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Journal of the Lepidopterists' Society



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Cover Illustration:

Hadena ectypa (Morrison, 1875), larva and adult. Larva collected 3 August 2009, photographed in the lab 15 August 2009. Adult collected (as larva) 28 July 2009, emerged from pupa 4 September 2009, photographed in the lab 6 September 2009. Both individuals collected at the Knightville State Wildlife Management Area in the town of Huntington, Hampshire County, Massachusetts, USA. Photos by Michael W. Nelson, Massachusetts Natural Heritage & Endangered Species Program. See article on page 1.

NOTES ON A RECENTLY DISCOVERED POPULATION OF *HADENA ECTYPA* (MORRISON, 1875)
(NOCTUIDAE: NOCTUINAE: HADENINI) IN MASSACHUSETTS

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ABSTRACT. *Hadena ectypa* (Morrison, 1875) (Noctuidae: Noctuinae: Hadenini) is a rarely encountered moth of conservation concern, inhabiting forest and woodland openings and edges in eastern North America. A population discovered in 2002 in Massachusetts (USA) is the first record of this species in New England. *Hadena ectypa* larvae from this population were reared in 2003, 2009, and 2010; the immature stages and life history are described. Parasitism by a species of *Eulophus* Geoffroy, 1762 (Hymenoptera: Eulophidae) and predation by *Toxomerus geminatus* (Say, 1823) (Diptera: Syrphidae) were observed. The native host plant of *Hadena ectypa* is *Silene stellata* (L.) W.T. Aiton (Caryophyllaceae), however, the population in Massachusetts uses introduced *Silene vulgaris* (Moench) Garcke as the primary larval host. *Hadena ectypa* could have adopted *S. vulgaris* as a novel host at any time during the past 200 years. *S. vulgaris* shares a number of traits with *S. stellata* that may have facilitated this host shift. Many of these traits are also shared by another introduced species, *Silene latifolia* Poiret, and while *Hadena ectypa* will feed on this plant in captivity, is not known to use it in the wild. The adoption of *S. vulgaris* as a larval host may allow *Hadena ectypa* to spread to new, weedier habitats, to increase its geographic range, and to increase its propensity for a second annual generation.

Additional key words: calyx, diapause, parasitoid, larval behavior, rearing

Hadena ectypa (Morrison, 1875) is a noctuid moth, one of 140 species in the Holarctic genus *Hadena* Schrank, 1802 (Hacker 1996; Troubridge & Crabo 2002). Fifteen species of *Hadena* occur in North America, most of which are western, with only *Hadena ectypa* and *Hadena capsularis* (Guenée, 1852) occurring in the east (Troubridge & Crabo 2002). *Hadena ectypa* is found from southeastern New York west to Minnesota and Kansas, and south to northern Georgia. It is a rare moth throughout its range, found most frequently in the Appalachian Mountains, from southern Ohio and West Virginia, south to Tennessee and North Carolina (Schweitzer et al. 2011). As larvae, species in the genus *Hadena* are specialized feeders on the flowers and seed capsules of “pinks,” herbaceous plants in the family Caryophyllaceae (Forster & Wohlfahrt 1971; Hacker 1996; Young 1997). Species in the genus *Silene* L. are particularly frequent hosts for *Hadena* (Robinson et al. 2002). The only published larval host for *Hadena ectypa* is starry campion, *Silene stellata* (L.) W.T. Aiton (Robinson et al. 2002), plus one record of a larva on fire pink, *Silene virginica* L. (Kephart et al. 2006). The habitat of *Hadena ectypa* is typically described as forest and woodland openings and edges, though it occurs in more open prairie and savanna habitats in the western part of its range (Metzler et al. 2005). The reported flight season for *Hadena ectypa* extends from late June through early August (Wyatt 1929; Forbes 1954; Rings et al. 1992; Schweitzer et al. 2011), with larvae developing in July and August (Wyatt 1929; Forbes 1954; Crumb 1956; Godfrey 1972).

METHODS AND RESULTS

Fieldwork. A population of *Hadena ectypa* was discovered in Massachusetts (USA), in Hampshire County, town of Huntington, at the Knightville State Wildlife Management Area (WMA). The initial discovery was made when a single adult was captured in a blacklight trap (15 Watt, Leroy Koehn design), set the night of 10-11 September 2002. As both the locality and the date of capture were unusual for *Hadena ectypa*, the identification of the specimen was confirmed by both T.L. McCabe (New York State Museum) and D.F. Schweitzer (NatureServe). Subsequent searches of the literature and collections (including the Harvard Museum of Comparative Zoology, the American Museum of Natural History, the New York State Museum, and the National Museum of Natural History) failed to find any records for *Hadena ectypa* to the north or east of southeastern New York state. Therefore the moth trapped in Huntington, Massachusetts in 2002 appears to represent the first record of *Hadena ectypa* in New England.

Not a single September collection date was found for museum specimens from the Northeast, nor could any reference to such a late flight season be found in the literature, with one exception. In what appears to be the first published life history account for *Hadena ectypa*, Wyatt (1929) describes the rearing of an unspecified number of individuals, collected from *Silene stellata* by A. Herz, one of which emerged on 5 September of the same year. The remaining individuals overwintered as pupae, emerging between 23 June and 25 July of the

following year. Therefore it appears that *Hadena ectypa* has a facultative second generation, which in the wild is probably partial as far north as Massachusetts. In the British Isles, a partial second generation occurs in several species of *Hadena* (Porter 1997).

The discovery of *Hadena ectypa* in Massachusetts presented another mystery: its native host plant, *Silene stellata*, is not known to occur in the state (FNA 2005; Magee & Ahles 2007; Dow Cullina et al. 2011; Haines 2011). On 29 July 2003, the Knightville WMA was visited in the hope of finding larvae of *Hadena ectypa*, and possibly even discovering a population of *S. stellata* in Massachusetts. The Knightville WMA site is at the bottom of a steep-sided ravine, forested with northern hardwoods, hemlock (*Tsuga canadensis* (L.) Carrière), and white pine (*Pinus strobus* L.). The Westfield River flows through the bottom of the ravine. The light trap that caught *Hadena ectypa* in 2002 was set in floodplain forest habitat on the west side of the river, approximately 50 m from the bank. The floodplain forest is on an approximately 100 m wide strip of flat terrain bordering the river, which also includes open fields maintained by infrequent mowing, and a dirt road running parallel to the river. Immediately to the west of the flat strip of terrain, the topography rises steeply and is densely forested.

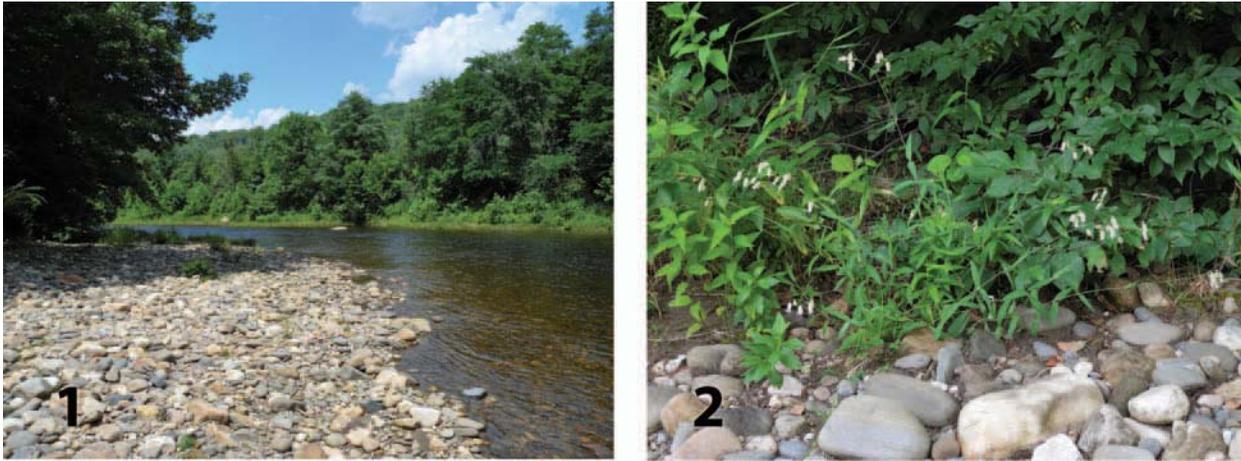
Various open areas within this predominantly forested habitat were searched for species of *Silene*, including the fields, margins of the dirt road, and the river banks. The river has a rocky substrate, with margins of accumulated cobble and sandy soils, which support a narrow strip of herbaceous vegetation between the river and the floodplain forest (Fig. 1). Approximately 450 m to the south of where the *Hadena ectypa* adult was trapped in 2002, growing amongst other herbaceous vegetation on the sandy river bank, a concentration of bladder campion, *Silene vulgaris* (Moench) Garcke, was found. Eight *Hadena ectypa* larvae were found on the *S. vulgaris*, ranging from the second through the fifth instar. Each larva was feeding on a green seed pod (ovary), hidden inside the inflated calyx of a flower just past bloom. In addition, one *Hadena ectypa* egg was found on *S. vulgaris*, laid on the green ovary inside the calyx of a flower. All eight larvae and the egg were collected for rearing. This discovery represents the first record of *Hadena ectypa* using *S. vulgaris* as a larval host, which is of particular interest because *S. vulgaris* is an introduced species from Europe (FNA 2005; Magee & Ahles 2007). At the request of MWN, Lynn Harper (Massachusetts Natural Heritage & Endangered Species Program) searched for additional larvae during a visit to the Knightville WMA on 7 August 2003. One fourth instar larva was found on

S. vulgaris, growing on the river bank at a second location approximately 700 m to the north of where the *Hadena ectypa* adult was trapped. This larva was also collected for rearing.

On 8 August 2004, and again on 23 June 2005, the Knightville WMA was visited in order to more extensively search for other species of *Silene*, and in particular any native species that could serve as larval hosts for *Hadena ectypa*. During the 2004 visit, in addition to searching the river banks, margins of the dirt road, and fields in the vicinity of where *Hadena ectypa* had been found previously, a nearby talus slope and wetland were explored. The canopy on the talus slope is sparse enough to allow growth of herbaceous vegetation in the understory. The wetland is a beaver pond surrounded by open marsh and wet meadow. No species of *Silene* were found on the talus slope or in the wetland. Ragged robin, *Silene flos-cuculi* (L.), was found during the 2005 visit. Like *Silene vulgaris*, *S. flos-cuculi* is an introduced species from Europe (FNA 2005; Magee & Ahles 2007). The *S. flos-cuculi* was growing on the bank and cobble bars along the west side of the river, immediately to the south of where *Hadena ectypa* had been found feeding on *S. vulgaris* in 2003. In 2005, *S. vulgaris* was found growing in the same area as *S. flos-cuculi*, and both plants were searched for eggs and larvae of *Hadena ectypa*. None were found, but it was probably still too early in the season.

The Knightville WMA was not revisited until 26 July and 17 August 2008. The stretch of riverbank where *Hadena ectypa* larvae were found on *Silene vulgaris* in 2003 was checked, and found to be overgrown with Japanese knotweed, *Fallopia japonica* (Houttuyn) Ronse Decraene (Polygonaceae), an invasive species introduced from Asia (FNA 2005; Magee & Ahles 2007). No *S. vulgaris* remained, but a search to the north found about a dozen *S. vulgaris* plants, scattered along an approximately 1 km stretch of the west bank of the river. A few *Silene flos-cuculi* plants were also found along this stretch, as well as a few white campion, *Silene latifolia* Poiré, another introduced species from Eurasia (FNA 2005; Magee & Ahles 2007) that had not been noted during previous visits. The *S. vulgaris*, *S. flos-cuculi*, and *S. latifolia* plants were all searched for *Hadena ectypa* eggs and larvae, but none were found. A few of the *S. vulgaris* plants, however, had feeding damage that may have been caused by *Hadena ectypa* larvae.

The Knightville WMA was visited on 28 July 2009 in order to determine if *Hadena ectypa* still persisted at this site. At the north end of the stretch of river where *Hadena ectypa* had been found in 2003, a half dozen *Silene vulgaris* plants were found growing on the sandy



FIGS. 1-2. 1) Habitat of *Hadenectypa* at the Knightville State Wildlife Management Area, town of Huntington, Hampshire County, Massachusetts, USA. This stretch of the Westfield River has a rocky substrate, with margins of accumulated cobble and sandy soils, which support a narrow strip of herbaceous vegetation between the river and the floodplain forest. Photographed 28 July 2009. 2) Bladder campion, *Silene vulgaris*, growing on the sandy river bank behind the cobble bar in Fig. 1. *Hadenectypa* was collected from this plant. Photographed 28 July 2009.

bank behind a cobble bar. The habitat (Fig. 1) and *S. vulgaris* (Fig. 2) were photographed at this location. Most of the *S. vulgaris* flowers were just past peak, with petals still present and ovaries small and green. Careful examination of flowers at this stage revealed the presence of *Hadenectypa*: four first instar larvae, each in its own flower, and two unhatched eggs, both laid on the ovary of a single flower. All four larvae and both eggs were collected for rearing. Also observed on 28 July 2009 were a number of small syrphid flies (Diptera: Syrphidae), including one mating pair, on and around the *S. vulgaris*. In addition, syrphid fly larvae were observed on the *S. vulgaris* flowers. On 3 August 2009 the Knightville WMA was revisited in order to determine if the *Hadenectypa* population extended further to the south of areas explored previously. At a site on the west bank of the river, approximately 2.6 km to the south of where *Hadenectypa* was found on 28

July 2009, a single third instar larva of *Hadenectypa* was found on *S. vulgaris*, and collected for rearing.

The Knightville WMA was revisited on 15, 18, and 20 July 2010. On 15 July 2010, at the same site where *Hadenectypa* was found on 28 July 2009, five large *Silene vulgaris* plants were thoroughly searched, with hundreds of flowers examined. A total of 25 *Hadenectypa* larvae were found (two in the second instar and 23 in the third instar), as well as seven shed head capsules (one from the first instar and six from the second instar), and two empty eggshells (both inside the same flower). Two second instar and six third instar larvae were collected for rearing. On 18 July 2010, the river banks to the north were searched, but the only sign of *Hadenectypa* was a single empty eggshell on one of six *S. vulgaris* plants about 800 m north of where *Hadenectypa* was found on 15 July. On 20 July 2010, the river banks to the south were searched. At one site



FIGS. 3-4. 3) *Hadenectypa*, adult male, reared in 2009. Wingspan 28.5 mm. 4) *Hadenectypa*, adult female, reared in 2010. Wingspan 30.0 mm.

approximately 1.8 km south of where *Hadena ectypa* was found on 15 July, one first instar, one second instar, and two third instar larvae were found on six *S. vulgaris* plants, as well as a shed second instar head capsule and seven empty eggshells. The first and second instar larvae were collected for rearing. At a second site about 850 m farther south (close to where *Hadena ectypa* was found on 3 August 2009), one first instar and two second instar larvae were found on four *S. vulgaris* plants, as well as two shed head capsules (one from the first instar and one from the second instar), and three empty eggshells. The first instar larva and one second instar larva were collected for rearing.

Rearing. In 2003, 10 individuals of *Hadena ectypa* were collected as one egg and nine larvae ranging from the second through the fifth instar. In 2009, seven individuals were collected as two eggs, four first instar larvae, and one third instar larva. In 2010, 12 individuals were collected as two first instar larvae, four second instar larvae, and six third instar larvae. Each individual was reared separately in its own plastic vial. In 2003, all larvae were initially fed flowers and ovaries of *Silene vulgaris*, and later switched to flowers and ovaries of *Silene latifolia*, which was accepted. In 2009 and 2010, all larvae were fed flowers and ovaries of *S. vulgaris* exclusively. A 1:1 mixture of peat and sand was provided for pupation. Rearings were kept on a shaded outside porch for a natural photoperiod and temperature regime.

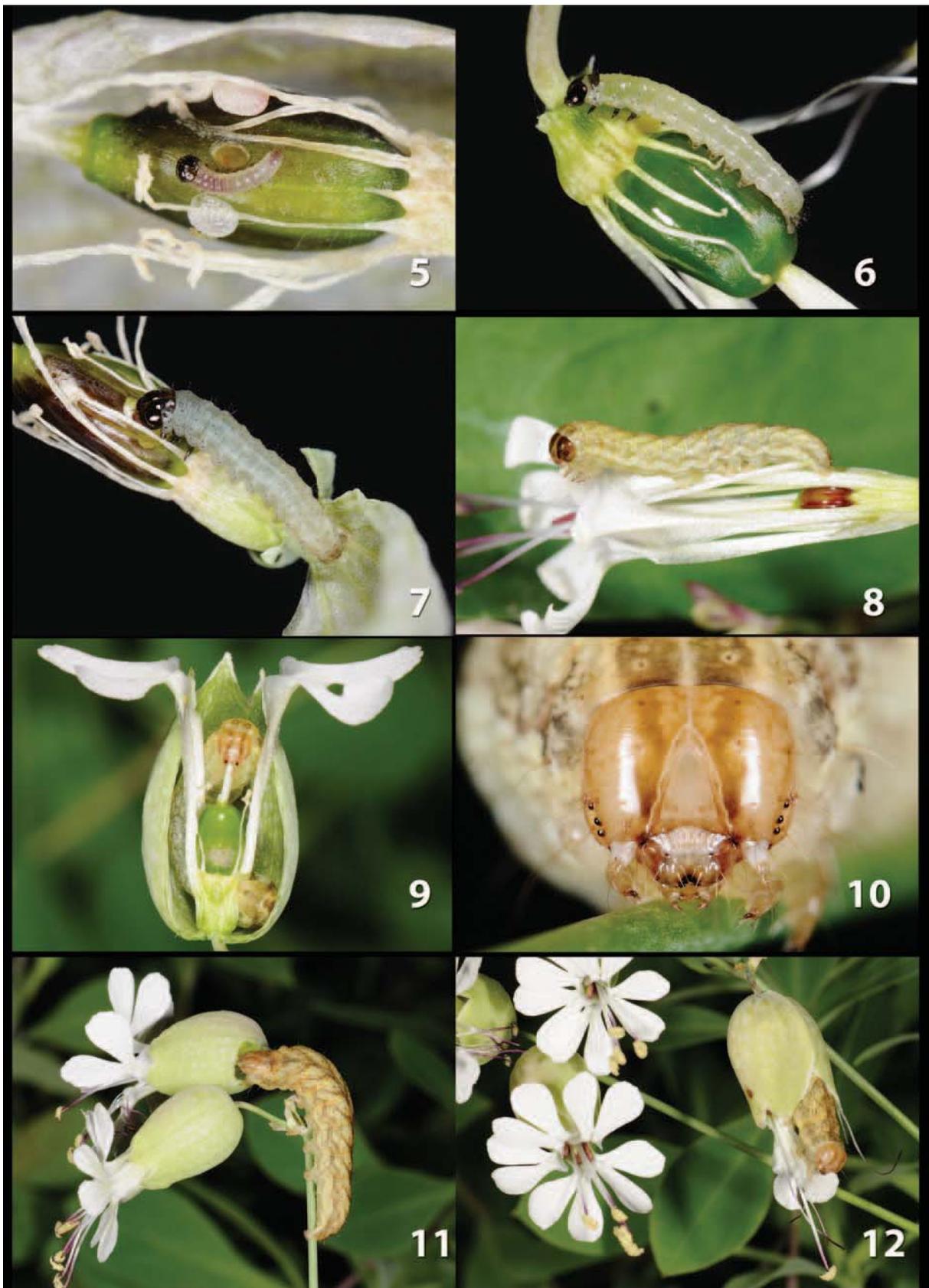
The *Hadena ectypa* egg collected on 29 July 2003 hatched on 31 July, and the fully-grown larva burrowed into the peat/sand mixture for pupation on 21 August, a total larval development time of only 21 days. Of the other eight individuals reared in 2003, one final instar larva was preserved, and the other seven burrowed into the peat/sand for pupation between 10 and 22 August. The eight individuals reared through pupation in 2003 emerged between 29 August and 27 September, with pupal periods ranging from 19 to 37 days (mean of 27 days). Of the seven individuals reared in 2009, three were preserved as larvae, and the other four burrowed

into the peat/sand for pupation between 11 and 17 August. These individuals emerged between 28 August and 9 September, with pupal periods ranging from 17 to 23 days (mean of 21 days). An adult male reared in 2009 is shown in Fig. 3. Of the 11 individuals reared in 2010, four were preserved as larvae, one was preserved as a pupa, and the other six burrowed into the peat/sand for pupation between 26 July and 13 August. These individuals emerged between 13 August and 4 September, with pupal periods ranging from 17 to 22 days (mean of 18 days). An adult female reared in 2010 is shown in Fig. 4.

One fifth instar *Hadena ectypa* larva collected on 29 July 2003 was found dead inside a calyx of *Silene vulgaris* on 3 August, along with 16 live eulophid larvae (Hymenoptera: Eulophidae) that had exited its body. The eulophids pupated almost immediately, and all 16 adults emerged on 10 August. Specimens were preserved, and later identified as belonging to the genus *Eulophus* Geoffroy, 1762 by Dr. Michael W. Gates at the Systematic Entomology Laboratory, Agricultural Research Service, U.S. Department of Agriculture. The specimens could not be identified to species, as the genus *Eulophus* is in need of revision, and species identification requires sorting through primary literature and type specimens that are not readily available.

On 20 July 2010, a syrphid fly larva (likely the same species observed on 28 July 2009) was inadvertently collected along with a *Silene vulgaris* flower and one second instar larva of *Hadena ectypa*. When the contents of the rearing vial were examined that evening, all that remained of the *Hadena ectypa* larva were the head capsule and cuticle. The syrphid larva was kept for rearing and identification. It was fed pre-pupal braconid larvae (Hymenoptera: Braconidae), of which it consumed four over the course of six days. The adult fly emerged on 2 August. The specimen was sent to Michael C. Thomas at the Connecticut Agricultural Experiment Station, who identified it as *Toxomerus geminatus* (Say, 1823).

FIGS. 5-12. [Opposite page] **5)** *Hadena ectypa* egg, hatchling larva, and empty eggshell, all on ovary of *Silene vulgaris* (the calyx has been peeled open). The hatchling has chewed a hole through the ovary wall to feed on the ovules within. Eggs 0.7 mm in diameter, 0.4 mm high. Hatchling larva 1.8 mm long, head capsule 0.35 mm wide. Photographed 29 July 2009. **6)** *Hadena ectypa*, second instar larva on ovary of *Silene vulgaris* (the calyx has been removed). Larva 4.5 mm long, head capsule 0.55 mm wide. Photographed 23 July 2010. **7)** *Hadena ectypa*, third instar larva feeding on ovary of *Silene vulgaris* (the calyx has been peeled back). Larva 6.0 mm long, head capsule 0.80 mm wide. Photographed 2 August 2009. **8)** *Hadena ectypa*, fourth instar larva feeding on petals of *Silene vulgaris* (the calyx has been removed). Larva 13 mm long, head capsule 1.3 mm wide. Photographed 5 August 2009. **9)** *Hadena ectypa*, fifth instar larva feeding on style inside calyx of *Silene vulgaris* (one side of the calyx has been removed). The larva has also chewed a hole through the ovary wall, exposing the ovules within. Larva 18 mm long, head capsule 1.8 mm wide. Photographed 5 August 2009. **10)** *Hadena ectypa*, sixth instar, frontal view of head. Head capsule 2.8 mm wide. Photographed 25 July 2010. **11)** *Hadena ectypa*, sixth instar larva making hole in calyx of *Silene vulgaris*. Larva 25 mm long, head capsule 2.7 mm wide. Photographed 12 August 2009. **12)** *Hadena ectypa*, sixth instar larva half inside calyx of *Silene vulgaris*, feeding on petals. Larva 25 mm long, head capsule 2.7 mm wide. Photographed 12 August 2009.



Deposition of specimens. The single wild-collected *Hadena ectypa* adult was pinned and spread, as were all reared adult moths. Pupal shells were pinned. Larvae and one pupa were preserved in 75% ethanol. *Eulophus* sp. parasitoids were mounted on points. *Toxomerus geminatus* was preserved in 75% ethanol. Specimens were deposited at the Massachusetts Natural Heritage & Endangered Species Program Insect Collection.

Description of immature stages. The following descriptions were prepared with either living specimens or photos of living specimens, and later checked and expanded by examining preserved material. All specimens (N = 29) were from the population at the Knightville State Wildlife Management Area in the town of Huntington, Hampshire County, Massachusetts, USA.

Egg (Fig. 5). Flattened spherical, 0.7 mm in diameter and 0.4 mm high. Micropylar rosette with 10–12 lobes. White in color, chorion with reticulate sculpturing. Black head capsule and lavender gut of first instar larva visible through eggshell prior to hatching.

First instar larva (Fig. 5). Length ~1.8 mm at hatching, growing to 3.0 mm. Head capsule 0.30–0.35 mm wide, smooth and shiny, solid black in color. Prothoracic shield brown upon hatching, becoming gray. Legs gray. Body smooth and pale, grayish white, almost colorless, with minute (<0.1 mm long), tan to dark brown setae, each seta arising from a small gray pinaculum. Spiracles round to slightly oval, outlined with gray. Gut of hatching larva lavender in color, visible through body wall (Fig. 5), fading shortly after hatching.

Second instar larva (Fig. 6). Growing to 5.5 mm in length. Head capsule 0.55–0.60 mm wide, smooth and shiny, solid black in color. Prothoracic shield and legs dark gray. Body smooth and pale, grayish white, almost colorless, with minute (~0.1 mm long), tan to brown setae, each seta arising from a small gray pinaculum. Spiracles round to slightly oval, outlined with gray. Anal shield and posterior of anal prolegs sclerotized, dark gray in color.

Third instar larva (Fig. 7). Growing to 8.0 mm in length. Head capsule 0.75–0.80 mm wide, smooth and shiny, dark brown to black in color. Prothoracic shield dark gray, bisected with a pale gray median stripe and flanked with pale gray on either side. Legs dark gray. Body smooth and pale, greenish gray, with faint, grayish-white dorsal and spiracular lines. Setae minute (~0.2 mm long), tan in color, each arising from a small gray pinaculum. Subdorsal pinacula smaller than lateral pinacula. Spiracles round to slightly oval, tan in color and outlined with gray. Anal shield and posterior of anal prolegs sclerotized and gray in color.

Fourth instar larva (Fig. 8). Growing to 13 mm in length. Head capsule 1.2–1.3 mm wide, smooth and shiny, yellowish tan in color with brown bar extending from vertex to base of frons; vertex and coronal region sometimes more extensively brown, obscuring bar (as in Fig. 8). Ocelli and mandibles dark brown. Color and pattern of prothoracic shield and legs as in the sixth instar. Body smooth and pale, whitish yellow in color, with darker, greenish-yellow markings, pattern elements as in the sixth instar. Dorsal and subdorsal setae with yellow ring around base. Supraspiracular area with greenish-yellow mottling. Spiracles oval, tan in color and outlined with black. Subspiracular area pale yellow, almost white. Ventrolateral area and venter pale yellow, almost colorless. Setae short (<0.3 mm), some on head, prothorax, venter, and ninth and tenth abdominal segments longer (0.3–0.5 mm). Setae tan in color, each thoracic and abdominal seta arising from a minute pinaculum. Subdorsal pinacula smaller than lateral pinacula.

NOTE: Several individuals reared in 2010 were unusually large in the third instar, and had a slightly wider head capsule than is typical at this stage. Furthermore, no fourth instar head capsules could be

found for these same individuals, after they molted to “fifth” instars of typical size and head capsule width. It is possible that these individuals consumed their fourth instar head capsules, or that the capsules were simply lost. However, this also suggests the intriguing possibility that some individuals, under conditions conducive to rapid growth, may skip an instar by combining the third and fourth instars into a single stage. This possibility should be investigated further.

Fifth instar larva (Fig. 9). Growing to 20 mm in length. Head capsule 1.7–1.8 mm wide, smooth and shiny, color and pattern as in the sixth instar. Ocelli and mandibles dark brown. Color and pattern of prothoracic shield and legs as in the sixth instar. Body smooth and yellow in color, with greenish-brown markings dorsally, pattern elements as in the sixth instar. Dorsal and subdorsal setae with yellow ring around base, lateral setae with slightly smaller yellow ring. Supraspiracular area with greenish-brown mottling. Spiracles oval, tan in color and outlined with black. Subspiracular area pale yellow. Ventrolateral area and venter pale yellow, almost colorless. Setae short (<0.4 mm), some on head, prothorax, venter, and ninth and tenth abdominal segments longer (0.4–0.7 mm). Setae tan in color, each thoracic and abdominal seta arising from a minute pinaculum. Subdorsal pinacula about same size as lateral pinacula.

Sixth instar larva (Figs. 10, 11, and 12). Growing to 28–32 mm in length and 4.0–5.0 mm wide at fourth abdominal segment. Head capsule (Fig. 10) 2.7–2.8 mm wide, rounded in frontal view, smooth and shiny; yellowish tan in color with faint, reticulate brown patterning, distinct, brown coronal/frontal stripe extending from vertex to base of frons, and short brown supraocellar stripe. Distance between dorsal adfrontal seta (AF2) and ventral posteriodorsal seta (P1) slightly less than distance between P1 and dorsal posteriodorsal seta (P2). Ocelli dark brown. Antennal base white, antenna yellowish tan. Anteclypeus white, labrum yellowish tan with dark brown edge at notch. Mandible yellowish tan proximally, brown distally, cutting edge dark brown, almost black. Mandible with six teeth on cutting edge, plus one large, triangular inner tooth, which is absent in *Hadena capsularis* (Godfrey 1972, Fig. 42 as compared to Fig. 40). Details of the hypopharyngeal complex are given in Godfrey (1972, p. 26 and Fig. 43). Edges of postgenal sclerites almost touch.

Prothoracic shield with concentration of brown dorsally, bisected with yellow median stripe and flanked with yellow on either side, each seta with yellow ring around base. On first thoracic segment, distance between second dorsal seta (D2) and second subdorsal seta (SD2) greater than distance between D2 and second extra dorsal seta (XD2). Legs yellowish tan, matching lighter portions of head capsule. Metathoracic coxae narrowly separated.

Body smooth and golden yellow in color, with brown markings dorsally, including two parallel dorsal lines, fused between segments, outlining a narrow and broken dorsal stripe flanked by an oblique dorsolateral dash on each segment, creating a “herringbone” pattern of chevrons pointing posteriorly. Each dorsolateral dash (“arm” of chevron) widest dorsally, tapering laterally. Dorsal and subdorsal setae with yellow ring around base (dorsal rings with brown “shadow” on side nearest dorsal line), lateral setae with smaller yellow ring. Supraspiracular area with pale brown mottling. Spiracles oval, tan in color and outlined with black. Height of spiracle on first thoracic segment 1.2 times height of spiracles on first through seventh abdominal segments; height of spiracle on eighth abdominal segment 1.3 times height of those on first through seventh segments. On second abdominal segment, distance between first subdorsal seta (SD1) and spiracle greater than distance between first lateral seta (L1) and spiracle; on eighth abdominal segment, distance between SD1 and spiracle less than distance between L1 and spiracle. Subspiracular area pale yellow; ventrolateral area and venter paler yellow, almost colorless. Setae short (<0.5 mm), some on head, prothorax, venter, and ninth and tenth abdominal segments longer (0.5–1.0 mm). Setae tan in color, each thoracic and abdominal seta arising from a minute pinaculum. Subdorsal pinacula about same size as lateral pinacula. Venter of first and second abdominal segments with setae arising from a prominent pinaculum (Crumb 1956). Crochets uniordinal, number on each proleg: third abdominal segment, 20–23; fourth, 20–24; fifth, 22–26; sixth, 22–28; and tenth, 28–32.



FIGS. 13-14. **13)** *Hadena ectypa*, pupa, lateral. Length 16 mm, width 5.0 mm at third abdominal segment. Photographed 20 August 2009. **14)** *Hadena ectypa*, pupa, ventral. Length 15 mm, width 5.0 mm at third abdominal segment. Photographed 7 August 2010.

Pupa (Figs. 13 and 14). Length 14.5–16.5 mm, width 4.5–5.0 mm at third abdominal segment. Head with bulging eyes and vertex, and dorsal concavity at the epicranial suture. Wings ending at posterior margin of fourth abdominal segment. Maxillae extending past wing margins in prominent ventral lip above articulation of fourth and fifth abdominal segments. Metathoracic legs ending in line with spiracle on fourth abdominal segment, antennae slightly shorter. Mesothoracic legs ending in line with posterior margin of first abdominal segment. Prothoracic legs and labial palpi barely visible. Tenth abdominal segment ending in elongated cremaster with single pair of stout hooks, both tapered and curved inwardly at apex. Integument thin, light orangish brown on wings and other appendages, somewhat thicker and darker, orangish brown on abdominal segments, and considerably thicker and darker brown on eyes, vertex of head, dorsum of head and thorax, and ninth and tenth abdominal segments. Integument smooth on wings and other appendages, with only faint, wrinkled sculpturing under magnification. Wrinkled sculpturing more prominent on head. Dorsum of head, thorax, and anterior half of first through fourth abdominal segments sculptured with numerous minute pits, anterior half of fifth through seventh abdominal segments with pits around entire perimeter, eighth and ninth abdominal segments with pits over entire surface, and tenth abdominal segment smooth. Minute setae present on vertex of head and on dorsum of thorax and abdomen.

Life history notes. In Massachusetts, *Hadena ectypa* adults are active in July, although a small number of individuals may emerge earlier. Moths emerge from their pupae in the early morning, but otherwise all adult activity, including feeding, mating, and oviposition, occurs nocturnally. The egg is laid inside the inflated calyx of a *Silene vulgaris* flower, deposited on the side of a green, immature seed pod (ovary), or on the base of a petal or stamen (Fig. 5). Normally only one egg is laid inside a single flower, but occasionally there are two, or rarely even three. The hatchling larva does not typically consume its eggshell. Instead, upon eclosion, it bores a hole into the ovary and begins to feed on the ovules within (Fig. 5). Normally the larva develops through the third instar inside the ovary of the initial flower. The larva is nearly colorless in the first three instars (Figs. 5, 6, and 7),

which is typical of larvae that feed inside their host plant.

In the fourth instar the larva develops a more distinctive color and pattern (Fig. 8), and by this stage the larva moves to a new flower to find food. Flowers that are blooming, or just past bloom, with a soft, green, immature ovary are preferred. In the fourth and fifth instars, the larva remains inside the inflated calyx of a *Silene vulgaris* flower, both feeding and resting while so hidden (Fig. 9). This presumably affords some protection from predators and parasitoids (Brantjes 1976; Biere et al. 2002; Biere & Honders 2006). The larva enters a calyx through the apical opening, or alternatively, it chews a hole in the base of a calyx (Fig. 11). A larva will sometimes consume an entire flower, including the calyx, but more often it will consume only the petals, stamens, pistil, and ovary, leaving behind an empty calyx when it moves to another flower. Many flowers and ovaries are consumed over the course of development, and a larva feeds exclusively on the plant's reproductive tissues through the fifth instar. In the sixth and final instar a larva will also consume the leaves of *S. vulgaris*, but continues to exhibit a preference for flowers and their ovaries. A sixth instar larva is too large to fit within the calyx of a flower without either the anterior or posterior end of its body protruding (Fig. 12). Many species of *Hadena* feed nocturnally in later instars, hiding under leaves at the base of the plant during the day (Forster & Wohlfahrt 1971; Hacker 1996; Porter 1997); it is likely that sixth instar larvae of *Hadena ectypa* behave similarly.

After each molt, the larva typically consumes its shed cuticle. Under warm conditions and with sufficient high-quality food, larval development is rapid and may be completed within three weeks. The larva burrows

into the soil for pupation, which typically occurs 2 to 3 cm below the surface, in a cell sparsely lined with silk. Most individuals have pupated by late August, and pupae overwinter until the following year. A small number of individuals may emerge in late August and September as a partial second generation.

DISCUSSION

On 24 July 2008, Nelson Bricker (a student of David L. Wagner at the University of Connecticut) found a single prepupal *Hadena ectypa* larva crawling across a road in Canaan, Litchfield County, Connecticut, USA. On 11 July 2009, Wagner returned to the Canaan site (with Alex Meleg and MWN), and found more than a dozen *Hadena ectypa* larvae feeding on *Silene vulgaris* growing along the roadside. The discovery of a second population of *Hadena ectypa* in New England, also feeding on exotic *S. vulgaris*, indicates that the use of this plant is not unique to the population in Huntington, Massachusetts.

Silene stellata, the native host of *Hadena ectypa*, occurs in New York state and Connecticut (FNA 2005; Magee & Ahles 2007). It is a rare plant of conservation concern in Connecticut. Fernald (1950) includes Massachusetts in the range of *S. stellata*, but currently it is not known to occur in the state (FNA 2005; Magee & Ahles 2007; Dow Cullina et al. 2011; Haines 2011). *Hadena ectypa* presumably occurs on *S. stellata* in New York, as this plant is not rare in parts of that state. *Hadena ectypa* may also use *S. stellata* in Connecticut, although this may have been more likely in the past given the plant's current rarity there. If *S. stellata* occurred in Massachusetts historically, it was probably quite rare, as this represents the northeastern edge of its geographic range. Thus it seems only a remote possibility that *Hadena ectypa* ever occurred on its native host plant in Massachusetts.

Specimens of *Hadena ectypa* from southeastern New York at the American Museum of Natural History date back to 1899. However, the first records from Massachusetts and Connecticut are those reported here. This may indicate that use of introduced *Silene vulgaris* as a larval host has facilitated a slight northeast expansion of the range of *Hadena ectypa*. Alternatively, it is possible that *Hadena ectypa* historically occurred on *Silene stellata* in western Connecticut, and maybe even western Massachusetts, but was sufficiently rare to avoid detection.

Native, introduced, and potential larval host plants. *Silene vulgaris* currently occurs across most of the Northeast (Magee & Ahles 2007), and indeed across most of North America (FNA 2005). While the precise site and date of the introduction of *S. vulgaris* from

Europe is not known, herbarium specimens from Massachusetts date back to 1846 (Sorrie 2005). *S. vulgaris* was also reported from Massachusetts by Cutler (1785). Therefore while it is possible that *Hadena ectypa* began to use *S. vulgaris* as a larval host in this area only recently, this host shift could have occurred at any time during the past 200 years. If *S. vulgaris* was first introduced to North America through a port city in the Northeast, such as New York, Boston, or Quebec, and subsequently spread south and west, then *Hadena ectypa* likely first encountered this plant in the region of southeastern New York, western Connecticut, and western Massachusetts. Since its introduction, *S. vulgaris* has spread throughout the entire range of *Hadena ectypa*. It therefore seems likely that *Hadena ectypa* uses *S. vulgaris* as a larval host in other parts of its range, although this has not yet been documented.

There are at least 22 species of *Silene* that occur within the geographic range of *Hadena ectypa*, including eight native species and 14 introduced species (FNA 2005). While it is not unlikely that *Hadena ectypa* uses other native *Silene* spp. as larval hosts, existing data indicate that *Silene stellata* is the primary native host. In addition to oviposition and larval development on *S. stellata*, *Hadena ectypa* adults imbibe nectar from the flowers of *S. stellata*, and in the course of both nectaring and oviposition provide pollination services to this plant (Kephart et al. 2006; Reynolds et al. 2011). Given the intimate ecological relationship between *Hadena ectypa* and *S. stellata*, it seems likely that this plant has particular traits that make it a more favorable larval host for *Hadena ectypa*, as compared to other native species of *Silene*. Traits of *S. stellata* that are beneficial to *Hadena ectypa* include: (1) white flowers with nocturnal scent, which attract nectaring and pollinating moths, and which also help *Hadena ectypa* females find plants upon which to oviposit (Kephart et al. 2006; Reynolds et al. 2011); (2) flowers with a large, inflated calyx, and space between the calyx and ovary, which allows a larva of *Hadena ectypa* to remain hidden from predators and parasitoids while feeding and resting (Brantjes 1976; Biere et al. 2002; Biere & Honders 2006); (3) many flowers per plant, each with a relatively large ovary with many seeds, making it more likely that a larva on any given plant (or small patch of plants) will have sufficient high-quality food to complete development; and (4) asynchronous, staggered flowering and fruiting phenology between plants, as well as asynchronous, staggered development of flowers and fruits on separate stems of individual plants, making food available for a longer period of time, which in turn may facilitate temporal resource tracking, as well as provide a late-

season food source for a facultative second generation of *Hadena ectypa*.

Like *Silene stellata*, *Silene vulgaris* has a peak flowering period of mid- to late summer. Furthermore, *S. vulgaris* shares with *S. stellata* all of the traits favorable to *Hadena ectypa* as listed above (Pettersson 1991a, b), making it a more suitable alternate host plant for *Hadena ectypa* as compared to other species of *Silene*, native or introduced. Indeed, behavioral aspects of the use of *S. vulgaris* by both adults and larvae of *Hadena ectypa* are nearly identical to those observed on *S. stellata* by Reynolds et al. (2011). In its native Europe, *S. vulgaris* is fed upon by at least nine species of *Hadena* (Pettersson 1991a, b; Kephart et al. 2006), indicating that it is a particularly suitable larval host plant for species of *Hadena* in general.

The favorable traits of *Silene stellata* and *Silene vulgaris* are also shared by *Silene latifolia*, another common and weedy species introduced to North America prior to 1850 (Sorrie 2005), which has since spread throughout the range of *Hadena ectypa*. However, unlike *S. stellata* and *S. vulgaris*, the flower of *S. latifolia* has a calyx that is densely covered in trichomes, as well as a constricted apical opening that is blocked by contracted petals during the day (Kephart et al. 2006). This may make access to the interior of the flower more difficult for *Hadena ectypa*. When the *Hadena ectypa* larvae reared in 2003 were initially offered sealed flowers of *S. latifolia*, they chewed away at the trichomes, but seemed to have difficulty accessing the interior of the calyx. Subsequently the calyces were split open, and the larvae responded by immediately entering them and feeding on the green ovaries, thereafter ignoring the trichome-covered calyces. It should be noted, however, that *S. latifolia* is used as a larval host by at least three other species of *Hadena* in its native Eurasian range (Kephart et al. 2006). Furthermore, Blair & Wolfe (2004) have shown that North American populations of *S. latifolia* invest less in defensive traits (dense calyx trichomes and thick ovary wall) as compared to European populations, perhaps because of ecological release from *Hadena* species and other herbivores in the native range (Wolfe 2002). It therefore seems quite possible that *Hadena ectypa* could adapt to the use of *S. latifolia* in North America.

Another possible barrier to the use of *Silene latifolia* by *Hadena ectypa* is that this plant is dioecious, and many populations have two to six times more staminate than pistillate flowers (Brantjes 1976). In Europe, *Hadena bicruris* (Hufnagel, 1766) feeds on *S. latifolia*, and females exclusively oviposit in the pistillate flowers of this plant (Brantjes 1976). This is important because staminate flowers do not have an ovary to feed a

developing larva, and moreover, staminate flowers drop off of the plant a few days after pollination (Brantjes 1976). It is not necessary for *Hadena ectypa* to discriminate between flowers of its native host, as *Silene stellata* is hermaphroditic, or between flowers of *Silene vulgaris*, as this species is gynodioecious. Therefore *Hadena ectypa* may not have the ability to discern pistillate from staminate flowers, and if it were to oviposit indiscriminately on flowers of *S. latifolia*, this plant could serve as a population sink.

Use of a novel host plant: effects on phenology, habitat, and geographic range. All of the *Hadena ectypa* adults reared in 2003, 2009, and 2010 emerged in August or September of the same year, confirming that this species has a facultative second generation. In insects with facultative induction of diapause, the choice between either continuous development or diapause is determined by environmental cues; typical cues include photoperiod, temperature, and food quality and quantity (Tauber et al. 1986; Leather et al. 1993). The captive rearings reported here were kept in a warm environment and offered an abundance of high-quality food; as a result, larval growth was rapid, and none of the reared individuals entered pupal diapause.

As far north as Massachusetts, it seems likely that most wild *Hadena ectypa* enter pupal diapause, although a partial second generation does occur, as indicated by the adult caught in a light trap the night of 10–11 September 2002. The offspring of moths breeding in September in Massachusetts must have a low probability of surviving to pupation, except in years with exceptionally warm weather in September and October. In addition to cooling temperatures, flowers and fruits of *Silene vulgaris* become scarce late in the season. However, the asynchronous, staggered flowering phenology of *S. vulgaris*, both between and within individual plants, may provide a sufficient late-season food source in some years. Interestingly, *S. vulgaris* continues to flower and fruit later in the season than *Silene stellata* (Gleason & Cronquist 1991; FNA 2005). Therefore the phenology of this novel, introduced host plant may increase survival of second-generation individuals of *Hadena ectypa*, and thereby increase the propensity for a second annual generation in this species. Future investigation of this topic could provide some interesting insights.

Hadena ectypa has always been considered a rare moth (Wyatt 1929). It is currently a species of conservation concern, subject to anthropogenic threats including habitat loss to development, grazing of larval host plants by artificially abundant deer, and degradation of habitat by invasive exotic plants (Schweitzer et al. 2011). Ironically, the introduction of

Silene vulgaris may “rescue” *Hadena ectypa*, as this plant is now relatively common and weedy in North America, with a much larger geographic range than *Silene stellata* (FNA 2005). Adoption of *S. vulgaris* as a larval host may allow *Hadena ectypa* to spread to new, weedier habitats, to increase its geographic range, and to increase its propensity for a second annual generation.

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SEASONAL TRENDS OF FOREST MOTH ASSEMBLAGES IN CENTRAL HOKKAIDO, NORTHERN JAPAN

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ABSTRACT. Seasonal trends of adult moth assemblages were investigated using portable light traps in a cool-temperate region in central Hokkaido, northern Japan. Light traps were set at monthly intervals from April to December 2005 in five stands. Seasonal changes in the numbers of species and individuals in each stand were unimodal with a peak in summer (July or August). The value of a similarity index between samples from successive months in each stand was always low, indicating that species composition changed greatly between successive months. Based on the seasonal occurrence of 248 species, the mean occurrence period in each species was only 1.8 months. Among these species, 91.5% were estimated to be univoltine and only 8.5% were estimated to be multivoltine. Most species occurred in the summer (July and/or August), although some occurred only in the spring or autumn. Thus, in the present study the high species turnover of adult moths during the active season was due to the short occurrence period of each species, which may be associated at least in part with univoltinism, synchronized adult eclosion, and short life spans of adult moths.

Additional key words: black light trap, life history, night-flying moth, phenology, seasonal occurrence.

Moths comprise one of the most diverse insect groups in forest ecosystems. About 140,000 species have been identified throughout the world (New 2004) and more than 5000 species are listed in Japan (Sugi 2000). Such high diversity of moths may be maintained by plant diversity (e.g. Neuvonen & Niemelä 1981) and plant architecture (Lawton 1983). In addition to this impressive diversity, moths are easily collected with light traps that are widely recognized as the standard tool for sampling night-flying moths (Southwood & Henderson 2000).

In forest ecosystems, moths are mostly herbivores in their larval stage and are thus particularly sensitive to environmental changes that affect plant quality and quantity as their diets. On the other hand, moths are an important food resource for other animals and their abundance affects the population dynamics of animals in higher trophic levels. Because of their pivotal role in maintaining biodiversity in forest ecosystems, moths are generally regarded as useful indicator taxa for monitoring insect biodiversity and habitat disturbance caused naturally or artificially in tropical and temperate

forests (Hammond & Miller 1998; Usher & Keiller 1998; Kitching et al. 2000; Summerville et al. 2004).

Seasonal patterns of larval moth assemblages have been investigated in relation to foliage quality, weather conditions and natural enemies (Feeny 1970; Niemelä & Haukioja 1982; Yoshida 1985; Butler & Strazanac 2000; Summerville et al. 2003; Murakami et al. 2005). However, only a few studies have focused on seasonal patterns of adult moth assemblages (Yoshida 1980; Yela & Herrera 1993; Butler et al. 2001). For example, Yoshida (1980) investigated seasonal fluctuations of species richness, abundance and diversity index of adult moth communities at four forest stands in Hokkaido, northern Japan. Yela & Herrera (1993) studied seasonal patterns of species richness and abundance of noctuid moths in Mediterranean mixed forests. However, few studies have investigated seasonal occurrence in each species except for pest species.

In temperate regions, moth assemblages consist of seasonal progressions of the occurrences of different species. The timing and duration of flight periods of adult moths depend on the various life history traits of each species, such as overwintering stage, voltinism (the number of generations per year), adult life span, and immature growth rate (Wolda 1988). These traits may be further influenced by weather conditions (e.g. temperature, precipitation and day-length) and availability of host-plants (e.g. quantity and quality). For example, Hunter & McNeil (1997) revealed effects of host-plant quality on diapause induction and subsequent voltinism in a tortricid moth.

In the present study, we investigated seasonal trends of night-flying moth assemblages in a cool-temperate region to contribute information about the regional moth diversity of Hokkaido. For this purpose, we sampled adult moths using portable light traps because light traps are useful tools to quantify the moth communities (Southwood & Henderson 2000). Using data collected from these traps, we estimated flight duration and voltinism of major species.

MATERIALS AND METHODS

The study was conducted from April to December 2005, which covers almost the entire season of adult moth flight, in five stands of three different forest types located in Sapporo, central Hokkaido, northern Japan (42°53'–43°00'N, 141°22'–26'E; 150–400 m a.s.l.). Study stands, which were always more than 10 ha in size and located more than 1 km apart, consisted of two deciduous broadleaved forests at Hitsujigaoka and Mizunenosawa, two larch (*Larix kaempferi* Carr.)

plantations at Shimomitaki (42 years old) and Mt. Yagyu (47 years old), and a Todo-fir (*Abies sachalinensis* Masters) plantation at Mt. Yagyu (48 years old). We used these forest types because these are the most common forest types in the cool-temperate region in Hokkaido. The deciduous broadleaved forests were dominated by linden (*Tilia japonica* Simonkai), cucumber tree (*Magnolia obovata* Thunb.), oak (*Quercus crispula* Blume), and maple (*Acer mono* Maxim.). Forest floors in the study stands were more or less covered with bamboo grasses (*Sasa kurilensis* (Rupr.) Makino et Shibata).

We used portable light traps developed by Okochi (2002). This trap was equipped with a 6 W black (ultraviolet) light fluorescent tube powered by a 9 V alkaline battery made up of six 1.5 V cells. The light lasted about 12 h per night. Every month we set two light traps in each stand on a night around the new moon (nine nights in total). Trapping nights were chosen to avoid rain and snow. The two traps were hung at a height of approximately 1.5 m at fixed locations, which were located 100 m apart in the central part of each stand. Early the next morning, moths caught in the traps were killed with ethyl acetate, preserved in a refrigerator, and at a later date identified to species. We used scientific names of moths in Inoue et al. (1982) and changes after Inoue et al. (1982) followed Sugi (2000), Sugi & Jinbo (2004) and Jinbo (2004–2008). In the following analysis, individuals identified to species (67–85% of sampling individuals in each stand) were used. Unidentified individuals were those with either extensive wing wear or from microlepidopteran moths (e.g. Tortricidae). All voucher specimens in this study were deposited in the collection of Hokkaido Research Center, Forestry and Forest Products Research Institute.

For seasonal trends of moth assemblages, the number of species, the number of individuals, and the Pielou's index (J') for evenness were calculated for each trap and expressed as the averages of the two traps in each stand. Pielou's index (J') was calculated as follows:

$$J' = \frac{-\sum_i p_i \ln p_i}{\ln S}$$

where p_i is the proportion of individuals found in the i th species and S is the total number of species. Similarity indices (C_λ) between samples from successive months in each trap were also calculated and averaged in each stand to quantify the seasonal

changes in species composition. A similarity index (C_λ) was calculated as follows:

$$C_\lambda = \frac{2 \sum_{i=1}^S n_{1i} \cdot n_{2i}}{(\lambda_1 + \lambda_2) N_1 \cdot N_2}$$

$$\lambda_1 = \frac{\sum_{i=1}^S n_{1i}(n_{1i} - 1)}{N_1(N_1 - 1)} \quad , \quad \lambda_2 = \frac{\sum_{i=1}^S n_{2i}(n_{2i} - 1)}{N_2(N_2 - 1)}$$

where n_{1i} and n_{2i} are the numbers of individuals in the i th species and N_1 and N_2 are the total numbers of individuals in samples 1 and 2, which are collected from successive months, respectively. S is the total number of species. The value of C_λ is 0 when two samples have no common species and is nearly 1 when two samples are identical (Morisita 1959).

The seasonal occurrence of each moth species was examined for the species in which a total of at least 10 individuals were collected. The mean duration of occurrence in each species was calculated from the number of months in which each species was collected. This value indicates an occurrence of moths based on the assumption that the flight period of a moth species was one month for a moth species that was sampled in one trapping date since we conducted a monthly sampling. Voltinism (univoltine or multivoltine) of these species was estimated based on the following criteria. We assigned a species to multivoltine if the species was (1) collected in discontinuous sampling months, (2) collected in more than two sampling months and had two peaks in their occurrence or (3) collected in more than three sampling months. The other species were assigned to univoltine. The estimated voltinisms were compared with the voltinisms reported for the same species in eastern Hokkaido (Iijima 1990). Iijima (1990) assigned 12 species to partial bivoltine (basically univoltine with a partial second generation only in favorable seasons), but these species were excluded from the present analysis.

RESULTS

Seasonal changes in species diversity and species composition. A total of 14,591 adult moths, consisting of 693 species in 29 families, was collected and identified in the five study stands. No moths were collected in December. The number of species was greatest in Geometridae followed by Noctuidae (Table 1). Seasonal changes in the mean number of

species in each stand were unimodal with a peak in July or August (Fig. 1). Seasonal changes in the mean number of individuals in each stand were also unimodal with a peak in August, except in the larch plantation at Mt. Yagyū where a peak occurred in July (Fig. 2). This peak was due to the high abundance of two dominant arctiids, *Ghoria collitoides* Butler and *Eilema cribrata* (Staudinger) in this month. On the other hand, mean evenness (J') showed a weak declining

TABLE 1. Numbers of species and individuals of forest moths collected in five stands in Sapporo in 2005.

Family	No. of species	No. of individuals
Incurvariidae	3	5
Tortricidae	46	638
Tineidae	3	15
Gracillariidae	1	1
Yponomeutidae	9	32
Argyresthiidae	1	1
Oecophoridae	4	14
Lecithoceridae	3	9
Gelechiidae	6	9
Carposinidae	1	3
Zygaenidae	1	3
Limacodidae	5	32
Pyalidae	67	969
Pterophoridae	1	1
Drepanidae	6	279
Thyatiridae	13	88
Geometridae	206	4684
Epiplemidae	2	8
Lasiocampidae	9	282
Bombycidae	2	20
Brahmaeidae	1	7
Saturniidae	6	224
Sphingidae	8	201
Notodontidae	51	899
Lymantriidae	11	644
Arctiidae	26	2763
Nolidae	7	55
Noctuidae	193	2703
Agaristidae	1	2
Total	693	14,591

Families were listed according to the taxonomic order adopted in Inoue et al. (1982)

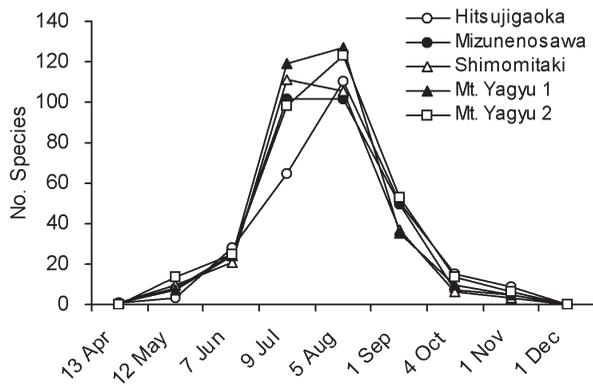


FIG. 1. Seasonal changes in the number of adult moth species in five stands in deciduous broadleaved forests (Hitsuji-gaoka, Mizunenosawa), larch plantations (Shimomitaki, Mt. Yagyu 1), and a Todo-fir plantation (Mt. Yagyu 2) in Sapporo, 2005. Values show the averages of two traps in each stand.

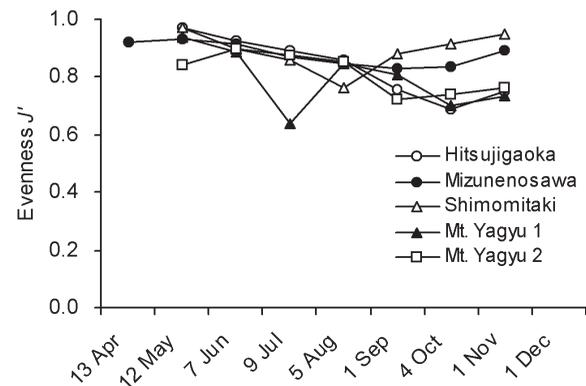


FIG. 3. Seasonal changes in evenness (Pielou's J') of adult moth assemblages in five stands in deciduous broadleaved forests (Hitsuji-gaoka, Mizunenosawa), larch plantations (Shimomitaki, Mt. Yagyu 1), and a Todo-fir plantation (Mt. Yagyu 2) in Sapporo, 2005. Values show the averages of two traps in each stand.

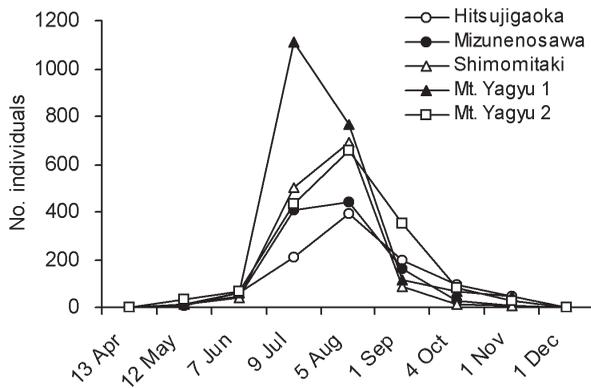


FIG. 2. Seasonal changes in the number of adult moth individuals in five stands in deciduous broadleaved forests (Hitsuji-gaoka, Mizunenosawa), larch plantations (Shimomitaki, Mt. Yagyu 1), and a Todo-fir plantation (Mt. Yagyu 2) in Sapporo, 2005. Values show the averages of two traps in each stand.

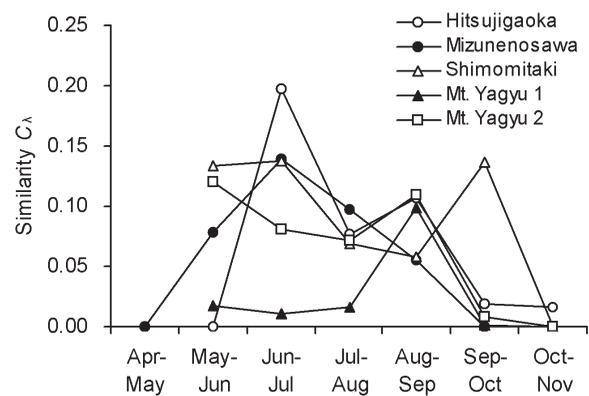


FIG. 4. Seasonal changes in the value of similarity index (C_λ) of adult moth assemblages between samples from successive months in five stands in deciduous broadleaved forests (Hitsuji-gaoka, Mizunenosawa), larch plantations (Shimomitaki, Mt. Yagyu 1), and a Todo-fir plantation (Mt. Yagyu 2) in Sapporo, 2005. Values show the averages of two traps in each stand.

trend as the season progressed, except in the larch plantation at Shimomitaki (Fig. 3). In the larch plantation at Mt. Yagyu, the lowest mean evenness was observed in July when two dominant noctuids, *Aventiola pusilla* (Butler) and *Mimachrostia fasciata* Sugi occupied 11.3% and 8.5% of the abundance, respectively. In the larch plantation at Shimomitaki, the lowest mean evenness was observed in August when two dominant arctiids, *Ghonia collitoides* and *Eilema cribrata* comprised 36.5% and 14.3% of the total abundance of moths, respectively.

Mean similarity indices (C_λ) between samples from successive months in each stand were always low (less than 0.2) (Fig. 4), although the indices fluctuated differently in each stand. The low similarity indices

indicate that species composition changed greatly between successive months.

Seasonal occurrence of each moth species. At least 10 individuals were collected from 248 species in five stands (Appendix 1). These species were listed in order of the increasing mean occurrence period, which was calculated from the average of sampling months weighted by the number of individuals collected in each month. Each species was collected within a short period. The mean duration of occurrence in each species was 1.8 months (range 1–4 months), and 90 species (36.3%) were collected in only one month. Among the 248 species, 14 species (5.6%) were collected only in spring (from April to June; Appendix 1). On the other hand, 25 species

(10.0%) occurred only in autumn (from September to November; Appendix 1). Especially, some geometrid winter moths occurred only in November (Appendix 1).

Of the 248 species, 227 species (91.5%) were assigned to univoltine and only 21 species (8.5%) were assigned to multivoltine (Appendix 1). Eleven of the multivoltine species were geometrids. Voltinisms estimated for 156 species (90.2%) were similar to the voltinisms reported for the same species in Iijima (1990), in which 148 species were classified as univoltine and 25 species were classified as bivoltine. There were only a few differences in the two studies: 14 species estimated to be univoltine were bivoltine in Iijima (1990), and three species estimated to be multivoltine were univoltine in Iijima (1990).

DISCUSSION

The present study shows that seasonal changes in the numbers of species and individuals of adult moths were markedly unimodal with a peak in summer (July or August) (Fig. 1, 2). Yoshida (1980) also found that the numbers of species and individuals were greatest in July or August in a deciduous broadleaved natural forest and a larch plantation in the Tomakomai Experimental Forest of Hokkaido University, which is located about 60 km from Sapporo. However, Yoshida (1980) showed multimodal seasonal patterns with peaks in summer and autumn in the number of individuals in a deciduous broadleaved secondary forest and a Todo-fir plantation. The peak abundance in autumn is probably caused by some dominant species that were extremely abundant that autumn (Yoshida 1980). Hirao et al. (2006) collected adult moths in a deciduous broadleaved forest at the same locality as Yoshida (1980) and reported that July possessed the highest number of species and individuals. These studies suggest that a unimodal seasonal pattern with a peak in summer (July or August) is a general trend for species richness and abundance in adult moth assemblages in the cool-temperate region of central Hokkaido. This information is critical to determine efficient sampling periods in a future study and provides a useful basis for comparative studies with other regions.

In contrast to the unimodal seasonal pattern reported here, seasonal changes in the number of species of adult moths in a mixed deciduous forest in southern Korea were bimodal with peaks in June and August (Choi 2008). In mixed hardwood forests in North America, no clear peak was detected in the number of species, although the number of individuals was highest between March and June (Landau et al. 1999) or in July and early August (Butler et al. 2001). In Mediterranean mixed forests, abundance and diversity of adult noctuid moths were markedly bimodal with two distinct peaks, in early

summer (mid-July) and in early autumn (late September to early October) (Yela & Herrera 1993). These studies demonstrate that seasonal trends of adult moth assemblages vary widely among regions. This difference may reflect different climate conditions among regions because climate variables are often important factors influencing moth abundance and diversity (Yela & Herrera 1993).

Seasonal changes of larval moth communities in forests have also been studied as an alternative measure of moth activity in forest ecosystems (Yoshida 1985; Yela & Herrera 1993; Butler & Strazanac 2000). Yoshida (1985) showed that the number of species and individuals of macrolepidopterous larvae on oak trees had two peaks, in June (spring) and August (summer). Butler & Strazanac (2000) sampled lepidopteran larvae at oak-dominated Appalachian forests from May to mid-August and showed that the numbers of species and individuals of larvae were higher in May and August. Yela & Herrera (1993) showed that the frequency of occurrence of noctuid larvae exhibited a distinct peak in the first half of June. Yela & Herrera (1993) also suggested that the duration of the pupal stage might affect the difference in the occurrence pattern between larvae and adults as a result of life history strategies adapted to the hot and dry summer season in Mediterranean habitats. This suggests that seasonal occurrence patterns of adults do not correspond to those of larvae.

The value of evenness (J') showed a decreasing trend as the season progressed except in the larch plantation at Shimomitaki (Fig. 3). In central Hokkaido, Yoshida (1980) also found that a relative diversity index, which is equivalent to evenness, decreased with season in deciduous broadleaved forests, a larch plantation, and a Todo-fir plantation, although the value of the index fluctuated considerably. These findings suggest either that dominant species occupy a relatively larger part of moth assemblages or that there are a large number of rare species in autumn.

Most (90.2%) of the voltinisms estimated in the present study were consistent with the voltinisms recorded in eastern Hokkaido (Appendix 1; Iijima 1990). In addition, more than 90% of the species were assigned to univoltine, suggesting that the univoltine life cycle is predominant for moths in Hokkaido. This may be caused by the relatively short growth period in the cool-temperate region in Hokkaido. For the species estimated to be univoltine in the present study but bivoltine by Iijima (1990), it is possible that we were simply unable to detect multivoltinism using our monthly sampling intervals. For the species estimated to be multivoltine in the present study but univoltine by Iijima (1990), these

species may be univoltine only in eastern Hokkaido where temperatures are relatively low in comparison to central Hokkaido. Further studies are needed to clarify the voltinism of these species.

Low values of the similarity index (C_{λ}) between samples from successive months (Fig. 4) show that species composition changed greatly between successive months. In a deciduous broadleaved forest in central Hokkaido, Hirao et al. (2006) also found that species composition of adult moth communities was distinctly partitioned into each month. These high species turnovers were due to the short occurrence period (1.8 months on average in the present study) of each species. For moth species to have short occurrence periods, species are likely to have a univoltine life history, synchronized adult eclosion, and short life spans for adult moths. In cool-temperate regions, relatively shorter growing season may result in one generation per year. General life expectancy of adult moths is assumed to be from one to three weeks (Zborowski & Edwards 2007), although we could not find any field studies that examined life span of adult moths. Similar life history traits seem to be common in moths because many moths have well-defined and characteristic periods of seasonal activity and, particularly in temperate regions, may fly for only short periods (New 2004).

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Appendix 1. Seasonal occurrence of adult moth species in which at least 10 individuals were collected in Sapporo in 2005.

	Species	Family	Sampling Date								Total	Voltinism
			13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct	1 Nov		
1	<i>Lithophane plumbealis</i> (Matsumura)	Noctuidae	1	16							17	U
2	<i>Odontosia sieversii</i> <i>japonibia</i> Matsumura	Notodontidae		15							15	U
3	<i>Perigrapha hoenei</i> Püngeler	Noctuidae		37	2						39	U
4	<i>Orthosia gothica jezoensis</i> (Matsumura)	Noctuidae		13	6						19	U
5	<i>Cerastis pallescens</i> (Butler)	Noctuidae		5	7						12	U
6	<i>Eupithecia clavifera</i> Inoue	Geometridae		6	19						25	U
7	<i>Pseuderannis lomozenia</i> (Prout)	Geometridae		1	16						17	U
8	<i>Eupithecia daemionata</i> Dietze	Geometridae		1	18						19	U
9	<i>Ellida arcuata</i> (Alphéraky)	Notodontidae			20						20	U
10	<i>Lassaba nikkonis</i> (Butler)	Geometridae			20						20	U
11	<i>Phyllodesma japonicus</i> <i>japonicus</i> (Leech)	Lasiocampidae			14						14	U
12	<i>Nola confusalis</i> (Herrich- Schäffer)	Nolidae			13						13	U
13	<i>Cusiala stipitaria</i> <i>stipitaria</i> (Oberthür)	Geometridae			10						10	U
14	<i>Trichopteryx hemana</i> (Butler)	Geometridae			10						10	U
15	<i>Paradarisa consonaria</i> (Hübner)	Geometridae			56	4					60	U
16	<i>Chlorissa inornata</i> (Matsumura)	Geometridae			11	4					15	U
17	<i>Cleora insolita</i> (Butler)	Geometridae			9	4					13	U
18	<i>Plagodis dolabraria</i> (Linnaeus)	Geometridae			10		2				12	M
19	<i>Togepteryx velutina</i> (Oberthür)	Notodontidae			12	8					20	U
20	<i>Marumba jankowskii</i> Oberthür	Sphingidae			22	41					63	U
21	<i>Spilosoma punctarium</i> (Stoll)	Arctiidae			4	27					31	U
22	<i>Hydrillodes morosus</i> (Butler)	Noctuidae			18	127					145	U
23	<i>Ptilodon jezoensis</i> (Matsumura)	Notodontidae			1	9					10	U
24	<i>Aethalura ignobilis</i> (Butler)	Geometridae			5	53					58	U
25	<i>Xerodes rufescentaria</i> (Motschulsky)	Geometridae			19	187	2				208	U

Appendix 1. Continued.

	Species	Family	Sampling Date								Total	Voltinism
			13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct	1 Nov		
26	<i>Stauropus fagi persimilis</i> Butler	Notodontidae			2	12	1				15	U
27	<i>Chytonix subalbonotata</i> Sugi	Noctuidae			1	35					36	U
28	<i>Calliteara pseudabietis</i> Butler	Lymantriidae			2	36	1				39	U
29	<i>Hypomecis punctinalis</i> <i>conferenda</i> (Butler)	Geometridae			1	70					71	U
30	<i>Parectropis similaria</i> <i>japonica</i> Sato	Geometridae				95					95	U
31	<i>Archips nigricaudana</i> (Walsingham)	Tortricidae				95					95	U
32	<i>Paracolax albinotata</i> (Butler)	Noctuidae				75					75	U
33	<i>Pheosiopsis cinerea</i> (Butler)	Notodontidae			4	55	4				63	U
34	<i>Ellida viridimixta</i> (Bremer)	Notodontidae			10	39	10				59	U
35	<i>Heterarmia costipunctaria</i> (Leech)	Geometridae				56					56	U
36	<i>Leptostegna tenerata</i> Christoph	Geometridae				54					54	U
37	<i>Lomaspilis marginata</i> <i>amurensis</i> (Hedemann)	Geometridae				51					51	U
38	<i>Apamea hampsoni</i> Sugi	Noctuidae				49					49	U
39	<i>Tortrix sinapina</i> (Butler)	Tortricidae				48					48	U
40	<i>Phthonosema tendinosar-</i> <i>ium</i> (Bremer)	Geometridae				43					43	U
41	<i>Hyperstrotia flavipuncta</i> (Leech)	Noctuidae				31					31	U
42	<i>Lomographa bimaculata</i> <i>subnotata</i> (Warren)	Geometridae				30					30	U
43	<i>Parapsestis argenteopicta</i> (Oberthür)	Thyatiridae				29					29	U
44	<i>Protoarmia faustinata</i> (Warren)	Geometridae				28					28	U
45	<i>Idaea invalida invalida</i> (Butler)	Geometridae				26					26	U
46	<i>Scopula duplinupta</i> Inoue	Geometridae				24					24	U
47	<i>Electrophaes corylata</i> <i>granitalis</i> (Butler)	Geometridae				19					19	U
48	<i>Menophra senilis</i> (Butler)	Geometridae				18					18	U
49	<i>Cabera purus</i> (Butler)	Geometridae				18					18	U
50	<i>Gandaritis maculata</i> (Swinhoe)	Geometridae				18					18	U

Appendix 1. Continued.

	Species	Family	Sampling Date							Total	Voltinism	
			13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct			1 Nov
51	<i>Olethreutes moderatus</i> (Falkovitsh)	Tortricidae				18					18	U
52	<i>Protoboarmia simpliciaris</i> (Leech)	Geometridae				17					17	U
53	<i>Eana argentana</i> (Clerck)	Tortricidae				16					16	U
54	<i>Archips audax</i> Razowski	Tortricidae				16					16	U
55	<i>Prometopus flavicollis</i> (Leech)	Noctuidae				12					12	U
56	<i>Chytonix albonotata</i> (Staudinger)	Noctuidae				11					11	U
57	<i>Rabta cristata</i> (Butler)	Notodontidae				11					11	U
58	<i>Euplexia koreaeplexia</i> Bryk	Noctuidae				10					10	U
59	<i>Eustroma aerosum</i> (Butler)	Geometridae				10					10	U
60	<i>Ghonia collitoides</i> Butler	Arctiidae				920	1				921	U
61	<i>Eilema cribrata</i> (Staudinger)	Arctiidae				347	3				350	U
62	<i>Actias aliena sjoeqvisti</i> Bryk	Saturniidae				106	1				107	U
63	<i>Idaea imbecilla</i> (Inoue)	Geometridae				136		1			137	M
64	<i>Callambulyx tatarinovii gabyae</i> Bryk	Sphingidae				33	1				34	U
65	<i>Taeniophora unio</i> (Oberthür)	Geometridae				32	1				33	U
66	<i>Ghonia gigantea gigantea</i> (Oberthür)	Arctiidae				83	3				86	U
67	<i>Torigea straminea</i> (Moore)	Notodontidae				23	1				24	U
68	<i>Scopula floslactata claudata</i> (Prout)	Geometridae				43	2				45	U
69	<i>Zanclognatha helva</i> (Butler)	Noctuidae				17	1				18	U
70	<i>Microcalicha sordida</i> (Butler)	Geometridae				17	1				18	U
71	<i>Marumba gaschkewitschii ecephron</i> (Boisduval)	Sphingidae				82	5				87	U
72	<i>Leucodonta bicoloria</i> (Denis et Schiffermüller)	Notodontidae			1	14	2				17	U
73	<i>Spilarctia seriatopunctata seriatopunctata</i> (Motschulsky)	Arctiidae				115	8				123	U
74	<i>Hypomecis roboraria displicens</i> (Butler)	Geometridae				39	3				42	U
75	<i>Shaka atrovittatus</i> (Bremer)	Notodontidae				26	2				28	U

Appendix I. Continued.

	Species	Family	Sampling Date							Total	Voltinism	
			13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct			1 Nov
76	<i>Perinephela lancealis pryeri</i> Munroe et Mutuura	Pyralidae				24	2				26	U
77	<i>Mimopydna pallida</i> (Butler)	Notodontidae				12	1				13	U
78	<i>Moma alpium</i> (Osbeck)	Noctuidae				23	2				25	U
79	<i>Agathia carissima carissima</i> Butler	Geometridae				30	3				33	U
80	<i>Cabera exanthemata insulata</i> Inoue	Geometridae				28	3				31	U
81	<i>Lomographa temerata</i> (Denis et Schiffermüller)	Geometridae			1	34	5				40	U
82	<i>Tethea ampliata ampliata</i> (Butler)	Thyatiridae				9	1				10	U
83	<i>Herminia tarsicrinalis</i> (Knoch)	Noctuidae				16		1			17	M
84	<i>Panthea coenobita idea</i> Bryk	Noctuidae				20	3				23	U
85	<i>Spilonota eremitana</i> Moriuti	Tortricidae				60	10				70	U
86	<i>Hexafrenum leucodera</i> (Staudinger)	Notodontidae				30	5				35	U
87	<i>Hydrelia sylvata</i> (Denis et Schiffermüller)	Geometridae				15	3				18	U
88	<i>Ptycholomoides aeriferana</i> (Herrich-Schäffer)	Tortricidae				64	7	3			74	U
89	<i>Anacronicta nitida</i> (Butler)	Noctuidae				84	20				104	U
90	<i>Gandaritis whitelyi whitelyi</i> (Butler)	Geometridae				8	2				10	U
91	<i>Eilema okanoi</i> Inoue	Arctiidae				35	10				45	U
92	<i>Syntypistis cyanea cyanea</i> (Leech)	Notodontidae			18	16	33				67	U
93	<i>Koyaga falsa</i> (Butler)	Noctuidae				15	8				23	U
94	<i>Abraxas sylvata microtate</i> Wehrli	Geometridae				12	8				20	U
95	<i>Archips ingentana</i> (Christoph)	Tortricidae				7	5				12	U
96	<i>Phthonosema invenustarium</i> (Leech)	Geometridae				22	16				38	U
97	<i>Semidonta biloba</i> (Oberthür)	Notodontidae				16	12				28	U
98	<i>Euproctis piperita</i> Oberthür	Lymantriidae				25	19				44	U
99	<i>Ectropis crepuscularia</i> (Denis et Schiffermüller)	Geometridae			26	1	68				95	M
100	<i>Geometra dieckmanni</i> Graeser	Geometridae				15	7	2			24	U

Appendix I. Continued.

	Species	Family	Sampling Date								Total	Voltinism
			13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct	1 Nov		
101	<i>Habrosyne dieckmanni roseola</i> Matsumura	Thyatiidae				7	6				13	U
102	<i>Belciades niveola</i> (Motschulsky)	Noctuidae				14	13				27	U
103	<i>Zaranga permagna</i> (Butler)	Notodontidae			2	6	13				21	U
104	<i>Fusapteryx ladislai</i> (Oberthür)	Notodontidae				5	6				11	U
105	<i>Nomis albopedalis</i> Motschulsky	Pyralidae				73	88				161	U
106	<i>Barsine pulchra</i> (Butler)	Arctiidae				15	19				34	U
107	<i>Herminia grisealis</i> (Denis et Schiffemüller)	Noctuidae				24	2	9			35	M
108	<i>Paracolax fascialis</i> (Leech)	Noctuidae				29	39				68	U
109	<i>Sphrageidus similis</i> (Fuessly)	Lymantriidae				46	69	3			118	U
110	<i>Crambus perlellus</i> (Scopoli)	Pyralidae				4	8				12	U
111	<i>Laciniodes denigratus</i> <i>ussuriensis</i> Prout	Geometridae				5	7	1			13	U
112	<i>Chrysoteuchia diplogramma</i> (Zeller)	Pyralidae				3	7				10	U
113	<i>Euthrix potatoria bergmani</i> (Bryk)	Lasiocampidae				44	90	3			137	U
114	<i>Jodis lactearia</i> (Linnaeus)	Geometridae				4	10				14	U
115	<i>Mitochrista miniata rosaria</i> Butler	Arctiidae				87	220				307	U
116	<i>Tyloptera bella bella</i> (Butler)	Geometridae				9	23				32	U
117	<i>Epodonta lineata</i> (Oberthür)	Notodontidae			3	2	19	1			25	M
118	<i>Holocryptis nymphula</i> (Rebel)	Noctuidae				20	4	11			35	M
119	<i>Nerice davidi</i> Oberthür	Notodontidae				3	9				12	U
120	<i>Dendrolimus superans</i> (Butler)	Lasiocampidae				7	24				31	U
121	<i>Hemitha aestivaria</i> (Hübner)	Geometridae				5	19				24	U
122	<i>Microphalera grisea</i> Butler	Notodontidae			7	2	14	10			33	M
123	<i>Hadennia incongruens</i> (Butler)	Noctuidae				2	10				12	U
124	<i>Endropiodes abjectus abjectus</i> (Butler)	Geometridae			6		70				76	M
125	<i>Olethreutes pryranus</i> (Walsingham)	Tortricidae				6	35				41	U

Appendix I. Continued.

	Species	Family	Sampling Date								Total	Voltinism
			13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct	1 Nov		
126	<i>Nerice bipartita</i> Butler	Notodontidae				3	18				21	U
127	<i>Hagapteryx admirabilis</i> (Staudinger)	Notodontidae				5	32				37	U
128	<i>Selenia tetralunaria</i> (Hufnagel)	Geometridae			8		112				120	M
129	<i>Zanclognatha griselda</i> (Butler)	Noctuidae				3	23				26	U
130	<i>Notodonta albicosta</i> (Matsumura)	Notodontidae				1	9				10	U
131	<i>Scopula takao</i> Inoue	Geometridae				1	10				11	U
132	<i>Auzata superba superba</i> (Butler)	Drepanidae				2	8	1			11	U
133	<i>Brabira artemidora artemidora</i> (Oberthür)	Geometridae			3		41		1		45	M
134	<i>Meganola fumosa</i> (Butler)	Nolidae				3	34				37	U
135	<i>Gonoclostera timoniorum</i> (Bremer)	Notodontidae				3	37				40	U
136	<i>Chrysoteuchia distinctella</i> (Leech)	Pyralidae				20	77	12			109	U
137	<i>Hydrelia shioyana</i> (Matsumura)	Geometridae				1	13				14	U
138	<i>Peridea gigantea</i> Butler	Notodontidae				4	60				64	U
139	<i>Zanclognatha subgriselda</i> Sugi	Noctuidae				1	15				16	U
140	<i>Cnethodonta grisescens grisescens</i> Staudinger	Notodontidae				2	31				33	U
141	<i>Talanga quadrimaculalis</i> (Bremer et Grey)	Pyralidae				1	16				17	U
142	<i>Parasa sinica</i> Moore	Limacodidae				1	17				18	U
143	<i>Barsine aberrans askoldensis</i> (Oberthür)	Arctiidae				1	18				19	U
144	<i>Abraxas niponibia</i> Wehrli	Geometridae				4	13	3			20	U
145	<i>Eilema japonica ainonis</i> (Matsumura)	Arctiidae				5	122				127	U
146	<i>Idioclora ussuriaria</i> (Bremer)	Geometridae				1	30				31	U
147	<i>Sophta subrosea</i> (Butler)	Noctuidae				2	69				71	U
148	<i>Idaea effusaria</i> (Christoph)	Geometridae					246				246	U
149	<i>Lithosia quadra</i> (Linnaeus)	Arctiidae					223				223	U
150	<i>Mimachrostia fasciata</i> Sugi	Noctuidae					209				209	U

Appendix 1. Continued.

Species	Family	Sampling Date									Total	Voltinism
		13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct	1 Nov			
151 <i>Aventiola pusilla</i> (Butler)	Noctuidae					165					165	U
152 <i>Gynaephila maculifera</i> Staudinger	Noctuidae					127					127	U
153 <i>Eilema nankingica</i> (Daniel)	Arctiidae					115					115	U
154 <i>Omiodes tristrialis</i> (Bremer)	Pyralidae					67					67	U
155 <i>Hypomecis lunifera</i> (Butler)	Geometridae					60					60	U
156 <i>Idaea auricruda</i> (Butler)	Geometridae					59					59	U
157 <i>Cosmia pyralina</i> (Denis et Schiffermüller)	Noctuidae					56					56	U
158 <i>Pelosia angusta</i> (Staudinger)	Arctiidae					36					36	U
159 <i>Idaea foedata</i> (Butler)	Geometridae					32					32	U
160 <i>Cyana hamata hamata</i> (Walker)	Arctiidae					29					29	U
161 <i>Gandaritis agnes festinaria</i> (Christoph)	Geometridae					29					29	U
162 <i>Trachycera hollandella</i> (Ragonot)	Pyralidae					27					27	U
163 <i>Sypnoides hercules</i> (Butler)	Noctuidae					23					23	U
164 <i>Peridea graeseri</i> (Staudinger)	Notodontidae					23					23	U
165 <i>Asthena sachalinensis</i> (Matsumura)	Geometridae					22					22	U
166 <i>Oncocera semirubella</i> (Scopoli)	Pyralidae				1	20		1			22	U
167 <i>Sinibotys obliquilinealis</i> Inoue	Pyralidae					22					22	U
168 <i>Cosmia moderata</i> (Staudinger)	Noctuidae					21					21	U
169 <i>Pelosia noctis</i> (Butler)	Arctiidae					19					19	U
170 <i>Phlogophora aureopuncta</i> (Hampson)	Noctuidae					18					18	U
171 <i>Phthonandria atrilineata atrilineata</i> (Butler)	Geometridae					17					17	U
172 <i>Dimorphicosmia variegata</i> (Oberthür)	Noctuidae					16					16	U
173 <i>Melanaema venata venata</i> Butler	Arctiidae					16					16	U
174 <i>Malacosoma neustrium testaceum</i> (Motschulsky)	Lasiocampidae					16					16	U
175 <i>Archips fuscocupreanus</i> Walsingham	Tortricidae					16					16	U

Appendix I. Continued.

	Species	Family	Sampling Date								Total	Voltinism	
			13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct	1 Nov			
176	<i>Cosmia camptostigma</i> (Ménétriès)	Noctuidae					15					15	U
177	<i>Arctornis l-nigrum ussuricum</i> Bytinski-Salz	Lymantriidae					15					15	U
178	<i>Sypnoides picta</i> (Butler)	Noctuidae					14					14	U
179	<i>Ivela ochropoda</i> (Eversmann)	Lymantriidae					13					13	U
180	<i>Rhyparioides nebulosa</i> Butler	Arctiidae					12					12	U
181	<i>Eupithecia gigantea</i> Staudinger	Geometridae					11					11	U
182	<i>Plemyria rubiginata japonica</i> Inoue	Geometridae					11					11	U
183	<i>Ancylolomia japonica</i> Zeller	Pyralidae					11					11	U
184	<i>Schrankia separatalis</i> (Herz)	Noctuidae					10					10	U
185	<i>Ceroprepes ophthalmicella</i> (Christoph)	Pyralidae					87	1				88	U
186	<i>Eilema griseola submontana</i> Inoue	Arctiidae					205	3				208	U
187	<i>Zanclognatha fumosa</i> (Butler)	Noctuidae				6	30	7				43	U
188	<i>Metabraxas clerica clerica</i> Butler	Geometridae					40	1				41	U
189	<i>Eulithis convergenata</i> (Bremer)	Geometridae					137	4				141	U
190	<i>Hupodonta lignea</i> Matsumura	Notodontidae					63	2				65	U
191	<i>Prodasynemis inornata</i> (Butler)	Pyralidae					60	2				62	U
192	<i>Lobogonodes erectaria</i> (Leech)	Geometridae		4		9	18	19				50	M
193	<i>Paratalanta ussurialis</i> (Bremer)	Pyralidae					34	2				36	U
194	<i>Deileptenia ribeata</i> (Clerck)	Geometridae				26	236	43				305	U
195	<i>Pachista superans</i> (Butler)	Geometridae					15	1				16	U
196	<i>Eilema deplana pavescens</i> (Butler)	Arctiidae					38	3				41	U
197	<i>Chasminodes albonitens</i> (Bremer)	Noctuidae					19	3				22	U
198	<i>Lymantria monacha</i> (Linnaeus)	Lymantriidae					311	50				361	U
199	<i>Diarsia canescens</i> (Butler)	Noctuidae			8		1	10	5			24	M
200	<i>Oreta pulchripes</i> Butler	Drepanidae				28		42				70	M

Appendix I. Continued.

Species	Family	Sampling Date								Total	Voltinism
		13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct	1 Nov		
201 <i>Palpita nigropunctalis</i> (Bremer)	Pyralidae				45	20	3	33		101	M
202 <i>Eulithis ledereri</i> (Bremer)	Geometridae				1	20	8			29	U
203 <i>Idaea biselata</i> (Hufnagel)	Geometridae				1	123	45			169	U
204 <i>Callidrepana palleola</i> (Motschulsky)	Drepanidae			9	1	106	73			189	M
205 <i>Hupodonta corticalis</i> Butler	Notodontidae					7	3			10	U
206 <i>Martania saxea</i> (Wileman)	Geometridae				16	4	35			55	M
207 <i>Eustroma melancholicum melancholicum</i> (Butler)	Geometridae				3	1	7			11	M
208 <i>Udea lugubralis</i> (Leech)	Pyralidae					13	9			22	U
209 <i>Gandaritis placida</i> (Butler)	Geometridae					21	16			37	U
210 <i>Geometra papilionaria subrigua</i> (Prout)	Geometridae					10	11			21	U
211 <i>Amphipyra schrenckii</i> Ménétriès	Noctuidae					11	16			27	U
212 <i>Asthena amurensis</i> (Staudinger)	Geometridae				2		8			10	M
213 <i>Morphaga bucephala</i> (Snellen)	Tineidae				2		8			10	M
214 <i>Hermonassa arenosa</i> (Butler)	Noctuidae					7	11			18	U
215 <i>Catocala dissimilis</i> Bremer	Noctuidae					6	14			20	U
216 <i>Cosmia unicolor</i> (Staudinger)	Noctuidae					4	11			15	U
217 <i>Sineugraphe bipartita</i> (Graeser)	Noctuidae					8	25			33	U
218 <i>Martania fulvida</i> (Butler)	Geometridae				2		25			27	M
219 <i>Chasminodes sugii</i> Kononenko	Noctuidae					37	220			257	U
220 <i>Garaeus specularis mactans</i> (Butler)	Geometridae					1	11			12	U
221 <i>Gandaritis fixseni</i> (Bremer)	Geometridae					1	26			27	U
222 <i>Triphaenopsis jezoensis</i> Sugi	Noctuidae					1	31			32	U
223 <i>Alcis medialbifera</i> Inoue	Geometridae						321			321	U
224 <i>Acleris dentata</i> (Razowski)	Tortricidae						126			126	U
225 <i>Chasminodes aino</i> Sugi	Noctuidae						92			92	U

Appendix I. Continued.

Species	Family	Sampling Date								Total	Voltinism
		13 Apr	12 May	7 Jun	9 Jul	5 Aug	1 Sep	4 Oct	1 Nov		
226 <i>Patagoniodes nipponellus</i> (Ragonot)	Pyralidae						48			48	U
227 <i>Ilema eurydice</i> (Butler)	Lymantriidae						34			34	U
228 <i>Myrteta angelica</i> Butler	Geometridae						32			32	U
229 <i>Saturnia japonica japonica</i> (Moore)	Saturniidae						13			13	U
230 <i>Xestia efflorescens</i> (Butler)	Noctuidae						12			12	U
231 <i>Timandra reompta ovidius</i> (Bryk)	Geometridae						11			11	U
232 <i>Rhopobota naevana</i> (Hübner)	Tortricidae						11			11	U
233 <i>Gypsonoma dealbana</i> (Frölich)	Tortricidae						11			11	U
234 <i>Ypsolopha albistriatus</i> (Issiki)	Yponomeuti- dae					2	6	5		13	U
235 <i>Bombyx mandarina</i> (Moore)	Bombycidae						9	10		19	U
236 <i>Ramobia basifuscaria</i> (Leech)	Geometridae						5	86		91	U
237 <i>Daseochaeta viridis</i> (Leech)	Noctuidae						2	50		52	U
238 <i>Saturnia jonasii fallax</i> Jordan	Saturniidae							95		95	U
239 <i>Telorta edentata</i> (Leech)	Noctuidae							21		21	U
240 <i>Ramobia mediodivisa</i> Inoue	Geometridae							46	1	47	U
241 <i>Venusia phasma</i> (Butler)	Geometridae							159	4	163	U
242 <i>Epinotia rasdolnyana</i> (Christoph)	Tortricidae							12	1	13	U
243 <i>Erannis golda</i> Djakonov	Geometridae								70	70	U
244 <i>Poecilocampa tamanukii</i> Matsumura	Lasiocampi- dae								64	64	U
245 <i>Operophtera brumata</i> (Linnaeus)	Geometridae								51	51	U
246 <i>Erannis defoliaria gigantea</i> Inoue	Geometridae								26	26	U
247 <i>Larerannis orthogrammaria</i> (Wehrli)	Geometridae								16	16	U
248 <i>Operophtera relegata</i> Prout	Geometridae								11	11	U
Total		1	94	438	4,922	5,475	1,604	523	244	13,301	

The number of individuals collected in five stands in each month is expressed. Species were listed in order of increasing mean occurrence period. To estimate voltinism (univoltine or multivoltine), we assigned a species to multivoltine if it was collected in discontinuous months, collected in more than two months and had two peaks in their occurrence pattern, or collected in more than three months. Voltinism: U, univoltine; M, multivoltine.

EIGHT NEW SPECIES OF *EUCOSMA* HÜBNER (TORTRICIDAE) FROM WESTERN NORTH AMERICA

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ABSTRACT. Eight new species of *Eucosma* Hübner (Tortricidae) are described from western North America: *E. angelana*, *E. blanchardi*, *E. candida*, *E. johnstoni*, *E. lafontainei*, *E. maculosa*, *E. mescalerana*, and *E. rufocostana*. *Eucosma conspiciendana* Heinrich and *Eucosma cataclystiana* (Walker) are reviewed due to similarity in forewing appearance to *E. rufocostana*. Illustrations of the adults and genitalia are provided.

Additional key words: Olethreutinae, Eucosmini, *conspiciendana*, *cataclystiana*.

In the Nearctic Region, the olethreutine lineage currently arranged under the genera *Phaneta* Stephens, *Eucosma* Hübner, and *Pelochrista* Lederer is represented by some 300 named species. The greatest diversity occurs in western North America, where there are numerous taxa yet to be recognized and described. This paper proposes names for eight new species, five from the desert southwest, two from the high plains east of the Rocky Mountains, and one from the Great Basin and central Rocky Mountain regions. Their placement in *Eucosma* is based on the presence of a costal fold on the male forewing and the lack of a large spine on the ventral margin of the male cucullus. Included are reviews of *Eucosma conspiciendana* Heinrich and *Eucosma cataclystiana* (Walker), which are similar in forewing appearance to one of the new species.

MATERIALS AND METHODS

This study is based on the examination of 366 specimens and 97 associated genitalia preparations from the following institutional and private collections: Charles D. Bird, Erskine, Alberta (CDB); The Natural History Museum, London (BMNH); Canadian National Collection, Ottawa (CNC); Laurence L. Crabtree, Bieber, California (LLC); Donald J. Wright (DJW); Essig Museum of Entomology, UC Berkeley (EME); George J. Balogh, Portage, Michigan (GJB); John S. Nordin, Laramie, Wyoming (JSN); and United States Museum of Natural History, Washington D.C. (USNM). Collections at Colorado State University, Fort Collins, Colorado (CSU) and Michigan State University, East Lansing, Michigan (MSU) are included amongst the paratype depositories for some of the new species. Morphological nomenclature follows Gilligan et al. (2008). Forewing length (FWL) is measured from base to apex including fringe, aspect ratio (AR) is defined as FWL divided by medial

forewing width, saccular angle refers to the angle formed by the ventral margin of the sacculus and the adjacent margin of the neck (see Wright 2011), and “≈” stands for “approximately equal to”.

SPECIES ACCOUNTS

Eucosma blanchardi, new species

(Figs. 1–3, 21, 31, 32, 47)

Diagnosis. *Eucosma blanchardi* resembles *Eucosma mescalerana* (described below) (Figs. 1–3 vs. Fig. 4), but the forewing has a less sharply defined median fascia, a paler apical region, and brown reticulations in the interfascial areas. The male genitalia of the two species are distinguished by subtle differences in valval shape (Figs. 21, 22), the number and size of the spines along the distal margin of the cucullus (fewer and stouter in *E. blanchardi*), and the presence/absence of a ridge on the medial surface of the valva at the proximal margin of the cucullus (present in *E. blanchardi*, absent in *E. mescalerana*). Females are easily separated by sterigma shape (Figs. 32, 34). Also, *E. blanchardi* lacks the sclerotized patch present on the ductus bursae in *E. mescalerana* (Figs. 31, 33).

Description. *Head:* Frons white; vertex with medial scales beige, lateral scales white with pale brown shading; labial palpus white, with some brownish-gray shading on lateral surface of second segment and with third segment concealed by long scales on ventral margin of second segment; antenna concolorous with vertex. *Thorax:* Dorsal surface white; tegula white with light brown basal and sub-apical spots; ventral surface white; legs brown, sometimes shading to tan, with white markings at mid-tibia, distal extremity of tibia, and distal extremity of each tarsomere. *Forewing* (Figs. 1–3): ♂ FWL 5.9–8.0 mm (mean = 6.5, n = 30), AR = 2.89; ♀ FWL 5.9–8.2 mm (mean = 7.1, n = 17), AR = 2.84; costal margin weakly convex; apical angle approximately 90°; distal margin weakly convex; dorsal markings brown to gray; interfascial areas white with extensive gray-brown reticulations; subbasal fascia well expressed from dorsum to cubitus, barely discernable from cubitus to costa; median fascia usually complete, often weakly expressed on radius and cubitus, and frequently with small cluster of black scales forming a dark dot at proximal margin of ocellus; ocellus with proximal and distal margins defined by white-edged lustrous beige bars; central field of ocellus white, frequently with fine brown reticulations, and crossed by up to

three longitudinal black dashes; costal strigulae well expressed from base to apex; scales along termen white with black to blackish-brown cross-bars; fringe scales whitish, those toward apex with dark cross-bars. *Hindwing*: Gray brown. *Male genitalia* (Fig. 21) ($n = 9$): Uncus semitriangular and well differentiated from dorsolateral shoulders of tegumen; socius long and narrow, with distal one-half tapering to narrowly rounded apex; vesica with 1–6 deciduous cornuti; valva with costal margin concavely curved at neck, apex evenly rounded, distal margin convex of nearly uniform curvature, anal angle moderately produced, neck long and tapering from saccular corner to cucullus, saccular angle obtuse; proximal margin of cucullus accentuated by weakly developed ridge on medial surface of valva; distal margin of cucullus with 5–9 spines spaced evenly from anal angle nearly to apex. *Female genitalia* (Fig. 31, 32) ($n = 7$): Papillae anales with ventrolaterally facing posterior lobes, laterally facing anterior lobes, long ventrally curving setae along lateral margins, and hook-tipped setae along margins of anal opening; lamella postvaginalis semirectangular, medial width $\approx 2 \times$ length, with posterior margin somewhat wider than ostium, and with several hair-like setae flanking shallow central trough; lamella antevaginalis ring-like and weakly sclerotized; posterior margin of sternum 7 roundly emarginated to one-half length of sterigma; ductus bursae lacking sclerotization; corpus bursae with two signa of distinctly different size; corpus bursae finely wrinkled, with interior surface lacking microspinules.

Holotype. ♂, Arizona, [Pima Co.], Madera Canyon, Santa Rita Mtns., R. W. Hodges, 4400 ft., 12 October 1959, USNM.

Paratypes. ARIZONA: Cochise Co., S. W. Res. Sta., 5 mi. W. Portal, J. R. Powers, 1 September 1959 (1 ♂, genitalia slide DJW 2410); same location and collector as holotype, 6 October 1959 (2 ♂), 12 October 1959 (1 ♂); [Pima Co.], Madera Canyon, Santa Rita Mtns., R. W. Hodges, 4880 ft., 24 July 1959 (1 ♂), 28 August 1959 (1 ♂), 13 September 1959 (1 ♀), 14 September 1959 (1 ♂), 16 September 1959 (1 ♂), 26 September 1959 (1 ♀, genitalia slide DJW 2065), 27 September 1959 (1 ♂; 1 ♀, genitalia slide DJW 2406), 29 September 1959 (1 ♀, genitalia slide DJW 2067); Santa Cruz Co., Pena Blanca Canyon, R. W. Hodges, 26 August 1959 (1 ♂). NEW MEXICO: Otero Co., Dog Cyn. Rd., south of Alamogordo, G. J. Balogh, 14 September 2004 (11 ♂, genitalia slides DJW 1743, 2407; 1 ♀, genitalia slide DJW 2063); Sierra Co., Hwy 195 near I-25 exit 83, G. J. Balogh, 15 October 2001 (1 ♂, genitalia slide DJW 1119); White Sands National Monument, E. H. Metzler, 25 August 2009 (3 ♂, genitalia slide DJW 2534), 14 September 2009 (3 ♀). TEXAS: [Brewster Co.], Big Bend N. P., Chihuahuan Desert near Nugent Mtn., A. & M. E. Blanchard, 21 September 1971 (1 ♂, genitalia slide USNM 90418; 1 ♀), 8 October 1969 (1 ♀, genitalia slide USNM 90420); Presidio Co., Shafter, A. & M. E. Blanchard, 9 September 1969 (1 ♂, genitalia slide USNM 90419), 16 October 1973 (1 ♂, genitalia slide USNM 90421). Depositories: BMNH, DJW, EME, GJB, MSU, USNM.

Etymology. The specific epithet honors André Blanchard for his many contributions to our knowledge of the Tortricidae of Texas.

Distribution and biology. Figure 3 is representative of 6 specimens (1 ♂, 5 ♀) I collected approximately 12 miles south of Silver City in Grant County, New Mexico on 9 August 1999. I did not include them in the type series because they are a little larger than the designated paratypes (mean FWL \approx 7.5 vs. 6.6 mm) and a little more strongly marked, but I am treating them as *E. blanchardi* based on similarity of genitalia and forewing pattern. The 49 specimens examined (32 ♂, 17 ♀) document a geographic range extending from southeastern Arizona to southwest Texas (Fig. 47). Adults fly from late July to mid-October.

Eucoisma mescalerana, new species

(Figs. 4, 22, 33, 34, 47)

Diagnosis. *Eucoisma mescalerana* is similar to *E. blanchardi*; differences are discussed in the diagnosis section for the latter species.

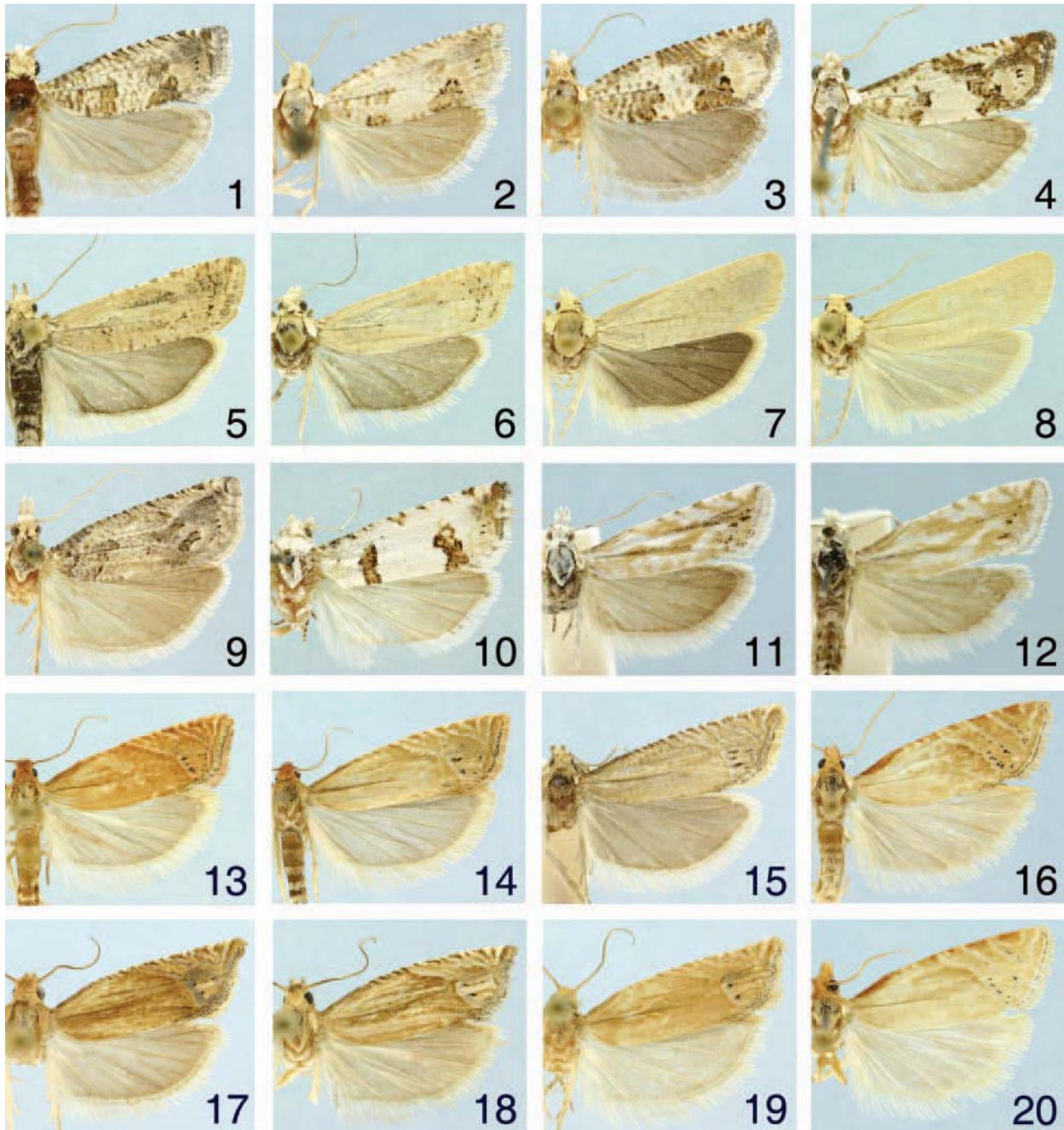
Description. *Head*: Frons and vertex white; labial palpus white, with gray-brown shading on lateral surface of second segment; antenna white. *Thorax*: Dorsal surface white; tegula white with brown basal spot; ventral surface white; fore- and mid-leg with anterior surfaces pale brown, posterior surfaces whitish; hind-leg whitish; mid-leg with white marks at mid-tibia and distal extremity of tibia; tarsi with whitish annular markings at distal end of each tarsomere. *Forewing* (Fig. 4): ♂ FWL 7.8–8.7 mm (mean = 8.2, $n = 3$), AR = 3.19; ♀ FWL 6.7–7.7 mm (mean = 7.4, $n = 3$), AR = 2.94; costal margin nearly straight; apex acute; distal margin straight; dorsal surface white with brown markings, the latter variably edged with black; male costal fold grayish brown; basal and subbasal fasciae represented by short mark on inner margin and by bar from inner margin to cell, respectively; median fascia complete, with cluster of black scales forming conspicuous dot at proximal margin of ocellus; postmedian band often interrupted by white sub-costal scaling; central field of ocellus white to pale tan, crossed by up to three black dashes, bordered on proximal and distal margins by white-edged lustrous beige bars, and capped anteriorly by patch of white-tipped gray scales; costal strigulae sharply defined from mid-costa to apex; scales along termen blackish gray with white apices; fringe scales whitish near tornus, shading to dark gray toward apex. *Hindwing*: Gray brown. *Male genitalia* (Fig. 22) ($n = 3$): Uncus a prominent lobe with rounded apex; dorsolateral shoulders of tegumen well developed; socius long and narrow, tapering gradually to narrowly rounded apex; vesica with 5–6 deciduous cornuti; valva with costal margin concave, apex rounded, distal margin weakly convex to nearly straight, anal angle moderately produced, ventral emargination of neck moderate, saccular angle obtuse; cucullus with medial surface covered with fine setae and with 12 or more spiniform setae along distal margin from anal angle nearly to apex. *Female genitalia* (Figs. 33, 34) ($n = 3$): Papillae anales with ventrally facing lobes extending posterior to anal opening, laterally facing surfaces flanking anal opening, long ventrally curving setae along lateral margins, and shorter often hook-tipped setae along anal opening; lamella postvaginalis nearly flat, with semitriangular posterolateral corners and shallow medial trough; anterior margin of ostium fused with sternum 7; membrane posterior to sterigma with irregular lines of hair-like setae extending to ventral extremities of tergum 8; sternum 7 with posterior edge emarginated to nearly full length of sterigma and with medial section weakly sclerotized compared to posterior and lateral margins; ductus bursae with small sclerotized patch near juncture with ductus seminalis; corpus bursae with large signum on ventral surface and small tack-like signum on dorsal surface.

Holotype. ♂: New Mexico, Chaves Co., Mescalero Dunes east of Roswell, G. J. Balogh, 22 September 2003, genitalia slide DJW 1122, USNM.

Paratypes. ARIZONA: Cochise Co., 5131 Bannock St., Pueblo Del Sol, Huachuca Mts., H. S. Wielgus, 22 June 1986 (1 ♀, genitalia slide DJW 1934); Cochise Co., Turkey Creek, Chiricahua Mts., 5600 ft., J. Brown, 1–2 August 1986 (1 ♂, genitalia slide DJW 1319; 1 ♀, genitalia slide DJW 1321); Santa Cruz Co., 2 mi. W. of Ft. Huachuca on Forest Serv. Rd. 827, D. J. Wright, 6 August 1999 (1 ♀, genitalia slide DJW 1153). NEW MEXICO: same data as holotype (1 ♂, genitalia slide DJW 1154). Depositories: DJW, EME, USNM.

Etymology. The specific epithet is derived from the name of the type locality, the Mescalero Dunes in southeastern New Mexico.

Distribution and biology. I examined 6 specimens (3 ♂, 3 ♀) from the southeast corner of Arizona and east



FIGS. 1-20. 1-3, *E. blanchardi*. 1, ♂ Otero Co., New Mexico. 2, ♀ Santa Rita Mts., Arizona; 3, ♀ Grant Co., New Mexico. 4, *E. mescalerana*, ♂ holotype, Chaves Co., New Mexico. 5-6, *E. maculosa*. 5, ♂ holotype. 6, ♂ Albany Co., Wyoming. 7-8, *E. lafontainei*, ♂, ♂ Albany Co., Wyoming. 9, *E. angelana*, ♂ Los Angeles Co., California. 10, *E. candida*, ♂ holotype. 11-12, *E. johnstoni*. 11, ♂ holotype. 12, ♂ Mojave Co., Arizona. 13-15, *E. conspiciendana*. 13, ♂ Sanpete Co., Utah. 14, ♂ Albany Co., Wyoming. 15, ♂ Monterey Co., California. 16, *E. rufocostana*, ♂ holotype. 17-19, *E. cataclystiana*, ♂, ♂, ♂, Adams Co., Ohio; Monona Co., Iowa; Larimer Co., Colorado. 20, *E. rufocostana*, ♂ Oneida Co., Idaho.

central New Mexico (Fig. 47). One record is from late June, the others from August and September.

***Eucosma maculosa*, new species**

(Figs. 5, 6, 23, 35, 36, 48)

Diagnosis. *Eucosma maculosa* is similar to *Eucosma lafontainei* (described below). The pale forewing is variably speckled with dark brown, the costal strigulae are weakly delimited by brown marks, and a pale grayish-brown streak extends from mid-cell nearly to the apex (Figs. 5, 6). The forewing in *E. lafontainei* (Figs. 7, 8) is immaculate except for a pale grid of fine yellow-brown reticulations. The male genitalia of the two species are similar (Figs. 23, 24), but in *E. maculosa* the uncus is somewhat more bulbous, the cucullus slightly more elongate, and the setae on the uncus, socii, and sacculus are finer and less densely distributed. The phallobase, which is bulbous in both species, is spherical in *E. maculosa* but comprised of two semispherical sections in *E. lafontainei*. Females of *E. maculosa* have large patches of scales on the lamella postvaginalis vs. a few hair-like setae in *E. lafontainei* (Figs. 36, 38), and in *E. maculosa* the posterior margin of sternum 7 more strongly overlaps the ostium. The male genitalia of *E. maculosa* resemble those of *Eucosma biquadrana* (Walsingham) (Wright 2008, Fig. 33), but the two species are easily separated by forewing color and maculation (Figs. 5, 6 vs. Wright 2008, Figs. 21, 22).

Description. *Head:* Frons and vertex creamy white to pale tan; labial palpus concolorous with vertex, with long scales of second segment a shade darker; antenna pale tan. *Thorax:* Dorsal surface tan; ventral surface creamy white; legs tan to pale brown, with whitish ring at distal end of each tarsomere. *Forewing* (Figs. 5, 6): ♂ FWL 9.5–11.7 mm (mean = 10.7, n = 12), AR = 3.50; ♀ FWL 10.9–11.7 mm (mean = 11.3, n = 2), AR = 3.23; costal margin straight; apex acute; termen nearly straight; dorsal surface pale yellowish white to tan, lacking fasciate markings but liberally speckled with brown/black scales, often with pale grayish-brown streak arising at about mid-cell and gradually widening toward apex; ocellus barely discernable, concolorous with wing, with transverse line of black scales through central field; costal strigulae weakly expressed from mid-wing to apex, separated by brown to blackish-brown costal marks; fringe scales concolorous with wing. *Hindwing:* Gray brown, with fringe paler. *Male genitalia* (Fig. 23) (n = 4): Uncus strongly developed and somewhat bulbous, with height ≈ basal width; dorsolateral shoulders of tegumen well defined; socii long, finger-like, and moderately setose; phallus cylindrical, with bulbous spherical base; vesica with 8–9 deciduous cornuti; valva with costal margin concave, apex evenly rounded, distal margin convex, anal angle weakly developed, ventral emargination of neck broad and shallow, saccular corner broadly rounded; cucullus with 4–5 spiniform setae on ventral two-thirds of distal margin. *Female genitalia* (Figs. 35, 36) (n = 2): Papillae anales ventrally facing and tapering from evenly rounded posterior lobes to more narrowly rounded anterior lobes, with ventral surfaces covered with short to medium length setae, lateral margins lined with long ventrally curving setae, and with numerous hook-tipped setae on anterior lobes; lamella postvaginalis nearly flat, shaped like a whale tail, with shallow central trough and large patches of scales (ca. 50, represented by sockets in Figs. 35, 36) on lateral projections; posterior margin of sternum 7 with medial projection shielding

ostium; ductus bursae without sclerotization; corpus bursae with two signa, one thimble-like, the other smaller and cone-like; membrane of corpus bursae finely wrinkled, with interior surface lacking microspinules.

Holotype (Fig. 5). ♂: Wyoming, Albany Co., T15N R75W S29, W. side Gelatt Lake, 7250 ft., J. S. Nordin, 41° 14.0' N, 105° 50.6' W, 18 July 2005, USNM.

Paratypes. WYOMING: Same locality and collector as holotype, 29 June 2006 (1 ♂), 15 July 2005 (1 ♂, genitalia slide DJW 1411), 16 July 2007 (1 ♂), 18 July 2005 (2 ♂), 20 July 2005 (1 ♂), 28 July 2005 (4 ♂, genitalia slides DJW 1410, 1927, 1928; 1 ♀, genitalia slide DJW 1666), 29 July 2005 (1 ♂); Albany Co., NW side Gelatt Lake, 7250 ft., J. S. Nordin, 9 July 2007 (1 ♀, genitalia slide DJW 1874). Depositories: BMNH, CNC, CSU, DJW, EME, USNM.

Etymology. The specific epithet comes from the Latin adjective *maculosus*, meaning spotted or speckled.

Distribution and biology. The type locality, located approximately 15 miles WSW of Laramie, Wyoming, is noted for its alkali soil, with sizable stands of *Atriplex gardneri* (Moq.) D. Dietr. (Gardner's saltbush) (Chenopodiaceae) along the lake shore. The larva of *E. maculosa* is probably a root borer in one or more species of Asteraceae, as is the case with most species of *Eucosma* with documented hosts (see e.g. Powell & Opler 2006). Species of Asteraceae identified at the type locality include: *Ericameria nauseosa* (Pall. ex Pursh) G. L. Nesom & G. Baird (rubber rabbitbrush), *Artemisia frigida* Willd. (prairie sagewort), and *Artemisia tridentata* Nutt. (big sagebrush). Adult capture dates range from 29 June to 29 July.

***Eucosma lafontainei*, new species**

(Figs. 7, 8, 24, 37, 38, 48)

Diagnosis. This species is distinguished from other Nearctic *Eucosma* by the uniformly pale yellowish forewing (Figs. 7, 8) together with the form of the female genitalia (Fig. 37). It most closely resembles *E. maculosa*, the differences being noted in the diagnosis for that species.

Description. *Head:* Uniformly yellowish white. *Thorax:* Dorsal surface concolorous with head; ventral surface a shade lighter; legs pale yellowish white and lacking tarsal annulations. *Forewing* (Figs. 7, 8): ♂ FWL 11.5–12.9 mm (mean = 12.3, n = 6), AR = 3.33; ♀ FWL 11.2–13.5 mm (mean = 12.4, n = 3), AR = 3.24; costal margin straight; apex acute; termen convex; dorsal surface uniformly pale yellow to pale tan, with extensive pale yellowish-brown reticulations; fasciate markings, ocellus, and costal strigulae not expressed. *Hindwing:* Pale gray brown to dark gray brown; fringe contrastingly lighter in dark specimens. *Male genitalia* (Fig. 24) (n = 6): Uncus strongly developed, with apex rounded to weakly indented medially; dorsolateral shoulders of tegumen well differentiated; socii large, finger-like, and densely covered with moderately stout setae; phallus cylindrical, with bulbous base divided into two semispherical lobes; vesica with 6–13 deciduous cornuti; valva with costal margin weakly concave, apex rounded, distal margin convex, anal angle weakly produced, ventral emargination of neck broad and shallow, saccular corner broadly rounded; cucullus with medial surface densely covered with moderately stout setae and with ca. 5 spiniform setae along distal margin. *Female genitalia* (Figs. 37, 38) (n = 3): Papillae

anales ventrally facing and tapering from evenly rounded posterior lobes to more narrowly rounded anterior lobes, with medial margins flanking anal opening somewhat raised, ventral surfaces densely setose, lateral margins lined with long ventrally curving setae, and numerous hook-tipped setae on anterior lobes; lamella postvaginalis nearly flat, in the shape of a whale tail, with very shallow central trough and several setae (6–12) on each lateral projection; posterior margin of sternum 7 with convex medial projection weakly shielding ostium; ductus bursae without sclerotization; corpus bursae with two signa of unequal size, membrane finely wrinkled, and interior surface lacking microspinules.

Holotype. ♂: Wyoming, Albany Co., T15N R75W S29, W. side Gelatt Lake, 7250 ft., J. S. Nordin, 28 July 2005, genitalia slide DJW 2422, USNM.

Paratypes. CANADA: Alberta, Dry Island Buffalo Jump Provincial Park, 51.939° N, 112.965° W, 760 m., C. D. Bird, 12 July 2003 (1 ♀, genitalia slide DJW 1899). COLORADO: [Pueblo Co.], 5 mi N. Pueblo, 5100 ft., Lafontaine and Bowen, 22 August 1975 (1 ♂, genitalia slide DJW 1164). WYOMING: same location and collector as holotype, 18 July 2005 (1 ♂, genitalia slide DJW 1412), 28 July 2005 (2 ♂, genitalia slides DJW 1408, 2423; 2 ♀, genitalia slides DJW 1409, 1930), 29 July 2005 (1 ♂, genitalia slide DJW 1929); Albany Co., NW side Gelatt Lake, 7242 ft., J. S. Nordin, 22 July 2009 (1 ♂). Depositories: CDB, CNC, CSU, DJW, EME, USNM.

Etymology. This species is named after J. Donald LaFontaine, one of the collectors of the earliest dated specimen in the type series.

Distribution and biology. I examined 10 specimens (7 ♂; 3 ♀) from the plains of eastern Colorado, southeastern Wyoming, and southern Alberta (Fig. 48). Capture dates range from 12 July to 22 August.

Eucosma angelana, new species

(Figs. 9, 25, 39, 40, 47)

Diagnosis. The combination of forewing appearance (Fig. 9) (brownish-gray coloration with fragmented median fascia) and male cucullus shape (Fig. 25) (broadly rounded apex with narrowly rounded and strongly developed anal angle) distinguishes *E. angelana* from other Nearctic *Eucosma*. The male genitalia most closely resemble those of *Eucosma matutina* (Grote) and *Eucosma fiskeana* Kearfott (Gilligan et al. 2008: 217 and 220), but the latter two species are smaller (mean FWL ≈ 7.6 mm and 9.2 mm, respectively, vs. 11.9 mm in *E. angelana*) and quite different in forewing color and maculation (Fig. 9 vs. Gilligan et al. 2008: 108, 114). The female genitalia resemble those of *Eucosma totana* Kearfott (Figs. 39, 40 vs. Wright 2005, Figs. 28, 32), but the forewing of the latter species has whiter interfascial areas and a distinctive chevron-shaped mark at the end of the cell (Fig. 9 vs. Wright 2005, Figs. 7, 8).

Description. *Head:* Lower frons creamy white; scales of upper frons and vertex creamy white, with variably expressed tan to brown cross-markings; labial palpus with medial surface and dorsal edge creamy white, lateral surface pale brown, third segment creamy white and concealed by long scales of second segment; antenna concolorous with vertex. *Thorax:* Scales of dorsal surface creamy white with grayish-brown cross-markings; ventral surface creamy

white; fore- and mid-leg with anterior surfaces brown, posterior surfaces creamy white; hind-leg paler; legs with whitish markings at mid-tibia, distal extremity of tibia, and distal end of each tarsomere. *Forewing* (Fig. 9): ♂ FWL 11.3–12.2 mm (mean = 11.7, n = 7), AR = 3.21; ♀ FWL 11.5–12.7 mm (mean = 12.2, n = 4), AR = 2.95; costa weakly arched at base, otherwise straight; apex acute; termen straight; dorsal surface brownish gray, heavily suffused with creamy white, with faint creamy-white streaks along radius, cubitus, and CuP; fasciate markings darker brown, often with some black edging; subbasal fascia an oblique bar from inner margin to radius, separated from costa by creamy-white sub-costal streak; median fascia weakly expressed and broken into three components: an outwardly oblique bar at mid-costa, a pretornal oblique bar arising on inner margin and bordering proximal margin of ocellus, and a bar at distal end of cell that aligns with dark scaling anterior to ocellus to form an apical streak; ocellus defined proximally and distally by lustrous beige bars; central field of ocellus concolorous with interfascial areas and marked by up to three black dashes, the latter often reduced to black dots; scales along termen white with dark brown cross-markings; fringe scales creamy white, sometimes with pale brownish cross-markings. *Hindwing:* Grayish brown. *Male genitalia* (Fig. 25) (n = 4): Uncus a well developed convex lobe; dorsolateral shoulders of tegumen well defined; socii finger-like, narrowing distally; vesica with 8–11 deciduous cornuti; valva with costal margin concave, apex broadly rounded, distal margin nearly straight toward anal angle, anal angle acute and strongly produced, ventral emargination of neck broad and U-shaped, saccular angle obtuse; cucullus with medial surface densely setose. *Female genitalia* (Figs. 39, 40) (n = 3): Papillae anales laterally facing and moderately setose; ostium circular; lamella postvaginalis widening posteriorly, with V-shaped emargination of posterior margin, acute posterolateral corners, and several hair-like setae flanking microspinulate medial section; lamella antevaginalis narrow and ring-like; posterior margin of sternum 7 weakly concave and separated from sterigma by thin band of membrane; ductus bursae lacking sclerotization but with microspinules on inner surface near juncture with ductus seminalis; corpus bursae with two signa of different size and with inner surface sparsely microspinulate.

Holotype. ♂: California, Los Angeles Co., Mint Canyon, Christopher Henne, 15 October 1941, genitalia slide JAP 4602, EME.

Paratypes. CALIFORNIA: same location and collector as holotype, 11 October 1941 (1 ♀, genitalia slide DJW 2415); Los Angeles Co., 6 mi. W. Lancaster, J. A. Powell, 2 October 1967 (8 ♂, genitalia slides JAP 2292, DJW 1312, 2416; 4 ♀, genitalia slide DJW 1313); 5 October 1964 (1 ♀, genitalia slide DJW 2056). Depositories: DJW, EME, USNM.

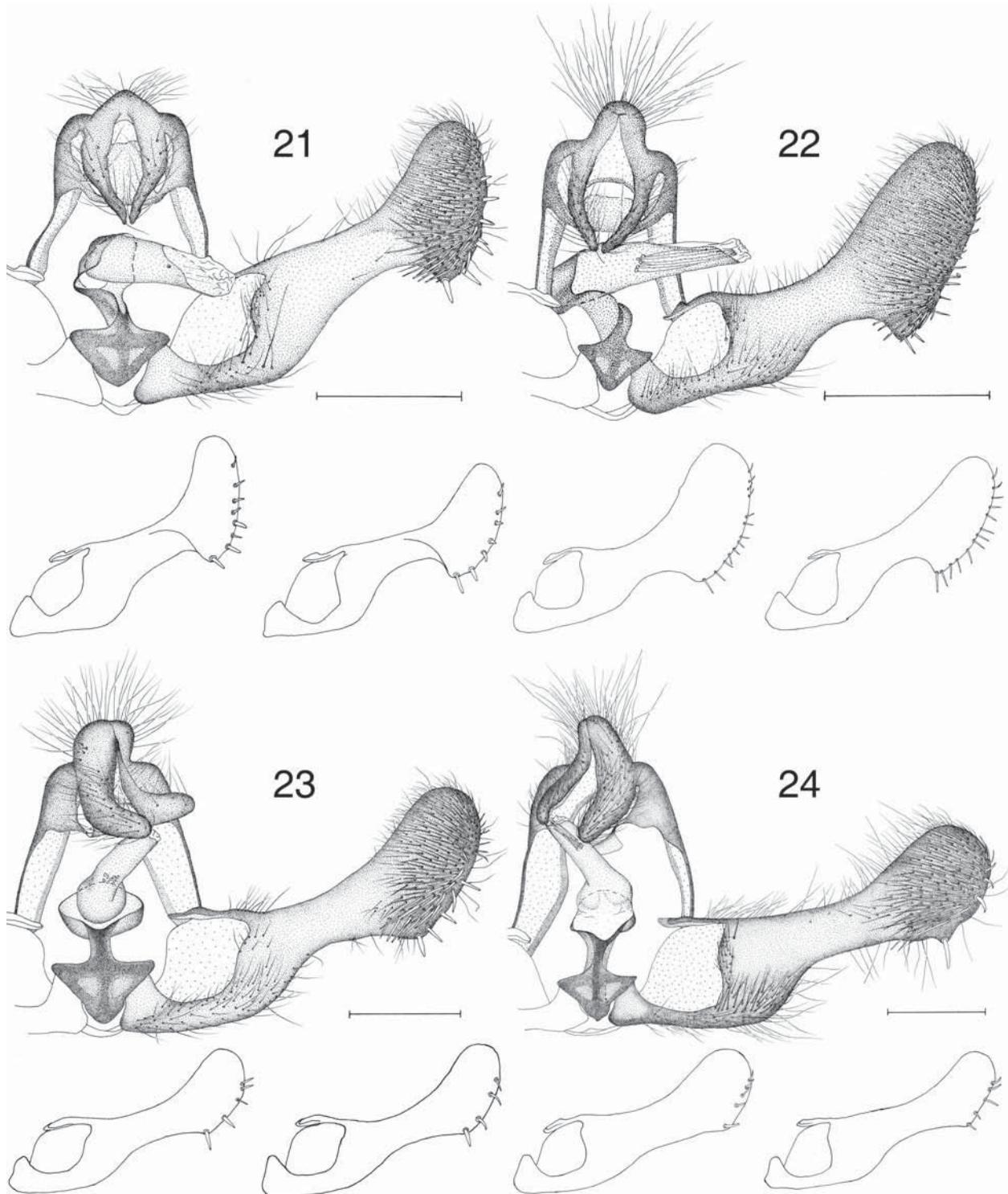
Etymology. The specific epithet refers to Los Angeles County, California, where the type series was collected.

Distribution and biology. I examined 15 specimens (9 ♂, 6 ♀) (Fig. 47), all captured during the first half of October. Those from the Lancaster site bear pin labels with the inscription “Artemisia”.

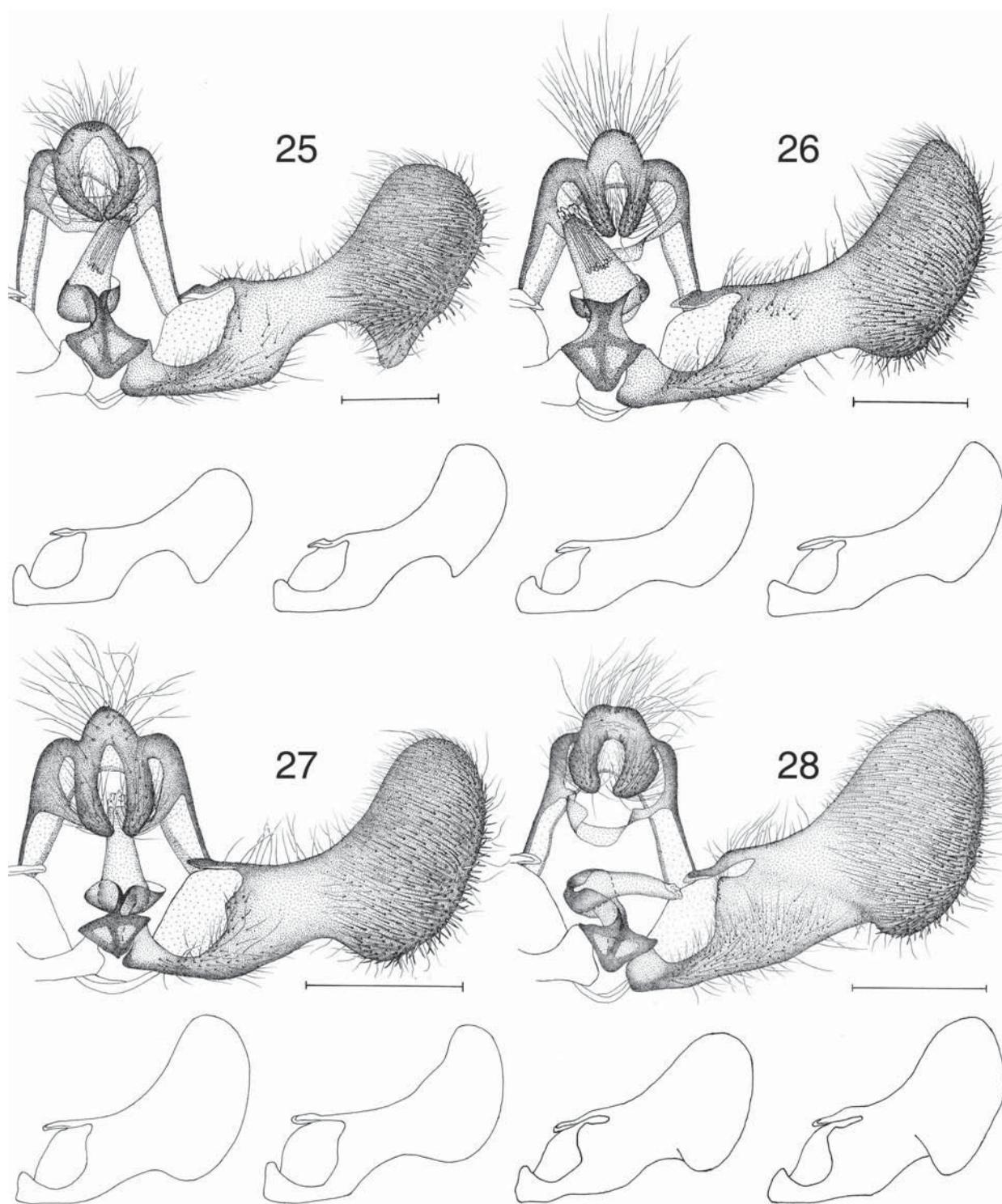
Eucosma candida, new species

(Figs. 10, 26, 47)

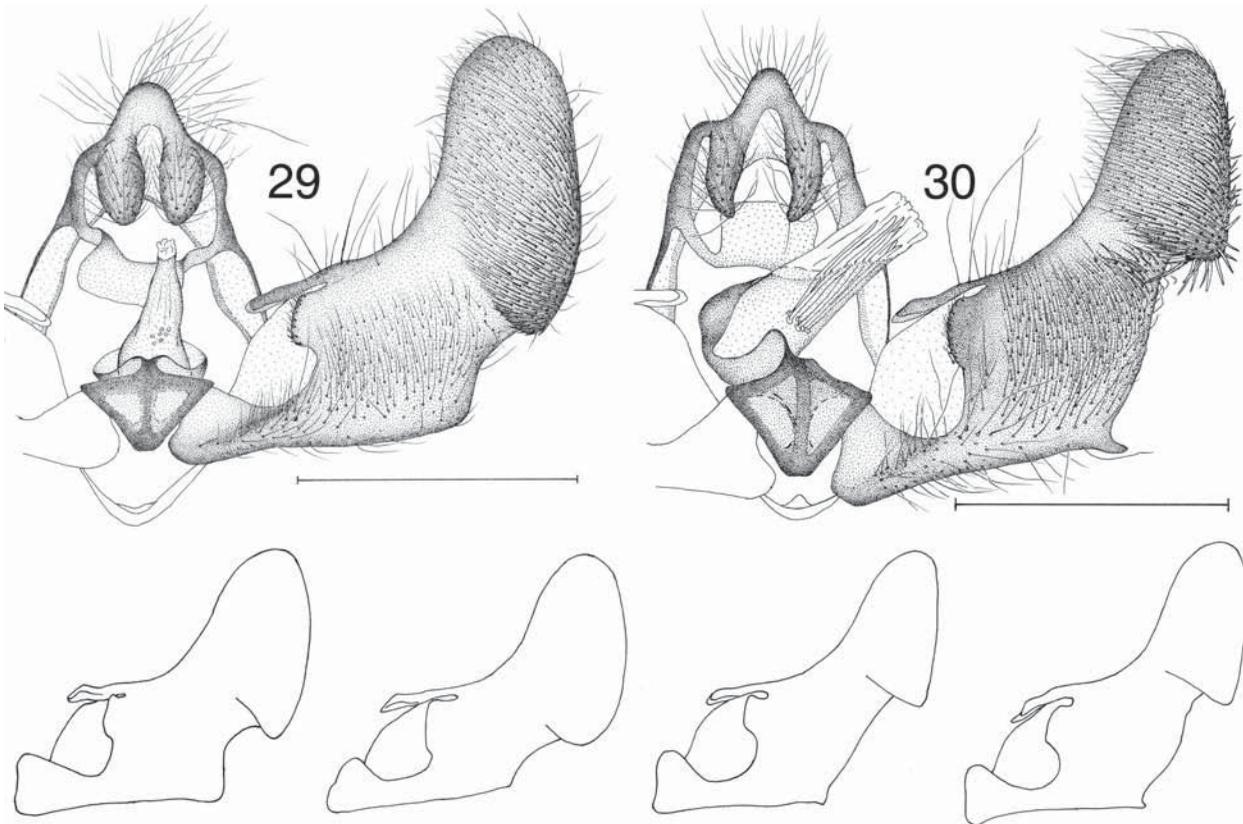
Diagnosis. This species is recognized by the combination of a bright white forewing and two incomplete brown fasciate markings on the inner margin. The male genitalia (Fig. 26) suggest an affiliation with *Eucosma snyderana* Kearfott (Wright 2007, Fig. 31), but *E. candida* lacks the brownish-gray suffusion in the forewing typical of that species (Wright 2007, Figs. 9–11).



FIGS. 21-24. *Male genitalia*. **21**, *E. blanchardi*, slides DJW 2410, 1743, USNM 90419. **22**, *E. mescalerana*, slides DJW 1319, 1154, 1122. **23**, *E. maculosa*, slides DJW 1411, 1928, 1927. **24**, *E. lafontainei*, slides DJW 2423, 1164, 1929. Scale bar = 0.5 mm.



FIGS. 25-28. Male genitalia. **25**, *E. angelana*, slides DJW 1312, JAP 2292, 4602. **26**, *E. candida*, slides DJW 1159, 1062, JAP 2476. **27**, *E. johnstoni*, slides DJW 2421, 1167, 2420. **28**, *E. rufocostana*, slides DJW 758, EME 5718, JAP 2490. Scale bar = 0.5 mm.



FIGS. 29–30. Male genitalia. 29, *E. conspicidana*, slides DJW 695, 1231, 1668. 30, *E. cataclystiana*, slides DJW 2517, 1141, 2514. Scale bar = 0.5 mm.

Description. *Head:* Frons, vertex, labial palpi, and antennae white. *Thorax:* Dorsal and ventral surfaces white; legs with femur and tibia white, sometimes shading to brown on anterior surfaces; tarsus brown with white annular markings at distal extremity of each tarsomere. *Forewing* (Fig. 10): ♂ FWL 10.4–11.3 mm (mean = 10.8, $n = 3$), AR = 3.50; costa straight; apex acute; termen straight; dorsal surface bright white with brown markings, the latter variably edged with black; subbasal fascia represented by blackish mark on costa and bar extending from inner margin nearly to radius, the two components separated by white sub-costal scaling; median fascia composed of mark at mid-cost and bar along proximal margin of the ocellus from inner margin to distal end of cell; ocellus inconspicuous, bordered proximally and distally by white to pale gray lustrous bars and surmounted by patch of pale gray scales; central field of ocellus white with two or three blackish-brown dashes; costal strigulae delimited by prominent brown marks; termen with blackish line from approximately CuA2 to apex but interrupted by two white terminal strigulae (on R5 and M2); terminal strigulae joined by narrow white bar proximal to dark terminal line; fringe scales white from tornus to R5, blackish gray at apex. *Hindwing:* Grayish brown, paler toward base. *Male genitalia* (Fig. 26) ($n = 3$): Uncus well developed, with rounded apex; dorsolateral shoulders of tegumen weakly hunched; socii finger-like; vesica with 9–10 deciduous cornuti; valva with costal margin concave, apex semitriangular, distal margin convex, anal angle weakly developed and broadly rounded, ventral emargination of neck shallow, sacular angle obtuse. *Female genitalia:* Unknown.

Holotype. ♂: California, Los Angeles Co., Hungry Valley, 4 air miles S. Gorman, J. A. Powell, 16 July 1975, genitalia slide DJW 1159, EME.

Paratypes. ARIZONA: Coconino Co., Hochderffer Hill, 12.5 mi. NNW Flagstaff, 8500 ft., J. G. Franclemont, 17 July 1964 (1 ♂, genitalia slide DJW 1062). CALIFORNIA: Ventura Co., Ozena Forestry Camp, upper Cuyana, C. W. Kirkwood, 18 July 1986 (1 ♂, genitalia slide JAP 2476). Depositories: EME, USNM.

Etymology. The specific name comes from the Latin *candidus*, meaning shining white.

Distribution and biology. The three known specimens, captured in mid-July, are from southern California and north central Arizona (Fig. 47).

Eucosma johnstoni, new species

(Figs. 11, 12, 27, 41, 42, 47)

Diagnosis. *Eucosma johnstoni* is distinguished by the following combination of characters: relatively small size (mean FWL \approx 7.6 mm), irregular brownish-yellow streaking on an otherwise whitish forewing (Figs. 11, 12), and genitalic structure (Figs. 27, 41, 42). It is similar to *Eucosma morrisoni* (Walsingham) in forewing appearance (Gilligan et al. 2008:103) and to *Eucosma serpentana* (Walsingham) in maculation, but these two species are larger (mean FWL \approx 8.6 mm and 8.4 mm, respectively), and *E. serpentana* has gray-brown to

blackish-brown markings with no yellowish coloration. The genitalia of *E. johnstoni* are easily distinguished from those of *E. morrisoni* (Figs. 27 & 42 vs. Gilligan et al. 2008: 215 & 268), the latter having the structure typical of the *Eucosma agricolana* (Walsingham) species group. The male genitalia of *E. johnstoni* and *E. serpentana* (Fig. 27 vs. Heinrich 1923, Fig. 207) differ in cucullus shape (apex and anal angle more rounded in *E. johnstoni*), in neck length (shorter in *E. johnstoni*), and in the presence in *E. serpentana* of ca. 6 stout setae along the distal margin of the cucullus (absent in *E. johnstoni*). The female genitalia of *E. johnstoni* have an unusually simple lamella postvaginalis (Fig. 42), a flat rectangular plate with weakly curled lateral margins.

Description. *Head:* Frons and vertex white; labial palpus white with brownish-gray shading on lateral surface of second segment and with long brownish-gray scales on second segment concealing third segment; antenna white, scape with pale brown dot on medial surface. *Thorax:* Dorsal surface white, variably suffused with brownish yellow; ventral surface white; legs white, shading to gray brown on anterior surfaces; tarsi darker with white annulations. *Forewing* (Figs. 11, 12): ♂ FWL 6.4–8.7 mm (mean = 7.7, n = 16), AR = 3.37; ♀ FWL 6.4–8.3 mm (mean = 7.3, n = 7); costa nearly straight; apex acute; termen weakly convex; dorsal surface white with brownish-yellow markings, including: a longitudinal streak extending along cubitus from base to CuA2, slanting from there to apex, and often overlaid with brownish-gray dash from mid-wing to ocellus; a streak arising at distal end of costal fold and merging with cubital streak anterior to ocellus; a narrow band along termen from tornus to apex; some irregular suffusion along inner margin; and narrow oblique dashes associated with strigulae on distal one-half of costa; ocellus inconspicuous, with a few black scales on a pale brownish-yellow central field and with barely distinguishable lustrous white bars at proximal and distal margins; some fringe scales white, others white with pale blackish-gray cross-markings, the markings roughly aligning to form two grayish lines parallel to termen. *Hindwing:* Grayish brown. *Male genitalia* (Fig. 27) (n = 6): Uncus semitriangular, with basal width ≈ 2 × height and apex narrowly rounded; dorsolateral shoulders of tegumen weakly hunched; socii long and finger-like; vesica lacking cornuti; valva with costal margin concave, apex evenly rounded, distal margin convex of nearly uniform curvature, anal angle weakly developed and broadly rounded, ventral emargination of neck shallow to moderate, saccular angle obtuse. *Female genitalia* (Figs. 41, 42): Papillae anales laterally facing and densely setose, lamella postvaginalis a semirectangular plate with lateral margins curled inward, lacking microspinulae, but with a few hair-like setae flanking medial section; lamella antevaginalis ring-like and very weakly sclerotized; posterior margin of sternum 7 weakly concave and separated from sterigma by narrow strip of membrane; ductus bursae with sclerotized ring anterior to juncture with ductus seminalis; corpus bursae with two small cone-like signa, one distinctly larger than the other.

Holotype (Fig. 11). ♂: Arizona, Mojave Co., 3 mi. S.E. Kingman, P. Opler & J. Powell, 3 June 1968, genitalia slide JAP 3656, EME.

Paratypes. ARIZONA: same data as holotype (8 ♂, genitalia slides DJW 1167, 2421; 5 ♀, genitalia slides JAP 3657, DJW 1169, 2419); Mojave Co., Hualapai Mtn., P. Opler & J. Powell, 2 June 1968 (1 ♂). CALIFORNIA: Orange Co., 7 mi N.E. El Toro, P. A. Opler, 8 June 1968 (3 ♂, genitalia slide JAP 2421). NEW MEXICO: Hidalgo Co., Lordsburg, E. C. Johnston, 9 May 1950 (2 ♂, genitalia slides DJW 2130, 2420; 2 ♀, genitalia slides DJW 2131, 2418). TEXAS: Brewster Co., Alpine, E. C. Johnston, 22 May 1950 (1 ♂). Depositories: CNC, CSU, DJW, EME, USNM.

Etymology. This species is named after E. C. Johnston, whose specimens from New Mexico and

Texas in 1950 appear to be the earliest records of this moth.

Distribution and biology. The 23 examined specimens (16 ♂, 7 ♀) document a range extending from Orange County in southern California to the vicinity of Big Bend National Park in west Texas (Fig. 47). Capture dates range from 9 May to 3 June.

Eucosma rufocostana, new species

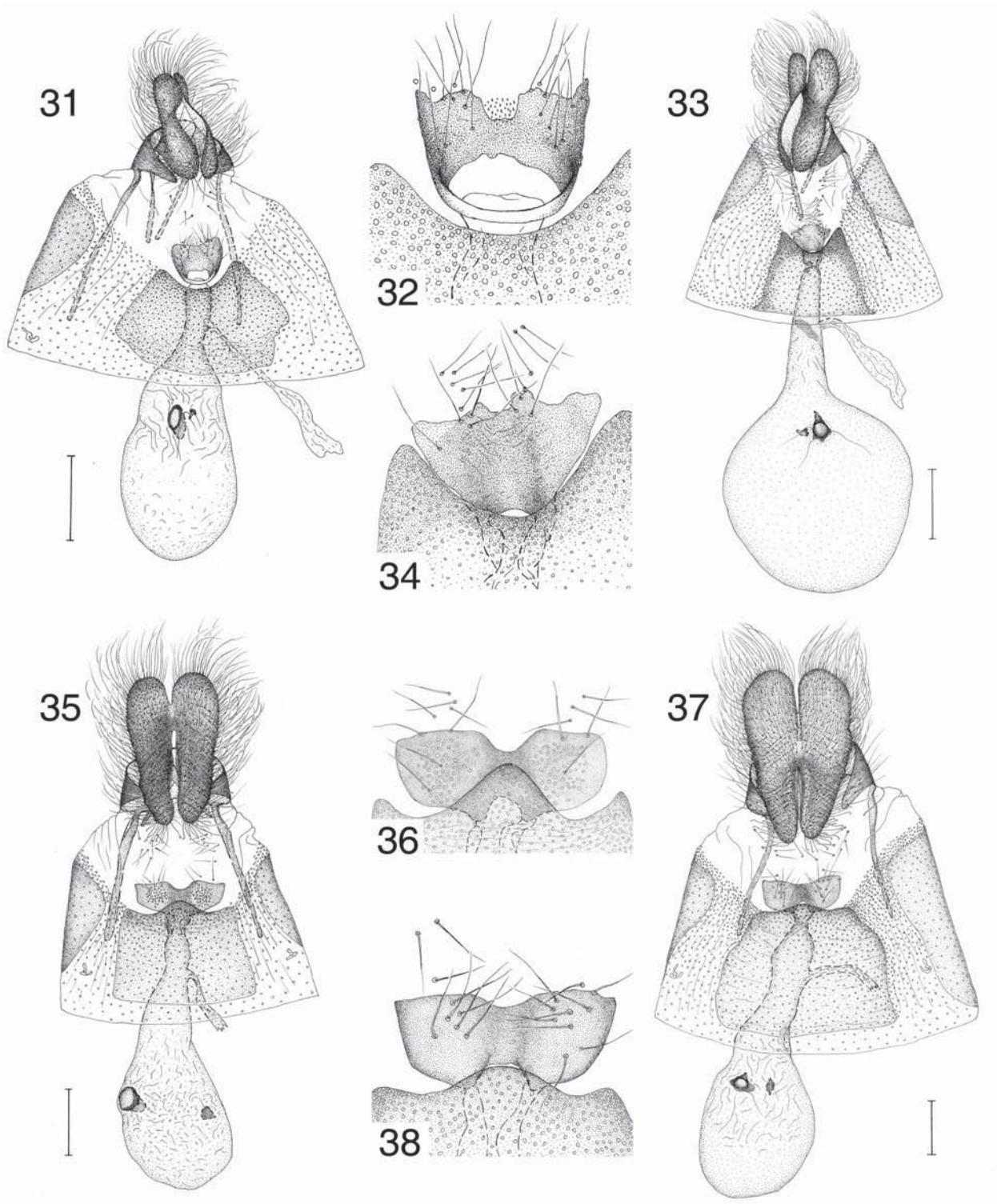
(Figs. 16, 20, 28, 48)

Diagnosis. *Eucosma rufocostana* is similar in forewing color and maculation to *E. conspiciendana* and *E. cataclystiana* (both reviewed below), but is larger (mean FWL = 10.6 vs. 8.4 and 8.0 mm, respectively) and has different male genitalia (Fig. 28 vs. 29 and 30). The conspicuous reddish-brown streak on the costal margin is usually sufficient to separate *E. rufocostana* from *E. conspiciendana* and *E. cataclystiana*.

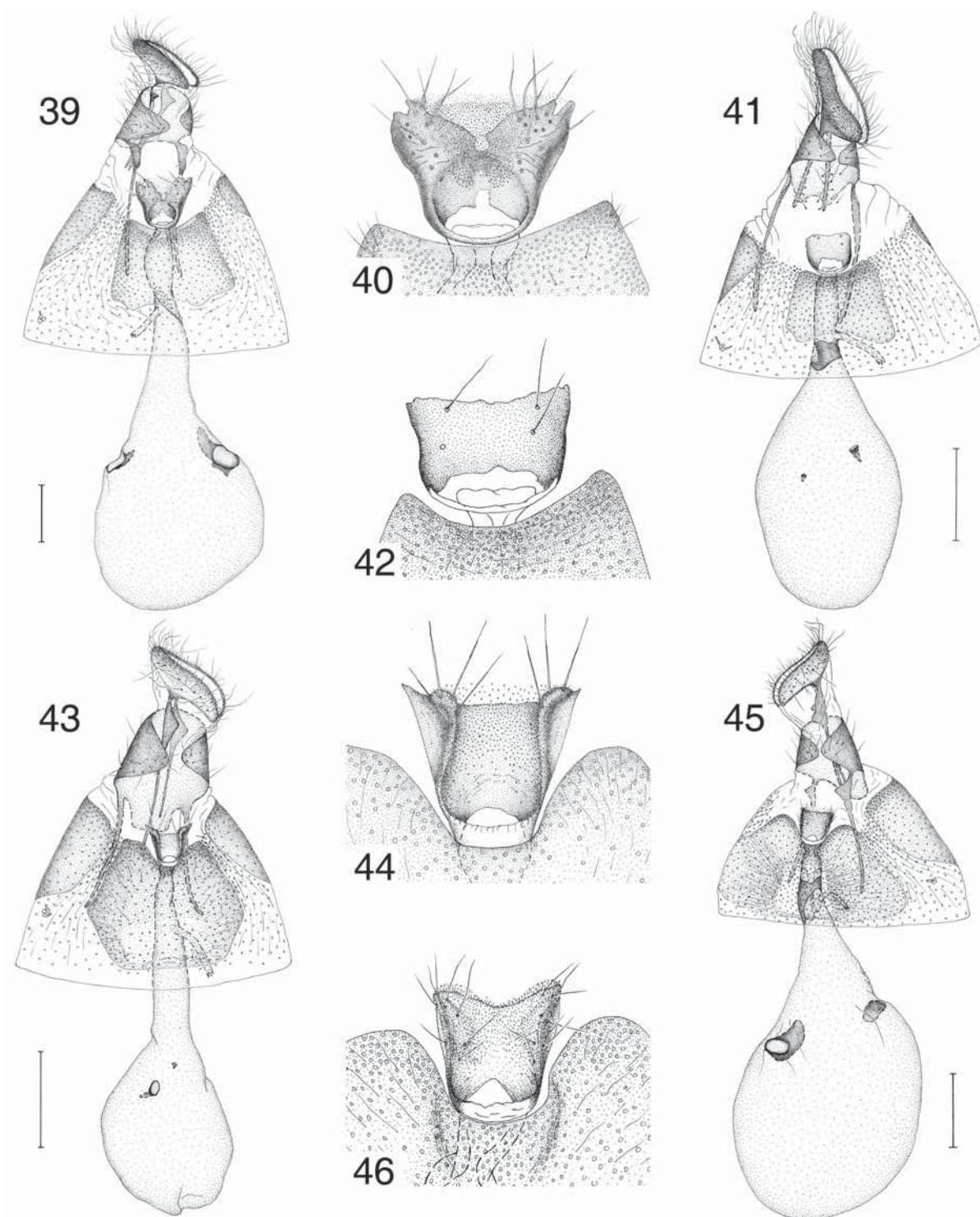
Description. *Head:* Lower frons creamy white; upper frons and vertex pale reddish brown; labial palpus reddish brown, shading to creamy white on medial surface and dorsal edge; antenna concolorous with vertex. *Thorax:* Dorsal surface pale brownish yellow; ventral surface creamy white; legs with anterior surfaces reddish brown, posterior surfaces creamy white; tarsi lacking pale annulations. *Forewing* (Fig. 16, 20): ♂ FWL 9.2–11.8 mm (mean = 10.6, n = 19), AR = 3.07; costa weakly convex; apex acute; termen straight; dorsal surface pale brownish yellow at base, shading to pale reddish brown on distal one-half of wing; costal margin reddish brown; basal and subbasal fasciae not expressed; median fascia represented by reddish-brown shade from mid-costa to proximal margin of ocellus; distal one-half of wing with whitish lines emanating from costal strigulae, separating apical portion of wing into pale reddish-brown oblique bands, the margins of which are sparsely dotted with black and/or silver scales; scales along termen white with black cross-markings, the cross-markings aligning to produce a thin black line preceded proximally by a white terminal line; fringe scales pale brownish yellow with reddish-brown tints. *Hindwing:* Pale grayish brown. *Male genitalia* (Fig. 28) (n = 8): Uncus broad, with apical margin straight to semitriangular and often weakly indented medially; dorsolateral shoulders of tegumen well differentiated; socii broad, with rounded apices; vesica lacking cornuti; valva with costal margin weakly concave, apex rounded, distal margin convex, anal angle rounded; cucullus with basoventral margin weakly overlapping ventral margin of neck and with medial surface densely covered with fine setae; neck wide and weakly differentiated from basal portion of valva; medial surface of valva with broad lobe projecting basally from distal margin of basal excavation. *Female genitalia:* Unknown.

Holotype (Fig. 16). ♂: Idaho, Oneida Co., Curlew National Grassland, 5 mi SSE of Holbrook, 4800 ft., 42° 06.234' N, 112° 36.958' W, D. J. Wright, 18 July 2001, USNM.

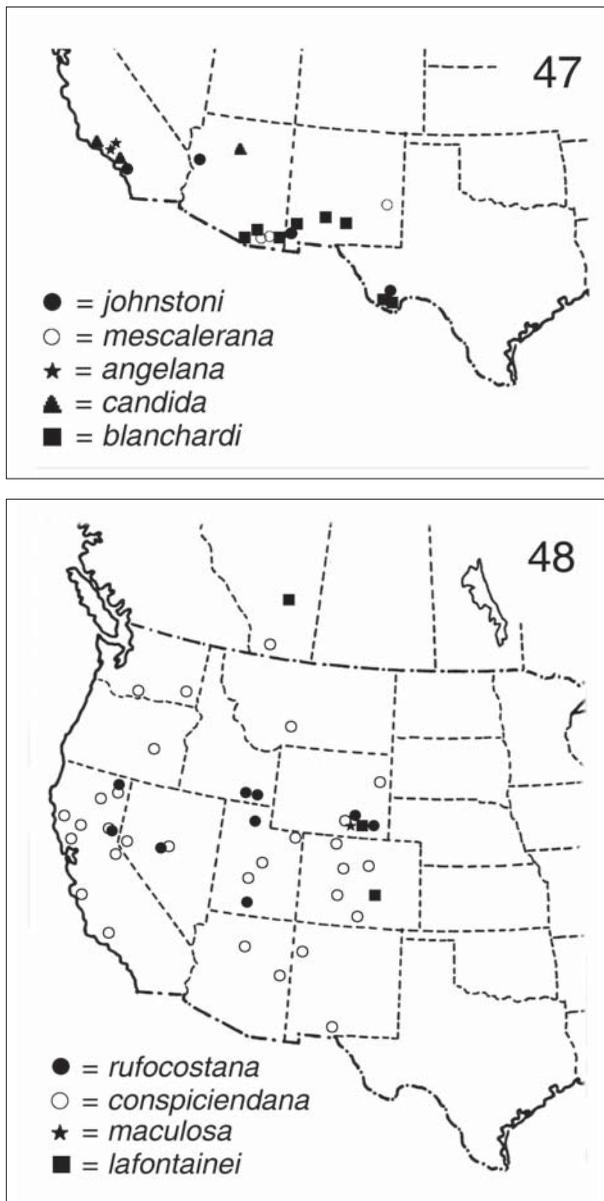
Paratypes. CALIFORNIA: Modoc Co., 8 mi S. Eagleville, J. A. Powell, 23 July 1968 (1 ♂, genitalia slide JAP 2490); Surprise Valley, 6 mi. E. Cedarville, 4500 ft., L. L. Crabtree, 30 June 2007 (1 ♂); Plumas Co., 2 mi SE Beckwourth, Sierra Valley, 4870 ft., L. L. Crabtree, 4 July 2010 (1 ♂). IDAHO: same data as holotype (1 ♂, genitalia slide DJW 2203); Oneida Co., Malad City, D. J. Wright, 18 July 2001 (1 ♂, genitalia slide DJW 758). NEVADA: Nye Co., 24 mi N Carvers, St. Hwy. 376, 5500 ft., L. L. Crabtree, 31 May 2002 (1 ♂), 3 July 2002 (1 ♂, genitalia slide DJW 2622). UTAH: Garfield Co., 3 mi. W. Bryce Jctn., 7552 ft., J. A. Powell, 28/29 June 1992 (5 ♂, genitalia slides EME 5718, DJW 2412); [Weber Co.], Ogden, G. F. Knowlton & L. E. Fronk, 28 July 1959 (1 ♂, genitalia slide EME 5719). WYOMING: Albany Co., T15N R73W S1, 2217 Sky View



FIGS. 31-38. Female genitalia. 31-32, *E. blanchardi*, slides DJW 2406, 2408. 33-34, *E. mescalerana*, slides DJW 1934, 1153. 35-36, *E. maculosa*, slides DJW 1874, 1666. 37-38, *E. lafontainei*, slides DJW 1899, 1930. Scale bar = 0.5 mm.



FIGS. 39-46. Female genitalia. 39-40, *E. angelana*, slides DJW 2056, 1313. 41-42, *E. johnstoni*, slides DJW 2419, 1169. 43-44, *E. conspiciendana*, slide DJW 2414. 45-46, *E. cataclystiana*, slides DJW 2555, 2556. Scale bar = 0.5 mm.



FIGS. 47–48. Geographic distribution of species.

Lane, J. S. Nordin, 28 July 2002 (1 ♂); NE of Pole Mtn, SE of Happy Jack Rd., J. S. Nordin, 2 July 2003 (1 ♂); W. side Gelatt Lake, 7250 ft., J. S. Nordin, 19 June 2006 (1 ♂, genitalia slide DJW 2204), 12 July 2004 (1 ♂), 15 July 2005 (1 ♂). Depositories: BMNH, DJW, EME, LLC, USNM.

Etymology. The specific name refers to the distinctive reddish-brown streak along the costal margin of the forewing.

Distribution and biology. I examined 19 male specimens collected at elevations between 4500 ft. and 8300 ft. in northeastern California, southern Idaho, central Nevada, Utah, and southeastern Wyoming (Fig. 48). They document a flight period extending from mid-June through July.

Eucosma conspiciendana Heinrich

(Figs. 13–15, 29, 43, 44, 48)

Eucosma conspiciendana Heinrich 1923:135, fig. 157; McDunnough 1939:48; Powell 1983:35; Brown 2005:318.

Discussion. *Eucosma conspiciendana* is similar in forewing appearance to *Eucosma cataclystiana* (Walker) (Figs. 13–15 vs. 17–19) but lacks the concave indentation of the termen typical of the latter species. The two taxa are easily separated by genitalia (Figs. 29, 43, 44 vs. 30, 45, 46); valval differences include cucullus size, neck length, and presence/absence of a nipple-like projection at the saccular corner; females differ in sterigma structure (Figs. 44, 46) and the presence/absence of a sclerotized band on the ductus bursae (Figs. 43, 45).

Description. *Head:* Lower frons creamy white; upper frons and vertex yellow gray to bright reddish brown; labial palpus with medial surface creamy white, lateral surface yellow gray to pale reddish brown; antenna concolorous with vertex. *Thorax:* Dorsal surface yellow gray, usually with reddish-brown tints; ventral surface whitish; fore- and mid-legs with anterior surfaces blackish gray to reddish brown, posterior surfaces whitish; hind-legs paler; tarsi with pale annulations. *Forewing* (Figs. 13–15): ♂ FWL 7.1–10.0 mm (mean = 8.7, n = 45), AR = 3.10; ♀ FWL 6.0–8.1 (mean = 7.3, n = 13), AR = 2.92; costal margin weakly convex; apex acute; termen nearly straight; dorsal surface yellowish gray to bright reddish brown; basal and subbasal fasciae not expressed; median fascia represented by indistinct dark shade extending obliquely from mid-costa to proximal margin of ocellus; distal one-half of wing with thin outwardly oblique white lines arising at costal strigulae and terminating on inner margin, anterior edge of ocellus and termen, the lines thinly and variably edged with silvery gray; ocellus inconspicuous, edged proximally and distally with white and a few lustrous gray scales; central field of ocellus pale reddish brown to yellowish gray, crossed by up to three black dashes; scales along termen whitish, with black cross-bars that form a thin line from tornus to apex; fringe concolorous with wing. *Hindwing:* Gray brown. *Male genitalia* (Fig. 29) (n = 14): Uncus a tapering lobe with rounded apex; dorsolateral shoulders of tegumen moderately developed and somewhat slouched; socii pendulous, broad medially, with rounded apices; vesica with 0–8 deciduous cornuti; valva with costal margin concavely curved at neck, apex broadly rounded, distal margin straight to weakly convex, anal angle acute and weakly developed, neck short and wide, sacculus long, saccular angle obtuse; medial surface of valva with rectangular lobe projecting basally from margin of basal excavation and with numerous fine setae distributed from sacculus and ventral margin of neck to three-fourths distance to costal margin; cucullus with basoventral margin weakly overlapping ventral margin of neck and medial surface densely covered with fine setae. *Female genitalia* (Figs. 43, 44) (n = 4): Papillae anales laterally facing and sparsely setose; lamella postvaginalis widening posteriorly (length ≈ medial width), with raised microspinulate ridges flanking medial trough and flaring at posterior margin toward posterolateral corners; lamella antevaginalis ring-like and very weakly sclerotized; sternum 7 with posterior margin incurved to two-thirds length of sterigma and with medial section very weakly sclerotized; ductus bursae entirely membranous; corpus bursae with moderately large signum on ventral surface and minute signum on dorsal surface.

Types. **Holotype:** ♂, Utah, [Tooele Co.], Stockton, T. Spalding, 4 July 1904, AMNH [not examined; genitalia illustrated by Heinrich (1923, fig. 157)]. **Paratypes.** CALIFORNIA: San Bernardino Co., Loma Linda (1 ♂), USNM; MONTANA: [Lake Co.], St. Ignatius (1 ♂), AMNH; UTAH: same as holotype except date, 29 June 1904 (1 ♀) [Heinrich (1923) misreported the date as VI-27-4], USNM; [Juab Co.], Eureka, T. Spalding, 31 May 1910 (1 ♂), USNM.

Distribution and biology. I examined 95 specimens (72 ♂, 23 ♀), documenting a range extending from the eastern slope of the Rocky Mountains to the west coast and from southern Alberta to the Mexican border (Fig. 48). Adults fly primarily in June and July.

Eucosma cataclystiana (Walker)
(Figs. 17–19, 30, 45, 46)

Paedisca cataclystiana Walker 1863: 378; Walsingham 1879: 46.

Eucosma cataclystiana: Fernald [1903]: 456; Barnes and McDunnough 1917: 169; Heinrich 1923: 135, fig. 156; McDunnough 1939: 48; Powell 1983: 35; Miller 1987:54; Brown 2005: 317; Gilligan et al. 2008:115.

Discussion. Walker described *E. cataclystiana* from two females. One was dissected in 1965, probably by W. G. Tremewan, and is labeled lectotype, but it seems the designation was not published. Brown (2005) cited this specimen as a holotype. For stability of nomenclature, the lectotype designation is given below. Walsingham (1879) redescribed the species, noting that he had encountered it in California. I examined seven specimens so determined by Walsingham, six of which proved to be *E. conspiciendana*, one *E. comatulana* (Zeller). So far as I know there are no valid records of *E. cataclystiana* from west of the Rocky Mountains. *Steganoptycha ochreana* Clemens, described from Virginia in 1864, was treated as a synonym of *E. cataclystiana* by Walsingham (1879), Barnes & McDunnough (1917), Heinrich (1923), McDunnough (1939), and Miller (1973), but Miller (1974) pointed out that it belongs in the synonymy under *Eucosma agricolana argentialbana* (Walsingham). All that remains of the lectotype are the right wings, which are pictured in Miller (1973, Fig. 31).

Description. *Head:* Frons creamy white to tan; vertex yellowish brown to reddish brown, with scales between antennae darker; antenna brown to blackish brown dorsally, tan ventrally. *Thorax:* Dorsal surface reddish brown to yellowish brown; ventral surface whitish; fore- and mid-legs with brown anterior surfaces, whitish posterior surfaces, and whitish tarsal annulations; hind-legs whitish, with darker tarsomeres and whitish tarsal annulations. *Forewing* (Figs. 17–19): ♂ FWL 6.6–9.2 mm (mean = 8.0, n = 27), AR = 3.03; ♀ FWL 6.6–8.9 mm (mean = 7.9, n = 9), AR = 3.03; costa weakly convex; apex acute; termen concave from apex to M3; dorsal surface pale yellowish tan with reddish-brown markings, including an irregularly defined streak along cubitus from base to ocellus and a median fascia weakly expressed as a narrow shade from mid-costa to ocellus; ocellus bordered proximally, distally, and posteriorly by lustrous gray scaling, the distal component usually reduced; central field of ocellus tan, crossed by two longitudinal brown streaks, the latter marked at proximal extremities and occasionally at distal extremities by black dots; ocellus capped anteriorly by patch of dark scales with pale apices; costal strigulae conspicuous from mid-costa to apex and usually accompanied by lustrous gray striae; termen with band from tornus to apex consisting of white scales with dark cross-markings; outer fringe scales yellowish brown to pale reddish brown. *Hindwing:* Brownish gray. *Male genitalia* (Fig. 30) (n = 9): Uncus semitriangular with rounded apex; dorsolateral shoulders of tegumen well developed; socii

finger-like, tapering toward apex; vesica with 9–12 deciduous cornuti (n = 5); valva with costal margin concavely curved at neck, apex rounded, distal margin nearly straight, anal angle acute, neck narrowing from saccular corner to cucullus, saccular corner with nipple-like projection; valva with broad basally-directed projection on margin of basal excavation; medial surface of neck densely setose; cucullus with basoventral margin overlapping neck, medial surface densely setose, and several spiniform setae at anal angle and along basoventral margin. *Female genitalia* (Figs. 45, 46) (n = 4): As in *E. conspiciendana* except: the ridges flanking the shallow central trough of the lamella postvaginalis are greatly reduced, the ductus bursae has a sclerotized patch posterior to the juncture with the ductus seminalis, and the two signa do not differ as much in size.

Type. Lectotype here designated: ♀, North America, genitalia slide 11531, BMNH. Paralectotype: ♀, same data, abdomen missing, BMNH.

Distribution and biology. *Eucosma cataclystiana* occurs throughout eastern North America, from southern Canada to the Gulf Coast. Its range extends as far west as the Rocky Mountains, where it is sympatric with *E. conspiciendana*. Capture dates range from late April to the end of September. *Euthamia graminifolia* (Linnaeus) Nutt. (flat-top goldenrod) was reported by Putman (1942) as a host in Ontario, Canada, the larva boring in the lower stem and rhizomes.

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COMPLEX MTDNA VARIATION AND SPECIES DELIMITATIONS IN THE *PHYCIODES THAROS* SPECIES GROUP (NYMPHALIDAE: MELITAEINI): A SECOND LOOK IN MICHIGAN AND OHIO

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ABSTRACT. The number and delimitation of species in the *Phyciodes tharos* species complex has puzzled lepidopterists for years. Previous analysis of mtDNA sequence data has suggested that *P. cocyta* is more closely related to *P. cocyta* than to *P. tharos*, in contrast to inferences from morphology and ecology. We sequenced the mitochondrial gene cytochrome oxidase I for 40 individuals of *Phyciodes tharos*, *P. cocyta*, and *P. cocyta* from Michigan and Ohio, a region at the boundaries of the geographic ranges of these species. Network and cladistic analyses reveal shared mtDNA lineages, indicating that limited hybridization occurs in this region between *P. cocyta* and the other two taxa but not between *P. tharos* and *P. cocyta*. Our evidence also supports the traditional phylogenetic assessment of *P. tharos* and *P. cocyta* as the two most closely related species in this species group. Data from nuclear genes are needed to more fully resolve this intriguing group of butterflies.

Additional key words: split network, Neighbor-Net, SplitsTree4, maximum-likelihood, introgression

Papilionoidea, the true butterflies, are no doubt the group of invertebrates most well-known to science—thousands of studies over hundreds of years having been published, especially on their ecology and evolution (Boggs et al. 2003). The taxonomy of butterflies is especially well known, with most of the worldwide taxa already described—a huge feat considering the size of the group (Ackery et al. 1999). Yet there still remain many groups of butterflies for which species boundaries remain unclear. The genus *Phyciodes*, comprised of ten currently recognized species (Pelham 2008) with mainly Nearctic distributions, is one such group.

Within *Phyciodes*, the *P. tharos* species group (*P. tharos*, *P. cocyta*, *P. cocyta*, and *P. pulchella*) has been especially interesting due to the species' phenotypic similarity, variability in diagnostic characters, and (with the exception of *P. cocyta* and *P. cocyta*) largely parapatric ranges with broad swathes of sympatry (Fig. 1) (Scott 1994). *Phyciodes tharos* and *P. cocyta* are of particular interest, having long been considered conspecifics. Oliver (1980), however, based on extensive breeding experiments that revealed a degree of hybrid breakdown between various populations of *Phyciodes tharos*, distinguished two entities which he called *tharos* Type A and *tharos* Type B. Scott (1994) assigned the name “*cocyta*” to Oliver's “*tharos* Type B” and raised it to full species status based on a few morphological characters and sympatry with *P. tharos* in some areas, despite incomplete reproductive

isolation in other areas. *Phyciodes batesii* and *P. pulchella* are more easily diagnosable, although extensive hybridization between *P. cocyta* and *P. cocyta* has also been observed in Colorado and Utah (Scott 1994, 1998). Recent authors have largely followed the lead of Scott (1994) in recognizing four distinct species in the *P. tharos* group, although agreement is by no means universal, especially as to whether *P. cocyta* should not be a subspecies of *P. tharos* (e.g. Glassberg 1999).

The advent of molecular analysis of DNA has been a great boon to butterfly systematics, augmenting knowledge of morphology and life histories (Sperling 2003). Wahlberg et al. (2003) conducted the first phylogenetic analysis of *Phyciodes* using DNA, with a parsimony analysis of 1450 base pairs of the mitochondrial gene cytochrome oxidase I (COI) from 140 *Phyciodes* specimens representing all ten species from across North American and Mexico. Wahlberg et al. (2003) attempted to sample specimens widely in order to capture as much geographic variation as possible. They found that the *tharos* species group formed a well-supported monophyletic clade (with the exception of two specimens). Within the clade they found that *P. tharos* was the most basal of the four species, which confirmed the suggestion of Scott (1994) based on genital and pupal characters. Surprisingly, though, they found that the haplotypes of *P. cocyta* and *P. cocyta* were interdigitated, grouping together to form several clades paraphyletic with respect to *P. pulchella*.

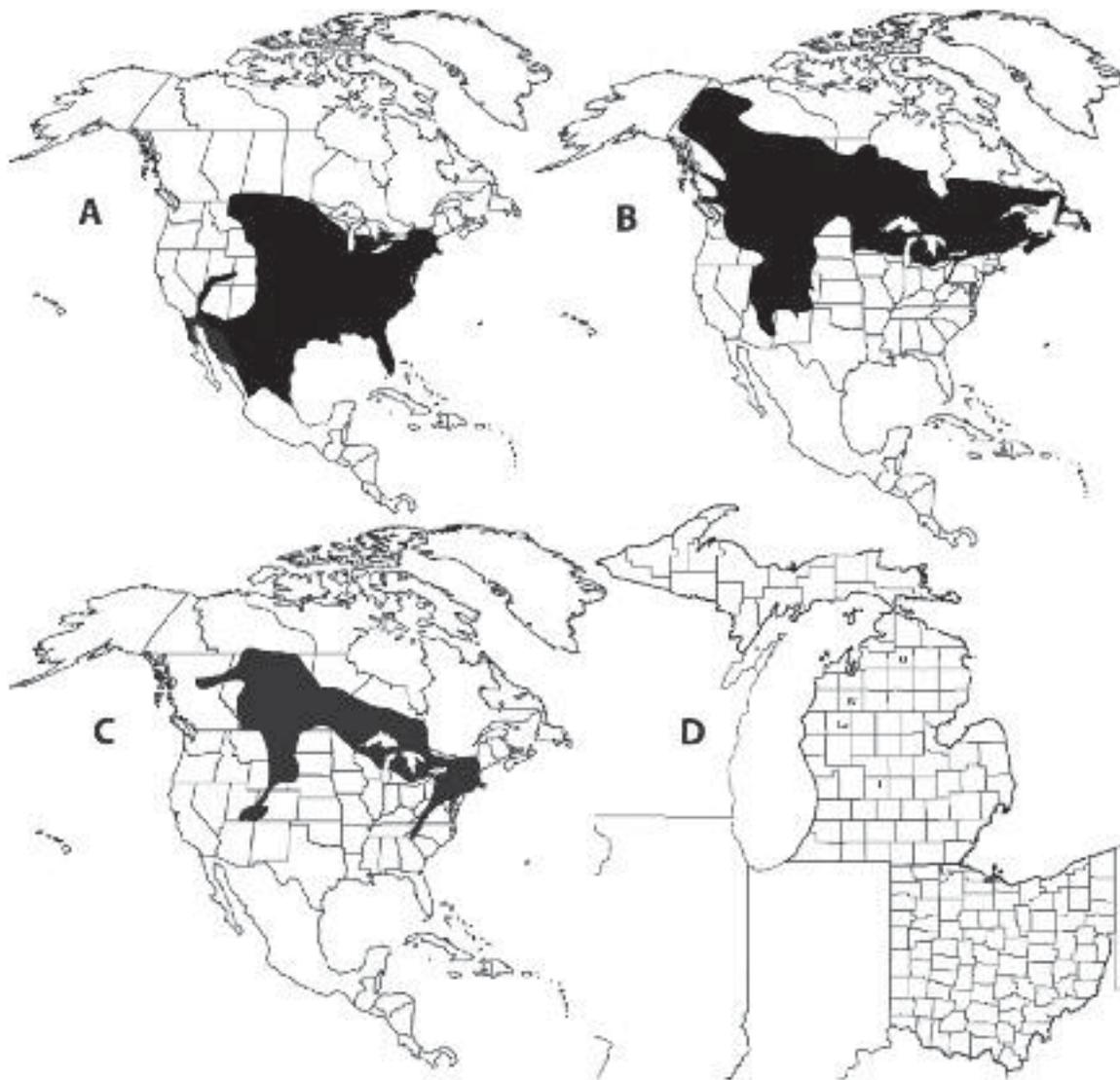


FIG. 1. Range maps of the three species in the *Phyciodes tharos* complex focused on in this study (A-C), and a map of Michigan and Ohio showing the location of the novel specimens collected for this study (D). **A:** *P. tharos*. **B:** *P. cocyta*. **C:** *P. batesii*. The range maps are modified from Opler et al. (2009) and Brock & Kaufman (2003). **D:** Letters indicate approximate locations within counties where specimens were collected for this study. O = Otsego Co.; W = Wexford Co.; La = Lake Co.; I = Ionia Co.; Lu = Lucas Co.

The inference that *P. cocyta* is most closely related to *P. cocyta* and sister group to *P. pulchella* contradicts the morphological and ecological evidence that *P. cocyta* is most closely related to *P. tharos*.

In this paper we re-investigate the relationships between *P. tharos*, *P. cocyta*, and *P. cocyta*. In contrast to Wahlberg et al. (2003), our approach was to sample *P. tharos*, *P. cocyta* and *P. cocyta* from a relatively small geographic area: the lower peninsula of Michigan and northwest Ohio, where the ranges of all three species coincide (Fig 1). This is a region not sampled by Wahlberg et al. (2003); their closest specimens to our study area were collected from Carleton Co., Ontario.

Since there is known to be incomplete reproductive isolation between these three species (Scott 1994), this area is a particularly interesting region to investigate the question of which species is most closely related to *P. cocyta*, and to see whether evidence of gene flow between species can be observed.

MATERIALS AND METHODS

Sampling and molecular techniques. Specimens of *Phyciodes* were collected between 06 June and 19 June 2006 throughout the northern part of the lower peninsula of Michigan. Since only *P. cocyta* and *P. cocyta* were found in Michigan, *P. tharos* was collected

in Ohio on 29 and 30 June 2006. All specimens were spread while fresh and are now stored at the Hillsdale College Insect Collection, Hillsdale, Michigan. Approximate collection localities are displayed in Fig 1; complete collection data are presented in Appendix 1. Identification to species level was made after examination of the color of the antennal clubs, the extent and pattern of reticulation and dark pigmentation on the dorsal wing surfaces, extent of dark coloration on the hindwings below, and overall size (Nielsen 1999; Scott 1986). In our estimation, none of the specimens from which reliable sequence data was extracted had a doubtful identification based on these characters.

Two legs were removed from each fresh specimen for DNA extraction, either immediately after capture or after several months storage in ethanol in refrigeration. Genomic DNA was extracted from the two legs of each specimen using the Qiagen DNeasy extraction kit. Two primer pairs were used to amplify 1450 base pairs of the COI gene: LCO1490-J-1514 (5'GGTCAACAAATCATAAAGATATTGG) and HCO2198-N-2175 (5'TAACTTCAGGGTGACCAAAAATCA) (Folmer et al. 1994), and C1-J-2183 (5'CAACAYTTATTTTGATTTTTTGG) and TL2-N-3014 (5'ATCCATTACATATAATCTGCCATA) (Simon et al. 1994). These primers were chosen based on their previous successful amplification in *Phyciodes* (Wahlberg et al. 2003). All COI fragments were amplified with standard polymerase chain reaction (PCR) techniques. PCR products were monitored for yield, specificity, and contamination using agarose gel electrophoresis and cleaned with ExoSAP-IT. PCR fragments were sequenced with a dye terminator cycle sequencing kit and an Applied Biosystems 3130 Genetic Analyzer. Only one strand of each fragment was sequenced, using the forward primer. Sequence quality was assessed by the Applied Biosystems software Sequencing Analysis 5.2 and by visual inspection of the chromatograms. Areas of poor sequence quality, such as the center of the COI gene where the fragments of the two sequencing runs overlapped, were trimmed. Sequences of entirely poor quality were discarded. Forty sequences of 1319 nucleotide characters were ultimately retained.

Data analyses. Seventy-eight COI sequences of *Phyciodes tharos*, *P. cocyta*, *P. cocyta*, *P. pulchella*, and *P. phaon* from Wahlberg et al. (2003 (accession nos. AF187747, AF187785, AF187789, AF187798, AF187800, AF187783, AF187807, AY156595-AY156686), were downloaded from GenBank. Those, together with our 40 novel sequences, were aligned in

Mesquite v. 2.6 (Maddison & Maddison 2009) using Clustal W v. 2.0.9 (Larkin et al. 2007) with default settings. Alignments were manually adjusted using the Align package in Mesquite (Maddison et al. 2007).

Our 40 novel sequences were opened with SplitsTree4 v. 4.10 (Huson & Bryant 2006) and a split network generated with Kimura-2 parameter (K2P) distance according to the Neighbor-Net method (Bryant & Moulton 2004); all other settings were set to default. Robustness of the splits was assessed with 1000 bootstrap repetitions.

In order to compare directly our data with Wahlberg et al. (2003), a phylogenetic tree was generated using the maximum-likelihood method implemented in Garli 1.0 (Zwickl 2006). We used the HKY+I+G model of evolution, which was selected by ModelTest 3.7 (Posada & Crandall 1998) as the most likely to fit our data according to the AIC criterion. During the analysis, Garli was allowed to estimate rate parameters, base frequencies, and proportion of invariable sites. Fifteen search replicates were performed to find the best tree of score -4897.3347. Two hundred bootstrap replicates were performed in order to estimate branch support. The tree was rooted with the three *P. phaon* sequences and two aberrant *P. pulchella* sequences (47-6 CA3 and 49-13 CA3).

RESULTS

Network analysis. Our 40 *Phyciodes* sequences are represented by a split network in Fig. 2. A split network can be thought of as a generalized combination of many phylogenetic trees; in fact, phylogenetic trees are a sub-category within split networks. With any data set, such as DNA sequences, any given character can be used to split a set of taxa into separate groups. For example, in this matrix

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w AACGTG
x ACCTGG
y TACGTG
z TACTTG
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the first column splits [w,x] from [y,z], the second column splits [x] from [w,y,z], the third column does not split any taxa, because it is constant, and the fourth column splits [w,y] from [x,z]. Any set of splits can be compatible or incompatible. A phylogenetic tree is a visual representation of a set of compatible splits; a split network can represent a set of splits whether compatible or incompatible. When all splits are compatible, they can each be represented graphically by a single branch: this is a phylogenetic tree. With most real data sets, however, this is not the case. Incompatible splits in a split network are represented

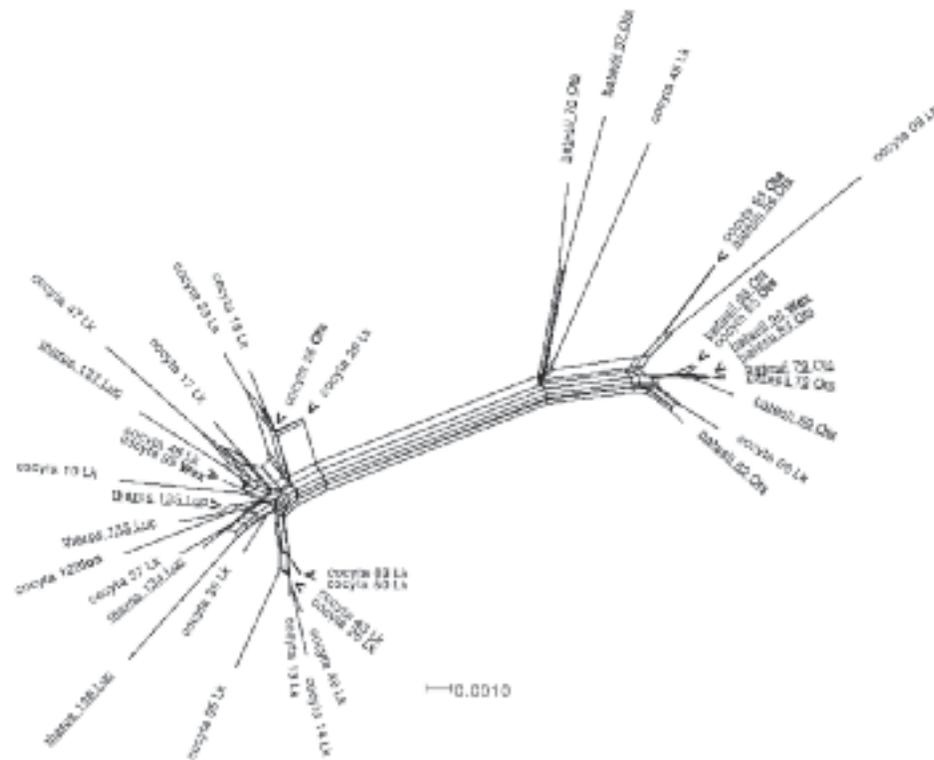


FIG. 2. A split network of 40 specimens of three species of Phyciodes, constructed by the Neighbor-Net method from 1319 base pairs of the cytochrome oxidase I gene. Each edge represents a split separating one or more taxa from the rest; multiple parallel edge indicate multiple incompatible splits. Length of edges corresponds to genetic distance according to the K2P model. Individuals of *P. tharos* and *P. batesii* are underlined. The specific epithet of the individual, a unique identifier, and the county of collection given at each terminal node. Lk = Lake Co.; Ots = Otsego Co.; Wex = Wexford Co.; Ion = Ionia Co.; Luc = Lucas Co. Bolded county abbreviations indicate either a specimen of *P. cocyta* not from Lake Co. or a specimen of *P. batesii* not from Otsego Co. Chevrons indicate either multiple specimens terminating at nodes too close to differentiate or a single specimen terminating with a branch too short to show.

by multiple parallel branches (Huson & Bryant, 2006). Hence a split network can incorporate a measure of uncertainty within a data set. The network in Fig. 2 was constructed by the Neighbor-Net method, in which the data matrix used to generate the split network is a matrix of the genetic distances between taxa.

The sequences in Fig. 2 separate into two clusters with a large relative distance between them, supported by 100% bootstrap support (not shown). All of the five *P. tharos* are in one cluster, all of the 10 *P. cocyta* are in the other, and the 25 *P. cocyta* are distributed among both (20 with the *P. tharos* grouping and five with the *P. cocyta* grouping). There is no one set of splits that encompasses one species exclusively. Of the five *P. cocyta* that group with the *P. cocyta*, two are two of the three *P. cocyta* from Otsego Co.—the location where

most of the *P. cocyta* in our study were collected, and the only place we sampled where *P. cocyta* was the most commonly encountered *Phyciodes* species. Four of the five *P. tharos* sequences are included in a group of six haplotypes separated from the rest by a single set of splits (Fig. 2). Of the two *P. cocyta* sequences that complete that group, one is the lone *P. cocyta* specimen from Ionia Co., by far the closest geographically to the location where the *P. tharos* specimens were collected (Fig. 1D).

Phylogenetic tree analysis. When we constructed a maximum-likelihood tree from our 40 novel sequences in addition to the 78 *Phyciodes* sequences from Wahlberg et al. (2003), the branching pattern and branch support closely resemble the parsimony tree found in Wahlberg et al. (2003) (Fig. 3). All the clades

TABLE 1. Number of haplotypes of three species of *Phyciodes* found in certain clades of the phylogenetic tree generated from the data of Wahlberg et al. (2003), the number of haplotypes of each species from our data added to those clades when our data was analyzed with that of Wahlberg et al. (2003), and the total number of haplotypes of each species in those clades (see Fig. 3).

	B "tharos" clade	C, D, E "cocyta/batesii" clades	F-H "pulchella" clades
Wahlberg et al. (2003)	15 <i>tharos</i> 2 <i>cocyta</i> 3 <i>batesii</i>	18 <i>cocyta</i> 8 <i>batesii</i> 1 <i>pulchella</i>	25 <i>pulchella</i> 1 <i>batesii</i>
Added	5 <i>tharos</i> 20 <i>cocyta</i>	5 <i>cocyta</i> 10 <i>batesii</i>	- -
	22 <i>cocyta</i>	23 <i>cocyta</i>	25 <i>pulchella</i>
Totals	20 <i>tharos</i> 3 <i>batesii</i>	18 <i>batesii</i> 1 <i>pulchella</i>	1 <i>batesii</i>

marked with capital letters by Wahlberg et al. (2003) as being important for discussion in their tree are also found in our tree, and with comparable branch supports. The phylogeny appears robust to the addition of new sequences and to the method of phylogenetic inference, parsimony or maximum likelihood. The topology of the tree can be summarized as three principal clades: a "tharos" clade (clade B), a "cocyta/batesii" clade (clades C, D, E), and a "pulchella" clade (clades F – H). All five of our novel *P. tharos* sequences and 20 of our 25 novel *P. cocyta* sequences clustered within the "tharos" clade; the remaining five *P. cocyta* sequences and all ten of our novel *P. cocyta* sequences clustered within the "cocyta/batesii" clade (Table 1).

DISCUSSION

Our results in Fig. 2 suggest that: 1. mitochondrial introgression may have taken place between *P. cocyta* and *P. cocyta* and between *P. cocyta* and *P. tharos*, and 2. that *P. cocyta* in our area of study is more closely related to *P. tharos* than to *P. cocyta*. The first inference is supported by the fact that none of the three species are separated into an exclusive cluster. It is also suggestive that of the two *P. cocyta* that cluster with the *P. tharos* sequences group A in Fig. 2, one is from Ionia Co., the closest location geographically to where all the *P. tharos* were collected. Similarly, two of the three *P. cocyta* collected from Otsego Co., where almost all of the *P. cocyta* were collected, cluster with the *P. cocyta* sequences despite three-quarters of the *P. cocyta* clustering at the *P. tharos* end of the figure. The second

inference is supported because 15 of the 20 *P. cocyta* sequences are far closer to the *P. tharos* sequences than to the *P. cocyta*. Moreover, when our data are added to that of Wahlberg et al. (2003) (Fig. 3), the same 15 *P. cocyta* sequences, as well as the five *P. tharos* sequences, come out in the "tharos" clade (clade B; Table 1). The *P. cocyta* from our study area are not only more similar to the *P. tharos* than the *P. cocyta* from our study area, but from all around the continent.

Species that are recently diverged and closely related are expected to sustain some gene flow (Coyne & Orr 2004). As long as they maintain genetic integrity across their range, this does not compromise their status as good species (Sperling 2003). Gene flow between recently diverged species is not unusual and has been documented in a wide variety of animal taxa (e.g. Nosil 2008; Friar 2007). The members of the *Phyciodes tharos* species complex are likely just such recently diverged species. They diverged on the basis of adaptation to different ecological pressures (Oliver 1980), and differences in flight periods in response to environmental conditions was likely a key factor in the speciation (Oliver 1980; Scott 1994). At the geographic boundary between species' ranges (especially of parapatric species, like *tharos* and *cocyta*) where ecological pressures are similar on both, hybridization is particularly likely.

Hybridization and mitochondrial introgression may best explain the pattern in our data (Fig. 2). Similar patterns, where mitochondrial lineages correlate better with geographic than phylogenetic distances between populations, have been observed in other Lepidoptera (Schmidt & Sperling 2008). It may not be the best explanation for the non-monophyly of especially *P. cocyta* and *P. cocyta* in Wahlberg et al. (2003), although non-monophyly in mitochondrial gene trees has been demonstrated to be an indicator of mitochondrial introgression in various other taxa (Linnen & Farrell 2007; Shaw 2002; Gompert et al. 2008). Nearly all of the *P. tharos*, *P. cocyta* and *P. cocyta* in Wahlberg et al. (2003) were sampled from or near areas where all three species are found and yet, unlike our data, different species collected from the same locality fell out in different parts of their tree.

Many species, especially recently diverged ones, are paraphyletic with respect to their gene trees due to gene introgression via hybridization or incomplete lineage sorting from variable ancestral populations (Maddison 1997; Funk & Omland 2003). Wahlberg et al. (2003) explained the patterns of non-monophyly of the species in the *P. tharos* complex as largely due to incomplete lineage sorting, but with hybridization and mitochondrial gene introgression playing a role

especially between *P. cocyta* and *P. cocyta*. Across the largely sympatric ranges of *P. cocyta* and *P. cocyta* (Fig. 1), there is only one place where morphology indicates hybridization may be currently occurring regularly between them: the Rocky Mountains of Utah and Colorado (Scott 1998). Elsewhere their phenotypes are quite distinct (Scott 1994, 1998). Confusion in species identification in the *P. tharos* species complex usually occurs when *P. tharos* and *P. cocyta* are confused, as in the case of Porter and Mueller (1998) whose conclusions in hybridization experiments between *P. tharos* and *P. cocyta* were challenged by a claim by J. Scott that they had misidentified a subspecies of *P. cocyta* as *P. tharos* (Wahlberg et al. 2003). Furthermore, hybridization and hybrid viability has been observed several times between *P. tharos* and *P. cocyta*, both in the laboratory and in the wild (Oliver 1980; Scott 1986b). Our data corroborate the conclusion of Wahlberg et al. (2003) that introgression has likely occurred between *P. cocyta* and both *P. cocyta* and *P. tharos*, but, in contrast to their conclusions, suggest that introgression between *P. cocyta* and *P. tharos* has been more widespread than between *P. cocyta* and *P. cocyta*, at least in our area of study.

The final word on the relationships between these butterflies has, of course, not yet been established. The keys to shedding more light on the questions in this species complex will be more intense sampling (e.g. Funk 1999) and the use of nuclear genetic markers. Numerous studies have shown the importance of sampling both mitochondrial and nuclear genes for phylogenetic analyses, since their different patterns of inheritance often lead to discordant gene trees (e.g. Berthier et al. 2006; Gomez-Zurita & Vogler 2003). Wahlberg and Freitas (2007) did analyze a mitochondrial gene and two nuclear genes for 11 species of the *P. tharos* species complex in a phylogeny of the Phycioidina tribe, but with ambiguous results: parsimony and Bayesian analyses of the combined genes gave very different arrangements of the *P. tharos* species complex. Until an analysis of nuclear genes can be incorporated into a much more intense sampling of the *P. tharos* species complex, we can only anticipate further elucidation of the complications in this fascinating group of butterflies.

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Please see Appendix on next page.

Appendix 1. Localities and dates for the specimens collected for this study. All specimens collected by the senior author.

#	Species	Location	County	Date
03	<i>Phyciodes cocyta</i>	Frank Smith Rd & Old MI 63	Lake Co., MI	06 June 2007
05	<i>Phyciodes cocyta</i>	Frank Smith Rd & Old MI 63	Lake Co., MI	06 June 2007
06	<i>Phyciodes cocyta</i>	Frank Smith Rd & Old MI 63	Lake Co., MI	06 June 2007
09	<i>Phyciodes cocyta</i>	Frank Smith Rd & Old MI 63	Lake Co., MI	06 June 2007
10	<i>Phyciodes cocyta</i>	Frank Smith Rd & Old MI 63	Lake Co., MI	06 June 2007
13	<i>Phyciodes cocyta</i>	Frank Smith Rd & Old MI 63	Lake Co., MI	06 June 2007
14	<i>Phyciodes cocyta</i>	Frank Smith Rd & Old MI 63	Lake Co., MI	06 June 2007
17	<i>Phyciodes cocyta</i>	G. H. Gordon Biological Station, Luther	Lake Co., MI	07 June 2007
18	<i>Phyciodes cocyta</i>	G. H. Gordon Biological Station, Luther	Lake Co., MI	07 June 2007
25	<i>Phyciodes cocyta</i>	Silver Creek Pathway, Pierre Marquette State Forest	Lake Co., MI	08 June 2007
29	<i>Phyciodes cocyta</i>	Silver Creek Pathway, Pierre Marquette State Forest	Lake Co., MI	08 June 2007
33	<i>Phyciodes cocyta</i>	Silver Creek Pathway, Pierre Marquette State Forest	Lake Co., MI	08 June 2007
37	<i>Phyciodes cocyta</i>	Silver Creek Pathway, Pierre Marquette State Forest	Lake Co., MI	08 June 2007
39	<i>Phyciodes cocyta</i>	King's Hwy & Old MI 63	Lake Co., MI	10 June 2007
43	<i>Phyciodes cocyta</i>	2 ½ Mile Rd & Old MI 63	Lake Co., MI	10 June 2007
45	<i>Phyciodes cocyta</i>	2 ½ Mile Rd & Old MI 63	Lake Co., MI	10 June 2007
46	<i>Phyciodes cocyta</i>	2 ½ Mile Rd & Old MI 63	Lake Co., MI	10 June 2007
47	<i>Phyciodes cocyta</i>	2 ½ Mile Rd & Old MI 63	Lake Co., MI	10 June 2007
49	<i>Phyciodes cocyta</i>	2 ½ Mile Rd & Old MI 63	Lake Co., MI	10 June 2007
50	<i>Phyciodes cocyta</i>	2 ½ Mile Rd & Old MI 63	Lake Co., MI	10 June 2007
53	<i>Phyciodes cocyta</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
54	<i>Phyciodes batesii</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
55	<i>Phyciodes cocyta</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
57	<i>Phyciodes batesii</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
59	<i>Phyciodes batesii</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
65	<i>Phyciodes cocyta</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
69	<i>Phyciodes batesii</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
70	<i>Phyciodes batesii</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
73	<i>Phyciodes batesii</i>	Crapo Lake Rd & Old State Rd	Otsego Co., MI	13 June 2007
79	<i>Phyciodes batesii</i>	Grignell Rd & Old State Rd	Otsego Co., MI	13 June 2007
82	<i>Phyciodes batesii</i>	Grignell Rd & Old State Rd	Otsego Co., MI	13 June 2007
84	<i>Phyciodes batesii</i>	Grignell Rd & Old State Rd	Otsego Co., MI	13 June 2007
96	<i>Phyciodes batesii</i>	Long Lake Campground, 8 mi NE of Cadillac	Wexford Co., MI	16 June 2007
99	<i>Phyciodes cocyta</i>	Long Lake Campground, 8 mi NE of Cadillac	Wexford Co., MI	16 June 2007
128	<i>Phyciodes cocyta</i>	Hawley Rd, 1 mi S of Ellison Rd	Ionia Co., MI	20 June 2007
133	<i>Phyciodes tharos</i>	Black Rd, Monclova	Lucas Co., OH	29 June 2007
134	<i>Phyciodes tharos</i>	Black Rd, Monclova	Lucas Co., OH	29 June 2007
135	<i>Phyciodes tharos</i>	Black Rd, Monclova	Lucas Co., OH	29 June 2007
136	<i>Phyciodes tharos</i>	Black Rd, Monclova	Lucas Co., OH	30 June 2007
137	<i>Phyciodes tharos</i>	Black Rd, Monclova	Lucas Co., OH	30 June 2007

POLLEN LOAD IN AN ACTIVE POLLINATOR, THE YUCCA MOTH *TEGETICULA YUCCASELLA*
(PRODOXIDAE)**Additional key words:** active pollination, evolutionary novelty, resource allocation

Insect pollination of flowers is a dominant trait among flowering plants, with estimates of 75% of all angiosperms relying on animal-mediated pollen dispersal (Committee on the Status of Pollinators in North America 2007). In almost all cases, this is a passive process in that a flower-visiting insect accidentally picks up pollen while visiting a flower for foraging purposes, and that pollen will be accidentally deposited on flowers subsequently visited. Conspecific pollen grains deposited onto stigmas may then complete ovule fertilization.

The probability that a pollen grain will reach the stigma of a conspecific flower is very low, and as a consequence pollen-to-ovule ratios in flowers in outcrossing species tend to be very high (Cruden 1977), commonly several thousand pollen grains per ovule. In some circumstances, there may be a selfish interest in the pollinator to cause pollination, such as when its larvae rely on developing seeds for completing their development. In Lepidoptera, there are at three known cases of this kind, including yucca moths (*Tegeticula* and *Parategeticula*; Prodoxidae; 20+ spp.; Riley 1872; Davis 1967; Pellmyr 2003), *Upiga virescens* (Pyrallidae) on the columnar senita cactus *Lophocereus schottii* (Holland & Fleming 1999; Fleming & Holland 1998), and *Epicephala* (Gracillariidae) on trees of Phyllanthaceae (500+ spp.; Kato et al. 2003; Kawakita & Kato 2004, 2009, 2010; Kawakita 2010). In the associations involving yucca moths, the female moth uses sex-specific unique tentacular mouthparts (Fig. 1.) to actively gather pollen of the larval host plant, and then uses some of that pollen to actively pollinate each flower in which she has oviposited. In *Epicephala*, the proboscis is used for the same purpose, and in the case of the senita cactus, the moth uses an abdominal scale brush for pollen collection and deposition. In so doing, the female assures that lack of pollination will not prevent development of seed-bearing fruit for her larval progeny.

While the pollen load carried by the female yucca moth was described in Riley's original papers (Riley 1872, 1873, 1892), the actual quantity of pollen that a female collects and transports has never been determined. Here I report on pollen loads carried by *Tegeticula yuccasella*, the most wide-ranging pollinator species (Davis 1967; Pellmyr 2003).

Forty-nine female *T. yuccasella* were collected in flowers of *Yucca filamentosa* in and around Spring Grove Cemetery in central Cincinnati, Ohio, USA (39.165°N 84.5229°W) during 24–29 June 1993 and 23–26 June 1994, at which time moths were abundant in the area. Moths were weighed individually within an hour of harvest on a Mettler AC100 balance (Mettler Toledo GmbH, Greifensee, Switzerland) to the nearest 0.00001g. The pollen load and the tentacles were then removed from each female with surgical forceps and scissors, respectively, and weighed separately to the same precision. Each pollen load was placed in clear mounting medium on a glass slide and the pollen grains were manually counted for each sample.

Investment in specific structures for pollen movement in the form of the unique tentacles of the female constitute a minor allocation as the tentacles constituted 0.16–1.24% of total body mass (median = 0.39%). This variation in part derives from variation in



FIG. 1. Head of female *Tegeticula yuccasella* carrying a pollen load under her head. Light arched structure in front of pollen is proboscis, darker brown structure placed against pollen load is left tentacle, used for pollen manipulation.

overall body mass attributable to different proportions of egg loads retained by females at the time of collection. Pollen loads varied within a considerable range, between 0–9670 grains, and an average of 3676 ± 2235 (SD). Three individuals carried no pollen when sampled, either because their supply had been depleted or they had yet to gather pollen. In circumstances where flower density is moderate and moth density is relatively high, as was the case at our study site, it was indeed common later during the activity period to find females searching at length to replenish their pollen supplies. Individual *Yucca filamentosa* flowers at the study site typically contained 150–200 ovules so there is very substantial demand on females to provide sufficient pollen; in addition, resource competition among simultaneously developing fruits result in early fruit abscission and consequent death of all moth larvae within it (Pellmyr & Huth 1994). There is indeed strong selection on females to gather and deposit ample pollen on flowers where she has oviposited, as the effects of pollination on probability of retention of the developing fruit with the feeding larvae is a key factor in determining the reproductive success.

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BOOK REVIEW

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THE BUTTERFLY ISLES: a Summer in Search of Our Emperors and Admirals, by Patrick Barkham. 372 pages, 16 plates; 8.5 × 6 in; ISBN 978-1-84708-127-8; Hardback. UK £20.00. Granta Publications, London; Publication date: 2010.

As far as I can tell, this book is only the second published account of a butterfly big year. As the only other member of this exclusive club, I was of course eager to read it, and I am in a privileged position to review it. Four years studying and working on butterfly conservation in England, many years ago, enhanced my desire to do so. Let me say from the outset, however, that I have attempted to avoid comparing Mr. Barkham's adventure with my own, apart from sympathizing with our common challenges, trials, and pleasures. A big year based on just 59 resident species of butterflies on a small archipelago can in no way be judged or measured against a similar endeavor staged on a large continent hosting 800 species (Pyle, 2010). I trust, therefore, that these comments will be taken as coming from what Nabokov described as “a fellow sufferer” of the *passio et morbus aureliani* rather than from any sort of competition.

The narrative begins with Barkham's long-ago hunt with his dad for the Brown Argus (*Aricia agestis*), followed by memories of six summers rambling with his “Jeremy Thomas” in hand—his field guide, tantamount to birding with your Roger Tory Peterson (Thomas, 1986). But “we ran out of summers, or steam,” he writes, “and my personal tally of British butterflies got stuck at 54.” The years since had afforded no time for butterflies. In 2009, he went forth to pick up the others, and in fact to try to see all 59 in one year: “Finally, I decided I must complete this unfinished business, in the course of one summer. Butterflies, I hoped, could be a way to unlock the ordinary, everyday beauty of the natural world that I hoped could still be experienced on our small island, if only I took time to seek it out. This is the story of my search for every British butterfly ... from beaches to forests, from central London to the Highlands of Scotland ... before it was too late.” And as he described both what he would need (“fine weather, good luck, and a lot of patience”) and what he hoped he might receive (“fleeting moments of wonder as we fly through our lives”), I fully understood.

As the accompanying map shows, the author did not actually visit very much of the British Isles: no Wales, no Northeast, barely into Scotland. He did, however, visit Northern Ireland for Real's Wood White (*Leptidea*

reali), relatively recently discerned in Britain from the ordinary (but uncommon) Wood White (*Leptidea sinapis*), of which more later.

Barkham is a professional writer, and the book is generally very handsomely written: “My love of butterflies began not with a blaze of colour but with a small brown job. That's what my mum called the common plodders of the butterfly world that would scarcely divert your gaze as they bimbled past.” “Wobbling down the street like a small boy on a bicycle was a white butterfly.” A memorable frog-mating sequence (“hurtling around cooing and groaning and fervently trying to find someone to love”) takes place in tandem with the first butterfly spotted, a Small Tortoiseshell (*Aglais urticae*). And then there's the raven that “gurgled as it lurked on the headland, as shifty as a hooded teenager in a park.” Duke of Burgundies (*Hemearis lucina*) “were repelled by an invisible force, and looped away from each other in the sky. Then each butterfly folded its wings together and plummeted like a meteor back to the warm grass.”

The author describes the collecting vs. watching dichotomy in Britain, which is far more starkly drawn on that fair but crowded isle than in the U.S., where netting and sampling remain alive and important. He portrays collectors as being of another era, colorful but well behind us, and he tells of the admitted excesses of some of the mega-collectors of yore. Britain may be one of the few countries where a big year could gain any credence absent voucher specimens for difficult species (certainly necessary in North America). Barkham doesn't carry a net even for catch-and-release, unlike his more knowledgeable father who sometimes does. In fact, he is even embarrassed to wear his binoculars, which he calls “The ultimate symbol of geekiness.” This, to one whose binoculars have been welded to his body for most of his life, seemed odd indeed. Happily, he gets over it.

Throughout, he draws upon plenty of engaging literary references and lepidopterological lore, with which Great Britain is abundantly supplied. He gives a memorable portrait of British butterfly culture, both of the earlier collecting era and of today's equally avid and idiosyncratic watchers, tickers, and photographers. Splendid portraits of particular lepidopterists—David Redhead, the inimitable Matthew Oates, Jeremy Thomas himself, and Butterfly Conservation's CEO Martin Warren, among others—peg them perfectly. I have been in the field with most of these, going back forty years, and young Barkham's sketches are spot-on.

Sometimes he seems wise for his years: “The countryside shrinks in winter; there really is less of it.”

Barkham gets a lot out of just 59 species. “If I had strolled straight through the meadow, I would have only picked up the two hefty Peacock butterflies pursuing each other around a patch of brambles. The lovely thing about looking for butterflies, however, is that it gives you an excuse to dither and then just be. I stood there, in the sunshine, in a meadow of pink and white flowering nettles and creamy cow-parsley flowers with their delicate, slightly bitter scent, with young hops and sticky goose grass straining to climb over it all.” But there is a serpent in the garden; the story also becomes a plaint for love gone wrong. His girlfriend, Lisa, “found the geekiness of all this quite cute. ‘Butterfly Boy’ was her new nickname for me. But she preferred to relax by flitting around parties in fancy dress with all her mates and I no longer had time to do any of this.” As the season progresses, Lisa makes game attempts to take part in some of his field trips, but the writing is on the wall: it’s going to be butterflies or her.

Mr. Barkham is no lepidopterist, and he knows it. Some of the evidence is startling: “Butterflies and moths are distinguished from other insects by having wings *made of* tiny scales” (emphasis mine). He gets better as he goes along, earnestly learning in the field and from mentors. Yet one gathers he read a lot more historical than contemporary lep lit. For example, he overdoes “pugnaciousness” in the old manner, apparently unaware of the contemporary interpretation of many male-male butterfly encounters as potential courtship pursuits. Even with the classical literature, he’s not always accurate. In retelling the well-worn story of Alfred Russell Wallace’s day-long headache after finding a resplendent birdwing, Barkham misattributes the attack to *Ornithoptera alexandrae*, the largest butterfly in the world, of Papua New Guinea; whereas the actual agent, as made clear by Wallace in *The Malay Archipelago* (1869), was the Golden Birdwing (*O. croesus*) of the Moluccas. Wallace never saw Queen Alexandra’s Birdwing, and a good thing; it might have given him a stroke.

Nor is the book free of grammar problems, an increasing plague in modern books where editing and proofing short-cuts are more and more the rule. He’s a pro, but his editors sometimes let him down: The Purple Emperor “eluded and taunted my dad and I for years”—it taunted *I*? “Anyone could train themselves ...” “Pupa” and “pupae” both used as the plural in the same sentence. And a number of misplaced modifiers: “Further on, stuck to the starry white blooms of greater stitchwort, we saw our first Common Blues of the summer.” It’s hard to watch butterflies when you’re

stuck to the flowers of greater stitchwort, but Patrick and his dad did it! (We all make such goofs, but that’s what editors are supposed to be for.) Another frequent lapse, one that I note all too often in this journal and the *NEWS*, is the failure to capitalize Lepidoptera—which, like every other taxon name above the level of species, is properly upper-cased. Readers could use a little more guidance with the lovely but quirky British common names. Barkham explains that the sole British metalmark, long known as the Duke of Burgundy, finally lost its unfortunate epithet “fritillary;” but not that some of the so-called British “fritillaries” are actually checkerspots; nor the relationship between the Brown Argus and the Scotch Argus (none); or that the Scotch Argus and the Mountain Ringlet are both actually species of *Erebia*. A gap is the total absence of scientific names, which would have been easy and helpful to include (here I have followed Asher et al, 2001).

The book is dedicated to the author’s father, John Barkham, an experienced naturalist who was the boon companion of Patrick’s butterfly-watching trips in his youth; and again, after a long hiatus, for some of the jaunts in 2009. Though undedicated and undernoted, his mother was also important, providing, in fact, his best single day: six new species at Kelling Heath on the Norfolk coast. Overall, Barkham had a lucky good year: sunny, with a big Painted Lady (*Vanessa cardui*) invasion, of which he gives a fine account in historical context. He’s a good researcher, as his work as a journalist might suggest. And that’s another salient point: he had to hold a job down all year, and often had to work when he wanted to be out (whereas on my big year, I was able to devote almost the entirety of the time to my admittedly larger task). Concerned with just 59 species, the book is able to include a complete set of British butterfly images—a built-in, very helpful field guide—in the middle. Painted by Brian Hargreaves, these were borrowed from Higgins and Riley’s popular Collins field guide (1970). Additional plates reproduce photographs from life by the author, depicting particularly memorable moments and butterflies. Fine pencil drawings by Helen Macdonald enhance each chapter heading.

Barkham’s treatment of conservation is thorough and thoughtful, as in a conflict between Marsh Fritillaries (*Euphydryas aurinia*) and windmills: “Which comes first: green energy or a rare and beautiful butterfly? ... Must we sacrifice the latter to our insatiable desire for power?” Almost every encounter touches on conservation or management, in the country that pioneered butterfly conservation yet still loses essential habitat annually, even as heroic efforts are made to save

and restore critical butterfly sites. He gives excellent accounts of the great successes, such as Jeremy Thomas and the reintroduction of the Large Blue (*Maculinea arion*), and Martin Warren and the Heath Fritillary (*Melitaea athalia*); and stirring reports of his meetings with these men and the butterflies they helped save, including an eye-witness account of an historic outbreak of the sometime-endangered Heath Fritillary. Having spent a summer myself seeking *M. athalia* on its historic sites in the early '70s, when it was nearly extinct and its ecology and management needs but little understood, I can especially appreciate Barkham's wonder at seeing thousands on the wing. But he also endured close calls, such as with the first butterfly saved by Jeremy Thomas's research and subsequent applied management, *Satyrrium pruni*: "The sun did find a small window in the cloud and the woodland rides were suddenly, capriciously, animated with dozens of indefatigable Meadow Browns, warring Large Skippers, beautiful Marbled Whites, bejewelled Common Blues and a couple of pristine, velvety Ringlets, the first of the year. But that modest, slightly tatty insect was the only Black Hairstreak I saw."

Mr. Barkham's narrative holds up well and brings us right along on the journey. There is high adventure to be had here, with the Purple Emperor (*Apatura iris*) and the Swallowtail (*Papilio machaon britannicus*); and low adventure, as when Barkham, butterfly-creeping around London parks, is mistaken for a skulker looking for a same-sex hook-up. And pathos: he finally loses his sweetie over a date with the emperor, when he opts for baiting it with rancid fish paste instead of a weekend country house party with her. All this takes place in a great chapter called "The Curse of the Purple Emperor." At least he succeeds in seeing this mythic beauty—57 of them, in fact—flying in tandem with Purple Hairstreaks (*Neozephyrus quercus*).

The author sees some of the best of wild Britain, from Arnside Knot to Meathop Moss; but also plenty of gridlocked, fummy motorways and unpleasant urban passages on the way to the desired habitats. He does not, as I did, have days on end in lonely landscapes with more wildlife than people (he could have, in northern Scotland; but he never made it up there, picking up the Scottish specialties farther south). He runs into "Butterfly Burnout" over the Lulworth Skipper at Lulworth Crumple on the Dorset Coast and Chalkhill Blues on Royston Heath (*Thymelicus acteon*, *Lysandra coridon*). But he can't give up now—he has more to go. He grows giggly in the seemingly futile search for #55, *Leptidea sinapis*, differentiated from Real's Wood White (*L. reali*) by that species' much longer penis. "My journey to find all fifty-nine species would end at fifty-

eight. It was not an heroic failure. It would be an inept failure, especially as the stumbling point was the humble Wood White, and the short-willed form at that."

At that point Mr. Barkham comes to a realization that must ultimately ground every good-hearted big year: "I too had no control over the weather, or the butterflies, or the traffic, or the hearts of those I loved. For some reason, I continued to cling to the idea that I could find what I was looking for if only I was smart enough, and disciplined enough, and organized enough, and knew the right back road through south London. I badly needed to learn not only patience, but acceptance." Of course, eventually he does find the Wood White.

And then the Final Four: the Scotch Argus (*Erebia aethiops*), as it "jittered and bashed its way clumsily through the stiff moor grass;" the Adonis Blue (*Polyommatus bellargus*), "the best of the blues ... this dashing electric-blue butterfly [that] had the power to incite great obsession" (how well I remember!); the Silver-spotted Skipper (*Hesperia comma*) on a round-headed rampion on the South Downs of West Sussex, which he watches copulate; and finally, the Brown Hairstreak (*Thecla betulae*), a winter search for the eggs of which had actually begun his year afield. "Watching so intently," he writes, "I became attuned to every pinprick in the landscape, the sway of every blade of grass and the blunder of every bee." Driving home, drained by his success, he realized that "it proved easier to see the butterflies than I imagined, but far harder to undertake the journey." To the last part, I can definitely relate! But even then it wasn't over, for there were surprises to come, and recoveries, that I will not spoil here. I'll just say that I found *The Butterfly Isles* to be a delightful, evocative, and thoroughly worthwhile read; and if he wouldn't be ashamed of his bins, I would very much enjoy going afield with Mr. Barkham. His was a very different butterfly big year from my own, to be sure, and no less for it. He has entered a memorable title in the uncrowded genre of natural history big years in general, whose masterpiece is Kenn Kaufman's *Kingbird Highway* (1997), and a worthy entry it is.

"Searching for the butterflies," Barkham reflected, "had given me the gift of becoming, for a moment, here and there at least, a small, harmonious part of the natural world." But it had also made him realize, in spite of his good luck with weather and numbers, that "what everyone instinctively suspects" is true: "Most of us no longer find our summer days routinely animated by dozens, let alone swarms, of butterflies." They really are fewer than they used to be. And yet, reflecting on his first Orange Tip of the year, the first he'd seen in a decade, he felt "Everything was all right with the world,

for another year at least, if the Orange Tips were dancing through a meadow by the Thames in April. The Apocalypse was not nigh, not quite yet.”

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BOOK REVIEW

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GIANT SILKMOTHS: COLOUR, MIMICRY & CAMOUFLAGE, by Philip Howse and Kirby Wolfe. 192 pages, 24 cm × 30 cm, soft laminate cover; ISBN 13: 978-1-906506-25-4; £25 (about US\$40); Papadakis, Winterbourne, Berkshire, England; Publication date: November 2011.

There are many books including several new ones that depict beautiful Saturniidae as images of pinned specimens. Even more books or articles show living saturniids as close-ups in their natural resting poses or alarm positions, but normally as only a page or two of images in a book about Lepidoptera or insects. *Giant Silkmotths* gives us dozens of enlarged images of living saturniids courtesy of Kirby Wolfe's now famous photography, and augments them with a very readable and intriguing text, so there really is no other book like this one. It is decidedly not "just another book with pretty pictures of saturniids." More than any other, the book will educate the reader about how saturniids live and interact in their natural ecosystems, with a primary focus on how they avoid predation by vertebrates. This book promises to become an instant classic like Howse's wonderful 2010 book *Butterflies: Messages from Psyche*, also published by Papadakis. Professor Howse is a renowned expert on insect ecology and behavior, with a distinguished career that includes pioneering work in environmentally-friendly pest control. Wolfe has to his credit a long series of sound taxonomic publications on saturniids, always embellished with his marvelous photographs of moths and caterpillars. He taught Spanish at the college level for years in California, and has made many excursions to collect Saturniidae in several countries of Central America and South America. The collaboration here between them has yielded a book that deserves to be widely available in personal and institutional libraries.

It has long been recognized that many saturniid moths have wing patterns that resemble dead leaves, complete with necrotic spots and holes. In others, the ubiquitous eyespots on the hindwings and often also the forewings have been widely accepted as evidence of mimicry of the eyes of vertebrates. It must surely be effective and therefore true, since so many species in almost all of the saturniid subfamilies and on different continents have these features. Even Charles Darwin cited examples of these in *The Origin of Species* to support some of his hypotheses. The text of *Giant Silkmotths* correlates closely with the photographs, usually on the same or adjacent page, making it very

instructive. Employing a writing style that is both engaging and compelling, the authors point out that they are only offering hypotheses instead of trying to force their views upon the users of the book. The book supports some points by providing other images such as a fox, a hare, a lizard, flowers, and some pieces of art. Howse and Wolfe delve into the perception and interpretation of images, whether in the minds of humans or birds or other saturniid predators. They also give information about structure and function of eyes in birds, humans, and other vertebrates. The reader is reminded at critical points that what we humans see and perceive can be very different from what birds see and perceive. Many tantalizing hypotheses are presented, inviting the possibility of controlled quantitative studies by others who might wish to test these. I can envision this book sparking the interest of a future graduate student who will write a thesis on vertebrate predation or insect ecology. The book is that important, and as I already indicated, fills a real gap in literature on Saturniidae.

Maybe I am too gullible or insufficiently skeptical, but when I read the authors' interpretations of what the diverse wing patterns represent on page after page, I said aloud to myself, "Why didn't I think of that?" or "Why couldn't I see that years ago—it is so obvious now?" Of course that is a bat hanging in a tree (p. 62); of course those are fungi growing out of a log (pp. 58–59); of course the forewing spots by the costal margin (stem of a plant) of a luna moth are berries or flower buds attached to it; of course those scalloped yellow markings on the forewings of *Citheronia laocoon* represent the feathers of a bird's wing. The book exposes many more of the remarkable images that are hidden in plain sight on the wings of saturniids. For the caterpillars, Howse and Wolfe have also decoded some secrets, such as a tiny frog sitting atop the thorax of a mature larva of *Bombyx mandarina* and toadstools growing in a row on the larva of *Automeris lauta*. They respectfully counsel us to view moths upside down and with wings folded in resting position, instead of as the standard pinned and spread specimens. For many saturniids, I was always determined to see the forewing apex as the anterior end of the head of a toad or snake or whatever. But look at the forewing of a *Polythysana* in one of your books or on the internet, and you will see, perhaps for the first time, that the bird has a sharp beak pointing toward the thorax, and the outer edge of the forewing is the crest on the head of that bird. Howse and Wolfe have trained me to see the wing patterns of

saturniids in new and exciting ways. However, I discussed this book by telephone with John Cody, a psychiatrist and an artist who paints mainly Saturniidae, and found him to be skeptical of many of these hypotheses.

In some ways, size is critical, which is why smaller moths like the normal geometrids and noctuids do not have eyespots. In other ways, size is not something a foraging bird has the time or capability to process. For example, when I collected and pinned a small gray cerambycid beetle of the genus *Astylopsis* in upper South Carolina many years ago, I was struck that the posterior end looked like the face of a rodent. If that beetle had crawled into a hole in a log, the rear end would look like a tiny mouse peering out of the hole, and one or both of the long antennae would fold back to make the mouse's tail or two. For years I thought it has

to be a mouse mimic, yet it was way too small, but now after reading the book by Howse and Wolfe, I realize it is indeed the image of a mouse (i.e., I was right all along!). All of these things about size, perception, and vision are explained in some detail in the book, with citations for further reading. Wolfe has added a valuable appendix about rearing and photographing moths.

In conclusion, if you buy this book, I guarantee that you will be glad that you did, because this review can only hint at the enjoyment that awaits users of this book.

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BOOK REVIEW

Journal of the Lepidopterists' Society
66(1), 2012, p. 56–57

LEARN ABOUT BUTTERFLIES IN THE GARDEN, by Brenda Dziedzic. 2011. Published by Brenda Dziedzic in Westland, MI, 48186. 506 color photos, 35 range maps, 2 diagrams. Paperback, 7.8 x 5.1 x 1 in., ISBN-10: 0615443036, ISBN-13: 978-0615443034. Available from Brenda Dziedzic, 1263 Springer St., Westland, MI 48186; Phone: 734-326-0578; e-mail: happybutterflying@yahoo.com; website: <http://butterfliesinthegarden.com>; Price \$25.14 (USA), \$33.64 (Canada/Mexico).

This book is a glossy, full-color pictorial guide to the life-history stages of some common butterflies and moths, along with gardening and rearing advice. According to the preface, Ms. Dziedzic is an Advanced Master Gardener—a certification awarded by the American Horticultural Society for horticultural training and performing volunteer services, and a self-taught butterfly enthusiast.

The gardening portion of the book is surprisingly brief, considering her experience in that realm, and primarily gives tips for a small backyard garden in the Great Lakes region of the United States. Nevertheless, her advice seems sound and to-the-point, and focuses on native plants that attract butterflies either as host plants or as food sources for adult butterflies. She also emphasizes aspects of the garden that help create an environment to attract butterflies by filling a variety of their needs, such as shelter from the wind, and spots for sunning or puddling (acquiring nutrients from damp soil). Her advice on rearing butterflies from eggs collected in the garden is detailed, but simple enough for a novice to follow. The author also provides rearing advice on her website (<http://butterfliesinthegarden.com/RaisingButterflies.aspx>).

The bulk of Dziedzic's book is composed of close-up photos of the life-history stages, from egg to adult, of 36 species of butterflies, skippers and moths, with descriptive captions, lists and some photos of host plants, and range maps. The photo captions include information such as the length of time for the various developmental stages, how the species overwinters, number of broods, host/larval food plants, and adult food preferences. I do not know why she chose these species, although presumably many are found in her

own garden. All but four have range maps that indicate wide-spread distribution across the United States, making the book useful for readers throughout the U.S. One species, the gypsy moth, *Lymantria dispar*, is a notorious pest of hardwood trees and was included, according to the author, to prevent accidental rearing.

Each species record contains over a dozen photos, several for each life stage: egg, larva, chrysalis, and adult. Dziedzic appears to have reared many of these species herself and, indeed, she took all but 39 of the 493 photos in this section. The photos are not just beautiful but also are helpful for the gardener who, in order to encourage butterflies in his or her garden, must recognize them in all their forms.

Diversity is the wrench tossed into the machinery of identification, whether you are a layperson or a seasoned field biologist. One of the most useful qualities of Dziedzic's photos is the diversity they reveal. The book includes photos showing different color morphs of larvae, e.g., the Question Mark, *Polygonia interrogationis* (p. 202), and dorsal and ventral surfaces of adult butterflies, e.g., the Red Admiral, *Vanessa atalanta* (p. 207). Photos also show changes over time in egg color, e.g., the Red-spotted Purple, *Limenitis arthemis* (p. 216), larval instars, e.g., the Common Checkered-skipper, *Pyrgus communis* (p. 244), and the developing chrysalis, e.g., the Clouded Sulphur, *Colias philodice* (p. 83).

There is one identification error in the book that was noted by the author in her cover letter to the editor. The photo on p. 33 indicating the ventral surface of the Giant Swallowtail, *Papilio cresphontes*, should read Eastern Tiger Swallowtail, *Papilio glaucus*.

Ms. Dziedzic's book offers concise advice and beautifully detailed photos for anyone who wants to encourage butterflies in the garden in all forms, including rearing them. This book would be an excellent addition to the library of the experienced entomologist interested in the life-history stages of these common Lepidoptera.

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BOOK REVIEW

Journal of the Lepidopterists' Society
66(1), 2012, p. 57–58

OLETHREUTINE MOTHS OF THE MID-WESTERN UNITED STATES, An Identification Guide. by Gilligan T. M., D. J. Wright, and L. D. Gibson. 334 pages, 106 B/W plates of genitalia; each adult habitus is also shown in color and some representative larvae are depicted in color. Hardback. ISBN: 978-0867271607. Ohio Biological Survey, Columbus, Ohio. Price: \$75.00 USD. Publication date: 2008.

Every now and then, a book comes along that makes one's work vastly easier. *The Olethreutine Moths of the Midwestern United States* is such a publication, and for that, I for one am grateful. This large-format book combines wonderful full-color habitus shots of specimens with photographs of male and female genitalia. It covers a fairly large geographic area and treats 306 species. Prior to this I often had to depend on more scattered and often antiquated literature to identify many of my olethreutine tortricids.

Opening the book is a brief section on historical perspectives that covers the big names in olethreutine taxonomy. It is refreshing to see our historical entomological forefathers brought to light and this history really helps illuminate the stories behind the names. Following is a concise, very well written section on morphology. The illustrations here are excellent, and assist greatly in explaining genitalic terminology. There is a color printing error in the wing venation figure, however, it is merely an aesthetic issue.

The species accounts section comprises much of the remainder of the book. It begins with a list of the species covered and 5 plates of life-sized photographs of all species for quick comparison. Here and throughout the species accounts, the book follows an intuitive numbering system, making the association of photos

and accounts easy. Each genus is introduced with a good synopsis and often has references for further information. The species accounts themselves have an attractive layout, with the text on the left and one or occasionally two large photographs of the whole insect on the right. Each account consists of the forewing length, flight period, distribution, biology, and remarks. For a few of the variable species, it might have been preferable to have included more than two photos. The genitalia photographs are large and there are many on the same page, allowing for easy comparison. My only complaint about the genitalia photographs is that only the ostium region is shown for most females. Inclusion of the corpus bursae for more species would have been helpful. In general, however, what is figured is more than sufficient.

Steven Passoa contributed to Part III, which updates McKay's treatment of olethreutine larvae. It provides detailed information on early stages of olethreutines and it is well illustrated. There is also rearing and preservation information for larvae followed by a key to common species. I would, however, have preferred this section to have been incorporated into the main text, because in this format it almost appears to be an afterthought to the rest of the book.

Overall, this is a marvelous book and deserves to be on the bookshelf of every lepidopterist. For myself, it has been a valuable and well-used tool for identifying olethreutine tortricids. Todd Gilligan, Don Wright, and Loran Gibson should be commended on such a wonderful work.

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ERRATUM:

The note beginning on page 270 of volume 65(4) was authored by Ignacio Castellanos, Pedro Barbosa, and Astrid Caldas. Dr. Caldas's name was not properly capitalized in the list of author affiliations on page 272, nor was she included in the Table of Contents. The editors of *Journal of the Lepidopterists' Society* apologize for this omission.

MANUSCRIPT REVIEWERS FOR 2011 (VOLUME 65)

Manuscript reviewers are anonymous contributors to the scientific rigor, clarity, and quality of text and illustrations in the papers published by the Journal of the Lepidopterists' Society. The reviewers' input is invaluable and always welcomed by authors, editors and readers. We hope their careful work continues to allow the Journal to increase quality and readership. On behalf of all the authors and the editorial staff of the Journal, respectful acknowledgement is given to the reviewers for contributions published in Volume 65.

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