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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 MZ95 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).

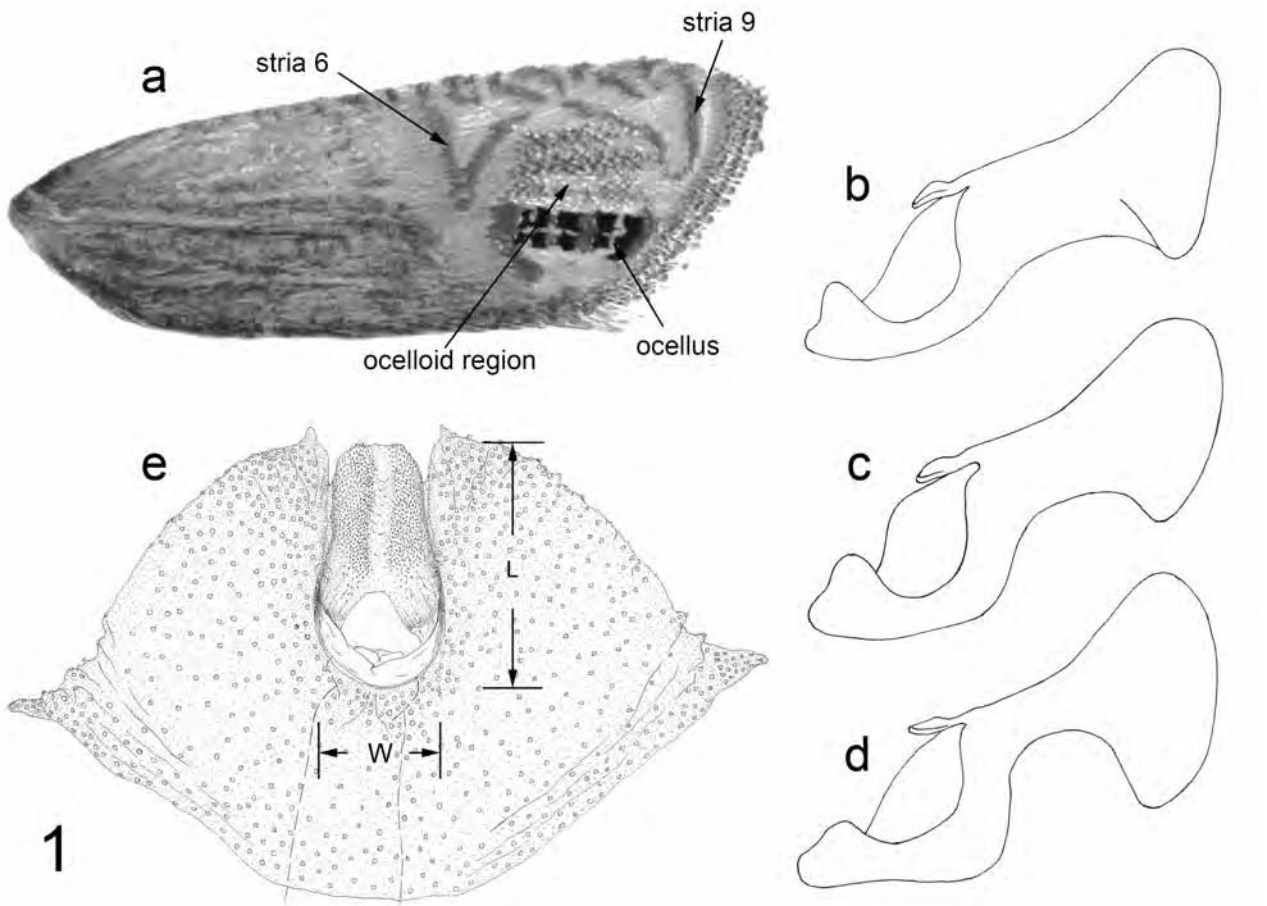



FIG. 1. **1,** *Eucosma refusana* group characters. **a,** forewing pattern, *E. autumnana*. **b–d,** valva shape, *E. amphorana*, *E. verna*, *E. autumnana*. **e,** sterigma-sternum 7, *E. amphorana*.

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.

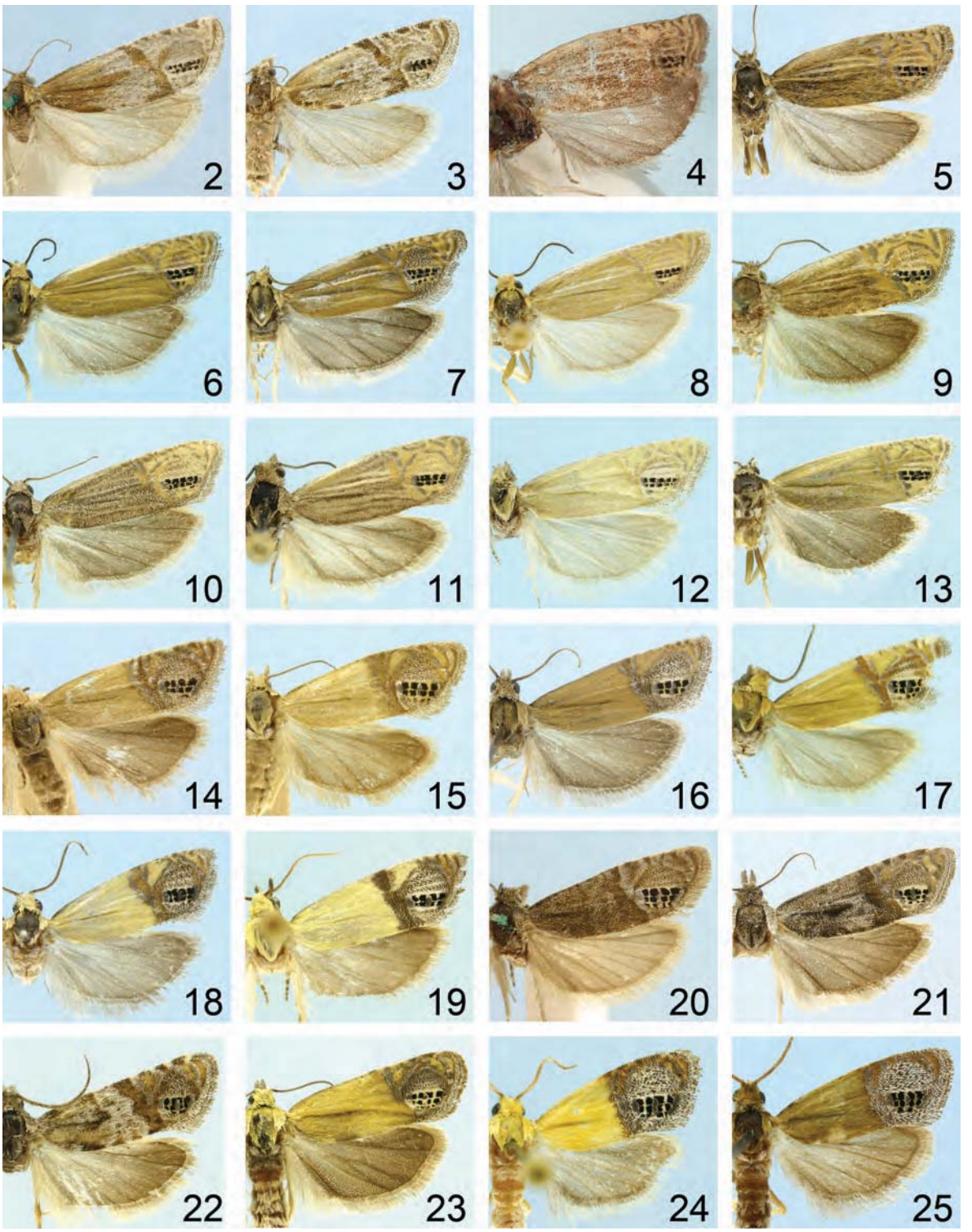
*Thiodia decempunctana*: Fernald [1903]:462; Heinrich 1923:44, fig. 120; McDunnough 1939:44.

*Eucosma decempunctana*: Barnes and McDunnough 1917:172.

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

TABLE 1. Comparison of selected characters.

| | FWL (mm) | | | AR | cornuti | | | SA° | | | NR | | | SR | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **Range** | **mean** | **n** | **mean** | **Range** | **mean** | **n** | **Range** | **mean** | **n** | **Range** | **mean** | **n** | **Range** | **mean** | **n** |
| *decempunctana* | 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 |
| *refusana* | 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 |
| *verna* | 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 |
| *autumnana* | 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 |
| *citricolorana* | 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 |
| *annetteana* | 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 |
| *millerana* | 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 |
| *amphorana* | 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 |
| *litorea* | 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 exihibit 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)

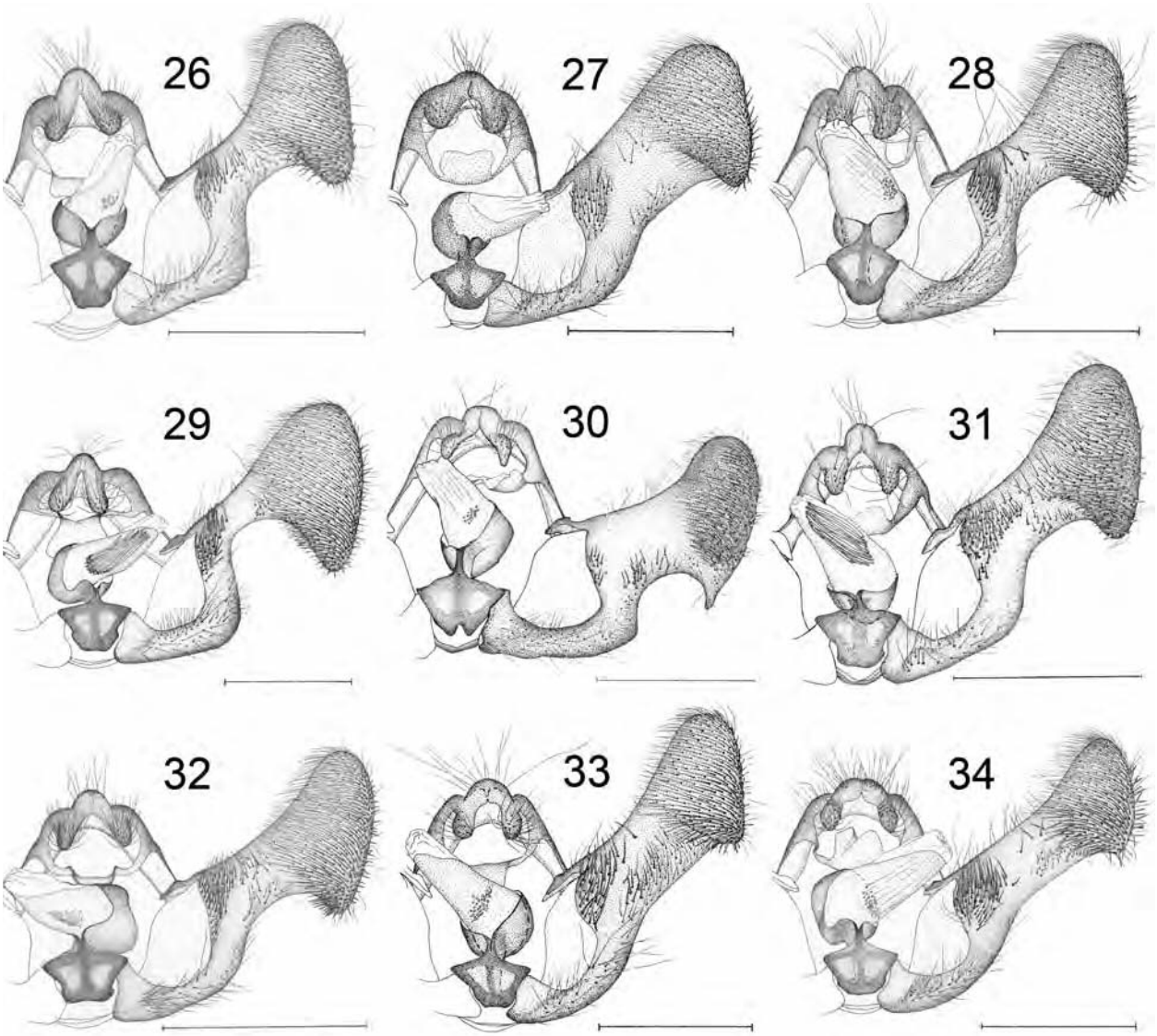
*Grapholita refusana* Walker 1863:382.
*Semasia refusana*: Walsingham 1879:63, pl. 74, fig. 10.
*Thiodia refusana*: Fernald [1903]: 463.
*Eucosma refusana*: Barnes and McDunnough 1917:172.
*Phaneta refusana*: Miller 1971:284; Powell 1983:33; Brown 2005:495; Pohl et al. 2010.

**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.

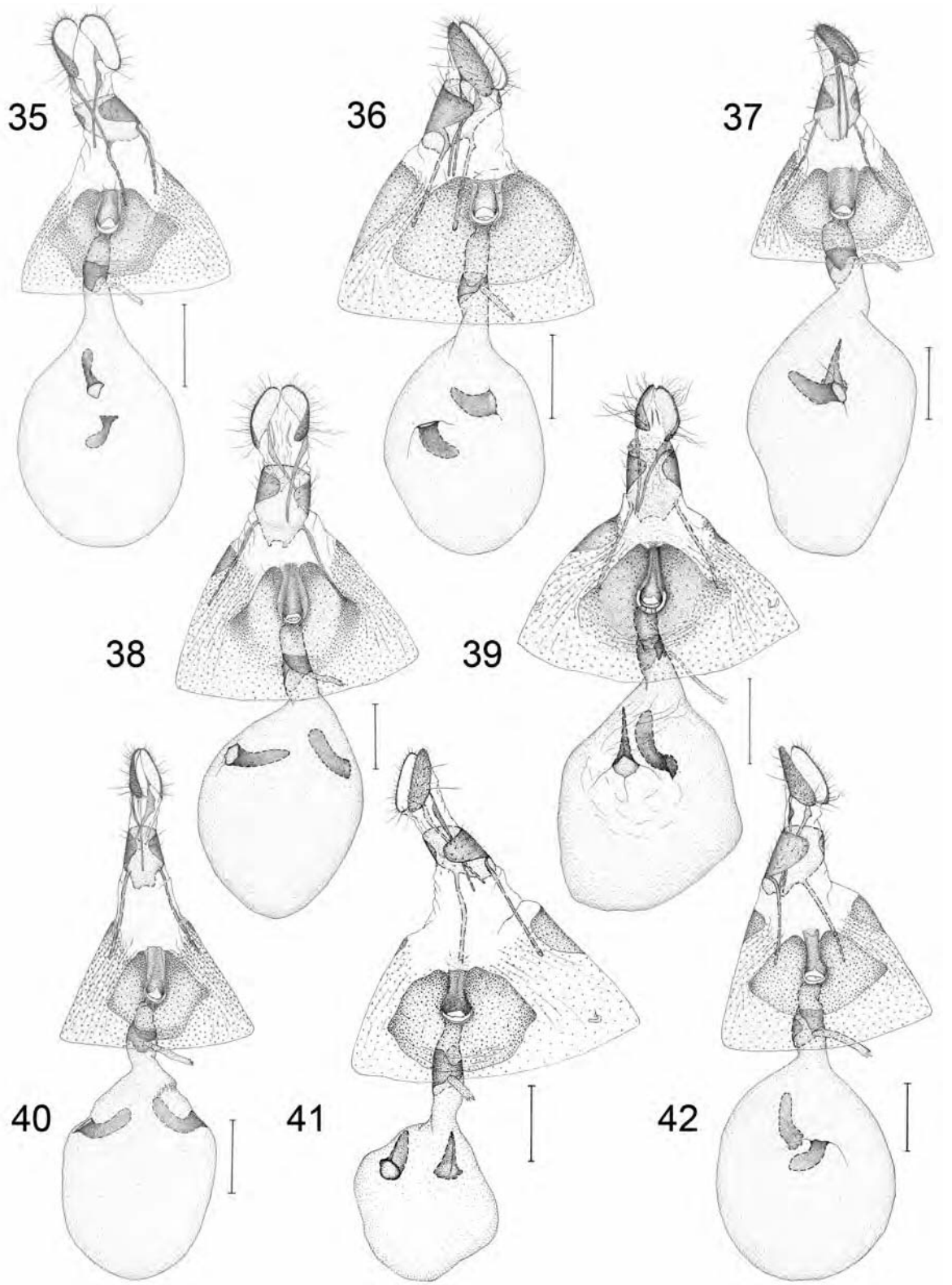
**Distribution and flight period.** We examined 91 individuals documenting a range from Maine to North Dakota, south to North Carolina and Mississippi. The Mississippi and North Carolina specimens were collected in March and April, the others from 24 August to 18 October.

*Eucosma citricolorana* (McDunnough 1942)
(Figs. 12, 13, 30, 46)

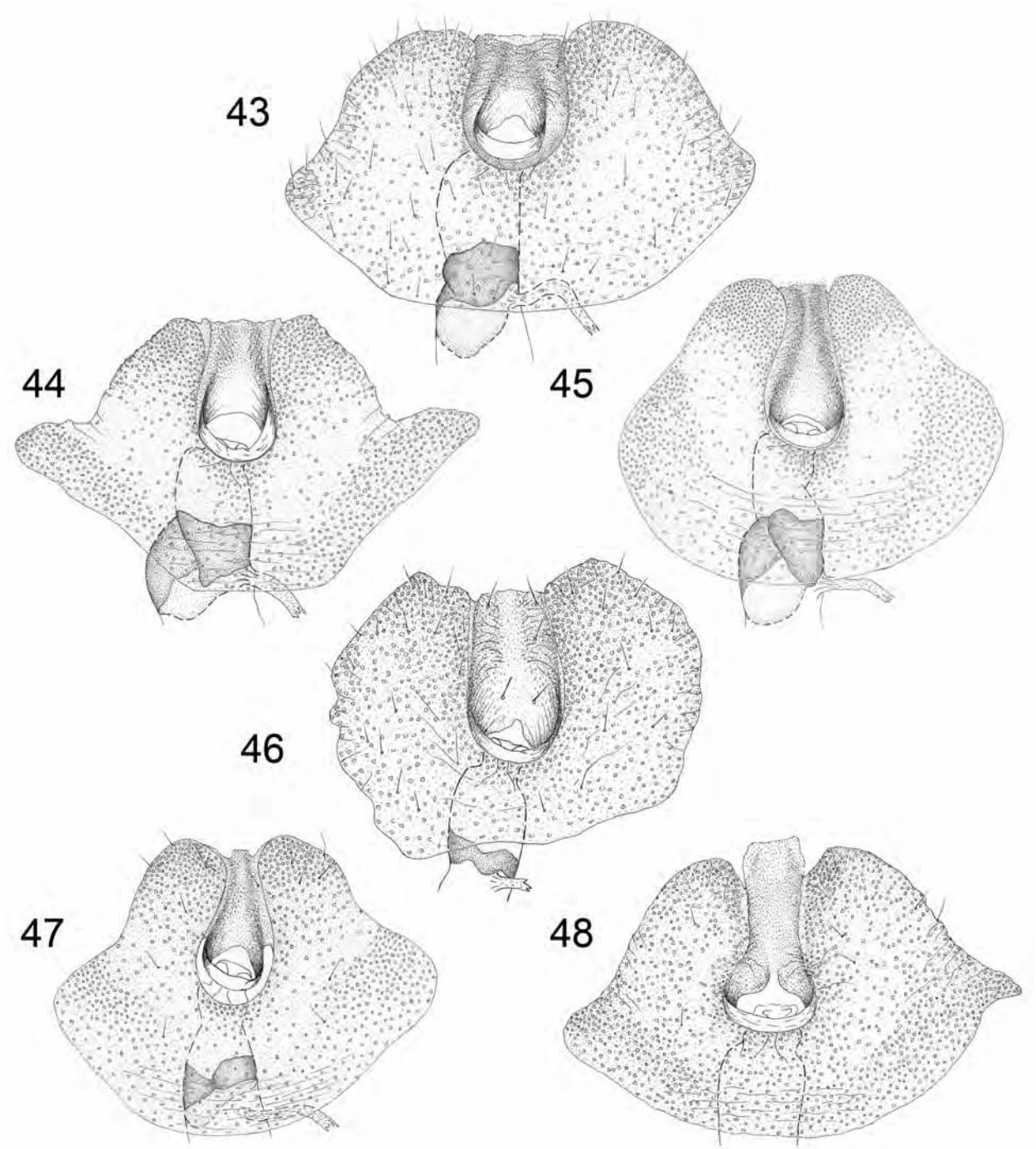
*Thiodia citricolorana* McDunnough 1942:66.

*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 $CuA_2$, 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. 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., Ohoopee 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 Ohoopee 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 Ohoopee 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 Ohoopee 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 Ohoopee Dunes Natural Area and the adjacent Nature Conservancy Preserve. That site differs from the others in having a large population of *C. pauciflosculosa*. 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 Ohoopee 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 Ohoopee Dunes (MacGown et al. 2009). Based on these distribution patterns, it is hypothesized that the Gulf Coastal dunes and the riverine dunes of Ohoopee 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 700km$^2$ 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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## LITERATURE CITED

AXELROD, D. I. 1985. Rise of the grassland biome, Central North America. Bot. Review 51:163–201.

BAIXERAS, J. 2002. An overview of the genus level taxonomic problems surrounding *Argyroploce* Hübner (Lepidoptera: Tortricidae), with description of a new species. Ann. Entomol. Soc. Am. 95:422–431.

BARONE, J. 2005. Historical presence and distribution of prairies in the Black Belt of Mississippi and Alabama. Castanea 70: 170–183.

BARNES, W. AND J. MCDUNNOUGH. 1917. Check list of the Lepidoptera of Boreal America. Herald Press, Decatur, Illinois. viii + 392 pp.

BEAUMONT, D. 2007. The geological origin of the blackland prairies, the Grand Prairie, and Edwards Plateau areas and their soils. Proc. NSOT-NPAT Joint Symposium for 2007: 5–11. [available online at http://npsot.org/symposium2007/home/index.shtml, accessed June 4, 2013]

BROWN, R. L. 2003. Paleoenvironment and biogeography of the Mississippi Black Belt. Evidence from insects. Pp. 11–26. *In* E. Peacock and T. Schauwecker (eds.). Blackland Prairies of the Gulf Coastal Plain: Nature, Culture, and Sustainability. University of Alabama Press, Tuscaloosa. 348 pp.

BROWN, R. L., J. F. G. CLARKE, AND D. H. HABECK. 1983. New host records for Olethreutinae (Tortricidae). J. Lepid. Soc. 37:224-227.

BROWN, R. L. AND J. A. POWELL. 1991. Description of a new species of *Epiblema* (Lepidoptera:Tortricidae: Olethreutinae) from coastal redwood forests in California with an analysis of the forewing pattern. Pan-Pacif. Entomol. 67:104–114.

DELCOURT, H. R. 1979. Late Quaternary vegetation of the eastern Highland Rim and adjacent Cumberland Plateau of Tennessee. Ecol. Monog. 49:255–280.

DELCOURT, P. A. AND H. R. DELCOURT. 1993. Paleoclimates, paleovegetation, and paleofloras during the Late Quaternary. Pp. 71–94. *In* Flora of North America Editorial Committee (ed.). Flora of North America North of Mexico, Vol. I. Oxford University Press, New York. 400 pp.

DESELM, H. R. 1988. The barrens of the western Highland Rim of Tennessee. Pp. 199–219. *In* D. H. Snyder (ed.). Proceedings of the First Annual Symposium on the Natural History of Lower Tennessee and Cumberland River Valleys. Austin Peay State University, Center for Field Biology of Land Between the Lakes. xii + 328 pp.

FERNALD, C. H. [1903]. *In* H. G. Dyar. A list of North American Lepidoptera. United States National Museum Bulletin. 52: xix, 448–489.

GILLIGAN, T. M., D. J. WRIGHT, AND L. D. GIBSON. 2008. Olethreutine Moths of the Midwestern United States. An Identification Guide. Ohio Biological Survey Bulletin New Series. Vol. XVI, No. 2, vii + 334 p.

GILLIGAN, T. M., D. J. WRIGHT, J. MUNZ, K. YAKOBSON & M. P. SIMMONS. 2013. Molecular phylogeny and revised classification of Eucosma Hübner and related genera (Lepidoptera: Tortricidae: Eucosmini). Systematic Entomology, doi: 10.1111/syen.12036.

GILLIGAN, T. M. AND D. J. WRIGHT. 2013. Revised world catalogue of *Eucopina*, *Eucosma*, *Pelochrista*, and *Phaneta* (Lepidoptera: Tortricidae: Eucosmini). Zootaxa 3746: 301–337.

HEINRICH, C. 1923. Revision of the North American moths of the subfamily Eucosminae of the family Olethreutidae. U.S.N.M. Bulletin. 123: iv, 1–298, pls 1–59.

HILL, J. G. 2005. Disjunct distributions of *Pseudopomala brachyptera* and *Campylacantha olivacea* (Orthoptera: Acrididae) in blackland prairies of Mississippi. Entomol. News 116:127–130.

HILL, J. G. 2009. The grasshopper (Orthoptera: Acrididae) fauna of sand dunes along the Little Ohoopee River, Emanuel County, Georgia, USA. Journal of Orthoptera Research 18:29–35.

HOFFMAN, R. A. AND J. K. JONES, JR. 1970. Influence of late-glacial and post-glacial events on the distribution of recent mammals on the northern Great Plains. Pp. 355–394. *In* W. Dort, Jr. and J. K. Jones (eds). Pleistocene and Recent Environments of the Central Great Plains. University of Kansas, Department of Geology, Special Publication No. 3. University Press of Kansas, Lawrence. x + 433 pp.x

JOHNSON, A. F. 1997. Rates of vegetation succession on a coastal dune system in northwest Florida. J. Coastal Res. 13: 373–384.

KAYE, J. M. 1974. Pleistocene Sediment and Vertebrate Fossil Associations in the Mississippi Black Belt: A Genetic Approach. Ph.D. dissertation, Louisiana State University, Baton Rouge.

KEARFOTT, W. D. 1907. New North American Tortricidae. Trans. Amer. Entomol. Soc. 33:1–98.

KING, J. E. AND W. H. ALLEN. 1977. A Holocene vegetation record from the Mississippi River Valley, southeastern Missouri. Quaternary Res. 8:307–323.

KLOTS, A. B. 1942. Type material of North American microlepidoptera other than Aegeriidae in the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist. 79: 391–424.

MACGOWN, J. A., J. G. HILL, AND M. DEYRUP. 2009. Ants (Hymenoptera: Formicidae) of the Little Ohoopee River dunes, Emanuel County, Georgia. J. Entomol. Sci. 44:193–197.

MARKEWICH, H. W. AND W. MARKEWICH. 1994. An overview of Pleistocene and Holocene inland dunes in Georgia and the Carolinas—morphology, distribution, age, and paleoclimate. U.S. Geol. Surv. Bull. 2069:1–32.

MARTIN, L. L. 1963. A specialized scientific paper in two parts. Part I — a new occurrence of *Atrytone dukesi* (Hesperiidae) in Ohio. Part II—a theory on the northern distribution of *Atrytone dukesi* (Hesperiidae). Unublished report, Wellington, Ohio. 20 pp.

MCDUNNOUGH, J. 1939. Check List of the Lepidoptera of Canada and the United States of America. Part II. Microlepidoptera. Memoirs of the Southern California Academy of Sciences 2: 1, 3–171.

_____ 1942. Tortricid notes and descriptions. Can. Entomol. 74:63–71.

_____ 1958. New microlepidoptera, with notes. Amer. Mus. Novit. 1917: 1–11.

METZLER, E. H., J. A. SHUEY, L. A. FERGE, R. A. HENDERSON, AND P. Z. GOLDSTEIN. 2005. Contributions to the understanding of tallgrass prairie-dependent butterflies and moths (Lepidoptera) and their biogeography in the United States. Bull. Ohio Biol. Surv. (N.S.) 15: 1–143.

MILLER, W. E. 1971. Identity of *Phaneta refusana* (Walker) with description of a new species (Tortricidae). Journal of the Lepidopterists' Society. 25: 4, 284–287.

_____ 1987. Guide to the olethreutine moths of midland North America (Tortricidae). U.S.D.A. For. Serv. Agric. Handbook 660:1–104.

PENFOUND, W. T. AND M. E. O'NEILL. 1934. The vegetation of Cat Island, Mississippi. Ecology 15:1–16.

POGUE, M. G. 2010. A new species of *Schinia* Hübner from the southeastern United States (Lepidoptera, Noctuidae, Heliothinae). ZooKeys 52:57–64.

POHL, G. R., G. G. ANWEILER, B. C. SCHMIDT AND N. G. KONDLA 2010. An annotated list of the Lepidoptera of Alberta, Canada; ZooKeys 38:1–549. doi: 10.3897/zookeys.38.383

POWELL, J. A. 1983. Tortricidae. Pp. 31–41. *In* R. W. Hodges. Check list of the Lepidoptera of America north of Mexico. E. W. Classey, London and the Wedge Entomological Research Foundation. 284 pp.

POWELL, J. A. AND P. A. OPLER. 2009. Moths of western North America. University of California Press, Los Angeles, xiii + 369 p.

ROSS, H. H. 1970. The ecological history of the Great Plains: evidence from grassland insects. *In* W. Dort, Jr. and J. K. Jones (eds). Pleistocene and Recent Environments of the Central Great Plains. University of Kansas, Department of Geology, Special Publication No. 3. University Press of Kansas, Lawrence. x + 433 pp.x

SCHIEFER, T.L. 1998. Disjunct distribution of Cerambycidae (Coleoptera) in the Black Belt Prairie and Jackson Prairie in Mississippi and Alabama. Coleop. Bull. 52: 278–284.

SMITH, B. A., R. L. BROWN, W. LABERGE, AND T. GRISWOLD. 2012. A faunistic study of bees (Hymenoptera: Apoidea) in the Black Belt Prairie of Mississippi. J. Kan. Entomol. Soc. 85:32–47.

Transeau, E. N. 1935. The prairie peninsula. Ecology 16:423–437.

WALKER, F. 1863. List of the specimens of lepidopterous insects in the collection of the British Museum. Part 28. Tortricites and Tineites. London.

WALSINGHAM, LORD (THOMAS DEGREY). 1879. Illustrations of typical specimens of Lepidoptera Heterocera in the collection of The British Museum. Part IV. North American Tortricidae. Department of Zoology, British Museum, London. 84 pp + 17 pls.

WATTS, W. A. 1980. The late Quaternary vegetation history of the southeastern United States. Ann. Rev. Ecol Syst. 11:387–409.

WHARTON, C. H. 1989. The natural environments of Georgia. Georgia Dept. Nat. Res. Bull. 114:1–277.

WHITEHEAD, D. R. 1967. Studies of full-glacial vegetation and climate in the southeastern United States. Pp. 237–248. *In* D. J. Cushing and H. E. Wright, Jr. (eds). Quaternary Paleoecology. Yale Univ. Press, New Haven. vii + 433 pp.

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