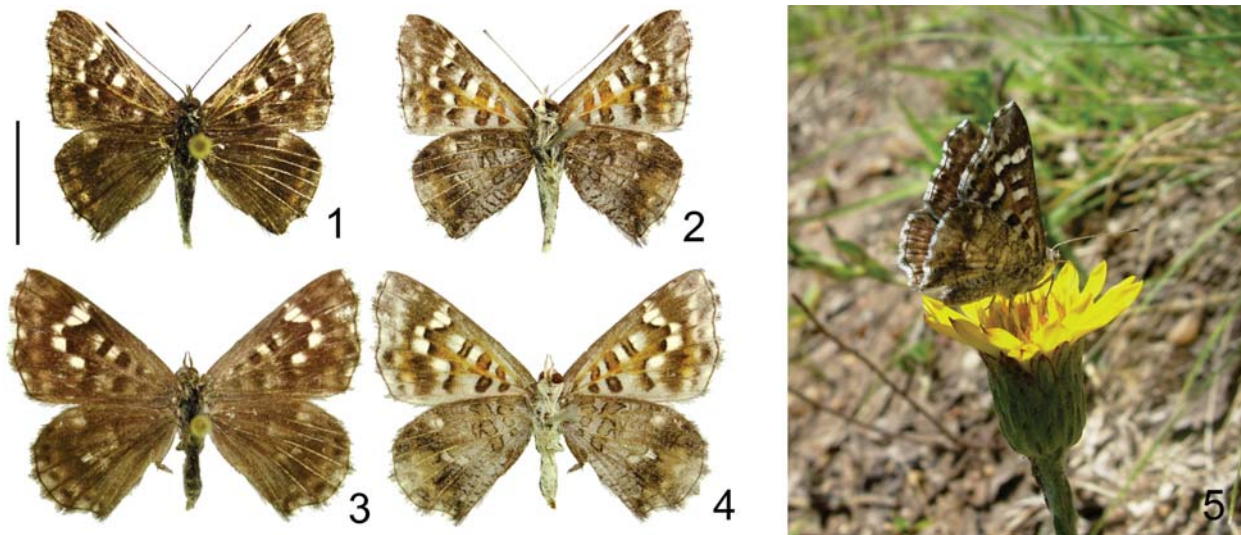
On 27 November 2012, three male and two female specimens of *A. cinericia* were recorded for the first time in Brazil, at Fundação Maronna, Alegrete municipality (55°42'58"W, 30°07'12"S), Rio Grande do Sul State, South Brazil. The area is located at the Pampa biome and is a transitional zone between forest and grasslands, a mixture of grassland with scattered shrubs. The individuals were collected on the bottom of a forested valley, at a forest edge, between 9 and 10 h and 18 h. The specimens are deposited at “Coleção de Lepidoptera do Departamento de Zoologia” (CLDZ), Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil, under the codes CLDZ 8227, CLDZ 8228, CLDZ 8229, CLDZ 8230 and CLDZ 8231.

Other records in South America were found in Buenos Aires (a single specimen in Museo Argentino Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires, Argentina), Corrientes (specimens at Instituto Miguel Lillo (IML), Tucumán and Museo de la Plata (MLP), Buenos Aires province) and Entre Ríos provinces, Argentina and, in more recent years (December 1995), in Parque Nacional El Palmar (nearby Arroyo Los Loros) (58°19'W, 31°51'S), located between the Colón and Concordia towns, Entre Ríos province, Argentina. On 4 December 2008, one male specimen was registered in Liebig (near Colón, Entre Ríos province) (58°15'W, 32°07'S) and observed on a xerophytic habitat, in the ecotone between grasslands and xeric trees vegetation (Fig. 5). It is possibly that flies in Misiones province and Paraguay too (Klimaitis & Núñez Bustos, in press).

Adults of this species are found on flowers or ground floors, sometimes on the ground where it camouflages quite well with the environment. Often shares habitat with *A. notialis*, much more common in the area. The knowledge of its host plant is still unknown but the specimen was seen nearby *Asclepias* Linnaeus and *Oxypetalum* R. Br (Beccaloni et al. 2008). All *Aricoris* species are known for its obligatory association with ants on the early immature stages (e.g. Kaminski & Carvalho-Filho 2012) but for *A. cinericia* there is a lack of information to this matter.

The scarcity of more specific inventories is one of the biggest causes of the lack of knowledge on the distribution of Neotropical butterflies, leading to a paucity of studies involving biology, occurrence and natural history of these insects. The Riodinidae fauna, in particular, is still poorly known, emphasizing the need of increasing efforts on this kind of inventory to fully characterize the patterns of distribution and occurrence of this family. Moreover, several species of Riodinidae have restricted spatial distributions and low population levels (Callaghan 1978, Brown 1993, New 1993), characteristics that hamper a correct evaluation of conservation status of most species. Given that the few records of *A. cinericia* in Brazil are in the highly endangered savannas and grasslands, a conservation plan for this Biome is urgent, since the general distribution of this species is apparently restricted to these open ecosystems. The use of the knowledge gathered from inventories allows studies on the biology of species, providing a useful tool for the conservation of these insects and their associated habitats.

The information about the conservation of the Campos (grasslands) is rare. According to Overbeck et al. (2007) there was approximately 25% decrease in the total area of native grassland in the last 30 years. In Rio Grande do Sul State, for example, only 0.14% of this vegetation is represented in preserved areas. The remaining habitats of Campos are losing area by the expansion of agricultural and silvicultural activities and, this ecosystem in austral South America have many portions of its distribution converted in these kind of systems. Thus, not only *A. cinericia* but all butterflies closed associated with this vegetation may be threatened, and the first step to their conservation is to create new legal protected areas (Overbeck et al. 2007, Dolibaina et al. 2011).



Figs. 1-5: 1-2) *Aricoris cinericia*, (♂), Dorsal and ventral surfaces. (CLDZ 8229 – Alegrete, Rio Grande do Sul, Brazil). 3-4) *A. cinericia*, (♀), Dorsal and ventral surfaces (CLDZ 8227 – Alegrete, Rio Grande do Sul, Brazil). 5) *A. cinericia*, (♂), feeding on a Asteraceae flower at Liebigh, Entre Ríos, Argentina. (Photo: Ezequiel Osvaldo Núñez Bustos). Scale bar = 1 cm.

ACKNOWLEDGEMENTS

We are grateful to Dr. Nicolás Mega (UFRGS) for the information about Fundação Maronna. We also thank M.Sc. Diego Rodrigo Dolibaina for its commentaries on the first draft of this manuscript. Ricardo Russo Siewert received a master fellowship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Cristiano Agra Iserhard a post-doctoral fellowship from Fundação de Amparo a Pesquisa do Estado de São Paulo (Fapesp – 2011/08433-8). This paper is part of the RedeLep “Rede Nacional de Pesquisa e Conservação de Lepidópteros” SISBIOTA-Brasil/CNPq (563332/2010-7).

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Submitted for publication 4 August 2013; revised and accepted 16 November 2013.

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