Full Issue

Source: The Journal of the Lepidopterists' Society, 69(1)

Published By: The Lepidopterists' Society

URL: https://doi.org/10.18473/lepi.v69i1.a8

Volume 69 Number 1
2015
ISSN 0024-0966

Journal of the Lepidopterists' Society

Published quarterly by The Lepidopterists' Society

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Journal of The Lepidopterists' Society (ISSN 0024-0966) is published quarterly by The Lepidopterists' Society, c/o Julian P. Donahue, Asst. Treasurer, 735 Rome Dr., Los Angeles, CA 90065-4040. Periodicals postage paid at Los Angeles, CA and at additional mailing offices. POSTMASTER: Send address changes to The Lepidopterists' Society, 735 Rome Dr., Los Angeles, CA 90065-4040.

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Cover illustration: Female *Euphydryas anicia eurytion* (Mead), from the newly designated type locality of *Melitaea eurytion*: the vicinity of Kenosha House, 2.16 km (1.34 mi) north of the summit of Kenosha Pass, Park County, Colorado (see the article by John V. Calhoun in this issue). Photographed 9 July 2014 by Andrew D. Warren.

Journal of the Lepidopterists' Society
69(1), 2014, 1–38

AN UPDATED ITINERARY OF THEODORE L. MEAD IN COLORADO IN 1871, WITH TYPE LOCALITY CLARIFICATIONS AND A LECTOTYPE DESIGNATION FOR *MELITAEA EURYTION* MEAD (NYMPHALIDAE)

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ABSTRACT. The discovery of the 1871 journal of Theodore L. Mead provides an opportunity to establish a more accurate itinerary of his exploration of Colorado that summer. The provenance of Mead's manuscripts, including this journal, is summarized. The history of Mead's expedition and the subsequent distribution of his butterfly specimens are reviewed. Despite the general belief that Mead participated in the Wheeler Survey, there is no evidence to support this claim. Information is presented on three significant localities where Mead collected butterfly type specimens: Kenosha House (figured and mapped), Turkey Creek Junction (=Bradford Junction; figured and mapped), and Twin Lakes (mapped). Based on Mead's actual whereabouts, type localities are clarified for 19 nominal taxa: *Pamphila colorado* Scudder, *Pamphila nevada* Scudder, *Hesperia dacotah* W. H. Edwards, *Hesperia napa* W. H. Edwards, *Anthocaris* [sic] *coloradensis* H. Edwards, *Colias hagenii* W. H. Edwards, *Argynnis helena* W. H. Edwards, *Argynnis meadii* W. H. Edwards, *Grapta hylas* W. H. Edwards, *Melitaea eurytion* Mead, *Melitaea calydon* Holland, *Phyciodes nycteis var. drusius* W. H. Edwards, *Phyciodes camillus* W. H. Edwards, *Phyciodes emissa* W. H. Edwards, *Erebia rhodia* W. H. Edwards, *Thecla ninus* W. H. Edwards, *Chrysophanus sirius* W. H. Edwards, *Lycaena daunia* W. H. Edwards, and *Lycaena melissa* W. H. Edwards. Based on the lectotype and type locality of *P. colorado*, *Hesperia comma oroplata* Scott should be treated as a synonym. The type locality of *M. eurytion* is fixed through a lectotype designation and the conceptual history of this nominal taxon is explored. Events related to the selection of the lectotype of *L. melissa* are reviewed in detail.

Additional key words: Bradford Junction, Kenosha House, William H. Edwards, Turkey Creek Junction, Twin Lakes

Born in Fishkill, New York, on 23 February 1852, Theodore L. Mead (Fig. 1) lived in New York City during his teen years. In July 1869, at the age of 17, he traveled to Coalburg (then "Coalburgh"), West Virginia, to spend the summer hunting butterflies with the celebrated lepidopterist William H. Edwards (1822–1909) (Mead 1935). Despite their thirty-year age difference, these enthusiastic naturalists developed a close friendship. Edwards benefited from Mead's youth in the field: "I can see with his eyes and hunt with his net quite as well as if I was out myself." Mead visited Coalburg many times to assist Edwards with collecting, rearing, and sorting specimens. Edwards (1900–1901) recalled that Mead "was in the fields and woods every day, and never returned without trophies in his net, and without information in the matter of larvae and food plants." Mead also became "the best of chums" with Edwards' son, William (Willie) S. Edwards (1856–1915). On 1 June 1882, Mead married Edwards' eldest daughter, Edith K. A. Edwards (1852–1927), forging a lifelong relationship with the Edwards family.

In December of 1870, Mead moved with his family from 233 W. 34th Street in New York City to 596 Madison Avenue, at the northwest corner of E. 61st Street ("first door above 61st Street;" the address of their building changed in 1873 to 674 Madison Ave.). Around that time, Mead purchased a small leather-bound market diary for the year 1871. As it turned out, 1871 proved to be a year of great personal and scientific achievement for Mead, who embarked on a months-long expedition to Colorado and beyond. He collected thousands of insects in Colorado, which resulted in the descriptions of 28 new taxa of butterflies between 1871 and 1931.

Beginning in the early 1930s and continuing for several decades, the lepidopterist F. Martin Brown (1903–1993) attempted to trace Mead's 1871 exploration of Colorado. He published two papers on the subject (Brown 1934, 1955a), which were based primarily on information in Mead ([1876]). Although Brown's attempts to trace Mead's movements were admirable, the lack of published data for many dates left gaps in the itinerary, especially during late July and September when Mead ([1876]) did not report the capture of any specimens. Brown later transcribed a portion of Mead's 1871 letter copybook at Rollins College (Winter Park, Florida), but he died before publishing the results. Continuing the work of her late husband, Grace Brown arranged for the publication of the letters relating to Colorado (Brown & Brown 1996).

In 2010, a series of fortuitous events led to my acquisition of Mead's 1871 journal (Calhoun 2010) (Figs. 2, 3). This daily record offers a unique glimpse into the life of an extraordinary 19-year-old naturalist, who would become one of the most esteemed entomologists and horticulturalists of his day. During 1871 alone, Mead traveled a staggering 19,433 km (12,075 mi) by horse, stagecoach, steamer, and train. He met and

corresponded with an astonishing number of famous (or soon to be famous) people, from politicians and religious leaders, to museum curators and fellow naturalists. Most important, the journal represents an authoritative itinerary of Mead's travels, resolving longstanding debates about the actual origins of his butterfly specimens. I completed a full transcription of the journal and included notes about the people, places and things mentioned (Calhoun 2013a). The present paper further revises Mead's itinerary and incorporates additional details about many of the butterfly taxa that were described from his specimens.

METHODS

The studies of Mead's travels by Brown (1934, 1955a) were reviewed and compared against Mead's 1871 journal. Correspondence of Mead and other lepidopterists, including letters transcribed by Brown and Brown (1996), were examined for additional information about Mead's itinerary. The original manuscripts are preserved in the following collections: the Spencer F. Baird correspondence (Smithsonian Institution Archives, Washington, D.C.; USNM); the files of F. M. Brown and correspondence of Henry Edwards (Archives of the Library of the American Museum of Natural History, New York, New York; AMNH); the William H. Edwards archives (Charles C. Wise, Jr. Library, West Virginia State Archives, West Virginia University, Morgantown; WVSA); the correspondence of William J. Holland (Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CMNH); the T. L. Mead manuscripts (Archives and Special Collections, Olin Library, Rollins College, Winter Park, Florida; RC, and the archives of the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History; MGCL); and the correspondence of F. H. Herman Strecker (Archives of the Field Museum of Natural History, Chicago, Illinois; FMNH). Photocopies of many of these manuscripts are preserved in the MGCL archives. Type locality information was obtained from numerous sources, including original descriptions, Pelham (2008, 2014), and the comprehensive studies of type specimens by Brown (1964, 1965, 1966b, 1967, 1969, 1970a, 1970b, 1973, 1977) and Brown and Miller (1980). Examined were images of relevant specimens, including lectotypes and neotypes, deposited in the following institutions: AMNH; the California Academy of Sciences (San Francisco, California; CAS); CMNH; the Museum of Comparative Zoology (Harvard University, Cambridge, Massachusetts; MCZ); the Natural History Museum of Los Angeles County (Los Angeles, California; LACM); and the Peabody Museum of Natural History (Yale University, New Haven, Connecticut). Mead's routes were determined using historical trail information compiled by G. Scott (1975, 1976, 1999, 2004). Many early roads had multiple designations (they were owned and/or used by various companies and stage lines), thus I attempted to select names that were most likely in use during 1871. Information about settlements in Colorado was obtained from numerous sources, including Benson (1994), Warren (1994), Eberhart (1986), and Bright (2004). In many instances, Mead's whereabouts were confirmed using his recorded mileage estimates and the online measurement tools of Google Earth.

RESULTS

Mead's Expedition of 1871. "I am studying up [on] Colorado, hoping to make an excursion of a few weeks thither next summer," wrote W. H. Edwards in early 1870. "If I can get to Colorado I will do more among the Butterflies in one month than ever has been done there and doubt not I could bring back a hundred new species" (23.ii.1870, USNM). Later that year, Edwards still hoped to head west: "I must either go to Colorado or get someone to go" (4.xi.1870, AMNH). He soon realized that he would not be able to make the trip himself and began searching for a capable replacement. Although he could easily secure a collector, it was more difficult to find "an observer" (24.xii.1870, AMNH). He complained about the lack of information offered by the Philadelphia entomologist James Ridings, who toured the Territory of Colorado in 1864: "When Ridings came back from a summer in Colorado I put him to the racks for information of habits and localities of the butterflies he took and if he had been on a real rack he could not have been more recalcitrant . . . the information was not in him" (ibid.). Edwards finally located an outstanding collector and observer in the form of young T. L. Mead, who in early 1871 confirmed that he was "determined to spend the season in Colorado" (19.iii.1871, AMNH). Edwards considered Mead to be an extremely competent butterfly collector and predicted that he would "bring back a thousand fold" more specimens and information from Colorado than previous collectors (28.ii.1871, MGCL). "He is accomplished in many departments of entomology but rather most so in the butterflies," Edwards wrote, adding that Mead was well-educated and "exceedingly genial" (23.v.1871, AMNH). Giddy with anticipation, Edwards declared, "This is the best opportunity that has ever occurred for us poor butterfly men" (ibid.).

Brown (1934, 1955a, Brown et. al. 1954) repeatedly claimed that Mead served as a collector with the Wheeler Survey in Colorado. Supervised by Lt. George M. Wheeler (1842–1905), the Wheeler Survey was

Figs. 1–3. Theodore L. Mead and his 1871 journal. **1,** Mead in 1874, three years after returning from Colorado (RC). **2,** journal. **3**, journal pages.

composed of separate expeditions that explored United States territories located west of the 100th meridian. Wheeler led the first expeditions in 1869 and 1871, after which the survey was expanded under authorization of the U.S. Government to more extensively map the western lands, as well as document the natural history and Native American populations of the region. Brown (1955a, 1955b, 1957, 1966a) studied the explorations of several survey naturalists.

Despite Brown's assertion, I found no evidence that Mead's trip was in any way associated with the Wheeler Survey. The most obvious discrepancy is that the Wheeler Survey of 1871 did not include Colorado and instead explored portions of California, Arizona, Nevada, and Utah (Bartlett 1962). Consequently, Mead could not have "accompanied the Denver party of the Wheeler Survey" as stated by Brown (1934). Mead ([1876]) did not mention any involvement in the actual survey and there are no such references among his manuscripts or those of W. H. Edwards. Their letters indicate that Mead merely accepted a proposal from Edwards to collect butterflies in Colorado. This is supported by Mead (1936), who remarked, "In 1871 Mr. Edwards . . . suggested a summer in Rocky Mountain country, sharing the expense and sharing the butterflies." In his autobiography, Edwards (1900–1901) made no mention of the Wheeler Survey, stating, "In May, 1871, Mr. Theodore L. Mead went on a collecting tour or Colorado . . . that I might describe and figure any new species." Mead was not mentioned in the preliminary report of the Wheeler Survey for the year 1871 (Humphreys 1872). Furthermore, Edwards ([1876]) did not include any of Mead's exclusive Colorado captures within a list of species reported by the Wheeler Survey (i.e. they were not considered part of the survey). Mead's only clear connection to the Wheeler Survey is his subsequent authorship of the *Report upon the Collections of Diurnal Lepidoptera* (Mead [1876]), which he wrote on behalf of the survey (see below). "Mr. Edwards recommended me to the naturalist of the Wheeler Expn as the proper person to write a report on the habits and distribution of their butterflies," Mead explained. "This I have promised to do & will incorporate in it all my observations on Colorado species . . ." (8.iii.1874, RC, AMNH). His use of the phrase "***their*** butterflies" implies his detachment from the survey. Mead was an invited author who simply added his own observations as an expert on the Colorado fauna. Other entomologists also authored survey reports without any direct involvement in the survey itself. Unfortunately, Brown's assertion was repeated by many subsequent authors, including myself (Calhoun 2010, 2013c).

Mead jumped at the chance to collect butterflies in such a beautiful and poorly-understood region. Edwards obtained the necessary railroad passes and suggested that Mead begin his trip during May of 1871. Edwards also urged Mead to continue beyond Colorado, with the expectation that he would "obtain many fine species and much information" from lepidopterists in California. Mead's family was wealthy and his father, Samuel H. Mead, Sr., spared no expense where his sons were concerned. His financial support of "Teddy's" ambitious western adventure was augmented by Edwards, who promised to "bear half the expense," provided his portion did not exceed $500 (28.ii.1871, MGCL).

Edwards felt obliged to compensate Mead for the specimens he expected to receive.

To prevent the loss of specimens during the trip, Edwards instructed Mead to "put the insects in papers and express them to me pretty frequently." Upon receipt, Edwards would mount some of the specimens and keep them segregated with the remainder of the papered Colorado material (28.ii.1871, MGCL). Edwards softened the papered specimens using "a towel wet & well wrung," folded four times, in which he placed the insects on a sheet of blotting paper. Larger specimens could be mounted in about 24 hours, while smaller specimens were ready in three or four hours (5.viii.1871, AMNH).

Edwards also devised a plan to allocate the specimens upon Mead's return. He suggested that they retain the first two pair of each butterfly species, while the next pair would be given to the American Entomological Society (AES) in Philadelphia, Pennsylvania. All remaining butterflies would be divided evenly between them. Other species of Lepidoptera, with the exception of the Sphingidae (which Edwards wanted to see), would mostly be kept by Mead with the expectation that he would donate some to AES. As for butterflies, Edwards wanted to "make the acquaintance of all the species taken" so that he could describe any new taxa. He also longed to receive biological information for inclusion in his book, *The Butterflies of North America*, which was well under way by that time (Calhoun 2013b).

In preparing for the journey, Mead asked his Aunt to construct his butterfly nets and he purchased other collecting equipment from the Brooklyn natural history dealer John Akhurst. He searched for helpful books about Colorado, purchasing *A Summer Vacation in the Parks and Mountains of Colorado* by Samuel Bowles (1869). After gathering together all the necessary materials, Mead started his trip on 17 May, first stopping at the home of Edwards in Coalburg before continuing westward on 23 May. Departing West Virginia, Willie Edwards accompanied Mead as far as Cincinnati before returning home on 26 May. In Chicago, Mead met up with his older brother, Samuel H. Mead, Jr. (1848–1875), and they traveled together for the remainder of the journey.

The Mead brothers arrived in Denver on 31 May. During their tour of Colorado, the book by Bowles (1869) must have come in handy, as they visited many of the same destinations. Mead described their travels as "nomadically going about hither and thither" in search of butterflies and game (Brown & Brown 1996). As originally proposed, Mead regularly sent shipments of papered butterflies back to Edwards as they were collected, packed in wooden cigar boxes. Mead wrote the date on each field envelope (e.g. "6/16," "7–13," or "June 12") and identified those species he did not recognize using a system of genus name and number, such as "Melitaea 1." He explained to Edwards, "As you see I only put the date on each paper because a good days catch takes four hours or more to put away and label and I keep an accurate record of my whereabouts" (Brown & Brown 1996). His "accurate record" was his journal, as mentioned in a letter to Edwards in August 1871 (Brown & Brown 1996). "I make it an invariable rule to label every specimen collected with date of its capture," he later wrote, "as I keep a daily record of them, I can give very precise localities" (3.ii.1873, RC). Mead had some trouble keeping track of the species he was collecting, thus he mounted a few specimens and retained them for comparison: "I intend to pin some caught by my brother and so obviate this difficulty" (Brown & Brown 1996). Upon receipt, Edwards grouped the papered specimens by species and inserted them into separate letter envelopes, which were then placed into a "strongly scented" cigar box to deter mold and insect pests (15.vi.1871, RC).

Mead sent thousands of specimens back to Edwards, who remarked that they were "mostly in good order" (5.viii.1871, AMNH). Edwards was overjoyed with Mead's work: "He climbs Mountains to their summits & collects everywhere" (ibid.). Reviewing what Mead had collected up to the end of July, Edwards supposed that it included 23 new species (4.viii.1871, RC). Edwards ultimately described exactly 23 new taxa, most before Mead even returned from his trip, including *Colias meadii*, *Argynnis meadii* (=*Speyeria callippe meadii*) and *Cercyonis meadii*. "I am delighted that such beautiful insects are to be called after me and appreciate highly the honor," wrote Mead upon learning of these names (Brown & Brown 1996). Entrusting Edwards to describe new discoveries, Mead did not consider himself "sufficiently acquainted with the Pacific Coast fauna to have undertaken the work" (20.ii.1873, RC).

Prior to describing new taxa, Edwards often sent some of Mead's specimens to the lepidopterist Henry Edwards (1827–1891) of San Francisco, California. For this purpose, W. H. Edwards (WHE) considered H. Edwards (HE) to be a "consulting entomologist." HE was allowed to keep most of the specimens, many of which he recorded in his collection catalog (now preserved at AMNH). Once WHE decided on a name for a new taxon, he informed HE so that the specimens could be labelled accordingly (20.ix.1871, AMNH). One shipment of specimens was sent on 9 July 1871, when WHE advised HE to regard them as having been sent directly by Mead. When later traveling through California in October of that year, Mead saw these

butterflies in the collection of HE and remarked in amazement that they looked "quite unfamiliar" (Brown & Brown 1996). Mead had collected so much material that he remembered little about individual specimens. Years later, Mead returned the favor and invited Edwards to examine his collection in New York: "I would be happy to have you take a look at my collection & enclose a note to the servants—they of course have had instructions not to receive visitors unknown to them without authority" (14.viii.1878, AMNH).

Citing the abundance of butterflies in Colorado, Mead (1877) wrote, "In no place outside of the tropics have I found a better collecting-ground . . . both as to variety of species and number of specimens." In an undated list, written soon after his return home, Mead tabulated the butterfly species that he had collected in Colorado (AMNH). Of 84 entries, 61 are identified by name. Mead (1877) summarized the more abundant species and groups that he encountered, along with the number of specimens he collected. He also tallied the total number of butterflies collected by month: 1,792 during June; 1,483 during July; 607 during August; and 43 during September. Edwards admitted that he was "embarrassed by the extent of the material" (3.xii.1871, AMNH).

Mead also collected other kinds of insects in Colorado. By his own count, he obtained 3,800 insects besides Lepidoptera, mostly on rainy days when butterflies were inactive (Mead 1877). He collected about 1500–2000 specimens of Coleoptera (15.xii.1872, RC) and about 50 specimens of Hemiptera (17.xii.1972, RC). He sold his beetles via the natural history dealer John Akhurst, who advertised them in the *Canadian Entomologist* (e.g. Akhurst 1873), thereby disposing of them "in a lump" (30.vi.1873, AMNH). Mead's moth captures were listed by other authors (e.g. Packard 1874) and several species were named in his honor. His moths included 318 specimens of Geometridae and Noctuidae (Mead 1877). In addition to collecting adult insects, Mead reared butterflies in Colorado and mailed examples of early stages to W. H. Edwards; those not alive were sent in carbolic acid. He even sent larvae home with instructions to his parents on what plants to feed them. Mead also sent home cactus plants, some of which were still alive four years later (17.xi.1875, AMNH). More significantly, he gathered fossils in the area now known as the Florissant Fossil Beds National Monument (Teller County) and is recognized as the first to make fossils from this site available for study (Brown 1981, Veatch & Meyer 2008). He sent insect fossils to W. H. Edwards, who forwarded them to S. H. Scudder for examination. Scudder, an accomplished insect paleontologist, mentioned some of these specimens in his publications (e.g. Scudder 1876) and described a fossil termite in Mead's honor (Scudder 1884). In 1873, Mead sent all his remaining fossils directly to Scudder, "leaves and all" (23.xii.1873, RC). This material is preserved at MCZ.

Departing Colorado via Cheyenne, Wyoming, on 27 September 1871, Mead and his brother arrived in Salt Lake City, Utah, the following day. After spending time in and around Salt Lake City, they proceeded to California on 4 October. After arriving at San Francisco two days later, they toured the city and met the prominent entomologists Hans H. Behr (1818–1904), James Behrens (1824–1898), H. Edwards, and Richard H. Stretch (1837–1926). They took a side trip to Yosemite Valley and returned to San Francisco prior to their scheduled departure of 3 November. Traveling south via streamer along the coast, Mead briefly disembarked on 17 November at Puntarenas, Costa Rica, where he collected a few butterflies. On 20 November the brothers arrived at Panama, where they spent nearly two weeks exploring along the coast. They collected about 1000 butterflies (most hesperiids) by "tramping from 8 to 10 mi a day through swamp & forest" (19.xii.1871, RC). On 3 December they took a train across Panama to the town of Aspinwall (now Colón) on the Caribbean Sea, where they boarded another steamer late that evening. Heading northward, they reached Kingston, Jamaica, on the afternoon of 6 December. They collected butterflies and sampled the local fare in Jamaica until the next afternoon, when they departed for the United States. They finally arrived back home at New York City on 14 December, concluding an arduous, but incredibly gratifying seven-month adventure.

Disposition of Mead's specimens. After Mead's return, he and W. H. Edwards divided up the butterflies from the trip (Edwards 1890), but it is unclear if they followed the plan precisely as Edwards had originally proposed. This took place at Edwards' home in Coalburg, where Mead visited from 28 February to 30 April 1872 (11.v.1872, AMNH). The task was completed during the first week of March and must have taken some time, as Mead had collected nearly 4,000 butterflies (10.iii.1872, AMNH; Mead 1877). "Now I am spending a few weeks with Mr. W. H. Edwards," Mead wrote his parents, "talking over my captures & having a good time generally" (13.iii.72, RC).

Nearly all of the butterflies that Edwards returned to Mead in 1872 were still in their original field envelopes. For Mead's portion of the take, Edwards decided not to remove them from the papers any more than was necessary to "make sense of the species" (10.vi.1871, RC). Long after he received his share of the take, Mead

continued to keep most of his Colorado specimens in papers, which made it easier to exchange them with correspondents. He explained, "In 1871 I collected four thousand specimens of Diurnal Lepidoptera all of which I put up in that manner [papers] finding it safe and convenient, while it would have been almost impossible to transport such a mass of pinned specimens without much risk and trouble" (30.xi.1872, RC). Referring to the papers that he used to store butterflies from Colorado, he recalled, "2 ½ inches square was about the most useful size—accommodating *Pieris*, *Chionobas* & etc while [for] *Lycaenas* 1 ¾ in. would do" (18.xii1872, RC). He advised recipients of his specimens, "if you lay the papers in a damp towel the butterflies will be relaxed in the course of from 12 to 24 hrs or more according to size" (28.v.1872, RC). Because most of his specimens remained papered, Mead was often "a good deal puzzled" about their identities. He therefore decided to mount one specimen of each unfamiliar species for future comparison. After that, "there was no more trouble" (24.xii.1872, RC). Mead took a particular interest in the Hesperiidae and this was the only group of specimens that he mounted entirely (19.iii.1874, RC).

In an undated letter to his parents, sent from West Virginia during his visit with Edwards in early 1872, Mead recounted his awkward conversation regarding Edwards' financial obligation for the trip. "He said that he was perfectly willing to pay half expenses for the time during which I was butterfly hunting," Mead wrote, "but intimated that the months during which I was not so engaged didn't count" (RC). Edwards asked Mead to propose an amount which he "thought was right," to which Mead suggested $400. Despite Edwards' earlier promise to pay up to $500, he was surprised at being "called upon to pay so much." Nonetheless, Edwards believed the amount was fair and that the butterflies were "fully worth it." Mead did not intend to ask Edwards for any money ("As it is I feel rather mean"), but the trip had cost more than expected. Edwards was short of funds, but promised to pay the balance within several months. They also agreed that Edwards would offer a "share" of Colorado butterflies to at least two lepidopterists for $100 each. If Mead contributed specimens, he would be given half the amount received.

While Mead was still in Coalburg, Edwards offered Colorado specimens to the lepidopterist F. H. Herman Strecker (1836–1901) of Reading, Pennsylvania. "Mr. Mead & I find that the expense of last summers' collecting in Colorado was very heavy," Edwards wrote, "More than expected" (23.iv.1872, FMNH). Edwards offered Strecker "a good lot" for a "contribution" of $100 (nearly $2,000 in today's economy). Edwards proposed to make this offer to no more than five lepidopterists, thereby giving each enough specimens "to make a good collection." Edwards assured Strecker that Mead's papered specimens were mostly in good condition, but admitted that "some of course are not." He indicated that there were a half a dozen specimens of each species, "frequently 10 or 20," but in some instances there were "considerably more" (10.v.1872, FMNH). Strecker ultimately declined this proposition and instead purchased only a handful of desirable specimens, a few of which are still contained in his collection at FMNH. In an attempt to cut out the middleman (i.e. W. H. Edwards), Strecker contacted Mead and offered to "expand [mount] all the specimens, have price lists printed and undertake to dispose of" his Colorado specimens for a twenty percent commission (4.ix.1872; MGCL). Mead, however, did not accept this proposal, probably realizing that such an agreement would mostly benefit Strecker in affording him access to the choicest specimens. Although Mead told other correspondents that he was "pretty well supplied with Rocky Mountn and Western rarities for exchange" (24.xii.1872, RC), he insisted that Strecker contact Edwards: "After Mr. Edwards has deposed of his, should there be still a demand I would probably be willing to sell some of mine" (10.ix.1872, RC).

By June 1873, Edwards had contacted four other people whom he hoped would be interested in the specimens (and be able to afford them), but none responded (27.vi.1873, AMNH). Edwards therefore decided to keep the specimens and offer them as "duplicates" to other lepidopterists. Mead was shocked to learn that some of his Colorado specimens were so highly prized: "I had no idea that they were so valuable but in [the] future shall consider the fact in making exchanges" (5.vii.1872, RC).

Although Mead reassured Edwards that he was in no hurry to receive the money owed, Edwards evidently paid the balance by June of 1873, professing, "I live on a salary myself, but I have no cigars to buy or whiskey to indulge in and I save money where some would spend it, and therefore do not feel that I am extravagant in spending what I do in the matter of Butterflies" (27.vi.1873, AMNH). Based on the material at CMNH, Edwards exchanged and/or sold the bulk of his share from Mead's 1871 trip. Edwards subsequently obtained additional Colorado specimens from other collectors, rendering Mead's material less valuable.

Over the years, Edwards and Mead provided Colorado butterflies to many correspondents. Among them was Samuel H. Scudder (1837–1911), who figured several in Scudder (1874). Scudder acquired many specimens during a three-day visit to Edwards' home in December 1873, when he "carried off" all the

Hesperiidae he wanted, including several undescribed species (13.xii.1873, AMNH). Scudder examined Mead's collection in New York in late 1873 (19.xi.73, RC) and obtained additional specimens directly from Mead during the early 1870s. Scudder also received some of Mead's specimens via Herbert K. Morrison (1854–1885), a professional collector who exchanged specimens directly with Mead for many years. A number of these specimens are labeled with specific locality data (e.g. "Apex Gulch," "T. C. Junction," "Twin Lakes"), which Mead personally conveyed to Morrison (1.iv.1873, RC). Scudder's collection is deposited at MCZ. Morrison's specimens are deposited in many institutional collections, including USNM.

Others who received Mead's Colorado material include Augustus H. Mundt (1847–1920), a jeweler and naturalist of Fairbury, Illinois. These specimens are now deposited in the collection of the Illinois Natural History Survey (Irwin 1966). The California lepidopterists H. Edwards, Hans Behr, and James Behrens obtained specimens from both W. H. Edwards and Mead (Mead also gave them some Colorado specimens when he visited California in late 1871). Henry Edwards' collection is deposited at AMNH. Behr's collection was tragically destroyed two years after his death in the San Francisco earthquake and fire of 1906. Prior to his death, Behrens donated his collection to what is now the Museum für Natur und Umwelt (Museum for Nature and the Environment), Lübeck, Germany. Another San Francisco lepidopterist, William G. Wright (1831–1912), obtained some of Mead's specimens (probably from W. H. Edwards) and several were illustrated in Wright (1905). Wright's collection is deposited at CAS.

William H. Edwards exchanged Mead's specimens with the Massachusetts entomologist Francis G. Sanborn (1838–1884), who in turn forwarded some to the naturalist Charles P. Whitney (1838–1928) of New Hampshire. Beginning in early 1872, Mead exchanged many specimens directly with Whitney: "I have given him already a considerable proportion of the more abundant Col^{o} species in exchange for N.E. [New England] Hesperians etc. not in my collection" (27.v.72, RC). Whitney's collection is now preserved at PMNH (see Calhoun (2013e) for information about the provenance of Whitney's collection).

Mead personally sent Colorado butterflies to the newspaperman and amateur lepidopterist Willard E. Yager (1855–1929) of Oneonta, New York, whose collection may be preserved in the Yager Museum of Art and Culture at Hartwick College in Oneonta. In 1873, Mead exchanged some Colorado butterflies with another New Yorker, the entomologist Joseph A. Lintner (1822–1898), whose collection was bequeathed to the Albany Museum of Natural History, Albany, New York. Mead also sent a few Colorado specimens to the farmer and naturalist George M. Dodge (1846–1912), then of Ohio, Illinois, whose collection is deposited at CAS (Calhoun 2013d). Per his original agreement with Edwards, Mead sent at least one box of butterflies in 1872 to E. T. Cresson of the American Entomological Society: "Today I express to you a box containing . . . a collection of Col^{o} Diurnals in papers, the joint gift from Mr. Edwards and myself to the Society" (24.v.72, RC). I recently found some of these specimens at The Academy of Natural Sciences (Philadelphia, Pennsylvania) labeled "Edwards and Mead."

Perhaps the most distant entomologists to obtain Mead's butterflies were the entomologist Jean B. A. D. de Boisduval (1799–1879) of Paris, France, and the natural history dealer Otto Staudinger (1830–1900) of Dresden, Germany. Edwards sent a few Colorado butterflies to Boisduval in 1873 and 1874 (Edwards' journal "D," WVSA), while Mead sold some to Staudinger in 1872 (13.iv.1873, RC). Those from Boisduval's collection may be deposited at USNM (see Calhoun 2004, 2006). Staudinger's collection is deposited at the Museum für Naturkunde in Berlin, Germany. Staudinger is credited with sparking Mead's interest in entomology in 1867 (Mead 1935, Calhoun 2013a), though Mead began collecting insects "sporadically" four years earlier (21.v.1874, RC). Untold numbers of butterflies changed hands between entomologists of the 19th century, scattering Mead's specimens to countless collections, though many are no longer recognizable as his.

It was fortunate that Mead was not a member of the Wheeler Survey of 1871, as many of the specimens brought back from explorations that year were accumulated and stored in Chicago, Illinois. On 8–10 October 1871, the Great Chicago Fire laid waste to much of that city, taking with it specimens from the survey (Yarrow [1876a]). The collections of Mead and Edwards were ultimately purchased by William J. Holland (1848–1932), who later served as the Director of the Carnegie Museum (CMNH), where his large personal collection is now preserved. In his autobiography, Mead (1935) erroneously dated the purchase of his collection as 1877; it was actually 1884. Apparently, Mead's collection had suffered from neglect and many specimens were in poor condition. "Mead had a great many very valuable things of his own collecting . . ." Edwards remarked, "I hope these may not have suffered," (16.xi.1884, CMNH). This problem is evident in the condition of some of Mead's specimens at CMNH (Brown 1970). Holland paid $460 for Mead's entire collection (7.vi.1884, RC). He purchased Edwards'

collection in 1885–1886 for $2,500 (Calhoun 2013b).

Mead's Report. William H. Edwards encouraged Mead in late 1871 to write up his observations on Colorado butterflies. Edwards even offered to publish them in his book, *The Butterflies of North America*, as a "highly interesting record to the present generation" (15.xi.1871, MGCL). Alternatively, Edwards suggested that Mead write a lengthy story about his experiences and publish them as "a magazine article." Mead did neither, but he was asked three years later, at the suggestion of Edwards, to write the section on diurnal Lepidoptera for the zoology report of the Wheeler Survey (Calhoun 2013c). Mead accepted the responsibility of drafting the report on diurnal Lepidoptera while he was a student at Cornell University in Ithaca, New York. "I will be glad to prepare a report on the insects," Mead wrote in reply, "but I would like to know how voluminous an account is desired" (29.i.1874, RC). He suggested a more detailed treatise that would result in a "sizable pamphlet—probably 60 or 70 pp." Mead wasted little time in sharing this distinguished honor with his closest correspondents. He was astonished by the official acknowledgement he received, conveying the thanks of Lt. Wheeler, which was addressed to "Prof. T. L. Mead." Mead quipped to his brother, "[I] wonder what he would say if he knew I was nothing but a miserable little Freshman . . ." (4.ii.1874, RC). He was astounded that an inexperienced college freshman would be entrusted with such an important task. Thus was the influence of W. H. Edwards and his admiration of Mead.

For the report, Mead combined the results of his own collecting in Colorado with those of Wheeler Surveys conducted from 1871 to 1874 in portions of southern Utah, New Mexico, and Arizona. As a consultant to the Wheeler Survey, Edwards contributed a list of all the butterfly species that were collected during the various Wheeler expeditions. Mead also included data from the Allen Expedition of 1871. Joel A. Allen (1838–1921), an assistant at the Museum of Comparative Zoology, spent nine months during 1871 with two assistants exploring portions of Kansas, Colorado, Wyoming, and Utah (Osborn 1916, Brown 1956). Mead met the Allen party near Montgomery City, Colorado, on 24 July 1871. He later examined Allen's butterfly specimens at MCZ (26.vi.1872, RC), some of which are still preserved in that collection, labeled "Colorado. / Allen." William H. Edwards was probably referring to Allen's expedition when he notified Mead that some of the same species had been brought back by other collectors in 1871 and "Many are at Cambridge" (15.xi.1871, MGCL). Mead was unfamiliar with some of the species collected in Utah and other areas outside Colorado, thus he asked Henry Edwards to provide notes on those species (8.iii.1874, AMNH) (he thanked Edwards in the published report for "notes upon some species whose habits were unknown to me"). Due to extreme delays, Mead's *Report* was not published until late 1876 (Calhoun 2013c). It served as the basis of the suggested type localities by Brown (1934) and the primary source of information about Mead's Colorado itinerary as charted by Brown (1955a).

Mead started to lose interest in entomology around 1877. By 1882, when he permanently moved to Florida, his lifelong interest in horticulture had become his passion. He left his Lepidoptera collection with his parents in New York, and it was from there in 1884 that W. J. Holland transported it to his home in Pittsburgh, Pennsylvania. Although Mead continued to maintain a passing interest in Lepidoptera for many years (Skinner 1922), he became infatuated with the hybridization of flowers, especially orchids and *Amaryllis* (Mead 1904, Mead 1935, Butler 2013, 2014). Census records from the early 20th century list him as a "florist" and "bulb farmer." Mead suffered through the devastating deaths of his young daughter, Dorothy, in 1892 and his wife, Edith, in 1927. Mead died of a stroke on 4 May 1936 at Memorial Hospital in Sanford, Florida, and was buried in Greenwood Cemetery (section B)—to this day a serene oasis nestled within the bustling tourist mecca of Orlando, Florida.

Mead's manuscripts and 1871 journal. In his last will and testament, dated 19 August 1933 (RC), Mead bequeathed to the Trustees of Rollins College all of his "scientific books and pamphlets and apparatus," as well as his "album of Colored Orchid Photographs." With the exception of a few miscellaneous items, he bestowed "all the rest and residue and remainder" of his property, "real personal and mixed," to his nieces Catherine T. Willis and Eleanor deGruyter of Charleston, West Virginia. Catherine (1884–1968), who was married to John A. Willis, Sr. (1877–1961), was the daughter of Anne S. Smith (1858–1930), the youngest daughter of W. H. Edwards and the sister of Mead's wife. For many years the Willis' lived in Edwards' former home in Coalburg, West Virginia (Calhoun 2013b). They received some of Mead's property, including many of his letters (a portion of which are preserved at MGCL). None of Mead's journals were listed among the items originally received by Rollins in 1936.

Although Rollins College received the bulk of Mead's manuscripts after his death, some material remained the property of Mead's friend, John "Jack" H. Connery (1908–1982), of Winter Park, Florida. For a time, Mead was a scoutmaster and Connery was one of his Eagle Scouts. Connery attended Rollins College, where he

taught ornithology classes and served as the director and curator of the Thomas R. Baker Museum. During the early 1930s, he was a photographer for the Bermuda expeditions of the famed zoologist William Beebe (Gould 2004). Documents at Rollins College indicate that upon Mead's death, Connery took charge of Mead's property, much of which was stored in a barn, presumably on Mead's property in Oviedo, Florida. Some of Mead's belongings were retained for a planned Mead memorial that later evolved into the Theodore L. Mead Botanical Garden in Winter Park. Dedicated in 1940, Connery was instrumental in the development of this property, which operates today as Mead Botanical Garden (Whitman 1939, Johnson 2008).

Records show that Connery received books from Mead's library, as well as "a large quantity" of his personal letters, manuscripts, photographs and many other items of "great historical interest." This is supported by a letter from Mead to Connery and his wife, Helen, dated 30 May 1933, three months before Mead drafted his will. Mead permitted them to have all the correspondence they wished, advising, "I don't believe anybody else would care for the diaries so you can have them when I have done with them" (RC). Mead mentioned the presence of "1877 diaries and later," thus revealing that other journals existed and at least some were likely received by the Connerys. Beginning around 1947, the majority of the manuscripts given to the Connerys were kept in a large trunk in a storeroom of Edwin O. Grover (1870–1965), a former Director of Libraries at Rollins College who later served as Vice President of the school until his retirement in 1947. In 1957, Grover and the Connery's asked that the trunk of Mead's manuscripts be placed on deposit with the remainder of Mead's manuscript collection at the Mills Memorial Library, which opened at Rollins College in 1951. The Mead manuscript collection was moved several times after arriving at Rollins and is now preserved in the Olin Library, which opened in 1985. Other Mead-related materials and documents are deposited at the John C. Hitt Library, University of Central Florida (Orlando, Florida), the Kroch Library, Cornell University (Ithaca, New York), Mead Botanical Garden (Winter Park, Florida), the Orange County Regional History Center (Orlando, Florida), and the Winter Park Public Library. John Connery's sons, John, Jr. and W. Edwin, also possess some items, including a few of Mead's orchid hybridization notebooks and a painted portrait of Mead (W. E. Connery, pers. comm.).

In 2010, I was extremely fortunate to acquire Mead's 1871 journal from James W. Tillery of Lehigh Acres, Lee County, Florida (Calhoun 2010) (Figs. 2, 3). Tillery discovered it among items in a storage unit, which had been rented by a local bookseller. The bookseller passed away and the unit's contents were auctioned. An obvious connection to Lee County could be made through J. H. Connery's youngest son, W. Edwin Connery of Cape Coral, Florida (whose middle name honors Edwin O. Grover of Rollins College). I discussed Mead and his manuscripts with W. E. Connery via telephone in April 2013. He did not recall ever seeing any of Mead's personal journals among his parents' belongings when they died. He suggested that the 1871 journal became separated from the other manuscripts many years ago and its subsequent presence in that region of Florida was merely a coincidence. Some of Mead's remaining yearly journals were seen by Paul Butler during a recent visit the former home of W. H. Edwards in Coalburg, West Virginia, though none are from the 1870s (P. Butler, pers. comm.). Butler is currently preparing a more lengthy biography of Mead for publication.

Preserved at Rollins College are five volumes of letter copybooks in which Mead duplicated the letters he wrote during the early 1870s. Within these bound volumes are letters written during 1 January–29 December 1870, 23 October–30 December 1871, 4 January–31 December 1872, 6 January–31 December 1873, and 1 January–20 March 1874. Unfortunately, the volume that would have included letters written during 1 January–22 October 1871 (covering Mead's time in Colorado) is missing. Among the F. M. Brown archives in the AMNH is information about this copybook, as well as some photocopied pages and a draft manuscript about Mead's Colorado trip. I obtained scans of these documents, which offer some insight into the fate of the missing volume.

In 1979, F. Martin Brown and the late lepidopterist Lee D. Miller (1935–2008) visited the Mills Memorial Library at Rollins College, where they examined some of Meads' manuscripts, including his letter copybooks. The reference librarian photocopied a portion of the 1871 copybook at Brown's request. In 1981, Brown requested additional photocopies of letters that were illegible in the original set. On 5 September 1984, Brown announced that he had finally completed the transcriptions of the letters in the copybook, yet some passages remained undecipherable. At that point, the librarian was unable to locate some of the materials, pointing out that the letters "apparently have been shifted." Brown reminded her that the copybook was "in an old trunk (box) down in the storeroom," referring to the trunk of Mead's manuscripts that the Connerys had previously donated to the college. It seems likely that the copybook was misplaced shortly after photocopies were sent to Brown in 1981. It probably lacked external identifying marks, such as Mead's name or a catalog

number, increasing the chance that once separated it was not properly returned. Mead's manuscripts have since been thoroughly cataloged and archived. Although Brown's photocopy of Mead's 1871 volume is incomplete and many pages are illegible, it offers a valuable glimpse into its contents, especially when combined with the transcriptions by Brown & Brown (1996).

Updated Colorado Itinerary. Based upon Mead's 1871 journal, I offer a corrected itinerary of Mead's exploration of Colorado (Table 1). The map included in Brown (1955a) is still a helpful reference to the locations visited by Mead, but some of the dates and estimated routes are incorrect. Three locations where Mead spent a great deal of time in Colorado serve as the type localities for multiple taxa described from his specimens. Kenosha House and Turkey Creek Junction were 19th century stagecoach stops in Park and Jefferson Counties, respectively. The third, Twin Lakes, is located in southern Lake County.

Kenosha House. Described by Mead as "a clean well-kept ranch," Kenosha House was a two-story stagecoach station constructed in 1861 (Fig. 4). Offering meals and lodging to weary travelers, the proprietors advertised "an excellent variety of tempting food," including venison, wild duck, and mountain strawberries (Anonymous 1870, Crump & Crump 2010). Kenosha House also had mail service, which allowed Mead to send letters to W. H. Edwards and others while lodging there. Mead often referred to the station as "Kenosha Ranch."

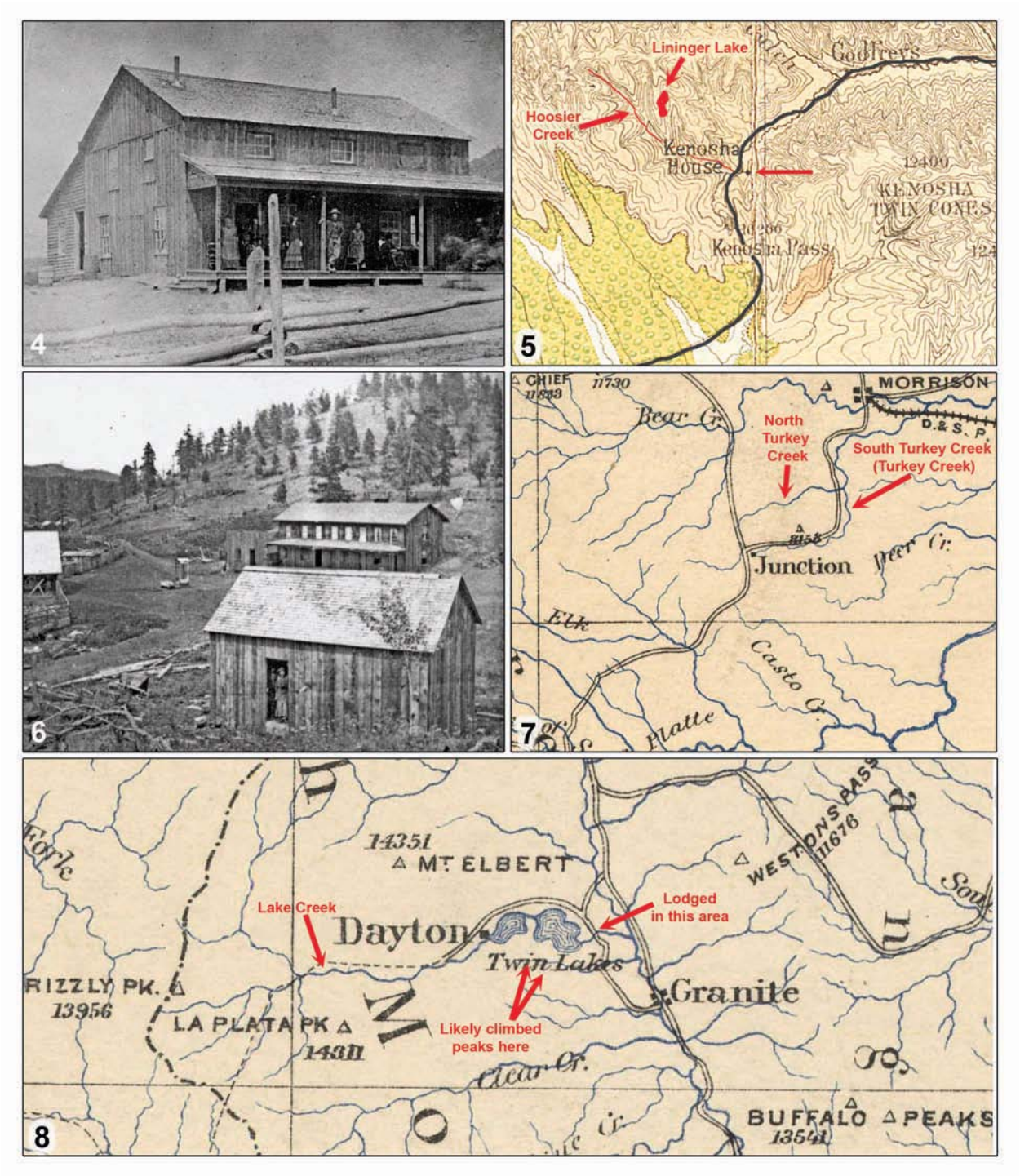
Disagreement exists regarding the location of Kenosha House, with some authors (e.g. Fisher 2006) placing it at the summit of Kenosha Pass, Park County. Scott et al. (2006) positioned it 0.8 km (0.5 mi) north of the pass. Although this location is consistent with the map of Wheeler (1876) and the trail map of G. Scott (1999), it does not agree with other accounts, including the map of Hayden (1877b), which shows it about 2.16 km (1.34 mi) (2.62 km/1.6 mi by road) north of the summit (Fig. 5). This is roughly where Brown (1955a) mapped it. Warren (1994) also located it there, directly opposite the current intersection of U.S. Hwy 285 and C.R. 58 (Lininger Lake Rd.), near the point where Hoosier Creek turns northward. This site corresponds with the records of the Colorado Office of Archaeology and Historic Preservation (S. Gilmor, pers. comm.). Mead ([1876]) stated that Kenosha House was located "four miles from the South Park," which is a relatively accurate distance from this site to the South Park basin along the old wagon road. This is consistent with a statement that the best view of the South Park basin could be had "about three miles beyond the Kenosha House" (Anonymous 1870).

The house stood on the east side of the Denver, Bradford & Blue River Road. Also known as the Denver, Turkey Creek & South Park Wagon Road, this trail was commonly known as the Denver & South Park Road (Hayden 1874); cumbersome names shorted by Mead to "South Park Road." The house was said to overlook a "beautiful valley that slopes up toward the mountains" (Anonymous 1870), clearly a reference to the valley of Hoosier Creek (Fig. 5). According to his journal, Mead collected butterflies as far as 4.8 km (3 mi) within the gulch "opposite the house" (Hoosier Creek) and along the wagon road toward South Park. He also explored "up a little brook" to a "pine lake." These are today's Lininger Ditch and Lininger Lake, located just northwest of the former site of Kenosha House (Fig. 5).

Gannett (1877) recorded the elevation of Kenosha House as 2935 m (9629 ft.), but current maps suggest it was closer to 2957 m (9700 ft.). GPS: 39.432627, -105.758828. This area serves as the type locality of the nominal taxa *Colias hagenii* W. H. Edwards, *Thecla ninus* W. H. Edwards, and *Melitaea eurytion* Mead.

Turkey Creek Junction. There also is disagreement about the location of this settlement. Brown (1934) initially associated it with "the junction of South Turkey Creek with Turkey Creek," but later equated it with Junction House (=Bradford Junction), formerly located in today's town of Conifer in Jefferson County (Brown 1955a). Scott et al. (1998) considered Turkey Creek Junction to be 0.8 km (0.5 mi) north of Tiny Town, a miniature village about 1.6 km (1 mi) southeast of the community of Indian Hills along South Turkey Creek Road. Fisher (2006) suggested that Turkey Creek Junction was probably "in the vicinity of what we call Tinytown . . . or between there and what is currently called Myers Ranch Open Space." The latter is now known as Meyer Ranch Park, located just east of the town of Conifer.

Distances recorded by Mead in his journal confirm that what he called "Turkey Creek Junction" was Bradford Junction, a community once situated 10.6 km (6.6 mi) southwest of Tiny Town and about 366 m (1200 ft.) higher in elevation. Mead later recalled that "Turkey Creek Junction" was "a very good collecting ground 28 miles from Denver on the S.P. [South Park] road" (1.iv.1873, RC). Identified as "Junction" on contemporary maps (e.g. Hayden 1877a, Wheeler 1877) (Fig. 7), this small settlement and stagecoach stop was established by Robert B. Bradford, who owned the property from 1860 to 1873. It was located at the junction of two main roads; the Mt. Vernon Wagon Road (which Mead called the "North Road") and the Denver & South Park Road (which Mead called the "South Park Road"). Bradford Junction existed where present-day



FIGS. 4–8. Mead's collecting localities. Maps are from Hayden (1877a, 1877b), with relevant features denoted in red. **4,** Kenosha House, ca. 1870 (courtesy History Colorado, scan 10027856). **5,** location of Kenosha House (road darkened). **6,** Bradford Junction ("Turkey Creek Junction"), ca. 1875, looking northwest from today's southeast corner of CR 73 and Barkley Road (courtesy Park County Local History Archives). The two-story building at center right is the Junction House. **7,** location of Bradford Junction (as "Junction"). **8,** the Twin Lakes region.

TABLE 1: Itinerary of T. L. Mead in Colorado

Date(s)	Location(s)	Proposed location(s) from Brown (1955a)	Details
31 May–4 June	Denver area (Denver Co.)	Late May–3 June: Denver	Reached Denver from Cheyenne, Wyoming, at 1900 hrs on 31 May. On 1 June collected butterflies along the South Platte River. On 3 June collected on the prairie southeast of Denver along Cherry Creek, a tributary of the South Platte River. On this date collected the lectotype of *Phyciodes emiss*a (=*Phyciodes pulchella camillus*) (see text).
5–7 June	Denver (Denver Co.) to Bradford Junction ("Turkey Creek Junction") (Jefferson Co.)	5–6 June: Turkey Creek Junction	Departed on the stage for Fairplay early in the morning on 5 June. Later that day collected butterflies in Turkey Creek Canyon along the Denver & South Park Road (mostly today's South Turkey Creek Road), reaching the "dinner station" (Bradford Junction) (Figs. 6, 7) at 1500 hrs. Collected 6.4 km (4 mi) along the Mt. Vernon Road (today's CR 73, north of Barkley Rd.) missing the stage and staying for two days. On 6 June started out at about 0700 hrs walking a round trip of 26 km (16 mi) northeast of Bradford Junction along the Denver & South Park Road (today's South Turkey Creek Rd. paralleling South Turkey Creek); collected the lectotype of *Argynnis meadii* (*Speyeria callippe meadii*) (see text). On 7 June walked 0.8 km (0.5 mi) along road collecting butterflies. Possibly collected this week the lectotype of *Anthocaris* [sic] *coloradensis* (=*Euchloe ausonides coloradensis*) (see text). Left Bradford Junction at 1330 hrs on 7 June and traveled all night by stage along the Denver & South Park Road 103 km (64 miles) towards Fairplay.
8–12 June	Fairplay vicinity (Park Co.)	10–12 June: Fairplay area	Reached Fairplay at 0500 hrs on 8 June. On 9, 10, and 12 June collected butterflies along nearby Beaver Creek. On 9 June also took a wagon to Buckskin Joe, a former mining town settled in 1859 northwest of Fairplay. On 10 June collected the lectotype of *Anthocaris* [sic] *julia* (=*Anthocharis sara julia*). On 11 June explored the woods on the south side of the Middle Fork South Platte River. On 12 June "went up Beaver Creek several miles" and collected the lectotype of *Pamphila* (=*Hesperia*) *nevada* (see text). Departed on the stage for Kenosha House and traveled all night along the Denver & South Park Road (today's I-285 corridor).
13–20 June	South Park area (Park Co.), including Kenosha House; Bradford Junction ("Turkey Creek Junction") (Jefferson Co.)	13–16 June: Fairplay area	After stopping to sleep along the way (probably at Hamilton, a mining camp northeast of Fairplay), departed at 0630 hrs on 13 June and traveled to Kenosha House (Figs. 4, 5), arriving at 1100 hrs. Traveled total of 45 km (28 mi) by stage. On 14 June explored along a brook that led to the "top of the mountains" where there was a lake (Hoosier Creek up to Lininger Lake). On 15 June walked along "a small rivulet," then along the Denver & South Park Road (today's I-285 corridor) towards South Park. On 16 June walked 4.8 km (3 mi) along the same road toward South Park and collected butterflies, including the lectotype of *Colias hagenii* (=*C. philodice eriphyle*) (Figs. 13, 14; see text). On 17 June walked "up" the same road and collected the lectotype of *Thecla ninus* (=*Callophrys spinetorum*). Departed for Bradford Junction on 20 June, arriving at 1030 hrs, traveling 61 km (38 mi) by stage.
21–28 June	Bradford Junction ("Turkey Creek Junction") (Jefferson Co.); Kenosha House (Park Co.)		On 21 June collected butterflies 3.2 km (2 mi) "down the road," probably southwest of Bradford Junction along the Denver & South Park Road (today's CR 73). On 22 June walked along the "gulch opposite the house" (probably the head of North Turkey Creek) collecting caterpillars. On 23 June collected "down the road," probably southwestward from Bradford Junction, about 2.4 km (1.5 mi). On 24 June walked northeastward along the Denver & South Park Road (today's South Turkey Creek Road) paralleling South Turkey Creek, possibly collecting the lectotype of *Lycaena daunia* (=*Glaucopsyche piasus daunia*) (see text). Collected along the same road on 25 June. On 26 June explored northward along the Mt. Vernon Wagon Road (now CR 73) and "branched up a small brook." On this walk collected the lectotype of *Phyciodes nycteis* var. *drusius* (=*Chlosyne nycteis drusius*) (see text). On 27 June walked 2.4 km (1.5 mi) along the Denver & South Park Road, possibly collecting several *Echinargus isola* (Reakirt), including a female that resulted in the description of *Lycaena alce*. Also walked along the Mt. Vernon Wagon Road. This week at Bradford Junction collected the syntypes of *Melitaea calydon* (=*Chlosyne palla calydon*) (see text). Departed for Kenosha House on 28 June, arriving at 12 midnight, traveling 61 km (38 mi) by stage

TABLE 1: Itinerary of T. L. Mead in Colorado (continued)

Date(s)	Location(s)	Proposed location(s) from Brown (1955a)	Details
29 June–5 July	Kenosha House, Fairplay (Park Co.)	2–5 July: Fairplay area	On 29–30 June collected butterflies "up the second large gulch on the right hand side of the creek" (probably Lininger Ditch from Hoosier Creek). On 2 July collected butterflies "up the gulch," probably up the creek just south of the house. On 3 July collected 4.8 km (3 mi) "down the gulch" (Hoosier Creek) and 1.6 km (1 mi) "down the road" (Denver & South Park Road). On 4 July collected the lectotypes of *Phyciodes camillus* (=*Phyciodes pulchella camillus*) (see text) and *Melitaea eurytion* (=*Euphydryas anicia eurytion*) (Figs. 16, 17; see text). Departed for Fairplay at 2300 hrs on 5 July.
6–8 July	Fairplay area (Park Co.) to Oro City (Lake Co.), including Mosquito Pass	6–7 July: Fairplay area; 8 July [Mosquito Pass]	Arrived at Fairplay at 0400 on 6 July, traveling 41.8 km (26 mi) overnight by stage on the Denver & South Park Road (today's I-285 corridor). On 6 July explored "up" Beaver Creek, where the lectotype of *Erebia rhodia* (=*Erebia epipsodea brucei*) was collected (see text). On this date possibly also collected the lectotype of *Argynnis eurynome* (=*Speyeria mormonia eurynome*). On 8 July left for Twin Lakes, following the Fairplay & California Gulch Wagon Road (today's State Hwy 9 to County Roads 12 and 3), crossing Mosquito Pass where the lectotypes of *Colias meadii* and *Erebia callias* were collected. Arrived at Oro City at about 1800 hrs. Oro City was a former gold mining town founded in 1860 on California Gulch near Leadville. Traveled 64 km (40 mi) by stage.
9 July	Oro City to Twin Lakes (Lake Co.)	Twin Lakes area	Departed for Twin Lakes at 0900 hrs and arrived at 1200 hrs. Traveled by stage 24 km (15 mi) along the wagon road paralleling the Arkansas River. Collected butterflies along the western side of Upper Twin Lake (the western lake) (Fig. 8). Possibly collected on this date the lectotypes of *Pamphila* (=*Polites*) *draco* and *Satyrus charon* (=*Cercyonis oetus charon*). It was proposed by Scott et al. (1998) that the lectotype of *Argynnis electa* (=*Speyeria hesperis* [*atlantis*?] *electa*) also originated from Twin Lakes.
10 July	Twin Lakes (Lake Co.), including peak south of the lakes (Chaffee Co.)	Twin Lakes area [La Plata Peak?]	On this date Mead ascended a peak, most likely just south of the lakes (see text) (Fig. 8). The lectotype of *Thymeticus* [sic] *hylax* (=*Oarisma garita* (Reakirt)) was probably collected on this date.
11 July	Twin Lakes (Lake Co.)	Twin Lakes area [La Plata Peak?]	Mead was stiff from the climb the day before and did not ascend any peaks. He collected in the vicinity of the lodging house (east side of the lakes) (Fig. 8) and walked about 4 km (2.5 mi) "up the road," probably towards Dayton (now the town of Twin Lakes) (Fig. 8). The lectotype of *Lycaena* (=*Plebejus*) *melissa* (Fig. 31) was collected on this date (see text).
12 July	Twin Lakes (Lake Co.), including peak south of the lakes (Chaffee Co.)	Twin Lakes area	Tried to walk up the mountain just SE of the peak climbed on 10 July (see text).
13 July	Twin Lakes (Lake Co.)	Twin Lakes area	Walked to "the head of the upper lake" (the northern shore of Upper Twin Lake) and collected the lectotypes of *Chrysophanus sirius* (=*Lycaena rubidus sirius*) (see text) and *Pamphila* (=*Hesperia*) *colorado* (Fig. 9) (see text).
14 July	Twin Lakes (Lake Co.)	Arkansas Valley	Walked over 9.7 km (6 mi) up Lake Creek, west of the lakes (Fig. 8). In total, walked 25.7 km (16 mi) along the road, which then did not continue beyond its intersection with Lake Creek, west of Dayton. This road is now State Hwy 82.
15–16 July	Twin Lakes (Lake Co.)	Probably Twin Lakes	Read and wrote letters; no field work.
17–18 July	Twin Lakes (Lake Co.)	"ascent of La Plata or Elbert may have been made at this time instead of 10–11;" 17 July: south of Kenosha House (Brown meant 17 June)	Did not ascend any mountains on these dates. On 17 July, collected around Dayton. On 18 July, walked about 1.9 km (1 mi) south of Twin Lakes, along the wagon road (now CR 30) leading to the town of Granite.

TABLE 1: Itinerary of T. L. Mead in Colorado (continued)

Date(s)	Location(s)	Proposed location(s) from Brown (1955a)	Details
19–20 July	Twin Lakes and California Gulch (Lake Co.)	July [15-20]—probably Twin Lakes until 17th	Left Twin Lakes on 19 July, traveling by stage on the wagon road 24 km (15 mi), to Oro City in the California Gulch. On 20 July "walked up the gulch and on the mountains" catching butterflies, possibly including the lectotype of *Argynnis helena* (*Boloria chariclea helena*) (see text).
21 July	California Gulch (Lake Co.) to Fairplay (Park Co.), including Mosquito Pass	Mosquito Pass	Left California Gulch "pretty early" and collected butterflies in the mountains along the Fairplay & California Gulch Wagon Road (today's County Roads 3 and 12 to State Hwy 9) across Mosquito Pass. Reached Fairplay about 1700 hrs, traveling 64.4 km (40 mi) by stage.
22 July	Fairplay to Mt. Lincoln and Montgomery City (Park Co.)	Mt. Lincoln	Traveled northward on horseback on the old wagon road paralleling the Middle Fork of the South Platte River (today's CR 9) to Montgomery City, a former gold mining town at the foot of Mt. Lincoln (most of the town now lies at the bottom of Montgomery Reservoir). Began ascent of Mt. Lincoln at about 1400 hrs, reaching summit at 1900 hrs. Returned to Montgomery City at about 2130 hrs.
23 July	Montgomery City (Park Co.)	Twin Lakes area	Read books nearly all day; no field work.
24 July	Montgomery City to Fairplay (Park Co.)	Twin Lakes area	Walked south to Fairplay, 19 km (12 mi), probably via the same route traveled northward on 22 July. Met the Allen expedition near Montgomery City.
25–27 July	Fairplay; Kenosha House to Bailey's Ranch (Park Co.)	Turkey Creek Junction; Denver	On 25 July took stage to Kenosha House (Figs. 4, 5). Collected butterflies in the vicinity on that day and the next. Departed Kenosha House at 1200 hrs on 27 July, traveling on horseback 33.8 km (21 mi) on the Denver & South Park Road to Bailey's Ranch, a stage stop and hotel built in 1864 by William N. Bailey (it later became the town of Bailey). Arrived at about 1750 hrs.
28 July	Bailey's Ranch (Park Co.) to Bradford Junction ("Turkey Creek Junction") (Jefferson Co.)	Turkey Creek Junction; Denver	Collected in the afternoon near Bailey's Ranch. Departed at 2000 hrs via the Denver & South Park Road, arriving at Bradford Junction at midnight after traveling 27.3 km (17 mi) on horseback.
29 July	Bradford Junction ("Turkey Creek Junction") (Jefferson Co.)	Denver	Local collecting "down the road," probably along the Denver & South Park Road (Fig. 7).
30 July	Bradford Junction ("Turkey Creek Junction") (Jefferson Co.) to Denver (Denver Co.)	Denver	Left Bradford Junction at 1000 hrs, traveling on horseback via the Denver & South Park Road, arriving at Denver at about 1630 hrs.
31 July–1 August	Denver (Denver Co.)	Apex Gulch	Made purchases around town; no field work.
2 August	Denver (Denver Co.) to Apex Gulch (Jefferson Co.)	[Apex Gulch]	Departed Denver on horseback ("Comanche") at about 1600 hrs, traveling 19.3 km (12 mi) to Apex Gulch. Brown (1955a) was unsure of the location of Apex Gulch, which was a stage stop and stream valley served by a wagon road west of Denver and south of Golden. A popular hiking and biking trail, Apex Trail, currently runs along a portion of the old Apex & Gregory Wagon Road, a toll road that led to the early mining camps of Central City. Heritage Square is located at the head of the gulch on the site of the former settlement of Apex.

TABLE 1: Itinerary of T. L. Mead in Colorado (continued)

Date(s)	Location(s)	Proposed location(s) from Brown (1955a)	Details
3 August	Apex Gulch and Wilson Junction (Jefferson Co.) to Idaho Springs (Clear Creek Co.)	Apex Gulch; Georgetown	Collected butterflies about 6.4 km (4 mi) west of Apex Gulch, along the Apex & Gregory Wagon Road. Stopped for lunch around 1500 hrs at Wilson Junction, a half-way house located between Denver and Georgetown, about 19.3 km (12 mi) east of Idaho Springs. Soon after continued westward to Idaho Springs on the Junction & Idaho Wagon Road (essentially following today's I-70 corridor), arriving at dark after traveling a total of 37 km (23 mi) on horseback ("Comanche").
4 August	Idaho Springs to Georgetown (Clear Creek Co.)		After lunch traveled from Idaho Springs to Georgetown, 22.5 km (14 mi) on horseback ("Comanche"), mostly on the Central City & Georgetown Wagon Road (today's I-70 corridor).
5 August	Georgetown (Clear Creek Co.) to Montezuma, and along the Snake River [Dillon] (Summit Co.)	Gray's Peak; also en route to Middle Park	Started early from Georgetown on horseback ("Comanche") on the Georgetown & Ten Mile Road, crossing the continental divide at Argentine Pass near Grays Peak (today's County Roads 381, 352 and 5). Although Mead ([1876] mentioned collecting a butterfly "on Gray's Peak," he does not document this in his journal or his letters, where he noted that he "escaped climbing the peak" (Brown & Brown 1996). He instead stated that he was "near" the peak and "close by Gray's Peak." All such specimens were collected at the base of the mountain below Argentine Pass, which is about 3658 m (12,000 ft.) in elevation. He also referred to "Gray's Peaks," a local term for the group of peaks in that area (Bowles 1869). Dined at Montezuma, a former mining camp established in 1865. Continued westward on the road (today's County Roads 5 and 4), stopping at a cabin along the Snake River, probably where the town of Dillon would later be established (now covered by the Dillon Reservoir). This is just southeast of the present town of Silverthorne. Travelled at total of 51.5 km (32 mi)
6–7 August	Middle Park, along Snake River [Dillon] (Summit Co.)	Middle Park	Collected locally near the present town of Silverthorne.
8 August	Middle Park, along Blue River north of Snake River (Summit Co.)	Along Blue River, Middle Park	Left camp at about 1100 hrs, traveling north on horseback ("Comanche") about 19.3 km (12 mi) along a trail paralleling the Blue River (probably today's State Hwy 9). Camped in "a little park" (grassy clearing).
9 August	Middle Park, along Blue River north of Snake River (Summit Co.)	Along Blue River, Middle Park	Started early heading north on the trail along the Blue River, traveling about 19.3 km (12 mi) before lunch. During afternoon stopped to camp about 8 km (5 mi) after crossing Blue River, probably on the east side of today's Green Mountain Reservoir. Traveled total of 40.2 km (25 mi) on horseback ("Comanche").
10 August	Middle Park, fork of Blue and Colorado Rivers (Grand Co.)	Middle Park	Rode on horseback ("Comanche") along the trail for 19.3 km (12 mi) and camped "near the mouth of the Blue River on the Grand in a wide grassy plain" (just south of where the town of Kremmling is now located). That portion of the Colorado River above the confluence with the Green River in Utah was then known as the Grand River.

TABLE 1: Itinerary of T. L. Mead in Colorado (continued)

Date(s)	Location(s)	Proposed location(s) from Brown (1955a)	Details
11 August	Middle Park, along Colorado River from Blue River to Williams Fork (Grand Co.)	Middle Park	Started out at about 1100 hrs, riding "very slowly" along the Grand (Colorado) River to Williams Fork (Williams River), which is a tributary of the Colorado River west of Hot Sulphur Springs. Stopped to camp for the night, apparently near the current town of Parshall. Traveled 17.7 km (11 mi) on horseback ("Comanche"), basically following the route of present-day U.S. Hwy 40.
12 August	Middle Park at Williams Fork (Grand Co.)	Middle Park	Briefly collected butterflies locally.
13 August	Middle Park at Williams Fork to Hot Sulphur Springs (Grand Co.)	Middle Park	Rode on horseback ("Comanche") about 2.4 km (1.5 mi) up Williams Fork to fish, and then continued on to Hot Sulphur Springs, 9.7 km (6 mi).
14 August	Hot Sulphur Springs (Grand Co.)	Hot Sulphur Springs	Walked towards the "Agate Patch" while collecting butterflies. This presumably refers to a large agate field located south of the Colorado River, west of Williams Fork, on a high sage plain.
15 August	Hot Sulphur Springs and east/southeast (Grand Co.)		Departed early from Hot Sulphur Springs, riding on horseback ("Comanche") southeast along the trail and wagon road (today's County Road 55 and U.S. Hwy 40 corridor) for 38.6 km (24 mi). Stopped for the night at a cabin, probably south of the town of Fraser.
16 August	Southeast of Hot Sulphur Springs (Grand Co.) to Georgetown (Clear Creek Co.), including Berthoud Pass	Near Berthoud Pass	Left camp early, possibly traveling southward along Hoop Creek on the Empire & Middle Park Wagon Road (east of today's U.S. Hwy 40), reaching Berthoud Pass at about 1400 hrs. Before reaching the pass collected butterflies, including the lectotype of *Grapta hylas* (=*Polygonia faunus hylas*) (see text). Continued on to Georgetown via the Central City & Georgetown Wagon Road (U.S. Hwy 40 and I-70 corridors), arriving at about 1930 hrs. Traveled 38.6 km (24 mi) on horseback ("Comanche").
17 August	Georgetown (Clear Creek Co.)		Stayed indoors all day; no field work.
18 August	Georgetown to Idaho Springs (Clear Creek Co.)		Visited the Burleigh Tunnel near Georgetown, and then traveled the Central City & Georgetown Wagon Road (today's I-70 corridor) to Idaho Springs, 24 km (15 mi) on horseback ("Comanche").
19 August	Idaho Springs (Clear Creek Co.) to Apex Gulch (Jefferson Co.)	Idaho Springs	Departed Idaho Springs "pretty early," collecting butterflies along the way. Probably near Idaho Springs captured the holotype of *Hesperia dacotah* (=*Polites mystic dacotah*) and the neotype of *Hesperia napa* (=*Ochlodes sylvanoides napa*) (see text). Dined at Wilson Junction (see 3 August) before reaching Apex Gulch. Traveled 37 km (23 mi) on horseback ("Comanche"), mostly following the Junction & Idaho Wagon Road (today's I-70 corridor) and the Apex & Gregory Wagon Road.
20 August	Apex Gulch (Jefferson Co.) to Denver (Denver Co.)	Near Denver	Left Apex Gulch at 0830 hrs and arrived at Denver at 1130 hrs, riding 22.5 km (14 mi) on horseback ("Comanche").
21–22 August	Denver (Denver Co.)		Spent time in Denver and apparently did not collect butterflies on these dates.

TABLE 1: Itinerary of T. L. Mead in Colorado (continued)

Date(s)	Location(s)	Proposed location(s) from Brown (1955a)	Details
23 August	Denver (Denver Co.) to Reed's Mills (Jefferson Co.)		Departed Denver at about 1100 hrs and stopped for the night at Reed's Mills (Reed Mill), a stage stop between Denver and Bradford Junction along the Denver & South Park Road (today's South Turkey Creek Road). Traveled 38.6 km (24 mi) on horseback ("Comanche").
24 August	Reed's Mills (Jefferson Co.) to Bailey's Ranch (Park Co.)		Rode the Denver & South Park Road from Reed's Mills to Bradford Junction (Figs. 6, 7), dined, and then continued on to Bailey's Ranch (see 25–27 July), arriving after 2100 hrs. Traveled 35.4 km (22 mi) on horseback ("Comanche").
25 August	Bailey's Ranch (Park Co.)		Walked about 6.4 km (4 mi) roundtrip collecting butterflies, probably along the North Fork South Platte River.
26 August	Bailey's Ranch to Kenosha House (Park Co.)	Bailey's Ranch	Collected in the vicinity of Bailey's Ranch, where the lectotype of *Satyrus meadii* (=*Cercyonis meadii*) was captured. Departed about 12 noon, following the Denver & South Park Road to Kenosha House (Figs. 4, 5), collecting along the way. Traveled 33.8 km (21 mi) on horseback ("Comanche").
27 August	Kenosha House (Park Co.)		Collected butterflies locally.
28 August	Kenosha House to Slaght's House (Park Co.)	20 miles from South Park on South Park Road	Walked 13 km (8 mi) northeast from Kenosha House along the Denver & South Park Road and dined at the home of Charles Hepburn (1813-?), who operated a stage station that was described as "quiet and homelike" (Anonymous 1870). Walked the same road another 13 km (8 mi) east to the home of Azel Slaght (1825–1902), who operated a stage stop that later became the town of Shawnee. Stayed the night there.
29 August	Slaght's House to Bailey's Ranch (Park Co.)	Kenosha House	After breakfast departed Slaght's and walked 8 km (5 mi) along the road to Bailey's Ranch (see 25–27 July) while collecting butterflies.
30 August	Bailey's Ranch (Park Co.)	South Park Road, east of Fairplay	Collected butterflies locally.
31 August	Bailey's Ranch area (Park Co.)		Walked southeast along the North Fork South Platte River collecting butterflies
1 September	Bailey's Ranch area (Park Co.)		Walked southeast and northwest along the North Fork South Platte River collecting butterflies. Departed on the stage for Kenosha House, arriving at 12 midnight, traveling 33.8 km (21 mi).
2 September	Kenosha House (Park Co.)		Did not feel well; no field work.
3–11 September	Kenosha House (Park Co.)	10 September: South Park	Explored locally, but rain during the period hindered field work. On 10 September walked "down the gulch," probably Hoosier Creek valley (Fig. 5), about 1.6 km (1 mi) to collect Diptera. Sold his horse ("Comanche") and left Kenosha House late on 11 September.

TABLE 1: Itinerary of T. L. Mead in Colorado (continued)

Date(s)	Location(s)	Proposed location(s) from Brown (1955a)	Details
12 September	Hamilton to Fairplay and Hartsel Ranch (Park Co.)		At about 0500 hrs reached Hamilton. Continued to Fairplay and ate breakfast. Traveled 45 km (28 mi) by stage to Fairplay. Took stage and stopped for the night at Hartsel Ranch (Station 39), which was located south of Fairplay along the Fairplay & Cañon City Road (today's State Hwy 9 and County Road 59). Owned by Samuel Hartsel (1834–1918), a pioneer cattleman from Pennsylvania, the ranch became the town of Hartsel. Traveled total of 66 km (41 mi) by stage since leaving Kenosha House.
13 September	Hartsel Ranch (Park Co.)		Did not feel well; no field work
14 September	Hartsel Ranch towards Florissant (Park Co.)		Left Hartsel Ranch heading southeast on the road towards Florissant (today's U.S. Hwy 24). Stopped after traveling 14.5 km (9 mi) on horseback, probably north of Sulphur Mountain.
15–17 September	Florissant (Teller Co.)		Arrived early in the evening of 15 September at the ranch of James Castello, traveling 33.8 km (21 mi) "through wood & dell dingle & gulch" on horseback. Castello (1814–1878) opened a trading post with his son in 1870 near the confluence of East Twin Creek and West Twin Creek (just north of today's U.S. Hwy 24). Castello later changed the name of the settlement from Twin Creek to Florissant. On 15 September visited local shale beds. On 16 and 17 September walked and rode to the shale beds and petrified tree stumps.
18–19 September	Florissant (Teller Co.) to Colorado City (El Paso Co.)		On 18 September rode on horseback to petrified stumps to the south, after which he rode 37 km (23 mi) south on the road (now U.S. Hwy 24) to "Litts' Ranch," where he stayed the night. This possibly refers to Cornelius Litts (1841–?), a farmer from New York. Based on Mead's mileage estimate, the ranch was located near Colorado City, which is now known as Old Colorado City, part of Colorado Springs. On 19 September walked and rode 16 km (10 mi) "all around a mountain" and "ahead down the road."
20 September	Colorado City (El Paso Co.) to Cañon City (Freemont Co.)	Near Cañon City	Took the stage to Cañon City, traveling the Colorado City & Cañon City Road (today's State Hwy 119 and County Road 132) 63 km (39 mi). This is the last location listed by Brown (1955a).
21 September	West of Cañon City, up the Arkansas River (Freemont Co.)		In the morning went up the Arkansas River west of Cañon City to collect butterflies. This is the last date in Mead's journal when he specifically mentions collecting butterflies in Colorado.
22 September	Cañon City (Freemont Co.) to Pueblo (Pueblo Co.)		Took the Cañon City to Pueblo Stageline (today's U.S. Hwy 50 corridor) to Pueblo, arriving at about 1700 hrs. Traveled 72.4 km (45 mi).
23 September	Pueblo (Pueblo Co.) to Colorado City (El Paso Co.)		Rode the stage 72.4 km (45 mi) to Colorado City along the stage line paralleling Fountain Creek, leaving at 1400 hrs and arriving at 2100 hrs.
24 September	Colorado City (El Paso Co.) toward Denver (Denver Co.)		Visited local tourist attractions near Colorado Springs (Garden of the Gods and Punch Bowl) and then took overnight stage for Denver (following today's I-25 corridor and U.S. Hwy 85). Traveled 120 km (75 mi).
25–26 September	Denver (Denver Co.)		Arrived at Denver at 1100 hrs on 25 September and stayed in town the next day.
27 September	Denver (Denver Co.) to Cheyenne, Wyoming		Departed Denver via Denver Pacific Railway at 0730 hrs, arriving in Cheyenne at 12 noon. Continued after lunch to Ogden, Utah via the Union Pacific Railroad. Traveled 1061 km (659 mi) by rail.

Barkley Road intersects County Road 73 within the town of Conifer. Bradford Junction was the basis of Conifer (Donovan 1995), though current maps erroneously suggest that Conifer is a small community south of Aspen Park along US Hwy 285. In reality, Aspen Park is merely a developed area within Conifer, not a separate town. The historic Yellow Barn now stands at the former site of Bradford Junction (Bentley 1985, Donovan 1995, Hood 2011).

Among several buildings at Bradford Junction was the large two-story Junction House, which offered food and lodging, though, according to Mead, some of its beds were infested with bedbugs: "[A]t night it entirely ceases to be a labor of love and becomes something quite different" (he pinned six bedbugs to his pillow one night) (Brown & Brown 1996). The house stood just southeast of the present-day Yellow Barn. A covered well, dug in 1862 and still present on the property, is visible in the middle of the road in front of the Junction House in a photograph taken ca. 1875 (Fig. 6). The surroundings were described as "very interesting, the forest delightful, the shrubbery voluptuous with foliage and flowers, the way often bordered with wild roses, perfuming the cool, bracing air" (Anonymous 1868). The house burned in 1878 and was rebuilt about five years later using a different design (Hood 2011).

The Junction House served as Mead's base of operations when he explored the region, which he generally referred to as "Turkey Creek." Upon his first arrival at Bradford Junction on 5 June, Mead called it "the dinner station," as he did not intend to spend any time there. He walked ahead along the wrong road while collecting butterflies and missed the stage, stranding himself for two days until the stage returned. This was a very fortuitous event, as his success collecting there prompted him to revisit the area two more times, leading to the discovery of several new butterfly taxa. Mead hunted butterflies as far as 6.4 km (4 mi) northward along the Mt. Vernon Wagon Road (today's CR 73) and 12.9 km (8 mi) northeastward along the Denver & South Park Road (today's South Turkey Creek Road), paralleling South Turkey Creek (then known as Turkey Creek). He also explored along the gulch "opposite the house," which is the head of North Turkey Creek (Shadow Mountain Drive now parallels the creek where an older road once existed). Also at Bradford Junction was a post office, from which Mead sent letters and specimens during his trip.

It is significant that I have found no other allusions to the name "Turkey Creek Junction" beyond those of Mead. The place names directory of the Jefferson County Historical Commission (Jeffco 2013) has no listing for this name, nor does the state historical society, History Colorado. Members of the local Conifer Historical Society are also unfamiliar with this name. The settlement was identified as "Junction" on period maps and stage schedules (Fig. 7). The most reasonable explanation is that Mead added the appellation "Turkey Creek" to geographically restrict his references (i.e. Junction within Turkey Creek Canyon) to prevent its confusion with other stage stops in Colorado also known as "Junctions." When citing Mead's data, it is more geographically accurate to refer to this locality as Bradford Junction.

Gannett (1877) recorded the elevation of Junction House as 2485 m (8153 ft.), but it is actually closer to 2454 m (8050 ft.). GPS: 39.534153, -105.309489 (Junction House). This area serves as the type locality of the nominal taxa *Anthocaris* [sic] *coloradensis* H. Edwards, *Lycaena daunia* W. H. Edwards, *Phyciodes nycteis* var. *drusius* W. H. Edwards, and *Melitaea calydon* Holland. The original type (now lost) of *Lycaena alce* W. H. Edwards was also from this vicinity.

Twin Lakes. A region with two large glacial lakes south of Leadville, Lake County (Fig. 8). Now a reservoir, the lakes were described in 1870 as "about two miles in width, and five miles in length, separated by a strip of forest land, about one-fourth mile in breadth" (Wallihan & Bigney 1870). Immediately surrounding the lakes were "clear, hard, sandy beaches," alternating with "walls of rock and low marshy meadows" (Bowles 1869). The western lake is known as Upper Twin Lake, while the eastern lake is Lower Twin Lake. Damming the lower lake during the late 19th century raised water levels by as much as 4.6 m (15 ft.), obliterating a large portion of the vegetation that grew around the lakes when Mead visited (Noel & Fielder 2001).

Mead's journal entries and mileage estimates indicate that he lodged in a "house" on the east side of Lower Twin Lake, west of the Arkansas River. Described as a "roadside ranch" by Mead, the lodging house was most likely owned by Samuel M. Derry (c. 1817–?), who also operated a hotel in the former community of Dayton (now Twin Lakes). Derry claimed ownership of much of the land surrounding the lakes (Anonymous 1908, Jackson & Driggs 1929) and Mead mentioned in his journal on 9 July that his brother went fishing for trout with "Mr. Derry." Mead remarked that his nearest neighbors at Twin Lakes were six miles away by road (Brown & Brown 1996), which presumably refers to Dayton, located about 9.7 km (6 mi) by road west of the point where Lake Creek crossed the old wagon road on the east side of Lower Twin Lake (Fig. 8). Mead explored much of the area around the lakes, including over 9.7 km (6 mi) westward along Lake Creek (west of the lakes) and southward about 1.6 km (1 mi) along the

road leading to the town of Granite, southeast of the lakes.

Mead also reached the peak of a mountain at an elevation of 1219–1524 m (4000–5000 ft.) "above [the level of] the lakes." Brown (1955a) suggested this was La Plata Peak, or possibly Mt. Elbert. Brown and Brown (1996) later proposed Quail Mountain. However, Mead's written comments suggest that he ascended an unnamed lower peak northeast of Quail Mountain, just south of the lakes. Without taking provisions, he started out on 10 July to simply "look around," but "walked a long distance up a gulch and finally concluded to go to the top of a peak," returning at "about suppertime." He most likely walked up Flume Creek, reaching an elevation of about 3840 m (12,600 ft.) (Fig. 8). Two days later, Mead and his brother unsuccessfully attempted to climb a steep peak "not quite so high" located just southeast of the first peak.

Elevation of the lakes approx. 2804 m (9200 ft.). GPS: 39.077576, -106.291290 (vicinity of Mead's likely lodging site). This area serves as the type locality of the nominal taxa *Thymeticus* [sic] *hylax* W. H. Edwards, *Hesperia colorado* Scudder, *Pamphila draco* W. H. Edwards, *Chrysophanus sirius* W. H. Edwards, *Lycaena melissa* W. H. Edwards, *Argynnis electa* W. H. Edwards, and *Satyrus charon* W. H. Edwards.

Type localities. Most of the Colorado specimens in Mead's collection were contained in field envelopes and it appears that they were purchased in this condition by W. J. Holland (Brown 1964, 1970). When these specimens were later mounted by Holland, that portion of Mead's envelope with his handwritten date was clipped out and affixed to the pin. Many of the specimens from Mead's collection at CMNH bear such clippings and this information is extremely valuable in determining collecting localities. Samuel H. Scudder also received Mead's butterflies in papers and, like Holland, affixed a portion of Mead's envelope onto the mounted specimens. Some of Mead's specimens at CMNH and MCZ possess small identification labels in Mead's hand (Fig. 17), suggesting they were already mounted when they were acquired by Holland and Scudder. "Generally I write my labels as printed ones are not always to be had," Mead remarked in August 1871 (Brown & Brown 1996).

Twenty-eight taxa of butterflies were described from specimens that Mead collected in Colorado in 1871. One additional taxon is represented by a neotype that was collected by Mead. Nineteen of these nominal taxa possess incorrect or imprecise type localities that were suggested by previous authors. Presented below are clarifications of these type localities based on Mead's whereabouts in accordance with Article 76 of ICZN (1999), including Recommendation 76A. Current nomenclature follows Pelham (2014).

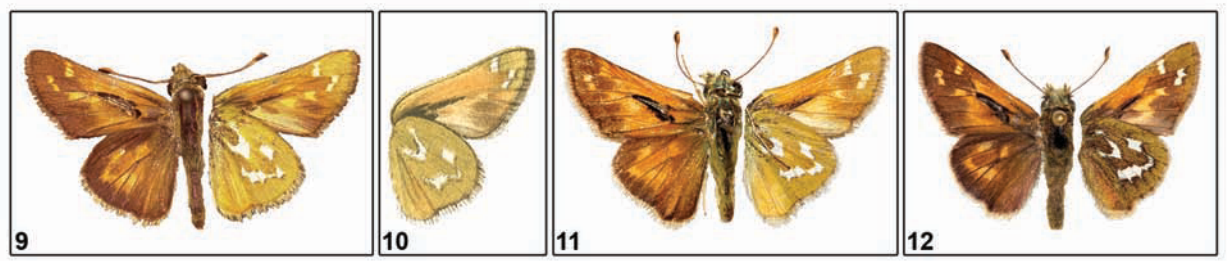
Pamphila colorado Scudder, 1874

(=*Hesperia colorado*; Hesperiidae)

Described from "Colorado, about the Georgetown and South Park Roads [Clear Creek and Park Cos.]," which Mead ([1876]) reiterated. The lectotype (MCZ) (Fig. 9) designated by Barnes and McDunnough (1916) is labeled "Colorado." Scott (1998) suggested a type locality of "Tennessee pass, 3150 m (=10300 feet), Lake–Eagle Cos. Colorado." Andrew D. Warren proposed Guanella Pass (Park/Clear Creek Cos.) (Pelham 2008), but maps do not show a trail through that area during the 1870s. Scott (2008b, 2008c) stated "evidently Kenosha Pass [Park Co.] or Guanella Pass [Clear Creek Co.], Colo."

Affixed to the lectotype is a portion of Mead's original field envelope with the penciled date of "7–13." This specimen was figured by Scudder (1874, Pl. 10, fig. 18) as "collected July 13, by T. L. Mead." A damaged male paralectotype at MCZ with the same date as the lectotype, was dissected and figured by Scudder (1874, Pl. 11, figs. 10, 11). Other butterflies at MCZ that Mead collected during mid-July 1871 bear dates written in his hand in either pencil or ink using the same format. Scudder (1874, Pl. 10, figs. 16, 17) also figured as *colorado* two females collected by Mead, one of which is dated 28 August. All these specimens were possibly papered duplicates that Scudder obtained when he visited Edwards' home in December 1873. Most of Mead's specimens of *Hesperia* from Colorado were examined by Scudder, who identified some as *Pamphila manitoba* (=*Hesperia comma manitoba* (Scudder)) (Scudder 1874). This undoubtedly prompted Mead ([1876]) to apply this name to two of his specimens, which represent high-elevation phenotypes of the Front Range subspecies *Hesperia colorado ochracea* Lindsey.

On 13 July 1871 Mead was at Twin Lakes, where he walked "up to the head of the upper lake" to collect butterflies. All the material from Twin Lakes was mailed to Edwards from Oro City on 20 July 1871. The female specimen that Mead captured on 28 August was taken along the Denver & South Park Road northeast of Kenosha House in northern Park County (Table 1), probably at an elevation of about 2621 m (8600 ft.). Mead ([1876]) mentioned collecting *colorado* along this road "during the latter part of August." Although the peak flight period of this butterfly is mid-August to early September, adults can emerge much earlier, especially during unusual conditions. Precipitation in Colorado during the spring of 1871 was below modern norms (Mock 1991). In fact, much of the United States was



Figs. 9–12. *Hesperia* specimens. **9**, lectotype of *Pamphila colorado* (male, dorsal/ventral) (MCZ-ENT0015299). **10,** ventral figure of lectotype from Scudder (1874) (image reversed). **11,** holotype of *Hesperia* comma *oroplata* (male, dorsal/ventral), Spring Creek, Fremont Co., CO (LACM). **12**, higher-elevation phenotype of H. *colorado* (male, dorsal/ventral), 3505 m/11,500 ft., Hoosier Pass, Park Co., CO (MGCL).

already suffering drought conditions by early spring. One of the worst natural disasters in history took place during October 1871 when fire storms swept across the Great Lakes region, causing the Great Chicago Fire (van den Dool 2012). Other captures by Mead in 1871 suggest that some other butterfly flight periods were advanced (see *C. hagenii* and *A. helena*, below).

To identify the lectotype (MCZ-ENT00015299) as the primary type of *colorado*, a red printed and handwritten label was affixed to its pin, which reads, "LECTOTYPE / *Pamphila colorado* / Scudder, 1874 / per Barnes & McDunnough (1916) / John V. Calhoun, 2013."

Type locality. As defined by the lectotype, the type locality is restricted to Twin Lakes, along the northern shore of Upper Twin Lake (the western lake), Lake County, Colorado.

Discussion. Skinner and Williams (1924) observed that "Individuals from high altitudes are darker green below than the type." Referring to Scudder's (1874) figure of the lectotype, Lindsey (1942) suspected that it "may very well be true *colorado*." Indeed, the lectotype (Fig. 9) and paralectotype from Twin Lakes are more brightly colored than higher-elevation butterflies (Fig. 12), which have long been considered to represent nominotypical *colorado*. Many authors, including MacNeill (1975), Stanford (1981), and Tilden and Smith (1986), considered nominotypical *colorado* to denote high-elevation populations of small dark butterflies. The lectotype, however, is more evocative of butterflies that are currently recognized as the subspecies *Hesperia colorado oroplata* (Fig. 11), described as *H. comma oroplata* by Scott (1981) to define more brightly-colored lower-elevation populations "from the Arkansas River Valley south of Buena Vista to the Royal Gorge, south to the Sangre de Cristo Mts. of New Mexico, and the San Luis Valley of Colorado." Unfortunately, Scott did not attempt to locate type specimens of *Pamphila colorado* (Scott 1998).

To establish a baseline of comparison from which to differentiate *oroplata*, and to prevent the use of the name *colorado* for populations at lower elevations, Scott (1998) suggested Tennessee Pass (3170 m/10,400 ft.) as the type locality of *colorado*, despite a lack of evidence that Mead had collected there. Without further explanation, Scott (2008b, 2008c) later revised the type locality to "evidently Kenosha Pass or Guanella Pass," which are 3048 m (10,000 ft.) and 3557 m (11,670 ft.), respectively. Scott (1998) considered "true" *colorado* to occur "at high altitude in Colorado in mountains along the continental divide . . . from about 10,000 feet upward," adding that "the darkest populations are at the highest altitudes of up to 12,400 feet or more." As an example of this taxon, Scott (1998, fig. 15) figured a male from Loveland Pass, Summit Co., Colorado, 3779.5 m (12,400 ft.) in elevation. Although this approach reflected the popular concept of this taxon, it is not supported by the lectotype. Thanks to Mead's journal, we can now establish with certainty that the lectotype of *colorado* was collected at a lower elevation.

The primary character used by Scott (1981) to distinguish *oroplata* was the "lighter yellowish rather than greenish brown" coloration of the ventral hindwings (Scott 1981). Additional cited attributes were "slight differences in genitalia, antenna length, number of micropyle spines & developmental period." This analysis, however, was based on the notion that *colorado* is restricted to higher elevations; populations that Scott (1975a, 1975b, 1986) considered to be genetically discrete. Scott's interpretation of *colorado* is inconsistent with the lectotype, which agrees with the original description of *oroplata* in that the ventral hindwings are "lighter yellowish," not greenish brown like those from higher elevations (Figs. 9, 11, 12). Scudder's (1874) figure of the lectotype faithfully portrays its more brightly-colored ventral hindwings (Fig. 10). Moreover, Scott (2006b) remarked that *colorado* is "evidently biennial like other alpine butterflies." This differs from *oroplata* and populations of "true" *colorado*, both of which are annually-brooded. Forewing lengths (base to apex) of the holotype of *oroplata* and the lectotype of *colorado* measure 15.0 and 14.4 mm, respectively.

The lectotype of *colorado* was collected at an elevation of roughly 2819 m (9250 ft.), within an area that Scott (1975) identified as a transition zone between *oroplata* and higher-elevation populations, which he and other authors attributed to nominotypical *colorado*. Fifty-six specimens that Scott collected within this area are deposited at MGCL (ex. W. W. McGuire colln.). They were captured 2.6 km (1.6 mi) north of the town of Granite, Chaffee County (2774 m/9100 ft.), and at Mt. Massive Trout Club, Lake County (2856 m/9400 ft.). These populations occur within 9.7 km (6 mi) of the type locality and represent typical *colorado* as defined by the lectotype. Any perceived differences between these populations and those within the range of *oroplata* are subtle at best. They form a smooth gradual cline, with populations at lower elevations producing slightly larger and tawnier adults with somewhat reduced dark maculation. Because the primary criteria that were originally used to differentiate *oroplata* also extend to the nominotypical subspecies, all these populations should be considered to represent H. c. *colorado*. As a result, the dusky biennial populations at higher elevations in Colorado require a new name (Warren & Calhoun 2015).

The female that Mead collected on 28 August, which was figured by Scudder (1874, Pl. 10, fig. 17), is applicable to *H. c. ochracea*. The second female figured as *colorado* by Scudder (1874, Pl. 10, fig. 16) actually represents *Hesperia nevada* (Scudder).

***Pamphila nevada* Scudder, 1874**

(=*Hesperia nevada*; Hesperiidae)

In addition to specimens from Nevada, California and Oregon, this species was described from "Colorado . . . on the mountains about the South park and in the Park itself [Park Co.]," which Mead ([1876]) reiterated. Barnes and McDunnough (1916) designated one of Mead's specimens as the lectotype and defined the type locality as "S. Park, Colo." Affixed to the lectotype (MCZ) is a portion of Mead's original field envelope dated "June 12." This specimen was figured by Scudder (1874, Pl. 10, fig. 1) as "collected June 12, by T. L. Mead." Scudder (1874, Pl. 10, figs. 3, 4) also figured male and female paralectotypes, dated 17 June and 23 June, respectively. A male paralectotype at CMNH was collected by Mead on 16 June (it is from Mead's collection, but Scudder examined all of Mead's *Hesperia* prior to describing this species). Colorado specimens of *nevada* from Scudder's collection were possibly papered duplicates that he obtained from Edwards in 1873.

Another male paralectotype at MCZ bears a portion of Mead's field envelope dated "6/17." Its claspers were figured by Scudder (1874, Pl. 11, figs. 3, 4), who stated that the specimen was "collected June 17, by T. L. Mead." This specimen also bears a second clipping from Mead's envelope reading "Mr. B." Mead's journal entry for that date indicates that Samuel M. Blair collected 70 butterflies. Blair (1842–1932), a miner and relative of the proprietor of Kenosha House, assisted Mead and W. H. Edwards in collecting and rearing butterflies from the area. "Mr. Blair is, I think, to be trusted to take good care of the insects and to collect more," Mead reported in July 1871 (Brown & Brown 1996). Mead initially took ownership of Blair's butterflies, but Blair later accepted an offer from Edwards to collect specimens in exchange for parts of his butterfly book. Blair's specimens were thereafter considered to be Edwards' property, though Mead saw this as an unfair arrangement, especially since he physically managed Blair's activities in Colorado. Mead eventually became dissatisfied with Blair, complaining that he lacked "that extreme accuracy necessary for scientific observations" (Brown & Brown 1996).

On 12 June 1871, Mead collected several miles up Beaver Creek near Fairplay (Table 1). On 16 and 17 June, he walked south from Kenosha House along the Denver & South Park Road. On 23 June, he collected along the same road just southwest of Bradford Junction (Table 1). Mead mailed the lectotype specimen to Edwards from Bradford Junction on 20 June 1871.

To identify the lectotype specimen (MCZ-ENT00015299) as the primary type of *nevada*, a red printed and handwritten label was affixed to its pin, which reads, "LECTOTYPE / *Pamphila nevada* / Scudder 1874 / per Barnes & McDunnough (1916) / John V. Calhoun, 2013."

Type locality. As defined by the lectotype, the type locality is restricted to along Beaver Creek, east/northeast of Fairplay, Park County, Colorado.

***Hesperia dacotah* W. H. Edwards, 1871**

(=*Polites mystic dacotah*; Hesperiidae)

Described from a single male collected by Mead in "Colorado," which Brown and Miller (1980) defined as "Georgetown, Clear Creek County, Colorado." Scott (2008b) suggested "Georgetown or eastward toward Idaho Springs." Although the holotype (CMNH) does not possess a date, it bears an identification label of W. H. Edwards reading "*napa* ♂= *dacotah*."

Soon after describing *dacotah*, Edwards (1872) questioned its recognition and concluded it was synonymous with the species he had previously described as *Hesperia napa* (=*Ochlodes sylvanoides napa*). Based on this treatment, Mead ([1876]) did not

separately list any records of *dacotah* from Colorado, nor did Edwards ([1876]) list it among the species recorded by the Wheeler Survey. These taxa were not again recognized as different species until Barnes & McDunnough (1916) treated *dacotah* as a variety of *P. mystic*.

Regarding *napa* (which was then considered to include *dacotah*), Mead ([1876]) stated that he "found a few specimens in August near Georgetown." One of Mead's specimens of *napa* at CMNH is dated "Aug 19" (see below). On 19 August, Mead was traveling from Idaho Springs — where he had arrived the previous day from Georgetown — to Apex Gulch (Table 1). Mead ([1876]) also mentioned the capture of another species at Idaho Springs on 19 August. These specimens were mailed to Edwards from Denver on 22 August 1871.

Type locality. Restricted to the vicinity of Idaho Springs, Clear Creek County, Colorado.

***Hesperia napa* W. H. Edwards, 1865**

(=*Ochlodes sylvanoides napa*; Hesperiidae)

Described from specimens collected in 1864 by James Ridings at "Empire City [Clear Creek Co.], Colorado Territory." One of Mead's specimens (CMNH) was designated as the neotype by Brown and Miller (1980), who implied the type locality to be "the vicinity of Georgetown, Clear Creek County, Colorado." However, Miller and Brown (1981) and Pelham (2008, 2014) reiterated the type locality as "Empire City, Colorado," and "Empire in Clear Creek County, Colorado," respectively. Mead ([1876]) stated that he "found a few specimens in August near Georgetown."

Affixed to one of Mead's specimens of *napa* from the Edwards collection (CMNH) is a portion of his original field envelope, which reads "*Hesperia* A / Aug 19." In a letter to Edwards, Mead mentioned taking "Hesp A" on 19 August at Idaho Springs (Brown & Brown 1996). On 19 August, Mead was traveling from Idaho Springs to Apex Gulch (Table 1). These specimens were mailed to Edwards from Denver on 22 August 1871.

Type locality. Restricted to the vicinity of Idaho Springs, Clear Creek County, Colorado.

Anthocaris [sic] ***coloradensis* H. Edwards, 1881**

(=*Euchloe ausonides coloradensis*; Pieridae)

Described as a possible new species from "Colorado," which Opler (1966) defined as "Turkey Creek Junction, Jefferson County, Colorado." This type locality was proposed on the advice of F. Martin Brown, who examined the male syntype and concluded that it is "without doubt one sent to Henry Edwards by W. H. Edwards from the material collected by T. L. Mead in 1871." Mead wrote of finding early stages of this species at Turkey Creek Junction in June 1871 (Edwards 1874). He later told H. Edwards, "only one of my [larval] specimens gave imago and it proved to be Ausonides . . ." (4.iv.1874, AMNH).

Two specimens (male and female) from H. Edwards' collection, acquired by AMNH in 1892, possess his handwritten labels identifying them as "types" of *coloradensis*. The male syntype was designated as the lectotype by Johnson (1976). Henry Edwards received one of Mead's specimens of this butterfly from W. H. Edwards in early July 1871. In the accompanying letter, W. H. Edwards asked if "*Anthocaris* 1" was *ausonides*; in agreement, H. Edwards scrawled that name on the page (8–9.vii.1871, AMNH). It could be assumed that it was this specimen to which Edwards (1881) referred when he wrote, "I have long had in my possession a ♂ example of *Anthocaris*, which appears to be distinct from any known form, but I hesitated to describe it until more material might present itself." However, Mead sent at least two additional Colorado specimens of *ausonides* to Edwards in 1872 (19.vi.1872, RC, AMNH). Edwards (1881) did not attribute the male type specimen to Mead and only casually mentioned that Mead's collection also contained this species. Henry Edwards evidently did not recall where he had obtained the male type specimen, which was received years before he described *coloradensis*. He exchanged hundreds, if not thousands, of butterflies after 1871 and it is possible that the specimen he mentioned in the original description was received from another correspondent at a later date.

Edwards' collection catalog at AMNH does not list any specimens by the name *coloradensis*. Entry no. 14 lists "*Anthocaris ausonides*" from California. Although Opler (1966) indicated that the lectotype of *coloradensis* was labeled "14," no such label or notation is currently affixed to the specimen. Possibly referring to the two *coloradensis* that Mead sent in 1872, entry no. 4277 lists an "*Anthocaris*" collected by Mead during June in "Rocky Mts. Col."

According to Edwards (1881), the female paralectotype was received from the physician James S. Bailey (1830–1883) of Albany, New York (Curtis 1884). Not only did Edwards correspond with Bailey, he visited Bailey's home and wrote his obituary (Edwards 1883). One of Bailey's sons, Theodore P. Bailey, also collected Lepidoptera. The elder Bailey provided Colorado Lepidoptera to several other contemporary entomologists, including Augustus R. Grote, who described new taxa from his moth specimens. Bailey did not personally travel to Colorado, but obtained "unprepared" specimens through another entomological correspondent who employed a resident of Colorado to collect butterflies and sugar for moths

(30.vii.1878, FMNH). Unfortunately, no letters from Bailey were found among Edwards' correspondence at AMNH.

Type locality. Although the source of the lectotype is uncertain, this taxon has been associated with "Turkey Creek Junction" for nearly fifty years and the species is known to occur there. The type locality is more accurately defined as the vicinity of Bradford Junction ("Turkey Creek Junction," within the present-day town of Conifer), Jefferson County, Colorado.

Colias hagenii W. H. Edwards, [1884]

(=*Colias philodice eriphyle* W. H. Edwards; Pieridae)

Described from "various localities, from So. Colorado to Montana and Dacotah (Bismarck)." Without explanation, Ferris (1971) attributed the type locality to "Durango, La Plata Co., Colorado." Brown (1973) designated one of Mead's specimens as the lectotype (Figs. 13, 14) and defined the type locality as "northeastern corner of South Park, Park Co., Colorado." Affixed to the lectotype (CMNH) is a portion of Mead's original field envelope dated "6/16." It also includes a fragment of Mead's notation identifying the specimen as a male "[Phil]odice" (Fig. 15), which is consistent with Edwards' (1887b) comment that Mead originally considered these specimens to represent "a variety of Philodice."

On 16 June 1871, Mead was lodging at Kenosha House, where he "found many *Colias*" during a walk of 4.8 km (3 mi) along the road "to the South Park" (Table 1). He apparently walked along the Denver & South Park Road (today's I-285 corridor) from Kenosha House over the summit of Kenosha Pass and down toward the South Park basin. Although Brown (1973) stated that the lectotype was from Edwards' collection, there is no such collection label on the specimen (Fig. 15). The presence of the envelope clipping infers that Holland acquired it from Mead and it was still papered. Mead mailed this specimen to Edwards from Bradford Junction 20 June 1871.

Type locality. As defined by the lectotype, the type locality is restricted to within 1.6 km (1 mi) south of the summit of Kenosha Pass, Park County, Colorado.

Discussion. Although most authors since Smith (1891) consigned *hagenii* to synonymy, Garth and Tilden (1963) and Pohl et al. (2010) resurrected this name to recognize subspecies of *Colias philodice* Godart. The original description of *hagenii* characterized a summer phenotype with broad black wing margins (Edwards [1884a]), though Edwards (1887a) eventually considered *hagenii* to be "seasonally dimorphic." Referring to specimens that would later be described as *hagenii*, Mead reportedly observed, "if there could be such a thing as a yellow Eurytheme, this was it" (Edwards [1884a], [1884b], 1887a). Mead's concept of *Colias eurytheme* Boisduval was of the summer phenotype, as the spring form of this butterfly was then thought to represent a different species, *Colias* ariadne W. H. Edwards. In his original description, Edwards ([1884]) stated that *hagenii* was "between *Philodice* and *Eurytheme* . . . add orange and *Hagenii* would be indistinguishable from *Eurytheme*."

There is still a great deal of disagreement regarding the status of *eurytheme*, *eriphyle*, and *philodice*. Although most lepidopterists now treat *eriphyle* as a subspecies of *philodice*, some consider it worthy of specific recognition. Likewise, the true nature of *hagenii* remains somewhat obscure and even Edwards' concept of this nominal taxon evolved over time. In his original description, Edwards (1884a) noted that some adults of *hagenii* have an "ochraceous tint." He also mentioned that the coloration is sometimes "not yellow, but of a peculiar shade, a sort of buff-yellow (better chrome-yellow), a shade not seen in *Philodice*" (Edwards 1884b). He observed that males "frequently show more or less of [this coloration], and occasionally have a flush of orange." During the 1880s, Edwards reared adults of *hagenii* from eggs that were received from Herman W. Nash of Pueblo, Colorado. Edwards (1887a) identified some of these reared adults as *eurytheme*, prompting him to consider *hagenii* as a yellow form of *eurytheme* (Edwards 1887b). He ultimately concluded that *hagenii* was synonymous with *eriphyle*, but still regarded the latter as a "tetramorphic form" of *eurytheme* (Edwards 1887b). The lectotype of *hagenii* is a slightly darker shade of yellow (Figs. 13, 14), but it is unclear if this coincides with Edwards' reference to an "ochraceous tint" or is simply due to the specimen's age and storage conditions. Many specimens from Holland's collection are discolored due to being stored in his cellar prior to their transfer to the Carnegie Museum in 1896–97 (Brown & Miller 1980).

Although the lectotype of *hagenii* (Figs. 13, 14) agrees with the original description, Fisher (2012) questioned its date (16 June) because he could not confirm the occurrence of the summer phenotype of *C. p. eriphyle* during mid-June in the Fairplay area. He argued that the specimen was probably not collected by Mead, but instead was reared from a batch of eggs that Edwards received from H. W. Nash. This is untenable, however, as the writing on the clipping affixed to the lectotype, including the penciled notation "Colo," is in Mead's hand (Fig. 15). It is also difficult to disregard Mead's accompanying journal entry about finding "many *Colias*" on its date of capture (16 June), or the fact that

FIGS. 13–15. *Colias hagenii*. **13,** lectotype (male, dorsal) (CMNH). **14,** lectotype (ventral). **15,** labels of lectotype.

he reportedly collected most of his specimens of *philodice* during June (Mead [1876]). Because Mead mailed specimens from Colorado on a regular basis, it is unlikely that he collected the specimen at a later date and incorrectly labeled its envelope.

Unusual weather conditions during 1871 could explain the presence of a summer phenotype of *eriphyle* near Kenosha Pass on 16 June. Other captures by Mead near Kenosha House suggest that the 1871 season was earlier than normal (see *P. colorado*, above, and *A. helena*, below). It is also possible that the specimen was not of local origin, but rather reached the area from lower elevations where the summer form appears earlier in the season.

***Argynnis helena* W. H. Edwards, 1871**

(=*Boloria chariclea helena*; Nymphalidae)

Described from specimens "Taken in Colorado by Mr. Mead." Brown (1934) suggested a type locality of "Mt. Elbert, Mosquito Pass, Mt. Lincoln and Hoosier Pass." Brown (1965) designated a lectotype and restricted the type locality to "Mosquito Pass, Lake–Park Counties, Colorado." Although the lectotype is undated, there are several other specimens in CMNH from Mead's collection that possess clippings from his field envelopes dated "7–20." Brown (1965) suspected that on 20 July 1871 Mead was "en route between Twin Lakes, Lake County, and Fairplay, Park County," noting that Mead was definitely on Mosquito Pass the following day. On 20 July, Mead explored in the vicinity of Oro City, within California Gulch, Lake County (Table 1). He walked "up the gulch and on the mountains," but did not reach the higher elevations of Mosquito Pass, located 9.7 km (6 mi) northeast of Oro City. In a letter dated 20 July, which accompanied a box of specimens that had been collected since the last shipment, Mead attributed all the butterflies he captured that day to California Gulch (Brown & Brown 1996).

Two additional dated specimens of *helena* that Mead collected are deposited at PMNH. A male bears a label written by C. P. Whitney dated "July 3 1871" and a female bears a label written by F. G. Sanborn dated "7 10." Mead was lodging at Kenosha House on 3 July when he mentioned collecting about 50 specimens of this species "further up and more in the mountains" (probably up Hoosier Creek valley west of the house) (Brown & Brown 1996). This is an early date for this species, suggesting that the 1871 season was advanced (this species does emerge in early July on occasion, as there are two fresh specimens at MGCL from Park County dated 3 July 1990 from an elevation of 3426 m/11,240 ft.). On 10 July, Mead climbed a peak south of Twin Lakes (Table 1) (Fig. 8), where he found "swarms" of this species at the summit (Brown & Brown 1996).

Type locality. Although Mead collected this species at multiple locations, the type locality is restricted to the vicinity of Oro City, California Gulch, Lake County, Colorado. This location is most suitable because of its proximity to the type locality previously proposed by Brown (1965) and its association with several specimens at CMNH where the lectotype is deposited.

***Argynnis meadii* W. H. Edwards, 1872**

(=*Speyeria callippe meadii*; Nymphalidae)

Described in part from a male specimen taken by Mead at "Turkey Creek Junction [Jefferson Co.], in Colorado," which Brown (1934) restricted to "Turkey Creek Junction, Colorado . . . probably the junction of South Turkey Creek with Turkey Creek, a few miles up in the foothills." Mead's male specimen (CMNH) was designated by Brown (1965) as the lectotype. According to Mead ([1876]), it was collected on 6 June 1871. On that date, Mead was at Bradford Junction ("Turkey Creek Junction") where he "took a lunch along & started down the road," walking 12.9 km (8 mi), then returned by the same route (Table 1). He stated in a letter (Brown & Brown 1996) that he followed Turkey Creek, apparently walking along the winding Denver & South Park Road (today's South Turkey Creek Road), which paralleled South Turkey Creek northeast of Bradford Junction (Fig. 7). The lectotype specimen was

mailed to Edwards from Bradford Junction on 20 June 1871.

Type locality. Restricted to within 9.7 km (6 mi) northeast of Bradford Junction ("Turkey Creek Junction," within the present-day town of Conifer), along South Turkey Creek, Jefferson County, Colorado.

Grapta hylas W. H. Edwards, 1872

(=*Polygonia faunus hylas*; Nymphalidae)

Described from "about 20 specimens taken in Colorado, in August 1871, by Mr. Mead." Brown (1934) defined the type locality as "near Berthoud Pass, with little doubt on the southern slope [Clear Creek Co.]." The lectotype (CMNH), designated by Brown (1967), bears a portion of Mead's original field envelope dated "8/16." On 16 August 1871 Mead was approaching Berthoud Pass from the north along the Empire & Middle Park Wagon Road (Table 1), when he stopped and collected 15 specimens of a new Grapta. Mead recorded in his journal that these specimens were collected "a little before reaching the pass." Two paralectotypes, which Mead collected on the same date, are deposited at CMNH (ex. Mead colln.). These specimens were mailed to Edwards from Denver on 22 August 1871.

Type locality. As defined by the lectotype, the type locality is restricted to the northern slope of Berthoud Pass, Grand County, Colorado.

Melitaea eurytion Mead, [1876]

(=*Euphydryas anicia eurytion*; Nymphalidae)

Described from "Colorado," which Brown (1934) defined as "Twin Lakes, California Gulch, Fairplay and probably Kenosha. Probably not at Turkey Creek Junction." Miller and Brown (1981) suggested "South Park, Park Co., Colorado." Scott et al. (2006) suggested "South Park, probably near Fairplay, Park Co., Colo." Fisher (2006) proposed "the vicinity of Fairplay or certainly between Fairplay and 'Kenosha House' within South Park [Park Co.]." Although Mead ([1876]) clearly intended to credit the name *Melitaea eurytion* to W. H. Edwards, modern rules of nomenclature (ICZN 1999, Art. 50.1) dictate that Mead be recognized as the author. For similar reasons, Barnes and Benjamin (1926) also attributed authorship to Mead.

Among the specimens of this taxon at CMNH is a somewhat rubbed male (Figs. 16, 17), which was figured as a "type" by Holland (1931, Pl. 57, fig. 15) and as "typical" by Scott et al. (2006, Pl. 5, top row). It bears a portion of Mead's original field envelope, reading "*Melitaea* 1" with the date "7/4" written in the same purple ink that Mead used for his journal entry on that date (Fig. 18). On 4 July 1871 Mead was lodging at Kenosha House (Table 1). This specimen was mailed to Edwards from Fairplay on 7 July 1871.

An undated female at CMNH (Figs. 19, 20) was also figured as a "type" by Holland (1931, Pl. 57, fig. 16) and as "typical" by Scott et al. (2006, Pl. 5, second row). This specimen bears a small label in Mead's hand identifying it as "*Melitaea Eurytion* Edw" (Fig. 21), suggesting it was mounted prior to being purchased by W. J. Holland. It also bears a larger typed label, probably prepared by Holland, which refers to the specimen as a "typr" (sic; type) with the notation "= *nubigena* fide Strkr," which likely refers to Strecker (1878), who wrote "*Eurytion* = *Nubigena*." Holland's (1931) figure of this specimen is too reddish, causing it to resemble the lower-elevation subspecies *Euphydryas anicia capella* (W. Barnes). New images from CMNH (Figs. 19, 20) reveal that it is actually quite dingy, probably due to its early storage conditions. Many specimens from Holland's collection were discolored due to being stored in his cellar prior to their transfer to the Carnegie Museum in 1896–97 (Brown & Miller 1980).

Scott et al. (2006) doubted the occurrence of this butterfly at Kenosha Pass, but adults were photographed there in early July 2008 by Thomas Bentley (Harp 2009, Warren et al. 2012), who indicated (pers. comm.) that they were "quite common." On 9 July 2014, Andrew D. Warren found this species to be abundant within the meadows along Hoosier Creek directly opposite the former site of Kenosha House, at elevations from 2970 and 3000 m (9744 and 9843 ft.). This species was evidently also common in that area in 1871, as at least twelve other specimens at CMNH were captured by Mead in the vicinity of Kenosha House between 14 June and 2 July. Two additional females, which Mead collected in the same area, are deposited at PMNH (YPM ENT429625 and YPM ENT799979) (Figs. 22, 23, 25, 26). These specimens are from the collection of C. P. Whitney, who received them from Mead in early 1872 (6.iii.1872, RC). Both bear Whitney's labels that attribute them to Mead (Figs. 24, 27). In its original condition, the discolored female at CMNH, identified by Mead as *M. eurytion*, was phenotypically analogous to the female at PMNH dated 4 July (Figs. 25, 26). Mead's specimens from the vicinity of Kenosha House were likely collected at elevations between 2941 and 3200 m (9650 and 10,500 ft.). Also included among Mead's material at CMNH are three specimens from near Fairplay (Park Co.) and one from Twin Lakes (Lake Co.). At the request of John E. Rawlins, I provided locality information for all of Mead's dated specimens of *E. anicia* from Colorado at CMNH.

Discussion. Reflecting his frustration with identifying specimens, Mead declared, "*Melitaea* is I

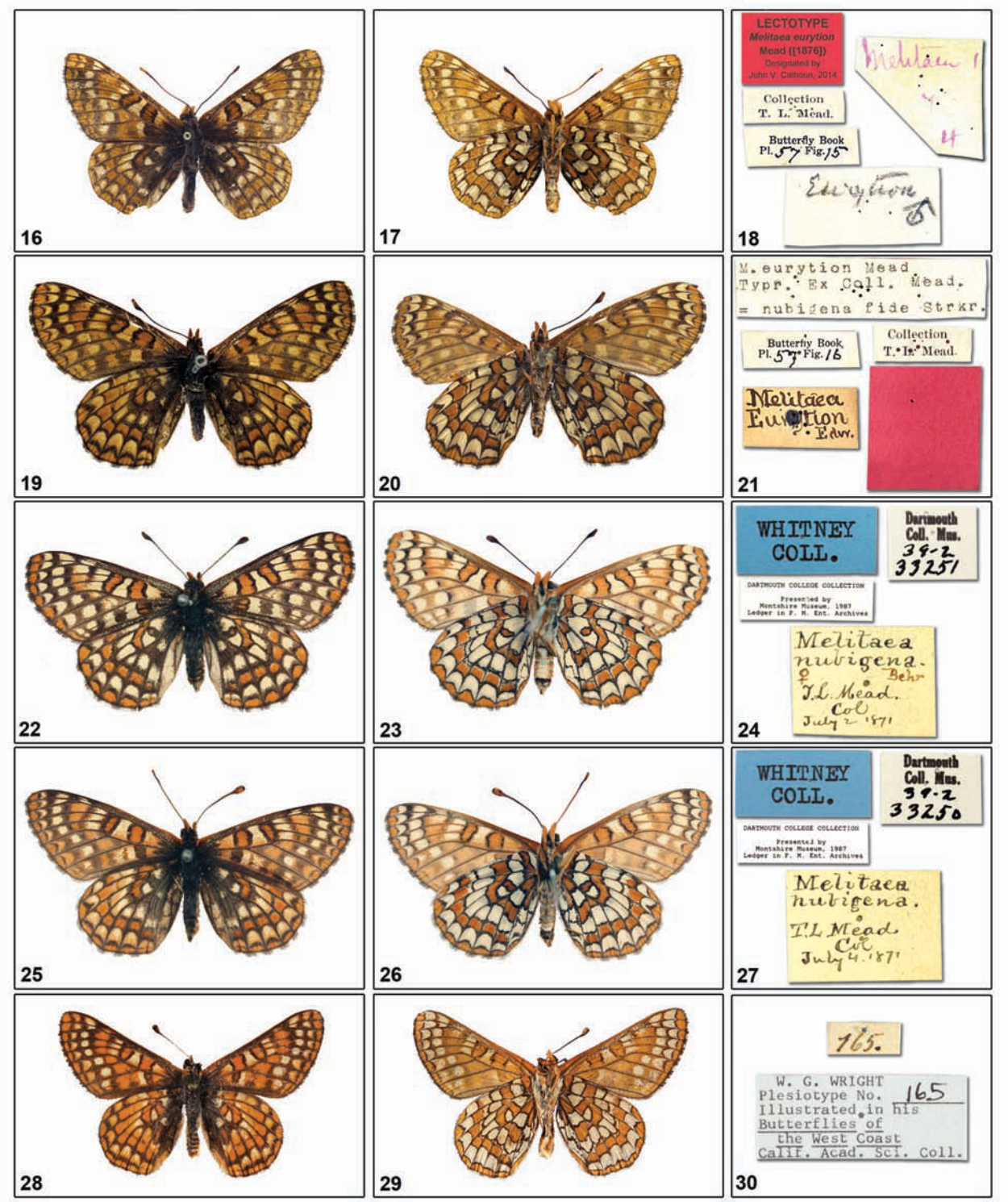
think about the most difficult genus we have . . ." (15.xii.1872, RC). His idea of *M. eurytion* applied to a particular color variation of the butterfly currently represented by this name and likely involved a second taxon. A review of the history of *Melitaea eurytion* is helpful in understanding Mead's concept of this butterfly.

On 9 July 1871, William H. Edwards (WHE) sent a batch of Mead's Colorado specimens to Henry Edwards (HE) for his opinion about their identities. In the associated letter, WHE asked if the species identified as "*Melitaea* 1" was "*anicia* or what," to which HE scrawled "not *anicia*" (AMNH). WHE informed Mead on 25 August 1871 (MGCL) that HE had determined the species as *Melitaea nubigena* Behr (=*Euphydryas editha nubigena*; a California taxon). In the collection catalog of HE (AMNH) is an entry for "*Melitaea nubigena*" from "Rocky Mts, Colorado" from "T. Mead," but these may refer to four other specimens, identified as "*nubigena*", which Mead sent during 1872 (18.i.1872, RC; 19.vi.1872, AMNH). The two female specimens at PMNH from the Whitney collection are labeled as *Melitaea nubigena*, as originally identified by Mead on the advice of HE (Figs. 24, 27). Still confused, WHE wrote on 21 March 1873, "There are some remarkable forms among Mead's Colo [Colorado] *Melitaeas* that I had labelled as *Nubigena* & I think there are 2 species mix'd" (AMNH). WHE was clearly flummoxed by the array of melitaeine phenotypes found by Mead and even proposed to call several specimens *Melitaea idas*, but he never published this name.

In late 1873, WHE proposed the name *Melitaea eurytion* (14.xii.1873, AMNH), but it was Mead ([1876]) who actually published it. Crediting the name to WHE, Mead wrote only two sentences about *eurytion*: "This species is found associated with *Nubigena* in Colorado, but is much rarer, and does not seem to range to quite so great elevations. The most obvious point of distinction from *Nubigena* is that the yellow spots of the latter are largely obscured in *Eurytion* by fulvous." Despite Mead's publication of the name, *Melitaea eurytion* was subsequently abandoned. Strecker (1878) was the first to argue that Mead's ([1876]) comments were not sufficient to serve as an original description. Even WHE disregarded *eurytion* and instead maintained that all these butterflies from Colorado were either *Melitaea anicia* E. Doubleday or *M. nubigena*, and he did not list *eurytion* as a synonym of either (Edwards [1876], 1877, [1885]). *Melitaea eurytion* was not included in any checklists until Barnes and Benjamin (1926) considered it to be a synonym of *anicia*. Holland (1931) resurrected the name to define specimens "from comparatively low altitudes" in Colorado. He figured two of Mead's specimens as "types," thus establishing the popular concept of this taxon. Brown et al. (1955a) also regarded *eurytion* as a full species. Miller and Brown (1981) considered *eurytion* to be a subspecies of *anicia*, yet acknowledged the name's tenuous nomenclatural availability. This treatment is generally accepted today.

Mead ([1876]) considered the butterfly that he called *Melitaea nubigena* to be "quite common throughout the mountain district of Colorado." He described several larvae that he believed to be this species, one of which suspended itself on 19 June and pupated the following day. He mentioned these same larvae in a letter to W. H. Edwards on 22 June, stating that he had found them in South Park (Brown & Brown 1996). From 8 to 20 June Mead explored around Fairplay and Kenosha House, where he collected many adults of this butterfly. His concept of *nubigena* was clearly synonymous with the taxon now known as *E. a. eurytion* and probably included populations from above timberline, which are currently recognized as the subspecies *E. a brucei* (W. H. Edwards). Mead ([1876]) also listed *Melitaea anicia* from Colorado, but stated, "I did not meet with it in the Territory." Like WHE, Mead apparently associated the darkest high-elevation phenotypes (i.e. extreme *brucei*) with nominotypical *anicia*. Lastly, Mead ([1876]) tentatively identified a single specimen from Bradford Junction as "*Melitaea chalcedon*" (=*Euphydryas chalcedona* E. Doubleday), but this was presumably based on an unusually dusky or aberrant individual.

In late 1873, WHE informed Mead of his concept of *eurytion*. Mead responded, "I found I could separate what I take to be *Eurytion* quite readily from the Nubigenas by the general appearance but in the details of markings I was unable to satisfactorily find the precise manner of difference except indeed in the greater proportion of yellow in *Nubigena*." By introducing the name *Melitaea eurytion*, Mead ([1876]) clearly attempted to segregate the more fulvous butterflies within montane populations of "*nubigena*" (=*anicia*) in Colorado. The undated female specimen in CMNH, which Mead personally identified as *M. eurytion* (Figs. 19–21), is consistent with this concept in having its pale spots "largely obscured with fulvous." Likewise, the pale spots of the analogous female from PMNH, collected on 4 July (Figs. 26, 27), are broadly infused with fulvous scales. Brown (1966b) supposed that Mead used the name *eurytion* to denote the "red form" of *E. a. brucei*, but Mead's named female does not agree with *brucei*, whose alpine populations contradict his account that *eurytion* "does not seem to range to quite so great elevations." Adults currently found near the former site of Kenosha House are



FIGS. 16–30. Mead's specimens of *E. a. eurytion* and *E. a. capella*. **16,** lectotype of *Melitaea eurytion* (male, dorsal) (CMNH). **17,** lectotype (ventral). **18,** labels of lectotype. **19**, paralectotype (female, dorsal) (CMNH). **20,** paralectotype (ventral). **21,** labels of paralectotype (largest label slightly reduced). **22,** paralectotype (female, dorsal) (PMNH; YPM ENT429625). **23,** paralectotype (ventral). **24,** labels of paralectotype (Whitney's handwritten label enlarged). **25,** paralectotype (female, dorsal) (PMNH; YPM ENT799979). **26,** paralectotype (ventral). **27**, labels of paralectotype (Whitney's handwritten label enlarged). **28,** *E. a. capella* (male, dorsal) (CAS). **29,** *E. a. capella* (ventral). **30,** labels of specimen.

extremely variable, with some showing characteristics of *E. a. capella* and a few resemble *E. a. brucei*. Populations in the vicinity of Kenosha Pass embody the popular notion that *eurytion* is a highly variable taxon (see Ferris 1981).

Mead's concept of *eurytion* probably extended to lower-elevation populations of *E. a. capella*. Although *capella* is variable, its yellow (or yellowish-white) pattern elements are typically fulvous, corresponding with Mead's original description of *eurytion*. On 21 June, while exploring along the road just south of Bradford Junction ("Turkey Creek Junction"), Mead mentioned finding "another species of *Melitaea* of the same size as No. 1, but without any yellow spots" (Brown & Brown 1996). At CMNH is a dated male *capella* which Mead collected along the same road two days later. In addition, a male *capella* was figured by Wright (1905, Pl. 19, fig. 165) with the statement "no data, from Colorado; T. L. Mead." This specimen (Figs. 28, 29) is deposited among the Wright "plesiotypes" at CAS and was listed by Tilden (1975). Unfortunately, it bears only one small label reading "165," which corresponds to the species/figure number used by Wright (1905) (Fig. 30). This specimen was most likely also captured in the vicinity of Bradford Junction. Because Mead ([1876]) did not separately mention fulvous lower-elevation populations (i.e. *capella*), it is reasonable to assume that he considered all ruddy phenotypes to represent *eurytion*.

Lectotype designation. To preserve nomenclatural stability and fix the type locality, I hereby designate the male syntype at CMNH (Figs. 16, 17) as the lectotype of *Melitaea eurytion*, Mead, [1876] in accordance with ICZN (1999, Art. 74.7). This specimen was selected because 1) it is from Mead's personal collection, 2) it is dated, 3) it is from an extant population where Mead collected many of these butterflies, 4) its illustration as a "type" by Holland (1931) helped forge the modern concept of *eurytion*, and 5) Scott et al. (2006) referred to this specimen as "typical" and nearly designated it as the lectotype. The specimen bears 1) a white handwritten rectangular label [*Eurytion* /♂] in the hand of W. J. Holland, 2) a small rectangular printed and handwritten label [Butterfly Book / Pl. 57 Fig. 15], 3) a small rectangular printed label [Collection / T. L. Mead], and 4) a portion of T. L. Mead's original field envelope, reading "*Melitaea* 1 / 7/4" in faded purple ink (Fig. 18). A red printed label [LECTOTYPE / *Melitaea eurytion* / Mead [1876] / Designated by / John V. Calhoun, 2014] (Fig. 18) has been affixed to the specimen. All other specimens of *eurytion* collected by Mead at CMNH, as well as those at PMNH, are paralectotypes. The specimens sent to Henry Edwards were not located by staff at AMNH. Additional paralectotypes of *eurytion* likely exist, as Mead's letter copybooks (RC) indicate that he also sent specimens of "*nubigena*" to J. Behrens, H. K. Morrison and others. Mead collected 297 specimens of "*Melitaea* and *Phyciodes*" in Colorado (Mead 1877).

Euphydryas anicia carolae T. Emmel & L. N. Harris is treated by most authors (e.g. Fisher 2006, Scott et al. 2006, Pelham 2008, 2014) as synonymous with *M. eurytion*. The type locality of *carolae* is 2.1 km (1.3 mi) south of Fairplay at an elevation of 3005 m (9860 ft.) (Emmel & Harris 1998). This location is about 32 km (20 mi) southwest of Kenosha House, where Mead collected the lectotype of *eurytion*. Fisher (2006) suggested that Emmel and Harris (1998) disregarded *eurytion* in the tradition of prior authors, but Thomas C. Emmel (pers. comm.) confirmed that he recognizes *eurytion* as a valid subspecies and *carolae* was described solely to differentiate populations of brightly colored *anicia* that occur in dry-meadows within open valley floors of northern South Park. However, Scott et al. (2006) observed that most adults from the *carolae* type locality "look like the *eurytion* types (some quite like the types)." Moreover, some of the adults found around Kenosha Pass are very similar to *carolae* (Andrew D. Warren, pers. comm.). The various phenotypes of *anicia* in Colorado need further study to better understand the extreme variability between, and within, populations.

Type locality. As defined by the lectotype, the type locality is restricted to the vicinity of Kenosha House, 2.16 km (1.34 mi) north of the summit of Kenosha Pass, Park County, Colorado.

Phyciodes nycteis var. *drusius* W. H. Edwards, 1884

(=*Chlosyne nycteis drusius*; Nymphalidae)

Described from "Colorado and Arizona," Brown (1966) designated a lectotype from one of Mead's specimens and defined the type locality as "Turkey Creek Junction, Jefferson County, Colorado." The lectotype (CMNH) bears Mead's small identification label dated "June 26," indicating that it was probably mounted prior to being purchased by Holland. On 26 June 1871 Mead collected butterflies along the Mt. Vernon Wagon Road and "up a small brook" north of Bradford Junction (Table 1). Specimens collected that day were mailed to Edwards from Fairplay on 7 July 1871.

Type locality. As defined by the lectotype, the type locality is restricted to within several kilometers north of Bradford Junction ("Turkey Creek Junction," within the present-day town of Conifer), Jefferson County, Colorado.

***Melitaea calydon* W. Holland, 1931**

(=*Chlosyne palla calydon*; Nymphalidae)

Edwards first proposed the name *calydon* in 1873 (14.xii.1873, AMNH), but never published it. Citing Edwards, Mead ([1876]) listed *M. calydon* without description in association with specimens that he collected at "Turkey Creek Junction." Holland (1931) resurrected the name *calydon* to define Colorado specimens that resembled *Melitaea* (=*Chlosyne*) *palla* Boisduval. He figured a pair of "types" and, following Mead ([1876]), suggested a type locality of "Turkey Creek Junction, Colorado." Mead ([1876]) reported that he collected specimens at that locality during 20–30 June 1871. Although he arrived at that locality on 20 June, he actually departed on 28 June (Table 1). Mead mailed the lectotype specimen to Edwards from Fairplay on 7 July 1871.

Type locality. The type locality is more accurately defined as the vicinity of Bradford Junction ("Turkey Creek Junction," within the present-day town of Conifer), Jefferson County, Colorado.

***Phyciodes camillus* W. H. Edwards, 1871**

(=*Phyciodes pulchella camillus*; Nymphalidae)

Described from specimens "Taken in Colorado by Mr. Mead." Brown (1966) designated a lectotype and defined the type locality as "Fairplay, Park County, Colorado." Affixed to the lectotype (CMNH) is a portion of Mead's original field envelope, dated "7–4," written in the same purple ink as Mead's journal entry for that date. On 4 July 1871 Mead was lodging at Kenosha House (Table 1). He mailed the lectotype specimen to Edwards from Fairplay on 7 July 1871.

Type locality. As defined by the lectotype, the type locality is restricted to the vicinity of Kenosha House, about 2.16 km (1.34 mi) north of the summit of Kenosha Pass, Park County, Colorado.

***Phyciodes emissa* W. H. Edwards, 1871**

(=*Phyciodes pulchella camillus*; Nymphalidae)

Described from "several specimens taken in Colorado by Mr. Mead." Brown (1966) designated a lectotype and defined the type locality as "Denver, Denver County, Colorado." The lectotype (CMNH) bears a portion of Mead's original field envelope with the date "6/3." On 3 June 1871 Mead was lodging in Denver, where he "walked out on the prairie and found plenty butterflies" (Table 1). He followed Cherry Creek, a tributary of the South Platte River that runs southeast from the center of the city. The lectotype specimen was mailed to Edwards from Denver the same day on which it was collected.

Type locality. Restricted to Denver, along Cherry Creek, Denver County, Colorado.

***Erebia rhodia* W. H. Edwards, 1871**

(=*Erebia epipsodea brucei* Elwes; Nymphalidae)

Described from "Colorado; from several specimens taken by Mr. Mead." Brown (1934) suggested the type locality of "Fairplay [Park Co.]." Brown (1964) designated a lectotype (CMNH), which bears a portion of Mead's original field envelope dated "7–6." On 6 July 1871 Mead collected "up" Beaver Creek near Fairplay (Table 1). This specimen was mailed to Edwards from Fairplay the following day.

Type locality. As defined by the lectotype, the type locality is restricted to along Beaver Creek, east/northeast of Fairplay, Park County, Colorado.

***Chrysophanus sirius* W. H. Edwards, 1871**

(=*Lycaena rubidus sirius*; Lycaenidae)

Described from specimens "taken in Colorado by Mr. Mead." Brown (1934) suggested a type locality of "Twin Lakes," as well as "Mt. Lincoln, South and Middle Park." Brown (1969) designated a lectotype and defined the type locality as "vicinity of Twin Lakes, Lake Co., Colorado." The lectotype (CMNH) bears a portion of Mead's original field envelope, which is dated "7–13." On 13 July 1871 Mead was indeed at Twin Lakes (Table 1). He walked "up to the head of the upper lake," where he found "lots of *Chrysophanus*." He collected at least 40 males and two females in a "grassy spot" (Mead [1876], Brown & Brown 1996). Additional specimens of *sirius* which Mead collected during his stay at Twin Lakes are deposited at CMNH (ex. Mead colln.), MCZ (ex. Scudder colln. via Morrison), and PMNH (ex. Whitney colln.). These specimens were mailed to Edwards from Oro City on 20 July 1871.

Type locality. As defined by the lectotype, the type locality is restricted to Twin Lakes, along the northern shore of Upper Twin Lake (the western lake), Lake County, Colorado.

***Thecla ninus* W. H. Edwards, 1871**

(=*Callophrys spinetorum spinetorum* (Hewitson); Lycaenidae)

Described from three specimens "Taken in Colorado by Mr. Mead." Brown (1934) cited Mead ([1876]), who stated that specimens were taken "on the South Park road four miles from the park." Shields (1966) defined this as "ca. 1 mi. E Kenosha Pass summit, U.S. Highway 285," which Brown (1970a) cited as "about 1 mile east of Kenosha Pass, Park County, Colorado." Although the lectotype is not dated, Mead ([1876]) reported that he caught all of his specimens at the same locality on 17 June 1871. On this date, he was collecting along the Denver & South Park Road near Kenosha House (Table 1). His comment about taking the specimens "four miles

from the park" denoted road miles from the South Park basin. Although the suggested type locality of Shields (1966) is essentially correct, the old wagon road (and existing U.S. Hwy 285) actually crossed the pass in a more north/south direction, not east/west. One mile east of the pass would place the collection site far off the road among the nearby peaks. Mead's specimens of ninus were mailed to Edwards from Bradford Junction on 20 June 1871.

Type locality. Restricted to the vicinity of Kenosha House, about 2.16 km (1.34 mi) north of the summit of Kenosha Pass, Park County, Colorado.

Lycaena daunia W. H. Edwards, 1871

(*Glaucopsyche piasus daunia*; Lycaenidae)

Described from specimens "Taken in Colorado by Mr. Mead." Based on Mead ([1876]), Brown (1934, 1970b) defined the type locality as "Turkey Creek, Jefferson Co., Colorado." Mead collected only three specimens during the last week in June, two of which are deposited at CMNH (ex. Edwards colln.). Neither is dated, but Mead spent 20–28 June at "Turkey Creek Junction" (Table 1), where on several occasions he walked along South Turkey Creek (Turkey Creek). His specimens from this period were mailed to Edwards from Fairplay on 7 July 1871.

Type locality. Based on the location of the settlement and Mead's documented activities, the type locality is defined as along South Turkey Creek, within 9.7 km (6 mi) northeast of Bradford Junction ("Turkey Creek Junction," within the present-day town of Conifer), Jefferson County, Colorado.

Lycaena melissa W. H. Edwards, 1873

(=*Plebejus melissa*; Lycaenidae)

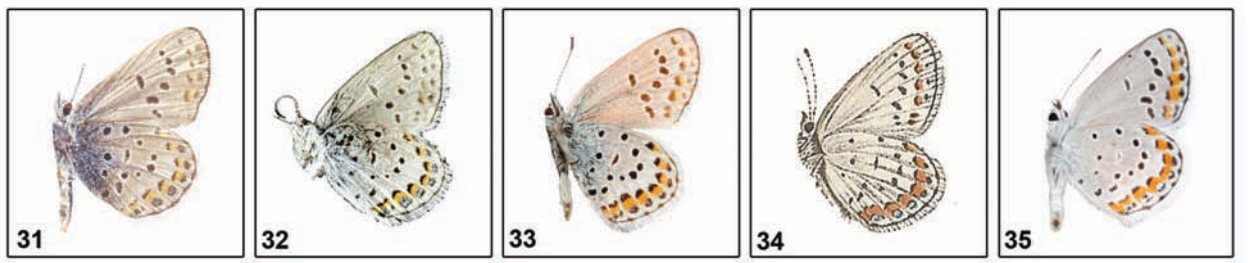
Described from "many specimens taken in Colorado by Mr. Mead, in the summer of 1871." Although Edwards (1873) mentioned that he had also received this species from Nevada and Arizona, it was implied that the description was based solely upon Mead's specimens from Colorado. Brown (1934) suggested a type locality of "Fairplay [Park Co.]," which Nabokov (1949) expanded to "Park Co., between Fairplay and Californian Gulch, on the way to Mosquito Pass, 9,500–13,188 ft. alt." Brown (1970b) designated a lectotype (Fig. 31) and defined the type locality as "vicinity of Twin Lakes, Lake Co., Colorado . . . probably taken on La Plata Peak," which Miller and Brown (1981) reinterpreted as "La Plata Peak, vic. Twin Lakes, Lake Co., Colorado." Scott (2006a) suggested "Tinytown [Jefferson Co.]." Andrew D. Warren agreed with Brown (1934) that Fairplay is a more likely type locality (Pelham 2008).

The lectotype (CMNH) designated by Brown (1970b) bears a portion of Mead's original field envelope dated "7–11." Mead was at Twin Lakes on 11 July 1871, but he did not climb any nearby peaks (Table 1). He was stiff after ascending a peak the previous day and instead collected in the vicinity of the lodging house (east of the lakes) and walked 4 km (2.5 mi) "above" the house, presumably northwestward along the road (now State Hwy 82). Mead remarked that this species was "very plentiful" around Twin Lakes, where it was "abundant by the first week in July" (Mead [1876], Brown & Brown 1996). In addition to the lectotype, at least two males and five females of *melissa* which Mead collected around Twin Lakes are deposited at CMNH (ex. Mead colln.). These specimens, including the lectotype, were mailed to Edwards from Oro City on 20 July 1871.

Type locality. As defined by the lectotype, the type locality is restricted to Twin Lakes, along the eastern side of Lower Twin Lake (the eastern lake), Lake County, Colorado.

Discussion. The type locality of *Lycaena melissa* (Fig. 31) is located about 16 km (10 mi) east of the type locality of *Lycaeides melissa pseudosamuelis* Nabokov (Fig. 32). The proximity of the type localities and similarity of the primary types prompted Scott (2006a) to speculate on the reasons why a drab high-elevation phenotype was chosen as the lectotype of *melissa*, even suggesting that F. Martin Brown was "peeved at Nabokov" and deliberately intended to force *pseudosamuelis* into synonymy. Although Brown (1950a, 1950b) disagreed with Nabokov's statistical methods, I have found no evidence that he had any such deliberate intentions regarding *melissa*. Appreciating Brown's motivation requires a review of the complex conceptual histories of the nominal taxa *Lycaena melissa* and *Lycaeides melissa pseudosamuelis*.

On 4 August 1871, W. H. Edwards informed Mead that three of his *Lycaena* species appeared to be new, but cautioned that he was not yet certain (RC). In early 1873, Edwards was unsure of the identity of Mead's "Lycaenas," particularly one "like *Scudderii*, Edw., that has passed for *Anna*"(16.i.1873, AMNH). Edwards was referring to *Lycaena scudderii* (=*Plebejus idas scudderii*) and *Lycaena anna* (=*Plebejus anna*), both of which he had previously described. Seeking another opinion, he sent several specimens to Henry Edwards, referring to them as "all of Mead's collecting in Colorado." After comparing his type of anna with Mead's specimens, W. H. Edwards wrote, "certainly the two seem distinct and I think the Coloradian is undescribed" (23.i.1873, AMNH). Within two months he had chosen a name: "The *Lycaena* like *Anna* I call *Melissa*" (9.iii.1873, AMNH). One of the male



FIGS. 31–35. *Lycaena melissa* and *Lycaeides m. pseudosamuelis*. **31,** lectotype of *L. melissa* (male, ventral), ca. 2819 m (9250 ft.) (CMNH). **32,** holotype of *L. melissa pseudosamuelis* (male, ventral), ca. 3048 m (10,000 ft.) (MCZ-ENT00027846). **33,** *L. melissa* paralectotype (male, ventral), [between Fairplay and Montgomery City, Park Co., CO], ca. 3048-3353 m (10,000-11,000 ft.), (leg. T. L. Mead) (PMNH, YPM ENT746876). **34,** ventral male figure of *melissa* from Plate 36 of Mead ([1876]) (image reversed). **35,** *Plebejus melissa* (male, ventral), Parker, Douglas Co., CO, ca. 1798 m (5900 ft.) (leg. A. D. Warren).

specimens that W. H. Edwards sent to H. Edwards eventually made its way back to Mead. It is deposited at CMNH (Brown 1970b) and was figured by Holland (1898, 1931; Pl. 31, fig. 25). Another specimen, a female, is deposited at AMNH and labeled "4880" in H. Edwards' hand. It corresponds to an entry in his collection catalog (AMNH) for an unidentified species of "*Lycaena*," which was collected by Mead during June in "Rocky Mts. Colorado."

In his original description of *Lycaena melissa*, Edwards (1873) defined a butterfly with a "complete sub-marginal row of large orange spots" on the ventral hindwings, as well as a row of orange spots on the ventral forewings. He characterized the female as having a "complete orange band" on the dorsal forewings and hindwings. However, Edwards typically chose one specimen of each gender from which to derive his original descriptions (Brown 1965). To define melissa, he presumably selected a pair that significantly differed from his concepts of *scudderii* and *anna* (Edwards 1873). Lower-elevation populations of *melissa* tend to be more brightly colored. Mead's specimens of *melissa* at CMNH suggest that he collected more from high elevations than from low, supporting the idea that Edwards cherry-picked the specimens he described.

Edwards' correspondence reveals that he intended to illustrate melissa with his description, but did not do so. Instead, he figured dorsal and ventral aspects of the male and female in Mead ([1876], Pl. 36, figs. 5–8) (Fig. 34). Edwards prepared the plates for that publication and undoubtedly selected the figured specimens (Calhoun 2013b). Because Edwards had exchanged much of his share of Mead's 1871 material by that time, the melissa specimens he figured were probably not those characterized in the original description. None of the *melissa* at CMNH were identified by Edwards as type specimens (Brown 1970b).

Barnes and McDunnough (1916) examined specimens at CMNH, including "presumable types from Colorado" and defined typical melissa as having "heavy red submarginal markings on the underside." They considered specimens in their possession from Colorado, Utah, Arizona, and New Mexico as "typical." Holland (1931, Plate 66, fig. 17) figured a brightly colored female from Colorado and identified it as a "type." Today, nominotypical *melissa* is generally recognized as a low-elevation taxon with well-developed ventral orange spots that occurs over a large portion of western North America (Downey 1975, Fisher 1981, 2009, Scott 1986, Lane & Weller 1994, Layberry et al. 1998, Gompert et al. 2008) (Fig. 35). Fisher (1981) considered this taxon to be most common in the Rocky Mountains at elevations of 1525–2135 m (5000–7000 ft.). Despite our modern interpretation of nominotypical *melissa*, this taxon was treated differently during the four decades between the publication of Holland (1931) and Downey (1975).

Around 1932, F. Martin Brown began researching Mead's itinerary in an effort to clarify the type localities of taxa attributed merely to "Colorado" by W. H. Edwards. Regarding *melissa*, Brown (1934) stated, "Mead gives Fairplay as the probable locality for the 1871 series." This assertion was derived from Mead's ([1876]) remark that specimens "were brought in by the expedition of 1871, probably from the vicinity of Fairplay." Brown, however, mistakenly assumed that Mead was a member of a larger survey party and likely interpreted Mead's comment to mean that another party member had collected the type series, but the locality was unknown. Rather, Mead's uncertainty about the locality implies that he was referring to a different expedition than his own. In several instances Mead ([1876]) cited the "expedition of 1871" in reference to other exploring parties. Mead was probably referring to the Allen Expedition, who was in the vicinity of Fairplay

in late July 1871 (Brown et al. 1956). It is also possible that Mead intended to cite the Wheeler Expedition of 1873, whose party collected in South Park, including Fairplay, during July and August (Yarrow [1876b]). Mead also listed *melissa* from Denver, and "In the South Park and about Twin Lakes." Based on what we now know about his itinerary, he was referring to his own specimens from those areas. Nonetheless, Brown's concept of nominotypical *melissa* was forever biased by Mead's reference to Fairplay, which is roughly 3048 m (10,000 ft.) in elevation.

While Brown (1934) began to shift the concept of nominotypical *melissa*, it was Nabokov (1949) who formally advocated the change. Among the *melissa* specimens that Nabokov examined at MCZ was a female collected by Mead on 8 July 1871. Nabokov stated that "Mead's label" read "Divide between the Arkansas and S. Platte Valleys." This specimen supported Brown's (1934) assertion that the type material was from the vicinity of Fairplay. In addition, Brown (1934) placed Mead on 8 July 1871 "on the divide between Fairplay and California Gulch" (i.e. Mosquito Pass), which corresponds with the data on the specimen. Nabokov therefore considered the type locality of *melissa* to be "Park Co., between Fairplay and Californian Gulch, on the way to Mosquito Pass, 9,500–13,188 ft. alt." Accordingly, Nabokov (1949) regarded Mead's female specimen as a topotype and figured it on his Plates 6 and 9. I examined images of this specimen and found that its label was not written by Mead, but by Herbert K. Morrison, who received the specimen from Mead on 20 February 1873 (Mead referred to it in his letter to Morrison as "*L. anna*?") (RC). Morrison probably sent this specimen to S. H. Scudder, whose collection is deposited at MCZ. Morrison's label, based on data provided by Mead, reads, "Divide between the / Arkansas & Platte / valleys July. 8.1871." In an effort to reconcile the locality label with Brown's (1934) allusion to Fairplay, Nabokov affixed a label to this specimen which reads, "vic. Fairplay, / Mosquito Pass / (see Brown 1934 J. N.Y. / Ent. Soc.) leg T. L. Mead." It is no secret that Nabokov greatly admired Brown's studies of Mead (Boyd & Pyle 2000).

Influenced by Brown's assumptions and encouraged by Mead's specimen, Nabokov (1949) concluded, "typical *melissa* is not the low level (sage belt, oak brush, alfalfa, prairie, etc.) form or forms, with richly ornamented underside and female upperside, but an altitudinal, comparatively drab race, little known to collectors." To conserve the "general concept of *melissa*," he considered the "richly ornamented" low-elevation populations as an extreme form. A male *melissa*, collected by Mead on 22 July 1871 between Fairplay and Montgomery City, Park Co., Colorado (PMNH, ex. C. P. Whitney colln.) (Fig. 33), is consistent with nominotypical *melissa* as interpreted by Brown (1934) and Nabokov (1949).

Nabokov (1944) was the first to mention "a curious Colorado form" of *melissa* with a reduced ventral orange band. He later described this form as the subspecies *L. m. pseudosamuelis* to "delimit the geographically adjacent type form of *melissa melissa* on the negative side of its pattern" (Nabokov 1949). He admitted that *pseudosamuelis* (Fig. 32) was the "weakest of *melissa* races in Colorado," with the "Fairplay typical form coming next, and the S. E. Colo. form bringing ssp. *melissa* to its maximum expansion in Colorado" (Figs. 33, 35). In essence, Nabokov described *pseudosamuelis* to narrow his definition of the nominotypical subspecies. Nabokov (1955) later characterized a population of *melissa* from above timberline in the Sierra Madre Range of Wyoming as a "colony of typical (alpine) *L. melissa melissa* as described by Edwards," thus confirming his belief that typical *melissa* is a high-elevation taxon separate from *pseudosamuelis*, which he limited to Pitkin and Lake Counties of Colorado.

Ten of the 17 type specimens of *pseudosamuelis*, including the holotype (Fig. 32), were collected by the Kansas lepidopterist John R. (J. E. Rice) Turner (1910–2000) along US Hwy 82 in the vicinity of the Red Mountain Inn, Lake Co., Colorado. The former Red Mountain Inn was a late 19th century stage stop along the Twin Lakes toll road, 9.7 km (6 mi) west of the town of Twin Lakes, at an elevation of about 3048 m (10,000 ft.) (Scott 2004) (this is about where the red arrow points to Lake Creek on Fig. 8). Turner's specimens are undated, but they were most likely collected during the 1940s (that section of the old toll road was designated as part of US Hwy 82 in 1927; it was paved in 1967 (CDOT 2012)). Possibly in an attempt to further segregate *pseudosamuelis*, Brown et al. (1955b) limited this taxon to populations "generally above 11,500 feet," ignoring the fact that the elevation of its type locality is 10,000 ft. Echoing Nabokov's analysis, Brown observed that specimens of *melissa* from the plains seem to "differ more from typical material caught at Fairplay than the Fairplay specimens differ from *pseudosamuelis*."

Brown's notion of typical *melissa* was reinforced during the 1960s when he examined Mead's specimens at CMNH and discovered that they incorporated both high-elevation and low-elevation phenotypes. Edwards received and examined all of Mead's material from Colorado as it was collected, thus Brown considered

Mead's entire catch to represent the type series (Brown 1970b). Agreeing with Nabokov (1949), Brown defined high-elevation populations as "true *melissa*" and low-elevation populations as the "better known atypical form." That Edwards himself was aware of the variation in *melissa* is suggested by the figures in Mead ([1876]), which Edwards prepared under his personal direction. The ventral male is especially evocative of a high-elevation phenotype (Figs. 33, 34). In fact, Nabokov (1949) considered all the specimens figured by Mead ([1876]) to represent "typical" (i.e. high-elevation) *melissa*.

In selecting a lectotype of *melissa*, Brown worked with CMNH curator Harry K. Clench, a specialist of Lycaenidae. Brown (1970b) recalled that when reviewing lycaeinid material at CMNH, he and Clench "spent days upon days at the Carnegie Museum studying, discussing and arguing about this and that related to the selection of the Edwardsian specimens to be designated the type." In November 1968 they selected one of three dated male specimens of *melissa* at CMNH which could be attributed to a high-elevation locality. Presumably because none of the available specimens at CMNH were from Park County, they chose one from another locality mentioned by Mead ([1876]): Twin Lakes (Lake County), which is the only high-elevation locality definitely represented among Mead's specimens in that collection (see Brown 1970b). Brown affixed a label to the specimen indicating that it was chosen as the lectotype by "F. M. Brown & H. K. Clench / XI 1968."

The lectotype designation for *melissa* was based on a high-elevation concept as defined by Nabokov and supported by Clench, both of whom Brown recognized as authorities on this group of butterflies. This action, however, created a potential conflict with *pseudosamuelis*, which Brown (1970b) did not address. This is all the more surprising given that Brown believed that the lectotype was collected on La Plata Peak, a mountain over 4267 m (14,000 ft.) in elevation —well within the domain of *pseudosamuelis* as previously defined by Brown himself—and located only 4.8 km (3 mi) from the type locality of *pseudosamuelis*. Moreover, Nabokov (1949) had previously questioned if populations from Twin Lakes represented nominotypical *melissa* or another subspecies (i.e. *pseudosamuelis*). Undoubtedly because of the proximity of the type localities, Brown subsequently treated *pseudosamuelis* as a junior subjective synonym of *melissa* in Miller and Brown (1981). Perhaps bowing to criticism from those who preferred conventional usage, *pseudosamuelis* was again listed as a subspecies of *melissa* by Miller and Brown (1983).

Despite the interpretation of nominotypical *melissa* by Brown and Nabokov, Downey (1975) reintroduced the concept of this taxon as a "lowland, brightly colored" sagebrush-prairie inhabitant. He recognized the subspecies *pseudosamuelis* as "the extreme of an altitudinal cline." Perhaps in protest, Downey made no mention of Brown's lectotype of *melissa* and instead reiterated the type locality of Nabokov (1949): "Park county, Colorado, between Fairplay and California Gulch." Ironically, Downey's acceptance of a high-elevation type locality contradicted his premise and contributed to the confusion.

Lane and Weller (1994) mapped the distribution of *pseudosamuelis* to include a very small area surrounding its type locality in Lake County. Scott (2008a) collected additional examples of *pseudosamuelis* at its type locality and defined its range as "several of the cold valleys of the northern Sawatch Range." Fisher (2009) observed that phenotypes resembling *pseudosamuelis* also occur at higher elevations in the southwestern mountains of Colorado. Scott (2006a) mentioned similar butterflies in the Bighorn Mountains of Wyoming, which he satirically referred to as "bighornimuelis." Scott (2008a) later associated those populations with the taxon now recognized as *Plebejus idas longinus* (Nabokov). Although *pseudosamuelis* was reported from New Mexico by Ferris (1976) and Holland (1984), these records were not listed by Toliver et al. (2001). Further complicating matters is the extreme similarity between *pseudosamuelis* and the taxon currently recognized as *Plebejus idas sublivens* (Nabokov). Nabokov (1949, 1950) mentioned their resemblance and subsequent authors (e.g. Brown et al. 1955b, Scott 2006a, 2008a, Fisher 2009) postulated on their potential relationship. Gompert et al. (2010) found that *idas* and *melissa* have hybridized extensively in portions of the central Rocky Mountains, resulting in substantial admixture and nuclear introgression. Although authors continue to associate *pseudosamuelis* with *melissa* (Pelham 2008, 2014, Fisher 2009, Scott 2008a, 2014), it may be more closely allied with *idas* (A. D. Warren, pers. comm.). Scott (2008c) included all *melissa* subspecies within his own concept of an *idas* superspecies, which he sardonically termed a "stenchospecies."

In an effort to fix the name *melissa* to a brightly colored lowland taxon, Scott (2006a, 2008c) asserted that Holland (1931) had designated a lectotype using a specimen from a low-elevation population. Holland referred to three figured specimens as "types:" a pair on Plate 31 and a female on Plate 66. Only the female on Plate 66 was identified as a type on the accompanying plate legend, which, Scott argued, demonstrates

Holland's intent to select that specimen as the sole name-bearing type (i.e. lectotype) per ICZN (1999, Art. 74.5), thereby invalidating the lectotype designation by Brown (1970b). Scott (2006a) suggested a type locality of "Tinytown" (Jefferson County), which is about 2073 m (6800 ft.) in elevation. I disagree with this reasoning, as Holland did not unambiguously select the female to serve as the unique type as required by the Code (ICZN 1999, Art. 74.5), nor was there any visible intent to do so. What Scott interpreted as a conscious act by Holland was likely nothing more than an editorial artifact.

The revised edition of The Butterfly Book by Holland (1931) was based upon a first edition of 1898, which included 48 plates. Only two specimens figured in Holland (1898) were identified as types on the accompanying plate legends (Pl. 30, figs. 9, 33). For the revised edition of 1931, Holland added 29 additional plates, many of which included specimens that were identified as types on the plate legends. In only a few instances did he go back and add "type" captions to the original 48 plates. Simply stated, Holland (1931) did not identify the two specimens as types on the legend for Plate 31 (figs. 25, 26) because he had not done so in Holland (1898). Finally, there is no explicit statement on the legend for Plate 66 of Holland (1931) to suggest any intent to select that female as the sole name-bearing type. In the text of this book, Holland referred to three figured specimens as "types" (plural) without further restriction. The plate legend does not supersede the textual reference and instead merely denotes one of the three "types" mentioned in the text. I therefore agree with Pelham (2014) that the lectotype designation of Brown (1970b) is valid.

ACKNOWLEDGMENTS

James W. Tillery found Mead's 1871 journal and recognized its importance. Wenxian Zhang and Darla Moore (RC) granted access to the manuscripts of T. L. Mead. Jacqueline Y. Miller and Andrew D. Warren (MGCL) hosted my visits to examine specimens and manuscripts under their care. For patiently responding to my many inquiries and providing useful images, I thank Rodney Eastwood and Rachel Hawkins (MCZ), Lawrence F. Gall (PMNH), Suzanne Rab Green (AMNH), Vincent F. Lee and Mike Narahara (CAS), John E. Rawlins and Jane Hyland (CMNH), Andrew D. Warren (MGCL), and Weiping Xei (LACM). Sarah Gilmor (History Colorado, Denver), Susan Morris (Conifer Historical Society, Conifer, Colorado), Hanah Q. Parris (Denver Public Library, Denver, Colorado), Gregory A. Rami and Mia Qaraman Reitmeyer (Archives of the Library, AMNH), and Christie Wright (Park County Local History Archives, Fairplay, Colorado) supplied information, as well as scans of articles, manuscripts, and historical photos. For bestowing additional helpful information and support, I thank Thomas Bentley, Michael M. Collins, Thomas C. Emmel, Nick V. Grishin, James L. Monroe, Chris C. Nice, and Jonathan P. Pelham. Paul Butler generously shared some of his research and publications about Mead's life. Michael E. Toliver kindly reviewed the manuscript and offered helpful comments. Finally, I thank Andy Warren, a respected authority on Colorado butterflies, for thoroughly reviewing drafts of the manuscript and providing much valuable input.

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Submitted for publication 27 May 2014; revised and accepted 25 August 2014.

Journal of the Lepidopterists' Society
69(1), 2015, 39–49

A NEW NAME FOR ALPINE POPULATIONS OF *HESPERIA COLORADO* (SCUDDER) (HESPERIIDAE, HESPERIINAE) IN COLORADO

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ABSTRACT. A reevaluation of the lectotype and type locality of *Pamphila* (=*Hesperia*) *colorado* Scudder indicates that populations in Colorado which were described as *Hesperia comma oroplata* Scott (=*H. colorado oroplata*) are synonymous. Based on an examination of numerous specimens, a new subspecies is described for alpine (mainly above timberline) populations in Colorado, which were previously attributed to the nominotypical subspecies. Patterns of geographic variation observed among subspecies of *H. colorado* in Colorado and bordering states are also reviewed.

Additional key words: cline, Colorado, *Hesperia comma oroplata*, *H. colorado idaho*, *H. colorado ochracea*

Based on the 1871 journal of Theodore L. Mead (1852–1936), the type locality of *Pamphila colorado* Scudder (now recognized as *Hesperia colorado*) was clarified by Calhoun (2015) to "Twin Lakes, along the northern shore of Upper Twin Lake (the western lake), Lake County, Colorado." A male specimen, figured by Scudder (1874, Pl. 10, fig. 18) as "collected July 13, by T. L. Mead," was designated as the lectotype by Barnes and McDunnough (1916). The claspers of a male paralectotype, collected by Mead on the same date as the lectotype, also were figured by Scudder (1874, Pl. 11, figs. 10, 11). Both of these specimens are deposited in the Museum of Comparative Zoology (Harvard University, Cambridge, Massachusetts; MCZ).

The lectotype (Fig. 1), and its type locality, are inconsistent with the popular notion that nominotypical *colorado* is a dark, biennially-brooded taxon that occurs in Colorado above 3048 m (10,000 ft.) in elevation (Calhoun 2015) (Figs. 2, 4-12). Rather, the lectotype fundamentally agrees with populations now recognized as *Hesperia colorado oroplata*, originally described by Scott (1981) as *Hesperia comma oroplata* to define more brightly-colored, lower-elevation populations "from the Arkansas River Valley south of Buena Vista to the Royal Gorge [in Colorado], south to the Sangre de Cristo Mts. of New Mexico, and the San Luis Valley of Colorado." The lectotype of *colorado* was collected at an elevation of roughly 2819 m (9250 ft.), within an area that Scott (1975) identified as a transition zone between *oroplata* and higher-elevation populations, which he and other authors attributed to nominotypical *colorado.* Populations within the purported transition zone (which includes the corrected type locality of *H. c. colorado*), as well as those within the range of *oroplata*, should all be considered to represent *H. c. colorado*. They form a smooth, subtle cline, with populations at lower elevations (i.e., *oroplata*, sensu Scott 1981) producing slightly larger and tawnier adults with somewhat reduced dark maculation.

We believe that the dusky, biennially-brooded populations at higher elevations in Colorado, previously identified as nominotypical *colorado*, should continue to be recognized on the basis of consistent morphological and biological differences. Scott (1975a, 1975b, 1986) likewise considered such populations to be genetically discrete. We therefore describe a new subspecies to characterize alpine populations that occur near and above timberline in north-central Colorado.We also review the general distributions of adjacent subspecies in Colorado and bordering states: *Hesperia colorado colorado*, *H. colorado ochracea* Lindsey and *H. colorado idaho* (W. H. Edwards).

METHODS

Specimens were examined (see below) from several collections, most notably the extensive holdings of *Hesperia* in the McGuire Center for Lepidoptera and Biodiversity (Florida Museum of Natural History, University of Florida, Gainesville, Florida; MGCL), and the C. P. Gillette Museum of Arthropod Diversity (Colorado State University, Fort Collins, CO; CSU), as well as the personal collection of Andrew D. Warren (Castle Pines, Colorado; ADW). Images of relevant specimens were obtained from other collections,

including MCZ. Fieldwork on various *H. colorado* populations has been conducted throughout Colorado nearly annually by the senior author since 1989, with a special focus on alpine habitats in the Mosquito and Front ranges since 2006. Elevations and coordinates cited herein were obtained from Google Earth.

RESULTS

Hesperia colorado sublima A. Warren & Calhoun, **new subspecies**

(Figs. 2-12)

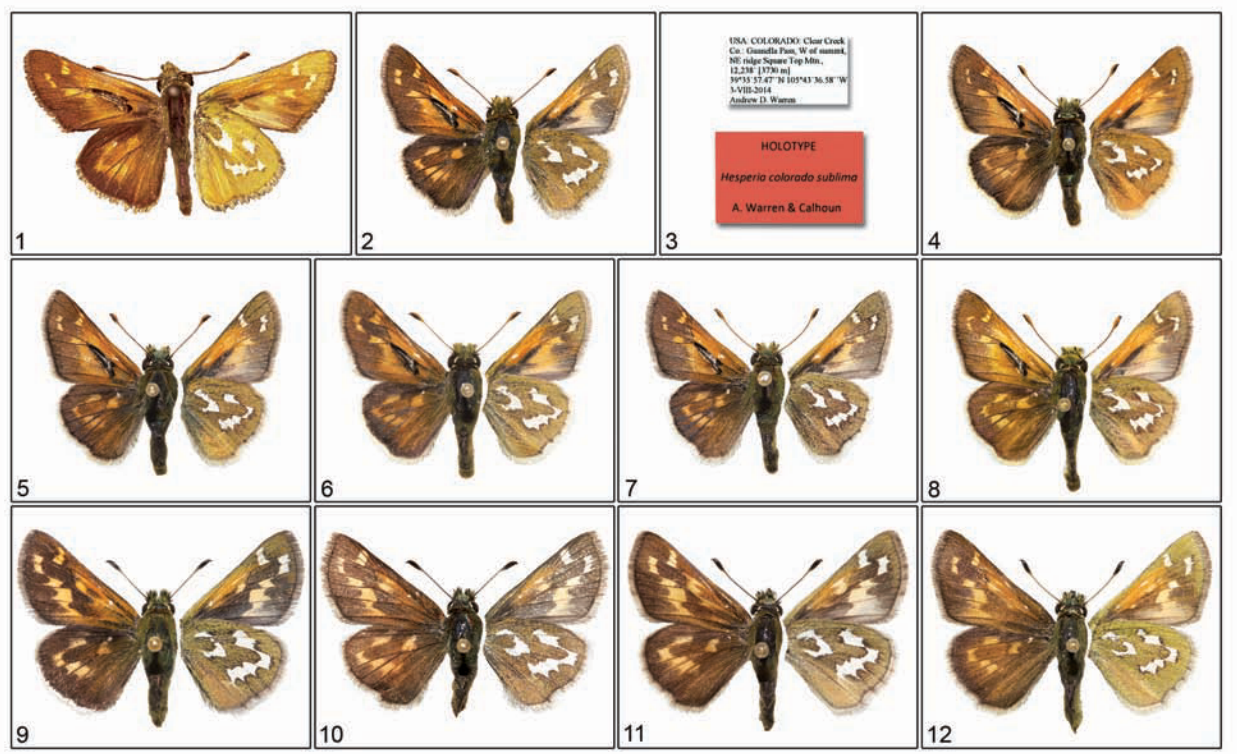
Diagnosis. This taxon is well recognized in the literature, thus we do not believe that a lengthy diagnosis is necessary here (but see remarks below). In general, *sublima* is separated from other subspecies of *Hesperia colorado* by its dark ground coloration on the dorsal and ventral surfaces, well-developed white ventral markings somewhat intermediate between those of *H. c. ochracea* and *H. c. idaho*, smaller adult size, alpine distribution (above about 3146 m/10,321 ft.), and mostly or entirely biennial voltinism. The ventral coloration of *sublima* is more olivaceous, sometimes significantly more greenish-brown, than in other subspecies. Its known distribution to date includes alpine habitats in the Front and Mosquito ranges of Colorado.

Description. Male (Figs. 2, 4–8), mean forewing length = 14.0 mm (13.7–14.3 mm, n = 10); *dorsal forewing* ground color dark orange, with broad brown-black outer margin variably extending into basal two-thirds of wing, often completely encircling the subapical spots; entire wing surface covered with sparse orange overscaling in fresh individuals; small, pale orange spots as follows: rectangular, subapical, in cells R_3, R_4 and R_5; square, distad in M_1 and M_2; trapezoidal, larger, in M_3, frequently conjoined with broad medial and basal orange areas, which extend to base of wing; broad, shiny, gray bipartite stigma in basal portions of cells CuA2 and CuA1, bordering the discal cell; stigma surrounded on all sides by dark black scales; fringe grayish brown, paler towards tornus. *Dorsal hindwing* with reduced tawny coloration, dark orange ground color may be poorly- or well-developed; costal margin dark black, outer margin brown-black, often with indistinct border basad; most of wing, save costal and anal margins, covered with sparse orange overscaling in most individuals when fresh; small, pale orange spots as follows: trapezoidal, in mid cell Rs; trapezoidal, rectangular or hourglass-shaped, distad, in M_1–M_2; trapezoidal, in mid M_3; rectangular, in mid CuA1, generally aligned with spot in M_3; rectangular or linear, poorly defined and often nearly concolorous with ground color in CuA2, usually aligned slightly basad of that in CuA1; trapezoidal, round or rectangular, at distal end of discal cell; fringe mostly grayish, as on forewing tornus. *Ventral forewing* pattern mostly like that of dorsal surface, orange ground color more restricted, stigma replaced by dark black patch, extending diffusely distad along vein CuA1; costal cell darkest orange, markings paler distad to yellowish or whitish in cell CuA2; distal third of wing with dense olivaceous or greenish-brown overscaling; spots positioned as on dorsal surface, but are white in color, save that in cell M_3, which is pale orange to whitish; pale areas in cells CuA1 and CuA2 with ill-defined to well-defined distal borders; fringe as on dorsal surface. *Ventral hindwing* ground color entirely olivaceous or greenish-brown to grayish; spots mainly as on dorsal surface but slightly larger, white, with very distinct borders, usually surrounded by blackish scales; an additional small, triangular spot variably present in cell $Sc+R_1$, aligned with or just basad of spot in Rs; spot at distal end of discal cell variably enlarged, often arching basad (or sometimes bipartite) into basal parts of cells Rs and $Sc+R_1$, and into the basal part of cells M_3 and/or CuA2; fringe as on dorsal surface.

Female (Figs. 9-12), mean forewing length = 15.1 mm (14.7 – 15.7 mm, n = 10); *dorsal forewing* largely like that of male, wings somewhat more produced and rounded at distal margin; orange ground color generally reduced to basal third of wing (though may be more extensive distad); stigma replaced by broad dark brown-black patch, medial orange areas replaced by variably well-defined spots; spots generally as on male, usually larger and paler, with additional large, rectangular or irregularly-shaped yellowish to pale orange spots in cells CuA1 and CuA2; yellowish spots at distal end of discal cell, often conjoined; fringe as on male. *Dorsal hindwing* generally patterned as on male, spots usually paler, additional triangular spot in cell $Sc+R_1$ sometimes present; fringe as on male. *Ventral forewing* as on male, but with broader median dark area and additional spots as on dorsal surface in CuA1, CuA2 and discal cell; fringe as on male. *Ventral hindwing* as on male, spots generally larger and bolder; fringe as on male.

Types. Holotype ♂ (Fig. 2) with the following labels (Fig. 3): white, printed: / **USA: COLORADO: Clear Creek / Co.**: Guanella Pass, W of summit, / NE ridge Square Top Mtn., / 12,238' [3730m], / 39°35'57.47"N 105°43'36.58"W / 3-VIII-2014 / Andrew D. Warren /; red, printed: HOLOTYPE / *Hesperia colorado sublima* / A. Warren & Calhoun /. The holotype is deposited at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (MGCL). **Paratypes.** All from **USA: COLORADO**. **Boulder Co.**: Arapahoe Pass, 17-VIII-1968, R. Stanford (1♂, CSU); nr. Ward Dam, Indian Peaks, 29-VII-1952, F. M. Brown (1♂, MGCL); Rollins Pass Rd., 8.6–9.4 rd. mi. NE Jct. East Portal Rd. (Rd. 16), 10,500'-11,000', 3-VII-2012, A. Warren (1♂, ADW); **Clear Creek Co.**: below Loch Lomond Res., Steuart Rd., 1.8 rd. mi NW Alice Rd., 11,033' [3363 m], 39°49'42"N 105°40'24"W, 3-VIII-2012, A. Warren (1♀, ADW); Grays Peak, 27-VIII-1941, R. Whittaker (1♀, MGCL); Guanella Pass, hilltop just W of summit, 11,700' [3566 m], 39°35'44.81"N 105°42'48.87"W, 18-VII-2006, A. Warren (10♂, 2♀, ADW); 18-VII-2012, A. Warren (3♂, 2♀, ADW); Guanella Pass, W of summit, NE ridge Square Top Mtn., 12,139'–12,238' [3700–3730 m], vic. 39°35'57.47"N 105°43'36.58"W, 22-VII-2012, A. Warren (54♂, ADW); 3-VIII-2014, A. Warren (61♂, 3♀, ADW) (Figs. 4–7, 9, 10); Loveland Pass, 29-VII-2000, T. Stoddard (2♂, ADW); Loveland Pass, 12,000–13,000', 12-VIII-1973, M. Fisher (1♂, MGCL); 10-VIII-1975, M. Fisher (1♂, MGCL); 22-VII-1989, M. Fisher (2♂, MGCL); Mt. Goliath, Mt. Evans Rd., 11,000', 6-VIII-1976, M. Fisher (1♂, MGCL; 1♂, ADW); **Clear Creek – Summit Cos.**: Loveland Pass, 12,000', 10-VIII-1975, M. Fisher (1♂, MGCL); **Gilpin Co.**: Corona Pass Rd., 10–12,000', 19-VIII-1973, R. Stanford (1♂, CSU); **Park Co.**: Boreas Pass, 11,500', 16-VIII-1957, A. C. Allyn (2♂, MGCL); Gold Dust Trail, Trout Creek trailhead, 1.7 mi WNW jct. Boreas Pass Rd. (FR 404), 10,348' [3154 m], 39°21'37"N 105°57'09"W, 14-VII-2006, A. Warren (1♂, ADW); Guanella Pass Rd. (FR 118), ca. 1 air mi S Clear Creek Co. line, along Duck Creek, 10,321' [3146 m], 39°33'13"N 105°43'16"W, 18-VII-2006, A. Warren (3♂, ADW); Hall Valley, 17-VIII-1941, R. Whittaker (2♂, MGCL); Hall Valley, 10,500-11,500', 29-VII-1968, M. Fisher (2♂, 1♀, MGCL); Hoosier Pass, 12,500', 12-VII-1985, M. Minno (1♂, MGCL); Hoosier Pass summit, 2-VIII-1994, R. Romeyn (2♂, MGCL); Horseshoe Mountain, NE ridge, 12,060' [3675 m], 39°11'42.66"N 106°09'30.94"W, 8-VII-1994, A. Warren (3♂, 1♀, ADW); 23-VII-1994, A. Warren (15♂, ADW); 1-VII-2006, A. Warren (1♀, ADW) (Fig. 12); 13-VII-2006, A. Warren (2♂, 1♀, ADW) (Figs. 8, 11); Jct. of FS 416 & 415, W of Alma, 30-VII-1980, L. Dorr (1♂, MGCL); Pennsylvania Mt., 18-VIII-1977 (1♂, CSU); Selkirk Campground, along upper Tarryall Ck., below Boreas Pass Rd., 10,466' [3190 m], 39°22'14"N 105°57'04"W, 14-VII-2006, A. Warren (1♂, ADW); W above Hoosier Pass, 11,500', 30-VII-1982, J. Scott (2♂, MGCL); 3-VIII-1982, J. Scott (8♂, MGCL); **Summit Co.**: W side Loveland Pass, 11,500', 16-VIII-1993, R. Stanford (1♂, CSU).

Etymology. Alluding to the occurrence of this taxon at high elevations, the name *sublima* (pronounced "sub-



FIGS. 1-12. Specimens of *Hesperia c. colorado* and *H. c. sublima* from Colorado (dorsal/ventral). Forewing lengths are base to apex. **1**, lectotype of *Pamphila colorado* (slightly enlarged), 13.vii.1871, [Twin Lakes, Lake Co.], ca. 2819 m (9250 ft.) (14.4 mm) (MCZ-ENT0015299). **2**, holotype of *H. c. sublima* (male), 3.viii.2014, Guanella Pass, Clear Creek Co., 3730 m (12,238 ft.) (14.3 mm) (MGCL). **3**, labels of holotype (slightly enlarged). Paratypes of *H. c. sublima*: **4**, male, 3.viii.2014, Guanella Pass, Clear Creek Co., 3700-3730 m (12,139-12,238 ft.) (13.8 mm) (ADW); **5**, male, 3.viii.2014, Guanella Pass, Clear Creek Co., 3700-3730 m (12,139-12,238 ft.) (13.9 mm) (ADW); **6**, male, 3.viii.2014, Guanella Pass, Clear Creek Co., 3700-3730 m (12,139–12,238 ft.) (14.0 mm) (ADW); **7**, male, 3.viii.2014, Guanella Pass, Clear Creek Co., 3700-3730 m (12,139-12,238 ft.) (13.9 mm) (ADW); **8**, male, 13.vii.2006, Horseshoe Mtn., Park Co., 3675 m (12,060 ft.) (14.1 mm) (ADW); **9**, female, 3.viii.2014, Guanella Pass, Clear Creek Co., 3700-3730 m (12,139-12,238 ft.) (14.7 mm) (ADW); **10**, female, 3.viii.2014, Guanella Pass, Clear Creek Co., 3700-3730 m (12,139-12,238 ft.) (15.7 mm) (ADW); **11**, female, 13.vii.2006, Horseshoe Mtn., Park Co., 3675 m (12,060 ft.) (14.8 mm) (ADW); **12**, female, 13.vii.2006, Horseshoe Mtn., Park Co., 3675 m (12,060 ft.) (15.0 mm) (ADW).

lime-a") is a feminine Latin adjective meaning lofty or elevated. It is in gender agreement with the feminine noun *Hesperia*. The English derivative "sublime" is a fitting tribute to the grandeur of this butterfly's montane habitat.

Remarks. *Hesperia colorado* displays considerable geographic variation in Colorado, largely corresponding with the major river drainages in the state. East of the Continental Divide and below timberline, two main groups of populations are found. *Hesperia colorado ochracea* occupies the South Platte River drainage in Larimer, Boulder, Gilpin, Clear Creek, Jefferson, Douglas, and eastern Park counties, and extends into Teller and El Paso counties. As suggested by Scott (1975), populations in far southern Teller County (Cripple Creek area) and far northeastern Fremont County (if present), may be intermediate between *H. c. ochracea* and *H. c. colorado*; we've examined just one male specimen from this area, which indeed does look intermediate. Records from Adams and Arapahoe counties (Stanford 2002) represent single individuals, presumably strays from the west or south. The distribution of *H. c. ochracea* includes montane habitats in the Front Range, including the Rampart Range, Kenosha Mountains, Tarryall Mountains, and the Pikes Peak area to the south. As with all sets of *H. colorado* populations in Colorado and neighboring states, adults from the lowest-elevation populations of *H. c. ochracea* (1676–2591 m/ 5500–8500 ft.) are the largest and tawniest, progressively becoming smaller and darker, above and below, with increasing elevation. Reports of *H. comma manitoba* (Scudder) from Colorado (Brown et al. 1956, Stanford 1981) represent higher-elevation populations of *H. c. ochracea* (2591-3048 m/ 8500-10,000 ft.), which appear to interact or intergrade with *H. c. sublima* in a few Front Range localities (e.g.,

Tolland [= East Portal], Gilpin Co., 2810 m/ 9220 ft.). To the north, in northern Larimer and Weld counties, Colorado, as well as all of southern Wyoming and far western Nebraska, *H. colorado idaho* replaces *H. c. ochracea.* There is a narrow zone of intergradation between these taxa in northwestern Larimer County, Colorado, roughly from north of the Cache la Poudre River to the Wyoming state line, which is the area where the southern end of the Laramie Mountains meets the northern end of the Front Range.

To the south of *H. c. ochracea* in Colorado, in the Arkansas and Rio Grande River drainages, flies *H. c. colorado* (including *oroplata*, sensu Scott 1981), in Lake, Chaffee, Fremont, Custer, Pueblo, Huerfano, Las Animas, central and eastern Saguache, Alamosa, Costilla, Conejos, Mineral and Rio Grande counties, extending into the upper San Juan River drainage in Archuleta and La Plata counties. Smaller, darker adults are found at higher elevations (roughly above 2896 m/ 9500 ft.), but below timberline, in the San Juan Mountains (San Juan, Hinsdale, southern Ouray and presumably Mineral counties; see below). *Hesperia c. colorado* also occurs in northern New Mexico, in Colfax, Los Alamos, Mora, Rio Arriba, Sandoval, San Miguel, Taos, and Union counties (Toliver et al., 2001). The distribution of *H. c. colorado* includes montane and canyon habitats in the upper Arkansas River Valley, Wet Mountains, Sangre de Cristo Mountains, Raton Mesa Complex, the eastern and southern slopes of the San Juan Mountains, and the Jemez Mountains in New Mexico. As with *H. c. ochracea* and *H. c. idaho* (see below), adults of *H. c. colorado* are largest and tawniest at lower elevations (2050–2740 m/ 6725–9000 ft.), where occasional adults, especially females, resemble *H. c. ochracea* (e.g., Wet Mountains, Custer County; Raton Mesa Complex, Las Animas-Colfax counties). Adults become somewhat smaller and darker above and below with increasing elevation, up to about 3500 m (11,483 ft.) in the Sangre de Cristo Mountains of Taos County, NM (Wheeler Peak). It is unclear exactly where *H. c. colorado* is replaced to the west by *H. c. idaho.* Specimens examined from the upper San Juan River drainage, on the south slope of the San Juan Mountains (e.g., Archuleta and La Plata counties, CO; western Rio Arriba Co., NM) are consistent with the phenotype of *H. c. colorado*, as are occasional adults from the western slope of the San Juan Mountains (e.g., Dolores and San Miguel counties, CO) and the La Sal Mountains of Utah. Material from the vicinity of Mesa Verde National Park, Montezuma County, CO (ca. 2591 m/ 8500 ft.), more closely resembles *H. c. idaho* than *H. c. colorado*, although very little material from this area has been examined. The few specimens seen from the Cochetopa Hills (Saguache Co., CO), a low point in the Continental Divide separating the Rio Grande and Gunnison River drainages northeast of the San Juan Mountains, as well as more extensive series from Monarch Pass, separating the Arkansas River drainage from the Gunnison River drainage, are analogous and could be assigned to either subspecies. For now, other than populations from the upper San Juan River drainage (listed as *H. c. colorado*), specimens from all of these areas are listed under *H. c. idaho* (see below), although relationships between the two taxa should be studied in more detail. Further research may suggest that these taxa are best considered synonymous.

Specimens from higher elevations (above 2835 m/ 9300 ft.) in the San Juan Mountains of Colorado, as seen elsewhere in the range of *H. colorado*, are smaller and darker than adjacent populations at lower elevations. A few of these specimens generally resemble *H. c. sublima*, but overall they have better-developed ventral markings, suggesting a closer affinity to *H. c. colorado* and/or *H. c. idaho.* We don't know if *H. colorado* flies above timberline (roughly 3530–3650 m/ 11,581–11,975 ft.) in the San Juan Mountains, or if any populations there are biennially-brooded; no such material has been encountered to date. For now, we consider all material in the San Juan Mountains above about 2835m (9300 ft.) to represent dark *H. c. colorado* and/or *H. c. idaho* "montane forms" (sensu Warren 2005), with the caveat that if biennial, truly alpine populations exist there, they may be more closely allied with *H. c. sublima.*

West of the Continental Divide in Colorado and north of the San Juan Mountains, throughout the Uncompahgre, Gunnison, Colorado, White and Yampa River drainages, and east of the Continental Divide in the North Platte (Jackson Co.) and potentially the Laramie River (far northwestern Larimer Co.) drainages, as well as in far northern Weld County, all populations below about 3200 m (10,500 ft.) are referable to *H. c. idaho.* This butterfly is very widespread in the state, flying in northwestern Saguache, Gunnison, Ouray, Montrose, Delta, Mesa, Pitkin, Summit, Eagle, Garfield, Rio Blanco, Moffat, Routt, Grand, Jackson, and perhaps far northwestern Larimer counties. Throughout the extensive overall range of this taxon, including essentially all of the Columbia and Great basins and most of the southern Rocky Mountains, patterns of altitudinal variation resemble those seen in Colorado, with larger, paler adults at lower elevations, and smaller, darker adults at higher elevations. The higher-elevation forms in the Pacific Northwest were termed "montane forms" (Warren 2005).

Finally, in Colorado's Front and Mosquito ranges starting at about 3146 m (10,321 ft.) and becoming common above timberline (3400–3650 m/ 11,155–11,975 ft.), flies *H. c. sublima.* In the Guanella Pass area of Clear Creek and Park counties, as well as along the northern edge of South Park (below Boreas Pass), individuals are rarely found as low as 3146 m (10,321 ft.), but *H. c. sublima* is far more abundant above timberline. The upper elevational limit for this taxon remains to be determined. The largest population with which we are familiar is that at the type locality, situated at 3700–3730 m (12,139–12,238 ft.) in elevation, but it surely ranges higher, perhaps up to 4200 m (13,780') or greater. We know of populations in Boulder (Indian Peaks Wilderness, Rollins [= Corona] Pass), Gilpin (Rollins [= Corona] Pass), Clear Creek (vic. Loch Lomond Reservoir, Loveland Pass, Grays Peak, Guanella Pass area, Mt. Goliath), Summit (Loveland Pass) and northern and western Park (Boreas Pass area, Hall Valley, Hoosier Pass, Horseshoe Mtn., Pennsylvania Mtn., W of Alma, possibly Craig Park) counties, and it likely also occurs in far southwestern Larimer (Longs Peak area) and far eastern Grand (Rollins [= Corona] Pass) counties at and above timberline. It is unknown if *H. c. sublima* extends into the Gore or Sawatch Ranges, and material examined from timberline in the Sangre de Cristo Mountains (Wheeler Peak, Taos Co., NM) represents typical *H. c. colorado.*

As far as we are aware, populations of *H. c. sublima* are mostly or entirely biennially-brooded, based on recent annual studies at Guanella Pass, Clear Creek County (see below). However, even in Clear Creek County, not all populations are synchronized to fly in the same year, and adults fly annually at some sites. We have records from Loveland Pass from even- and odd-numbered years. To the southeast on Mt. Goliath and Guanella Pass, adults apparently only fly in even-numbered years. Most records from the Mosquito Range (Hoosier Pass, Horseshoe Mountain, W of Alma) are from even-numbered years, but the record from Pennsylvania Mountain is from an odd-numbered year, and one of the specimens from Hoosier Pass, likewise, is from an odd-numbered year. Records exist from both even and odd-numbered years from Hall Valley (far northern Park Co.). Sites where adults occur annually may indicate the presence of two discrete biennial populations occurring sympatrically, as has been noted for other alpine and arctic butterfly taxa (e.g. Ferris & Brown 1981).

The population of *H. colorado* at the summit of Tennessee Pass, Eagle-Lake counties, at about 3170 m (10,400 ft.), is interesting in several respects. This population, about 380 m (1250 ft.) below timberline, is significant in that it was employed by Scott (1975, 1981) as a baseline of comparison when developing his concept of the lower-elevation subspecies *H. c. oroplata.* To define *H. c. colorado* as a dark high-elevation taxon (distinct from *oroplata*), Scott (1998) suggested Tennessee Pass as its type locality. However, most adults that we examined from this locality, especially reared adults mentioned by Scott (1975), are closer to topotypical *H. c. colorado* or *H. c. idaho* than they are to *H. c. sublima* as defined herein, although several (about 35%) are indistinguishable from *H. c. sublima.* From the summit of Tennessee Pass, populations at lower elevations to the south are typical *H. c. colorado*, and those at lower elevations to the north, in Eagle County, are *H. c. idaho*, although these two sets of populations, as elsewhere where the ranges of *H. c. colorado* and *H. c. idaho* meet, are quite similar in appearance. Just above the summit of Tennessee Pass, to the southeast, is Ski Cooper ski area, with ski runs extending southeast nearly to timberline on Buckeye Peak, which constitutes the southernmost end of the Gore Range, although it is essentially attached to the Mosquito Range via Climax and Fremont Pass; to the west of Tennessee Pass lies the Sawatch Range. Tennessee Pass therefore appears to represent a unique population of *H. colorado*, with apparent influences from *H. c. colorado* to the south, *H. c. idaho* to the north, and probably, *H. c. sublima* at higher elevations to the east. Collection records suggest that adults fly every year on Tennessee Pass. Variability in this population suggests that continued surveys for *H. colorado* at and above timberline in the Gore and Sawatch ranges should be conducted to determine the western and southern distributional limits of *H. c. sublima.* Most of the potential habitats in these ranges lie within wilderness areas that are off limits to motor vehicles, thus surveys there would require significant effort.

Hesperia colorado sublima is apparently endemic to Colorado. In Wyoming, all material we've examined from at and above timberline in the Snowy and Wind River ranges corresponds with smaller, darker "montane forms" of *H. c. idaho*; the population above timberline on the Beartooth Plateau, on the Wyoming-Montana border, appears closest to *H. comma manitoba.* Given that we haven't detected *H. c. sublima* from alpine habitats in the Sangre de Cristo Mountains (populations there are referable to *H. c. colorado*, as noted above), and populations at higher elevations in the San Juan Mountains appear to be "montane forms" of *H. c. idaho* and or *H. c. colorado*, it appears not to extend into New Mexico. To date, all known populations of *H. c. sublima* occur along or near the Continental Divide, in ranges

where, in a broad sense, *H. c. ochracea* occurs at lower elevations to the east and *H. c. idaho* (or *H. c. colorado* further south) occurs at lower elevations to the west. It is possible that *H. c. sublima* evolved through mixing between *H. c. ochracea* and *H. c. idaho*. While its overall morphology and distribution generally supports this idea, *H. c. sublima* has clearly developed a unique biology, with respect to *H. c. ochracea*, *H. c. idaho* and *H. c. colorado*, in being mostly or entirely biennially-brooded.

The integrity of *H. c. sublima* as a taxon is perhaps best seen in Park County. *Hesperia colorado* is apparently absent from the floor of South Park, constituting one of the only major gaps in the montane distribution of the species in Colorado. Thus, populations on the far southeastern side of the Front Range and east side of the Mosquito Range in Park County (western and northern parts of the county) don't directly abut *H. c. ochracea* to the east, as they do farther north in the Front Range in Clear Creek, Gilpin and Boulder counties. The population of *H. c. sublima* on Horseshoe Mountain is at least 48 km (30 mi) from the nearest populations of *H. c. ochracea* to the east (Wilkerson Pass, potentially Tarryall Creek, potentially E side of Kenosha Pass). These Park County populations have enabled us to define an unambiguous lower distributional limit for *H. c. sublima*, and demonstrate that the taxon is not merely part of a gradual cline between *H. c. ochracea* and *H. c. idaho* or *H. c. colorado*.

The senior author has studied populations of *H. c. sublima* on multiple occasions, mainly at two sites: Horseshoe Mountain, west of Fairplay in Park County (Mosquito Range), and at the type locality above Guanella Pass in Clear Creek County (Front Range). On Horseshoe Mountain, at around 3675 m (12,060 ft.), adults are found primarily on a gently sloping ridgeline just above timberline. Males vigorously defend hilltop perches, and females are usually found nearby, in relatively dry, grassy areas. Adults were sampled in 1994 and 2006, each year in small numbers.

The type locality of *H. c. sublima*, above Guanella Pass in Clear Creek County, has been the focus of field studies on this taxon since 2006. Adults have been found here in 2006 (18 July), 2012 (18 and 22 July) and 2014 (3 August), and were not found, despite intensive searches under ideal field conditions, in 2009 (17 July), 2011 (25 August- a very delayed season), or 2013 (20 and 31 July), suggesting that adults fly only on even-numbered years at this site. Here, males are usually encountered on hilltops or ridgelines above timberline and females may be found anywhere in the landscape, but usually on drier hillsides and ridges. Small numbers of individuals regularly occur on the hilltop 0.2 km (0.12 mi) to the south-southwest of the upper (west) summit parking lot, at 3566 m (11,700 ft.), but adults are far more abundant on the northeastern ridge of Square Top Mountain, about 1.17 km (0.73 mi) to the west of the upper parking lot, at 3700-3730 m (12,139-12,238 ft.). In 2012, adults were very abundant on the northeastern ridge of Square Top Mountain on 22 July, when up to 8 males could frequently be seen at one time, flying around perching sites along the ridgeline, and in pursuit of passing females. On 3 August 2014, adults of *H. c. sublima* were again very abundant on the northeastern ridge of Square Top Mountain, active from 1000 hrs. to about 1300 hrs., when clouds terminated butterfly activity for the day.

Perhaps due to the shorter overall season for butterfly activity in alpine habitats, adults of *H. c. sublima* normally fly two weeks to one month earlier than populations of *H. colorado* below timberline. Mid-July to early August is usually the peak flight period for *H. c. sublima*. Depending upon elevation, annual variation in snowpack, and summer weather, the normal peak flight period for *H. c. colorado*, *H. c. idaho* and *H. c. ochracea* in Colorado is mid-August to early September, with fresh males first beginning to emerge in mid- to late July. For example, in 2014 (a somewhat delayed season), when *H. c. sublima* was at or near its peak flight on Guanella Pass, adults of *H. c. idaho* on the West Slope were just beginning to emerge, and no adults of *H. c. colorado* or *H. c. ochracea* had yet been seen on the East Slope. Despite this, under extreme conditions, adults of all subspecies may fly long before or after the typical peak periods. Evidence from T. L. Mead's 1871 journal, as well as his collected specimens, suggests that some butterfly flight periods were considerably advanced that season compared to modern average norms (Calhoun 2015.). This presumably explains the seemingly early collection date of 13 July for the lectotype and a paralectotype of *Pamphila colorado*. It is also worth noting that Mead apparently collected above timberline in Colorado only in the Mosquito and Sawatch ranges. While we have yet to confirm *H. c. sublima* from the Sawatch Range, adults have mainly been found in even-numbered years in the Mosquito Range, suggesting that Mead would not likely have encountered this taxon in 1871.

Additional material examined. The following specimens were examined during the course of this study, in addition to type material of *H. c. sublima* listed above. For *H. c. colorado* and *H. c. idaho*, we list data from all specimens examined, but for *H. c. ochracea*, which is very abundant in collections, we only list complete data from populations immediately adjacent

to *H. c. sublima* or otherwise discussed in the text.

***Hesperia colorado sublima*: USA: COLORADO: Boulder Co.:** "Sunset", 30-VII-1951, B. Weber (1♂, 1♀, MGCL) [excluded from type series since site could not be located]; **Park Co.**: Craig Park, 10,500', 27-VI-1939, R. Whittaker (1♂, MGCL) [while like *sublima*, this is the only high-elevation specimen examined from the Kenosha-Platte River ranges, territory dominated by *ochracea* at slightly lower elevations to the east; the locality should be revisited to study variation there]; **County unknown**: "Kingston" [possibly referring to a former mining town by this name in Gilpin Co.], 12-VIII-1951, H. A. Freeman (1♂, 1♀, MGCL) [excluded from type series due to imprecise locality information].

***Hesperia colorado sublima / H. c. colorado / H. c. idaho* transition zone: all from USA: COLORADO. Eagle-Lake Cos.**: Tennessee Pass, 10,424', 23-VIII-1969, J. Scott (1♂, MGCL); 15-VIII-1971, J. Scott (13♂, 4♀, MGCL); 9-VIII-1972, J. Scott (11♂, 7♀, MGCL); egg laid about 10-VIII-1972, pup. 29-IX-1972, emg. 14-X-1972, J. Scott (1♂, MGCL); egg laid about 10-VIII-1972, pup. 29-IX-1972, emg. 16-X-1972, J. Scott (1♂, MGCL); egg laid about 10-VIII-1972, pup. 5-X-1972, emg. 21-X-1972, J. Scott (1♀, MGCL); egg laid about 10-VIII-1972, pup. 7-X-1972, emg. 21-X-1972, J. Scott (1♂, MGCL); egg laid about 10-VIII-1972, pup. 7-X-1972, emg. 24-X-1972, J. Scott (1♀, MGCL); egg laid about 10-VIII-1972, pup. 8-X-1972, emg. 22-X-1972, J. Scott (1♂, MGCL); egg laid about 10-VIII-1972, pup. 8-X-1972, emg. 24-X-1972, J. Scott (1♀, MGCL); egg laid about 10-VIII-1972, pup. 9-X-1972, emg. 26-X-1972, J. Scott (1♀, MGCL); egg laid about 10-VIII-1972, pup. 10-X-1972, emg. 26-X-1972, J. Scott (1♀, MGCL); egg laid about 10-VIII-1972, pup. 11-X-1972, emg. 27-X-1972, J. Scott (1♀, MGCL); egg laid about 10-VIII-1972, pup. 12-X-1972, emg. 28-X-1972, J. Scott (1♀, MGCL); 1-VIII-1982, J. Scott (2♂, MGCL); 9-VIII-1996, R. Stanford (1♂, 1♀, CSU).

***Hesperia colorado colorado* "montane form" (San Juan Mts. above 2835 m (9300 ft.): all from USA: COLORADO. Hinsdale Co.**: Mill Creek Campground [2885 m/ 9465 ft.], 10 mi SW Lake City, 27-VII-1996, P. Opler & E. Buckner (1♀, CSU); North Creek, 20-VII-1993, D. & J. Lindsley (3♂, 1f, MGCL); nr. N. Clear Creek Falls, 10,000', 6-VIII-1983, R. Klopshinske (1♂, MGCL); Quiet Valley, Hwy. 149, 9600', 31-VIII-1955, F. M. Brown (6♂, 16♀, MGCL); **San Juan Co.**: Silverton, 16-23-VIII (1♀, MGCL); 2 mi N Silverton at Mineral Ck., 9500', 4-IX-1983, R. Klopshinske (5♂, 3♀, MGCL).

***Hesperia colorado colorado* (incl. *oroplata*, sensu Scott 1981): USA: COLORADO: Alamosa Co.**: Great Sand Dunes, 20-VIII-1958 (1♂, MGCL); Great Sand Dunes Nat. Mon., 8300', 31-VIII-1977, F. M. Brown (1♂, MGCL); 26-VIII-1980, F. M. Brown (8♂, 4♀, MGCL); 18-IX-1980, F. M. Brown (3♂, 1♀, MGCL); Sand Dunes, 7800', 20-VIII-1976, B. Weber (5♂, 1♀, MGCL); **Archuleta Co.**: vicinity of Blanco River Campground, 7200', 28-VII-1988 (1♂, 1♀, MGCL); **Chaffee Co.**: Bear Creek, 5-IX-1997, R. Romeyn (4♂, 2♀, MGCL); big hilltop, 2 mi E Buena Vista, 17-VIII-1971, J. Scott (6♂, MGCL); Greens Creek, 8800', 27-VIII-1974, J. Scott (1♂, MGCL); Lost Creek, 2 mi W Maysville, 9200', 6-IX-1974, J. Scott (2♂, 1♀, MGCL); Otero Pumping Station, between Riverside and Princeton, 17-VIII-1971, J. Scott (1♂, MGCL); Pine Creek, 17-VIII-1971, J. Scott (3♂, 1♀, MGCL); Salida, Spiral Drive, 10-IX-1971, J. Scott (1♂, MGCL); Trout Creek, off Rt. 285, 4-IX-1993, B. Kondratieff (1♂, CSU); 1.6 mi N Granite, 16-VIII-1971, J. Scott (23♂, 1♀, MGCL); 2 mi SE Salida, 2-VIII-1965, J. Scott (2♂, MGCL); 4 mi S Poncha Springs, 29-VIII-1972, J. Scott (1♂, MGCL); **Conejos Co.**: Aspen Glade Campground, 21-VIII-1965, J. Scott (1♀, MGCL); Bighorn Creek, 8900', 16-VIII-1999, P. Pineda (1♂, CSU); Conejos River, near River Springs Guard Station, 14-IX-1968, G. Scott (1♀, MGCL); FS Rd. 250 at Alamosa C.G., above Terrance Res., 8950', 20-VIII-1996, A. Warren (3♂, 3♀, ADW); FS Rd. 271 nr. Cat Ck., N of Terrance Res., 8950', 20-VIII-1996, A. Warren (1♀, ADW); Rd. to Platoro, 20.8 mi W of Hwy. 15 jct. 9300', 13-VIII-1971, T. Emmel (4♂, 1♀, MGCL); Rito Hondo, 21-VIII-1965, J. Scott (1♂, CSU); **Costilla Co.**: nr. Fort Garland, 5-IX-1969, M. Fisher (1♀, MGCL); 5-IX-1969, R. Stanford (1♂, CSU); W La Veta Pass, US 160, 9200', 18-VIII-1992, R. Stanford (1♀, MGCL); **Custer Co.**: Bigelow Divide, 16-VIII-1952, D. Eff (2♂, MGCL; 2♂,1♀, ADW); 24-VIII-1952, D. Eff (1♂, MGCL); Hardscrabble Canyon, 22-VIII-1972 (2♂, CSU); Querida, 1-IX-1962, J. Scott (1♂, MGCL); Silver Park, 1-IX-1962, J. Scott (1♀, MGCL); **Fremont Co.**: Cotopaxi, 23-VIII-1969, R. Stanford (5♂, CSU); Currant Ck., 15 mi NW Canyon City, 1-IX-1974, M. Fisher (2♀, MGCL); Kerr Gulch, 19-VIII-1973, J. Scott (1♂, MGCL); Kuntz Gulch, 26-VIII-1970, J. Scott (1♀, MGCL); nr. Cotopaxi, 5-VIII-1969, M. Fisher (2♂, MGCL); Oak Creek, 19-IX-1968, J. Scott (2♂, MGCL); Oak Creek, nr. Cotopaxi, 23-VIII-1969, M. Fisher (10♂, 2♀, MGCL); Spring Ck., 15-VIII-1965, J. Scott (2♂, MGCL); 31-VII-1969, J. Scott (1♂, MGCL); 2-VIII-1969, J. Scott (1♂, MGCL; 1♂, CSU); 7-VIII-1969, J. Scott (1♀, MGCL); 1 mi NE Calcite, 29-VII-1965, J. Scott (3♂, MGCL); 3 mi SW Cotopaxi, 3-VIII-1965, J. Scott (1♂, MGCL); **Huerfano Co.**: nr. La Veta, 7600', 9-IX-1973, R. Stanford (2♀, CSU); **Lake Co.**: Mt. Massive Trout Club, 15-VIII-1971, J. Scott (1♂, MGCL); 16-VIII-1971, J. Scott (31♂, MGCL); **La Plata Co.**: Radio Hill, SW of Durango, 20-VIII-1980, J. Scott

(1♂, MGCL); Rockwood, Elbert Ck., at N end Shalona Lake, 7500', 19-VIII-1996, A. Warren (2♂, 6♀, ADW); **Las Animas Co.**: Lift to peak on Raton Pass, 13-IX-1969, M. Fisher (6♀, MGCL); N of Rd. to Sugarite Ski Lodge, 7550', 9-VIII-1988, J. & F. Preston (1♂, MGCL); North Lake, 8-IX-1973, M. Fisher (1♂, 1♀, MGCL); nr. North Lake, 86-9000', 8 mi N Stonewall, 9-IX-1973, R. Stanford (10♂, 11♀, CSU); Raton Pass, 13-VIII-1951, H. A. Freeman (3♂, MGCL); 13-IX-1969, R. Stanford (1♂, CSU); S side San Francisco Pass, S slope, Raton Mesa Complex, N of Sugarite Canyon SP, 4.5 mi S CO Rd. 12.5 on Co. Rd. 85.5, 8000', 6-VIII-1996, R. Holland (3♂, CSU); Stonewall, 21-VIII-1980, J. Scott (1♂, MGCL); **Mineral Co.**: Wolf Creek Camp, 8400', 20-VII-1952, J. & F. Preston (1♂, MGCL); **Rio Grande Co.**: Del Norte area, "D" Mt., 7-VIII-1976, M. Fisher (1♂, MGCL); **Saguache Co.**: Bonanza Rd., 1 mi S Villa Grove, 7800', 20-VIII-1966, S. Ellis (1♀, MGCL); Harry Ck., E side Marshall Pass, 5-IX-1975, J. Harry (2♂, 2♀, MGCL); Poncha Pass, 9000', 11-VIII-1979, J. & F. Preston (1♂, 1♀, MGCL); Raspberry Ck., 8200', 22-VIII-1965, J. Scott (2♂, MGCL); Rito Alto Ck., 9-VIII-1970, J. Scott (1♂, MGCL); Wild Cherry Ck., 16-VIII-1974, J. Scott (1♂, MGCL); 1 mi E of North Cochetopa Pass, CO 14, 9500', 11-VIII-1996, R. Stanford (2♂, ADW); 1 mi W Villa Grove, 7800', 20-VIII-1966, S. Ellis (1♀, MGCL); 5 mi W Villa Grove, 4-VIII-1969, J. Scott (1♂, MGCL); 7 mi W La Garita, 4-VIII-1970, J. Scott (1♂, CSU; 1♂, MGCL); 13 mi S Parlin, 8800', 30-VII-1933, Chadwick & Davenport (1♂, MGCL); **NEW MEXICO: Colfax Co.**: Bartlett Mesa, 8100', 22-VIII-1980, J. Scott (1♂, MGCL); NM 21, 5 mi NW Rayado, 6800', 17-IX-1995, S. Cary (1♂, CSU); Porcupine Trail Camp, Philmont Scout Ranch, nr. Cimmaron, 24-VIII-1958, C. P. Slater (1♂, MGCL); Raton Mesa, 24-VIII-1969, J. Scott (2♂, MGCL); 24-VIII-1979, J. Scott (2♂, MGCL); 21-VIII-1980, J. Scott (8♂, 4♀, MGCL; 1♀, CSU); Red Hill, Johnson Mesa, E of Raton, 8400', 27-VII-1996, R. Holland, S. Cary (1♂, CSU); Sodapocket Campground, Sugarite State Park, 8000', 3-IX-1992, J. & F. Preston (10♂, 8♀, MGCL); **Los Alamos Co.**: nr. Los Alamos, 8000', 16-IX-1973, R. Stanford (3♂, 5♀, CSU); USFS Rd. 1, 8000–9000', 4 mi W Los Alamos, E slope, Jemez Mts., 31-VII-1984, S. Cary (1♂, CSU); **Mora Co.**: Chacon, 26-VIII-1978, J. Scott (1♂, 1♀, MGCL); Ocate Mesa, 10 mi NW Ocate, 16-VIII-1987, S. Cary (2♂, CSU); **Rio Arriba Co.**: Bear Spring, FS 64, 2 mi N FS 77, 9000', 31-VIII-1985, R. Holland (1♀, CSU); FS 77, 0.5 mi N NM 96, Santa Nino, nr. Gallena, N Jemez Mts., 8000', 31-VIII-1985, R. Holland (2♂, 1♀, CSU); Tusas Ridge, W of Tres Piedras, 5-IX-1969, R. Stanford (1♂, CSU); 2 mi E NM 112 on NM 96, N Jemez Mts., 1-IX-1985, R. Holland (1♀, CSU); 2 mi N Gallina on FS 8, 8000', Jemez Mts., 1-IX-1985, R. Holland (2♀, CSU); 4 mi W Deadman Lookout, N. ext. Jemez Mts., 8700', 8-IX-1984, R. Holland (5♂, 11♀, CSU); 14 mi NW Chama, 21-VIII-1969, J. Schaffner (1♀, ADW); **Sandoval Co.**: Agua Sarca, nr. Mesa Poleno, 8000', N slope Jemez Mts., 12-VIII-1984, R. Holland (1♀, CSU); 9-IX-1984, R. Holland (3♂, 2♀, CSU); Bear Paw Lake, NW slope Jemez Mts., 7600', 31-VII-1984, R. Holland (1♂, CSU); 9-IX-1984, R. Holland (5♂, 3♀, CSU); Sec. 20, 5 mi N NM 126 on FS 376, W-cent. Jemez Mts., 8200', 1-VIII-1984, R. Holland (2♂, CSU); 1 mi S Regina, 7500', NW slope Jemez Mts., 9-IX-1984, R. Holland (2♂, 5♀, CSU); **San Miguel Co.**: Santa Fe Nat. For., Pecos, 31-VII-1989, P. Milner (1♂, MGCL); **Taos Co.**: Arroyo Hondo, 1 mi NE Nat. For. boundary, 7500', 24-VIII-1985, R. Holland (2♂, CSU); Big Arsenic Spring, Rio Grande Gorge, 9-VIII-1986, S. Cary (1♀, CSU); Chawa Lama Overlook, E side, Rio Grande Gorge, 7000', 24-VIII-1985, R. Holland (5♂, CSU); Ranchito, 27-VIII-1978, J. Scott (1♂, 2♀, MGCL); Red River, 8900', 27-VIII-1960, H. A. Freeman (2♂, 1♀, ADW); 28-VIII-1960, H. A. Freeman (1♂, ADW); Red River Pass, 9850', 27-VIII-1960, H. A. Freeman (2♀, ADW); Wheeler Peak Tr., 3500m, 2-VIII-1989, P. Milner (1♂, MGCL); **Union Co.**: Capulin Mt., Crater Rim Trail, 8000', 20-VIII-1969, F. M. Brown (4♂, MGCL); Capulin Volcano, summit, 8700', 22-IX-1996, R. Holland (1♂, 2♀, CSU); Sierra Grande, E slope, 16-VIII-1997, S. Cary (1♂, 1♀, CSU); trail from Sierra Grande parking area to summit, NE slope, 7200'–8700', 20-VII-1997, S. Cary (1♂, CSU); 17-VIII-1997, S. Cary (2♂, CSU).

***Hesperia colorado idaho*: USA: COLORADO. Delta Co.**: Coal Creek, nr. Somerset, 2-VIII-1969, M. Fisher (1♀, MGCL); Crystal Creek Campground, 6600', 20-VIII-1965, M. Fisher (2♂, MGCL); Crystal River Canyon, 6600', 20-VIII-1965, M. Fisher (1♂, 1♀, MGCL); Leroux Ck. Rd., 7500', 9-VIII-1962, S. Ellis (1♂, 2♀, MGCL); 23-VIII-1962, S. Ellis (4♂, 3♀, MGCL); 3-IX-1962, S. Ellis (3♂, 4♀, MGCL); 25-VII-1964, S. Ellis (1♀, MGCL); 7-VIII-1964, S. Ellis (2♂, MGCL); 15-VIII-1964, S. Ellis (4♂, MGCL); 21-VIII-1964, S. Ellis (1♂, MGCL); 31-VIII-1964, S. Ellis (1♂, MGCL); Ponkey's Peak, 0.5 mi N Crawford, 7386', 17-VIII-1966, M. Fisher (1♂, 1♀, MGCL); 10–15 mi E Somerset, 18-VII-1971, D. Lindsley (3♂, MGCL); **Eagle Co.**: Hwy. 141, ca. 5.5 mi N of Wolcott, 2317m, 39°46'11"'N 106°40'52"W, 28-VII-2014, A. Warren (13♂, ADW); Hwy. 141, ca. 8.5 mi N of Wolcott, 2496m, 39°48'30"N 106°40'35'W, 10-VII-2012, A. Warren (2♂, ADW); Hwy. 141, mi. 17.2, along Colorado River just NW of Bond, 2038m, 39°53'03"N 106°41'46"W, 10-VII-2012, A. Warren (1♂, ADW); 28-VII-2014, A. Warren (4♂, ADW); Minturn, 1-VIII-1984, D. L. Bauer (1♂,

MGCL); W of Wolcott, 8500', 27-VII-1964, S. Ellis (2♂, MGCL); 5 mi W Gypsum, 6500', 11-VIII-1972, M. Fisher (15♂, 13♀, MGCL); 5 mi W jct. 131 & Rd. to Burns, 13-VIII-1972, M. Fisher (1♀, MGCL); 7 mi NE State Bridge, 7000', 13-VIII-1972, M. Fisher (1♂, 2♀, MGCL); **Garfield Co.**: Rim Road above Tichner Dr., 9200', 9-VIII-1996, C. Slater (1♂, 1♀, CSU); Roan Plateau, JQ5 Trail, 6000', 7-VIII-1996, C. Slater (2♂, 2♀, CSU); **Grand Co.**: Beaver Creek Jct., 12-VIII-1967, R. Stanford (5♂, CSU); Co. Rd. 50, 0.2-2.2 rd. mi SE Hwy. 40, 2330–2435m, from 40°03'06''N 106°07'42''W to 40°01'57''N 106°06'42''W, 25-VII-2014, A. Warren (4♂, ADW); Co. Rd. 50, 3 mi SE jct. US Hwy. 40 (8 mi SW Hot Sulphur Spgs.), 7-VII-1989, A. Warren (1♂, ADW); E side Gore Pass, milepost 21, SH 134, 8600', 15-VIII-1980, J. & F. Preston (9♂, 10♀, MGCL); Lake Granby, 19-VIII-1978, M. Minno (5♂, MGCL); Lost Bob Gulch, Shadow Mtn., 10,000', 6-VIII-1955, F. M. Brown (1♂, MGCL); Parshall, 19-VIII-1911 (1♂, CSU); 21-VII-1974, T. Dickel (1♂, MGCL); 6-VIII-1974, T. Dickel (1♂, 1♀, MGCL); Shadow Mtn. Dam, 8375', RMNP, 27-VII-1999 (1♂, CSU); 6-IX-1998 (1♂, CSU); Soda Springs Ranch, Hwy. 34 at S end Grand Lake, 17-IX-1998, S. J. Warren (6♀, ADW); Vasquez Mountain summit, ca. 4 air mi SE Hot Sulphur Spgs., 10,118' [3084 m], 40°02'28''N 106°02'33''W, 2-IX-2011, A. Warren (12♂, 1♀); W side Gore Pass (Hwy. 134), vic. mi 12, Jct. NF 250 & NF 241, ca. 1 mi SE Routt Co. line, 2680m, 40°04'20''N 106°37'08''W, 2-VIII-2014, A. Warren (1♂, ADW); **Gunnison Co.**: Almont Summit, 25-VII-1993, D. Lindsley (1♂, 1♀, MGCL); Black Sage Pass, FR 887, vic. summit, 2970m, 39°29'28''N 106°27'07''W, W of Tomichi Creek, 8-VIII-2014, A. Warren (6♂, 2♀, ADW); Blue Mesa Reservoir, 31-VII-1972, T. Scovell (1♂, MGCL); Blue Mesa Summit, 22-VIII-1970, M. Fisher (3♂, 3♀, MGCL); bottom of Black Canyon, 6500', 30-VIII-1955, F. M. Brown (5♂, 3♀, MGCL); Coal Creek, nr. Somerset, 21-VIII-1968, M. Fisher (3♂, MGCL); East Muddy Creek, 7-VIII-1964, S. Ellis (1♀, MGCL); Gothic, 6-VIII-1954, F. M. Brown (1♀, MGCL); 7-VIII-1961, W. Howe (1♂, MGCL); 12-VIII-1962, B. Baker (1♂, MGCL); 27-VII-1971, D. Lindsley (2♂, MGCL); Hwy. 92, 9800', 19-VIII-1976, B. Weber (1♂, MGCL); Marcellina Mtn., 30-VII-1971, D. Lindsley (1♀, MGCL); Mt. Crested Butte, 3000m, 17-19-VII-1998, V. Lukhtanov (3♂, 8♀, MGCL); Muddy Creek, 10-VIII-1961, S. Ellis (1♀, MGCL); 15-VIII-1961, S. Ellis (1♀, MGCL); N end Paonia Reservoir, 7500', 25-VII-1989, M. Fisher (1♂, MGCL); nr. Chair Mtn., Muddy Creek, 10-VIII-1961, K. Tidwell (1♀, MGCL); nr. Somerset, 8-VIII-1961, R. & C. Kendall (6♂, 1♀, MGCL); Old Monarch Pass Rd., 8000', 19-VIII-1952, F. M. Brown (7♂, 7♀, MGCL); Old Monarch Pass, W side, 9000', 21-VIII-1983, M. Fisher (8♂, MGCL); Rte. 50 nr. Blue Mesa, 1-VIII-1981, E. Olson (1♂, 1♀, MGCL); S end Hwy. 50 bridge, Blue Mesa Reservoir, 8000', 17-VIII-1970, F. M. Brown (17♂, 12♀, MGCL); Taylor Park, 2860m, 1-2-VIII-1983, P. F. Milner (5♂, 1♀, MGCL); Tomichi Creek, Co. Rd. 888, 2 mi N Hwy. 50, 2641m, 38°27'03''N 106°24'20''W, 8-VIII-2014, A. Warren (12♂, 7♀, ADW); West Muddy Creek, 27-VII-1964, R. Davis (2♂, 2♀, MGCL); **Jackson Co.**: North Dunes SRA, 18-VIII-1996, P. Opler (1♂, 1♀, CSU); **Mesa Co.**: Lands End Rd., between SOB and Coal Creeks, Grand Mesa, 10,200', 12-VIII-1985, J. & F. Preston (1♂, 1♀, MGCL); Lands End Rd., Grand Mesa, 9600', 21-VIII-1966, M. Fisher (2♂, 2♀, MGCL); Unaweep Canyon, West Creek, 5400', 4-VIII-1969, M. Fisher (1♂, 1♀, MGCL); 19-VIII-1968, M. Fisher (1♂, MGCL); 25-VIII-1967, M. Fisher (1♂, MGCL); 2 mi S Mesa, 6500', 31-VII-1971, S. Steinhauser (1♂, MGCL); 6 mi S Mesa, 6600', 25-VII-1971, S. Steinhauser (1♂, 1♀, MGCL); **Moffat Co.**: Craig, 30-VIII-1994, D. L. Bauer (1♂, 1♀, MGCL); Entrance, Dinosaur Nat. Mon., 6600–7000', 25-VII-1969, M. Fisher (4♂, MGCL); Hwy. 40, 0.3 mi E Elk Springs, 10-IX-1996, I. Leeuw (3♀, ADW); 5-IX-1997, I. Leeuw (4♂, 3♀, ADW); Vermillion Ck., Co. Rd. 10, 4 mi SE mi. 9 (9 mi N Jct. 318), 1-IX-1991, A. Warren (1♂, 2♀, ADW); 1.5 mi E Maybell, 31-VIII-1991, A. Warren (1♀, ADW); 4 mi E Elk Springs on US 40, 20-VIII-1978, M. Minno (3♂, MGCL); **Montezuma Co.**: Mesa Verde National Park, 23-VIII-1958, D. Eff (2♂, 1♀, MGCL); 30-VII-1972, M. Fisher (1♂, MGCL); **Montrose Co.**: Black Canyon, 13-VIII-1964, S. Ellis (14♂, 2♀, MGCL); 18-VIII-1964, S. Ellis (2♂, MGCL); S Rim Black Canyon, 8200', 28-VIII-1955, F. M. Brown (17♂, 24♀, MGCL); 17-VIII-1962, T. W. Davies (6♂, 11♀, MGCL); **Ouray Co.**: Canyon Creek, Ouray, 8500–9000', 22-VIII-1970, F. M. Brown (12♂, 3♀, MGCL); East Dallas Creek, end of Ouray Co. Rd. 7, 24-VIII-1970, F. M. Brown (2♂, 1♀, MGCL); Hayden Mtn., 9300', 29-VIII-1955, F. M. Brown (4♂, 8♀, MGCL); Log Hill Mesa, N of Ridgewood, 19-VIII-1996, A. Warren (1♂, 1♀, ADW); NE Cedaredge at Surface Ck., 7500', 28-VIII-1983, R. Klopshinske (6♂, 1♀, MGCL); nr. Ouray, 7500–7800', 16-20-VIII-1959, F. M. Brown (6♂, 7♀, MGCL); nr. Ouray, 7800', 7-VIII-1960, F. M. Brown (1♂, MGCL); nr. Ridgeway, jct. US 550 & Ouray Co. Rd. 8, 23-VIII-1970, F. M. Brown (5♂, MGCL); Ouray, 8000', 28-VIII-1969, F. M. Brown (3♂, 2♀, MGCL); Owl Creek Pass, 8000', 28-VII-1963, S. Ellis (1♂, MGCL); SE Ridgeway, 7000', 27-VIII-1983, Klopshinske (1♀, MGCL); Willow Swamp, 9000', E Fork Dallas Creek, 5-VIII-1998, P. Pineda (1♂, CSU); 1 mi E Ridgeway, 21-VIII-1964, S. Ellis (8♂, 3♀, MGCL); 22-VIII-1970, M. Fisher (5m, 1♀, MGCL); 2.5 mi N Ouray, 7500', 20-VIII-1970, F. M.

Brown (13♂, 4♀, MGCL); 3 mi S Ridgeway, 7000', 20-VIII-1983, R. Klopshinske (1♂, 1♀, MGCL); 4 mi N Ouray, 7500', 19-27-VIII-1970, F. M. Brown (14♂, 7♀, MGCL); **Pitkin Co.**: Aspen, 7-VIII-1968, R. Stanford (6♂, MGCL); 15-VIII-1971, R. Stanford (1♀, CSU); Conundrum Creek Trail, Aspen, 18-VIII-1988, L. Harris (3♀, MGCL); Redstone area, 3-VIII-1983, P. F. Milner (1♂, MGCL); 7 mi N Redstone, 29-VII-1976, D. Eff (1♂, MGCL); Rio Blanco Co.: Rd. 64 at White Riv., 22-VIII-1991, Kondratieff & Kippenhan (2♀, ADW); 6 mi E Meeker, 5-VIII-1985 (1♂, CSU); **Routt Co.**: W side Gore Pass on CO 134, 9000', 15-VIII-1997, B. Brinkman (2♂, 2♀, ADW); **San Miguel Co.**: Leopard Ck., 8500', 20-VIII-1959, F. M. Brown (6♂, 2♀, MGCL); **Summit Co.**: Boulder Creek CG, 23-VII-1967, R. Stanford (1♂, CSU); CO 91, 1 mi S Wheeler Jct., 9-VIII-1996, R. Stanford (1♂, 1♀, CSU); Keystone, 9300', 16-VIII-1993, R. Stanford (1♂, 1♀, CSU); Montezuma, 30-VII-1984, D. Bauer (1♀, MGCL); nr. Keystone, 9600', 4-VIII-1973, R. Stanford (2♂, CSU); nr. Keystone Ski Area, 9300', 4-VIII-1973, M. Fisher (1♂, MGCL); 10-VIII-1975, M. Fisher (5♂, MGCL); **Weld Co.**: Pawnee Nat. Grassland, 12 mi E Grover, 1-IX-1973, R. Stanford (1♂, 3♀, CSU); 1 mi S Wyoming line, due N of Raymer, 30-VIII-1985, J. Scott (4♂, 3♀, MGCL); **UTAH: Grand Co.**: Gateway (state line) Rd., 10.5 mi E jct. La Sal Mtn. Loop Rd., 18-VIII-1996, A. Warren (4♀, ADW); La Sal Mtn. Loop Rd., 0.6 mi SW jct. Castleton Rd., 16-VIII-1996, A. Warren (1♂, ADW); La Sal Mtn. Loop Rd., 2.4 mi S jct. Castleton Rd., 16-VIII-1996, A. Warren (8♂, 4f, ADW); La Sal Mtn. Loop Rd., 5.3 mi S jct. Castleton Rd., 16-VIII-1996, A. Warren (1♂, ADW); La Sal Mtn. Loop Rd., 6.2 mi S jct. Castleton Rd., 16-VIII-1996, A. Warren (6♂, 4♀, ADW); La Sal Mtn. Loop Rd., 8.9 mi S jct. Castleton Rd., 16-VIII-1996, A. Warren (1♂, ADW); **San Juan Co.**: La Sal Mtn. Loop Rd., 13 mi E jct. US Hwy. 191, 16-VIII-1996, A. Warren (1♂, ADW).

***Hesperia colorado idaho / H. c. ochracea* transition zone: all from USA: COLORADO. Larimer Co.:** Cherokee Park SWA, Middle Unit, Rd. 80C, 10 mi WNW Hwy. 287, 31-VIII-2008, A. Warren (7♂, 2♀, ADW); Cherokee Park SWA, Rd. 80C, 6 mi W Hwy. 287, 31-VIII-2008, A. Warren (1♂, 1♀, ADW); Hewlett's Gulch, 7-X-1997 (1♀, CSU); Middle Cherokee Park, 6000', 31-VIII-1987, J. Keeler (1♂, MGCL); Virginia Dale, 14-VIII-1980, L. Brown (2♂, 3♀, MGCL); 15-VII-1982, J. M. Nelson (1♀, MGCL).

***Hesperia colorado ochracea:* all from USA: COLORADO. Boulder Co.**: 7♂, 3♀ (CSU); 47♂, 46♀ (MGCL); **Clear Creek Co.**: Clear Creek Canyon, 21-VIII-1977, I. Finkelstein (1♂, 1♀, MGCL); Fall River Rd., 9000', 7-IX-1968, R. Stanford (1♂, CSU); hill SE of Empire, 9400', 22-VIII-1971, J. Scott (5♂ , MGCL); Idaho Springs, 3 mi E, 3-VIII-1984, D. L. Bauer (2♂, MGCL); 2 mi E Idaho Springs, 13-VIII-1968, R. Stanford (1♂, CSU); **Douglas Co.**: 71♂, 39♀ (ADW); 12♂, 34♀ (CSU); 82♂, 42♀ (MGCL); **Elbert Co.**: 3♂, 7♀ (ADW); 34♂, 15♀ (MGCL); **El Paso Co.**: 4♂, 2♀ (ADW); 9♂, 3♀ (CSU); 74♂, 31♀ (MGCL); **Gilpin Co.**: Blackhawk, 2440m, 1-IX-1983, C. Slater (1♀, CSU); Chase Creek, 2500m, 12-VII-1977, C. Slater (1♂, CSU); 18-IX-1973, C. Slater (1♂, CSU); CR 7 at Smith Gulch, 10-VIII-1996, C. Mills III (14♂, 3♀, MGCL); Golden Gate Canyon State Park, Smith Hill Rd., 4-VII-1996, C. Mills III (5♂, 1♀, MGCL); Macy Gulch, 8200', 30-VIII-1987 (1♂, 2♀, CSU); **Jefferson Co.**: 49♂, 11♀ (ADW); 10♂, 6♀ (CSU); 128♂, 56♀ (MGCL); **Jefferson-Douglas Co.**: 2♂, 1♀ (CSU); **Larimer Co.**: Bear Lake Rd., below Eagle Cliffs, 8075', RMNP, 25-VIII-1999 (1♂, CSU); Big Thompson Cyn., Round Mtn. Trail, 10-VIII-1996, D. Leatherman (1♂, CSU); Black Canyon Trail, 7800', RMNP, 3-IX-1997 (2♂, CSU); Cow Creek, 7850', RMNP, 3-IX-1997 (1♀, CSU); Cow Creek Trail, 8150', RMNP, 6-IX-1998 (1♀, CSU); 14-VIII-2002 (1♂, CSU); Deer Ridge Trail, 8875', RMNP, 15-VIII-1998 (1♂, CSU); Fern Lake Trail, 8200', RMNP, 13-VIII-1998 (1♂, CSU); 20-VIII-2002 (1♂, CSU); Fort Collins, 20-IX-1975, M. Epstein (1♀, CSU); Glacier View Meadow, 7000', 30-VIII-1985, H. & M. Evans (2♂, CSU); Kelly Flats Campground in Cache la Poudre Canyon, 6750', 7-VIII-1987, J. & F. Preston (1♂, MGCL); Lory SP, 4 mi W Fort Collins, 13-X-1991, P. Opler (1♀, CSU); Moraine Park, Fern Lake, 8100', RMNP, 3-4-IX-1994, R. Muckenthaler (1♂, CSU); Pennock Pass, 7500', 31-VIII-2002, P. Opler & E. Buckner (1♂, 3♀, CSU); RMNP Headquarters, 3-IX-1995, P. Opler (1♂, CSU); Viestenz-Smith Park, 12-X-1991, P. Opler (1♂, 1♀, CSU); **Park Co.**: Bailey, 25-VIII-1941, R. Whittaker (1♀, MGCL); Eleven Mile Canyon, 8000–8400', SW of Lake George, 2-IX-1973, R. Stanford (1♀, CSU); Little Blue Mountain, 25-31-VII-1989, A. Warren (1♂, ADW); near Pipe Springs Campground, E of Wilkerson Pass, 9450', 16-VIII-1980, J. & F. Preston (2♂, 1♀, MGCL); Tappan Creek, 8000', 23-VIII-1948, F. M. Brown (6♂, 15♀, MGCL); **Teller Co.**: Big Spring Ranch, 4 mi SW Florissant, 8600', 8-VIII-1971, T. Emmel (1♀, MGCL); 15-VIII-1971, T. Emmel (1♂, MGCL); Cripple Creek, 31-VIII-1975, B. H. (1♂, MGCL- intermediate towards *colorado*?); Crystola Canyon, 8000', 25-VIII-1973, M. Fisher (2♂, 3♀, MGCL); 3-IX-1973, M. Fisher (2♀, MGCL); Crystola Creek, 8-9000', 3-IX-1973, R. Stanford (1♂, 5♀, CSU); Florissant Fossil Beds, 8400', R71W T13S sec 14, 17-IX-1976, F. M. Brown (1♂, MGCL); Pikes Peak Research Station, 7 mi S Florissant, 11-VIII-1985, M. Minno (2♂, 1♀, MGCL); Trail Creek, 84-8800', 2-IX-1973, R. Stanford (1♂, 1♀, CSU); 3 mi N Florissant,

8250', 3-IX-1973, M. Fisher (1♂, MGCL); 4 mi W Divide, 9500', 21-VIII-1948, F. M. Brown (10♂, 6♀, MGCL); **Teller-Park Co**.: S Platte River, 72-7500', 3-IX-1973, R. Stanford (1♂, 3♀, CSU).

***Hesperia colorado ochracea / H. c. sublima* transition zone: all from USA: COLORADO. Gilpin Co**.: East Portal, 21-VIII-1968, R. Stanford (4♂, CSU); 2-VIII-1969, R. Stanford (2♂, CSU); 3-VIII-1969, R. Stanford (1♂, CSU); 22-VIII-1969, M. Fisher (2♀, MGCL); 22-VIII-1969, R. Stanford (1♂, CSU); 27-VIII-1969, R. Stanford (2♂, CSU); 29-VII-1972, R. Stanford (1♂, CSU); 30-VII-1972, R. Stanford (1♂, CSU); 19-VIII-1973, R. Stanford (1♂, CSU); Tolland, 12-VIII-1951, H. A. Freeman (2♂, 3♀, MGCL); Toll Ranch [Tolland?], 28-VII-1977, J. Scott (1♂, MGCL); 30-VII-1977, J. Scott (1♂, MGCL); 4-VIII-1977, J. Scott (2♀, MGCL). Tolland (= East Portal) is situated at about 2810m (9220'), around 39°54'11'N 105°38'37''W.

ACKNOWLEDGMENTS

We thank Paul A. Opler and Boris C. Kondratieff for access to specimens in the C. P. Gillette Museum of Arthropod Diversity, Colorado State University, and William W. McGuire for making large series of *Hesperia* specimens available for study at the McGuire Center for Lepidoptera and Biodiversity, University of Florida. For images of the type material, we thank Rodney Eastwood and Rachel Hawkins (MCZ). The senior author thanks William Bernstein, Joel Cox, Tom Ortenburger, Ray Stanford and Sally Warren for assistance with fieldwork in Colorado and bordering states. We also thank Jonathan P. Pelham and two anonymous reviewers for reviewing and improving this manuscript.

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Submitted for publication 15 September 2014; revised and accepted 23 October 2014.

Journal of the Lepidopterists' Society
69(1), 2015, 50–57

ANATOMICAL STUDY ON THE MORPHOLOGY OF THE REPRODUCTIVE SYSTEMS AND THE SCALE BRUSHES OF *DIORYCTRIA RUBELLA* HAMPSON (PYRALIDAE, PHYCITINAE)

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ABSTRACT. The morphology of the reproductive systems and the coupling mechanism between the male and the female genitalia during copulation in *Dioryctria rubella* Hampson are described. Differing from those in other genera of Phycitinae moths, the corpus bursae possesses a well-developed signum, and the seminal duct does not exhibit a bulla seminalis, instead arising from the ventral surface of the corpus bursae. The ultrastructural observation shows that the spines on the inner surface of the ductus bursae and the cervix bursa are complementary to that of cornuti on the outer surface of vesica in position and direction, which elucidates the matching mechanism between the ductus bursae and the vesica. The male possesses well-developed scale brushes, which consist of six pairs of overlapped structures. Finally, the morphological differences of scale brushes between *D. rubella* and other *Dioryctria* species and related genera, and their function during copulation are discussed.

Additional key words: *Dioryctria rubella*, reproductive system, scale brushes, ultrastructure

The pine shoot moth, *Dioryctria rubella* Hampson (Pyralidae), ranges over more than 20 provinces in China, and also occurs in Philippines, Japan, Russia and many European countries (Liang et al. 2011). The larva bores into the terminals and cones and thereby causes severe losses to the cones and seeds of *Pinus massoniana*, *P. thunbergii*, and *P.taeda*. It is quite difficult to control this insect pest because of its concealed foraging habit and overlapping generations, and methods for managing this insect, such as chemical, physical and biological control have been improved for over 30 years (Wu et al. 1986; Zhao et al. 1992; Liang et al. 2011). Knowledge of the morphology of the reproductive organs is prerequisite to studies of reproductive biology as well as to investigations of sex pheromone. Up to now, only a few studies on the morphology of reproductive systems have been reported in Pyralidae. Fatzinger (1970) detailed the internal reproductive systems of *Dioryctria abietella*. This is the only species of genus *Dioryctria* in which reproductive organs have been researched. Only eight other species of Pyralidae have had their reproductive morphology described (Srivastava & Srivastava 1959; Ye & Lu 1964; Song et al. 1965; Davis 1968; Beals & Berberet 1976; Miskmen et al. 1983; Jones et al. 1984; Liao 1988; Song et al. 2012). Although Wang & Song (1985) described briefly the genitalia morphology of this moth, the morphology of the reproductive systems of *D. rubella* has not been reported in detail before.

The scale brushes play an important role in releasing of the male sex pheromone in Lepidoptera (Birch et al. 1990). Simonsen & Roe (2009) described morphology of the scale brushes in male Phycitinae moths and discussed their phylogenetic value. In this paper, we describe the anatomical structures of male and female reproductive systems and the scale brushes of *D. rubella* in detail so as to supply some basic information for further studies on reproductive biology and the sex pheromone. Anatomical terminology follows Klots (1970) and Kristensen (2003).

MATERIALS AND METHODS

Insect materials. The larvae and pupae were field–collected from April to October in 2013, from Sanjie, Anhui province, China. They were kept in the 15–20 mm long larval feeding tunnels, which were natural or man-made. The terminals were plugged into the matrix which can absorb water, and covered with glass tubes to avoid evaporation. Afterwards, the terminals were maintained at 25–28 degrees centigrade and about 62% RH on a 14:10 (L:D) cycle. The adults were collected and used as anatomical materials, they were either dissected instantly or fed with 0.5% honey water prior to study. All samples (30 females, 25 males) used for dissection were alive and unmated.

Anatomy. Moths were dissected in Ringer solution (6.5g NaCl, 0.14g KCl, 0.12g $CaCl_2$, 0.2g $NaHCO_3$, 0.01g NaH_2PO_4, and diluted with water to 1000ml) under the light microscope JN-JSZ6S. Meanwhile, the structures of reproductive systems were observed, measured and described. The photographs were captured using a computer and video camera mounted

on a stereoscopic microscope, afterwards, figures were sketched according to the printed photographs. The dissecting structures were kept in stationary liquid (40% formaldehyde, 1.25ml glacial acetic acid, 10g chloral hydrate, and diluted with water to 100ml) for further observation.

Scanning electron microscopy. In order to investigate the relationship between the ductus bursae and the vesica, the ultrastructure in the inner surface of the ductus bursae were observed under the scanning electron microscopy (SEM). The ductus bursae was fixed in stationary liquid mentioned above for three weeks. Then, it was washed with 0.1 M phosphate buffer, pH 7.2, for 20 mins, operated twice. Afterwards, the sample was dehydrated in a graded acetone, 30%, 50%, 70%, 90% for 15 mins respectively, 100% for 20 mins and three times, then submitted to the critical point drying method, using superdry CO_2. Finally, the sample was placed on metallic support, coated with a thin layer of gold and examined under the SEM FEI Quanta 200.

RESULTS

Internal female reproductive organs. The internal female reproductive organs (Fig. 1) of *D. rubella* are composed of paired ovaries, a pair of lateral oviducts, one common oviduct, a genital chamber, the spermatheca along with its gland, and accessory glands.

The ovaries are secured within the abdomen by fine tracheae and some fat bodies, and normally loop back and forth 2 or 3 times within the abdomen. Each ovary is composed of 4 ovarioles, with an average length of 10.05 mm, which connects to the calyx of each lateral oviduct. The ovarioles fuse at their apex, contact closely throughout their length, and each of them is composed of a thin membranous tunica propria containing oocytes from 7 to 10, with newly emerged female containing the greater number.

The common oviduct branches anteriorly into two lateral oviducts, with an average length of 0.90 mm, and slightly constricts before joining the genital chamber. The lateral oviduct expands into the base of ovarioles. The seminal duct and the spermathecal duct open into the anterior end of the genital chamber, while the common duct of the accessory glands opens into the dorsum of the posterior region of the genital chamber, slightly anterior of the opening to the rectum. The genital chamber terminates into a fleshy, telescopic ovipositor equipped with numerous sensory hairs and an ovipore.

The spermathecal duct, 1.25 mm long, convolutes into 10 small spiral loops. The convolute directions of the loops are reversed at the center of the spermathecal duct. The spermathecal chamber, which opens through

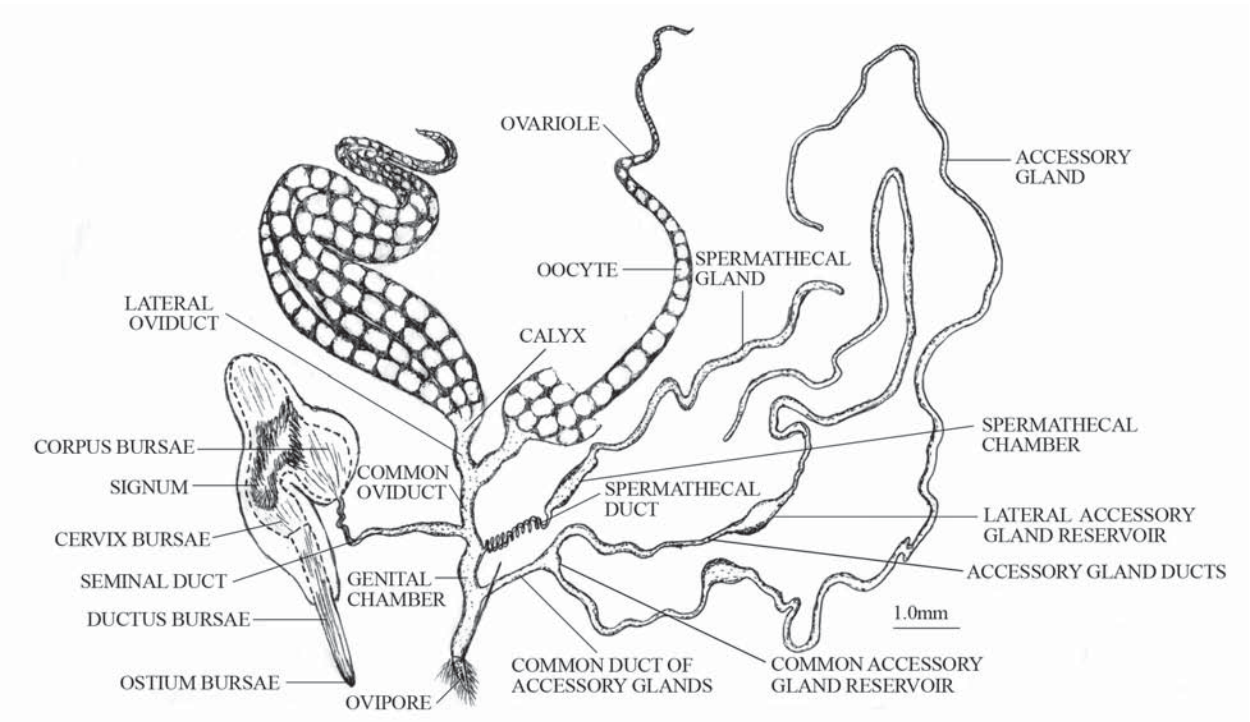


FIG. 1. Female reproductive system of *D. rubella*

the spermathecal duct, is an elongated sac. The spermathecal gland appears as a diverticulum of the spermathecal chamber and it terminates into 2 branches or not, depending on the individuals.

The common duct of the accessory gland attaches to the genital chamber and distally expands into an indistinctive common accessory gland reservoir. The separate accessory gland ducts attach to the common reservoir respectively. Each accessory gland also possesses a kidney-shaped reservoir near its base, the lateral accessory gland reservoir, with an average length of 0.96 mm. The anterior half of the accessory gland duct is finer than the posterior one. These reservoirs dilate or contract depending on the contents of the accessory glands. Each accessory gland arises from the anterior end of the lateral reservoir and is folded several times in the abdomen.

External female reproductive organs. The bursa copulatrix is a large, membranous organ (Fig. 1). The sclerotized ductus bursae, 2.68 mm in length, about eight times as long as width, is noticeably narrowed and musculated, anteriorly joins the cervix bursae and opens externally in the intersegmental cuticula of the 7th and 8th abdominal sternites through the ostium bursae. The membranous, U-shaped corpus bursae arise as a pouch from the cervix bursae. The internal surface armed with numerous spines, more than 500, about 0.18 mm long, which form a ring-like signum. The seminal duct arises from the ventral surface of the corpus bursae, coils three times at its anterior half near the corpus bursae, and slightly enlarges toward the posterior half near its junction with the genital chamber. There was not a bulla seminalis in the enlarged region, nor eggs found inside

The posterior opening of the genital chamber, the ovipore, is located below the anus. The papillae anales are derived from the 10th segment; they are weakly sclerotized and terminate in a nipple–shaped terminus. The papillae anales are covered with numerous long sensory hairs, and the hairs are 0.3 mm long in average. The margin of the papillae anales bears the posterior apophyses. There are a pair of lateral sclerites in the 8th abdominal segment, which bear a pair of anterior apophyses. Both of posterior and anterior apophyses are slightly sclerotized (Fig. 2).

Internal male reproductive organs. The internal male reproductive organs (Fig. 3) of *D. rubella* include two testes, a pair of vasa deferentia, the ductus ejaculatorius duplex, a ductus ejaculatorius simplex, and a pair of accessory glands.

The two testes are encased by a scrotum which appears as a thin, transparent membrane and form a complex testis. The complex testis is 1.04 mm in

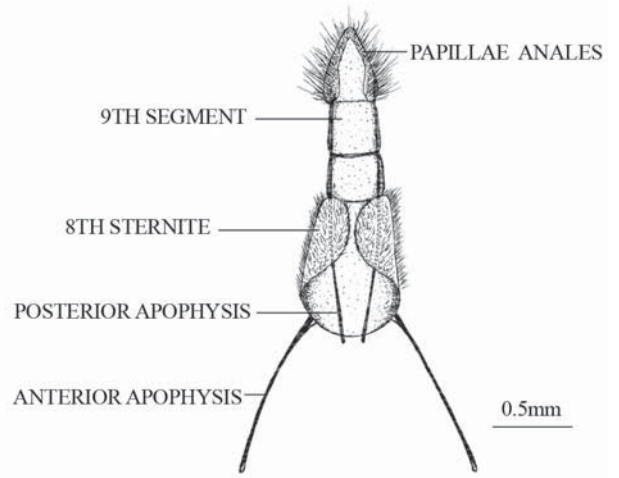


FIG. 2. Terminal female abdominal segments of *D. rubella*.

diameter, supported by tracheae and other viscera in the dorsal abdominal cavity between the 3rd and 4th segments, and easily distinguished by the brilliant claret-red of the scrotum. The paired vasa deferentia arise from the ventral surface of the testis and join to the ductus ejaculatorius duplex respectively. Each vas deferens possesses two seminal vesicles, which appear as two significant dilations, the anterior enlargement and posterior enlargement, each of them is 0.82 mm long. The anterior enlargements cross at their middle parts.

The ductus ejaculatorius duplex consists of 2 tubular organs, fusing at their posterior terminals to form the ductus ejaculatorius simplex and giving rise to the accessory glands at their anterior terminals. Each branch of the ductus ejaculatorius duplex receives one vas deferens, and the junctions are near the accessory glands and locate at the one third of ductus ejaculatorius duplex. The accessory glands are uniform,

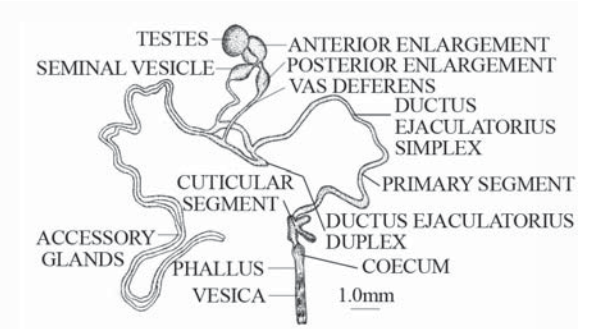


FIG. 3. Male reproductive system of *D. rubella*.

remain in close contact throughout their length and are intertwined among other organs within the abdominal cavity. Both of accessory glands are slightly club shaped at their terminals.

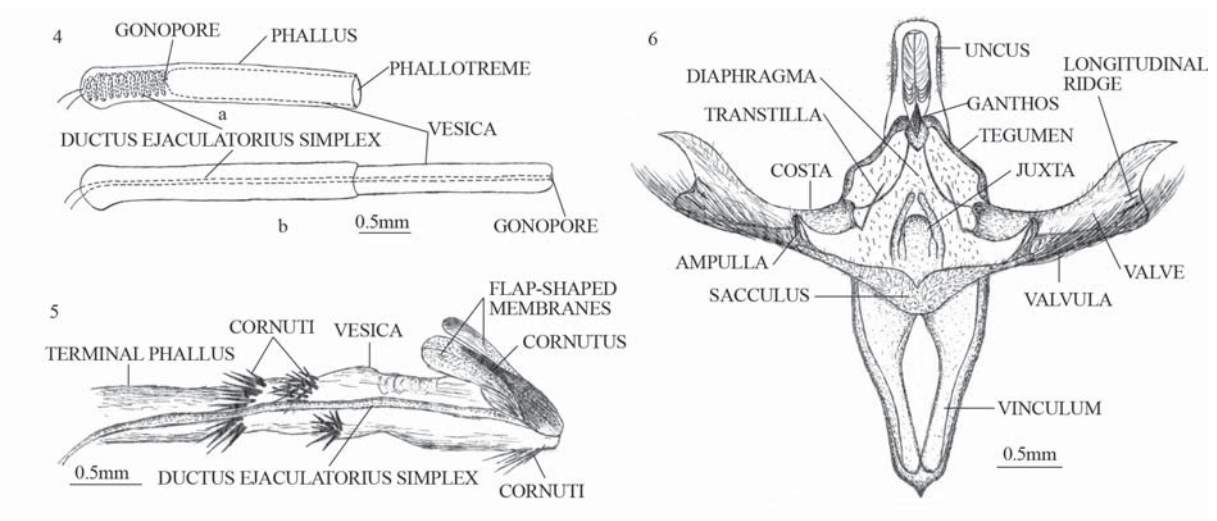
The anterior end of the tubular ductus ejaculatorius simplex connects to the ductus ejaculatorius duplex and posteriorly extends to the vesica. The ductus ejaculatorius simplex consists of 2 morphological areas, the primary segment and the cuticular segment. The primary segment appears as a thin, membranous tube, the cuticular segment is muscular area, differentiated by a lateral diverticulum and terminates into the phallus.

External male reproductive organs. The phallus is dorsolaterally supported by the transtilla with striptyped muscles attaching to the margin of the 9th tergum, ventrally supported by the juxta. The phallus, which bears a caecum at the phallobase, is slender, strongly sclerotized tubular-shaped, and about seven times as long as wide. The ductus ejaculatorius simplex within the phallus combines with well–developed muscles fibers, convolutes into many spiral loops and joins to the base of vesica. These structures make the vesica possible to evert or invaginate freely during copulation. The terminal phallus is a tubular structure and the vesica is located in the lumen. Owing to its eversible and retractable abilities, the vesica, together with the phallus, constitute a telescopic structure.

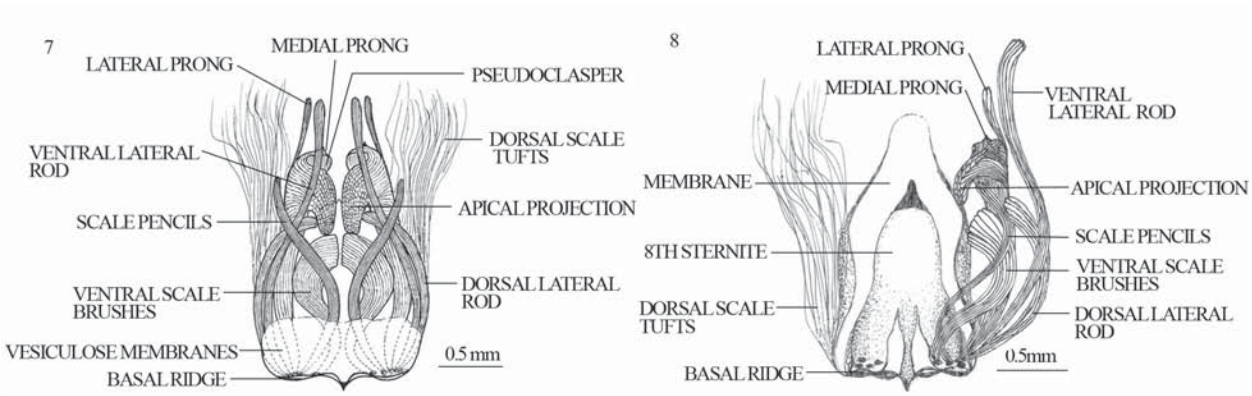
The membranous vesica, which is invaginated in the lumen of the phallus and forms a true gonopore (Fig. 4b), the primary gonopore or aperture of the ductus ejaculatorius simplex, opens externally at the apex membranous vesica. The opening at the terminal phallus, which results from the invagination of vesica, is actually a false gonopore, the secondary gonopore or the phallotreme (Fig. 4a). The phallotreme disappears along with the evaginable vesica, and the surface of vesica exposes one large spine-like cornutus, with an average length of 0.78 mm (cornutus in Fig. 5), five to ten slender cornuti on the opposite side to the cornutus (cornuti in Fig. 5), and one to three sets of smaller straight cornuti (cornuti in Fig. 5) (with an average of 72), 0.28 mm long. The direction and position of cornuti vary with the position of vesica. When the vesica everts, the cornuti point to the phallobase (Fig. 5). After the vesica invaginating, the cornuti point to the terminal phallus. The cornutus is surrounded by two flap-shaped muscular membranes (flap-shaped membranes in Fig. 5), and the membranes is surrounded by a layer of longitudinal muscle fibers.

When the vesica is in invagination (Fig. 4a), the phallus is about 2.71 mm long, thereinto the vesica is 1.86 mm long. The relative position of the eversible vesica and the phallus is shown in Fig. 4b, and the eversible vesica and the phallus are totally 4.57 mm in length. This is correlated with the telescopic structure of the phallus and the vesica.

The genital capsule of *D. rubella* is composed of the highly modified 9th and 10th abdominal segments (Fig. 6). The anal tube passes beneath the 9th tergum. Uncus with rounded apex, which formed from the 10th segment, is attached to the mid-dorsal surface of the



FIGS.. 4–6. Male genital. **4.** The schematic diagram of the phallus and the vesica in male *D. rubella*. **a.** The telescopic structure. **b.** The phallus with eversible vesica. **5.** Eversion of vesica in male *D. rubella*. **6.** Male genitalia of *D. rubella* (the phallus has not been sketched).



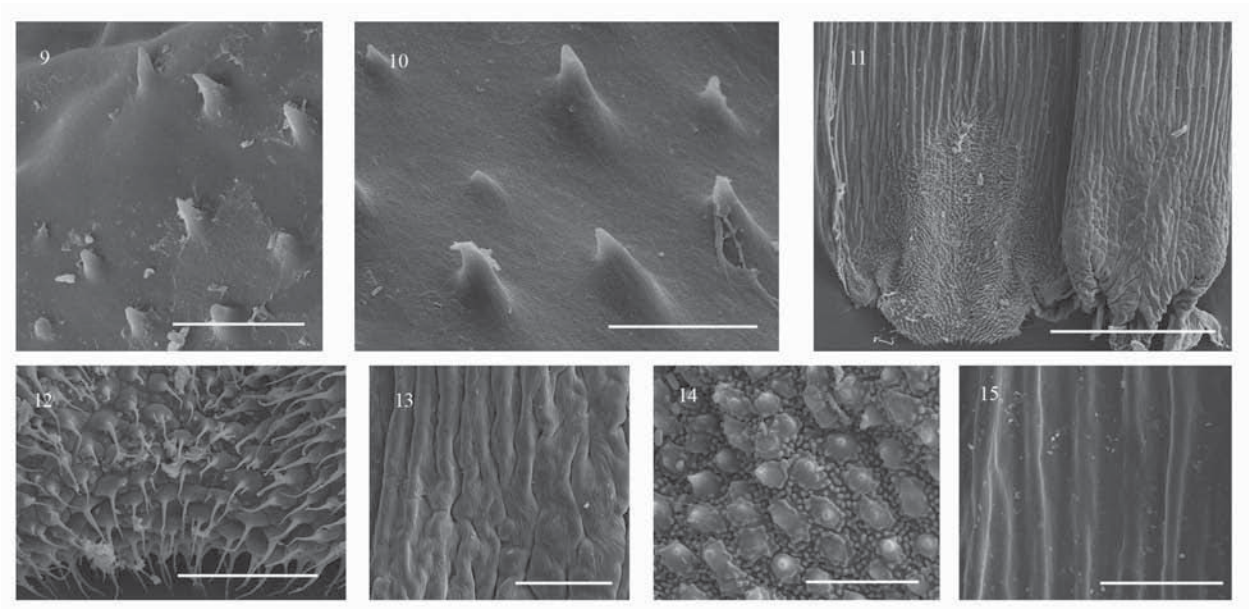
FIGS. 7–8. The modified scale brushes from the 8th abdominal sternite of male *D. rubella*, ventral visual. **7.** Overlapped sight. **8.** Unfolded sight, with partly removed.

9th tergum. Both sides of the uncus are parallel, with the sunken margin. The sclerotized gnathos is small pear-like with protruding cuspides, and connects to the sclerotized shield-shaped tegumen by the hardened, arcuate, and wide arms of both sides. The paired gnathos giving ventrolateral support to the anal tube. The diaphragma, a membranous ventral body wall behind the valve bases and ahead of the 10th segment sclerotizations, is the place where the anal tube and the phallus pass through. Most of the diaphragma derives from intersegmental membrane between the 9th and 10th segment (Klot 1970). The juxta, which is the most consistently developed diaphragma sclerotization, closely associated with the vinculum, round-shaped with two finger-type arms terminally equipped with fine hairs. Another kind of diaphragma sclerotization is transverse bridge, the transtillas, which is between the upper basal valve corners, extending above the phallus. The paired valves derive from the 9th segment (Ferro & Akre 1975), articulate with the vinculum along the posterior margin, and are armed with numerous setae, which are primarily serving to clasp the female abdominal apex during copulation (Kristensen 2003). The dorsal costa widens terminally and tapers to a long, sclerotized, falcate process, with the following three longitudinal ridges. The ventral valvula connected to the sacculus is membranous and bears many long setae. The sclerotized sacculus is located in the base-ventral of the valve and covered with shorter setae. The mediodorsal, hooked, sclerotized ampulla, ventrally connected to the terminal sacculus and dorsally associated with costa, also armed with numerous short setae. The vinculum is fused with the lateral margin of the 9th tergum. The vinculum joins the tegumen with its two arms, and ventral part sinks as a "V".

Scale brushes in male adult. The scale brushes (Fig. 7) originate from the basal ridge of the strongly sclerotized and U-shaped the 8th sternite (Fig. 8), are composed of six pairs of overlapped structures. A bigger U-shaped, slightly sclerotized membrane is ventrally attached to the 8th sternite, and dorsolaterally attached to the male genitalia. The most dorsal components are a pair of dorsal scale tufts lateral to the 8th sternite, which are comprised by multiple very long piliform scales. Two pairs of long rods originate laterally from the base of the 8th sternite. The dorsal lateral rods are short and thick, while the ventral lateral rods are very long. The pseudoclaspers originate from the latero-basal portion of the 8th sternite, medially and posteriorly to the two pairs of lateral rods. These structures are composed of a thick shaft and head with a curved inner margin, a large downward pointed ventral hook, apical projection, medial prongs and lateral prongs. Ventral to the pseudoclaspers are a pair of large ventral scale brushes, which are laterally curved, originate from the centro-dorsal of the 8th sternite. The scale pencils are a pair of long and narrow structures, loosely composed of a few scales, originating ventro-laterally to the ventral scale brushes.

The six pairs of scale brushes are equipped with many parallel and scaly ridges on surface, and they are flexible at the base, so that they can unfold. The scale brushes are covered with vesiculose membranes (Fig. 7).

Scanning electron microscopy of the inner wall of the ductus bursae. The inner wall of the cervix bursa and the ductus bursae are armed with some spines (Figs. 9–10), which are evenly distributed at one side of the base of the ductus bursae, with an average length of 10.0 µm (Fig. 10). The setae are unevenly distributed on the internal surface of ostium bursae



FIGS. 9–15. SEM micrographs of the inner surface of the ductus bursae. **9.** Anterior end of the ductus bursae, showing spiculate surface (Scales 20 μm). **10.** The inner wall of the cervix bursae (Scales 20 μm). **11.** The ostium bursae (Scales 300 μm). **12.** Dense, long setae of the ostium bursae (Scales 40 μm). **13.** Plicated muscles of the ostium bursae (Scales 50 μm). **14.** Membranes joining to the ostium bursae (Scales 10 μm). **15.** Middle part of the ductus bursae (Scales 50 μm).

(Fig. 11), one side is equiped with dense, long setae (Fig. 12), and the remainder is plicated muscles (Fig. 13). However, the spiculate surface and the setaceous surface are on opposite sides of the ductus bursae. The membranes, which attached to the ostium bursae are sags and crests, with some big humps surrounded by numerous small ones (Fig. 14). The remainder part of the ductus bursae is smooth, with longitudinal rumples (Fig. 15).

DISCUSSION

In general, the morphological characters of reproductive organs in *D.rubella* are similar to that of *D. abietella* and other Pyralidae species (Fatzinger 1970; Srivastava & Srivastava 1959; Ye & Lu 1964; Song et al. 1965; Davis 1968; Beals & Berberet 1976; Miskmen et al. 1983; Jones et al. 1984; Liao 1988; Song et al. 2012). However, there are some obvious differences, for example, the seminal duct of some species in the genus *Passadenoides*, *Etielloides* and *Endotricha* arises from corpus bursae near the junction of ductus bursae and corpus bursae (Ferris 2004; Ren & Li 2006; Sun & Li 2009). As for *D. rubella* and some other *Dioryctria* species, it arises from the ventral surface of the corpus bursae (Fatzinger 1970; Wang & Song 1985). Furthermore, no bulla seminalis such as described in *D. abietella* has been found in *D. rubella*, which seems to be acting as a pumping organ to assist movement of sperm through the seminal duct (Fatzinger 1970). Callahan & Cascio (1963) suggested that peristaltic movements of the seminal duct were also beneficial to sperm transmission in species which lack a bulla seminalis, and the seminal duct in *D. rubella* may function in this way.

D. rubella is of the U-shaped corpus bursae and the well-developed signum equipped with widespread, numerous spines. These are similar to some *Dioryctria* moths (Wang & Song 1985), and different from other species of the genus *Endotricha*, which the corpus bursae are round and the signum is indistinctive (Sun & Li 2009), the signum even absent in some *Etielloides* and *Lipographis* moths (Ren & Li 2006; Ferris 2012). The signum aids in retaining the spermatophore in the corpus bursae as the phallus is removed and the ultimate shape of the spermatophore is determined by the corpus bursae (Ferro & Akera 1975). The developed signum and the U-shaped corpus bursae may imply a strong retaining capacity and the U-shape of the spermatophore in *D. rubella*.

In *D. rubella*, the exact mating process has still not been reported. Some speculations may be inferred according to the morphology of external reproductive organs. There is a fine matching between the outer surface of vesica and the inner surface of the ductus bursae as well as the cervix bursae. The spines on the inner surface of the ductus bursae and the cervix bursae

are complementary to the cornuti on the outer surface of vesica, moreover, the directions of spines and the cornuti are opposite to each other, which give the male a firm hold on the female during copulation and spermatophore formation (Ferro & Akera 1975; Callahan 1958). In ditrysian Lepidoptera, the phallus and the vesica insert into the ductus bursae and the cervix bursa during copulation, and *D. rubella* may copulate in the same way.

Male scent structures from abdomen of Pyralidae have many descriptive terms, such as coremata (Bradley 1968; Bradley 1969), corema (Wang & Song 1985), scale tufts (Mutuura & Munroe 1974; Ren & Li 2006), hair pencils (Sasaerila et al. 2003), culcita (Ren et al. 2011; Liu & Li 2012), scale brushes (Simonsen & Roe 2009). In this paper, we adopt the Simonsen's term and describe the scale brushes structure of *D. rubella* in detail. Simonsen & Roe (2009) examined structural morphology of scale brushes within the genus *Dioryctria* and two closely related genera by the scanning electron microscopy. Though variable in size and shape, the scale brushes of these species are clearly comprised by overlapped scales except for *Pyla criddlella*, which only has a pair latero-ventral scale tufts on the 8th sternite. The ultrastructures of the scale brushes are diversiform in species of genus *Dioryctria* and *Sciota*. There existed numerous pores on the cuticula of the scale brushes in *Sciota termitalis*, *D. pseudotsugella* and *D. fordi*, and some secretions were found around the pores (Simonsen & Roe 2009). They suggested that the scale brushes of these species might have excretory functions. The pores are neither found in *D. rubella*, nor in *D. abietivorella*, *D. auranticella*, and *D. yiai*, which may imply that the scale brushes only function to emit sex pheromone in these species. Whether the vesiculose membranes associated with the scale brushes in *D. rubella* have the excretory function of sex pheromone still need to be investigated.

In some Pyralidae species, sex pheromone is emitted from the scale brushes when the male is close to the female (Phelan & Baker 1990). During the study on the reproductive behavior of *D. rubella*, we found that some females ran after the males. Whether male sex pheromone exists in *D. rubella* still need to be further studied. Phelan & Baker (1990) suggested that male species equipped with well-developed scale brushes exhibited a more complex, interactive courtship sequence. It may imply a higher sequence of courtship behavior in *D. rubella*.

ACKNOWLEDGEMENTS

We owe our gratitude to our supervisor and members of our group. This study was supported by the following sources: the National Science and Technology Support Project (2012BAD19B0703), the Funding Project of Nanjing Municipal Construction Bureau & the Management Office of Dr. Sun Yat-Sen's Mausoleum (200409), Nanjing Forestry University Southern Modern Forestry Collabotative Innovation Center and A Project Funded by the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD).

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Submitted for publication 26 May 2014; revised and accepted 29 August 2014.

Journal of the Lepidopterists' Society
69 (1), 2014, 58–62

ULTRAVIOLET COLORATION IN TIGER SWALLOWTAIL BUTTERFLIES (*PAPILIO GLAUCUS* GROUP, PAPILIONIDAE) WITH A METHOD FOR OBJECTIVELY QUANTIFYING ADULT BUTTERFLY WING WEAR

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ABSTRACT. Tiger swallowtail butterflies in the genus *Papilio* have an ability to visually distinguish between a large array of colors including those in the ultraviolet spectrum (UV). However, very little is known about UV reflectance patterns in these butterflies. Using a combination of UV photography and spectral analysis, we here show that several areas on the wings of tiger swallowtails reflect UV light including areas of blue scaling and the anterobasal region of the hind wings. We also discuss how a low level of UV reflectance from the wing membrane itself may be combined with UV photography to quantify wing wear. This technique could be used to objectively place wild-caught individuals into wear classes, approximating their age. Finally, we examine male mating preferences for pristine or artificially aged females and present preliminary results that suggest a strong preference for those that are pristine.

Additional key words: ultraviolet coloration, wear class, *Papilio*, Papilionidae, mate choice

Tiger swallowtail butterflies in the genus *Papilio* have color vision that is among the broadest in the animal kingdom, with an ability to discern color across a spectral range that extends both into the ultraviolet (300 – 400 nm) and the infrared (700–800 nm; Briscoe 2000). Despite this broad visual acuity, surprisingly little is known about the extent of UV reflectance in these butterflies. UV wing coloration is extremely important in a wide variety of other butterfly species, predominately in relation to conspecific recognition and mate selection (Silberglied 1979). Recently, we reported that blue scales on the wings of these butterflies are UV reflective (Aardema & Scriber 2013). Here we expand upon this observation and additionally report a formal way to objectively quantify wing wear of adult *Papilio* butterflies, which may be used to estimate adult age. We also report a preliminary investigation on the implications UV reflectance may have for mating preferences in these butterflies.

MATERIALS AND METHODS

We first assessed ultraviolet coloration in tiger swallowtails by photographing the wings of dead specimens using an XNite330nm UV pass filter attached to a Nikon Coolpix 990 digital camera (3.34 megapixels). This filter has a peak transmission at 330nm of 85% and has 50% transmission at 270nm and 375nm. It also has a small transmission peak of 10% in the infrared at 725nm. With this combination of filter and camera, we photographed the dorsal and ventral sides of a single fore and hind wing from 15 *Papilio glaucus* and *P. canadensis* specimens (3 yellow-morph males of both species, 3 yellow-morph females of both species, and 3 dark-morph female *P. glaucus*). This was done in a darkened room with a circular black light for illumination following techniques previously described (Acorn 2002). We additionally examined the spectral reflectance signature of blue, yellow and black wing areas using an Ocean Optics s2000 miniature fiber optic spectrophotometer. We measured three roughly 1 cm^2 squares of wing, each that had only one solid color (yellow, black or blue) from four pristine Levy County, Florida yellow-morph females (Fig. 1A). Reflectance of color was measured in comparison to a white standard (WS-1 Diffuse Reflectance Standard, Ocean Optics).

During the course of our investigations, we also noticed that scale loss on the wing revealed a low level of UV reflectance from the underlying wing membrane. Such reflectance of the cuticle is not uncommon in insects and led us to consider the possibility of using measures of UV reflectance to quantify scale loss. Wing wear has been used in a large number of studies to approximate the age of individual adult butterflies (e.g. Boggs 1987, Lederhouse & Scriber 1987, Kemp 2000). Therefore, methods to objectively quantify wing wear may be of some value to Lepidopteran researchers.

Starting with a pristine forewing, we artificially removed scales using transparent adhesive tape. This was done by firmly pressing the tape to the wing and then slowly removing it, taking scales off in the process. To remove additional scales, we simply reapplied a new piece of tape to the same area. In this way we sequentially reproduced four wear classes (1–4) following Lederhouse and Scriber (1987). Wear class 1 corresponds to a "fresh" individual whereas wear class 4 is considered "very worn" (no scale loss versus substantial scale loss). Visual examples of the four wear classes can be seen in Figure 2 (column 1). This method appears to reproduce patterns of scale loss that closely resemble those observed in wild-caught specimens (data not shown).

For each of the four classes we photographed UV reflectance using the same methods described above. We quantified the amount of UV reflectance using two distinct measures with the freely available program ImageJ (Abramoff et al. 2004). For each UV picture we first used ImageJ to convert it to an 8-bit, black and white image. We then enhanced the contrast of the image using a pixel saturation point of 0.4%. Our first quantification of wing wear based on UV reflectance used the average gray scale measure of the pixels found along a straight line stretching from the wing base to the tip. The gray scale ranges from 0 (black) to 255 (white). Our second measure of wing wear was based on the total area of UV reflectance. To calculate this, we first converted each picture to a binary image. This resulted in the UV reflecting areas becoming black regions whereas the remaining areas were white (Fig 2, column 4). Using ImageJ we measured the total area of the UV reflecting regions. The presence of a ruler in each photograph allowed us to calibrate the scale for each picture.

Finally, we postulated that these butterflies themselves may potentially utilize the UV reflectance that comes with increasing wing wear to assess reproductive potential in members of the opposite sex. Specifically, we predicted that younger looking individuals with less scale loss would be preferred over older looking individuals, independent of mating status. In tiger swallowtail butterflies older males are more likely to have previously mated and thus have a smaller spermatophore to pass on to a female (Lederhouse et al. 1990). Correspondingly, older females have also likely mated and will have fewer eggs available for fertilization. To examine the potential influence of scale loss and UV reflectance on mate selection, we conducted two-choice male preference trails in two populations of tiger swallowtail. The first was in northern Michigan (*P. canadensis*) and the second was in central Florida (P. *glaucus*). In both populations, methods followed those described in Aardema and Scriber (2013). Briefly, we prepared pairs of females, one that's wings were left pristine and another one that had ~50% of her scales removed haphazardly from both sides of the wing by us using transparent adhesive tape as described above. We handled both artificially aged and pristine females for a similar amount of time to reduce potential handling affects. Within each pairing, the females were of approximately the same size as measured by forewing length from base to tip (± 1 mm). A wooden dowel was placed horizontally through the top of a 2 m long vertical stake so that equal halves stuck out in opposite directions. This allowed us to tether females approximately one meter apart by a fine thread at the ends of the dowel. We used between four and six female pairs placed a minimum of eight meters from one another in areas where there were abundant nectar plants.

Males flying by these females would alter their flight path and engage them if interested. Typically this involved repeatedly circling the females on their tethers. Upon contact with a male the females would generally become enlivened and flutter rapidly at the ends of their strings, spiraling in tight circles. At this point the male would either land on one of the females and initiate copulation or in some cases fly off. In most instances the male engaged both females of a pair before copulation was initiated. While they were tethered, we checked each pair of females at least once every five minutes. After we observed a mating being initiated or else found a copulation in progress, we would gently remove the male from the female. We retained all males. For further details see Aardema and Scriber (2013).

Our null hypothesis was that there would be no preference for one treatment over another and that mating frequencies would be approximately 50/50. Alternatively, if either pristine females or artificially aged females were preferred we would expect a statistically significant deviation from 50/50. To evaluate male mating preferences we used a χ^2 goodness-of-fit test.

Results

Our ultraviolet photography of wing coloration revealed distinct areas that reflected UV light and other areas that appear to be entirely UV absorbent (Fig 1, A & B). Most of the UV reflective areas occur in blue regions of the wings in both species and sexes. The anterobasal area of the hind wing also shows a high degree of UV reflectance. Black and yellow colored areas were UV absorbent. All our photographs revealed

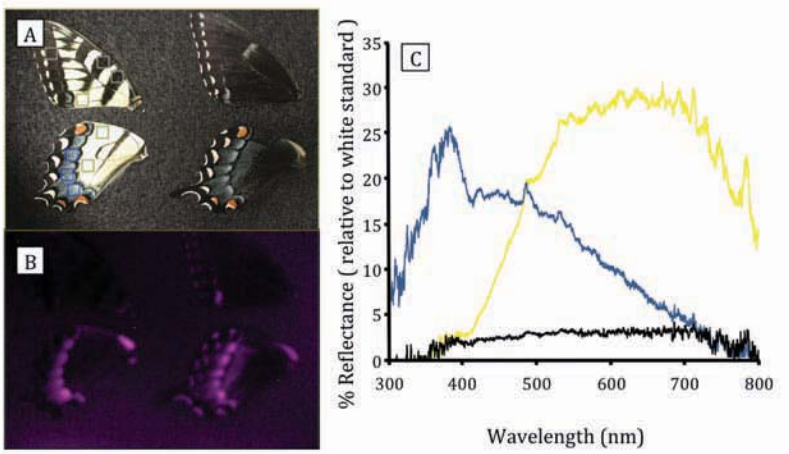
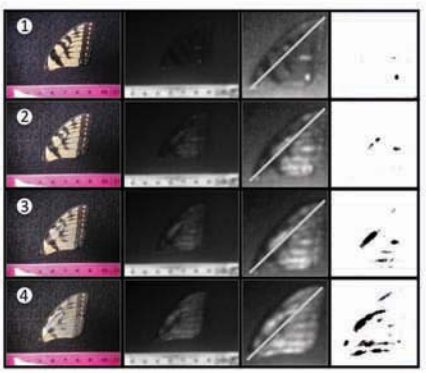


FIGURE 1



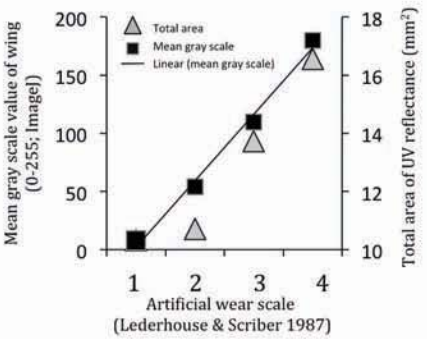


FIGURE 2

FIGURE 3

FIG. 1. Examples from our photographic and spectral examination of ultraviolet reflectance in tiger swallowtail butterflies. All examined butterflies showed very similar patterns (photographic: n=15, spectral: n=4). **A**: Representative visual image of the dorsal side of yellow morph (left) and dark morph (right) female P. *glaucus*. The nine squares on the yellow-morph female's wing represent the approximate locations of our sampling for the spectral analysis. Gray squares correspond to 'black' regions, gold squares correspond to 'yellow' regions, and blue squares correspond to 'blue' regions. **B**: The same wings as in 'A' but photographed using a UV pass filter to reveal UV coloration. Areas that reflected UV light appear purple whereas areas that absorbed UV light appear black. **C**: An example of the reflectance spectrum patterns of blue, yellow and black coloration from a single yellow morph, P. *glaucus* female. This figure shows a clear UV signature (300–400 nm) for blue coloration and virtually no UV reflectance for yellow and black coloration.

FIG. 2. Examples of wings classified as wear class 1–4 (rows from top to bottom). From left to right, Column 1: Visual images of wings showing increasing scale loss. Column 2: UV images of wings showing increasing scale loss. Column 3: UV images enhanced for contrast using ImageJ to estimate the mean gray scale along a linear transect from wing base to tip. Column 4: UV pictures converted to binary images to estimate the total area of scale loss based on UV reflectance.

FIG. 3. Correlation between subjective wear class (1–4) and two measures of wing wear based on UV reflectance. The left Y-axis shows the mean gray scale estimate along a line drawn from the base of the wing to the tip (after image was enhanced for contrast). The right Y-axis shows the total area of UV reflectance (after binary conversion). Both measures correlate strongly with wing wear (Mean gray scale $R^2 = 0.991$; Total area $R^2 = 0.926$).

very similar patterns across the 15 individual specimens we examined. In agreement with our photographic results, our spectral analysis revealed a strong UV signature for blue coloration, but virtually no UV reflectance for yellow or black coloration (Figure 1, C). Again, these results were very consistent across samples.

Both measures of UV reflectance were strongly correlated with our wear class categories (Fig. 3). For our test sample, the mean gray scale gave a slightly higher correlation between the wear classes than did the total area of UV reflectance (mean gray scale $R^2 = 0.991$; total area $R^2 = 0.926$), but both were highly significant ($p<0.001$). How much variance would be observed around these points remains to be determined.

In our assessment of male mating preferences for pristine or artificially aged females, we observed 38 copulations in total, 30 in Michigan and eight in Florida (Table 1). While the χ^2 has been shown to work reasonably well even with small expected values, it is generally agreed that the average expected value across categories should be at least 5 (Roscoe & Byars 1971). Therefore, we only statistically examined mating preferences for the Michigan population and for both populations combined. This assessment of male preference for artificially aged or pristine females revealed a clear choice for pristine females (Table 1). In both Michigan and Florida at least 75% of all initiated copulations were with a pristine female rather than an artificially aged female.

TABLE 1. The results of our two-choice mating trials comparing male preferences for pristine and aged females (no scale loss vs. wings artificially aged to category 4).

Population (Species)	# pristine female pairings	# aged female pairings	p value[1]
Michigan (*P. canadensis*)	24	6	0.001
Florida (*P. glaucus*)	7	1	NA
ALL	**31**	**7**	**<0.001**

[1] These p values are based on 2-tailed χ^2 test with 1 degree of freedom and expected frequencies for both categories of 50%.

DISCUSSION

We have shown that tiger swallowtail butterflies have extensive UV reflectance on their wings, predominately in areas that are blue as well as the anterobasal region. However, it should be noted that UV images such as those described here only capture reflectance in a small part of the UV spectrum (Rutowski & Macedonia 2008). It is possible that our description of UV coloration in tiger swallowtails may be rather different from the way these insects view one another, in addition to how other butterfly species, predators, etc. view them.

Another point to consider is that tiger swallowtail females generally have significantly more blue coloration on their wings and therefore more UV reflectance than males (Aardema & Scriber 2013). Unlike in many other Lepidopteran systems, this coloration does not seem to be utilized for conspecific recognition or mate choice (Aardema & Scriber 2013). It is possible that UV and blue coloration relates to enhanced mimicry of the pipevine swallowtail (*Battus philenor*) by dark-morph *P. glaucus* females. However, *B. philenor* have wings that reflect almost no UV light (Aardema & Scriber, unpublished data). More testing will be needed to determine if the ultraviolet coloration of tiger swallowtail butterflies has ecological or behavioral significance.

Beyond the basic observations of UV in these butterflies, we have proposed that techniques similar to those described here could be used to objectively quantify wing wear in butterflies. Such methods are in contrast to many systems currently employed which use some form of subjective wear class. These systems may be affected by observer biases or differences between observers. Interestingly, our observation of increasing UV reflectance with wear in tiger swallowtails is the opposite pattern to that observed in *Colias eurytheme*. In this species the scales have evolved to reflect a maximal amount of UV, and this reflectance declines with increased wing wear (Kemp 2006). Recently it was shown that UV coloration in butterflies could evolve very rapidly (Wasik 2014). Therefore, it is not surprising that different species exhibit differences in how their UV coloration is affected by wear. Regardless of whether UV coloration increases or decreases, when changes in UV reflectance correlate with wing wear, these patterns could be used to objectively quantify the wing wear of individuals, and correspondingly age. However, species-specific calibrations would likely be in order.

Finally, the results of our mate-choice study lend preliminary support to our hypothesis that older looking individuals are less desirable as potential mates. However, we were only able to examine male mate choice for worn or fresh appearing females. It remains to be determined whether females also discriminate among males based on wing wear and/or the exposure of the underlying wing membrane with corresponding increases in UV reflectance. Furthermore, whether UV reflectance is the actual cue that indicates an individual's age to conspecifics of the opposite sex requires

additional research to determine. Ultimately, these results should be viewed as preliminary and follow-up research is warranted.

ACKNOWLEDGMENTS

We would like to thank Rodrigo Mercader and Gabe Ording for helpful discussions during the early stages of this project. Shane Empie and John Acorn provided advice on UV photography. We thank Jay Sobel for assistance with spectrophotometry. Ange Kosnik, Brittany Sonke, Howard Romack and William Houtz assisted with the rearing of females for tethering experiments.

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Submitted for publication 18 August 2014; revised and accepted 20 September 2014.

Journal of the Lepidopterists' Society
69 (1), 2014, 63–72

TWO NEW SPECIES OF *PELOCHRISTA* LEDERER (TORTRICIDAE) FROM EASTERN UNITED STATES, WITH REVIEWS OF FIVE SIMILAR SPECIES

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ABSTRACT. *Pelochrista sullivani*, new species, and *Pelochrista lynxana*, new species, are described, respectively, from coastal savannah habitat in Mississippi and North Carolina and from prairie/glade habitat in Kentucky, Mississippi, and Ohio. Four species with similarities to the new taxa are reviewed, *Pelochrista matutina* (Grote), *Pelochrista fiskeana* (Kearfott), *Pelochrista pandana* (Kearfott) and *Pelochrista symbolaspis* (Meyrick), with *P. pandana* being recognized as a junior synonym of *P. fiskeana*. Also reviewed is *Pelochrista notialis* (Miller), a taxon once confused with *P. matutina*.

Additional key words: Eucosmini, *fiskeana*, *pandana*, *matutina*, *notialis*, *symbolaspis*

The primary purpose of this paper is to make names available for two species of *Pelochrista* Lederer from eastern United States that have been encountered during the past two decades in coastal savannah habitat in Mississippi and North Carolina and in prairie/glade openings in Kentucky, Mississippi, and Ohio. The first, *Pelochrista sullivani*, new species, resembles *Pelochrista matutina* (Grote) in forewing appearance and is nearly identical in male genitalia to *Pelochrista symbolaspis* (Meyrick), a little known species from west Texas. The second, *Pelochrista lynxana*, new species, resembles *P. sullivani* in genitalia and forewing pattern but differs from that species in color and habitat preference. Reviews are provided for *P. matutina*, *P. symbolaspis*, and *Pelochrista fiskeana* (Kearfott), the last species having similarities with *P. matutina* and *P. lynxana* in male genitalia and forewing appearance, respectively. Also reviewed are *Pelochrista notialis* (Miller), a species that Heinrich (1923) confused with *P. matutina*, and *Pelochrista pandana* (Kearfott), which is treated here as a junior synonym of *P. fiskeana*.

Generic assignments for the species mentioned here follow the recently revised world catalogue of *Eucosma* and *Pelochrista* by Gilligan and Wright (2013), which in turn is based on a phylogenetic analysis of the *Eucosma-Pelochrista* lineage by Gilligan et al. (2014).

MATERIALS AND METHODS

I examined 355 specimens and 74 associated genitalia preparations from the following institutional and private collections: American Museum of Natural History, New York (AMNH); George J. Balogh, Portage, Michigan (GJB); Florida State Collection of Arthropods, Gainesville, Florida (FSCA), Loran D. Gibson, Florence, Kentucky (LDG); C. E. Harp, Littleton, Colorado (CEH); E. C. Knudson, Houston, Texas (ECK); Mississippi Entomological Museum, Mississippi State, Mississippi (MEM); The Natural History Museum, London (BMNH); United States Museum of Natural History, Washington D. C. (USNM); and Donald J. Wright (DJW).

Morphological terminology follows Gilligan et al. (2008). Forewing length (FWL) is defined as the distance from base to apex including fringe, aspect ratio (AR) as FWL divided by medial forewing width. Saccular angle (SA) refers to the angle-like projection of the valva at the juncture of the ventral margins of the sacculus and neck, and neck ratio (NR) is defined as neck width divided by basal valva width, the first measurement taken at the narrowest point of the neck, the second from base of costa and to ventral margin of sacculus, perpendicular to the latter. The SA and NR are reported as averages of a few such calculations. Adult images and genitalia drawings were edited in Adobe Photoshop CS5, and "n" signifies the number of observations supporting a particular statement.

SPECIES ACCOUNTS

Pelochrista fiskeana (Kearfott 1905) (Figs. 1–4, 21, 27, 30)

Eucosma fiskeana Kearfott 1905:358; Barnes & McDunnough 1917:171; Heinrich 1923:127; McDunnough 1939:47; Powell 1983:35; Brown 2005:319; Gilligan et al. 2008:114.

Pelochrista fiskeana: Gilligan & Wright 2013:320.

Eucosma pandana Kearfott 1907:17; Barnes & McDunnough 1917:170; Heinrich 1923:127; McDunnough 1939:47; Powell 1983:35; Brown 2005:325, **new synonymy**.

Pelochrista pandana: Gilligan & Wright 2013:325.

Eucosma sardiopa Meyrick 1912:34. Unnecessary replacement name for *pandana*.

Discussion. Kearfott (1905) described *P. fiskeana* from three syntypes (2 ♂, 1 ♀) collected by W. F. Fiske at Tryon, North Carolina. Klots (1942) interpreted Heinrich's (1923) statements "Type – In American

Museum" and "Type locality – Tryon, North Carolina" as the designation of a lectotype. Since there is only one syntype of *P. fiskeana* in the AMNH, those remarks constitute a valid designation of the name bearing specimen. That specimen has a green "LECTOTYPE" label attached by Klots.

Pelochrista pandana was described from five syntypes, three from Kerrville, Texas, and two from Cochise County, Arizona. Heinrich (1923) pointed out that the Arizona specimens (1 ♂, USNM; 1 ♀, AMNH) are conspecific with *Pelochrista corosana* (Walsingham). The Texas syntypes are females, two in the AMNH, one in the USNM. In this case, Heinrich's (1923) remarks "Type – In American Museum" and "Type locality – Kerrville, Texas" do not identify a unique specimen, so for stability of nomenclature, one of the two specimens in the AMNH is designated below as the lectotype and has been labeled as such.

I examined the syntypes of *P. fiskeana* and *P. pandana* and found no consistent differences in genitalia, color, or forewing pattern, hence the new synonymy. In some *P. pandana* (Fig. 4) the interfascial areas of the forewing are nearly concolorous with the fasciate markings, but the fasciae are still detectable thanks to faint white edging along their margins. I attribute this condition to intraspecific variation.

Pelochrista fiskeana can be confused with *Pelochrista milleri* Wright based on forewing appearance (Wright 2007, figs. 1, 2; Gilligan et al. 2008, species 164, 175), but the two species have substantially different genitalia (Figs. 21, 27 vs. Wright 2007, figs 3, 4).

Types. *Eucosma fiskeana*. Lectotype: ♂, North Carolina, [Polk Co.], Tryon, W. F. Fiske, 2 August 1903, abdomen missing, AMNH. Paralectotypes: Same location and collector as lectotype, 10 August 1903 (1 ♂, slide 70471) USNM, 11 August 1903 (1 ♀, slide WEM 176924) USNM. *Eucosma pandana*. Lectotype here designated (Fig. 3): ♀, Texas, [Kerr County], Kerrville, AMNH. Paralectotypes: same data as lectotype (1 ♀) AMNH, (1 ♀, slide DJW 3157) USNM.

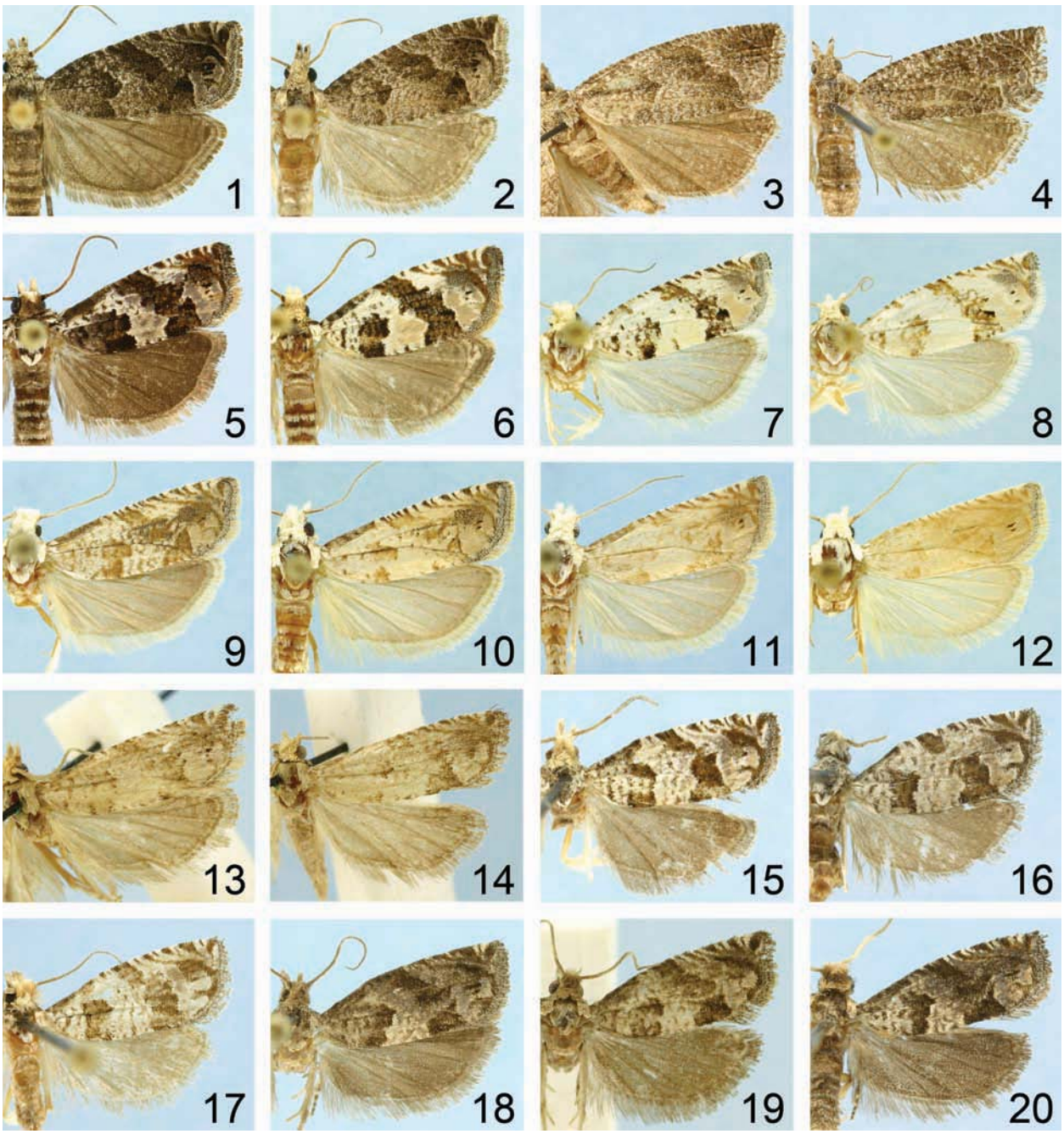
Description. *Head.* Frons pale tan; vertex scales brownish gray with tan apices; labial palpus with medial surfaces of first and second segments tan to white, lateral surfaces brownish gray to blackish gray, third segment blackish brown; antenna brown; scape with blackish mark on dorsal surface. *Thorax.* Dorsal surface brown to dark gray brown; fore- and mid-legs with anterior surfaces blackish brown, posterior surfaces tan; hind-legs largely tan; fore- and mid-legs with tan marks at mid-tibia and distal end of tibia; tarsi with tan annulations. Forewing (Figs. 1–4): ♂ FWL 7.0–11.6 mm (mean = 9.2, n = 53), AR = 2.55; ♀ FWL 7.6–13.5 mm (mean = 10.4, n = 20), AR = 2.58; male with costal fold; costa weakly arched; apical angle approximately 90°; termen straight; dorsal surface brown to blackish brown; fasciae dark brown, thinly edged with white, usually contrasting with paler interfascial areas; subbasal fascia chevron-shaped, nearly complete, often weakly interrupted by paler scaling on radius and A_{1+2}; median fascia complete, band-like, outwardly oblique from mid-costa to pre-tornal portion of inner margin; postmedian band narrow, extending from costa to mid-termen, often constricted or interrupted on radius; ocellus well-defined to obscure, with lustrous gray bars on proximal, distal and posterior margins; central field of ocellus concolorous with interfascial areas and crossed by up to four black dashes; distal one-half of costa with inconspicuous paired whitish strigulae and associated lustrous gray striae; termen with thin white line from M_2 to apex, followed distally by band of white-tipped blackish-gray scales from tornus to apex; fringe gray brown. Hindwing: Gray brown. *Abdomen.* Male genitalia (Fig. 21) (n = 12): Uncus barely differentiated from dorsolateral shoulders of tegumen, with apical margin weakly indented medially; socii short and fingerlike; phallus short and stout; vesica with 24–50 deciduous cornuti; valva with costal margin concave at neck and weakly convex toward apex, ventral emargination moderate, NR = 0.60, saccular corner broadly rounded, mean SA = 154°; cucullus with dorsal lobe strongly developed, apex round to flattened, distal margin nearly straight near apex and weakly concave toward anal angle, anal angle tongue-like, setation of medial surface sparse at anal angle, moderately course along distal margin, fine otherwise. Female genitalia (Figs. 27, 30) (n = 5): Papillae anales facing laterally, with margins of anal opening curling medially; apophyses posteriores distinctly shorter than apophyses anteriores; lamella postvaginalis ovate to semi-rectangular, microtrichiate; lamella antevaginalis ring-like and outwardly projecting from surface of sterigma; posterior margin of sternum 7 concavely emarginated to one-half length of sterigma and laterally diverging from sterigma; scaling of sternum 7 uniform except for dense band along posterior margin; ductus bursae with sclerotized patch near juncture with ductus seminalis; corpus bursae with two large semi-circular signa of nearly equal size, one near juncture with ductus bursae, the other in anterior one-half of corpus bursa.

Distribution and flight period. I examined 80 specimens (58 ♂, 22 ♀) documenting a range from North Carolina, Ohio, and Illinois, south to Florida, Mississippi, and Texas. Adults fly from mid-April (in Texas) to October (in Texas), with most collections occurring in June, July or August.

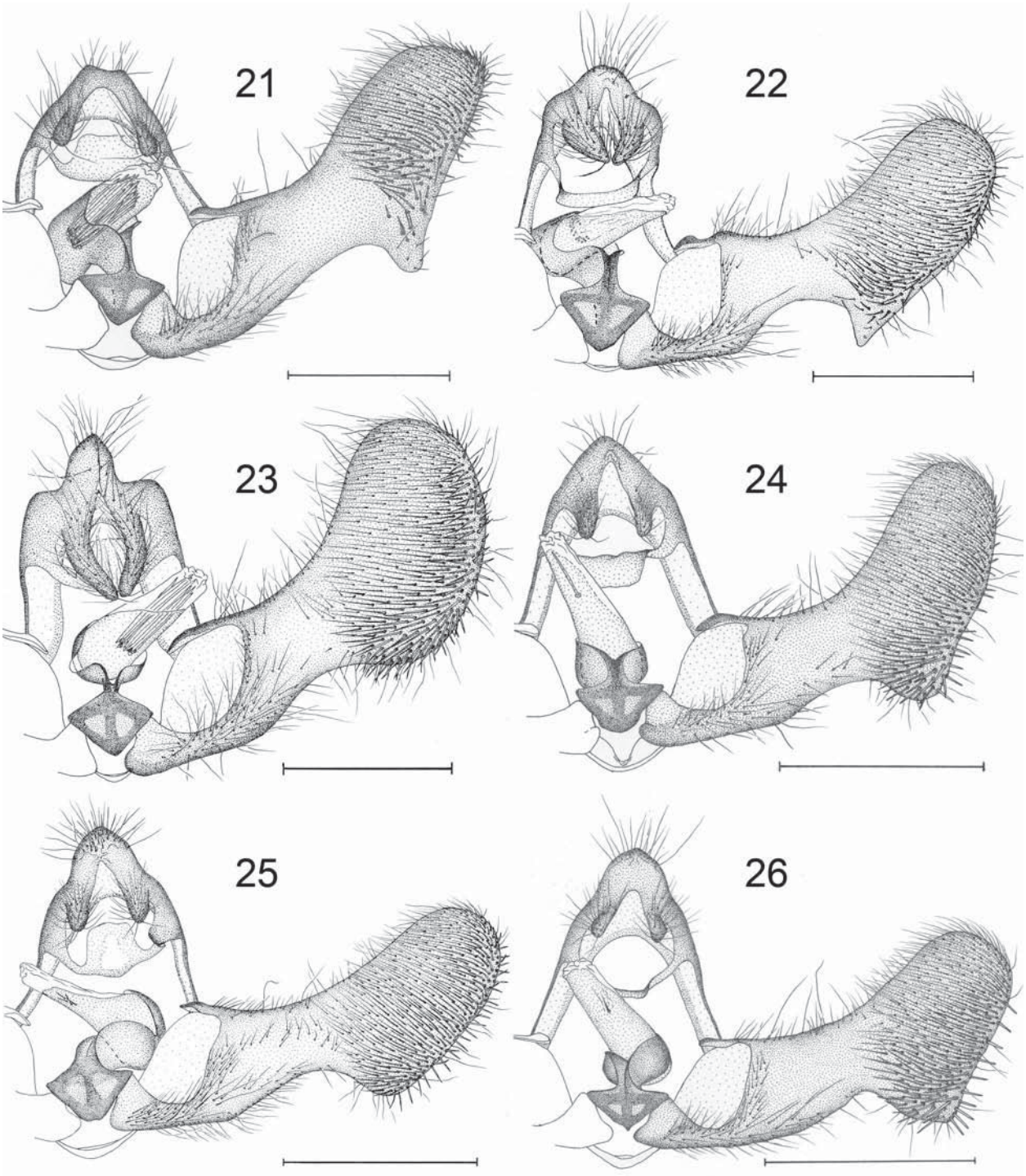
Pelochrista matutina (Grote)
(Figs. 5–8, 22, 28, 31)

Penthina matutina Grote 1873:92, plate 2, fig. 9.
Paedisca matutina: Fernald 1882:41.
Eucosma matutina: Fernald [1903]:459; Barnes & McDunnough 1917:170; McDunnough 1939:47; Powell 1983:34; Miller 1985:243; Miller 1987:51; Brown 2005:323; Gilligan et al. 2008:108.
Pelochrista matutina: Gilligan & Wright 2013:324.
Eucosma grotiana Kearfott 1908:170; Barnes & McDunnough 1917:170; Heinrich 1923:106; McDunnough 1939:46; Powell 1983:34; Miller 1985:243; Brown 2005:323.
Pelochrista grotiana: Gilligan & Wright 2013:324.

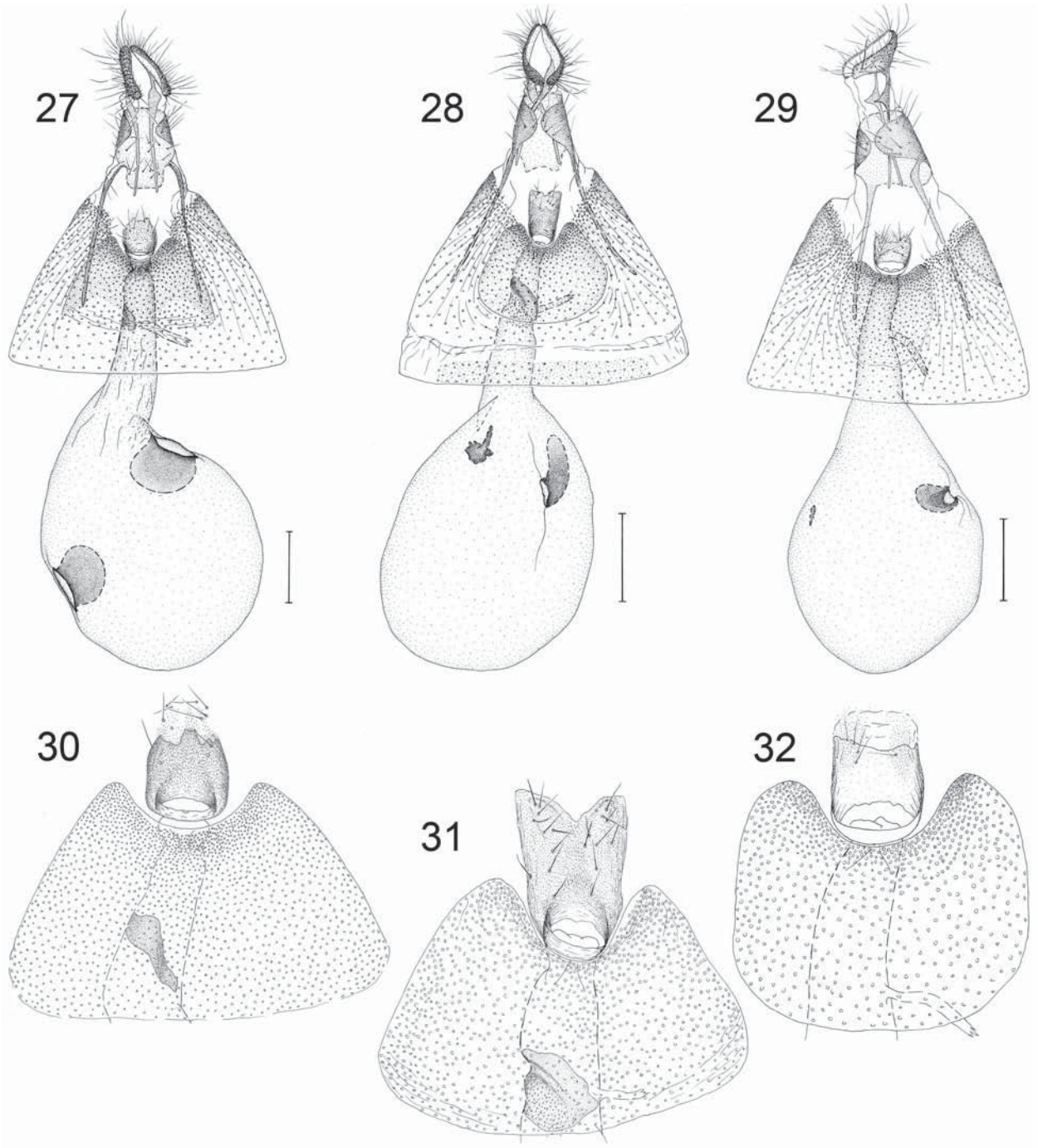
Discussion. Grote (1873) described *P. matutina* from a single specimen collected in Texas by G. W. Belfrage. The Grote collection was sold to the BMNH (Kearfott 1908:171), and Heinrich (1923), not having seen the type but believing it to be in the BMNH, misidentified *P. matutina*, illustrating the genitalia (fig. 199) of a specimen he considered likely to have been compared with the type by Fernald. Miller (1985), without comment on the fate of the holotype, designated a neotype for *P. matutina*, a ♀ in the BMNH that lacks an abdomen. The neotype is alleged to be the



FIGS. 1–20. **1–4,** *P. fiskeana*. **1–2,** ♂, ♂, Adams Co., Ohio. **3,** *P. pandana* ♀, lectotype, Kerr Co., Texas. **4,** *P. pandana* ♀, Washington Co., Texas. **5–8,** *P. matutina*. **5**, ♂, Bullitt Co., Kentucky. **6,** ♂, Adams Co., Ohio. **7–8,** ♀, ♀, Morton Co., Kansas. **9–12,** *P. notialis*. **9–10,** ♂, ♂, Yuma Co., Colorado. **11,** ♂, Morgan Co., Colorado. **12,** ♀, Baca Co., Colorado. **13–14**, *P. symbolaspis* syntypes. ♂, ♂, Brewster Co., Texas. **15–17,** *P. sullivani*. **15,** ♂, holotype, Cateret Co., North Carolina. **16,** ♂, Cateret Co., North Carolina. **17,** ♂, Jackson Co., Mississippi. **18–20,** *P. lynxana*. **18,** ♂, holotype, Adams Co., Ohio. **19**, ♂, Bullitt Co., Kentucky. **20,** ♂, Chickasaw Co., Mississippi.



FIGS. 21–26. Male genitalia. **21,** *P. fiskeana*, slide DJW 1294. **22,** *P. matutina*, slide DJW 3047. **23,** *P. notialis*, slide DJW 3030. **24,** *P. symbolaspis*, slide DJW 3325. **25,** *P. sullivani*, holotype, slide DJW 3029. **26,** *P. lynxana*, slide DJW 3237. Scale bar = 0.5 mm.



FIGS. 27–32. Female genitalia. **27, 30,** *P. fiskeana*. **27,** slide DJW 3049. **30,** *P. pandana* syntype, slide DJW 3157. **28, 31,** *P. matutina*, slides DJW 1151, 3043. **29, 32,** *P. notialis*, slides DJW 3033, 421. Scale bar = 0.5 mm.

only other specimen of the species belonging to Grote that was collected before 1874. Miller (1985) illustrated the wings of that specimen with a photograph from the AMNH that probably was taken by N. Obraztsov. He also proposed the name *E. notialis* for the species Heinrich misidentified and illustrated as *E. matutina*.

Kearfott (1908) based *E. grotiana* on 15 specimens from Colorado, Illinois, Iowa, and New Mexico and distinguished it from E. *matutina* by size (wing span 15–22 vs. 12–16 mm), color of markings (dark in the former, fawn in the latter), and the presence of a brown spot on the base of the antenna (absent in *E. matutina*). Klots (1942) credited Heinrich (1923) with the designation of a lectotype, based on the statements "Type – In American Museum" and "Type locality – Iowa," but there are three syntypes in the AMNH that fit that description. Klots attached a green "LECTOTYPE" label to one of those Iowa specimens, which in turn prompted Miller (1985) to attribute the lectotype designation to Klots. For the sake of nomenclatorial stability, I include below a designation of that specimen as the lectotype. The synonymy of *grotiana* and *matutina* was proposed by Miller (1985) without explanation.

Pelochrista matutina is superficially similar to *P. sullivani* (described below) and to *Pelochrista mescalerana* (Wright) (Figs. 5–8 vs. 15–17 and Wright 2012, fig. 4) but is easily separated from those taxa by differences in genitalia (Figs. 22, 28 vs. 25, 33 and Wright 2012, figs. 22, 33).

Types. *Penthina matutina*. Neotype (designated by Miller 1985): ♀, abdomen missing, BMNH. *Eucosma grotiana*. Lectotype (here designated): ♀, Iowa, C. P. Gillette, AMNH. Paralectotypes: IOWA: Ac. Cat. 121 (1 ♂) AMNH; Ac. Cat. 118, C. P. Gillette (1 ♀) USNM; Ames (1 ♀) AMNH. COLORADO: 2610 (1 ♂, slide DJW 3299) AMNH; 628 (1 ♀) USNM; 2610 (1 ♂, slide 70363) USNM; Clear Creek (1 ♂) USNM; Clear Creek, Oslar, 23 July 1904 (1 ♂) AMNH, 16 July 1904 (1 ♂) USNM; Denver, Oslar (1 ♂) USNM; Oslar 22 June 1905 (1 ♂) USNM. ILLINOIS: Chicago, July 1900 (1 ♂) USNM. NEW MEXICO: Pecos, [Cockerell], 25 August (1 ♀) USNM. This accounts for 14 of the 15 syntypes. The fifteenth is a male *Gypsonoma haimbachiana* (Kearfott) in the AMNH labeled: Colorado, Bear Creek, Oslar, 23 August 1904, slide DJW 3298.

Description. *Head.* Frons and vertex white, dark specimens with upper vertex suffused with brown; labial palpus white with brown shading (pronounced in dark specimens) on lateral surface of second segment; antenna white to pale brown; scape with brown spot on dorsal surface (pale to absent in light specimens). *Thorax.* Dorsal surface white with some brown speckling; fore- and mid-legs with anterior surfaces brown, posterior surfaces tan to whitish; hind-legs tan to white; tarsi with whitish annulations. Forewing (Figs. 5–8): ♂ FWL 5.8–10.2 mm (mean = 7.6, n = 57), AR = 2.62; ♀ FWL 5.7–9.9 mm (mean = 7.6, n = 44), AR = 2.66; male with costal fold; costa weakly arched; apical angle approximately 90°; termen straight; interfascial areas white, often with brown transverse reticulations; fasciae pale brown to dark brown, often speckled with black; subbasal fascia represented by bar from inner margin to cell and associated dark mark on costa, the two components separated by white subcostal band from base to median fascia; median fascia complete and band-like, from mid-costa to pre-tornal portion of inner margin; area between subbasal and median fasciae often suffused with gray (in dark specimens) or pinkish tan (in whiter specimens); ocellus bordered proximally and distally by lustrous gray to pinkish-tan bars; central field of ocellus white, crossed by up to four short black dashes; costal strigulae between median fascia and apex white, paired, and sharply defined; termen with salt-and-pepper colored band from tornus to apex; fringe white to pale brown, darker toward apex. Hindwing: Dark gray brown to pale gray brown. *Abdomen.* Male genitalia (Fig. 22) (n = 13): Uncus with apex angulate to rounded; dorsolateral shoulders of tegumen well-defined and weakly slouched; socii finger-like, tapering distally; vesica with 13–34 deciduous cornuti; valva with costal margin concave, ventral emargination moderate, NR = 0.62, saccular corner angulate, mean SA = 142°; cucullus with dorsal lobe strongly developed, apex rounded, distal margin weakly convex to nearly straight, ventral lobe triangular, setation of medial surface sparse at anal angle, moderately course along distal margin, fine otherwise. Female genitalia (Figs. 28, 31) (n = 5): Papillae anales laterally facing and moderately setose; apophyses posteriores distinctly shorter than apophyses anteriores; lamella postvaginalis semi-rectangular and densely microtrichiate, with length greater than width; lamella antevaginalis ring-like and projecting outward from surface of sterigma; posterior margin of sternum 7 concavely emarginated to one-third length of sterigma; scaling of sternum 7 uniform except for moderately dense band along posterior margin; membrane between sterna 6 and 7 with two shallow pockets; ductus bursae contorted by sclerotized patch at juncture with ductus seminalis; inner surface of said patch microtrichiate; corpus bursae with two signa of unequal size.

Distribution and flight period. The 145 specimens examined (87 ♂, 58 ♀), along with various literature records, indicate a range extending from Maine, Wisconsin, and Montana, south to Alabama, south Texas and New Mexico. Most adults were collected from early July to early September, with a few records in May, June, and October.

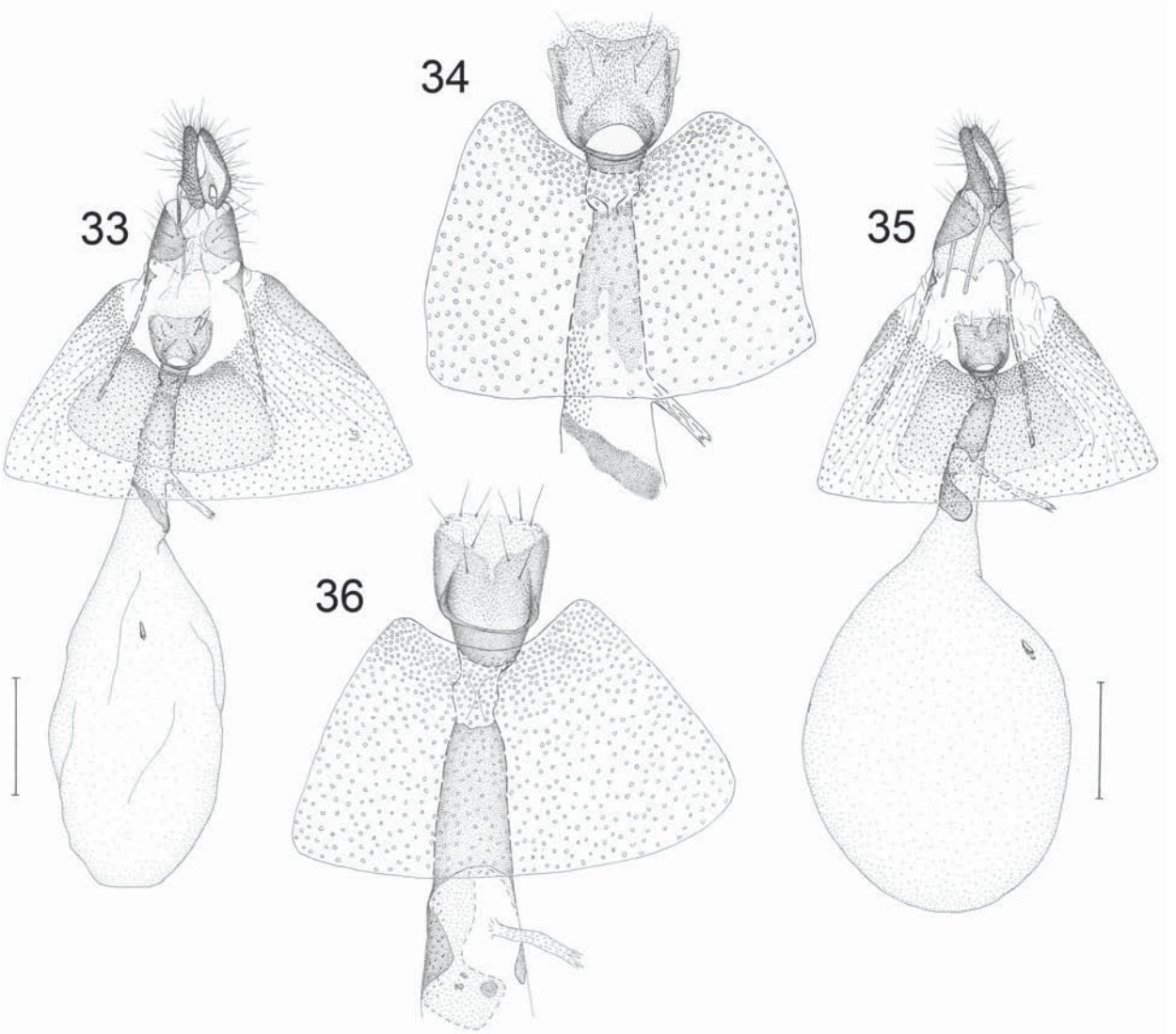
Pelochrista notialis (Miller)
(Figs. 9–12, 23, 29, 32)

Eucosma notialis Miller 1985:244; Brown 2005:324.
Eucosma matutina not Grote 1873:92, Heinrich 1923:109, misidentification.
Pelochrista notialis: Gilligan & Wright 2013:325.

Discussion. *Pelochrista notialis* is not particularly close to the other taxa treated here (based on genitalia) but is included because Heinrich (1923) misidentified it as *P. matutina*. That confusion endured until Miller (1985) recognized the distinction between the two taxa. The two species do have maculational similarities (Figs. 9–12 vs. 5–8), but *P. notialis* is more yellowish than whitish, with considerably less contrast between fasciae and interfascial areas.

Holotype. ♂ Texas, [Kerr County], Kerrville, H. Lacey, 6 June, slide 70599, USNM.

Paratypes. Same location and collector as holotype,



Figs. 33–36. Female genitalia. **33, 34,** *P. sullivani*, slides DJW 3028, 3027. **35, 36,** *P. lynxana*, slides DJW 3255, 3252. Scale bar = 0.5 mm.

16 March (1 ♂, slide 89796) USNM; no locality, 3/7, (1 ♂, slide CH 11 May 1920) AMNH; Hemphill Co., E. C. Knudson, 2 July 1978 (2 ♂, slides ECK 636, WEM 224842) ECK; Travis Co., E. C. Knudson, 13 April 1979 (1 ♂, slide ECK 628) ECK.

Description. *Head.* Frons and vertex white to pale yellow brown; labial palpus whitish with brown shading on lateral surface of second segment; antenna concolorous with vertex. *Thorax.* Dorsal surface white to pale brownish yellow; fore- and mid-legs with anterior surfaces brown, posterior surfaces paler, with whitish mark at mid-tibia and distal end of tibia; hind-legs white to pale brownish yellow; tarsi with pale annulations, often obscure on hind-legs. Forewing (Figs. 9–12): ♂ FWL 5.9–8.4 mm (mean = 7.3, n = 28), AR = 2.95; ♀ FWL 7.0–8.5 mm (mean = 7.6, n = 6), AR = 2.88; male with costal fold; costa nearly straight; apical angle approximately 90°; termen straight; interfascial areas pale brownish yellow to white, variably reticulated with brown; fasciae brown to yellow brown and variably expressed; subbasal fascia represented by bar from inner margin to cell, interrupted on A_{1+2}, and separated from costa by band of whitish scales along radius; median fascia composed of three components: an outwardly oblique bar at mid-costa, an irregularly shaped patch at distal end of cell, and a triangular mark on inner margin bordering proximal edge of ocellus; costal strigulae between median fascia and apex sharply defined by short dark dashes; ocellus obscure to moderately well-defined, the proximal and distal margins edged by lustrous whitish bars, the central field with two small blackish dashes; termen with salt-and-pepper colored band from tornus to apex; fringe scales whitish to pale yellowish brown. Hindwing: Pale gray brown to pale yellowish brown. *Abdomen.* Male genitalia (Fig. 23) (n = 11): Uncus strongly produced, with apex angulate and ventral surface divided by prominent medial line; dorsolateral shoulders of tegumen well-defined; socii long and finger-like; vesica with 13–19

deciduous cornuti; valva with costal margin concave, ventral emargination shallow, NR = 0.76, mean SA = 153°; cucullus with dorsal lobe strongly developed, apex broadly rounded, distal margin convex of nearly uniform curvature, ventral lobe weakly produced, anal angle broadly rounded, setation of medial surface fine. Female genitalia (Figs. 29, 32) (n = 2): Papillae anales laterally facing; lamella postvaginalis rectangular, plate-like, width greater than length, with lateral margins curled inward; lamella antevaginalis ring-like; sternum 7 with posterior margin roundly emarginated to one-half length of sterigma; setation of sternum 7 uniform except for dense band along posterior margin; ductus bursae lacking sclerotization; corpus bursae with two signa, one much smaller than the other.

Distribution and flight period. I examined 44 specimens (38 ♂, 6 ♀) from Baca, Morgan, Otero, Weld, and Yuma Counties in Colorado, and from Brown, Cottle, Culberson, Hemphill, Jeff Davis, and Kerr Counties in Texas. Colorado adults fly in July and August; the Texas records are from mid-April to the end of July.

Pelochrista symbolaspis (Meyrick)
(Figs. 13, 14, 24)

Eucosma symbolaspis Meyrick 1927:334; Clarke 1958:391, Plate 194, figs. 4, 4a.
Epiblema symbolaspis: McDunnough 1939:48; Powell 1983:35; Brown 2005:286.
Pelochrista symbolaspis: Gilligan & Wright 2013:328.

Discussion. This species is poorly known to North American taxonomists due to a lack of specimens in institutional collections. Meyrick (1927) described it from a series of 18 specimens collected near the town of Alpine in west Texas. Sixteen of the syntypes (all males) are in the BMNH, (K. Tuck, pers. comm.), including a lectotype designated and illustrated by Clarke (1958). The fate of the other two syntypes is unknown, and no specimens other than the types have been reported. McDunnough (1939) placed *E. symbolaspis* in *Epiblema* Hübner, and subsequent authors followed suite until Gilligan & Wright (2013) transferred it to *Pelochrista* based on Clarke's illustrations of the lectotype and on the similarity it bears to the two new taxa described below. I examined four of the syntypes and found two of them to be an undescribed species of *Pelochrista* with genitalia similar to those of *Pelochrista womonana* (Kearfott).

Lectotype. ♂, Texas, Brewster County, Alpine, 7000 ft., April 1926, slide 6387, BMNH.

Paralectotypes. Same data as lectotype except for elevation (7000–8000 ft.) and date (April or May), (15 ♂, not all conspecific with lectotype, slides DJW 3325, 3333) BMNH.

Description. *Head.* Frons whitish; vertex pale tan; labial palpus with medial surface whitish, lateral surface tan with dark brown mark on second segment; antenna concolorous with vertex. *Thorax.* Dorsal surface tan; tegula tan, shading to brown at base; legs with anterior surfaces brown, posterior surfaces tan; tarsi with conspicuous whitish annulations. Forewing (Figs. 13, 14): ♂ FWL 6.3–7.2 mm (mean = 6.8, n = 2), AR = 3.17; male with costal fold; costa nearly straight; apex acute; termen straight; dorsal surface with diffuse brown fasciate markings and tan interfascial areas, the later with brown transverse reticulations; subbasal fascia represented by slightly oblique band from inner margin to cell; median fascia consisting of a dark mark at mid-costa, an ill-defined mark at distal end of cell, and an obscure semi-triangular mark on inner margin adjacent to proximal edge of ocellus; ocellus pale, moderately contrasting with surrounding area, defined proximally and distally by lustrous fawn to gray bars, with central field marked by one or two blackish-brown dashes; costal strigulae between median fascia and apex white, paired, and clearly defined; termen with inconspicuous brown line from tornus to apex; fringe brownish. Hindwing: Pale gray brown. *Abdomen.* Male genitalia (Fig. 24) (n = 1): Uncus triangular and barely differentiated from dorsolateral shoulders of tegumen; socii short and finger-like; phallus weakly tapering toward apex, with base closely surrounded by anellus; vesica with 1 deciduous cornutus; valva with costa concave, ventral emargination shallow, NR = 0.72, SA = 155°; cucullus with dorsal lobe strongly produced, apex rounded, ventral one-half of distal margin slightly indented, ventral lobe moderately developed, anal angle rounded, setation moderately stout near anal angle and distal margin, fine otherwise. Female genitalia: Unknown.

Distribution and biology. The type series was collected in April and May in Brewster County, Texas, about 70 miles north of Big Bend National Park.

Pelochrista sullivani, **new species**
(Figs. 15–17, 25, 33, 34)

Diagnosis. *Pelochrista sullivani* is similar to *P. matutina* in color and maculation but differs from that taxon in size (mean FWL = 5.9 vs. 7.7 mm) and genitalia. Genitalic differences include: uncus strongly vs. moderately developed with angulate vs. rounded apex, dorsolateral shoulders of the tegumen less clearly defined, anal angle rounded vs. triangular, vesica with 1–4 vs. 13–34 deciduous cornuti, sterigma less elongate, ductus bursae not contorted near ductus seminalis, corpus bursae with only one signum (Figs. 25, 33, 34 vs. 22, 28, 31). *Pelochrista sullivani* resembles *P. symbolaspis* and *P. lynxana* (described below) in size, male genitalia, and forewing maculation but has white interfascial areas without the brown and dark brownish-gray suffusion, respectively, in the latter two species. Moreover, *P. sullivani* is known only from coastal savannah in Mississippi and North Carolina, *P. symbolaspis* from west Texas, and *P. lynxana* from remnant prairie/cedar glade habitat in the eastern Midwest and northern Mississippi.

Holotype (Figs. 15, 25). ♂, North Carolina, Carteret County, Millis Road Savannah, J. Bolling Sullivan, 24 August 1993, slide DJW 3029, USNM.

Paratypes. MISSISSIPPI. Harrison County, Long Beach, R. Kergosien, 3 July 1997 (1 ♀), 16 September 1995 (1 ♀); Jackson County, Sandhill Crane NWR, J. A. MacGown, 30.4594° N, 88.6911° W, 25 April 1995 (8 ♂, slides DJW 983, 3249), 29 August 1995 (1 ♀), 7 September 1994 (3 ♀); Jackson County, Shepard State Park, R. Kergosien, 6–11 September 1995 (1 ♀), 9–15 September 1995 (2 ♂), 12–18 September 1995 (1 ♂). NORTH CAROLINA. Same location and collector as holotype, 14 August 1993 (1 ♀, slide DJW 3028), 17

August 1993 (1 ♂, 1 ♀), 24 August 1993 (5 ♂), 27 August 1993 (1 ♂), 9 September 1993 (1 ♀, slide DJW 3027), 11 September 1993 (2 ♂). Paratype depositories: MEM, USNM, DJW.

Description. *Head.* Frons and vertex white; labial palpus white with gray-brown mark on lateral surface of second segment and some gray-brown shading on long scales projecting from ventral margin of second segment; antenna white. *Thorax.* Dorsal surface whitish, suffused with gray brown; fore- and mid-legs with anterior surfaces dark brown, posterior surfaces whitish; hind-legs whitish; tarsi with whitish annulations, prominent on fore- and mid-legs, obscure on hind-legs. Forewing (Figs. 15–17): ♂ FWL 5.1–6.8 mm (mean = 6.0, n = 30), AR = 2.67; ♀ FWL 4.9–6.5 mm (mean = 5.8, n = 11), AR = 2.60; male with costal fold; costa with basal one-half weakly arched, distal one-half straight; apical angle approximately 90°, termen nearly straight; dorsal surface with brown fasciate markings and white interfascial areas, the later with gray-brown transverse reticulations; subbasal fascia nearly complete, often interrupted on radius and/or A_{1+2}; median fascia band-like, extending from mid-costa to pretornal portion of inner margin, often interrupted or at least constricted at distal end of cell by whitish interfascial scaling; postmedian band narrow, usually interrupted near costa, bending around anterior margin of ocellus and connecting to narrow band along termen from M_2 to tornus; ocellus with lustrous gray to beige bars on proximal, distal, and posterior margins and with whitish central field crossed by two blackish dashes; costal strigulae sharply defined from subbasal fascia to apex; termen with thin white line from M_2 to apex; fringe scales dark gray with white apices, distal row somewhat lighter. Hindwing: Uniformly gray brown. *Abdomen.* Male genitalia (Fig. 25) (n = 4): Uncus with strongly developed angulate apex; dorsolateral shoulders of tegumen slouched and weakly differentiated from uncus; socii short and finger-like; phallus tapering toward apex; vesica with 1–4 short deciduous cornuti; valva with costal margin concave, ventral emargination somewhat shallow, NR = 0.69, SA = 155°; cucullus with dorsal lobe strongly developed, apex semicircular, distal margin weakly convex to nearly straight, ventral lobe moderately developed, anal angle rounded, setation of medial surface moderately course near distal margin and anal angle, fine otherwise. Female genitalia (Figs. 33, 34) (n = 6): Papillae anales facing laterally, with margins of anal opening curled medially; sterigma with inwardly-directed cylindrical projection from ostium nearly to constriction of ductus bursae and with narrow flange-like development along anterior one-half of ostium; lamella postvaginalis broadening somewhat posteriorly (width of posterior margin about 1.5 times ostium diameter); posterior margin of sternum 7 concavely emarginated to about one-half length of sterigma and diverging laterally from sterigma; sclerotization of ductus bursae consisting of two components, one semi-cylindrical, extending from constriction anterior to ostium nearly to juncture with ductus seminalis, the other band-like and anterior to ductus seminalis; interior surface of ductus bursae opposite ductus seminalis microtrichiate; corpus bursae with one greatly reduced, almost scar-like signum.

Etymology. This species is named after J. Bolling Sullivan, whose collections in southeastern United States have contributed substantially to our knowledge of the Lepidoptera of that region.

Distribution and flight period. The specimens in the type series were collected in longleaf pine savannah near the Gulf Coast of Mississippi and in coastal savannah in North Carolina. Capture dates indicate two primary broods per year, spring and late summer.

Pelochrista lynxana, **new species**
(Figs. 18–20, 26, 35, 36)

Diagnosis. *Pelochrista lynxana* resembles *P. sullivani* in size and forewing maculation, but the vertex, lateral surface of the labial palpus, antenna, and interfascial areas of the forewing are grayish brown rather than white. The male genitalia of the two species (Figs. 25, 26) differ slightly in the shape of the anal angle, the apex being somewhat truncated in *P. lynxana*. In females, the sclerotization of the ductus bursae consists of one component in *P. lynxana* vs. two in *P. sullivani* (Fig. 36 vs. 34). This species has been collected in remnant prairie/cedar glade habitat in Ohio, Kentucky, and northern Mississippi; *P. sullivani* is known only from coastal savannah in southern Mississippi and North Carolina. *Pelochrista symbolaspis* is similar to *P. lynxana* in male genitalia and forewing maculation but is paler, slightly larger (mean FWL = 6.8 vs. 5.8 mm), and is known only from west Texas. Several eastern Eucosmini, such as *Pelochrista palabundana* (Heinrich), *Pelochrista womonana* (Kearfott), and *Sonia divaricata* Miller resemble *P. lynxana* in size, color, and forewing pattern but differ from it substantially in genitalia (see Gilligan et al. (2008): species 148, 174, and 204, respectively).

Holotype (Fig. 18). ♂, Ohio, Adams County, 1 mi. SE of Lynx, D. J. Wright, 1 August 1997, slide DJW 3238, USNM.

Paratypes. KENTUCKY. Bullitt County, S side Rt. 480, 6.9 mi. E. Rt. 61, L. D. Gibson, 22 July 1989 (1 ♂, slide LDG 46), 9 September 1988 (1 ♂, slide LDG 151). MISSISSIPPI. Chickasaw County, Tombigbee National Forest, 30.9258° N, 88.8492° W, R. L. Brown and J. G. Hill, 4 September 2005 (14 ♂, slides DJW 3251, 3253; 3 ♀, slides DJW 3252, 3254, 3255); Lowndes County, T17N R16E S34, Black Belt Prairie, R. L. Brown and D. Pollock, 24 August 1993 (3 ♀, slide DJW 3256); Oktibbeha County, Osborn Prairie, R. L. Brown and L. Koehn, 30 August 1997 (2 ♂, 3 ♀). OHIO. Adams County, 1 mi. SE of Lynx, 25 July 1997 (2 ♂), 25 July 1998 (3 ♂), 29 July 1989 (1 ♀, slide WEM 149901), 1 August 1997 (2 ♂, slide DJW 3237); Erie County, Resthaven Wildlife Area, D. J. Wright, 20 July 1990 (2 ♂, slide WEM 189902). Paratype depositories: AMNH, MEM, USNM, DJW.

Description. *Head.* Frons whitish; vertex gray brown; labial palpus with medial surface white, lateral surface and long scales on ventral margin brownish; antenna concolorous with vertex. *Thorax.* Dorsal surface brown, sometimes suffused with grayish white; fore- and mid-legs with dark brown anterior surfaces, grayish-tan posterior surfaces; hind-legs similar but paler; tarsi with prominent white annulations. Forewing (Figs. 18–20): ♂ FWL 5.4–6.7 mm (mean = 5.8, n = 30), AR = 2.63; ♀ FWL 5.5–6.5 mm (mean = 5.9, n = 9), AR = 2.48; male with costal fold; costa weakly arched basally, nearly straight distally; apical angle approximately 90°, termen straight; maculation as in *P. sullivani* except: fasciae blackish-brown; interfascial areas gray to gray brown, often with some whitish suffusion in basal area and on inner margin between subbasal and median fasciae; median fascia complete; white line on termen from M_2 to apex absent; central field of ocellus gray brown. Hindwing: Uniformly gray brown. *Abdomen.* Male genitalia (Fig. 26) (n = 7): Uncus, tegumen, socii, and phallus as in *P. sullivani*; vesica with 1–3 short deciduous cornuti; valva as in *P. sullivani* except: NR = 0.70, saccular corner broadly rounded, SA =

153°; cucullus with apex convex and often somewhat flattened, distal margin nearly straight and sometimes weakly indented near anal angle, basoventral margin often bent medially, anal angle usually angulate. Female genitalia (Figs. 35, 36) (n = 5): As in *P. sullivani* except: lamella postvaginalis more rectangular; sclerotization of ductus bursae extending from constriction anterior to ostium nearly to juncture with ductus seminalis and continuing beyond said juncture as tongue-like semi-spiral projection.

Etymology. This species is named after the town of Lynx in Adams County, Ohio, which is located within approximately one mile of the type locality.

Distribution and flight period. The types were collected in prairie/glade habitat in northern Ohio, southern Ohio, central Kentucky, and northeastern Mississippi. Adults fly from late July to early September.

DISCUSSION

I vacillated for some time between two possible interpretations for the moths described here as *P. sullivani* and *P. lynxana*: two distinct species vs. two color forms of a single species. The genitalia differences cited above are subtle and conceivably could be attributed to intraspecific variation. The color differences are conspicuous in most cases, but there is some intergradation in northeast Mississippi between the two primary phenotypes. Ultimately, the differences in habitat preference (coastal savannah vs. remnant prairie/cedar glade) persuaded me adopt the present position. From that perspective, *P. sullivani* and *P. lynxana* appear to be weakly differentiated species separated by their distinctly different habitats. Perhaps other considerations such as host plants and molecular data will help clarify this situation sometime in the future.

ACKNOWLEDGEMENTS

I thank J. W. Brown, R. L. Brown, D. Grimaldi, and J. E. Hayden for the loan of specimens under their care. George Balogh, Loran Gibson, Chuck Harp, and Edward Knudson provided additional specimens. Todd Gilligan and an anonymous reviewer provided helpful comments on the manuscript.

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Submitted for publication 3 August 2014; revised and accepted 20 September 2014.

Journal of the Lepidopterists' Society
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PARIDES VERCINGETORIX (PAPILIONIDAE): FIRST RECORD FROM SURINAME

Additional key words: Papilioninae, Troidini, Guianas, Guiana Shield, Surinam.

Parides vercingetorix (Oberthür 1888) (Papilionidae, Papilioninae, Troidini) is one of the rarest Papilionidae of South America (Collins & Morris 1985, Tyler et al. 1994). Rothschild & Jordan (1906) stated that only two specimens were known, one female described by Boisduval as *Papilio coelus* (Boisduval 1836) and one male, the type of *P. vercingetorix*. Nowadays, still only a handful of specimens are known, most of them collected by Le Moult in the early 1900s. Until recently, all came from northern (Montsinery) and northwestern (Mana, St. Laurent du Maroni, St. Jean du Maroni, Plateau des Mines near Gite Moutouchi) French Guiana (http://parides.genus.free.fr/coel.html). Recently (2012), a male was collected from Saül, central French Guiana (collection C. Castelain; Diringer 2012).

In southern Suriname (N 03 26 28, W 055 22 22, about 275 km south of Paramaribo), at 10th November 2012, a freshly emerged *P. vercingetorix* female (FIGURE) was collected in primary forest along a track leading from the Tapanahony river to Poti hill, a small granite inselberg, about 90 km north of the Brazilian border. The butterfly was flying along the herbal layer, showing the typical behavior of searching for hostplants.

This finding extends the distribution of this rare species in about 250 km west from Saül to southern Suriname. Nothing is known about its biology, however, all specimens known were collected in the months of February, October and November. As these are months in which little collecting is generally done, this may partly explain the paucity of collected specimens.

ACKNOWLEDGMENT

My gratitude to Frans Barten for editing the figure.

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Submitted for publication 12 July 2014; revised and accepted 4 October 2014.

FIG. 1. Female *Parides vercingetorix*, collected on November 10, 2012, on track from Tapanahony river to Poti hill, Suriname; forewing length 55 mm, proboscis 22 mm; dorsal (left) and ventral (right) view.

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MANUSCRIPT REVIEWERS FOR 2014 (VOLUME 68)

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 contribtuions published in volume 68.

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NOTE FROM THE EDITOR

At the 2014 annual meeting, the Executive Committee of the Lepidopterists' Society approved using the 3rd issue of Volume 69 (2015 calendar year) to include peer-reviewed manuscripts that include undergraduate students as co-authors. The goals of this effort are, in part, to showcase the exceptional work that the "next generation" of Lepidopterists are performing and to expose future scholars of Lepidoptera to our Society's outlet for publication. The same instructions to authors and the same criteria used during our standard peer-review process will apply to articles that appear in the special section, tentatively titled: "Focus on the Future: Research from Emerging Lepidopterists". I'm open to tweaking that, however. Should you **or a colleague outside the Society that uses Lepidoptera as focal taxa in research** wish to submit an article for this special issue please indicate so in the cover letter (or email) that accompanies your manuscript submission. Questions—please email me (**keith.summerville@drake.edu** or call **515-271-2265**).

Thanks, and I look forward to seeing your submissions!

Keith Summerville
Drake University
Editor, Journal of the Lepidopterists' Society

NOTICE TO CONTRIBUTORS

The Lepidopterists' Society has since its inception valued the contributions of both professional and amateur Lepidopterists. We maintain a policy of accepting for publication in the Journal articles from both groups, while maintaining high standards of scholarship. The Journal of The Lepidopterists' Society is a quarterly publication welcoming articles addressing any aspect of the study of Lepidoptera, including systematics, natural history, behavior, ecology, distribution and biogeography, and evolution. Categories are Articles, Profiles, General Notes, and Advances in Methodology. Instructions for electronic submission appear below.

Short articles, especially those of a less quantitative nature, may be more appropriate for publication in the ***News of the Lepidopterists' Society***. Content for the ***News*** typically includes natural history and life cycle observations, techniques for collecting, rearing and observation, photography, state records, book reviews and notices of new publications, and current events. Such material should be sent to the editor: James Adams, School of Sciences and Math, 650 College Dr., Dalton State College, Dalton, GA 30720-3778; email: **jadams@daltonstate.edu .**

Send ***Journal*** submissions electronically to: **ksummerville@drake.edu** or to the editor at the above address. Contributors should feel free to recommend one or two reviewers upon submission of their manuscript.

Before submitting manuscripts or electronic files, consult instructions on the Society's web site at **http://www.lepsoc.org/**.

Authors should provide an electronic copy of the manuscript in a standard PC or Macintosh-based word processing format.

Abstract: Include an informative abstract for Articles, Profiles, and Technical Comments.

Additional key words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Write with precision, clarity and economy, and use the active voice and the first person whenever appropriate. Make title explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Use metric units for measurements, and a 24-h clock (0930 h, not 9:30 AM) to express time. Underline only where *italics* are intended.

Literature cited: References to Articles, Profiles, General Notes, and Technical Comments should be given as Sheppard (1959) or (Sheppard 1959, 1961a,b) and listed alphabetically under the heading Literature Cited, in plain text (**do not capitalize author names**) and without underlining as follows:

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

—— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

Illustrations: Electronic submissions are expected. Initial submissions may be low-resolution *.jpg format, but final illustrations should be *.tif format with image layers flattened, saved at a resolution of at least 350 ppi (137 pixels per cm). Illustrate only half of symmetrical objects such as adults with wings spread, unless whole illustration is crucial. Bear in mind that your illustrations will be sized to fit a *Journal* page (plan to make lettering sufficiently large) and that the figure legend will appear at the bottom of the page (*Journal* page: 16.5 cm width, 22.5 cm height). One-column illustrations should be a minimum of 1000 pixels wide; two-column illustrations should be at least 2200 pixels wide. Figures, both line drawings and photographs, should be numbered consecutively in Arabic numerals; do not use "plate." Type figure legends double-spaced at the end of the manuscript following Literature Cited. Use a separate paragraph for each legend. Color illustrations are encouraged; contact editor or consult our web site for submission requirements and cost.

Tables: Number tables consecutively in Arabic numerals. Label them in plain text (e.g., Table 1.) and use a concise and informative heading. Type each table on a separate sheet and place after the Literature Cited section, with the approximate desired position indicated in the text. Avoid vertical lines and vertical writing.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting the identity of organisms can be found. Kinds of reports that require vouchering include descriptions of new taxa, life histories, host associations, immature morphology, and some experimental studies.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes will be charged to authors at the rate of $3.00 per line. A purchase order for reprints will accompany proofs.

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Correspondence: Address all matters relating to the *Journal* to the editor. Address book reviews directly to the *News* editor.

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