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Cover illustration: Drawing of *Papilio palamedes* Drury by John Abbot, completed ca. 1816–1818. Submitted by John Calhoun, courtesy of the Alexander Turnbull Library, Wellington, New Zealand.

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JOHN ABBOT'S BUTTERFLY DRAWINGS FOR WILLIAM SWAINSON, INCLUDING GENERAL COMMENTS ABOUT ABBOT'S ARTISTIC METHODS AND WRITTEN OBSERVATIONS

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ABSTRACT. Between 1816 and 1818, artist-naturalist John Abbot completed 103 drawings of insects for English naturalist William Swainson. The history of these illustrations is reviewed, leading up to their rediscovery in 1977 in the Alexander Turnbull Library, Wellington, New Zealand. Four of these drawings are figured. The adults in the 21 butterfly drawings are identified and the figures of larvae and pupae are assessed for accuracy. The illustrated plants are also identified and their status as hosts is examined. Aspects of Abbot's life history notes are discussed, including his spelling, grammar, and use of Latin names. His notes for Swainson are transcribed and analyzed. A review of Abbot's artwork indicates that he duplicated many of his compositions for 20–25 years. He sometimes portrayed erroneous figures of larvae, pupae, and hostplants. Figures of immatures were sometimes fabricated using other species as models. He also applied duplicate figures of larvae to more than one species. Abbot may have sent another set of insect drawings to Swainson in 1830. Ninety-nine smaller drawings at the Turnbull Library are attributed to both Abbot and Swainson. Six of these illustrations are figured. Abbot's notes for Swainson suggest that at least three butterfly species are now more abundant than during the early nineteenth century, while three others are probably less widespread than formerly.

Additional key words: Georgia, larvae, Lepidoptera, pupae, hostplants, watercolors

“To the scientist and the naturalist comes, then, the artist, to wait upon both, ever ready to translate into form and line the forms of the butterflies, to fix the colours of brocaded wings”—Vere Temple.

Thousands of natural history illustrations were rendered by Georgia artist-naturalist John Abbot (1751–ca.1840), but relatively few have been analyzed by more recent authors. Abbot's bird drawings have received the most attention through the studies of Faxon (1896), Rhodes (1918), Allen (1951), Larson & Rogers-Price (1983), Simpson (1984, 1993), Griffin ([1990]), and Rogers-Price (1992, 1997). Spider drawings were reviewed by Chamberlin & Ivie (1944). Scudder (1872, 1888–1889) documented a large number of Abbot's unpublished butterfly drawings, but his identifications were incomplete and partially inaccurate. Miscellaneous drawings of birds, insects, and spiders were figured and identified in biographical accounts, most notably by Rogers-Price (1983) and Gilbert (1998, 2000).

While conducting research for Calhoun (2003) I realized Abbot's profound influence on North American entomology. Abbot documented many species of

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Lepidoptera long before they were scientifically described. His drawings and specimens contributed to the original descriptions of numerous species. For many years, Abbot's illustrations and notes were the primary source of life history information for the Lepidoptera of America. Edwards (1868–1872) stated, “Even among our old and common species, the larvae are but little more known than in the days of Abbot.” Scudder (1888, 1888–1889) similarly remarked, “the transformations of not a few of our butterflies are even now known only through the observations and illustrations of Abbot.” Abbot's work is still valuable in understanding the life histories of poorly known species. His original drawings also help to clarify taxonomic concepts and historical distributions (Calhoun 2003). However, some of his illustrations and written observations are the source of dubious information that continues to plague the literature. Authors have repeated many of Abbot's erroneous hostplant associations without realizing their origin. Because of these discrepancies, extreme caution must be exercised when consulting Abbot's drawings for life history information. To fully appreciate Abbot's contributions, it is essential to analyze his artwork within its original context and over the course of his career in

America. I previously discussed Abbot's work in Calhoun (2003, 2004, 2005, 2006). I now present a review of Abbot's butterfly drawings in the Alexander Turnbull Library, Wellington, New Zealand. I also continue to investigate the artistic methods and manuscript notes that Abbot used to document his observations of American Lepidoptera.

METHODS

Digital images of drawings were received from the Alexander Turnbull Library. The adult butterflies were identified and the figures compared with those in other sets of Abbot's drawings that are deposited elsewhere. Figures of butterfly larvae and pupae were analyzed for accuracy using written descriptions, line drawings, and photographs of living specimens. Botanist Mark A. Garland provided identifications of the depicted plants, which were then evaluated as hosts. Also consulted were relevant manuscripts preserved in the Carl A. Kroch Library (Cornell University), Ernst Mayr Library (Museum of Comparative Zoology, Harvard University), Gray Herbarium (Harvard University), and the Linnean Society of London.

RESULTS

Background. Since his youth, the English naturalist William Swainson (1789–1855) was familiar with John Abbot through the published drawings in Smith & Abbot (1797) and Abbot's numerous specimens that were contained in the natural history cabinets of London. Swainson obtained some of Abbot's insect specimens in 1813 through Abbot's London agent, John Francillon (Swainson correspondence, Linnean Society of London). In September 1816, Swainson wrote directly to Abbot about his desire to purchase additional specimens, as well as drawings of the insects of Georgia. He later asked specifically for illustrations of butterflies and sphinx moths that were not figured in Smith & Abbot (1797). Without divulging Swainson's name, Abbot boasted to the Swiss naturalist Heinrich (Henry) Escher-Zollikofer (1776–1853) that he had received a letter from "a Gentleman in England of my acquaintance, who desires me to collect for him a General collection of Insects, and also wants to purchase a collection of Drawings" (Kroch Library, Cornell University). Abbot replied to Swainson in December 1816 that he had "commenced making a set of Quarto (large size) Drawings of the changes of Insects with notes, of such Insects that are not figured in Smiths Lepidoptera Insects of Georgia, indeed it is a continuation of that Work" (Linnean Society of London). Abbot expected to complete about 100 drawings by the time he collected all the insects that

Swainson wanted, but stated that he could "readily make at least 200 such Drawings not figured in Smiths work, among them is many of the principal Insects both for size & beauty" (Linnean Society of London). By the time Abbot sent his reply, Swainson had already departed London for a two-year expedition to Brazil. His letter was forwarded to Brazil by Swainson's father, John Timothy Swainson.

Abbot hoped that more of his drawings would eventually be published like those in *The Natural History of the Rarer Lepidopterous Insects of Georgia* (Smith & Abbot 1797). Abbot was probably unaware of this book for some time, but was familiar with it by 1813 when he referred to "Smiths Lepidoptera" in a letter to Escher-Zollikofer. Abbot also wrote Latin names from this book on drawings that he began in 1813 (Calhoun 2004). He repeatedly referred to his sets of drawings as "a continuation of Smiths Lepidoptera," presumably to induce patrons to publish them as such. The proposed Lepidoptera drawings for Swainson were to be completed in a comparable format, which Abbot described as "Quarto, containing the larva, & Fly, Male & female if any difference, on one of the plants it feeds on, or the particular plant, in Watercolors" (letter to H. Escher-Zollikofer, Kroch Library). Like his other life history illustrations, they would invariably portray only mature larvae and include pupae.

When Abbot was working on his drawings for Swainson, he was also attempting to complete a set for Escher-Zollikofer. In April 1817, Abbot sent 50 drawings to Escher-Zollikofer and applied 48 others to Swainson's order. Abbot often juggled specimens and drawings between patrons. By August 1817, he had completed at least 56 more drawings, telling the South Carolina botanist Stephen Elliott, "I have now 104 [drawings], finished for a 2d Vol. [of "Smiths Lepidoptera"]" (Gray Herbarium, Harvard University). Upon completion of the set for Swainson, Abbot entered notes about the habits and biology of each species in a separate manuscript.

Abbot finally sent his watercolors and accompanying notes to Swainson with 900 insect specimens on 1 May 1818. He advised, "I have sent under the cork at the bottom of the box (being a false bottom) 104 Q [quarto] Drawings of the changes of the Insects of Georgia making a 2d Vol. of Smith" (Linnean Society of London). The drawings were placed under the cork to conceal them from customs inspectors and avoid duty fees. Abbot asked Swainson, "If you shou'd not approve of them yourself, beg the favor to dispose of them to the best advantage for me" (Linnean Society of London). Although Abbot intended to provide 104 drawings, the same number published in Smith & Abbot (1797), he

apparently misplaced one of them prior to shipment. Despite Abbot's description, the set included more than just Lepidoptera.

Swainson examined the drawings upon his return to London in August 1818. He was immediately critical. In his reply to Abbot, Swainson complained that the drawings were "not so highly finished as those must have been from which the Plates in Dr Smith's work were taken," adding, "the greatest objection is that they are much smaller in size so they can never be bound uniformly with that work" (Linnean Society of London). In Abbot's defense, his original drawings for Smith & Abbot (1797) were of a comparable size, but the published plates were printed on larger paper. Per his earlier request, Swainson argued that he wanted only drawings of butterflies and sphinx moths, not the variety of insects that Abbot had included. As a friendly gesture, Abbot had already discounted the cost of the drawings from seven shillings and six pence to six shillings, but Swainson offered to pay only five shillings in light of his objections. At five shillings each, the cost of the drawings would have totaled £25 15s, currently valued at about £1,340 (\$2,520 US). Swainson also complained about Abbot's insect specimens, stating, "I should have liked a greater variety instead of 4 & 5 of a species." Swainson asked that replacement drawings be sent with another shipment of insect specimens. If Abbot could not provide more drawings, Swainson proposed to keep some from the first set and "dispose of the remainder if possible" (Linnean Society of London). Abbot acquiesced in June 1819, writing, "I will draw over again for you those that you want...and will leave you to dispose of those already sent at the best price you can get" (Linnean Society of London). In lieu of monetary payment for the drawings and specimens, Swainson offered to exchange Brazilian insects from his recent expedition. Swainson collected about 20,000 insect specimens during his trip (Natusch & Swainson 1987). Abbot graciously accepted and arranged for the Brazilian insects to be sent directly to Heinrich Escher-Zollikofer in Switzerland, who would then pay Abbot. However, Abbot apparently never completed the replacement drawings and Swainson kept the entire first series. As payment for Abbot's specimens, Swainson later sent Brazilian insects to Escher-Zollikofer, but Abbot was mortified to learn that the shipment was heavily damaged upon receipt.

Swainson ultimately lost interest in a project to publish more of Abbot's drawings, relating many years later, "another series of 103 subjects, not included in that which has been published, was executed for us, with the intention of forming two additional volumes to those edited by Dr. Smith, but the design is now

abandoned" (Swainson 1840). It is uncertain what species would have been included in such a book, since Swainson would likely have used the replacement drawings that Abbot intended to send. Because of his dissatisfaction with the drawings, Swainson missed a perfect opportunity to describe the numerous "nondescript" species that they portrayed, most of which remained unnamed for many years. Nonetheless, Swainson (1821) published an abbreviated version of one of the moth drawings to accompany his description of *Thyreus abbottii* (now *Sphecodina abbottii*), which dubiously honored Abbot with an incorrect double-t spelling of his name—a common mistake still made today. Abbot and Swainson continued to correspond for many years. A letter that Abbot wrote in January 1835 was possibly his last to Swainson (Alexander Turnbull Library). In November 1836, after learning that yet another shipment of Swainson's Brazilian insects for Escher-Zollikofer had arrived in deplorable condition, Abbot remarked, "I have had no dealings with him since" (letter to H. Escher-Zollikofer, Cornell University).

Swainson moved from England to New Zealand in 1840. After Swainson's death, his extensive correspondence was brought to England by one of his daughters and placed in the care of the botanist Sir Joseph D. Hooker. In 1900, the 934 letters, including nine from Abbot, were acquired for £50 by the Linnean Society of London (Günther 1899–1900). Albert C. L. G. Günther, then President of the Linnean Society, knew from these letters that Swainson had received drawings from Abbot, but their whereabouts were unknown. Prior to his departure to New Zealand, a large portion of Swainson's library and natural history collections were auctioned in June 1840 (Chalmers-Hunt 1976). Abbot's drawings, however, were not part of this sale. In September 1841, four months after Swainson's arrival in New Zealand, a ship carrying much of the remainder of his library sunk off the coast of South Africa en route to his new home (Parkinson 1984). Günther (1899–1900) bemoaned the possibility that Abbot's drawings were forever lost in this disaster, stating, "No one could appreciate their value better than Swainson, and their exquisite beauty and accuracy must have exercised a very beneficial influence on the work of his own pencil and brush." Swainson was also an accomplished artist who personally illustrated most of his publications (see Parkinson 1989).

The fate of these Abbot watercolors remained a mystery until 1977 when a librarian at the Alexander Turnbull Library discovered an uncataloged collection of drawings. Parkinson (1978) initially associated them with drawings that Abbot supposedly shipped to

Swainson in 1835, but Wilkinson (1982) correctly identified them as those completed between 1816 and 1818. In 1866, eleven years after Swainson's death, the drawings were deposited into the Colonial Museum in Wellington, New Zealand. There they remained until 1876 when they were given to Walter B. D. Mantell, son of famed British paleontologist Gideon A. Mantell. The Turnbull Library acquired the library of W. B. D. Mantell in 1927 from the widow of his son, Walter G. Mantell (Parkinson 1983a, 1984, Parkinson & Rogers-Price 1984).

During the early 1980s, the Alexander Turnbull Library Endowment Trust embarked on an ambitious project to publish these drawings as Abbot had hoped. They would be issued in annual fascicles consisting of six to ten plates each. The text would be formatted similar to that of Smith & Abbot (1797), but Abbot's notes for each drawing would be photographically reproduced from his manuscript. The drawings themselves would be reproduced as six-color photolithographic prints measuring 40.0 × 25.0 cm (15.7 × 9.8 in) and printed on Process Dove 25 percent rag paper. The first fascicle was offered in May 1983 for \$50 NZ. Individual plates could be ordered for \$10 NZ (editor's note in Rogers-Price 1984). Six plates were included in this fascicle: one katydid and five butterflies from drawing nos. 6, 10, 11, 12, 21, and 28 (ATLET 1983). The insects were identified by Matthew E. Dakin, John G. Franclemont, and Paul E. S. Whalley. The plants were determined by C. Richie Bell. The second fascicle of ten plates was being prepared in 1984 for publication the following year, but poor sales of the first fascicle forced the discontinuation of the project, leaving the remainder of the drawings unidentified (M. Calder pers comm., P. Parkinson pers comm.). Although Parkinson (1978) listed all the drawings, he tentatively identified them using only Abbot's manuscript names.

Analysis. In January 2003, I received digital images of all 103 drawings, as well as photocopies of Abbot's accompanying notes. The drawings are unbound, but appear to have once been protected between pink marbled boards, which are preserved with the drawings. The front board bears a pasted paper label, probably created by Swainson, reading, "Original drawings of insects by J. Abbott." On the verso of the board is the bookplate of W. B. D. Mantell and a Turnbull Library classification label dated 1929.

The drawings are rendered in watercolor and graphite on cream-colored wove paper and most measure 34.2 × 24.6 cm (13.5 × 9.7 in). Twenty-five of them possess watermarks of "T G & Co." This paper was manufactured by Thomas and Joshua Gilpin, whose mill was located north of Wilmington, Delaware from 1787

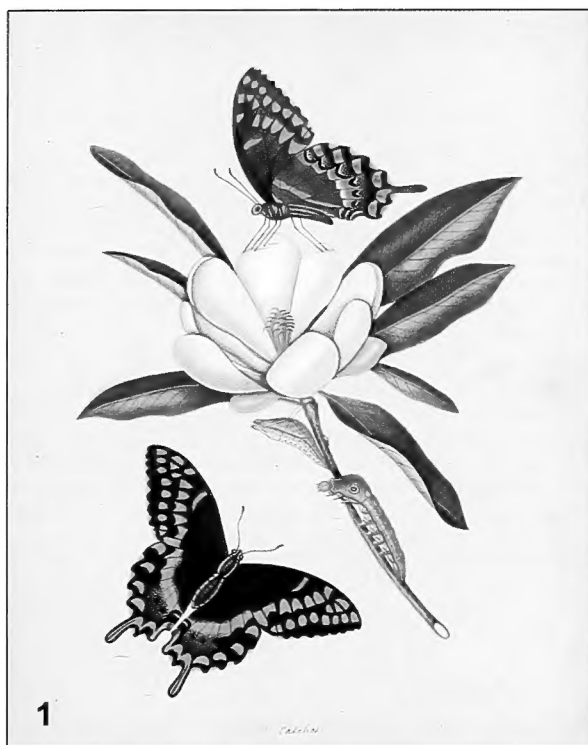
until 1837 (Gravell & Miller 1979). Three other sheets bear the watermarks of "Ruse & Turners 1810" and "W B." The Ruse & Turners paper mill operated in England from 1805 until 1845 (Churchill 1935). Beginning in 1808, William Barber (Barbour) produced paper with the "W B" watermark from mills located in Berks County, Pennsylvania (Gravell & Miller 1979). This reveals that Abbot was using American paper by this time, which he probably purchased in Savannah. He initially employed English papers, such as those from the Whatman mills (Calhoun 2006a).

Although high in quality, these watercolors are not as detailed as the original drawings for Smith & Abbot (1797), which were completed *ca.* 1783–1792 (see Calhoun 2006a). At the top right of each drawing are numbers written by Abbot that correspond to the entries in his notes. Several drawings bear names and other notations in Swainson's hand.

The set includes illustrations of Coleoptera (7 spp.), Hemiptera (1 sp.), Hymenoptera (1 sp.), Lepidoptera (85 spp.), and Orthoptera (2 spp.). Seventeen of the watercolors (nos. 3, 6, 8, 10–12, 14, 17, 18, 21, 32, 35, 37, 49, 53, 72, 78) were figured by Parkinson (1978), Reynolds (1983), Rogers-Price (1983, 1984), Parkinson & Rogers-Price (1984), and Calhoun (2003, 2004). The Lepidoptera drawings are like those published in Smith & Abbot (1797), depicting adults, early stages, and a supposed hostplant (Figs. 1–4). They include 21 species of butterflies.

The accompanying eleven pages of annotations, entitled "Notes to the Drawings of Insects," are written in Abbot's hand on cream wove paper measuring 34.0 × 20.5 cm (13.4 × 8.1 in). The entries are numbered to correspond to the drawings and several sheets bear undated watermarks of "J M," indicative of paper manufactured after 1817 by John Matthews of Pennsylvania (Gravell & Miller). The pages have been stitched into a fawn wove paper cover. The front cover bears a misspelled ink title, probably written by Swainson, reading, "DISCRIPTION OF ABBOTTS DRAWINGS." Preserved with this collection is a leather cover that may have been removed from boards that once protected the notes. It bears gilt tooling and edging, as well as a gilt crest in the center. The crest possibly pertains to the Mantell family.

With the help of six other specialists, I compiled a nearly complete list of identifications for all the insects and plants in these drawings. This list was provided to the Turnbull Library in September 2003. As part of my study of John Abbot's butterflies, I present a review of the butterfly drawings that are preserved in the Turnbull Library with transcriptions of Abbot's accompanying manuscript notes (Table 1).



FIGS. 1-4. John Abbot butterfly drawings in the Alexander Turnbull Library. 1, *Papilio palamedes* (E-272-f-009) (erroneous hostplant). 2, *Asterocampa clyton* (E-272-f-016) (erroneous larva, pupa, and hostplant). 3, *Pyrgus communis* (E-272-f-023). 4, *Callophrys henrici* (E-272-f-027).

TABLE 1. Adult butterflies, early stages, and plants depicted in John Abbot drawings in the Alexander Turnbull Library. Also Abbot's original manuscript entries for each (Abbot's grammar and spelling are preserved). Insect nomenclature follows Opler & Warren (2002). Adult insect figures: D=dorsal, V=ventral, m=male, f=female. Early stages: L=larva, P=pupa, a=acceptable, u=unacceptable. Status of figured hostplants (in brackets): C=confirmed, NC=needs confirmation, E=erroneous.

Drawing No.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot
8	<i>Papilio glaucus</i> L. Df, Vf, La, Pa	<i>Styrax americanus</i> Lam. (Styracaceae) [C] "Styrax laevigata" is a synonym of <i>S. americanus</i> . "Swamp Ash" (probably <i>Fraxinus pennsylvanica</i> Marsh.) (Oleaceae) and "Hicory" [hickory] (<i>Carya</i> sp.) (Juglandaceae) are also confirmed hostplants.	8. <i>Papilio Glaucus</i> . The Caterpillar feeds on the <i>Styrax laevigata</i> , Swamp Ash and Hicory, Tied itself up 11 th Octr Changed 13 th bred 2 ^d April. It also breeds again in the Summer. The Caterpillar is very rare, and the Butterfly not common.
NOTES: only the dark form of the female is portrayed. This drawing was figured by Parkinson (1978) and Parkinson & Rogers-Price (1984). Duplicate figures by Abbot were reproduced for Plates 8 and 9 of Boisduval & Le Conte (1829-[1837]). "Glaucus" is penciled on the drawing in Swainson's hand. It is interesting that Abbot followed contemporary wisdom in treating this form as a separate species from the butterflies in drawing no. 10, especially since he reared both and noted that each fed on "Swamp Ash". Moreover, he portrayed slightly different immatures in these drawings. Abbot possibly knew the truth about this form, but was hesitant to refute more "learned" naturalists who were also paying customers.			
9	<i>Papilio palamedes</i> Drury Dm, Vm, La, Pa	<i>Magnolia virginiana</i> L. (Magnoliaceae) [E]	9. Large yellow spotted black swallow tailed Butterfly. Feeds on the Bay figured. Tied up 30 th May, changed the 31 st bred 14 th June. Another that changed the 18th Sepr was bred the 24 th March. The Caterpillar is not common to be met with. But the Butterfly is frequent all over the Country.
NOTES: see Fig. 1. Duplicate figures of the larva and pupa by Abbot were reproduced for Plate 5 of Boisduval & Le Conte (1829-[1837]). "Calchas," a misspelling of the junior synonym <i>Papilio calchas</i> Fabricius, is penciled on the drawing in Swainson's hand. <i>Magnolia virginiana</i> is often listed as a hostplant of this species, but it is toxic to the larvae (Scriber 1986, Scriber et al. 2000). Brooks (1962) noted that larvae of <i>P. palamedes</i> would not accept this plant in Georgia. Two other Abbot drawings of <i>P. palamedes</i> with <i>M. virginiana</i> are preserved at The Natural History Museum, London. They are duplicates of one another, but slightly different from the drawing in New Zealand and probably completed about a decade earlier. Scudder (1888-1889) examined one of these and identified the depicted plant as <i>Magnolia glauca</i> (L.), now considered to be a synonym of <i>M. virginiana</i> . This drawing was figured by Rogers-Price (1984) and Gilbert (1998, 2000). Scudder's discussion of this drawing is the source of all subsequent claims that this butterfly feeds on <i>M. virginiana</i> . Abbot portrayed this butterfly only with <i>M. virginiana</i> . He identified the plant in two duplicate drawings as "Magnolia glauca," but this appears to have been an aesthetic substitution or he incorrectly recalled the host when he later illustrated the life history of this butterfly. Scudder (1888-1889) also remarked that Florida naturalist William Wittfeld reported the hostplant to be "red bay," which Wittfeld identified as " <i>Magnolia glauca</i> ." However, Wittfeld probably associated the wrong Latin name with his report of "red bay," which is applicable to <i>Persea borbonia</i> (L.) Spreng., the only acceptable host of this butterfly in Florida (Scriber et al. 2000). <i>Magnolia virginiana</i> is known as "sweet bay." The pupa is too colorful, but conceptually accurate.			
10	<i>Papilio glaucus</i> L. Dm, Vm, La, Pa	<i>Ptelea trifoliata</i> L. (Rutaceae) [C] "Swamp Ash" (probably <i>Fraxinus pennsylvanica</i> Marsh.) (Oleaceae) is also a confirmed hostplant.	10. <i>Papilio Turnus</i> . Feeds on the <i>Ptelea trifoliata</i> , and Swamp Ash, Tied itself up 19 th June. changed 20 th bred 4 th July. May be met with thinly scattered over all parts of the Country.
NOTES: see drawing no. 8. This drawing was reproduced in ATLET (1983) and figured by Rogers-Price (1983). Duplicate figures by Abbot were reproduced for Plates 6 and 7 of Boisduval & Le Conte (1829-[1837]). "Turnis", a misspelling of the junior synonym <i>Papilio turnus</i> L., is penciled on the drawing in Swainson's hand. Abbot also used this name.			
11	<i>Papilio cresphontes</i> Cramer Dm, Vm, La, Pa	<i>Zanthoxylum clava-herculis</i> L. (Rutaceae) [C] "Prickly Ash" refers to <i>Z. clava-herculis</i> . "Orange tree" (<i>Citrus</i> sp.) (Rutaceae) is also a confirmed hostplant.	11. <i>Papilio Thoas</i> . Feeds on the Prickly Ash, and the Orange tree, Tied up the 6 th May, changed the 7 th bred the 27 th another that changed the 15 th May, was bred 3 ^d June, and another that changed the 30 th June, bred 19 th July. Is to be met in the Gardens of the City of Savannah, and the neighbourhood, but not a few miles back in the inland parts.
NOTES: this drawing was reproduced in ATLET (1983) and figured by Parkinson & Rogers-Price (1984). Duplicate figures by Abbot were reproduced for Plates 12 and 13 of Boisduval & Le Conte (1829-[1837]). The cultivation of orange trees was probably responsible for the occurrence of this butterfly "in the Gardens of the City of Savannah." The name " <i>Papilio Thoas</i> " (i.e. <i>Papilio thoas</i> L.) was used for <i>P. cresphontes</i> until these very similar butterflies were recognized as different species many years later.			

TABLE 1. Continued.

Drawing No.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot
12	<i>Ascia monuste</i> (L.) Dm, Df(2), Vf, La, Pa	<i>Cleome gynandra</i> L. (Capparaceae) [C] "Cleome pentaphilles," a misspelling of <i>C. pentaphylla</i> L., is a synonym of <i>C. gynandra</i>	12. <i>Papilio Danai</i> Cleome. Feeds on the <i>Cleome pentaphilles</i> . Tied up 16th July, changed 17 th , bred 23 ^d . Many of the female Butterflies varies being of a dingy black as figured. This Butterfly is some Summers very plenty in Savannah breeding in the Gardens & yards where the plant grows in plenty but is rare in the Inland parts.
13	<i>Cercyonis pegala</i> (Fabricius) Dm, Df, Vf, La, Pa	<i>Panicum</i> sp, possibly <i>P. dichotomiflorum</i> Michx. or <i>P. rigidulum</i> Nees (Poaceae) [NC]	13. Great meadow brown Butterfly. Feeds on the grass figured, and other grasses, Tied up 19 th June, changed 20 th bred 5 th July. Frequents the pine woods &c. Is not common.
14	<i>Herneupychia sosybius</i> (Fabricius) Dm, Df, Vm, Lu, Pa	<i>Carex</i> sp., possibly <i>C. hyalinolepis</i> Steudel (Cyperaceae) [NC]	14. Small Ringlet. Feeds on the Twisted Grass, figured, and other Grasses, Tied up Aug 23 ^d changed 24 th bred 1 st Sepr. Frequents the Swamps and fields, is not very common
15	<i>Asterocampa celtis</i> (Boisduval & Le Conte) Dm, Df, Vm, Lu, Pa	<i>Celtis</i> cf. <i> tenuifolia</i> Nutt. (Celtaceae) [C] "Sugarberry" refers to the figured <i>Celtis</i> .	15. <i>Papilio Portlandia</i> . Feeds on the Sugarberry, tied up 6 th May, changed 7 th bred 20 th . Is very rare.

NOTES: this drawing was figured by Calhoun (2004) and a duplicate drawing was figured by Gilbert (1998). Duplicate figures by Abbot were also reproduced for Plate 16 of Boisduval & Le Conte (1829-[1837]) (Calhoun 2004). Pencil on the drawing in Swainson's hand is "no 12". Abbot's name for this species is derived from the Linnaean classification system, where *Papilio* is the genus and *Danai* is a group that includes the Pieridae. "Cleome" is a name that Abbot coined based on the hostplant. Abbot's notes aptly describe the irregular migratory presence of the subspecies *A. m. phileta* (Fabricius) in coastal Georgia (Calhoun 2004).

NOTES: portions of a duplicate drawing by Abbot were reproduced for Plate 59 of Boisduval & Le Conte (1829-[1837]) (the figure of the larva was reversed). The plant was identified in ATLET (1983) as *Panicum* [sic] *agrostoides* Sprengel, now considered to be a synonym of *P. rigidulum*. This drawing prompted Parkinson (1983b) to question the subspecific arrangement of *C. pegala*, particularly the identity of *C. pegala abbotti* Brown. This subspecies was named in honor of John Abbot by Brown (1969), who believed that the butterflies figured by Boisduval & Le Conte as *Satyrus alope* (= *C. pegala alope* Fabricius) actually portrayed an undescribed subspecies found in southeastern Georgia and northern Florida. Parkinson argued that the adult figures in the drawing in New Zealand, as well as the duplicates in Boisduval & Le Conte (1829-[1837]), are inconsistent with this phenotype as defined by Brown (1965). I agree, as Abbot's figures are consistent with *C. p. pegala* that occurs in eastern Georgia. Abbot's English name for this butterfly was derived from its superficial resemblance to the common European butterfly, *Maniola jurtina* (L.), known in Britain as the "meadow brown" since the early eighteenth century. In 1769, Abbot illustrated specimens of this species that he had collected in England, using this name to identify them (Library of the Carnegie Museum of Natural History).

NOTES: this butterfly is known to feed only on grasses (Poaceae). Abbot may have collected the wrong plant for his illustration, possibly confusing it with the host of *Neonympha areolatus* (J. E. Smith), which feeds on sedges (Cyperaceae). Abbot supplied the same notes and used the name "Twisted Grass" for the plant illustrated in another drawing of *H. sosybius* now deposited at The Natural History Museum, London. That drawing portrays a twisted-leaved species of yelloweyed grass, probably *Xyris caroliniana* Walter, not a true grass but a member of the Xyridaceae and an erroneous host. Because Abbot figured a different plant for Swainson, he crossed-out "Twisted" to reflect this change. To Abbot, sedges were simply "grasses." The depicted larva lacks the pair of posterior appendages that are present in this species. Abbot included a more accurate larva in at least two other drawings of this species, but later applied it to *Cyllopsis gemma* (Hübner). Abbot's English name for this butterfly was derived from its remote similarity to the widespread European species, *Aphantopus hyperantus* (L.), which has been known as the "ringlet" in Britain since the mid-eighteenth century. In 1769, Abbot illustrated specimens of this species that he had collected in England, using this name to identify them (Library of the Carnegie Museum of Natural History).

NOTES: portions of a duplicate drawing by Abbot were reproduced on Plate 57 of Boisduval & Le Conte (1829-[1837]) to accompany the original description of this species. The larva, and possibly also the pupa, is *A. clyton* (drawing no. 16). Boisduval & Le Conte (1829-[1837]) and Scudder (1858-1859) identified the depicted plant as *Celtis occidentalis* L. (Celtaceae). Abbot repeatedly misapplied the name "*Papilio Portlandia*" (i.e. *Papilio portlandia* Fabricius) to this species (see text).

TABLE 1. Continued.

Drawing No.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot
16	<i>Astererocampa clyton</i> (Boisduval & Le Conte) Dm, Vm, Lu, Pu	<i>Vaccinium stamineum</i> L. (Ericaceae) [E] "Sugarberry" refers to <i>Celtis</i> .	16. Orange coloured Butterfly. Feeds on the Sugarberry. Tyled up 20 th May. changed 21 st bred 9 th June. Is very rare
<p>NOTES: see Fig. 2. The immatures and plant in this drawing are all unrelated to the adults (see text). Despite the figured <i>Vaccinium</i>, this butterfly is known to feed only on <i>Celtis</i> trees (Celtaceae). Abbot identified the plant in a duplicate drawing as "Wild gooseberry." Two additional drawings of this species by Abbot portray the same figures. Abbot incorrectly associated the larva, and possibly also the pupa, with the closely related <i>A. celtis</i>, which feeds on the same hostplants (see drawing 15). He probably found few immatures of these species and misidentified those that he later collected for his drawings. Abbot ultimately fabricated immatures for <i>A. clyton</i>, modeling them after <i>Polygonia interrogationis</i> (Fabricius) (see text). Abbot probably observed that the adults of these species even shared similar color forms, reinforcing this perceived relationship. He duplicated these erroneous figures for all his subsequent life history illustrations of <i>A. clyton</i>. Boisduval & Le Conte (1829-[1837]) apparently recognized this mistake. Although their Plate 56 of <i>Apatura clyton</i> was credited to Abbot, it appears to have been constructed using figures from other sources, including an altered version of Abbot's larva of <i>A. celtis</i> (actually <i>A. clyton</i>). The hostplant on the published plate was equally erroneous, being a species of <i>Ilex</i>, possibly <i>I. decidua</i> Walt. (Aquifoliaceae). Scudder (1888-1889) identified the larva as <i>P. interrogationis</i> and the pupa as <i>Polygonia comma</i> (Harris). I have found no evidence that Abbot encountered <i>P. comma</i> in Georgia, nor does the depicted larva resemble that species.</p>			
17	<i>Chlosyne gorgone</i> (Hübner) Dm, Df, Vf, La, Pa	<i>Helianthus divaricatus</i> L. (Asteraceae) [C] "Cross wort" apparently refers to <i>H. divaricatus</i> (see Calhoun 2003). This is possibly a misapplication of an English name for the British yellow-flowered herb, <i>Cruciata laevipes</i> Opiz (Rubiaceae). "Sunflower" probably indicates another species of <i>Helianthus</i> .	17. Cross wort Fritillary Butterfly. Feeds on the Cross wort, and sunflower, Tyled itself up by the tail 16 th May, changed 17 th bred 26 th . Frequents the Oak Woods of Burke County but is not common.
<p>NOTES: this drawing was figured in Parkinson & Rogers-Price (1984) and Calhoun (2003). Duplicate figures by Abbot were reproduced for Plate 46 of Boisduval & Le Conte (1829-[1837]) to accompany the original description of the enigmatic taxon <i>Melitaea ismeria</i> (Calhoun 2003, 2004, 2005, 2006b). The depicted larva is conceptually consistent with <i>C. gorgone</i>. "Fritillary" is a misspelling of the British name "Fritillary."</p>			
18	<i>Libytheana carinenta</i> (Cramer) Dm, Vm, La, Pa	<i>Celtis</i> cf. <i>tenuifolia</i> Nutt. (Celtaceae) [C] "Sugarberry" and "Hackberry" refer to <i>Celtis</i> .	18. Snout Butterfly. Feeds on the Sugarberry, or Hackberry, Tyled up 28 th April. changed 29 th bred 8 th May. Is rare.
<p>NOTES: this drawing was figured in Calhoun (2004). With the exception of the adult figures, most of a duplicate drawing by Abbot was reproduced for Plate 64 of Boisduval & Le Conte (1829-[1837]) (Calhoun 2004). Scudder (1888-1889) identified the plant in duplicate drawings as <i>Celtis occidentalis</i>. Species of <i>Libytheinae</i> have long been called "Snout" butterflies.</p>			
19	<i>Pyrisitia lisa</i> (Boisduval & Le Conte) Dm, Df, Vm, La, Pa	<i>Senna occidentalis</i> (L.)Link (Fabaceae) [C] "Cassia tochida persova" is an allusion to <i>Cassia foetida</i> and its author, C. H. Persoon (see text); a synonym of <i>S. occidentalis</i> . "Cassia chamaecusta" is a misspelling of <i>Cassia chamaecrista</i> L., which is a synonym of <i>Chamaecrista fasciculata</i> (Michx.)Green (Fabaceae). This is also a confirmed hostplant.	19. Little yellow Butterfly. Feeds on the Cassia tochida persova but is most frequent on the Cassia chamaecusta. Tyled up 6 th Sepr changed 7 th bred the 13 th .
<p>NOTES: duplicate figures were reproduced for Plate 19 of Boisduval & Le Conte (1829-[1837]) to accompany the original description of this species.</p>			

TABLE 1. Continued.

Drawing No.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot
20	<i>Eurema daira</i> (Godart) Dm, Df, La, Pa	<i>Chamaecrista fasciculata</i> (Michx.)Greene [C] "Cassia chamaecrista" is a misspelling of <i>Cassia chamaecrista</i> L., which is a synonym of <i>Chamaecrista fasciculata</i> .	20. Black streaked little yellow Butterfly. Feeds on the <i>Cassia chamaecrista</i> Tied itself up 27 th August changed 28 th bred 5 th Sep. Both these kinds [this and <i>E. lisa</i> ; drawing no. 19] is common in all parts of the Country in Autumn, and settles so many together at times to suck moist places in roads &c, that I seen 20 in the compass of a hat, but this species is not quite so common as the last.
NOTES: the winter (dry season) form of the species is portrayed. A portion of a duplicate drawing by Abbot was reproduced for Plate 18 of Boisduval & Le Conte (1829–[1837]) (Calhoun 2004).			
21	<i>Thorybes bathyllus</i> (J. E. Smith) Dm, Df, Vf, La, Pa	<i>Desmodium</i> sp., possibly <i>D. paniculatum</i> (L.)DC. (Fabaceae) [C] "Begger's lice" refers to the figured <i>Desmodium</i> .	21. Brown Skipper. Feeds on the Beggars lice, spun up in the leaves 18 th Octr bred 20 th April. is not very common.
NOTES: this drawing was reproduced in ATLET (1983). It was also figured by Reynolds (1983) and Rogers-Price (1983). Portions of a duplicate drawing by Abbot were reproduced for Plate 74 of Boisduval & Le Conte (1829–[1837]). Like the Abbot drawing used for the original description of <i>Papilio bathyllus</i> in Smith & Abbot (1797), the females in this composition may portray <i>Thorybes confusus</i> Bell (Calhoun 2006a). The plant was identified in ATLET (1983) as <i>Desmodium fernaldii</i> B.G.Schub. (Fabaceae).			
22	<i>Erynnis martialis</i> (Scudder) Dm, Df, Vf, La, Pa	<i>Indigofera caroliniana</i> Mill. (Fabaceae) [E] In this case, "Wild Indigo" apparently refers to <i>Indigofera</i> , not a species of <i>Baptista</i> (Fabaceae).	22. Least Dingy Skipper. Feeds on the Wild Indigo. spun up in the leaves 25 th June. bred 8 th July. Frequents the Oak woods. is much less common than the other Dingy Skippers.
NOTES: this species is known to feed only on <i>Ceanothus americanus</i> L. (Rhamnaceae) in eastern North America. In fact, Abbot illustrated this skipper with <i>C. americanus</i> for an earlier composition, calling the plant "Red shank or red Root." His notes for other drawings also refer to "Red Root or red shank." Abbot's mistaken recollection of an alternate host may have resulted in the inclusion of <i>I. caroliniana</i> . He called all the species of the genus <i>Erynnis</i> "Dingy Skippers," after the European <i>Erynnis tages</i> (L.), which has long been called the "dingy skipper" in Britain			
23	<i>Pyrgus communis</i> (Grote) Dm, Df, Vf, La, Pa	<i>Sida acuta</i> Burm. f. (Malvaceae) [C]	23. Black and white Skipper. Feeds on the plant figured. Spun up in the leaves 25 th June bred 7 th July. Is to be met with in the Oak woods and fields, is not common.
NOTES: see Fig. 3. "Thymale" (a misspelling of the genus name <i>Thymele</i> Fabricius) is penciled on the drawing, probably in Swainson's hand. The skippers portrayed in this drawing are almost certainly <i>P. communis</i> , as there is no evidence that the similar <i>Pyrgus albescens</i> Plötz occurred in Georgia during Abbot's lifetime (see text).			
24	<i>Problema bulenta</i> (Boisduval & Le Conte) Dm, Df, Vm, La, Pa	<i>Panicum</i> sp., possibly <i>P. dichotomiflorum</i> Michx. or <i>P. virgatum</i> L. (Poaceae) [NC] "Broad grass" refers to this or a similar species of grass. Abbot misidentified the figured plant as " <i>Zozani aquatica</i> ", a misspelling of <i>Zizania aquatica</i> L. (Poaceae).	24. Feeds on the Broad grass, <i>Zozani aquatica</i> folding itself up in the leaf, changed 25 th bred 6 th Augt. Frequents Rice fields, ditches, and the sides of ponds in the lower parts of Georgia—is not common.
NOTES: duplicate figures by Abbot were reproduced for Plate 67 of Boisduval & Le Conte (1829–[1837]), representing the "original description" of this species (see text). Little is known about the biology of this skipper. Larvae have been found on <i>Spartina cynosuroides</i> (L.)Roth (Poaceae) in New Jersey (Cromartie & Schweitzer 1993) and southward it has been associated with <i>Zizaniopsis miliacea</i> (Michx.) Döll & Asch. (Poaceae) (Opler & Krizek 1984). Larvae have also been found and reared on <i>Phragmites australis</i> (Cav.)Trin. ex. Steud. (Poaceae) (Schweitzer 2006). Although confined females will oviposit on <i>Panicum</i> (Cromartie & Schweitzer 1993), Abbot probably did not find larvae on it. This skipper may feed on <i>Z. aquatica</i> as Abbot indicated, or he confused this grass with the similar <i>Z. miliacea</i> . <i>Problema bulenta</i> was possibly more plentiful in southern Georgia where rice plantations offered additional wetland habitat (see text). Although Abbot did not provide an English name for the insect in this drawing, he used "Broad grass Skipper Butterfly" for duplicate drawings.			

TABLE I. Continued.

Drawing No.	Figured adults and early stages	Plant species and host status	Manuscript entry by J. Abbot
25	<i>Ancyloxypha numitor</i> (Fabricius) Dm, Df, Vm, La, Pa	<i>Justicia ovata</i> (Walter)Lindau (Acanthaceae) [E]	25. <i>Least Skipper</i> . Feeds on the plant figured, changed 12 th Sepr bred 22 ^d . Is frequent in Rice fields and Meadowy parts of brooks
NOTES: this species is a grass-feeder. <i>Justicia</i> grows in the wet habitats where this skipper occurs, thus Abbot may have confused the host. However, an earlier composition of <i>A. numitor</i> includes a different erroneous host, <i>Asclepias verticillata</i> L. (Apocynaceae), which occurs in dry soils. Abbot ambiguously referred to both plants as "the plant figured," suggesting that he did not recall the proper host or inserted these more colorful plants to enhance his compositions.			
26	<i>Satyrium liparops</i> (Le Conte) Dm, Df, La, Pa	<i>Crataegus</i> sp., possibly <i>C. viridis</i> L. (Rosaceae) [C] "Parsley haw" refers to <i>Crataegus</i> . "Oaks" (<i>Quercus</i>) (Fagaceae) are also fed upon by <i>S. liparops</i> .	26. <i>Brown hair Streak Butterfly</i> . Feeds on the Parsley haw, and Oaks, Tied up 16 th April, changed 18 th bred 5 th May. This species frequents the Oak woods on the edge of Ogechee River swamp. is very rare.
NOTES: unlike his other butterfly compositions, the ventral surface of the adult is not portrayed. Another drawing by Abbot was reproduced on Plate 31 of Boisduval & Le Conte (1829-[1837]) to accompany the original description of this species, which remained poorly understood for over a century (See Calhoun 2004, 2005). For other drawings, Abbot called this species the "Ogechee Brown hair Streak Butterfly," a misspelled reference to the occurrence of this species in the vicinity of the Ogechee River of eastern Georgia.			
27	<i>Callophrys henrici</i> (Grote & Robinson) Dm, Df, Vm, La, Pa	<i>Vaccinium corymbosum</i> L. (Ericaceae) [C] "Swamp huckleberry" probably refers to the figured <i>Vaccinium</i> , but the same plant is portrayed in drawing no. 28 under a different name. "Judas tree" refers to redbud (<i>Cercis canadensis</i> L.) (Fabaceae). The adults that Abbot saw frequenting the blossoms of redbud may have included ovipositing females, as this tree is also a confirmed host.	27. <i>Black brown hair streak Butterfly</i> . Feeds on the Swamp huckleberry, tied itself up 18 th April, changed the 20 th bred 6 th May. The Butterfly frequents the blossoms of the Red bud or Judas tree, on the borders of Swamps, is far from common.
NOTES: see Fig. 4. Duplicate figures by Abbot of the larva and pupa were reproduced for Plate 31 of Boisduval & Le Conte (1829-[1837]). Abbot spelled "tied" in the notes for this drawing, but spelled it "Tyed" elsewhere. See the text and Calhoun (2006a) for discussions of Abbot's uneven spelling and grammar. Pupae of this species typically overwinter, but Abbot's notes suggest that his larva developed into an adult during the same season.			
28	<i>Calycopis cecrops</i> (Fabricius) Dm, Df, Vm, Lu, Pa	<i>Vaccinium corymbosum</i> L. (Ericaceae) [NC] "Black Huckleberry" apparently refers to the depicted <i>Vaccinium</i> , but the same plant is portrayed in drawing no. 27 under a different name.	28. <i>Small purple Hair streak Butterfly</i> . Feeds on the Black Huckleberry &c. tyed up 28 th April. changed 20 th bred 20 th May. the Butterfly is frequent in most parts of the Country.
NOTES: the female butterfly in this drawing was misidentified in ATLET (1983) as the Neotropical species <i>Strymon martialis</i> Herrich-Schäffer. The depicted plant was identified in ATLET (1983) as <i>Gaylussacia frondosa</i> (L.) Torrey & A. Gray ex Torrey. The larva of this species is not green, but rather brown or pinkish-brown.			
29	<i>Cupido comyntas</i> (Godart) Dm, Df, Vm, Lu, Pa	<i>Phaseolus polystachios</i> (L.) Britton et al. (Fabaceae) [C] "Red Root or redshank" was Abbot's name for <i>Ceanothus americanus</i> L. (Rhamnaceae), an unlikely host for this legume-feeder.	29. <i>Least blue Butterfly</i> . Feeds on the kind of wild pea figured, Red Root or redshank &c. Tyed itself up June 16 th bred 24 th is not common in the lower parts of the Country.
NOTES: duplicate figures were reproduced for Plate 36 of Boisduval & Le Conte (1829-[1837]). The larva exhibits dark pattern elements that are not associated with this species.			

DISCUSSION

Life History notes. Abbot arranged most of his sets of elaborate life history drawings in loose order, grouping similar species such as butterflies, moths, and beetles. He recorded information about each species on a separate manuscript, which he often entitled “Notes to the Drawings of Insects.” These remarks, largely copied from a set of master notes, included names, hostplants, rearing dates, habitats, and other pertinent information.

Although Abbot employed a legible English round-hand writing style, his spelling and grammar were decidedly irregular. Walton (1921) attributed this to several possible factors, including the approach of senility, but Abbot’s grammar improved over time (Calhoun 2006a). Dow (1914) believed that Abbot’s misspellings “reveal the man,” yet they reveal just as much about the period in which he lived. Spelling was not standardized during much of Abbot’s life. It was largely phonetic, often resulting in different spellings of the same word within a single document. For example, Abbot typically wrote “tyed,” but he spelled the word “tied” in the notes for a drawing that he sent to Swainson (Table 1, no 27). He even varied the spellings of people’s names. Following the conventions of the period, Abbot’s punctuation was sporadic and he routinely capitalized nouns within sentences. Swainson was similarly criticized for his spelling and grammar. Günther (1899–1900) observed that Swainson was “loose in his style of writing; he persistently misspelt not only technical terms, but also the names of foreign authors, and even of some of his familiar friends and correspondents.” Deane (1905) referred to Swainson’s “crude method of writing and expressing himself.” The widely publicized journals of the Lewis and Clark Expedition (1803–1806) contain countless examples of such casual spelling and sentence structure.

Abbot identified most of the insects and plants in his drawings using either English or Latin names. While a few of the English insect names were of local origin in America, Abbot invented others based on appearance, habitats, hostplants, and localities. Examples include “Orange colored Butterfly,” “Broad grass Skipper Butterfly,” “Swamp brown Butterfly,” and “Georgia Skipper Butterfly.” He also adopted names used in Britain, such as “Meadow Brown,” “Ringlet,” and “Dingy Skipper” (Table 1). His general names of “swallow tailed Butterfly,” “Frittillary” (sic.), “Hair streak,” and “Skipper” are also of British origin, dating to the seventeenth and eighteenth centuries. Abbot used some of these names for drawings that he completed before leaving London (Library of the Carnegie Museum of Natural History). Some of his new

names, such as “Great Purple hair Streak Butterfly,” are still used.

By the time Abbot finished his drawings for Swainson, he was more often employing Latin names to identify American insects and plants. A set of early drawings that Abbot completed in London between 1766 and 1772 (Houghton Library) indicates that he was willing to use Latin names when he knew them. However, his access to scientific publications in America was limited. The notebooks of Dru Drury (1725–1804) at The Natural History Museum, London, record that Abbot subscribed to at least a portion of Drury’s “*Illustrations of Natural History*” (Drury 1770–1782), but Abbot did not always abide by its Latin names. Most of the Latin names that he initially used for American species are Linnaean and were probably suggested by Augustus G. Oemler (1770–1854), a naturalist of Savannah, Georgia, whom Abbot met in 1805. Oemler’s influence is supported by the lack of Latin names in Abbot’s earlier notes for Smith & Abbot (1797). Oemler was familiar with Linnaean classification, as shown by his 1834 remark that Abbot “never knew any thing of Linneus’ [sic] Classification till I demonstrated it to him” (Dow 1914) (this is misleading, as Abbot was probably long familiar with the work of Linnaeus). In an 1851 letter to Thaddeus W. Harris (Mayr Library), Oemler stated that he “had no new work on insects presenting modern classification,” implying that he possessed older publications, like those by Carolus Linnaeus (Carl von Linné) and perhaps also Johann C. Fabricius. Oemler may be responsible for Abbot’s repeated misapplication of the name “*Papilio Portlandia*” (i.e. *Papilio portlandia* Fabricius) for drawings of the butterfly *Asterocampa celtis* (Boisduval & Le Conte), which was not named until 1835 (Table 1, no. 15). In an 1851 letter, Oemler asked T. W. Harris to “correct some errors I may have committed in naming” the insects in Abbot’s drawings (Mayr Library).

John Francillon (1744–1816) may also have suggested Latin names to Abbot. Francillon served as Abbot’s London agent for many years, selling his specimens and illustrations to European patrons. He was acquainted with the prominent naturalists of the period, amassing a large library and collection of insects. At the time of his death, Francillon possessed up to 4,000 of Abbot’s insect specimens (King 1817, 1818) and nearly 3,000 of his drawings. Countless others passed through his hands during their long relationship. Francillon’s collection of Abbot drawings is now preserved at The Natural History Museum, London. Many bear Linnaean and Fabrician names that were written by an unidentified contemporary naturalist. Francillon later added these names to his accompanying transcriptions of Abbot’s

notes (Calhoun 2005). By 1813, Abbot was also using Latin insect names that were first proposed in Smith & Abbot (1797).

Abbot's master set of notes seems to have initially included only English names. His use of Latin names became more frequent as he grew older. His early name for the butterfly *Papilio palamedes* Drury was descriptive, but cumbersome: "Large yellow spotted black swallow tailed Butterfly." By the time he completed the drawings for Swainson, he had begun calling this species "*Papilio Chalcas*," a synonym of *P. palamedes*. More often than not, his Latin names were misspelled and they varied between sets of drawings. He probably did not own the reference publications and may have relied on memory. Among the drawings for Swainson, he identified a plant as "*Cassia tochida persova*," which is a severely corrupted spelling of *Cassia foetida* and its author, C. H. Persoon (Table 1, no. 19). In notes for Augustus Oemler (Houghton Library) he wrote the same name as "*Cassia tochida persoon*." Notes for an earlier drawing for John Francillon merely identified the plant as "yellow Indigo." In his notes for Swainson, Abbot also referred to "*Cassia chamaecusta*" instead of *Cassia chamaecrista* L. (Table 1, nos. 19, 20). Additional spellings of this plant for Oemler are almost unrecognizable; "*Cassia Arameecrista*" and "*Cassia Acamaecusta*." In earlier notes for Francillon he identified this plant as "Sensitive Flower." If Abbot did not know the identity of the plant, he referred to it as "the plant figured" or "the flower figured." He generally considered his written observations to be "rude notes" that did not require absolute accuracy (Calhoun 2006a).

Abbot frequently varied his written information on hostplants, thus the plants in his drawings are not always consistent with his accompanying notes. Abbot often updated his remarks to reflect new observations and also sought to keep the information from becoming too stale and repetitive. While some of the hostplants mentioned in his notes are erroneous, his other comments about the life cycles of Lepidoptera are essentially accurate. For most butterflies, he recorded the dates that each species "tyed up" (larva suspended prior to pupation), "changed" (pupated), and "bred" (eclosed as an adult). For skipper butterflies of the family HesperIIDae, he recorded when the larva "spun up" or "spun up in the leaves" (pupated). Later on, Abbot usually omitted the dates when a species "tyed up." Regardless of a species' voltinism, he usually only documented a single brood and repeated this information, with little revision, for subsequent drawings. The American naturalist Titian R. Peale claimed that Abbot received larvae from others and

"generally only learned what species they belonged to when the butterfly or moth came from the chrysalid or pupa" (dos Passos 1951). This may have been true in some cases, but Abbot personally collected eggs and larvae in nature and reared them on the associated plants. He wrote that he had "taken" larvae on given plants and commented on the abundance of the caterpillars in nature, indicating that he actively searched for them in the field. Mature larvae were probably most often collected.

When discussing the abundance of insects in Georgia, Abbot used vague terms like "rare," "uncommon," "not very common," "frequent," and "abundant." Abbot wrestled with these definitions, stating in 1835, "I find it very difficult to know what Insects are rare & what are common, except a very few kinds" (transcribed letter to T. W. Harris, Mayr Library). Clearly frustrated, he observed that insects were "very local," noting that some occurred "on one side of a Creek, & none on the other." "Every Year," he remarked, "I have observed some few kinds to be plenty, if not common & then not to be met again with, for years after." Unfortunately, this uncertainty makes it very difficult to reconcile his comments with what we know today about the abundance of these species.

Duplication. Out of convenience, Abbot evidently relied on templates to produce duplicate illustrations of insects and birds. He probably maintained pattern books of individual figures, as well as entire compositions. The insect templates were numbered and corresponded to entries in his master set of notes. For a time, Abbot numbered his insect drawings and notes to coincide with the numbers that he used for his template compositions. These numbers were probably also used by Abbot and Francillon to take orders for specific drawings. Based on the numbers that Abbot used, his templates were arranged in order of completion. If so, the first butterfly template that he completed was of the dark form female of *Papilio glaucus* L., followed by *Papilio palamedes* Drury. The yellow form of *P. glaucus* was identified as no. 274. Abbot did not use these numbers for the drawings for Smith & Abbot (1797), indicating that he began using composition templates after about 1795. By the time Abbot completed his set for Swainson, he had begun listing his drawings in numerical order. Abbot's many references to Burke County, Georgia, suggest that the majority of his templates had been completed by 1806 when he moved from Burke County to Savannah, Chatham County.

An examination of Abbot's work indicates that he likely traced all of his figures. This is most obvious in six butterfly illustrations for Augustus Oemler (Houghton Library) that include uncolored plant figures, whose

graphite outlines are unbroken and clearly traced. Even when not using templates, he probably first sketched his figures on scrap pieces of paper to conserve his more expensive drawing paper. Abbot may have placed his templates and sketches against a brightly lit window pane, then traced the backlit images onto blank sheets. He could thereby produce multiple drawings and layouts with minimal effort. To avoid sending duplicates to the same patron, Abbot kept records of the illustrations that he sold. In 1818, he complained that he had “lost or mislaid the list of the last Drawings” that he had sent to Heinrich Escher-Zollikofer (Kroch Library). Despite his numerous duplicates, he did not rely entirely on templates and frequently rendered new figures to minimize repetition. This is especially true for his drawings that did not include plants.

Although Rogers-Price (1983) claimed that most of Abbot’s compositions appear only once within his existing corpus of artwork, this does not apply to his elaborate life history drawings of Lepidoptera. My comparison of over 180 of Abbot’s butterfly life history drawings reveals that he duplicated the majority of his compositions for 20–25 years. For others, he updated the layouts with new figures of adult insects and plants, replacing them to reflect new observations or merely to invigorate the designs. These revised compositions were copied for the remainder of his career, joining those that he had previously duplicated. Conversely, he illustrated the early stages of most species only once and duplicated these figures for subsequent drawings. He began this practice no later than during the preparation of his drawings for Smith & Abbot (1797). For a few species, he created alternate figures of larva and pupa that were also duplicated. Errors that were committed during the creation of his templates were consequently repeated for multiple drawings. These errors were reiterated for many years thereafter, as Scudder (1888–1889) reproduced many of Abbot’s figures. Holland (1898, 1931) copied many of Scudder’s reproductions, thus conveying the errors well into the twentieth century. Most, if not all, of the adult specimens in Abbot’s Lepidoptera drawings did not develop from the larvae and pupae portrayed with them.

The butterfly compositions for Smith & Abbot (1797), completed *ca.* 1783–1792, were not duplicated, probably because Abbot intended them for publication (he did duplicate some larvae and pupae for later drawings). Sometime around 1800, Abbot began producing a new series of butterfly life history compositions. With few exceptions, he duplicated these for many years, probably into the mid-1820s. During the late 1820s, the elderly Abbot seems to have

switched to less complex geometric designs of adults without hostplants or immatures. He perhaps abandoned the production of larger illustrations shortly after 1830, but continued to produce small drawings of single insects until at least 1835 (see below). Abbot’s compositions, numbering methods, names, and other notations aid in dating drawings of unknown provenance. Duplication is also common among Abbot’s bird drawings, where similarities are associated with dates of completion (Simpson 1984, 1993).

All 22 butterfly watercolors for Swainson are duplicated in other sets of Abbot’s illustrations, including the life history drawings that formed the basis of plates in Boisduval & Le Conte (1829–[1837]) (Table 1). These drawings, derived from three separate sets that are believed lost, were probably completed between 1810 and 1815. The Swainson set also shares duplicate figures of adults, larvae, and pupae with other plates in Boisduval & Le Conte (1829–[1837]) that were reproduced from drawings now in the Thomas Cooper Library (University of South Carolina) (Calhoun 2004). Based on comments in Abbot’s correspondence, these drawings were begun in 1813. Abbot even shared identical figures of plants between different insect species. A drawing of a katydid (*Amblycorypha floridana* Rehn & Hebard) for Swainson includes the same representation of *Ipomoea pandurata* (L.) G. Meyer (Convolvulaceae) as a drawing of a butterfly (*Achalarus lyciades* (Geyer)) for Oemler. Abbot also had a penchant for copying bird illustrations by other artists (Simpson 1984, 1993), but I have not found this to be true of his insect drawings.

Artistic license. The botanist William Baldwin of Savannah, Georgia, wrote in 1811, “I have looked over, with great pleasure, the interesting drawings of the amiable Mr. Abbott... They are, as far as I am qualified for judging, exquisitely beautiful and scientifically accurate.” Four years later, Baldwin complained, “Abbott’s drawings, though beautiful, are generally very defective” (Darlington 1843). Scudder (1888, 1888–1889) perceived “a mark of carelessness in some of the figures of early stages which is not found in others.” These contradicting interpretations expose the true nature of Abbot’s artwork. The quality and accuracy of Abbot’s drawings are inconsistent, seemingly supporting Swainson’s (1840) claim that Abbot employed “one or two assistants, whose copies he retouched.” Faxon (1896) suggested that Abbot may have redrawn bird sketches that he received from “assistants” without confirming their accuracy. However, there are no references to such assistants among Abbot’s numerous surviving letters and manuscripts, including those for Swainson. More likely,

Abbot's haste to fulfill orders sometimes resulted in a measure of complacency.

During the course of my research, it quickly became apparent that Abbot's illustrations frequently deviate from reality. Some of his Lepidoptera drawings include figures of larvae, pupae, and plants that are inconsistent with the associated adults. Larvae can be very difficult to assign to species, while a few are clearly fictitious (Calhoun 2003, 2004, 2006a). He sometimes applied the same figure of a larva to more than one species. The majority of these discrepancies are likely due to misidentifications, presumption, and a lack of proper subjects.

Contrary to my previous assumptions (Calhoun 2006a), it is likely that Abbot did not always create his template when he reared each species. Instead, he probably returned to the field at a later date to collect specimens for his compositions. This disconnect would explain why he associated some larvae and pupae with the wrong species. It would also account for Abbot's inaccurate and outright inventive figures. For those larvae and pupae that he failed to relocate in nature, evidence suggests that he fabricated figures using other species as models and also "borrowed" figures from illustrations of other species. Among the drawings for Swainson, this is shown in his compositions of the life histories of the butterflies *Asterocampa celtis* (Boisduval & Le Conte) and *Asterocampa clyton* (Boisduval & Le Conte) (Table 1, nos. 15 & 16). Abbot mistakenly applied the larva (and probably also the pupa) of *A. clyton* to the closely related *A. celtis*. Apparently thinking that he could not find the early stages of *A. clyton*, he fabricated figures for this species, modeling them after *Polygonia interrogationis* (Fabricius), another orange butterfly that he found feeding on the same *Celtis* trees (Celtaceae) (Fig. 2).

In search of specimens to illustrate, Abbot probably forgot which plants had previously yielded certain larvae and confused many plants, particularly grasses and legumes. He repeatedly reminded correspondents that he was no botanist, "only an admirer of Natures Beauties" (Linnean Society of London). Collecting specimens after the fact would greatly increase the probability of such errors. Abbot may have forced some larvae to feed on plants not normally fed upon in nature. He probably also found wandering mature larvae on adjacent plants that did not serve as hosts, leading him to assume that they were feeding on those plants. In addition, he confused similar species of Lepidoptera, resulting in erroneous hostplant associations (Calhoun 2006a).

Some of Abbot's dubious hostplants may prove to be valid. An example is his drawing for Plate 11 of Smith &

Abbot (1797), in which he associated *Polygonia interrogationis* with *Tilia americana* (L.) (Malvaceae). I initially considered this to be a possible forced captive rearing (Calhoun 2006a), but have since discovered that Titian R. Peale also recorded finding this butterfly "feeding on Linden" (*Tilia* sp.) in the vicinity of Washington, D.C. during the early nineteenth century (specimens in the Academy of Natural Sciences of Philadelphia). Despite the likely validity of some unconfirmed hosts, Abbot apparently inserted some plants strictly for their aesthetic appeal (Calhoun 2006a) (Figs. 1, 2). Using unpublished and published references, including Allen *et al.* (2005), Minno *et al.* (2005), Robinson *et al.* (2002), and Wagner (2005), I have attempted to evaluate the validity of the associated figures in Abbot's drawings for Swainson (Table 1). Larvae and pupae were considered to be acceptable if they exhibited fundamental characteristics of the given species.

It should be mentioned that Abbot's adult butterflies and moths can also be problematic. They often possess primitive bodies, simplified legs, distorted wing shapes, and imprecise color patterns. These inconsistencies became more prevalent as Abbot grew older and were recognized during the preparation of Boisduval & Le Conte (1829–[1837]). Subscribers of this book criticized the accuracy of the legs and bodies on the color plates, prompting Boisduval to promise that the defects would be corrected for future fascicles (Calhoun 2004). As a result, the original figures that were subsequently reproduced for the book show corrections to bodies, legs, and antennae. In addition, many of the dorsal figures used for the book are markedly asymmetrical, with one side more refined than the other. I previously attributed this to Abbot's carelessness (Calhoun 2004), but the figures were undoubtedly altered at a later date. Possibly based on specimens from Boisduval's collection, the wing modifications vary from minor color enhancements to nearly complete over-painting to create more precise figures. The colors are richer and the wing profiles tend to be more accurate than the figures that Abbot was producing at that time. These changes were probably made by Charles Émile Blanchard, an accomplished young artist who also contributed illustrations for the book (Calhoun 2004). Only the altered wings were used by the engraver to create the dorsal figures on the published plates (Calhoun 2005). The artistic style of the unaltered wings is more consistent with Abbot's other drawings, including those for Swainson.

Additional drawings for Swainson. Swainson's surviving correspondence with Abbot abruptly ceases in 1820, followed by only one additional letter from 1835.

However, there is a clue that Abbot produced a set of drawings for Swainson in 1830. In a letter to Thaddeus W. Harris, dated 4 June 1839, the British lepidopterist Edward Doubleday wrote, "A few days since I found at a Booksellers 84 drawings by Abbot containing 150 figures of Georgian Coleoptera & about 350 of Lepidoptera. They are bound in a small folio volume, & did belong to Swainson" (Mayr Library) (misquoted by Scudder (1869) to read, "& did not belong to Swainson"). Doubleday sent these drawings to Harris in 1839 as a token of their friendship. After Harris' death in 1856, they were purchased for the Boston Society of Natural History. They were later examined by Samuel H. Scudder who attributed them to an "inferior copyist" (Scudder 1888). Dow (1914) likewise proclaimed that they were by "a pupil or imitator" of Abbot. These drawings were acquired in 1946 by Harvard University, where they are now preserved in the Houghton Library. I personally examined these watercolors and found that they are consistent with other drawings that Abbot completed during the late 1820's, which were unknown to Scudder and Dow. Moreover, the set includes Abbot's handwritten title page, dated 1830. There is no reason to believe that these drawings were created by anyone other than Abbot. Because there is no known physical evidence that suggests Swainson's ownership, the bookseller must have informed Doubleday about their prior history. Swainson perhaps sold these drawings in preparation for his trip to New Zealand, as he offered drawings and specimens for sale in early 1839 (Parkinson 1984, Natusch & Swainson 1987). A forthcoming publication will discuss these drawings in more detail.

William Swainson was possibly also the intended recipient of Abbot's template drawings of insects, or at least a portion of them. Abbot wrote to Swainson in 1835, "I have now sent You with this Letter...my book of Drawings of Insects" (Swainson correspondence, Alexander Turnbull Library; reproduced by Parkinson 1978). He offered this "book of Drawings" to Swainson for seven guineas, currently valued at about £550 (\$1,038 US). It was shipped with "about 650 Drawings of single Insects on small papers," which Abbot separately referred to as "other Drawings." He stated that this shipment included "all the Drawings of Insects at this time in my possession." Parkinson (1978) proposed that the "book of Drawings" was the set of 103 watercolors now in New Zealand, but he soon realized that these were completed many years earlier (Parkinson 1983). Gilbert (1998) suggested that this was a copy of Smith & Abbot (1797), but it is highly unlikely that Abbot would have sent a copy of this book all the way back to England where it was published. Abbot

shipped his "book of Drawings" at the bottom of a box, beneath a layer of paper and plant specimens to conceal it from customs inspectors. He told Swainson that "no person or yourself would think there was any thing under the paper, if I did not inform you of it." The bulky folio volumes of Smith & Abbot (1797) would hardly escape notice under a thin layer of paper. Although this could refer to the set of drawings that Abbot completed in 1830, his possessive description ("my book of Drawings") implies that these were illustrations of more personal significance. There is also no evidence that Abbot produced any more insect drawings after 1835. He was then 84 years old and was possibly divesting himself of his possessions. He perhaps desired to entrust these unique illustrations to one of his few remaining correspondents. Unfortunately, they do not appear to have survived and may have been lost when the ship carrying a portion of Swainson's library sunk in 1841. It is also possible that Swainson sold them prior to leaving England in 1840.

The fate of the 650 small drawings that Abbot sent to Swainson is obscure. Like his "book of Drawings," Abbot offered the entire set to Swainson for seven guineas. Along with the 103 larger illustrations, the Turnbull Library received 99 smaller watercolors that were also owned by Swainson. Among them are 61 drawings of beetles that Parkinson (1978, 1983a) attributed to Abbot. The library catalog also ascribes them to Abbot, *ca.* 1830 (ref. nos. E-265-q-001 through 061). According to the library catalog these drawings vary in size from 13.0 × 17.2 cm to 23.2 × 17.0 cm (5.1 × 6.8 in – 9.1 × 6.7 in). Handwritten verso notations associate the figured specimens with the cabinets of "Papa," George Humphrey, Dru Drury, and others. The inscriptions denote that the specimens were collected in Australia, Britain, North America (including Georgia and Virginia), and South America. Many of the specimens originated from Cayenne, French Guiana. On one of the drawings is written, "From New Holland [Australia], in my own collection." I examined a digital photograph of one of these illustrations and found the writing to be in Swainson's hand.

Regarding allusions to "Papa's Cabinet," Abbot's father had little interest in natural history, while Swainson's father was a founding member of the Linnean Society of London who maintained collections of mollusks and insects (Swainson 1840, Natusch & Swainson 1987). Specimens from "Papa's Cabinet" were drawn on the same sheets as others that were collected in England in 1804, yet Abbot's father died in 1787 (Rogers-Price 1983). By 1804 Abbot had been living in America for over thirty years.

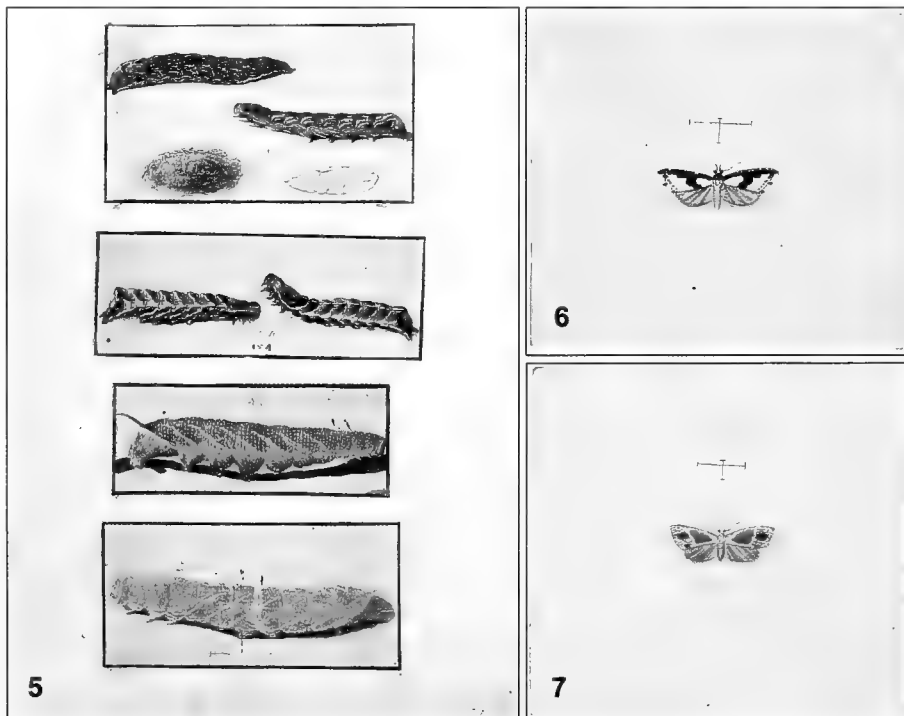
George Humphrey (1745–1830) was one of the

leading naturalist-dealers in London who included insects among his collections (Chalmers-Hunt 1976). Humphrey encouraged a young William Swainson to study natural history; "When, however, I could steal an hour to visit or had permission to spend a day with Mr. Humphrey, it was the greatest happiness of my life" (Swainson 1840). Swainson recalled that his youth was "divided between drawing and collecting" (Swainson 1840).

This evidence indicates that these watercolors were actually completed by Swainson before he began traveling abroad in 1806. The British specimens that were collected in 1804 were likely captured by Swainson himself. Those from Cayenne, French Guiana, may have been collected by Julius P. B. Rohr (1735–1792) who traveled to the Antilles and portions of South America (including Cayenne) in 1783, sending a large number of insects back to Europe (Zimsen 1964). Humphrey was a popular natural history dealer who organized the sale of specimens brought back from such expeditionary voyages. All the specimens from Georgia, and possibly also those from Virginia, likely came from Abbot. Many are credited to the collection of Humphrey, who may have obtained them directly from Abbot. Swainson wrote on one of the drawings "from Mr Abbot of Georgia." The drawing of another

specimen from Georgia bears Swainson's inscription, "Gave me by Mr Humphrey who received it from North America." Humphrey also owned bird specimens that were probably collected by Abbot prior to 1790 (Simpson 1984, Rogers-Price 1997). Humphrey may have obtained additional Abbot specimens in 1805 when the insect collection of Dru Drury was auctioned in London. This is suggested by Swainson's inscriptions on some drawings that read "from Mr Drury's Collection" and "from the cabinet of Mr Drury." Drury possessed a large number of Abbot's specimens from Georgia and Virginia (Wilkinson 1984). Some of the specimens from Cayenne may also have come from Drury, who purchased them from the statesman-naturalist Pierre Victor Malouet (1740–1814), Governor of French Guyana from 1776 to 1779 (Drury 1770–1782).

Abbot was also familiar with Humphrey, whom he met prior to leaving London in 1773. In his unfinished autobiography entitled "Notes on my Life" (ca. 1834), Abbot recalled that in the summer of 1773 he was briefly employed by an unnamed gentleman to make natural history drawings, particularly shells, through the recommendation of "a Mr Humphreys" (Mayr Library). Nearly 50 years later, Abbot wrote to Swainson in 1818, "I think you know an old acquaintance of mine, a Geo. Humphreys dealer in shells and Natural Curiosities, is he



FIGS. 5–7. Small drawings attributed to William Swainson and John Abbot. 5, European moth larvae, Swainson, ca. 1804. 6, moth, *Nigetia formosalis* Walker, Abbot, ca. 1835. 7, moth, possibly *Maliatha synochitis* (Grote & Robinson), Abbot, ca. 1835.

dead, or still living. If alive where does he reside at present as I wou'd wish to write to him." Swainson replied that "Mr. G. Humfrey is still living but very old. Yet with all his spirits he is a very worthy character." Swainson did not provide Humphrey's address, leading Abbot to respond in 1819, "not knowing where Mr Humfreys lives, I have enclosed a Letter for him" (Linnean Society of London). Remarkably, these letters include four different spellings of Humphreys' name. Swainson also varied the spelling of Humphrey's name on his small drawings at the Turnbull Library.

Thirty-eight other small drawings are mostly attributed to Abbot by the Turnbull Library catalog. I examined digital photographs of several of these illustrations. One of them (ref. no. E-265-q-066), watermarked 1801, depicts two moths sketched in pencil. Three others (ref. nos. E-265-q-063 through 065) portray the early stages of European Lepidoptera. Another (ref. no. E-265-q-067), also watermarked 1801, illustrates a European ichneumon wasp. The size of these drawings is consistent with the 61 beetle drawings and they are most likely the work of Swainson, completed prior to 1806. Six smaller drawings (E-265-q-066-1 through 066-4, E-265-q-073-1, E-254-q-073-2), measuring from 3.0 × 7.5 cm to 4.5 × 12.0 cm (1.2 × 3.0 in – 1.8 × 4.7 in), are pasted onto two larger sheets of paper. They also depict the early stages of European moths. Handwritten numbers, at least one written with the same paint used for the associated illustration, are not in Abbot's hand. They are characterized by a robust paint application, unlike Abbot's subtle transparent watercolors (Fig. 5). They are probably also by Swainson.

The remaining 27 watercolors (ref. nos. E-265-q-80 through 106) depict single adult moths on papers as small as 9.3 × 9.2 cm (3.7 × 3.6 in). I examined digital photographs of two of these drawings (Figs. 6, 7). They lack inscriptions, but the size, format, and artistic style are consistent with Abbot's other small drawings at The Natural History Museum, London, and others attributed to Abbot at the American Philosophical Society Library, Philadelphia (Calhoun 2006c). They likewise portray species that occur in Georgia. In this case, Parkinson (1978) was correct in attributing them to Abbot and they are possibly all that remain of the numerous small watercolors that were sent to Swainson in 1835. Abbot's advanced age (84 years) surely contributed to the lack of detail in these figurers. Some are very difficult to identify (Fig. 7).

Georgia, then and now. Even in Abbot's time the wilderness of Georgia was rapidly being transformed. Between 1790 and 1800 the population of Georgia doubled from 82,000 to 162,000. By 1820 it had reached

340,000 (Coleman 1977a). In Burke County, where Abbot lived for many years, the population swelled from 30,000 in 1790 to over 150,000 in 1820 (Hillhouse 1985). Prior to 1810 the growing population of Georgia was limited to the lands between the Ocmulgee and Savannah Rivers, the same area that Abbot explored. Stretching to the west were untamed Indian territories. Abbot noted in 1813 that the settled lands of Georgia yielded a "comparative small Quantity of Insects, one great cause may be the annual burning of the woods which must destroy an immense quantity of Insects" (letter to H. Escher-Zollikofer, Kroch Library). Five years later, Abbot told Swainson, "this Country fails much" to provide as many insects and birds as it "furnished formerly" because the countryside was "being more cleared and settled, and the woods being burnt every spring for the benefit of their cattle" (Linnean Society of London). By 1820 the frontier had moved beyond the lands between Augusta and Savannah where Abbot made his home (Coleman 1977b). After 56 years of studying the insects of Georgia, Abbot recalled in 1832, "as to the number of Butterflies I can recollect having caught 75 or 6 different Species, but dont know if I can take half that number of a Year now." He added, "it was much better formerly" (letter to H. Escher-Zollikofer, Kroch Library). In 1834, he reported to T. W. Harris that "there is many kinds I have formally [formerly] met with, that I now cant find a single specimen of" (Mayr Library). Among the butterfly species portrayed for Swainson, *Erynnis martialis* (Scudder) (no. 22) was possibly more frequent in eastern Georgia than it is today.

At least three butterflies that Abbot illustrated for Swainson may actually be more abundant today: *Hermeuptychia sosybius* (Fabricius) (no. 14, "not very common"), *A. celtis* (no. 15, "very rare"), and *Libytheana carinenta* (Cramer) (no. 18, "rare") (Table 1). The hostplants of these species thrive in secondary habitats that are created in the wake of human activity. I have personally found *L. carinenta* to be locally abundant near *Celtis* (Celtaceae) trees growing along a roadside in the Savannah River floodplain of Burke County. Nearby, *H. sosybius* flew in a disturbed grassy clearing. Nonetheless, such local abundance could have been interpreted by Abbot as generally rare or uncommon.

Abbot also illustrated *Pyrgus communis* (Grote) (no. 23) (Fig. 3), which he considered "not common." This species has been greatly affected by the recent spread of the very similar *Pyrgus albescens* Plötz into eastern North America (see Burns 2000). For reasons unknown, many populations of *P. communis* have been completely

displaced by *P. albescens*. This process was rapid in Florida where *P. communis* may no longer occur (Calhoun 2002). *Pyrgus albescens* reached McIntosh County in southeastern Georgia by 2000 (Calhoun 2002) and Richland County, South Carolina by 2002 (John M. Burns pers comm.). In April 2006, I discovered a thriving population of *P. albescens* not far from Abbot's former home in Burke County. No *P. communis* were found among them.

Problema bulenta (Boisduval & Le Conte) (no. 24), considered "not common" by Abbot, may have been more widespread in wetlands associated with coastal rice plantations that have long since disappeared (Table 1). Rice was a major crop in colonial Georgia, comprising as much as one third of all exports (Spalding 1977). Abbot illustrated this species at least as early as the 1790s, but it remained unknown beyond his drawings for over a century. The first published illustration of the species in Boisduval & Le Conte (1829–[1837]) was reproduced from an Abbot drawing that was completed ca. 1813 (Calhoun 2004). No text was included with this illustration, but entomologists generally assumed that Abbot had found it in Georgia. This is confirmed by Abbot's mention of its occurrence in the "lower parts of Georgia" in his notes for other drawings of the species (Table 1). The species remained unknown beyond Abbot's illustrations, thus subsequent authors either doubted its validity or tentatively associated it with other taxa. Abbot was vindicated in 1925 when *P. bulenta* was rediscovered in coastal marshes near Wilmington, North Carolina (Jones 1926). It is now known to be a localized coastal inhabitant from Georgia to New Jersey and is locally abundant in tidal marshes of the Savannah River in Georgia. This is probably the same general area where Abbot first encountered this species.

Those who take the time to enjoy Abbot's illustrations will learn much about the butterflies of an unspoiled Georgia. Exploring within his compositions will expose many secrets about the artist himself.

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EFFECT OF TEMPERATURE VARIABLES ON ULTRAVIOLET TRAP CATCHES OF *ACTIAS LUNA*
AND *DRYOCAMPA RUBICUNDA* (SATURNIIDAE) IN WAYNE NATIONAL FOREST, OHIO

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ABSTRACT. Counts of the luna moth, *Actias luna* (Linnaeus) and the rosy maple moth *Dryocampa rubicunda* (Fabricius) from ultraviolet traps in southeastern Ohio reveal that different temperature factors affect catch size. High and low counts of *A. luna* (Saturniinae) were generally not influenced by short term temperature trends, difference temperatures, or maximum temperatures on the trap day itself. Conversely, high counts of *D. rubicunda* (Ceratocampinae) were associated with maximum temperatures, indicating a response to more immediate factors. It is recommended surveys of saturniids include sampling days that cover a wide range of temperatures. Influences of life history characteristics and body sizes on temperature responses are discussed.

Additional key words: *Actias luna*, *Dryocampa rubicunda*, light trap, emergence temperature, flight temperature, photoperiod, life history strategy, body size, saturniids, moonlight, diapause, survey

This study investigated the influences of warming trends, daily temperature differences, maximum temperatures, low temperatures, and average temperatures on ultraviolet light catches of *A. luna* and *D. rubicunda* in southern Ohio from 1995 to 1998. Knowledge of the environmental factors affecting development, phenology, and behavior may be especially useful for biologists who inventory, survey, or monitor populations of saturniids in forested regions of the northeastern USA.

Light trapping studies with moths have investigated their diversity, abundance, migration times, population trends, development, phenology, and life history cues (Gregg *et al.* 1994, Thomas & Thomas 1994, Robinson & Tuck 1993, Frank 1988, Bowden 1982, Worth 1979). Moth emergence and flight times to light traps are affected by abiotic factors such as photoperiod, moonlight, temperature, wind speed, wind direction, functioning of the light trap, and background illumination (Manley 1993, Bowden 1982, Wright 1970). Certain environmental conditions break diapause and initiate adult development while other conditions stimulate emergence. For example, Wright (1970) reported photoperiod played a significant role in the number of days required for emergence of unchilled *Actias luna* pupae; a 16-hour photophase resulted in earlier emergence than a 24-hour photophase. Truman (1985) noted eclosion in giant silkmoths was determined by light-dark cycles and was regulated by the brain with the release of eclosion hormone. Young (1997) discussed the effectiveness of ultraviolet traps and lunar cycles; catch size is partly dependent upon trap light contrasts with their background.

Heinrich (1993, 1997) noted that large saturniid moths shiver to warm up flight muscles to 37° C, a response that depends, in part, upon ambient temperatures. In Georgia and Florida, *Automeris io* (Fabricius) emerged from late morning to mid-

afternoon if temperatures were above 10°C with no heavy rain, dense fog or high wind (Manley 1993). Calling behaviors in the evening were also initiated above 10°C but sudden drops below 8° C resulted in pairs remaining in copula throughout the night.

Stamp and Casey (1993) reported the abrupt appearance of moths, butterflies, and caterpillars at the beginning of the Santa Rosa, Costa Rica, rainy season was cued by temperature drops of 6°C, not by the onset of rain. After a long, dry, hot period, cool air pulses were associated with enormous numbers of moths attracted to lights. Additionally, pupal eclosion of *Rothschildia lebeau* (Guerin-Meneville) (Saturniidae) in airtight plastic bags was more affected by temperature drops than humidity levels; moths in wet bags eclosed an average of 1–2 days later than moths in dry bags.

Unlike adult Sphingidae that harvest fuel and water from flowers, adult Saturniidae mate and die in a relatively short time after eclosion (Janzen 1984). The male generally flies for two to three days after emergence in search of pheromone plumes. Fast, accurate flight to a female may be paramount for reproductive success. Conversely, females specialize in finding suitable host plants for oviposition, a more refined activity that requires fluttering, careful positioning around oviposition sites, and wing strength to support egg bearing weight. Increased catches of female saturniids may occur when light traps are placed near a concentration of host plants (Tuskes *et al.* 1996).

Light trap catches are affected by environmental factors that influence the entire sequence of a moth's life history such breaking diapause, development, eclosion, oviposition, and flight periods.

MATERIALS AND METHODS

Moths were captured with ultraviolet light traps from 1995–1998 at 6 trapping stations in southeastern Ohio mixed-hardwood forests. One set of 3 traps was located

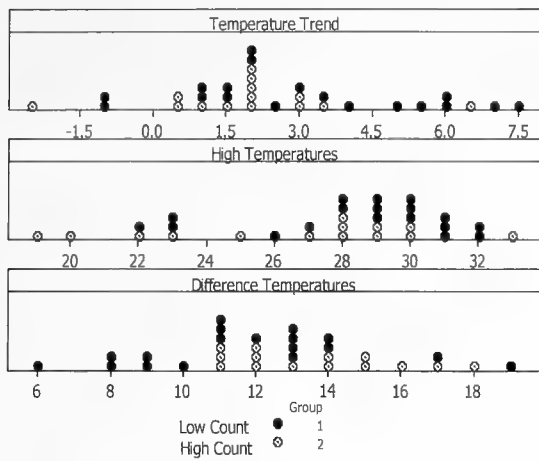


FIG 1. Low and high count samples of *A. luna* caught at different temperature variables by blacklight trapping in Lawrence County, Ohio, from May to August 1995–1998. Mean comparisons of temperature trends, high temperatures, and difference temperatures between the high and low count groups were not significantly different (t-test, $p > 0.05$) ($n = 16$ for low count samples, $n = 23$ for high count samples).

within the Vinton Furnace Experimental Forest near Dundas in Vinton County while another set of 3 traps was located within Wayne National Forest near Kitts Hill in Lawrence County. These different county trap sites were approximately 69.7 kilometers apart. Researchers turned on trap lights for one night a week from dusk to dawn using preset timers and then emptied collection chambers the day after lights turned off. The weekly trapping period ran from April 25 to August 14 in 1995–1997; moths were trapped biweekly in 1998 from May 6 to August 16. A total of 71 samples was analyzed for both county sites, excluding days with thunderstorms, rain, mist and heavy fog. A sample count consisted of summing the number of moths from the three traps on one county site for one trapping night. Each trap consisted of a 20-liter (5 gallon) plastic pail placed beneath a 10 cm, 8 watt ultraviolet Sylvania GTE fluorescent bulb powered by a 12-volt battery between Plexiglas baffles. Traps were hung from limbs approximately 1.5 m above the ground near ridge crests. Insects that fell through the funnel entrances were killed by ethyl acetate.

Temperature and precipitation data were compiled from Climatological Data, 1995–1998, National Oceanic and Atmospheric Administration (NOAA) at Portsmouth, Sciotoville and Athens Ohio. The Portsmouth Station is approximately 25 km due west of Lawrence County trap sites and Athens Station is approximately 25 km due east of the Vinton County trap sites. The nearest station with mist and heavy fog data was Huntington, West Virginia, approximately 70 km from both sites. Nightly moth catches were

designated as either high count samples or low count samples for each species. High count samples contained any count equal to or above the four year trap median in that county; low count samples were any count occurring below the four year trap median in that county (Table 1).

Moonlight data also came from the NOAA, National Weather Service Forecast, in Huntington, West Virginia. On nights with greater than 80% of the moon's disk illuminated ($N = 21$), only 42.8% of *A. luna* catches and 33.3% of *D. rubicunda* catches were ranked as high counts. These results did not account for the influence of cloud cover on moonlight luminescence.

The first analysis compared temperature trends, difference temperatures, and maximum temperatures between high and low count groups of each species in each county. Maximum temperatures were the highest temperatures recorded either on the trap day itself or one to two days preceding the trap day, a time period corresponding to adult emergence and adult life span. Temperature trends were the sums of the 3 to 5 day warming or cooling trend leading up to the maximum temperature. Difference temperatures (maximum minus minimum) were recorded on the trap day itself.

Temperature variables were compared with independent sample t-tests (unequal variances) using Minitab (Release 14: 2004), and checked for normality (Rosner 2000). All hypothesis tests were 2-tailed with a maximum probability of type-1 error set at 0.05. A linear regression analysis determined if maximum

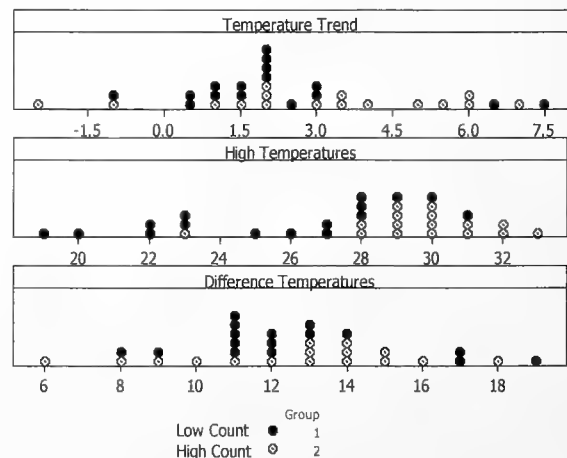


FIG 2. Low and high count samples of *D. rubicunda* caught at different temperature variables by blacklight trapping in Lawrence County, Ohio, from May to August 1995–1998. Mean comparison of high temperatures were significantly different between the high and low count groups (t-test, $p < 0.05$) ($n = 19$ for low count samples, $n = 20$ for high count samples). Temperature trends and difference temperatures were not significantly different.

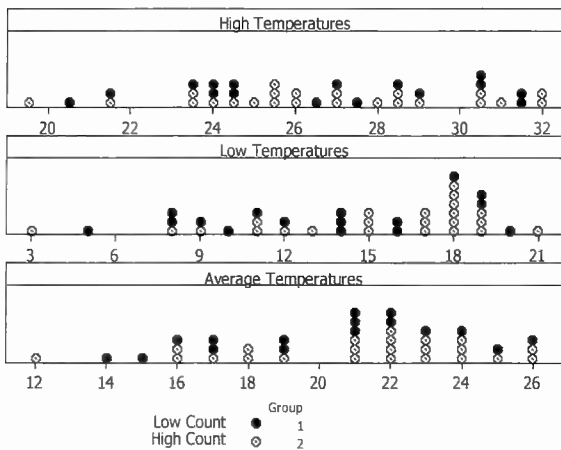


FIG 3. Low and high count samples of *A. luna* caught at different temperature variables by blacklight trapping in Vinton County, Ohio, from May to August 1995–1998. Mean comparisons of high temperatures, low temperatures, and average temperatures between high and low count groups were not significantly different (t-test, $p > 0.05$) ($n = 16$ for low count samples, $n = 23$ for high count samples).

temperatures could reliably predict moth counts. Residual plots were checked for normality, unequal variances, and independence (Durbin-Watson Test) while scatter diagrams were screened for outliers and influential observations (Rosner 2000). Moth counts required square root transformations to reduce unequal residual variances. Finally, we investigated the influence of catch day maximum temperatures, minimum temperatures, and average temperatures on moth groups. These data were also compared with independent sample t-tests (unequal variances) after checking for normality.

RESULTS

At both county sites, the rosy-maple moth, *D. rubicunda*, was trapped in higher counts (mean = 34.25

TABLE 1. Mean counts (\pm SE), medians, and high group counts of *Actias luna*, and *Dryocampa rubicunda* using catch data from ultraviolet light trapping in Lawrence and Vinton counties, southeastern Ohio 1995–1998 (N = number of trapping days).

Species	Lawrence County			High Group Count
	N	Mean	Median	
<i>A. luna</i>	32	3.37 (0.64)	2.00	>2
<i>D. rubicunda</i>	32	34.25 (5.37)	25.00	>25
Vinton County				
<i>A. luna</i>	39	4.18 (0.65)	3.00	>3
<i>D. rubicunda</i>	39	36.51 (7.57)	25.00	>25

TABLE 2. Comparison of temperature trends, difference temperatures, and maximum temperatures (\pm SE) between designated high and low count groups using ultraviolet light trap catch data from Lawrence County, Ohio 1995-1998. Asterisk indicates means are significantly different (t-tests, $p < 0.05$)

Variable	Group Type	<i>A. luna</i>			
		N	Mean	t	P
Temperature Trend	Low	18	0.95 (0.53)	1.52	0.14
	High	14	3.16 (0.59)		
Difference Temperature	Low	18	13.61 (0.62)	-1.92	0.07
	High	14	11.72 (0.76)		
Maximum Temperature	Low	18	30.15 (0.63)	1.94	0.07
	High	14	26.06 (0.88)		
<i>D. rubicunda</i>					
Temperature Trend	Low	16	2.20 (0.53)	-1.02	0.31
	High	16	3.05 (0.64)		
Difference Temperature	Low	16	12.43 (0.74)	-0.23	0.82
	High	16	12.67 (0.77)		
Maximum Temperature	Low	16	* 27.63 (0.76)	-3.40	0.00
	High	16	30.84 (0.56)		

± 5.37 at Lawrence) than was *A. luna* (mean = 3.37 \pm 0.64 at Lawrence) (Table 1).

Temperature trends, difference temperatures, and maximum temperatures were not significantly different between low and high count groups of *A. luna* (t-test; $p > 0.05$ for all comparisons) in Lawrence County (Table 1) (Fig 1). Conversely, low and high count groups of *D. rubicunda* differed significantly ($t = -3.40$; $p = 0.00$) in relation to maximum temperatures (27.63 \pm 0.76 and 30.84 \pm 0.56 respectively) (Table 2) (Fig. 2).

Temperature trends, difference temperatures, and maximum temperatures were also not significantly different between low and high count groups of *A. luna* (t-test; $p > 0.05$ for all comparisons) in Vinton County (Table 3) (Fig. 3). Low and high count groups of *D. rubicunda* differed significantly ($t = -2.72$; $p = 0.01$) on maximum temperatures (27.28 \pm 0.24 and 29.82 \pm 0.57, respectively) in this county (Table 3) (Fig. 4).

In a comparison of maximum, minimum, and average temperatures on the trap day itself between the different groups of *A. luna*, only minimum temperatures (17.85 \pm 1.20 and 13.94 \pm 1.00) were significantly different in Lawrence County (Table 4).

TABLE 3. Comparison of temperature trends, difference temperatures, and maximum temperatures (\pm SE) between designated high and low count groups using ultraviolet light trap catch data from Vinton County, Ohio 1995–1998. Asterisk indicates means are significantly different (t-tests, $p < 0.05$).

Variable	Group Type	<i>A. luna</i>			
		N	Mean	t	P
Temperature Trend	Low	16	2.86 (0.81)	-0.85	0.40
	High	23	3.70 (0.59)		
Difference Temperature	Low	16	15.25 (1.00)	-0.09	0.93
	High	23	15.36 (0.61)		
Maximum Temperature	Low	16	29.09 (0.63)	0.88	0.38
	High	23	28.23 (0.73)		
<i>D. rubicunda</i>					
Temperature Trend	Low	19	2.75 (0.77)	-1.23	0.22
	High	20	3.93 (0.65)		
Difference Temperature	Low	19	15.31 (0.83)	-0.01	0.99
	High	20	15.32 (0.76)		
Maximum Temperature	Low	19	*27.28 (0.24)	-2.72	0.01
	High	20	29.82 (0.57)		

TABLE 4. Comparison of maximum, minimum, and average temperatures in Celsius between high count groups and low count groups of *A. luna* catches in southeastern Ohio from 1995–1998. These temperatures were recorded on the catch day.

Variable	County	Group	<i>A. luna</i>			
			N	Mean (SE)	t	P
Maximum Temp.	Lawrence	Low	18	28.29 (0.73)	1.28	0.22
		High	14	26.62 (1.10)		
	Vinton	Low	16	26.51 (0.86)	-0.15	
		High	23	26.68 (0.68)		
Minimum Temp.	Lawrence	Low	18	17.85 (1.20)	2.46	0.02
		High	14	13.94 (1.00)		
	Vinton	Low	16	13.26 (1.10)	-1.29	
		High	23	15.12 (0.91)		
Average Temp.	Lawrence	Low	18	22.62 (0.80)	1.70	0.10
		High	14	20.46 (0.98)		
	Vinton	Low	16	20.03 (0.90)		-0.86
		High	23	21.03 (0.76)		

TABLE 5. Comparison of maximum, minimum, and average temperatures between high count groups and low count groups of *D. rubicunda* catches in southeastern Ohio from 1995–1998. These temperatures were recorded on the catch day.

Variable	County	Group	<i>D. rubicunda</i>			
			N	Mean (SE)	t	P
Maximum Temp.	Lawrence	Low	16	25.48 (0.87)	-3.99	0.00
		High	16	29.64 (0.57)		
	Vinton	Low	19	25.03 (0.79)	-3.23	0.00
		High	20	28.11 (0.53)		
Minimum Temp.	Lawrence	Low	16	14.31 (1.4)	-2.21	0.04
		High	16	17.97 (0.82)		
	Vinton	Low	19	12.22 (1.10)	-3.23	0.00
		High	20	16.39 (0.69)		
Average Temp.	Lawrence	Low	16	19.83 (0.98)	-3.33	0.00
		High	16	23.53 (0.53)		
	Vinton	Low	19	18.75 (0.84)	-3.60	0.00
		High	20	22.40 (0.56)		

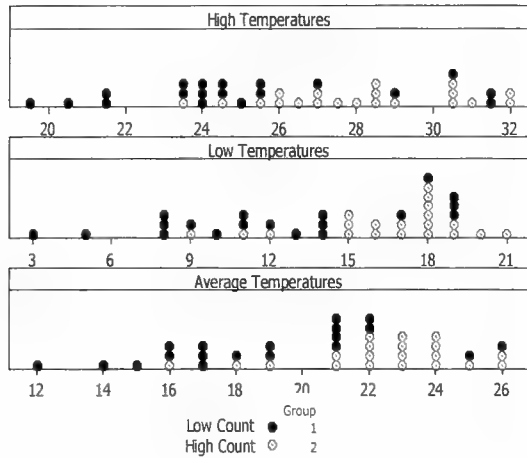


FIG 4. Low and high count samples of *D. rubicunda* caught at different temperature variables by blacklight trapping in Vinton County, Ohio, from May to August 1995–1998. Mean comparisons of high temperatures, low temperatures, and average temperatures were significantly different between the high and low count groups (t-test, $p < 0.05$) ($n = 19$ for low count samples and $n = 20$ for high count samples).

Maximum, minimum, and average temperatures of *D. rubicunda* groups differed significantly (t-test; $p < 0.05$) in both counties (Table 5).

In Lawrence County, *A. luna* counts did not significantly increase or decrease with increasing maximum temperatures ($df = 1$, $R^2 = 0.08$, $p = 0.12$) (Fig 5), but higher counts of *D. rubicunda* were associated with higher maximum temperatures ($df = 1$, $R^2 = 0.43$, $p = 0.00$) (Fig. 6).

The overall patterns of high *A. luna* counts occurring throughout a range of temperatures and high *D. rubicunda* counts occurring at generally higher temperatures is present in Fig. 7 from Vinton County.

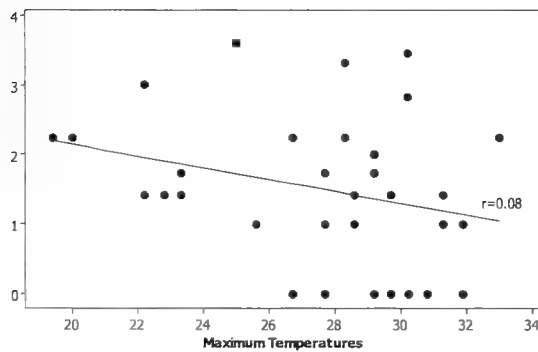


FIG 5. Relationship of maximum temperatures (x) to *A. luna* moth counts (y) on different sampling days in Lawrence County, Ohio, from May to August 1995–1998. Moth counts required square root transformations. The regression equation is $y = 3.835 - 0.084x$.

DISCUSSION

High counts of *A. luna* in ultraviolet light traps were generally not influenced by maximum temperatures, differences in daily temperatures, or short term temperature trends at trapping times. In contrast, high catches of *D. rubicunda* were influenced by maximum temperatures on the catch day itself and by maximum temperatures one to two days preceding the trap night. *D. rubicunda* responded more to immediate maximum temperature cues than did *A. luna*.

Allen (1976) reported that *D. rubicunda* oviposition rates reached a peak during the first 10 days of July in northern Pennsylvania, New York, and New England, a

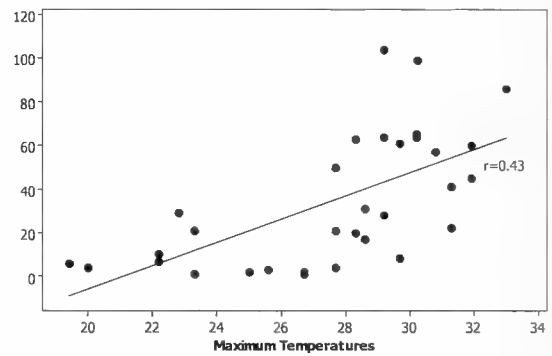


FIG 6. Relationship of maximum temperatures (x) to *D. rubicunda* moth counts (y) on different sampling days in Lawrence County, Ohio, from May to August 1995–1998. Moth counts required square root transformations. The regression equation is $y = -9.045 + 0.515x$.

time period corresponding to the highest mean temperatures in these locations (NOAA 2002). For example, the mean normal temperature of Warren, Pennsylvania, in July from 1971–2000 was 21.1°C compared to a mean of 20.4°C in August. Additionally, Bouseman and Sternburg (2002) noted that *A. luna* pupae from Illinois emerged in May and June, monthly periods associated with cooler temperatures than July (NOAA 2002). In Danville Illinois, the mean temperature in June was 22.1°C compared to 24.1°C in July.

Populations of *D. rubicunda* are univoltine both in the northeastern United States and eastern Canada with adult emergences from mid-May to mid-July (Allen 1976). In South Carolina, first broods appear from the end of April to May while second broods appear from late June through mid-September. Additionally, multivoltine populations are found in southern states (Bouseman 1982). In Canada and the northern states, *A. luna* is univoltine while in the more southern Ohio River Valley, it is bivoltine. Similar to *D. rubicunda*,

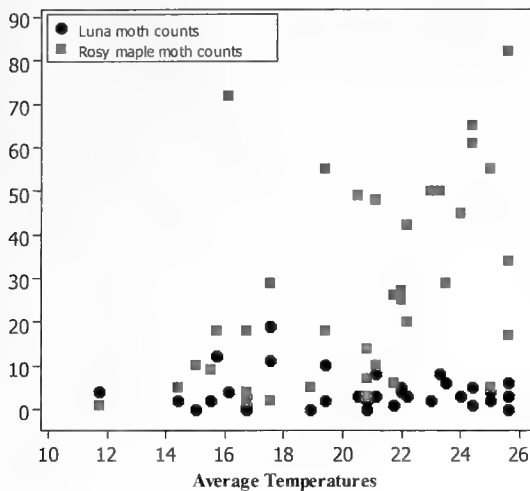


FIG. 7. Dual plot of *A. luna* and *D. rubicunda* counts on Vinton County for the entire trapping period (1995–1998). Compared to high count samples of *A. luna* ($N \geq 2$ for a high count sample), high count samples of *D. rubicunda* ($N \geq 25$ for a high count sample) generally occurred at higher temperatures.

multivoltine populations of *A. luna* are also present in southern states (Tuskes *et al.* 1996). Both temperature and photoperiod influence *Actias* emergence; diapause is terminated by photoperiod while cool weather delays emergence in some species (Miyata 1971, 1974, 1986).

The different origins and life history strategies of saturniids may also influence emergence and flight temperatures. *D. rubicunda*, a member of the subfamily Ceratocampinae with tropical origins, may be more innately adapted to flight in high midsummer temperatures with humid weather (Tuskes *et al.* 1996). Conversely, the genus *Actias* is a more temperate Asiatic group with species such as *Actias artemis artemis* (Bremer & Grey) and *Actias gnoma tomariactias* (Bryk) found in Japan (Miyata, 1981, Nassig & Peigler 1984, Tuskes *et al.* 1996).

Larger-sized females of *A. luna*, *Hyalophora cecropia* (Linnaeus) (Saturniinae) and *Eacles imperialis* (Drury) (Ceratocampinae) travel longer distances to disperse smaller clutches of ova compared to some of the smaller-sized females of Ceratocampinae and Hemileucinae that lay their all their eggs in one or two large clutches (Tuskes *et al.* 1996). These smaller species also have gregarious, brightly colored larvae. Similarly, *D. rubicunda* (Ceratocampinae) lays clutches of 10–30 eggs that hatch into colonial larvae colored with black patches adjacent to dorsal and sub-dorsal tubercles, characteristics associated with warning coloration and distastefulness. *D. rubicunda* may spend limited time in flight due to its life history strategy. Conversely, *A. luna* flies longer distances to disperse

single eggs or small groups of eggs, a strategy that benefits larvae from competition with other larvae and from detection by predators and parasitoids (Young 1997). Risk is spread out over a larger area.

Size also plays a role in the ability to be active at different temperatures. Denno and Dingle (1981) suggested that larger bodied insects in temperate summer environments were more buffered against short-term environmental changes than smaller bodied insects. The larger *A. luna* (male forewing 45–60 mm, last instar length 70 mm) may better control overheating or overcooling compared to the smaller *D. rubicunda* (male forewing 17–29 mm, last instar length 45–55 mm from Tuskes *et al.* 1996). Unlike the luna moth, *D. rubicunda* may be restricted to flying at higher temperatures.

Trapping result differences probably reflect differences in both emergent temperature responses and flight temperature responses of the two species.

This study recommends that surveys of saturniids by ultraviolet traps include sampling dates that cover a wide range of temperatures and not just days considered optimal. Larger-sized saturniids may be caught in significant numbers at both high and low temperatures while smaller-sized saturniids may be more abundant at high temperatures.

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WHAT DO MONARCH POPULATION TIME SERIES TELL US ABOUT EASTERN AND WESTERN POPULATION MIXING?

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ABSTRACT. Time series for the annual variation in the size of the central Mexican overwintering population, the California (western) summer breeding population (4th of July Count) and the California coastal wintering population (Thanksgiving Count) are examined. The California summer and following wintering populations are found to correlate with the size of the previous winter's central Mexico population in support of the hypothesis that monarchs migrating north in the spring from Mexico contribute to the western population

Additional key words: *Danaus plexippus*, Annual census, Time series, Climate dependence, Mexico, California

The monarch (*Danaus plexippus*) butterfly has long been of interest because of its remarkable migratory pattern. There are two North American populations of monarchs; one that summers east of the Rocky Mountains and migrates to and overwinters in the mountain forests in central Mexico, and another population west of the Rocky Mountains that winters along the central and southern California coast and disperses east and north in the summer (Urquhart 1987, Brower 1995a).

The recognition of this pattern has arisen and been supported by extensive mark/recapture results, particularly for the eastern population (Monarch Watch). Unlike birds, but similar to the migratory Painted Lady (*Vanessa cardui*) butterfly, any particular individual of the eastern population does not make the complete trip from the wintering grounds to the northernmost summer grounds. Instead the returning overwintered individuals breed along the Gulf Coast and their offspring continue the migration northward (Malcolm *et al.* 1993, Knight *et al.* 1999). Additional breeding generations complete the northeastern recolonization (Brower 1996). The temporal variation in the recolonization rate has been shown to be remarkably stable from year to year (Davis and Howard, 2005). The return migration to the overwintering areas is made by the final fall generation that enters reproductive diapause (Urquhart 1960) and flies to Mexico (Urquhart and Urquhart, 1978).

The extent to which the two populations may mix is largely unknown. Some mark-release-recapture results (Monarch Watch) have trajectories that hint at mixing. Directions of movement of individuals in the west have also been interpreted as indicating migration paths that might lead to population mixing (Pyle 1999). However mitochondrial DNA sequencing indicates very little heterogeneity between the eastern and western North American populations, and even between the North and South American populations (A. Brower *et al.* 2004). L.

Brower and Pyle (2004) have summarized the evidence for some interchange between the eastern and western populations.

The purpose of this study is to examine correlations in year-to-year Monarch fluctuations at the eastern and western population overwintering sites and at western population breeding sites for clues as to whether the western population is supplemented by Monarchs from the eastern population overwintering area in Mexico.

METHODS AND DATA SOURCES

This study makes use of three annual census counts. The first is the 4th of July Butterfly Count, the longest running monarch butterfly monitoring program. It was initiated by the Xerces Society in 1975 and is presently under the auspices of the North American Butterfly Association (NABA). Butterflies within a 15-mile diameter circle are counted. There are five count circles west of the Rocky Mountains for which counts have been performed every year during the last decade, and at which Monarchs are seen on a regular basis. These are Cosumnes River (38 21 N, 121 27 W), Mt. Diablo (37 57 N, 121 52 W), Willow Slough (38 34 N, 121 44 W), Dardanelles (38 22 N, 119 45 W) and San Joaquin Co. (38 9 N, 121 18 W). The number of butterflies observed has been divided by the number of party-hours reported in an attempt to correct for differences in observer effort and coverage from year to year. Issues related to these counts have been discussed by Swengel (1990). Many counts have observers that have participated in a particular count circle for a number of years, helping to make observed changes in butterfly numbers from year to year more accurate. One count circle, Willow Slough, CA, has been counted by the same observer, Art Shapiro, for all but one of the last 27 years (NABA 1999)! The count results are presently published yearly by NABA (4 Delaware Rd., Morristown, NJ 07960).

The second census, the Monarch Program

Thanksgiving Count of the overwintering population in California, is patterned after the 4th of July Butterfly Count, takes place during a 2-week period around Thanksgiving. Approximately 100 overwintering sites in 15 California counties are surveyed. The largest numbers of Monarchs are between San Francisco and Los Angeles. The first count was in 1997. The results for the seven years 1997–2003 have been compiled by Dennis Frey and Shana Stevens and are posted on the Monarch Program website (www.monarchprogram.org/tagging.htm). The results from the first four years have been discussed by Frey and Schaffner (2004). The 1997–2003 data, as well as 4th of July Butterfly Count data for the period 1977–1999 has been examined by Koenig (2006). He looked for spatial synchrony, the extent to which the populations vary in size from year to year in unison over considerable geographical distances. A modest (correlation coefficient about 0.3) but statistically significant correlation was found for the Thanksgiving counts over distances as large as 1000 km. With only three years overlap with his 4th of July data set he did not compare trends between the two data sets.

The third count, the Monarch Butterfly Biosphere Reserve census, estimates the size of the overwintering population in Mexico. The eastern breeding population

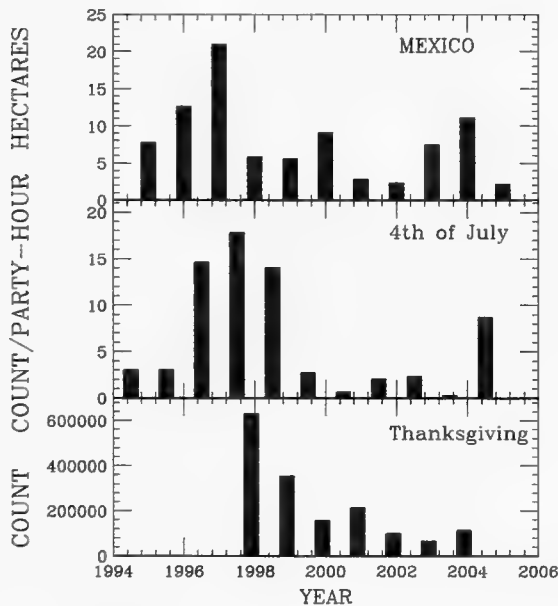


FIG. 1. Comparison of wintering (eastern) population in Mexico (top), California (western) summer population (middle) and California Thanksgiving Count (bottom). The Mexican population size is expressed as hectares occupied. The placement of the bars reflects the time of year at which the census is performed, eg. the bar for the 1996–1997 Mexican wintering population is plotted at 1996.9. The 4th of July data is the sum of the counts/party hour for 5 California sites.

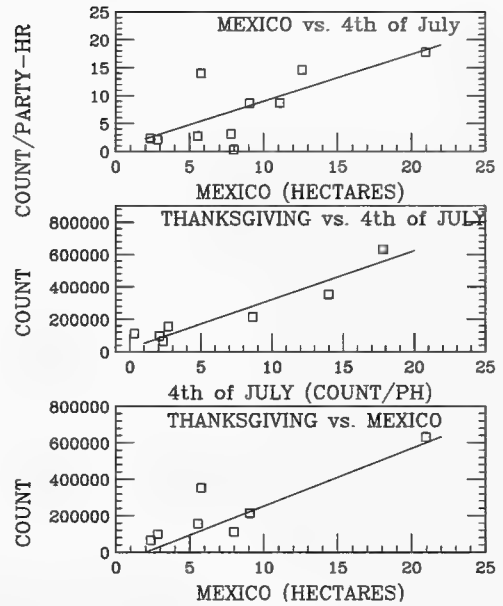


Fig. 2. Regression plots for the three pairs of variables.

of monarchs winter in high-altitude oyamel forests in central Mexico. Garcia-Serrano *et al.* (2004) have described a monitoring program initiated in 1993 under the auspices of the Monarch Butterfly Biosphere Reserve. All known colonies within and outside the reserve are monitored. Rather than attempting to count individual butterflies, the surface area occupied by colonies was measured. The data collection takes place during the last two weeks in December at a time when the colonies have consolidated and are least active. In January an estimate of the mortality at each site was assessed. (This mortality estimate reflects bird and mouse predation as well as mortality due to unknown causes. It does not capture the mortality associated with winter storms that occur later in the winter).

Estimates of the areas occupied by overwintering monarchs are from updates appearing on the Monarch Larvae Monitoring Program (www.mlmp.org) and Journey North (www.learner.org/jnorth/tm/monarch/PopulationMexico.html) websites. Since I am interested in estimating the influence of the size of the wintering population on the following summer and fall monarch numbers, I have reduced by 75% the December count for the 2001–2002 winter due to the severe winter storm in January of 2002 (Brower, Kust *et al.* 2004). There was also a significant winter storm effect on the 2003–2004 winter population but as estimates for the mortality differ greatly (Monarchwatch: www.monarchwatch.org/update/2004/0216.html) I have not attempted a correction for this season.

The largest area occupied by monarchs since the initiation of this project was about 20 hectares (ha) in Dec. 1996. Using previous estimates of butterfly densities of approximately 10 million butterflies/ha (Calvert & Brower 1986, Brower 1995b) would suggest a population of 200 million. More recent density estimates (Brower *et al.* 2004; Calvert 2004) would lead to a much larger population total. During some years however the area occupied by monarchs was only about 1/10th of this.

COMPARISON OF MEXICAN WINTERING POPULATION,
CALIFORNIA SUMMER POPULATION, AND CALIFORNIA
WINTERING POPULATION TIME SERIES

Population estimates for the Mexican wintering population are available for about a decade and for the California wintering population ("Thanksgiving" count) for seven years going back to 1997. There are five count circles in California where monarchs were regularly observed during the 4th of July Count and for which data are available over the last decade. The count per party hour values for these sites have been added and compared with the Mexican wintering population and the California wintering population estimates in Fig. 1. The most striking observation from this figure is that the California summer population and the California wintering population exhibit a maximum in the summer and fall following the winter with the largest population in Mexico, in spite of the general tenet that the Mexican wintering population remigrates to eastern and central North America via the gulf coast rather than to the west coast.

Multiple regression has been used to explore the correlation between the Mexican wintering population, the 4th of July summer counts, and the California wintering population (Thanksgiving counts). The data used for this analysis are given in Table 1, along with the regression equations obtained. The results of the regression analysis are displayed in Fig. 2. The sum of the count/party-hour for the five California 4th of July counts is found to be strongly correlated with the previous winter's Mexican population, $R^2=0.57$, $p=0.019$. The Thanksgiving count is also strongly correlated with the previous winter's Mexican population, $R^2=0.78$, and $p=0.008$. As expected from the two previous correlations, the Thanksgiving count correlates well with the 4th of July count/party-hour sum, $R^2=0.89$, $p=0.001$. Thus well over half of the fluctuation from year-to-year in the western 4th of July count and the western Thanksgiving count can be explained in terms of the size of the Mexican wintering population.

Two possible explanations for these strong

TABLE 1. Monarch counts from three kinds of censuses. The wintering census in Mexico are characterized by the number of hectares occupied, and are listed for the year in which Jan. of the particular winter occurs. The 4th of July results are the sum of the monarch's per party hour for 5 California sites. The Thanksgiving counts are the number of monarchs observed summed over all sites surveyed.

Year	Mexico	4th of July	Thanksgiving
1994		3.03	
1995	7.8	3.08	
1996	12.6	14.61	
1997	20.97	17.81	631140
1998	5.77	13.99	353272
1999	5.56	2.71	156659
2000	9.05	8.64	214198
2001	2.83	2.08	98418
2002	2.35	2.33	65375
2003	8.0	0.31	111909
2004	11.12	8.69	

Linear regression performed on these data give the following relations:

$$4\text{th July}=0.84 \cdot \text{Mexico} + 0.60$$

$$\text{Thanksgiving}=3,120 \cdot 4\text{th July} + 1960$$

$$\text{Thanksgiving}=2810 \cdot \text{Mexico} + 1410$$

These relations are illustrated by the straight lines in Fig. 2

correlations are: firstly, there is some climate variation effect common to both populations, and, secondly, that the western population is supplemented by monarchs from the Mexican overwintering population. The first possibility does not seem likely as it would seem to require the spring and summer climate in the east to be favorable the year before a favorable spring and summer climate in the west. This requirement arises because the peaks in the summer 4th of July count and the California Thanksgiving count lag the peak in the Mexican count by one half and one year, respectively. A second explanation is that some fraction of the eastern Mexican wintering population may migrate to the west in the spring and contribute to the western population in the following summer and fall. Such a hypothesis was put forward independently by L. Brower and S. Gauthreaux in 1996 (see Brower and Pyle, 2004). Since the eastern wintering population is about two orders of magnitude larger than the western wintering population, it would require only a very small fraction of the Mexican overwintering population to noticeably influence the western breeding and subsequent fall wintering population. Brower and Pyle make the further suggestion that the long-term survival of the western population of monarchs may depend on occasional replenishment from the Mexican winter population. This mechanism may also have enabled an expansion of the western population to exploit changes in coastal tree species distributions in historical times. The western

population's wintering grounds are presently primarily in Eucalyptus trees, which are not native to the U.S. and were introduced by settlers in the 1850's (Lane 1993). Lane has reviewed the historical evidence for the use of other tree species by overwintering Monarchs.

SUMMARY

The time correlation of the year-to-year fluctuations in monarch numbers have been examined at several different locations and seasons from which it has been inferred that the western population is supplemented by contributions from the eastern population. This inference, based only on time series correlations, was possible independent of the mechanism responsible for the fluctuations.

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Mia Monroe called to my attention the existence of the Thanksgiving Count program and encouraged me to examine these data for climate correlations. Lincoln Brower and Ann Swengel made helpful comments on a draft manuscript. I thank Robert Michael Pyle for an informative conversation. I thank Jane V. Scott of NABA who made a copy of the 2003 Report after it was out of print and my copy had gone astray in the mail.

This work complies with the current laws of the United States.

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DIETARY BASIS FOR DEVELOPMENTAL PLASTICITY OF AN ANDROCONIAL STRUCTURE IN THE SALT MARSH MOTH *ESTIGMENE ACREA* (DRURY)(LEPIDOPTERA: ARCTIIDAE).

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ABSTRACT. Larvae of the salt marsh moth *Estigmene acrea* (Dru.) feed on a variety of herbaceous plants including some that contain secondary plant substances called pyrrolizidine alkaloids (PAs). The salt marsh moth uses PAs in defense against predators and parasites and as pheromone precursors while non-PA plants are used for general nutrition. This study focuses on the development of their androconial organs, coremata, and on the role of pyrrolizidine alkaloids as morphogens stimulating coremata growth. During the pupal period, the development of the coremata can be divided into five discrete stages. Dietary PAs fed to laboratory raised final instar larvae were found to accelerate coremata development in stages four and five, to increase the number of coremata scales and to enhance coremata size compared to larvae without a PA dietary supplement. As part of the developmental process, dietary PAs stimulated the formation of a network of stellate cellular inclusions in the secretory cells at the base of each androconial scale. In addition, dietary PAs shortened the duration of the pupal stage for males but not females. The effects of PAs as morphogens in *E. acrea* are compared to those for the South Asian arctiines *Cretonotus gangis* and *C. transiens* in which the developmental role of PAs was first discovered.

Additional key words: coremata, hydroxydanaidal, morphogen, pyrrolizidine alkaloids

INTRODUCTION

Over twenty years ago the unusual mating systems of the arctiine moths *Cretonotus gangis* and *C. transiens* were described (Schneider *et al.*, 1982; Boppré and Schneider, 1985). In these South Asian insects males gather in aggregations and inflate impressive quadrid abdominal coremata. Females are attracted to the aggregation by a pyrrolizidine alkaloid-derived pheromone hydroxydanaidal released by these structures (Wunderer *et al.*, 1986). Moreover, the size and development of the male's coremata are determined by larval access to pyrrolizidine alkaloids (Schneider *et al.*, 1982; Egelhaaf *et al.*, 1992). The mating systems of the *Cretonotus* species represent stunning examples of sex role reversal—males attracting females instead of the opposite (which normally occurs in moths)—the evolution of which is of considerable interest to behavioral ecologists. Little is known about the details of these interesting mating systems largely due to the difficulty in obtaining specimens and observing the behavior under natural conditions. It was recently discovered that the common New World species *Estigmene acrea*, also an arctiine, has many similarities to the *Cretonotus* species in behavior and ecology (Willis and Birch, 1982; Davenport and Conner, 2003; Jordan *et al.*, 2005). We herein describe the developmental events that give rise to the coremata in male *Estigmene acrea* and the effects of pyrrolizidine alkaloids on this developmental process. We compare our results to those previously reported for *Cretonotus* (Schneider *et al.*, 1982; Egelhaaf *et al.*, 1992).

The salt marsh moth, *Estigmene acrea*, hereafter referred to as *Estigmene*, has an unusual dual mating system (Willis and Birch, 1982). Early in the evening

males gather in groups and inflate their abdominal coremata (Figure 1a). As in *Cretonotus gangis* and *C. transiens*, hereafter referred to as *Cretonotus*, females are attracted to the aggregation and mate. Later in the evening unmated *Estigmene* females revert to a more traditional lepidopteran mating scheme in which they release a blend of sex pheromones (Hill and Roelofs, 1981; del Mazo-Cancino *et al.*, 2004) and attract males. This alternative mating strategy was also noted in *Cretonotus*.

The larvae of the salt marsh moth are polyphagous and frequently include plants containing pyrrolizidine alkaloids (PAs) in their diet (Hartmann *et al.*, 2005). PAs are toxic secondary plant substances based on a bicyclic nitrogen-containing pyrrolizidine ring found sporadically in many plants, particularly in certain Asteraceae, Boraginaceae, and Fabaceae (Hartmann and Ober, 2000). Several arctiid species sequester them as defenses against predators and parasites (Weller *et al.*, 1999; Hartmann and Ober 2000; Singer *et al.*, 2004; Hristov and Conner 2005). As in *Cretonotus*, larval *Estigmene* preserve the alkaloids through metamorphosis, and derivatives of the alkaloids serve as precursors for the male courtship (coremata) pheromone, hydroxydanaidal (Hartmann *et al.*, 2003; Hartmann *et al.*, 2004; Hartmann *et al.*, 2005; Jordan *et al.* 2005).

The coremata of male *Estigmene* consist of two inflatable tubes emanating ventrally from intersegmental membranes between abdominal segments seven and eight. The coremata are invested with elongate androconial scales that increase their surface area for the release of the pyrrolizidine alkaloid-derived pheromone hydroxydanaidal (Krasnoff and Roelofs, 1989; Jordan *et al.* 2005). The size of the

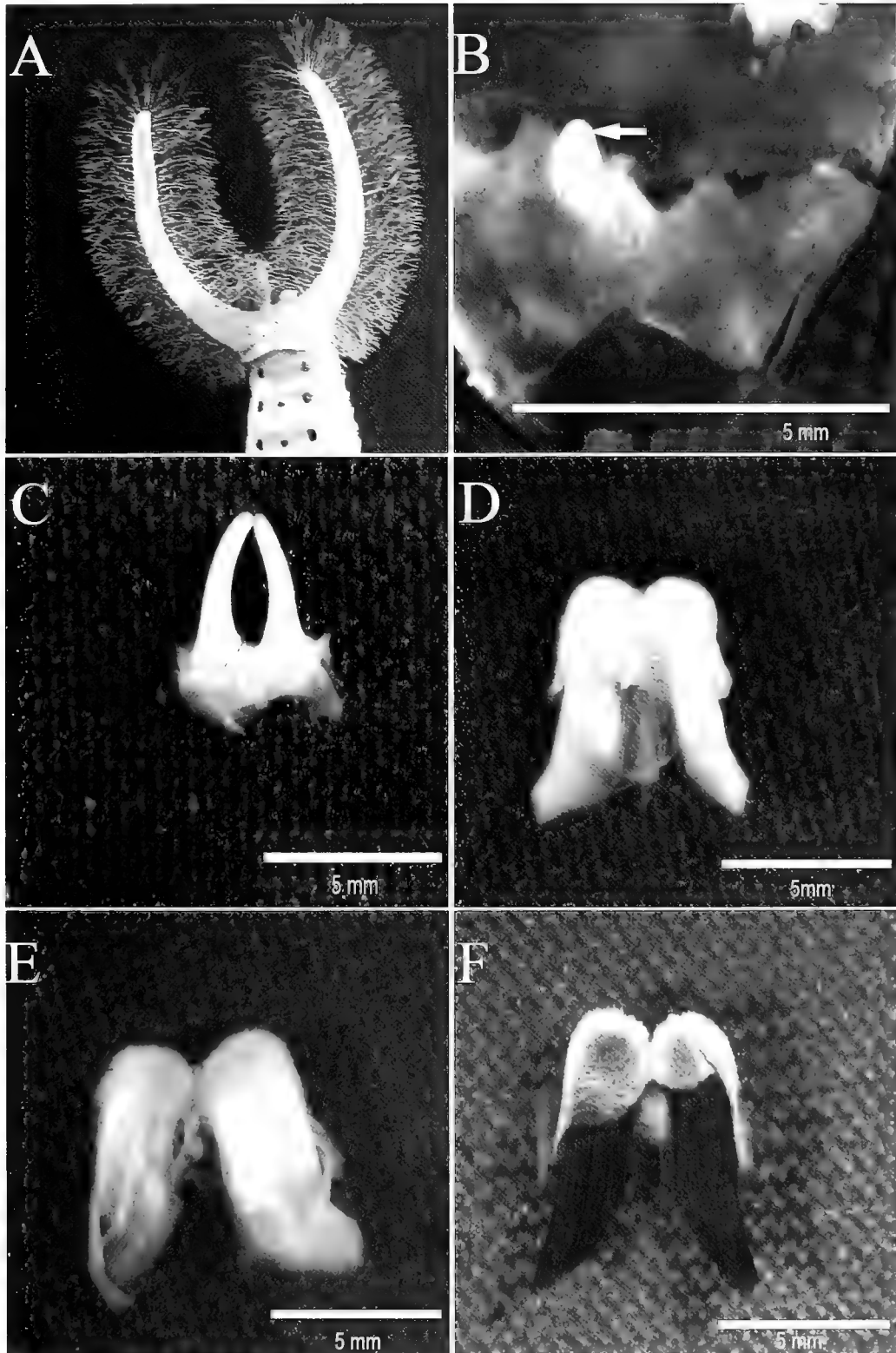


FIG. 1. (A) Artificially inflated core-mata of adult male *Estigmene acrea*; (B-F) five different stages of core-mata development: (B) stage one—the rapid proliferation of epidermal imagnal disks; (C) stage two—development of the imagnal disks into anteriorly oriented fingerlike projections; (D) stage three—the projections begin to regress and invaginate and form terminal buttons; (E) stage four—the core-matal scales develop within a fine sheath (F) stage five—the core-matal scales sclerotize and melanize, marking complete development.

coremata and their pheromone load in the adult male depend upon the quantity of pyrrolizidine alkaloids consumed in the larval stage (Davenport and Conner, 2003). Pyrrolizidine alkaloids thus have a specific morphogenetic effect stimulating coremata growth. We herein show how the PAs exert their effects on the development of the coremata of *Estigmene* and compare our results with those obtained earlier for *Cretonotus*. We propose *Estigmene acrea* as a readily accessible model for studying the behavior and evolution of sex role reversal in a pheromonal communication system.

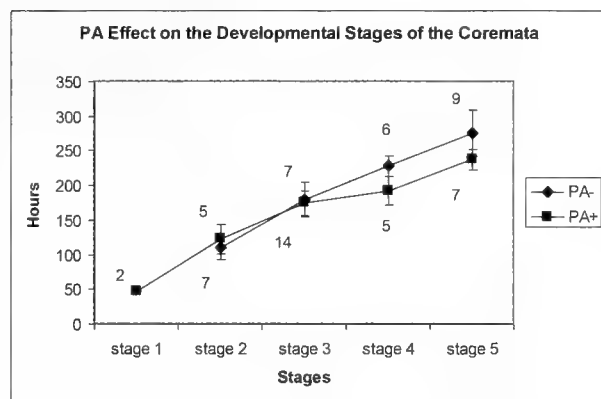


Fig. 2. Effect of dietary PAs on the rate of development of the coremata of *Estigmene acrea*. Symbols represent means, error bars represent standard deviations of the mean. Sample sizes are shown for PA+ males above the curve and for the PA- males below the curve.

METHODS

To determine the effects of dietary pyrrolizidine alkaloids on the development of coremata, we raised larvae of *Estigmene acrea* obtained from St. Charles Parrish, Louisiana, on a commercially available insect diet (salt marsh caterpillar diet, Bioserv # F9743B). Two hundred larvae were raised in disposable plastic petri dishes containing 1 to 5 cm³ of diet (depending on larval size), replaced daily. Larvae were raised at room temperature (average 23°C). Larvae and pupae were exposed to a 16 hour light: 8 hour dark photoperiod. During the early hours of their final larval instar one-half of the larvae (designated PA+) were supplemented with 5 cm³ of the diet containing 2.5 mg of the PA monocrotaline (Davenport and Conner, 2003). Once they had ingested all of the alkaloid diet, the PA+ larvae were returned to the normal diet feeding schedule. Controls animals (designated PA-) were offered an equal amount of PA-free diet. Monocrotaline was obtained from the Fairfield Chemical Company, Blythewood, South Carolina, and was certified 99% pure. Larvae were allowed to complete development to

the pupal stage. After pupation, the pupae were then sexed, and the males and females were separated. Pupal tissues from four males were fixed in Bouin's fixative (Fisher Scientific) every 12 hours beginning with the onset of pupation and ending with eclosion. After a 48 hour fixation period, abdomens were rinsed and stored in 5ml of 70% ethanol. Abdomens were dissected in 70% ethanol and the development of the coremata assessed using light microscopy and documented by digital photography using an Olympus SZX-ILLK100 dissecting scope fitted with an Optronics digital camera. Developing coremata were assigned to five discrete stages of development (based on the findings of this study) and their age in hours noted. Thin sections of 20 (10 PA+ and 10 PA-) male pupae were prepared using a vibratome. The sections were stained using using a 1% Neutral Red solution in 0.1M acetate buffer for 1 minute. Stained sections were dehydrated using an ethanol series, followed by xylene. Sections were coverslipped using Permount (Fisher Scientific) and examined under a Zeiss Axioplan™ 40C microscope using normal light. Digital images were taken with a Hamamatsu® color chilled CCD camera.

The final number of androconial scales associated with single corema of 10 PA+ and 10 PA- males was assessed by snipping the scales from the uninflated corema and manually counting them. The scale counts were compared using a *t*-test (SPSS® 14.0 for Windows, SPSS Inc.).

RESULTS

The coremata of *Estigmene acrea* develop from epidermally derived imaginal discs as in *Cretonotus* (Egelhaaf *et al.*, 1992). Their growth and development are diet dependent. Visible growth of the disks begins approximately 48 hours after pupation and is complete just prior to adult eclosion.

The development of the coremata can be broken down into five discrete stages (Figure 1 b-f):

1. Epidermal imaginal disks associated with the intersegmental membrane between the seventh and eighth abdominal segments begin to proliferate rapidly. (Note this stage was never observed in PA- males probably because of the smaller size of the structures. Its presence is inferred from our observations in PA+ animals and the presence of the later stages in PA- animals.)

2. Imaginal disks develop into anteriorly oriented fingerlike projections.

3. Projections begin to regress, invaginate, and form terminal buttons.

4. Coremata scales develop within a fine acellular sheath.

5. Coremata scales separate, sclerotize, and melanize, marking complete development.

The timing of the initial stages of development of PA+ males were not distinguishable from those of control animals. However, PA+ males reached stages four and five more quickly than did the PA- males (Figure 2: Mann Whitney U test, $P < 0.005$). PA+ males also developed more rapidly than PA- males, eclosing in 252 ± 2.5 hours ($n = 10$). PA- males eclosed in 324 hours ± 7.4 hours ($n = 10$), requiring an average of 3 additional days to complete pupal development. No difference was detected in the length of the pupal stage

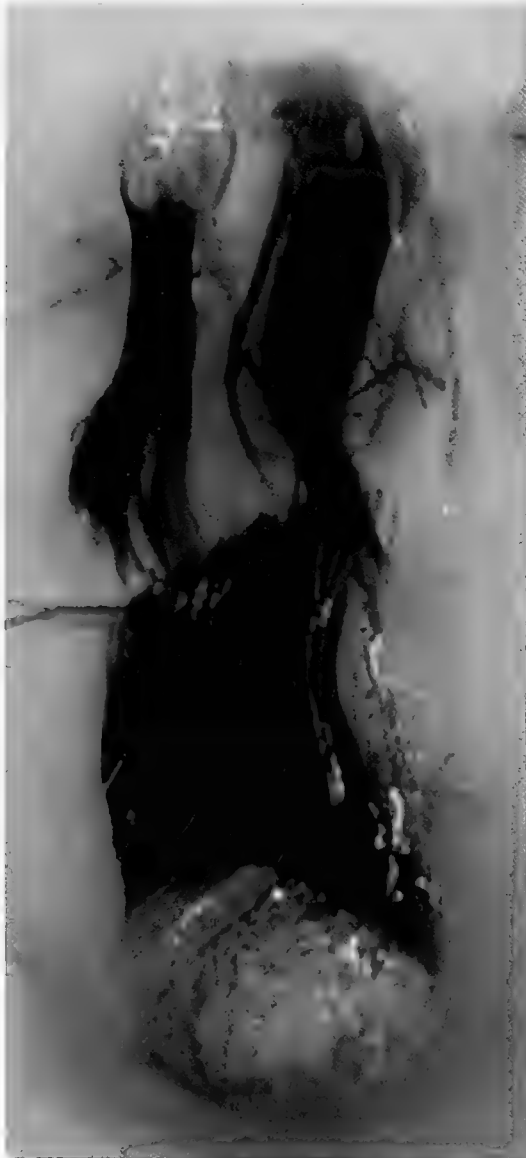


FIG. 3. Coremata of *Estigmene acrea* at 100% development; (top) 2 PA- coremata from a male that received no monocrotaline in its final larval instar, and (bottom) corema from a PA+ male that received 2500 μg of monocrotaline in the final larval instar.

in females of the two categories. The resultant coremata of the PA+ males were roughly twice the size of those of PA- males (Figure 3) and had more scales (490 ± 30.8 [$n=10$] scales for PA+ males versus 197 ± 23.6 [$n=10$] for PA- males, Figure 4: t -test $p < 0.001$). Since each scale has a socket and trichogen cell (secretory cell) at its base, the difference in the number of scales affected these components as well. The secretory cells associated with each scale are visible through the very thin cuticle of the coremata. This effect is heightened by the use of ultraviolet (360 nm) illumination (Figure 5).

Thin sections revealed the intimate relationship between each scale, its cuticular socket, and an underlying trichogen cell (Figure 6a). A network of densely staining (neutral red) stellate cellular inclusions (5–10 microns in diameter) can be seen in chains traversing the secretory cells, the sockets and the lumen of the scent scales (Figure 6b). These inclusions were only seen in PA+ animals.

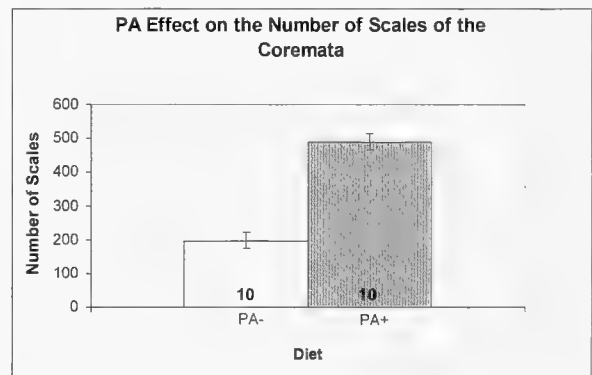


FIG. 4. Effect of dietary PAs on the number of coremata scales of *Estigmene acrea*. Mean values and standard deviations are plotted. (PA+ = 2500 μg monocrotaline). Sample sizes are indicated within each.

DISCUSSION

As in *Cretonotus*, pyrrolizidine alkaloids play a vital role in sexual signaling of *Estigmene* by regulating the development of the androconial structures that release male courtship pheromones. PAs accomplish this by acting as morphogens triggering the accelerated growth and development of the coremata from their epidermal imaginal disks in the pupal stage. Under the influence of PAs, coremata grow more rapidly and reach a greater final size.

Our results are in many respects similar to those Egelhaaf *et al.* (1992) obtained for the arctiid *Cretonotos transiens*. PAs had a pronounced effect on the developmental trajectory of the coremata of both *Cretonotos* and *Estigmene*, although the effect was notably larger (10X) in the former. The developmental stages of the two groups are essentially identical except

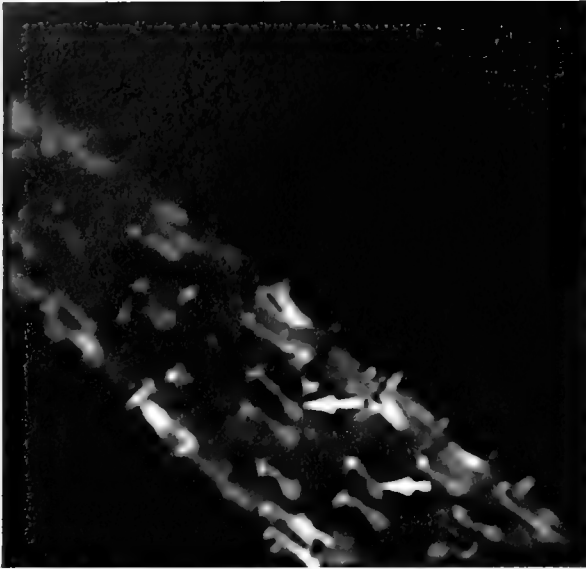


FIG. 5. Fluorescent image of artificially inflated coremata of adult male *Estigmene acrea* that received monocrotaline in its last larval instar viewed under UV (360 nm.) illumination, arrows show individual secretory cells below each scale. .

that the coremata of *Cretonotos* are quadrifid. Egelhaaf *et al.* did not note cellular inclusions specific to PA+ animals that we have described. Since these inclusions were found only in PA+ males, we posit that they are involved in transport of the male courtship pheromone from its origin in the secretory cells to its release point.

Hartmann *et al.* (2004, 2005) showed that *Estigmene* larvae process ingested PAs in a series of steps. The PAs

are first hydrolyzed to the simple necine base retronecine, which is re-esterified to form insect-specific alkaloids (eg. Cretonotine B). In males, these insect-specific alkaloids are used to produce the courtship pheromone, hydroxydanaidal. We do not yet know which of these alkaloidal materials stimulates coremata growth. It seems unlikely that it is hydroxydanaidal because this compound does not appear until well after the coremata are fully formed (Nickisch-Rosenegk, *et al.*, 1990, Hartmann *et al.*, 2004).

The strength of the morphogenetic effect of PAs, which has now been detected in *Cretonotos* and *Estigmene*, acts as a measure of the importance of PAs in their natural history and in the sexual system of each species. It should be noted that not all PA-feeding arctiids show the effect. Methods identical with those described herein did not detect this effect in *Pyrharctia isabella* (E. McCammack and W. E. Conner, unpublished data). Krasnoff and Roelofs (1989) argued that the alkaloid-based pheromonal communication system of *P. isabella* has become vestigial in that species and McMammack and Conner's findings support their contention.

The pupal stage of male *Estigmene* exposed to PAs in their larval stage is significantly shortened. Egelhaaf *et al.* (1992) did not note an effect on the duration of the pupal stage in *Cretonotos*, but a similar effect was noted for larvae and adult females in the arctiid *Utetheisa ornatix* (del Campo *et al.* 2005). For *Utetheisa* it was argued that the shortening of life stages

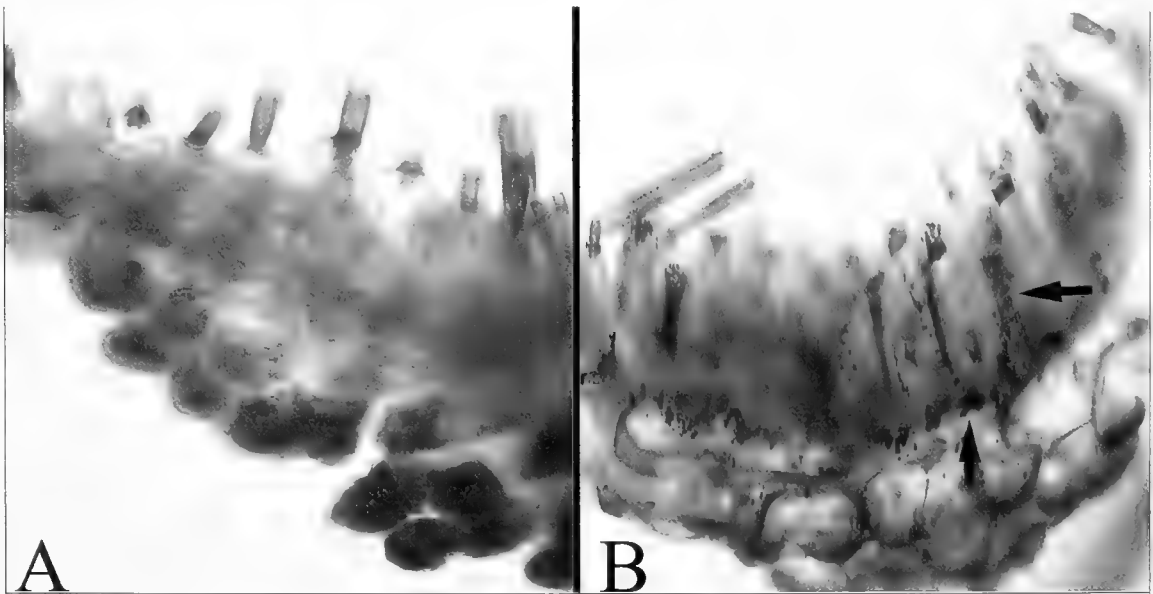


FIG. 6. Ultra thin cross sections of coremata: (A) section magnified at 20X from a male that received no PAs in its larval state (B) section magnified at 10X from a male that received 2500 µg of monocrotaline in its last larval instar, arrows highlight heavily stained stellate cellular inclusions

in the presence of PAs is a competitive strategy to gain a numerical advantage over slower growing PA-deprived individuals given a patchy host plant environment. The significance of pupal shortening in male *Estigmene* is unknown but it could conceivably be part of a similar adaptive strategy.

Overall the behavior, physiology, and development of *Estigmene* are similar to that of *Cretonotus*. The exact phylogenetic relationship of the two genera is not yet known, but they are likely to be closely related (Ferguson, 1985). It is possible that their reliance on PAs as morphogens and behavioral regulators stems from a common PA-feeding ancestor (Weller *et al.*, 1999). Because of the behavioral, developmental, and ecological similarities between *Cretonotus* and *Estigmene* we propose the latter as a model system that will provide insight into the behavior and evolution of the extraordinary sex role reversal behavior in both species.

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NOTES ON NEARCTIC *EUCOSMA* HÜBNER: A NEW SPECIES, A RESURRECTED SPECIES, AND THREE NEW SYNONYMIES (TORTRICIDAE)

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ABSTRACT. Three new synonymies are proposed in Nearctic *Eucosma*: *E. fandana* Kearfott (= *E. gandana* Kearfott), *E. snyderana* Kearfott (= *E. sperryana* McDunnough), and *E. irroratana* (Walsingham) (= *E. perdricana* (Walsingham)). *Eucosma kandana* Kearfott is resurrected as a valid species name after having been treated for more than eighty years as a junior synonym of *perdricana*. *Eucosma curlewensis*, new species, is described from southern Idaho, Utah, Nevada, and southern California. Reviews are included of five additional taxa: *E. invicta* (Walsingham), *E. subinvicta* Kearfott, *E. spaldingana* Kearfott, *E. hazelana* Klots, and *E. handana* Kearfott, each of which bears some resemblance to one or more of the aforementioned species. Lectotypes are designated for *invicta*, *spaldingana*, *perdricana*, *irroratana*, and *handana*. Adults and genitalia of each species are illustrated, though females of *hazelana* and *irroratana* are currently not known.

Additional key words: Olethreutinae, Eucosmini

Species described by early North American tortricid specialists commonly were based on few representatives of the proposed new taxa, often on a single specimen. The attendant lack of understanding of variation resulted in the creation of a large number of synonyms, some of which are only now being recognized. This paper addresses several such problems in the genus *Eucosma* Hübner. It also proposes a name for a new species of *Eucosma* from western United States.

Eucosma fandana Kearfott and *E. gandana* Kearfott are relatively large lemon-yellow species that historically have been separated by the presence in *fandana* (Fig. 2) of longitudinal, white, forewing streaking, a feature lacking in *gandana* (Fig. 3). Each name is based on a single female. The holotypes were the only specimens of these taxa known to Heinrich (1923), and his study did not include an assessment of the female genitalia, so subsequent determinations have been based solely on forewing maculation. Material now available in collections makes it clear that the forewing streaking in *fandana* is variable and grades into the obsolescent form associated with *gandana*. There are no significant genitalia differences in the two forms, so it seems that the two names refer to a single species. There is another western species of similar size with lemon-yellow coloration, *E. canariana* Kearfott, but its forewing features yellow streaking on a silvery-white ground. An illustration of the adult (Fig. 4) is included for comparison.

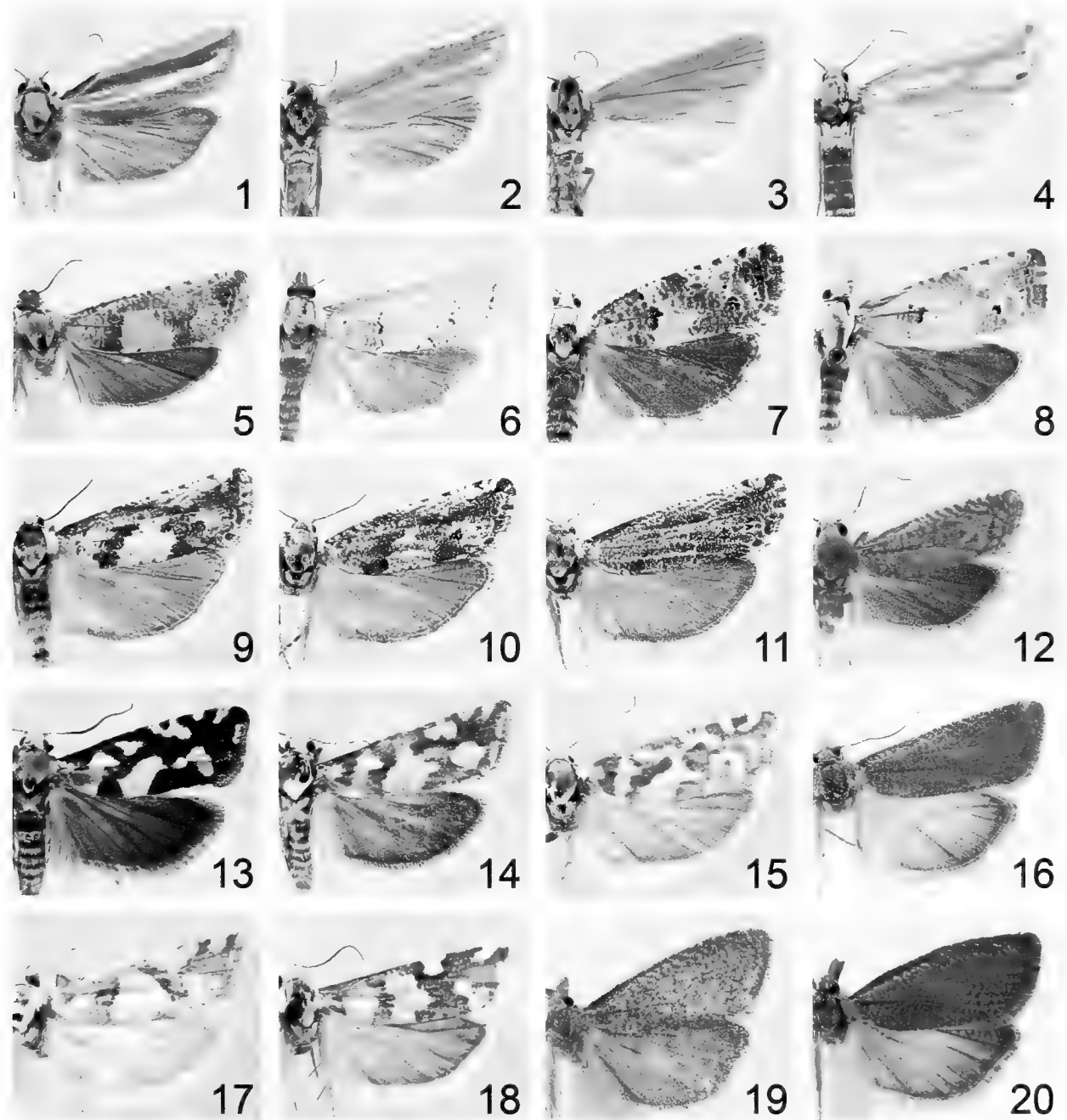
Each of *E. snyderana* Kearfott and *E. sperryana* McDunnough was described from a single male. In examining a long series of *snyderana* specimens from Albany Co., Wyoming, it became apparent that the *sperryana* forewing pattern (Fig. 11) is just one of the variations (Figs. 9–11) found in *snyderana*. The genitalia of the two holotypes are indistinguishable, so *sperryana* should be regarded as a junior synonym of

snyderana. Two other western species, *E. invicta* (Walsingham) and *E. subinvicta* Kearfott, can easily be confused with *snyderana*. Heinrich (1923) suspected that *subinvicta* is “only a race of *invicta*,” but there are consistent differences in both maculation and genitalia that support the case for two species. Diagnostic features of *snyderana*, *invicta*, and *subinvicta* are discussed below.

Walsingham (1879) described *E. irroratana* and *E. perdricana* based on five and two male specimens, respectively, collected during his 1871 expedition to California and Oregon. He noted the similarity of the two species but considered the smaller size and lack of lustrous gray irrorations in the *perdricana* syntypes as grounds for proposing the second name. Kearfott (1907) described *E. kandana* from six specimens collected by Tom Spalding in Stockton, Utah. Heinrich (1923) had access to the *kandana* cotypes and to a specimen of *irroratana* that had been given to Busck by Walsingham for deposit in the United States Museum of Natural History (USNM). He had seen no authoritatively identified specimens of *perdricana* but concluded on the basis of Walsingham's description that *kandana* was a synonym of *perdricana*. The forewing patterns of these species are similar (Figs. 12, 19), and *kandana* is smaller than *irroratana* (a distinguishing character attributed to *perdricana* by Walsingham), but the male genitalia are different (Figs. 29, 30). Consequently, *kandana* must be reinstated as a valid species name. I examined one of the *perdricana* syntypes, two *irroratana* syntypes, and one *irroratana* topotype and found no substantial differences in forewing pattern or male genitalia. The *perdricana* syntype (Fig. 19) is somewhat worn but does show faint traces of the lustrous scaling characteristic of *irroratana* (Fig. 20). The smallest *irroratana* specimen was only slightly larger than the *perdricana* syntype, suggesting that size

is not a diagnostic character. I believe these are sufficient reasons for treating the two names as synonyms. *Eucosma handana* Kearfott, a western species that is similar in maculation and male genitalia to *irroratana*, is also reviewed.

Finally, I propose the name *Eucosma curlewensis* for a new taxon collected recently in Idaho but first noticed during faunal studies in southern California (Brown & Bash, 1997; Powell, 1994). Two western species with potential for being confused with *curlewensis*, *E.*



FIGS. 1-20. 1. *E. fandana*, ♂ Billings Co., North Dakota. 2, 3. *E. fandana*, ♀, ♀ Alamosa Co., Colorado. 4. *E. canariana*, ♂ Sanpete Co., Utah. 5. *E. invicta*, Lectotype ♂. 6. *E. invicta*, ♂ Natrona Co., Wyoming. 7. *E. subinvicta*, ♀ Coconino Co., Arizona. 8. *E. subinvicta*, ♂ Riverside Co., California. 9, 10, 11. *E. snyderana*, ♂, ♂, ♂ Albany Co., Wyoming. 12. *E. kandana*, ♂ Oneida Co., Idaho. 13, 14. *E. curlewensis*, ♂, ♂ San Diego Co., California. 15. *E. curlewensis*, ♂ Oneida Co., Idaho. 16. *E. handana*, ♂ Benton Co., Washington. 17. *E. spaldingana*, ♂ Toole Co., Utah. 18. *E. hazelana*, Holotype ♂. 19. *E. perdricana*, Lectotype ♂. 20. *E. irroratana*, Lectotype ♂.

hazelana Klots and *E. spaldingana* Kearfott, are also reviewed.

I examined the primary types of all the species mentioned above except *E. canariana*, and I've listed below in the species accounts the data and depositories of all specimens that I could locate and confirm as members of the various type series.

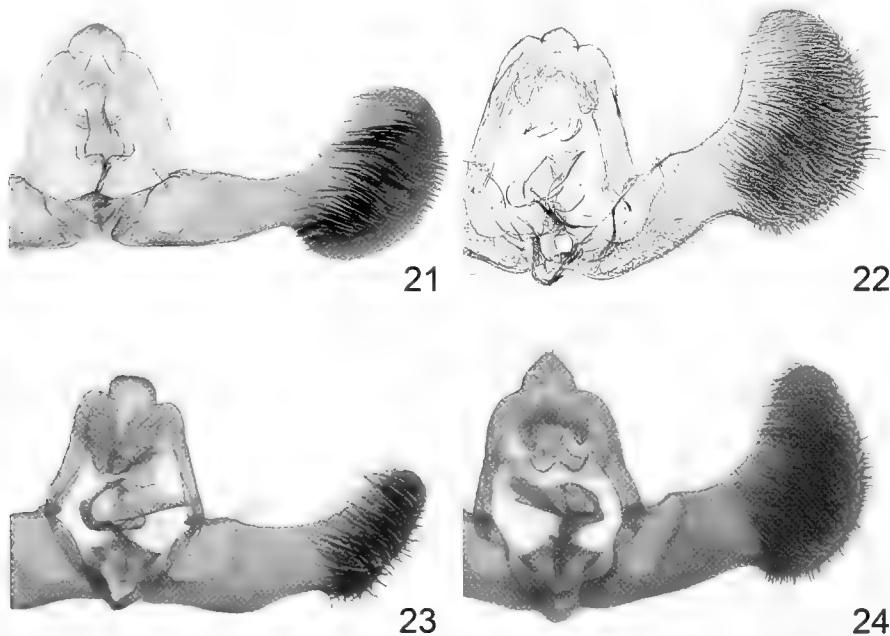
MATERIALS AND METHODS

This study is based on an examination of 403 adult specimens and 85 genitalia preparations from the following collections: American Museum of Natural History (AMNH), George Balogh, Canadian National Collection (CNC), Colorado State University (CSU), Los Angeles County Museum of Natural History (LACM), Mississippi Entomological Museum (MEM), The Natural History Museum, London (BMNH), USNM, University of California, Berkeley (UCB), and D. J. Wright (DJW).

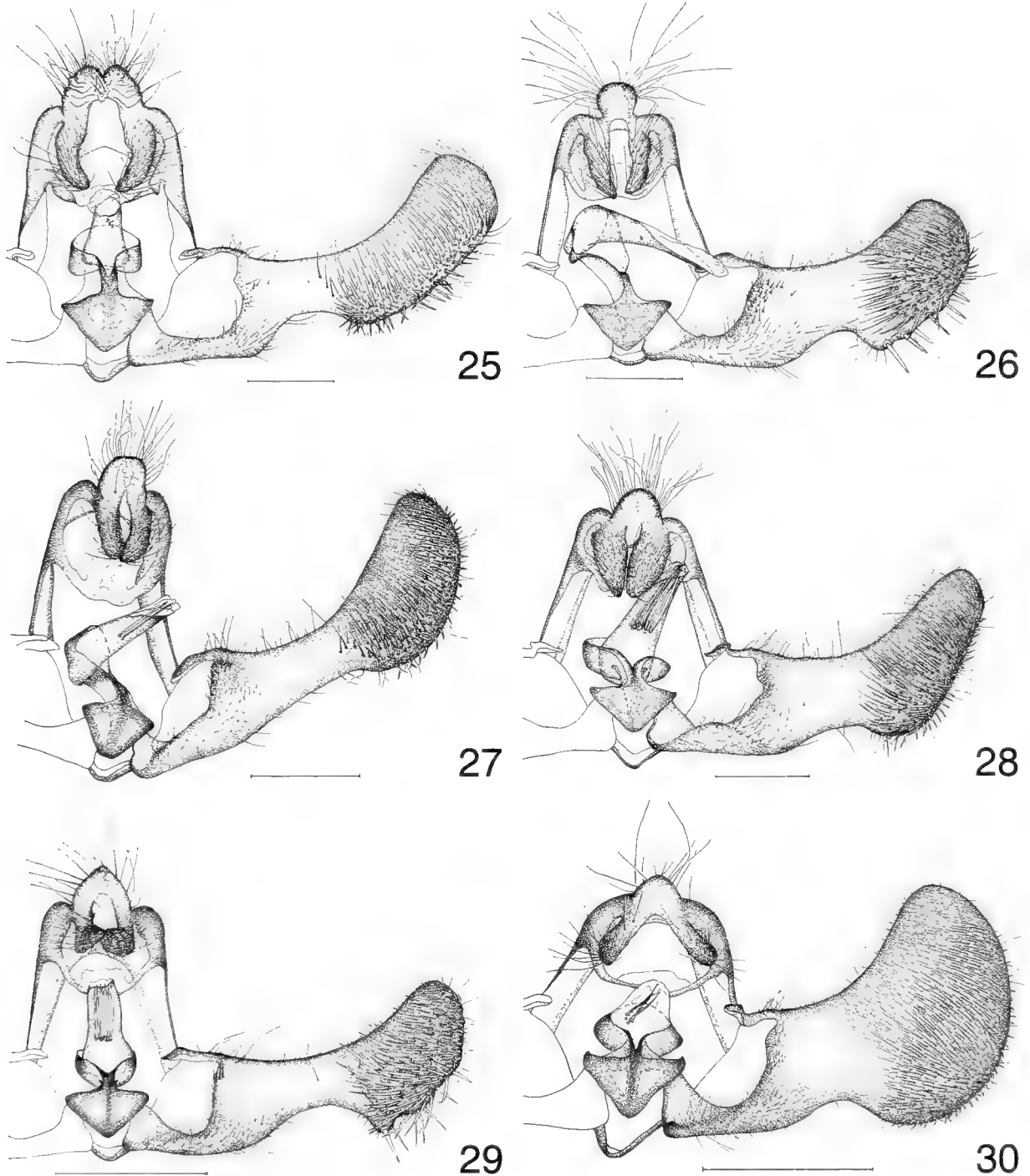
Due to the extreme similarity among many species of *Eucosma*, the potential for future recognition of additional synonymy in the genus, and the possibility of mixed series of syntypes, it is necessary to designate lectotypes for these taxa to stabilize the nomenclature of the group. For *invicta*, *perdricana*, and *irroratana* I selected specimens chosen by Obraztsov for this purpose, his designations having never been published. As for *spaldingana* and *handana*, Klots (1942) reported 7 and 3 syntypes, respectively, in the AMNH, including

lectotypes whose designations he attributed to Heinrich (1923). The material I received on loan from AMNH consisted of 6 specimens of *spaldingana* and 3 of *handana*, of which none bears the green LECTOTYPE label typically affixed to such specimens by Klots. Pinned on the floor of each unit tray was a green label with the notation "needs LECTOTYPE." Whatever the explanation for these discrepancies, in neither case can Heinrich's comment (1923:84, 102) "Type in American Museum" be interpreted as the selection of a particular specimen, so I'm choosing a lectotype for each species from among the syntypes in the AMNH. Each of the remaining species treated here currently has a holotype or lectotype, either by virtue of having been based on a single specimen or by prior designation.

Forewing length (FWL), defined as distance from base to apex (including fringe), is used as a measure of specimen size. Aspect ratio (AR), defined as FWL divided by medial forewing width, provides a rough measure of forewing geometry and is reported as the average, rounded to two decimal places, of corresponding values calculated for a small sample of specimens. The number of measurements or observations supporting a particular statement is indicated by n. The adult images were edited in Adobe Photoshop CS, and those in Figures 8, 17, and 18 were flipped horizontally so that what appears to be the right forewing is in fact the left forewing. Forewing pattern terminology follows Brown & Powell (1991) as modified



FIGS. 21-24. Genitalia of lectotypes. 21. *E. invicta*, slide BMNH 11574. 22. *E. irroratana*, slide BMNH 11512. 23. *E. spaldingana*, slide DJW 1548. 24. *E. handana*, slide DJW 1505



FIGS. 25-30. Male genitalia. 25. *E. fandana*, slide DJW1490. 26. *E. curlewensis*, slide DJW 1501. 27. *E. hazelana*, slide DJW 1067. 28. *E. spaldingana*, slide DJW 1503. 29. *E. kandana* slide DJW 766. 30. *E. perdricana*, Lectotype, slide BMNH 11509. Scale bars = 0.5 mm.

by Baixeras (2002).

SPECIES ACCOUNTS

Eucosma fandana Kearfott

(Figs. 1, 2, 3, 25, 35)

Eucosma fandana Kearfott 1907:19; Barnes and McDunnough 1917:169; Heinrich 1923:81; McDunnough 1939:45; Powell 1983:34.

Eucosma argyraula Meyrick 1912:34, invalid replacement name.

Eucosma gandana Kearfott 1907:20; Barnes and McDunnough 1917:169; Heinrich 1923:83; McDunnough 1939:45; Powell 1983:34, **new synonymy**.

Eucosma chloroleuca Meyrick 1912:34, invalid replacement name.

Types. *Eucosma fandana*. Holotype: ♀, Denver, Colo., Oslar, genitalia slide DJW 1488, AMNH [type locality and collector reported by Kearfott (1907) but not present on pin labels]. *Eucosma gandana*. Holotype: ♀, Denver, Colo., 10 Sept. 0? [year illegible], Oslar, genitalia slide DJW 1489, AMNH.

Remarks. Typical *fandana* (Fig. 2) has a lemon-yellow forewing with two, white, longitudinal steaks. The anterior streak runs just posterior to the costa, arising at the distal end of the costal fold and terminating at the apex, leaving a very narrow band of yellow coloration along the costa itself. The posterior streak is broader and runs anterior to the cubital vein from the base to just short of the termen, where it bends toward the apex. In darker specimens (Fig. 1), yellowish brown replaces some of the lemon-yellow coloration. Often the anterior streak is suffused with yellow, and occasionally both streaks are strongly suffused with yellow (Fig. 3). The latter results in the phenotype associated with the name *gandana*. Forewing statistics: ♂ FWL: 10.7–15.7 mm (mean = 13.5, n = 13), AR = 3.36, ♀ FWL: 12.4–15.2 mm (mean = 13.9, n = 7), AR = 3.28.

The male genitalia (Fig. 25) (n = 4) has the following features: Uncus well developed, medially divided into two lobes, and

moderately wrinkled (an unusual feature in *Eucosma*); anellus well developed, not closely surrounding aedeagus; vesica lacking deciduous cornuti; interior surface of aedeagus usually with two clusters of *ca.* four very small setae (visible at 100×), one at anterior extremity, the other located medially; cucullus semirectangular with mildly concave costal margin, length *ca.* 2.5 × width. Female genitalia (Fig. 35) (n = 4): Papillae anales facing ventrally and densely setose; sterigma with triangular posterolateral projections, width of posterior margin *ca.* 4 × ostium diameter, lateral projections sparsely scaled; corpus bursae with only one signum.

Distribution and flight period. The 27 specimens (19 ♂, 8 ♀) I examined indicate that this moth occurs in the high plains east of the Rocky Mountains from Colorado north into Saskatchewan and Manitoba. Capture dates range from 7 July to 24 September, but the majority of the records are from August and the first half of September.

Eucosma snyderana Kearfott

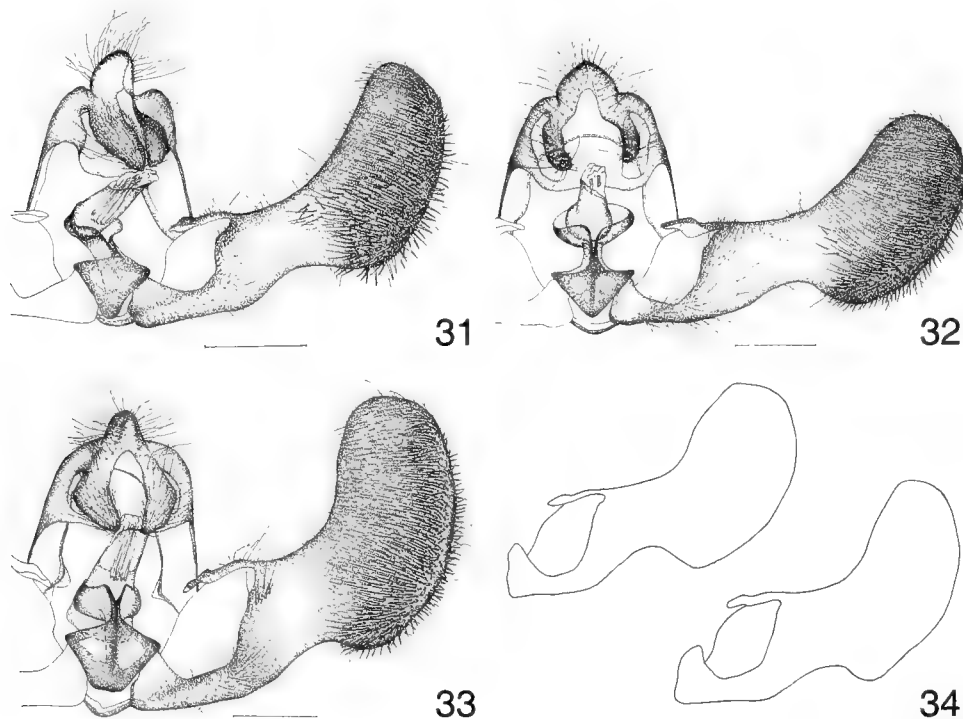
(Figs. 9–11, 31, 38)

Eucosma snyderana Kearfott 1907:89; Barnes and McDunnough 1917:171; Heinrich 1923:107; McDunnough 1939:46; Powell 1983:34.

Eucosma sperryana McDunnough 1942:69; Powell 1983:34, **new synonymy**.

Types. *Eucosma snyderana*. Holotype: ♂, Blackfoot, Idaho, 3 June, A. J. Snyder, genitalia slide CH 16 Dec 1919, AMNH. *Eucosma sperryana*. Holotype: ♂, Opal, Wyo., 24 June 1933, G. & J. Sperry, genitalia slide no. 77, CNC.

Remarks. Forewing maculation in *snyderana* (Figs. 9–11) consists primarily of three brown and gray markings: a subbasal fascia partially

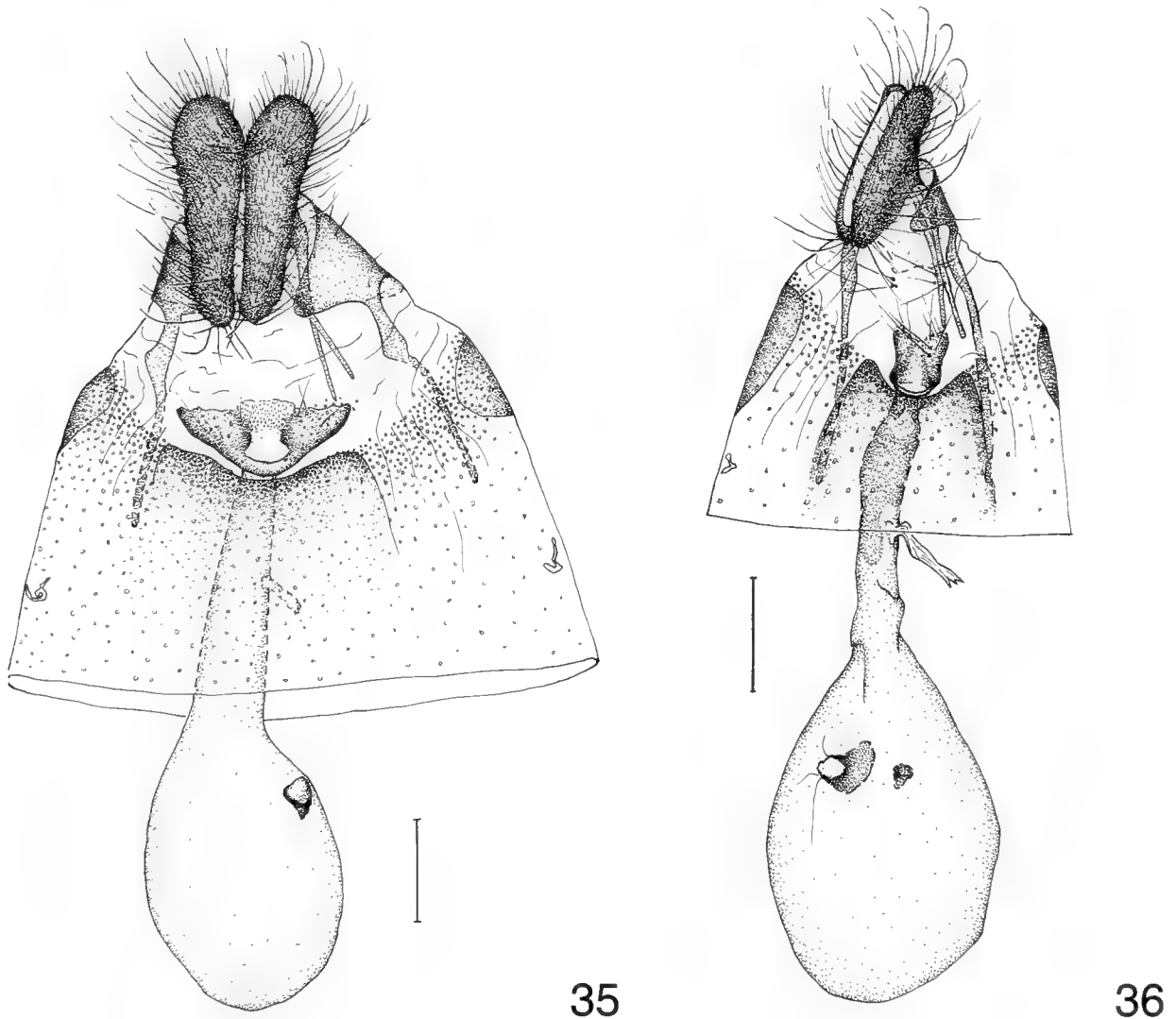


FIGS. 31–34. Male genitalia. 31. *E. snyderana*, slide DJW 267. 32. *E. invicta*, slide DJW 160. 33, 34. *E. subinvicta*, slides DJW 1550, 1551, 1552. Scale bars = 0.5 mm.

expressed as an outwardly oblique bar from dorsum to radius; a median fascia composed of a narrow longitudinal streak from mid costa to distal end of cell together with a broader transverse band along the basal margin of the ocellus, the latter terminating on the pretornal portion of the dorsum; and a subtriangular patch anterior to the ocellus that connects to an apical dash. Some specimens (Fig. 9) have a white interfascial spot extending from mid dorsum to radius and a moderate amount of white coloration in the basal area. The phenotype associated with the name *sperryana* (Fig. 11) has the forewing suffused with brown and gray to the extent that the fasciae are largely obscured. Most specimens (Fig. 10) are intermediate in this respect. In all phenotypes the distal one half of the costa is white, with dark marks delimiting the strigulae. Forewing statistics: ♂ FWL: 12.7–16.5 mm (mean = 14.4, n = 24), AR = 3.34, ♀ FWL: 12–14.6

mm (mean = 13.5, n = 13), AR = 3.12.

The male genitalia of *snyderana*, *invicta* and *subinvicta* (Figs. 31–34) are similar but distinguishable. In each case the uncus is semitriangular and well developed. In *invicta* its base is noticeably broader, with basal width *ca.* 2 × height; in the other two species these dimensions are nearly equal. In *snyderana* and *subinvicta* the ventral surface is produced into a wedge-shaped ridge, the ridge line being particularly sharp in *snyderana*. The anellus in *invicta* is cuplike and loosely surrounds the base of the aedeagus, in *subinvicta* it is closely approximate to the aedeagus, and in *snyderana* it is intermediate in this respect. Both *snyderana* and *subinvicta* have deciduous cornuti in the vesica; *invicta* does not but does possess two small sclerotized patches toward the distal end of the aedeagus. In *subinvicta* the valva is somewhat variable in shape (Figs. 33, 34). Compared to the other



FIGS. 35-36. Female genitalia. 35. *E. fandana*, slide DJW 1489. 36. *E. kandana*, slide DJW 1549. Scale bars = 0.5 mm.

two species it has a more strongly concave costal margin and is wider basally and at the neck. The apex of the cucullus is angular in *snyderana*, evenly rounded in *invicta*, and intermediate in *subinvicta*. The female genitalia of the three species are quite similar. Subtle differences can be detected in the shape of the sterigma (Figs. 37-39), but this character is sufficiently variable in each species as to render identification on this basis unreliable. In *invicta* there are numerous, long, hairlike setae on the posterolateral corners of the sterigma and on the membrane between the sterigma and the ventral extremities of tergum VIII. Only a few such setae are found in *subinvicta*, and *snyderana* is intermediate in this regard but closer to *invicta*.

Distribution and flight period. I examined 76 specimens (63 ♂, 13 ♀) from California, Idaho, Oregon, Utah, Washington, and Wyoming. The flight period

extends from mid May to early July.

Eucosma invicta (Walsingham)

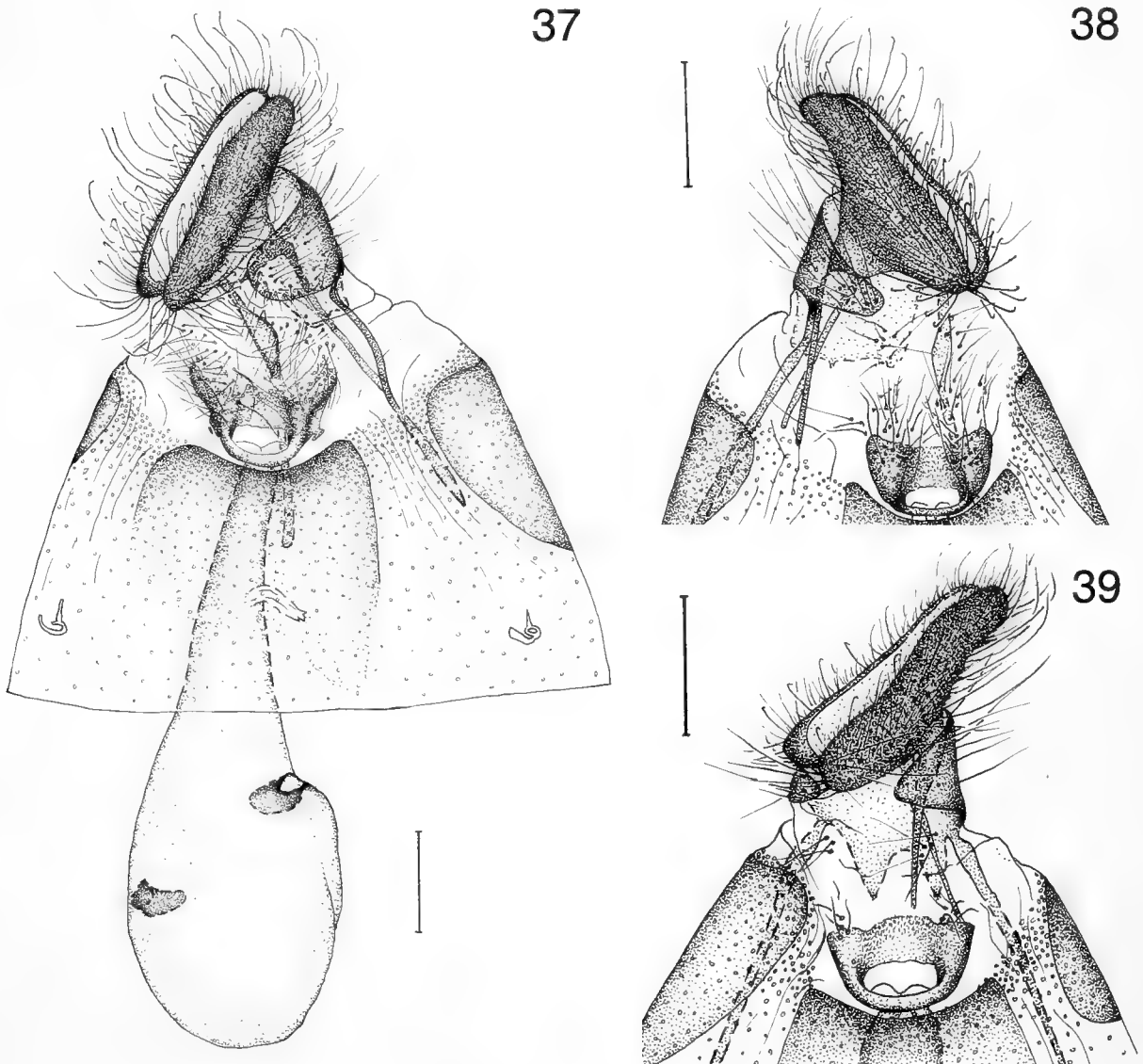
(Figs. 5, 6, 21, 32, 37)

Paedisca invicta Walsingham 1895:509.

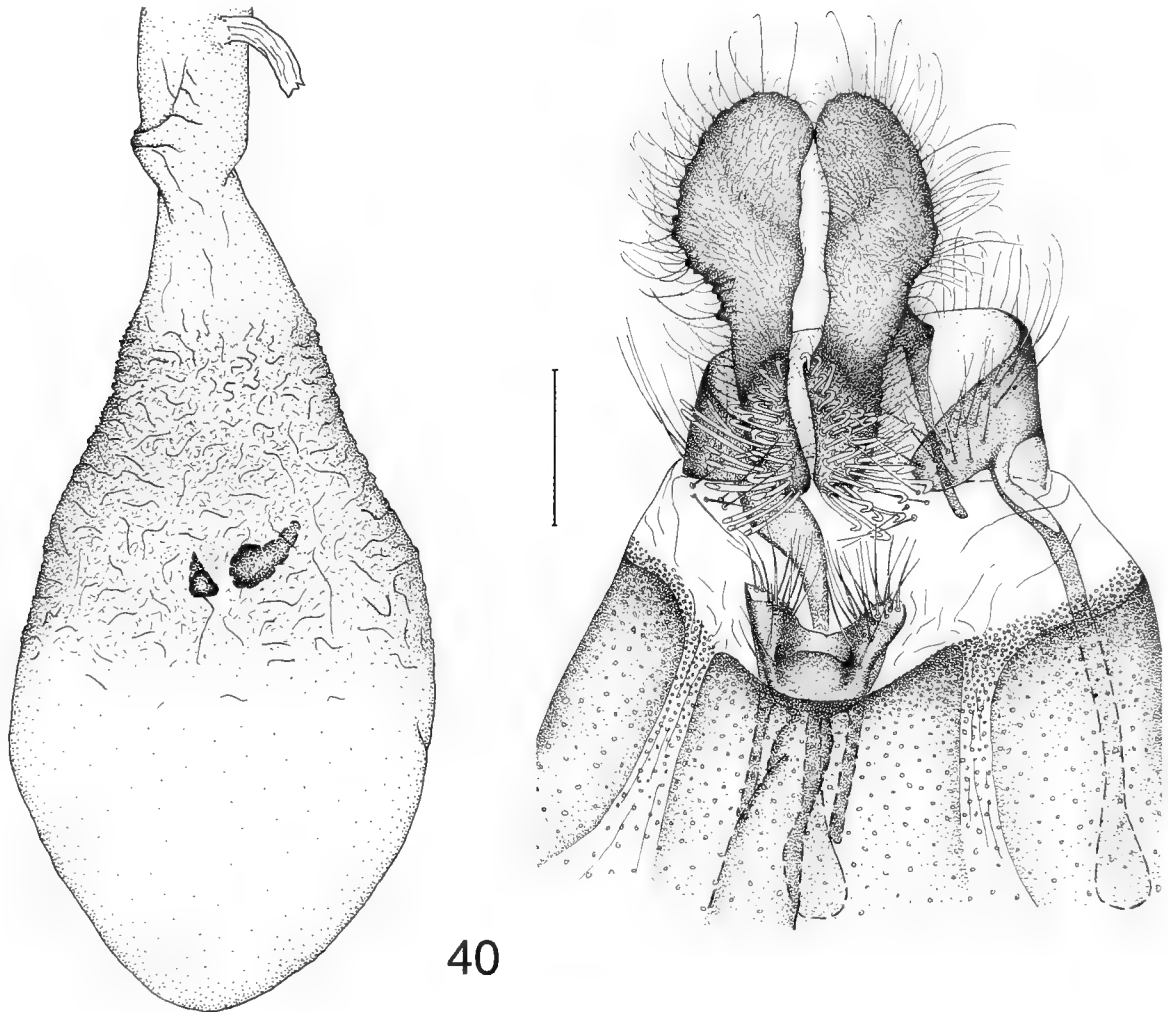
Eucosma invicta: Fernald [1903]:460; Barnes and McDunnough 1917:171; Heinrich 1923:107; McDunnough 1939:46; Powell 1983:34.

Types. Lectotype here designated (Figs. 5, 21): ♂, Larimer Co., Colorado, 5000 ft., July 1891, Smith, genitalia slide 11574, BMNH. Paralectotypes: same data as lectotype (8 ♂, genitalia slide 11575), BMNH.

Remarks. Forewing coloration is variable in both *invicta* (Figs. 5,



FIGS. 37-39. Female genitalia. 37. *E. invicta*, slide DJW 1555. 38. *E. snyderana*, slide DJW 1492. 39. *E. subinvicta*, slide DJW 1514. Scale bars = 0.5 mm.



40

FIG. 40. Female genitalia. *E. curlewensis*, slide DJW 1499. Scale bars = 0.5 mm.

6) and *subinvicta* (Figs. 7, 8), and pale phenotypes of the two species are quite similar. Nevertheless, Kearfott (1907) observed (and my investigations confirm) that head color is a reliable diagnostic character: rose brown in *invicta*, white in *subinvicta*. Well marked specimens of *invicta* (Fig. 5) display at least partial subbasal and median fasciae, which are often suffused with the rose-brown color of the head. In pale specimens (Fig. 6) these features can be difficult to discern. The maculation always includes a white interfascial spot at mid dorsum. Its proximal margin tends to be straight, perpendicular to the dorsum, and thinly lined with black scales, and in darker specimens it is preceded basally by a brown to gray bar from dorsum to radius. The strigulae on the distal one half of the costa are weakly defined and sometimes coalesce into a white costal streak. Forewing statistics: ♂ FWL: 11.5–17.2 mm (mean = 14.6, n = 28), AR = 3.24, ♀FWL: 13.5–16.6 mm (mean = 14.8, n = 6), AR = 3.05.

Genitalia characters are discussed under *snyderana*.

Distribution and flight period. I examined 50 specimens (40 ♂, 10 ♀) from Alberta, California,

Colorado, Kansas, Montana, Nevada, New Mexico, Saskatchewan, Utah, and Wyoming. Most records are from August and September, but I found one each from April and June and three from July.

Eucosma subinvicta Kearfott
(Figs. 7, 8, 33, 34, 39)

Eucosma subinvicta Kearfott 1907:33; Barnes and McDunnough 1917:171; Heinrich 1923:107; McDunnough 1939:46; Powell 1983:34.

Types. Holotype: ♀, Williams, Ar[izona], genitalia slide DJW 1547, AMNH. Paratypes: Williams, Ariz., 1 July (1 ♀, genitalia slide 70382), 25 July (1 ♀), USNM.

Remarks. Typical *subinvicta* forewing maculation (Fig. 7) includes a white spot at mid dorsum, a gray basal patch, and a gray median fascia. The forewing in pale phenotypes (Figs. 8) is strongly suffused

with white throughout. The basal patch is bordered distally by a thin line of black scales that widens over the cubitus to form a conspicuous black mark. In most cases the line jogs inwardly on 1A+2A. In pale specimens only the black mark is expressed. A second black mark occurs on the proximal margin of the ocellus. The distal one half of the costa is white, with dark marks delimiting the costal strigulae. Forewing statistics: ♂ FWL: 10.2–15.5 mm (mean = 13.6, n = 28), AR = 2.97, ♀ FWL: 10.7–15.9 mm (mean = 13.5, n = 21), AR = 2.98.

Genitalia characters are discussed under *snyderana*.

Distribution and flight period. I examined 60 specimens (36 ♂, 24 ♀) from Arizona, southern California, and Utah. Most records are from July and August. Two series of specimens from Glendora, California, one collected in May, the other in September, suggest the possibility of two broods in southern California.

Eucosma kandana Kearfott, revised status

(Figs. 12, 29, 36)

Eucosma kandana Kearfott 1907:20; Barnes and McDunnough 1917:169.

Eucosma argillacea Meyrick 1912:34, invalid replacement name.

Eucosma perdricana: (not Walsingham, 1895) Heinrich 1923:99; McDunnough 1939:46; Powell 1983:34.

Types. Lectotype designated by Klots (1942): ♂, Stockton, Utah, Tom Spalding, [4–17 August: reported by Kearfott (1907) but not present on pin labels], genitalia slide CH 16 Dec 1919, AMNH. Paralectotypes: Stockton, Utah, Tom Spalding (1 ♀, genitalia slide DJW 1549), AMNH; 4 July 1904 (1 ♂, ♀, ♂ genitalia slide USNM 70672), 1 August 1904 (1 ♀), 7 August 1904 (1 ♀), USNM.

Remarks. The forewing of *kandana* (Fig. 12) is brownish gold with fine white mottling. The only markings are the thin dashes on the distal one half of the costa separating the white costal strigulae. The inconspicuous ocellus is bordered basally and distally by whitish transverse bars and usually has a few black scales in its central field. The scales along the terminal margin of the membrane have brown to blackish-brown medial marks and lighter apices. Forewing statistics: ♂ FWL: 6.3–9.4 mm (mean = 8, n = 10), AR = 3.01, ♀ FWL: 8–9.3 mm (mean = 8.8, n = 5), AR = 2.96.

Male genitalia (Fig. 29) (n = 6): Uncus semitriangular; dorsolateral shoulders of tegumen well developed; aedeagus with 5–11 deciduous cornuti; valva with costal margin concave, ventral margin broadly invaginated, cucullus with apical one third tapering to evenly rounded apex, ventral angle with rounded projection supporting one or two large spiniform setae, distal margin with ca. five stout setae and with a mild convex projection above the anal angle, medial surface with numerous stout setae. Female genitalia (Fig. 36) (n = 1): Papillae anales facing laterally and densely setose; sterigma semirectangular; length ca. 1.5× width, lateral margins weakly concave; ductus bursae uniform in width, with large sclerotized patch between ostium and juncture of ductus seminalis; corpus bursae with two signa.

Distribution and flight period. I examined 22 specimens (16 ♂, 6 ♀) from California, Colorado, Idaho, Montana, Oregon, Utah and Washington. Capture dates range from 15 June to 10 August.

Eucosma irroratana (Walsingham)

(Figs. 19, 20, 22, 30)

Paedisca irroratana Walsingham 1879:48.

Eucosma irroratana: Fernald [1903]:457; Barnes and McDunnough 1917:170; Heinrich 1923:101; McDunnough 1939:46; Powell 1983:34.

Paedisca perdricana Walsingham 1879:49, new synonymy.

Eucosma perdricana: Fernald [1903]:457; Barnes and McDunnough 1917:170.

Types. *Paedisca irroratana*. Lectotype here designated (Figs. 20, 22): ♂, Head of Noyo R., Mendocino Co., Calif., 8–11 June 1871, Wlsm. 91898, genitalia slide 11512. Paralectotypes: same data as lectotype (3 ♂, Wlsm. 91899, 91900, 91901); past Little Lake, Mendocino Co., Calif., 12 June 1871, (1 ♂, Wlsm. 91905). *Paedisca perdricana*. Lectotype here designated (Figs. 19, 30): ♂, Burney Falls, Shasta Co., California, 18–20 July 1871, Walsingham, genitalia slide 11509, BMNH. Paralectotype: same data as lectotype (1 ♂), BMNH.

Remarks. Besides the five syntypes mentioned above, there are six additional specimens that were collected by Walsingham but not mentioned in his description of *irroratana*. The associated data are: Head of Noyo R., Mendocino Co., Calif., 8–11 June 1871 (3 ♂, Wlsm. 91902, 91903, 91904); past Little Lake, Mendocino Co., Calif., 12 June 1871 (1 ♂, Wlsm. 91906); Scott's Valley, Lane Co., Calif., 17–19 June 1871 (2 ♂, Wlsm. 91907, 91908). Walsingham's specimen ledger, kept by Durrant, accounts for their disposition: #91902 was given to Zeller, #91904 was given to the USNM, and the remaining 4 were retained by Walsingham. Today, all but #91904 are in the BMNH. A twelfth specimen, residing in the USNM, bears a yellow "Fernald Collection" label and may well belong to the original series. Its red bordered, hand written, determination label, characteristic of certain specimens Walsingham is known to have given to C. H. Fernald, includes the inscription "Cal. Type," but there is no other collection data associated with this specimen. Inquiries to several North American collections produced no additional specimens correctly determined as either *irroratana* or *perdricana*.

The forewing of *irroratana* (Figs. 19, 20) is brown, with very fine, transverse, tan striations. This background is variably irrorated with lustrous gray scales, particularly on the distal one third of the wing. Anterior to the tornus there is a heavier concentration of lustrous scales and a fine speckling of black scales but no well defined ocellus. Forewing statistics: ♂ FWL: 9.2–13.7 mm (mean = 11.4, n = 5), AR = 2.84.

Male genitalia (Figs. 22, 30): Uncus short, semitriangular and apically rounded; socii moderately long and fingerlike; aedeagus with 2–4 deciduous cornuti (n = 2); valva broad basally, with costal margin concave, apex moderately acute but rounded, distal margin roundly convex, ventral margin weakly invaginated; cucullus with medial surface finely and densely setose, distal margin lacking stout setae. Female genitalia: Unknown.

Distribution and flight period. I examined 5 male specimens. Walsingham collected *irroratana* in early to mid June in Mendocino and Lake Counties in northern California. The two *perdricana* types came from nearby Shasta County, California, on 20 July.

Eucosma handana Kearfott

(Figs. 16, 24, 42)

Eucosma handana Kearfott 1907:20; Barnes and McDunnough 1917:169; Heinrich 1923:102; McDunnough 1939:46; Powell 1983:34.

Eucosma ceramitis Meyrick, 1912:34, invalid replacement name.

Types. Lectotype here designated (Fig. 24): ♂, Stockton, Utah, Tom Spalding, genitalia slide DJW1505, AMNH. Paralectotypes: Stockton, Utah, Tom Spalding (2 ♂, genitalia slide DJW1591, AMNH; 1 ♂, USNM); Stockton, Utah, 20 July 1903, Tom Spalding (1 ♂, genitalia slide DJW1590, USNM).

Remarks. This species may prove to be a variation of *irroratana*, but there are subtle differences in the males, and females of the latter species are not available for comparison. The *handana* types are moderately worn and probably faded. Their forewings show only the faintest indications of transverse tan striations, and they have no discernable lustrous scaling. The costal margin in *irroratana* is

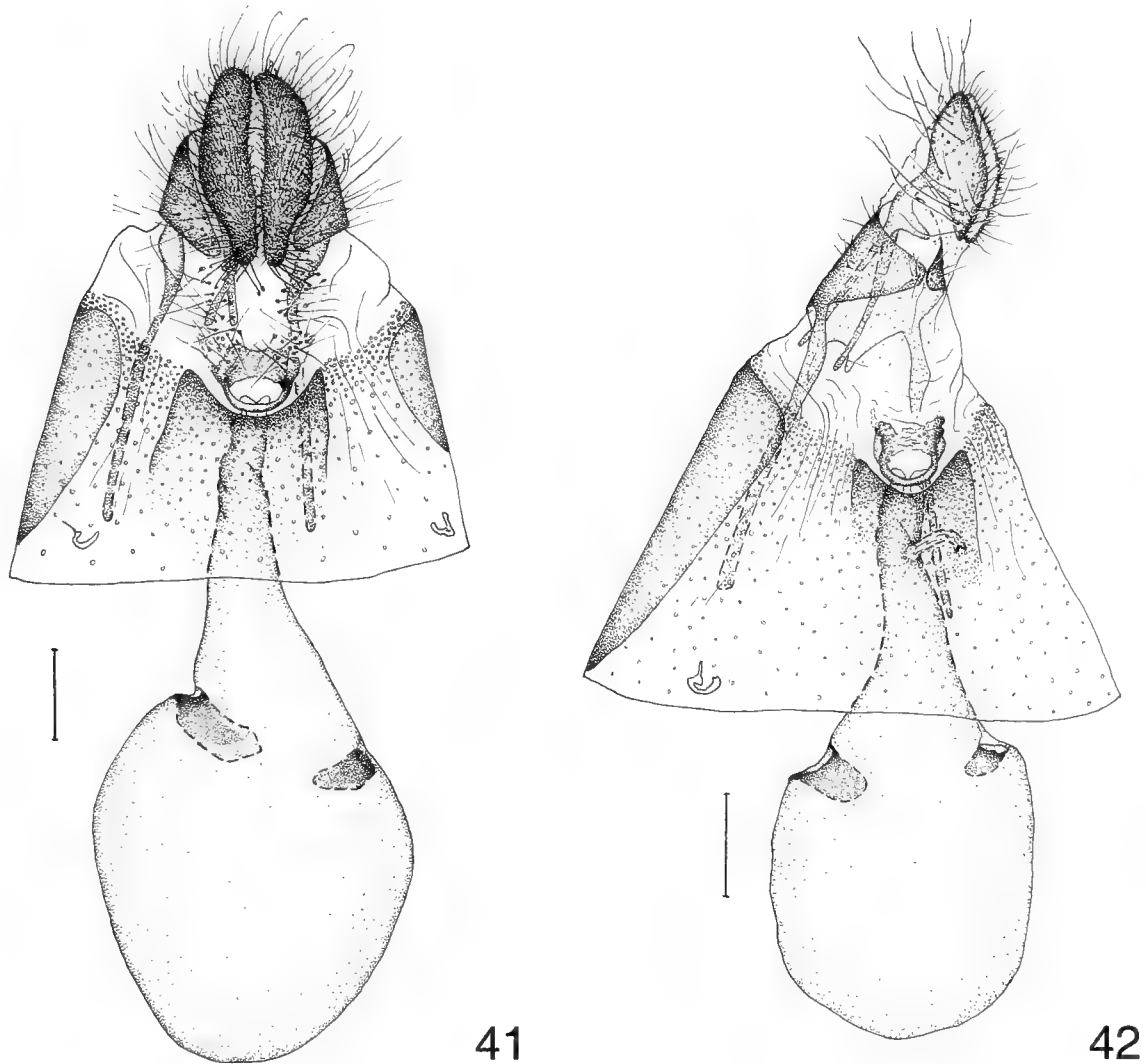


FIG. 41-42. Female genitalia. 41. *E. spaldingana*, slide DJW 1504. 42. *E. handana*, slide DJW 1506. Scale bars = 0.5 mm.

moderately convex. It is nearly straight in *handana*, producing a slightly more elongate forewing appearance.

The male genitalia (Fig. 24) are similar to those of *irroratana* (Fig. 30), but the cucullus appears to be somewhat narrower, with apex more acutely angled, and the vesica has *ca.* 14 deciduous cornuti ($n = 5$) vs. 2-4 ($n = 2$) in *irroratana*. Female genitalia (Fig. 42) ($n = 1$): Papillae anales facing laterally, with posterior and anterior extremities acutely angled, medial margin convex, and lateral surfaces moderately setose; sterigma semirectangular, anterior margin rounded and ring like, lateral margins with convex medial projections, lamella postvaginalis with shallow medial trough and mildly invaginated posterior margin; corpus bursae with two blunt-tipped signa located near juncture with ductus bursae.

Distribution and flight period. I examined 13 specimens (12 ♂, 1 ♀) from Nevada, Utah, and

Washington. Capture dates range from 24 May to 4 August.

Eucosma curlewensis, new species

(Figs. 13-15, 26, 40)

Diagnosis. Forewing color and maculation (Figs. 13-15), though variable, are usually sufficient to identify this moth. Paler phenotypes (Figs. 14, 15) can be confused with *hazelana* or, if worn or greasy, with *spaldingana*, but the three species are clearly separated by male genitalia (Figs. 26-28). Females of *curlewensis* are distinguished by the clusters of thick hook-tipped

setae at the anterior extremities of the papillae anales, the lip on the sterigma projecting over the anterior margin of the ostium, the long anterior extensions of the sterigma, and the unusually stout apophyses anteriores, with their wide, paddle-shaped anterior extremities.

Description. **Head:** Frons and vertex white; labial palpus white, lateral surface of second segment with pale brown shading; antenna white to pale brown, dorsal surface of scape with very pale brown shading. **Thorax:** Dorsal surface white with some brown lateral scaling; tegula brown basally, white apically; ventral surface white; legs with posterior surface white, anterior surface concolorous with forewing markings, particularly on foreleg. **Forewing** (Figs. 13–15): ♂ FWL: 6.6–12.6 mm (mean = 11, n = 43), AR = 3.27, ♀ FWL: 10.5–13.2 mm (mean = 11.9, n = 16), AR = 3.05; dorsal surface white with orange-brown to blackish-brown markings: three, irregular, transverse bands that might be interpreted as basal, subbasal, and median fasciae, the first two generally complete from costa to dorsum, the last frequently interrupted on radius and/or cubitus; a variably shaped mark on distal one fourth of forewing connecting to median fascia, costa, apex and tornus, defining three or four white costal spots, a white bar on terminal margin, and a white variably shaped spot anterior to tornus; a white interfascial spot between basal and subbasal fasciae, another between subbasal and median fasciae, the latter outwardly oblique from dorsal margin to cell and thereafter angling inward toward costa; fringe white to light brown, occasionally with some black scaling along distal margin of membrane. **Hindwing:** Uniformly light gray brown to dark gray brown, fringe lighter. **Male genitalia** (Fig. 26) (n = 11): Uncus a strongly developed, dorsally setose lobe, apex angular or rounded, ventral surface with variably developed medial ridge; socii long, narrow, and moderately setose; gnathos band like; aedeagus long, tapering distally, vesica with 1 or 2 deciduous cornuti; valva with costal margin concave, ventral margin moderately invaginated; cucullus semirectangular, with distal corners and ventral angle rounded, distal margin with ca. 5 stout setae distributed along ventral two-thirds, medial surface with short tack like setae along margin of basal opening. **Female genitalia** (Fig. 40) (n = 4): Papillae anales ventrally facing, wider posteriorly, with anterior extremities projecting ventrally, setae on lateral margins long, hairlike, and curving ventrally, those on ventral surface short, fine, and densely distributed, anteroventral projections with clusters of thick hook-tipped setae; tergum VIII with long hair-like setae; apophyses anteriores very stout, anterior extremities paddle shaped; lamella postvaginalis widening posteriorly, with shallow medial trough and pronounced medial invagination of posterior margin, posterolateral corners of sterigma with numerous, long, hair-like setae; lamella antevaginalis with rounded lip projecting over anterior margin of ostium; sterigma with long (ca. 2 × ostium diameter), narrow, anterior projections at anteroventral corners; corpus bursae with two signa, membrane finely wrinkled and thickened from signa to juncture with corpus bursae.

Holotype. ♀, Idaho, Oneida Co., Curlew NG [National Grassland], 4 mi. ENE of Holbrook, 25 July 2003, D. J. Wright, deposited in USNM. Type locality at: 42° 10.97' N, 112° 35.12' W.

Paratypes. **CALIFORNIA:** Los Angeles Co., Santa Catalina Island, Toyon Bay, J. Bennett, 13 August 1983 (1 ♂, genitalia slide JAP 6716); Santa Catalina Island, D. Meadows, 22 September 1932 (1 ♂, genitalia slide JAP 5304); Orange Co., Rcho Miss Viejo, N. Bloomfield, 15–18 September 1999 (1 ♂, genitalia slide DJW 691); San Diego Co., NAS Miramar, N. Bloomfield, 24 July 1997 (2 ♂), 1 August 1997 (2 ♂, 1 ♀), 3 August 1997 (2 ♂); San Diego Co., MCAS Miramar, N. Bloomfield, 3 August 1998 (1 ♂), 16 August 1998 (1 ♂), 6–9 September 1998 (3 ♂); San Diego Co., Torrey Pines St. Res., Sorrento Vy Marsh, N. Bloomfield, 19–26 July 2005 (3 ♂, genitalia slide DJW 1544), 27–30 July 2005 (2 ♂, 1 ♀, ♂ genitalia slide DJW 1543, ♀ genitalia slide DJW 1499), 1–7 August 2005 (4 ♂, 1 ♀), 8–15 August 2005 (2 ♂, 1 ♀); Santa Barbara Co., Santa Rosa Island, Lower Cherry Cyn., J. A. Powell, 21 September 2000 (1 ♂); Santa Barbara Co., 3 mi. N. Refugio Beach, J. S. Buckett, 18 July 1965 (1 ♂, genitalia slide JAP 1930). **IDAHO:** Oneida Co., Curlew NG, 4 mi. ENE of

Holbrook, D. J. Wright, 25 July 2003 (1 ♂), 26 July 2003 (3 ♀, genitalia slide DJW 1498); Oneida Co., Curlew NG, T14S R32E S30, D. J. Wright, 28 July 2003 (2 ♀); Oneida Co., Curlew NG, 5 mi. SSE of Holbrook, D. J. Wright, 18 July 2001 (1 ♂, genitalia slide DJW 786), 1 August 2001 (10 ♂, 3 ♀, ♂ genitalia slides DJW 1497, 1501). **NEVADA:** Elko, G. H. & J. L. Sperry, 2 August 1938 (1 ♀). **UTAH:** Eureka, Tom Spalding, 20 July 1911 (1 ♂, genitalia slide DJW 1509). Paratype depositories: AMNH, BMNH, CNC, CSU, LACM, MEM, USNM, UCB, and DJW.

Etymology. The specific epithet derives from the name of the type locality, Curlew National Grassland.

Distribution and flight period. I examined 79 specimens (62 ♂, 17 ♀) from the following states and counties: California: Los Angeles, Orange, San Diego, and Santa Barbara; Idaho: Oneida; Nevada: Elko; Utah: Beaver and Juab. One individual was collected in June, the rest between 18 July and 22 September. All September records were from southern California.

Discussion. The variation in forewing color appears to be geographically dependent (light orange-brown (Fig. 15) in Idaho, Nevada, and Utah to dark blackish-brown (Fig. 13) in southern California), but the various phenotypes exhibit no differences in genitalia

There are relatively few species of Nearctic *Eucosma* for which the female genitalia has been illustrated, so there isn't much of a context in which to interpret the characters observed here in *curlewensis*. Nevertheless, some of them appear to be quite unusual. The large clusters of long, stout, hook-tipped setae on the papillae anales have not been observed in other North American species of *Eucosma*. Hair like setae with hooked apices are not uncommon, particularly on the medial margins and anterior extremities (Wright: 2005), but they don't usually occur in such large dense clusters. Setae of comparable thickness were reported by Miller (1974) on the ventral extensions of the papillae anales in *E. smithiana* (Walsingham) and *E. barbara* Miller; they were few in number, quite stubby, and had only weakly curved apices. Another apparently unique feature of *curlewensis* is the well developed lip on the anterior margin of the ostium. A number of species of *Eucosma* and *Pelochrista* have a medial extension of the posterior margin of sternum VII that partially overlaps the ostium, but to my knowledge this is the first reported case in which the projection is an integral part of the lamella antevaginalis. Finally, I am aware of no other member of the genus with such long, rod like, anterior extensions of the sterigma (presumably for muscle attachment).

Eucosma spaldingana Kearfott

(Figs. 17, 23, 28, 41)

Eucosma spaldingana Kearfott 1907:19; Barnes and McDunnough 1917:169; Heinrich 1923:84; McDunnough 1939:45; Powell 1983:34.

Types. Lectotype here designated (Fig. 23): ♂, Stockton, Utah, Tom Spalding, 28 July 1903, genitalia slide DJW 1548, AMNH. Paralectotypes: Stockton, Utah, Tom Spalding, 20 July 1903 (2 ♂, AMNH), 26 July 1903 (1 ♂, USNM), 28 July 1903 (1 ♂, USNM), 29 July 1904 (1 ♂, USNM), 30 July 1904 (1 ♂, genitalia slide 70195, USNM), 7 August 1904 (1 ♂, AMNH), 11 Aug 1904 (1 ♂, AMNH), [no date] (1 ♂, AMNH).

Remarks. This moth has a silvery-white forewing with light reddish-brown markings (Fig. 17). The basal, subbasal, and median fasciae, though usually well defined as transverse reddish-brown bands, are often weakly expressed toward the costa. White interfascial spots occur between the basal and subbasal fasciae and between the subbasal and median fasciae, the latter being quite large and semitriangular. There is an irregularly shaped reddish-brown mark on the apical one third of the forewing that connects to the median fascia, costa, apex, and termen, forming a white, triangular, costal spot, a small white preapical spot, a narrow white bar on anterior one half of termen, and a medium sized white spot anterior to tornus. Forewing statistics: ♂ FWL: 10.5–13.5 mm (mean = 12.1, n = 34), AR = 3.19, ♀ FWL: 12–14.5 mm (mean = 13.4, n = 6), AR = 3.06.

Male genitalia (Figs. 23, 28) (n = 4): Uncus a well developed, dorsally setose lobe; socii broad basally and tapered distally; vesica with ca. 15 deciduous cornuti; valva with costal margin concave, distal margin straight, ventral angle evenly rounded, and ventral margin weakly invaginated; cucullus tapered from ventral angle to apex, distal margin lacking stout setae. Female genitalia (Fig. 41) (n = 1): Papillae anales facing ventrally and densely setose, narrow anterior extremities with clusters of moderately long, hook-tipped setae; sterigma with ring like anterior margin, lamella postvaginalis widening posteriorly, posteroventral corners and membrane between sterigma and ventral extremities of tergum VIII with numerous, long, hair like setae; corpus bursae with two signa.

Distribution and flight period. I examined 66 specimens (58 ♂, 8 ♀) from California, Nevada, and Utah. All but five (1 dated 21 May, 1 dated 19 June, and 3 dated 29 September) were captured between 2 July and 30 August.

Eucosma hazelana Klots

(Figs. 18, 27)

Eucosma hazelana Klots 1936:1; McDunnough 1939:45; Powell 1983:34.

Types. Holotype: ♂, Fountain Valley School, Colorado Springs, Colo., 20–31 Aug. 1932, genitalia slide ABK 18 Dec. 1932, AMNH. Paratype: S. W. Col., July 1899, Dietz, genitalia slide 70718, USNM. [Klots (1936) reported a damaged male paratype in AMNH labeled "Col.", but I did not examine it.]

Remarks. The color and maculation of the forewing of *hazelana* (Fig. 18) is similar to that of *spaldingana*, but the white ground color does not have a silvery hue, the fasciate markings are usually stronger, the interfascial spot at mid dorsum is not triangular, and the white spots on the costa and above the tornus are not as large. Forewing statistics: ♂ FWL: 7.7–11.6 mm (mean = 9.9, n = 5), AR = 3.35.

Male genitalia (Fig. 27) (n = 4): Valva with costal margin concave, apex angular but rounded, distal margin roundly convex, neck long and narrow; cucullus lacking stout setae on distal margin; aedeagus with 2 or 3 deciduous cornuti. Female genitalia: Unknown.

Distribution and flight period. I was able to locate only 5 specimens of this species: 2 from Colorado, 1 from southeastern Montana, and 2 from Coahuila, Mexico. Capture dates range from July [day unknown] in Colorado to 23 September in Mexico.

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DON MEADOWS, NEARLY FORGOTTEN AS A LEPIDOPTERIST

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ABSTRACT. Don Meadows was the first lepidopterist to collect extensively on any of the California Channel Islands, when he lived on Santa Catalina during 1927-1934. He published annotated lists of the butterflies, sphingids, and tiger moths of the island, and he collected more than 260 species from Catalina, the most comprehensive survey of Lepidoptera for any site in California at that time. Meadows is credited with having proposed the Channel Islands Biological Survey of the Los Angeles County Museum, and he supervised the initial 1939-40 expeditions. He published several papers, including new taxa from the islands, and at least three patronyms were proposed in his honor. However, by the late 1940's his interest in insects had waned; in 1950 he sold his collection to the Smithsonian Institution, and he disappeared as a lepidopterist. During the subsequent 44 years Don Meadows became an acclaimed historian and bibliophile of southern California, published several books and numerous articles, and was the subject of two booklets of tributes from admirers, none of whom cared about of his life as a lepidopterist.

Additional key words: island biogeography, microlepidoptera

Anyone who studies Lepidoptera of southern California, and particularly its Channel Islands, soon comes across the name of Don Meadows. He published several papers on Lepidoptera, proposed new taxa, had patronyms named in his honor, and was an organizer of

and participant on the 1939-41 Los Angeles County Museum Biological Survey expeditions. Yet his name does not appear in major bibliographies of biographies of entomologists (e.g., Gilbert 1977), nor is there any mention of him in the lepidopterists' biographies/



Personnel aboard the California Fish and Game Commission Patrol Boat "Bluefin", at the start of the Third Expedition of the Los Angeles County Museum-Channel Islands Biological Survey, Long Beach Harbor, California, July 21, 1939. This expedition included a week of work on each of four islands. Left to right: George Kanakoff, invertebrate zoologist; Jewell Lewis; Don Meadows, Expedition leader; Capt. Walter Engelke; C. H. Groat, Supervising Fish Warden; Russell Sprong; Arthur Woodward, archaeologist; M. B. Dunkle, botanist; Lloyd Martin, entomologist; Jack von Bloeker, mammologist [*Long Beach Sun* Photo]

bibliographies or deposition of collections compiled for the 25th year Commemorative Volume of The Lepidopterists' Society (Kendall *et al.* 1977). Indeed, he is not even mentioned in Orsak's *Butterflies of Orange County* (1977), where he had collected extensively as a youth.

I was amazed and chagrined to learn only recently that Don Meadows had been a well known author and historian living in Orange County until the mid 1980s, decades after I began compiling records of his work on the Channel Islands. He and his wife, Frances, lived in the hills overlooking the Santa Ana Valley, virtually within sight of the Santa Ana Freeway, which I traversed many times, yet I never met him. Meadows was a man of many interests and talents, and was widely known and respected for research and teaching carried out after leaving his Lepidoptera interests behind. Much of the following story is gleaned from a volume of tributes written in the 1970s by friends who knew him as a historian and bibliophile, less so as a naturalist, published by the Friends of the Library, University of California, Irvine (Heiskell 1982) and from a summary of his life published by friends when he died (Bigandi 1995).

Donald Charles Meadows was born in 1897 in Indiana, where his father, Charles W. Meadows, was employed by a local newspaper. After visiting relatives in California, the senior Meadows moved the family there in 1903, when Donald was five years old. They settled in the town of Orange, where Don's interest in California history is said to have begun after a visit to the Spanish mission ruins at San Juan Capistrano when he was 10 years old, and in natural history at about the same time. He collected insects, particularly butterflies and moths, and learned to identify the local birds as a young boy. He was educated in Orange County public schools, and at Pomona College, where he studied under William Hilton and Phillip Munz and obtained a degree in biology in 1922, after spending time in the Navy during WW I. Don began to collect books and other historical literature on California and Baja California while a college student, a passion that continued for the rest of his life.

After graduation, Meadows worked for a newspaper in Long Beach until 1925, then took a teaching position in the Long Beach public schools, first in junior high, where he met his wife, Frances, a librarian at the school. After two years he conceived the idea of doing a biological survey of Santa Catalina Island, which recently had been taken into the Long Beach school system, and Don requested a transfer to Avalon High School. During their residency there, 1927 to 1934, the

Meadows built a home overlooking Avalon but returned to the mainland for the summer months. Meadows surveyed diurnal Lepidoptera extensively over the island, and collected moths at lights primarily at Avalon. During the first three seasons, and especially 1929-30, Don collected moths at lights of the Club House, which was located on Country Club Drive at the mouth of Avalon Canyon.

In 1930-31, at the height of the great depression, Don took a leave of absence from his teaching position in order to complete a M.S. degree in Entomology, with the hope of obtaining a position teaching zoology at Santa Ana Junior College. He moved with his family to Berkeley to complete the degree at University of California. He conducted his thesis research under the direction of H. B. Herms, a medical entomologist, on the biology and ecology of a salt marsh-inhabiting horsefly (Meadows 1931). The fly had been misidentified as *Tabanus gilanus* Townsend, an Arizona species, but Meadows' voucher specimens were later determined to be *T. laticeps* Hine, and his detailed study is cited as such (Middlekauff and Lane 1980). The thesis research failed to convert Don to a dipterist, but the experience at Berkeley had a profound effect on him as a lepidopterist. Evidently he was inspired by his association with faculty, including E. O. Essig and E. C. Van Dyke, and students, Harry Lange, Gort Linsley, Bob Usinger, and Bob Wind, among others, to broaden and increase his survey efforts on Catalina Island. In March Meadows expanded his collecting repertoire by designing a light trap, an incandescent bulb hung over a 9-inch funnel (sketch in his field notebook), which he deployed outside a window on the top floor of Agriculture Hall on campus, and for the first time lists of species in his notebook began to include microlepis. Probably he was influenced by H. H. Keifer, as that was during Keifer's active period of research with microlepidoptera, working in Sacramento (Powell 1990), and Meadows' notebook entries mention identification of his specimens by Keifer. Immediately upon his return to Catalina Meadows began to inventory by light trapping in a canyon back of the high school, resulting in a dramatic increase in the numbers of collection records and species compared to his efforts

TABLE 1. Numbers of species and date records for moths collected by Don Meadows on Santa Catalina Island, 1927-1934 (LACM, USNM; excludes Sphingidae, Catocala)

	Sept. 1927- May 1930		Sept 1931- May 1934	
	species	records	species	records
Microlep	2	2	~70	<200
Pyraloid	5	5	<35	<180
Macromoth	48	90	<133	<790

in 1927–30 (Table 1). Also, in 1932–1933, he enlisted one of his 8th grade students, Noel Turner, to run a light trap at Middle Ranch, where he lived, located at 650 ft. elevation on the Pacific side of the island.

Entries in his field note books (which for the Catalina years are housed in the archives of the Santa Barbara Natural History Museum, SBNHM) include many lists of birds and butterflies, notes on macromoth larvae, etc., from various parts of the island and provide glimpses of his moth sampling. For example, in late September to November, 1929, he collected at the Club House lights on 20 dates, recording lists of macros and on Sept. 14 “a great many silver lined crambid moths” [*Crambus occidentalis* Grote], Sept 20 “33 [specimens] nice stuff,” Oct. 23 “54 specimens”, and on Feb. 7, 1930 “8 geos, 4 noctuids, two of the beautiful flecked green variety” [38 years later named *Feralia meadowsi* Buckett]. After the light trapping program began, Meadows did not record species names and specimen numbers and evidently limited his collections by time available for spreading, as Sept. 18/19, 1932: “Collection fine, 2 or 3 hundred micros and about 100 noctuids, only 50 specimens saved, mostly the noctuids, no time to mount them all.” On June 10, 1932, he counted the Catalina collection, 2,375 specimens, including 90+ butterflies, 602 Noctuidae, 475 Geometridae, 367 Pyralidae, 46 Tortricidae, 416 micros.

Meadows was the first to collect microlepidoptera on any of the islands, and several species have been new to science, named from his specimens. In total he accumulated more than 400 records for 100+ species of micros and pyraloids, all represented by nicely spread specimens. He was featured in a newspaper article as the ‘Moth Man of Catalina’, which stated that he had captured more than 400 different species, many of them new to entomology (Los Angeles Times, Sunday Magazine, Feb. 16, 1933, Buckett 1968). That number was optimistic, but I have recovered records in the National Museum of Natural History (USNM) and Los Angeles County Museum of Natural History (LACM) of about 260 species, the most comprehensive local inventory of Lepidoptera in California up to that time.

After the Catalina experience, Meadows returned to Long Beach and taught high school biology for the remainder of his career. He published several notes on the birds of the island, two papers on the butterflies, sphingids, and arctiids (Meadows 1936, 1939), and compiled an annotated list of 160 species of macrolepidoptera (1943, unpublished). More influential than his Catalina survey, Don Meadows is credited by Comstock (1939) as having initiated a proposal to the authorities of the LACM for a biological survey of all the Channel Islands. Whereas beetles and some other

insects, in addition to vertebrates and plants, had been collected on the islands in the late 1800s and early 1900s, exceedingly few Lepidoptera were known other than from Catalina after the resort town of Avalon was established in 1887. A five-year project was approved by the Board of Directors in December 1938, and trips began in February 1939. Meadows acted as field supervisor on the first five of the expeditions in 1939–40. He worked on six of the islands, along with other lepidopterists, Lloyd Martin and Chris Henne, one or both of whom took part in most of the trips. Altogether 13 expeditions were conducted, visiting each of the eight islands at least twice before the last trip was abruptly terminated in December 1941 by the bombing of Pearl Harbor (Comstock 1946).

Meadows (1943a) estimated that 40,000 insect specimens were collected, of which about 5,000 were Lepidoptera. Thus the 1939–41 LACM expeditions laid the foundation for all subsequent inventory of insects, and Meadows’ visionary proposal was a pivotal event in the development of our knowledge of the insects of the California Channel Islands. According to his son, Don hoped to use his Channel Islands study of Lepidoptera as the basis for a Ph.D. thesis, and in 1940–42 he approached both the University of Southern California and University of California, Los Angeles, regarding prospects of such a project. However, the required residency and course work could not be arranged while maintaining his full time teaching position.

During that following decade, Meadows described a noctuid from San Clemente Island (1942) and published articles on butterflies (1943b) and biology, and attempted to identify the moths from the 1939–41 expeditions. His ms draft lists of Catalina and Channel Island macrolepidoptera (1943a) indicated plans to publish lists, but evidently he tried to identify all the species without seeking assistance from specialists, and the project bogged down. During four summers following WW II Don worked as a park ranger and naturalist at Big Basin State Park in the Santa Cruz Mountains, California, and wrote an extensive handbook on the history and biology of the park (Meadows 1950), which included lists of the butterflies (25 species) and a few moths, and mentioned more than 60 species of moths had been collected in the park.

However, by about that time his interest in Lepidoptera and natural history had waned, probably in part because he had been unable to pursue further graduate studies, and he may have felt he could not do justice to two compelling avocations. He sold his private collection of insects to the Smithsonian in 1950 (Clarke 1974). It contained about 10,000 specimens and included butterflies, macrolepidoptera, and pyraloids

from southwestern United States, in addition to its emphasis on Catalina Island, as well as some of the specimens he collected on the Channel Islands expeditions to other islands. Curiously, all of his microlepidoptera went to the LACM, and I was unable to find any archival record as to why this division was made. Although Don had been a member of the Lorquin Society in Los Angeles, he evidently dropped out of contact with other lepidopterists by the time the Lepidopterists' Society was founded in 1947. His decision was finite; there was virtually no contact with lepidopterists or the LACM after 1950. In correspondence as late as 1952 he said he was working on a book on the natural history of the islands, but that project did not come to fruition.

Meadows' decision was biologists' and lepidopterists' loss, and historians' gain. Thereafter he increasingly wrote and lectured on California and Baja California history, particularly of Orange County and the Spanish Missions era, and published about 50 articles and books between 1951 and 1980, in addition to 31 reviews of books on history and travel in the southwest, especially Baja California (F. Meadows 1980). He taught California history in night school at Orange Coast College in Santa Ana before retirement in 1960. The Meadows historical library grew to more than 4,000 volumes and enormous numbers of pamphlets, manuscripts, and other ephemera, probably the best collection of southern Californiana ever assembled. The Meadows library was purchased by The University of California, Irvine, in 1972, through a grant from the University's contingency funds administered by President Hitch, and is held intact—all well indexed and available in the UCI archives—the Meadows papers alone occupy 90 linear feet of shelf space (Gibson 1995).

Don Meadows and his wife moved to Yuba City, California, in 1985, to be near his son and family, where she died in 1989 at the age of 90, and he in November 1994, two months into his 98th year, and nearly half a century after his days as a lepidopterist had ended. His life was celebrated in two collections of tributes written by 24 friends and admirers, the first published by the Friends of the U.C. Irvine Library (Heiskell 1980), and the second as a memorial after his passing was published privately by friends in Orange County (Brigandi 1995). He is acclaimed as a historian and researcher, bibliophile, outstanding teacher, professional writer and a friend, confidant, critic, and mentor to a diverse group of admirers, none of whom had any appreciation of his contributions as a lepidopterist.

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APPENDIX

Taxa described by Don Meadows:

Anthocaris cethura catalina Meadows, 1937
Hemihyalea edwardsii ochrous Meadows, 1939
Zosteropoda clementi Meadows, 1942

Patronyms:

Arachnis picta meadowsi Comstock, 1942
Sericosema wilsonensis meadowsaria Sperry, 1948
Feralia meadowsi Buckett, 1968

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ENIGMOGRAMMA BASIGERA (NOCTUIDAE, PLUSIINAE) AS A SPECIALIZED TRANSIENT PEST OF *LOBELIA* IN NEW JERSEY.

The plusiine tribe Argyrogrammatini is primarily an Old World tropical group but a few species occur in the New World, including five in the eastern United States (Lafontaine and Poole, 1991). Four of these currently occur in New Jersey, but probably only as occasional to abundant migrants. The fifth, *Argyrogramma verruca* (Fabricius), apparently has not been collected there in more than 60 years. LaFontaine and Poole (1991) referring to the tribe globally state that as far as known larvae are polyphagous on various herbs.

In 1998 the second author was cultivating over 700 cardinal flower (*Lobelia cardinalis* Linnaeus) plants from local seed stock in outdoor pots placed in tubs of shallow water at Heislerville, Cumberland County, New Jersey. In early August significant defoliation began to appear, especially of basal rosettes. Several species of Noctuidae were involved but overwhelmingly the culprits were green plusiine loopers, and in mid August an adult *Enigmogramma basigera* (Walker) eclosed from one of them. Soon after, a new wave of defoliation started and some large plants were almost completely eaten and most plants were damaged. By late August, the defoliators were nearly all Plusiinae, and over 20 more *E. basigera* eclosed. The larvae appeared consistent (verified by both DFS and Tim McCabe) with previous descriptions (e.g. LaFontaine and Poole, 1991) and an illustration of one of them is provided here by McCabe (Fig. 1). No plusiine larvae appeared on any other species of cultivated or wild plants growing with or near the cardinal flowers. A brief life history account follows.

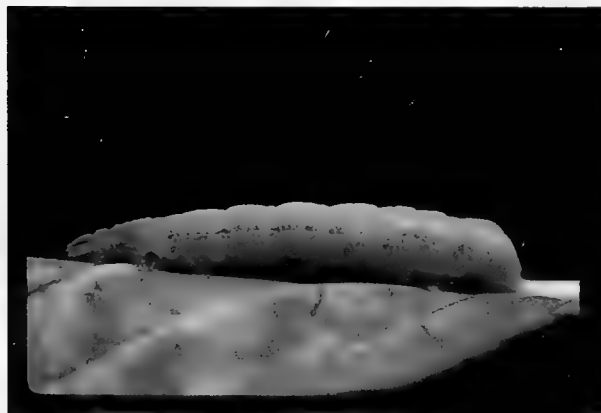


Fig. 1. Larva of *Enigmogramma basigera*.

Eggs were laid in groups of approximately 6–20 on a *Lobelia* leaf, usually on the underside. They hatched in about five days and the first two instars stayed on the original leaf, scraping it from the underside. Older larvae dispersed and became solitary, but often remained on the same plant if there was sufficient foliage. They hid, often on the underside of a basal leaf, when not feeding. The larval stage lasted about 20 days in summer. Fairly substantial cocoons were spun on the undersides of *Lobelia* leaves or on the outside of flower pots just above water level. The pupal stage lasted about a week or slightly more in summer, but cocoons spun 17 September eclosed 30 September and 3 October with none on the two intervening cool days (maxima 21°C). Larval abundance peaked in early September, which represented at least a second local brood. While many larvae were removed in September, several dozen were not and many were seen as late last instars or cocoons. With lows around 10–14°C and highs about 17–21°C in early October, larvae consumed food at about a third the rate they did in summer. Caged adults were sluggish and mostly inactive at night under such conditions and no new eggs were seen on the outdoor plants after mid September. The last wild adults were seen around 1 October and a few reared ones eclosed later that month, but no eggs or larvae appeared in October. Cooler conditions may have prevented reproduction, or perhaps the last adults emigrated. No feeding damage was seen on basal rosettes over winter or in spring, and although cardinal flower cultivation continued for two more years, no *E. basigera* in any stage has been observed again at this site or on wild cardinal flowers through 2006. However, DFS collected a female nectaring on Buddleia in September 2002 at nearby Port Norris.

Lobelia siphilitica Linnaeus was also accepted whether or not offered with cardinal flower, but larvae refused many other herbs. They refused *Hydrocotyle umbellata* Linnaeus (Apiaceae), a previously reported foodplant (Lafontaine and Poole, 1991), if even poor quality *Lobelia* was present, and usually even in its absence if they had eaten any earlier the same night. Larvae starved for twelve hours or more would eat *Hydrocotyle* but consumption was perhaps half as fast as with cardinal flower leaves, and *Hydrocotyle* probably is not really a suitable foodplant. Five larvae that were

about two days into the penultimate instar were forced to eat *Hydrocotyle* for one night and were then placed with foliage of the following plants, Chenopodiaceae: *Chenopodium album* Linnaeus, Asteraceae: *Aster lateriflorus* Linnaeus (also flower buds), *Bidens* sp., *Cichorium intybus* Linnaeus, *Taraxacum officinale* Weber (dandelion), *Krigia* sp., and a *Lactuca* cultivar (Boston lettuce); Commelinaceae: *Tradescantia virginica* Linnaeus, *Commelina* sp. ("Wandering Jew"); Plantaginaceae: *Plantago lanceolata* Linnaeus, Violaceae: *Viola*^p *papilionacea* Pursh-Rydberg, Phytolaccaceae: *Phytolacca americana* Linnaeus, Solanaceae: *Physalis* sp., *Solanum* sp. (nightshade); and two grasses: a *Panicum* seedling and a mature *Setaria* species. After they completely refused to feed on any of these through two nights, cardinal flower foliage was added the next day and all five located it and fed within an hour. Similar results were obtained in a second trial using these same five larvae as late ultimates and, after they ate all of the *Lobelia cardinalis*, one of them also ate some *Hydrocotyle* after only 6–8 hours. Three other starved last instars refused water hyacinth (Pontederiaceae: *Eichhornia crassipes* (Mart) Solms), two others refused *Polygonum* sp. (Polygonaceae) and *Hibiscus mocheutos* Linnaeus (Malvaceae) and all five opted to starve for 48 hours. These mal-treated larvae were not runty as adults but they required nearly an extra week as larvae. An ability to recover from starvation and/or malnutrition for at least one to three days (even twice in the last two instars) is noteworthy because if larvae defoliate a *Lobelia*, finding another one could take substantial time. We do not know if such larvae could successfully mature on *Hydrocotyle*, which would be much easier to locate in some habitats.

Enigmogramma basigera does not appear to be a generalist, and is probably a *Lobelia* specialist. It is possible that prior feeding on *Lobelia* influenced subsequent host rejection, but the first author has reared hundreds of species of Lepidoptera over the past 40 years and has never encountered prolonged complete refusal to switch among normally suitable

foodplants. Furthermore larvae were starved or forced to feed on *Hydrocotyle* before they rejected 19 genera in eleven families, including even dandelion and lettuce which nearly all polyphagous herb feeding Noctuidae readily accept. Dussourd (2003) also reports *L. cardinalis* as a foodplant for *E. basigera* and describes larval leaf-trenching behavior, but does not discuss whether larvae are polyphagous or specialists. He does note that a polyphagous leaf-trenching argyrogrammatine, *Trichoplusia ni* (Linnaeus), failed to mature on *L. cardinalis*. Foodplants of other *Enigmogramma* are apparently unknown. Our observations also suggest that *E. basigera* does not overwinter in New Jersey. If adults do not function well at about 10–20°C, they probably could not maintain normal activity in winter north of central Florida, although larvae probably could overwinter farther north. The first author collected a wild larva of another plusiine, *Autographa precatationis* (Guenee), in his yard at Port Norris on basal rosettes of either *Conyza* or *Erigeron* in late November 2005 and reared it outdoors. It continued to feed, mostly on dandelion, molted on 1 January and 28 February, began to spin a cocoon on 27 March, and the adult eclosed 1 May. *E. basigera* probably has similar habits on *Lobelia rosettes*, but not as far north.

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ABOUT DISTASTEFULNESS AND MIMICRY: A COMMENT ON PETER SMETACEK'S ARTICLE
(J. LEP. SOC., VOL. 60:82–85)

I am writing in response to Smetacek's (2006) conclusion that *Papilio polyctor*, *P. protenor*, and *P. polytes* are distasteful to avian predators and thus chemically defended. Smetacek's experiment on butterflies and wild birds was an immense effort involving years of observations, which I highly appreciate. However, the results presented in his article are interesting and suggestive, not conclusive.

Smetacek's study had limited experimental controls, which compromised reliability of the small dataset. The methods did not fully describe motivational states and prior experiences of the birds, and how these factors were controlled or contributed to the data. These are key aspects of palatability experiments and must be addressed in order to draw conclusions from the predators' behavior. The article mentioned, "The birds at times arrived and devoured everything in sight and at other times ignored everything, including controls, having evidently found sufficient food elsewhere." We do not know how much of the variation in measured palatability was introduced by this lack of control, motivational states of the birds and their prior experience with unpalatable prey.

The author's explanation for persistence of the non-mimetic female form of *P. polytes*—that it persists because it is distasteful—conflicts with earlier data. Ohsaki (1995, not cited in Smetacek 2006) has shown that in nature a much higher percentage of non-mimetic females of *P. polytes* have beak marks on their wings compared to the mimetic females. Ohsaki's data suggests that the non-mimetic female form is palatable

and suffers higher rates of predatory attack, whereas the mimetic female form is attacked much less frequently and has a Batesian mimetic advantage. Moreover, the nature of female-limited mimic–non-mimic polymorphism and variation in frequencies of female forms over most of the geographic range of *P. polytes* is in line with theories of Batesian polymorphism, not Müllerian polymorphism. Thus, based on theory and empirical evidence, balanced polymorphism and other traditional explanations (e.g. Turner 1978, and references therein) still seem more satisfactory in explaining the mimic–non-mimic polymorphism in *P. polytes*. Parallel mimic–non-mimic polymorphism in *P. glaucus* and other *Papilio* species is also instructive.

The idea—that a classic Batesian mimic is actually a Müllerian mimic—is intriguing but controlled experiments are required before a definitive conclusion can be reached.

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AUTHOR'S RESPONSE TO TECHNICAL COMMENT

First, all *Papilio* larvae are believed to be unpalatable, as stated in the Introduction of my paper. On the basis of the data presented, I concluded that *P. polytes*, *polyctor* and *protenor* are also distasteful in the adult stage.

Concerning the misgiving about limited experimental controls compromising the reliability of the small dataset, the normally acceptable ratio is 1:1; this has been exceeded in my experiments as noted in Column 2 of Table 1. As stated, the *Papilio* species were offered together with the controls. Therefore, it made little

difference to the result of the experiments whether the birds arrived hungry or sated. Perusal of the paper will show that the number of times the birds ignored the presentation does not in any way affect the interpretation of data.

With reference to the contention that I have not fully described "motivational states and prior experiences" of the birds and "how they were controlled or contributed to the data", all information that was noteworthy on this subject may be found in the last two paragraphs of the Materials and Methods section. My limited

acquaintance with the wild birds and the language barrier precluded greater familiarity with their "prior experiences" with unpalatable prey. However, it is noted in the paper that only the non-mimetic female form of *polytes* was used in the experiments and on three occasions the wing scales of a *Papilio* were wiped off and the wing shape altered. I trust that these require no further explanation.

As a matter of fact, I cannot recall any palatability experiment where the "key aspects" mentioned by Kunte have been "fully addressed", particularly when using wild birds or else birds caught from the wild.

Concerning Ohsaki (1995), despite the elegant mathematics, I believe that his conclusions are not valid because putative beak marks cannot be construed to be an indicator of palatability, nor of the relative preferences of avian predators. An analogy will clarify my point of view better: during the Second World War, the R.A.F. undertook a survey of bullet and flak damage to all its airplanes as they returned from sorties. Each bullet hole and shrapnel mark was entered on a diagram, with a view to discovering and subsequently strengthening the parts most often damaged. The inherently flawed reasoning became apparent when a junior officer asked, "What about the planes that *didn't* come back?"

Similarly, Ohsaki's discovery that the non-mimetic form of *polytes* had more putative beak marks than the mimetic form in a S.E. Asian forest, cannot be safely interpreted any further. For this reason, I did not rely upon or refer to his paper.

I cannot agree with Kunte that putative beak marks constitute "empirical evidence" of palatability, while actual tasting, eating, rejection, and distress behavior by birds is ignored altogether.

Concerning Batesian mimicry, suffice it to say that as mentioned in the first sentence of the paper, the basic premise is that, of two or more similar looking species, one is palatable and the other is unpalatable. If predators, in this case birds, avoid the "palatable" species, reject it after long examination and even exhibit distress behavior on occasion after eating it, then the species is not entirely palatable and therefore the relationship not Batesian, for while there are varying degrees of distastefulness in Müllerian mimicry relationships, there is no scope for the mimic being even slightly distasteful if the relationship is to be deemed Batesian. All other considerations are secondary. That entirely palatable species exist and the birds in the experiment could distinguish them is evident from the figures presented for controls in Table 1 and the second paragraph of the Results section.

Referring to the applicability of theories of Batesian polymorphism, etc. to the distribution of *polytes*, while ignoring its distastefulness is, to my mind, putting the cart before the horse.

With reference to the "small dataset", while 18 specimens of *polytes* are certainly not as many as one could have wished, that one to three of these specimens were offered on 49 occasions should not be ignored, nor the fact that less than half were eaten; on 7 occasions a specimen was rejected after being manipulated for over 5 seconds and distress behavior was observed after a bird ate part of a specimen, as noted in the last paragraph of the Results section. Those readers familiar with feeding birds will agree that rejection after manipulation for 5 seconds or more is a decisive rejection. As observed above, if a species is to be deemed a Batesian mimic, there is no scope for it to be even slightly distasteful. Therefore, I feel entirely justified in treating *polytes* as distasteful and its relationship with *P. aristolochiae* as Müllerian.

Concerning *polyctor* and *protenor*, the distastefulness is so evident that to go on offering specimens will not prove very much more, unless the number of times the presentation was ignored is treated as significant, a course which I believe is not advisable in the present case.

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Journal of the Lepidopterists' Society
61(1), 2007, 59

ANNUAL MEETING ANNOUNCEMENT
THE 2007 NATIONAL MEETING OF THE LEPIDOPTERISTS' SOCIETY

JULY 12 TO JULY 15
BAKERSFIELD, CALIFORNIA

The 2007 National Meeting of the Lepidopterists' Society will be held in Bakersfield, California, from July 12 to July 15. All members of the Lepidopterists' Society are invited to the annual meeting. The 2007 meeting, a combination meeting of the Pacific Slope Section with the National Meeting, will be near a number of prime collecting and observing locations for Lepidoptera. Recent spring rains promise an excellent summer flight for both butterflies and moths. Although Bakersfield is the 11th largest city in California, with a population of over 300,000, many people may not be aware of the advantages of the location of the city for the lepidopterist.

Bakersfield is located about 120 miles north of Los Angeles, and about 230 miles southeast of San Francisco, near the southern end of the Great Central Valley. Near this location are a variety of landforms which are of importance to the lepidopterist.

At its southern end, the Great Central Valley is known as the San Joaquin Valley, and in the distance of 250 miles from the Sacramento River Delta area the elevation rises only some 390 feet in elevation, or about one and a half feet per mile. Much of Bakersfield sits at around 380 feet elevation. However, to the west the Tumbler Range rises to an elevation of near 5000 feet, to the south the area of Mount Pinos (see related article in the News) rises to a maximum elevation of over 8700 feet, and to the east the Greenhorn Range rises into the Sierra Nevada Range to upwards of 8000 feet elevation areas accessible by road about two hours drive out of Bakersfield. The Kern River flows from near 12,000 feet elevation in the Sierra Nevada south through the Greenhorn Mountains and from Lake Isabella west through Bakersfield.

The collecting areas in these areas are blessed with many Lepidoptera because two National Forests protect the higher elevations. To the south of Bakersfield lies the Los Padre National Forest and to the northeast lies the Sequoia National Forest.

For those who are unaware of the landforms of the state, California can be divided into a number of important life zone regions. There is one area where the coast range, the Great Central Valley, the Sierra Nevada, the Basin and Range Province, the Mojave

Desert and the Transverse Ranges all come together. Only near Bakersfield do five life zones of the state meet.

Over 140 species of butterflies and over 1000 species of moths occur within one and a half hour's drive of Bakersfield, in Kern and Tulare counties. Of course, these Lepidoptera occur in many different months, with collecting actually possible all year long. Many, of course will be regularly flying in the middle of July, when the meeting will be held.

The mountains surrounding the Kern River Canyon, and extending about thirty miles in either direction are known as the Greenhorn Mountains. They are a low (for California) mountain range bordered roughly by Rt 58 west of Tehachapi extending northward past the Kern River another thirty miles to the vicinity of Kernville, where the Sierra Nevada range begins. Route 155 marks the northern border of the Greenhorn Mountains. Lake Isabella is nestled in the Greenhorn Mountains and provides a number of camping areas, especially from the lake area to the north.

Meeting events will include the traditional Friday night barbeque, which will be held at the California Living Museum, (CALM) a museum of California wildlife. Saturday night will include the banquet and honoring of the Comstock Award, a Pacific Slope Section award. Thursday will be the Executive Council meeting and collecting opportunities.

For spouses and those accompanying meeting attendees, there are events possible for entertainment. The Historical Society is planning a tour for Old Bakersfield, The Education Committee is working on workshops for students and possibly teachers Thursday at CALM and there are local areas of interest such as Pioneer Village and California State University, Bakersfield to visit. Day trips into the Sierra Nevada are recommended for all.

Detailed information about the meeting is available in the News of the Lepidopterists' Society. The host, Kelly Richers, may be contacted at krichers@bak.rr.com or kerichers@wuesd.org e-mail addresses, or at his address of 9417 Carvalho Court, Bakersfield, CA 93311. Telephone numbers include home (661) 665-1993 or cell (661) 201-7357.

MANUSCRIPT REVIEWERS FOR 2006 (VOLUME 60)

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 all of us. Let us hope that their careful work continues to allow the Journal to grow in quality and readership. On behalf of all authors and editorial staff of this Journal, respectful acknowledgements are given to the reviewers for contributions published in volume 60.

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Sheppard, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.

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