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Volume 63 Number 1

29 Apr 2009

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, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, CA 90007-4057. Periodicals postage paid at Los Angeles, CA and at additional mailing offices. POSTMASTER: Send address changes to The Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, CA 90007-4057.

Cover Illustration: *Omiodes continuatalis*, an endemic Hawaiian crambid moth formerly thought to be extinct, but recently rediscovered. Photo by William P. Haines. (See journal article on page 11).



JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

Volume 63

2009

Number 1

Journal of the Lepidopterists' Society
63(1), 2009, 1–10

A NEW SPECIES OF *DRASTERIA* HÜBNER (NOCTUIDAE: CATOCALINAE: MELIPOTINI) FROM ARIZONA, WITH COMMENTS ON THE GENUS

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ABSTRACT. *Drasteria walshi* n. sp. (Noctuidae: Catocalinae) from southeastern Arizona is described and illustrated. The new species belongs to the *D. fumosa*-*D. divergens* species group. *Drasteria walshi* is distinguished from related species of *Drasteria* by wing color and pattern, and structure of male and female genitalia. Taxonomic problems in *Drasteria* are discussed.

Additional key words: taxonomy, *Drasteria*, new species, Arizona, Nearctic

The genus *Drasteria* Hübner, 1818, with more than 60 described species, is the largest genus in the tribe Melipotini (sensu Fibiger & Lafontaine 2005). It is exclusively Holarctic in distribution, with 27 species known from the Nearctic region and 35 species known from the Palearctic region. No species are known to occur in the tropics or Southern hemisphere. The only comprehensive study of the Palearctic species of the genus was published by John (1910) almost a hundred years ago. Since then, a dozen new species and subspecies of *Drasteria* have been described from the Palearctic region. The Palearctic species of *Drasteria* are in need of revision because the status of many taxa remains unresolved, and some widely distributed species may actually be complexes of closely related species, as is the case for *Drasteria rada* (Boisduval, 1848) (Metlevski *et al.*, unpublished data). Richards (1939) revised the Nearctic species of *Drasteria*, and few changes have occurred in the taxonomy of Nearctic species since then. Some taxonomic problems pointed out by Richards, such as the relationship between *D. tejonica* (Behr, 1870) and *D. howlandii* (Grote, 1864), or the status of *D. nichollae* (Hampson, 1926), have not been resolved yet. Richards' 1939 revision downgraded to subspecies (race by Richards) a number of taxa

originally described as separate species by other workers. Poole's 1989 catalog of the world Noctuidae (Poole 1989) did not recognize any taxa at the subspecies level and synonymized all the names applicable to the taxa treated as subspecies by Richards. As a result, all *Drasteria* names synonymized by Poole have been excluded from the lists of Nearctic fauna, such as *Nomina Insecta Nearctica* (Poole & Gentili 1996). Nevertheless, the status of many taxa treated by Richards as subspecies of other *Drasteria* species remains unclear. *Drasteria hastingsii* (H. Edwards, 1878) is now recognized as a valid species, and Wagner *et al.* (in press) provide evidence that *Drasteria graphica atlantica* Barnes & McDunnough, 1918 represents a full species. It is likely that others, such as *D. sabnosa abrupta* (Barnes & McDunnough, 1918) or *D. adumbrata alleni* (Grote, 1877), are also valid species.

In addition, our current investigations suggest that some North American species of *Drasteria* are actually complexes of closely related species. For example, populations of *D. inepta* (Edwards, 1881) from Colorado and northern New Mexico are not conspecific with populations from southeastern Arizona and southwestern New Mexico. Finally, discoveries of new

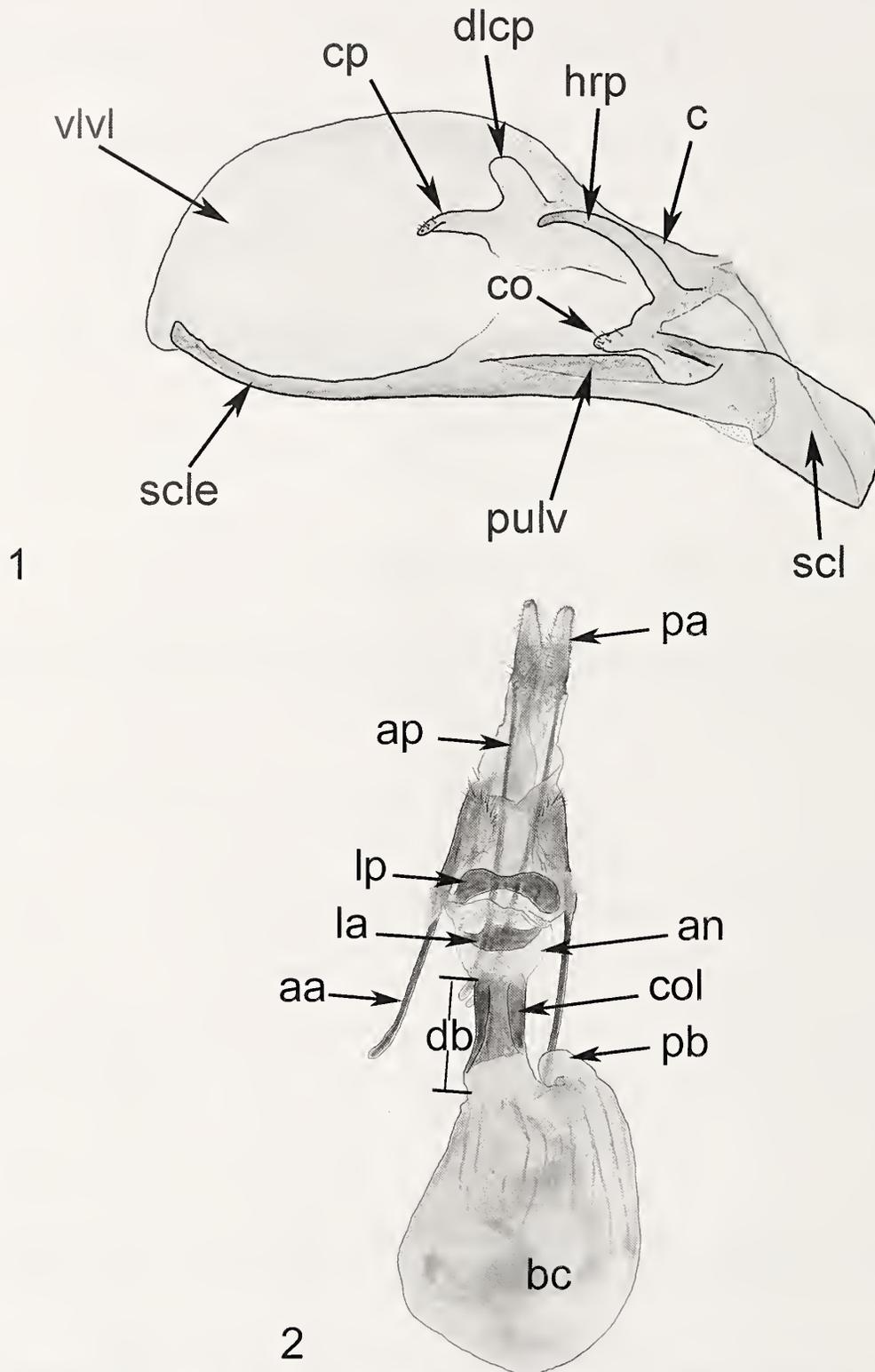


FIG. 1. Medial surface of *Drasteria* male valve (based on a left valve of *D. pallescens* (Grote & Robinson, 1866)) (c - costa; co - conus; cp - costal process; dlcp - dorsal lobe of costal process; hrp - harpe; pulv - pulvinus; scl - sacculus; scle - saccular extension; vlvl - valvula).

FIG. 2. Female genitalia of *Drasteria* (based on *D. sinuosa* (Staudinger, 1884)) (aa - apophyses anteriores; an - antrum; ap - apophyses posteriores; bc - bursa copulatrix; col - colliculum; db - ductus bursae; la - lamella antevaginalis; lp - lamella postvaginalis; pa - papilla analis; pb - pseudobursa).

species of *Drasteria* in North America are still occurring. *Drasteria convergens* Mustelin, 2006, was described recently from California, and below we describe a new species from southeastern Arizona.

The terminology used here for structures of the male valva follows the scheme shown in Fig. 1. We use the term “harpe” in a broad sense since the problem of homologies of valval structures, to which this term is applicable in various groups of Noctuidae, remains unresolved. For this reason we follow with some modifications the broad definition of the term “harpe” given by Kuznetsov & Stekolnikov (2001), and define the harpe as various and not necessarily homologous sclerotized structures on the inner surface of valva, that are not derived from the costa or sacculus. Here we use the term “harpe” for the long and slender process (processus basalis valvae in John 1910) arising from a sclerotised, angled ridge on the inner surface of proximal part of the valva. We also use the term “conus” for the small process located just below the harpe, and

the term “pulvinus” for the shelllike process arising laterad from the inner side of the basal part of the saccular extension. The last two terms were introduced by John (1910) for *Drasteria* but have not been used since. Terminology for male genitalia other than valva follows Goater *et al.* (2003).

Species of *Drasteria* have aedeagi with a very complex vesica, consisting of a number of diverticula of different sizes. The complexity of the vesica of species of *Drasteria* was shown only recently (Goater *et al.* 2003; Mustelin 2006); previous taxonomic works on the genus have not made mention of the vesica. Our current investigations show the number and relative position of diverticula are good characters for grouping members of the genus into species groups. Thus, we include a detailed description of the vesica in the species description.

Terminology for female genitalia follows Kühne (2005) and is shown in Fig. 2. Terminology for wing patterns is shown in Fig. 3.

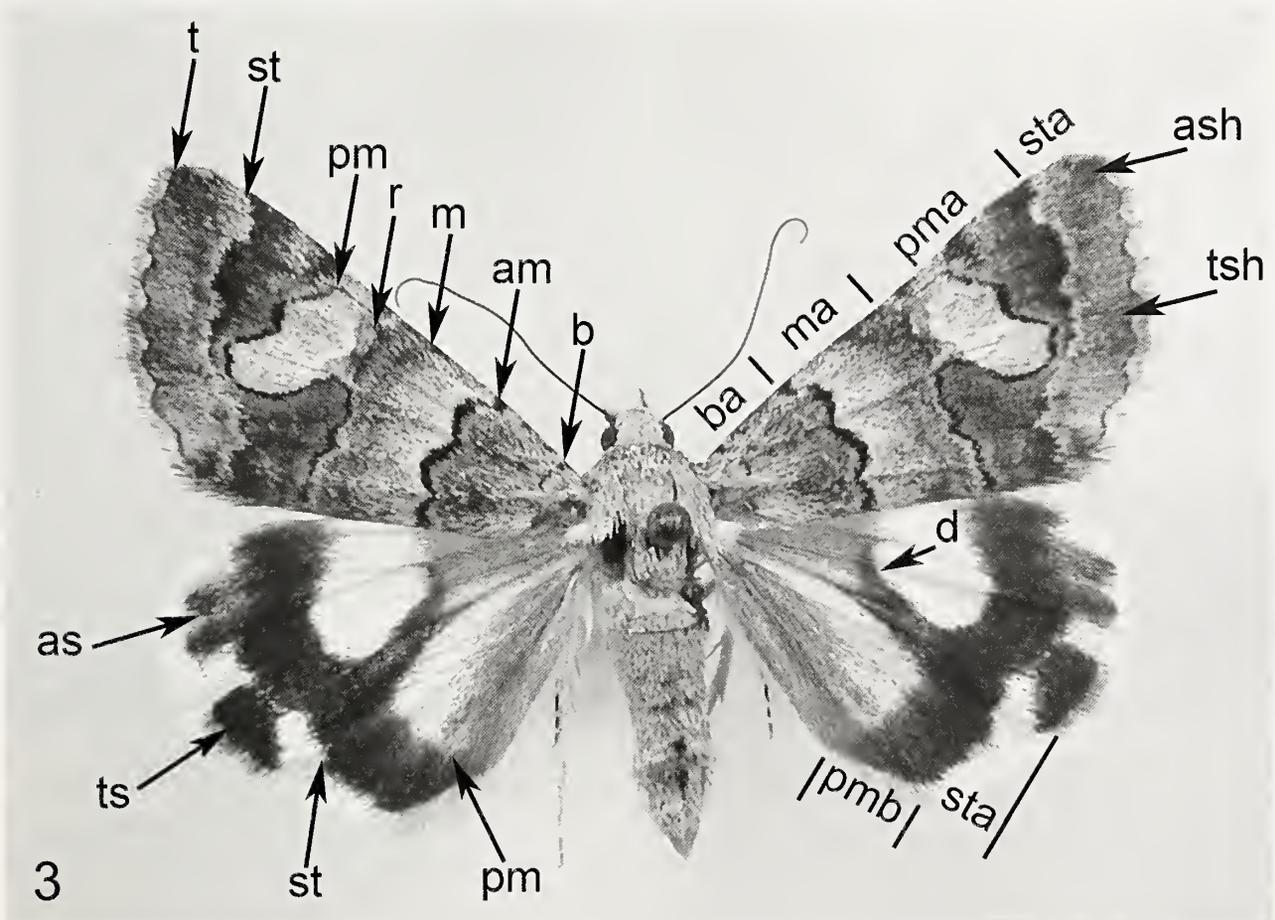
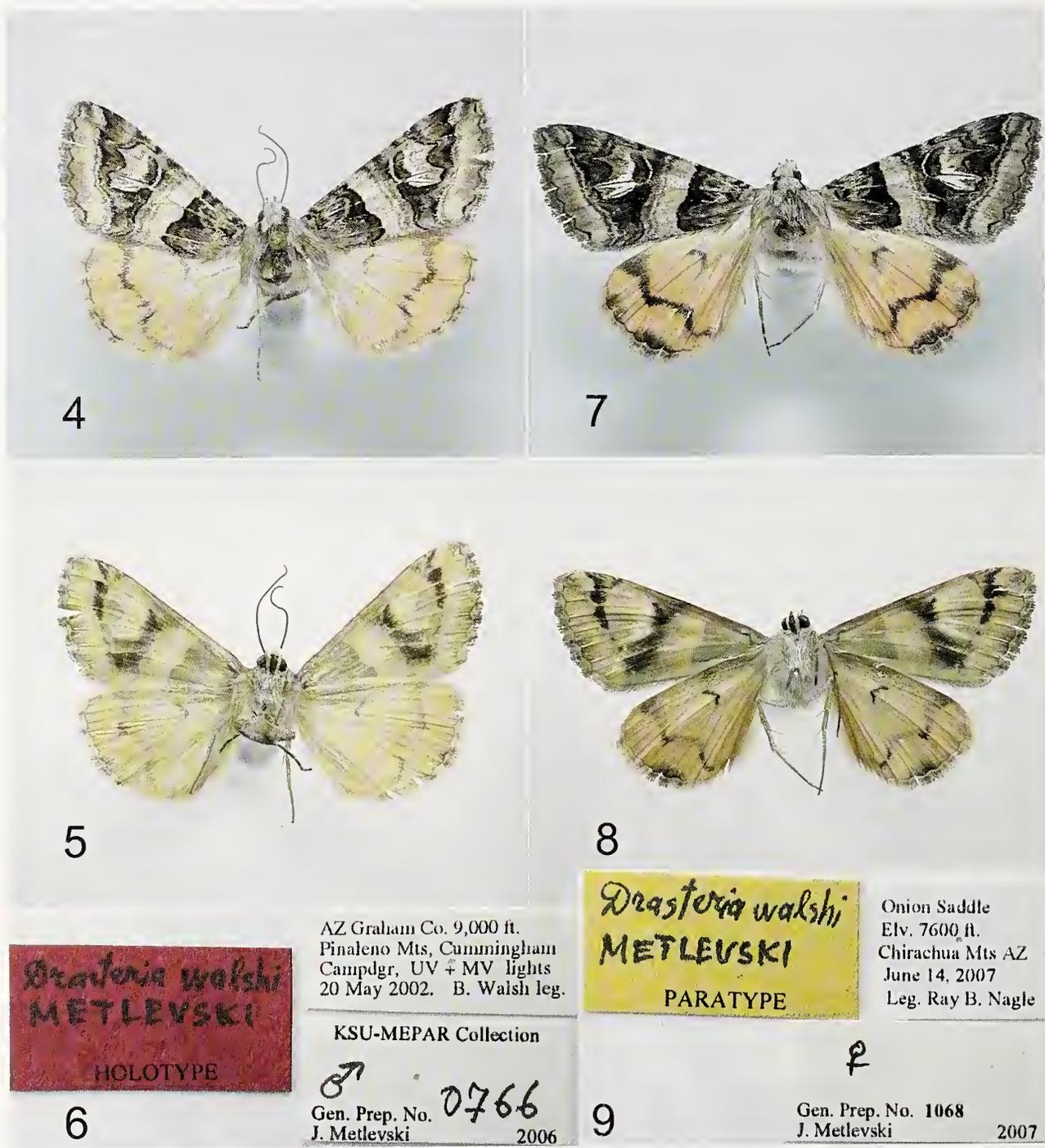


FIG. 3. Wing pattern of *Drasteria*, dorsal surface (based on *D. christophi* (Alpheraky, 1895)) (am – antemedial line; as – apical spot; ash – apical shadow; b – basal line; ba – basal area; d – discal spot; m – medial shadow; ma – medial area; pm – postmedial line; pma – postmedial area; pmb – postmedial band; r – reniform spot; st – subterminal line; sta – subterminal area; t – terminal line; ts – terminal spot; tsh – terminal shadow).



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Drasteria walshi
METLEVSKI
HOLOTYPE

AZ Graham Co. 9,000 ft.
Pinaleno Mts, Cunningham
Campdgr, UV + MV lights
20 May 2002. B. Walsh leg.

Drasteria walshi
METLEVSKI
PARATYPE

Onion Saddle
Elv. 7600 ft.
Chirachua Mts AZ
June 14, 2007
Leg. Ray B. Nagle

KSU-MEPAR Collection

♂
Gen. Prep. No. 0766
J. Metlevski 2006

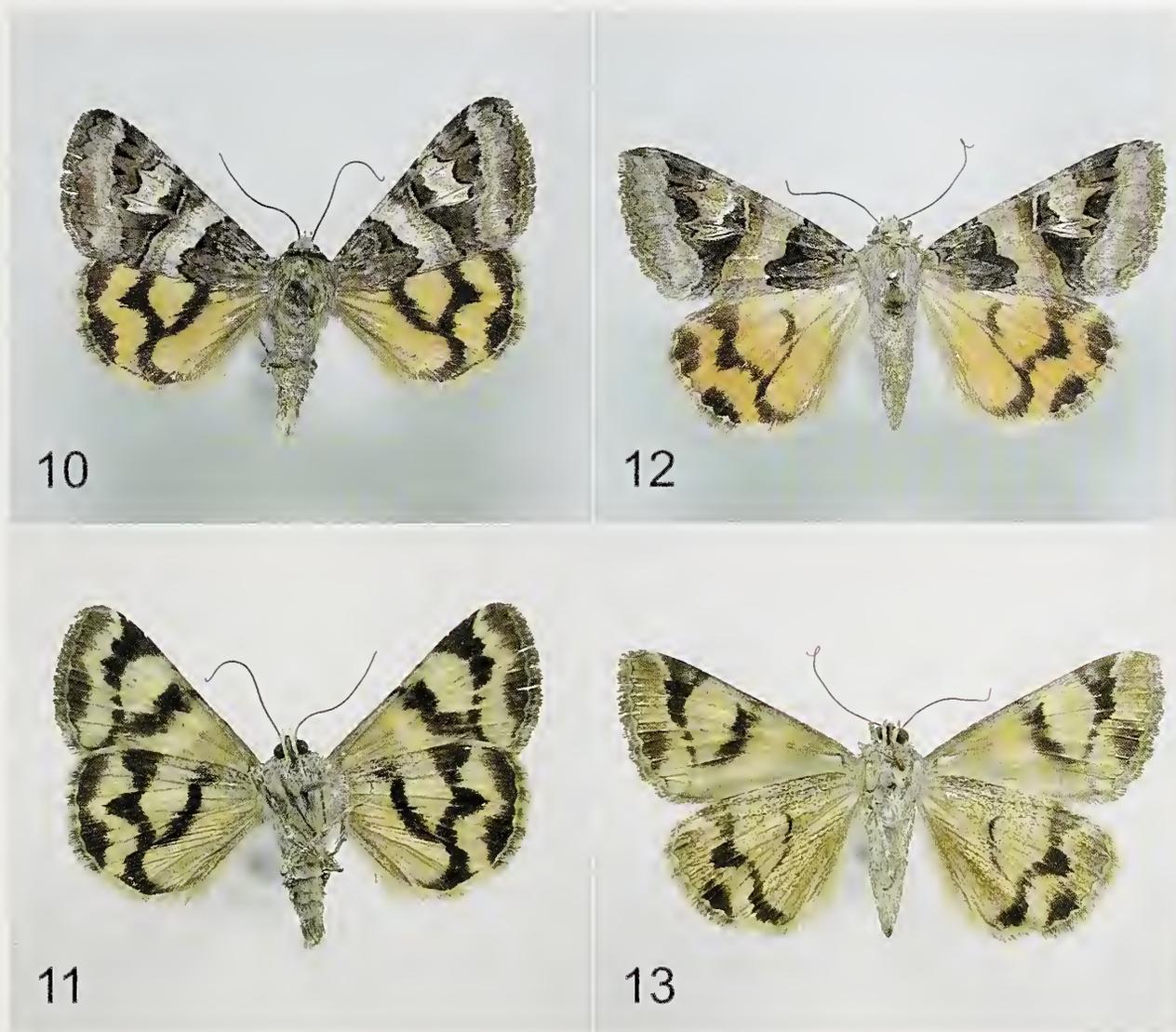
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Gen. Prep. No. 1068
J. Metlevski 2007

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FIGS. 4-9. *Drasteria walshi*. 4-6, holotype. 4, dorsal surface. 5, ventral surface. 6, pin labels. 7-9, female paratype, Chirachua Mts. 7, dorsal surface. 8, ventral surface. 9, pin labels.



Figs. 10-13. *D. divergens*. 10-11, male, White Pine Co., Nevada. 10, dorsal surface. 11, ventral surface. 12-13, f. socia, female, Santa Barbara, California. 12, dorsal surface. 13, ventral surface.

Abbreviations for institutions and collections used in the text are as follows: KSU-MEPAR = Kansas State University Museum of Entomological Prairie Arthropod Research; BW = Bruce Walsh collection (Tucson, AZ); RN = Ray B. Nagle (Tucson, AZ) collection.

***Drasteria walshi* Metlevski, new species**

(Figs. 4-9, 18-20)

Diagnosis. *Drasteria walshi* is most similar to *D. divergens* (Figs. 10-13, 21, 23), especially to the form with orange hind wings, *D. divergens* f. *socia* (Behr, 1870) (Figs. 12, 13). The following features can be used to differentiate *D. walshi* from *D. divergens*: in *D. walshi* the underside of the wings is pinkish, while they are yellow to pale yellow in *D. divergens*; in *D. walshi*

the terminal spots on the underside of the wings are obscured or completely absent, while in *D. divergens* there are strong black terminal spots on the underside of the wings; in *D. walshi* the discal spot is a thin dark comma-like line not connected to the postmedial band, compared to a strong black discal spot connected to the postmedial band (at least vein CuA2 is black from the postmedial band to the discal spot, but usually the connection is much stronger) in *D. divergens*.

Among other species of *Drasteria* occurring in southeastern Arizona only one, *D. tejonica* (Behr, 1870), has forewings with similar pattern and colored hind wings. *Drasteria tejonica* however is noticeably smaller in size and has much stronger black pattern on the hind wings (Figs. 14-17). Males of *D. tejonica* (Figs. 14-15)



Figs. 14-17. *Drasteria tejonica*, Pima Co., Arizona. 14-15, male. 14, dorsal surface. 15, ventral surface. 16-17, female. 16, dorsal surface. 17, ventral surface.

can be easily separated from *D. walshi* by the coloration of the hind wings, which are white basally in *D. tejonica*.

In males, the costal processes of the valvae of *D. walshi* arc robust, elongate, sinuous and pointed at the tip (Fig. 18). This readily distinguishes *D. walshi* from *D. divergens* (Fig. 23), as well as from any other species in the genus. Female genitalia of the new species (Fig. 20) could be confused only with those of *D. divergens* (Fig. 21) and *D. fumosa* (Fig. 22). The antevaginal plate in *D. walshi* is more than 3 times longer than the colliculum, while just slightly longer in *D. divergens* and about 2 times longer in *D. fumosa*. The antevaginal plate of *D. walshi* is semi-rectangular in shape, compared to triangular with a blunt tip in *D. fumosa*. The shape of the antevaginal plate of *D. walshi* is similar

to that of *D. divergens*: both species have a rectangular anterior portion and a slightly narrower posterior portion. However, in *D. walshi* the broader anterior portion is about half the length of the narrower posterior portion, while in *D. divergens* the length of both parts is subequal.

Description. *Head:* Light brownish gray; labial palpus light grey, with some dark brownish gray scales on the external side of first and second segments; antenna filiform in both sexes.

Thorax: Covered with long flattened and slightly spatulate hairs dorsally, with long simple hairs ventrally; patagia light brownish gray, with a dark brown longitudinal stripe; remainder of thorax little darker and with light pinkish tint; tegulae slightly rimmed with dark brown hairs on external margin; legs same color as thorax except for tarsi, which are darker brownish gray with a ring of light gray scales at distal end of each segment.

Forewing: Length 19–23 mm; males and females similar; ground color light brownish gray with light pinkish tint; basal line double, black, enclosed area light brownish gray; basal area brownish gray in anterior half, dark gray in posterior; antemedial line double, internal

and external lines black, enclosed area filled with dark brown, internal line making a strong long tooth toward base of wing between veins A and Cu and two small teeth at veins A and Sc, entire antemedial line almost straight from costa to vein A, abruptly curving inward after vein A; medial area very light brownish gray, somewhat darker in outer part and at costa; medial line brown, not strongly contrasting, double, the internal line thin, external one wider; both lines strongly expanded and becoming dark brown or almost black at costa; reniform spot dark brown, black rimmed, with strong whitish outline on outer margin and thin whitish outline followed by thin black line on inner margin; postmedial line double, area enclosed between internal and external lines dark brown except at costa where pinkish, internal line strong and black through its entire length, external one weaker, marked with dark brown or black scales, almost disappearing in the middle; postmedial line turning abruptly toward the apex at vein R_1 and almost parallel to costal margin until vein R_3 , then bending again and curving outward, includes strong tooth pointed outward at vein M_1 and another smaller tooth at vein M_3 , curving inward in between; making an abrupt turn at vein CuA_1 , continuing along this vein toward base of reniform spot then turning toward posterior margin of wing, curving slightly outward between base of reniform and vein A, turning toward anal angle of wing at vein A; area between reniform spot and postmedial line brownish grey to brown, filled with brown and light brownish grey scales, veins M_1 and CuA_1 within this area dark brown with strong whitish outlines joined with similar outline on inner margin of reniform spot; postmedial area dark gray, pinkish along postmedial line at costa; subterminal line slightly incurved between costa and vein R_3 , then slightly wavy and subparallel to inner margin of wing, at vein A_1 turning toward anal angle of wing, dark brown at veins, otherwise black in anterior half of wing, mostly brown, with some black scales between veins in posterior half; 4 strong black arrow marks arising from subterminal line between veins in anterior half of wing, and pointing toward base of wing; subterminal line with a thin pale brownish gray outline along outer side, immediately followed by dark brown line; subterminal area light brownish gray, somewhat darker in place where terminal shadow is located; apical shadow obvious, as a dark brown path, connected to dark brown outer outline of subterminal line; terminal line fine, wavy, obvious, dark brown to almost black; fringe pinkish at base, otherwise grayish brown, checkered. Underside pale pinkish to pinkish; reniform spot dark brown to black; dark brown transversal shadow extending from the middle of costa through inner edge of reniform toward the anal angle, ending well before anal angle between veins CuA_2 and A; subterminal line greasy pinkish with dark edges at costa, otherwise dark brown to black, convex, wide at costa, rapidly narrowing toward posterior edge of wing becoming a thin line at its posterior end, meeting transversal shadow at vein CuA_2 and not extending after this point, outer edge of subterminal line wavy, inner edge evenly convex; terminal and apical shadows brownish, obscured and sometimes barely visible; terminal line thin, dark brown, wavy, vanishing at anal angle; fringe pinkish at base, otherwise grayish brown, lighter toward anal angle.

Hind wing: Ground color orange pink, a few dark brown scales at anal margin and occasionally a few brownish scales near base of wing and on Cu stem; discal spot a narrow dark grayish brown line along cross-vein, not connected to postmedial band; postmedial band dark grayish brown to black, narrow through most of its length but strongly widened between vein R_1 and costa, subparallel to outer margin between anal angle and vein CuA_2 , approaching vein CuA_2 curving abruptly mesad, and at vein CuA_2 angling toward apex, then turning toward costa between veins M_2 and M_3 ; outer margin of postmedial band turning sharply outward at vein R_3 ; terminal and apical spots narrow patches, dark grayish brown to black, with obscure inner edge, almost disappearing in some specimens; terminal line obvious through most of its length, vanishing near anal angle, dark grayish brown to black, thin, wavy; basal portion of fringe pink, outer portion pink orange, greasy orange brown at terminal spot, with some blackish scales between basal and outer layers at terminal and apical spots. Underside pale pinkish to pinkish, some brown or brownish scales along costal margin; discal spot similar to that on upper side but weaker; postmedial band intermittent, marked by few brown scales at costal margin, remaining remnants present only between veins M_1 and M_2 , and between vein CuA_2 and anal angle; terminal spot a dark brown to blackish shadow, weak, in some specimens almost disappearing; apical spot absent; terminal line weaker than on upper side, otherwise similar; fringe same as upper side.

Abdomen: Ochreous gray, with some scattered dark brown scales.

Male genital capsule (Fig. 18): Uncus strong, curved, pointed at tip, dorsally with a low longitudinal crest and dense hairlike setae in third distal quarter; scaphium long, narrow, articulated at base of uncus;

valvae obovate, slightly asymmetrical, left valve slightly smaller, narrower in the middle and with more sinuous dorsal margin; valvula rounded, acute at ventro-distal angle, with a small tuft of setae on inner surface at ventro-distal end; area occupied by coremata small, subbasally on outer side of valva, extending along sclerotized base of valva from ventral edge of base of costa to ventral side of distal half of saccus; saccus about 4 times as long as wide, its dorsal edge slightly concave; saccular extension strong, slightly curved, ending just before tip of valvula in a small free prong-like projection turned inward toward genital capsule; pulvinus strong, broad, broader on left valva, tip of pulvinus with robust elongate setae; harpe curved, slender, smoothly narrowing to tip, apex flattened and rounded; conus present on both valvae, left one tapered, about 2 times as long as wide, right one minute, short; tip of conus bearing few microscopic setae; costa moderately sclerotized, with costal process present on both valvae; costal process prominent, broad based, strongly elongated, sinuous, tapered, pointed at tip; costal process on left valva shorter, directed along longitudinal axis of valva; costal process on right valva longer, directed slightly dorsad, reaching dorsal margin of valvula; saccus short, V-shaped; juxta symmetrical, about 2 times as long as wide, with deep V-shaped incision on dorsal margin and two short, curved, and divergent ventroanterior arms.

Aedeagus (Fig. 19): strong, straight, tubular, membranous in distal half dorsally but with a small sclerotized area at base of vesica, otherwise well sclerotized, its membranous portion finely spiculate; coecum short, slightly flattened dorsoventrally at tip; ventral plate of carina strongly sclerotized, long, narrow, slightly expanded at top, basal half of right margin with a strong longitudinal fold; dorsal plate of carina absent; inflated vesica short, turned dorsad, with a complex system of diverticula (insertion on Fig. 19): *diverticula arising on ventral side right of carinal plate* (2 large and 4–5 very small): **1.** diverticulus next to the tip of carinal plate, broad, about twice as long as wide, distally rounded, spiculate on right side, directed caudad, tip slightly turned left; **2.** group of 4–5 aligned small spiculate diverticula, next right to diverticulus 1, followed by diverticulus 3; **3.** the biggest diverticulus, two times longer than next longest diverticulus, slightly narrowing to the tip, finely spiculate, directed right laterodorsad, perpendicular to longitudinal axis of aedeagus; *diverticula arising on ventral side left of carinal plate* (1 bigger and 1 very small): **4.** diverticulus next to tip of carinal plate, short, bifurcated at tip, spiculate, directed left laterad, perpendicular to longitudinal axis of aedeagus, one of tips turned cephalad; **5.** very small, lobelike, with no spicula, between diverticulus 4 and tip of aedeagus; *diverticula arising at left dorsolateral angle of vesica* (2 bigger and 1 very small): **6.** globular, expanded distally, as long as wide, finely spiculate, directed dorsocaudad, with a narrow fingerlike projection arising left ventrolaterally and directed ventrad; **7.** second longest, tapering, finely spiculate, curved, directed cephalad, tip curving right dorsocephalad; **8.** very small, short, narrowing at tip, with no spicula, between diverticulus 7 and base of vesica; *top of vesica* exposed dorsad, bearing 1 small diverticulus and 1 small lobe: **9.** minute diverticulus, with no spicula, arising on right side close to diverticulus 2; **10.** small lobe with no spicula, close to the base of diverticulus 6; *posterior side of vesica:* **11.** bearing a small lobe with no spicula between diverticulus 1 and top of vesica.

Female genitalia (Fig. 20): Ovipositor telescopic; papillae analis with moderately sclerotized longitudinal band dorsally, weakly sclerotized in other parts, narrow, about 5 times as long as wide, strongly narrowing in distal third, tips rounded, membranous; surface of papillae with short scattered setae, which are denser on tips, some long setae at the base and tips of papillae analis; apophyses long and slender, posterior ones about 1.7 times longer than anterior; lamella postvaginalis (postvaginal plate) a V-shaped sclerotized band, its ends not connected to eighth segment's sclerotization; antrum wide, with almost parallel lateral edges, about 2 times as long as wide, dorsoventrally flattened, with large sclerotized antevaginal plate ventrally, otherwise membranous; antevaginal plate occupying almost whole ventral side of antrum, semi-rectangular in shape, slightly narrowing distally, with slightly convex posterior edge; ductus bursae short, slightly longer than wide, about 2 times narrower and 2.5–3 times shorter than the antrum; colliculum as long as wide, its left edge slightly longer than the right one, edges of colliculum not overlapping; bursa copulatrix asymmetrically ovate, membranous, with some

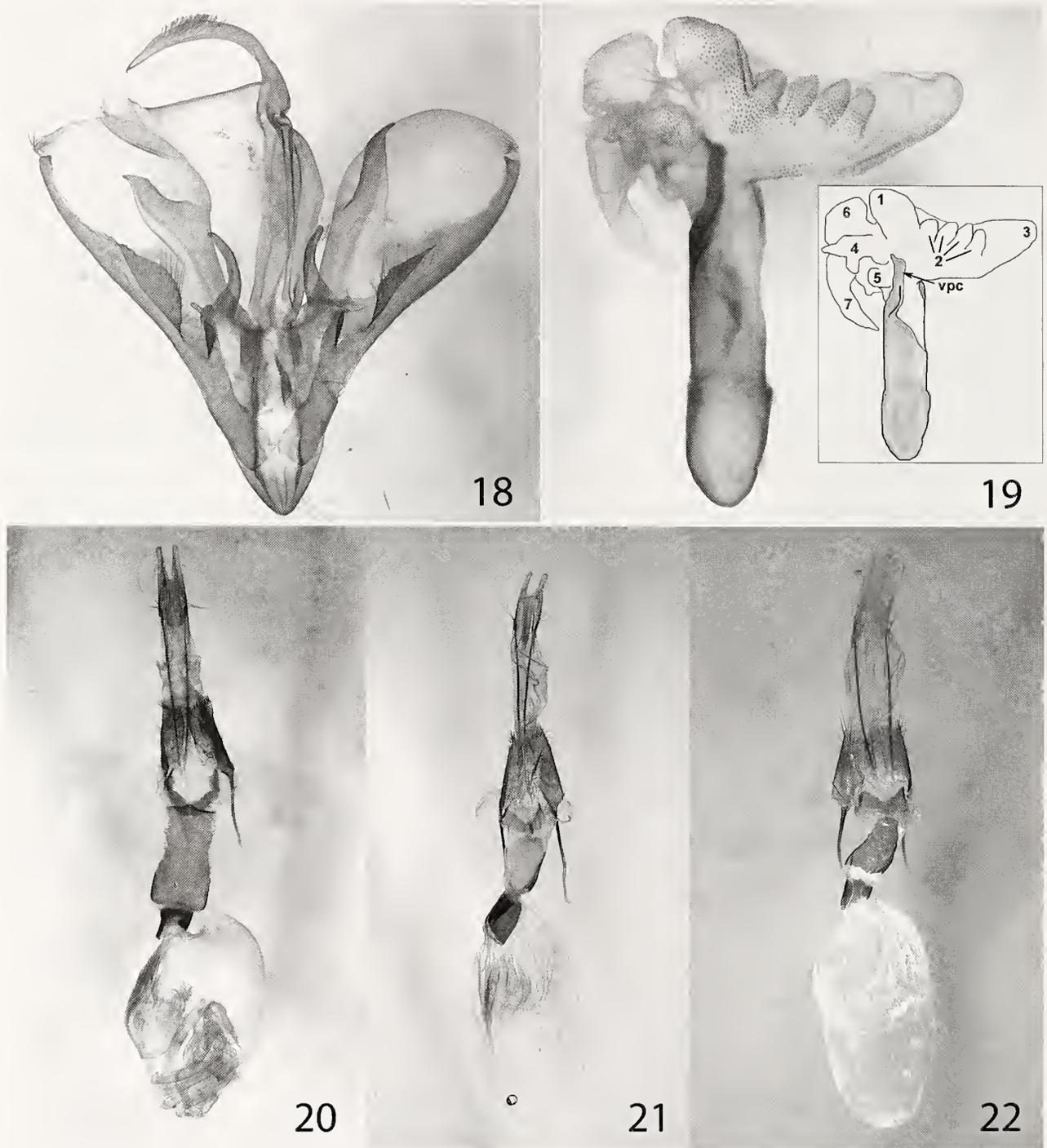


FIG. 18-22. **18.** Male genital capsule of *D. walsli* (posterior), holotype. **19.** Aedeagus of *D. walsli* with vesica everted (ventral view), holotype. Inset: vpc – ventral plate of carina; 1-7 – numbers of diverticula according to the description. **20.** Female genitalia of *D. walsli* (ventral view), paratype, genital prep. by Jan Metlevski No. 945. **21.** Female genitalia of *D. divergens* (ventral view), Tuolumne Co., California, genital prep. by Jan Metlevski No. 774. **22.** Female genitalia of *D. fumosa* (ventral view), Pima Co., Arizona, genital prep. by Jan Metlevski No. 963.



FIG. 23. Male genital capsule of *D. divergens* (posterior), genital prep. by Jan Metlevski No. 794.

longitudinal wrinkles on left side anterad of insertion of ductus bursae, otherwise smooth; insertion of ductus bursae posteriorly, slightly left; internal wall of bursa copulatrix in posterior half of bursa with very minute spines, most visible at wrinkled area, becoming smaller and barely visible laterad, and disappearing anteriorad; pseudobursa arising posteriorly, right of insertion of ductus bursae, coiling dorsad and to right, making 0.5 coil; ductus seminalis arising from the tip of pseudobursa.

Holotype. ♂, "AZ, Graham Co. Pinaleno Mts. Cunningham Campgrd. 9000 ft. UV + MV lights. 20 May 2002. B. Walsh leg.," "Genitalia Prep. by J. Metlevski No 766", deposited in KSU-MEPAR (Figs. 4–6, 18, 19).

Paratypes. (3 ♂ and 3 ♀): 1 ♂, same label data as holotype, in BW; 1 ♀, "AZ, Graham Co. Pinaleno Mts. Cunningham Campgrd. 9000 ft. Ponderosa pine habitat. 14 June 2005. UV + MV lights. B. Walsh leg.," "Genitalia Prep. by J. Metlevski No 945", in BW (Fig. 20); 1 ♂, "AZ, Graham Co. Pinaleno Mts. Cunningham Campgrd. 9000 ft. Ponderosa pine habitat. 5 June 2007. B. Walsh leg.", in BW; 1 ♀, "AZ, Cochise Co., Chiricahua Mts. Onion Saddle, 7700 ft, Ponderosa Pine/Oak habitat, 14 June 2007. B. Walsh leg.," "Genitalia Prep. by J. Metlevski No 1084", in BW; 1 ♀, "AZ, Cochise Co., Chiricahua Mts. Onion Saddle, 7600 ft, June 14 2007. Leg. Ray B. Nagle", "Genitalia Prep. by J. Metlevski No 1068", in RN (Fig. 7–9); 1 ♂, same label data as above, "Genitalia Prep. by J. Metlevski No 1069", in RN.

Variation. Specimens from the Chiricahua Mountains have the hind wings a slightly brighter ground color and with a stronger dark pattern compared

to specimens from the Pinaleno Mts.

Biology. Unknown. Specimens have been collected in the second half of May and first half of June.

Distribution. Pinaleno Mountains (Mt. Graham) and Chiricahua Mountains in southeastern Arizona.

Etymology. *Drasteria walshi* is named in honor of Bruce Walsh, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, in recognition of his invaluable efforts in studying the lepidopteran fauna of southeastern Arizona.

Discussion. Female genitalia of *Drasteria walshi* have a greatly enlarged antevaginal plate, which occupies most of the ventral side of the antrum and is longer than the colliculum. This condition of the antevaginal plate links *D. walshi* with *D. fumosa* (Strecker, 1898) and *D. divergens* (Behr, 1870), which are the only other Nearctic species in the genus sharing this character state. In the male genitalia, the aedeagus also provides characters linking *D. walshi* with the two species mentioned above in that the general structure of the vesica, such as the relative position and number of

diverticula, of *D. walshi* is most similar to that of *D. divergens* and *D. fumosa*.

All known specimens of *Drasteria walshi* have been collected in the Pinaleno and Chiricahua Mountains at altitudes between 7500–9000 feet (approximately 2300–2750 m) in ponderosa pine or mixed ponderosa pine/oak forest habitats. Both the Pinaleno Mts. and Chiricahua Mts. are isolated high mountain massifs surrounded by lowland plains grasslands and deserts.

ACKNOWLEDGEMENTS

We thank P. A. Opler and B. C. Kondratieff (Colorado State University), J. H. Boone (Field Museum, Chicago), E. H. Metzler (Alamogordo, New Mexico), and R. B. Nagle (Tucson, Arizona) for loans of specimens used in this study. We are grateful to T. Mustelin (San Diego, California), D. L. Wagner (University of Connecticut) and two anonymous reviewers for reviewing the manuscript. This article is Contribution No. 08-395-J from the Kansas Agricultural Experiment Station (KAES) and was supported in part by KAES Hatch Project No. 583 (Insect Systematics).

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Received for publication 1 July 2008; revised and accepted 9 December 2008

BIOLOGY AND DISTRIBUTION OF A RECENTLY REDISCOVERED ENDEMIC HAWAIIAN
LEAFROLLER MOTH, *OMIODES CONTINUATALIS* (CRAMBIDAE)

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ABSTRACT. The endemic Hawaiian leafroller moth *Omiodes continuatalis* was documented by early entomologists to be one of the most common species encountered during initial collecting trips in the Hawaiian Islands at the end of the 19th century. The species was declared extinct in 1982, and while subsequent surveys have resulted in their “rediscovery”, it is evident that *O. continuatalis* populations have experienced declines and localized extinctions throughout their historical range. The objective of our research was to document the life history, biology, general morphology, and behavior of this little studied species. To complete the investigation, we observed both wild caught and laboratory reared *O. continuatalis*. We also conducted light trap surveys to document the current distribution of *O. continuatalis* across the Hawaiian Islands. We have integrated our findings from this study with all available historical data on *O. continuatalis*, to create a document which can be referenced for future research relating to the biology or conservation of this species.

Additional Key words: pyraloid, light trap, fossorial, development, extinction

The genus *Omiodes* Guenée, 1854 (Lepidoptera: Crambidae) occurs in tropical and subtropical regions of Oceania, Southeast Asia and the Americas, and contains over 100 species, including 23 species endemic to the Hawaiian Islands. The subject of this research, *Omiodes continuatalis* (Wallengren, 1860), is a generalist grass-feeding species, originally documented from all of the high Hawaiian Islands, with the exception of Kahoolawe (Zimmerman 1958). The Reverend Thomas Blackburn found *O. continuatalis* to be one of the most common moths encountered during collecting trips in Hawaii prior to 1880 (Zimmerman 1958). Swezey reported the species from “drier, lower” habitats, but does not provide specific collection localities beyond a single reference to a population in Olinda, Maui (Swezey 1907; Zimmerman 1958). Despite their early documented widespread abundance, 100 years later the species was declared extinct by the U.S. Fish and Wildlife service, and other agencies (Gagné & Howarth 1982; IUCN 2007). *Omiodes continuatalis* and 13 other *Omiodes* species were listed as “extinct or possibly extinct” based on reviews of museum collections which indicated that specimens had not been collected for

several decades. Non-target impacts of the biological control agents introduced for the coconut and sugar cane leafroller pest species were blamed for the extinctions (Gagné & Howarth 1982). However, data from surveys of more recent museum collections completed in 2003 revealed extant *O. continuatalis* populations (Haines *et al.* 2004). Specimens were identified from light trap samples collected at five mesic forest study sites on both the leeward and windward sides of Hawaii Island (Haines *et al.* 2004). In addition, field collections completed in 2003 confirmed *O. continuatalis* to be abundant at several localities on East Maui (Haines unpublished data).

In the past, *O. continuatalis* larvae have been collected from native pili grass *Heteropogon contortus* (L.), as well as introduced species such as kikuyu grass *Pennisetum clandestinum* (Hochst. ex Chiov.) and Hilo grass *Paspalum conjugatum* Berg. (Zimmerman 1958). Like other species in the group, *O. continuatalis* larvae are leaf-rollers, and use silk to bind plant foliage together to create a refuge in which they feed and take shelter. Early observations by Swezey describe how *O. continuatalis* larvae typically feed near the base of their

host plants, within the grass matrix or in leaf litter at the soil surface (Zimmerman 1958). This behavior is uncharacteristic of other Hawaiian *Omiodes* larvae, which generally feed higher on host plant foliage, fastening or rolling the tips of leaves together (Swezey 1907). *Omiodes continuatalis* larvae were also noted to be physically distinct from larvae of other *Omiodes* species, in that they attain a greater body width and often exhibit pinkish-green coloration in contrast to the monochromatic green coloration displayed by larvae of other *Omiodes* species (Zimmerman 1958).

Unlike the sugarcane leafroller *O. accepta* (Butler, 1877), *O. continuatalis* is not considered a pest and consequently few data have been collected to document its life history. *Omiodes continuatalis* appear to share similar habitat requirements, feeding habits and physical characteristics with *O. accepta* (Zimmerman 1958), and initially seemed likely to have comparable biology and development. The objective of this chapter is to describe the complete life history of *O. continuatalis*, providing new information on its biology, ecology, general morphology and life history, and to integrate recent findings with information gathered by early naturalists, to create a document that can serve as a reference for future research on the biology and conservation of *O. continuatalis*.

MATERIALS AND METHODS

We collected data for this laboratory and field study from February 2005 to March 2008.

Insect rearing. We established laboratory colonies of *O. continuatalis* using wild female moths captured from UV light traps set on Kailili Road in Kokomo, Maui (484m) and at the University of Hawaii Kula Agricultural Research Station (975m), Maui. Moths were collected alive in plastic specimen vials, and held at ambient temperature until being transferred into rearing cages. Moths were easily identified using the key to *Omiodes* species in Zimmerman (1958), as *O. continuatalis* is a very distinctive species. Rearing cages were composed of hand-made 61cm×46cm×31cm PVC-framed sleeve cages covered with fine insect mesh sleeves. Moths were fed a 30% honey/70% water solution, and were provided potted sugarcane, pili grass and/or Hilo grass, on which to oviposit. We obtained young sugarcane starts from Hawaii Commercial and Sugar (HCS) and Hawaii Agricultural Research Center (HARC) fields, while pili grass and Hilo grass were propagated from seed. These plants provided food and served as host plants for colony larvae. The substrate in each host plant pot consisted of a 50/50 blend of Sunshine Mix 5® potting soil and vermiculite. All moth colonies and host plants were housed in the University

of Hawaii at Manoa, Gilmore Hall greenhouses, and University of Hawaii, Kula Agriculture Research Station greenhouses. In Manoa, temperatures ranged seasonally from a mean low of 18.7°C in the winter to a mean high of 24.3°C during the summer (Manoa Lyon Arboretum weather station), and plants were watered three times each day. In Kula, temperatures ranged from a mean low of 11.1°C in the winter 2006, to a mean high of 24.4°C during the summer 2006 (UH Kula weather station), and plants were watered twice daily. We collected additional wild *O. continuatalis* moths and integrated them into laboratory colonies periodically to replenish adult stock and maintain genetic diversity.

Biology and morphology. To elicit oviposition, we isolated female moths in vials lined with wax-paper and temporarily denied them access to a food source. These stressful conditions commonly stimulate female moths to oviposit. Eggs deposited in each egg mass were then counted under a Leica dissecting microscope to determine the total number present, and the minimum and maximum number of eggs per mass. In order to quantify mean egg size, we selected 50 eggs randomly from 50 *O. continuatalis* egg masses, and measured them at the widest point using an ocular micrometer in a Wild Heerbrugg microscope.

We obtained data on *O. continuatalis* larval development and morphology by observing 100 individual larvae develop from egg to pupal stage. Larvae were stored in individual 2-oz Solo® cups (ventilated with 3–6 holes in the lid). Cups were cleaned and larvae provided with fresh sugarcane foliage every 2–3 days. We measured the head capsule width of each larva daily to document larval growth; head capsule widths were measured at their widest point, as above for eggs. We also recorded changes in larval morphology following each larval molt. Only head capsule widths of larvae which survived from egg to pupal stage (n = 52) were used to assess instar duration and size ranges. We completed a one-way analysis of variance to document variation in head capsule width by instar.

Behavior. Data relating to *O. continuatalis* larval behavior were collected based on observations of individual larvae contained in laboratory colonies, or from colony larvae deployed on potted host plants at selected Maui field sites. We collected data opportunistically, observing behaviors in the field during larval deployment and retrieval, and in the laboratory during daily colony maintenance and larval feedings. Adult *O. continuatalis* were isolated and observed individually to assess adult lifespan under laboratory colony conditions.

Distribution. Field sites were selected to be surveyed based on accessibility and the presence of *O.*

continuatalis host plants. We collected *Omiodes continuatalis* adults using two types of UV light traps: sheet light traps and bucket light traps. Sheet light traps consisted of an 18" UV light bulb placed in front of a large, white bed sheet suspended vertically. Bucket light traps were constructed with an 18" UV light bulb attached to three 10.2cm×25.4cm clear plastic flight intercept vanes, and secured on top of an 8 liter bucket with bungee cords. Each bucket trap was baited with a killing agent such as cyanide or a Hot Shot No-Pest Strip®. Individual moths landing on sheet light traps were collected alive, however insects collected from bucket traps were always dead. We set at least one of the two trap types at each field site to survey for *O. continuatalis* adults. When an initial survey yielded numerous *O. continuatalis* specimens, we revisited sites to replenish and diversify laboratory colonies. Visual surveys of and sweep netting for adult *O. continuatalis* were also completed at field sites to complement data collected from light trapping. To quantify total survey effort, the number of nights and the number of traps that were used, were multiplied to obtain the total number of "trap nights" completed at each survey location.

RESULTS AND DISCUSSION

Biology. *Omiodes continuatalis* are highly attracted to UV light, and both male and female moths were regularly collected from light traps. In addition, *O. continuatalis* appeared to be more attracted to UV light traps than other *Omiodes* species. Once drawn to a light, *O. continuatalis* adults frequently remained around the light for long periods of time, in contrast to the sedge-feeding species *O. anastrepta* Meyrick, 1899, which are not as readily attracted to light traps, even when adults are observed flying in close proximity to a trap. Over the course of one year, adult *O. continuatalis* were collected, on multiple occasions, from light traps at Kokomo, Makawao, and Kula, on Maui (Table 1). Data from these surveys indicate that *O. continuatalis* is multivoltine, with more than three generations per year. Considerable climatic seasonal variation exists at mid-high elevation localities, so if *O. continuatalis* populations are multivoltine at these three mid-high elevation field sites, it is likely that populations are also multivoltine and not seasonal at low elevation sites, where seasonal changes in temperature and rainfall may be even less restrictive to *O. continuatalis* development. Based on mitochondrial genetic data, *O. continuatalis* populations do not exhibit much structure, either within or among islands (Haines, unpublished data), suggesting that moths are strong dispersers. Because of this, we do not suspect that populations on islands other than Maui

exhibit very different morphology or life history characteristics from those observed in our colonies.

Laboratory colonies of *O. continuatalis* were maintained continuously from July 2005–December 2005, and from March 2006–March 2008. In laboratory colonies, the moths were most successfully reared on sugarcane host plants, as compared with pili grass and hilo grass, which the moths were previously documented feeding on in the field. At one point during rearing of the colony, some larvae escaped from cages and were discovered feeding on *Canavalia pubescens*, Hook. & Arn. (Fabaceae) an endemic Hawaiian legume which was being grown in the same greenhouse as food for another caterpillar species (*O. monogona* Meyrick, 1888). The *O. continuatalis* larvae were caged with *C. pubescens*, and surprisingly, multiple generations were reared on the plant. There are no previous records of this grass-feeding species surviving on a dicot host, yet it survived through four generations on *C. pubescens* with no obvious morphological or reproductive disadvantages. The success of the moth on this host plant over multiple generations indicates that its host range in the wild might be broader than previously expected, although oviposition preference may be more important than nutritional suitability as a determinant of host range. While the utilization of this host plant was unexpected given the documented life history of the species, it may be explained by recent molecular analysis of the genus. Phylogenetic analysis based on mitochondrial DNA shows that *O. continuatalis* is the sister species, and the closest relative, of *O. monogona*, the sole Hawaiian *Omiodes* species which feeds on fabaceous host plants (Haines unpublished data). Other tropical *Omiodes* species are documented to feed on Fabaceae, thus this dietary shift may reflect a reversion to an ancestral host plant retained in the evolutionary 'memory' of some Hawaiian *Omiodes*. Evolutionary memory is the idea that larvae may retain an ability to feed on ancestral hostplants on which they are no longer found in nature (Janz & Nylin 1998). This discovery has important implications not only for the conservation of the species, but also for the evolution of host plant shifts in the genus.

Adult *O. continuatalis* (Fig. 1) lived a maximum of 18 days under laboratory conditions. In cages, *O. continuatalis* females were observed ovipositing on both the upper and lower surfaces of host plant vegetation, and females did not avoid ovipositing on material such as wood, plastic, wax paper and screen mesh. Egg masses ranged in size from a single egg, to a maximum of 73 eggs, with a mean of 7.25 (\pm 0.81 S.E.) per individual egg mass ($n = 115$). A limited survey of *O. continuatalis* females ($n = 33$) indicated that gravid



FIG. 1. Adult *Omiodes continuatalis* moth.

females can lay more than 400 eggs over their lifetime, and up to 122 eggs in a 24 hour period. Egg masses are composed of even rows or clusters of flattened eggs, slightly overlapping one another (Fig. 2). Eggs have a mean width of 1.22mm (± 0.025) ($n = 50$), are light yellow in color, and exhibit fine surface reticulations and an iridescent sheen. *Omiodes continuatalis* eggs took four days to hatch at 32°C, and eight days to hatch 22°C.

Morphology. Swezey broadly described the life history and physiology of *O. continuatalis* (summarized by Zimmerman 1958). Zimmerman (1978) later provided limited descriptions and illustrations of larval morphology, including a larval key to most Hawaiian *Omiodes* spp. However, no detailed research has been reported that fully characterizes the life history and larval stages of *O. continuatalis*.

Based on head capsule width measurements from 52 individuals, we observed *O. continuatalis* larvae transitioning through seven to nine developmental instars (Fig. 2). In a previous study, *O. continuatalis* larvae were observed transitioning through as many as 10 instars prior to pupation (King & Rubinoff 2008). Analyses of variance of head capsule widths by instar indicates that mean head capsule widths for instars 1 through 9 are significantly different from one another (Figure 2; $df = 8$; $F = 1823.68$; $P = <0.001$). Due to considerable overlap in head capsule widths in each instar (Fig. 3), it is difficult to distinguish discrete larval instars at any stage of development based on measurements alone.

Upon eclosion, larval head capsules are reddish-

brown in color and have a mean width of 0.35mm (range: 0.32–0.38). The reddish-brown coloration persists throughout the entire larval stage. Unlike the larvae of other Hawaiian *Omiodes* species which maintain bright green body coloration (Swezey 1907), *O. continuatalis* larval coloration is comparatively less vivid. The abdomen is a gradient of off-white to light olive, and once larvae begin feeding they acquire the approximate pigment of the vegetation they are digesting. Larvae may molt to the second instar (mean: 0.45mm, range: 0.40–0.50) and the third instar (0.64mm, 0.50–0.74mm) after three to five days. In the third instar, larvae develop a single black head spot on each of the head capsule lobes, as well as two black spots on the prothoracic shield. *O. continuatalis* larvae continue to molt every three to five days (4th: 0.92mm, 0.66–1.10mm; 5th: 1.28mm, 0.90–1.42mm; 6th: 1.78mm, 1.3–1.96mm), growing in size and developing more intricate patterns of melanization on the prothoracic shield, as well as tubercles on the 2nd and 3rd thoracic segments and the 7th–10th abdominal segments. During the penultimate instar (6th; 7th: 2.32mm, 1.8–2.52mm; 8th: 2.84mm, 2.34–3.56mm), *O. continuatalis* larvae acquire a faint pink tint, while the



FIG. 2. *Omiodes continuatalis* larvae exhibit changing patterns of melanization on the prothoracic shield during nine developmental instars. A. Cluster of eggs. B. First instar. C. Second instar. D. Third instar. E. Fourth instar. F. Fifth instar. G. Sixth instar. H. Seventh instar. I. Eighth instar. J. Ninth instar.

head, thoracic and abdominal spots are reduced. Molts to the final instar (7th; 8th; or 9th: 3.19mm, 2.86–3.50mm) also occur in three to five days. At this stage, head spots disappear completely, and the thoracic and abdominal segments become very pink. Immediately prior to pupation, *O. continuatalis* larvae become pale and begin to shrink in size to form prepupae. It is common for lepidopterous larvae to change color prior to pupation, when the procuticle increases in area in the cuticle column above the epidermal cells (Chapman 1998). Pre-pupae develop into pupae over 1–2 days, and remain as pupa for 13–17 days. In total, immature *O. continuatalis* development was 36–57 days.

Behavior. Early instar larvae feed on the surface and inner tissue of host plant foliage, often near the midrib of the leaves. *Omiodes continuatalis* larvae cannot be characterized as gregarious, like the larvae of *O. blackburni* (Butler, 1877) which share the same shelters throughout most of their development, however early instar *O. continuatalis* larvae often feed in close proximity to one another. Aggregations of larvae on host plants especially in the first and second instars are a natural result of larvae emerging from eggs laid in clusters. General observations from this research suggest that first instar *O. continuatalis* larvae are more likely to survive when feeding together. First instar larvae that were separated, and made to feed independently, frequently failed to feed successfully and progress to the subsequent instar. The reasons for this increased mortality are not clear, but may involve the cumulative benefit of aggregated larvae feeding cooperatively during early instars. Research indicates that cooperative feeding behavior has many advantages for lepidopterous larvae, including increasing feeding efficiency on physically tough host plant material (Clark & Faeth 1997). It is possible that *O. continuatalis* larvae exhibit this type of cooperative feeding due in part to the fact that they have evolved on grasses, which are tougher than many dicot host plants and contain higher concentrations of silica (Fahn 1982). When *O. continuatalis* larvae reach the third instar they continue to consume the surface and inner tissue of host plant leaves, but fed independently from other larvae more frequently than in the early stages. Third instar larvae began to fasten silk threads across the foliage and/or roll-up foliage to create a protected shelter in which to retreat. During the fourth instar and/or when larvae attain a head capsule width of 1mm, they begin to feed on the entire leaf structure. Some larvae were observed to feed predominantly inside their shelters, while others migrated back and forth between their shelter and feeding areas elsewhere on the host plant. Late instar

larvae primarily feed outside the shelters they construct. Feeding patterns were easily discerned based on areas of feeding damage on field deployed host plants, and host plant material provided to isolated *O. continuatalis* larvae.

In colony, *O. continuatalis* larvae occupied all available space on the host plants provided, from the sheaths at the very base of the sugarcane, to the top of each blade. In contrast, when placed at lower densities on host plants in the field, larvae generally stayed on the green sugarcane foliage on the mid to upper portion of the plant. When foliage was available at the base of the plant, larvae often constructed shelters there, using both fresh and dead vegetation as materials. This behavior is consistent with early observations of larval feeding habits made by Swezey (Zimmerman 1958). Additional observations by King & Rubinoff (2008) indicate that some *O. continuatalis* larvae display a more unusual habit, burrowing beneath the soil surface at the base of their host plants for shelter. In some cases, larvae were recovered up to 14cm below the soil surface. This fossorial behavior was observed in early, middle and late instar larvae, and is not pupation behavior.

Another behavior we observed during laboratory colony rearing was larval cannibalism. *O. continuatalis* larvae, specifically late instars, were observed feeding on other live *O. continuatalis* larvae. This behavior was more common on occasions when larval density was high and host plant resources were decreasing, but still available. Most frequently, late instar larvae were observed feeding on middle instar larvae. In one case a ninth instar larva was found feeding on another ninth instar larva. In all cases, the larvae being consumed did not appear to fight or try to avoid the predation, but remained stationary during the attack. The cannibalistic

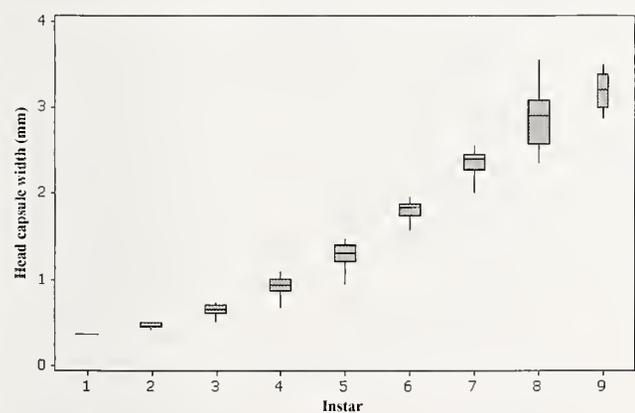


FIG. 3. Boxplot of headcapsule widths of *Omiodes continuatalis* larvae by instar. Medians and inter-quartile ranges are represented for each instar, and box widths are proportional to sample size.

TABLE 1. Locations surveyed for *O. continuatalis* on the main Hawaiian Islands.

Island	Location	Elevation (m)	Method	Date	Trap nights	<i>O. continuatalis</i> present	Surveyor(s)
Kauai	Pu'u Ka Pele Forest Reserve	855	light trap	8/6/08	1	No	W. Haines
	Koke'e State Park, Camp Sloggett	1060	light trap	5/16/05, 10/6/07	3	No	W. Haines, C. King
	Mohihi Road, Koke'e State Park	1110	light trap	6/2/04	2	No	W. Haines
	Koke'e State Park, Koke'e Museum	1130	light trap	8/7/07	2	No	W. Haines
	Na Pali Kona FR, Pihea trail	1140	light trap	8/7/07	1	No	W. Haines
	Koke'e State Park, Nualolo Trail	1170	light trap	8/8/07	1	No	W. Haines, M. Mecklen
	Na Pali Kona FR, Alakai Swamp Trail	1180	light trap	8/7/07	3	No	King Haines, Rubinoff
	Na Pali Kona FR, Pihea trail	1200	light trap	5/18/05, 7/23/06, 8/18/06	4	No	Eiben, Haines, Rubinoff
	Koke'e State Park, Near Awaawapuhi Trail	1245	light trap	6/3/04	1	No	W. Haines
	Na Pali Kona FR, Kalalan Lookout	1255	light trap	8/17/06	2	No	J. Eiben, D. Rubinoff
Oahu	Aina Haina, Niuki Circle	2	light trap	3/24/05	1	No	C. King
	Mokuleia Beach	2	light trap	5/1/05	1	No	W. Haines, C. King
	Sandy Beach	3	light trap	3/6/05, 6/20/05	2	No	W. Haines, C. King
	Ewa, open grass lot	15	light trap	5/21/05	1	No	C. King
	Diamond Head Crater, wetland	80	light trap	4/3/05, 2/15/08	4	No	W. Haines
	Palolo Valley	80	light trap	2/25/08, 2/26/08, 2/27/08, 2/28/08	4	No	W. Haines
	HARC Maunawili	160	light trap	5/26/05, 6/22/05	3	No	C. King
	Lyon Arboretum, sugarcane patch	228	light trap	1/27/07	2	No	C. King
	Lanipo Trail	240	light trap	5/29/05	1	No	W. Haines, C. King
	Dole pineapple field	256	light trap	3/12/05	1	No	Haines, King, Vorsino
	Hawaiiloa Ridge Trail	425	light trap	6/14/06	1	No	J. Eiben, W. Haines
	Wiliwilimui Trail, access	440	light trap	6/6/06	1	No	W. Haines
	Wa'ahila Ridge	475	light trap	6/8/06	1	No	W. Haines
	Kahanahaiki Valley	605	light trap	2/24/07	1	No	C. King
	Mt. Tantalus	613	light trap	6/3/05, 6/22/05	2	No	W. Haines, C. King
	Wiliwilimui Trail, Summit	731	light trap	6/24/06	1	No	W. Haines
	Ko'okau Mountains, Konahuanui Trail	762	light trap	6/1/06	1	No	W. Haines
	Palikea Trail	777	light trap	5/15/06	1	No	W. Haines
	Mokuleia FR, along Mt. Kaala Road	1100	light trap	6/15/07	2	No	W. Haines
	Waianae-Kai FR, near Ka'ala NAR boundary	1190	light trap	6/15/07	1	No	W. Haines
Ka'ala NAR, bog	1200	light trap	6/15/07	1	No	W. Haines	
Ka'ala NAR, DOFAW shed	1210	light trap	6/15/07	1	No	W. Haines	
Maui	Kanaha Beach Park	3	light trap	3/20/05	1	No	C. King
	Mahiko Gulch sugarcane field	76	light trap	6/1/05, 7/13/06	2	No	C. King
	West HCS sugarcane field	137	light trap	6/6/06	1	No	C. King
	Iao Valley	183	light trap	6/5/06	1	No	C. King
	Waiehu Valley Trail	183	light trap	7/6/06	1	No	C. King
	Haliimaile sugarcane field	274	light trap	6/1/05	1	Yes	C. King
	University of Hawaii Agricultural Park	305	light trap	6/1/06	1	No	C. King
	Waihe'e Ridge Trail	305	visual survey	6/8/05	0	Yes	W. Haines
	2955B Kaili'ili Rd, Kokomo	484	light trap	3/19/05°	15	Yes	W. Haines, C. King
	Pu'u Kukui Watershed, Kahuanui Valley	485	light trap	4/5/06	2	No	W. Haines
Waihe'e Ridge Trail	670	light trap	6/8/05	1	No	W. Haines	

° dates = 3/19/05, 5/25/05, 6/1/05, 7/19/05, 9/3/05, 9/23/05, 2/8/06, 3/7/06, 4/18/06, 7/8/06, 3/9/07, 4/19/07, 5/18/07, 8/17/07, 2/6/08

TABLE 1. Continued

Island	Location	Elevation (m)	Method	Date	Trap nights	<i>O. continuatalis</i> present	Surveyor(s)
Maui	Makawao Forest Reserve, Site 1	750	light trap	3/23/05	1	No	W. Haines
	Makawao Forest Reserve, banana patch	762	light trap	6/19/06, 7/14/06, 7/15/06	8	Yes	W. Haines
	Makawao Forest Reserve, Site 5	825	light trap	3/23/05	1	Yes	W. Haines
	Kipahulu Valley Delta Camp, HALE	860	light trap	1/15/04, 9/14/04	4	No	W. Haines, D. Rubinoff
	Makawao Forest Reserve	914	light trap	3/19/05, 5/25/05, 6/1/05	4	Yes	W. Haines, C. King
	Makawao Forest Reserve, Site 2	915	light trap	3/23/05	1	Yes	W. Haines
	Makawao Forest Reserve, Site 6	930	light trap	3/23/05	1	Yes	W. Haines
	UH Kula Field Station	975	light trap	3/9/07 ^o	5	Yes	C. King
	Makawao Forest Reserve, Site 4	1050	light trap	3/23/05	1	No	W. Haines
	Waipoli Road, Kula	1065	light trap	6/20/04	2	Yes	W. Haines
	Haleakala Ranch	1280	visual survey	6/23/06	0	Yes	C. King
	Makawao Forest Reserve	1280	light trap	6/3/06, 8/17/07	2	Yes	W. Haines, C. King
	Makawao Forest Reserve, Site 3	1330	light trap	3/23/05	1	Yes	W. Haines
	Kula FR	2073	light trap	6/4/06	1	No	C. King
Molokai	Moomomi Preserve	10	light trap	7/5/05	1	No	W. Haines
	Molokai Forest Reserve, TNC Barracks	915	light trap	7/7/05, 12/30/05	3	No	W. Haines
	Kamakou Preserve, Kamakou Flats	1105	light trap	5/18/04	2	No	W. Haines
	Kamakou Preserve, Puu Kolekole	1130	light trap	5/19/04, 7/7/05	2	No	W. Haines
	Kamakou Preserve, Pepeopae Bog	1240	light trap	5/19/04, 7/6/05	2	No	W. Haines, D. Rubinoff
Lanai	Lanai Cane Management Area	365	light trap	7/3/05	1	No	W. Haines
	Kanepuu Preserve	520	light trap	7/2/05	1	No	W. Haines
	Kanepuu Preserve	544	light trap	3/6/08	2	Yes	D. Rubinoff, P. Sehmitz
	Munroe Trail	1000	light trap	7/3/05	1	No	W. Haines
Kahoolawe	Base Camp, south of Kanapou Bay	5	light trap	1/14/06	1	Yes	S. Meyers
Big Island	Pahala sugarcane field	292	light trap	6/10/05	1	No	C. King
	Honokaa sugarcane field	303	light trap	6/9/05	2	Yes	C. King
	Glenwood, Omega Rd.	700	light trap	2/6/05	2	No	W. Haines
Big Island	Clenwood, Near Kahaualea NAR	700	light trap	2/6/05, 7/30/06	6	No	W. Haines
	Ka'u, Kaiholena	770	light trap	7/31/06	2	No	W. Haines, J. Giffin
	Ola'a FR	822	light trap	2/5/05	1	No	W. Haines
	Ola'a FR	975	light trap	2/5/05	1	No	W. Haines
	Ka'u, Kaiholena	975	light trap	7/31/06	1	No	W. Haines, J. Giffin
	Kahuku Ranch, HAVO	1005	light trap	5/18/06	3	No	W. Haines, D. Rubinoff
	Volcano Village	1128	light trap	6/8/05, 11/26/05	2	No	C. King
	Ola'a Tract, HAVO	1150	light trap	5/17/06	4	No	W. Haines
	Escape Rd./Thurston, HAVO	1155	light trap	4/16/05, 6/29/05, 5/18/06	3	No	W. Haines, C. King
	Kilauea Field Station, HAVO	1158	light trap	2/5/05	1	No	W. Haines
	Kipuka Puauulu, HAVO	1200	light trap	10/15/04	1	Yes	W. Haines
	Ola'a Tract, Pu'u Unit	1300	light trap	5/17/06	1	No	W. Haines, D. Rubinoff
	Waikii	1432	light trap	6/11/05	1	No	C. King
	Mama Loa Strip Road, HAVO	1500	light trap	10/14/04	1	Yes	W. Haines
	Kona Forest Unit, Hakalan Nat'l Wildlife Refuge	1615	light trap	4/12/05	2	No	C. King
	Keamoku flow, HAVO	1707	light trap	4/15/05, 6/28/05	3	No	C. King

^o dates = 3/9/07, 4/7/07, 4/19/07, 5/10/07, 5/18/07

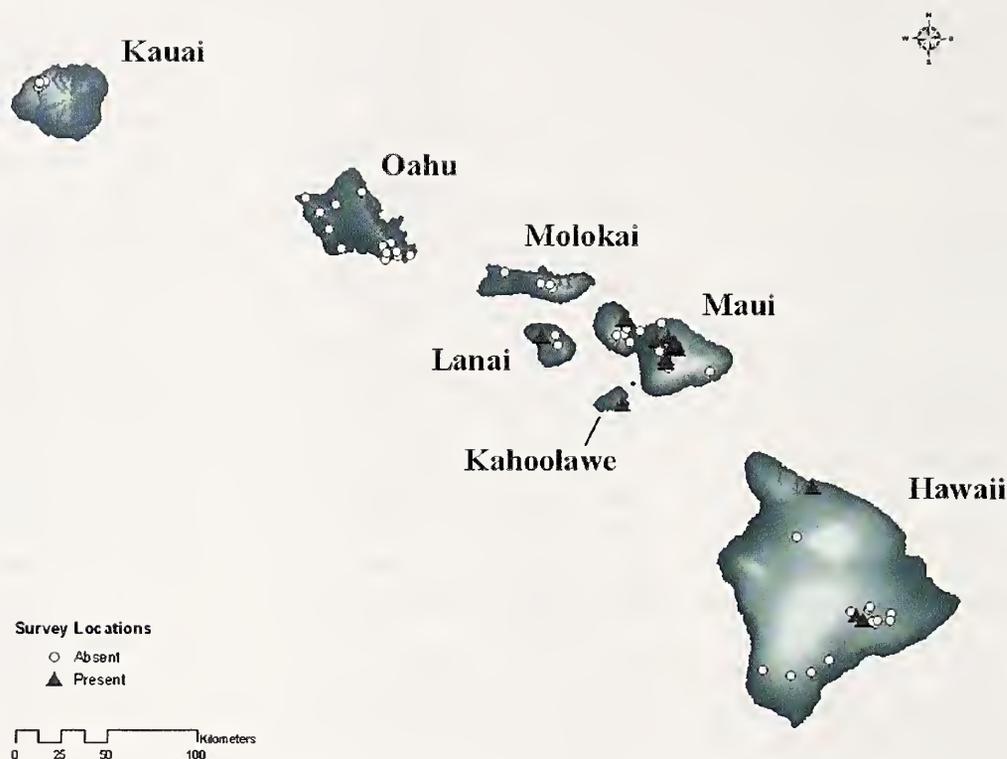


FIG. 4. Map of current distribution of *Omiodes continuatalis* in the Hawaiian Islands, based on recent field survey data.

larvae began their attacks at the tenth abdominal segment, working forward and consuming the entire contents of the abdomen. The only structures not consumed by the cannibalistic larvae were the head capsule and the cuticle. Thus, the end product of such an encounter resembled a shed head capsule and cuticle following a developmental molt. Perhaps the behavior has never been documented in *Omiodes* larvae because Hawaiian *Omiodes* species have not been reared in colony prior to this investigation. Cannibalism, prompted by competition for limited resources such as host plant resources and over-wintering sites, has been documented in non-Hawaiian crambid species (Baskauf 2003), so it is possible that *O. continuatalis* larvae may exhibit the behavior in the natural environment under high density conditions.

Distribution. We completed more than 166 trap nights of surveys at 85 field sites for populations of *O. continuatalis* across the Hawaiian Islands (Table 1). While previous collecting records show *O. continuatalis* to be present in mostly dry or mesic habitats (Zimmerman 1958; Haines *et al.* 2004), our surveys

show that *O. continuatalis* populations are present in dry, mesic and also wet habitat types (Table 1) (Fig. 4). On Hawaii Island, *O. continuatalis* was collected from three mesic habitats: Kipuka Puaulu (1195m) and Mauna Loa Strip Road (1492m) on Mauna Loa in Hawaii Volcanoes National Park, and a remnant sugarcane field near the town of Honokaa (303m). All of these sites receive a mean annual rainfall (MAR) of 1500–2000mm. On Maui, *O. continuatalis* were collected from seven distinct field sites: Waihee Ridge trail (305m), Haliimaile/Haleakala Hwy sugarcane field (274m), Kokomo (484m), UH Kula field station (975m), Makawao Forest Reserve (914m, 1280m), and Haleakala Ranch (1280m). With the exception of Waihee Ridge, which is located on West Maui, all of the field sites are located on East Maui. The two Makawao Forest Reserve sites and the Haleakala Ranch site are wet habitats (2000–3000mm MAR). Waihee is a mesic habitat (1500mm MAR), as is Kokomo (1500–2000mm MAR), while Haliimaile/Haleakala Hwy sugarcane field and the UH Kula field station are dry habitats, due to their position in the rain shadow of East Maui (MAR

<750mm). *O. continuatalis* were also collected on the islands of Kahoolawe and Lanai. Both of these islands are exceedingly dry (630mm MAR) as they are also located in the rain shadows of Maui and Molokai.

Based on survey data of *O. continuatalis*, it is clear that this species can persist in diverse habitat types ranging from dry to wet. *O. continuatalis* also occurs in habitats exhibiting varying levels of alteration and disturbance. The species is present in predominantly native forest habitat (e.g. Mauna Loa, Makawao Forest Reserve), as well as areas where native habitat has been converted to pastureland (e.g. Haleakala Ranch), and/or agricultural land (e.g. Honokaa and Haliimaile sugarcane fields). Their persistence appears possible so long as the habitat contains sufficient host plant resources, in the form of native or introduced grasses, to support larval development. Given their widespread distribution, their palpable ability to adapt to significant changes in habitat, and their ability to utilize invasive grasses as host plants, *O. continuatalis* would seem an unlikely candidate to face high risk of declines and/or extinction. Nevertheless, the current distribution of *O. continuatalis* on the islands of Maui, Kahoolawe, Lanai and Hawaii represents a significant range reduction for a species which was previously common, but is now extirpated from, Kauai, Oahu, and Molokai.

It is possible that the reduction in distribution is not as great as these survey data might indicate. Even small variations in season, moon phase, air temperature, precipitation and wind speed can affect light trap catch on a given day. Therefore, it is possible that *O. continuatalis* may have gone undetected at sites where light trapping occurred on only one occasion. The Kailili Road study site in Kokomo, Maui was surveyed frequently due to the consistent *O. continuatalis* trap catch. Even so, there were at least two occasions where *O. continuatalis* adults were not observed. Furthermore, during surveys on Hawaii Island, *O. continuatalis* was not collected from light traps at the Keamoku flow on Mauna Loa, where the species has been previously recorded (Haines *et al.* 2004). Thus, it is possible, that *O. continuatalis* are present at additional field sites on Maui, Kahoolawe, and Hawaii Island. Accordingly, the species may remain undetected on other islands despite extensive negative data from these survey efforts. This hypothesis seems more plausible at sites where traps were only set-up for 1–2 trap nights, as opposed to field sites like Kokee State Park or the Alakai Swamp on Kauai where more than 18 trap nights have cumulatively been completed, and no *O. continuatalis* have yet been detected.

Potential factors influencing the decline and restricted distribution of *O. continuatalis* were not

quantified under the scope of this research. Given the persistence of the moth in severely degraded habitats, it seems unlikely that habitat destruction or habitat alteration alone could be significant limiting factors for the species. There are habitats on the islands of Kauai, Oahu and Molokai, both pristine and disturbed, which we presume contain suitable resources to support *O. continuatalis*, and yet the species has still not been “rediscovered” on these islands. If habitat destruction and alteration are not consistently affecting the persistence of this species across the Hawaiian Islands, then what other factors may be contributing to their declines? The intentional and accidental introduction of natural enemies into the Hawaiian Islands has been viewed suspiciously by entomologists for over a century (Perkins 1897; Zimmerman 1958; Howarth 1983; Henneman & Memmott 2001), and some of these parasitoids and predators appear to suppress populations of other *Omiodes* species (Zimmerman 1958; Bess 1974). Additional research is currently underway to examine the mortality factors, specifically parasitism, which may be affecting *O. continuatalis* populations. However, the individual and compound effects of introduced predators, such as ants and spiders, are also likely mortality factors, and their effects on *Omiodes* species remain to be investigated.

ACKNOWLEDGEMENTS

We thank A. Areinas (Hawaii Agricultural Research Center) and M. Nakahata (Hawaii Commercial & Sugar Company) for providing plant material, and D. Oka and G. Otani (University of Hawaii Kula Agricultural Research Station) for field preparation and greenhouse assistance. J. Patu provided essential laboratory assistance. Access permits were granted by S. Meidel (Haleakala Ranch), G. Shishido and B. Gagne (Department of Land and Natural Resources, Division of Forestry and Wildlife), and C. Haines and G. Haines (Pacific Produce). Special thanks to M. Wright, C. Hooks, J. Eiben, L. Leblanc and L. Kaufman (University of Hawaii, Department of Plant and Environmental Protection Sciences) for valuable input on research methods, and also W. Haines (University of Hawaii, Department of Plant and Environmental Protection Sciences) for access to unpublished data. Anonymous reviewers provided valuable feedback on this publication.

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Received for publication 23 May 2008; revised and accepted 9 Dec 2008.

A NEW SPECIES OF *MORRISONIA* (NOCTUIDAE) FROM
SOUTHEASTERN NORTH AMERICA

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ABSTRACT. We describe *Morrisonia triangula*, (Noctuidae: Hadeninae: Orthosini) from material collected from Virginia to Texas. Illustrations of adults and their genitalia are provided. The generic placement is discussed.

Additional key words: *Achatia*, *Egira*, *Himella*, *Orthosia*

For at least 40 years collectors in the southeastern United States have been aware of an undescribed species of hadenine provisionally placed in the genus *Morrisonia* by Jack Franclemont. Apparently, Franclemont never collected the species but was aware of it from material sent to him for identification by Charles Kimball prior to the latter's publication of the Lepidoptera of Florida in 1965. Kimball (1965) mentions 5 specimens collected in Escambia Co., Florida, 4 in April of 1961 and one in May of 1962. Additional material, much of which is in the U. S. National Museum, was collected in the period from 1960-80 in Virginia, the Carolinas, Louisiana and Texas by several eastern collectors. Kimball (1965) indicated that Franclemont would describe the species but a manuscript was never completed. In this paper we describe the new species and discuss some of the current taxonomic problems posed by the "genus" *Morrisonia*.

MATERIALS AND METHODS

Specimens were examined from the National Museum of Natural History, Washington, DC (USNM) and Furman University, Greenville, SC (FU). Data were provided by Steve Roble on material in the Virginia Department of Natural Resources (VDNR), Richmond, VA; by Steven Hall on specimens in the North Carolina Heritage Program (NCHP), Raleigh, NC; and by Richard Brown on material in the Mississippi State Museum (MSM), Starkville, MS. Data were also provided from the personal collections of James K. Adams; Vernon Brou, Abita Springs, LA; Chuck Ely, Nacogdoches, TX; Irving Finkelstein, Atlanta, GA; Howard Grisham, Maysville, AL; Ed Knudson, Houston, TX; Hugo Kons, Gainesville, FL;

Tom Neal, Gainesville, FL; Brian Scholtens, Charleston, SC; Jeff Slotten, Gainesville, FL; and J. Bolling Sullivan.

Genitalia were prepared by digestion in 10% potassium hydroxide, dissected in water, and photographed with a Nikon Coolpix 995 camera attached to a Nikon SMZS00 microscope. Additional photographs were provided by Donald Lafontaine (see Lafontaine 1998). Recently collected specimens were sent to Paul Hebert at the University of Guelph for barcode COI analyses (Ratnasingham & Hebert, 2007).

Morrisonia triangula sp. nov. Sullivan & Adams
(Figs. 1–2)

Description. *Head:* Antennae fasciculate, setae exceeding shaft diameter at base in male, shorter than shaft diameter in female; scape straw with rusty scales intermixed; antennal dorsum scaled with alternating straw and rusty bands. Palps upturned, slightly longer than eye diameter, tan, dark brown and reddish scaled. Frons straw above tongue, short scaling but dorsal half of frons protruding with ventral part deep maroon, dorsal part straw, tan with reddish scales; a distinct dark line visible across upper part of frons. Area lateral to eye blackish scaled, tan scales below tongue. *Thorax:* Neck with a mixture of reddish and straw scales, largely erect. Collar a mixture of white, straw, tan and deep maroon scales forming a series of horizontal bands; scaled tuft behind collar. Tegulae reddish brown with some white scales; scaling underneath mostly white. Legs with reddish scaling dorsally, brown with cream scales ventrally; single pair of spurs on L2, two pairs on L3. *Abdomen:* two reddish dorsal scale tufts on first two segments, 2nd tuft small. Dorsum of abdomen tan with scattered reddish scales; underneath more reddish but similar.

Forewing: Pattern without obvious cross lines, dominated by a black basal and anal dash and a black triangular wedge at mid costa; whitish scaling in costal area before wedge, distal to wedge are 5 whitish costal spots, the most distal the largest; cream elliptical mark between dashes, marginal line black, scalloped; anal dash with smaller dash on costal side, whitish scaling on vein along anal dash; wing base above and below basal dash

darkened; orbicular and reniform spots lightly outlined, filled with the surrounding light gray ground color of the forewing; orbicular oblong, posterior to triangular black wedge; reniform kidney shaped, just distal to triangular wedge. *Hindwing*: Fuscous with marginal black band and tan marginal scales forming fringe. *Underside*: With distinct discal spots; perceptible PM (post-medial) line. Reddish on marginal half of forewing; black scaling on veins distal to PM line giving a striated appearance; basal half of forewing with blackish scaling. Hindwing with similar scaling, black scales densest on costal edges of both wings.

Male genitalia (Fig. 6): Valvae symmetrical, extending beyond uncus when viewed laterally, flared toward apex; costal region sclerotized, saccular region membranous; digitus arising from costa and curving ventrally well beyond saccular edge; elasper C-shaped, deriving from well developed medial plate; flared apical portion of valva setose with corona; uncus gently tapering and arching ventrally, slender, subbasal setae on dorsal side; gnathos and socii absent; anal tube slightly sclerotized ventrally; tegumen arms broad, forming inverted V; penicillum well developed and located on pointed flap at posterior end of tegumen; vinculum V-shaped, well developed; pleurite slender, curving up to dorsal side of tegumen; justa flaring posteriorly, with deep V in middle, posterior edges rounded; aedeagus rounded at base, sclerotized and tapering to a gentle curving apex; vesica with 3 or more spirals, basal spiral with longitudinal row of short cornuti, largest cornuti in short row above long, longitudinal row, diverticula on first and second spirals, ribbon-like band of embedded cornuti beginning on second spiral, cornuti patch (6–10 long cornuti) ventral to second diverticulum, distal end of vesica membranous.

Female genitalia (Fig. 9): Lightly sclerotized anal papillae, anterior and posterior hypophyses equal in length; ostium a simple flared opening, ductus sclerotized to bursa; accessory bursa arising ventrally, spiralled with sperm duct arising near tip; bursa a well defined sack with 4 evenly spaced longitudinal signa extending 2/3 toward anterior end, walls of bursa striated.

Types: *Holotype*: Male (Fig. 1): U. S. A. North Carolina: Craven Co., Croatan National Forest, Road 169, 2 iv. 2000, J. B. Sullivan. *Paratypes*: (11 males, 8 females) – North Carolina: Collection data same as holotype (2 males); Craven Co., Croatan National Forest, Road 147, 11 iv. 2000 (2 males, 1 female); 23 iv. 2006 (2 males, 1 female); 12 v. 1996 (1 female); 6 vi. 2006 (1 female); Croatan National Forest, Road 3046, 26 vi. 1995 (1 female) J. B. Sullivan. Georgia: Lumpkin Co., Blood Mountain, .25 mi. S of Neel's Gap, 3100', 27 v. 2006 (1 female). Louisiana: St. Tammany Parish, sec 24T6SR12E, 4.2 mi. NE of Abita Springs, 30 iii. 1998 (1 male); 10 iv. 1998 (1 male); 25 iii. 2002 (1 male); 28 iii. 2004 (1 female). Texas: Tyler Co., Big Thicket National Preserve, Turkey Creek Unit, 15–16 iv. 1994 (2 males); 8 iv. 1995 (1 female). The holotype will be deposited into the U. S. National Museum and paratypes into the Canadian National Collection, British Museum, Florida State Collection of Arthropods, Texas A&M University, and the Texas Lepidoptera Survey (with Charles Bordelon and Edward C. Knudson, Houston, TX).

Etymology. The name *triangula* is an adjective describing the distinctive triangular mark along the forewing costa. We suggest Triangle-barred *Morrisonia* as the common name.

Diagnosis. *Morrisonia triangula* is abundantly distinct in maculation and genitalia from other species of *Morrisonia* and from other hadenine species encountered in the Eastern United States. In pattern it

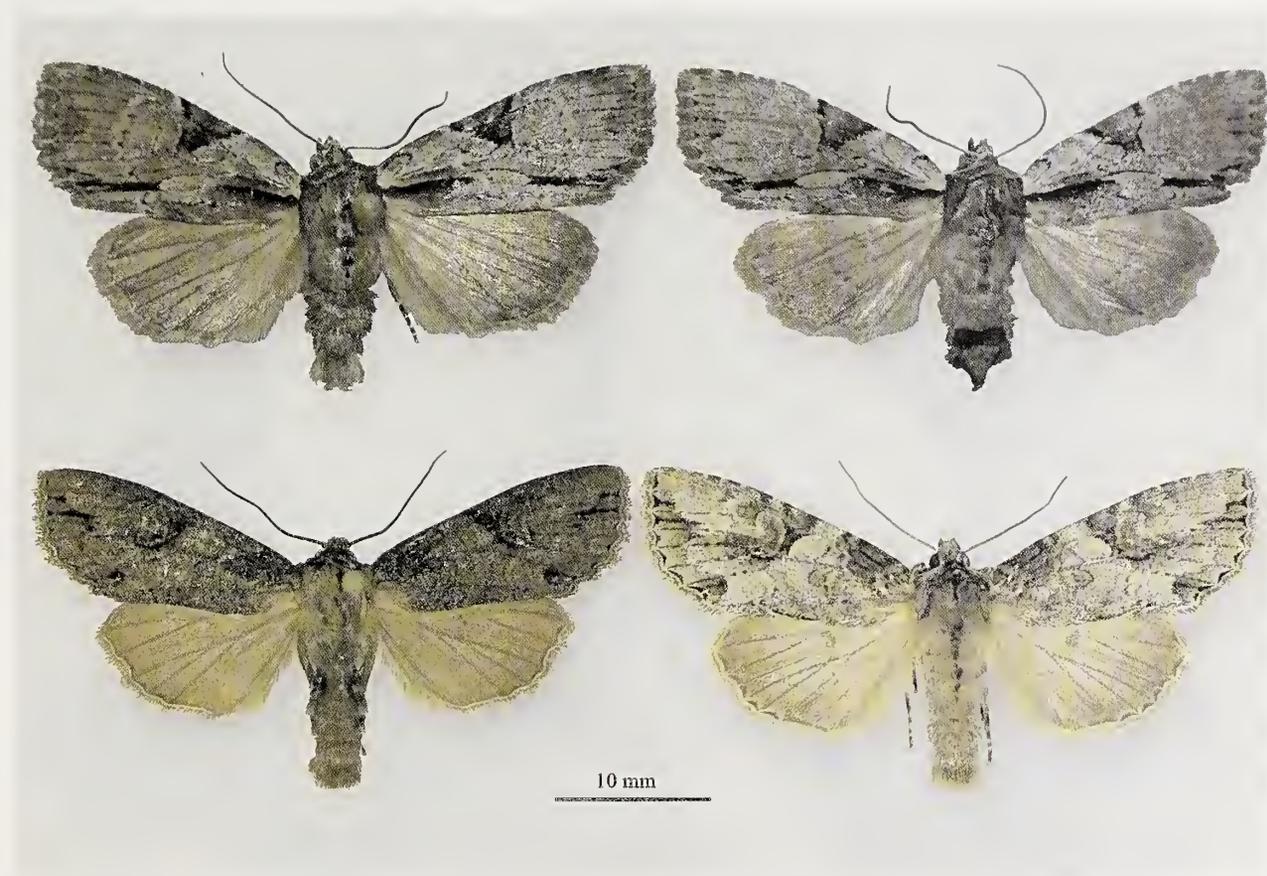
resembles less heavily marked forms of *M. evicta* (Grt.) but is larger, has the distinct costal triangle and except perhaps for a few mountain localities, is allopatric. If the two species do fly together, one would expect *M. evicta* to be on the wing earlier in the spring, *M. triangula* more closely resembles *M. latex* (Gn.) (Figs 3, 4) in size and ground color, and, to some extent, in the major dark markings of the forewing. The two species certainly occur in similar habitats in the mountains and possibly on the coastal plain.

When the wing pattern is obscured, the genitalia of either sex can be used to distinguish the species. Males of *M. triangula* lack hair pencils at the base of the abdomen as do *M. confusa* (Hbn.) and *M. latex*. The digitus is almost basal in *M. confusa* but crosses the membranous sacculus more distally in *M. latex* and *triangula*. In *M. latex* the membranous area is swollen distally, in *triangula* it tapers evenly. The everted vesica of *triangula* is unique in the genus because it has no large cornutus nor comb-like concentrations of smaller cornuti. Instead, it has a ribbon-like band of small cornuti.

Distribution and Habitat. This species occurs from the southeastern corner of Virginia along the coastal plain to all of Florida and west to east Texas. There are very few piedmont records (which may reflect a lack of collecting in this area). In the mountains it occurs from Avery Co. in North Carolina to the foothills in NE Alabama. County records are as follows: **VIRGINIA**: City of Suffolk, City of Virginia Beach, Isle of Wright; **NORTH CAROLINA**: Bladen, Brunswick, Carteret, Craven, Cumberland, Hoke, Macon, Martin, Moore, Onslow, Pender, Union; **SOUTH CAROLINA**: Charleston, Greenville, Oconee; **TENNESSEE**: Cocke; **GEORGIA**: Fulton, Long, Lumpkin, Rabun, Towns, Union; **FLORIDA**: Alachua, Escambia, Liberty, Monroe, Okaloosa; **ALABAMA**: Bibb, Conecuh, Sumpter; **MISSISSIPPI**: Forrest, Franklin, George, Hancock, Harrison, Jackson, Pearl River, Pike; **ARKANSAS**: Ashley, Union; **LOUISIANA** (Parishes): Iberville, St. Tammany, West Feliciana, Winn; **TEXAS**: Hardin, Jasper, Polk, Sabine, Tyler.

Collections of this moth are not limited to a specific habitat. It occurs in swamps, savannahs, pinelands and mesic hardwood sites throughout the Coastal Plain. Mountain sites are equally undistinguished.

Flight Season. In the Coastal Plain of North Carolina the extended flight period runs from late March into June and perhaps early July. Most males fly in mid April and most females are in flight in May–June. Mountain records (above 4000') are May through mid July. For other states with numerous records, the recorded flight periods are as follows: **Mississippi**:

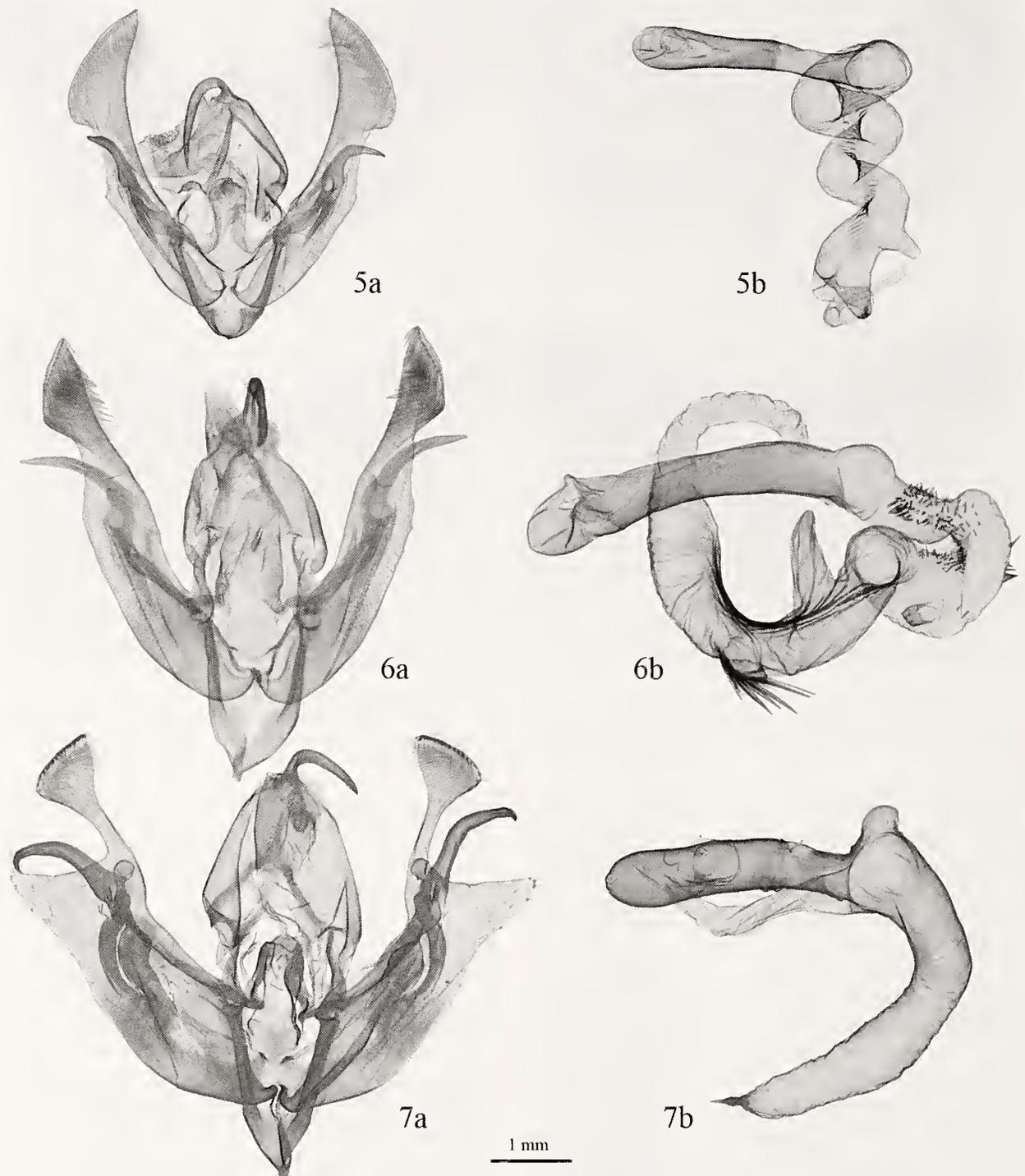


FIGS. 1–4. Adult *Morrisonia triangula* Sullivan and Adams. Male. Little Deep Creek Rd., Croatan National Forest, Craven Co., N. C. April 2, 2000, J. Bolling Sullivan. 2. *Morrisonia triangula* Sullivan and Adams. Female. Croatan National Forest Rd. 147, Craven Co., N. C. April 11, 2000, J. Bolling Sullivan. 3. *Morrisonia latex* (Guenée). Male. East side of Carp Ridge, 45°24.63'N, 76°03.45'W, Ontario, 14 June 2003, J. Troubridge. 4. *Morrisonia latex* (Guenée). Female. Temiscouata Co., Québec, 16 June 1993, Henry Hensel.

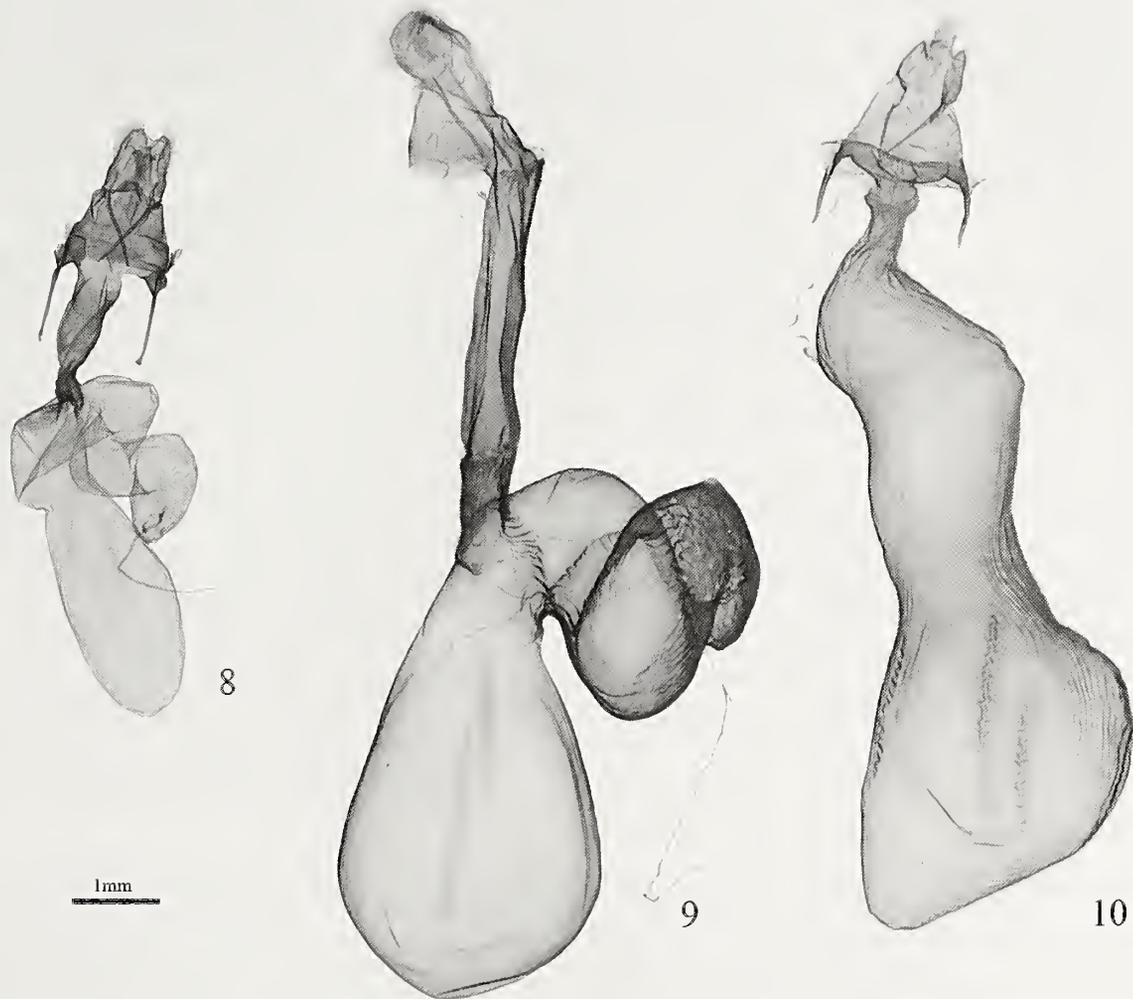
March 27–June 2; Louisiana: March 12–June 15; Texas: April 8–May 22; South Carolina: May 21–July 25 (the latest recorded specimen, from the mountains [Oconee Co.]); Georgia: April 23–May 27; Florida: March 17–May 23; Alabama: June 3–June 12. There is no evidence for a second brood.

Generic Placement. The genus *Morrisonia* is attributed to Grote (1874), with *evicta* as the type species, but no characters are given in his work to help delineate the genus. Hampson (1898–1913) included taxa from North America and New Zealand but species from New Zealand have since been removed (Dugdale 1988). Forbes (1954) characterized the genus as follows: “vestiture always mixed, the division of the tuft on upper part of face obvious; collar usually with suggestion of a central ridge, and concave on either side; double dorsal tufts of thorax distinct; several distinct tufts on abdomen.” Since Forbes’ treatment of the genus, *M. distincta* Hbn. has been moved to the genus *Achatia* (Hodges et al. 1983) and *Mamestra latex* (Gn.) has been moved into *Morrisonia* (Poole 1989). Other North

American genera placed in the tribe Orthosiini by Lafontaine (2007) are *Acerra*, *Stretchia*, *Perigonica*, *Orthosia*, *Himella*, *Egira* and *Achatia*. Members of the tribe are united by characters of the larval hypopharynx and spinneret (Fibiger & Lafontaine 2005), characters which we have not evaluated. Genitalic variation in this tribe and within several of the genera is extreme (Ronkay et al. 2001). The genus *Morrisonia* is no exception. What characters then seem to place this new species in *Morrisonia*? Two external characters other than wing pattern support placement of the new species in *Morrisonia*. First, the vestiture is coarse, a mixture of scales and hairs, and in most of the other genera only hair scales are present. Second, there is a well-differentiated line across the frons that occurs in the other *Morrisonia* species but is extremely faint when present (rarely) in other genera. Comparison of related species and genera (*Egira alternans* (Wlk.), *variabilis* (Sm.), *dolosa* (Grt.), *crucialis* (Harv.), *rubrica* (Harv.), *cognata* (Sm.); *Stretchia inferior* (Sm.); *Perigonica angulata* (Sm.); *Himella fidelis* Grt.; *Orthosia praeses*



FIGS. 5-7. Male genitalia of *Morrisonia*. **5a,b.** *Morrisonia evicta* (Grote). **a.** Valves, Dunrobin, Ontario (CNC 13538). **b.** Aedeagus. Same data as male valves. **6a, b.** *Morrisonia triangula* Sullivan and Adams. **a.** Valves, Wedge Plantation, 7miN McClellanville, South Carolina (CNC 13964). **b.** Aedeagus. same data as male valves. **7a,b.** *Morrisonia latex* (Guenée). **a.** Valves, North Gower, Ontario (CNC 13539). **b.** Aedeagus. same data as male valves.



FIGS. 8–10. Female genitalia of *Morrisonia* spp. 8. *Morrisonia evicta* (Grote). Female. Aweme, Manitoba (CNC 13560). 9. *Morrisonia triangula* Sullivan and Adams. Female. Key Largo, Florida (CNC 13542). 10. *Morrisonia latex* (Guenée). Female. Lac Mondor, Ste Flore, Québec (CNC 13540).

(Grt.), *rubescens* (Wlk.), *hibisci* (Gn.), *alurina* (Sm.), *pacifica* (Harv.), *revicta* (Morr.), *pulchella* (Harv.), *mys* (Dyar), *erythrolita* (Grt.), *garmani* (Grt.) and *segregata* (Sm.) and all 5 *Morrisonia* species using CO1 barcoding techniques (Hebert et al. 2006) reveals that, whereas most species sort with their supposed congeneric members, there are often inclusions of one or two additional non congeneric species in each generic cluster. In the case of *Morrisonia* both *evicta* and *triangula* sort together but may be separated from the other *Morrisonia* species by *Orthosia hibisci* or *rubescens*. Examination of the male and female genitalia (Figs. 5, 6, 8, 9) shows that *M. evicta* and *triangula* are quite similar in all characters and the pair is most similar to *M. mucens* (Hbn.). *M. confusa* and *M. latex* have genitalia which are quite divergent from the *mucens*, *evicta*, *triangula* complex. Significant

divergence is seen in the CO1 data from *M. latex* but not *M. confusa*.

Diverse assemblages of species are characteristic of *Orthosia*, *Egira*, and perhaps other orthosiine genera with multiple species (Ronkay et al. 2001). Finding good generic characters is difficult at best. For *M. mucens*, *evicta* (Fig. 5) and *triangula* (Fig. 6) we could list the spiral vesica with groups of cornuti but no major spine, a short diverticulum near the apex of the vesica, and the valva, diaphanous along its ventral edge, indented from the ventral side past the midpoint and expanded distally. The valve process derives from the costal plate; the medial plate often produces a small process. In females (Figs. 8, 9) the appendix bursa is coiled, the ductus bursa well sclerotized, and the ostium simple. These same characters are either missing or highly modified in *M. confusa* and *latex* (Fig. 10).

Morrisonia confusa and *latex* are polyphagous (Covell 2005; Rings *et al.* 1992). Most records for *Morrisonia evicta* are from *Prunus*, although *Kalmia* and *Corvus* are listed also, perhaps erroneously (Wagner *et al.* 2008). Jaek Franelemont reared *Morrisonia mucens* from Water Oak (*Quercus nigra* L.) as reported in Godfrey (1972). While most orthosiines require tender new foliage, both *M. confusa* and *M. latex* develop comparatively slowly on older, hardened summer foliage. *M. confusa* is exceptional among noctuids in taking as long as 6–7 months to mature (Wagner 2005). The habits of *M. confusa* and *M. latex* are strikingly different from each other and completely different from the other spring feeding orthosines. *M. confusa* begins the year feeding externally on new growth as do the other species, but in the last instar it fashions a shelter on old summer foliage, densely lines it with silk, and continues to feed for upwards of 5–6 months. *Morrisonia latex* also feeds throughout the summer but rests on bark by day (at least in the last instar), a habit completely unique to other orthosines (Wood & Butler 1989; Wagner *et al.* 2008). Based on the sum of differences in larval morphology, behavior, and life history, *M. evicta*, *confusa* and *latex* could easily be placed in three separate genera.

Thus, everything points to inclusion of *triangula* in the genus *Morrisonia*, considering that it seems to be the closest relative to *evicta*, the type species. In fact it is a better fit than some of the other species currently placed there. When the larval biology of *triangula* is known, hopefully, it will confirm this placement rather than add more heterogeneity to yet another genus in the Orthosini.

ACKNOWLEDGEMENTS

We would like to acknowledge the following persons who contributed data, insight or both: Vernon Brou, Richard Brown, Chuck Ely, Irving Finkelstein, Howard Grisham, Steven Hall, Paul Hebert, Ed Knudson, Hugo Kons, Don Lafontaine, Tim McCabe, Tom Neal, Steve Roble, Dale Schweitzer, Brian Scholtens, Darryl Searcy, Jeff Sloten, John Snyder and Dave Wagner. Figures were prepared by Jocelyn Gill.

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Received for publication 31 January 2008; revised and accepted 20 October 2008

TINACRUCIS NOROESTA, NEW SPECIES, NORTH AMERICA'S LARGEST TORTRICINE MOTH
(TORTRICIDAE: ATTERIINI)

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ABSTRACT. The Neotropical tribe Atteriini is briefly characterized, and *Tinacrucis noroesta* is newly described in order to make the name available for a forthcoming book on moths of western North America. This species, the northernmost of the tribe, occurs in the Sierra Madre Occidental, Mexico, and mountains of southern Arizona, where it was first collected in 1927. The larvae are believed to be polyphagous leaf rollers on broadleaf trees and shrubs but have not been discovered in the field.

Additional Key words: Egg mass adornment scaling, sexual dimorphism, Chihuahua, Durango, Arizona, leaf-roller.

The Atterini comprises one of the smallest and most well defined tribes of the Tortricinae. Its monophyly is convincingly supported by a suite of uniquely derived morphological and behavioral characters associated with oviposition (Powell 1986). The adults are among the largest tortricid moths in the Western Hemisphere, FW length ranging to 22 mm. Females are conspicuously larger than males, and there is pronounced sexual dimorphism in wing shape and color patterns in some genera (*Anacrusis*, *Tina*, *Tinacrucis*), whereas the sexes are similar in other genera (e.g., *Atteria*, *Templemania*). The eggs are laid in imbricate, overlapping patches, presumably a synapomorphy with Archipini and Sparganothini. Females possess obvious patches of corethrogyne scales covering the venter of A6 and A7; a thick pad of long, thin, dark scales on A6, which are spread over the egg mass and its periphery, and an enormous patch of upright, thicker scales on A7 that are curled at the tips, which are glued to the substrate in clumps, like a fence surrounding the egg mass. Most atteriines are nocturnal, but *Atteria* are diurnal and brightly colored, evidently specific Batesian mimics of *Pseudatteria* (Tortricinae: Polyorthini). Atteriine larvae are similar to sparganothines but are much larger leaf rollers. The distance between V setae on A9 is greater (1.5–2X) than on A8, the crochets are bi- or triordinal, and there is a well developed anal fork. I have reared several species of *Templemania*, *Tina*, and *Tinacrucis* from eggs to maturity on synthetic diet, which suggests atteriines are polyphagous, and Dan Janzen and others have reared field collected larvae of Costa Rican *Anacrusis* from several unrelated plant families, enhancing that assumption. The Atteriini includes about 40 described species assigned to eight genera, in addition to numerous undescribed taxa in Central and South America. A few species range into northern Mexico, one into Arizona.

Tinacrucis Powell, 1986, is distinguished by having elaborate antennal setulae in males, the costa sinuate in both sexes (unmodified in male *Anacrusis* and *Templemania*), markedly different size and FW pattern between the sexes (though not as extreme as in *Tina*), greatly enlarged A8 tergum, forming a hood enclosing the male genitalia. *Tinacrucis* includes six named species and several undescribed in Mexico and Central America. I have reared broods of several of them from single female egg masses, enabling association of the markedly differing sexes.

I have been aware of the species described here for 50 years, based on males taken by J.A. Kusche in the Chiricahua Mountains, Arizona, in 1927, but until recent years, we lacked sufficient material to confirm conspecificity of the Arizona species with specimens collected in Durango, Mexico. This species is described now because we discuss it in our forthcoming book, *Moths of Western North America* (Powell & Opler in press), scheduled for publication by the University of California Press in May, 2009. A treatment of the Sparganothini and Atteriini, by J. W. Brown and Powell, is in preparation for *Moths of America North of Mexico*, an appropriate place for this description, but it will be published later. Both of those volumes will include color images of the new species.

Tinacrucis noroesta Powell, new species
(Figs. 1, 2, male, female from
El Salto, Durango, Mexico)

This is the largest tortricine moth in America north of Mexico. Males have a relatively narrow FW with sinuate costa, pale beige to yellowish reticulated with rust lines and irregularly mottled with rust-brown. Females are larger with broader wings, pale chocolate- to rust-brown with faint darker and white banding in costal area when fresh and with huge masses of modified scales ventrally on abdominal segments 6 and 7.



FIG. 1. *Tmacrucis noroesta* Powell ♂ — Mexico, Durango, W of El Salto, VII.5.1964 (J. Martin) CNC.



FIG. 2. *T. noroesta* Powell ♀ — Mexico, Durango, W of El Salto, VII.1.1964 (J. Martin) CNC.

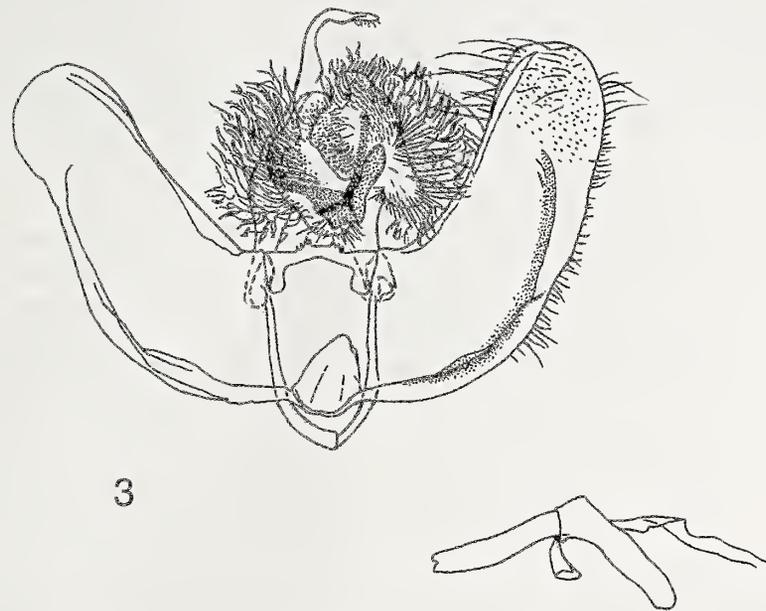


FIG. 3. *Tinacruis noroesta*, male genitalia, ventral aspect, valvae spread; aedeagus, lateral aspect shown to right; a, aedeagus with vesica extended, revealing the deciduous cornuti.

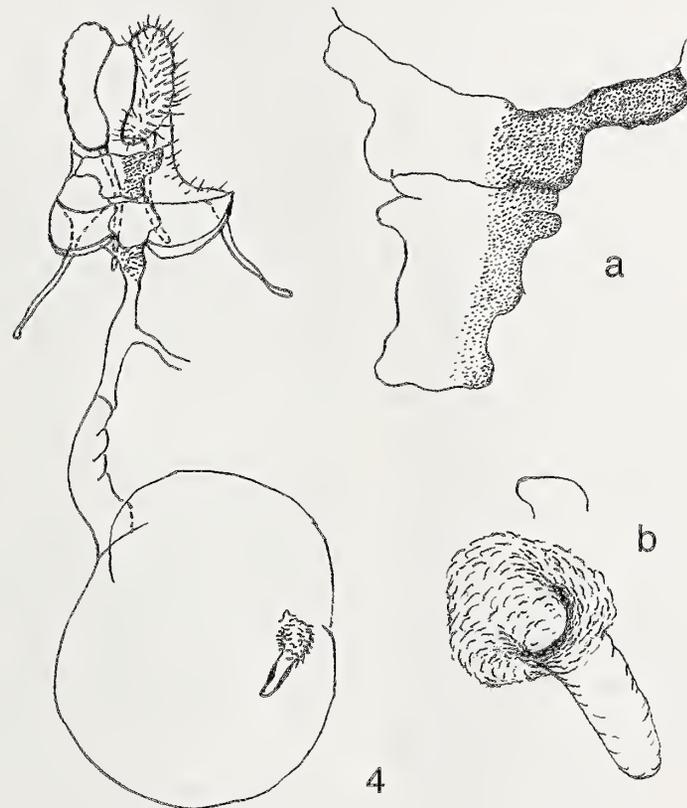


FIG. 4. *T. noroesta*, female genitalia, ventral aspect; a, detail of translucent ventral plate of A9; b, detail of signum, dorsal aspect.

Description. MALE. *Forewing*. Length 14.7–16.3 mm (n = 25), narrower than female, length 2.6–2.8 × width, costa sinuate, concave beyond middle, apex produced and subtended by concave terminal margin; ground color pale beige to yellow, reticulate with rust-brown along veins and numerous cross lines between veins, confined by rust-brown clouding to irregular blotches, basally, in cell, and subterminal area (resembling skeletonized spots on a fallen leaf); costal area beyond middle whitish in fresh specimens. *Hindwing*. Broad, pale cream colored, tinged with rust apically; underside variably mottled by rust in costal and apical areas, which is visible from above. *Abdomen*. Scaling pale beige to rust tinged caudally, venter paler, with segmental dark, medial spots. *Genitalia*. As in fig. 3 (drawn from paratype, El Salto, JAP slides 2893; n = 8); uncus only slightly flared apically, socii densely covered with elongate scales; joined tip of gnathos elongate, slightly flared; a pair of dentate projections on posterior margin of transtilla usually widely separated but adjacent in one specimen from Jalisco; basal half of valva with weakly projecting saccular ridge recessed from anterior margin; vesica with a compact group of 8 blade-like, deciduous cornuti situated in two rows; after dehiscence, the attachment scars are visible at high magnification (100X) on the withdrawn vesica near the phallobase/aedeagus junction.

FEMALE. *Forewing*. Length 17.0–20.0 mm (n = 6); broad, length 2.45–2.55 × width; costa weakly concave beyond middle; ground color milk chocolate- to rust-brown, showing faint transverse, whitish and dark bands on costal half beyond middle on fresh specimens; underside rust tinged; fringe narrowly rust. *Hindwing*. As in male. *Abdomen*. Scaling pale beige dorsally; venter paler, with large, medial, black spots on segments 3–5; A6 with a thick patch of thin, dark brownish scales; A7 with a conspicuous patch of upright, pale to dark scales, each bent at the tip. *Genitalia*. As in fig. 4, a, b (drawn from paratype, Summerhaven, JAP slide 9080; n = 3); papillae anales broad, darkly pigmented, with raised setiferous nipples; sterigma a broad bowl subtending A9, which is modified as a translucent plate covered with tiny spicules, more densely at margins (4a); signum a densely wrinkled patch at bursa surface, preceded by a small, blind pouch, projected inwardly as a broad, weakly wrinkled, hollow blade (4b).

Holotype female: ARIZONA, Pima Co., Summerhaven, 7,800', Santa Catalina Mountains, emerged 10 December 1997, larva reared on synthetic diet from egg deposited by female collected 29 August 1997 (R. B. Nagle, JAP lot 97H9) in Essig Museum of Entomology, University of California, Berkeley.

Paratypes (35 ♂, 7 ♀): MEXICO, CHIHUAHUA, Sierra de la Catarina, 7,900', 18 rd. mi. NE Buenaventura, 1 ♂ VIII.21.1976 (J. & K. Donahue, LACM). DURANGO, 10 mi. W of El Salto, 9,000', 1 ♂ VI.13.1964, 5 ♂, 1 ♀ VII.5/29.1964 (J. Martin, CNC), 1 ♂ VII.30.1964 (Chemsak & Powell, EME), 1 ♂ VIII.8.1964 (Powell, EME). JALISCO, 18 km SW Sayula, 1 ♂ X.18.1992 (J. McCarty, EME). USA: ARIZONA, Apache Co., Greer, White Mts., 3 ♂ VIII.6/8.1962 (E. & I. Mumroe, CNC), 2 ♂ VIII.5.1986 (R. Leuschner, RL), ♂ Alpine, 8,200', VIII.3.1986 (R. Leuschner, RL). Cochise Co., Barfoot Ridge, 8,500', Chiricahua Mts., 2 ♂, VIII.6.1927 (J. Kusche, CAS); Barfoot Park, 1 ♀ IX.27.1987 (N. McFarland, EME); Rustler Park, 3 ♂ VII.30.1987, 1 ♂ VII.24.1989, 1 ♂ VIII.7.1997 (R. & J. Robertson, EME), 1 ♂ VIII.6.1991 (Robertson & Powell, EME); Pinery Canyon, 6,500', Chiricahua Mts., 1 ♂ VIII.6.1991 (Robertson, EME); Pinery Canyon 6800' 1 ♀ VIII.1.2005 (K. Richers, KR); Miller Canyon, 6,200', Huachuca Mts., 1 ♂ VIII.7.1974 (Powell, EME). Graham Co., Soldier Creek Camp, 9,350', Graham Mts., 1 ♀ VIII.16.1974 (R. & J. Wielgus, USNM); Mt. Graham, Cunningham Campgr., 3 ♂ VII.20.2007 (C. Ferris, CF, EME). Pima Co., same data as holotype, 5 ♂, 2 ♀ VII.24 to VIII.29, 1991 to 1999 (EME, RN), 1 ♀ VIII.1996, eggs infertile (EME), 1 ♂ VII.21.1998, (D. Ferguson, USNM).

Diagnosis. The geographically nearest congener is *Tinacruis apertana* (Walker), with which *T. noroesta* flies in the mountains of Durango, Mexico. I have reared *T. apertana* in Nuevo Leon from eggs, confirming association of the sexes. The two are similar, but the FW of *apertana* males has more extensive network pattern on a paler, cream yellowish ground, defining a broad, brown costal triangle; females of *apertana* have cream-tan FW, more or less uniformly strigulate with thin, brownish, transverse lines, with a brownish bar from mid-costa curving towards the tornus, and a poorly defined subterminal patch, contrasted with the more uniform rust tan of *noroesta*. *T. sebasta* (Walsingham), which was described from Guatemala and occurs in Mexico, has the reticulate pattern restricted to the basal half of the male FW, and the female FW pattern is similar to that of *apertana* but darker tan. The uncus of *T. apertana* has a wide, T-shaped apex, and that of *sebasta* is broadly spatulate subapically, tapering to the tip, whereas it is narrow, only weakly flared in *noroesta*. *T. apertana* and *sebasta* have narrower valvae than does *noroesta*, with a more distinct saccular ridge. The female signum is short and broad in *T. apertana*, elongate in *sebasta*, more slender than in *noroesta*.

In addition we have two male specimens from Mexico, Sinaloa, 8 road miles W of El Palmito, 6,400', X.12.1975 (Chemsak & Powell, EME), which are similar but differ in several respects. They are slightly larger than the other *T. noroesta* specimens, and their colors are richer, more contrasting yellow and brown. The male genitalia have a slender uncus, not flared. The dentate projections of the transtilla are closely adjacent, and there are slight differences in the valva. These specimens are provisionally considered to represent another population of *T. noroesta*.

ACKNOWLEDGEMENTS

Carolyn Mullinax made the drawing of the male genitalia. Several collectors made special efforts in response to my pleas to collect this remarkable species in Arizona and Mexico: the late John Chemsak, Ron Leuschner, Ray Nagle, the late Ron Robertson, and Ron Wielgus. Paratypes are deposited in the California Academy of Sciences (CAS); Canadian National Collection, Ottawa (CNC); Essig Museum of Entomology, UC Berkeley (EME); Los Angeles County Museum of Natural History (LACM); Ron Leuschner, Manhattan Beach, California (RL); Ray Nagle, Tucson, Arizona (RN); K. Richers, Bakersfield, California (KR); and U.S. National Museum of Natural History, Washington, D.C. (USNM).

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Received for publication 27 Aug 2008; revised and accepted 17 Nov 2008.

MELITARA WALKER (PYRALIDAE) IN WESTERN CANADA: THE DOCUMENTATION OF *M. SUBUMBRELLA* (DYAR) IN THE PRAIRIE PROVINCES DEMONSTRATES THE VALUE OF REGIONAL COLLECTIONS AND SPECIES LISTS.

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ABSTRACT. The moth genus *Melitara* comprises 8 recognized species of medium sized to large micromoths that all feed on *Opuntia* cacti as larvae. One species, *M. dentata* is widespread in western North America, including the southern parts of the Canadian provinces British Columbia, Alberta and Saskatchewan. We report the presence of a second species, *M. subumbrella* in southern Alberta and Saskatchewan, a species hitherto widely believed to extend no farther north than southern Idaho and Wyoming. Closer examinations of *Melitara* collections in major Canadian museums and public collections revealed several additional *M. subumbrella* specimens from Alberta, including specimens from the 1940s. Two specimens were actually reported by K. Bowman (1951) under a previous taxonomic arrangement, but were subsequently overlooked by later workers on North American Phycitinae. Combined with subtle differences in mitochondrial DNA, this leads us to conclude that *M. subumbrella* has been present in Canada for a long time. This provides an excellent example of the scientific value of continuous insect collecting, well-curated regional collections, and regional faunal lists.

Additional key words: Disjunctive distribution, mitochondrial DNA, cactus-feeding

The pyralid genus *Melitara* Walker, a prominent group of cactus-feeding phycitines, is found throughout much of the USA, southwestern Canada, and northern Mexico. One species, *M. prodenialis* Walker, is widespread throughout the east, and another species, *M. dentata* (Grote), is widespread in the west. The remaining 6 species are all restricted to Mexico and the southwestern USA with only *M. subumbrella* (Dyar) extending north to Wyoming and southern Idaho, and west to southern California (Heinrich 1956; Mann 1969; Neunzig 1997). Bowman (1951) reported *M. dentata* and *Olycella* [= *Melitara*] *nephelepasa* from Alberta, but his records were ignored by later workers. The latter is referable to *M. subumbrella*, which was considered to be a synonym of *M. nephelepasa* at the time (McDunnough 1939). A full list of currently recognized species of *Melitara* and their reported range is given in Table 1. Neunzig (1997) included the genus *Olycella* Dyar in *Melitara*, with the three species *O. subumbrella*, *O. junctionella* (Hulst) and *O. nephelepasa* (Dyar) (Heinrich 1939, 1956). This synonymy has later been shown to be systematically justified (Simonsen 2008). It is not currently clear whether *Melitara* and *Olycella* (both sensu Heinrich 1956) are reciprocally

monophyletic and thus deserve subgenus status. All species in the genus feed strictly on prickly pear cactus in the genus *Opuntia* (Mann 1969) and are thus restricted to habitats with *Opuntia*.

Identifying *Melitara subumbrella*. Both *M. subumbrella* and *M. dentata* are large micromoths with wingspans exceeding 50 mm. With their stout bodies and rectangular wings they have a superficial similarity to medium sized Noctuoidea. The resting moth with its large porrect palps, and the wings coiled cigar-like around the body is fairly easy to identify as a phycitine (Fig. 1). Fresh specimens can fairly easily be identified to species without dissection (at least in areas where only *M. subumbrella* and *M. dentata* occur). Both species have white hind wings and gray forewings (sometimes with a yellowish cast—especially in older collection specimens). *Melitara dentata* has a fairly elaborate zigzag pattern across the forewing, whereas *M. subumbrella* has uniformly gray forewings almost devoid of any pattern (Fig. 2a, b). Old, faded, and especially denuded specimens can be much harder to identify. In this case dissection is often necessary. Females are easy to identify based on genitalic dissections as *M. subumbrella*. The species formerly



FIG. 1. Live *Melitara dentata* displaying typical Phycitinae posture with the wings rolled around the abdomen and the antennae pressed down along the back. CAN: AB: Buffalo: 50.848°N -110.696°W: 16 viii 2006. Photo: JJD.

grouped in *Olycella* are the only members of *Melitara* with a signum on the corpus bursae (Heinrich 1939, 1956; Neunzig 1997). The males are harder to identify, but the shape of the valves differs slightly between the two species. In *M. dentata* the valve has a fairly pointed apex with curved dorsal and ventral margins. The costa extends almost to the apex of the valve (Fig. 3a). In *M. subumbrella* the valve has a much broader and blunter apex, and the costa does not extend as far (Fig. 3b). Finally, the flight period is often a very good way to tell the species apart. All *M. subumbrella* from Canada were collected between May 15 and July 2, whereas all *M. dentata* were collected between July 27 and October 25, so there is only a small risk of an overlap in flight time between the two species. This pattern where *M. subumbrella* is a late spring to early summer flyer, and *M. dentata* is a late summer to fall flyer seems to be the same in the western USA, though some *M. dentata* are reported from early July (Neunzig 1997).

Herein we report on an examination of *M. subumbrella* specimens, to determine if Canadian populations are distinct from those farther south. To do so, we examined morphological and genetic characters.

MATERIALS AND METHODS

Morphology. To search for morphological differences, two male and one female *M. subumbrella* from Grasslands National Park SK, one male and one female *M. subumbrella* from central USA, and several male and female *M. dentata* were examined. Abdomens were dissected and macerated in 10% KOH, and stained in Chlorazol Black in a 70% ethanol solution by TJS, both for use in this study and others (e.g. Simonsen 2008). Terminology follows Heinrich (1956), Klots (1970) and Neunzig (1997).

Molecular analysis. To test for genetic differences between the Canadian and USA populations, we

sequenced 740 bp from the cytochrome oxidase subunit I (COI) gene from three specimens from Grasslands National Park and one from Colorado. DNA was extracted from legs with the QIAgen's DNEasy extraction kit (QIAgen Sciences, Maryland, U.S.A). PCR reactions were performed using the Jerry – Pat primer pair (Simon *et al.* 1994), and the PCR cycling profile was: 95.0°C for 2 minutes followed by 35 cycles of denaturing (95.0°C for 30 sec.), annealing (45.0°C for 30 sec.) and extension (72.0°C for 2 minutes). PCR products were purified using the QIAgen's PCR Purification Kit, and the PCR primers were also used for direct sequencing. Sequencing was done with an ABI Prism 377 DNA sequencer using Big Dye®. Consensus sequences from the two sequencing directions were constructed using Sequencher 4.1 and aligned by eye. The sequences are deposited on GenBank under accession numbers FJ422995–FJ423000.

Phylogenetic analysis. An exhaustive maximum parsimony (MP) analysis was carried out in PAUP* 4.10b (Swofford 2002). The haplotype distributions were analyzed in MacClade 4.0 (Maddison & Maddison 2000). The tree was rooted using a *M. dentata* specimen from Alberta as outgroup.

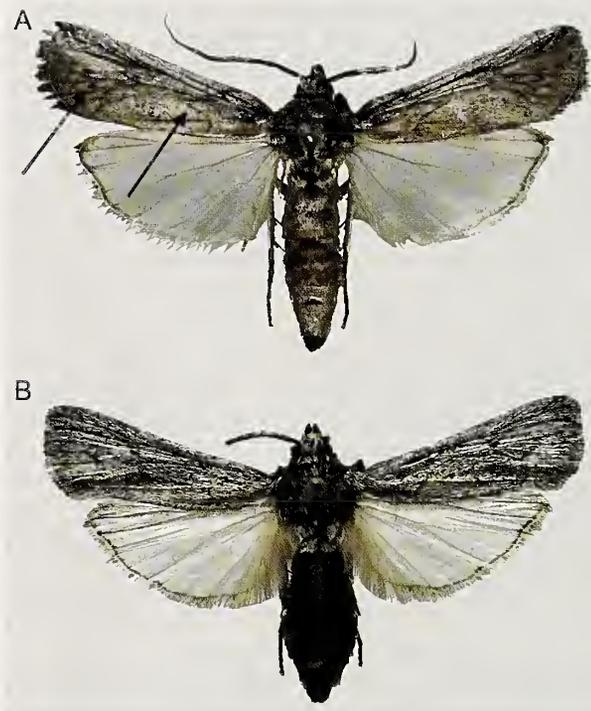


FIG. 2. *Melitara dentata* (a) and *M. subumbrella* (b) displaying subtle, yet clear differences in forewing pattern (arrows point to the zigzag pattern on the forewing of *M. dentata*).

TABLE 1. Currently recognized species of *Melitara* and their distributions following Heinrich (1956), Mann (1969), and Neunzig (1997).

Species	Distribution
<i>Melitara prodenialis</i> Walker	Southeastern U.S.A. from Texas and Florida to New York
<i>Melitara dentata</i> (Grote)	Interior western North America from north western Mexico, Arizona and western Texas to southwestern Canada.
<i>Melitara texana</i> Neunzig	Texas
<i>Melitara doddalis</i> Dyar	Southern Arizona, southern New Mexico and western Texas.
<i>Melitara apigramella</i> Blanchard & Knudson	Southwestern Texas
<i>Melitara junctionalla</i> Hulst	Southern Texas and eastern Mexico.
<i>Melitara nephelepesa</i> (Dyar)	Central Mexico
<i>Melitara subumbrella</i> (Dyar)	Southwestern USA from southeastern California and western Texas to southern Idaho, Wyoming and Nebraska.

RESULTS

Morphology. When dissected, males from Grasslands National Park were found to be indistinguishable from males from Colorado, USA. The dissected female from Grasslands National Park, showed a very subtle difference. The signum on the corpus bursae was less developed than the corresponding structure in specimens from Colorado.

Molecular analysis. The MP analysis resulted in a single tree 62 steps long (Fig. 4). The four specimens from Grasslands National Park all shared the same haplotype; whereas the specimen from Colorado differed in three base pairs, corresponding to a difference of 0.4%. *M. dentata* differed in 59 base pairs compared to all four *M. subumbrella* specimens, corresponding to a difference of 8.0%.

DISCUSSION

***Melitara* in Canada.** In 2004 GRP collected five specimens of *M. subumbrella* in Grasslands National Park, Saskatchewan. In his annotated list of Lepidoptera in Alberta, Bowman actually reported two specimens of *M. subumbrella* from the Medicine Hat region (Bowman 1951), though he listed them as *Olycella nephelepesa* (following McDunnough 1939). *Melitara subumbrella* is technically a new record for Canada. However, a simple update of Bowman's (1951) checklist, following the synonymy reported in Munroe (1983) would yield the report of this species in Alberta. Both the specimens and Bowman's paper have been overlooked by later workers on the genus in North America (e.g. Heinrich 1956; Mann 1969; Neunzig 1997). One of Bowman's specimens was located in the University of Alberta Strickland Museum. Four other specimens were misidentified as *M. dentata* in the same collection, including another specimen collected by

Bowman in 1940 near Medicine Hat. The latter is obviously Bowman's second specimen which later must have been misplaced in a tray with *M. dentata*. The three remaining specimens were collected in 2005 at two different localities in southeastern Alberta. This inspired us to examine other public collections that we felt could hold either overlooked or misidentified specimens of *M. subumbrella* from western Canada. Examinations of the materials in the collections of the Canadian Forest Service (Edmonton, AB), Royal Alberta Museum, (Edmonton, AB), Olds College (Olds, AB), Royal Saskatchewan Museum (Regina, SK) and the Canadian National Collection, (Ottawa, ON) revealed one *M. subumbrella* from Lethbridge, AB collected by C. E. Lilly in 1949, and one from Onefour, AB collected by GRP in 1995. The same examinations also showed that *M. dentata* occurs from south-central

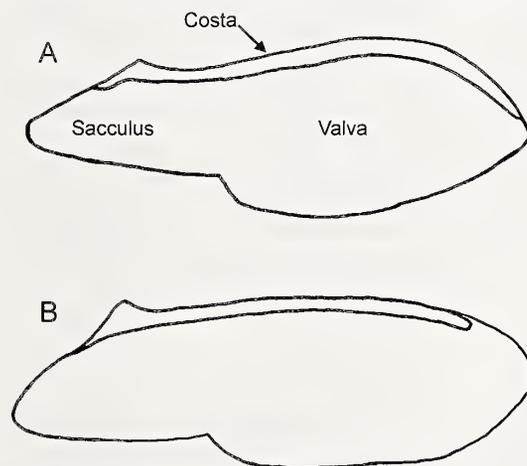


FIG. 3. Differences in male genitalia between *Melitara dentata* (a) and *M. subumbrella* (b). Note the more pointed apex of the valve and that the costa extends to the apex in *M. dentata*.

Saskatchewan to the southern interior of British Columbia (Table 2), a more widespread Canadian distribution than reported recently by Neunzig (1997), who only listed the species from southern Alberta. The distributions of both species based on the collection data are shown in Fig. 5. These records underscore the importance of regional collectors, and their published lists and collections, in determining species ranges. Local collectors typically have extensive knowledge of productive collecting localities, and often amass extensive collections of excellent quality (Ferris 1986; Hendra 2005, 2007). These collections and publications

are a neglected resource that can yield many exciting finds to the diligent taxonomist.

Two prickly-pear species, *Opuntia fragilis* (Nutt.) Haw. and *O. polyacantha* Haw., occur (sometimes abundantly) throughout the southern parts of Canada's Prairie Provinces (personal painful observations). Though Fragile Prickly-pear Cactus (*Opuntia fragilis*), a possible host plant for *M. dentata* (Mann 1969; Neunzig 1997), occurs scattered in remnants of the Peace River grasslands in northwestern Alberta (Royer & Dickinson 2007), there are no records of *M. dentata* from that region. It is, however, quite possible that *M. dentata*

TABLE 2. Records of *Melitara* in Canada based on the collections listed in the text. Collection acronyms: CNC: Canadian National Collection of Insects, Arachnids and Nematodes; NFRC: Northern Forestry Centre Research Collection; OC: Olds College; RSM: Royal Saskatchewan Museum; UASM: University of Alberta, Strickland Museum.

Species	Locality	Coll. period	Year	No.	Collection
<i>M. dentata</i>	Grasslands National Park, SK	24/7-12/9	2002	6	RSM
<i>M. dentata</i>	Buffalo Pond Provincial Park, SK	7/8-25/8	1974, 1984-85	3	RSM
<i>M. dentata</i>	Wood Mountain Park, SK	4/9	2002	2	RSM
<i>M. dentata</i>	Fort Qu'Appelle, SK	12/8-31/8	1976, 1991	2	RSM
<i>M. dentata</i>	St. Victor, SK	14/8	2002	1	RSM
<i>M. dentata</i>	Matador, SK	7/8	2002	1	RSM
<i>M. dentata</i>	Eastend, SK	reared	1974	1	RSM
<i>M. dentata</i>	Saskatchewan Landing Provincial Park, SK	10/8	1951	1	RSM
<i>M. dentata</i>	Seout Lake, SK	27/8	1968	4	CNC
<i>M. dentata</i>	Swift Current, SK	8/8	1936	1	CNC
<i>M. dentata</i>	Tolman Bridge, AB	3/8-25/10	2000-2, 2006	13	UASM, NFRC, OC
<i>M. dentata</i>	Taber, AB	14-15/8	1999, 2005	2	OC
<i>M. dentata</i>	Medicine Hat, AB	17/8	1943	1	UASM
<i>M. dentata</i>	Edgerton, AB	24-25/8	2002	1	UASM
<i>M. dentata</i>	Steveville Bridge, AB	13/8	1999	2	UASM, NFRC
<i>M. dentata</i>	Buffalo, AB	16/8	2006	1	UASM
<i>M. dentata</i>	Champion, AB	3/8	1961	12	CNC
<i>M. dentata</i>	Coaldale, AB	4/8	1961	8	CNC
<i>M. dentata</i>	Manyberries, AB	10/8	1951	1	CNC
<i>M. dentata</i>	Lethbridge, AB	26/7-24/8	1921-22, 1949, 1986	6	CNC
<i>M. dentata</i>	Willow Creek Canyon, AB	29/7	1961	4	CNC
<i>M. dentata</i>	Kamloops, BC	5/8-9/8	1937, 1956	4	CNC
<i>M. dentata</i>	Nicola, BC	29/8-6/9	1922-23	4	CNC
<i>M. dentata</i>	Oliver, BC	1/8-15/9	1923, 1953	113	CNC
<i>M. subumbrella</i>	Grasslands National Park, SK	2/6	2004	5	NFRC
<i>M. subumbrella</i>	Onefour, AB	19/6	1995	1	NFRC
<i>M. subumbrella</i>	Lost River Valley w. of Onefour, AB	20-21/5	2005	1	UASM
<i>M. subumbrella</i>	Medicine Hat, AB	31/5	1940	2	UASM
<i>M. subumbrella</i>	Oldman River Hwy. 36, s of Vauxhall, AB	18/5	2005	2	UASM
<i>M. subumbrella</i>	Lethbridge, AB	15/5	1949	1	CNC

does occur in the Peace River region, as suitable habitats in the region are fairly poorly collected, especially during *M. dentata*'s main flight period (G. G. Anweiler pers. com.).

The status of *Melitara subumbrella* in Canada. The three oldest specimens of *M. subumbrella* from southern Alberta show that the species was present in the province 60–70 years ago. The presence of recently collected individuals from different localities in southeastern Alberta and Saskatchewan clearly demonstrates that *M. subumbrella* occurs at multiple localities in western Canada. It is also not unthinkable that the species still is overlooked and is more widespread, not only in southwestern Canada, but also in Montana, though an examination of the *Melitara* specimens in the entomological collection of Montana State University in Bozman did not result in additional specimens.

Are Canadian *M. subumbrella* different from *M. subumbrella* in the U.S.A.? Ideally, many more specimens from both Canada and the U.S.A. should have been included to strengthen the results of the molecular analysis. Unfortunately such material was not available. Nonetheless, the difference reported here is well within variations that have been found in other

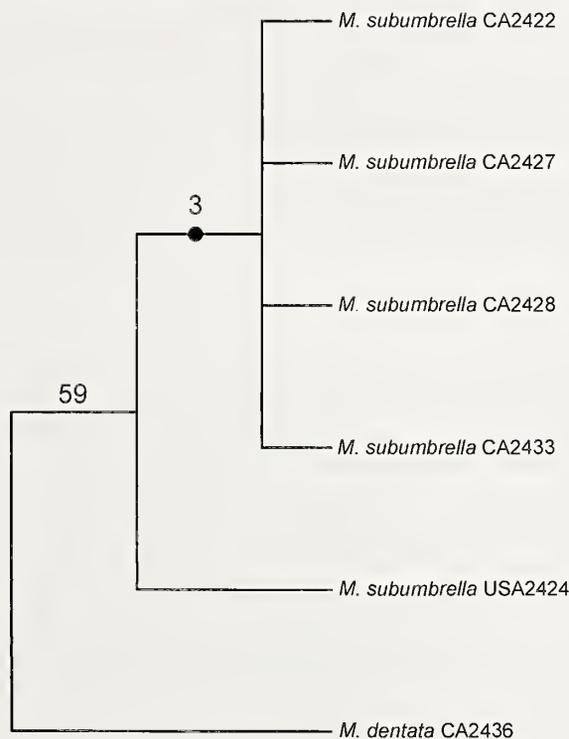


FIG. 4. Haplotype tree showing relationship between *Melitara subumbrella* in Canada and west central USA. The closed circle marks the clade comprising the four Canadian specimens. The six digit code after the species name is the specimen ID. The numbers indicate the number of unique base pair changes.

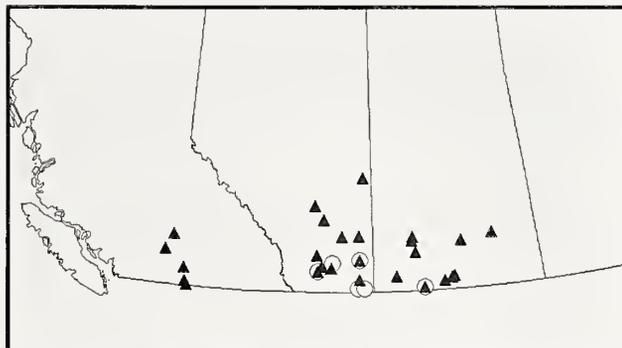


FIG. 5. Distribution map for *Melitara* in western Canada based on the records listed in Table 2. An open circle marks a *M. subumbrella* locality, and a closed triangle marks a *M. dentata* locality.

insect populations considered to be conspecific (e.g. Simonsen *et al.* 2008; Cognato 2006; Laffin *et al.* 2005a, b; Scheffer & Grissel 2003). The slight difference in female genitalia may well represent individual variation. It is not known whether the species is present in Montana, and the variation thus could be continuous. Despite the apparent geographical isolation, these differences do not in our opinion justify separate taxonomic status (subspecies or otherwise) for the Canadian *M. subumbrella* populations. The species should be sought after in Montana to determine whether the distribution is continuous or the Canadian populations are disjunct.

ACKNOWLEDGEMENTS

We wish to thank Paul Opler, of the Gillette Museum, Colorado State University for loans of specimens from the U.S.A. and for permission to extract DNA from these. We thank the following people and institutions for help and assistance: Jean-François Landry, Canadian National Collection, Ray G. Poulin, Royal Saskatchewan Museum, Tyler Cobb, Royal Alberta Museum, Ken Fry, Olds College and Michael A. Ivie, Montana State University, Bozman. Felix A. H. Sperling, Gary G. Anweiler, Danny Shpeley, Marie Djernaes and Lisa Lumley, all of the University of Alberta, and Brenda Laishley, Canadian Forest Service, Edmonton, AB, are thanked for help, advice and discussions. Financial support was provided by The Carlsberg Foundation, Copenhagen, Denmark (post doc salary for T. J. Simonsen), NSERC (a Discovery Grant to Felix A. H. Sperling paid for lab work and various expenses), and Natural Resources Canada (support for faunistics work by G. R. Pohl).

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Received for publication 5 June 2008; revised and accepted 27 October 2008.

NOT ALL BILATERAL GYNANDROMORPH BUTTERFLIES ARE INTERSPECIFIC HYBRIDS: NEW
PAPILIO SPECIMENS FROM FIELD POPULATIONS

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ABSTRACT. Bilateral gynandromorphs (half male, half female) have previously been reported in interspecific hybrids. However, we report 6 new nearly perfect bilateral gynandromorphs, three (one *Papilio canadensis*, and two *P. glaucus*) of which were collected from areas not near hybrid zones. New interspecific gynandromorphs also are described for apparent *P. rutulus* x *P. multicaudatus* hybrids. By using hand-paired interspecific hybrids we have generated both diapausing and direct developing (non-diapausing) gynandromorphs. While X (or Z)-linked regulation of diapause in these *Papilio* may be similar throughout the male and female halves of the individual, the dark melanic color [Y (or W)-linked] is distinctly different. Wing color regulation is differentially implemented on dorsal and ventral surfaces as seen in sexual mosaics described here. The developmental irregularities resulting in bilateral gynandromorphs and sexual mosaics are not solely due to interspecific genetic incompatibilities. However, genetic factors seem to play a major role in their expression. The existence of dark melanic female patchy patterns supports the suggestion that control of the W (=Y)-linked *b*⁺ melanic gene is both cell-specific and sex-specific in its ability to suppress the BAS enzyme activity that normally shunts dopamine to the yellow papiliochrome pathway. Interspecific hybrids involving dark mothers (with the Y-linked *b*⁺ gene) mated to *P. multicaudatus*, *P. rutulus*, and *P. canadensis* males (all species lacking the dark morph) have also produced hybrid daughters with “intermediate” suppression of melanism giving a dusty colored appearance (differing from color mosaics). This uniform “dusty” coloration often has been referred to as “cinnamon,” and may reflect incomplete genetic penetrance.

Additional key words: melanic wing color, sex chromosomes, *Papilio glaucus*, *P. canadensis*, *P. rutulus*, *P. multicaudatus*, *P. appalachiensis*

Lepidoptera that have developed abnormally to produce mosaic color patterns and a mixture of other traits, often representing intersexes (part female and part male) have frequently been described (Clarke & Ford 1980; Ayala & Kiger 1984; McCafferty & Bloodgood 1986). If such developmental errors occur early in development (perhaps from fertilization of a binucleate oocyte; Blanchard & Descimon 1988) the result might be a perfect (or near-perfect) bilateral gynandromorph with one half being male and one half female (Clarke & Clarke, 1983).

A large number of gynandromorphs have been reported in Lepidoptera from at least 10 different species of Papilionidae, eight species of Lycaenidae, four Hesperidae, ten Pieridae, four Nymphalidae, and several families of moths including Saturniidae,

Pyralidae, Geometridae, and Lymantriidae (reviewed in Scriber & Evans 1988b; see also Sibatani 1980, 1983a, b; Shucy & Peacock 1985). Cockayne (1935) provides numerous additional records, and the Milwaukee Public Museum's James R. Neidhoefer Collection has several hundred mosaics and at least 150 bilateral gynandromorphs. David and Marc Perlman in Illinois have also compiled a large collection of mosaics and gynandromorphs.

A number of suggestions have been advanced to potentially explain these developmental abnormalities including: extreme temperatures (Standfuss 1900; Drescher & Rothenbuhler 1963; Riotte 1978), ultraviolet light (Nekrutenko 1965), viral infections (Gardiner 1972; Blau 1978; Sevastopulo 1973), translocations of parts of the sex-chromosomes and/or

autosomes (Blanchard & Descimon 1988; Scriber & Evans 1987; Marec et al. 2001), and background uranium radiation-induced somatic mutations and the Chernobyl nuclear power plant disaster (Dantchenko et al. 1995). Interspecific hybrid crosses have also been suspected as a potential cause of mosaic/gynandromorphs (Whicher 1915; Cockayne 1935; Clarke & Sheppard 1953; Clarke et al. 1977; Platt 1983; Blanchard & Descimon 1988; Scriber & Evans 1988a, b). In *Papilio* such gynandromorphs have been found to be most often the result of interspecific (or intersubspecific) crosses (Scriber & Evans 1988b). Asymmetrical color mosaics may also result from such interspecific crosses, but are more often seen from the central parts of a species geographic range, or from intraspecific pairings, which suggests that mosaic gynandromorphs could be the result of more complex and basically different developmental processes than bilateral gynandromorphs (Clarke & Clarke 1983; Blanchard & Descimon 1988).

The evidence we had collected from 1979–1986 with the Papilionidae in eastern North America suggested that perhaps only interspecific hybridization would generate bilateral gynandromorphs, and at that time we had never found a “natural” (i.e. field-collected) bilateral gynandromorph (Scriber & Evans 1988b). However, we have subsequently collected interesting mosaics and near-perfect bilateral gynandromorphs from field populations, some of which were not clearly near a hybrid zone where introgression from different species was obvious. We report on some of these interesting aberrations here.

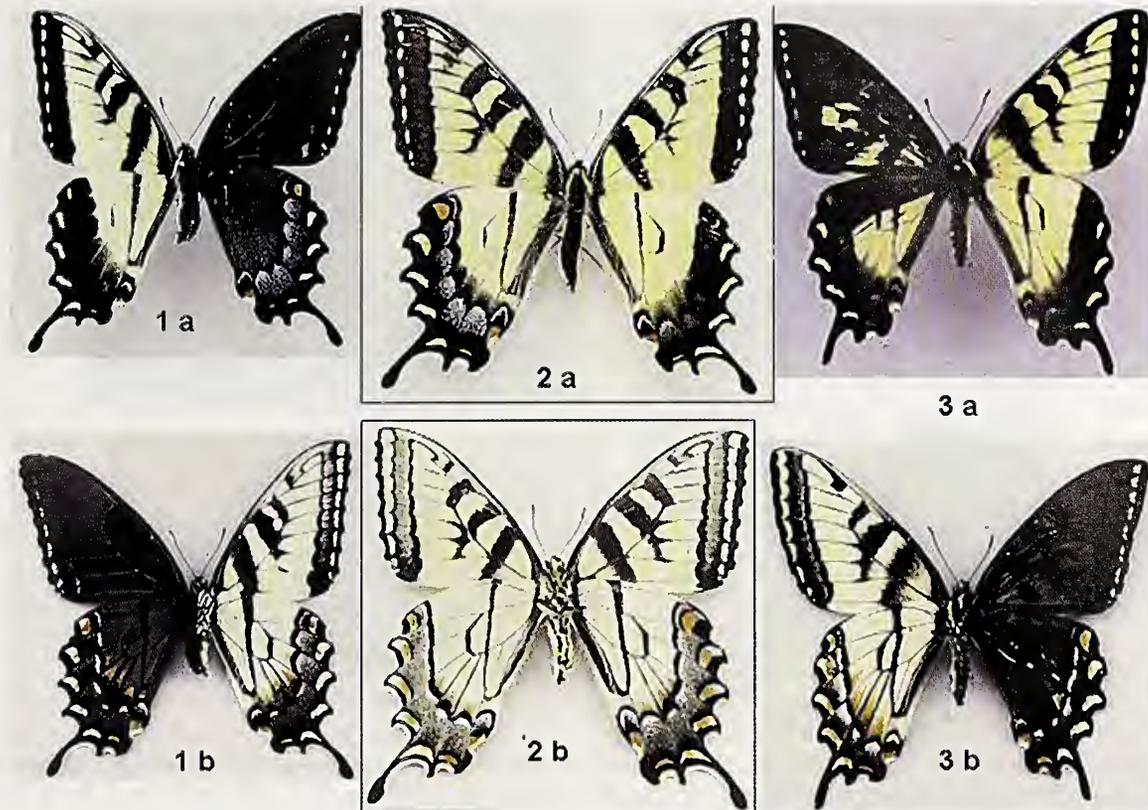
Tiger Swallowtail Gynandromorphs and Color/Sexual Mosaics. For an earlier study (Scriber & Evans 1988b), we reared nearly 30,000 butterflies from more than 4,000 families of *Papilio glaucus* and *P. canadensis* (previously considered subspecies *P. glaucus canadensis*; Hagen et al. 1991). Of these individuals we observed 6 of 34 color mosaic adults, all of which possessed basic dark (mimetic) wing patterns of females interrupted by yellow patches or blotches on one to three of the individual wings. These yellow patches represent either the non-mimetic female, or male type pattern. Such color mosaics may represent intersexes or gynandromorphs with part male and part female asymmetric traits. They may be either gynandromorphs or sexual mosaics (Blanchard & Descimon 1988; Cockayne 1935; Ford 1955; Sevastopulo 1973). In *Papilio glaucus* and *P. alexiades* Hopffer, both polymorphic yellow and black forms are found (Scriber et al. 1996). Only these two *Papilio* species have the polymorphic dark and yellow morph females, clearly showing the color contrast in gynandromorphism/

mosaicism. One such *P. glaucus* female (with one yellow half and one mostly dark half) has recently been figured and described by Bradshaw (2000).

In addition to these 34 color mosaics, we also observed three perfect bilateral gynandromorphs (including one that is half dark female and half yellow male) and two “nearly” perfect bilateral gynandromorphs basically half dark and half yellow (Scriber & Evans 1988a, b). These perfect bilateral gynandromorphs were all offspring from interspecific hybrid crosses. Furthermore, while the dark color of the female half was expressed in the pairing of a dark Ohio female with a *P. alexiades* Mexican male (Fig. 1), the female half of the second gynandromorph [a dark female *P. glaucus* from South Carolina (with the b⁺ gene) mated with a *P. canadensis* male from Marinette Co., Wisconsin] had the dark potential suppressed (Fig. 2; Scriber et al. 1996). The third gynandromorph (a yellow *P. glaucus* from Pennsylvania mated with a *P. canadensis* from Juneau Co., Wisconsin) had the female half yellow because it likely lacked the Y-linked dark gene from the mother and also probably received an X-linked suppressor gene from the *P. canadensis* father (Scriber et al. 1996).

Such gynandromorphs are not only fascinating in appearance, but also with regard to physiology. Both of these *P. glaucus* × *P. canadensis* bilateral gynandromorphs emerged in the second year and did not develop directly as did many of their “normal-looking” brothers. This reflects an X-linked obligate diapause that is hemizygous in the female hybrids (and the female half of these gynandromorphs; XY or ZW), but heterozygous in its sibling male hybrids (XX or WW), which allows direct development and adult male ecdysis without diapause. Apparently the two halves of both gynandromorphs were cued to eclose as adults in the next season rather than directly (at the 16:8 L:D photophase, 23°C rearing conditions; Scriber & Evans 1988b).

Of the 9,000 or more field collected specimens during this study (1979–1987; Scriber & Evans 1988a, b) we never collected an obvious bilateral or nearly bilateral gynandromorph. The closest was one reared from a field-collected female from Jasper Co. Texas (Fig. 4). However, we collected many color mosaics (dark and yellow patterns being the most obvious). In fact, 33 of the 39 color mosaics were field-captured individuals (6 were lab-reared from hand-paired hybrids). While most of these field-collected color mosaics were from Georgia, Ohio, Illinois, and Texas, one family from a female captured in Dane Co., Wisconsin produced 17 of the color mosaics. It is possible that some introgression from *P. canadensis*



FIGS. 1–3. 1. A bilateral gynandromorph (from brood #4210) from a lab cross of a dark morph *P. glaucus* female (Adams Co., Ohio) mated to a wild collected male *P. alexiarses garcia* from Nuevo Leon, Mexico. (a) dorsal, (b) ventral. 2. A bilateral gynandromorph (from brood #628) from a lab cross of a dark morph *P. glaucus* female (Pickens Co., South Carolina) mated to wild collected male (*P. canadensis* from Marinette Co., Wisconsin (collected 1–5 July 1983 by Don Caine). (a) dorsal, (b) ventral. 3. A gynandromorph, or sexual mosaic, which appears to be more than 60% male (from brood #2830) from a dark morph *P. glaucus* female (reared from eggs obtained from a dark morph female wild collected in Clay Co., West Virginia) bred to a wild collected *P. rutulus* male (reared from eggs obtained from a wild female collected in Sacramento Co., California). (a) dorsal, (b) ventral.

could have occurred in this geographic area since it is very near the hybrid zone (Luebke *et al.* 1988). In fact, the famous 19th century Strecker collection (Strecker 1878; Walsten 1977; Ehle 1981; Shapiro 1981a, b; Clarke & Clarke 1983) of *P. glaucus* color (or sexual) mosaics (which had been on loan from the Chicago Field Museum to the Allyn Museum) may reflect such introgression in those mosaics near the *Papilio glaucus*/*P. canadensis* hybrid zone in the Midwest and Pennsylvania (Scriber *et al.* 2003). Here we review our hypothesis in light of new information.

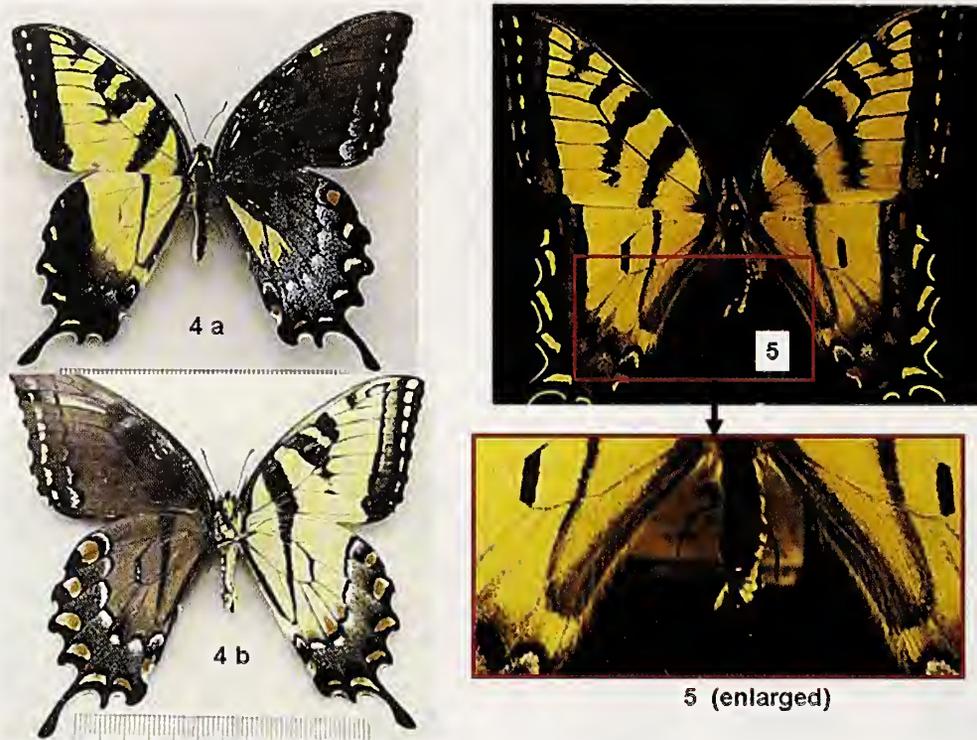
We reared these hybrid larvae only through to pupation on black cherry (*Prunus serotina*) leaves, since this host is used by both *P. canadensis* and *P. glaucus* (and by all four other species in the *P. glaucus* group; Scriber 1996). If we had attempted to rear these gynandromorphs on tulip tree, *Liriodendron tulipifera* (this *P. glaucus* favorite is toxic to *P. canadensis*; Scriber 1982) or on quaking aspen, *Populus tremuloides* (this *P. canadensis* favorite is toxic to *P. glaucus*, Lindroth *et al.*

1988), these insects might have survived to become adults, as normal hybrids, since detoxification enzymes are inherited autosomally, and are used inside the gut, they can be expressed throughout the insect regardless of whether they are produced by one or both halves (male or female) of the gynandromorphs (Scriber 1986; Scriber *et al.* 1989).

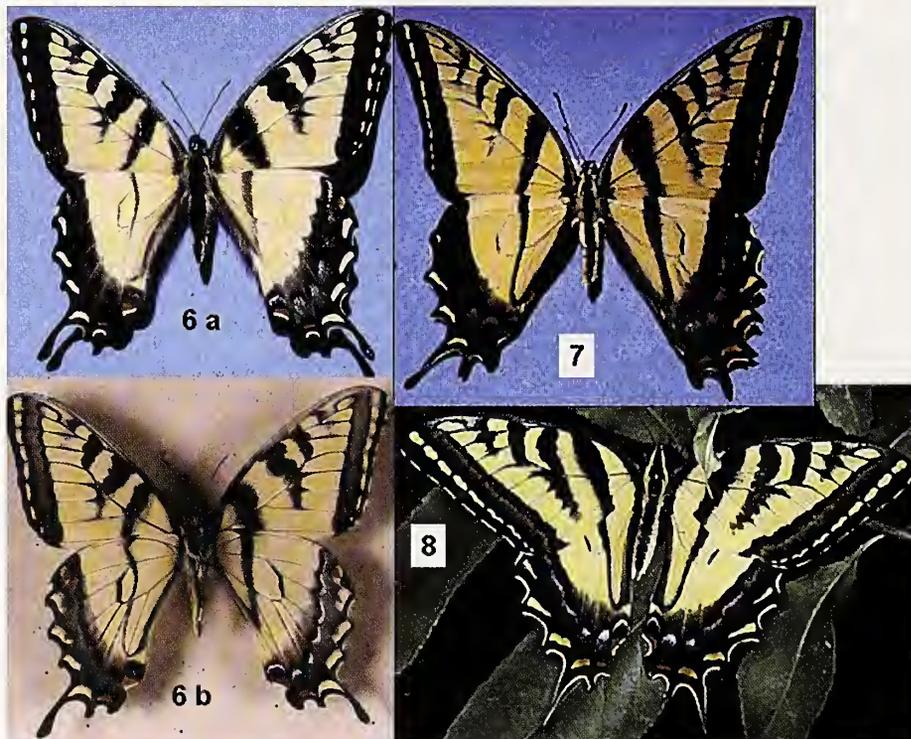
RESULTS

We collected a female *Papilio canadensis* from Cheboygan Co., Michigan during the period 9–12 June 1997. Larvae were reared on black cherry. One of the resulting adults was a nearly perfect bilateral gynandromorph with blue hindwing color and female genitalia on the right, and with male genitalia and coloration on the left (Fig. 5).

Another near-perfect bilateral gynandromorph was actually collected in the field on 15 June 1996 in southwestern Vermont near the New York border (H.R.). This specimen has basically female blue



FIGS. 4-5. 4. A nearly perfect gynandromorph or sexual mosaie (from brood #1091) from a wild collected dark morph (*P. glaucus* female from Jasper Co., Texas. (a) dorsal, (b) ventral. 5. A bilateral gynandromorph lab-reared from a family that was derived from a female *P. canadensis* collected in Charlevoix Co., Michigan, 9-12 June 1997 (a) dorsal, (b) close-up (In collection of Mark Deering).



FIGS. 6-8. 6. A bilateral gynandromorph of *P. canadensis* collected (H.R.) in Bennington Co., Vermont on 15 June 1996 (a) dorsal, (b) ventral. 7. A bilateral gynandromorph collected (H.R.) on 3 June 1989 in Lincoln Co., Wyoming. Possibly *P. rutulus* female (left half) and *P. multicaudatus* male (right half). 8. A hybrid (lab-paired, lab-reared) of a *P. rutulus* female x *P. multicaudatus* male (brood #7806).

coloration on the right hindwing and slightly heavier (wider) black bands (as in females) on the right forewings (Fig. 6; this specimen appears to possess 2 male elaspers and no ovipositor).

The third nearly perfect bilateral gynandromorph is one collected from Lincoln Co. (Wyoming) on 3 June 1989. This individual appears to be half female *P. rutulus* and half male *P. multicaudatus* (Fig. 7). Both species lack the dark morph females and probably the Y-linked b^+ gene (Scriber *et al.* 1990, 1996). The right hindwing has the extra "tail" and the right forewing appears somewhat similar to *P. multicaudatus* in banding. The left female half looks *rutulus*-like. For comparison, we also present a female from an interspecific lab pairing of *P. rutulus* female \times *P. multicaudatus* male (Fig. 8, brood #7806). In this specimen, the two species traits appear somewhat intermediate throughout and did not segregate into the two halves (one female and one male, as in the interspecific gynandromorph; Fig. 7).

A field-captured, nearly-perfect bilateral gynandromorph between the nymphalids *Limenitis arthemis arthemis* (Drury) and *L. a. astyanax* (F.) was captured in the same area of the southwestern Vermont/New York border as the *P. canadensis* gynandromorph (not figured) and may be part of an active hybrid zone. These *Papilio* and *Limenitis* species (sub-species) complexes have significant introgression and exhibit centers within their hybrid zones in New England, as they do across the Midwest in Michigan and Wisconsin (Platt & Brower 1968; Scriber 1996).

We have also lab-reared a dark nearly perfect bilateral gynandromorph from a dark, east Texas *P. glaucus* mother (brood #8858, Janice Bossart). A specimen photo sent to us by Loretta Lutman of Ashboro, North Carolina (Randolf Co.) also appears to be a wild, bilateral gynandromorph of *P. glaucus*, with the female half dark (Fig 9).

Perfect bilateral gynandromorphs, with half expressing male traits and the other female traits, are extremely rare. Color/sexual mosaics with asymmetrical blotches or patterns of color (or other mixed gender traits) are somewhat more common than bilateral gynandromorphs among these swallowtails, but they are still quite rare. Earlier studies with nearly 30,000 lab-reared North American *Papilio* resulted in 30–40 color mosaics (approximately 0.001 % of reared adults was an obvious color and/or sexual mosaic; Scriber & Evans 1988b). It is easiest to find color (or sexual) mosaics in *P. glaucus* when the female is of the dark morph, but the hindwing blue color of females is also helpful in spotting them (Fig. 10). One thing that is clearly characteristic of color mosaics is that the dorsal and ventral patterns are

determined independently; a few examples are illustrated in Figs. 11–16. Another mosaic from Illinois shows asymmetry (Fig. 17). It is also possible to have bilateral differentiation as in size or color for the same sex and single species individual larvae, pupae, and adults (see Scriber & Hagen 1990).

DISCUSSION

We describe six new and nearly perfect bilateral gynandromorphs from field collections in northern Michigan, southwestern Vermont, Montana and Texas. Four of these are likely to represent interspecific or intersubspecific hybrids (Figs. 5–7, and the *Limenitis* from Bennington Co. Vermont, collected by HR). While perfect and near-perfect bilateral gynandromorphs appear to be often generated by interspecific hybridization, we report two gynandromorph specimens from Texas and North Carolina (Fig. 9) and East Texas (J. Bossart and JMS, not figured here) that were not near the *P. canadensis/glaucus* hybrid zone.

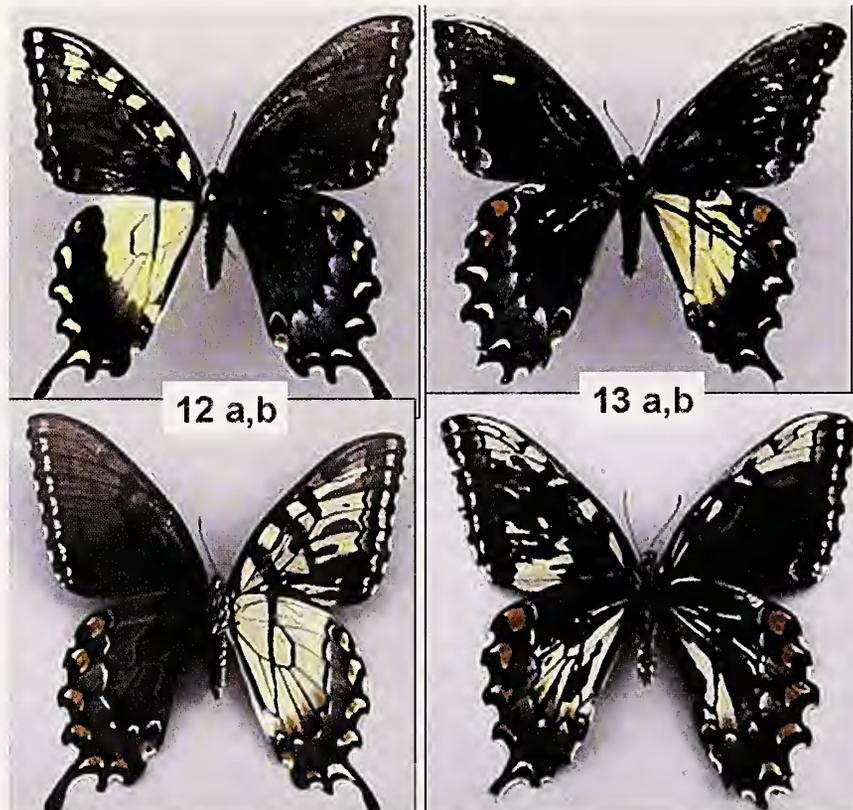
The somewhat unique ability of individual butterflies with one half male and one half female to develop as larvae, pupae, and live adults capable of flight (e.g. Scriber *et al.* 1995; Connors 2000) is fascinating, but still poorly studied and understood. The dramatic differences in wing color with partial dark morph females and yellow-patterned males enables us to easily detect individual bilateral gynandromorphs or asymmetrical sexual mosaics, but the yellow morph female gynandromorphs of tiger swallowtail butterflies are no less fascinating.

Here we have presented one example of interspecific bilateral gynandromorphs that were bred from *Papilio glaucus* female and *P. canadensis* male parents (Fig. 2; see also Scriber *et al.* 1995). This interspecific pairing united genes in the resulting gynandromorph that have segregated into the two gender-differentiated halves with the heterogametic female [XY (=ZW)] possessing the Y-linked black (b^+) gene of dark morph females plus the X-linked suppressor (s^+ ; Scriber *et al.* 1996), resulting in the yellow (suppressed) tiger pattern for the female half (Fig. 2). This contrasts with the interspecific (*P. glaucus* \times *P. alexiavres*) gynandromorph with the dark melanic (b^+) gene and no suppressor (s , an enabler), where the female half is black (Fig 1).

The biochemical pathways (temporally and spatially regulated by enzymes, including dopa carboxylase) are apparently coordinated by multiple enzyme activities of the melanin (black) and papiliochrome (yellow) specific pathways. These enzyme regulations must be conducted simultaneously in the same gynandromorphs (Koeh *et al.* 2000a), all of which is coordinated by the single major Y-linked factor (Scriber *et al.* 1996) on the female



FIGS. 9–11. **9.** A natural bilateral gynandromorph of *P. glaucus* from Randolph Co., North Carolina (photo from Loretta Lutman). **10.** A sexual mosaic (gynandromorph) with mostly male characters (except the blue coloration in the left hindwing) brood 2025, from a wild-collected yellow female, Clark Co., Georgia. **11.** A color/sexual mosaic (lab-reared from a female collected in Ohio, 1989) (a) dorsal, (b) ventral.



FIGS. 12–13. **12.** A gynandromorph or sexual mosaic, which appears to be more than 60% female (from brood #3622) from a pure *P. glaucus* lineage (in which the mother was the daughter of a dark morph female collected in Hocking Co., Ohio and mated to a male from Adams Co., Ohio). (a) dorsal, (b) ventral. **13.** A gynandromorph or sexual mosaic, which appears to be more than 75% female but with male claspers (from brood #3935) from a wild collected dark morph *P. glaucus* female (Scioto Co., Ohio). (a) dorsal, (b) ventral.

side of the individual; but these genes are either not expressed, or not present, on the male half of the individual. The activity of other sex-linked traits such as obligate diapause regulators would explain the direct development (non-diapause) of both halves of the *P. glaucus*/*P. alexiaries* gynandromorph and the one year delay (diapause) of the *P. glaucus*/*P. canadensis* gynandromorph (with both the hemizygous female and the heterozygous male having the X-linked obligate diapause gene, *od*⁺). Other sex-linked traits such as oviposition preferences could not be analyzed, but in the future researchers could examine the sex-linked diagnostic allozymes and mitochondrial DNA variation with regard to distribution in the two halves of such gynandromorphs.

In melanic females, black melanin replaces the background yellow papiliochrome (Koch *et al.* 1998). The key enzyme involved is BAS (n-β-alanyl-dopamine-synthase), which shunts (suppresses) dopamine from the melanin pathway into the production of the yellow papiliochrome pigment (probably in response to dosage of the Z (=Y)-linked *b*⁺ gene products; Scriber *et al.* 1996). The mixed mosaics we figure here appear to reflect the fact that melanism is both sex-specific and pattern-specific (cell autonomous), and therefore melanic specimens of *P. glaucus* are not just null mutants as in some ebony *Drosophila* strains (Koch *et al.* 2000b). The suppressor/enabler gene (*s/s*⁺) that permits dark female expression of the *b*⁺ melanin gene has been identified on the Z (=X) chromosome (Scriber *et al.* 1996), and may involve tyrosine hydroxylase, or linked factors that are involved in production of dopa (common to both melanin and papiliochrome pathways) (Koch *et al.* 2000a, b). The late incorporation of tyrosine into melanin may also be involved in the incomplete penetrance (where yellow scales are brownish) suggesting that sex-linked control genes and their sex-linked modifiers exert their effects by differential interpretation of the patterning signal (e.g. the delay in development of melanic scales is female-specific) (Ffrench-Constant & Koch 2003).

The specific melanin (*b*⁺) modifier genes (*s*⁺/*s*⁻) on the Z-chromosome, remain to be identified, but we have isolated the tyrosine hydroxylase gene from the Z-chromosome of *P. glaucus* (Putnam *et al.* 2007). The Z-chromosome also carries other genes of major significance in this species, including oviposition preferences (Scriber 1993; Mercader & Scriber 2007; Mercader *et al.* 2009), diapause regulation (Rockey *et al.* 1987a, b), post-diapause emergence delays (Scriber *et al.* 2008), and allozymes (lactate dehydrogenase (Ldh), and phosphogluconate dehydrogenase (Pgd)), which

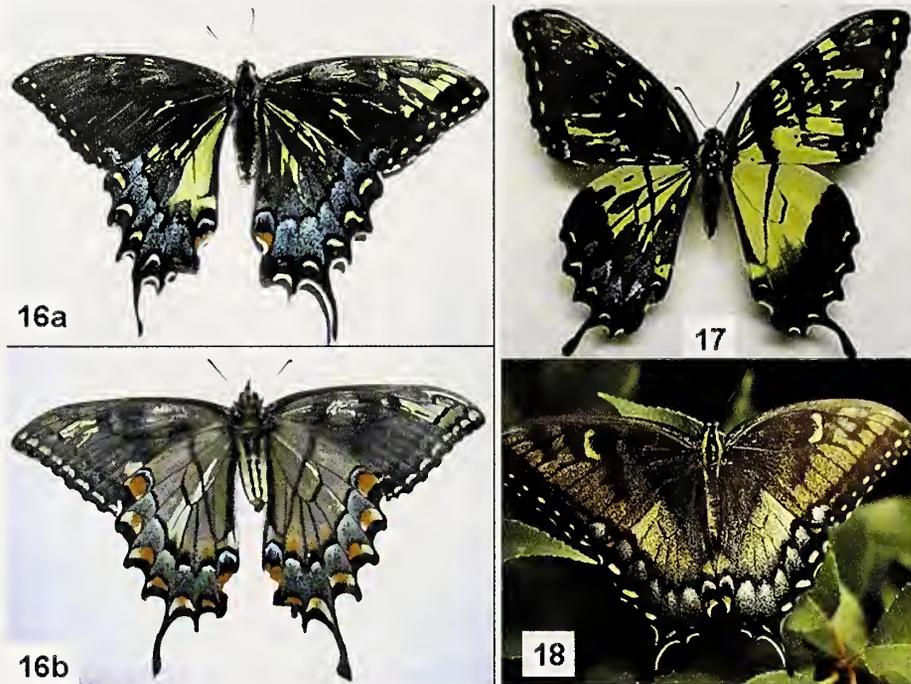
appear to be species-diagnostic for *P. glaucus*, *P. canadensis*, and *P. appalachiensis* (Hagen *et al.* 1991; Scriber & Ording 2005; Scriber *et al.* 2008). The genetic incompatibilities of some recombinant hybrid genotypes appear to involve the Haldane effect in the heterogametic female pupae (Hagen & Scriber 1995). The delayed emergence of recombinant hybrid swarms (*P. appalachiensis*; Pavulaan & Wright 2002; Scriber & Ording 2005) may be controlled by the Z-linked obligate diapause gene (*od*⁺; Scriber *et al.* 2008) or a closely linked post-diapause developmental rate controlling gene on this Z-chromosome, such as identified for the delayed mid-July flight of European corn borer (Dopman *et al.* 2005). The *tpi* allozyme locus appears to correspond closely with this factor in the corn borer, and we have determined that it is also Z-linked in *P. glaucus*/*P. canadensis* (Hagen & Scriber 1989; Scriber 1994).

Females of *P. glaucus* that are intermediate in their expression of melanism (with different degrees of “dusted” or “cinnamon” appearance; Fig 18) can be a result of rearing and/or pupal eclosion at higher temperatures (Ritland 1986). Such intermediate melanism may reflect variable penetrance, suggesting that the black melanin is superimposed over the yellow papiliochrome (Koch *et al.* 1998), which may appear brown in color (Ffrench-Constant & Koch 2003). However, we have also seen such intermediate melanism in hybrid daughters of dark females mated to *P. multicaudatus* (Fig 9), to *P. rutulus* (Scriber *et al.* 1995), and to *P. canadensis* (from Dane Co. WI, not figured here). Most *P. canadensis* males have X-linked suppressors (*s*⁺) that completely prevent the expression of melanism in hybrid daughters of dark mothers (Scriber *et al.* 1996). Here we report the partial expression of melanism (“cinnamon” with striations) in daughters of a primary F-1 hybrid pairing between a dark *P. glaucus* mother mated with a male *P. canadensis* from central Michigan (in Isabella Co. on the cooler side of the historical hybrid zone; see below). These are not color mosaics as described earlier. These “cinnamon” intermediates of this Michigan *P. canadensis* father and dark *P. glaucus* mother, reared and emerged at 22° C, were also not due to high temperatures (28–30° C) as in Fig. 18 (see Ritland 1986).

This result suggests that the wild Isabella Co. male parent of this pairing (#20011) had at least one Z-linked enabler (*s*⁻), which permitted expression of the Y-linked dark gene (*b*⁺). The introgression of the X-linked enabler has also been documented in daughters of another Isabella Co. *P. canadensis* male mated to a dark *P. glaucus* mother (#20015; Scriber *et al.* in prep.) and



FIGS. 14–15. **14.** A gynandromorph or sexual mosaic which appears to be more than 50% female (from brood #4196) from a lab cross of a dark morph *P. glaucus* female (Champaign Co., Illinois) mated to a hybrid male (mother of which was the daughter of a dark morph *P. glaucus* female collected in Georgia and whose father was a *P. canadensis* collected in Lincoln Co., Wisconsin. (a) dorsal, (b) ventral. **15.** A female color mosaic (from brood #3770) from a dark morph *P. glaucus* female (the daughter of a wild dark morph *P. glaucus* female, #3104, collected in Athens Co., Georgia) mated to a wild *P. canadensis* male (collected in Tompkins Co., New York). (a) dorsal, (b) ventral.



FIGS. 16–18. **16.** A field-reared *P. glaucus* from Lancaster Co. PA 2004 (pupa from Wm. Houtz). **17.** A specimen from David and Marc Perlman (photo provided, pers. comm. to JMS). **18.** An intermediate “dusty” or “cinnamon” type reared from Dane Co., Wisconsin at high temperatures (28–30° C).

also in daughters of several males of the hybrid swarm late flight at the New York/Vermont border where no dark females (with the W-linked b^+ gene for melanism; Scriber *et al.* 1996) have ever been collected (the nearest collection of a dark female is roughly 150 miles south; Scriber *et al.* in prep). The Z-linked enabler has also been detected in males captured from the hybrid swarm of late flight individuals in *P. appalachiensis* populations from West Virginia, but here, on the warmer side of the hybrid zone (Scriber *et al.* 2009b), the W-linked gene for melanism (b^+) does also occur as evidenced by recombinant hybrid-like dark females (Pavulaan & Wright 2004; Scriber & Ording 2005; Scriber *et al.* 2009a, b).

Individual species diagnostic traits moving northward across the historical hybrid zone include: 1) autosomal tulip tree detoxification (Scriber 1986, 2002; Scriber *et al.* 1999), 2) several wing color traits (Luebke *et al.* 1988), 3) some X-linked traits such as the allozyme allele Pgd-100 (Hagen & Scriber 1989; Hagen *et al.* 1991; Scriber *et al.* 2008), and 4) oviposition preferences (Scriber *et al.* 1991; Mercader & Scriber 2007; Mercader *et al.* 2009). However, other X-linked species diagnostic traits (including Ldh-100 allozyme alleles and bivoltine potential (od^-); Rockey *et al.* 1987) as well as the Y-linked dark gene (b^+) and certain mitochondrial DNA alleles have not moved northward across the historical hybrid zone (Stump *et al.* 2003; Scriber *et al.* 2008). The divergent selection pressures on different parts of the X-chromosome (and differential movement of these parts) in the genomes of both *P. glaucus* and *P. canadensis* may be historically old (Putnam *et al.* 2007). However, recent origins of interspecific introgression and recombination combined with strong divergent selection on different regions of the X-chromosome may have been catalyzed by recent climate warming, possibly leading to the Mountain Swallowtail (potential hybrid species), *P. appalachiensis* (Pavulaan & Wright 2002; Scriber & Ording 2005). We will continue to investigate the linkage relationships of the dark morph enabler gene (s^-) with other parts of the X-chromosome and how it may be involved in the easily detected sexual color mosaics.

ACKNOWLEDGEMENTS

This research was supported in part by the College of Natural Science, and the Michigan Agricultural Experiment Station (Project MICL #01644), NSF grants (DEB 9220122, DEB 9981608, DEB 0716683), and the Ray and Bernice Hutson Endowment of the Department of Entomology. We thank Matt Ayres, Janice Bossart, Jessica Deering, Robert Dowell, Cheryl Frankfater, Robert Hagen, Robert Lederhouse, Matt Lehnert, Jim Maudsley, James Nitao, Michelle Oberlin, and Patti Tidwell for assistance in the field and lab. Thanks are extended to David and Marc Perlman and Joseph Zeligs for their color mosaic pho-

tos and to Loretta Lutman for the photo of the wild bilateral gynandromorph. We thank Austin P. Platt and Charles V. Covell for very helpful reviews.

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Received for publication 26 February 2008; revised and accepted 9 December 2008.

PITHING AND MINING BY A PUNKIE: THE UNUSUAL FEEDING STRATEGIES OF *NOLA CILICOIDES* (GROTE, 1873) (NOCTUIDAE: NOLINAE)

Additional key words: *Lysimachia ciliata*, leafmining, plant defense, hypertrophied tactile setae, leaf shelter

Herbivorous insects have evolved innumerable strategies for coping with plant defenses. Among these are efforts made by insects to incapacitate a plant's ability to transport defensive substances through its vascular or lactifer systems to sites of feeding injury. One means of doing such is to trench, vein cut, or otherwise breach the delivery systems of the host so that milky latexes, resins, and gums cannot be transported to the feeding site (Dussourd & Eisner 1987; Dussourd 1993). Another strategy is to girdle the host, either as an adult (e.g., ovipositing females) or as a larva (Forcella 1982; Dussourd 1993; Hanks 1999; Albanese *et al.* 2007). A third option is mass assault: bark beetles are a classic example. Adults attack host trees in such numbers that individuals under siege cannot individually "pitch out" all the invading beetles (Wood 1982). Here we report an example of a fourth option available to herbivores for thwarting a host's defensive system: the hollowing (pithing) of non-woody stem tissues.

In early July 2007 we found young (approximately 3rd instar) larvae of *Nola cilicoides* (Grote) (Noctuidae: Nolinae) pithing upper stems of fringed loosestrife (*Lysimachia ciliata* L.) (Primulaceae). Larvae tunneled into the side of new shoots, removed pith and associated vascular tissues, backed out, then crawled further up the compromised stem to feed on flowers and young leaves.

Nola cilicoides (Fig. 1) occurs from southern Canada to northern Florida and west to Arkansas (Forbes 1960; Handfield 1999; Ferge & Balogh 2000; Covell 2005). In the Northeast the moth is local and uncommon in swamps, floodplains, wet meadows, damp woods, and other mesic to wet community types. Dyar (1899) did not provide life history information for *N. cilicoides* in his study of the early stages of Nearctic nolines. McCabe, in Rings *et al.* (1992), reported that the larva of *N. cilicoides* feeds on new leaves and flowers of fringed loosestrife (*Lysimachia ciliata*). Collection dates for adults in Connecticut and New York normally range from mid June into July, with the occasional specimen taken as early as late May or as late as August and September—we are unsure of the number of generations. In Georgia there are least three full broods (James Adams pers. comm.).

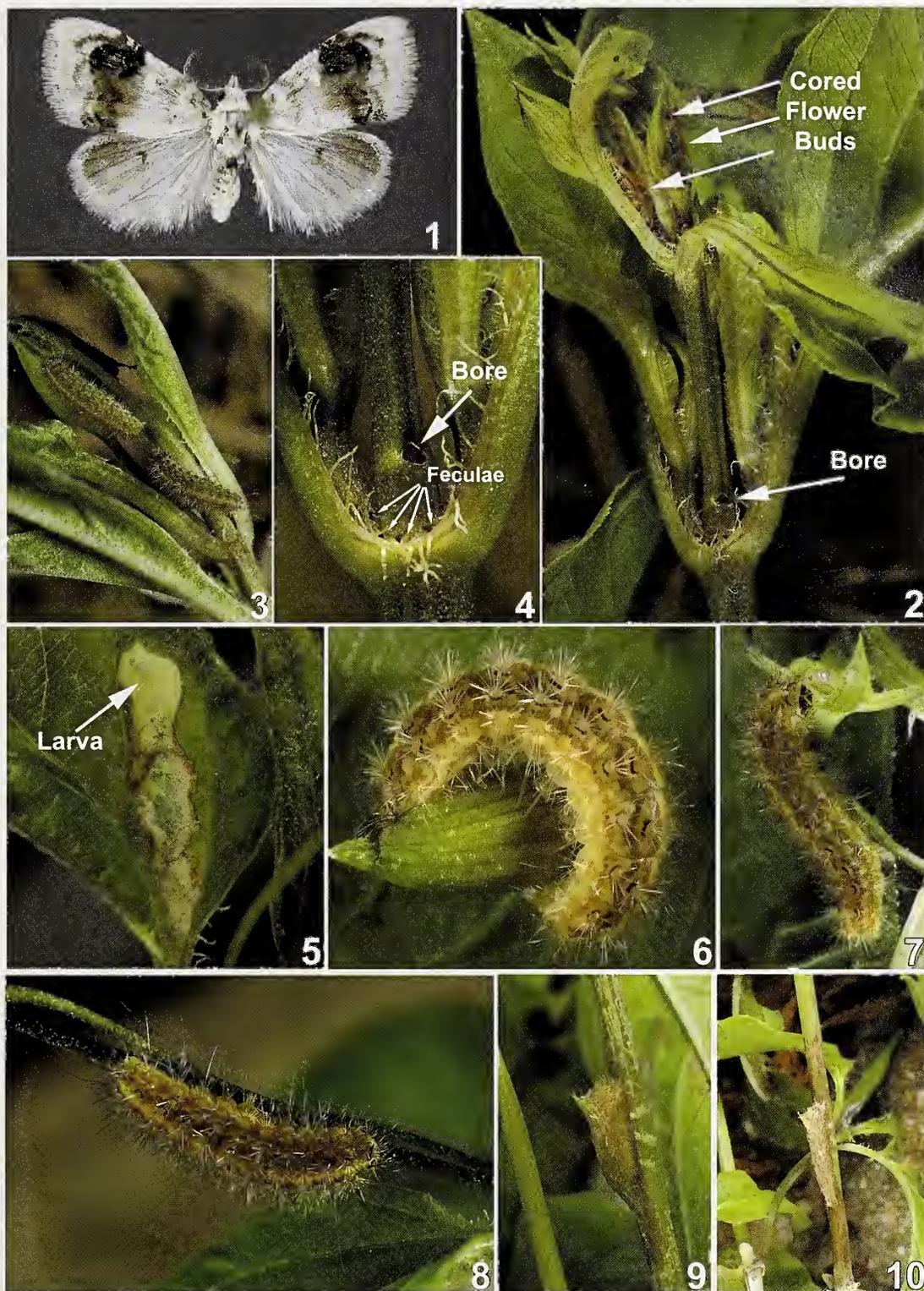
Study Site and Methods. Observations were made

on a colony of *N. cilicoides* located in Lebanon, Connecticut along a powerline cut south of Burnham Road and north of Route 87 (N41° 39' 15.5" W72° 14' 07.6"). Rearing was done in plastic bags and 40 dram plastic vials. Larvae were reared at 21–23° C with photoperiods set to match those outdoors in central Connecticut. Larval and adult vouchers and digital images have been deposited at the University of Connecticut.

Results. On 6 and 11 July, 2007, young larvae of *N. cilicoides* were found feeding on the shoots of fringed loosestrife plants that were coming into flower. Larvae were located by surveying for loosestrife plants with flagging shoots. Each flagged shoot had a small entry hole and small area of cored pith, 5–10 centimeters below the shoot apex (Figs. 2, 4). On each flagged plant, we located 1 or 2 approximately 3rd instar *N. cilicoides* feeding externally (Fig. 3), distal from the wound, on floral buds, flowers, and new leaves. Larvae showed a preference for buds and flowers (Figs. 6, 7) over leaves. Some larvae tied together adjacent leaves and flowers, forming a weak shelter, but silk deposition was sparse and their shelters were poorly defined.

Larval densities were low; only five caterpillars were found on roughly 200 plus fringed loosestrife stems that were searched in early July. In the vicinity of the colony and at other locations in New London and Tolland counties, we searched for, but did not find, larvae on either swamp loosestrife [*L. terrestris* (L.) Britton, Sterns, & Poggenb.] or whorled loosestrife (*L. quadrifolia* L.).

On 9 and 19 August, 2007, we returned to the same stand of fringed loosestrife in Lebanon, ostensibly to look for cocoons. While we failed to find cocoons on more than 60 checked stems, and any evidence on newly bored shoots, we discovered something surprising: young *Nola cilicoides* larvae, 2–3 mm in length mining leaves of fringed loosestrife. Larvae had entered through the lower epidermis, often adjacent to a vein, and then tunneled into the lamina, removing parenchymatic tissues, leaving a full depth blotch mine (Fig. 5). All but one mine had a single entrance/exit hole on the lower leaf surface; the one exception had three entry holes. Dark green to black frass collected in the



FIGS. 1-9. *Nola cilioides* (Grote), all Lebanon, New London Co., Connecticut except adult from Whitefield, New Hampshire. 1. Adult female. 2. Shoot damaged by single larva (arrows point to entry points). Note wilted section of stem above bore hole. 3. Middle instars feeding on young leaves. 4. Detail of 2. 5. Occupied leafmine. 6. Last instar "coring" flower bud with head fully inserted. 7. Last instar feeding on remains of what was previously an open flower. 8. Last instar. While not fully visible, SD setae extend close to all four edges of the image (see text). 9. Cocoon under construction, upper end with abdominal terminus visible. 10. Finished cocoon. Note discolored area of stem above and below cocoon where bark strips were removed.

mine, i.e., little had been expelled. The smallest mine located, was only a few mm in diameter and contained the cadaver of a larva 1.25 mm in length.

In the wild, we found approximately 3rd instar larvae grazing on patches of parenchyma from leaf undersides—scraping away small patches of leaf tissue without feeding through to the upper leaf surface—as late as mid September, indicating that at least some *N. cilicoides* larvae vacate their mines to feed externally, before the onset of winter.

Beginning as early as late August, our captive (lab-reared larvae) spun small, circular to oval, cocoons between overlapping leaves. Cocooned larvae were foreshortened, only 2.6–2.8 mm in length, and evidently had entered a non-feeding diapause in which they would pass the winter. [*Meganola spodia* Franclemont, an oak-feeding noline, also overwinters as a partially grown larva (Butler 1989).]

The full grown larva is 10–12 mm in length (n=8). It is typical for a noline: the prolegs are absent on A3 and secondary setae are present, grouped onto five (dorsal, subdorsal, lateral, subventral, and ventral) warts. Both the dorsal and subdorsal warts have an incomplete black ring around their bases (Figs. 6, 7). The ground color is dirty yellow-orange above, more yellow laterad, and mostly unpigmented below the subspiracular stripe; the creamy to pale orange middorsal stripe is weak over T1. Subdorsal warts on T1–T3 and A7–A9 bear one exceptionally long seta that extends well beyond the body (see below). The head, prominently marked with black (Fig. 7), is drawn into the prothorax at rest.

July-collected, lab-reared larvae formed their pupal cocoons along a stem (Figs. 9, 10), but extensive searches of plants in the wild, including those with wilted tips, did not yield any cocoons. The central chamber of cocoons measured roughly 3 mm x 10 mm. The lower end of the cocoons had an additional 5 mm-long "tail" that tapered downward; the upper end was higher in profile (n=3) (Figs. 9, 10). Like other nolines, numerous strips of stem epidermis "bark" were collected and then woven into the wall of the cocoon. Our caterpillars positioned more than 40 narrow strips of bark, removed from adjacent areas of the stem, into their cocoon walls. Eclosion occurred 1–2 weeks after pupation.

Discussion. The greatly elongated setae that extend from the SD warts at either end of the body of *Nola* larvae (Fig. 8 and caption) presumably serve as an "early warning" system for the larvae. Those issuing from T3 are the longest: in one individual, the longest SD seta extended forward 5.8 mm on a larva only 10 mm in overall length. The rearward-projecting SD seta on A9 of this same caterpillar measured 3.6 mm. In addition,

the subdorsal warts on these segments are oriented in such a way (in living larvae) that the hypertrophied setae are directed well forward on the thoracic and rearward on the abdominal segments. Analogous long dorsal or subdorsal setae also have been reported from choreutids (e.g., *Brenthia*), pyralids (e.g., *Monoloxis*), as well as other noctuids (e.g., *Abablemma* Walker) (Aiello & Solis 2003; Rota 2003, 2008; Wagner *et al.* 2008; Rota & Wagner 2008).

Although *Lysimachia ciliata* has not been investigated, the tissues of other *Lysimachia* species have been found to contain a variety of bioactive compounds including flavonoids, triterpenoid saponins, and phenolic acids (Chang *et al.* 2004). To what degree these are transportable or serve in defense remains unstudied. Our thesis presupposes that *N. cilicoides* larvae tunnel out the pith of their hostplant to incapacitate its vascular tissues—we acknowledge that the pithing behaviors reported here may have little to do with circumventing the plant's ability to translocate antiherbivory substances. Perhaps pithing and the subsequent flagging help the larva to construct its leaf shelter, prevent subsequent growth and maturation of the shoot, enhance survivorship from attacks by natural enemies, or in some other way improve or enhance larval performance or survival. Regardless, the stereotypical behavior is commonly expressed, and stem boring and bud coring represent unique traits for Nearctic nolines, which tend to be rather unspecialized leaf feeders (Forbes 1960; Wagner 2005; Wagner *et al.* 2010).

As noted above, larvae preferentially sought out flower buds and flowers over leaf tissues. A preference for reproductive tissues has been reported for other nolines. *Nola sorghiella* Riley feeds on the seed heads of sorghum and various other grasses and appears to be completely tied to reproductive tissues (our wild-collected larvae failed when offered only leaves). In the Old World, spiny bollworms of the genus *Earias* are major pests of cotton flowers (Pinhey 1975; Kitching & Rawlins 1998).

More surprising was the finding that *N. cilicoides* larvae engage in leaf mining. Leafmining is rare among noctuids. In the East only a handful of apameines mine, and most of these only for the first one or two instars (Wagner *et al.* 2010; Eric Quinter pers. communication). It is exceptional for a "leafminer" to bear secondary setae; more commonly, setae tend to be reduced or absent among leafmining clades (cf. Stehr 1987). We did not observe leafmining behaviors prior to our August visits. Interestingly, life histories with stem mining in spring generations and leafmining in late summer generations have been reported for a number

of European Momphidae (Koster 2002). In North America, *Mompha solomonella* Adamski & Brown, tunnels in shoots of *Cephalanthus occidentalis* L. (Rubiaceae) in the spring, but second and subsequent generations mine leaves (Wagner *et al.* 2004).

Much remains to be elucidated about the biology *Nola cilicoides*. As noted, the selective advantages of pithing and ultimate explanation for this exceptional behavior have yet to be determined. Both observational and controlled studies are needed to better understand the roles of the hypertrophied tactile setae of *Nola* and other lepidopterans. We are also in a quandary about the phenology and broodism of *N. cilicoides* in New England. We were only able document the existence of a single brood—one that produced its pithing larvae in early July. Either we missed a small spring brood, or the partially grown larvae that spun overwintering cocoons in August, waited until early July of the following season to break their diapause.

ACKNOWLEDGMENTS

Tim McCabe, as so many times before, guided DLW's initial efforts. Deane Bowers, Dave Dussourd, Laura McLoud, Jessica McShane, April Rodd, and Bo Sullivan read drafts of the paper. An anonymous reviewer offered many helpful suggestions. Andrea Farr assembled the plates. Both authors were supported on a grant from the CT-Department of Environmental Protection Wildlife Division through the State Wildlife Grants Program; additional support was provided by Northeast Utilities.

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Received for publication 6 Nov 2007; revised and accepted 28 May 2008

Journal of the Lepidopterists' Society
63(1), 2009, 52–57

EUGENE G. MUNROE

(8 SEPTEMBER 1919–31 MAY 2008)

I recently wrote an obituary for Eugene Munroe for the *Bulletin of the Entomological Society of Canada* [2008. 40 (1): 142–146]. Unfortunately there was not enough space for his list of publications. In 2000, I wrote a detailed account of Gene's life and professional career for a *Festschrift* in *Tropical Lepidoptera* [11:1–6]; the list of publications was incomplete. Gene's impressive publication list is published in its entirety here. See also the 2008 *Pyraloid Planet* [2:2] for reminiscences by colleagues. Michael Shaffer, The Natural History Museum, London, generously reviewed this version of Gene's publications.

To learn more about Gene's life, accomplishments, enthusiasm for research, and love of Lepidoptera, refer to the publications mentioned above. Here, I would like to briefly share some historical information regarding the Lepidopterists' Society and Gene. He was a Charter and Honorary Life Member of the Lepidopterists' Society. In preparation for the First Annual Lepidopterists' Society Meeting, Dec. 29th–30th, 1950, held at the American Museum of Natural History, New York, the President, J. H. McDunnough, appointed three committees, Program, Local Arrangements and Nominating. Gene was appointed member of the Nominating Committee. Also, at the first meeting Gene participated (1951e) in a symposium entitled "Geographic subspeciation in the Lepidoptera" where Charles Remington also presented the introduction. Gene was involved in the first annual Season Summary as a coordinator (1947b, 1949b,c, 1951b) for Area 7, the Northeast, and later as editor (1951d) of the Season Summary. He served as President of the society in 1958. In 2004 Gene received the Karl Jordan medal from the Lepidopterists' Society.

Gene Munroe passed away 31 May 2008 at the age of 89 in Ontario, Canada.

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Received for publication 30 September 2008; revised and accepted 17 January 2009.

Journal of the Lepidopterists' Society
63(1), 2009, 58

MOTH CATCHER: AN EVOLUTIONIST'S JOURNEY THROUGH CANYON AND PASS. By Michael M. Collins. 176 pages, 13 color plates; ISBN 978-0-87417-725-1 (hardcover), ISBN 978-0-87417-735-0; US\$49.95(hardcover), US\$18.95 (paperback). Univ. of Nevada Press. Publication date: 2007.

Two threads run through the stories of most lepidopterists that contribute to their life-long obsessive fascination with some aspect of entomology, whether they are professionals or avid amateurs. The first is some event of life-changing discovery to light the fire; the second is the timely connection with one or more knowledgeable and nurturing mentors to fuel the fire so that it burns throughout a lifetime. Such is indeed the case with Mike Collins, who shares with us the beginnings and many subsequent years of his own journey as a lepidopterist—in this case pursuing the life history, behaviors and interspecific relationships of western North American Saturniidae.

Migrating from his native Iowa to the western mountains, Mike quickly passed beyond the usual goal of building a large collection of adult specimens and focused on questions of biology and evolution, prompted first by the late Walter R. Sweadner's monograph on the evolution of the genus *Hyalophora*. Seminal to his later researches, Sweadner's treatise on natural hybridization begged for substantiating research. The evolutionary relationships among the 3 *Hyalophora* species—*cecropia*, *gloveri* and *euryalus*—became the major focus of Mike's research. Mike provided important supporting evidence for Sweadner's ideas in collections and by rearing *H. gloveri* and *H. euryalus* from areas of sympatry and allopatry. The discovery and elucidation of the hybrid zone where these two species come together in Monitor Pass in eastern California proved to be a major discovery. This story is the centerpiece of the book.

The sibling nature of *Heunleuca eglanteriua*, *nuttalli* and *hera* and their isolating mechanisms was another problem in Mike's voyage of research and discovery. His research on these and other saturniids was woven into his undergraduate years at UC Berkeley, and PhD work under Art Shapiro at UC Davis.

Friendships with several of our colleagues and stories of field adventures together spice the narrative. The account of his first meeting with Art Shapiro gave

me a knowing chuckle. A short biography of Sweadner, and Mike's meeting with his widow and daughter, was of special interest to me, as was a photo of this man who inherited W. J. Holland's curatorial mantle at the Carnegie Museum, but for a tragically short period.

Collins' style is anecdotal, written in the first person, and easily readable. He uses it effectively when describing people and research projects without the cumbersome data found in his scientific publications. There are numerous short treatises on topics pertinent to systematics and ecology: western montane ecology (plant and animal), Neo-Darwinism, industrial melanism, DNA sequencing, speciation (biological species concept versus phylogenetic species concepts), and pre-mating and post-mating barriers, to name a few. The book thus serves as a good primer for bright young people interested in entering the field of population ecology.

Mike's lifelong passion for his chosen specialty in entomology—isolating mechanisms among closely related saturniid moths in the majestic West—shines through from beginning to end. My minor comments concern uneven referencing: some of the major literature cited (*i.e.* Sweadner's monograph, p.24), are mentioned generally (no complete title and other citation details), but not included in the Bibliography. The reader must scout these out from other sources. Also, some less scientifically trained readers might benefit from definitions of more of the scientific terms employed (*genoune*, p. 44; "*relict*", p. 56). Other terms are well defined or explained.

It is always fascinating to see how our colleagues began their journeys with Lepidoptera—how and from whom they drew inspiration, nurturing and training—and then see a summary of their career-long contributions to the science. Mike's story is an enjoyable and informative addition to this lore.

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Received for publication 10 Dec 2008; revised and accepted 17 Jan 2009

MANUSCRIPT REVIEWERS FOR 2008 (VOLUME 62)

Manuscript reviewers are anonymous contributors to the scientific rigor, clarity, and quality of text and illustrations in the papers published by the Journal of the Lepidopterists' Society. The reviewers' input is invaluable and always welcomed by authors, editors and readers. We hope their careful work continues to allow the Journal to increase quality and readership. On behalf of all the authors and the editorial staff of the Journal, respectful acknowledgement is given to the reviewers for contributions published in Volume 62.

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