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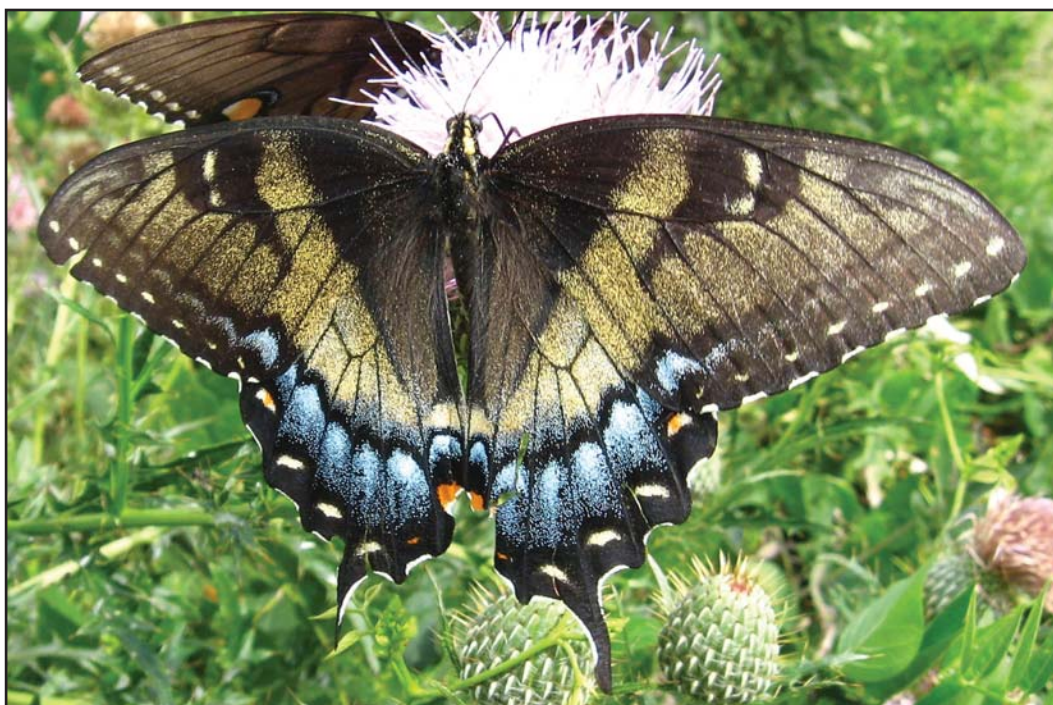
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Cover illustration: "Trigon"-type female *Papilio glaucus* L., 17 August 2010, 1400 h, taking nectar from *Cirsium* sp., J. I. Case Wetland Wildlife Refuge, Terre Haute (Vigo Co.), Indiana near SE corner of lake. Copyright © Roger Carpenter.

THE “TRIGON” WING PATTERN VARIANT IN FEMALE *PAPILIO GLAUCUS* (PAPILIONIDAE)
IN AN INDIANA POPULATION

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ABSTRACT. A small percentage of adult dark-morph female eastern tiger swallowtails, *Papilio glaucus* L. (Papilionidae), display wing coloration patterns intermediate between those of normal yellow-morph and normal dark-morph females. One of these patterns (which, for the sake of convenience, I refer to in this paper as the “trigon” pattern) involves normal melanization of the scales in the basal portions of the dorsal wing surfaces but incomplete melanization of the scales in the central portions, resulting in the appearance of an inverted triangle (trigon) centered on the insect’s body when the wings are outstretched. Between mid-July and mid-August 2010, I observed trigon-type female *P. glaucus* in the Terre Haute (Vigo Co.), Indiana region for the first time since I had begun systematically observing the *P. glaucus* in the area in 2002. Five trigon-type females out of 2,388 females were observed, suggesting that the trigon type comprised about 0.2% of the local female *P. glaucus* population. An examination of photographs of *P. glaucus* posted on an insect/spider identification website by users from throughout *P. glaucus*’s range revealed a notable increase in the percentage of trigon-type females in 2010, suggesting that the Vigo Co. increase was not a localized phenomenon. I concluded that the unusually high temperatures that prevailed in the summer of 2010 affected wing pigment production during pupal development, thereby serving to make the trigon phenotype more prevalent that year. Other evidence further suggests that in general the prevalence of the trigon phenotype is associated with elevated temperatures (e.g. severe heat events). The findings of the present study suggest that if record high temperatures continue to prevail throughout *P. glaucus*’s range during pupal development times, dark female *P. glaucus* expressing the trigon (and other intermediate) color patterns could become more prevalent, potentially altering the dynamics of dark female *P. glaucus*’s mimetic relationship with *Battus philenor* in the most impacted populations.

Additional key words: melanin, papiliochrome, temperature-sensitive phenotypic variation, wing pattern development, climate change

The eastern tiger swallowtail, *Papilio glaucus* L. (Papilionidae), ranges throughout the eastern half of the United States from New England west to the Great Plains and south to northeastern Mexico (Tyler et al. 1994). “Normal” adult females occur in both a yellow morph similar in appearance to the male and a dark morph in which the yellow is replaced with black dorsally and brown ventrally (Fig. 1a–b). In addition, a small percentage of female *P. glaucus* exhibits “intermediate” color patterns, which appear to involve the incomplete melanization of a genetically dark form (Ritland 1986).

In one type of rare dark-morph variant, the scales in the basal areas of the dorsal side of both the forewings and the hindwings are melanized, “filling in” the regions between the thorax and the inner edge of the proximal set of “tiger” stripes. The remaining wing surface, excluding the distal “tiger” stripes and marginal black bands, is generally yellow, although in some individuals it can appear “dusted” with varying proportions of dark scales. Because the proximal one-third of the dorsal wing surface is melanized and the resulting pattern gives the impression of an inverted triangle centered on the body when the outstretched wings are viewed from the dorsal side, I refer, for the sake of convenience, to this otherwise unnamed pattern as the “trigon” pattern. Both naturally occurring and experimentally produced females of this type have been reported in the literature (e.g. Edwards 1884 Fig. 5.2–3; Clark 1932 Fig. 38.2, also figured in Clark & Clark 1951 Fig. 21h; Ehle 1981

Fig. 1.2; Ritland 1986 Fig. 1.4; Scriber et al. 1987 Fig. 3a; Tyler et al. 1994 Fig. 94l) and photographs of these individuals have appeared online. The trigon pattern appears to represent a categorically distinct and consistent intermediate phenotype.

Between mid-July and mid-August 2010, I observed five trigon-type female *P. glaucus* in the Terre Haute (Vigo Co.), Indiana region (Fig. 1d–h). Although other intermediate females displaying an overall “dusting” of yellow and black scales but lacking the trigon pattern were also observed (e.g. Fig. 1c), such females are observed every year at low numbers, usually comprising ~0.5–1.0% of the female population. The sightings of the trigon-type females in 2010 marked the first time that I had observed this type since I had begun systematically observing the *P. glaucus* in the Terre Haute area in 2002. This paper discusses the 2010 observations and possible reasons for the appearance of this phenotypic variant.

METHODS AND MATERIALS

I observed trigon-type female *P. glaucus* while collecting data on the percentages of males, yellow females, and dark females at the J. I. Case Wetland Wildlife Refuge at Hawthorn Park in Terre Haute (39°29′20.0″ N, 87°19′05.0″ W) and at my home in Terre Haute during July and August 2010. I photographed all of these females with a digital camera at 2816 × 2112 pixel resolution on the dorsal side, where the trigon pattern is the most conspicuous, and

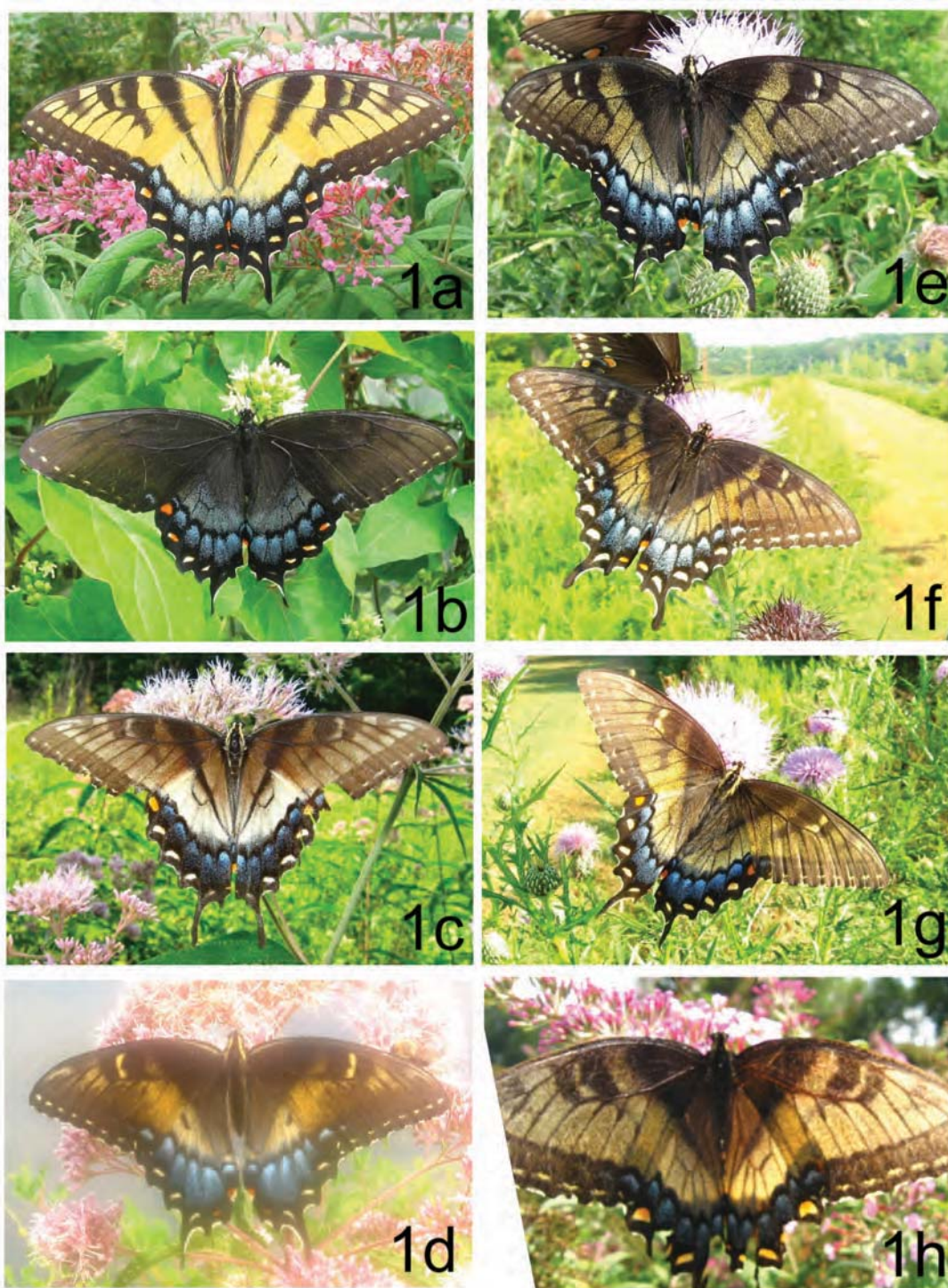


FIG. 1. "Normal" and "trigon"-type adult female *Papilio glaucus* from Vigo Co., Indiana. (a) Normal yellow female, 29 July 2006, author's home. (b) Normal dark female, 23 July 2004, author's home. (c) Intermediate non-trigon-type female, 7 August 2010, J. I. Case Wetland Wildlife Refuge. (d) Trigon-type female, 21 July 2010, 1333 h, taking nectar from *Eutrochium fistulosum* (Barratt) Lamont, J. I. Case Wetland Wildlife Refuge near SW corner of lake. FW length: 49.5 ± 3.3 mm. (e) Trigon-type female, 17 August 2010, 1400 h, taking nectar from *Cirsium* sp., J. I. Case Wetland Wildlife Refuge near SE corner of lake. FW length: 50.0 ± 3.3 mm. (f) Trigon-type female, 22 August 2010, 0919 h, taking nectar from *Cirsium* sp., J. I. Case Wetland Wildlife Refuge near SE corner of lake. FW length: 53.9 ± 3.3 mm. (g) Trigon-type female, 24 August 2010, 1009 h, taking nectar from *Cirsium* sp., J. I. Case Wetland Wildlife Refuge near SE corner of lake. FW length: 51.8 ± 3.3 mm. (h) Trigon-type female, 19 August 2010, 1303 h, taking nectar from *Buddleja davidii* Franch., author's home. FW length: 55-60 mm. All photographs © Roger Carpenter.

recorded data relevant to each observation (e.g. date, time, location, behavior).

Although I did not obtain morphometric data, I estimated forewing length from photographs in which the wings were positioned parallel to the camera lens and the body was fully visible. Assuming an average body length of 26.7 mm (based on previous sampling of second-brood female *P. glaucus* in Vigo Co.), forewing length in pixels was divided by body length in pixels and the resulting value was multiplied by 26.7 to derive forewing length in millimeters. The confidence interval (95%) was based on the standard deviation derived from the body length data (SD = 1.7 mm; 95% CI $\pm$ 3.3 mm).

I estimated the proportions of trigon-type females in both the female and dark female samples (CI = 95%). In addition, I performed *z*-tests of proportions (two-tailed) to determine 1) if the proportions of trigon-type females observed at the Refuge and at my home, respectively, significantly differed and 2) if the proportions of trigon-type males and that of females, respectively, significantly differed. Statistical analyses were performed using SPSS v20.0 software (IBM Corp. 2011).

RESULTS

At the Refuge, I observed four trigon-type females out of a total sample of 2,325 females ($0.17 \pm 0.17\%$). These individuals are illustrated in Fig. 1d–g. At my home, I observed one trigon-type female out of a total sample of 63 females ($1.6 \pm 3.1\%$). This individual is illustrated in Fig. 1h. The overall percentage in the combined sample (*n* = 2,388) was $0.21 \pm 0.18\%$, suggesting that the true population percentage of trigon-type females lay between 0.03% and 0.39%. A *z*-test of proportions revealed that the difference between the proportion of trigon-type females in the Refuge sample and that in the home sample was significant, *z* = -2.425, *P* = .016. The overall percentage of trigon-type dark females in the combined sample (*n* = 1,273) was $0.39 \pm 0.34\%$, suggesting that the true population percentage of trigon-type dark females lay between 0.05% and 0.73%.

In my sample, the trigon pattern appeared to be restricted to females. None of the 2,281 males in my Refuge sample or the 55 males in my home sample (total *n* = 2,336) exhibited this wing pattern. A *z*-test of proportions revealed that the difference between the proportion of trigon-type males and that of females was significant, *z* = 2.213, *P* = 0.027.

The bodies of all five trigon-type females had the yellow- and black-striped pattern more typical of yellow morphs than of dark morphs. Neither the wings nor the bodies exhibited any obvious structural abnormalities and, apart from the variant wing pattern, appeared

normal compared to other female *P. glaucus*.

DISCUSSION

The significant difference in the proportion of trigon-type females at the Refuge and that at my home is probably due to the small number of *P. glaucus* in the home sample as opposed to a non-statistical effect. In addition, the significant difference in the proportion of male and female trigon-type *P. glaucus* reflects the fact that no males of this type were observed. Scriber and Evans (1987) reported a wild-caught partly trigon-type male from Dane Co., Wisconsin (Fig. 6a–b), and Shull (1987) reported a similar male from Nashville (Brown Co.), Indiana (pl. 19), but the trigon patterns in these males were incomplete, appearing more prominently on the dorsal forewings. Scriber and Evans hypothesized that their male may have inherited a translocated melanizing gene from a dark mother or predecessor, and the appearance of Shull's male (whose body is also black) suggests the presence and expression of dark female genes. The facts that none of the 2,300+ males in my 2010 sample (or samples for other years) showed evidence of even a partial trigon pattern and that almost all of the trigon-type *P. glaucus* that have, to my knowledge, been depicted in the literature and elsewhere have been female support the hypothesis that "trigonation" is fundamentally the product of female genetics.

In explaining the occurrence of the trigon-type females observed in 2010, two possibilities can probably be discounted. First, hybridization between *P. glaucus* and other *glaucus*-group species is known to produce variant wing patterns (Clarke & Willig 1977; Scriber & Evans 1988a,b; West & Clarke 1988; Scriber 1990; Scriber et al. 1990; Scriber et al. 2009), but no other *glaucus*-group species occurs within ~350 km of Vigo Co. (*P. canadensis* in central Michigan). In addition, hybridization between *P. glaucus* and other swallowtail species that are sympatric with it in Vigo Co. (*P. troilus*, *P. cresphontes*, *P. polyxenes asterius*, *Battus philenor*, and *Eurytides marcellus*) is doubtful. *P. troilus* is the most common (pers. obs.) and genetically compatible (Caterino et al. 2001), but Scriber and Lederhouse (1988) reported that numerous attempts at hand-pairing *P. glaucus* females with *P. troilus* males produced only one successful pairing and no viable eggs. Such difficulties in producing *glaucus* $\times$ *troilus* offspring under controlled laboratory conditions suggests that successful hybridization between these two species is even less likely to occur in nature. In addition, the absence of non-*glaucus* features in the trigon-type females I observed further suggests they were not *glaucus* $\times$ *troilus* hybrids.

P. cressphontes is very rare in Vigo Co.; I observed only two in 2010 (and only three between 2002 and 2009), which suggests that even casual encounters between *glaucus* and *cressphontes* in Vigo Co. are highly infrequent. Hereau and Scriber (2003) reported a male *P. polyxenes* and a dark female *P. glaucus* in copulo in the field, but the authors pointed out that *glaucus* and *polyxenes* are separated by the greatest genetic distance of any two papilionid species reported mating in nature (except for a female *B. philenor* and a male *E. marcellus*, Rausher & Berenbaum 1983), making viable offspring from such pairings unlikely. *B. philenor* and *E. marcellus* are genetically even more distant, belonging to entirely different tribes (Troidini and Leptocircini, respectively). Therefore, hybridization between *P. glaucus* and other swallowtail species is improbable.

Second, the possibility that the trigon pattern arose in multiple individuals through random mutation is unlikely because of the uniformity of the pattern. In addition, it seems unlikely that all of the females I observed came from a single mother that passed on a heritable mutation. The first (Fig. 1d) was observed one month before the remaining four, making it unlikely that the former came from the same brood(s) as the latter. Although the remaining four, which were observed within a one-week period, could have come from the same brood, three (Fig. 1e–g) were observed at the Refuge and one (Fig. 1h) at my home, which are several kilometers apart. In addition, the low survival rate of members of a particular brood into adulthood also argues against the possibility that all four came from the same brood. Consequently, at least two (and likely several) mothers carrying the same transmissible mutation would probably have had to be involved. Although possible, it seems unlikely that several such mothers would be clustered in the same area at the same time but not at other times.

The most convincing explanation for the occurrence of the trigon-type females I observed is the unusually high temperatures that prevailed in the Terre Haute area throughout July and August 2010. Ritland (1986) found that the genetically dark female offspring of wild-caught dark female *P. glaucus* reared at higher temperatures were more likely to produce incompletely melanized color patterns than those reared at lower temperatures. For instance, broods reared at 22°C produced normal dark females. Those reared at 25°C, however, produced some females that exhibited an increase in the proportion of yellow scales relative to that found in normal dark females. Those reared at 28°C produced some females that displayed the most dramatic lack of melanization. One of these females (Fig. 1.4) is prototypical of the trigon phenotype.

Ritland speculated that heightened temperatures interfered with the melanization process during pupal development, thereby producing incompletely melanized dark females.

In July 2010, the mean temperature in Vigo Co. was 25.3°C (SD = 2.3°C), while in August, the mean temperature was 24.9°C (SD = 3.0°C). For both months combined, the mean temperature was 25.1°C (SD = 2.7°C). The mean high temperature for July and August combined was 31.3°C (SD = 2.3°C). The summer of 2010 was, in fact, the hottest summer in Vigo Co. since 1995. Since all of the trigon-type females I observed would have pupated between mid-July and mid-August, when the mean temperature was 26.3°C (SD = 2.2°C) and the mean high temperature was 31.8°C (SD = 2.4°C), conditions would have been ideal for producing incompletely melanized dark females, if temperature were in fact the main determining factor.

To obtain a rough measure of the situation in other parts of *P. glaucus*'s range in 2010, I examined photographs of *P. glaucus* that users of the insect/spider identification website *Bug Guide* (2013) had taken between 2002 and 2012. The results of this analysis are presented in Table 1. In the 2010 sample (n = 26), at least five females displayed the trigon pattern (19.2%). In addition, a sixth female that did not display the trigon pattern was strongly intermediate in coloration, displaying a heavy “dusting” of black scaling on a predominately yellow surface. By contrast, the data for only two other years (2006 and 2007) revealed trigon-type females. In the 2006 sample (n = 22), only one female was of the trigon type (4.5%), while in the 2007 sample (n = 19), only one was of this type (5.3%). None of the females from these two years displayed a non-trigon intermediate pattern. The samples for the remaining years revealed no trigon-type or intermediate females. Although the *Bug Guide* data should be interpreted with caution, given their unsystematic nature and small sample sizes for some years, between-year comparisons nonetheless suggest that trigon-type female *P. glaucus* were more common in 2010 than in other years.

Given that the 2010 observations took place over an area of >500,000 km², it is clear that the relative abundance of trigon-type female *P. glaucus* in 2010 was a consequence not of local factors, but of a widespread phenomenon that affected *P. glaucus* throughout a substantial portion of its range (e.g. temperature).

The observation dates for the 2010 trigon-type female *P. glaucus* displayed on *Bug Guide* (23 July–26 August) overlap those in my sample (21 July–24 August), suggesting that all of these females pupated sometime between mid-July and mid-August. Perhaps

TABLE 1. Percentages of Photographs of Trigon-Type Female *Papilio glaucus* Posted on the *Bug Guide* Website (<http://bugguide.net>), 2002–2012.

Year	Female	Intermediate	Trigon	Trigon %
2002	0	0	0	0.0%
2003	4	0	0	0.0%
2004	0	0	0	0.0%
2005	10	0	0	0.0%
2006	22	0	1	4.5%
2007	19	0	1	5.3%
2008	17	0	0	0.0%
2009	7	0	0	0.0%
2010	26	1	5	19.2%
2011	9	0	0	0.0%
2012	6	0	0	0.0%
Total	120	1	7	5.8%

NOTE. Lighter versions of the 2010 trigon-type females were photographed in Waterloo Park, Elkridge (Howard Co.), MD (28 July, <http://bugguide.net/node/view/433902>), Danville (Hendricks Co.), IN (22 August, <http://bugguide.net/node/view/445641>), and Mt. Olive Cemetery near Knoxville (Knox Co.), TN (26 August, <http://bugguide.net/node/view/447462>). Darker versions of these females were photographed in Montgomery Co., PA (23 July, <http://bugguide.net/node/view/432146>) and Whitewright (Grayson Co.), TX (31 July, <http://bugguide.net/node/view/600454>). The 2010 intermediate female was photographed in Avery Co., NC (29 August, <http://bugguide.net/node/view/463111>).

significantly, the highest mean July–August temperature that occurred between 2002 and 2010 for the five *Bug Guide* locations combined that reported trigon-type females in 2010 occurred in 2010. For three locations (Danville, IN; Knoxville, TN; Elkridge, MD), the highest mean July–August temperature occurred in 2010, while for the remaining two (Montgomery, PA; Whitewright, TX), the second highest occurred in 2010.

Trigon-type *P. glaucus* appear to have become more abundant in other years with unusually hot summers. For example, James Wiker, who has collected Lepidoptera in Illinois since the 1960s and has co-authored field guides on the skippers and the sphinx moths of Illinois (Bouseman et al. 2006; Wiker et al. 2010), has acquired a number of specimens of *P. glaucus* displaying variant wing patterns. Of these that I have examined, at least three are trigon types (Randolph Co., 27 July 1980; Menard Co., 21 August 1995; Alexander Co., 28 August 2007). Although these specimens were not collected in 2010, they nonetheless pupated during periods when especially severe heat events affected their pupation sites (e.g. the Chicago heat wave of

1995). In addition, the trigon type depicted in Ehle (1981 Fig. 1.2) was also collected during the heat wave year of 1980.

Interestingly, the wild-caught partly trigon-type male figured in Scriber and Evans (1987 Fig. 6a–b) was collected on 10 August 1983, and the previous one-month period (at some point during which it would have pupated) was the hottest mid-July to mid-August period in Dane Co., Wisconsin since 1955 (mean = 24.1°C, mean high = 30.6°C). The male depicted in Shull (1987), which was collected on 21 August 1984, pupated under similar temperatures (mean = 24.1°C, mean high = 29.2°C). If these males did in fact inherit translocated melanizing genes, then the expression of these genes might have been susceptible to the effects of heightened temperatures, as they appear to be in certain dark females.

Finally, the non-trigon-type intermediate females I observed in 2010 (e.g. Fig. 1c) tended to be lighter than the ones I had observed in the previous eight and subsequent two years, again suggesting that elevated temperatures have an increased demelanizing effect in dark female *P. glaucus*.

My findings not only lend support to Ritland’s hypothesis that high temperatures can produce incompletely melanized dark female *P. glaucus*, but also suggest that temperature is an influencing factor not only in the laboratory but also in nature. (In addition, my findings suggest that inbreeding, which occurred in Ritland’s studies, probably does not contribute to the production of the trigon form in nature, since inbreeding is unlikely to occur in the highly mobile naturally occurring *P. glaucus* population.)

The pathways that lead to the production of the yellow and black scales that dominate the *glaucus* color pattern are relatively well understood (Koch et al. 1998; Koch et al. 2000a,b; ffrench-Constant & Koch 2003), and this understanding suggests how intermediate phenotypes, including the trigon phenotype, can occur. In particular, during the wing pigmentation process, each wing cell appears to behave autonomously, having a unique threshold of responsiveness to the signal to initiate melanin synthesis; above this threshold, the cell will undergo papiliochrome synthesis and become pigmented yellow, while below this threshold, the cell will undergo melanin synthesis and become pigmented black (ffrench-Constant & Koch 2003). Ritland’s (1986) findings strongly suggest that at higher levels, temperature can affect this threshold, causing biochemical changes (see ffrench-Constant & Koch 2003 for details) that lead to papiliochrome synthesis in cells that would normally undergo melanin synthesis and resulting in atypical mixtures of yellow and black scales.

In addition, the incompletely melanized dark females illustrated in Ritland (1986 Fig. 1) suggest that in dark females there is a positive relationship between the distance that a “background” (i.e. non-stripe, non-margin) wing scale lies from the body and the likelihood that the scale will fail to melanize. Scales in the more distal areas of the wing appear to fail to melanize more frequently than those in the more proximal areas, suggesting that in dark females, the more proximal the scale is, the more resistant to papiliochrome synthesis it is. This would explain why “dusted” forms are more common than trigon forms, since the conditions required to produce the heightened demelanization seen in the latter are more extreme (i.e. less common) than those required to produce the lessened demelanization seen in the former. In addition, this would explain why “reverse” trigon patterns (i.e. yellow basally and black distally) are not observed in dark female *P. glaucus*.

Otherwise, the fact that Ritland did not produce a totally yellow-appearing dark female suggests that in dark female *P. glaucus*, the trigon (i.e. least melanized) pattern may represent the upper limit of temperature-sensitive demelanization. Of course, if completely demelanized dark females can and do exist in nature, then some seemingly “yellow” females are in fact dark females “in disguise” and go unrecognized for what they really are.

In Vigo Co., the 2011 July–August mean and mean high temperatures were comparable to those for 2010 (mean = 25.0°C, SD = 3.0°C; mean high = 31.5°C, SD = 2.6°C), while the 2012 July–August mean and mean high temperatures were higher than those for the previous two years (mean = 26.4°C, SD = 3.7°C; mean high = 34.2°C, SD = 3.9°C). Even so, I did not observe trigon-type female *P. glaucus* during the summers of 2011 and 2012. The apparent lack of trigon types during these two years, however, may be the result less of environmental factors than of sampling deficiencies. The number of *P. glaucus* present at the Refuge before mid-July is too low to permit adequate sampling before this time, which means that almost all of the individuals in my Refuge samples (>99%) are observed after mid-July. Unfortunately, changes in the schedule and pattern of mowing activity at the Refuge in 2011 and 2012, which destroyed the majority of larval and imaginal hosts by mid-July, virtually eliminated the *P. glaucus* population there and made adequate sampling impossible for those two years. In addition, the *Bug Guide* samples of female *P. glaucus* for 2011 and 2012 were comparatively small (9 and 6, respectively), providing limited examples. Even so, the facts that I had not observed a trigon type before 2010 among the

thousands of female *P. glaucus* that I had previously encountered in the Vigo Co. area and that the trigon types posted on *Bug Guide* clustered in 2010 suggest that in 2010, conditions favored the production of the trigon phenotype.

If the idea proposed here that elevated temperatures were responsible for the increase in the occurrence of trigon-type female *P. glaucus* in 2010 is correct, then this raises the interesting possibility that if record high temperatures continue to prevail throughout *P. glaucus*'s range during pupal development times, genetically dark female *P. glaucus* expressing the trigon (and other demelanized) color patterns could become more prevalent. If so, such an increase in incompletely melanized forms could potentially alter the dynamics of dark female *P. glaucus*'s mimetic relationship with *Battus philenor* in the most impacted populations.

ACKNOWLEDGEMENTS

I would like to thank Mark Scriber of Michigan State University for clarifying issues related to male “trigon”-type *P. glaucus* and informing me of French-Constant and Koch's (2003) synthesis of findings related to the wing pigmentation process in *P. glaucus*. In addition, I would like to thank both Mark Scriber and David Ritland of Erskine College for their critical reviews of earlier drafts of this paper and their helpful suggestions for improvement of the final version. Finally, I would like to thank Jim Wiker for sharing his data regarding variant *P. glaucus* in Illinois.

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THE LEPIDOPTERA OF WHITE SANDS NATIONAL MONUMENT 6: A NEW SPECIES OF
CHIONODES HÜBNER, [1825] (LEPIDOPTERA, GELECHIIDAE, GELECHIINAE)
DEDICATED TO RONALD W. HODGES AND ELAINE R. SNYDER HODGES
IN THE YEAR OF RON'S 80TH BIRTHDAY, 2014.

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ABSTRACT. A new species of *Chionodes* Hübner, [1825] (Lepidoptera, Gelechiidae, Gelechiinae), *C. hodgesorum*, is described from White Sands National Monument, Otero County, New Mexico. Ron and Elaine Hodges were special mentors in my study of Lepidoptera. Thus this description to honor Ron and Elaine is published in the year of Ronald W. Hodges' 80th birthday, 2014. Images of the imago and male and female genitalia are included, and a map of New Mexico showing the type-locality is provided.

Additional key words: biological diversity, endemism

DEDICATION

As a young student studying Noctuidae at Michigan State University I often encountered specimens collected by Ron Hodges. Eventually, on a trip to the U.S. National Museum in Washington, DC, I had the good fortune to meet him. On that first visit, Ron and his wife Elaine took me, an unknown person, to lunch in the Castle of the Smithsonian Institution. Ron spent several hours, on that visit and in many additional visits, tutoring me about the fine arts of studying smaller moths. Thanks to Ron I now work in all families of Lepidoptera, including the ones I pretended not to exist when I was a student. This paper, my fourth paper (Adamski & Metzler 2000; Metzler & Adamski 2002; Metzler & Lightfoot in press) describing species of the Gelechioidea, is testament to Ron's influence on me.

Elaine, an artist with extra ordinary skills, also tutored me by allowing me to watch over her shoulder for hours while she produced the most exquisite illustrations. She never hesitated to teach while she was working. Elaine passed in 2006—my friendship with Ron continues.

Ron and Elaine both served on the Executive Council of The Lepidopterists' Society. Both are the kind of people I hope we all desire to be.

Hodges (1999) revised the species of *Chionodes* Hübner, [1825] in America north of Mexico. As evidence of the poorly known status of the genus, 115 species (62%) of the 187 species treated were new to science. The distributions of many species appear to be highly disjunct. Additional collecting of small moths should fill in some gaps as well as disclosing undescribed species. Hodges (1999) specifically mentioned the need for more collecting in southern New Mexico.

Prior to 2006 when White Sands National Monument invited me to conduct a ten-year study of moths at the Monument, almost nothing was known about the insect fauna of the white gypsum dunes ecosystem in the Tularosa Basin (Schneider-Hector 1993) in southern New Mexico, USA. During the first six years of the study, 2007 through 2013, a new species of *Chionodes* was collected and is described herein.

MATERIALS AND METHODS

Moths and other night flying insects were collected in U.S.D.A. type black-light traps, as described in Smith et al. (1974), in diverse habitats in White Sands National Monument. A detailed description of the study methods is in Metzler et al. (2009).

Specimens of moths were retained for further study. The specimens were sorted and identified. Of them selected specimens were spread and labeled. All non-lepidopteran insects (by-catch) from the traps were placed in 95% EtOH and deposited in the Museum of Southwestern Biology at the University of New Mexico, Albuquerque, New Mexico.

Genitalia of selected moth specimens were examined following procedures outlined in Clarke (1941), Hardwick (1950), Lafontaine (2004), and Pogue (2002). Abdomens were removed from the moths, placed in 95% EtOH for a short time, and soaked in 10% KOH for about 30 minutes at 50°C. Genitalia were dissected in water, stained with Chlorazol Black in water and Safranin O in absolute EtOH, dehydrated in 99.9% propanol under glass chips, and slide mounted in Euparal.

Terminology for elements of wing pattern, morphology, and genital structures follows Hodges (1999) and Scoble (1995). Terminology for color comes from wing markings and regions of the wing follows Mikkola et al. (2009). Forewing lengths were measured to the nearest 0.1mm, from the base to the apex excluding fringe, using an ocular micrometer in the



FIGS. 1–4. *Chionodes hodgesorum* adults; 1. male holotype (Genitalia on slide USNM 144565); 2. female paratype; 3. male paratype; 4. female paratype.

eyepiece of a Wild™ model M5 stereo-microscope at magnification of 6x.

Photographs of adults were taken with a Nikon® model D200 camera with bellows and Micro-NIKKOR™ 105mm 1:2.8 macro lense. Illumination was provided by an Aristo DA-10 lightbox manufactured by Aristogrid™. Photographs of the mounted male and female genitalia were taken with a Nikon™ model D200 camera mounted on the photo tube of a Zeiss™ Lumipan Universal Research Microscope using a Leitz™ 1x plan objective and bright field transmitted light. Photographs were processed with Microsoft Windows™ versions of Zerene Stacker™ and Adobe Photoshop CS6™ software.

The coordinates for latitude and longitude on the labels of the specimens from the studies are in degrees and decimal minutes. Specimens of Lepidoptera cited in this paper are deposited in the following collections:

- EHM Eric H. Metzler, Alamogordo, NM, for subsequent transfer to MSUC.
- MSUC Albert J. Cook Arthropod Research Collection, Department of Entomology, Michigan State University, East Lansing, MI
- UNM Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM
- USNM U. S. National Museum of Natural History (Smithsonian Institution), Washington, DC

RESULTS

Chionodes hodgesorum Metzler, new species (Figs 1–10)

Diagnosis. *Chionodes hodgesorum* is a black and yellow moth with pale-gray reflective hindwings. Of similar species of *Chionodes* in the *sistrella*-complex, *C. hodgesorum* and *C. oecus* Hodges, 1999 occur sympatrically at White Sands National Monument. *Chionodes hodgesorum* is noticeably larger (forewing length = 1.5 x the forewing length of *C. oecus*). The

similar *Chionodes xanthophilella* (Barnes & Busck, 1920), not recorded from White Sands National Monument, is the same size as *C. oecus*. In addition to *C. hodgesorum*'s larger size, structures of the male genitalia can readily separate *C. hodgesorum* from its congeners. The basal portions of the valvae of *C. hodgesorum* are straight with the apices bent mesally; the basal portions of the valvae of *C. oecus* are strongly C shaped, and the valvae of *C. xanthophilella* are broadly curved laterally with the apices directed mesally.

Description. Adult male (Figs. 1, 3). *Head*: Front, clypeus, and vertex pale yellow, scales appressed to surface. Labial palpi directed slightly laterally from base, upcurved to center of front; first segment brown, second segment basal one-third brown, distal two-thirds pale yellow, ventral surface shaggy, dorsal and lateral surfaces with scales appressed, third segment apically pointed, pale yellow, scattered brown scales near apex. Haustellum scaled, pale yellow. Antenna scaled, dorsal surface dark brown black, ventral surface of each segment alternating dark black brown and paler brown. *Thorax*: Dorsum pale yellow, tegulae and patagia dark brown black, scales appressed; underside pale yellow, scales appressed. Foreleg with dorsal surface pale yellow, ventral surface dark brown scales appressed, apex of tibia and each tarsomere pale yellow. Midleg dorsally pale yellow, ventrally dark brown, scales appressed laterally and ventrally, shaggy fringe dorsally; tarsomeres pale yellow, ringed with dark brown basally, scattered setae on ventral surface. Hindleg pale yellow mesally and ventrally, scales appressed, dirty yellow dorsally, shaggy, alternating brown and pale yellow laterally, scales appressed, tarsomeres dorsally, ventrally, and mesally pale yellow, laterally alternating pale yellow and dark brown, scattered setae on ventral surface. Forewing: Length 8.1–8.7 mm (mean 8.5 mm, n = 5). Costal half black to 2/3 length, a more or less complete pale-yellow fascia at 2/3 length, costal scales from fascia to apex fuscous, subcostal scales from fascia to apex black with scattered yellow scales. Black costal region with 2 or 3 subcostal vague pale-yellow spots. Posterior half yellow, with 1 or 2 shallow semicircular yellow markings intersecting the black region at or near antemedial line (not always present), postmedial line, and the fascia at 2/3 wing length. Basal streak black, narrow, inconspicuous, extending apically to yellow fascia, interrupted by yellow semicircular markings. Terminal line comprised of scattered black scales, apex mostly black intermixed with pale-yellow scales; fringe pale fuscous. Underside fuscous gray, costa at base edged with black, fading to dark fuscous apically, sub apical 1/5 pale yellow, posterior margin narrowly lined with pale yellow, outer margin at tornus lined with pale yellow; fringe gray fuscous. Hindwing reflective gray-fuscous, veins overlaid with fuscous scales, costa pale-

gray overlaid with fuscous scales, apex with small patch of pale-yellow scales, fringe gray-fuscous. *Abdomen*: Dorsum segments 1 through 3 moderate to grayish-yellow, then pale-yellow to distal end; underside pale-yellowish gray, intermixed with fuscous scales. Genitalia (Figs. 5, 6): uncus broadly rounded, spoon-shaped, setae on the ventrolateral margin; culcitula absent; gnathos base sclerotized, lobed laterally asymmetrical, lobes may be bifurcate; gnathos sharply curved at .2x length, shallowly curved to subapical region, sharply curved apically, 2 or 3 minute scobinations on inside of subapical surface, apex bluntly pointed; tegumen elongate, broadly A shaped, slightly narrowed apically, each arm gradually narrowing to junction with vinculum; vinculum = 1.1x length of tegumen, abruptly narrowed anteriorly from junction with tegumen extended anteriorly, and elongated (vinculum + saccus) with a blunt apex; posterolateral lobe of vinculum membranous, sclerotized basally, sparse setae; saccus not differentiated from vinculum; valvae slightly asymmetrical, both nearly parallel to tegumen, slightly sinuous, shallowly curved outwardly along basal 1/3, shallowly curved mesally along apical 1/6, with shallow sculpting along a sharply pointed apex. Aedeagus with distal part sculpting complex, several narrow longitudinal fin-like structures; caecum = slightly more than 2x length of distal part.

Adult female (Figs. 2, 4). Appearance similar to male. Forewing length 7.8–8.9 mm, (mean 8.5 mm, $n = 9$). Frenulum acanthae multiple. Genitalia (Fig. 7): Ovipositor telescopic; papillae anales membranous, sparsely setose, with most setae clustered apically; apophyses posteriors extending anteriorly to between 8th and 9th segments; 9th abdominal ventrolateral margins extended to form anterior apophyses; anterior apophyses extending anteriorly to base of antrum; antrum sclerotized laterally with narrow longitudinal folds; ductus bursae membranous, short, slightly bulbous; corpus bursae ovoid; signum an inward excavation with broad marginal dentitions.

Holotype. Adult male, pinned with labels as follows: "USA: NM: Otero Co. White Sands Nat[ional] Mon[ument], edge of dunes habitat, 106°11.32'W, 32°45.72'N 4,000', 14 Sept. 2009 wsnm9, Eric H. Metzler uv tr[a]p, Access # WSHA 00131" "HOLOTYPE USNM *Chionodes hodgesorum* Metzler" [red handwritten label] "U.S.N.M ♂ 144,565 E.H. Metzler Holotype [green handwritten label]. (USNM).

Paratypes. 4 ♂, 12 ♀: all are "USA: NM: Otero Co. White Sands Nat Mon, Access # WSHA 00131" details as follows: edge of dunes habitat, 32°45.724'N, 106°11.315'W, 4,000', 10 June 2013, WSHA9, Eric H. Metzler uv trp, 1 ♂, 5 ♀; edge of dunes habitat, 106°11.32'W, 32°45.72'N, 4,000', 14 Sept. 2009, wsnm9, Eric H. Metzler uv trp, [slide E.H.M. 515] 1 ♂; interdune vegetation, 106°11.59'W, 32°45.57'N 4,006', 21 Aug 2007, WSNM2, Eric H. Metzler uv trp, slides USNM 144566 & E.H.M. 517] 2 ♀; interdune vegetation, 106°11.38'W, 32°46.69'N 4,000', 17 May 2010, WSNM8, Eric H. Metzler uv trp, 1 ♀; edge of dunes, 11–12 June 2007, 32°45.704'N 106°11.240'W, 4,001 ft. Coll. E.H. Metzler & D. Adamski, Blacklight, 2 ♂, 1 ♀; edge of dunes habitat, 106°11.32'W, 32°45.72'N, 4,000', 5 Sept. 2013, WSNM9, Eric H. Metzler uv trp, 2 ♀; interdune vegetation, 106°10.84'W 32°46.64'N 4,000', 5 Sept. 2013, WSNMF, Eric H. Metzler uv trp, 1 ♀ (EHM, MSUC, UNM, USNM).

Systematics. This new species is placed in the genus *Chionodes* Hübner based on the presence of the caecum on the aedeagus (Hodges 1999).

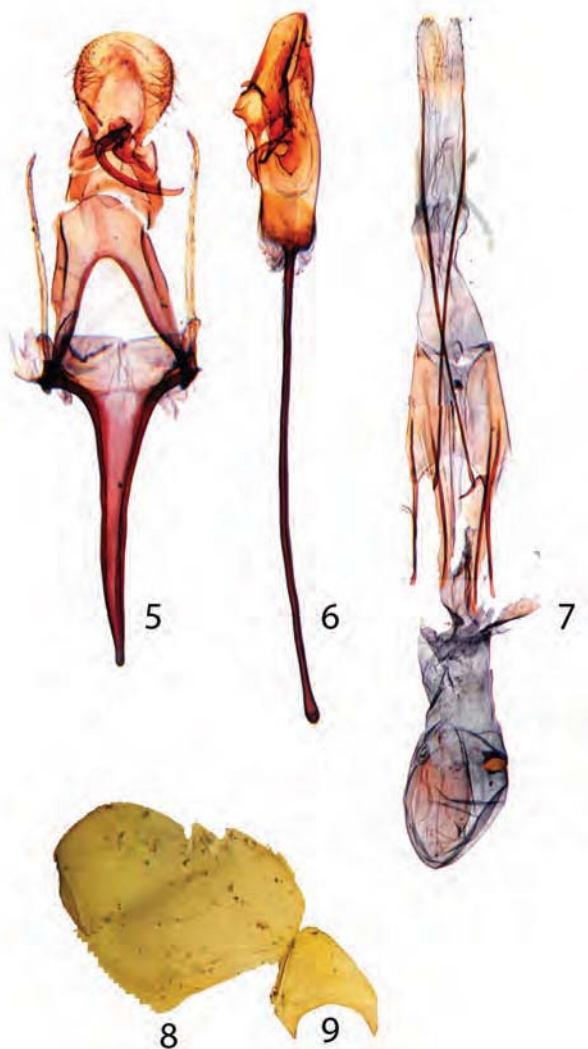
Etymology. The specific name of this species, *hodgesorum*, honors Ronald W. Hodges and his late wife, Elaine R. Snyder Hodges, both of whom are my mentors and personal friends. Both contributed significantly to my study of Lepidoptera.

Distribution. *Chionodes hodgesorum* occurs in the gypsum dunes at White Sands National Monument.

Phenology. Emergences of fresh specimens in the early summer and autumn suggest two broods. Other details of its life history are unknown.

DISCUSSION

Hodges (1999) cautioned that "All species in the *sistrella*-complex" which includes *C. hodgesorum* "are variable to highly variable in coloration, maculation, and genital characters," and in personal conversations, when Hodges was preparing the revision of *Chionodes*, he told me this group of moths can be extremely difficult. Fortunately, for users of Hodges' (1999) revision, he qualified the variability and provided detailed diagnoses,



FIGS. 5–9. *Chionodes hodgesorum* genitalia and male seventh abdominal segment (on slide USNM 144565); 5. male genitalia Holotype (on slide USNM 144565); 6. male aedeagus Holotype (on slide USNM 144565); 7. female genitalia paratype (on slide USNM 144566); 8. male seventh abdominal segment tergum Holotype (on slide USNM 144565); 9. Male seventh abdominal segment sternum Holotype (on slide USNM 144565).



FIG. 10. *Chionodes hedgesorum* distribution map. *Chionodes hedgesorum* is known only from White Sands National Monument, Otero Co., New Mexico.

key characters, and descriptions which allowed me to focus on the features of each species which either included it or excluded it from consideration as I distinguished *C. hedgesorum*. When I sent photographs of the adult and genital preparations to Ron Hodges, he agreed with my diagnosis. One male specimen of *C. hedgesorum* has a hint of orange in the yellow area of the forewing.

In 2006, the U.S. National Park Service invited me to initiate a ten-year study of the moths at White Sands National Monument, Otero County, NM. A primary purpose of the study was to compile an inventory of moths in various habitats within the Monument, and to describe new species discovered during the study. Descriptions of species from the Monument are important because the names facilitate cataloging, protecting, and communicating information about their significance.

More than 600 species of moths (unpublished data), including ca. 30 species new to science (unpublished data), were recorded in the first six years of the study from black-light traps along a 2.4 km transect in the southeastern corner of the dunes of the Monument. Most of the new species from the Monument are apparently endemic to the white dunes, and several are

white species (Kain 2000). The number of endemic species of moths to White Sands National Monument compared to all of North America is the highest for a single location. These numbers seem more impressive in consideration of the small study area and the short time of the study to date.

The diagnosis of the genus *Chionodes* and identification of its many species rely heavily on genital characters. The species described here is an excellent example of a species, which requires dissection for positive identification. I dissected 2 males and 2 females. They were remarkably consistent in structure.

The dearth of collections of smaller moths in southern New Mexico (Hodges 1999) means it is not possible to conclude that *C. hedgesorum* is endemic to White Sands National Monument. Nonetheless, the high rate of endemism, ca. 5%, of the number of recorded species of moths at White Sands National Monument, and the failure to detect this species until now, suggests that this species may be endemic to the white gypsum dunes.

This is the 8th in a series of papers to document the Lepidoptera at White Sands National Monument (Metzler et al. 2009, 2010a, 2010b, in press; Metzler & Forbes 2011a, 2011b, 2011c, 2012; Metzler & Lightfoot in press), and the 7th species of Lepidoptera described as new to science from the study.

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REVIEW OF THE *EUCOSMA REFUSANA* (WALKER) SPECIES GROUP (TORTRICIDAE), WITH
DESCRIPTIONS OF TWO NEW SPECIES AND DISCUSSION OF BIOGEOGRAPHIC INFLUENCES
ON SPECIES DISTRIBUTION

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ABSTRACT. Eight closely related species of *Eucosma* Hübner are reviewed: *E. refusana* (Walker), *E. decempunctana* (Walsingham), *E. amphorana* (Walsingham), *E. annetteana* (Kearfott), *E. autumnana* (McDunnough), *E. citricolorana* (McDunnough), *E. scotiana* (McDunnough), and *E. verna* Miller. *Eucosma scotiana* is recognized as a junior synonym of *E. annetteana*, and two new members of the group, *Eucosma litorea* sp. n. and *Eucosma millerana* sp. n., are described. Distributional patterns and biogeographic relationships for members of the group are discussed.

Additional key words: Olethreutinae, Eucosmini, coastal sand dunes, inland riverine dunes, prairie remnants

The *refusana* group consists of eight recognized Nearctic *Eucosma* Hübner and two new species, *E. litorea* and *E. millerana*, described below. Three of these species, *E. autumnana* (McDunnough 1942), *E. verna* (Miller 1971), and *E. amphorana* (Walsingham 1879) are well represented in collections, the first two being widely distributed in eastern North America, the last occurring from Washington to southern California. The group namesake, *E. refusana* (Walker 1863), was misidentified by North American taxonomists for nearly a century. Prior to 1971 it was confused with *E. verna*, and for some years thereafter it was presumed to be known only from the holotype. The rest of the group consists of *E. annetteana* (Kearfott 1907) and *E. scotiana* (McDunnough 1958), two poorly understood species from eastern North America, and *E. decempunctana* (Walsingham 1879) and *E. citricolorana* (McDunnough 1942), little known species from Oregon and Saskatchewan, respectively. This review proposes names for the two new species and provides refined interpretations of the previously recognized taxa based on examination of the primary types, comparison of male and female genitalia, and updated distributional data from material accumulated during the past several decades. *Eucosma scotiana* is treated as a junior synonym of *E. annetteana*.

Until recently, the previously described species considered here were placed in *Phaneta* Stephens due to the absence of a costal fold on the male forewing, but the phylogenetic analysis by Gilligan et al. (2013) concluded that these as well as nearly all other Nearctic *Phaneta* belong in *Eucosma*. The generic assignments of

other Eucosmini mentioned here follow Gilligan and Wright (2013).

MATERIALS AND METHODS

We examined 422 adult specimens and 113 genitalia preparations from the following institutional and private collections: American Museum of Natural History, New York (AMNH); George J. Balogh, Portage, Michigan (GJB); C. D. Bird, Erskine, Alberta (CDB); Canadian National Collection, Ottawa, Ontario (CNC); Robert P. Dana, Minneapolis, Minnesota (RPD); Essig Museum of Entomology, UC Berkeley (EME); Florida State Collection of Arthropods, McGuire Center for Lepidoptera and Biodiversity, Gainesville, Florida (FSCA); Loran D. Gibson, Florence, Kentucky (LDG); Mississippi Entomological Museum, Mississippi State University (MEM); Museum of Comparative Zoology, Harvard University (MCZ); Canadian Forest Service, Edmonton, Alberta (CFS-E); The Natural History Museum, London (BMNH); J. S. Nordin, Laramie, Wyoming (JSN); G. R. Pohl, Sherwood Park, Alberta (GRP); Strickland Museum, University of Alberta, Edmonton (UASM); United States National Museum of Natural History (USNM); Donald J. Wright (DJW).

Adults and genitalia were examined with a Leica MZ9s stereomicroscope equipped with an ocular micrometer. Genitalia were also examined with a Leica DME compound microscope. Morphological terminology follows Gilligan et al. 2008, with costal striae labeled in accordance with the numbering system for the associated strigulae proposed by Brown and Powell (1991) and modified by Baixeras (2002).

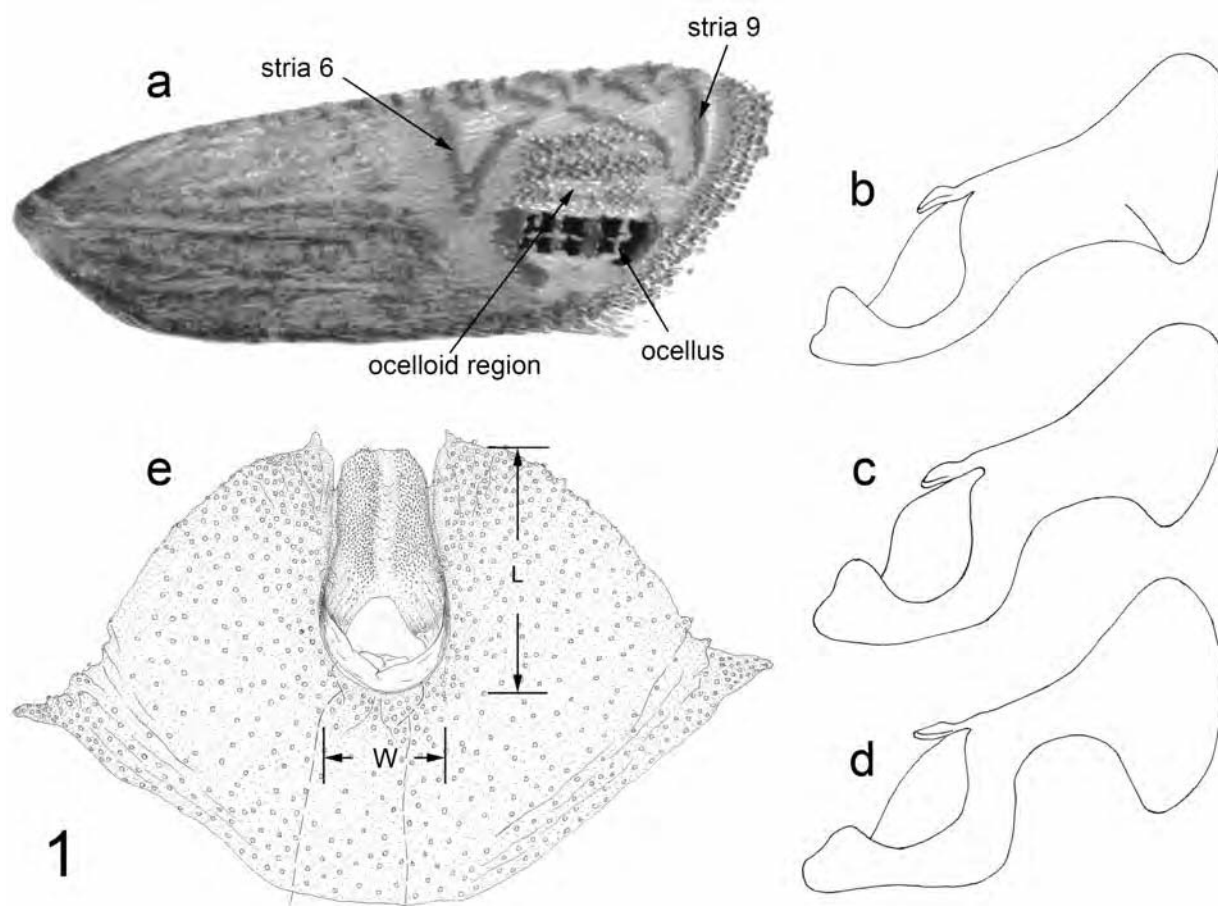


FIG. 1. **1**, *Eucosma refusana* group characters. **a**, forewing pattern, *E. autumnana*. **b–d**, valva shape, *E. amphorana*, *E. verna*, *E. autumnana*. **e**, sterigma-sternum 7, *E. amphorana*.

Forewing length (FWL), the distance from base to apex including fringe, is reported to the nearest tenth of a millimeter. Forewing aspect ratio (AR) is defined as FWL divided by medial forewing width. Conspicuous features of male valva geometry include the saccular angle (SA), the angular projection formed at the junction of the ventral margins of the sacculus and neck, and the neck ratio (NR), defined as neck width divided by basal valva width, the former measurement taken at the narrowest point of the neck, the latter from near the saccular corner to the base of the costa. In females, sterigma aspect ratio (SR) is defined as sterigma length divided by sterigma width at mid-ostium (see Fig. 1e, L/W). The SA, NR, and SR were measured on projected images of the genitalia, the first reported to the nearest degree, the last two as averages of several such calculations rounded to two decimal places. The number of cornuti in the male vesica was determined by counting sockets, the values sometimes being best possible estimates based on condition of the genitalia preparations. Table 1 provides a summary of these data.

The setose portion of the medial surface of the valva located at the distal margin of the basal excavation is referred to here as the basal setal patch (BSP). Adult images and scanned genitalia drawings were edited in Adobe Photoshop CS5.

For the sake of nomenclatorial stability, lectotypes are designated for *E. amphorana*, *E. decempunctana*, and *E. annetteana*, the first two based on unpublished selections by Obraztsov, the last clarifying an ambiguous designation attributed to Heinrich (1923) by Klots (1942).

GROUP CHARACTERS

This section describes the morphological characters that define the *refusana* group. It serves as a core for the species descriptions that follow, allowing each account to focus on exceptions and/or features peculiar to the individual taxon.

Forewing (Fig. 1a): Costa weakly arched to nearly straight; apex acute; termen straight to weakly convex; males without costal fold; dorsal surface divided by

color and/or maculation into a proximal portion (ca. two-thirds) and a distal portion (ca. one-third); proximal portion yellow, gray, brown, or some blend thereof; distal portion with circular ocelloid region extending from tornus nearly to costa; subcostal area anterior to ocelloid region bounded proximally and distally by two lustrous gray striae, numbers 6 and 9, extending from costa to cubitus and M_2 , respectively; anterior margin of ocelloid region edged with lustrous gray arc (usually with one or more interruptions) that converges with the posterior extremities of striae 6 and 9 and bounds a semi-circular region crossed by indistinct dark streaks along R_5 , M_1 , and M_2 ; ocellus consisting of two or three rows of black dots, the rows capped proximally and distally by lustrous gray transverse bars and divided into groups of one to three dots by lustrous gray marks; most species with thin brown line on CuP, moderately expressed from base to mid-wing, fading to an indistinct dark shade near tornus (e.g. Figs. 7, 12, 16, 23, 24); some species with brown median band from mid-costa to inner margin separating proximal and distal portions of forewing (e.g. Figs. 2, 15, 19, 21); termen with band of whitish scales with brown to blackish-brown cross-marks, the cross-marks sometimes arranged in a thin dark line from tornus to apex; outer fringe scales gray brown.

Hindwing: Pale to dark gray brown, often darker along margins; fringe pale.

Male genitalia (Figs. 26–34): Uncus moderately developed, sometimes with distal margin medially indented, usually with medial line of division on ventral surface; tegumen with well-defined dorsolateral shoulders; socii short and finger-like; phallus straight, relatively stout, moderately tapering distally; vesica with cluster of deciduous cornuti; valva (Fig. 1b–d) with costal margin weakly concave to nearly straight, ventral emargination varying from deep and U-shaped

to long and shallow, neck well-defined, saccular corner angular to broadly rounded, SA usually obtuse; cucullus with apex rounded, distal margin convex to straight, anal angle weakly to strongly developed, basoventral margin sometimes extending in ridge-like manner onto medial surface of neck (Fig. 1b), setation of medial surface dense and relatively fine, margins lacking contrastingly stouter setae; BSP usually semi-triangular, weakly raised, and covered with stiff moderately long setae.

Female genitalia (Figs. 35–48): Papillae anales laterally facing and moderately setose; sterigma (Fig. 1e) elongate (SR ca. 1.5–3.1); lamella postvaginalis rectangular to tapering posteriorly; lamella antevaginalis ring-like; posterior margin of sternum 7 invaginated to full length of sterigma and connected with lateral margins of lamella postvaginalis by a band of sclerotized membrane, the width of which is sometimes useful in distinguishing between species; scaling of sternum 7 dense on posterior and lateral extremities, relatively sparse elsewhere; ductus bursae with sclerotized ring posterior to juncture with ductus seminalis; corpus bursae with two signa of nearly equal size.

SPECIES ACCOUNTS

Eucosma decempunctana (Walsingham 1879)
(Figs. 2, 3, 26, 35)

Semasia decempunctana Walsingham 1879:58, pl. 73, fig. 6.

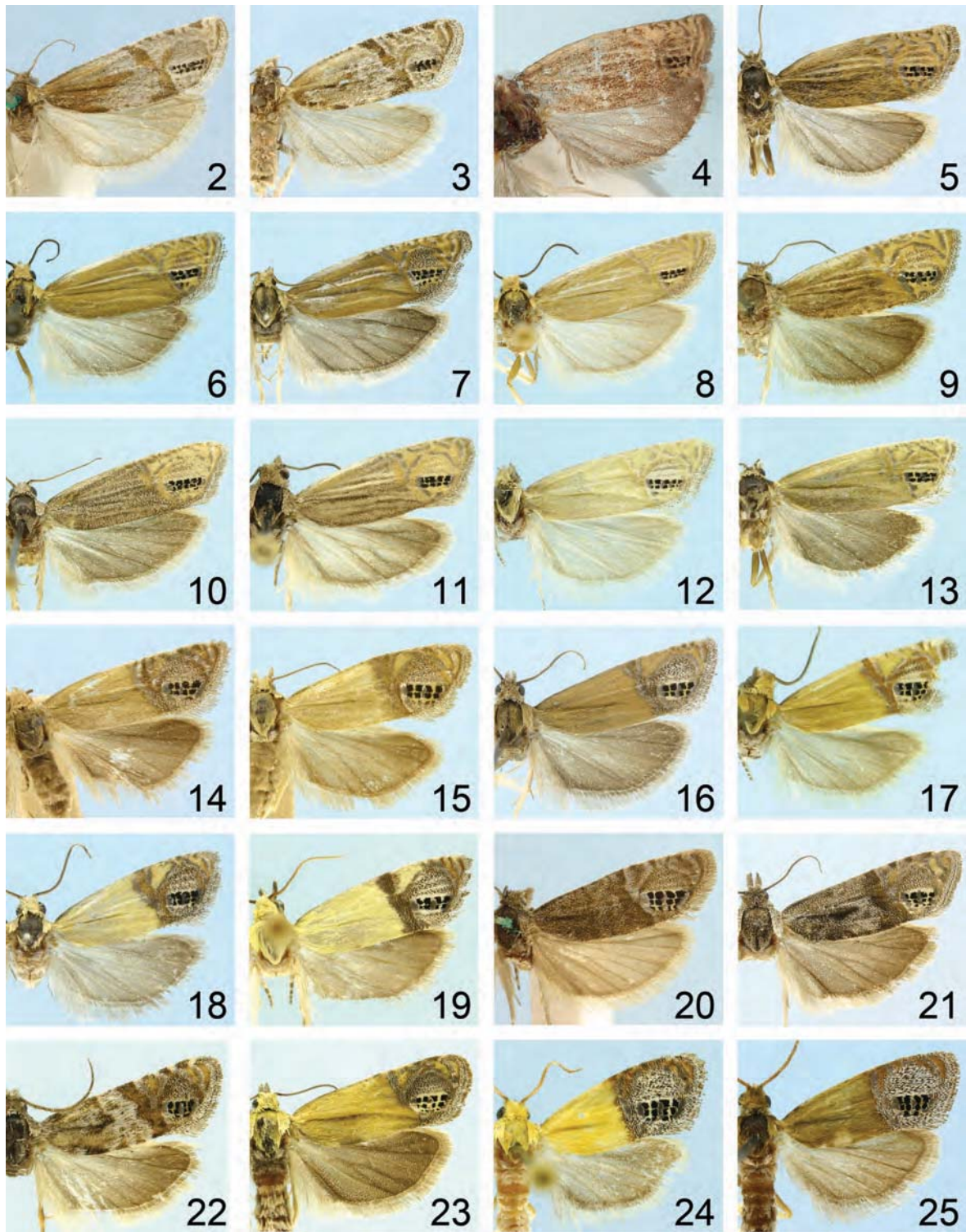
Thiodia decempunctana: Fernald [1903]:462; Heinrich 1923:44, fig. 120; McDunnough 1939:44.

Eucosma decempunctana: Barnes and McDunnough 1917:172.

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

TABLE 1. Comparison of selected characters.

Species	FWL (mm)			AR	cornuti			SA°			NR			SR		
	Range	mean	n		Range	mean	n	Range	mean	n	Range	mean	n	Range	mean	n
<i>decempunctana</i>	6.9-8.4	7.7	7	3.29	20	20	2	98-106	102	3	0.43-0.45	0.44	3		2.20	1
<i>refusana</i>	6.9-8.3	7.7	13	2.89	17-34	25	4	109-136	125	5	0.70-0.81	0.74	5	1.54-1.63	1.59	2
<i>verna</i>	6.9-9.4	7.9	61	3.12	17-50	33	15	102-127	114	15	0.38-0.61	0.48	15	1.73-2.40	2.06	8
<i>autumnana</i>	6.5-9.6	7.7	72	3.08	27-38	33	9	83-95	88	9	0.29-0.38	0.32	9	2.28-2.78	2.48	6
<i>citricolorana</i>	7.3-10.1	9.0	32	3.20	26-41	32	4	90-114	103	4	0.56-0.62	0.59	4	1.52-2.04	1.81	3
<i>annetteana</i>	5.3-8.1	6.6	63	3.00	16-38	30	16	112-137	123	16	0.48-0.69	0.56	16	2.58-3.36	2.80	7
<i>millerana</i>	4.9-6.7	5.8	45	3.04	39-47	42	5	110-129	121	5	0.48-0.65	0.55	5	2.92-3.32	3.12	5
<i>amphorana</i>	7.1-10.1	8.3	30	3.01	22-35	29	5	114-141	131	5	0.65-0.83	0.71	5	1.79-2.04	1.92	2
<i>litorea</i>	5.1-7.7	6.0	22	2.71	21-26	23	3	133-149	143	3	0.62-0.73	0.69	3	1.96-2.28	2.11	3



FIGS. 2-25. 2-3, *E. decempunctana*. 2, lectotype. 3, ♀ Deschutes Co., Oregon. 4-5, *E. refusana*. 4, holotype. 5, ♂, Alberta. 6-8, *E. verna*. 6, ♂ Wyandot Co., Ohio. 7, ♂ Sandoval Co., New Mexico. 8, ♂ Wyandot Co., Ohio. 9-11, *E. autumnana*. 9, holotype. 10, ♂ Billings Co., North Dakota. 11, ♂ Oktibbeha Co., Mississippi. 12-13, *E. citricolorana*. 12, holotype. 13, ♀ Alberta. 14-17, *E. annetteana*. 14, ♂ lectotype. 15, ♀ Hamilton Co., Ohio. 16, ♂ Oktibbeha Co., Mississippi. 17, *E. scotiana* holotype. 18-19, *E. millerana*. 18, holotype. 19, ♂ Oktibbeha Co., Mississippi. 20-23, *E. amphorana*. 20, ♂ lectotype. 21, ♀ Contra Costa Co., California. 22, ♂ Santa Barbara Co., California. 23, ♀ Contra Costa Co., California. 24, *E. litorea* holotype. 25, ♂ near *litorea*, Baldwin Co., Alabama.

Discussion. *Eucosma decempunctana* is distinguished from all other members of the group by forewing appearance (pale gray with rusty-brown markings) (Figs. 2, 3). It might be confused with some gray forms of *E. amphorana* (Figs. 20–22), but males of the two species have quite different genitalia (Figs. 26, 33), and females exhibit subtle differences in sterigma shape (see diagnosis under *E. litorea*).

Lectotype (Fig. 2) here designated: ♂, Oregon, Wasco Co., to Fort Dalles, Walsingham, 15–22 April 1872, slide 11589, BMNH.

Paralectotypes. There are six males in the BMNH with collection data identical to that of the lectotype, all labeled as paratypes by Durrant (K. Tuck, pers. comm.). One has been dissected (slide DJW 3149). Only three of these specimens qualify as paralectotypes since Walsingham mentioned only four syntypes in the description.

Description. *Head.* Frons grayish white; vertex brown with obscure whitish medial streak; labial palpus with medial surface grayish white, lateral surface gray brown with some whitish suffusion on second segment; antenna with dorsal surface brown, posterior surface whitish; scape with ventral surface whitish. *Thorax.* Dorsal surface brown; tegula with pale brown apex; legs with anterior surfaces brown, posterior surfaces whitish; tarsi with whitish annulations. Forewing (Figs. 2, 3): ♂ FWL 7.2–8.4 mm (mean = 7.9, $n = 6$), AR = 3.35; ♀ FWL 6.9 mm ($n = 1$), AR = 2.94; dorsal surface pale gray with irregularly defined rusty-brown basal patch and narrow rusty-brown median band; anterior portion of ocelloid region grayish white, lacking dark streaking along veins; ocellus with two rows of four to six black dots on a white ground; costa with three prominent gray-brown marks delimiting pale gray strigulae between medial band and apex. *Abdomen.* Male genitalia (Fig. 26) ($n = 3$): Vesica with 20 cornuti ($n = 2$); valva with costal margin concave, ventral emargination moderate, NR = 0.44, mean SA = 102° , anal angle moderately developed. Female genitalia (Fig. 35) ($n = 1$): Typical of the group, with SR = 2.20.

Distribution and flight period. We examined the lectotype, two syntypes, and four additional specimens (3 ♂, 1 ♀). Of the last four, one (in the AMNH) is labeled “CAL”, two (in the USNM) lack data, and the female (in the USNM) was collected in April in Deschutes County, Oregon.

The *refusana-verna-autumnana-citricolorana* subgroup. The four species in this subgroup are sufficiently similar in size, color, and maculation to render determination based on forewing appearance unreliable (Figs. 4–13), but they are readily separated by the shape of the male valva (Figs. 27–30). *Eucosma citricolorana* is unique among the four in having a bluntly pointed anal angle (Fig. 30); the others differ from one another in the depth of the ventral emargination of the neck, with NR = 0.74, 0.48, and 0.32, respectively. Females of the four species exhibit subtle differences in the shapes of the sterigma and sternum 7 and in the development of the sclerotized band connecting those structures (Figs. 43–46). The mean SR values are 1.59, 2.06, 2.48, and 1.81 respectively, but there is considerable overlap in some

value ranges, particularly for *E. autumnana* and *E. verna* and for *E. refusana* and *E. citricolorana* (Table 1).

McDunnough (1942) distinguished *E. autumnana* from what he considered to be *E. refusana* (likely *E. verna*) by flight period (autumn vs. spring), and Miller (1971) agreed as regards *E. autumnana* and *E. verna*. The 71 specimens we examined of *E. verna* were captured between 9 March (Mississippi) and 7 July (Wyoming). Of the 91 specimens we examined of *E. autumnana*, those from the northern part of the range were collected from late August to early October, but the Mississippi specimens were collected only in March and April.

Eucosma refusana (Walker 1863)
(Figs. 4, 5, 27, 36, 43)

Grapholita refusana Walker 1863:382.

Semasia refusana: Walsingham 1879:63, pl. 74, fig. 10.

Thiodia refusana: Fernald [1903]: 463.

Eucosma refusana: Barnes and McDunnough 1917:172.

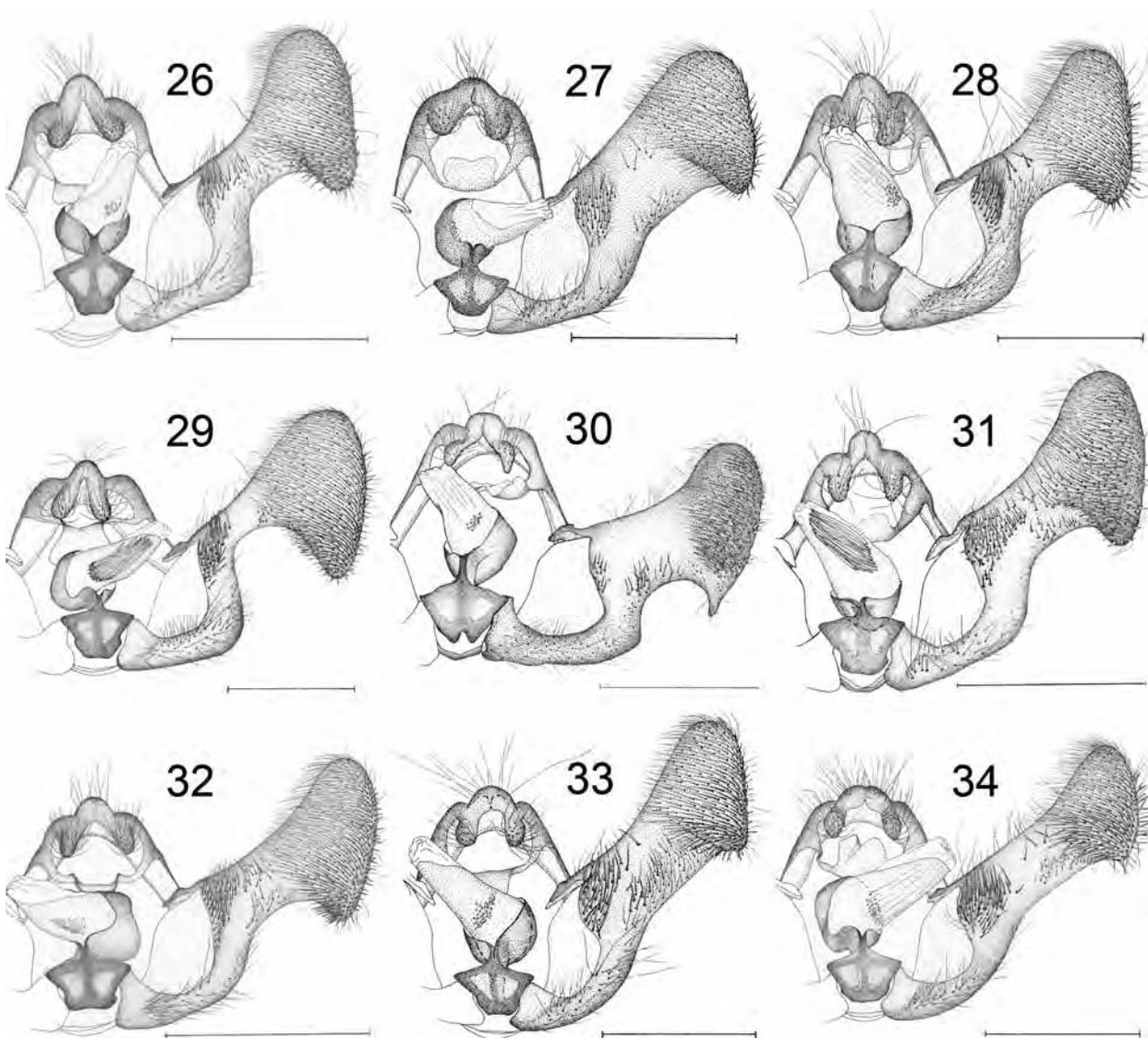
Phaneta refusana: Miller 1971:284; Powell 1983:33; Brown 2005:495; Pohl et al. 2010.

Discussion. This species was described from a single male by Walker (1863) and then redescribed and illustrated by Walsingham (1879). Heinrich (1923) confused *E. refusana* with the species later described by Miller (1971) as *E. verna*, illustrating under the former name the male genitalia of the latter species. Consequently, literature records of *E. refusana* prior to 1971 must be viewed as unreliable. Miller (1971) examined the holotype at the BMNH and, finding no other correctly identified specimens, suggested that this might be a rare boreal species. In fact, *E. refusana* has been known from Alberta for quite some time. The first specimens, now in the UASM, were collected by K. Bowman at Edmonton in 1924. During the last decade it was found at several Alberta localities by G. Pohl, A. Ngui, and C. Bird, and in 1999 it was collected by M. Sabourin in the vicinity of Minneapolis, Minnesota.

Eucosma refusana differs from other members of the subgroup in the relatively shallow ventral emargination of the valval neck (Fig. 27) and in the broad band of sclerotization separating the sterigma from sternum 7 (Fig. 43).

Holotype (Fig. 4). ♂, Canada, [Ontario], St. Martin's Falls, Albany River, Hudson Bay, G. Barnston, 1844–17, slide 4891, BMNH.

Description. *Head.* Frons and vertex creamy white with pale



FIGS. 26–34. Male genitalia. **26**, *E. decempunctana*, slide DJW 3149. **27**, *E. refusana*, slide DJW 625. **28**, *E. verna*, slide DJW 2679. **29**, *E. autumnana*, slide DJW 1091. **30**, *E. citricolorana*, slide DJW 1560. **31**, *E. annetteana*, slide DJW 1447. **32**, *E. millerana* holotype, slide DJW 3215. **33**, *E. amphorana*, slide DJW 2922. **34**, *E. litorea*, slide DJW 1563. Scale bar = 0.5 mm.

brown tints; labial palpus creamy white with pale brown shading at distal end of second segment and on lateral surface of third segment; antenna concolorous with vertex. *Thorax*. Dorsal surface pale brown; fore- and mid-legs with anterior surfaces pale brown, posterior surfaces whitish; hind-legs whitish; tarsi with weakly contrasting pale annulations. Forewing (Figs. 4, 5): ♂ FWL 7.1–8.3 mm (mean = 7.8, $n = 10$), AR = 2.92; ♀ FWL 6.9–8.1 mm (mean = 7.5, $n = 3$), AR = 2.78; proximal portion of dorsal surface brown, variably suffused with brownish yellow, with whitish subcostal streak from base to mid-costa and two or three obscure longitudinal whitish lines in cell; median band absent; anterior portion of ocelloid region with brownish streaking along veins; ocellus with two rows of black dots on a pale yellow ground. *Abdomen*. Male genitalia ($n = 7$) (Fig. 27): Vesica with 17–34 cornuti; valva with costal margin straight, ventral emargination long and shallow, neck wide and gradually broadening toward cucullus, NR = 0.74, saccular corner broadly rounded, mean SA = 125°, BSP weakly raised; cucullus with anal angle weakly developed,

basoventral margin extending in ridge-like fashion over ventral one-third of medial surface of neck. Female genitalia ($n = 3$) (Figs. 36, 43): Typical of the group; sclerotized band joining lamella postvaginalis and sternum 7 relatively broad compared to other members of the subgroup; sterigma relatively short (SR = 1.59 vs. > 1.80).

Material examined. ALBERTA: Edmonton, K. Bowman, 10 May 1924 (1 ♂, genitalia on pin; 1 ♀), 15 May 1934 (1 ♂), UASM; Red Deer, K. Bowman, 16 June 1927 (1 ♂), UASM; Strathcona County, N. Cooking L. Natural Area, vic. Wye Rd. and Rge. Rd. 211, 53.4804° N, 112.9913° W, G. R. Pohl, 15 May 2006 (1 ♀, slide DJW 3265), GRP; 8 km SE Sherwood Park, 53.4779° N, 113.2291° W, G. R. Pohl, 5 May 2006 (♂, slide DJW 3264), GRP; 14 km W. Edmonton, Wagner Fen Natural Area, A. Ngui (1 ♂, genitalia on pin), CFS-E; Big Knife Provincial Park, 52.494° N, 112.222° W, 675 m, C. D. Bird, 14 May 2003 (1 ♂), CDB; 8 km NW Winfield, 53.01° N, 114.50° W, 900 m, 14 May 2005, C. D. Bird (1 ♂), CDB. MANITOBA: Cartwright, E. F.

Heath (1 ♂, slide 124082), USNM; SASKATCHEWAN: Oxbow, F. Kaub, 28 May 1907 (1 ♂, slide 69964), USNM; MINNESOTA: Anoka County, Carlos Avery Wildlife Management Area, M. Sabourin, 1 May 1999 (1 ♂, slide DJW 625; 1 ♀, slide DJW 627), DJW.

Distribution and flight period. The 13 specimens (10 ♂, 3 ♀) we examined, together with the holotype, indicate a range for *E. refusana* that includes Alberta, Manitoba, Ontario, Saskatchewan, and Minnesota, the adults flying in May and June.

Eucosma verna (Miller 1971)

(Figs. 1c, 6–8, 28, 37, 44)

Phaneta verna Miller 1971:286; Powell 1983:33; Miller 1987:43; Brown 2005:497; Gilligan et al. 2008:94.

Thiodia refusana: Heinrich (not Walker 1863) 1923:43, fig. 119; McDunnough 1939:44.

Discussion. *Eucosma verna* most closely resembles *E. autumnana* (Figs. 6, 7 vs. 9–11), but pale specimens (Fig. 8) might be confused with *E. citricolorana* (Figs. 12, 13). *Eucosma autumnana* tends to be less uniform in color, particularly in the northern part of its range, the golden-yellow ocelloid region usually contrasting with the brownish proximal portion of the forewing. Most specimens of *E. verna* have a conspicuous white streak along the costa, a feature that is frequently lacking or muted in *E. autumnana*. Flight period separates these two species in the North (spring vs. fall), but in the South they both fly in March. Males are distinguished from those of *E. autumnana* by the moderate vs. deep emargination of the ventral margin of the valval neck (Figs. 28, 29), females are distinguished by the more strongly developed and pointed lateral projections of sternum 7 (Fig. 44, 45).

Holotype. ♂, Manitoba, Aweme, N. Criddle, 21 May 1904, slide 85, AMNH.

Paratypes. Miller (1971) mentioned 17 additional specimens from Colorado, Connecticut, Michigan, New Jersey, Pennsylvania, Ontario, and Nova Scotia but did not refer to any of them as paratypes.

Description. *Head.* Frons whitish; vertex brownish yellow; labial palpus with first segment white, medial surface of second segment white, lateral surface of second segment gray brown, third segment gray brown; antenna brown; ventral surface of scape white. *Thorax.* Dorsal surface yellow brown; fore- and mid-legs with anterior surfaces brown, posterior surfaces whitish; hind-legs whitish; tarsi with pale annulations, those on hind-legs obscure. Forewing (Figs. 6–8): ♂ FWL 7.0–9.0 mm (mean = 7.9, n = 47), AR = 3.14; ♀ FWL 6.9–9.4 mm (mean = 7.8, n = 14), AR = 3.06; dorsal surface as in *E. refusana* but less mottled in general appearance; white costal streak nearly always prominent. *Abdomen.* Male genitalia (n = 15) (Figs. 1c, 28): Vesica with 17–50 cornuti; valva with costal margin concave, ventral emargination moderate, NR = 0.48, mean SA = 114°, anal angle moderately developed. Female genitalia (n = 6) (Figs. 37, 44): Typical of the group; lamella postvaginalis tapering posteriorly; SR = 2.06.

Distribution and flight period. The range of *Eucosma verna* extends from Nova Scotia to British Columbia, south to Florida, Mississippi, and New Mexico. The 71 specimens we examined were captured between 9 March and 7 July, the vast majority flying in May and June.

Eucosma autumnana (McDunnough 1942)

(Figs. 1a, d, 9–11, 29, 38, 45)

Thiodia autumnana McDunnough 1942:66.

Phaneta autumnana: Miller 1971:287; Powell 1983:33; Miller 1987:43; Brown 2005:492; Gilligan et al. 2008:94.

Discussion. See comments under *E. verna*.

Holotype (Fig. 9): ♂, Quebec, Lac Ste. Marie, T. N. Freeman, 7 September 1935, slide TOR-1064, CNC.

Paratypes. Same data as holotype (1 ♂, 2 ♀), CNC; Ontario, Pt. Colborne, D. Gray, 15 October 1934 (1 ♂), CNC.

Description. *Head.* Frons whitish; vertex gray brown; labial palpus with first segment white, medial surface of second segment white, lateral surface of second segment gray brown, third segment gray brown; antenna with dorsal surface brown, lateral surface whitish; ventral surface of scape white. *Thorax.* Dorsal surface gray brown; fore- and mid-legs with anterior surfaces brown, posterior surfaces whitish; hind-legs whitish; tarsi with pale annulations. Forewing (Figs. 1a, 9–11): ♂ FWL 6.5–9.5 mm (mean = 7.6, n = 62), AR = 3.09; ♀ FWL 7.2–9.6 mm (mean = 8.4, n = 10), AR = 3.01; dorsal surface as in *E. verna* except proximal portion dark grayish brown, distal portion golden-yellow (at least in northern specimens); white costal streak and white lines in cell varying from absent to prominent. *Abdomen.* Male genitalia (n = 9) (Figs. 1d, 29): Vesica with 27–38 cornuti; valva with costal margin weakly concave, ventral emargination deep and U-shaped, NR = 0.32, mean SA = 88°, anal angle strongly produced. Female genitalia (n = 6) (Figs. 38, 45): Typical of the group; lamella postvaginalis tapering posteriorly; SR = 2.48.

Distribution and flight period. We examined 91 individuals documenting a range from Maine to North Dakota, south to North Carolina and Mississippi. The Mississippi and North Carolina specimens were collected in March and April, the others from 24 August to 18 October.

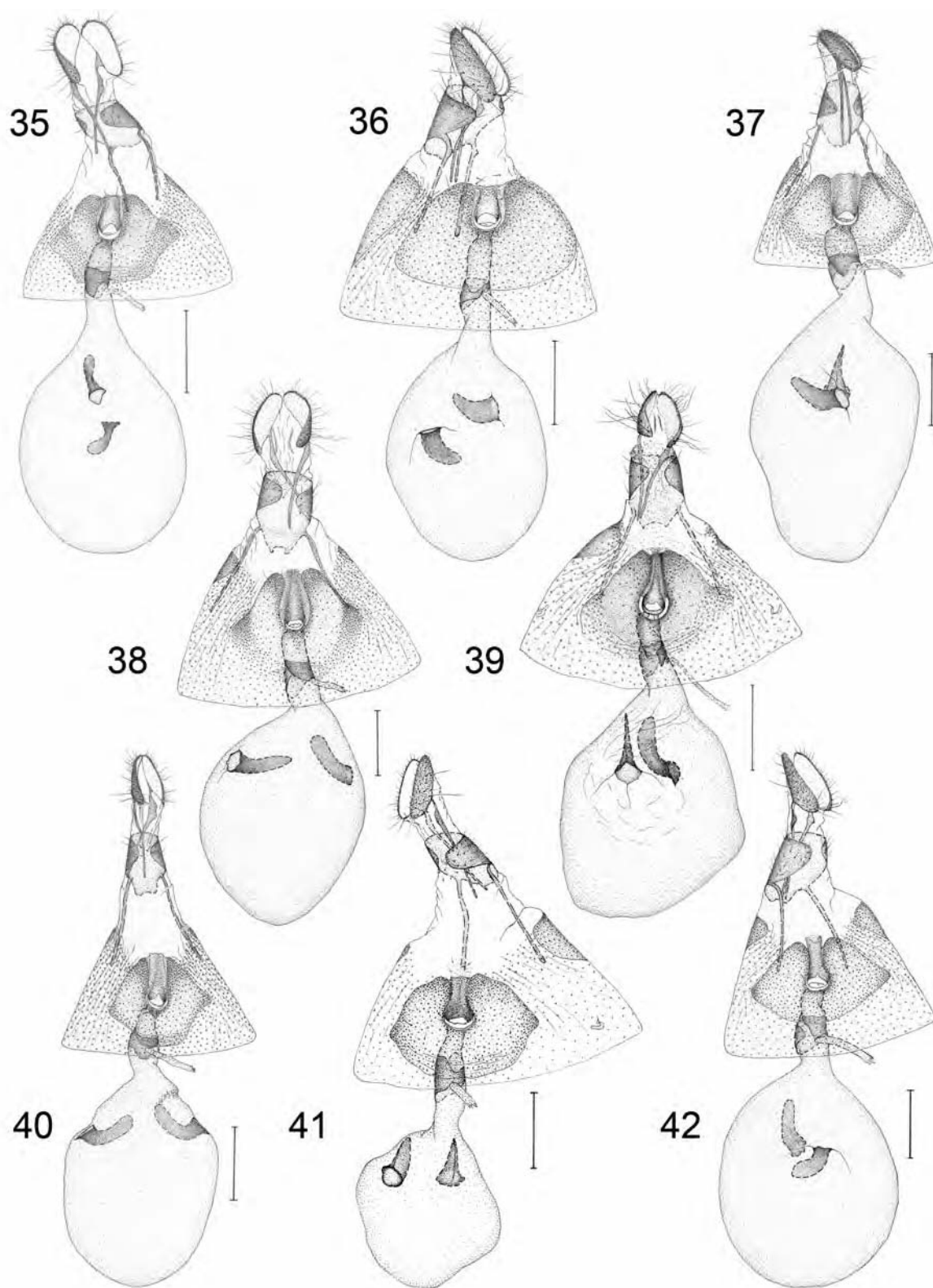
Eucosma citricolorana (McDunnough 1942)

(Figs. 12, 13, 30, 46)

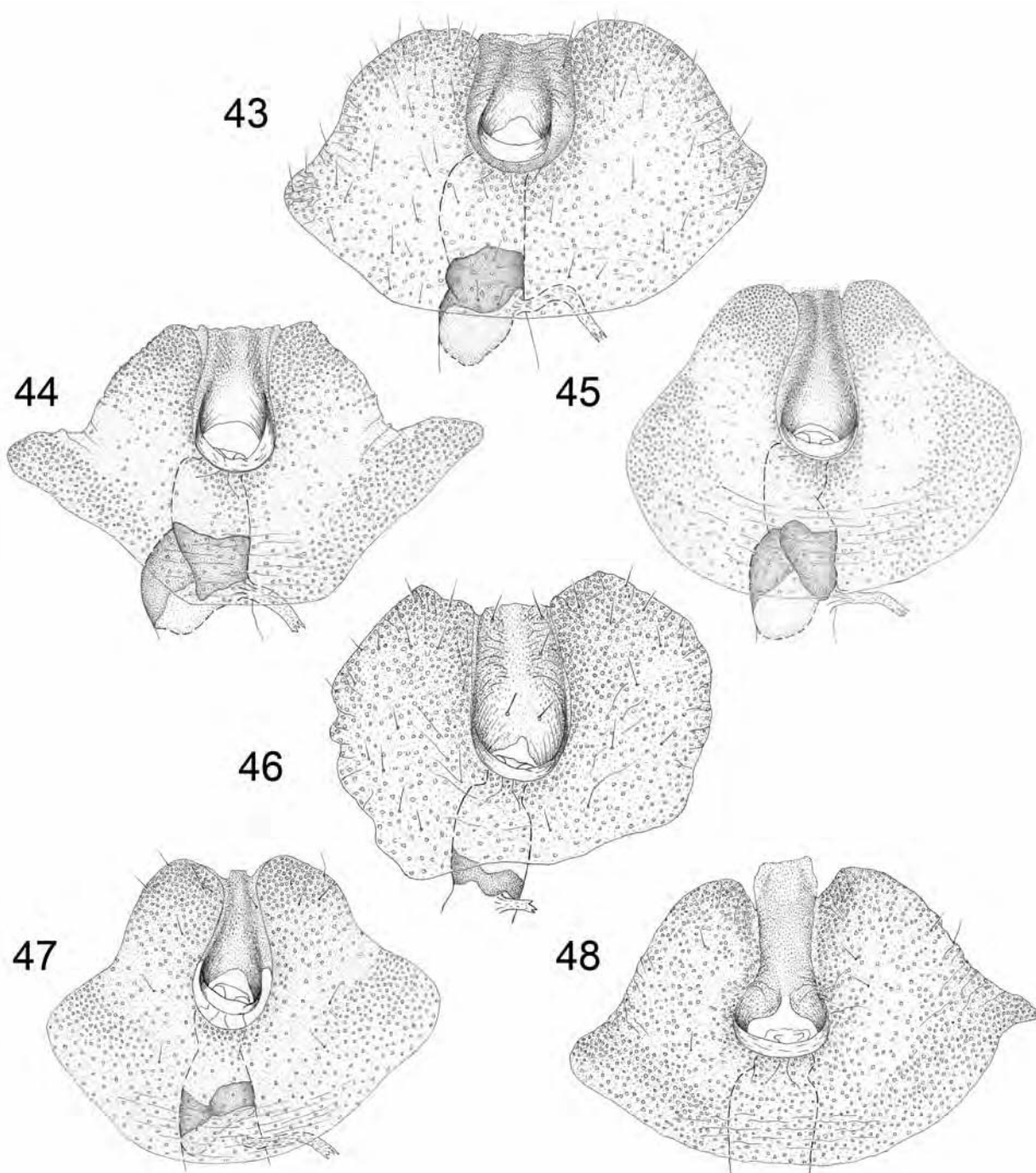
Thiodia citricolorana McDunnough 1942:66.

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

Discussion. Until recently, *E. citricolorana* was known only from the holotype and one paratype (both males). The holotype resembles *E. refusana*, *E. verna*, and *E. autumnana* in forewing pattern (Figs. 4–12) but is paler in color (except for unusually pale examples of *E. verna*) and barely exhibits the white streaking along the costa often found in the latter three species. In 2010, Pohl et al. reported a female of *E. citricolorana* from Alberta. That specimen was not collected in association with a male, so its determination was necessarily tentative. Its forewing (Fig. 13) is more strongly suffused with gray than is that of the male type. More recently, J. Nordin collected both sexes of *E. citricolorana* flying together diurnally near Laramie, Wyoming, and comparison of these individuals with the Alberta female confirmed the identity of the latter specimen. In the Wyoming series, the forewing is strongly suffused with gray in both males and females.



FIGS. 35–42. Female genitalia. **35**, *E. decempunctana*, slide DJW 3240. **36**, *E. refusana*, slide DJW 627. **37**, *E. verna*, slide DJW 3194. **38**, *E. autumnana*, slide DJW 3102. **39**, *E. annetteana*, slide TOR 610. **40**, *E. millerana*, slide DJW 3216. **41**, *E. amphorana*, slide DJW 2921. **42**, *E. litorea*, slide DJW 3121. Scale bar = 0.5 mm.



FIGS. 43–48. Sterigma-sternum 7. **43**, *E. refusana*, slide DJW 3265. **44**, *E. verna*, slide DJW 3232. **45**, *E. autumnana*, slide DJW 3269. **46**, *E. citricolorana*, slide DJW 3266. **47**, *E. annetteana*, slide TOR 1609. **48**, *E. litorea*, slide DJW 3120.

The distinctively shaped anal angle of the male valva (Fig. 30) separates this taxon from other members of the subgroup. Females are distinguished by the extremely narrow sclerotized band connecting the lamella postvaginalis to sternum 7, the relatively small size of sternum 7, and the relatively narrow sclerotized band on the ductus bursae (Fig. 46).

Holotype (Fig. 12). ♂, Saskatchewan, Saskatoon, K. M. King, 4 July 1924, slide TOR-981, CNC.

Paratype. ♂, Saskatchewan, Cypress Hills, A. R. Brooks, 5 June 1939, slide TOR-1608, CNC.

Description. *Head.* Frons white to tan; vertex tan to gray brown laterally, pale yellow to tan medially; labial palpus with medial surface whitish, lateral surface of second segment white to gray brown, lateral surface of third segment gray brown; antenna with dorsal surface tan to gray brown, posterior surface whitish; scape with ventral surface whitish. *Thorax.* Dorsal surface straw yellow to gray brown; legs with anterior surfaces brown to gray brown, posterior surfaces tan to whitish; tarsi with whitish annulations. Forewing (Figs. 12, 13): ♂ FWL 7.9–10.1 mm (mean = 9.2, n = 27), AR = 3.23; ♀ FWL = 7.3–8.2 mm (mean = 7.6, n = 5), AR = 3.05; proximal portion of dorsal surface straw yellow with variable gray suffusion; distal portion straw yellow except for ocelloid region and gray costal striae (paratype with gray-brown edging on costa from base to mid-wing); anterior portion of ocelloid region white to pale yellow with brownish streaks along veins; ocellus with two rows of black dots on a white ground and a greatly reduced third row often indicated by just a few black scales. *Abdomen.* Male genitalia (n = 4) (Fig. 30): Vesica with 26–41 cornuti; valva with costal margin concave, ventral emargination moderate and U-shaped, NR = 0.59, mean SA = 103°, BSP reduced; cucullus with anal angle strongly produced and bluntly pointed. Female genitalia (n = 3) (Fig. 46): Typical of the group; sternum 7 somewhat reduced and very narrowly connected to sterigma; lamella postvaginalis rectangular; SR = 1.81; sclerotized band on ductus bursae narrow.

Additional material examined. ALBERTA: vic. Fort Assiniboine, 55.301° N, 114.828° W, D. Macaulay, 22 June 2002 (1 ♀, slide DJW 3266), CFS-E. WYOMING: Albany Co., South Lodgepole Creek, S. of Happy Jack Rd., 41.252° N, 105.393° W, 8146 ft., J. S. Nordin, 9 June 2013 (4 ♂, slide DJW 3272; 3 ♀, slide DJW 3273), 12 June 2013 (3 ♂, 1 ♀, slide DJW 3279), 14 June 2013 (15 ♂, slide DJW 3278), 15 June 2013 (3 ♂), DJW, JSN, MEM.

Distribution and flight period. We examined 32 specimens (27 ♂, 5 ♀) ranging from northwest Alberta to southeast Wyoming, with adult flight occurring from 5 June to 4 July. The Wyoming specimens were collected in light traps and by diurnal sweeping, the latter by flushing the moths from stands of *Thermopsis montana* Nutt. (Fabaceae) (mountain goldenbanner).

The *annetteana-scotiana-millerana* subgroup. *Eucosma annetteana* was described by Kearfott (1907) from seven syntypes collected at Cincinnati, Ohio by Annette F. Braun. *Eucosma scotiana* was described by McDunnough (1958) from a holotype and seven paratypes collected by D. C. Ferguson in Nova Scotia. McDunnough recognized the similarity of the two species but separated them by the presence in *E. scotiana* of an “oblique orange-brown line” separating the proximal portion of the forewing from the ocelloid region, stating that this character was not mentioned by Kearfott in the description of *E. annetteana*. McDunnough considered *E. scotiana* to be a “denizen of the Hudsonian Zone” and therefore not likely to

have its range extend as far south as Cincinnati. These diagnostic comments have been insufficient for sorting the *annetteana-scotiana* material that has accumulated in recent decades.

We examined 143 specimens in this subgroup from Nova Scotia, Illinois, Massachusetts, Minnesota, Mississippi, New Jersey, Ohio, South Carolina, and Texas. They all possess the brown median band that McDunnough considered diagnostic for *E. scotiana*. We found no morphological characters that reliably separate the types of *E. annetteana* from those of *E. scotiana*. However, included in our sample were representatives of three populations, one in Mississippi, two in Minnesota, that differ consistently from *E. annetteana-scotiana* in forewing coloration. We treat them here as the new species, *E. millerana*.

Eucosma annetteana (Kearfott 1907)

(Figs. 14–17, 31, 39, 47)

Thiodia annetteana Kearfott 1907:42; Heinrich 1923:43, fig. 90; McDunnough 1939:43.

Eucosma annetteana: Barnes & McDunnough 1917:171.

Phaneta annetteana: Powell 1983:33; Brown 2005:492; Gilligan et al. 2008:93.

Thiodia scotiana McDunnough 1958:7, **new synonymy**. *Phaneta scotiana*: Powell 1983:33; Brown 2005:496.

Discussion. *Eucosma annetteana* resembles *E. scotiana* in forewing appearance and genitalia. Both species have a prominent median band and a dull yellow proximal portion of the forewing, the latter with varying amounts of brown to gray-brown suffusion. Variability in male genitalia consists of subtle differences in the structure of the cucullus: the distal margin is convex with curvature moderate to nearly straight; the ridge-like projection of the basoventral margin onto the medial surface of the neck is present but often weakly expressed in the *E. annetteana* types and Mississippi specimens, absent in the *E. scotiana* types, and present or absent in coastal specimens from Massachusetts to South Carolina. In females of both species the lamella postvaginalis tapers posteriorly, and the lamella antevaginalis is well-separated from sternum 7 by a band of membrane.

Types. *Thiodia annetteana*. Lectotype (Fig. 14) here designated: ♂ Ohio, Cincinnati, Annette F. Braun, 13 April 1905, AMNH. This specimen bears a green LECTOTYPE label attached by Klots. He (1942) attributed the designation to Heinrich (1923), but Heinrich's comment “*Type* – in American Museum” is ambiguous due to the presence of three syntypes in the AMNH, hence the present designation. Paralectotypes.

OHIO: Cincinnati, Annette F. Braun, 2 April 1903 (2 ♂, slide by CH 21 May 1917), USNM; 13 April 1905 (1 ♂, slide DJW 1447; 1 ♀), AMNH; 19 May 1906 (1 ♂, slide 69960), USNM; 23 May 1904 (1 ♂), USNM. *Thiodia scotiana*. Holotype (Fig. 17): ♂, Nova Scotia, St. Paul Island, Cabot Strait, D. C. Ferguson, 23 July 1955, slide TOR 1058, CNC. Paratypes: Nova Scotia, Peggy's Cove, Halifax County, D. C. Ferguson, 31 August 1957 (1 ♀, slide DJW 3073), CNC; same location and collector as holotype, 25 July 1955 (1 ♂, slide DJW 3051), AMNH. This accounts for 2 of the 7 paratypes mentioned by McDunnough (1958); the others (4 ♂, 1 ♀), according to his comments, were retained in his personal collection.

Description. *Head.* Frons white; vertex pale yellowish brown; labial palpus with first segment white, medial surface of second segment white, lateral surface of second segment pale brown with some white suffusion, third segment brown; antenna brown dorsally, white ventrally; ventral surface of scape white. *Thorax.* Dorsal surface brown to yellowish brown; fore- and mid-legs with anterior surfaces brown, posterior surfaces whitish; hind-leg whitish; tarsi with weakly contrasting pale annulations. Forewing (Figs. 14–17): ♂ FWL 5.5–8.1 mm (mean = 6.7, n = 49), AR = 3.02; ♀ FWL 5.3–7.2 mm (mean = 6.4, n = 14), AR = 2.95; proximal portion of dorsal surface dull brownish yellow to grayish yellow, with thin brownish edging on costal margin; median band brown with lustrous gray edging; anterior portion of ocelloid region filled with white-tipped brown scales, with streaking along veins obscure to absent; ocellus with two conspicuous rows of black dots, sometimes a partial third, on a whitish ground. *Abdomen.* Male genitalia (n = 19) (Fig. 31): Vesica with 16–38 cornuti; valva with ventral emargination moderate, NR = 0.56, mean SA = 123°; ridge-like extension of basoventral margin of cucullus onto medial surface of neck weakly expressed to absent. Female genitalia (n = 7) (Figs. 39, 47): Typical of the group; SR = 2.80; lamella postvaginalis tapering posteriorly; lamella antevaginalis well separated from sternum 7 by band of membrane.

Additional material examined. ILLINOIS: Putnam Co., M. O. Glenn, 29 April 1939 (1 ♂, slide DJW 3180; 2 ♀, slide DJW 3179), 3 May 1939 (1 ♂). MASSACHUSETTS: [Barnstable Co.], West Barnstable, C. P. Kimball, 26 April 1949 (1 ♂, slide DJW 3230), 27 April 1949 (1 ♂, slide DJW 3224), 30 April 1949 (1 ♂), 18 September 1949 (1 ♂); [Dukes Co.], Martha's Vineyard, F. M. Jones, 9 August (1 ♂), 17 August (1 ♂), 18 August 1930 (1 ♂, slide DJW 3182), 31 August 1944 (1 ♂), 1 September 1944 (1 ♂), 2 September (3 ♀, slides DJW 3186, 3187), 4 September (1 ♂), 5 September 1944 (1 ♂, slide DJW 3181), 8 September 1944 (1 ♂); [Middlesex Co.], Holliston, 29 August (1 ♂); Nantucket, 20 August 1941, C. P. Kimball (1 ♂), September 1907 (1 ♀). MISSISSIPPI: Oktibbeha Co., T19N R15E S16, D. M. Pollock, 9 March 1990 (7 ♂, slides DJW 3109, MEM 595), 23–30 March 1992 (1 ♂, slide DJW 3117); Osborn Prairie, R. L. Brown, 12 March 2003, (3 ♂, slide DJW 3108). NEW JERSEY: [Atlantic Co.], Hammonton, 3 September 1903 (1 ♀), 6 September 1903 (1 ♂). OHIO: Hamilton Co., Cincinnati, A. F. Braun, 13 April 1905 (5 ♂, slide DJW 3177; 2 ♀, slide TOR 1610), 13 April 1908 (1 ♂), 23 April 1904 (1 ♀, slide DJW 3175), 24 April 1906 (1 ♂, slide DJW 3178), 24 April 1907 (1 ♂, slide DJW 3176), 25 April 1912 (1 ♀), 27 April 1906 (2 ♂; 1 ♀, slide TOR 1609), 30 April 1904 (1 ♂). SOUTH CAROLINA: [Charleston Co.], McClellanville, The Wedge, R. W. Hodges, 18 March 1968 (1 ♂, slide DJW 3114), 19 March 1968 (2 ♂), 21 March 1968 (1 ♂, slide DJW 3222). TEXAS: [Lee Co.], Fedor, 1 April 1897 (2 ♂, slide DJW 3223).

Distribution and flight period. We examined 65 individuals (51 ♂, 14 ♀) establishing a range from Nova Scotia to Illinois, south to South Carolina, Mississippi, and southeast Texas. Specimens from west of the Appalachian Mountains were collected in March and April, those from the east coast mostly in August and September, with a few April captures from the Cape Cod region of Massachusetts.

Eucosma millerana, new species

(Figs. 18, 19, 32, 40)

Diagnosis. *Eucosma millerana* is similar to *E. annetteana* but differs from the latter taxon in color and flight period. The vertex, thorax, and proximal portion of the forewing are bright lemon yellow vs. dull yellow with brown and/or gray suffusion in *E. annetteana*, and the markings in the distal portion of the forewing are blackish brown vs. orange brown. *Eucosma millerana* appears to be a midwestern species, where it flies in August and September; adult flight in midwestern populations of *E. annetteana* occurs in March and April. On average, *E. millerana* is slightly smaller than *E. annetteana* (mean FWL = 5.8 vs. 6.6 mm), but the value ranges overlap considerably (Table 1). The genitalia of the two species appear to be indistinguishable, though the cornuti count is somewhat larger in *E. millerana* (mean = 42 vs. 30), and the sterigma is slightly more elongate (SR = 3.12 vs. 2.80) (see Table 1).

Description. *Head.* Frons whitish; vertex pale yellow; labial palpus with first segment and medial surface white, lateral surface of second segment gray brown with pale yellow patch at distal extremity, lateral surface of third segment dark brownish gray; antenna brown to dark brownish gray dorsally, yellowish white ventrally; ventral surface of scape whitish. *Thorax.* Dorsal surface pale yellow; fore- and mid-legs with anterior surfaces brown to dark brownish gray, posterior surfaces yellowish white; hind-legs yellowish white; tarsi with pale yellowish annulations. Forewing (Figs. 18–19): ♂ FWL 4.9–6.7 mm (mean = 5.8, n = 36), AR = 3.05; ♀ FWL 5.0–6.7 mm (mean = 5.9, n = 9), AR = 3.01; proximal portion of dorsal surface lemon yellow, with costal edge brownish gray; median band orange brown with lustrous gray edging; costal strigulae between median band and apex lemon yellow; anterior portion of ocelloid region with obscure white lines separating blackish-brown streaks along veins; ocellus with two rows and often a partial third row of black dots, all on a white background. *Abdomen.* Male genitalia (Fig. 32) (n = 5): Vesica with 39–47 cornuti, valva with costal margin concave, ventral emargination moderate, NR = 0.55, saccular corner rounded, mean SA = 121°; cucullus with ventral angle moderately developed. Female genitalia (Fig. 40) (n = 5): Typical of group; SR = 3.12; lamella antevaginalis separated from posterior margin of sternum 7 by band of membrane; membrane of corpus bursae weakly contorted by crescent-shaped band of internal microprotuberances anterior to juncture with ductus bursae.

Holotype. ♂, Minnesota, Clay Co., Blanket Flower Science & Natural Area, 46.6820° N, 96.2022° W, R. P. Dana, 23–24 August 20012, slide DJW 3215, deposited in the USNM.

Paratypes. MINNESOTA: Same data as holotype, (9 ♂, slide DJW 3217; 1 ♀, slide DJW 3218); Clay Co., Blanket Flower Science & Natural Area, 46.6897° N, 96.2138° W, R. P. Dana, 23–24 August 2012 (1 ♀, slide DJW 3216); Swift Co., Chippewa Prairie Preserve, 45.1537° N, 96.0070° W, R. P. Dana, 29–30 August 2011 (5 ♂, slide DJW 3025; 1 ♀, slide DJW 3024). MISSISSIPPI: Oktibbeha Co., Osborn Prairie, D. J. Wright, 26 August 2003 (3 ♂, slides DJW 1337, 3015); Osborn Prairie, 33.5114° N, 88.7356° W, R. L. Brown, 30 August 2003 (1 ♀), R. Patterson, 6 September 2006 (12 ♂, slide MEM 2740; 5 ♀, slides DJW 3023, MEM 2741), R. L. Brown, 7 September 2003 (1 ♂), 20 September 2007 (11 ♂), J. A. MacGown, 8 September 1997 (3 ♂). Paratype depositories: AMNH, CNC, DJW, EME, FSCA, MEM, RPD, USNM.

Etymology. The specific epithet commemorates our late colleague, William E. Miller.

Distribution and flight period. We examined 77 specimens (67 ♂, 10 ♀) collected between 23 August and 20 September in remnant

prairie habitat in Clay and Swift Counties, Minnesota and in Oktibbeha County, Mississippi.

The *amphorana-litorea* subgroup. The grouping of *E. amphorana* and *E. litorea* is based on similarity of their genitalia.

Eucosma amphorana (Walsingham 1879)

(Figs. 1b, e, 20–23, 33, 41)

Semasia amphorana Walsingham 1879:63, pl. 74, fig. 9.

Thiodia amphorana: Fernald [1903]:462; Heinrich 1923:42, fig. 86; McDunnough 1939:44.

Eucosma amphorana: Barnes and McDunnough 1917:172.

Phaneta amphorana: Powell 1983:33; Brown 2005:492; Powell and Opler 2009:132.

Discussion. *Eucosma amphorana* is variable in forewing color, ranging from nearly uniform brownish gray (Fig. 20) to largely lemon yellow (Fig. 23), with numerous intermediate phenotypes. Powell and Opler (2009) reported what appear to be seasonal influences on these forms in some California localities and the lack thereof in others.

Lectotype (Fig. 20) here designated: ♂, Oregon, Grant Co., Camp Watson, Walsingham, March–April 1872, BMNH(E) #819905, slide 11588, BMNH.

Paralectotypes: Same data as lectotype (5 ♂; 1 ♀, slide 11551), BMNH. This accounts for seven of the eight syntypes reported by Walsingham (1879).

Description. Gray phenotype (Fig. 20). *Head.* Frons grayish; vertex gray; labial palpus with first segment white, second segment largely white on medial surface, gray on lateral surface, third segment dark gray dorsally; antenna gray dorsally, with line of white scales on posterior surface; ventral surface of scape whitish. *Thorax.* Dorsal surface gray; legs with anterior surfaces gray, posterior surfaces whitish; tarsi with whitish annulations. Forewing: Proximal portion of dorsal surface brownish gray, variably suffused with grayish white; basal and subbasal fasciae partially expressed and confluent, forming a dark gray-brown basal patch from inner margin to mid-cell; median band brown and moderately wide; anterior portion of ocelloid region with white-tipped blackish-gray scales, the streaking along veins obscure; ocellus with three rows of black dots, the posterior row weakly and/or partially expressed; costa from median band to apex with three brown marks separating white to pale gray strigulae. Yellow phenotype (Fig. 23). As in gray phenotype except: vertex, dorsal surface of thorax, and proximal portion of forewing yellow to grayish yellow; basal patch and median band reduced to weakly contrasting (sometimes barely discernible) grayish-yellow shades; costal marks delimiting strigulae not as clearly expressed. Intermediate phenotypes (Figs. 21, 22). General appearance somewhat mottled; basal portion of forewing pale gray; subcostal region between median band and apex yellowish. Aggregated forewing statistics: ♂ FWL 7.1–10.1 mm (mean = 8.3, n = 18), AR = 3.05; ♀ FWL 7.4–9.6 mm (mean = 8.4, n = 12), AR = 2.94. *Abdomen.* Male genitalia (n = 5) (Figs. 1b, 33): Vesica with 22–35 cornuti; valva with costal margin weakly concave, ventral emargination long and shallow, neck moderately long and broad, NR = 0.71, saccular corner broadly rounded, mean SA = 131°, anal angle weakly produced, basoventral margin of cucullus with ridge-like extension onto medial surface of neck. Female genitalia (n = 5) (Fig. 41): Typical of the group; sterigma narrowing abruptly at posterior

margin of ostium; lamella postvaginalis rectangular; SR = 1.92.

Distribution and biology. *Eucosma amphorana* was reared by Clarke from *Grindelia* (Asteraceae) in Whatcom Co., Washington (Brown et al. 1983) and by Powell from *Grindelia camporum* Greene and *Isocoma menziesii* (Hook. & Arn.) G. L. Nesom in Contra Costa Co., California (Antioch NWR) and Santa Barbara Co., California (San Miguel Island), respectively. A more complete discussion of the life history is presented in Powell and Opler (2009). We examined 30 specimens (18 ♂, 12 ♀) documenting a range from the northwest corner of Washington to southern California. There appear to be two primary flight periods, spring and fall, with a few adults emerging in midsummer. Many of the records are from reared specimens.

Eucosma litorea, new species

(Figs. 24, 34, 42, 48)

Diagnosis. *Eucosma litorea* differs from other members of the *refusana* group in having an especially large ocelloid region which, aside from the ocellus, is filled with blackish scales with white apices, producing a uniform salt-and-pepper effect. It is somewhat similar in forewing appearance to *E. millerana* and to the yellow form of *E. amphorana* (Fig. 24 vs. Figs. 18–19 & Fig. 23) but lacks the well-developed median band in the former species and the grayish-yellow basal patch in the latter. *Eucosma litorea* differs subtly in forewing geometry from its fellow group members as indicated by AR = 2.71 vs. 2.89–3.29 in the other species. The male genitalia of *E. litorea* most closely resemble those of *E. amphorana* (Figs. 33, 34) but lack the ridge-like extension of the basoventral margin of the cucullus onto the medial surface of the neck. The female genitalia of these two species are essentially identical but differ from the other members of the group in that the sterigma narrows abruptly at the posterior margin of the ostium to form a rectangular lamella postvaginalis with width noticeably smaller than ostium diameter.

Description. *Head.* Frons white; vertex lemon yellow; labial palpus white with some gray-brown flecking on lateral surface of second segment, third segment sometimes gray brown; antenna concolorous with vertex; scape often with pale gray-brown scaling on dorsal surface, particularly in males. *Thorax.* Dorsal surface lemon yellow; fore- and mid-legs with anterior surfaces grayish brown, posterior surfaces white; hind-leg whitish; tarsi with brown annulations. Forewing (Fig. 24). ♂ FWL 5.1–6.2 mm (mean = 5.8, n = 15), AR = 2.74; ♀ FWL 5.7–7.7 mm (mean = 6.5, n = 7), AR = 2.65; proximal portion of dorsal surface bright lemon yellow; scales in anterior portion of ocelloid region and along termen black with white apices, producing salt and pepper effect; subcostal area anterior to ocelloid region orange brown, crossed by lustrous gray striae; stria 9 extending from costa to termen; striae 8 and 7 following anterior margin of ocelloid region in the distal and basal directions, respectively; stria 6 extending from costa to inner margin, with an interruption on CuA₂, its proximal margin edged with orange brown; ocellus with three rows of four black dots on a white ground, the rows divided into groups of two dots by a medial gray transverse bar. *Abdomen.* Male genitalia (n = 6) (Fig. 34). Uncus with basal width ca. 2 × height; vesica with 21–26 cornuti; valva with costal margin nearly straight except for slight bend at distal end of neck, ventral emargination long and shallow, ventral and costal margins of neck nearly parallel, NR = 0.69, saccular corner broadly rounded, mean SA = 143°, cucullus with apex narrowly rounded, distal margin convex of nearly uniform curvature, anal angle weakly developed. Female

genitalia ($n = 3$) (Figs. 42, 48). Typical of the group; lamella postvaginalis rectangular, width approximately $2/3$ ostium diameter; $SR = 2.11$.

Holotype. ♂, Alabama, Baldwin Co., Bon Secour NWR, 30.2286° N, 87.8308° W, R. L. Brown and D. Pollock, 8–9 August 1994, deposited in the USNM.

Paratypes. ALABAMA: Baldwin Co., Bon Secour NWR, 30.2286° N, 87.8308° W, R. L. Brown and D. Pollock, 8–9 August 1994 (14 ♂, slides SML 2739, DJW 1563, 3022; 5 ♀, slides SML 2738, DJW 3120), D. M. Pollock, 15 June 1994 (1 ♂), 21 June 2001 (1 ♂), R. L. Brown, 15 June 1994 (1 ♂), 16 June 2000 (1 ♂), 1 August 2000 (1 ♂), 21 October 2000 (1 ♂), T. L. Schiefer, 15 October 1996 (2 ♂), L. D. Gibson, 20 June 2008 (1 ♂); T9S R3E Sec. 30W, R. Brown and D. Pollock, 13–14 October 1991 (2 ♂), T9S R2E Sec. 25S, R. Brown and D. Pollock, 12–16 October 1991 (6 ♂; 1 ♀); Weeks Bay NER Reserve, 30.4175° N, 87.8396° W, R. L. Brown, 2 August 2000 (1 ♂); Plash Island, end of Hwy 6, 16–19 June 1986 R. L. and B. B. Brown (2 ♂; 1 ♀, slide DJW 3121). FLORIDA: Gulf Co., St. Joseph State Park, J. B. Heppner, 10–12 April 1999 (1 ♂, slide JBH 2553); Okaloosa Co., Ocean City, H. O. Hilton, 26 April 1963 (1 ♀), 30 April 1963 (1 ♀), 13 May 1963 (1 ♂), 20 May 1963 (1 ♂, slide JAP 2184), 23 May 1963 (2 ♂, slide JAP 2473); Shalimar, H. O. Hilton, 24 May 1964 (1 ♂); Santa Rosa Co., Pensacola, S. Hills, 17 May 1961 (1 ♂); GEORGIA: Emanuel Co., Ochopee Dunes Natural Area, 32.5375° N, 82.4611° W, 19 Jun. 2002, R. L. Brown (7 ♂; 2 ♀). Paratype depositories: AMNH, CNC, DJW, EME, MEM, FSCA, MCZ, USNM.

Etymology. The specific epithet derives from the Latin *litoreus*, meaning of the shore

Distribution and biology. Most of the types (41 ♂; 9 ♀) come from sand dune habitat on the northeast coast of the Gulf of Mexico (Baldwin Co., Alabama; Gulf, Okaloosa, and Santa Rosa Cos., Florida), but a few (7 ♂; 2 ♀) were collected at inland sand dunes along the Ochopee River in Emanuel Co., Georgia. There appear to be three primary flight periods: mid-April to late June, August, and October.

Remarks. Figure 25 is representative of six male specimens collected 10–14 March 1990 in sand dune habitat 1 mi E. of Oyster Bay, Baldwin Co., Alabama. They agree with *E. litorea* in all respects except color, the bright lemon yellow being replaced by dull olive brown. They may represent another new species or perhaps a dark form of *E. litorea*, but that decision must await the availability of additional material.

BIOGEOGRAPHIC RELATIONSHIPS

Some members of the *E. refusana* species group have distributional patterns similar to those of many other Lepidoptera that occur in grasslands and other open habitats. Metzler et al. (2005) tabulated Lepidoptera associated with tall grass prairie habitat in the upper Midwest, estimating levels of prairie-dependency, but that study did not include species in the *refusana* group. *Eucosma amphorana* and *E. decempunctana* occur in the Pacific coastal states, *E. refusana* in Minnesota and the Prairie Provinces of Canada, and *E. citricolorana* in Saskatchewan, Alberta, and southeast Wyoming. *Eucosma annetteana*, *E. autumnana*, and *E. verna*, are distributed from the Atlantic coast to the Midwest, with disjunct populations of all three in Mississippi. In addition, there are a few century-old records of *E. annetteana* from southeastern Texas and some recent collections of *E. verna* in New Mexico and Wyoming. The distributions of the new species, *E. millerana* and *E. litorea*, are more restricted and disjunct.

Eucosma litorea is known only from coastal dunes in Alabama and Florida and inland dunes of the Ochopee River in Georgia. The type locality of *E. litorea*, Bon Secour National Wildlife Refuge, includes a dune habitat (Fig. 49) that is characteristic for the Gulf Coast, as described by Penfound and O'Neill (1934) and Johnson (1997). The fore dunes are low in elevation and dominated by *Uniola paniculata* L. (sea oats), although other herbaceous plants are present. The hind dunes (or barrier dunes) are higher in elevation and are covered with a mixture of *Quercus geminata* Small (sand live oak), *Chrysoma pauciflosculosa* (Michx.) (woody goldenrod), *Ceratiola ericoides* Michx. (sand rosemary), *Balduina angustifolia* (Pursh), *Clinopodium coccineum*



FIGS. 49–50. *Eucosma litorea* and *Eucosma millerana* habitats. **49**, Fore and hind dunes, Bon Secour NWR, Baldwin Co., Alabama. **50**, Black Belt Prairie (Osborn Prairie remnant), Oktibbeha Co., Mississippi.

(Nutt. Ex Hook.), and various other herbaceous plants. Specimens of *E. litorea* were collected in both fore dunes and the adjacent hind dunes at Bon Secour.

Eucosma litorea was also collected at inland riverine dunes of the Ochoopee River in Georgia, which are of aeolian origin during the past 30,000 years (Markewich and Markewich 1994). The dominant trees include *Q. laevis* Walter (turkey oak), *Q. margaretta* Ashe (dwarf post oak), and *Pinus palustris* Mill. (long-leaf pine), but the shrubby and herbaceous vegetation is remarkably similar to that of the coastal dunes, including woody goldenrod, sand rosemary, and the previously mentioned species that occur at Bon Secour. *Eucosma litorea* was collected in only one of four sites sampled in the Ochoopee Dunes Natural Area and the adjacent Nature Conservancy Preserve. That site differs from the others in having a large population of *C. pauciflorescens*. Also collected at this site was *Schinia psamathea* Pogue (Noctuidae), a species that otherwise occurs only at locations on the Gulf Coast (Pogue 2010) where woody goldenrod is present. The biogeographic connections between the coastal dunes and the Ochoopee dunes are supported by surveys of ants, which record the rarely collected *Nylanderia phantasma* Trager in both locations and report other ant species with disjunct distributions between the Gulf Coast and Ochoopee Dunes (MacGown et al. 2009). Based on these distribution patterns, it is hypothesized that the Gulf Coastal dunes and the riverine dunes of Ochoopee River, Georgia were connected at some time during the past 30,000 years by a corridor of habitat suitable to explain the shared species of moths, ants, and plants.

Four species in the *refusana* group occur in Mississippi, and all are restricted to remnants of the Black Belt Prairie. A biogeographic analysis of species of Lepidoptera and other insects localized in the Black Belt prairie (Brown 2003) revealed five distributional patterns, of which two are present with the *E. refusana* group: 1) Black Belt + Great Plains, and 2) Black Belt + Great Plains + Atlantic Coastal Plain. The disjunct distribution of *E. millerana* between the Black Belt and the Great Plains (Minnesota) is shared with ten other species of Lepidoptera, including *Epiblema iowana* McDunnough, *Sonia fulminana* (Walsingham), and *Pelochrista ridingsana* (Robinson), as well as several species of Cerambycidae, Acrididae, and Apoidea (Brown 2003, Hill 2005, Smith et al. 2012). The disjunct distribution of *E. verna*, *E. autumnana*, and *E. annetteana* in the Black Belt, Great Plains, and Atlantic Coastal Plain is shared with *Eucosma canusana* (Wright), *Eucosma giganteana* (Riley), *Pelochrista graciliana* (Kearfott) (Brown 2003) and other species of Lepidoptera.

The Black Belt is the most southeastern prairie of the tall prairie type. It extends in a crescent-shape from McNairy County, Tennessee across east-central Mississippi and east to Russell County, Alabama (Brown 2003). An estimated 700km² of Mississippi and Alabama were covered by prairie during the 1830's based on an analysis of plat maps prepared from surveys of the General Land Offices in the two states (Barone 2005). Most of this prairie was converted to agricultural use during the ensuing years, and only small isolated remnants now remain. However, the Black Belt may have been a major refugium for the prairie biota during the Wisconsin glaciation.

Vertebrate fossil assemblages in the Black Belt from 33,000 to 16,000 years ago show a rich fauna of grazers, e.g., mammoth, bison, camel, and three species of horses (*Equus* L.), as well as browsers, e.g., mastodon, sloth, peccary, and deer (Kaye 1974). This combination of browsers and grazers, the latter predominating, suggests that grasses with a mixture of trees and shrubs covered the Black Belt during the Sangamon interglacial and Wisconsin glacial stages. The presence of western species of extinct *Equus* and other vertebrates suggest that a grassland corridor existed between the Black Belt and the Great Plains before the Wisconsin glacial stage and the subsequent development of the meandering Mississippi River. Thus, species of *Eucosma* and other insects with current localized distributions in the Black Belt may have had a continuous distribution with conspecific populations in grasslands of the Great Plains before the Wisconsin glaciation.

The woodlands and grasslands in the Central Great Plains and upper Atlantic Coast were replaced during the Wisconsin glacial maximum (20,000–15,000 years ago) by a boreal forest from approximately 34° N latitude to the tundra bordering the Laurentide ice sheet (Axelrod 1958, Whitehead 1967, Watts 1980, Delcourt 1979). The southern Great Plains in Texas and northern Mexico have been cited as areas where grasslands may have persisted during the glacial maximum (Ross 1970, Hoffman & Jones 1970). The Blackland Prairies of Texas are of the same Cretaceous age as the Black Belt Prairie of Mississippi (Beaumont 2007), and these prairies may have served as refugia for species such as *E. annetteana* and others during the Wisconsin glaciation.

The post-glacial Hypsithermal period between 9,000 and 4,000 years ago may have provided another time for exchange of species between the Black Belt, Great Plains, and Atlantic Coastal Plain. During this period a prairie peninsula (Transeau 1935) extended from the Great Plains southward into Missouri, east to the

Atlantic Coast, and southward along the Coastal Plain (King & Allen 1977, Axelrod 1985, Delcourt & Delcourt 1993). Metzler et al. (2005) cited an unpublished report by Martin (1963), who hypothesized that the northern Plains and Atlantic Coastal areas were repopulated following the Wisconsin glaciation by populations moving northward from Florida and Gulf Coast refugia through the Mississippi River Valley and along the Atlantic Coast. In contrast, Brown (2003) hypothesized that the Black Belt was the principal refugium of the prairie biota because of the greater number of endemic as well as shared species between the Black Belt and the Central Great Plains compared with those shared with the blackland prairies in Texas and the grasslands of the Gulf Coast and Florida. The exact dispersal route from the Black Belt to the prairie peninsula is unknown. The possibilities include an archipelago of fragmented grasslands across the barrens and cedar glades of Tennessee and Kentucky (DeSelm 1988) and a corridor along the Arkansas River valley, where many prairie remnants occur.

In summary, the distributions in the *E. refusana* group reveal patterns of disjunctions and past biogeographic connections that are supported by analyses of distributions of other species of Lepidoptera and other insects. Additional distributional records of these species may be found in the future in relictual grasslands such as blackland prairies in Arkansas, Louisiana, and Texas as well as glades and barrens in Tennessee and Kentucky.

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THREE NEW SPECIES OF LEAF-MINING GELECHIIDAE (LEPIDOPTERA) FROM CANADA AND NORTHEASTERN UNITED STATES

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ABSTRACT. Three new species of leaf-mining Gelechiidae are described: *Xenolechia ceanothiae* Priest, whose larvae feed on *Ceanothus americanus* L. (Rhamnaceae); *Gnorimoschema shepherdiae* Priest, on *Shepherdia canadensis* (L.) Nutt. (Elaeagnaceae); and *Scrobipalpula manierreorum* Priest, on *Eurybia (Aster) macrophylla* (L.) Cassini (Asteraceae). Their leaf mines were initially discovered in the understory in Michigan forests. Barcoding revealed additional records for two of these species from several regions of Canada. Photographs of the imago and illustrations of the male and female genitalia, larval and pupal chaetotaxal maps are provided. Scanning electron micrographs of selected features of the larva for each species supplement illustrations. Comparative diagnoses of adult morphological characters are presented to distinguish the new species from other North American congeners. Photographs of the leaf-mines for each species are also included. DNA barcodes for each species are shown to be distinct from related North American congeners. The first occurrence of *Gnorimoschema vibei* Wolff in North America is confirmed by barcoded specimens from Kuujuaupik in northern Quebec, Canada.

Additional key words: chaetotaxy, DNA barcode, Gelechiidae, leaf-miners, taxonomy

Occurrence of leaf-mining life style in larvae of Gelechiidae is widespread but scattered among several, unrelated genera in different tribes (Powell 1980). Among Litini for example, leaf-mining is prevalent in the genus *Coleotechnites*, which are primarily miners in conifer needles (Powell & Opler 2009). Some species in several gelechiid genera are leaf-miners whereas other congeners have different larval habits such as leaf-tiers, webbers, or stem borers: the genera *Chrysoesthia*, *Nealyda*, *Stereomita* (Anomologini), some *Gnorimoschema*, *Scrobipalopsis*, *Scrobipalpa*, and *Scrobipalpula* (Gnorimoschemini) all comprise several species with leaf-mining larvae (Huemer & Karsholt 1999, 2010; Povolný 1991; Powell & Povolný 2001).

Among leaf-miners discovered and reared by RJP during a long-term survey of leaf-mining Lepidoptera at two sites in Michigan were three species of Gelechiidae. DA determined that they were undescribed, one being a species of *Xenolechia* (Litini), the other two being Gnorimoschemini. JFL and VN recognized the Gnorimoschemini as conspecific with two undescribed species of Gnorimoschemini from Canada that they had previously DNA barcoded and studied as part of an overview of the Gnorimoschemini of Alberta (Nazari &

Landry 2012). Thus we decided to combine our results to present a more complete picture of these new species.

The purpose of this paper is to describe these three new species, compare their adult external features, genitalia morphology, immature features, and DNA barcodes to congeners, and present observations on their life history.

MATERIALS AND METHODS

Michigan study sites. The study site where leaf-mines of *Xenolechia ceanothiae* and *Gnorimoschema shepherdiae* were found is located near Lake Huron in northeastern Lower Michigan, Presque Isle County (T34N-R07E, Sec. 14 ne ¼ ; N 45° 20.819' W 83° 32.061'). This State Park was originally purchased by the Nature Conservancy for protection of one of the largest known occurrences of Dwarf Lake Iris. Soil at this site is well drained, dark brown, and a very gravelly sandy loam (Knapp 1993). The host plants of *X. ceanothiae* and *G. shepherdiae* grow in a second growth forest of *Betula papyrifera* Marsh. (Paper Birch), *Populus tremuloides* Michx. (Quaking Aspen), *Prunus virginiana* L. (Choke Cherry) and *Quercus rubra* L. (Red Oak). The understory is composed of *Amelanchier* spp.

(Serviceberry), *Ceanothus* spp. (New Jersey Tea) *Cornus* spp. (dogwood), *Viburnum* spp. (Arrow-wood), *Shepherdia canadensis* (L.) (Soapberry), and various forbes.

Larvae of *X. ceanothiae* and *G. shepherdiae* were first recovered in July 1998. This site was visited an additional 25 times between June and October from 1998–2010. Two trails, each approximately 1 km lined intermittently with host shrubs, were visually searched for mines.

The study site where leaf-mines of *S. manierreorum* were found is located at the Huron Mountain Club, Marquette County, Michigan. This private holding, located along south central Lake Superior, encompasses most of the Huron Mountains and several lakes. It is approximately 20,000 acres (8,094 ha) with about 8,000 acres (3,237 ha) of virgin forest. This old growth forest is a habitat for a diverse combination of hemlock-northern hardwood ecosystems (Simpson et al. 1990).

Larvae of *S. manierreorum* were first recovered in August 2004 (Lot 1523). This site was visited an additional 13 times between June and October from 2004–2010. Host plants were found growing along the sides of a gravel road for a distance of approximately 1 km. This road segment was visually searched for mined leaves.

Rearing method. Field collected leaves with mines were placed in 1-quart clear plastic freezer bags. Each live miner was assigned a specimen number, placed in a separate freezer bag to rear. Sample active miners were photographed according to Priest (2007). Individual pupae were placed in vented glass vials. Vials were then placed on slightly moistened paper toweling in a 1-gallon plastic box with tight fitting lid. Larvae recovered from late June to mid-July emerged as adults from late July to early August. Larvae recovered from late August to late October were wintered in a 1-gallon plastic box. The box was sheltered out-of-doors and checked weekly for adequate moisture. Warming began by mid-February to force emergence. Vacated mines were preserved in glassine envelopes, some larvae, pupae, and all parasitoids were preserved in 80% EtOH, and adults spread according to Landry & Landry (1994).

A portion of the viable larvae were carefully extracted from their leaf-mines, placed in mildly boiling H₂O for a few seconds, and stored in 40 % EtOH for 24 hrs. After a day, all larvae were stored in 80 % EtOH. Pupae were collected and stored directly in 80 % EtOH. Preserved larvae and pupae were used for studies using light-microscopy and scanning electron microscopy and for making associations with the reared adults.

Specimen preparation. For SEM study, larvae and pupae were cleaned in a full-strength solution of Formula 409™ detergent, and subsequently rinsed in

water and dehydrated in increasing concentrations of ethanol (10, 25, 50, 70, 95 %), ending with absolute ethanol. After dehydration, specimens were critical point dried using a Tousimis critical point dryer, mounted on SEM stubs using carbon paste, and coated with gold-palladium (40/60 %), using a Cressington sputter coater. Forewings were disarticulated from the mesothorax of pinned specimens and mounted on stubs using carbon adhesive tabs. The fine-structure of the larva and pupa, and the male sex scales on the undersurface of the forewing was studied with an Amray 1810 scanning electron microscope at an accelerating voltage of 10 kV.

Morphological examinations and measurements of the adults, larvae, and pupae were made using a Leitz RS dissecting microscope with a calibrated micrometer. Genitalia were dissected by DA as described by Clarke (1941), except that Mercurochrome™ and Chlorazol Black were used as stains; those dissected by JFL and VN were prepared as described by Landry (2007). The male and female genitalia are described as how they are oriented naturally on the body and not how they are figured. The Methuen Handbook of Colour (Kornerup and Wanscher 1978) was used as a color standard. The larval description is based upon the last instar. Larval nomenclature follows Stehr (1987). Pupal nomenclature follows Mosher (1916). Plant names follow Voss & Reznicek (2012).

DNA barcode analysis. Specimens or tissue samples (a leg) were shipped to the Canadian Centre for DNA Barcoding in Guelph for sequence analysis. Laboratory protocols at this facility have been greatly optimized, and the current iteration can be accessed at <http://www.ccdb.ca>. In short, a small tissue sample is lysed and genomic DNA extracted using an automated, silica-based method; the COI barcode region is amplified via PCR using one or more primer sets (Hebert et al. 2013) and successful amplicons are then bi-directionally sequenced (deWaard et al. 2008). The resultant sequences, along with the voucher data, images, and trace files, are deposited in the Barcode of Life Data Systems (BOLD) (Ratnasingham & Hebert 2007; www.barcodinglife.org), with sequences > 600bp subsequently deposited in GenBank.

Two 'technical' outgroup taxa were selected for each of the three new species to illustrate the level of intraspecific variation versus interspecific divergence. The two taxa with the closest Barcode Identification Numbers (BINs) (Ratnasingham & Hebert 2013) in BOLD were used: on average selected species showed more than 5% divergence. Neighbor-joining trees and genetic distances were calculated with MEGA 5.05 (Tamura et al. 2011) using the Kimura two-parameter (K2P) model of base substitution (Kimura 1980). Details

of the barcoded specimens and their photographs are available through the following dataset (<http://dx.doi.org/10.5883/DS-3GELECHI>). The same DOI provides access to the sequence records, trace files, and primer sequences used for PCR amplification, together with GenBank accession numbers.

Photography. Pinned specimens were photographed with a Canon EOS 60D with a MP-E 65mm macro lens. They were placed on the tip of a thin plastazote wedge mounted on an insect pin, with the head facing toward the pin and the fringed parts of the wings facing outward. This ensured that there was nothing between the fringes and the background. Specimens were photographed over a white background. Lighting was provided by a ring of 144 LEDs covered with a white diffuser dome (Fisher 2012 and references therein). The camera was attached to a re-purposed stereoscope fine-focusing rail. Sets of 20–35 images in thin focal planes were taken for each specimen and assembled into deep-focused images using Zerene Stacker and edited in Adobe Photoshop.

Slide-mounted genitalia were photographed with a Nikon DS-Fi1 digital camera mounted on a Nikon Eclipse 800 microscope at magnifications of 100–400×. Nikon's NIS 2.3 Elements was used to assemble multiple photos of different focal planes into single deep-focus images which were further adjusted with Adobe Photoshop.

Leaf mines were photographed (Priest 2007) with a Canon EOS Digital Rebel and EF-S60mm f/2.8 macro USM lens.

Deposition of specimens. Holotypes are deposited in the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Paratypes and immature stages obtained from this study are deposited in the USNM, the Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa (CNC), and Michigan State University, East Lansing, Michigan (MSUC); some specimens used in the DNA analysis are deposited in the Biodiversity Institute of Ontario, University of Guelph, Ontario (BIOUG). The authorship of the new species is attributed to Ron Priest.

RESULTS

Gelechiinae: Litini

Xenolechia ceanothiae Priest, new species

(Figs. 1, 4, 9–25)

Adult diagnosis. *Xenolechia ceanothiae* is similar to *X. ceanothiella* (Braun) in forewing coloration and pattern with five tufts of black scales but *X. ceanothiella* is overall paler from more extensive white suffusion.

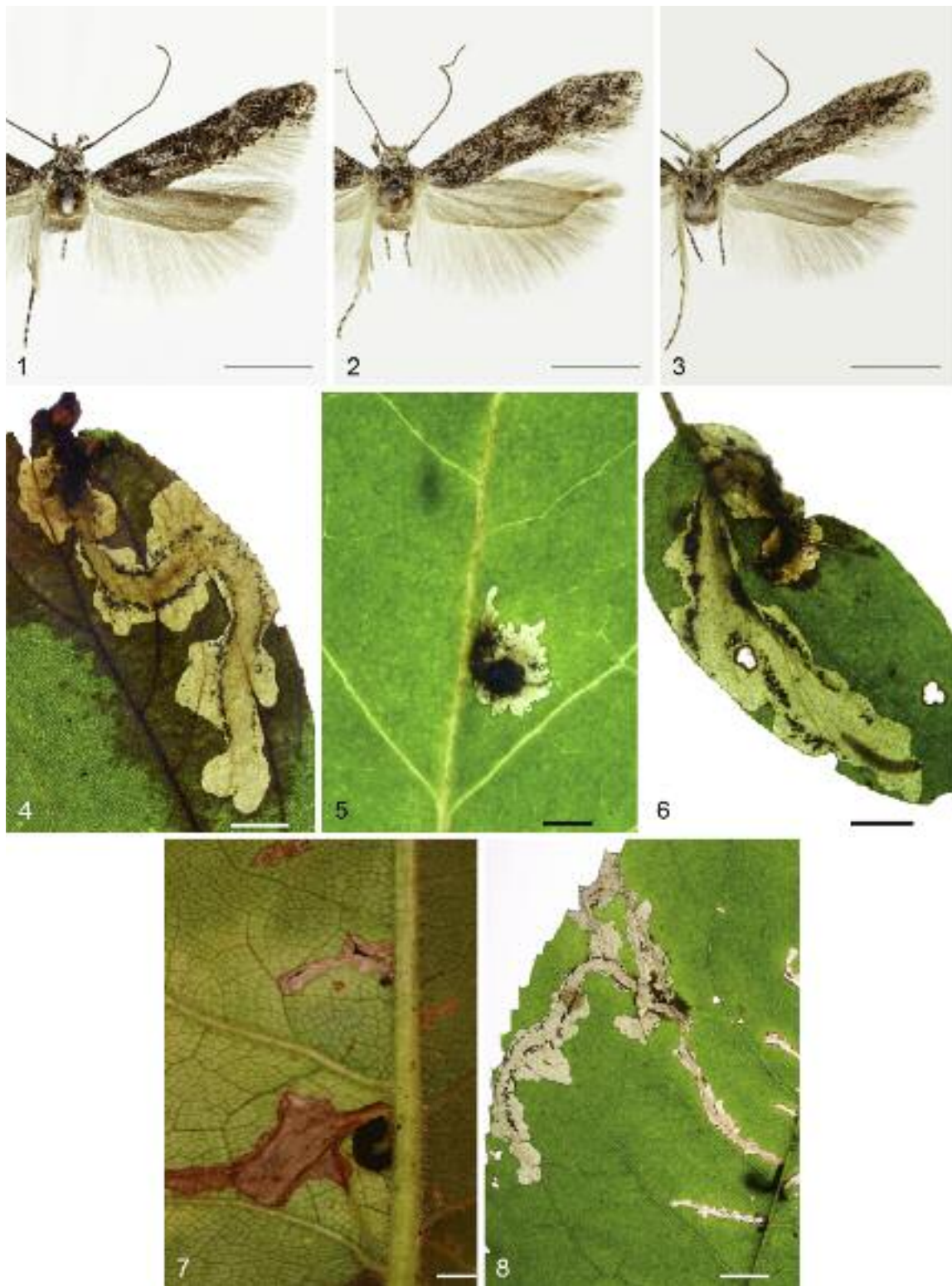
Xenolechia ceanothiella also uses *Ceanothus* as host plant but is so far known only from California. In *X. ontariensis* Keifer, which geographically overlaps *ceanothiae*, the scale tufts are less contrastingly dark than in *X. ceanothiae/ceanothiella* and the ground color is pale grey rather than white, with a pronounced pattern of dark grey irrorations, giving an overall speckled aspect. However, because of possible variation and wear, the only sure way to identify the species is by examination of the genitalia.

In male genitalia, *X. ceanothiae* is markedly different from all other *Xenolechia* in having the uncus lobes darkly melanized with a scabrous inner margin, subangular medial incision, and latero-apical notch, the tegumen with anterior arms narrower ($< \frac{1}{2}$ width) than the dorso-medial portion, the paired processes of the juxta are incurved and shaped like heavy pincers with the apices mucronate and darkly melanized, the vinculum-juxta junction constricted, and the phallus slenderly tubular, markedly arched and hinged on a elongate ventral juxta lobe. Other *Xenolechia* have the uncus lobes evenly melanized with a smooth inner margin, pointed apex and either an evenly U-shaped or V-shaped medial incision, the tegumen arms are at least as wide as the dorso-medial portion, the paired processes of the juxta are digitate and distally tapered, the vinculum-juxta junction is broad, and the phallus is a broad, stout, straight tube with an extremely short, nearly indistinct ventral lobe connected to the juxta.

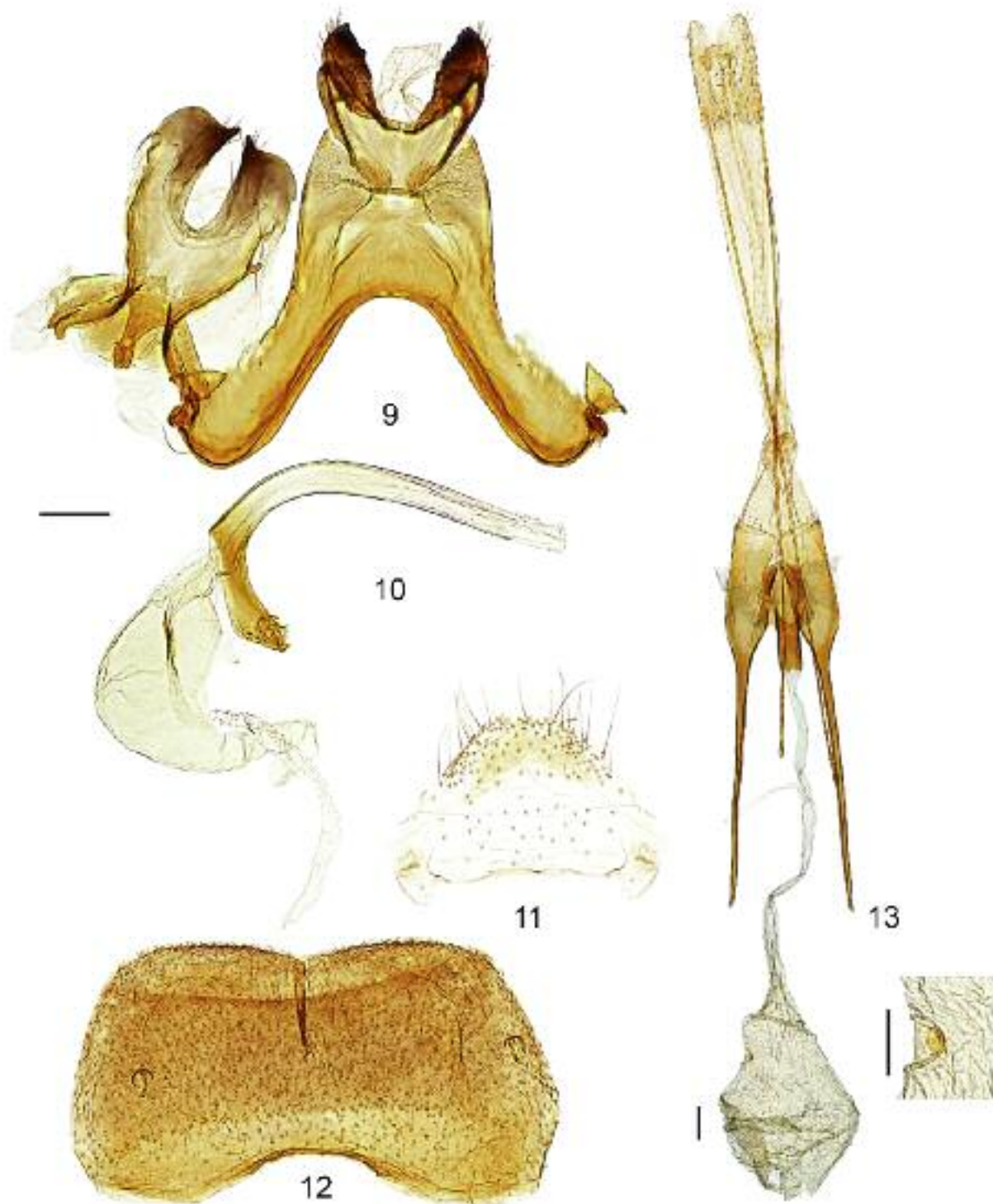
In female genitalia, *X. ceanothiae* has sternum 8 longer than wide, nearly as long as segment 7 with the posterior margin lined with a row of setae; an elongate sclerotized antrum which is about as long as sternum 8; sterigma a pair of elongate plates joined caudo-medially; and greatly reduced or absent signum. Other *Xenolechia* have sternum 8 wider than long and shorter than segment 7, without setae along the posterior margin; no sclerotized antrum; differently shaped sterigma, either with transverse, narrowly elongate, or tongue-like sclerites; and well developed, rhomboid signum with serrate edges.

Adult description. *Head:* Fronto-clypeus white. Scales on vertex with basal 2/3 white, apical 1/3 dark gray or basal 2/3 brownish gray, apical 1/3 dark brownish gray (some specimens intermixed with few white scales). Scape of antenna dark brownish gray with gray scales along apical margin, flagellomeres of flagellum dark brownish gray basally, brownish gray or pale gray apically on upper surface, brown on undersurface. Outer and inner surfaces of labial palpus dark brownish gray, segment 2 with a diagonal white band near 2/3 and white scales along apical margin, terminal segment with a white basal band, a white band near 2/3, and white apically. Proboscis white.

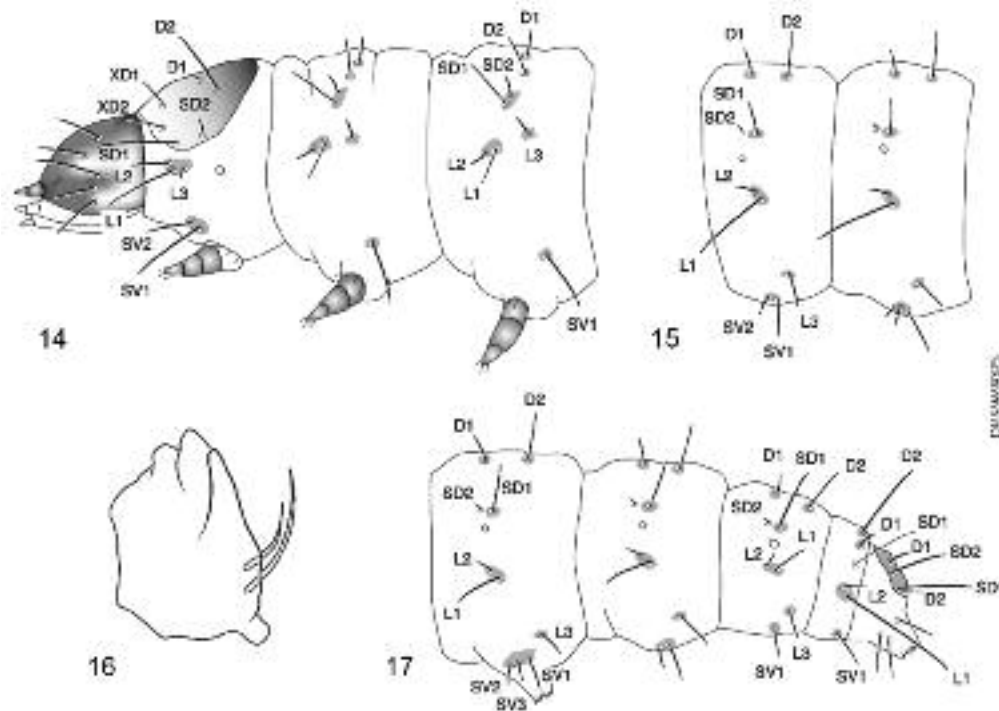
Thorax: Scales on mesonotum with basal 2/3 white, distal 1/3 dark brownish gray. Tegula patterned as mesonotum or basal 1/4 dark brownish gray, distal 3/4 with white scales with dark brownish gray on distal 1/4–1/5. Foreleg dark brownish gray with a suffuse white apical tuft on femur; tibia with a suffuse white band slightly beyond base, a



FIGS. 1–8. Adults, dorsal aspect. Scale = 2 mm. **1.** *Xenolechia ceanothiae*, holotype. **2.** *Gnorimoschema shepherdiae*, holotype. **3.** *Scrobipalpula manierreorum*, holotype. Figs. **4–8.** Larval leaf mines. **4.** *Xenolechia ceanothiae*, leaf mine of late-instar larva on *Ceanothus americanus*; scale = 5 mm. Figs. **5–6.** Leaf mines of *Gnorimoschema shepherdiae* on *Shepherdia canadensis*. **5.** Early instar; scale = 2.5 mm. **6.** Late instar; scale = 5 mm. Figs. **7–8.** Leaf mines of *Scrobipalpula manierreorum* on *Eurybia* (*Aster*) *macrophylla*. **7.** Early instar; scale = 2.5 mm. **8.** Late instar; scale = 5 mm.



FIGS. 9–13. *Xenolechia ceanothiae* genitalia. **9.** Male genitalia, ventral view, with vinculum-valvae unrolled to the left (slide MIC6817, specimen CNCLEP00099605). **10.** Phallus, lateral view. **11.** Eight tergum. **12.** Eight sternum. **13.** Female genitalia (slide MIC6818, specimen CNCLEP00098457); inset, close-up view of rudimentary signum. Scale = 100 μ m, except inset = 50 μ m.



FIGS. 14–17. *Xenolechia ceanothiae*, larval mandible and chaetotaxal maps. **14.** Head and T1–T3. **15.** A1–A2. **16.** Mandible. **17.** A6–A10.

suffuse white band near middle, and a white tuft along apical margin; tarsomeres with a narrow white band along apical margin. Midleg dark brownish gray with a suffuse white apical band on femur; tibia with a suffuse white band slightly beyond base, a suffuse white band near middle, and a white band on apical end adjacent to paired spurs; tarsomeres as above. Hindleg dark brownish gray a suffuse white apical tuft on femur; tibia with a suffuse white band slightly beyond base, a white band adjacent to middle pair of spurs, and a white band adjacent to apical pair of spurs; tarsomeres as above. Forewing (Fig. 1), length 4.5–6.0 mm ($n = 21$) dark brownish gray with a suffuse, white oblique band from 1/5–2/5, a suffuse white costal spot near 4/5, and a suffuse, white spot on tornus, and six black scale tufts; basal tuft small, near proximal end of CuP; three tufts above CuP (one small tuft within oblique band above radius, one large tuft along distal margin of band beneath radius, and one large tuft near distal end of CuP, proximal to tornus), two tufts below CuP (one large tuft along basal margin of band, one large tuft along distal margin of band). Fringe scales white, tipped with dark brownish gray. Undersurface brown except, anal area pale brown. Hindwing translucent pale gray.

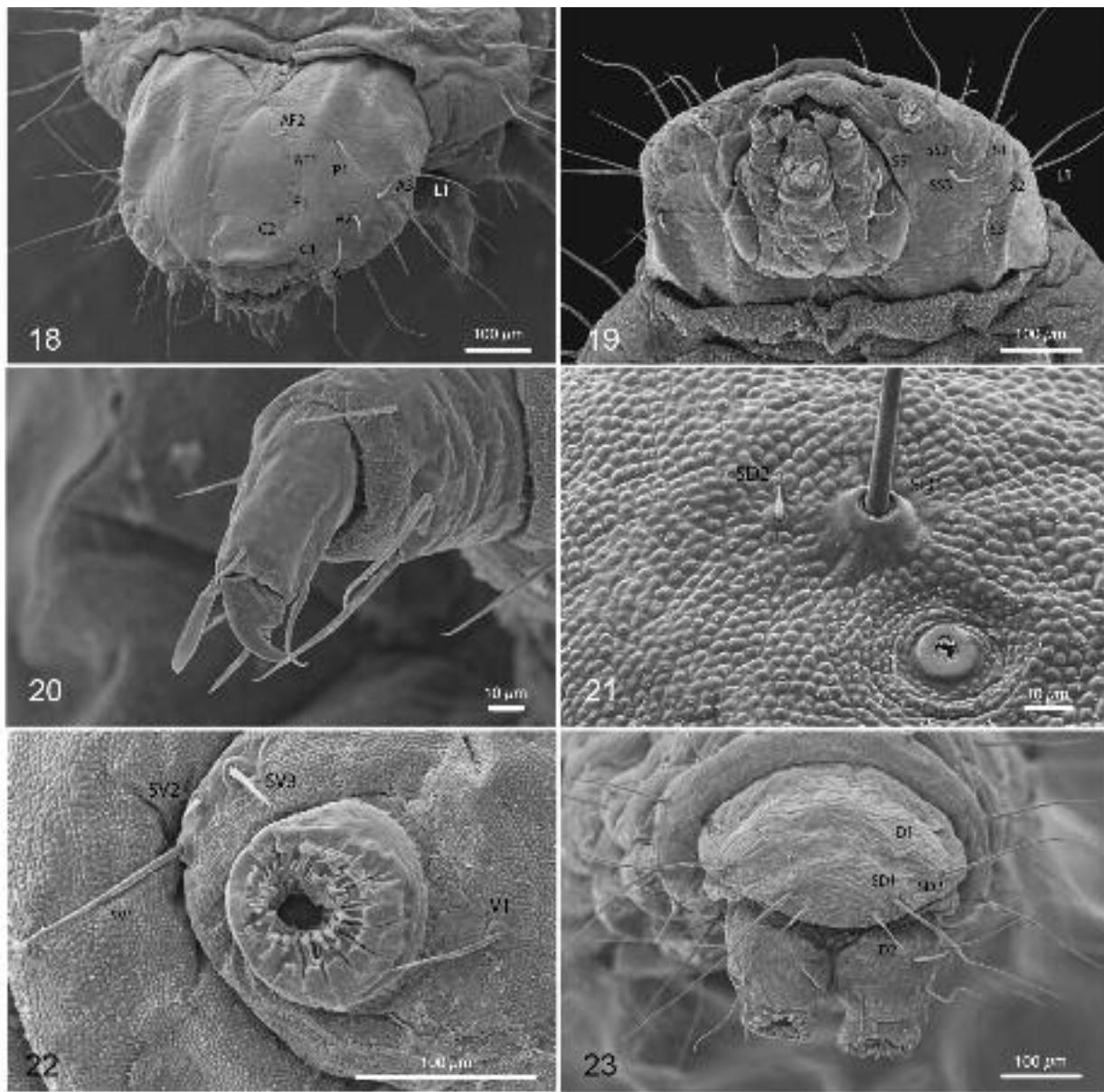
Male abdomen (Figs. 11–12): Tergum 8 broadly conical, wider than long, without coremata. Sternum 8 transversely subrectangular, posterior margin roundly emarginate.

Male genitalia (Figs. 9–10): Uncus lobes darkly melanized, inner margins finely serrate, medial incision subangular, latero-apical corners notched (side view). Tegumen with anterior arms narrower ($< \frac{1}{2}$ width) than dorso-medial portion, anterior notch slightly deeper than length of dorso-medial portion. Paired processes of juxta incurved, shaped like heavy pincers, apices mucronate and darkly melanized. Vinculum with short antero-medial process; junction with juxta constricted. Phallus slenderly tubular, arched, with slender antero-ventral lobe hinged to juxta; cornuti absent; ductus ejaculatorius with thin sclerite inside crescentic bulbous.

Female genitalia (Fig. 13): Ovipositor about 5× length of sternum 8. Apophysis anterioris straight, extended from gradually widened base. Apophysis posterioris about 2.5× length of apophysis anterioris, very thin. Sternum 8 elongate, nearly as long as segment 7, posterior margin lined with a row of setae, anteriorly with deep medial incision with sides forming pair of elongate sclerotized lateral plates posterad of ostium, caudally joined. Antrum sclerotized, straight-sided, nearly as long as sternum 8. Ductus bursae about as long as S8+AA, membranous, narrow, anterior end widened into corpus bursae, inception of ductus seminalis at 1/3 anterad of antrum. Corpus bursae subspherical, signum minute or absent.

Larva description. (Figs. 14–23): Length 8.0–10.2 mm ($n = 7$). Body pale gray; head with epicranium reddish brown; frons and basal area flanking frons dark orange; ecdysial line, stemmatal area, and dorso-posterior and ventrolateral margins dark brown; thoracic legs brown; pinacula unpigmented or pale brown; prothoracic shield with a wide unpigmented area demarcating dorso-longitudinal axis, bisecting two pale golden-yellow halves mottled with many brown spots, posterior and postero-lateral margins brown gradually becoming pallid anteriorly; anal shield pale golden yellow; spiracles on A2–A7 about same diameter of setae sockets on segments; spiracles on T1 and A8 about twice diameter of spiracles on A2–A7.

Head (Figs. 14, 16, 18–19): Epicranium slightly flattened dorso-ventrally; mouthparts semi-prognathous; an elongate, triangular frons demarcated by afrofrontal sclerites; scleritised widened distally, forming a broadly rounded ecdysial line; ecdysial suture short, bisecting adfrontal sclerites disto-medially; epicranial notch deep forming two large hemispheres; AF2 near apex of adfrontal sclerite, at least 5× longer than AF1; distance between AF2 and AF1 about 1/2 distance between AF1 and P1; P1 slightly longer than AF2; P2 approximate, dorso-lateral to, and about 1/3 length of P1; distance between AF1 and F1 about 2–3× distance between AF2 and AF1; C2 about 5× longer

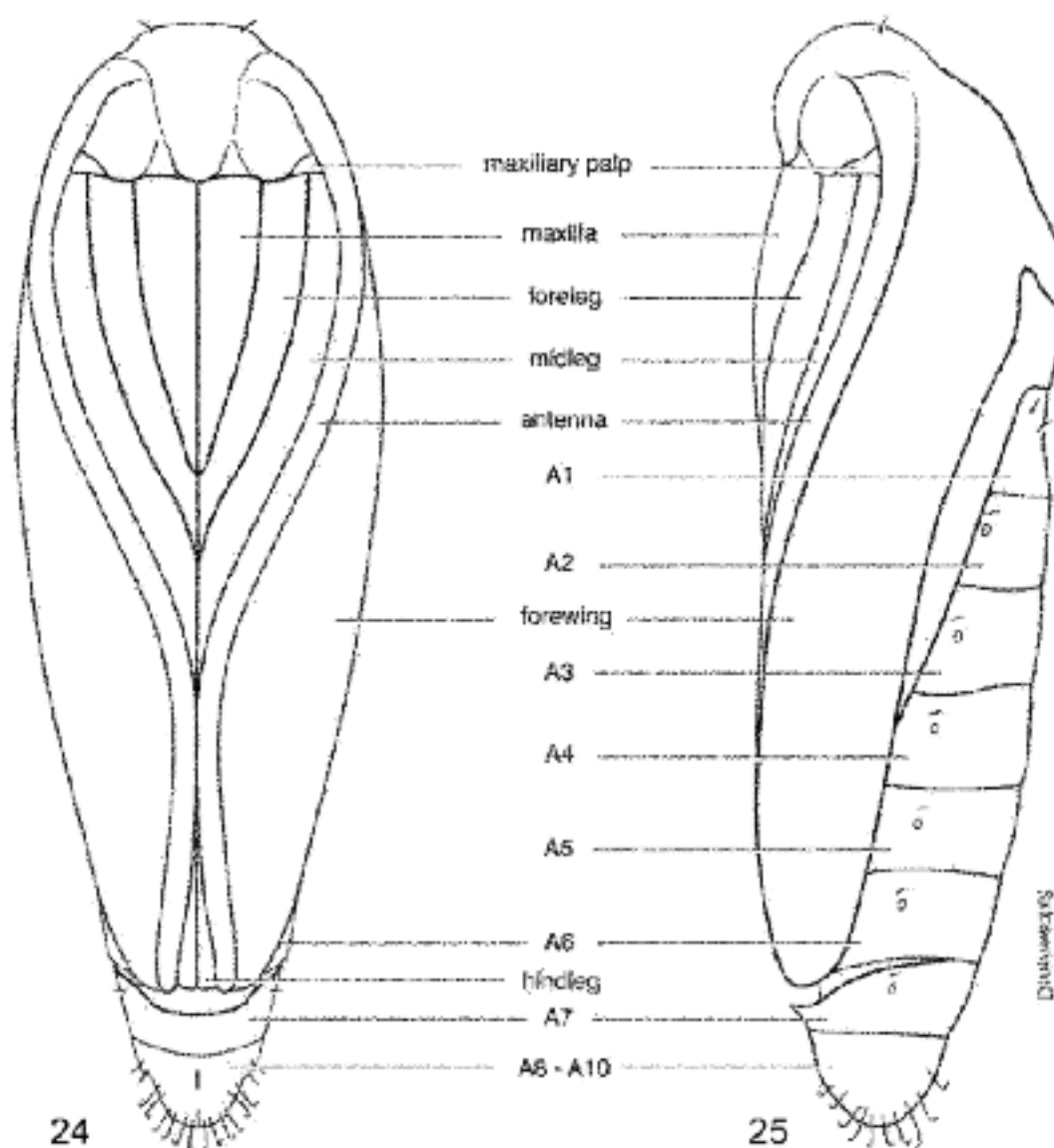


FIGS. 18–23. *Xenolechia ceanothiae*, scanning electron micrographs of larva. **18.** Head chaetotaxy, frontal view. **19.** Head chaetotaxy, ventral view. **20.** Right tarsus on T2. **21.** SD1 and SD2 on A8, left side. **22.** Right proleg on A5. **23.** Anal plate chaetotaxy on A10.

than C1; A3 dorso-posterior to stemma 2, about 5–6× A2 and about 1/3 longer than A1; six stemmata in a C-shaped pattern; S3 ventral to S2; S2 approximate and below stemma 1; S1 below stemmata 3; L1 posterior to stemma 1; SS1 beneath area between antenna and condyle of mandible; mandible with two apical dentitions, one dentition along dorsal surface, and two subequal setae near base of condyle (Fig. 16); SS2 and SS3 approximate, both beneath area between stemmata 5–6; labrum with six pairs of setae, two subequal median pairs, two equal fronto-marginal pairs, and two subequal latero-marginal pairs

Thorax (Figs. 14, 20): Prothoracic shield (Fig. 14) with SD1 about 2–2.5× longer than XD2 and XD1; SD1 posterior to XD2, XD1 posterior XD2; distance between XD2 and SD1 about 1/2 distance between XD2 and SD2; D2 about 4× longer than SD2; SD2 about 1/3

length of XD1 and XD2; D2 slightly shorter than SD1, posterior to SD2 and D1; distance between D2 and D1 at least 1/2 distance between D2 and SD2; D1 slightly shorter than SD2, closer to median longitudinal axis than XD1; L-group with L1 slightly ventral to L2 and L3, and about 2× longer than L2 and 5× longer than L3, pinaculum anterior and slightly dorsal to spiracle; SV2 slightly shorter than SV1; V1s along a transverse line across posterior margins of coxae (not shown), about 1/3–1/4 distance as distance between V1s on T2–T3; tarsus (Fig. 20) with two pairs of setae ventro-posterior and dorso-posterior to claw; ventro-posterior setae equal in lengths, dorso-posterior pair subequal, with a flattened seta with an obtuse apical margin. T2–T3 (Fig. 14): D2 about 2× length of D1, each seta on same pinaculum; SD1 3× longer than SD2, SD2 equal in length to D1, each seta on separate pinacula, anterior to D-group pinaculum; L1 2–2



FIGS. 24–25. *Xenolechia ceanothiae*, pupa. **24.** Ventral view. **25.** Lateral view.

1/2× longer than L2 and L3; L1 and L2 on same pinaculum, anterior to SD-group pinaculum; L3 slightly dorsal and posterior to L1, slightly anterior to SV1; V1s between coxae near middle (not shown).

Abdomen: A1–A2 (Figs. 15, 21–23): D2 about 2× longer than D1; SD1 dorso-posterior to spiracle on A1, and about 1/2 distance to spiracle on A2; SD2 minute, anterior to SD1 pinaculum; L1 about 6× longer than L2, both on same pinaculum; L2 ventral to spiracle on A2, L2 ventro-posterior to spiracle on A1; L3 about equal in length to L2, in straight line with or slightly anterior to D2; SV-group bisetose on A1, trisetose on A2, each group on same pinaculum; A3–A6 as above except, SV-group on a sclerotized band at base of proleg, and crochets uniserial, uniordinal, in a circle (Fig. 22). A7 (Fig. 17): as above except, SV-group bisetose (on same pinaculum), with SV1 2× length of SV2, and V1s slightly closer (not shown); A8 as above except, SV-group unisetose; A9 with all setae in near straight line, D2 about 4× D1; SD1 hairlike, slightly shorter than D2; L-group bisetose, with L2 about 6× longer than L1, each slightly diagonal on same pinaculum; SVs and Vs

as above. A10 (Figs. 17, 23): anal plate with SD2 and SD1 about 2× distance apart than distance between SD1 and D2; SD2 and SD1 of equal lengths, about 4× D2; D2 straight or slightly divergent; D1 equal in length to D2, anterior to SD1 and posterior to SD2; prolegs with crochets uniordinal.

Pupa description (Figs. 24–25). Length 5.5 – 6.3 mm (n = 3): smooth; golden yellow, with thin brown lines demarcating sclerites; vertex rounded; fronto-clypeus convergent, broadly rounded distally; labial palpi slightly visible; antennae broadly rounded encircling sclerites of maxillae, forelegs and midlegs, meeting medially slightly beyond midlength, extending distally in parallel, diverging distally slightly exposing mesothoracic legs; mesothoracic legs shorter or extending to lengths of antennae and forewings; maxillary palpi and forelegs extending to a common point anterior to midlegs; abdominal spiracles slightly raised; segments A6 and A7–10 movable; A6 divided ventrally, scars of prolegs absent; cremaster with 6 pairs of hooked setae present on dorsal and ventral surfaces of A9+A10.

Type material. Holotype ♂, “MICHIGAN, Presque Isle Co[unty], NE, T34N-R07E, S 14 [= 45.349°N, 83.541°W], Em[er]g[e]d: 26 Feb. 2006, Surv[eyor] [= Collector]: RJ Priest”, “Reared Ex. *Ceanothus americanus*, Rec[o]v[red] [= date collected]: 25 Oct. 2005, Lot: RJP1689.11”, [specimen #] “USNMMENT 00719471”, “DNA 2011 [blue label]”, “♂ Genitalia Slide by D. Adamski, USNM 83529” [green label] (USNM).

Paratypes: 13 ♂, 8 ♀. MICHIGAN: same data as holotype except: ♂, em. 28 Feb 2006, larva 25 Oct 2005, lot RJP1689.18, specimen # USNMMENT 00719470, DNA barcoded, genitalia slide USNM 83553 by D. Adamski (USNM); 1 ♂, em. 27 Feb 2006, larva 25 Oct 2005, lot RJP1689.8 (MSUC); 1 ♂, em. 27 Feb 2006, larva 25 Oct 2005, lot RJP1689.7 (MSUC); 1 ♂, em. 27 Feb 2006, larva 25 Oct 2005, lot RJP1689.6 (MSUC); 1 ♂, “26 Feb 2006, larva 25 Oct 2005, lot RJP1689.19 (MSUC); 1 ♂, em. 25 Feb 2006, larva 25 Oct 2005, lot RJP1690.2 [pupal exuvium in gelatin capsule beneath specimen] (MSUC); 1 ♂, em. 25 Feb 2006, larva 25 Oct 2005, lot RJP1689.14 (MSUC); 1 ♂, em. 1 Mar 2006, larva 25 Oct 2005, lot RJP1690.4, genitalia slide by D. Adamski, USNM 83528 (USNM); 1 ♀, em. 3 Mar 2006, larva 25 Oct 2005, lot RJP1689.9, specimen # USNMMENT 00719473, genitalia slide by D. Adamski, USNM 83531 (USNM); 1 ♀, em. 5 Mar 2006, larva 25 Oct 2005, lot RJP1690.6 (MSUC); 1 ♀, em. 7 Mar 2006, larva 25 Oct 2005, lot RJP1690.5, specimen # USNMMENT 00719472, DNA barcoded, genitalia slide by D. Adamski, USNM 83530 (USNM); 1 ♀, em. 7 Mar 2006, larva 25 Oct 2005, lot RJP1689.3, specimen # CNCLEP00098457, genitalia slide MIC 6807 (CNC); 1 ♀, em. 10 Mar 2006, larva 25 Oct 2005, lot RJP1689.4 (MSUC); 1 ♀, em. 7 Mar 2006, larva 25 Oct 2005, lot RJP1689.1 (MSUC); 1 ♂, em. wintered, larva 26 Sept. 2006, lot RJP1777.1 (MSUC); 1 ♀, em. wintered, larva 26 Sept. 2006, lot RJP1777.2 (MSUC); 1 ♀, em. wintered larva 26 Sept. 2006, lot RJP1777.3 (MSUC); 1 ♂, em. wintered, larva 12 Oct 2007, lot RJP1855.11 (MSUC); 1 ♂, em. wintered, larva 12 Oct 2007, lot RJP1855.1 [pupal exuvium on minuten beneath specimen], specimen # CNCLEP00098456, slide MIC (CNC); 1 ♂, em. wintered, larva 12 Oct 2007, lot RJP1855.10 (MSUC); 1 ♂, em. 28 Feb 2006, larva 25 Oct 2005, lot RJP1689.10 (MSUC).

Molecular data (Table 1, Fig. 60). BIN = BOLD:AAV3168. Full barcodes from three paratypes of the new species were obtained which were compared to those of *X. aethiops* (Humphreys & Westwood) (BOLD:AAE1445) and *X. ontariensis* (BOLD:AAC6357). The former is a Holarctic species and we analyzed barcodes of 14 specimens from Alberta, Ontario, Saskatchewan, British Columbia, France, and Spain. For *X. ontariensis*, we analyzed 26 barcodes of specimens from Alabama, Arkansas, Michigan, Manitoba, Oklahoma, Quebec, and Tennessee. *Xenolechia ceanothiae* differs by 11–12.5% (72–82 base pairs) from the other two species (which differed from each other by 6.85%, or about 45 base pairs). Intraspecific haplotype divergence was nil for *X. ceanothiae* and $\leq 0.5\%$ for the other two species.

Etymology. The species epithet, *ceanothiae*, is derived from the generic name of host, *Ceanothus*.

Placement of *ceanothiae*. Diagnostic characters of *Xenolechia* (Lee & Brown 2008a), which are shared by the new species, include the deeply bifid uncus, the absence of gnathos and valvae (or the latter undistinguishably fused with the vinculum), and hindwing veins M_3 and CuA_1 separate. However, none of these states is unique to the genus and the hindwing venation state is probably plesiomorphic. Placement of *ceanothiae* in *Xenolechia* is tentative and represents a best fit among currently recognized genera of Litini. The new species differs markedly from all other species of *Xenolechia* in several features of male and female genitalia, notably the slender, dorsally arched phallus

with a distinct, hinged, vertically oriented juxta, and rudimentary or absent signum. It is also hugely divergent in DNA barcode from either *X. ontariensis* or *X. aethiops*. This suggests that it may represent a distinct lineage which may warrant generic recognition. Although a phylogenetic analysis of the Litini showed strong support for the the monophyly of the *Xenolechia* (Lee & Brown 2008b), only one species out of eight described, *X. ontariensis*, was analyzed. A more encompassing species-level phylogenetic analysis would be required to re-assess generic limits.

Biology. Host: *Xenolechia ceanothiae* is a leaf-miner of *Ceanothus americanus* L. and *C. herbaceus* Raf. [Rhamnaceae].

Mine and larval behavior (Fig. 4). The mine is initiated at the leaf apex. It is full depth with the larva consuming all chlorophyll tissue between both epidermal surfaces. Frass is accumulated internally at the basal area. This frass area serves as a retreat when the larva is not feeding or disturbed. The mine is enlarged as a wide lobed track. As it develops, subsequent frass particles are aligned in long double rows laterad of the mine axis (Fig. 4). These rows guide the larva as it quickly retreats backwards to its basal frass retreat. This species feeds with its ventral side upward. Pupation was observed (RJP lot 0948) both inside and outside their mines.

Seasonal occurrence. *Xenolechia ceanothiae* was first recovered from the type locality in mid-September 1999. Since that recovery an additional 24 visits, at irregular times between mid-June and late October, were made. Seventeen visits were made between mid-June to early September without mines seen. They were only observed from mid-September into late October. Adults emerged only after wintering. It appears that *X. ceanothiae* has one generation per year in northeastern Lower Michigan. No adults were collected or observed under field conditions.

Parasitoid. *Hypomicrogaster ecdytolophae* (Muesebeck) (Braconidae).

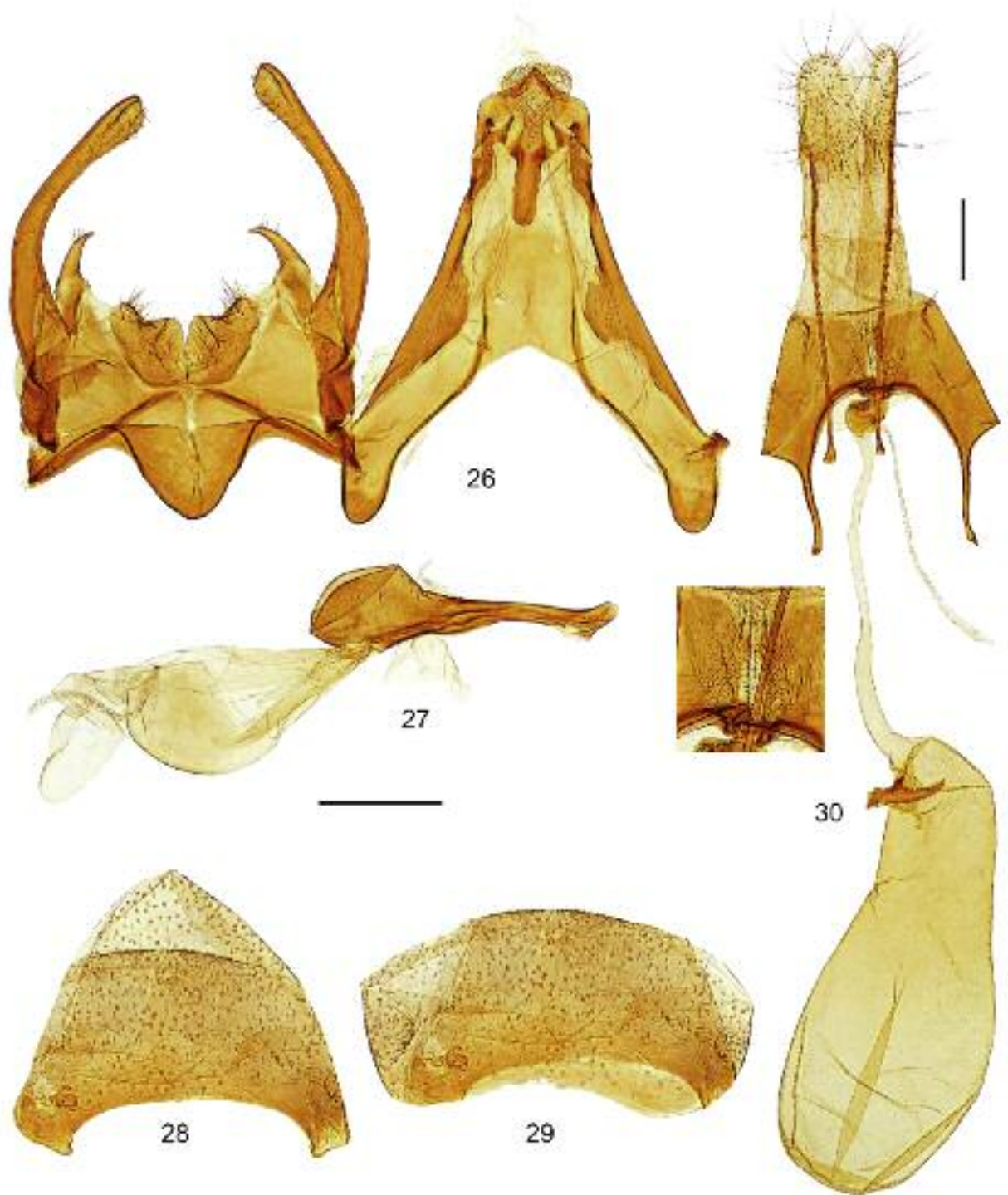
Distribution (Fig. 59). The species is recorded only from the type locality in upper Michigan but may be expected to occur more widely given that its larval host is distributed over the eastern half of North America; in Canada the host plant is restricted to southern Ontario and Quebec.

Gelechiinae: Gnorimoschemini

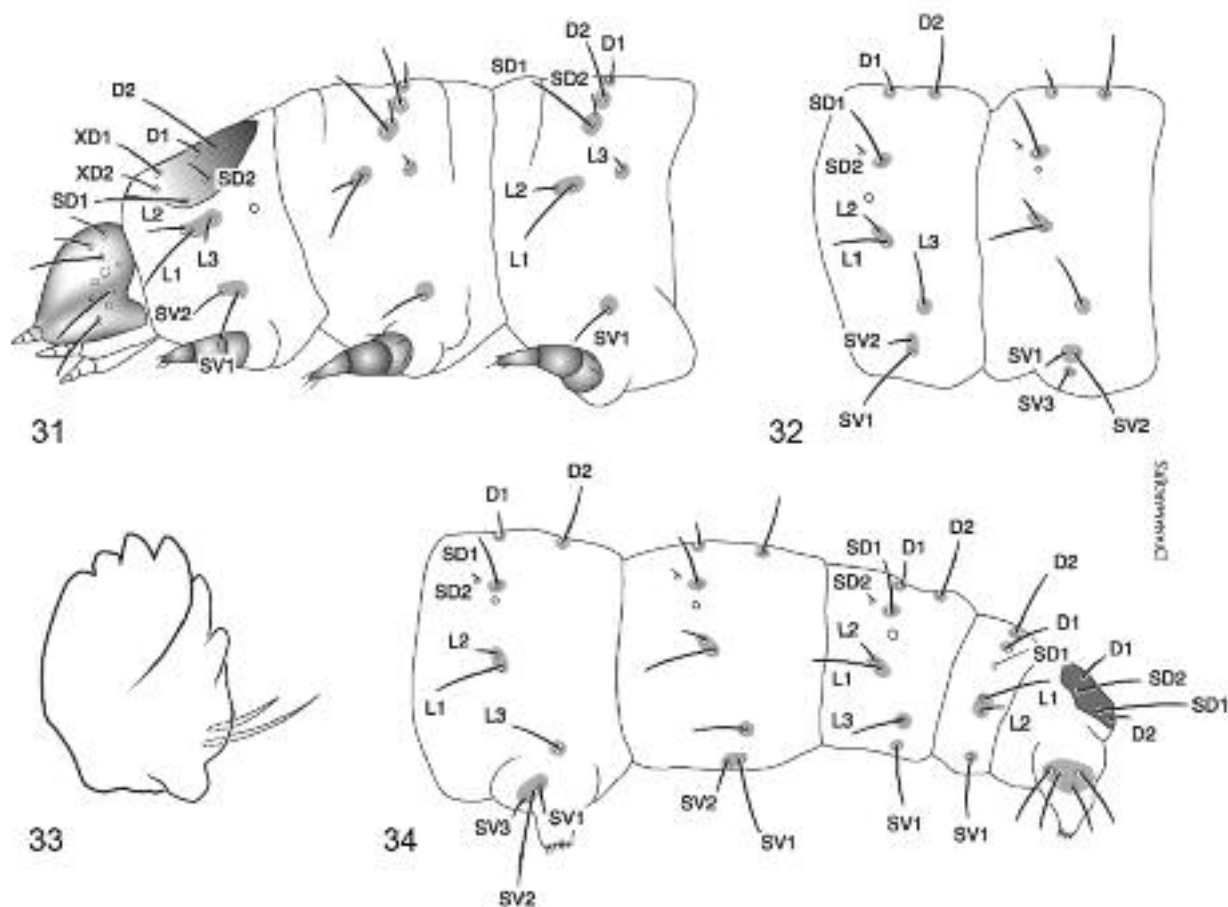
***Gnorimoschema shepherdiae* Priest, new species**

(Figs. 2, 5–6, 26–40)

Adult diagnosis. There are no distinguishing external characters to recognize members of



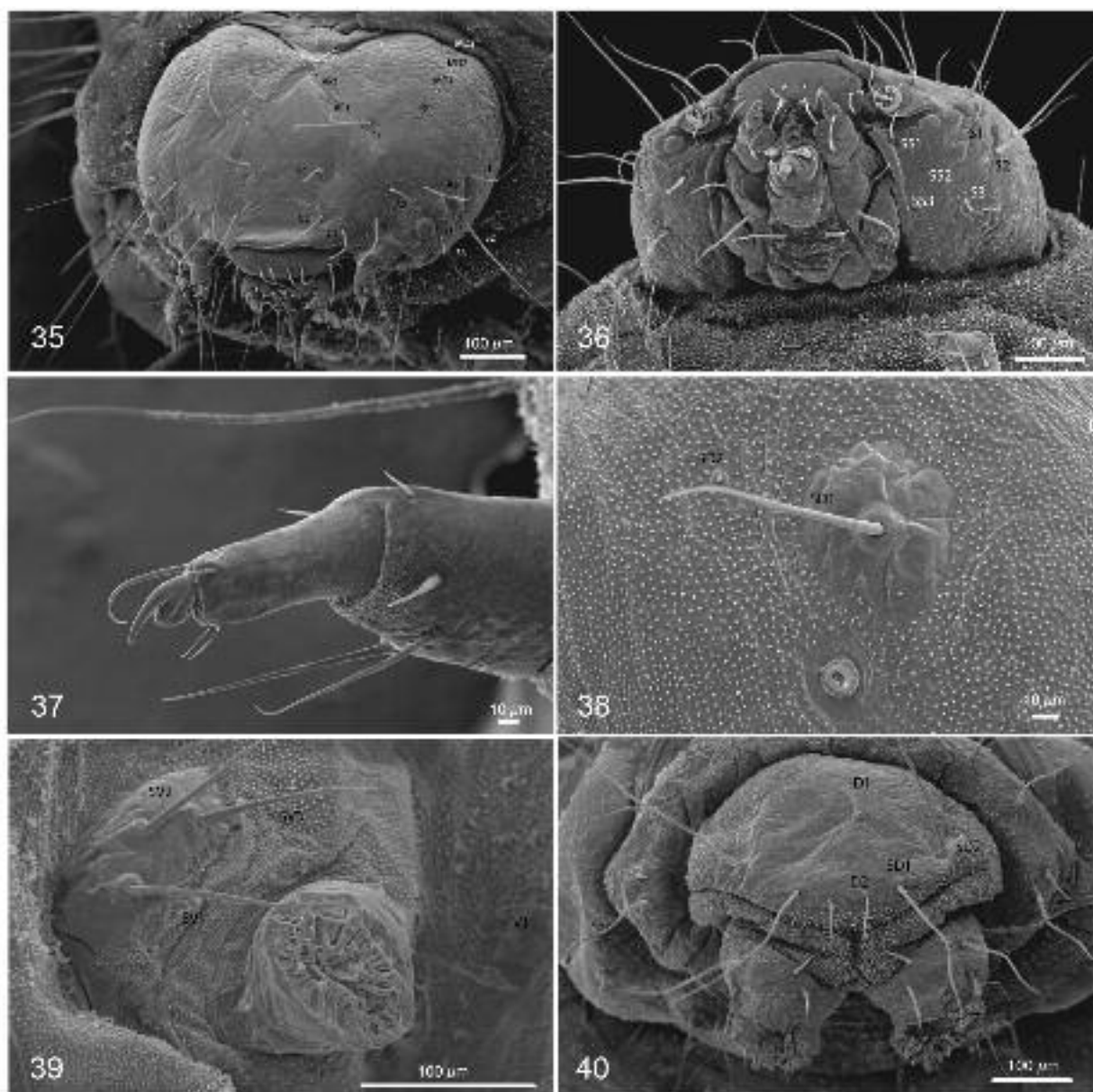
FIGS. 26–30. *Gnorimoschema shepherdiae* genitalia. **26.** Male genitalia, ventral view, with vinculum-valvae unrolled to the left (slide MIC5298, specimen CNCLEP00061397). **27.** Phallus. **28.** Eight tergum. **29.** Eight sternum. **30.** Female genitalia (slide MIC5931, specimen JD0263); inset, close-up view of ostium bursae area. Scale = 100 μ m.



FIGS. 31–34. *Gnorimoschema shepherdiae*, mandible and chaetotaxal maps. **31.** Head and T1–T3. **32.** A1–A2. **33.** Mandible. **34.** A6–A10.

Gnorimoschema, but the species share an overall more or less diagnostic configuration of the genitalia. In male genitalia, they are recognized by the combination of a medio-apically pointed uncus, tongue-like gnathos, markedly V-shaped tegumen from divergent pedunculi, incurved valva with a slight medial constriction and subclavate or clavate apex, sacculus lobes prominently developed, vincular processes reduced or stumpy, and phallus with a markedly bulbous base. In female genitalia, the antrum is not developed, the signum has a short and thick base and a thick spine and is near the point of inception of the ductus bursae. Most species of *Gnorimoschema* cannot be confidently identified from external aspect, and many display a tremendous amount of intraspecific variation in forewing pattern and colouration. However, the genitalia afford good differences and usually differ in a combination of features of proportions and shapes of structures that define species-specific, diagnostic appearances.

Among the numerous Nearctic species of *Gnorimoschema*, *G. shepherdiae* is most similar to *G. vibei* Wolff (known from Greenland and northern Quebec) in both male and female genitalia. In male *G. shepherdiae*, the distal process of the gnathos is very straight-sided, the sacculus is moderately incurved with the apex sharply pointed, and the vincular processes have an angulate margin and are separated by narrowly V-shaped median incision; in *G. vibei*, the distal process of the gnathos is slightly but distinctly tapered, the sacculus is sharply incurved with a rounded apex, the vincular processes have a slightly sinuate margin and a wide V-shaped incision. In female *G. shepherdiae*, S8 is transverse with the anterior margin roundly concave, the antrum is not prominent (indistinct), the corpus bursae is distinctly widened, ovoid in its anterior two-thirds, and the signum has a more slender, less curved hook; in *G. vibei*, S8 is elongate with the anterior margin forming a double concavity caused by a short but



FIGS. 35–40. *Gnorimoschema shepherdiae*, scanning electron micrographs of larva. **35.** Head chaetotaxy, frontal view. **36.** Head chaetotaxy, ventral view. **37.** Right tarsus on T2. **38.** SD1 and SD2 on A5, right side. **39.** Right proleg on A5. **40.** Anal plate chaetotaxy on A10.

distinctly protruded antrum, the corpus bursae is more narrow with the anterior third very slightly widened, and the signum has a thicker, more sharply curved hook.

We report here the first occurrence of *G. vabei* in Canada based on barcoded specimens from Kuujjuarapik in northern Quebec (CNC). This species was so far known only from western Greenland (Wolff 1964). New, unpublished information about its life history will be provided by in an upcoming book on the Lepidoptera of Greenland (Karsholt et al. in press).

Adult description. *Head:* Fronto-clypeus and vertex white, some scales agouti patterned with basal 2/3 white, tipped with brown with a narrow white margin. Scape white intermixed with brown scales or brown intermixed with few white scales; flagellomeres of flagellum basally brown, apically white on upper surface, white on undersurface. Ocellus behind antennal base along margin of compound eye. Outer surface of labial palpus with segment 2 brown intermixed with white scales along apical margin; scales agouti-pigmented, giving a “calico” pattern to ground color; scales divergent from midline on undersurface, forming a brushlike appearance; terminal segment with variable pattern, white with brown mid and subapical bands, or suffused; inner surface of labial palpus as above or paler. Proboscis white.

Thorax: Mesonotum and tegula with white scales tipped with brown. Legs calico patterned. Foreleg: femur brown; tibia with a suffuse white band slightly beyond base, a suffuse white band near middle, and a white tuft along apical margin; tarsomeres with a narrow white band along apical margin. Midleg with femur white intermixed with few brown scales; tibia with a suffuse white band slightly beyond base, a suffuse white band near middle, and a white band on apical end adjacent to paired spurs; tarsomeres as above. Hindleg with femur white; tibia with a suffuse white band slightly beyond base, a white band adjacent to middle pair of spurs, and a white band adjacent to apical pair of spurs; tarsomeres as above. Forewing (Fig. 2), length 5.0–6.3 mm ($n = 52$) calico patterned; brown intermixed with white and few grayish-orange scales; three suffuse white bands alternate from base with three bands (with brown scales intermixed with grayish-orange scales) to 2/3; distal 1/3 mostly white intermixed with white scales tipped with brown and brown scales and few grayish orange scales. Fringe scales white tipped with brown. Undersurface brown except for pale-brown fringe scales. Hindwing translucent pale brown.

Abdomen: Upper surface pale brown, undersurface white.

Male abdomen (Figs. 28–29). Tergum 8 subtriangular, weakly sclerotized, anteriorly roundly emarginate, antero-lateral angles inwardly directed. Sternum 8 transverse, about 2× wider than long, weakly sclerotized, posterior margin even rounded.

Male genitalia (Figs. 26–27). Tegumen with depth of anterior notch about two-thirds length of dorso-medial portion, apical part straight-sided and demarcated by constriction from rest of dorso-medial portion, pedunculi divergent forming broad V-shape. Uncus transverse, about 1.5× wider than long, apical margin medially produced into triangular point, sides parallel, without setae. Gnathos with short, triangular proximal arms, distal process tongue-shaped, parallel-sided. Culcitula developed, with dense, coarse microtrichiae. Vinculum transverse, about 1.8× wider than long, vincular processes short, hump-like, setose, medially separated by shallow, V-shaped incision, area around processes with wrinkled cuticle delineating an inverted trapezoid area. Saccus conical, broad, short, extended slightly anterad of antero-lateral angles of vinculum. Sacculus of valva pincer-like, inwardly curved, sharply pointed, extended to about half-length of cucullus, with a few sparse apical setae. Cucullus of valva incurved, apex extended slightly beyond apex of uncus, medial section constricted, apex somewhat dilated, with sparse, fine setae. Phallus with bulbous basal third, distal two-thirds straight with apex slightly upcurved and ended in short hook.

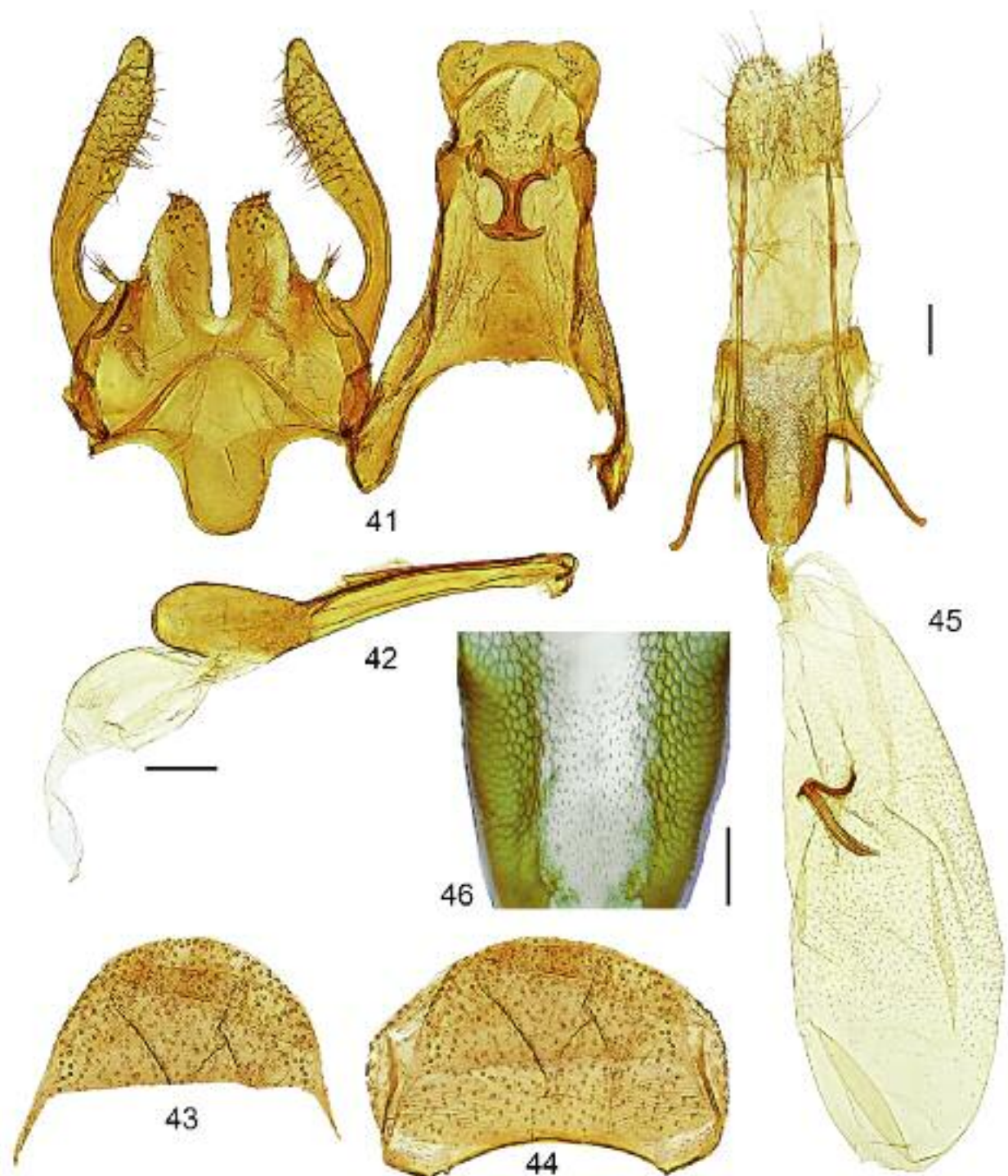
Female genitalia (Fig. 30). Ovipositor 1.8× length of S8 (to antero-lateral angle), papillae anales membranous. Anterior apophysis nearly straight, slightly shorter than S8. Posterior apophysis about 2.5× length of anterior one. S8 sclerotized, distal half transverse, anterior margin thickened, deeply, semi-circularly concave, depth of concavity about equal to length of distal half, antero-lateral angles prominent; postero-lateral angle with small, shallow invagination and a few very short setae; median area unmelanized, through-like, covered with very fine microtrichiae. Ostium bursae rimmed by extension of thickened S8 margin. Ductus bursae with membranous section about as long as S8 + ovipositor, with globular colliculum with sclerotized inner wall with insertion of ductus seminalis. Corpus bursae elongate-obovoid, broader in anterior two-thirds, wall membrane smooth, without microtrichiae nor spicules but with very fine, almost faint transverse wrinkles. Signum with thick, straight base and slightly curved, finely serrate hook, situated near inception ductus bursae.

Larva description (Figs. 31–40). Length 7.0–7.9 mm ($n = 8$). Body pale gray; head golden yellow except, clypeus, labrum, ecdysial line, genal and stemmatal areas, and dorso-posterior and ventro-posterior margins brown; thoracic legs and all pinacula brownish orange; prothoracic shield with a wide unpigmented area demarcating dorso-longitudinal axis, bisecting two pale golden-yellow halves, posterior and postero-lateral margins brown gradually becoming pallid anteriorly; anal shield pale golden yellow with a large brown spot anterior to D1 spiracle on T1 slightly larger than spiracles on A2–A7; spiracle on A8 about twice diameter of spiracles on A2–A7.

Head: (Figs. 31, 35–36): Epicranium slightly flattened dorso-ventrally; mouthparts semi-prognathous; an elongate, triangular frons demarcated by a frontal sclerite; sclerites widened distally, forming a broadly rounded ecdysial line; ecdysial suture short, bisecting a frontal sclerite disto-medially; epicranial notch deep forming two large hemispheres; AF2 slightly longer than AF1; AF1 and AF2 equidistant to distance between AF1 and P1; P1 slightly above and about 3× P2; distance from F1 to AF1 nearly equidistant to distance between F1 and C2; C2 slightly longer than C1; A3 above stemma 2, about 5–6× A2, and about 1/3 longer than A1; six stemmata in a C-shaped pattern, with stemma 3–4 approximate; S3 ventral and slightly posterior to S2; S2 approximate and below stemma 1; S1 below area between stemmata 3–4; L1 posterior to stemma 1; SS1 beneath area between antenna and condyle of mandible; mandible with three apical dentitions, two subequal dentitions along dorsal surface, and two subequal setae near condyle (Fig. 33); SS2 and SS3 approximate, both beneath area between stemmata 5–6; labrum with six pairs of setae, two equal median pairs, two equal fronto-marginal pairs, and two subequal latero-marginal pairs; SS2 and SS3 approximate, both beneath area between stemmata 5–6.

Thorax (Figs. 31, 37): Prothoracic shield with SD1 about 2–2.5× longer than XD2 and XD1; XD2 anterior to SD1 and XD1; distance between XD2 and XD1 about 2× distance between XD2 and SD1; SD2 about 1/4 as long as D2; distance between SD1 and SD2 equal to distance between SD1 and XD2; D2 slightly shorter than SD1, posterior to SD2 and D1; distance between D2 and SD2 at least twice distance between D2 and D1; D1 slightly shorter than SD2, closer to median longitudinal axis than XD1; L-group pinaculum and L-group diagonally oriented, with L2 more dorsal than L1 and L3 or L1 slightly lower than L2 and L3; L1 about 2.5× longer than L2, with L3 slightly shorter than L2, on same pinaculum anterior to spiracle; SV-group bisetose, with SV2 1/3–1/2× as long as SV1; V1s approximate, close to a transverse line across posterior margins of coxae (not shown). T2–T3 (Fig. 31): D2 about 2× length of D1, each seta on separate pinaculum, with D2 pinaculum slightly larger than D1 pinaculum; SD1 3–4 times of SD2, each seta on same pinaculum, on slight diagonal, anterior to D-group pinaculum; L1 2–2 1/2× longer than L2, each seta on same pinaculum, on acute diagonal, anterior to SD-group pinaculum; L3 slightly shorter than L2, on pinaculum posterior to area between SD-group pinaculum and L-group pinaculum, and slightly anterior to or in straight line with SV1; V1s between coxae near middle, about 2–2 1/2 × distance between V1s on T1 (not shown); tarsus (Fig. 37) with two pairs of setae ventro-posterior and dorso-posterior to claw; ventro-posterior setae equal in lengths, dorso-posterior pair subequal, with a broad hooklike seta on outer surface.

Abdomen: A1–A2 (Figs. 32, 34, 38–40): D2 2–2 1/2 × longer than D1; SD1 on pinaculum dorso-posterior to spiracle; SD2 minute, dorso-anterior to SD1 (Fig. 32); spiracle about 3× distance from SD1 on A1 than on A2; L1 2–2 1/2 × longer than L2, each seta on same pinaculum; L-group pinaculum on A2 at least twice distance from spiracle as distance from L-group pinaculum to spiracle on A1; L3 about equal in length to L1, in straight line with or slightly anterior to D2; SV-group on A1 bisetose, SV1 about 3× length of SV2, each seta on same pinaculum, slightly posterior to L-group pinaculum (L1–L2); SV-group on A2 trisetose, SV1 and SV2 on same pinaculum, parallel with longitudinal body axis; SV3 on separate pinaculum; distance between V1s as in T2 and T3 (not shown). A3–A6 (Fig. 34): as above except, SV-group pinaculum directly above spiracle, SV-group on a sclerotized band at base of proleg, and crochets uniserial and biordinal; A7–A10 (Fig. 34, 40): as above except, SV-group bisetose, with SV1 2× length of SV2, and V1s slightly closer; A8 as above except, SV-group unisetose; A9 with all setae in near straight line, D2 about 2× D1; SD1 hairlike, shorter than D2; L-group bisetose and on same pinaculum, with L1 at least 3× length of L2 (setae and pinaculum slightly diagonal); SVs and V1s as above (V1s not shown); A10 (Figs. 34, 40): anal plate with SD2 and SD1 at least 2× distance apart than distance between SD1 and D2; SD2 and SD1 of equal lengths, about 4–5× D2; D2 convergent; D1 anterior to space between D2 and SD1; crochets biordinal.



FIGS. 41–46. *Scrobipalpula manierreorum* genitalia. **41.** Male genitalia, ventral view, with vinculum-valvae unrolled to the left (slide MIC5722, specimen POHL-10-00172). **42.** Phallus. **43.** Eight tergum. **44.** Eight sternum. **45.** Female genitalia (slide MIC5784, specimen 08BBLEP-00325). **46.** Close-up view of antrum near ostium bursae. Scale = 100 μ m, except inset = 50 μ m.

Pupa. Undescribed. Although pupal exuviae were obtained during this study, we prefer not to describe this stage until freshly preserved pupae are available.

Type material. Holotype ♂, “MICHIGAN: Presque Isle Co[unty], NE, T34N-R07E, S 14, [= 45.349°N, 83.541°W], Em[er]g[e]d: 15 Feb. 2006, Sur[eyor] [= Collector]: RJ Priest”, “Reared Ex. *Shepherdia canadensis*, Rec[o]l[y]red [date collected]: 25 Oct. 2005, Lot: RJP1688.4”, [specimen #] “USNMENT 00719474”, “DNA 2011” [blue label], “♂ Genitalia Slide by D. Adamski, USNM 83549”, [green label], [pupal exuvium attached to pin] (USNM).

Paratypes: 13 ♂, 18 ♀. MICHIGAN: 2 ♂, 6 ♀, same data as holotype except: 1 ♂, em. 15 Feb 2006, larva 25 Oct 2005, lot RJP1688.5 [metathorax and abdomen attached to paper card beneath specimen] (MSUC); 1 ♂, em. wintered, larva 12 Oct 2007, lot RJP1854.5, specimen # USNMENT 00719450, genitalia slide by D. Adamski, USNM 83550 (USNM); 1 ♀, em. 16 Feb 2006, larva 25 Oct 2005, lot RJP1688.44, specimen # USNMENT 00719452, genitalia slide by D. Adamski, USNM 83551 (USNM); 1 ♀, em. 16 Feb 2006, larva 25 Oct 2005, lot RJP1688.13 [pupal exuvium in gelatin capsule beneath specimen] (MSUC); 1 ♀, em. 20 Jul 2007, larva 29 Jun 2007, lot RJP1815.1 [pupal exuvium attached to minuten beneath specimen] (MSUC); 1 ♀, em. wintered, larva 24 Aug 2006, lot 1743.1 [pupal exuvium attached to minuten beneath specimen] (MSUC); 1 ♀, T34N-R07E, S 15 [= 45.343°N, 82.572°W], em. 1 Aug 2002, larva 18 Jul 2002, lot RJP1305.1, specimen # USNMENT 00719451, genitalia slide by D. Adamski, USNM 83552, USNM (USNM); 1 ♀, em. 29 Jul 2002 larva 18 Jul 2002, lot RJP1305.2 [pupal exuvium attached to minuten beneath specimen] (MSUC). ALBERTA: 1 ♀, Banff Nat Pk, Storm Mountain, low alpine dry slope, adjacent to train track and Bow River, 15–20 Jun 2012, BIOBus 2012, 2 malaise traps, specimen # BIOUG03504-A02 (CNC); 1 ♂, Banff Nat Pk, 2 km North from Johnston Lake, 6–13 Jul 2012, Whittington, wetland, lodgepole pine/spruce, specimen # BIOUG06777-A01 (CNC); 1 ♀, Jasper Nat Pk, dunes, 18 May 2006, J. J. Dombroskie, C. Schmidt, specimen # JD0263 (CNC); 1 ♂, Jasper Nat Pk, dunes, 18 May 2006, J. J. Dombroskie, C. Schmidt, specimen # JD0182 (CNC); 1 ♀, Jasper Nat Pk, highway 16 / 93A junction, 20–27 Jun 2012, Clayton SyFchuk, thinned out lodgepole pine stand, valley basin, specimen # BIOUG02884-D11 (CNC); 1 ♀, Jasper Nat Pk, highway 16 / 93A junction, 4–11 Jul 2012, B. Sharp, thinned out lodgepole pine stand, valley basin, specimen # BIOUG03585-B07 (CNC); 1 ♀, Jasper Nat Pk, Palisades Centre, 02 Jun 2007, J. J. Dombroskie, specimen # JD2414 (CNC); 1 ♀, Jasper Nat Pk, Palisades Centre, 02 Jun 2007, J. J. Dombroskie, specimen # JD2415 (CNC); 1 ♀, Jasper Nat Pk, Whistlers Cmpgrd., Pine forest, 23 Jun 2010, BIOBus 2010, UV Light Trap, specimen # 10BBCLP-3075 (CNC); 1 ♂, Jasper Nat Pk, Whistlers Cmpgrd., Pine forest, 27 Jun 2010, BIOBus 2010, UV Bucket Trap, specimen # 10BBCLP-3108 (CNC); 2 ♂, Nordegg, 12 Jun 1921, J. McDunnough, specimens # CNCLEP00084604 (not barcoded), genitalia slide MIC 6363, # CNCLEP00090702 (not barcoded), genitalia slide MIC 6311 (CNC); 1 ♀, Nordegg, 13 Jun 1921, J. McDunnough, specimen # CNCLEP00090701 (not barcoded), genitalia dissection MIC 6310 (CNC); 1 ♀, Nordegg, 19 Jun 1921, J. McDunnough, specimen # CNCLEP00090703 (not barcoded), genitalia slide MIC 6312 (CNC); 1 ♀, Nordegg, 20 Jun 1921, J. McDunnough, specimen # CNCLEP00084579 (not barcoded), genitalia slide MIC 6350 (CNC); 1 ♀, Tolman Bridge, E bank of Red Deer River, 24 Jul 2003, J.-F. Landry, at mercury light, specimen # CNCLEP00007388 (CNC); 1 ♂, Abraham Lake, Allstones Lake trail, 01 Jul 2007, Pohl, G. R., specimen # POHL-10-00147 (CNC); 1 ♀, Wood Buffalo Nat Pk, Benchmark weather station, 31 May–07 Jun 2012, Nicole Labine, aspen stand, specimen # BIOUG05849-A05 (CNC). BRITISH COLUMBIA: 1 ♂, Lumby, 15 Jul 1957, Freeman & Lewis, specimen # CNCLEP00087115 (not barcoded), genitalia slide MIC 7029 (CNC). MANITOBA: 1 ♂, Churchill, 13 km E Churchill, Eastern Creek, 16 Jul 2007, P.D.N. Hebert, specimen # 07PROBE-10061, genitalia slide MIC 5442 (CNC); 1 ♂, Churchill, summer 2007, P.D.N. Hebert, specimen # 07PROBE-10739 (CNC). QUEBEC: 1 ♂, Gatineau, Aylmer, 48 rue Notre-Dame, 13 Jun 1996, J.-F. Landry, at MVL, specimen # CNCLEP00086250, genitalia slide MIC 4656 (CNC). YUKON: 1 ♂, 2 km N Carcross, sand dunes, 23 Jun 2004, B.C.

Schmidt, specimen # CNCLEP00061397, genitalia slide MIC 5928 (CNC).

Molecular data (Table 1; Fig. 60). BIN = BOLD:AAI5479. Full barcodes from 20 specimens, including the holotype and three paratypes of *G. shepherdiae* were obtained which were compared to those of *G. saphirinella* (BOLD:AAI5502) and *G. vibei* (BOLD:AAI0935). We analyzed barcodes of 8 specimens of *G. vibei* from Greenland and Quebec. For *G. saphirinella*, we analyzed 20 barcodes of specimens from Arizona, California, Colorado, Kansas, Mississippi, New Mexico, Oklahoma, and Texas. *Gnorimoschema shepherdiae* differs by 8.7% (57 base pairs) from *G. vibei* and 10.9% (71 base pairs) from *G. saphirinella*. The two ‘outgroup’ species differ from each other by 9.1%, or about 60 base pairs), whereas intraspecific haplotype variation was <1%.

Etymology. The species epithet, *shepherdiae*, is derived from the generic name of host, *Shepherdia*.

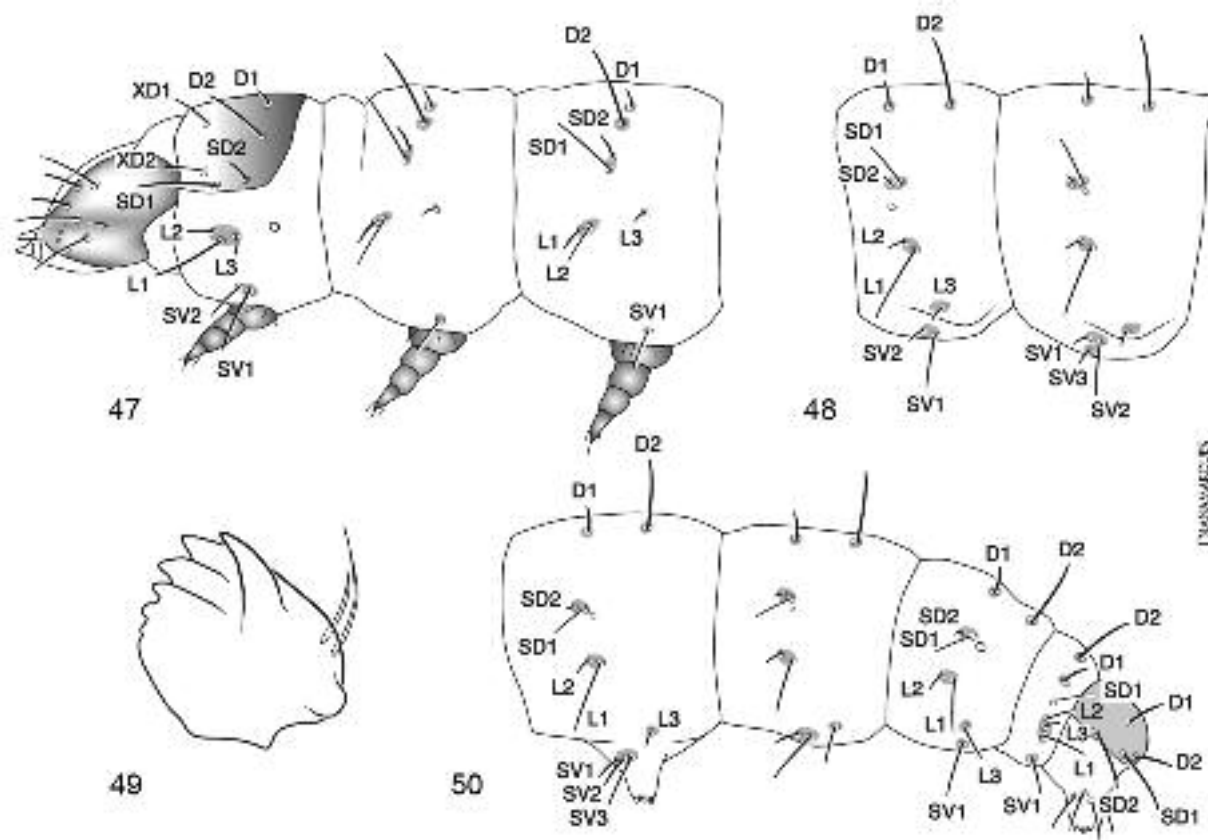
Biology. Host: *Gnorimoschema shepherdiae* is a leaf-miner of *Shepherdia canadensis* (L.) Nutt. (Elaeagnaceae).

Mine and larval behavior (Figs. 5–6). The mine usually begins at the midvein. Frass is concentrated at the base forming a retreat for the larva when not feeding or when it is disturbed (Fig. 5) (rearing lot RJP1828.1). Expansion of this full depth mine continues as a wide track with a series of short lobes. A shelter is constructed within the base of the mine where frass is concentrated. When the shelter is large enough to conceal the larva subsequent frass is arranged into two parallel rows along the primary mine axis (Fig. 6). These rows provide a guide for the larva to quickly retreat into its frass tube. The mature mine is tentiform with many small wrinkles on the upper surface. From early instar to mature larva, feeding occurs with the larval body ventral side upward. Most leaves can support full development of only one larva although two may mature in larger leaves. When the larvae of the June–July generation stop feeding they exit via a crescent-shaped cut at the terminus of their mines. An off-white cocoon is constructed presumably in the soil or leaf litter prior to pupation. Larvae of the next generation overwinter in their mines and exit during the spring.

Seasonal occurrence. Two generations were observed in Michigan. Larvae occurring from late June to mid-July produced adults by late July. Larvae occurring from late August to early October produced adults only after overwintering. The timing of observations of larval mines in the field in Michigan and flight periods of moths collected in Canada suggests that *Gnorimoschema shepherdiae* is bivoltine.

Parasitoids. *Pnigalio maculipes* (Crawford) (Eulophidae) and *Agathis gibbosa* (Say) (Braconidae).

Distribution (Fig. 59). The species is here recorded from Alberta, British Columbia, Manitoba, Michigan, Quebec, and Yukon. Its host plant is widespread across Canada and the northern half of United States and known records suggest that *G. shepherdiae* may be distributed as widely as its host.



FIGS. 47–50. *Scrobipalpula manierreorum*, mandible and chaetotaxal maps. 47. Head and T1–T3. 48. A1–A2. 49. Mandible. 50. A6–A10.

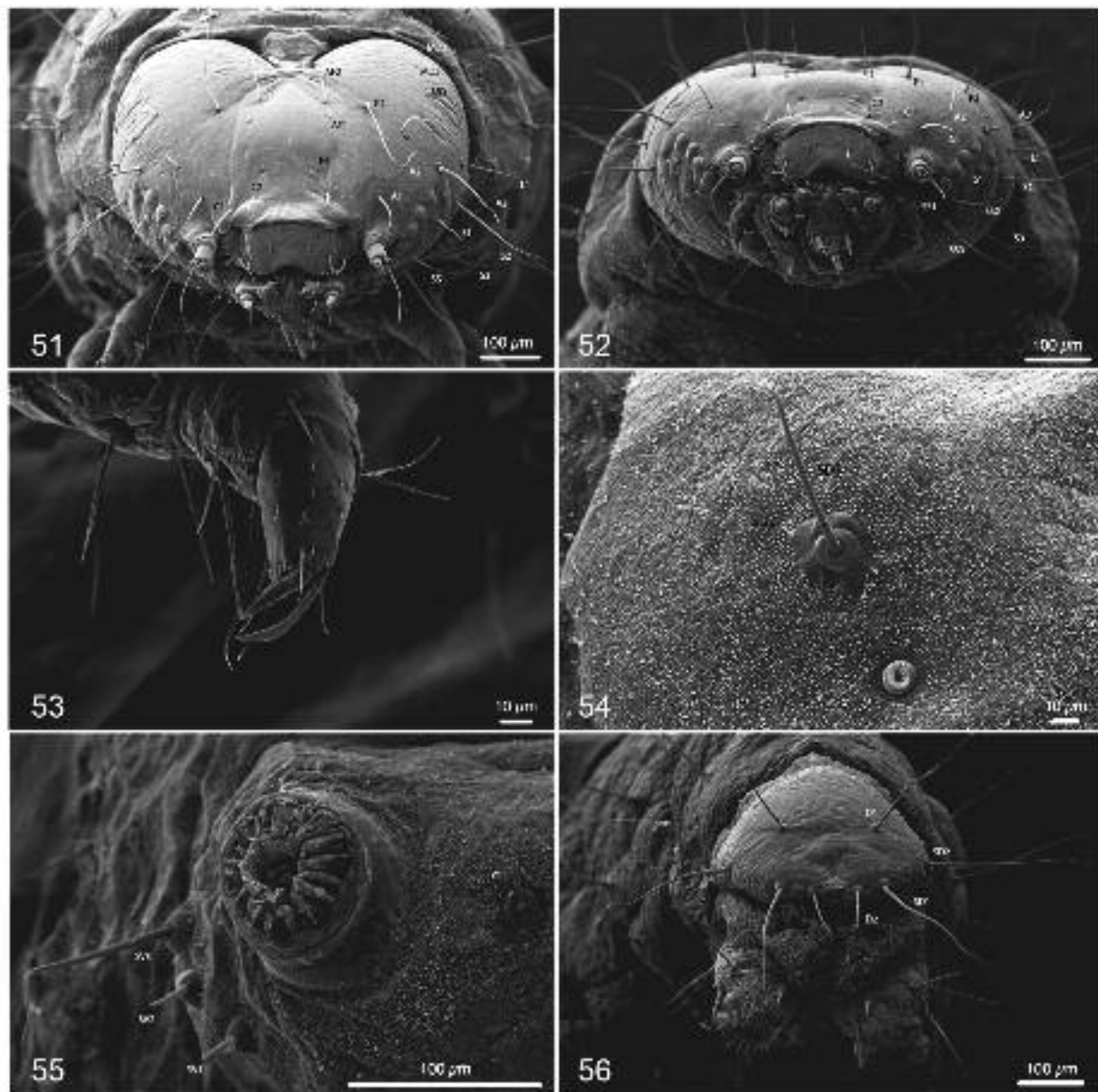
***Scrobipalpula manierreorum* Priest, new species**
(Figs. 1, 7–8, 41–58)

Adult diagnosis. In male genitalia, members of *Scrobipalpula* are recognized by the shape of the distal process of the gnathos which is expanded, forming an ax-blade-like structure; the paired processes of the vinculum are broad, elongate, extended to about 1/3 the length of the valva (cucullus) with a deep, median incision; the sacculus is very short, reduced, stub-like. There are no external diagnostic characters to recognize members of this genus.

Scrobipalpula manierreorum is similar to *S. artemisiella* (Kearfott) in forewing pattern but the latter has markedly different genitalia in both sexes. The male and female genitalia are most similar to those of *S. polemoniella* (Braun) [whose larvae are leaf-miners on *Polemonium*, (Polemoniaceae) and which probably overlaps geographically where both food plants occur]. *Scrobipalpula manierreorum* has the uncus slightly wider than long with the distal edge of transversely

straight; the gnathos distal process medially narrow and concave and the apex narrowly transverse; the vincular processes with a narrowly U-shaped median incision; and a broad, short saccus about one-third as wide as the distance between the antero-lateral angles of the vinculum and broadly rounded lateral margins; *S. polemoniella* differs mostly in the more triangular vincular processes separated by a V-shaped median incision, and straighter lateral margins of the vinculum.

In female genitalia, *Scrobipalpula* have the antrum funnel-like and extended to half or nearly the length of the anterior apophyses with the surface laterally covered with mesh-like microsculpture and medially with dense, fine microtrichiae, the corpus bursae is proportionally large and elongate (as long or longer than the 8th segment and extended ovipositor combined) with a slender, thorn-like signum with a slender base situated slightly posterad of the middle of the bursa. The mesh-like microsculpture is also present in several species of *Scrobipalpa* but differently distributed, and the antrum is not extended into an elongate funnel.

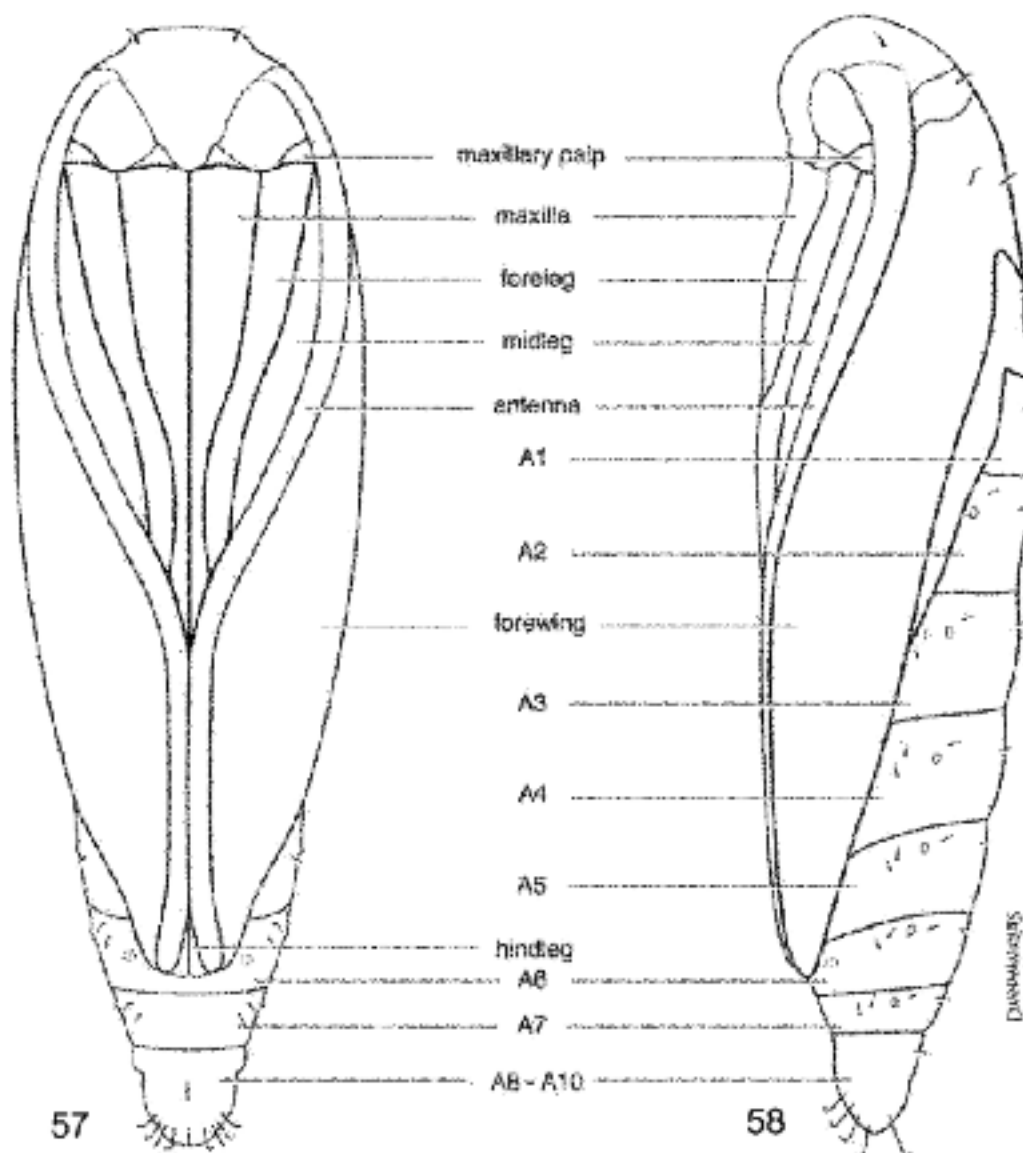


FIGS. 51–56. *Scrobipalpula manierreorum*, scanning electron micrographs of larva. **51.** Head chaetotaxy, frontal view. **52.** Head chaetotaxy, ventral view. **53.** Left tarsus on T3. **54.** SD1 and SD2 on A4, left side. **55.** Left proleg on A3. **56.** Anal plate chaetotaxy

Scrobipalpula manierreorum females have the antrum large and longer than S8 with anterior end somewhat rounded and only slightly narrowed; the corpus bursae very large, oblong, longer than the combined length of S8 and the extended ovipositor; a very short, slightly dilated colliculum; and divergent anterior apophyses. In *S. polemoniella* the antrum is triangular in outline and pronouncedly narrowed anteriorly and about the length of S8, the colliculum is more elongate, and the corpus bursae is narrowly oblong and subequal to the combined 8th segment + ovipositor.

Adult description. *Head:* Fronto-clypeus white. Vertex with agouti-patterned scales, with basal 2/3 white, tipped with brown with a narrow white distal margin. Scape of antenna with brown scales tipped with white, flagellomeres of flagellum dark brown basally, pale brown apically. Ocellus behind antennal base along margin of compound eye. Outer surface of labial palpus with segment 2 white intermixed with brown scales tipped with brown; terminal segment brown basally and apically with a broad white band between; inner surface as above but paler. Proboscis white.

Thorax: Mesonotum and tegula with agouti-patterned scales. Legs calico patterned. Foreleg: femur brown; tibia with a suffuse white band slightly beyond base, a suffuse white band near middle, and a white tuft along apical margin; tarsomeres with a narrow white band along apical margin. Midleg with femur brown intermixed with few white scales brown scales; tibia with a suffuse white band slightly



FIGS. 57–58. *Scrobipalpula manierreorum*, pupa. 57. Ventral view. 58. Lateral view.

beyond base, a suffuse white band near middle, and a white band on apical end adjacent to paired spurs; tarsomeres as above. Hindleg with femur white; tibia with a suffuse white band slightly beyond base, a white band adjacent to middle pair of spurs, and a white band adjacent to apical pair of spurs; tarsomeres as above. Forewing (Fig. 3), length 3.7–6.5 mm ($n = 39$) with white scales tipped with dark brown intermixed with brown, white, and grayish-orange scales; cell with two short, dark-brown streak, one near middle, one near distal end; a broad, suffuse, grayish-orange streak extending from base to apex. Fringe agouti. Underside brown except, fringe pale brown. Hindwing translucent pale brown.

Abdomen: Pale brown on upper surface, white on undersurface.

Male abdomen (Figs. 43–44). Tergum 8 transversely semicircular, wider than long, antero-lateral angles prolonged into short, thin, tapered extensions, without coremata (removed by dissection?). Sternum 8 transversely subtrapezoidal, posterior margin evenly convex, anterior margin shallowly, roundly emarginate.

Male genitalia (Figs. 41–42). Tegumen with pedunculi slightly longer than half length of dorso-medial portion, depth of anterior notch about 0.5 length of dorso-medial portion, its width slightly longer than length of dorso-medial portion. Uncus transversely subquadrate, posterior margin straight, anterior margin concave, lateral angles rounded, ventrally with paired patches of short setae. Gnathos with distal process hatchet-like, narrow, medial stem elongate and constricted, basal arms short, articulated to apical margin of tegumen. Vinculum transversely broad, about 2.5× wider than long (exclusive of vincular processes). Saccus tongue-shaped, short, broadly rounded, about one-third as wide as distance between antero-lateral angles of vinculum and broadly rounded lateral margins. Vincular processes about as long as vinculum, extended to about half length of valvae, with narrow, U-shaped median incision (gap), apex outwardly mucronate, distal upper surface with several short, sparse setae. Cucullus of valva extended slightly beyond apex of uncus, basal third incurved, distal two-thirds moderately dilated, setose; sacculus of valva

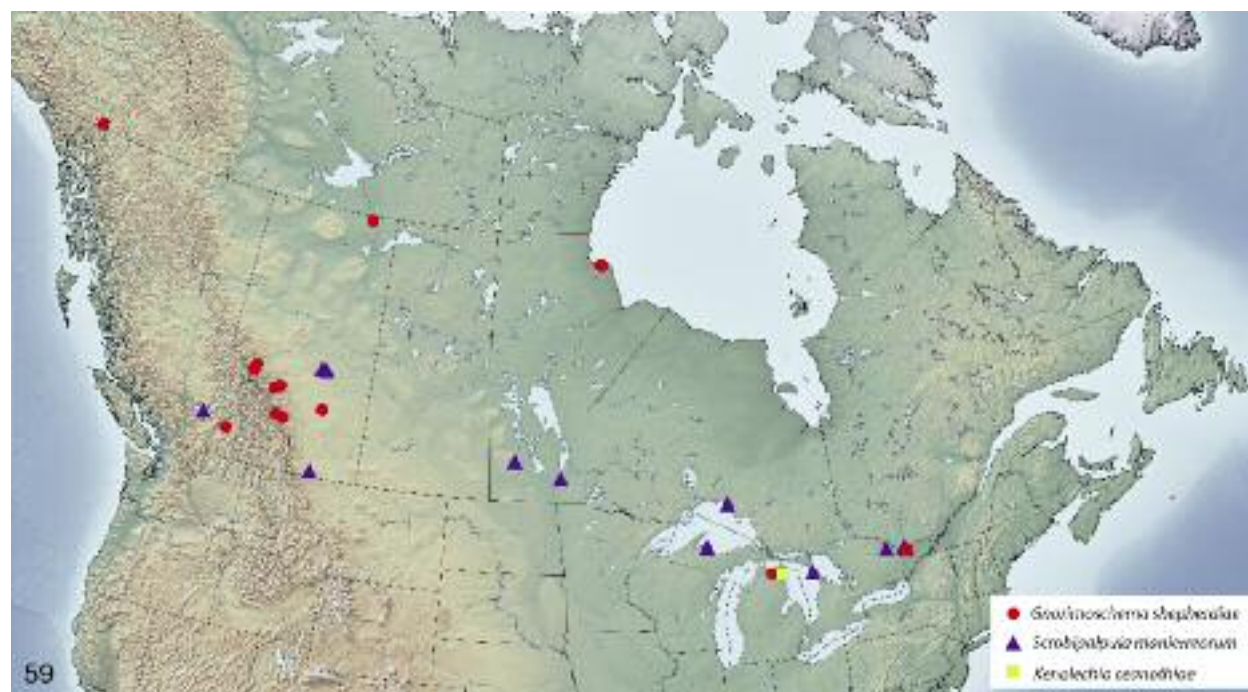


FIG. 59. Distribution map showing known localities of the three new species. The type locality of both *G. shepherdiae* and *X. ceanothiae* is the same in northern Michigan but the symbols were slightly offset so that both are visible.

very short, stubby, apically setose. Phallus with moderately dilated basal third, distal two-thirds very slightly arched, junction between swollen base and narrower distal part angulate, apex split into pair of downcurved hooks.

Female genitalia (Figs. 45–46). Ovipositor nearly 6× length of S8 (exclusive of antrum). Apophyses anteriores slightly curved, divergent, with slightly widened base. Apophysis posterioris about 3.4× length of apophysis anterioris, very thin, straight. Segment 8 slightly transverse, 1.5× wider than long. S8 laterally sclerotized with surface longitudinally wrinkled, medially membranous with dense, fine microtrichiae extended onto antrum surface. Antrum prominently developed, elongate-conical, extended nearly to apex of anterior apophyses, anterior end slightly roundly narrowed, lateral surface bulged into ridges covered with mesh-like microsculpture, medial area through-like and covered with dense, posteriorly directly microtrichiae. Ostium bursae situated at anterior end of antrum. Ductus bursae very short, < 1/2 length of antrum, internal wall with sclerotization (colliculum). Corpus bursae very large, oblong, slightly longer than combined length of S8 and extended ovipositor, inner surface covered with very fine, sparse spicules except in anterior 1/4. Signum slender, thorn-like, slightly curved, with slender, sharply curved base, and situated slightly posterad of middle of corpus bursae.

Larva description (Figs. 47–56). Length 5.5–8.2 mm ($n = 7$). Body pale gray; head golden yellow except, clypeus, labrum, ecdysial line, genal and stemmatal, and dorso-posterior and latero-posterior margins brown; thoracic legs and all pinacula brownish orange; prothoracic shield with a wide unpigmented area demarcating dorso-longitudinal axis, bisecting two pale golden-yellow halves, posterior and postero-lateral margins brown gradually becoming pallid anteriorly; anal shield pale golden yellow; spiracle on T1 slightly larger than spiracles on A2–A7; spiracle on A8 about twice diameter of spiracles on A2–A7.

Head (Figs. 47, 51–52): Epicranium slightly flattened dorso-ventrally; mouthparts semi-prognathous; an elongate, triangular frons demarcated by a frontal sclerites; sclerotized widened distally, forming a broadly rounded ecdysial line; ecdysial suture short, bisecting

adfrontal sclerites distomedially; epicranial notch deep forming two large hemispheres; AF2 at least 4× longer than AF1, distance between AF2 and AF1 slightly greater than distance between AF1 and P1; P1 about 3× and slightly above P2; distance from F1 to AF1 twice distance of distance from F1 and C2; C2 and C1 about equal in lengths; A3 above stemma 1, about 5–6× A2 and about 1/3 longer than A1; six stemmata in a C-shaped pattern, with stemma 1–5 approximate; S3 anterior, in vertical line with, or posterior S2; S2 approximate below area between stemmata 1–2; S1 below area between stemmata 2–3; L1 posterodorsal to stemma 1; SS1 beneath area between antenna and condyle of mandible; mandible broadly curved dorsally, with three apical dentitions, one subapical dentition, and two subequal setae at base near condyle (Fig. 49); labrum with six pairs of setae, two equal median pairs, two equal fronto-marginal pairs, and two subequal latero-marginal pairs; SS2 and SS3 approximate, both beneath area between stemmata 5–6.

Thorax (Figs. 47, 53): Prothoracic shield with SD1 about 1/3× longer than XD2 and XD1; XD2 and XD1 equal in lengths; XD2 and XD1 in straight line, slightly anterior to SD1; distance between XD2 and XD1 about 3× distance between XD2 and SD1; D2 about 4× longer than SD2; D1 slightly shorter than SD2, posterior to SD2 and D2; distance between D2 and D1 slightly shorter than distance between D2 and SD2; D1 closer to median longitudinal axis than XD1; L-group with L2 and L3 flanking L1, with L1 equidistant and ventral to both setae; pinaculum anterior and slightly ventral to spiracle; L1 at least 2× longer than L2, with L3 slightly shorter than L2; SV-group bisetose, with SV2 1/3–1/2 as long as SV1; V1s along a transverse line across posterior margins of coxae, separated about 1/4× less than distance of V1s on T2–T3 (not shown); tarsus (Fig. 53) with two pairs of setae ventroposterior and dorsoposterior to claw; ventroposterior setae equal in lengths, dorsoposterior pair subequal, with a broadened seta with an inwardly-curved, slightly flattened apical half.

T2–T3 (Fig. 47): D2 about 4–5× length of D1, each seta on separate pinaculum, with D2 pinaculum slightly larger than D1 pinaculum; SD1 3× length of SD2, each seta on same pinaculum, on



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TABLE 1. Mean sequence divergence (K2P) for the barcode region of the COI gene for the three new species described herein and three pairs of closely allied species. Shaded diagonal cells indicate mean intraspecific divergence.

<i>Xenolechia</i>	<i>ceanothiae</i>	<i>aethiops</i>	<i>ontariensis</i>
<i>ceanothiae</i> (n=3)	0	-	-
<i>aethiops</i> (n=14)	12,52	0,52	-
<i>ontariensis</i> (n=26)	11,02	6,85	0,26
<i>Gnorimoschema</i>	<i>saphirinella</i>	<i>vibei</i>	<i>shepherdiae</i>
<i>saphirinella</i> (n=20)	0,91	-	-
<i>vibei</i> (n=8)	9,15	0,28	-
<i>shepherdiae</i> (n=20)	10,9	8,72	0,45
<i>Scrobipalpula</i>	<i>tussilaginis</i>	<i>sacculicola</i>	<i>manierreorum</i>
<i>tussilaginis</i> (n=7)	0,17	-	-
<i>sacculicola</i> (n=15)	3,69	0,23	-
<i>manierreorum</i> (n=21)	5,03	4,76	0,14

slight diagonal, anterior to D2 pinaculum; L2 2–2 1/2× longer than L1, each seta on same pinaculum, on acute diagonal, anterior to SD-group pinaculum; L3 slightly shorter than L1, on pinaculum posterior to area between SD-group pinaculum and L-group pinaculum, and slightly anterior to or in straight line with SV1; V1s between coxae near middle. (not shown).

Abdomen: A1–A2 (Figs. 48, 50, 54–56): D2 2–2 1/2 times longer than D1; SD1 on pinaculum dorso-posterior to spiracle on A1, dorso-anterior to spiracle on A2, with distance between SD1 and spiracle at least 2× on A1 than on A2; SD2 minute, on same pinaculum as SD1 (Figs. 48, 50, 54); SD1 at least twice distance farther from spiracle on A2 than on A1; L1 about 4× longer than L2, each seta on same pinaculum, with L2 posterior to spiracle on A1 and in vertical line to spiracle on A2; L3 about equal in length to L2, in straight line with or slightly anterior to D2, posterior and slightly dorsal to SV-group; SV-group on A1 diagonally oriented, bisetose, SV1 about 2× length of SV2, each seta on same pinaculum, posterior to L-group pinaculum (L1–L2); SV-group trisetose on A2, SV1 and SV2 diagonally orientated on same pinaculum; SV3 on separate pinaculum; distance between V1s as in T2 and T3 (not shown). A3–A6 (Figs. 50, 55): as above except, SV-group on a sclerotized band at base of proleg; crochets uniserial, uniordinal, in a circle, decreasing in size laterally. A7–A10 (Figs. 50, 56): as above except, SV-group bisetose, and V1s slightly closer; A8 as above except, SV-group unisetose; A9 with all setae in near straight line except, L2 lies anterior to L1 and L3 on same pinaculum; D2 about 2× D1; SD1 hairlike, slightly shorter than D2; SV1 about as long as L2; V1s as above (not shown); A10 (Figs. 50, 56): anal plate with SD2 and SD1 about 2× distance apart than distance between SD1 and D2; SD2 and SD1 of equal lengths, about 2× length of D2; D2s parallel; D1 anterior to space between D2 and SD1, and in near transverse line with SD2; crochets uniordinal.

Pupa description (Figs. 57–58). Length 5.5–6.3 mm (n = 7): smooth; golden yellow, with thin brown lines demarcating sclerites; vertex rounded; frontoclypeus bilobed; clypeus U-shaped; labial palpi hidden; antennae broadly rounded encircling sclerites of maxillae, forelegs and midlegs, meeting medially slightly beyond midlength, extending distally in parallel, diverging distally slightly exposing mesothoracic legs; mesothoracic legs shorter or extending to lengths of antennae and forewings; maxillary palpi extending beyond foreleg; midleg abruptly narrowed distally, extending to area between apices of maxillary palpi and apices of forelegs; a pair of prolegs scars present on A6; abdominal spiracles slightly raised; segments A5, A6, and A7–10 movable; cremaster with several pairs of hooked setae present on dorsal and ventral surfaces of A9–10.

Type material. **Holotype** ♂, “MICHIGAN: Marquette Co[unty] ne/nw, T51N-R28W, S 09 [= 46.837°N, 87.854°W], Em[er]g[e]d. 17 Feb. 2006, Surv[eyor] [= Collector]: R.J. Priest”, “Reared Ex *Eurybia*

(*Aster*) *macrophylla*, Rec[o]v[red] [= date collected]: 13 Sept. 2005, Lot: RJP1654.30”, [specimen #] “USNM 00719453”, “DNA 2001” [blue label], “♂ Genitalia Slide by D. Adamski, USNM 83546” [green label]. [pupal exuvium in gelatin capsule beneath specimen] (USNM).

Paratypes: 12 ♂, 12 ♀. MICHIGAN: 5 ♂, 2 ♀; same data as holotype except: 1 ♂, em. 15 Feb 2006, larva 13 Sept. 2005, lot RJP1654.3, [pupal exuvium attached to minuten beneath specimen] (MSUC); 1 ♂, em. 12 Feb 2006, Surv: RJ Priest, lot RJP1654.6 (MSUC); 1 ♂, em. wintered, larva 28 Aug 2007, lot RJP1835.6, [pupal exuvium attached to minuten beneath specimen] (MSUC); 1 ♂, em. wintered, larva 28 Aug 2007, lot RJP1835.9, specimen # USNM 00719454, DNA barcoded, genitalia slide by D. Adamski, USNM 83547 [pupal exuvium attached to minuten beneath specimen] (USNM); 1 ♀, em. wintered, larva 28 Aug 2007, lot RJP1835.2, specimen # USNM 00719465, DNA barcoded, genitalia slide by D. Adamski, USNM 83548, [pupal exuvium attached to minuten beneath specimen] (USNM); 1 ♂, T51N-R28W, S 10 [= 46.83°N, 87.844°W], Emgd: wintered, larva 17 Sept. 2006, lot RJP1768.2, [pupal exuvium attached to minuten beneath specimen] (MSUC); 1 ♀, T51N-R28W, S 01 [= 46.844°N, 87.81°W], Emgd: wintered, larva 28 Aug 2007, lot RJP1834.9, specimen # USNM 00719466, DNA barcoded [right forewing missing] (USNM). ALBERTA: 1 ♂, Edmonton, 01 Jun 2010, J. J. Dombroskie, specimen # JD7399 (CNC); 1 ♀, Milk River Ridge, 10km north jct. Rte 820 & Rte. 501, at light, 24 Aug 1998, G.R. Pohl, specimen # POHL-10-00183, genitalia slide MIC 5723 (CNC); 1 ♂, Strathcona County, 8km SE Sherwood Park, 16 Jun 2008, G. R. Pohl, aspen forest, MVL, specimen # POHL-10-00172, genitalia slide MIC 5722 (CNC). MANITOBA: 1 ♂, near Winnipeg, Bird Hill Prov. Pk. Meadow, 4 Jul 2008, J. Sones, S. McCubbin, J. Straka, N. Jeffery & J. Cossey, UVL, specimen # 08BBLEP-05873 (CNC); 1 ♀, Riding Mountain Nat. Pk, mixed wood, medium stage aspen stand, 19–26 Jun 2012, BIObus 2012, specimen # BIOUG03169-F12 (CNC). ONTARIO: 1 ♀, Algonquin Park, Shaw Woods, South JK, 9 Jun 2012, Alex Smith, Uncut Forest, specimen # BIOUG06751-G06, genitalia slide MIC7183 (CNC); 1 ♀, Bruce Peninsula Nat. Pk, off trail nr visitors centre, 7–14 Jun 2012, Alina Mcmillan, Cedar stand – boreal forest, specimen # BIOUG05835-B02 (CNC); 1 ♀, Bruce Peninsula Nat. Pk, off trail nr visitors centre, 14–21 Jun 2012, Alina Mcmillan, Cedar stand–boreal forest, specimen # BIOUG03957-C04 (CNC); 1 ♀, Bruce Peninsula Nat. Pk, off trail nr visitors centre, 21–28 Jun 2012, Scott Parker, Cedar stand– boreal forest, specimen # BIOUG05835-D01 (CNC); 2 ♂, Pukaskwa Nat Pk, Park road entrance, 30 Jun 2008, BIObus 2008, UVL, specimens # 08BBLEP-00329, 08BBLEP-00331 (CNC); 1 ♀, Pukaskwa Nat. Pk, Park road entrance, 30 Jun 2008, BIObus 2008, UVL, specimen # 08BBLEP-00325, genitalia slide MIC5784 (CNC). QUEBEC: 1 ♂ 2 ♀, Gatineau, Aylmer, chemin

Boucher, 15 May 1998, B. Landry, MVL, specimens # CNCLEP00077453, CNCLEP00077475, CNCLEP00077476 (CNC); 1♀, Gatineau Park, chute de Luskville, 14 Jun 1990, J.-F. Landry, MVL, specimen # CNCLEP00086253, genitalia slide MIC5778 (CNC).

Other material excluded from the type series because the specimen was ground up for other DNA analysis:

BRITISH COLUMBIA: 1♂, 10 km W Kamloops, New Afton Mine, 6–13 Jun 2013, Chrystal Simon, Wetland Protected Area (control side) – Site 3, specimen # BIOUG07668-E11 (BIOUG).

Molecular data (Table 1, Fig. 60). BIN = BOLD:AAG9100. Full barcodes from 21 specimens, including the holotype and two paratypes of *S. manierreorum* were obtained which were compared to those of *S. sacculicola* (Braun) (BOLD:ABY8834) and *S. tussilaginis* (Stainton) (BOLD:ACF4414). We analyzed barcodes of 15 specimens of *S. sacculicola* from Alberta, Colorado, Louisiana, Manitoba, Michigan, Oklahoma, Ontario, Quebec. For the Palearctic *S. tussilaginis*, we analyzed barcodes of 7 specimens from Austria, Denmark, England, and Italy. *Scrobipalpula manierreorum* differs by 4.8% (31 base pairs) from *S. sacculicola* and 5% (33 base pairs) from *S. tussilaginis*. The two 'outgroup' species differ from each other by 3.7%, or about 24 base pairs). Intraspecific haplotype divergence is $\leq 0.25\%$ in all three species.

Etymology. The species epithet, *manierreorum*, is named in honor of William and Anne Manierre, both recently deceased, who supported this research.

Biology. Host: *Scrobipalpula manierreorum* is a leaf-miner of *Eurybia* (*Aster*) *macrophylla* (L.) Cassini (Asteraceae).

Mine and larval behavior (Figs. 7–8). Larval mines are usually initiated at the midvein although some were observed to begin along a secondary vein of the leaf. There is only one larva per mine but as many as 14 mines were observed initiated on a single leaf. Frass is initially suspended externally by webbing, forming a small clump at the base of the mine on the lower surface of the leaf. Additional frass extends from the basal clump and forms a curved tube (Fig. 7), which serves as a retreat when the larva is not feeding or when it is disturbed. The mine is full depth, with all chlorophyll eaten between upper and lower epidermal layers and develops into a branching track. As the mine extends subsequent frass is formed into a double row along the main mine axis (Fig. 8) (rearing lot RJP1989.2a). This double frass row serves to guide the larva directly into its retreat when disturbed. Unlike larvae *G. shepherdiae* and *X. ceanothiae*, the larva of *S. manierreorum* feeds with its dorsal surface facing upwards.

When feeding is complete, the larva exits its mine via the frass tube and presumably pupates in the leaf litter or soil. Five cocoons were observed in rearing bags. When sand or frass was available this substrate was used to ring the cocoon exterior. Cocoons are oval and tannish-grey to white. They measure from 3.5–6.0 × 1.4–3.0 mm [mean = 4.8 × 1.9 mm].

Seasonal occurrence. *S. manierreorum* was first reared in August 2004 as part of an ongoing survey of leaf miners of dicotyledonous plants by RJP that began at the type locality in 2000. Since then an additional 13

visits, at irregular times between early June and early October, were made. Active mines were recovered between mid-August to early September. Adults appear after overwintering. This species was observed to have one generation per year in Marquette County of Upper Michigan and likely also in Lower northeastern Michigan. This is the only site that *S. manierreorum* has been repeatedly collected. The type locality of *X. ceanothiae* in northeastern lower Michigan is also believed to harbor this species, but no adults of have been reared for confirmation. No adults were collected or observed under field conditions in Michigan. Observations of larval mines in Michigan together with Canadian collection records indicate that *S. manierreorum* may be bivoltine.

Parasitoids. *Schoenlandella minuta* (Cresson) (Braconidae) and *Campoplex* sp. (Ichneumonidae).

Distribution (Fig. 59). The species is here recorded from Alberta, British Columbia, Manitoba, Michigan, Ontario, and Quebec. Its host plant is distributed in the eastern half of North America west to Manitoba. The occurrence of *S. manierreorum* in Alberta and British Columbia suggests that it may be using other species of aster as larval host.

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MASS FLIGHTS OF *LYMANTRIA DISPAR JAPONICA* AND *LYMANTRIA MATHURA*
(EREBIDAE: LYMANTRIINAE) TO COMMERCIAL LIGHTING, WITH NOTES ON
FEMALE VIABILITY AND FECUNDITY.¹

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ABSTRACT. Adult *Lymantria dispar japonica* (females only) and *Lymantria mathura* (both sexes) flew to commercial lighting during the night in Takizawa Village, Iwate Prefecture, Japan, in large numbers during the first week of August 2008. Males of *L. d. japonica* were conspicuously absent while 93.8% of responding females were mated and subsequently laid an average of 419.2 eggs each post-flight. For *L. mathura* females, only 33.9% were mated during the first half of the night and each mated female carried on average 717.4 eggs (max. 1065). Egg counts were facilitated by a newly developed egg mass matrix digestion process and an approximation of egg count based on egg mass dry weight was calculated. These two moth species have dissimilar behavioral strategies—*L. d. japonica* is diurnal, mated during the afternoon pre-flight and females flew to the lighting after mating. In contrast, *L. mathura* is nocturnal and both sexes responded to the lighting; females generally arrived as virgins (unfertilized) to then mate with males as the night progressed. Lack of a moth flight in 2009 illustrated dramatic interannual population fluctuation prevalent among many lymantriine moths. An illustration of a 2013 mass flight in Ono City, Fukui Prefecture, suggests a more frequent occurrence of such flights in both time and space.

Additional key words: Noctuoidea, proteinase K digestion, female nocturnal flight, dispersal; flight activity; reproduction; Japanese gypsy moth; Asian pink moth

Unexpected events can provide unique opportunities to gain biological insights with both fundamental and applied importance. One such occasion was a chance encounter with massive nocturnal flights of lymantriine moths attracted to commercial lighting in the village of Takizawa (39.75° N, 141.07° E), just north of Morioka, Iwate Prefecture, Honshu, Japan. Takizawa is nestled in a valley surrounded with hills covered with abundant *Quercus* and *Larix* forests. Gerhard Gries (Simon Fraser University) and PWS were on a field trip in the area conducting unrelated field trapping experiments (Gries et al., 2009a; 2009b). During the evening hours of August 1, 2008, while driving through the well-lit commercial center of Takizawa, we observed a massive evening flight of lymantriine moths. That evening and six evenings to follow, we photographed and observed so many flying moths that the quantity of moths was suggestive of snow. Subsequently we became aware that the flight was more regional than at first appearance. Furthermore, a 2013 illustration is added during the review process that shows evidence of a flight of *Lymantria dispar japonica* (Motschulsky) (Japanese gypsy moth) at Ono City, Fukui Prefecture. We suggest that mass flights likely occur over more widespread

areas of Honshu and may occur more frequently than ever imagined.

Flights of *L. d. japonica* and *L. mathura* Moore (Asian pink moth¹) occur infrequently and they must have originated from population outbreaks. Such outbreak events in Honshu are recorded for both species [for *mathura* see Nishitani, 1918; for *japonica* see Inoue and Arisawa, 1984 or Sato and Sotodate, 1975 (these references are in Japanese and are annotated in Schaefer et al. 1988a but are omitted from the Literature Cited section herein)]. The observed female flights and the physiological condition of the females provide insight into the threat of invasion into new environments.

That females of *L. mathura* have the ability to fly has never been in dispute but the flight ability of *L. dispar* females has often been questioned. This is due in part to a fundamental behavioral polymorphism. In the North American and European forms of the gypsy moth, *L. d. dispar*, females are so aerodynamically configured that they are incapable of sustained flight. This is not the case with Asian forms, where flight-capable females demonstrate the capacity of both sustained and ascending flight. In eastern Asia, there are often

¹This name has recently been introduced as a replacement name for “Pink gypsy moth”, which is a misnomer and misleading reference to “gypsy moth” to which it should not be associated. *L. mathura* and *L. dispar japonica* are congeners but are not closely related based on behavior, molecular evidence, and on appreciably different sex pheromone communication systems.

concentrations of egg masses at outdoor light sources – demonstrative evidence of female flight. Historically, there has been a reluctance to acknowledge that females of the Asian forms of gypsy moth are capable of flight. This trait was observed by Schaefer (1978) in Hokkaido where females flew to white birches to deposit their eggs. Since the early 1990's, there has been increasing concern about female Asian gypsy moths being attracted to seaport lighting and subsequent egg deposition on containers or seagoing ships, hence the potential for international invasion of these moth species. This invasion potential has at times impaired commerce (Yokochi, 2007).

Aspects of gypsy moth female flight that have received recent attention include female flight as a genetic trait (Keena et al. 2008); comparisons among various gypsy moth populations (Reineke and Zebitz, 1998); attractiveness to specific light sources or mitigation efforts (Wallner et al. 1995; Iwaizumi and Arakawa, 2010) and details of the female flight behavior including timing of flights and dispersal capabilities (Carlton et al. 1999; Iwaizumi et al. 2010). Although these issues have been addressed, no studies have focused on the importance of viability and fecundity of flight capable females.

The question of female viability and fecundity in both *L. d. japonica* and *L. mathura* prompted collection of females to determine if these flight capable females were viable. Individual females were collected to determine what percent of females arriving at the lights were carrying viable eggs. This finding would help to clarify the relative threat represented by flight capable females as they sought oviposition sites which might have been on shipping containers or seagoing ships in ports that might export egg masses to environments where these moth species do not currently exist.

MATERIALS AND METHODS

Between 21:00 and 01:00 h. on August 1–7, PWS repeatedly observed and photographed massive nightly flights of lymantriine moths attracted to commercial lighting in Takizawa. The abundance of moths represented an unusual opportunity to investigate some important aspects of behavior using methodology described below. During the same week visits to Mizunashi revealed evidence that the flight was more regional in extent as was the subsequent discovery of a video of clouds of moths at a floodlight-lite baseball field in Kuji. All three locations are in Iwate Prefecture, northern Honshu.

Flight Composition. To characterize the species composition of the flight, adult moths were counted (near midnight of August 5–6) and recorded including

the numbers of each sex of both *L. d. japonica* and *L. mathura*, or any other congeners, on walls, buildings, signs, or paved surfaces near a public parking lot and all-night gas station. Species and sex of all specimens were determined on each surface and data summarized. Data were converted to sex ratios.

Female Viability and Fecundity. On August 4, collections of live females of each species were made near the lighting either from pavement surfaces or from walls or lighted signs but all were within reach by hand. Each female was immediately placed inside a folded newsprint triangular envelope (ca. 20 cm hypotenuse) in which the living female was sealed. Confined females were expected to lay their complement of eggs within the envelope before they died. All envelopes were stored in an outdoor insectary at the Forestry and Forest Products Research Institute in Morioka until the following spring. Then they were placed in a deep-freezer to kill the eggs. The collection was then shipped to USDA, ARS, Beneficial Insects Introduction Research, quarantine facility, Newark, Delaware, where the envelopes were refrozen until processing.

The egg masses of the two species were processed differently. Those of *L. d. japonica* were vacuum de-haired, using the technique described in Schaefer et al. (1988b), scored as being embryonated (by the darkened appearance of developed neonate larvae within the egg shell) or not. For a random subsample, eggs were counted on a counting dish made by covering the bottom surface of a petri dish with a plastic surface containing conveniently spaced parallel plastic ridges approximately 1.5 times higher than the diameter of a single egg. This dish allowed eggs to readily align into rows while the eggs were counted dry using a convenient magnification on a dissecting microscope.

Eggs of *L. mathura* were first removed (with some difficulty) from the newsprint of the envelopes in which they were laid and then dry weighed using an Ohaus-C, Pioneer Electronic balance (Ohaus Corp., Parsippany, NJ). Because *L. mathura* females insert their eggs en mass under bark scales while secreting fluids from the accessory glands that firmly cement individual eggs into a hardened matrix, direct egg counts were impossible without first processing these egg clusters in a digestion solution. The solution was obtained by dissolving 25 mg of proteinase K (Sigma Chemical Co., St. Louis, MO) in 5 mL of buffer (50 mM TRIS, plus 5 mM CaCl₂ at pH 8.0). This digestion process was devised by KGS. Digestion was allowed to proceed at room temperature for 2 to 5 days after which the solution was removed with a disposable plastic pipette. Any remaining clumps were teased apart with forceps and dissecting scalpel. Loosened eggs, setal hairs and matrix debris were all

washed onto the same plastic counting dish described above and counted under a shallow film of tap water. Fertile (embryonated) eggs, infertile eggs, and a few eclosed larvae were tallied.

Return Visit in 2009. Our 2008 data did not fully explain the time of female *L. mathura* mating. PWS returned to Takizawa in August 2009 expecting to capture additional female *L. mathura*. The intent was to segregate collections before and after 2200 h and to record numbers of pairs in copulo throughout the night.

RESULTS

Scenes of the moths at commercial lighting in Takizawa convey some of the abundance of moths that week (Figs. 1, 2) and accumulated gypsy moth egg masses (Fig. 3) at Mizunashi (39.88° N, 141.30° E, about 50 km from Takizawa) suggest that the flight was more widespread than just in Takizawa. See discussion for reference to a video that dramatically illustrates the same event and further suggests a more regional occurrence of our witnessed mass moth flight. During the manuscript submission and review process, another similar mass flight (Fig. 4) occurred at Ono City, Fukui Prefecture, Honshu (35.94° N, 141.49° E) further suggesting a re-occurring nature of these mass flights.

Counts made at Takizawa totaled 918 moths of four lymantriine species (Table 1). Among 65 live-isolated *L. d. japonica* females, 93.8% laid apparently full compliments of eggs that in every case were embryonated. The remaining 6.2% of females failed to produce any eggs. A random subsample (N = 16) of eggs per egg mass laid within the envelopes averaged 419.3 eggs per female (=mass) (S.D. = 62.2, range 311–523). Infertile eggs numbering <1% were disregarded.

Based on 56 confined *L. mathura* females, 53.6% of them laid some eggs but all were infertile (i.e. non-embryonated). An additional 12.5% laid no eggs at all, while only 33.9% of females laid fertile eggs that later embryonated indicating that these females had mated before being collected. Among this latter group were four females observed in copulo and so noted at the time of collection. This observation suggests that active mating occurred during the nocturnal hours and maximum egg viability would increase through the night. The subset of embryonated *L. mathura* egg masses averaged 717.4 eggs per female (N = 19, S.D. = 227.2, range 296–1065). Total eggs produced was the sum of a mean of 8.0 (S.D. = 4.2) eclosed larvae; 38.8 (S.D. = 36.0) infertile eggs; and 670.5 (S.D. = 227.2) fertile (embryonated) eggs per female.

Dry weights of the individual *L. mathura* egg masses (averaged 0.1642 gm (S.D. = 0.0518)) obtained prior to

digestion permitted an estimate of the egg count using a regression line expressed by $Y = 4203.64 X + 27.29$ ($R^2 = 0.92$; $P < 0.05$) where X = Dry weight of *L. mathura* egg mass and Y = Number of eggs contained in that egg mass.

A single *L. fumida* Butler female, another nocturnal species, failed to oviposit and was therefore likely unmated. No females of *L. monacha* (Linnaeus) appeared in the count but a single male was registered.

DISCUSSION

Four species of sympatric *Lymantria* (*dispar*, *mathura*, *monacha*, *fumida*) with coincident adult flights responded to the same commercial lighting, and were recorded in the count. Only one other species (*bantaizana*) is known to be present in the general area (Gotoh et al. 2004).

The magnitude of the 2008 moth flight can be further appreciated by viewing an on-line video at <https://www.youtube.com/watch?v=RvS-PPZ1w3w> (First viewed April 2013) which shows moths attracted to lights at a baseball field in Kuji, Iwate Prefecture. This video was uploaded by Toshiro Komatsu on the same date that Schaefer and Gries first encountered the flight in Takizawa village. Kuji is on the east coast of Iwate Prefecture at a distance of ca. 50 km NE of Takizawa. The video was taken 7–9 PM a few days before being uploaded (Toshiro Komatsu, per. comm. to Y. Higashiura) and it shows the “resemblance of snow” mentioned previously and further suggests both the overall magnitude and the regional extent of this tremendous moth flight. Although it is difficult to identify both species in the video, we believe that both *L. dispar japonica* and *L. mathura* were present, just as we documented a few days later in Takizawa.

The two most numerous species responded differently to the commercial lighting qualifying the potential threat of dispersal and possible establishment of new populations of these two important Asian moths (Pogue and Schaefer, 2007). For *L. d. japonica*, in which males are diurnally active, the males were conspicuously absent in the evening flight and must have remained inactive in the darkened forested hills surrounding Takizawa. Data showed that the overwhelming majority of females had successfully mated, with nearly 94% of all females of *L. d. japonica* fertilized and carrying an average of 420 eggs per female. Field observations by PWS over many seasons beginning in 1975, indicates that mating occurs during afternoon hours preceding any possible evening flight by females. This strategy suggests a very high dispersal potential with a corresponding probability of establishment in a new environment, either on a local or global scale.

TABLE 1. Numbers and sex ratios of lymantriine moths at commercial lighting in Takizawa Village, Iwate Prefecture, Honshu, Japan, during the night of August 5, 2008.

<i>Lymantria</i> spp.	Male	Female	Sex Ratio (M:F)
<i>mathura</i>	620	97	86.5 : 13.5 (6.4 : 1)
<i>dispar japonica</i>	5	194	2.5 : 97.5 (1 : 39)
<i>monacha</i>	1	0	—
<i>fumida</i>	0	1	—

In contrast, for *L. mathura*, in which males are nocturnal, both sexes responded to the commercial lighting with a much higher percentage of males compared to females (Table 1). Progression of the normal flight season might come into play in these species as in both cases, males generally eclose before females. To what extent earlier male emergence might change with the progression of the flight season remains unknown. For *L. mathura*, there was no evidence of behavioral dimorphism in response to lighting as there was in *L. d. japonica*.

It is interesting to note that in a somewhat analogous situation in the Russian Far East (involving a different subspecies of *L. dispar* and different lighting sources), the responses to commercial lighting sources were dissimilar (Wallner et al. 1995). For *L. mathura* the male:female ratio was similar to that in Japan but for *L. dispar asiatica* Vnukovskij in Russia the ratio was reversed. Wallner et al. (1995) reported the male:female ratio to be 11:1 while in Takizawa it was 1:39. It may also have resulted from the light source being positioned reasonably close to the moth infested forest and the artificial lighting may have simulated daylight conditions and stimulated males to become active and induced flight to the light sources. It remains unclear why these differences resulted, but it may also be due to subspecific behavioral differences or reactions to different lighting qualities, particularly since in Russia, the greatest capture of moths was at fluorescent blacklight lamps.

Regarding female viability at the time of flight, specimens examined indicated that only 34% of *L. mathura* females but nearly 94% of *L. d. japonica* females were viable at the time of capture. Since female *L. d. japonica* call diurnally and the males respond and mate, it is understandable that by evening most of the females will have mated. Mated females then are likely to take flight during the evening of the day they eclose (Charlton et al. 1999). With *L. mathura*, a strictly nocturnal species, eclosure of adults occurs during the afternoon (based on numerous observations of recently eclosed females on tree boles over many years) but mating does not occur in daylight hours. Flight follows

within a few hours after sunset, which may help to explain why so many of the collected females were infertile. All evidence suggests that the percentage of fertilized females will likely increase as night progresses. This was further suggested by a field notebook entry on the night of August 4–5 that in Takizawa more *L. mathura* pairs of moths were observed in copulo with each passing hour. As for *L. mathura* fecundity, our estimate of 717.4 eggs/female is appreciably more than the 258 eggs/egg mass recorded in Korea (Lee and Lee, 1996). We surmise, based on these two different estimates, that once mated, females may distribute their full egg compliment among 2 or 3 separate egg masses.

Recent experiments demonstrate antagonistic effects of *L. dispar* pheromone on attraction of male *L. mathura* (Gries et al. 2009a) but temporal differences in behavior between these two species tend to minimize any antagonism or interference with their respective pheromone communication systems even though they share the same habitat and compete for the same food sources (Nishio, 2000; Schaefer 2012). The important differences in behavioral events then result in females of the two sympatric species arriving at commercial lighting in different physiological conditions, mated for *L. d. japonica* and unmated for *L. mathura*. The importance of oviposition as the next behavioral event has a significant bearing on egg mass placement and the possible risk of invasion to new habitats.

The field trip in 2009 was expected to reveal some of the nocturnal flight activity observed in 2008, although the visit to Takizawa occurred slightly later in the season (August 10–20), there was no evidence of a 2009 moth flight. Walls, signs, storefronts etc. showed no evidence of new egg masses as they had the previous August. The outbreak had apparently collapsed during the 2009 spring season. Katsunori Nakamura, (Forestry and Forest Products Research Institute, Morioka), a local forest entomologist, indicated that early in the season there had been numerous larvae of both species present, but that diseases (likely both fungus and virus) had dramatically decimated existing populations resulting in too few adults to produce a 2009 moth flight.



FIGS. 1–4. (1, 2) Nocturnal illustrations of illuminated commercial surfaces on which moths had settled in Takizawa, Iwate Prefecture, Japan, August 1–6, 2008. Identifiable are both sexes of *Lymantria mathura* and lesser numbers of females only of *Lymantria dispar japonica*. (3) Accumulated *L. d. japonica* egg masses from females that had flown to Mizunashi school building lights during the same week. Note variability in individual egg mass color. (4) Morning after results of a 2013 *L. d. japonica* moth flight at Motomachi, Ono City, Fukui Prefecture, Japan. Photo taken July 27, 2013 by Mizuki Mizutani and used with permission. (Photos 1–3 by Paul Schaefer).

Evidence of a 2013 mass flight (even though apparently only *L. d. japonica*) (Fig. 4) suggests that similar mass flights may occur more frequently than first thought. It would be helpful to know just what factors are responsible for driving population outbreaks that result in the observed mass flights of females, and more particularly, do all females participate or is it restricted to only a subset of dispersal capable females.

The conspicuous lack of an adult moth flight in 2009 also illustrates the dramatic interannual fluctuations in the population dynamics of lymantriine moths, in this case, both *L. d. japonica* and *L. mathura*. In nearly 40 years of experience partly described in Schaefer (1989),

PWS has observed defoliating population levels of other lymantriine moths including *L. d. asiatica* Vnukovskij in Mongolia and Korea; *L. d. dispar* (L.) in New England; *Orgyia cana* Henry Edwards in California; *Gynaephora rossii* (Curtis) in the alpine zone of Mt. Daisetsu (elev. 2290 m) and *Ivela auripes* (Butler) both in Hokkaido, Japan; *Leucoma salicis* (L.) in Maine; *Lymantria fumida* Butler and *L. lucescens* (Butler) both in Honshu, Japan; *Euproctis chrysorrhoea* (L.) in Maine and Massachusetts; *Lymantria xyliina* Swinhoe in Taiwan; and *Orgyia antiqua badia* Henry Edwards locally in British Columbia, Canada. Such widely distributed outbreak events tend to reinforce a contention that

population outbreaks are an integral part of the population dynamics of lymantriine moths. To understand why and how such outbreaks appear and then often abruptly vanish, as experienced in Takizawa, is clearly a subject requiring further long-term study.

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HOST PLANT RECORDS OF *ANTHERINA SURAKA* (BOISDUVAL, 1833) (SATURNIIDAE) IN MADAGASCAR

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ABSTRACT. The larval stage of *Antherina suraka* (Boisduval) (Saturniidae) consumes leaves of plant species from 23 families. These host plant species belong mainly to families in the subclass Rosidae, although those in the family Oleaceae and Apocynaceae from another subclass (Asteridae) are nearly as numerous as those in the family Rosaceae. Documentation and field surveys from 2008 to 2011 in different regions of Madagascar enabled an update of the list of the host plants of *A. suraka*. As few records of host plants exist and no immature stages were found in the dry areas, in contrast with other regions of Madagascar, further studies of *A. suraka* in these special ecosystems will provide interesting ecological data. The discovery of several host plant species endemic to Madagascar showed that, although *A. suraka* has adapted to feed on non-native species in disturbed sites throughout its range, it remains reliant on native forests. Determination of its host availability in each region constitutes an important step in prioritizing the conservation of the edges of the remaining endangered forests, as it might help establish sericulture that can reduce deforestation by improving the livelihood of local people.

Additional key words: silkworm, food plants, deforestation, conservation.

Madagascar, the fourth largest island in the world located 400 km off the southeast coast of Africa, is known for its high biodiversity with an extraordinary level of endemism (Myers et al. 2000). Nearly 80 % of its plants (Schatz 2001) and vertebrates are not found anywhere else in the world (Goodman & Benstead 2005). It was separated 150–160 million years ago from mainland Africa and 88–95 million years ago from India (Rabinowitz et al. 1983, Storey et al. 1995, Wells 2003). Thus, the island has been isolated for 85 million years, which has allowed its living inhabitants to evolve independently, giving rise to adaptive radiations in many taxa and high levels of endemism at the genus or species level (Paulian & Viette 2003). In addition, biodiversity has been enhanced in relatively recent times by colonization by some living groups, including insects such as swallowtail butterflies (Papilionidae) (Zakharov et al. 2004, Condamine et al. 2013). The topography ranges from the mountainous central part of the island to the flat littoral areas and also features various geological barriers such as rivers, volcanic mountains and karsts, which offer additional opportunities for biological diversification. The climate regionally differs depending on elevation and the dominant winds. Both the variety of topography and climate led to the extremely high diversity of habitats. Thus, authors such

as DeWit (2003) have characterized Madagascar as a continent.

However, this unique biodiversity in Madagascar is severely endangered because of destructive practices such as slash-and-burn agriculture, gathering wood for fuel, timber logging and mining activities (Mittermeier et al. 1999, Fritz-Vietta et al. 2011). Protecting the forests requires integrating local people into conservation projects, as they rely heavily on forest resources. Efforts are being made to implement integrated conservation management. One solution is to provide a new income stream for local farmers (Marcus 2001), as implemented by a non-governmental organization, Conservation through Poverty Alleviation International (CPALI), which works in the Northeast of Madagascar and trains farmers for silk production of local species of silkworms, thus reducing overexploitation of the remaining forests of Madagascar.

Worldwide, the main commercial silk-producing species are the domesticated silkworm, *Bombyx mori* L. (Bombycidae), and several wild silkworms from other families, mainly Saturniidae (Peigler 1993). In Madagascar, the Saturniidae or Emperor Moths are important primarily for their beauty, attracting insect collectors from around the world, but they have surprisingly been unused traditionally for silk

production (Peigler 2004). Instead, a species of *Borocera* (Lasiocampidae) commonly called Landibe, has been mainly used throughout the country since ancestral times for manufacturing different garments, from funeral shrouds to traditional ceremony clothes (Razafimanantsoa et al. 2012).

This study focused on *Antherina suraka* (Boisduval, 1833) (Saturniidae), a species endemic to Madagascar and the Comoros Islands (Paulian 1951, Griveaud 1961, Viette 1965). Our investigation of host plant utilization by this species was restricted to the island of Madagascar, where *A. suraka* has been recently identified as a potential source for commercial wild silk production (Razafimanantsoa et al. 2006).

Collecting records in the Botanical and Zoological Park of Tsimbazaza (Parc Zoologique et Botanique de Tsimbazaza, PBZT) and the French National Museum of Natural History (Musée National d'Histoire Naturelle, MNHN) show that *A. suraka* is widely distributed throughout the island. Few specimens of *A. suraka* in these collections are labeled with any host plant data and their exact origins are rarely specified. This lack of information is not surprising as most of the specimens were collected as adults at lights, like other wild silk moths observed by Peigler (2004). Adding information about the host plant range of a phytophagous insect will aid significantly in understanding its natural history. In the literature, the larvae of *A. suraka* are recorded as consuming leaves of a variety of plant species (Bouvier 1936, Paulian 1951, Griveaud 1961, Stone 1991, Kurz 1991, Bowers 1993, Lampe 2010, Meister 2011) growing in diverse habitats. Of the plant species mentioned by these authors, only a small percentage were recorded from dry areas, although *A. suraka* is present in both dry and humid areas, two of the main types of vegetation in Madagascar. Further field exploration would therefore be necessary to complement these host records.

Information about host plants is important as it can serve as a tool to locate or rear a species for further biological studies or to maintain mass-rearing of the insect for economic purposes such as sericulture. Collating the distribution records of all host plants with distribution records for *A. suraka* would provide a versatile and useful tool for implementing conservation measures. Nonetheless, circumspection is recommended in this regard as the presence of a host species in a region does not necessarily imply that the population of *A. suraka* living there optimally utilizes that species. As an example, over 90% of individuals of *Rothschildia lebeau* (Guérin-Méneville) (Saturniidae) recorded in a dry forest in Costa Rica were found living on only three species out of the 11 food plants recorded

for the species in this region (Janzen 2003). Thus, larvae of *A. suraka* might use an alternative host plant as palatability of leaves might vary with altitudinal gradients (Erelli et al. 1998) and environmental conditions such as light availability (Osier & Jennings 2007) and drought (Gutbrodt et al. 2011).

The aim of the current study was to update the list of the host plants utilized by *A. suraka* throughout its range by recording larvae consuming leaves in specific regions of Madagascar and to collate these records with previous reports. The list of food plants recorded during our study is by no means exhaustive; rather, it is an attempt to shed additional light on the natural history of *A. suraka*, a spectacular representative of the endemic fauna that may provide, via silk production, a new income opportunity for the riparian farmers, which may

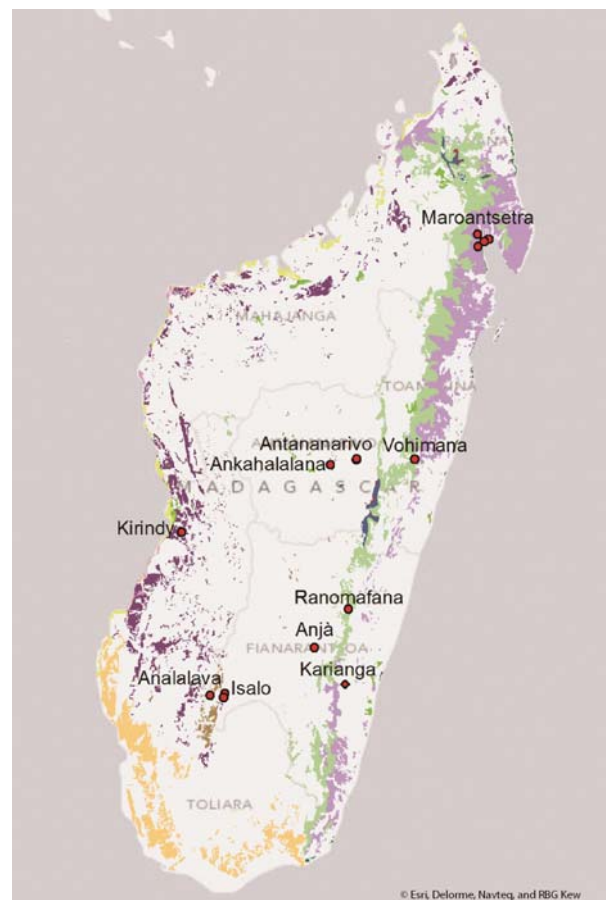


FIG. 1. Collecting sites of *Antherina suraka* (Saturniidae) in Madagascar. Dot colours: red - collecting site; light purple - evergreen humid forest (low altitude); green - evergreen humid forest (mid-altitude); blue - evergreen humid forest (low mountain); brown - evergreen sclerophyllous woodland; dark purple - deciduous, seasonally dry, western forest; tan - deciduous, dry, southern forest. Base map from World Light Gray through ArcGIS® software; primary vegetation map by Du Puy and Moat (1996). Copyright © Esri and the Royal Botanical Garden, Kew. All rights reserved.



FIGS. 2–7. (2) *Antherina suraka* live cocoon collected among grasses under a host plant. (3) *Antherina suraka* female on alert. (4) *Antherina suraka* third-instar larva feeding on leaf of *Weinmannia* sp. (Cunoniaceae) in Vohimana Forest in Madagascar. (5) *Antherina suraka* final-instar larva on *Maesa lanceolata* (Primulaceae) in Ranomafana National Park. (6) *Bakerella grisea* (Loranthaceae) in Ranomafana National Park, on which larvae of *Antherina suraka* were found but did not survive. (7) *Antherina suraka* final-instar larva on *Ischnolepis tuberosa* (Apocynaceae) in Anjà Forest.

TABLE 1. Sites visited during investigation of from 2008 to 2011.

Region	Site	Subsite	Latitude/Longitude/ Altitude	Year of Collection
Evergreen humid forest				
North - East	Maroantsetra	Ambalamahogo	-15.354833/49.55575 /35m	2010
		Anantoraka	-15.476/49.661028 /13m	2010
		Vodiriana	-15.553778/49.560778 /26m	2010
		Maroantsetra Town	-15.438914/49.739508 /10m	2009 and 2010
Central - East	Vohimana Forest	Near the Researcher Village	-18.92147/48.51195 /792m	2008, 2010 and 2011
South - East	Ranomafana National Park	Along the National Road	-21.258138/47.419027 /792m	2010
	Karianga	Karianga Town	-22.416667/47.366667 /263m	2008
City green patch				
Central	Antananarivo City	Ambatomaro		2009 and 2010
		Ambohitsaina	-18.91548/47.553083 /1323m	2010
		Ambohimandra	-18.92855/47.545217 /1293m	2010
Rupicolous vegetation (on rocky area)				
South-Central	Anjà Forest		-21.85015/46.83545 /984m	2009 and 2010
Fire-resistant forest				
Midwest	Arivonimamo	Ankahalana	-19.00814/47.12083 /1334m	2010
South-Central	Isalo National Park	Oasis	-22.62273/45.35155 /838m	2010 and 2011
		Mangily circuit	-22.5612667 /45.3705000/	2011
Deciduous dry forests				
South-West	Analalava Forest	South Tanambao	-22.583916/45.1279833 /712m	2010 and 2011
South-West	Kirindy Reserve	Research Center	-20.0671/44.6574667 /55m	2010 and 2011

TABLE 2. Larval food plant species for *Antherina suraka* recorded from the literature and local farmers. Naturalized plants defined as non-native species established in Madagascar and on which leaves *A. suraka* larvae were found, versus non-native species on which they were fed in captivity. Classification and origins of the plants compiled from tropicos.org, including the Madagascar catalogue (Missouri Botanical Garden, 2013).

Scientific Name	Origin	Family	Location of Record	Source of Record
ASTERIDAE				
<i>Mascarenhasia</i> sp.	Native	Apocynaceae	Isalo/Analalava	Information from villagers
<i>Nerium oleander</i> L.	Naturalized	Apocynaceae	Unmentioned but probably in gardens mainly in Antananarivo	Bouvier 1936, Griveaud 1961, Meister 2011
<i>Strophanthus</i> sp.	Native/naturalized	Apocynaceae	Unmentioned	Griveaud 1961, Meister 2011
<i>Polyscias bakeriana</i> (Drake) R. Vig.	Native	Araliaceae	Maroantsetra	CPALI
<i>Maesa lanceolata</i> C. Don.	Naturalized	Primulaceae	Vohimana, Mantadia, Mandraka, Ranomafana, Ambatofinandrahana	Griveaud 1961, Razafimanantsoa et al. 2005, Ranaivosolo (pers. com.), LRK 630
<i>Fraxinus pennsylvanica</i> Marshall	Non-native	Oleaceae	Rearing facility	Peigler (pers. com.)
<i>Ligustrum sinense</i> Lour.	Naturalized	Oleaceae	Antananarivo	Farmers who rear them
<i>Ligustrum japonicum</i> Thunb.	Naturalized	Oleaceae	Antananarivo	Farmers who rear them, Meister 2011
<i>Ligustrum ovalifolium</i> Haask.	Non-native	Oleaceae	Unmentioned	Meister 2011
<i>Ligustrum vulgare</i> L.	Non-native	Oleaceae	Unmentioned	Meister 2011
<i>Syringa vulgaris</i> L.	Non-native	Oleaceae	Rearing facility	Peigler (pers. com.)
CORE EUDICOTS				
<i>Liquidambar</i> sp.	Non-native	Altingiaceae	Unmentioned	Probst (pers. com. in Stone 1991), Meister 2011
ROSIDAE				
<i>Mangifera indica</i> L.	Naturalized	Anacardiaceae	Antananarivo	Griveaud 1961
<i>Rhus typhina</i> L.	Non native	Anacardiaceae	Rearing facility	Peigler (pers. com.)
<i>Schinus molle</i> L.	Naturalized	Anacardiaceae	Antananarivo	Griveaud 1961, Meister 2011
<i>Carpinus betulus</i> L.	Non-native	Betulaceae	Unmentioned	Meister 2011

TABLE 2. Continued

Scientific Name	Origin	Family	Location of Record	Source of Record
<i>Brassica</i> sp.	Naturalized	ROSIDAE (continued) Brassicaceae	Unmentioned	Griveaud 1961
<i>Terminalia catappa</i> L.	Naturalized	Combretaceae	Maroantsetra	CPALI
<i>Fagus</i> sp.	Non-native	Fagaceae	Unmentioned	Probst (pers. com. In Stone 1991), Meister 2011
<i>Quercus</i> sp.	Non-native	Fagaceae	Rearing facility	Kurz 1991
<i>Eugenia</i> sp.	Native and naturalized	Myrtaceae	Large distribution	Griveaud 1961, Meister 2011
<i>Psidium guajava</i> L.	Naturalized	Myrtaceae	Large distribution	CPALI
<i>Crataegus laevigata</i> (Poir.) DC.	Non-native	Rosaceae	Unmentioned	Meister 2011
<i>Crataegus monogyna</i> Jacq.	Non-native	Rosaceae	Unmentioned	Meister 2011
<i>Eriobotrya japonica</i> (Thunb.) Lindl.	Naturalized	Rosaceae	Antananarivo	Rakotoarisoa pers. com.
<i>Malus floribunda</i> Siebold ex Van Houtte	Non-native	Rosaceae	Rearing facility	Lampe 2010
<i>Malus "hillieri"</i>	Non-native	Rosaceae	Unmentioned	Meister 2011
<i>Prunus</i> sp. (plum, cherry)	Naturalized	Rosaceae	Rearing facility	Kurz 1991
<i>Rosa</i> sp.	Naturalized	Rosaceae	Rearing facility	Bowers 1993
<i>Salix babylonica</i> L.	Non-native	Salicaceae	Unmentioned	Meister 2011
<i>Salix caprea</i> L.	Non-native	Salicaceae	Unmentioned	Meister 2011
<i>Acer campestre</i> L.	Non-native	Sapindaceae	Unmentioned	Meister 2011
<i>Litchi chinensis</i> Sonn.	Naturalized	Sapindaceae	Unmentioned	Mamy Ratsimbazafy (pers. com.)
<i>Vitis vinifera</i> L.	Naturalized	Vitaceae	Unmentioned	Meister 2011

help to reduce the constant human pressure on the endangered unique forests of Madagascar.

MATERIALS AND METHODS

Areas of investigations selected as potential field sites were based on records from different authors who captured adults of *A. suraka* at these locations (Craig 2007, Rafamantanantsoa 2005, Razafimanantsoa et al. 2006) as well as from local farmers and field biologists who have found the species in these regions. Ten main sites were selected for the study (Table 1). A map of Madagascar was created using World Light Gray base map from ArcGIS® software by Esri, Delorme and Navteq. The sites were plotted on this base map from the coordinates recorded in the field using a handheld Global Positioning System (GPS) device (eTrex - Garmin Inc.). A refined map of primary vegetation of Madagascar by Du Puy & Moat (1996), produced by the Royal Botanical Gardens, Kew, was superimposed on the base map to show the distribution of the selected sites across different ecosystems of Madagascar, as characterized by different climates. The East Coast, directly exposed to the trade winds, has the highest rainfall; the Central Highlands are drier and cooler and the West Coast is considerably drier as the trade winds do not reach it sufficiently to provide significant humidity. Thus, parts of the Southwest and the Deep South experience extremely low rainfall and are semi-desert areas. Consequently, extremely varied vegetation types characterize the island (Figure 1): thicket vegetation covers the extreme south of the country, savanna woodlands and grasslands with patches of dry deciduous forests characterize the west, and these types are separated from the humid evergreen dense forests of the east by chains of mountains along the length of the island. Predominant grasslands cover the Central Highlands.

Eggs, larvae and cocoons of *A. suraka* were collected from November 2008 to January 2009, from March to May 2010 and during February and March 2011. Two teams of investigators, each comprising two or three entomologists, worked simultaneously at different sites during these periods. In addition, local guides assisted the teams during the surveys to facilitate investigation of potential habitats and host plants. Larvae were located by inspecting feeding damage on leaves of all previously recorded host plants. Vegetative parts of the plant on which larvae were found were preserved for identification and use as vouchers, which were deposited at PBZT and the California Academy of Sciences (CAS). As the larvae of *A. suraka* pupate in cocoons scattered on the ground, cocoons were collected under dead leaves of known or suspected

larval host plants or on grasses on the surrounding soil (Figure 2). Adults (Figure 3) were captured over a six-hour period (from 21:00h to 03:00h) using light-traps comprising a black-light (Bioquip Inc., 2804 AC/DC, 12 volts, 15 watts) powered by a portable automobile battery and hung or placed close to a white-sheet screen 2 × 1.60 m in dimensions. Specimens were generally killed and stored in glassine envelopes to document the presence of the species in the study areas. When females and males were simultaneously captured, they were kept alive and allowed to copulate in portable net cages.

For confirmation of host plants, field-collected larvae were reared in the laboratory on foliage of the plants on which they were found by placing them on freshly cut twigs with leaves in a container filled with water. Twigs and water were replaced every two to five days depending on the species of plant.

RESULTS

The larvae of *A. suraka* feed on approximately 44 species of plants belonging to 23 families in 15 plant orders (Tables 1 and 2). Host plant species belong primarily in families placed in the subclass Rosidae (28), the highest number of species (7) falling in the family Rosaceae. Other families of Rosidae were represented by one or, occasionally, two or three species. Although only six families of the subclass Asteridae and two of Core Eudicots were accepted as hosts, the family Oleaceae and Apocynaceae of Asteridae comprised the second and third highest numbers of host plants in term of species (respectively 6 and 4) after Rosaceae. Most of the host families listed here for *A. suraka* are shared food plants with other species of Saturniidae (Collins & Weast 1961, Griveaud 1961, Stone 1991, Lampe 2010, Meister 2011). Hostplants of *A. suraka*, *Weinmannia* sp. (Cunoniaceae) and *Eugenia* sp. (Myrtaceae) are, for example, hosts of the Comet Moth, *Argema mittrei* (Guérin-Méneville), another Malagasy-endemic species belonging to the family Saturniidae (Pinhey 1972, Stone 1991).

In total, ten species of plants that are endemic to Madagascar were newly recorded as hosts of *A. suraka* (Table 3). We found larvae of *A. suraka* consuming foliage of *Weinmannia* sp. in the Vohimana forest in 2008 (Figure 4), but when reared on it in the laboratory they failed to pupate. Leaves of *Ischnolepis tuberosa* Jum. & H. Perrier (Apocynaceae, Asclepiadoideae), a species with toxic latex, as well as *Bakerella grisea* (Scott-Elliot) Balle (Loranthaceae), which is a plant parasite, were eaten by the larvae of *A. suraka*. Both species were found in close proximity to the known host *Maesa lanceolata* G. Don (Figure 5). *Ischnolepis*

TABLE 3. Newly recorded food plants of *Antherina suraka*. Vouchers deposited in Botanical and Zoological Park of Tsimbazaza and California Academy of Sciences.

Scientific name	Family	Location of record	Fieldwork/Life cycle status	Voucher
	ASTERIDAE			
<i>Ischnolepis tuberosa</i> Jum. & H. Perrier	Apocynaceae	Anja	January 2009/Complete	LRK 629
<i>Foetidia asymetrica</i> H. Perrier	Lecythidaceae	Kirindy	February 2011/Cocoon found under trees	AS1
<i>Pyrostria nerifolia</i> (Homolle ex Arènes) Razafim., Lantz & B. Bremer	Rubiaceae	Kirindy	February 2011/cocoons found under trees	AS2
	CORE EUDICOTS			
<i>Bakerella grisea</i> (Scott-Elliot) Balle	Loranthaceae	Ranomafana	May 2010/failed to pupate	No voucher
	ROSIDAE			
<i>Terminalia tropophylla</i> H. Perrier	Combretaceae	Kirindy	February 2011/Cocoons found under trees	AS3
<i>Weinmannia</i> sp. L.	Cunoniaceae	Vohimana	November 2008/failed to pupate	No voucher
<i>Suregada capuronii</i> Leandri	Euphorbiaceae	Kirindy	February 2011/Cocoons found under trees	AS4
<i>Baudouinia sollyaeformis</i> Baill.	Fabaceae	Kirindy	February 2011/Cocoons found under trees	AS5
<i>Gravia cyclea</i> Baill.	Malvaceae	Kirindy	February 2011/Cocoons found under trees	AS6
<i>Cedrelopsis grevei</i> Baill.	Rutaceae	Kirindy	February 2011/Cocoons found under trees	AS7

tuberosa grows on rocks close to *M. lanceolata* in Anjà. All larvae of *A. suraka* recorded there were feeding on the needle-like leaves of *I. tuberosa* (Figure 7) and all of them successfully eclosed as adults when reared on this plant. No larvae were found on the leaves of *M. lanceolata* during our visit in Anjà in 2009, but the local people recorded them on *M. lanceolata* in 2013. The larvae found feeding on *Bakerella grisea* were on a plant immediately adjacent to *M. lanceolata* at the edge of the rainforest in Ranomafana (Figure 6), but they died without reaching the pupal stage whereas those feeding on leaves of *M. lanceolata* easily reached the adult stage. It thus appears that a female may have deposited some eggs on the leaves of *B. grisea* by mistake. In December 2008, larvae of *A. suraka* were found feeding on leaves of *M. lanceolata* and *Weinmannia* sp. in the Vohimana Forest, but neither larvae nor adults could be found in 2010 at the same sites. Definite host species of *A. suraka* were recorded from the northern (Maroantsetra), central (Vohimana) and southern (Ranomafana) parts of the eastern side of Madagascar, where the evergreen humid forest lies (Table 1). At Karianga, another site in the vicinity of a rainforest, no larvae were found on any leaves inspected in November 2008, but two *A. suraka* adults were captured at light and on a tree during the day.

In the dry forest of Kirindy, between two and seven old cocoons of *A. suraka*, the ages estimated at about one year post-eclosion, were found among grasses below each of the seven plant species discovered as hosts in 2011. Although no larvae were found feeding on the leaves of these plants during our surveys, the presence of cocoons at a distance of 0.25–0.75 m from the trees or even between their twigs was considered to be evidence that *A. suraka* feeds on them. Adding credence to this association is the fact that larvae of *A. suraka* typically wander from the foliage to the bottom of their host tree to find a suitable substrate, such as grasses or dead leaves, in which to spin a cocoon. Because some saturniids may crawl across distances of ten meters or more if no suitable substrate near a host tree is encountered, rearing experiments would be needed to confirm this putative association between *A. suraka* and these host tree species.

In Isalo National Park and Analalava Forest, where various types of vegetation including dry and rupicolous forests as well as fire-resistant ones such as the Tapia (*Uapaca bojeri* Baill., Phyllanthaceae) forest occur, adults of *A. suraka* were captured at light in 2010 and 2011 but no larvae or cocoons were found on or near possible host plants. *Mascarenhasia* sp. (Apocynaceae) was reported by local villagers in Analalava as a host, but this could not be confirmed as no larvae were found

feeding on this plant. Adults of *A. suraka* were recorded from another Tapia forest in the Midwest of Madagascar at Ankahalalana (Arivonimamo) in 2001 (H. A. Razafindralava pers. com.), but no specimens were captured during our trapping there in March 2010.

DISCUSSION

As our study was not exhaustive, further investigations should be undertaken to record all of the host plants of *A. suraka*. We had to select sites taking into account accessibility by road and required logistics during the limited time of the year when larvae can be found. Records of specimens of *A. suraka* from the 1940s to 1960s in the PBZT and MNHN insect collections indicated that some other sites, including in the far north and south of Madagascar, need further investigation to update the distribution area of the species and extend its possible host range.

The number of host plant species in the diverse families that we recorded shows that *A. suraka* is polyphagous, as are most other species of Saturniidae (Tuskes et al. 1996, Janzen 2003). The species shows host preferences that may vary in space and time due to microhabitat differences (Janzen 2003) or environmental stresses such as drought and light availability, as mentioned earlier. Also, the natural history of *A. suraka* in dry and sclerophyllous forests is not as well-known as it is in rainforests. We could not determine the period of the year when the larval stages of *A. suraka* can be found in these particular ecosystems, particularly in Kirindy, Analalava Forest, Isalo National Park and Ankahalalana. Only old cocoons, from which pupae were thought to have emerged in the previous year, were found in Kirindy in February 2011. Our rough estimation of the life cycle of the species based on the weather conditions and our capture of adults in April 2010 led us to expect to find larvae in March, April and May; however, larvae would not be expected to survive for extended periods during this season as the leaves of the trees in Kirindy Forest would likely already have senesced or fallen at this time of the year.

All ten newly recorded food plants of *A. suraka*, seven of them in a dry deciduous forest, are endemic species of forests in Madagascar. No local rearing was possible during our stay in the dry areas as we could not find local specimens but future projects that involve rearing *A. suraka* on these hostplants would be necessary to determine definitively whether the species can complete its cycle on these hostplants. Although some populations of *A. suraka* have adapted well to non-native or naturalized plants, such as *Ligustrum* sp. (Oleaceae) and other temperate plants grown for

farming (Kurz 1991, Bowers 1993), this study shows that *A. suraka* still relies on vegetation of native forests in different parts of the island. Forest edges are greatly threatened, partly because of slash-and-burn agriculture that tends to encroach upon these ecotones as distant land becomes depleted (Styger et al. 2007). As most of the *A. suraka* larvae and their host plants were found at the edges of forests along paths or roads, the species can probably be used as an indicator of habitat loss in the riparian zones of forests. In addition, it is evident that human disturbance of the surrounding habitats of protected areas can cause more damage within the areas than thought before (Laurance et al. 2012). Difficulty in collecting specimens in some areas where *A. suraka* was found in earlier years may indicate a continuing loss of habitat. Slash-and burn agriculture surrounding protected areas is so common (Styger et al. 2007, Dirac Ramohavelo 2009) that it possibly has an impact on the fauna and flora of most of the study sites. Road construction and other activities related to mining could change the ecotopes of forests such as Vohimana, where the same area in which we collected *A. suraka* turned from an abandoned, formerly cultivated hill at the edge of the forest to an open, red-soil area within one year.

Knowing the geographical distribution of *A. suraka* and its host plants might help to prioritize conservation of forest borders through implementation of silk production activities. Sericulture might help not only to conserve the species but also to improve the livelihood of local people, reducing overexploitation of the forests by virtue of their greater economic security (Razafimanantsoa et al. 2006, Kakati & Chutia 2009, Raina et al. 2011).

The organization, Conservation through Poverty Alleviation International (CPALI, www.cpal.org) has been working on such a project in Maroantsetra for several years by providing a market for the cocoons produced by local farmers. Unlike the common wild silk textile, unwoven textiles from individual cocoons sewn together are used by CPALI to make sheets for curtains, lampshades and jewelry. All members of a family engaged in silk production can benefit from the new silk activities: men and women are involved in planting the host plants and rearing *A. suraka*, and women in particular engage in later processing stages, including preparing and sewing the cocoons together. Expanding such activities to other regions will be feasible if more information on the host plants of various wild silkworm species is gathered. From the data obtained from this study, we suggest that Anjà, Vohimana and Ranomafana are possible areas to establish *A. suraka* rearing projects as the local host plants are already known and the local people are likely to be receptive to new work

alternatives since they are already involved in other development projects through community associations. For the remaining areas that are mainly dry deciduous or sclerophyllous forests, and where *Antherina suraka* larvae were difficult to find partly because of high levels of environmental stress on the forest such as frequent forest burns, other alternative conservation plans are needed, as these sites with unique ecosystems contain endemic animals and host plants at potential risk of extirpation or extinction.

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MITES INHABITING A LEPIDOPTERAN EGG

Additional key words: Acari, ecosystem engineering, Cerrado, Mimallonidae

Lepidopteran eggs are highly variable in morphology, showing different shapes and sizes according to family, genus and/or species (Stehr 1987). After hatching, many species eat their egg shells (see examples in Braby & Nishida 2007), while others open a hole through which they hatch and leave the rest of the chorion intact (see examples in Kaminski et al. 2013). In some cases, the empty egg shell can remain for days or weeks in a shape similar to the original (e.g. egg shells of *Parrhasius polibetes* (Stoll, 1781) (Lycaenidae) may endure on the inflorescences of their hostplants for several weeks; L. L. Mota, pers. obs)

In April 2013, a lepidopteran egg shell was found attached to the lateral of a Myrtaceae leaf, in an area of Cerrado savanna belonging to the Laboratório Nacional de Luz Síncrotron (22°48'S, 47°03'W), in Campinas, Southeast Brazil. The egg was elongated (1.3 mm long and 0.4 mm wide), with longitudinal ribs, and one extremity was open with irregular edges, suggestive of biting marks left by the caterpillar while hatching (Fig. 1). It was attached to the leaf longitudinally, so the structure resembled a tunnel with one side closed. Its shape and position in the leaf are similar to the described for the Mimallonidae genus *Lacosoma* Grote, 1864 (Dyar 1900, Peterson 1961; 1966). A caterpillar was found on a nearby leaf on the same branch, and was possibly the one which hatched from this egg. It was under a net constructed of silk and frass, also similar to that described for early and mid-instar larvae of a *Lacosoma* species (Dyar 1900). These evidences strongly suggest the egg belonged to the family Mimallonidae.

With stereomicroscopy observation, four unidentified mites (Acari) were found inside the egg, at the opposite extremity to the opening (Fig. 1a). Feces and at least six elliptical mite eggs (0.09 mm long) were also present at this region (Fig. 1b). The mites stayed in the same position even with intense hand and pin manipulation. Under stereomicroscope light they started to move and only one of them left the egg, walked around the chorion and the leaf and entered the egg shell a few minutes later (Fig. 1c–d). Previously, no mites were found walking in the leaf outside the egg shell.

The presence of the mites, their feces and eggs inside this lepidopteran egg shell suggests they were consistently using the chorionic structure as a shelter and reproduction site. Mites use many leaf structures as shelters, such as acaridomatias (O'Dowd & Willson 1989,

Willson 1991), former lepidopteran shelters (Lima et al. 2013), rolled leaves (Fournier et al. 2003), and even adhesive traps of carnivorous plants (Antor & García 1995). Some mites tend to establish preferentially near wall structures, especially in gaps between two walls (Kawasaki et al. 2009), so the egg shell of this Mimallonidae seems to be a perfect site for them, representing a long structure with two parallel walls. The benefits proportioned by the egg shell could be related to diminishing predation risk and maintaining microclimatic conditions (which could prevent them from desiccating), as found for other kinds of shelters used by mites (Kawasaki et al. 2009, Lima et al. 2013). The mites and eggs were positioned as far as possible from this aperture, where it would be most difficult for a predator larger than the opening of the egg to reach, and where they were in contact with a third wall structure, possibly providing optimal microclimate conditions. It is interesting to note that egg shells with other shapes, such as round or flat, or with hatching apertures positioned in a different place, could differ as well in the conditions provided for mites.

Even though this is a single record, it is, as far as we know, the first record of opportunistic use of a lepidopteran egg shell as a shelter, and offers evidence that empty eggs can increase the environmental complexity of leaves or other substrates. This effect would be possibly more intense in the case of eggs oviposited aggregately, or in plants that host a high abundance of eggs. Organisms that change the availability of resources to others are considered ecosystem engineers (Jones et al. 1994). It is known that some lepidopterans act this way by leaving leaf shelters (Vieira & Romero 2013) after caterpillar use, and by the vacant space left by mining species (Kagata & Ohgushi 2004). We suggest that another way through which lepidopterans—and other insects as well—could act as ecosystem engineers is through the differentiated microhabitat created by egg shells left empty after hatching. This would apply for systems in which some small arthropod species largely use these structures, and is an interesting, yet unrecorded, possibility.

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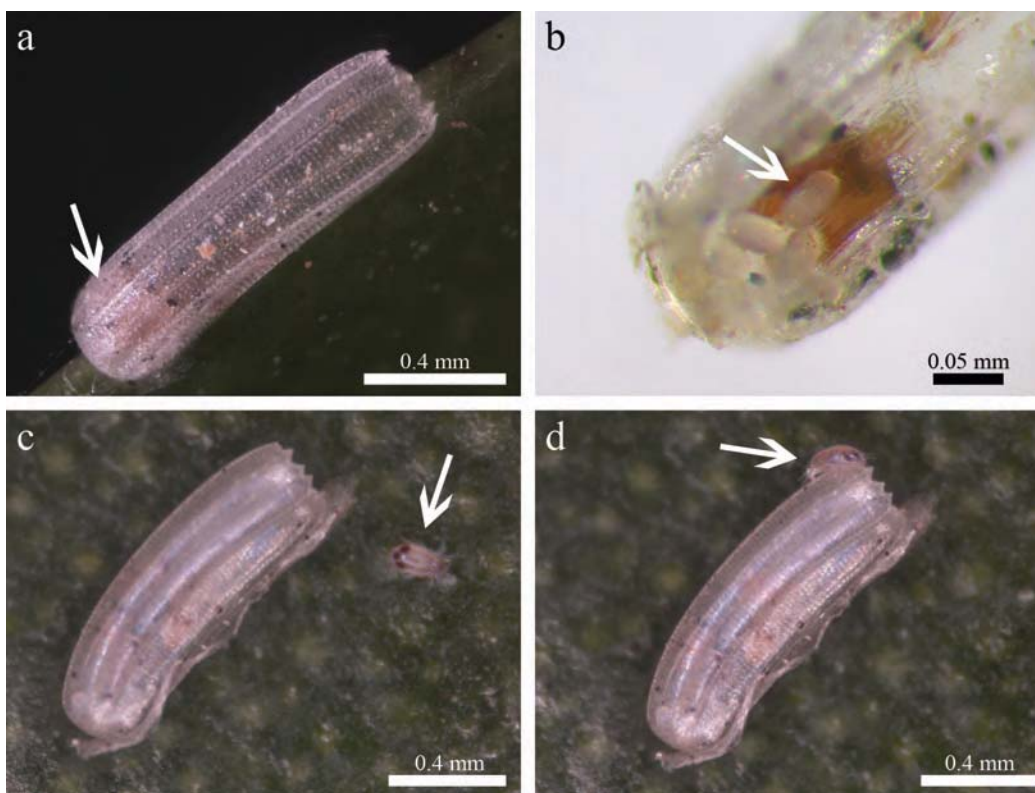


FIG. 1. **a)** Hatched Mimallonidae egg in dorso-lateral view, with mites (arrow) at the opposite extremity to the egg opening; **b)** Mite eggs (arrow) inside the Mimallonidae egg; **c)** Lateral view of the Mimallonidae egg after heating and hand manipulation, with a mite (arrow) that exited the egg interior; **d)** The same mite (arrow) close to the egg aperture.

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OVIPOSITING OFF THE HOST PLANT BY TWO TROPICAL NYMPHALID BUTTERFLIES

Additional key words: Enemy-free space, Heliconiinae, Ithomiini, Passifloraceae, Solanaceae

The choice for oviposition sites by an insect can be a compromise between opposing needs; females must select a suitable site while considering several different factors, such as plant nutritional content, concentration of chemical substances, presence of competitors, predators, and optimal physical conditions, always considering places that confer superior fitness to their offspring (Jaenike 1978, Thompson 1988, Thompson & Pellmyr 1991). Among all the above factors, predation and parasitism have been considered as particularly strong forces influencing female oviposition behavior (Sendoya et al. 2009, Carrasco & Kaitala 2009, De-Silva et al. 2011). To minimize the risks of predation and parasitism, females need to find a safe place to lay their eggs, where the contact with natural enemies is minimized, known as “enemy-free space” (Price et al. 1980). In temperate climates, selecting oviposition sites away from the host plant is a common strategy, not only related to enemy avoidance, but also to prevent oviposition on plants vulnerable to senescence (Wiklund 1984, Gompert et al. 2006). The behavior of ovipositing away from the host plant, however, is considered rare in tropical environments (Singer 1984, De Silva et al. 2011). In a recent paper, however, De Silva et al. (2011) showed that the neotropical ithomiine *Oleria onega* Hewitson usually oviposits away from its host plants, showing evidence that this behavior is at least partially related to high predation risks on the host plant. In the present paper, the behavior of ovipositing away from the host plant is reported for the tropical nymphalid butterflies *Ithomia drymo* Hübner (Danainae: Ithomiini) and *Eueides aliphra* Godart (Heliconiinae: Heliconiini). Field work was carried out at the “Reserva Municipal Biológica da Serra do Japi”, an area of semi-deciduous mesophytic forest in the municipalities of Jundiá and Cabreúva, in the state of São Paulo in Southeastern Brazil (a complete and detailed description of the area can be found in Morellato 1992); observations were made near the Research Station (centered on 23°13'S 46°55'W). On April, 15, 2011, a single *I. drymo* female was observed showing typical behavior of searching for host plants, fluttering with an irregular flight and touching the leaves of several shrubs on the forest edge. After testing the leaves of an *Aureliana* sp. (Solanaceae), one of their known host plants in Serra do Japi, the female flew 20 cm away from

the host plant and laid an egg on a dead leaf of a nearby non-host plant species (Fig. 1A). The female repeated this behavior seven times, resulting in seven eggs laid on dead leaves and twigs in the vicinity of the potential host plant (Fig. 1A). Additional searching revealed at least three additional eggs on neighboring dead vegetation, as well as five eggs on mature leaves of the host-plant. A similar behavior was observed in *E. aliphra*. On April, 14, 2011, a single female was observed ovipositing on a *Passiflora amethystina* vine (Passifloraceae), a plant previously recorded as host for this butterfly (Dell'Erba et al. 2005). Besides ovipositing on its host plant, the female was also observed laying eggs on a non-host Solanaceae (without foraging ants), and also on dead leaves, both nearby to the vine (Fig. 1B). Additional searching revealed other eggs on dead leaves and twigs in the vicinity of the host plant. Although the reasons for ovipositing away from the host plant have not been investigated in the present study, the hypothesis of escape from natural enemies seems the most plausible; ants are commonly present tending homopterans on solanaceous plants and visiting extrafloral nectaries of passion vines in the study area. In the case of *I. drymo*, although it has been reared several times from at least six different solanaceous host plant species at several different localities (Drummond & Brown 1987, Brown & Freitas 1994, Beccaloni et al. 2008, and more than 10 unpublished rearing records by the author), the behavior of ovipositing away from the host plant has never been recorded before in this species. Conversely, the behavior of ovipositing on dead tendrils and off the host plant has been reported for some heliconiines such as *Agraulis Boisduval* & Le Conte, *Dryadula* Michener, *Dryas* Hübner, and *Philaethria* Billberg, and has been suggested as an escape strategy to avoid natural enemies (see discussion in Benson et al. 1975). The present results suggest that this behavior could be more common than previously reported in the tropics. For example, this behavior was also observed in the nymphalid *Blepipolis batea* (Hübner) (Satyrinae: Brassolini) in 1990 (AVLF pers. obs., cited by Brown 1992: 150). However, this was a single event, and an oviposition mistake cannot be discarded. The lack of field observations of actual oviposition events could explain why the behavior of ovipositing away from the host plant has remained rarely reported for tropical butterflies.



FIG. 1. **A.** *Ithomia drymo* ovipositing on a dead twig of a non-host plant (arrow); in the right box, a detailed view of the egg (arrow); **B.** *Eueides aliphera* ovipositing on a dead non-host plant leaf held by the tendrils of its host plant (arrow); in the right box, a detailed view of two eggs (arrows).

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NEW RECORD OF THE ENDANGERED BRAZILIAN SWALLOWTAIL *HERACLIDES HIMEROS* BAIA
(ROTHSCHILD & JORDAN, 1906)

Additional key words: conservation, dry forest, endangered species, Paraíba

In the current list of threatened species in Brazil, 57 species of Lepidoptera are listed, nine of which are in the family Papilionidae (Machado et al. 2008). One of these species is *Heracles himeros* (Hopffer, 1865), a butterfly known from few extant populations, which is poorly studied in comparison with other Papilionidae (Tyler et al. 1994). The two described subspecies are considered threatened: the endangered *Heracles himeros himeros* (Hopffer, 1865), from coastal Rio de Janeiro and Espírito Santo, and the critically endangered *Heracles himeros baia* (Rothschild & Jordan, 1906), known from few specimens from the Brazilian states of Bahia, and Tocantins (Collins & Morris 1985, Tyler et al. 1994, Brown & Freitas 2008a,b, Freitas & Marini-Filho 2011). Although the nominal subspecies, *H. himeros himeros* has been extensively studied in most aspects (immature stages, population ecology and natural history, see Tyler et al. 1994, Brown et al. 1995), there is a lack of basic information about the biology of *H. himeros baia*. In addition, except for a recently collected male from Caetité, Bahia (collected in January, 2000), this subspecies has not been recorded for over 70 years (last collecting date was 1939, from an individual of unknown locality in Bahia, in the BMNH, London), and the available data shows that this butterfly is unknown from conservation areas.

Recently, a population of *H. himeros baia* was found in the “Parque Estadual Pico do Jabre” (PEPJ) (7°15'06"S e 37°22'56"W), located at Serra de Teixeira, in the west of Plateau of Borborema, between the municipalities of Maturéia and Mãe D'água, Paraíba State, NE Brazil. The PEPJ consists of 851 ha with altitudes varying from 780 to 1,000 m (maximum altitude of 1,197 m). The vegetation is montane semideciduous forest, surrounded by semi-arid vegetation (i.e., caatinga), with great physiognomic heterogeneity and a dry season that lasts at least eight months per year (Tabarelli & Silva 2003, Agra et al. 2004, Prado 2009, Rodal et al. 2008). The area is part of the altitude wetlands of the states of Pernambuco and Paraíba, known locally as “brejos de altitude” (Braga et al. 2002, Cabral et al. 2004, Tabarelli & Santos 2004).

Butterfly surveys were recorded monthly from April 2011–April 2012, as part of a broader project studying butterfly diversity in the PEPJ (Kerpel et al. in prep.).

Visual surveys were carried out from 0800 h to 1600 h in six transects: three at low altitudes (780 to 900 m) and three near the top of Pico do Jabre (1,065 to 1,197 m). Each transect was surveyed for 80 minutes, and times of surveys by transect were randomized; the total sampling effort was 96 h.

Adults of *H. himeros baia* were observed from 1045 h to 1330 h within the forest in two transects, both above 1,000 m of altitude. These two transects correspond to the best-preserved sectors in the study area, and also where the potential host plant, *Pilocarpus spicatus* Saint Hill. (Rutaceae) occurs, which according to Agra et al. (2004) occurs only above 900 m of altitude in the study site. A total of 28 *H. himeros baia* were captured and released, with the majority recorded during the wet season (Fig. 2). The number of individuals observed per day varied from one to six, which is slightly lower than those obtained for *H. himeros himeros*, where almost 20 individuals are observed per day in a given site (using the same method of transect counts, see Tyler et al. 1994 and Brown et al. 1995).

In a conservation perspective, the present results are important for at least four reasons: 1) this is the only known population of *H. himeros baia* in recent times; 2) this record, the first in the state of Paraíba, is the northernmost point of occurrence of the subspecies, expanding in about 1000 km its known extent of



FIG. 1. Male *Heracles himeros baia* collected on June 06, 2011, on Parque Estadual Pico do Jabre, Maturéia, Paraíba State; dorsal (left) and ventral view (right).

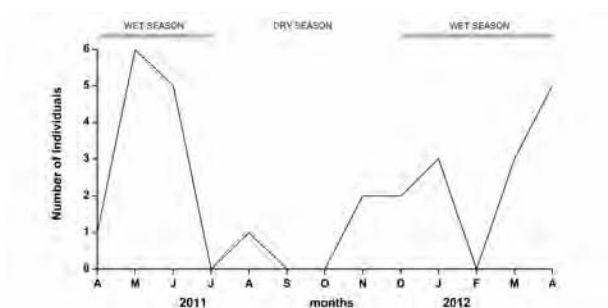


FIG. 2. Monthly numbers of *H. himeros baia* recorded in Parque Estadual Pico do Jabre, Maturéia, Paraíba State, between April, 2011 and April, 2012.

occurrence (sensu IUCN 2013); 3) this is the first record for the biome caatinga (previous records were for the Cerrado savanna and Atlantic Forest); and 4) this is the only population of *H. himeros baia* inside a conservation unity. In view of the present results, and considering its sparse and low-density populations, and fast flight, which makes it difficult to distinguish from the widespread *Heracles astyalus* Godart 1819, it is possible that other populations of *H. himeros baia* persist within its geographical range, thus potentially changing its conservation status.

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EDITOR'S NOTE

(with with credit to Dr. Larry Gall for helping develop this text)

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