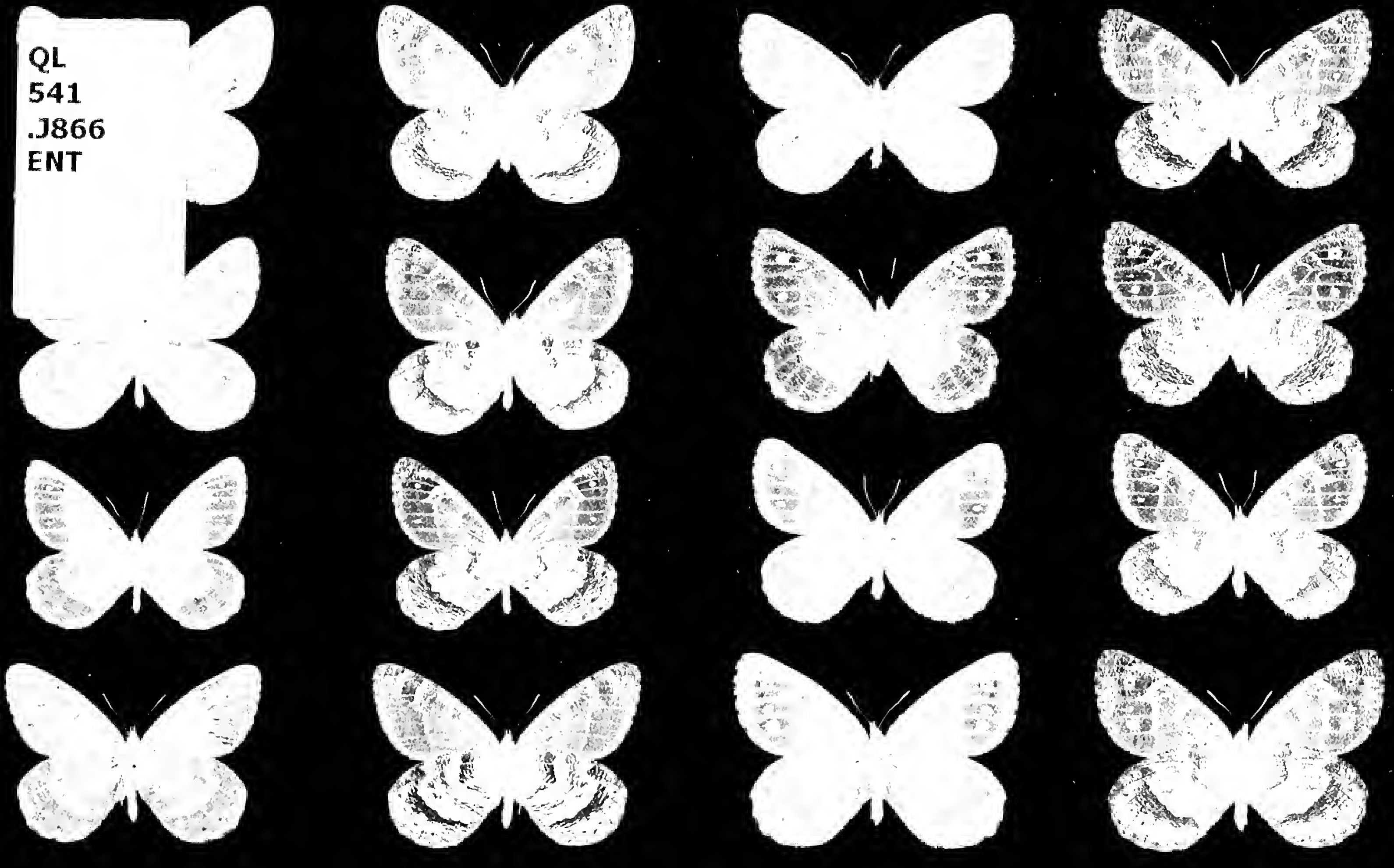

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A new species of *Oeneis* from Alaska, United States, with notes on the *Oeneis chryxus* complex (Lepidoptera: Nymphalidae: Satyrinae)

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Abstract. *Oeneis tanana* A. Warren & Nakahara is described from the Tanana River Basin in southeastern Alaska, USA. This new taxon belongs to the *bore* group of *Oeneis* Hübner, [1819] and is apparently closest to *O. chryxus* (E. Doubleday, [1849]) by morphology, including its larger size and similarity of the female genitalia. In wing patterns and *COI* mitochondrial DNA barcode sequences, it is reminiscent of *O. bore* (Esper, 1789). A review of *O. chryxus* subspecies suggest that some may be better treated as species-level taxa. Evolutionary scenarios within the *chryxus* complex of taxa are discussed. While we hypothesize that *O. tanana* is best considered a species-level taxon, we have not identified any single character that unambiguously separates it from *O. chryxus*. Further study is needed to elucidate the species- or subspecies-level status of *O. tanana*, and to determine if it may have evolved through hybridization between *O. chryxus* and *O. bore*.

Key words: Beringia, butterflies, cryptic species, hybrid species, Nearctic, speciation, taxonomy, Yukon Territory.

Introduction

Butterflies of the genus *Oeneis* Hübner, [1819] are Holarctic in distribution, and occupy a wide range of habitat types, including montane and boreal forests, taiga, grasslands and steppe, alpine and arctic tundra, with several species occurring in sparsely vegetated, rocky terrain (*e.g.*, Ferris 1980; Troubridge et al. 1982). While the nomenclature of Nearctic members of *Oeneis* can be considered relatively stable (*e.g.*, dos Passos 1961, 1964; Miller & Brown 1981; Ferris 1989; Pelham 2008, 2015), new taxa continue to be described (Troubridge et al. 1982; Troubridge & Parshall 1988; Guppy & Shepard 2001; Scott 2006; Holland 2010), and some unresolved taxonomic issues remain (*e.g.*, Hassler & Feil 2002). However, a large number of unresolved taxonomic questions persist among the much richer fauna of Palaearctic *Oeneis*, where species-level boundaries in some groups remain poorly defined (*e.g.*, Murayama 1973; Lukhtanov 1983; Korshunov & Gorbunov 1995; Bogdanov et al. 1997; Gorbunov 2001; Korshunov 2002; Korshunov & Nikolaev 2003; Korb 2005; Chernov & Tatarinov 2006). Progress in improving our knowledge of relationships in *Oeneis* is nonetheless being made; a recent molecular study (Kleckova et al. 2015) has

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helped resolve many of the issues related to the composition of species groups in the genus, a process initiated over 120 years ago.

Elwes & Edwards (1893) were the first to investigate the morphology of the male genitalia of *Oeneis*. They noted that *O. chryxus* (E. Doubleday, [1849]), *O. alberta* Elwes, 1893, *O. bore* (Esper, 1789) and *O. taygete* Geyer, [1830] (now often considered conspecific with *O. bore*) all shared the presence of a similar "tooth" on the valvae, not found in other *Oeneis* species. Dos Passos (1949) referred to Nearctic taxa with this character as members of the "*taygete* group." Based on this character, Gross (1970) united *O. bore, O. taygete, O. nevadensis* (C. Felder & R. Felder, 1867), *O. macounii* (W. H. Edwards, 1885), *O. chryxus, O. ivallda* (Mead, 1878), and *O. alberta* under "Gruppe C" in his review of the genus; this group of taxa was subsequently called the "*bore* group" by Lukhtanov (1984), Gorbunov (2001), Lukhtanov & Eitschberger (2001), Pelham (2008, 2015) and Kleckova et al. (2015). With the exception of various Palaearctic taxa associated with *O. bore, O. pansa* Cristoph, 1893 and *O. ammon* Elwes, 1899 (*e.g.*, Korb 1998; Korshunov 2002; Korshunov & Nikolaev 2003; Tsvetkov 2006; Yakovlev 2011), the *bore* group is Nearctic in distribution.

The *Oeneis chryxus* complex currently includes nine taxa, which are usually considered to be subspecies of *O. chryxus* (*e.g.*, Ferris 1989; Pelham 2008, 2015). These include *O. c. strigulosa* McDunnough, 1934 [Type Locality in Ontario], *O. c. calais* (Scudder, 1865) [Type Locality in Quebec], *O. c. caryi* Dyar, 1904 [Type Locality in NE Alberta], *O. c. chryxus* [Type Locality in W Alberta], *O. c. altacordillera* Scott, 2006 (Type Locality in Colorado], *O. c. socorro* R. Holland, 2010 [Type Locality in New Mexico], *O. c. valerata* Burdick, 1958 [Type Locality in the Olympic Peninsula, Washington], *O. c. ivallda* [Type Locality in Placer County, California] and *O. c. stanislaus* Hovanitz, 1937 [Type Locality in Alpine County, California]. Since 2006, however, some authors have recognized more than one species-level taxon in the *chryxus* complex, as detailed below (see Discussion).

While curating the genus *Oeneis* in 2010 at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, ADW encountered a series of distinctive Alaskan specimens, collected near the town of Tok in the southeastern part of the state, which had previously been determined as *O. chryxus*. The large size and overall dark aspect of these specimens contrasted sharply with other populations of *O. chryxus*. A brief review of the male genitalia by JPP and ADW in 2011 confirmed the placement of these *Oeneis* in the *bore* group. A subsequent search of the Kenelm Philip collection (currently housed at the University of Alaska Museum, Fairbanks) by ADW and KMD in 2015 revealed a large number of additional specimens from multiple localities bordering the Tanana River in southeastern Alaska. Further searches revealed many additional specimens in private collections, especially those of CDF and Jack Harry, the latter recently donated to the McGuire Center.

In an effort to determine the taxonomic status of these Alaskan specimens, genitalia of males and females were compared to those of *O. chryxus* from Yukon Territory and *O. bore* from Alaska. In addition, legs were sampled from all North American taxa in the *bore* group (except *O. c. socorro*) by VL in 2011 and NVG in 2015, from which sequence data from the "barcode" region of *COI* were obtained. Herein we present the results of these studies, and describe the distinctive Alaskan *Oeneis* as a new species, yet note that further elucidation of its taxonomic status is needed (see Discussion).

MATERIALS AND METHODS

Specimens examined are deposited in the following collections: private collection of Clifford D. Ferris, Laramie, Wyoming, USA (CDF); Private collection of Jim P. Brock, Tucson, Arizona, USA (JPB); Kenelm W. Philip collection, currently housed at the University of Alaska Museum, Fairbanks, Alaska, USA (as of January, 2016) (KWP); private collection of Martin Cesanek, Bratislava, Slovakia (MC); McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (MGCL); Triplehorn Insect Collection, Ohio State University, Columbus, Ohio, USA; material recently acquired from David Parshall, photos examined (OSUC).

Full data are provided for all specimens examined of the new species (see Types section, below), as well as for all specimens of *O. chryxus* from Alaska (6), British Columbia (103), and Yukon Territory (466), more-or-less as presented on specimen labels (see Additional Material Examined). Information between brackets "[ ]" in the listing of specimen data represents additional or corrected information. We also examined 3,670 additional specimens of the *O. chryxus* complex (as defined above) in the MGCL, as follows: Michigan (215), Wisconsin (24), Quebec (7), Ontario (391), Manitoba (177), Saskatchewan (2), Northwest Territories (5), Alberta (183), Montana (111), Wyoming (461), Colorado (862 *chryxus* + *altacordillera*), New Mexico (44), Utah (159), Nevada (65 *chryxus*, 93 *ivallda*), Idaho (119), Washington (142 *valerata*, 48 *chryxus*), California (562).

The distribution map (Fig. 7) was generated using SimpleMappr (<http://www.simplemappr.net>) based on existing locality information and additional data. When not provided on specimen labels, coordinates were estimated using Google Earth, often in combination with details provided in The Milepost (Morris 2015). All known localities from Alaska are included on the map, as are most localities in Yukon Territory, although a few localities from Yukon Territory that we have thus far been unable to pinpoint have not been mapped.

Wing lengths were measured with a digital Vernier caliper, from base to greatest length at the apex of the right forewing. Adult abdomens, legs, and palpi were soaked in hot KOH for 3-10 min prior to dissection, dissected, and subsequently stored in glycerine. Chlorazol black was used to stain female genitalia. Dissected specimens are indicated by "SN" numbers in the list of specimen data. External and genitalic morphology was studied using a Leica MZ 16 stereomicroscope and drawings were produced with a camera lucida attached to the Leica MZ 16 stereomicroscope. The terminology for wing venation follows the Comstock-Needham system described in Miller (1970), and the terminology for wing pattern elements follows Peña & Lamas (2005). Nomenclature of the genitalia mostly follows Klots (1956), but we follow Peña & Lamas (2005) in using the term aedeagus, and Muschamp (1915) in using the term 'brachia' for structures often called the 'gnathos'. Finally, we follow Austin & Mielke (2008) in referring to the part of the genitalia typically termed the 'vinculum' as 'combined ventral arms of tegumen and dorsal arms of saccus'.

Standard *COI* barcodes (658-bp 5' segment of mitochondrial *cytochrome oxidase subunit I*) were studied. *COI* sequences were obtained from 53 specimens representing the following species: *O. bore*, *O. chryxus*, *O. macounii*, *O. nevadensis*, *O. ammon* and the new species described below. We did not include *O. alberta* in the final *COI* analysis as this species is very distinct from both *O. bore* and the *O. chryxus* complex with respect to morphology and ecology, though it shares its barcodes with other members of the *O. bore* group (most likely due to a mitochondrial introgression). Legs from the samples labeled by letters BPAL and CCDB (43 specimens) were processed at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) using the standard high-throughput protocol described in deWaard et al. (2008). DNA was extracted from a single leg removed from each voucher specimen employing a standard DNA barcode glass fiber protocol (Ivanova et al. 2006). All polymerase chain reactions (PCR) and DNA sequencing were carried out following standard DNA barcoding procedures for Lepidoptera as described by Hajibabaei et al. (2005). This set of voucher specimens is housed at MGCL, and can be identified by the corresponding unique BOLD Process IDs that were automatically generated by BOLD (Barcode of Life Data System). Photographs of these specimens are available in BOLD at <http:// www.barcodinglife.org/>. Legs from the samples labeled with the letters NVG and OSUC were processed in the Grishin lab using Macherey-Nagel (MN) NucleoSpin® tissue kit according to the protocol described in Cong & Grishin (2014). The following pairs of primers were used to amplify the barcode in two overlapping segments: sCOIF (forward, 5' -ATTCAACCAATCATAAAGATATTGG-3') -Ven-m2COIR (reverse, 5'- GGTAAACTGTTCATCCTGTTC3'), and Meg-mCOIF2 (forward, 5'-CCTCGWATAAATAAYATAAGATTTTG-3') -sCOIR (reverse, 5' -TAAACTTCTGGATGTCCAAAAAATCA-3'). NVG voucher specimens are housed at MGCL, except OSUC vouchers are at OSUC. Newly generated sequences and accompanying data were submitted to GenBank and received accession numbers KU552034-KU552042 and KU570409-KU570424.

The barcode analysis involved 74 *COI* sequences (including eight *O. norna* samples that were selected as an outgroup). Among them there were 21 published sequences (Lukhtanov et al. 2009; Pohl et al. 2009; Dewaard et al. 2014a,b; Kleckova et al. 2015) downloaded from GenBank. Sequences were aligned using BioEdit software (Hall 1999) and edited manually. Phylogenetic hypotheses were inferred using Bayesian methods as described previously (Vershinina & Lukhtanov 2010; Talavera et al. 2013). Briefly, Bayesian analyses were performed using the program MrBayes 3.2 (Ronquist et al. 2012) with default settings as suggested by Mesquite (Maddison & Maddison 2015): burn-in=0.25, nst=6 (GTR + I + G). Two runs of 10,000,000 generations with four chains (one cold and three heated) were performed. Chains were sampled every 10,000 generations. The average value of the Potential Scale Reduction Factor (PSRF) was 1.000 and the average standard deviation of split frequencies was 0.009516 to the end of the analysis, indicating that convergence was achieved, and a good sample from the posterior probability distribution was obtained. The consensus of the obtained trees was visualized using software FigTree v 1.3.1 (Rambaut 2009).

Results

Oeneis tanana A. Warren & Nakahara, sp. nov.
(Figs. 1, 3-4, 6a-c)

Zoobank LSID: urn:lsid:zoobank.org:act:AC40896F-1D0B-4090-A52F-94EBD739D62F

MALE. **Head**: Eyes brownish, naked; labial palpi (Figs. 3d,e) first segment short, covered with long dark-brown hair-like modified scales ventrally, 3-4 times as long as segment width, white scales laterally, longer white hair-like scales dorsally; second segment similar to first in scale orientation, about three times longer than first segment; third segment similar to first and second segments in scale orientation, shorter than first segment in male, same length in female; antennae approximately two-fifths length of forewing costa, 40 segments (n=1), pedicel about half as long as scape, with distal 15-16 segments comprising club. **Thorax**: Dorsally black, covered with golden hair-like modified scales; ventrally black, golden hair-like modified scales sparse. Legs (Figs. 3b,c): Foreleg tarsus slightly longer than tibia, femur slightly shorter than tibia; midleg and hindleg similar in length; femur black, adorned with long dark-brown hair-like modified scales ventrally, greyish scales scattered dorsally; tarsus and tibia of midleg and hindleg covered with greyish scales, dark brown hair-like modified scales present on distal half of tibia, tibia and tarsus adorned with spines, pair of relatively short tibial spurs located at ventral side of distal end of tibia. **Abdomen**: Eighth tergite elongated, approximately 1.5 times longer than seventh tergite, dorsal surface apparently weakly sclerotized; eighth sternite small, approximately two-thirds length of seventh sternite, apparently uniformly sclerotized.

Genitalia (Figs. 4a-e): Tegumen shaped somewhat like a 'megaphone' in lateral view, dorsal margin of tegumen slightly concave; uncus tapered towards end, slightly curved in lateral view, curved posterior end of uncus rounded in lateral view, slightly longer than dorsal margin of tegumen in lateral view, dorsally seteous; brachia almost pararell to uncus in dorsal view, apex slightly hooked, roughly half length of uncus; ventral arms of tegumen partially fused to anterior margin of tegumen, thus form of anterior edge of tegumen somewhat like a plate in dorsal or posterior view; appendix angularis present; saccus relatively short, similar in length to brachia, dorsal arms of saccus combined with ventral arms of tegumen; juxta present; valva with scattered setae, positioned at approximately 30º angle to horizontal, distal half of valva roughly trapezoidal in lateral view with angular apex, 'tooth' present at middle section of dorsal margin of valva in lateral view, middle section of ventral margin of valva convex in lateral view, basal one third of dorsal margin concave; aedeagus similar in length to tegumen plus uncus, almost straight in lateral view, adorned with a variable number of short spins, open anterodorsally.

Wing venation and shape (Fig. 3a): Mean forewing length = 26.7 mm (n = 20). Forewing recurrent vein absent; basal swelling of forewing cubital vein absent; hindwing humeral vein developed; shape typical of other members of the *O. chryxus* complex. Wing pattern (Figs. 1a-l): *Dorsal forewing* ground color dark brown; androconial dark scales approximately 1mm in width, present at distal end of discal cell along cubital vein, base of cells M_3, Cu_1 and Cu_2; color and density of androconial scales highly variable; black submarginal ocellus in cell M_1 often with indistinct creamy pupil in center; submarginal ocelli variably present in cells M_3, Cu_1, with or without pale pupils; submargin and margin of forewing variably overscaled with reddish or pale ochre, sparse or absent over and adjacent to wing veins, creating a series of irregularly-shaped patches separated by dark wing veins; fringe scales white and greyish. *Dorsal hindwing* ground colour same as forewing, with variable intensity of reddish or pale ochre overscaling; black ocellus in cell Cu_1 variable in development, from bold to absent, often with indistinct creamy pupil in center; fringe scales white and greyish. *Ventral forewing* ground colour greyish-ochre; costal region (area basal to subcostal vein) mosaic of black and white, extending to apex, then along margin to cell R_5, and variably to cells M_2 or M_3; numerous dark brown fragmented markings in discal cell, dark brown streak along M_2-M_3; dark brown undulating band extending from costa, distal to discal cell, fading distally in cell M_2, curved inwards below M_3 and extending to cell Cu_2; black ocellus in cell M_1 generally with creamy pupil in center; ocelli in cells M_3 and Cu_1 variably present, smallest in M_3, with or without pale pupil; outer margin of forewing darker; fringe as described for upperside. *Ventral hindwing* ground colour indiscernible; wing veins highlighted with a variable amount of whitish scaling; costal region (area above subcostal vein) mosaic of black and white, extending along length of costa; pattern elements as follows, from base to distal margin: basal area mosaic of dark brown irregular markings with dark ochre background, followed by a whitish area with sparse dark brown irregular markings; dark brown sinuate band extending from costa to outer margin, approximately 1mm in width, roughly traversing in an outward direction until cubital vein, then roughly inward below cubital vein; area distal to this band mosaic of dark brown irregular fragmented markings with dark ochre and/or greyish white ground colour; second dark brown sinuate band extending from costa to outer margin, similar in width to previous band, roughly traversing in outward direction until origin of M_3, then roughly inward below this point; area distal to this band broadly white, wider than previous band; area distal to this (submargin and margin) mosaic of dark brown irregular fragmented markings with dark ochre and/or greyish ground color, darkest along margin; trace of pale submarginal ocelli variably present in cells Rs, M_1, M_2 and M_3, black ocellus in cell Cu_1 variably present, often with creamy pupil in center; fringe as described above.

FEMALE. Similar to male, except as follows: foretarsus not segmented although adorned with spines; mean forewing length = 26.9 mm (n = 10); wing shape rounder and broader, lacking forewing androconia and surrounding darkened area. Genitalia (Figs. 4f-h): Lamella antevaginalis well developed, vertical projection under ostium bursae present and sclerotized, anterior portion of lamella antevaginallis forming a plate below this vertical projection; weakly sclerotised ventral region present in seventh and eighth intersegmental membrane, apparently fused with anterior portion of lamella antevaginalis; most of ductus bursae sclerotised; ductus seminalis located at base (posterior end) of corpus bursae; corpus bursae roughly oval, extending to third abdominal segment; two brown signa located at ventral side of corpus bursae, signa prominent and parallel to each other, spines of signa developed.

COI 'Barcode' sequence: vouchers CCDB-05786 D08, KWP:Ento:29760, NVG-5202, NVG-5203, 658 base pairs:

AACTTTATATTTTATTTTAGGAATTTGAGCAG
GTATAGTAGGAACATCTCTTAGTCTTATTATTC
GAACAGAATTAGGTAACCCAGGATCTTTAATTG
GAAATGACCAAATTTATAATACTATTGTTACAGCT
CATGCTTTTATTATAATTTTTTTTATAGTTATAC
CAATTATAATTGGGGGATTTGGAAATTGACTAAT
TCCTCTAATACTTGGAGCCCCTGATATAGCCTTC
CCCCGAATAAATAATATAAGATTTTGACTTTTAC
CCCCTTCTTTGATACTTTTAATTTCAAGCAATAT
TGTTGAAAATGGAGTAGGAACAGGATGAACAATT
TACCCCCCTCTCTCATCTAATATTGCCCATAGAG
GATCTTCTGTTGATTTAGCAATTTTTTCTTTA
CATTTAGCTGGAATTTCTTCTATTTTAGGAGCT
ATTAATTTTATTACAACAATTATTAATATACGAAT
TAATAATATAACTTATGATCAAATACCTTTATTT
GTTTGAGCTGTAGGAATTACAGCTTTATTATT
ATTACTCTCTCTTCCTGTATTAGCTGGGGCAAT
CACTATACTTCTTACAGATCGAAATTTAAATACT
TCATTTTTTTGATCCAGCAGGAGGGGGAGACCCT
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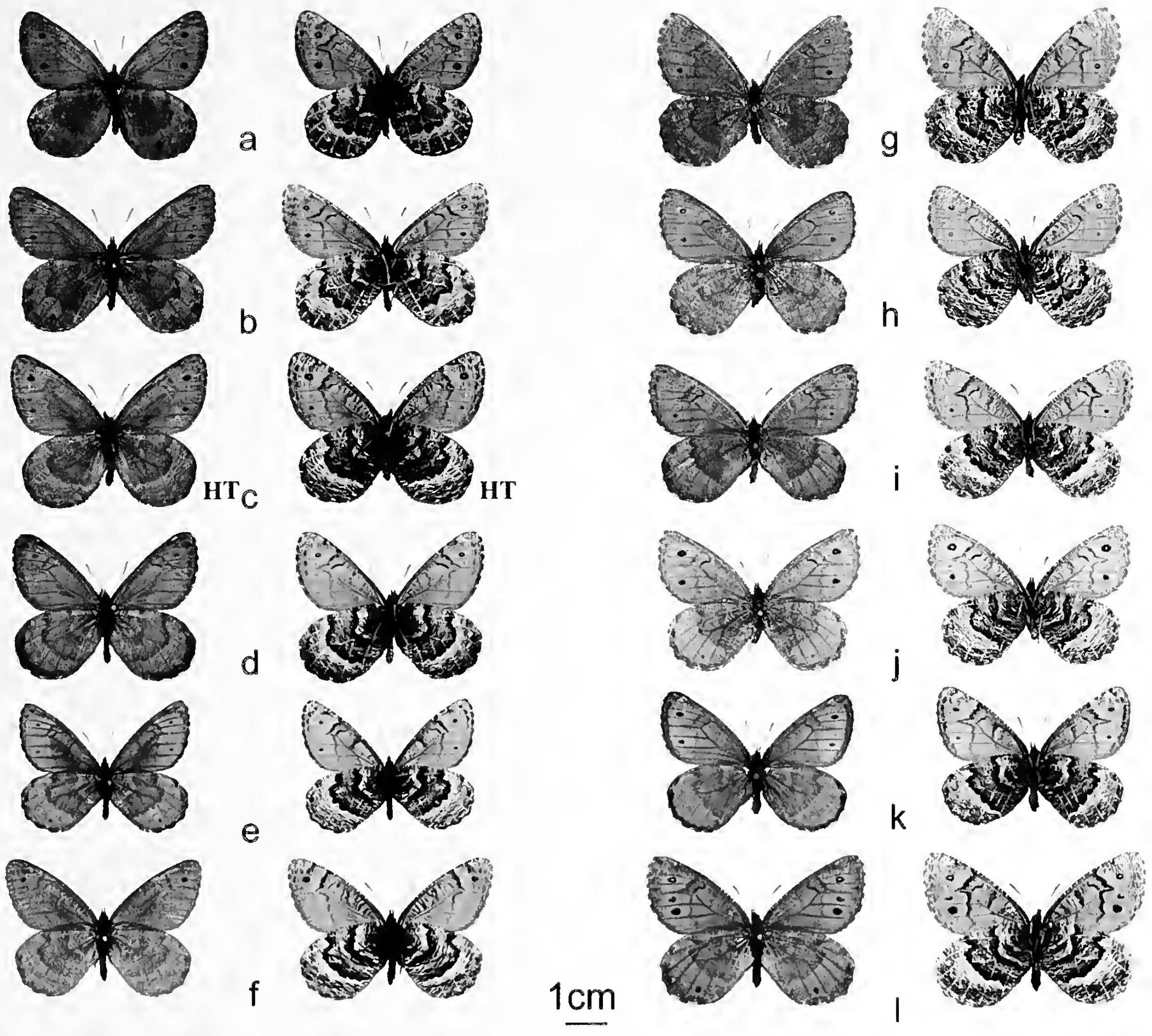

Figure 1. Males (a-f) and females (g-l) of *Oeneis tanana* from the type locality, 5 mi. S of Tok, Alaska, showing individual variation observed in the population. Each specimen is figured in dorsal (left) and ventral (right) views. HT = holotype. Specimens collected by M. Douglas (a-e, g-k, 17-18 June 1999) and J. Harry (f, 10 June 1999; l, 17 June 1999), in MGCL.

Types. Holotype male (Fig. 1c) with the following labels: white, printed: AK: TANANA VALLEY / 5 MI. S. OF TOK, TOK / CUT-OFF AT BUTCH / KUTH RD. VI-17-18-99 / LEG. M.G.Douglas /; white printed: J. D. Turner ex / Malcolm Douglas / colln. / MGCL Accession # 2009-26 /; red, printed: HOLOTYPE / *Oeneis tanana* / A. Warren & Nakahara /. The holotype is deposited in the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida (MGCL). Paratypes (326♂, 79♀) from: USA: ALASKA: Alaska Hwy., mi. 1270, 2000', 11-VI-1999, J. L. Harry (9♂, 1♀ MGCL); Alaska Hwy. (Hwy. 2), mi. 1289.55, 63°13,9'N 142°17.9'W, 1800', 15-VI-1997, C. D. Ferris (13♂, 1♀ CDF); Alaska Hwy., mi. 1289.55, Midway Lake, gravel flats on hillside above road, 15-VI-1997, K. W. Philip (7♂, 2♀ KWP; UAM100190535-UAM100190543); Alaska Hwy., mi. 1316, 20-VI-1955, J. & F. Preston (1♂ MGCL); Alaska Hwy. (Hwy. 2), mi. 1354.2, 1800', 63°35'N 143°55'W, 15-VI-1995, C. D. Ferris (2♀ CDF); Alaska Hwy., mi. 1371, 28-VI-1970 (1♀ MGCL); Alaska Hwy. (Hwy. 2), mi. 1410, 1250', 61°56.7'N 145°23.7'W, 15-VI-1995, C. D. Ferris (1♂, 1♀ CDF); Alaska Hwy., mi. 1410, Spruce Road, powerline cut in taiga, grass and flowers, 1240', 17-VI-1997, K. W. Philip (2♂ KWP; UAM100060877, UAM100060878); Alaska Hwy., mi. 1410, 12 mi. SE Delta Jct., 1200', 15-VI-2001, J. L. Harry (1♀ MGCL); Anderson, 1 mi. E, 500', 4-VI-1999, J. L. Harry (1♂, MGCL); Hwy. 1, 5 mi. S Tok, 1700', 10-VI-1999, J. L. Harry (18♂, 2♀ MGCL); 12-VI-1999, J. L. Harry (21♂ MGCL); 13-VI-1999, J. L. Harry (13♂ MGCL); 17-VI-1999, J. L. Harry (26♂, 6♀ MGCL); 18-VI-1999, J. L. Harry (1♂, 1♀ MGCL); Hwy. 1, 5 mi. S of Tok, 1700', 63°16'N 143°02'W, 13-VI-1995, C. D. Ferris (2♂, 1♀ MGCL SN-15-145-♂, SN-15-155-♂, SN-15-149-♀); 14-VI-1995, C. D. Ferris (8♂ MGCL; incl. SN-15-147, SN-15-154, SN-15-156, SN-15-157); 14-15-VI-1995, C. D. Ferris (46♂, 17♀ CDF); 6-VII-1995 C. D. Ferris (1♀ MGCL, SN-15-151); Hwy. 1, 5.0 ± 0.5 mi. S of Tok, [1700'], 63°16.04'N 143°01.9'W, 5-VI-1997, C. D. Ferris (1♂, 1♀ CDF); 14-VI-1997, C. D. Ferris (52♂, 21♀ CDF); 1-VII-1997, C. D. Ferris (3♂, 4♀ CDF); Nenana, 400' [351'], 4-VI-1999, J. L. Harry (6♂ MGCL); 6-VI-1999, J. L. Harry (1♂ MGCL); Northway Airport, 1700', 11-VI-1999, J. L. Harry (1♂ MGCL);

Northway Airport, 7 mi. off Alaska Hwy., flower-filled lawns and fields, 1700', 15-VI-1997, K. W. Philip (1♀ KWP UAM100190552); Old Alaska Hwy., 3 mi. NE Tok, 1600', 12-VI-1999, J. L. Harry (2♂ MGCL); Richardson Hwy., mi. 229 [vic. Black Rapids], [2083'], 26-VI-1971, C. D. Ferris (1♀ CDF); Tanana River, 21 mi. SW Fairbanks, 400' [Bonanza Creek Experimental Forest], 18-V-1997, J. L. Harry (1♀ MGCL); Tanana Valley, 5 mi. S of Tok, Tok Cutoff at Butch Kuth Rd., 17-18-VI-1999, M. Douglas (53♂, 7♀ MGCL); Tok, 17-VI-1971, L. Jennings (1♂ KWP; UAM100379347); 9-VI-2005, Szymczyk (1♂ JPB); Tok Cutoff, 5 mi. S of Tok, Butch Kuth Ave., roadside flowers in open aspen/spruce forest, 13-VI-1995, K. W. Philip (11♂, 3♀ KWP; UAM100379326-UAM100379329, UAM100379344-UAM100379346, UAM100379367-UAM100379369, UAM100379384-UAM100379387); 14-VI-1995, K. W. Philip (25♂, 3♀ KWP; UAM100379330-UAM100379343, UAM100379370-UAM100379383).

Additional material examined

Oeneis tanana: "nr. Nome, Alaska", no date, no collector indicated (1♀ MGCL). This specimen was not included in the type series, since it is the only known specimen of *O. tanana* labeled from outside the Tanana River drainage, and it lacks the collection date and name of the collector; we suspect it is mislabeled. Considerable collecting efforts have been made in the Nome area, yet no material of *O. tanana* has been reported.

Oeneis chryxus: CANADA: BRITISH COLUMBIA (74♂, 29♀): Alaska Hwy. km. 600, 11-VII-1984, J. & F. Preston (1♂ MGCL); Alaska Hwy., mi. 392, mountain S of Summit Pass, 4000-7000', 22-VII-1948, W. Hovanitz (1♀ MGCL); Alaska Hwy., mi. 400, Summit Lake, 4200-5000', W. Hovanitz (2♂, 2♀ MGCL); Alaska Hwy., mi. 409, McDonald Ck., 6-VII-1948, W. Hovanitz (2♂ MGCL); Alaska Hwy. mi. 415, Racing R., 6-VII-1948, W. Hovanitz (4♀ MGCL); Alaska Hwy., MP 417, 18-VI-1970, A. O. Detmar (1♂ MGCL); Atlin, 600-900m, 22-VI-1991, J. Reichel (1♂, 1♀ MGCL); Atlin, 800m, 26-VI-1991 (1♂ MGCL); 23-VI-1991 (1♀ MGCL); Atlin Rd., 3 mi. N of Atlin, 2300', 30-VI-1985, C. D. Ferris (4♂, CDF); Atlin Rd., 3 mi. N of Atlin to Snafu Creek, 30-VI-1985, C. D. Ferris (1♂ CDF); Coalmount, 5-VII-1968, S. Shigematsu (4♂ MGCL); Crater Mtn., W of Keremos, 1-VII-1981, C. D. Ferris (2♂ CDF); Creston, Thompson Pk., 15-VII-1976 (3♂ MGCL); Gibson Pass, Manning Park, 5000', 16-VII-1979, C. Guppy (2♂ MGCL); 23-VII-1983 (1♂ MGCL); Haines Hwy., mi. 78, 4-VII-1971, C. D. Ferris (7♂, 1♀ CDF); Jct. of Cassiar Hwy. & Boya Lake Rd., 2200', 10-VI-1986, C. D. Ferris (12♂, 4♀ CDF); Kelly Lake – Canoe Creek Rd., nr. Jesmond, 3100-4400', 23-VII-1984, J. & F. Preston (2♀ MGCL); 24-VII-1984, J. & F. Preston (1♂, 1♀ MGCL); [Manning] Park, 5000', Valley View, 7-VII-1961, H. Kimmich (1♀ MGCL); Mt. Princeton, 29-30-V-1964, H. Kimmich (1♂ MGCL); Otter Lake C.G., nr. Princeton, 9-VII-1976 (2♂, 1♀ MGCL); Pavilion – Kelly Lake Rd. at Diamond S Ranch, N of Lillooet, 3900', 24-VII-1984, J. & F. Preston (1♂ MGCL); Pavilion – Kelly Lake Rd., 8.5 mi. N Pavilion, 4300', 24-VII-1984, J. & F. Preston (2♂, 3♀ MGCL); Pink Mtn., halfway up, on road to lookout, 4-VII-1985, C. D. Ferris (2♂ CDF); Pink Mtn., mi. 147, Alcan Hwy., 9-VII-1978 (2♂ MGCL): Pink Mtn., mi. 147, Hwy. 97, 5000', VI-VII-1980, N. Tremblay (1♀ MGCL); Princeton, 27-VI-1966 (1♂ MGCL); Princeton, Cardinal Ranch, 27-VI-1966, B. Weber (1♀ MGCL); Stagleap Cyn., Kootenay Dist., 27-VII-1987, D. L. Bauer (1♂ MGCL); Summerland area, Okanagan Valley, 25-VI-1983, J. Reichel (1♂ MGCL); Tompson Mt., Kootenay Dist., 25-VII-1981, D. L. Bauer (2♂ MGCL); 5 mi. S Clinton, 26-VI-1964 (14♂, 5♀ MGCL).

YUKON TERRITORY (317♂, 149♀): Alaska Hwy., bog nr. Johnson's Crossing, 22-VI-1948 (1♂, 1♀ MGCL); Alaska Hwy., mi. 825, 15-VI-1957, J. & F. Preston (1♂ MGCL); Alaska Hwy., mi. 895-900, nr. Whitehorse, 22-VI-1948 (1♀ MGCL; SN-15-152); Alaska Hwy., mi. 976, nr. Mendenhall, 23-VI-1948 (2♂ MGCL); Campbell Hwy., km. 521, 1800', 12-VI-1979, J. & F. Preston (1♂ MGCL); Campbell Hwy., km. 533, 1700', 12-VI-1979, J. & F. Preston (13♂, 10♀ MGCL); Campbell Hwy., km. 563, 1400', 12-VI-1979, J. & F. Preston (1♂ MGCL); Campbell Hwy., km. 564-568, nr. Carmacks, 62°03'54.24''N 135°57'00.94"W, 560-650m, 11-VI-2008, M. Cesanek (15♂, 5♀ MC); Carcross Desert area, Hwy. 2 (Klondike Hwy.), in open woods at desert edge, 2170', 60°14'14''N 134°41'41''W, 29-VI-1985, C. D. Ferris (10♂, 2♀ CDF); Dawson, 13-VI-1911, ex Barnes coll., "holotype" of "yukonensis" (1♂ MGCL); 14-VI-1911, ex Barnes coll., "allotype" of "yukonensis" (1♀ MGCL); 10-VI-1981, N. Tremblay (30♂, 8♀ MGCL); Dawson Hwy., mi. 12.6, 16-VI-1962, J. Legge (1♂ MGCL); Dawson-Mayo Loop, mi. 69, W of Whitehorse, 21-VI-1970, D. Eff (2♂ MGCL); Dempster Hwy., mi. 10, 10-VI-1981, J. Johnstone (1♂ MGCL; 1♂ OSUC 618404); 10-VI-1981, N. Tremblay (22♂, 4♀ MGCL; 3♂, 9♀ OSUC 618391-618399, 618401-618403); 10-11-VI-1981, N. Tremblay (2♂ MGCL); 11-VI-1981, N. Tremblay (4♂, 2♀ MGCL; 1♂ OSUC 618379); 19-VI-1981, N. Tremblay (1♀ MGCL); VI-VII-1981, N. Tremblay (3♂ MGCL); 10-VI-1982, N. Tremblay (1♂ OSUC 618428); no date, N. Tremblay (1♂ OSUC 618405); Dempster Hwy., mi. 45-97, 14-VI-1981, N. Tremblay (1♂ MGCL); Dempster Hwy., mi. 84, 11-VI-1981, N. Tremblay (18♂, 4♀ MGCL); Dempster Hwy., mi. 96, 23-VI-1981, N. Tremblay (2♂ MGCL); Dempster Hwy., mi. 97, 14-VI-1981, N. Tremblay (1♂ MGCL); Dempster Hwy., mi. ?, 18-VI-1981, N. Tremblay (1♀ MGCL); 6-VI-1984, N. Tremblay (1♂ MGCL); Haines Jct., 6-VI-1966 (1♂ MGCL); 9-VI-1966 (4♂ MGCL; incl. SN-15-158); 10-VI-1966 (1♂ MGCL); 12-VI-1966 (3♂ MGCL; incl. SN-15-161); 13-VI-1966 (1♀ MGCL); 16-VI-1966 (1♂, 1♀ MGCL); 17-VI-1966 (1♀ MGCL); 21-VI-1966 (2♂ MGCL); 22-VI-1966 (1♂ MGCL); 24-VI-1966 (1♂, 1♀ MGCL); 25-VI-1966 (4♂, 1♀ MGCL; incl. 3♂ SN-15-160, SN-15-159, SN-15-146); 28-VI-1966 (1♂ MGCL); 29-VI-1966 (9♂, 4♀ MGCL; incl. 1♀ SN-15-148); 1-VII-1966 (1♂, 1♀ SN-15-169 MGCL); 12-VI-1967 (2♂, 1♀ MGCL); 14-VI-1967 (1♂ MGCL); 18-VI-1967, obtained from J. Ebner (1♂, CDF); 19-VI-1967, J. A. Ebner (1♂ MGCL); 21-VI-1967, J. A. Ebner (1♂ MGCL); 23-VI-1967, J. A. Ebner (1♂ MGCL); 24-VI-1967, J. A. Ebner (1♂ MGCL); 27-VI-1967, obtained from J. A. Ebner (2♀ CDF); 9-VI-1968 (1♂ MGCL); Haines Rd., mi. 87, 30-VI-1966 (1♀ MGCL); Horse Creek, mi. 12.6 Dawson-Mayo Loop, 24-VI-1964, A. H. Legge (2♂, 1♀ MGCL); 24-VI-1964, D. Eff (5♂, 4♀ MGCL); Hwy. 7, Atlin Rd., 2100', 29-VI-1985, C. D. Ferris (1♂ CDF); Hwy. 11 (Silver Trail), km. 31.5 (SW of Mayo), 27-28-VI-1985, C. D. Ferris (9♂, 3♀ CDF); 4-VI-1987, C. D. Ferris (2♂, CDF); 6-VI-1991, C. D. Ferris (10♂, 3♀ CDF); Jubilee Mtn., 1000-1500m, 5-VII-1977, A. Reif (1♂, 1♀ MGCL); Klondike Hwy., mi. 132, N of Yukon River, 20-VI-1975, D. K. Parshall (1♀ OSUC 618388); Lake Laberge, 30 mi. N Whitehorse, 10-VI-1985, J. & L. Troubridge (4♂ MGCL); 14-VI-1985, T. Kral (4♂ MGCL); 15-VI-1985 (2♂ MGCL); 18-VI-1985, T. Kral (2♂ MGCL); Lake Laberge, Hwy. 2, 46.4 km. N Whitehorse, 11-VI-1981, D. K. Parshall (1♂ OSUC 618439); 1-VII-1981, D. K. Parshall (1♂ OSUC 618442); 1-VII-1982, D. K. Parshall (2♂ OSUC 618390, 618441); 11-VII-1982, D. K. Parshall (1m OSUC 618440); 14-VI-1983, D. K. Parshall (9♂ OSUC 618327, 618408-618415); 15-VI-1983, D. K. Parshall (1♂ OSUC 618322); 23-VI-1983, D. K. Parshall (3♀ OSUC 618378, 618446-618447); 25-VI-1983, D. K. Parshall (3♀ OSUC 618443-618445); 14-VII-1983, D. K. Parshall (3♂, 2♀ OSUC 618455-618459); 6-VI-1984, J. P. Ross (2♀ OSUC 618406-618407); 12-VI-1985 (4♂, 1♀ OSUC 618339, 618448-618451); 13-VI-1985, D. K. Parshall (12♂, 5♀ OSUC 618324, 618331-618338, 618430-618437); 14-VI-1985, D. K. Parshall (3♂ MGCL; 13♂, 14♀ OSUC 618323, 618325, 618340-618354, 618418-618427); 15-VI-1985, D. K. Parshall (5♂, 5♀ OSUC 618321, 618326, 618328, 618355-618359, 618453-618454); 16-VI-1985, D. K. Parshall (4♀ OSUC 618360-618363); 18-VI-1985, D. K. Parshall (6♀ OSUC 618364-618368, 618452); 19-VI-1985, D. K. Parshall (1♂, 4♀ 618369-618373); 20-VI-1985, D. K. Parshall

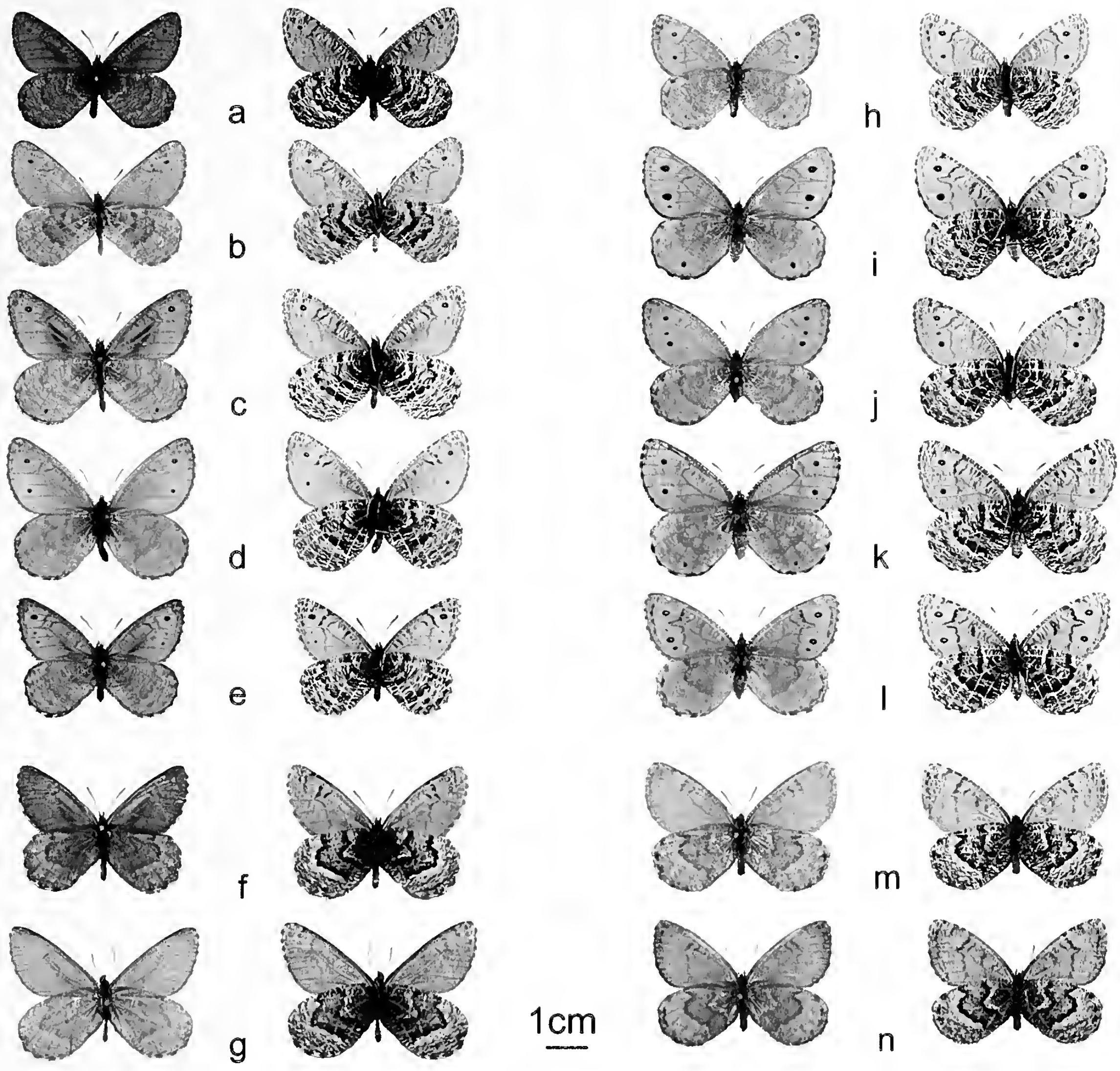

Figure 2. Males (a-e) and females (f-j) of *Oeneis chryxus* from Yukon Territory, Canada, and males (k-l) and females (m-n) of *O. bore* from Alaska (f-g) and Yukon Territory (m-n), in MGCL. Each specimen is figured in dorsal (left) and ventral (right) views. *Oeneis chryxus* from Yukon Territory: a, nr. Snafu Lake on Atlin Rd., 2600', 7 June 1991, J. & F. Preston; b, Dempster Hwy., mi. 97, 14 June 1981, N. Tremblay; c, Dempster Hwy., mi. 10, 10 June 1981, N. Tremblay; d,i,k,l, Campbell Hwy., km. 533, 12 June 1979, J. & F. Preston; e,j, 0.8 mi. N of Lewes Lake Rd. on Hwy. 2, 6 June 1991, J. & F. Preston; h, Whitehorse, 11 June 1966. *Oeneis bore* from: f, Murphy Dome, 17 June 1972, J. & F. Preston; g, Murphy Dome, 16 June 1999, M. Douglas; m, Dempster Hwy., mi. 97, 17 June 1981, N. Tremblay; n, Dempster Hwy., mi. 96, 24 June 1981, N. Tremblay.

(4♀ 618374-618377); Lake Laberge, Hwy. 2, mi. 29, 3-VI-1985, J. Zeligs (1♂ MGCL); 18-VI-1985, J. Zeligs (1♂ MGCL); Mts. SW of Haines Jct. (5-18 mi.), 3-4000', 22-VI-1967 (1♂ MGCL); N of Stewart Crossing, Hwy. 2, 22-VI-1983, [D. K. Parshall] (3♂, 5♀ OSUC 618330 [*this specimen with *O. tanana* barcode, Fig. 10c -d], 618380-618386); N of Stewart Crossing, Klondike Hwy., mi. 24, 20-VI-1975, D. K. Parshall (2♂ OSUC 618329 [*this specimen with *O. tanana* barcode, Fig. 10a -b], 618389); nr. Snafu Lake on Atlin Rd., 2600', 7-VI-1991, J. & F. Preston (4♂ MGCL); St. Elias Mts., Nickel Ck., 14-VI-1985, B. Grooms (1♂ MGCL); Stewart Crossing, Klondike Loop Rd., 1600', 13-VI-1979, J. & F. Preston (1♂, 2♀ MGCL); Twin Lakes, Hwy. 2, km. 115, 14-VI-1983, D. K. Parshall (2♀ OSUC 618416-618417); 28-VI-1983, D. K. Parshall (1♂ OSUC 618438); Whitehorse, 10-VII-1919, "paratype" of "yukonensis" (1♀ MGCL); 6-9-VI-1923 (1♂ MGCL); 8-VI-1923 (1♂ MGCL); 9-VI-1923 (2♂ MGCL); 17-VI-1923, J. Kusche (2♂ MGCL); 8-VI-1966 (1♂ MGCL); 9-VI-1966, H. Ebner (1♂ MGCL); 10-VI-1966 (1♂ MGCL); 11-VI-1966 (1♀ MGCL); 13-VI-1966 (1♀ MGCL); 2-VI-1982 (1♀ OSUC 618429); 1-VII-1982, B. Grooms (1♂ MGCL); Whitehorse, 2500', 24-VI-1981, G. Anweiler (1♂ CDF); 8-10-VI-1982, J. P. Ross (3♂, 5♀ CDF); Whitehorse, Baxter coll. (1♂ MGCL); Yukon Hwy. 2 (from Skagway, AK), km. 126, 2550', 6-VI-1991, J. & F. Preston (5♂ MGCL); 0.8 mi. N of Lewes Lake Rd. on Hwy. 2, 2700', 6-VI-1991, J. & F. Preston (6♂, 1♀ MGCL); 1.4 mi. S of Lewes Lake Rd.,

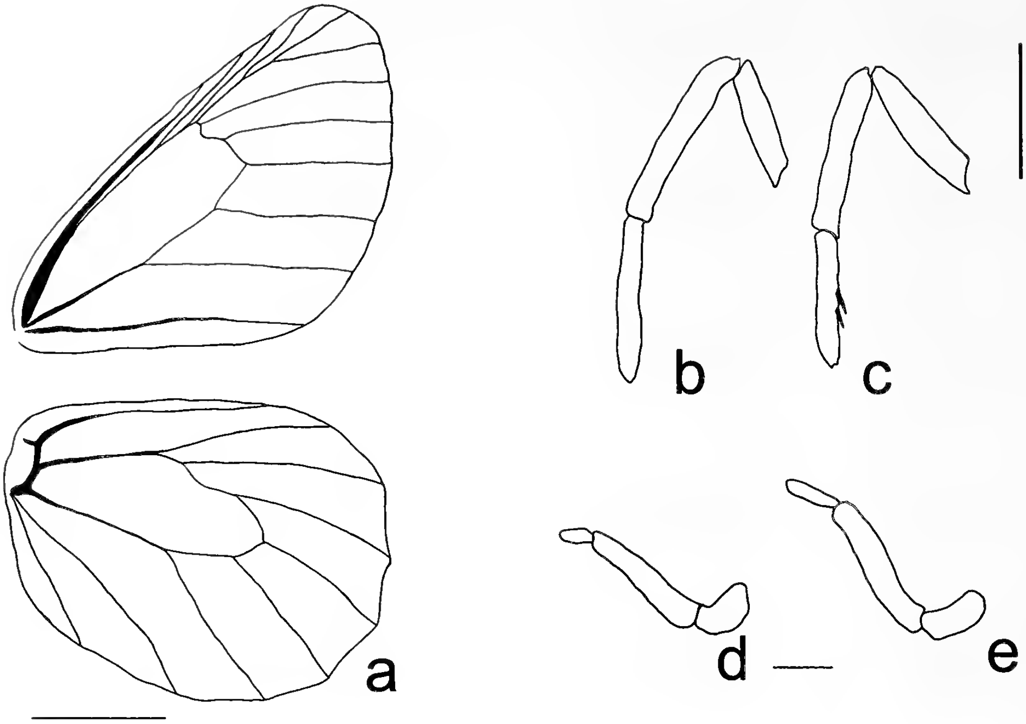

Figure 3. Morphology of *Oeneis tanana* from 5 mi. S of Tok, Alaska: a, male wing venation; b, male foreleg; c, female foreleg; d, male labial palpus; e, female labial palpus. Illustrations by Shinichi Nakahara. Scale bar = 10 mm for a, otherwise 1 mm.

W of Hwy. 2, 2550', 6-VI-1991, J. & F. Preston (1♂, 1♀ MGCL); 20 mi. S Burwash Landing, 1-VII-1948 (1♂ MGCL SN-15-150); "Alaska" [old specimen, most likely from Whitehorse area] (1♂ MGCL). Note: Much of the material from the Haines area, including that attributed to J. Ebner, was likely collected by Dr. A. M. Pearson, who collected for Ebner in the Haines area for several years in the 1960's.

USA: ALASKA: Eagle, 2-VII-1901, S. Hall Young (1♂ MGCL); 27-VI-1903, Reed Heilig, "paratype" of "yukonensis" (1♂ MGCL); Kathul Mtn., N side Yukon River, 6 mi above mouth Kandik R., 29-VI-1975, E. Holsten (3♀ KWP; UAM100379423-UAM100379425); 5-VIII[sic!?]-1975, E. Holsten (1♀ KWP; UAM100379422).

Etymology. This butterfly is named for the Tanana River, which flows through southeastern and central Alaska. Tanana is a Koyukon (Athabascan) word meaning "trail river", though the term is also applied to an Athabaskan indigenous group (Bright 2004).

Diagnosis. Adults of *O. tanana* average larger than those of Yukon *O. chryxus*. The mean forewing length of male *O. tanana* is 26.7 mm (range 24.6 to 29.4 mm, n = 20), vs. 24.8 mm (range 19.6 to 27.4 mm, n = 20) in Yukon *O. chryxus*. Females of *O. tanana* also average larger, with a mean forewing length of 26.9 mm (range 24.9 to 31.3 mm, n = 10), vs. 26.1 mm (range 21.0 to 29.1 mm, n = 10) in Yukon *O. chryxus*. Adults of *O. tanana* can usually be identified by the following traits, compared to Yukon *O. chryxus*: 1) larger size, 2) darker overall upperside coloration, with paler areas dark ochre or reddish, 3) darker ventral forewing coloration, 4) bolder dark ventral hindwing transverse bands, 5) expanded whitish areas on the ventral hindwing, 6) valvae average more robust. While none of these individual characters are strictly diagnostic, when considered together, essentially all specimens can be reliably identified to taxon. In addition, adults of *O. tanana* are separated from those of Yukon *O. chryxus* by their unique *COI* barcode sequences (but see below), which are identical to those found in adjacent populations of *O. bore*, with the exception of a single base-pair substitution at site 300: G->A (site number corresponds to the sequence given above).

Distribution. All localities where *O. tanana* is confirmed to occur are within the Tanana River Basin, in southeastern and central Alaska, including the lower north slope of the Alaska Range (Fig. 7). Available records suggest that *O. tanana* is widely distributed in appropriate habitats throughout the Tanana River drainage, at least from the Northway area (Northway Airport and Alaska Hwy. mi. 1270), northwest to Nenana, a roughly 400 km. (250 mi.) range centered along the Tanana River. Altitudinal records range from 107 m (351') at Nenana to 635 m (2083') along the Richardson Highway (mi. 229) and Delta River, which drains into the Tanana River to the north. A very small part of the Tanana River Basin extends into Yukon Territory (Moran 2007), but it is unknown if *O. tanana* occurs there. Likewise, it remains unknown how far down the Tanana River Basin *O. tanana* may occur, or if it occurs along the Yukon River Basin downstream or upstream of its junction with the Tanana River at Tanana. Most of this region has not been surveyed for butterflies. All specimens we have examined of *O. tanana* were collected in odd-numbered years, with the exception of a single female from Alaska Highway mile 1371, labeled from 1970. No collector's name is provided on the

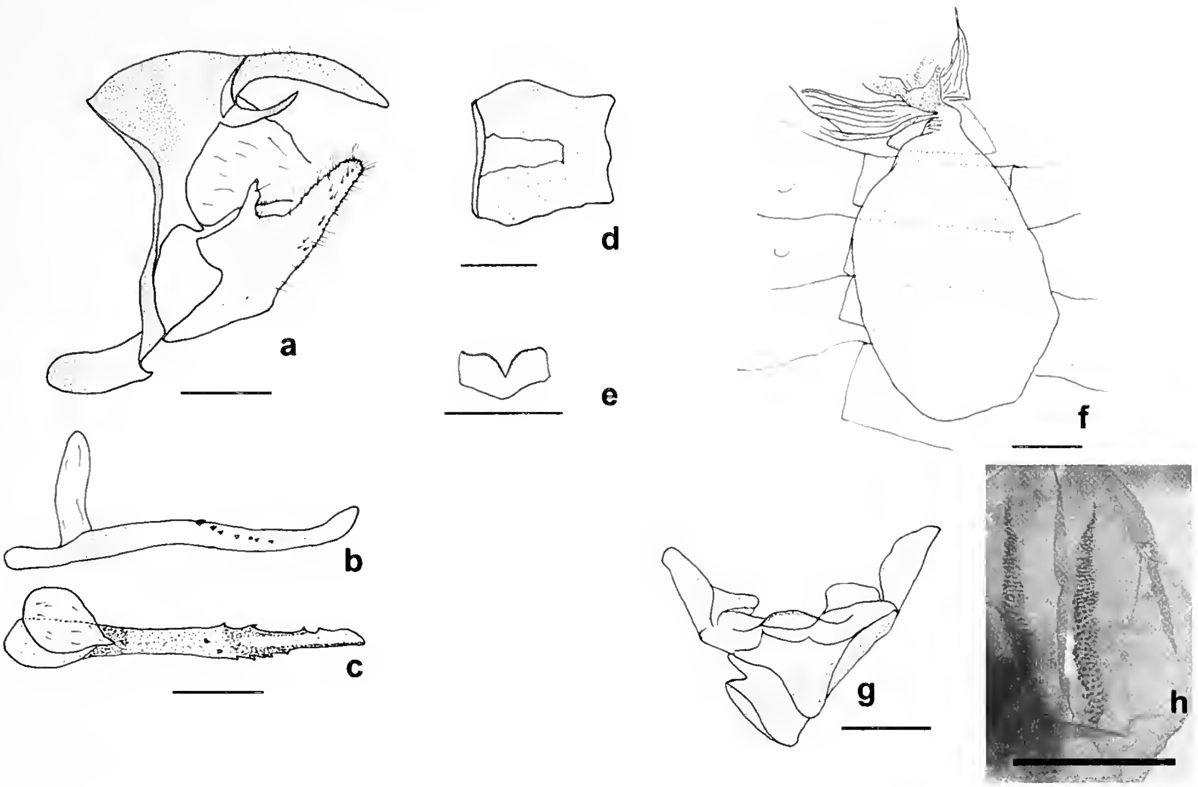

Figure 4. Male and female genitalia of *Oeneis tanana* from 5 mi. S of Tok, Alaska: a, male genitalia (SN-15-156) in left lateral view; b, aedeagus in left lateral view; c, aedeagus in dorsal view; d, eighth tergite in dorsal view; e, juxta in dorsal view; f, female genitalia (SN-15-151) in dorsal view; g, lamella antevaginalis in front view; h, signa. Illustrations by Shinichi Nakahara. Scale bar = 1 mm.

label, and the possibility of a labeling error cannot be ruled out. The earliest specimen of *O. tanana* we have seen is from 18 May (1997, 21 mi. SW Fairbanks), and the latest is from 6 July (1995, 5 mi. S of Tok), with most records from the second and third weeks of June.

Habitat. Adults of *O. tanana* fly in open, dry, grassy areas and clearings in boreal forest. In disturbed areas, they tend to frequent abandoned roads and trails, undeveloped dirt/gravel roads (Fig. 8), and power line cuts. They are fairly sedentary and in response to a disturbance fly short distances, usually in straight lines, to settle again. The butterflies generally sit on the ground or perch on rocks, or on low vegetation, with wings folded over the back unless basking. While colonies are isolated, numerous individuals are frequently present at occupied sites. Aside from grasses, sedges and various arctic forbs, the principal vegetation at the type locality includes black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), quaking aspen (*Populus tremuloides* Michx.), occasional birch (*Betula* sp.), and willows (*Salix* sp.). *Oeneis tanana* flies in sympatry with *O. jutta* (Hübner, [1806]) at Nenana, Alaska Hwy. mi. 1410, and in the vicinity of Tok (including at the type locality), and it flies with both *O jutta* and *O. philipi* Troubridge, 1988 at Northway Airport. No information on the early stages or larval foodplants of *O. tanana* is known to date, although grasses and/or sedges presumably serve as the larval foodplants, as reported for other taxa in the *O. chryxus* complex (James & Nunnallee 2011).

Discussion

Like *O. chryxus*, the genitalia of *O. tanana* possess a tooth-like projection of the dorsal margin of the valva, denticles on the valva in a single series, a strongly sclerotized ventral swelling of the lamella antevaginalis, and a left-skewed vertical plate of the lamella antevaginalis. Lukhtanov & Eitschberger (2001) noted the first three of these characters as diagnostic of the *bore* group. Based on the presence of these characters, *Oeneis tanana* is clearly a member of the *bore* group. Despite the phenotypic differences (adult size and wing color and pattern) between *O. tanana* and *O. chryxus*, the genitalia of these two species are very similar. Subtle differences in genitalia of both sexes indicated in Figs. 4-5 apparently reflect individual variation. To date, we have not identified any diagnostic characters in the genitalia that serve to unambiguously separate these two taxa, although the valvae of *O. tanana* average somewhat more robust than those of *O. chryxus* (Fig. 6), and are generally

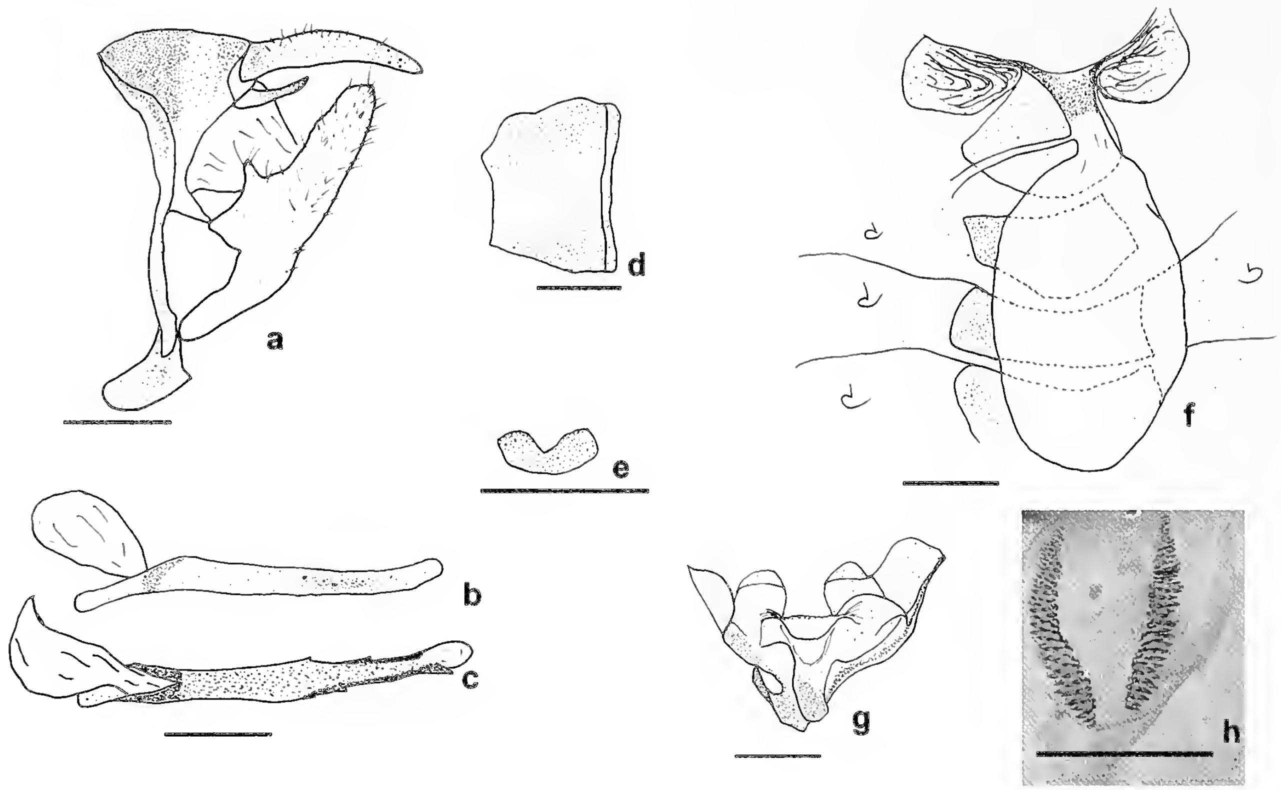

Figure 5. Male and female genitalia of *Oeneis chryxus* from Haines Junction, Yukon Territory, Canada: a, male genitalia (SN-15-158) in left lateral view; b, aedeagus in left lateral view; c, aedeagus in dorsal view; d, eighth tergite in dorsal view; e, juxta in dorsal view; f, female genitalia (SN-15-169) in dorsal view; g, lamella antevaginalis in front view; h, signa. Illustrations by Shinichi Nakahara. Scale bar = 1 mm.

slightly larger than those of *O. bore*. This result is not surprising, considering the lack of consistent genitalic differences reported among other North American members of the *bore* group. On the other hand, female genitalia of *O. tanana* and *O. chryxus* differ from those of *O. bore* by the position of the vertical projection of the lamella antevaginalis, which is skewed to the left in *O. tanana* and *O. chryxus*. Thus, genitalic characters suggest that *O. tanana* is morphologically closer to *O. chryxus* than *O. bore*, although the molecular data discussed below indicate the opposite.

Very little information on *O. tanana* is available in the literature. We are not aware of any previously published images of adult or immature *O. tanana*, other than the very recent images of adults of both sexes (as *O. chryxus caryi*) by Philip & Ferris (2015). Distributional records for *O. chryxus* in Alaska provided by Philip (1996, 1998, 2006) and Magoun & Dean (2000) all refer to *O. tanana*; we have examined specimens from all but one of these sites. The only molecular study that has focused on the *chryxus* complex is that by Nice & Shapiro (2001), who studied haplotype variation in 440 base pairs of mitochondrial *COII* among various western USA populations. Many samples were analyzed from California (*O. c. ivallda* and *O. c. stanislaus*), with others from Idaho, Nevada, Montana, Utah, Colorado, and New Mexico, as well as two specimens from Tok, Alaska (all considered to be *O. c. chryxus*). The specimens from Tok (now recognized as *O. tanana*) were found to possess a unique haplotype (type 'E') not shared with any other populations in the analysis, but no discussion of this population or haplotype was provided.

COI barcode analysis and morphology of the *chryxus* complex

The dendrogram resulting from our analysis of *COI* barcode sequences (Fig. 9) is complex, yet largely corroborates traditional treatments of the *bore* group based on morphology. *Oeneis alberta*, which was included in initial analyses, was omitted from our final tree since it appears polyphyletic, invariably sharing *bore* group haplotypes, yet its status as a species-level taxon, closely related to *O. chryxus*, has not been challenged. The close relationship between *O. bore* and *O. chryxus*, as suggested by many authors based on similarities in the male genitalia (*e.g.*, Elwes & Edwards 1893; Gross 1970; Gorbunov 2001; Lukhtanov & Eitschberger 2001), is corroborated by our analysis, in that the taxa don't appear reciprocally monophyletic. These irregularities in barcodes are likely a reflection of evolutionary closeness of taxa within the *bore* group and are possibly the result of mitochondrial introgression. This scenario would presumably explain the placement of *O. nevadensis* barcodes as derived within the *chryxus* complex, while *O. macounii* sequences are basal to all of these. All indications from morphology suggest that *O. nevadensis* and *O. macounii* are sister taxa, and their close relationship has not been questioned. Despite being obscured by apparent introgression, groupings on the dendrogram do appear to be highly informative, and may be indicative of cryptic diversity within the *chryxus* complex.

Oeneis chryxus is distributed among five barcode clusters, which closely correspond with morphological and biogeographical attributes. The first group includes the Rocky Mountain *O. chryxus* populations, comprising *O. c. chryxus*, with samples included from Colorado, Montana, Alberta, British Columbia, and Yukon Territory (see discussion below regarding Yukon material). These sequences are the least derived of the *chryxus* complex, as also indicated for *COII* by Nice & Shapiro (2001). Across this range, *O. c. chryxus* shows various degrees of localized morphological diversification, but barcodes suggest that all of these populations are very closely related. While not included in this study, the southernmost Rocky Mountain population, *O. c. socorro*, described from Mt. Withington, Socorro County, New Mexico, appears to be closely related to typical *O. c. chryxus* to the north (Holland 2010), based on morphology, habitat, and distribution, although an affiliation with *O. c. altacordillera* (see below) cannot yet be ruled out.

The second barcode group of the *chryxus* complex includes just *O. c. valerata*. This taxon is endemic to alpine habitats in the Olympic Mountains of Washington. While Burdick (1958) cited similar material from Vancouver Island, we know of no valid records from there. The presence of this taxon in its own barcode group suggests it is genetically rather distinct from other groups in the *chryxus* complex, presumably as a result of a long history of isolation on the Olympic Peninsula.

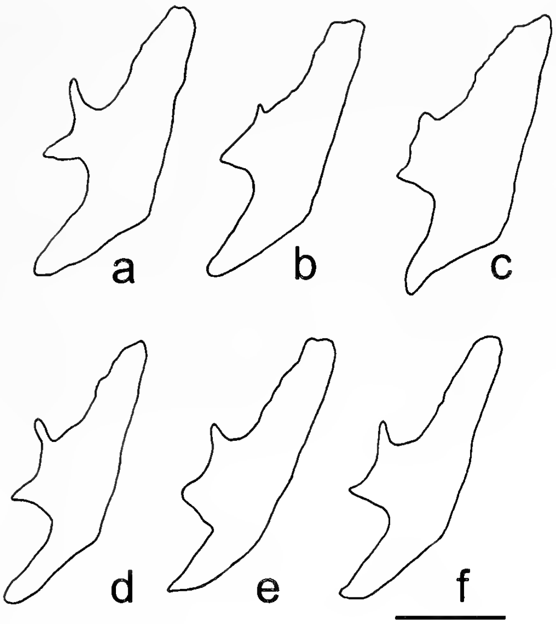

Figure 6. Variation in valvae of *Oeneis tanana* and *O. chryxus*: a-c, *Oeneis tanana* (SN-15-145; SN-15-155; SN-15-157); d-f, *Oeneis chryxus* (SN-15-158; SN-15-159; SN-15-160). Illustrations by Shinichi Nakahara. Scale bar = 1 mm.

The third barcode cluster includes the Sierra Nevadan taxa *O. c. ivallda* and *O. c. stanislaus*, together with a single specimen of *O. c. chryxus* from Utah. Many authors have treated the pallid *O. c. ivallda* as a species-level taxon while considering *O. c. stanislaus* to be a subspecies of *O. chryxus*, based on its similar tawny coloration (*e.g.*, dos Passos 1961, 1964; Gross 1970; Murayama 1973; Emmel 1975; Miller & Brown 1981; Pyle 1981; Garth & Tilden 1986; Tilden & Smith 1986). These taxa were studied in detail by Porter & Shapiro (1991) and Nice & Shapiro (2001), who found that they are very closely related, clearly conspecific as treated by Hovanitz (1937, 1940), and likely resulted from Pleistocene colonization of the Sierra Nevada via dispersal from the Rocky Mountains across the Great Basin. Our results corroborate these conclusions, as *O. c. ivallda* and *O. c. stanislaus* are not separable based on barcode sequences. In addition, the inclusion of a single Utah specimen in this group is consistent with the notion that Sierra Nevadan populations originated through cross-Great Basin dispersal, and some haplotypes are apparently still shared (Nice & Shapiro 2001).

The fourth barcode cluster includes the boreal North American taxa *O. c. calais* and *O. c. strigulosa*, with samples included from Michigan, Ontario and

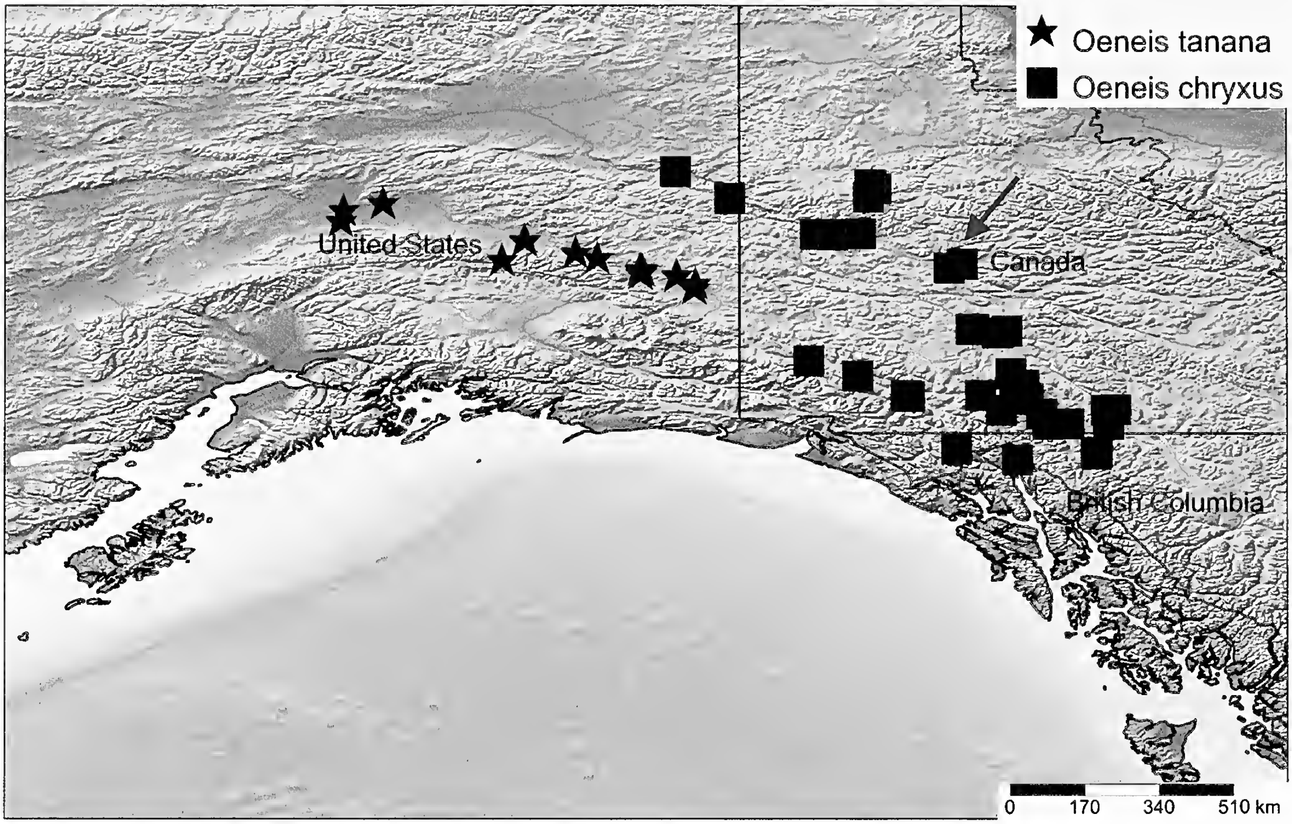

Figure 7. Distribution of *Oeneis tanana* (stars) and *O. chryxus* (squares) in Alaska and northwestern Canada. Red arrow indicates the Stewart Crossing area, Yukon Territory, where a few individuals with *O. tanana*-type *COI* sequences have been found (see discussion in text).

Manitoba. These two taxa are very closely related; it is often not possible to separate them in collections other than by locality, and barcodes failed to clearly distinguish them. This group occupies the central and northeastern North American boreal forests, from Quebec and Ontario, westward into Northwest Territories and northern Alberta, and it appears to be allopatric with respect to the distribution of *O. c. chryxus* in Alberta and British Columbia (Bird et al. 1995; Guppy & Shepard 2001), although access to most regions of potential sympatry or parapatry is extremely limited. As discussed below, the holotype specimen of *O. c. caryi* is fairly typical of specimens found in the western populations of this group. *Oeneis. c. calais* (including *O. c. strigulosa* and/or *O. c. caryi*) has been considered a species-level taxon by various authors (Scudder 1865; Cary 1906; Scott 2006; Kondla 2010).

The fifth cluster of the *chryxus* complex is the recently described *O. c. altacordillera*. This taxon inhabits high-elevations in the southern Rocky Mountains, generally above 3048 m (10,000') elevation, and is frequently found at or just above treeline. While its overall distribution remains to be determined, it appears to be endemic to Colorado and perhaps northern New Mexico (Warren 2011), yet adults from some populations in Colorado are not easily assignable to either taxon based on wing morphology (Scott 2006; pers. obs. ADW 2015). Given the marked difference in barcode haplotypes between typical *O. c. altacordillera* and *O. c. chryxus* from lower elevations in Colorado and elsewhere in the Rocky Mountains (also see Nice & Shapiro 2001), an extensive barcode survey will likely resolve questions about the overall distribution of *O. c. altacordillera*, as well as the identity of the lectotype of *O. c. chryxus* (Shepard 1984; Scott 2010). While Scott (2006) described *O. c. altacordillera* as a subspecies of *O. c. calais* (which was treated as a species-level taxon), an arrangement followed but questioned by Kondla (2010), our results suggest the two taxa are not very closely related, and that *O. c. altacordillera* may best be considered a species-level taxon.

Oeneis tanana is positioned in our dendrogram (Fig. 9) as the most derived grouping within a clade of Arctic American *O. bore*. All five barcode sequences obtained from Alaskan *O. tanana*, from three sites in the Tanana River Valley, were identical, and differ from those of nearby populations of *O. bore* by a single base-pair at site 300: G->A. This is a non-synonymous substitution, which translates to a S->N substitution in protein. The significance of this is not yet known.

Upon searching the BOLD database (Ratnasingham & Hebert 2007), we found a single sequence (HBNK245-07) of *Oeneis* from Yukon Territory that is a perfect match to those of *O. tanana*, from along the Stewart River (and Silver Trail) near Mayo. We therefore obtained barcodes from five additional specimens taken nearby, from the vicinity of Stewart Crossing, approximately 40 km. (24 mi.) southwest of Mayo, also along the Stewart River. Two of these specimens, from "N of Stewart Crossing" (Fig. 10, from OSUC) also possess barcodes typical of *O. tanana*, while three others, from "Stewart Crossing" (MGCL) have barcodes like those of other *O. chryxus* in Yukon Territory. The two specimens (Fig. 10) with barcodes typical of *O. tanana* are fairly dark above, compared to other *O. chryxus* from the province (Fig. 2), and have a ventral hindwing banding pattern reminiscent of Alaskan *O. tanana*, yet they are smaller and somewhat tawnier above than most Alaskan *O. tanana*. The three specimens with barcodes of *O. chryxus* are tawnier above and have a less contrasting ventral hindwing pattern; they appear typical of other *O. chryxus* specimens from the region. A much larger sampling of barcodes from populations in the area will be needed to determine if variation in phenotypes correspond to differences in barcode haplotypes.

The significance of the presence of barcode haplotypes typical of *O. tanana* among specimens from along the Stewart River in Yukon Territory remains unknown. It could indicate that *O. tanana* occurs disjunctly in Yukon Territory, perhaps as a somewhat smaller and tawnier form, at least along the Stewart River, in exact or near sympatry with *O. chryxus*. It could also indicate that haplotypes of *O. tanana* have introgressed into some Yukon populations of *O. chryxus*, but that only one phenotypically variable species actually occurs in the Stewart River area. Extensive study of populations along the Stewart River and nearby regions of central Yukon Territory will be needed to resolve this issue.

Taxonomic status and distribution of Yukon-Alaska *Oeneis chryxus*

Oeneis chryxus is widely distributed in Yukon Territory, with records from even and odd-numbered years, where it inhabits dry, open barrens and subarctic steppe (Ferris et al. 1983; Lafontaine & Wood 1997). Various authors have considered Yukon populations of *O. chryxus* to represent *O. c. caryi* (Layberry et al. 1998; Guppy & Shepard 2001), although Burdick (1958) noted that this is incorrect. The type specimen of *O. c. caryi*, as figured by Burdick (1958) and Warren et al. (2015), is markedly different than any material we have examined from Yukon Territory, and, other than the enlarged forewing ocelli, appears to fall within the normal range of variation seen in the western populations of *O. c. calais*. Further studies are needed to confirm the taxonomic status of *O. c. caryi*, although we believe *O. c. caryi* should probably be considered synonymous with *O. c. calais*; alternatively, if *O. c. calais* is considered to be a species-level taxon, *O. c caryi* might be considered its western subspecies, as implied by McDunnough (1934) and treated by Kondla (2010).

Figure 8. Habitat of *Oeneis tanana*, 8 miles south of Tok, Alaska, 25 June 2007. Photo by David Shaw.

Thus, the name *O. c. caryi* does not apply to populations of *O. chryxus* in northern British Columbia, Yukon Territory, or those barely entering eastern Alaska (see below). While the erection of a new subspecies name might be justifiable for these populations, we feel they are close enough to nominotypical *O. chryxus* in phenotype to tentatively associate them with that taxon. The similarity of *COI* sequences between Yukon and Rocky Mountain material to the south (British Columbia, Alberta, Montana, Colorado) also supports this arrangement, given that barcodes from Yukon specimens are extremely similar or identical to those from further south in the Rocky Mountains.

Oeneis chryxus was first reported from Alaska by Holland (1900), based on a single female taken at

Figure 9. Dendrogram generated from Bayesian analysis of *COI* barcode sequences from taxa in the bore group of *Oeneis*, with *O. norna* as the outgroup. See text for details of the analysis. Colored groupings identify taxa and populations discussed in the text.

Eagle City, on 10 July 1899, by Reverend S. Hall Young. We have examined two male specimens from Eagle, one collected by Young in 1901, and another collected by Reed Heilig in 1903, both of which are typical of *O. chryxus* found to the east in Yukon Territory. One of the specimens bears a blue "paratype" label reading "klondikensis FC", affixed by Frank Chermock. This name was never formally proposed, but was apparently intended to represent *O. c. "caryi"* of recent authors (*e.g.*, Layberry et al. 1998; Guppy & Shepard 2001). The "holotype" and "allotype" of "klondikensis", which we also examined, are from Dawson, Yukon Territory, and a second "paratype" we examined is from Whitehorse. More recently, Guppy & Shepard (2001) indicated the presence of *O. chryxus* in the Alaska Panhandle, in the vicinity of Skagway. While we have not examined specimens from this area, this material is likely to be morphologically like adjacent *O. chryxus* populations in southern Yukon Territory and far northwestern British Columbia.

Thus, with the delimitation of *O. tanana*, it appears that *O. chryxus* just barely penetrates into Alaska from Yukon Territory, along the Yukon River corridor, where it is known from two sites just 9.5 km. (5.9 mi.- at Eagle) and 60 km. (37 mi.- at Kathul Mtn.) west of the Canadian border (Fig. 7). Despite considerable collecting efforts by various researchers along the Taylor and Steese highways, which traverse the Yukon-Tanana uplands separating the Yukon and Tanana rivers, *O. chryxus* remains unreported from the region (the record from the central Yukon-Tanana highlands indicated by Philip and Ferris (2015) represents a misplaced Kathul Mountain record). Likewise, *O. chryxus* appears to barely extend into the Alaska Panhandle near Skagway, presumably from widespread populations just to the north in northwestern British Columbia.

Oeneis tanana appears to be allopatric with respect to *O. chryxus* in Alaska, and it might be endemic to Alaska (but see above). Available records suggest that Alaskan *O. tanana* populations are separated from the nearest known population of *O. chryxus* in Alaska (at Eagle) by about 185 air km. (115 mi.), and are separated from the nearest known population of *O. chryxus* in Yukon Territory (at Nickel Creek) by about 210 air km. (130 mi.).

Hypothesized evolutionary history of *Oeneis tanana*

The confirmed distribution of *Oeneis tanana* lies within the Tanana River Basin in Alaska, most or all of which was apparently never glaciated during the last glacial maximum in the late Pleistocene, roughly 28,000 to 14,000 years ago (Dyke 1999; Goetcheus & Birks 2001; Harrington 2005). During this time, the Tanana River Basin, together with the larger and contiguous Yukon River Basin (including lower elevations along the Yukon River drainage in northern and central Yukon Territory) formed the southeastern limits of eastern Beringia (*sensu* Elias & Brigham-Grette 2007), a region widely recognized as a refugium for many plants and animals during the glacial cycles of the Pleistocene (*e.g.*, Guthrie 2001; Pruett & Winker 2005; Geml et al. 2006; Zazula et al. 2006; Elias & Brigham-Grette 2007; Fritz et al. 2012; DeChaine et al. 2013; Edwards et al. 2014). The Tanana and Yukon River basins were identified as distinct sub-refugia during the Pleistocene for two fish taxa (Stamford & Taylor 2004; Campbell et al. 2015), and four species of trees (Roberts & Hamann 2015), and we believe the region likely served as a refugium for *O. tanana* as well.

We hypothesize that during the last glacial maximum, *O. tanana* persisted in the Yukon-Tanana basins, while *O. chryxus* was isolated in a southern Rocky Mountain refugium, similar to what has been documented for *Rhodiola integrifolia* Raf. (Crassulaceae) (DeChaine et al. 2013). Under this scenario, *O. chryxus* dispersed northward along the Rocky Mountain cordillera as the ice sheets retreated, while *O. tanana* remained within the Yukon-Tanana basins. This scenario is supported by the close similarity of *COI* barcode haplotypes among cordilleran *O. chryxus* from Colorado to Yukon Territory (also see Nice & Shapiro 2001), and uniqueness of *O. tanana* haplotypes, although the possibility of isolated refugia for *O. chryxus* in the northern Rocky Mountains cannot be ruled out (Marr et al. 2008; Savidge 2012). We hope that this hypothesis will be investigated in the future in a detailed phylogeographic study.

Given the similarity of *COI* haplotypes between *O. tanana* and Arctic American populations of *O. bore*, introgression between the two taxa has likely occurred, perhaps during the Pleistocene. Although adults of *O. tanana* average consistently larger than those of nearby *O. bore*, the ventral hindwing pattern of *O. tanana* is often inseparable from that of *O. bore*, due to the bold transverse bands and broad whitish areas bordering them. The dark dorsal coloration of *O. tanana* is also suggestive of *O. bore*. While overall, the morphology of *O. tanana* is seemingly closer to that of *O. chryxus* than to *O. bore*, these traits, as well as the *COI* haplotypes, suggest some degree of influence from *O. bore*. While much additional study is required, we feel it is possible that *O. tanana* could have evolved through hybridization between *O. bore* and *O. chryxus*; this highly speculative hypothesis should be tested through molecular studies. While such a mode of speciation is widely accepted in plants (*e.g.*, Soltis 2013), it has only recently been seriously investigated in animals, including butterflies (Gompert et al. 2006; Mavárez et al. 2006; Mallet 2007; Kunte et al. 2011; Abbott et al. 2013; Dupuis & Sperling 2015; Lukhtanov et al. 2015).

Taxonomic rank for *Oeneis tanana*: species or subspecies?

The last two new "species" of *Oeneis* described from North America (Troubridge et al. 1982; Troubridge & Parshall 1988) have proven to be very closely related to or conspecific with described taxa in the northeastern Palearctic region. *Oeneis excubitor* Troubridge, Philip, Scott & J. Shepard, 1982 has been treated as a subspecies of *O. alpina* Kurentsov, 1970 by most subsequent authors (Scott 1986; Lafontaine & Wood 1997; Layberry et al. 1998; Warren et al. 2015). *Oeneis philipi* has apparently close relatives in the northeastern Palaearctic, sometimes called *O. rosovi* Kurentsov, 1970, a name that has been applied as a senior synonym of *O. philipi* (Lafontaine & Wood 1997; Lafontaine & Troubridge 1998; Layberry et al. 1998). However, as noted by Lukhtanov (1989), the two syntypes of *O. rosovi* appear to represent two different species, so until a lectotype is designated, the application of this name to any populations remains problematical (Pelham 2008). *Oeneis tanana*, in contrast, does not appear to have any close relatives in the Palaearctic; its overall morphology and *COI* haplotypes clearly place it within the *bore* group, apparently most closely related to the entirely Nearctic *chryxus* complex.

When we initiated this project, we held no preconceived notions about the taxonomic rank of *O. tanana*. All we knew, based on overall morphology of large series of adults, is that they were different from *O. chryxus* in Yukon Territory. As our investigation progressed, and molecular and biogeographic information was analyzed from other members of the *chryxus* complex, we eventually determined that, based on currently available information, *O. tanana* is best considered a species-level taxon. The apparent lack of discrete genitalic characters to separate *O. tanana* from other members of the *chryxus* complex is not surprising in the genus *Oeneis*, since closely related species frequently cannot be reliably distinguished via genitalic morphology (*e.g.*, Troubridge & Parshall 1988). While *O. tanana* is apparently allopatric with respect to *O. chryxus* in Alaska, its barcode haplotype is quite distinct from those found in cordilleran *O. chryxus*, and almost all adults examined from Alaska are easily separated from Yukon-Alaska *O. chryxus* based on their wing morphology. Only the very smallest and tawniest Alaskan individuals of *O. tanana* (*e.g.*, Fig. 1e,k) can potentially be mistaken for Yukon-Alaska *O. chryxus*. Yet in these situations, *O. tanana* tends to have bolder ventral hindwing markings than what is normally seen in Yukon-Alaska *O. chryxus*.

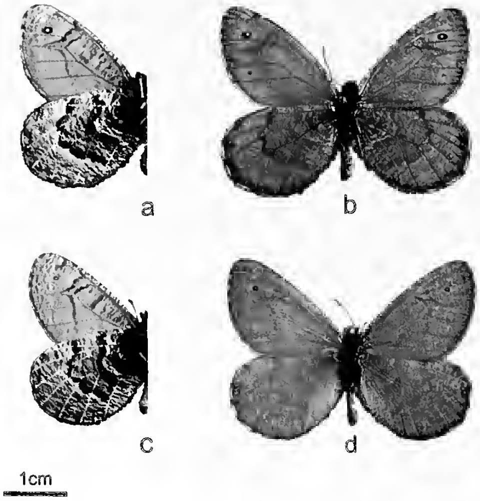

Figure 10. Male *Oeneis* from north of Stewart Crossing, Yukon Territory, Canada, possessing *COI* barcode sequences typical of Alaskan *O. tanana*: a-b, 20 June 1975, D. K. Parshall, OSUC 618329; c-d, 22 June 1983, D. K. Parshall, OSUC 618330. Photos courtesy of Luciana Musetti.

However, many questions remain about the overall distribution of *O. tanana* with respect to *O. chryxus*. The apparent gap of 210 km. in distributions of the two taxa along the Alaska Highway centered on the Yukon – Alaska border should be carefully studied for the possible occurrence of either species or intermediate forms. Likewise, additional surveys along the lower Tanana River, and along the Yukon River downstream of the Kathul Mountain area in Alaska should be conducted to detect the possible occurrence of members of the complex. In addition, populations along the Yukon River and its tributaries in Yukon Territory should be carefully studied and barcoded to determine the significance of *O. tanana* barcodes in the region. Thus, future studies could reinforce our hypothesis that *O. tanana* represents a species-level taxon, or they could indicate that subspecies-level status for *O. tanana* may be more appropriate.

While much additional study of the *O. chryxus* complex, employing multiple genetic markers and additional surveys in remote regions, will be required to fully understand relationships within the group, our results suggest that *O. chryxus* of most contemporary authors may comprise five species-level taxa: *O. chryxus* (including *O. c. ivallda, O. c stanislaus, O. c. chryxus*, and presumably *O. c. socorro*), *O. calais* (including *O. c. strigulosa* and *O. c. caryi*), *O. valerata, O. altacordillera* and *O. tanana*, with *O. tanana* apparently being the most distinctive of them all, morphologically. It is also possible, based on available data, to argue that the Sierra Nevadan taxa (*O. c. ivallda* and *O. c stanislaus*) represent a sixth species-level taxon, closely related to *O. chryxus*.

On the other hand, the main groupings in the *chryxus* complex can be interpreted as subspecies-level taxa, depending on one's species concept; indeed, none of them appear to be sympatric in distribution, with the possible exceptions of *O. c. chryxus* and *O. c. altacordillera* in Colorado, *O. c. chryxus* and *O. c. calais* in Alberta, and *O. chryxus* and *O. tanana* in Yukon Territory. Under this scenario, *O. chryxus* would be considered a diverse array of mainly allopatric populations, each of which possessing unique genetic attributes and sometimes highly divergent wing morphologies, distributed across a broad range of habitat types and biogeographical regions in North America. However, as noted above, recent authors have treated *O. c. calais* (including *O. c. strigulosa* and *O. c. caryi*) as a species-level taxon, which our results suggest is a reasonable interpretation. Based on our current knowledge, if *O. c. calais* is considered a species-level taxon, distinct from *O. chryxus*, the other main groupings within the *chryxus* complex should also be treated at the species-level, at least including *O. c. valerata, O. c. altacordillera* and *O. tanana*, which appear to be the most divergent members of the complex.

Regardless of its taxonomic status as a species or subspecies, *O. tanana* represents a unique entity within the genus *Oeneis* which deserves much additional study. A better understanding of its evolutionary history may be helpful in understanding mechanisms of diversification within the genus, both in the Nearctic and Palaearctic regions, and may further elucidate the geological history of eastern Beringia. Placing a name on this entity, as we have done herein, is the first step in this process.

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Editor's note

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Remarks on the recent publication of Titian R. Peale's "lost manuscript," including new information about Peale's Lepidoptera illustrations

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Abstract. The recent book *The Butterflies of North America: Titian Peale's Lost Manuscript* introduces over two hundred previously unpublished drawings of butterflies and moths by the naturalist-artist Titian Ramsay Peale. In many instances, this book provides inaccurate and insufficient information about Peale's illustrations and the specimens they portray. A number of species are misidentified and the nomenclature is sometimes outdated. A detailed analysis of these illustrations reveals that many of the depicted specimens still exist. It was also discovered that Peale copied over fifty of his larvae, pupae, and plants from at least ten published works. With the assistance of twelve other lepidopterists and botanists, the insects and plants portrayed in Peale's illustrations are re-identified. New information about Peale's abandoned work, *Lepidoptera Americana*, is also presented.

Key words: John Abbot, butterflies, larva, Mexico, moths, North America, plants, pupa, South America.

Introduction

Titian Ramsay Peale II (1799-1885) (Fig. 1) was a talented artist and naturalist, whose family was enormously influential in the development of the arts in America. His father, artist-naturalist Charles Willson Peale (1741-1827), painted some of the most familiar portraits of the colonial period and founded one of the first museums in America. In addition to producing lithographs for his own publication, *Lepidoptera Americana* (Peale 1833), Titian R. Peale contributed illustrations for Thomas Say's *American Entomology* (1817, 1824-1828), Charles L. Bonaparte's *American Ornithology* (1825-1833), and John Cassin's *Mammalogy and Ornithology* (1858). Contrary to popular belief, he rendered only some of the plates for these publications. Until recently, these remained the most widely recognized examples of his artwork, though he also produced a few illustrations for other publications (e.g. James 1822; Bonaparte 1824; Green 1827; Doughty & Doughty 1830-1834). With the publication of *The Butterflies of North America: Titian Peale's Lost Manuscript* (Peale et al. 2015) we become familiar with over two hundred of Peale's previously unpublished Lepidoptera illustrations, reproduced from manuscripts in the rare book collection at the American Museum of Natural History (AMNH).

Peale's manuscript

As suggested by its title, the first part of Peale et al. (2015) highlights illustrations for Peale's proposed work, "The Butterflies of North America, Diurnal Lepidoptera: Whence They Come, Where They Go, What They Do." This manuscript, comprised of three volumes of drawings and over 400 pages of handwritten descriptive text, was donated to AMNH in 1916 by wealthy New York financier Ogden Mills (1856-1929) (Tower 1917), who served on the AMNH Board of Trustees and was a generous benefactor to the museum. (His son, Ogden L. Mills, served as Secretary to the Treasury of the United States). Evidence suggests that this manuscript was mostly completed between the years 1874 and 1880, after Peale had retired from the U.S. Patent Office in Washington, D.C. and moved back to the Philadelphia area.

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Some of these illustrations were completed earlier, as he mentions in his text that he borrowed several specimens from the collection of the Entomological Society of Philadelphia, an organization that existed under that name from 1859 to 1867. While living in Washington, D.C., Peale occasionally made the trek to Philadelphia, particularly to visit his older brother, Benjamin Franklin Peale (Poesch 1961).

All of the illustrations from this manuscript are reproduced in Peale et al. (2015), but only 13 pages of the accompanying text are included. Although this manuscript is titled "Butterflies of North America," it incorporates several species of moths, and Peale's definition of North America is somewhat unconventional. He intended to limit himself "to the diurnal species," feeling that the time was insufficient to include both moths and butterflies, but found it "necessary to take them as they come to hand" (letter dated 19.ix.1875, Field Museum of Natural History, Chicago, Illinois; FMNH). Peale struggled with the definition of North America, asking the Pennsylvania lepidopterist F. H. Herman Strecker "What do you think of the limits of North America? – what is the limit South and Southeast?" (ibid.). In the introduction of his text Peale wrote, "[T]his subject cannot be divided by state lines, - there is nothing political in it, and so we must select some other stand point." He ultimately included the area from the Gulf of St. Lawrence southward to the West Indies, Mexico, and Central America, as well as northern South America. The accuracy of Peale's illustrations is, for the most part, extraordinary. Many of the depicted butterflies can be identified to subspecies, even without knowing their origin. The early stages are largely accurate, and those derived from other sources (see below) were enhanced by Peale to look more realistic. Some of the plants, however, are somewhat loosely portrayed and difficult to identify with certainty. Although the title of Peale et al. (2015) implies that the original manuscript was forgotten after Peale's death, at least nine of its illustrations were published or figured in other studies, and six pages were publicly exhibited prior to 2015 ([Skinner] 1892; Poesch 1961; Sellers 1980; Haifley 1981; Foutch 2011).

LEPIDOPTERA AMERICANA

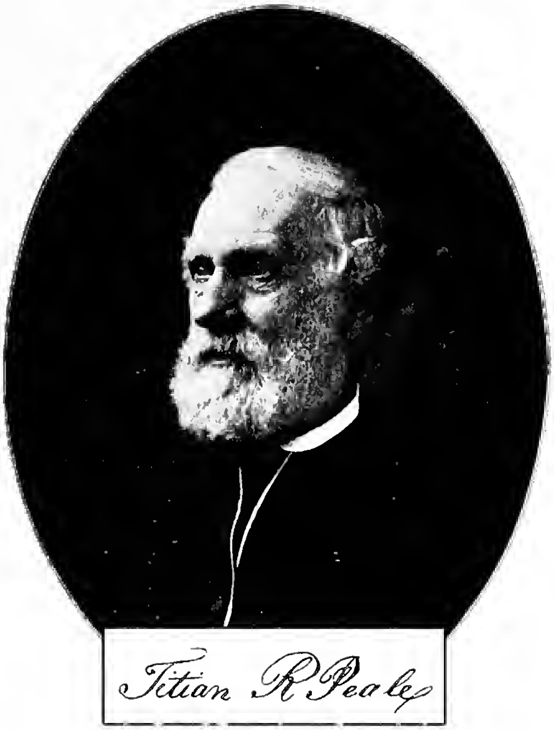
The second part of Peale et al. (2015) examines *Lepidoptera Americana* (Peale 1833), Peale's initial attempt to publish a treatise on North American butterflies and moths. Featured is Peale's personal copy, which was donated to AMNH in 1817 by Peale's nephew, John M. Hoffmire (1833-1919) (Tower 1918). Included with this copy is a double-sided sheet of "Proposals" for publishing the work, dated March 1833. Although Peale et al. (2015) reproduce ten lithographs for *Lepidoptera Americana*, only Plates 2, 3, 4, and 7 (with 14 pages of accompanying text) were actually included in the single published installment. *Lepidoptera Americana* is essentially a prospectus, and Peale himself referred to it as such (Foutch 2011). He issued the four plates and text as an example of what prospective subscribers could expect, but there is some disagreement about whether this work was actually published. However, Peale distributed colored copies to a number of "scientific friends" and donated colored and uncolored copies to "Scientific Libraries" (Peale 1884). These actions, as well as details of the piece itself, comply with Articles 8 and 9 of ICZN (1999, and amendments) as constituting a published work. After the first installment was published, Thomas Say attempted to persuade Peale to include descriptions of the early stages of each species, though he doubted that Peale would do so (13 August 1834, Museum of Comparative Zoology, Harvard University). At least nine additional plates were printed in expectation of continuing the series, six of which are included in Peale's copy at AMNH. Copies of these and three other trial plates (four dated 1836) were donated by Peale in 1884 to the Academy of Natural Sciences of Philadelphia (Pennsylvania; ANSP) ([Nolan] 1885). Although Peale enlisted 28 subscribers to *Lepidoptera Americana*, it was not enough to fund its publication. Peale most likely abandoned the project before the summer of 1838, when he left to participate in the United States Exploring Expedition (Wilkes Expedition).

Rhodes (2015) claims that only four copies of *Lepidoptera Americana* are known to exist, yet eight copies were listed by dos Passos (1965), two of which are preserved at AMNH (the second possibly being a combination of two copies that were reportedly sold to the University of Minnesota around 1942; see dos Passos 1965). Individual plates are also deposited in the American Philosophical Society Library (Philadelphia, Pennsylvania; APS). In addition, we confirmed the existence of a previously undocumented copy at the University of New South Wales (Sydney, Australia; UNSW). Bound in marbled boards and lacking a title page, it contains text and plates 2-8 (5, 6, and 8 were not published in the original installment). This copy evidently came to Australia via the entomologist William S. Macleay (1792-1865), whose signature appears on the verso of the front cover. Macleay probably received it directly from Peale, whom he met in Philadelphia in 1836 (Macleay 1838). Three years later, Macleay moved to Sydney, where he spent the remainder of his life. He remained in contact with Peale, even sending him specimens from Australia.

Of special interest, Macleay's copy of *Lepidoptera Americana* offers evidence that Peale later changed his mind about how this work would be issued. The printed "Proposals" sheet originally stated that it would be "issued in Numbers of four Plates" and that a number would be "regularly published every two months." The price of copies printed on "fine paper, with coloured plates," would be ten dollars per year, and would be payable "on the delivery of the first number" (dos Passos 1965; Foutch 2011). The "Proposals" page in the Macleay copy includes ink corrections by Peale, denoting that the book would be issued in entire volumes of 25 plates at a price of ten dollars each (Fig. 2). He did not, however, provide an indication of how often the volumes would appear. This new approach was probably proposed by Peale around the year 1836.

Peale's sketchbook

The last part of Peale et al. (2015) presents an assortment of illustrations from Peale's sketchbook, "Lepidoptera. Larva. Food-plant, Pupa. &c.," which was acquired by AMNH in 1918 from Peale's nephew, J. M. Hoffmire (Dickerson 1918). This collection includes over 100 drawings, most of which are reproduced in Peale et al. (2015). Dates written on the drawings indicate that they were rendered during two discrete periods: 1833-1837 and 1873-1880. In the intervening years, Peale traveled with the Wilkes Expedition, wrote his ill-fated zoological volume for the expedition, operated (and lost) the family museum, and worked at the U.S. Patent Office. He also suffered the deaths of his wife and three of his children during this time. He complained that while serving as examiner of patents, he was unable to indulge in his beloved pastime for many years (letter dated 10,vii.1871, FMNH). One rendering of the life history of a *Morpho* butterfly [possibly *M. epistrophus* (Fabricius, 1796)] was drawn in Brazil in 1838, while Peale was traveling with the Wilkes Expedition. The accuracy of Peale's drawings of larvae varies greatly, with some being unidentifiable. This is not unexpected, as they were rendered during different periods in Peale's life. An editorial error, or perhaps to fill space, several of the thirty-two small reproductions on pages 244 and 245 of Peale et al. (2015) are duplicates of larger images on the preceding pages. Although it is stated in the caption for the drawing on page 240 that only two butterflies are portrayed among the caterpillar studies, eleven butterfly species are included among these drawings (including six on pgs. 244 and 245).

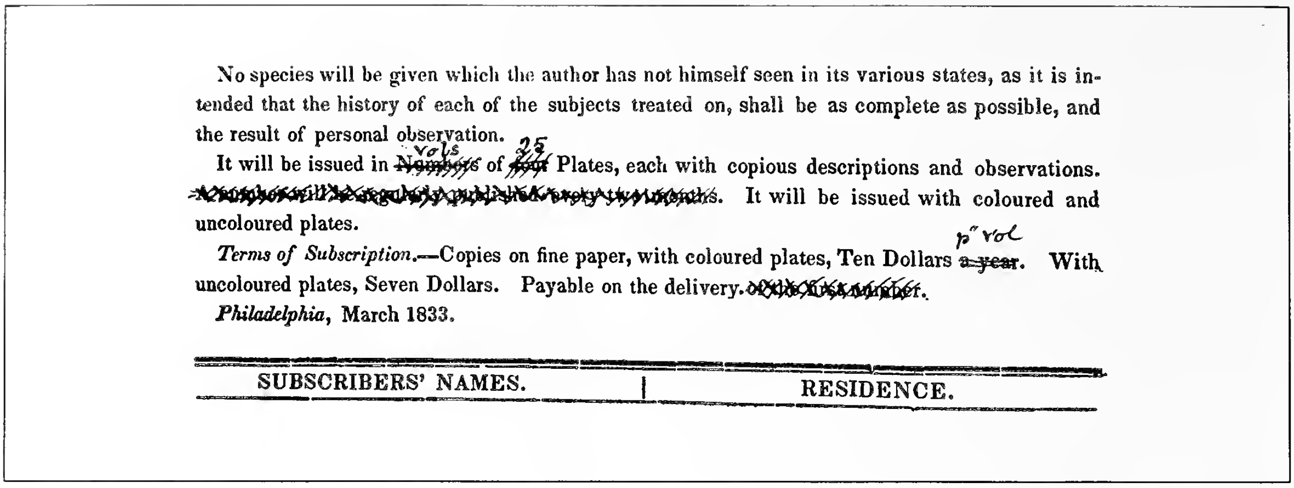


Titian R. Peale

Figure 1. Titian R. Peale, c. 1875 (American Philosophical Society) (signature from 1826; J. Calhoun coll.).

Analysis

We feel that Peale et al. (2015) understate the scientific merits of Peale's illustrations. An art historian, Haltman (2015) mostly explores the philosophical aspects of Peale's work in the book's introduction, perceiving that Peale "reworked the material reality of living specimens – motion to stillness, change (or metamorphosis) to stasis, weightlessness to gravity – into aesthetic fictions serving to document, sanitize, and even theorize the work of science," adding, "His later work would even, at times, invoke the possibility of a resurrection metaphysical in nature, beyond the pictorial resurrection he provided." In composing his Lepidoptera illustrations, Peale generally followed the artistic traditions of his predecessors. Adult butterflies and moths were typically depicted as specimens, suspended in space or sitting on leaves of the food plants on which the early stages are positioned. Peale was extremely creative, but he seemed more pragmatic when it came to illustrating his beloved Lepidoptera, fashioning arrangements that best enabled the identification of their subjects. The layout of larva, pupa, food plant, and adults of



No species will be given which the author has not himself seen in its various states, as it is intended that the history of each of the subjects treated on, shall be as complete as possible, and the result of personal observation.

It will be issued in ~~Numbers~~ vols of ~~four~~ 25 Plates, each with copious descriptions and observations. ~~A number will be regularly published every two months.~~ It will be issued with coloured and uncoloured plates.

Terms of Subscription.—Copies on fine paper, with coloured plates, Ten Dollars ~~a year~~ p" vol. With uncoloured plates, Seven Dollars. Payable on the delivery ~~of the first number~~.

Philadelphia, March 1833.

SUBSCRIBERS' NAMES.	RESIDENCE.

Figure 2. Verso of the "Proposals" sheet from the copy of *Lepidoptera Americana* in Australia (UNSW Library).

Battus philenor (Linnaeus, 1771) on Plate XVIII is a practical and appealing means to depict these figures within the limited space available. It was less likely composed, as interpreted by Haltman (2015), as a metaphor for metamorphosis, with a caterpillar crawling towards its own pupa, and then ultimately flying away as a butterfly at the top of the page. In fact, Peale's composition is likely an homage to the similar composition of this species by John Abbot on Plate III in Smith & Abbot (1797). Furthermore, Peale copied his larva and pupa for this illustration from figures on Plate 11 of Boisduval & Le Conte (1829-[1837]), which were based on Abbot's drawings (see below). While Peale was undeniably imaginative, he was bound by convention, resulting in compositions that were largely driven by convenience and scientific purpose.

The captions in Peale et al. (2015) are too brief and often include incorrect or insufficient information. Within the introduction it is stated that the portrait of Peale, dated "ca. 1850," portrays Peale "at about thirty years of age," but this would make him 51 years old. This portrait, done with the help of his brother, Rembrandt Peale, and preserved at AMNH, is believed to have been completed c. 1825-1835 (Poesch 1961). A contemporary brass plate affixed to the frame of this painting is the culprit, erroneously dating it as "ca. 1850." Among Peale's Lepidoptera illustrations, Plate XIX portrays two species, *Battus devilliers* (Godart, [1824]) and *Papilio oxynius* (Geyer [1827]), yet the caption mentions only *B. devilliers*. The caption for the subsequent plate mentions only *P. oxynius*, while two species are actually depicted, *Mimoides thymbraeus* (Boisduval, 1836) and *Battus polydamas* (Linnaeus, 1758). Plate XCVII portrays four different species – not two as indicated – and gives the range of *Anaea troglodyta* (Fabricius, 1775) as including Central America, where this species does not occur.

Fascinating details regarding some of the specimens that Peale portrayed were omitted from Peale et al. (2015). For example, the image of Plate XV received only the brief caption, "An apparent blue/dark variant of the Spicebush Swallowtail, *Papilio troilus* var." There is so much more to its story. In his text for this drawing, Peale noted that the depicted specimen was collected by a friend at Washington, D.C. in 1847. Peale was a correspondent of the Pennsylvania lepidopterist F. H. Herman Strecker, who learned about this aberrant specimen and cited it in Strecker (1878) as "One example in coll. Peale." Strecker was obsessed with aberrations or "monstrosities" and would attempt to acquire such specimens at practically any cost. Peale wrote in his collection notes at ANSP that the specimen of *Papilio troilus* Linnaeus, 1758 was ultimately sent to Strecker in June 1877 in exchange for a specimen of *Urania sloanus* (Cramer, 1776), a striking Jamaican moth that was extinct by the early 1900s. Strecker personally delivered the specimen to Peale in Philadelphia (card from Peale dated 27.v.1877, FMNH). Peale portrayed his prize *U. sloanus* on Plate CXXXVIII, and this specimen still exists in the ANSP collection. The specimen of *P. troilus* is deposited with Strecker's collection at the FMNH, and his handwritten collection catalog confirms that it was received from Peale. Strecker (1900) partially based his description of *P. troilus* var. *radiatus* on this specimen, which was attributed to "Washington, D.C., Titian R. Peale."

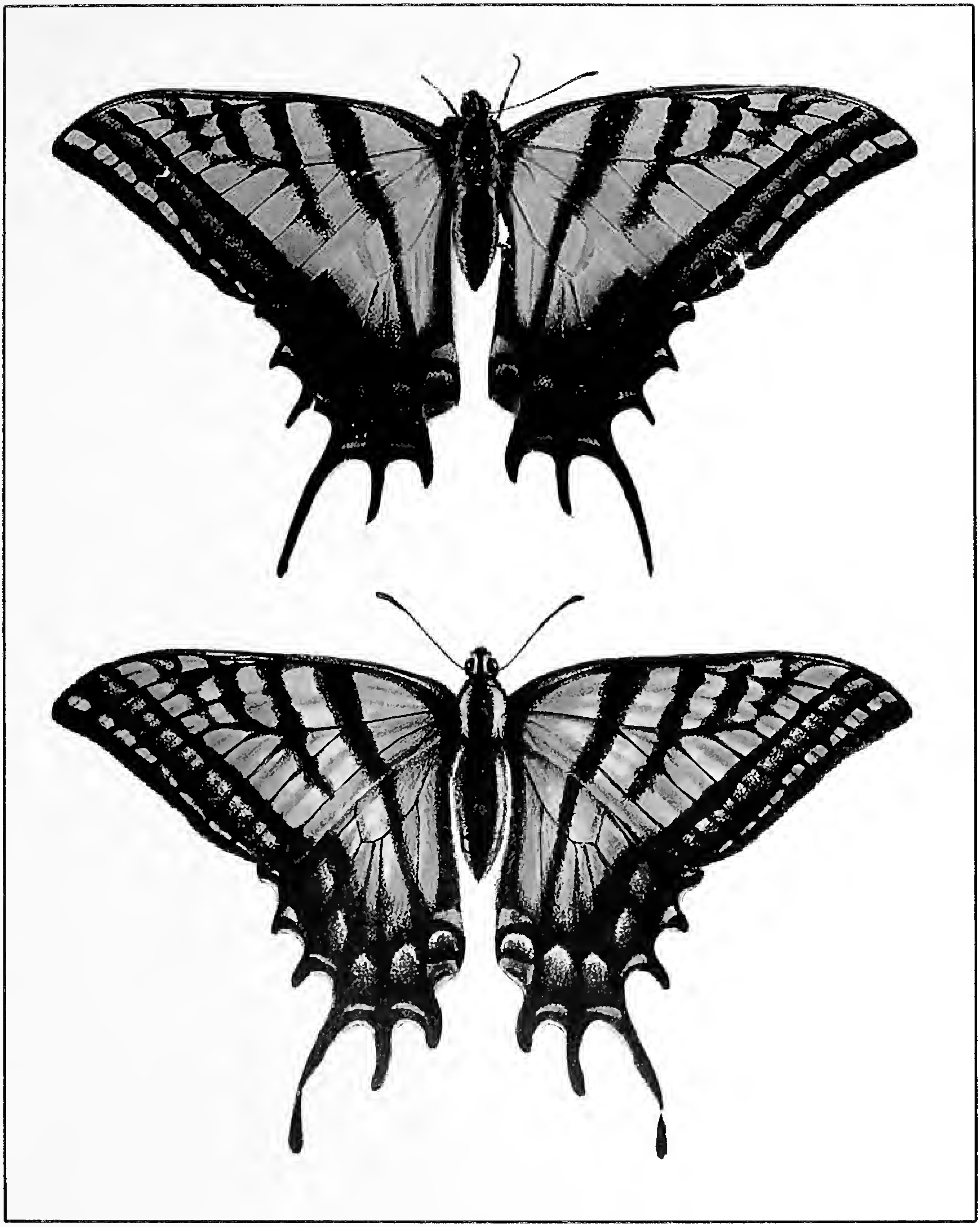


Figure 3. *Papilio multicaudata.* **Top**: specimen in Peale's collection at ANSP, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835. **Bottom**: hand-colored lithograph from Pl. III of Peale's manuscript, originally printed for *Lepidoptera Americana* (AMNH Library image b1083009_2).

Another remarkable account involves the name *Papilio multicaudata* W. F. Kirby, 1884, which Peale originally proposed for a large butterfly that he received in 1835 from John Millington (Fig. 3, top), a civil engineer who lived in Mexico for several years. Referring to the multiple tails on the hindwing of this species, Peale used the name *Papilio multicaudata* on a lithograph of Millington's specimen, which was printed in 1836 for the continuation of *Lepidoptera Americana* (Fig. 3, bottom). To create Plate III for his "Butterflies of North America," Peale simply clipped out the figures of this species from one of the previously printed plates. Because Peale never published his proposed name, he was "scooped" by the French entomologist Jean B. A. D. de Boisduval, who, based on another specimen from Mexico, scientifically described this species in 1836 as *Papilio daunus*. Consequently, Peale dutifully employed this name on his Plate III. The name *P. daunus*, however, had already been used for another species of butterfly, thereby invalidating Boisduval's name. In an incredible twist of fate, Peale's name (*P. multicaudata*) was later published by Kirby (1884) in reference, no less, to Peale's unpublished plate for *Lepidoptera Americana*. This made *P. multicaudata* the next available name for this species to replace the preoccupied name *P. daunus*. Following the strict rules of zoological nomenclature, Kirby is recognized as the author of *P. multicaudata* (Brower 1958) and we still use this name today. A mere technicality deprives Peale of the superb name that he proposed nearly fifty years earlier. The inclusion of such anecdotes about the depicted specimens would have greatly enhanced the value of Peale et al. (2015) and made Peale's story all the more compelling. In the introduction for his manuscript, Peale reminds us that an emphasis on mere names "leaves us without further useful information," and as a result, "many a marvelous history is lost."

Most disappointing in Peale et al. (2015) are the many inaccurate or imprecise identifications. Examples include the figures of *Euchloe ausonides* (Lucas, 1852) on Plate XXXII, which are identified as *Euchloe olympia* (W. H. Edwards, 1871). Plate CIV is identified as "A satyr, either *Hermeuptychia hermes* or *sosybius*, which live in the southeastern and mid-Atlantic United States." The name used by Peale for the figured butterfly, *Neonympha phocion*, is a preoccupied synonym of the southeastern species now recognized as *Neonympha areolatus* (J. E. Smith, 1797), which the figures clearly portray. Moreover, *Hermeuptychia sosybius* (Fabricius, 1793) is a very dissimilar species, and it was recently shown that *Hermeuptychia hermes* (Fabricius, 1775) does not occur within the United States (Cong & Grishin 2014). Plate CXI is claimed to depict "various color morphs" of *Cercyonis sthenele* (Boisduval, 1852), but four of the five figures portray two different subspecies of *Cercyonis pegala* (Fabricius, 1775). Plate CXLI is identified as the Neotropical moth *Eumorpha satellitia* (Linnaeus, 1771), but it actually represents *Eumorpha pandorus* (Hübner, 1821), a widespread species in the eastern United States. Peale reared this species from larvae found in 1833 (probably at Philadelphia), as indicated on his drawing on page 203, which in 1880 he incorporated into Plate CXLI. He also illustrated larvae of this species much earlier, around 1817 (drawing at APS). Although the early stages of the moth figured on page 182 are identified as "An inchworm species, possibly of the genus *Eupithecia* (Family Geometridae)," they represent the common geometrid moth *Prochoerodes lineola* (Goeze, 1781), a species also portrayed by Peale in a lithograph intended for *Lepidoptera Americana*. Possibly the result of a transcription error, the larva on page 190 is identified as "*Agrius cingulatus* (family Sphingidae)," when it actually portrays the noctuid moth *Acronicta oblinita* (J. E. Smith, 1797); the previous two drawings depict *Agrius cingulata* (Fabricius, 1775). Although the butterflies on Plate CV are correctly identified as *Cyllopsis gemma* (Hübner, [1809]), it is stated that the figures do not "match this particular species in upper or under surface." In reality, Peale's figures are reasonably accurate portrayals of this distinctive butterfly.

The nomenclature in Peale et al. (2015) is awkward, employing outdated scientific names and unconventional common names. Examples include the genus *Pieris* Schrank, 1801 for *Pontia protodice* (Boisduval & Le Conte, [1830]) (Plate XXXIII), and the genus *Eurema* Hübner [1819] is applied to species now generally placed into the genera *Abaeis* Hübner [1819] and *Pyrisitia* Butler, 1870 (Plates XLIII and XLIV). The incorrect spelling "*charitonius*" is used for *Heliconius charithonia* (Linnaeus, 1767) on Plate LII [see Brower (1994)]. The Old World genus *Precis* Hübner [1819] is used for *Junonia coenia* Hübner [1822] on Plate LXXVIII. The junior synonym *Cycnia antica* Walker, 1856 is used to identify the moth *Cycnia tenera* Hübner, 1818 on Plate CXXXVIII, as well as its larva on page 184 [though not acknowledged in the book, Plate CXXXVIII also portrays adults of the similar *Cycnia inopinatus* (H. Edwards, 1882)]. Common (English) names include "Pallid Swallowtail" for the Pale Swallowtail (Plate IV), "Great Smokies Fritillary" for the Diana Fritillary (Plate LX), and "Coontie Hairstreak" for the Atala (Plate CXXV). The Great Southern White (Plate XXXIV) is mistakenly called "The Great

Figure 4. Early stages and food plant of *Limenitis arthemis astyanax*. **a**. Figures by J. Abbot as published on Pl. 10 of Smith & Abbot (1797); **b**. Figures from Peale's Pl. LXXXVIII (AMNH Library image b1083009_98). Red circles show obvious similarities between the illustrations.

Southern Sulphur," and the Eyed Brown (Plate CIII) is erroneously called a "Pearly Eye." Most of the unusual common names of butterflies were proposed by Scott (1986), who attempted to "correct" those he believed were misleading (Scott 2008), though the new names were not generally adopted. Most of the scientific names for butterflies in Peale et al. (2015) also agree with Scott (1986), suggesting this was the primary source used for nomenclature.

The responsibility of identifying all the species and preparing the captions for Peale et al. (2015) was entrusted to David A. Grimaldi (Curator of the American Museum of Natural History's Division of Invertebrate Zoology), who is a highly respected and knowledgeable entomologist. However, this onerous task is beyond the ability of any one person, especially one who is not a lepidopterist. As lepidopterists, we spent a great deal of time closely scrutinizing each of the illustrations in this volume. We ultimately enlisted the help of seven other lepidopterists, including those who specialize in moths and the identification of larvae. We also solicited the assistance of five botanists to identify plants. At our request, staff members of the AMNH Research Library graciously provided scans of Peale's entire handwritten manuscript for "The Butterflies of North America." This text discloses the sources of many of the depicted specimens, which was particularly helpful in identifying Neotropical species. The detailed results of our analysis of Peale's illustrations, page by page in Peale et al. (2015), are presented in Table 1.

As part of our analysis, we also consulted the exhaustive online database of Peale's insect specimens, which are deposited at ANSP and the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania; CMNH) (Gelhaus et al. 2004). We discovered that many of the butterflies and moths that Peale portrayed still exist, including adults that resulted from larvae depicted in his sketchbook (Fig. 3). The ability to associate illustrations with actual specimens is a valuable means to connect library and museum collections (Pethers & Huertas 2015). Such an investigation of Peale's source material would have been a valuable addition to Peale et al. (2015). The results of our examination of Peale's figured specimens also are included in Table 1.

In addition to specimens that Peale personally collected in New York, Pennsylvania, New Jersey, Florida, Colombia ("New Grenada"), and Brazil, he figured butterflies that were received from many distinguished friends and correspondents: Baron Friedrich K. J. F. von Gerolt (1797-1879), a Prussian diplomat and mineralogist who lived and traveled in Mexico during the 1820s-1840s (Rowen 2012); Hans B. Hornbeck (1800-1870), a Danish physician who lived in the Virgin Islands from 1824 to 1844 (Acevedo-Rodríguez [1996]); John E. Le Conte (1784-1860), an American naturalist who owned property in Georgia and coauthored *Histoire générale et iconographie des Lépidoptères et des chenilles de l'Amérique septentrionale* by Boisduval & Le Conte (1829-[1837]), an early influential book on North American butterflies; Frederick E. Melsheimer (1782-1873), a prominent Pennsylvania entomologist; John Millington (1779-1868), an English civil engineer who lived in Guanajuato, Mexico, from 1829 to 1832 (Tarleton 1966); Thomas Nuttall (1786-1859), an English zoologist and botanist who, during the summer of 1834, crossed the Rocky Mountains and reached the Pacific Ocean in Washington as part of the Wyeth Expedition, then spent the summer of 1835 exploring northern Oregon and southern Washington (Pennell 1936); Charles Pickering (1805-1878), a fellow Philadelphian who participated with Peale as a naturalist for the Wilkes Expedition, during which he explored the interior of Oregon Territory (now Washington, from Puget Sound to Ft. Colville) in 1841 (Barry 1929); Felipe Poey (1799-1891), a celebrated Cuban zoologist; William Rich (1800-1864), a botanist who also participated in the Wilkes Expedition and traveled overland with Peale in 1841 from the Columbia River of Oregon to northern California (Poesch 1961; Eyde 1986); Ramón de la Sagra (1797-1871), a Spanish botanist who lived in Cuba between 1821 and 1835 (Fey & Racine 2000); Thomas Say (1787-1834), a pioneering American entomologist and conchologist; John K. Townsend (1809-1851), an American naturalist who accompanied T. Nuttall on the Wyeth Expedition in 1834 across the Rockies to the Pacific Northwest, then traveled with Nuttall during the summer of 1835 in northern Oregon and southern Washington (Townsend 1839). In addition to adult specimens, some of the larvae that Peale portrayed in his sketchbook were presented by others, including Robert E. Griffith, Jr. (1798-1850), a Philadelphia physician and member of the Academy of Natural Sciences.

Peale also borrowed specimens to illustrate. Some were received from the lepidopterist F. H. Herman Strecker (1836-1901) of Reading, Pennsylvania, and others came from the collections of the Entomological Society of Philadelphia (ESP; founded 1859) and its successor, the American Entomological Society (AES; founded 1867). The latter collection was deposited "in perpetuity" with ANSP in 1915 (Rehn 1959). In 1963, however, ANSP

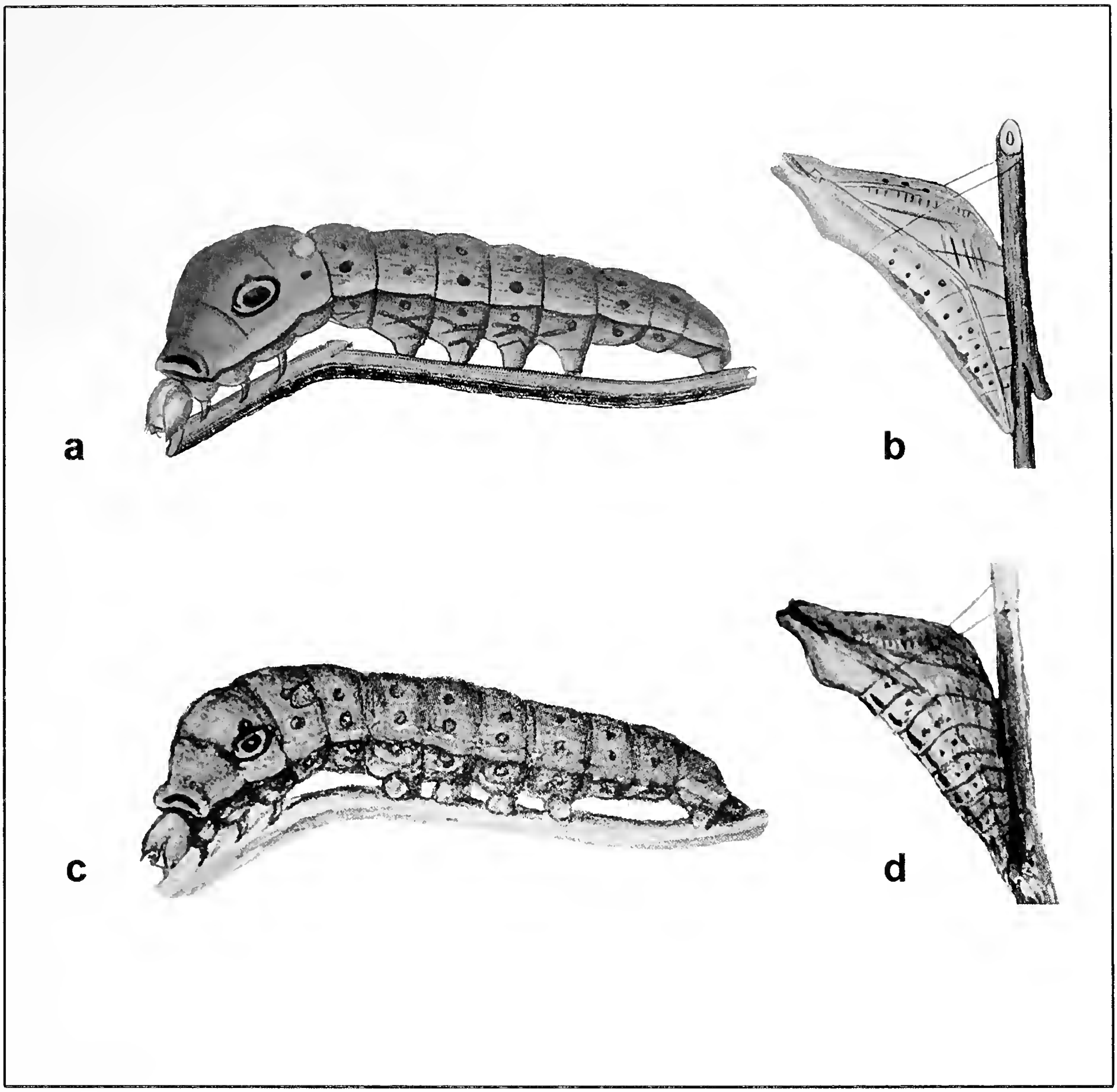


Figure 5. Early stages of *Papilio palamedes*. **a, b**. Figures by John Abbot from Pl. 5 of Boisduval & Le Conte (1829-[1837]); **c, d**. Duplicate figures by Peale for his Pl. XVI (AMNH Library image b1083009_16).

negotiated an exchange of the bulk of its general Lepidoptera collection for the Orthoptera collection at CMNH (Gelhaus et al. 2004). The specimens that Peale figured from the ESP and AES collections were almost certainly sent to CMNH as part of this exchange (J. D. Weintraub pers. comm.). Peale's collection, which was kept at ANSP beginning in 1876 (Stone 1915), was officially presented to the Academy by his second wife, Lucinda Peale, in 1888 (Ridings 1889; Foutch 2011). Some of his specimens, which had been deposited in the general collection at ANSP, were inadvertently sent to CMNH in 1963.

Grimaldi (2015) identifies Peale as "America's first lepidopterist," and bestows him with the distinction of "the first serious American naturalist of Lepidoptera." Although Peale is certainly among the more important early lepidopterists in America, the English naturalist John Abbot (1751-c.1840) is arguably the first American lepidopterist. Though not an American by birth, Abbot spent over sixty years in Georgia, where he reared countless species of Lepidoptera for the first time. He documented their life histories in thousands of illustrations and accompanying notes, many of which stood for nearly two centuries as the only such records for those species. Peale was familiar with Abbot's work and even met him while traveling through Georgia (Edwards 1887-1897). In fact, our analysis of Peale's artwork reveals that he derived at least thirty-six of his figures of larvae, pupae, and food plants in his manuscript "The Butterflies of North America" from Abbot's earlier drawings, as published in Smith & Abbot (1797) (Fig. 4), and especially Boisduval & Le Conte (1929-[1837]) (Fig. 5). Only twice did Peale actually admit to copying figures from these publications, in the text for Plates VI (Fig. 6) and CI. Furthermore, Peale obviously took cues from these publications about which food plants to portray in his butterfly illustrations. Because some of these plants could be found where Peale lived, he was able to incorporate known hosts into illustrations of species that he did not personally rear. The life history information presented in Smith & Abbot (1797) and Boisduval & Le Conte (1929-[1837]) was derived almost exclusively from the drawings and writings of Abbot. Not only did Peale indirectly borrow figures and information from Abbot, he also copied figures of larvae and pupae from other publications, including Macleay (1834) (Pl. CXXVI), Poey (1832) (Pl. XXXIX), Stoll (1787-1790) (Pls. LI, LXXXVI), and Westwood (1834) (Pl. XXXI). In some cases, Peale's depiction of adults from one locality, along with the early stages from another, resulted in the portrayal of two different subspecies on the same plate (e.g. Pl. XXXIV). In the text for Plates XXXI, XCVII, and CXXXIII, Peale also planned to include small illustrations of early stages and food plants, which he traced from figures in Westwood (1834) and Riley (1870, 1876) without attribution.

We also discovered that Peale copied some of his plant figures from published works, particularly the multivolume book on North American trees by the French botanist François André Michaux (1770-1855). Peale began the practice of copying Michaux's figures during the 1830s, when he was working on *Lepidoptera Americana* (Peale 1833). He most likely employed the English edition of Michaux's work, rather than the original French edition, published 1810-1813. The leaves and fruit of sassafras (*Sassafras albidum* (Nuttall) Nees) on Plate 3 of Peale (1833) were derived from Plate 81 of Michaux (1817-1819). For his planned Plate 5 of *Lepidoptera Americana*, Peale duplicated the figure of black gum (*Nyssa sylvatica* Marshall) from Plate 110 of Michaux (1817-1819). For Plates VI, VII, and XCVI (Fig. 6) of his "Butterflies of North America," Peale relied on Michaux's treatise for figures of pawpaw (*Asimina triloba* (Linnaeus) Dunai), willow oak (*Quercus phellos* L.), and devilwood (*Osmanthus americanus* (Linnaeus) Benth. & Hook f. ex A. Gray). For Plate V, Peale adapted the leaf and fruit of *A. triloba* from elements of Plate II of Audubon (1827-1838). He likely copied plants from other publications as well. As a result of such duplication, some of Peale's illustrations are almost entirely derivative, with only the adult butterflies representing original renderings (e.g. Pls. V, VI) (Fig. 6).

Peale apparently infused his illustrations with plagiarized material when it was necessary to convey a more complete story than was possible through his own experiences. He was aging and undoubtedly suffered more difficulties in collecting suitable material to illustrate. He also was lured by the great amount of published material available at ANSP. Surprisingly, Peale criticized other naturalists for similar conduct, arguing that it was "difficult to collect reliable original matter – few persons with time and means are willing to devote themselves to the labor of careful observation . . ." (introduction to "Butterflies of North America," AMNH). One wonders if his choice to incorporate derivative matter ultimately impacted his chances of publishing his opus. Others may have noticed that his work was not entirely original. Nonetheless, borrowing figures from other publications was not unusual during the nineteenth century. Figures from Plates 3 and 4 of *Lepidoptera Americana* (Peale 1833) were copied for Plate 12 of Duncan (1841), which was reproduced as Plate CXVII in Kirby (1897).

Like Abbot, Peale also duplicated his own figures and compositions. Such repetition was a convenient, time-saving practice when rendering figures of the same species (Calhoun 2007). During the preparation of "The Butterflies of North America," Peale repeated some of the figures that he had included on unpublished plates for the anticipated continuation of *Lepidoptera Americana* (Peale 1833). In several instances he repurposed fragments of those unpublished lithographs, clipping the figures out and pasting them onto the plates for his proposed new book (Pls. III, IV, XLIII). He also copied his earlier life history studies for illustrations in "Butterflies of North America."

Although Grimaldi (2015) states that "all the species for which life histories and host plants are

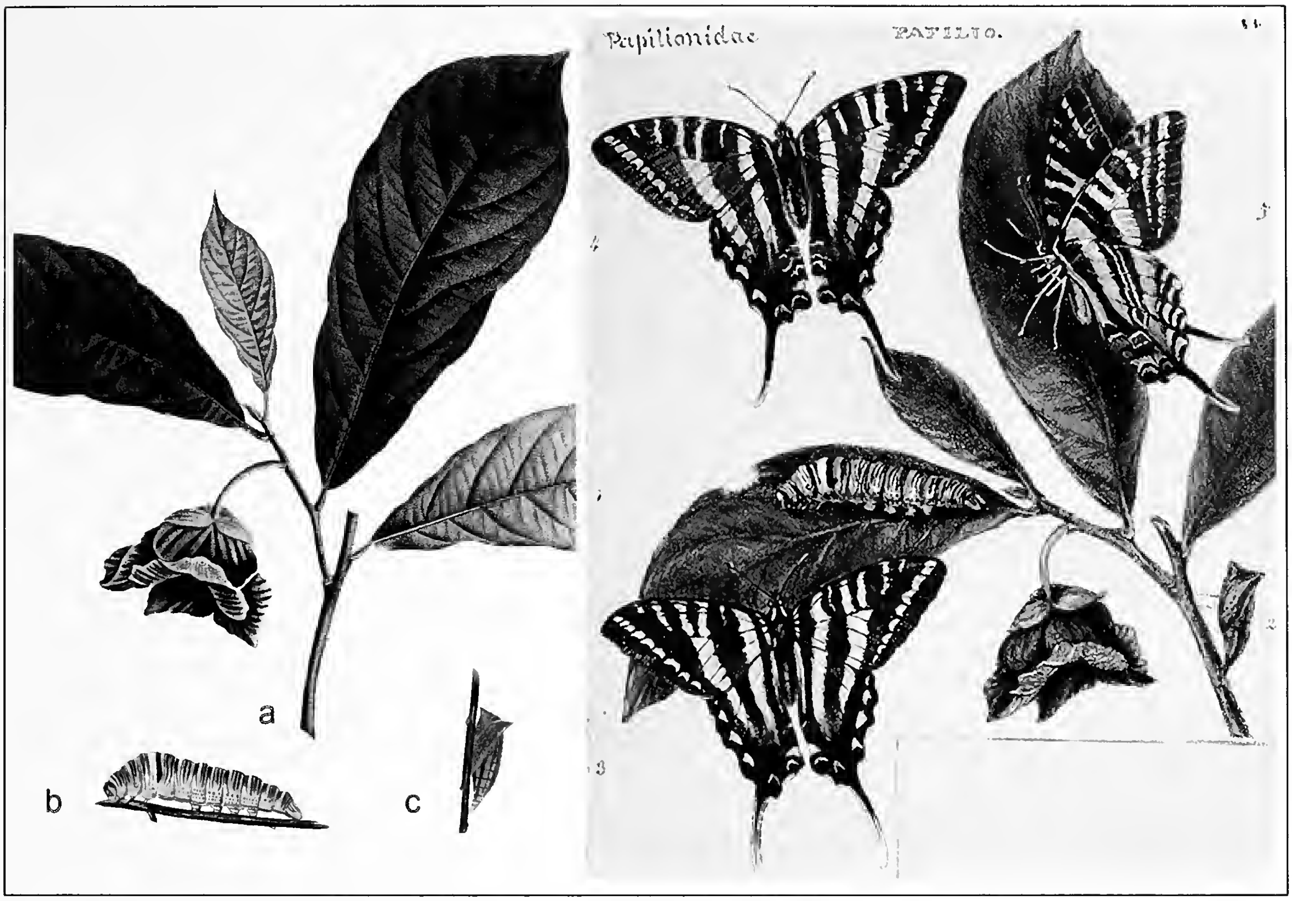


Figure 6. Early stages and food plant of *Eurytides marcellus*. **Left**: **a**. *Asimina triloba* from Pl. 60 of Michaux (1817-1819); **b**, **c**. larva and pupa by John Abbot from Pl. 2 of Boisduval & Le Conte (1829-[1837]) (pupa image reversed). **Right**: Peale's Pl. VI (AMNH Library image b1083009_5).

depicted are those that occur in the eastern United States, gathered in Red Bank and Ocean Grove, New Jersey," this does not take into account the many early stages that Peale derived from secondary sources, as well as his portrayal of species from other regions (e.g. Pls. XXXIX, LV). These previously overlooked aspects of Peale's work do not diminish his contributions, but instead offer valuable insights into his artistic methods and philosophy.

Peale aspired to publish a comprehensive work on North American Lepidoptera based on his illustrations and observations. The year before he died, he explained that his manuscript, "The Butterflies of North America," was the natural continuation of his disappointing *Lepidoptera Americana*: "This is not the labor of a day, but that of a life . . . a labor of love . . . [which doesn't] furnish much nourishment for the body" (Peale 1884). Both of Peale's attempts to publish his ambitious work failed, leaving his dream tragically unfulfilled. A century ago, Stone (1915) lamented, "There is something pathetic in the history of the natural history interests of the Peales . . . there are today no adequate results to stand forth as a monument to the earnest efforts of this notable family." Peale et al. (2015) only partially satisfy this debt, as the decision to omit the entire text of Peale's "lost manuscript" deprives us of his true vision. Not only do Peale's meticulous commentaries place his labors into the proper scientific context, they also remind us that his drawings are more than just images of pretty butterflies and metaphors for rebirth. They symbolize the embodiment of an extraordinary lifetime of discovery. A greater attention to accuracy, and the inclusion of more information, would have elevated Peale et al. (2015) from an eye-catching celebration of Peale's artistic accomplishments to a valuable scientific contribution. Such a fusion of art and science is precisely what Peale intended.

Table 1. Lepidoptera and plants figured in Peale et al. (2015), by page number. Latin names of butterflies follow Pelham (2015) and Warren et al. (2015). English names of butterflies follow NABA (2011-2015) and Warren et al. (2015). Latin and English names of moths follow MPG (2012). Botanical names mostly follow USDA (2015). Localities of figured specimens are from Peale's accompanying text. Unless otherwise noted, the plants figured are known hosts of the associated species of Lepidoptera.

Page no.	Insect species	Plant species	Notes
20.	Tiger Swallowtail, *Papilio glaucus* Linnaeus, 1758	Tuliptree, *Liriodendron tulipifera* Linnaeus	The name used by Peale, *Papilio turnus*, is a junior synonym of the name *P. glaucus*. See drawing on pg. 28.
28	Tiger Swallowtail, *Papilio glaucus* Linnaeus, 1758		Peale conceded that dark females are merely a form of this species, though he erroneously mentions in his notes that "black males are very uncommon." The female portrayed (along with its pupal exuvia) resides in Peale's collection at ANSP (box 1A, nos. 4, 6). It was reared from a larva that Peale found in 1834 at Camden, New Jersey. See drawing on pg. 20.
29	Two-tailed Swallowtail, *Papilio multicaudata* W. F. Kirby, 1884		Hand-colored lithographs cut from an unpublished plate for *Lepidoptera Americana,* printed in 1836 (Fig. 3). The name used by Peale, *Papilio daunus*, is a preoccupied name for this species. He first used the name *multicaudata* in association with the unpublished plate. This name was later published by Kirby (1884) in reference to Peale's plate, making Kirby the accepted author of this name, though it was originally coined by Peale (Brower 1958). The figured specimen, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, resides in Peale's collection at ANSP (box 26, no. 3). The caterpillar of this species is not always scarlet as stated in the published caption. It is green, but becomes more reddish as it approaches pupation. This illustration was figured by Foutch (2011).
30	Pale Swallowtail, *Papilio eurymedon* Lucas, 1852		Hand-colored lithographs cut from an unpublished plate for *Lepidoptera Americana,* printed in 1836, for which he proposed the name *Papilio lewisii* in honor of the American explorer Meriwether Lewis. This name was eventually published by Kirby (1884), but it is a junior synonym of *P. eurymedon.* The figured specimen was collected by Thomas Nuttall in the Rocky Mountains in 1834. Although dos Passos (1965) claimed that the figured specimen was in Peale's collection at ANSP, it is not present.
31	Zebra Swallowtail, *Eurytides marcellus* (Cramer, 1777) (spring fm.)	Pawpaw, *Asimina triloba* (Linnaeus) Dunal	This species does not occur in Cuba as indicated. The name used by Peale, *Papilio ajax*, was suppressed by the ICZN in 1954. The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 1 of Boisduval & Le Conte (1829-[1837]). The plant was adapted from elements of Plate II of Audubon (1827-1838). See drawing on pg. 32.
32	Zebra Swallowtail, *Eurytides marcellus* (Cramer, 1777) (late spring form and summer fm. 'lecontei Rothschild & Jordan, 1906)	Pawpaw, *Asimina triloba* (Linnaeus) Dunal	The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 2 of Boisduval & Le Conte (1829-[1837]) (Fig. 6). In the text for this drawing, Peale admitted that he copied those figures. The two adult specimens portrayed were collected in Georgia by John E. Le Conte. The plant was copied from Plate 60 of Michaux (1817-1819) (Fig. 6). See drawing on pg. 31.
33	Cuban Kite Swallowtail, *Eurytides celadon* Lucas, 1852	Willow oak, *Quercus phellos* Linnaeus	The name used by Peale, *Papilio sinon*, is preoccupied (type material suggests that it applies to *E. marcellus*). Peale's specimens were received from Felipe Poey of Havana, Cuba. The plant is not a host, but was inserted to enhance the composition.
34	Telesilaus Swallowtail, *Protesilaus telesilaus* (C. & R. Felder, 1864) ssp.	Smooth Solomon's seal, *Polygonatum biflorum* (Walter) Elliott	The name used by Peale, *Papilio archesilaus*, now applies to the subspecies *Protesilaus protesilaus archesilaus* (C. & R. Felder, 1865). Peale reportedly collected three specimens of this species in New Grenada (Colombia) during August and September 1832. This species occurs in Central and South America. The plant is not a host, but was inserted to enhance the composition.
35	Giant Swallowtail, *Papilio cresphontes* Cramer, 1777	Plant unidentifiable	The name used by Peale refers to a similar species, *Papilio thoas* Linnaeus, 1771. The figured specimen, collected in 1852 at East Rockport, Ohio, by Jared P. Kirtland, resides in Peale's collection at ANSP (box 18, no. 2). The larva and pupa are based on figures rendered by John Abbot in Georgia, as published on Plate 13 of Boisduval & Le Conte (1829-[1837]).

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
36	Androgeus Swallowtail, *Papilio androgeus epidaurus* Godman & Salvin, 1890	Indian shot, *Canna indica* Linnaeus	The name used by Peale, *Papilio polycaon*, is a junior synonym of the name *P. androgeus* Cramer, 1775. In addition to Central America as indicated in the published caption, the depicted subspecies occurs in Mexico and the Greater Antilles. The hindwing of the female does not accurately portray the multiple tails that are typically present. The plant is not a host, but was added to enhance the composition.
37	Machaonides Swallowtail, *Papilio machaonides* Esper, 1796		The name used by Peale, *Papilio lycoraeus*, is a junior synonym of the name *P. machaonides*. Peale attributed the figured specimen to "St. Domingo" (=Hispaniola).
38	Bahamian Swallowtail, *Papilio a. andraemon* (Hübner, [1823])		The figured specimen was collected by Felipe Poey near Havana, Cuba. This subspecies occurs in Cuba and Jamaica.
39	Black Swallowtail, *Papilio polyxenes asterias* Stoll, 1782	Common rue, *Ruta graveolens* Linnaeus	The early stages were derived from an earlier drawing by Peale, which is reproduced on pg. 244 (second row, far left).
40	Spicebush Swallowtail, *Papilio t. troilus* Linnaeus, 1758	Sassafras, *Sassifras albidum* (Nuttall) Nees	Although it is stated in the published caption that the "forewing marginal spots are depicted as white instead of the actual yellow," these spots vary from white to yellowish. Peale derived the figures of the pupa and one of the larvae from his earlier drawing reproduced on pg. 245 (top row, second from left).
41	Spicebush Swallowtail, *Papilio t. troilus* Linnaeus, 1758, ab. radiatus Strecker 1900		In the text for this drawing, Peale stated that this specimen was collected by a friend at Washington, D.C., in 1847. It was referred to by Strecker (1878, 1900) as "One example in coll. Peale," and "Washington, D.C., Titian R. Peale," respectively. Peale wrote in his collection notes at ANSP (box 40, no. 7) that this specimen was sent to F. H. Herman Strecker in June 1877 in exchange for a specimen of *Urania sloanus* (see entry for the drawing, pg. 138). Strecker's collection catalog at FMNH confirms that this specimen of *P. troilus* was received from Peale.
42	Palamedes Swallowtail, *Papilio p. palamedes* Drury, 1773		The red spots are not exaggerated as stated in the published caption. The figured specimen is from Alabama. The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 5 of Boisduval & Le Conte (1829-[1837]) (Fig. 5). The depicted nominotypical subspecies does not occur in Mexico, where it is replaced by *P. p. leontis* (Rothschild & Jordan, 1906).
43	Magnificent Swallowtail, *Papilio g. garamas* (Geyer, [1829])		The name used by Peale, *Papilio asclepius*, is a junior synonym of the name *P. garamas*. A specimen in Peale's collection at ANSP (box 17, no. 4), collected in Mexico and received from Baron Gerolt in 1846, probably served as the model for these figures. The depicted nominotypical subspecies occurs in Mexico.
44	Pipevine Swallowtail, *Battus p. philenor* (Linnaeus, 1771)	Virginia snakeroot, *Aristolochia serpentaria* Linnaeus	The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 11 of Boisduval & Le Conte (1829-[1837]), who also identified the food plant of this species as *Aristolochia serpentaria*, thereby giving Peale an appropriate (and locally available) host to portray.
45	Fig. 1: De Villiers' Swallowtail, *Battus devilliers* (Godart, [1824]); Fig. 2: Oxynius Swallowtail, *Papilio oxynius* (Geyer, [1827])		Although the published caption states that *B. devilliers* "lives in southern Florida," all known Florida records are dubious. The figured specimen of *B. devilliers* was received from Felipe Poey in Cuba. The specimen of *P. oxynius* (a Cuban species) was from the collection of the American Entomological Society (probably now at CMNH). The published caption on pg. 46 was presumably intended for this page.
46	Fig. 1: White-crescent Swallowtail, *Mimoides t. thymbraeus* (Boisduval, 1836); Fig. 2: Polydamas Swallowtail, *Battus polydamas thyamus* (Rothschild & Jordan, 1906)		The specimen of *M. thymbraeus* was loaned from the collection of the Entomological Society of Philadelphia (probably now at CMNH). The figured specimen of *P. p. thyamus* is from St. Thomas, Virgin Islands, and corresponds to a female in Peale's collection at ANSP (box 61, no. 1), which was collected by Hans B. Hornbeck in 1838. This subspecies occurs in the Virgin Islands and Puerto Rico. The published caption was presumably intended for page 45.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
48	Green-patch Swallowtail, *Battus laodamas copanae* (Reakirt, 1863)		The figured specimen was from the collection of the Entomological Society of Philadelphia (probably now at CMNH). Strecker (1872-1878) mentions this specimen, believing it to be one of only two known at that time (the other being the holotype in Strecker's collection, now at FMNH). The depicted subspecies occurs from Mexico to Costa Rica.
49	Variable Swallowtail, *Mimoides p. phaon* (Boisduval, 1836)		Peale implied that the figured specimens were from Mexico. They were loaned from the collection of the Entomological Society of Philadelphia (probably now at CMNH). This subspecies occurs from Mexico to Panama.
50	True Cattleheart, *Parides eurimedes* (Stoll, 1782) ssp.		The name used by Peale, *Papilio mylotes*, is now applied to a different subspecies of *P. eurimedes* (see drawing on pg. 51). Peale collected the two figured specimens with "one sweep of a net" near Cartagena, Colombia, in 1831 or 1832. This species is distributed from Mexico to South America.
51	True Cattleheart, *Parides eurimedes mylotes* (H. Bates, 1861)		The figured specimens are from Mexico, and were borrowed from the collection of the Entomological Society of Philadelphia (probably now at CMNH). This species is distributed from Mexico to South America.
52	Cuban Cattleheart, *Parides g. gundlachianus* (C. & R. Felder, 1864)		The figured specimens were borrowed from the collection of the Entomological Society of Philadelphia (probably now at CMNH), having been received from Felipe Poey of Havana, Cuba. This illustration was figured by Sellers (1980).
53	Poey's Swallowtail, *Papilio caiguanabus* Poey [1852]		The figured female was borrowed from the collection of the American Entomological Society (probably now at CMNH).
55	Clodius Parnassian, *Parnassius clodius claudianus* Stichel, 1907	Milkweed, *Asclepias* Linnaeus sp.	Peale proposed (but never published) the name "*Parnassius townsendii*" for this species in honor of John K. Townsend, who collected the figured female on "the Columbia River" (Oregon or Washington) in 1835. A discolored female at CMNH from Peale's collection, labeled "Columbia R.," is undoubtedly this specimen. Peale believed that the English entomologist Edward Doubleday had robbed him of his description of this species in 1847 when he named this species *Parnassius smintheus*, the name that Peale used on this plate. Peale should have described the depicted butterfly, as it actually represents a different species, which was not named *P. clodius* until 1855. The plant is not a host, but was inserted to enhance the composition.
56	Caribbean Swallowtail, *Papilio pelaus atkinsi* M. Bates, 1935	Plant unidentifiable	The depicted subspecies occurs in Cuba.
57	Melite Mimic White, *Enantia melite* (Linnaeus, 1763) ssp.	Plant unidentifiable	Peale collected the figured specimens on "the Island of St. Catherine," which refers to Santa Catarina Island off the coast of Brazil. Peale visited this island with the Wilkes Expedition in 1838. This species is distributed from Mexico to South America.
58	Figs. 1-2: Pure-banded Dartwhite, *Catasticta t. teutila* (Doubleday, 1847); Figs. 3-4: Mexican Dartwhite, *Catasticta n. nimbice* (Boisduval, 1836)		The name used by Peale, *Euterpe sebennica* (misspelled "*Sebenica*"), is a junior synonym of the name *teutila* (*Euterpe*). The figured female of this species, acquired in 1846 and identified as "*Euterpe sebenica*" from Mexico, resides in Peale's collection at ANSP (box 17, no. 1). The depicted nominotypical subspecies occurs in central Mexico. The figured specimen of *C. n. nimbice*, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, resides in Peale's collection at ANSP (box 27, nos. 12, 13). This subspecies is distributed from Texas to southern Mexico.
60	Social White, *Eucheira s. socialis* Westwood, 1834		This subspecies occurs in central and southern Mexico. Two specimens in Peale's collection at ANSP (box 27, nos. 19, 20), collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, likely served as the models for this figure. Peale copied the figures of the silk pupal nest from an illustration that accompanied the original description of this species by Westwood (1834, Pl. 6). In the text for this illustration, Peale planned to include figures of the pupa and adult antennae of this species, which he traced from Westwood (1834). In 1883, Peale loaned this illustration to Henry C. McCook, a naturalist and minister in Philadelphia (Foutch 2011).

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
61	Checkered White, *Pontia protodice* (Boisduval & Le Conte, [1830])	Common dandelion, *Taraxacum officinale* F.H. Wiggers	The plant is not a host, but was inserted to enhance the composition.
62	Fig. 1: Pine White, *Neophasia m. menapia* (C. & R. Felder, 1859); Figs. 2-3: Sara Orangetip, *Anthocharis sara* Lucas, 1852 ssp.; Figs. 4-5: Falcate Orangetip, *Anthocharis midea annickae* dos Passos & Klots, 1969; Figs. 6-7: Large Marble, *Euchloe a. ausonides* (Lucas, 1852)	Plant unidentifiable	The figured specimen of *N. menapia* was collected in 1835 on the Columbia River by Thomas Nuttall, who gave it to Peale in 1836. A male *E. ausonides* in Peale's collection at ANSP (box 16, no. 3), identified as "*Anthocaris Olympia*" from Oregon, is undoubtedly the figured specimen of this species. Peale proposed (but never published) the name "*Anthocaris pickeringii*" for this specimen, in honor of Charles Pickering, who had collected it. Peale implied that he collected the figured *A. midea* in Pennsylvania or Virginia. With the exception of *E. ausonides*, Peale previously included these figures on an unpublished lithograph for *Lepidoptera Americana*, printed in 1836 (ANSP).
65	Adults: Great Southern White, *Ascia monuste eubotea* (Godart, 1819); early stages: *Ascia monuste phileta* (Fabricius, 1775)	Probably Spiderwisp, *Cleome gynandra* Linnaeus	The figured specimens were received from Jamaica, and a female at CMNH from Peale's collection, labeled "Jamaica," possibly served as the model for the figured females. Although Peale mentioned that he was unsure of "having seen them in "New Grenada" (Colombia), there is a specimen labeled as such at CMNH from his collection. The larva and pupa in this drawing are based on figures drawn by John Abbot in Georgia, as published on Plate 16 of Boisduval & Le Conte (1829-[1837]), who also identified the food plant of this species as *Cleomes pentaphylla* Linnaeus (=*C. gynandra*), also based on a drawing by Abbot (Calhoun 2004), thus giving Peale an appropriate plant to portray. In his text for this drawing, Peale noted that this African plant was cultivated in local gardens. The subspecies *A. m. eubotea* occurs from Cuba to the Virgin Islands, while the subspecies *A. m. phileta* is found in the southeastern United States and the Bahamas. This illustration was figured by Haifley (1981).
66	Cabbage White, *Pieris r. rapae* (Linnaeus)	Probably winter cress, *Barbarea vulgaris* W. T. Aiton	The specimen portrayed as fig. 4 was possibly part of the type series of *Pieris rapae* var. *immaculata* Skinner & E. Aaron, 1889 (two paratypes from Peale's collection are deposited at ANSP and CMNH). Based on the original description of *immaculata*, Peale's specimens of this form were collected around Philadelphia, Pennsylvania. The early stages were derived from an earlier drawing by Peale, which is reproduced on pg. 245 (bottom row, far right).
68	Florida White, *Glutophrissa drusilla poeyi* (Butler, 1872)	Plant unidentifiable	The figured specimens were collected by Felipe Poey near Havana, Cuba. This subspecies occurs in the Bahamas, Cuba, and the Cayman Islands (not "from Florida to Brazil," as indicated in the published caption). The name used by Peale, *Pieris margarita*, is a nomen nudum and junior synonym of the name *Papilio drusilla* Cramer, 1777.
69	Figs. 1-2: Orange-barred Sulphur, *Phoebis philea huebneri* Fruhstorfer, 1907; Figs. 3-4: Statira Sulphur, *Aphrissa statira cubana* d'Almeida, 1939		The name used by Peale for figures 1 and 2, *Callidryas thalestris*, applies to a different subspecies of *P. philea*. A male *P. p. huebneri* at CMNH from Peale's collection, labeled "Cuba," is a close match to these figures. The figured male *A. s. cubana*, also a Cuban subspecies, was presented to Peale by Thomas Say.
70	Cloudless Sulphur, *Phoebis sennae eubule* (Linnaeus)	Partridge pea, *Chamaecrista fasciculata* (Michaux) Greene	The figured butterflies were collected in Georgia by John E. Le Conte. The subspecies *P. s. eubule* occurs in the eastern United States, Canada, and probably parts of Cuba. Different subspecies occur elsewhere. The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 24 of Boisduval & Le Conte (1829-[1837]), who also identified the food plant of this species as "*Cassia chamaecrista*" (=*Chamaecrista fasciculata*), thereby giving Peale an appropriate (and locally available) host to portray.
72	Orbed Sulphur, *Aphrissa o. orbis* (Poey, 1832)	Pride-of-Barbados, *Caesalpinia pulcherrima* (Linnaeus) Swarz	The figured specimens were received from Felipe Poey of Havana, Cuba. The figures of the early stages are mirror-image reproductions of uncolored figures in Poey (1832), who provided details on their coloration and mentioned the food plant. A discolored adult male *A. orbis* at CMNH, labeled "Cuba" from Peale's collection, was probably also received from Poey. Peale's depiction of *C. pulcherrima* is inaccurate and was possibly copied from another source.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
74	Figs. 1-2: Yellow Angled-Sulphur, *Anteos maerula* (Fabricius, 1775); Figs. 3-4: White Angled-Sulphur, *Anteos clorinde* (Godart, [1824])		The figured specimen of *A. maerula*, collected near Mexico City by Baron Gerolt and given to Peale in 1846, resides in Peale's collection at ANSP (box 17, nos. 7, 8). This species feeds on additional Fabaceae, not just species of *Cassia* as indicated in the published caption. The figured "female" (male) of *A. clorinde*, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, resides in Peale's collection at ANSP (box 28, no. 21).
75	Clouded Sulphur, *Colias p. philodice* Godart, 1819	Red clover, *Trifolium pratense* Linnaeus	The figures at lower right portray a small individual of this species, which Peale misidentified as *Nathalis plauta* E. Doubleday, 1847, a butterfly that occurs in South America. Peale indicated that he caught "*N. plauta*" near Holmesburg, Pennsylvania, on 2 August. The model for these figures, a male at CMNH from Peale's collection labeled "*Nathalis plauta*" was collected 2 August 1876 along Pennypack Creek, Holmesburg (Philadelphia), Pennsylvania. The early stages of *C. philodice* were derived from an earlier drawing by Peale, which is reproduced on pg. 245 (third row, far right).
77	Southern Dogface, *Zerene c. cesonia* (Stoll, 1790)	American wisteria, *Wisteria frutescens* (Linnaeus) Poiret	This species is not montane in nature as indicated in the published caption, but primarily occurs at lower elevations, down to sea level. The figured specimen was collected in Georgia by John E. Le Conte. The depicted nominotypical subspecies ranges from the southern United States and Cuba, southward to Colombia. The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 22 of Boisduval & Le Conte (1829-[1837]), who noted that this species feeds on "*glycine*" (=*Glycine* Willdenow), an Old World genus previously used for species now placed into *Wisteria* Nuttall. This gave Peale an attractive (and locally available) food plant to portray.
78	Sleepy Orange, *Abaeis nicippe* (Cramer, 1779)	American senna, *Senna hebecarpa* (Fernald) Irwin & Barneby	Hand-colored lithograph from *Lepidoptera Americana* (see drawing on pg. 168). Peale personally reared this species and implied that the figured individuals were from Pennsylvania.
79	Little Yellow, *Pyrisitia l. lisa* (Boisduval & Le Conte, [1830])	Partridge pea, *Chamaecrista fasciculata* (Michaux) Greene	The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 19 of Boisduval & Le Conte (1829-[1837]), who identified one of the food plants as "*Cassia*," probably giving Peale the idea to portray the butterfly with the locally available *C. fasciculata*, which was once placed in the genus *Cassia*.
80	Figs. 1-2: Salome Yellow, *Eurema salome jamapa* (Reakirt, 1866); Figs. 3-4: Dina Yellow, *Eurema d. dina* (Poey, 1832)	Plant unidentifiable	The figured specimen of *E. salome*, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, resides in Peale's collection at ANSP (box 28, no. 8). This specimen is identified as "*Terias Mexicana*," the same name that Peale used for these figures, which refers to the similar species *Eurema mexicana* Boisduval, 1836. The subspecies *E. s. jamapa* occurs from the southwestern United States southward to Panama. Peale noted that his specimens of *E. dina* were received from Felipe Poey and Ramón de la Sagra of Cuba. A female of this species at CMNH from Peale's collection was evidently acquired at a later date, as it is labeled "St Dom'go (=Hispaniola) and represents the subspecies *E. d. mayobanex* (M. Bates, 1939).
81	Figs. 1-2: Red Cracker, *Hamadryas amphinome fumosa* (Fruhstorfer, 1915); Figs. 3-4: Guatemalan Cracker, *Hamadryas guatemalena* (H. Bates, 1864) ssp.		The name used by Peale for figures 3 and 4, *Ageronia fornax*, refers to a different species, *Hamadryas fornax* (Hübner, [1823]). Peale found *H. a. fumosa* "not uncommon" in New Grenada" (Colombia) in 1831 or 1832. A specimen of *H. a. fumosa* from Peale's collection at ANSP, labeled "N. Grenada" probably served as the model for these figures.
82	Figs. 1-2: Gray Cracker, *Hamadryas februa ferentina* (Godart, [1824]); Figs. 3-4: Variable Cracker, *Hamadryas feronia* (Linnaeus, 1758) ssp.; Figs. 5-6: Arete Cracker, *Hamadryas arete* (Doubleday, 1847)		Peale identified figures 5 and 6 as *Ageronia arethusa*, which is a preoccupied junior synonym of another species, *Hamadryas laodamia* (Cramer, 1777). The figured specimen of the South American *H. arete* was possibly borrowed from the collection of the Entomological Society of Philadelphia.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
83	Monarch, *Danaus p. plexippus* (Linnaeus, 1758)	Swamp milkweed, *Asclepias incarnata* Linnaeus	Peale's write-up for this illustration is an enlarged version of the text that he had previously published for this species in *Lepidoptera Americana* (Peale 1833, Pl. 7).
84	Queen, *Danaus gilippus berenice* (Cramer, 1779)	Possibly purple milkweed, *Asclepias purpurascens* Linnaeus	Peale possibly collected the figured specimens in the Florida Keys during the winter of 1824-1825. This subspecies is found in the southeastern United States, Bahamas, Cuba, and the Cayman Islands. Other subspecies of *D. gilippus* occur on other West Indian islands, and from the southwestern United States southward to Brazil. The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 39 of Boisduval & Le Conte (1829-[1837]).
85	Adults: Soldier, *Danaus eresimus tethys* W. Forbes, [1944]; Early stages: *Danaus e. eresimus* (Cramer, 1777)		The figured male was collected in Cuba. Peale copied the figures of the larva and pupa (reportedly from Suriname) from Plate 6 of Stoll (1787-1790).
86	Top: Zebra Longwing, *Heliconius charithonia ramsdeni* W. Comstock & F. Brown, 1950; Bottom: Sapho longwing, *Heliconius sapho* (Drury, 1782) ssp.		The depicted subspecies of *H. charithonia* occurs in Cuba. *Heliconius sapho* is distributed from Mexico to South America.
87	Figs. 1-2: Probably Cuban Clearwing, *Greta cubana* (Herrich-Schäffer, 1862); Figs. 3-4: Klug's Clearwing, *Dircenna klugii* (Geyer, 1837)	Golden columbine, *Aquilegia chrysantha* A. Gray	*Dircenna klugii* occurs from the southwestern United States to Central America. Peale noted that the plant, which he identified, "is not given as the food plant of the caterpillar . . . ."
88	Adults: Gulf Fritillary, *Agraulis vanillae incarnata* (N. Riley, 1926); Early stages: Gulf Fritillary, *Agraulis vanillae nigrior* Michener, 1942	Passionflower, *Passiflora* Linnaeus sp.	The figured butterflies most closely resemble the subspecies *A. v. incarnata,* but Peale mentions early stages from the southern United States, which are applicable to *A. v. nigrior.* This illustration was figured by Foutch (2011).
89	Figs. 1-2: Julia Heliconian, *Dryas iulia* (Fabricius, 1775) ssp.; Figs. 3-4: Mexican Silverspot, *Dione moneta poeyii* Butler, 1873		The figured specimen of *D. m. poeyii* was collected by John Millington at Guanajuato, Mexico, and given to Peale in 1835. Peale's collection at ANSP contains two specimens of this species, both collected by Millington, though neither closely match the figured male. This subspecies is distributed from the southwestern United States to Central America.
90	False Fritillary, *Anetia pantheratus clarescens* (A. Hall, 1925)		The figured specimen was collected in Cuba, where this subspecies is restricted.
91	Mexican Fritillary, *Euptoieta hegesia meridiania* Stichel, 1938; Variegated Fritillary, *Euptoieta claudia* (Cramer, 1775)		Incomplete graphite sketches. A specimen of *E. h. meridiania* in Peale's collection at ANSP (box 28, no. 19), collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, likely served as the model for one of the sketches. This subspecies is found from southern Texas to Argentina. The name used by Peale, *Euptoieta mexicana,* does not apply to any known species in this genus. The small slip of paper figured at the bottom of the page refers to Glover (1856), who listed and figured the larva of *E. claudia* under the name "*Argynnis columbina*" (=*Papilio columbina* Fabricius, 1793), a junior synonym of the name *Papilio hegesia* Cramer 1779.
92	Regal Fritillary, *Speyeria i. idalia* (Drury, 1773)	Plant unidentifiable.	A male specimen of this species, collected in 1831 in the vicinity of Philadelphia (box 37, no. 2), is a close match to the figured male. The early stages were derived from an earlier drawing by Peale, which is reproduced on pg. 245 (bottom row, far left). The larvae were probably those found by Peale in New Jersey in 1833.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
93	Diana Fritillary, *Speyeria diana* (Cramer, 1777)	Plant unidentifiable	Peale borrowed the figured specimens from F. H. Herman Strecker in September 1876 ("I was at work on them an hour after their arrival... They will make a beautiful plate"; letter to Strecker dated 23.ix.1876, FMNH). The name "Great Smokies Fritillary" as used in the published caption, is not generally used for this popular species. Despite the comment that this species has "become quite rare," it is still locally common. Perhaps this statement was meant for *S. idalia* (see drawing on pg. 92), which is virtually extinct east of the Mississippi River.
94	Great Spangled Fritillary, *Speyeria cybele cybele* (Fabricius, 1775).		
95	Probably Variable Checkerspot, *Euphydryas c. chalcedona* (Doubleday, [1847]) or Snowberry Checkerspot, *Euphydryas colon* (W. H. Edwards, 1881)		Peale proposed the name "*Melitaea latercolor*" for this species in 1833, but did not publish it. Peale's collection at ANSP (box 15, no. 15) contains a specimen of *Euphydryas editha* (Boisduval, 1852) from "Oregon" (Washington), received from Charles Pickering (presumably collected in 1841), which is identified as "*Melitaea latercolor*," thus he obviously confused these similar species. *Euphydryas colon* occurs in Oregon and southwestern Washington. Peale previously included these figures on an unpublished lithograph for *Lepidoptera Americana*, printed in 1836 (ANSP).
96	Crimson Patch, *Chlosyne j. janais* (Drury, 1782)		The figured specimen, collected near Mexico City by Baron Gerolt and given to Peale in 1851, resides in Peale's collection at ANSP (box 16, no. 21). The depicted nominotypical subspecies occurs from Texas to Colombia. Peale obviously intended to include an unknown species of *Eurema* Hübner [1819], which he dubbed "*paulus*." No species of Pieridae is currently known by this name.
97	Eastern Comma, *Polygonia comma* (T. Harris, 1841)	Stinging nettle, *Urtica dioica* Linnaeus	The name used by Peale, *c-album*, refers to the similar European species *Polygonia c-album* (Linnaeus, 1758), which was used for *P. comma* until this species was described in 1841. The figured males were reared from larvae that Peale found in 1875 near Holmesburg (Philadelphia), Pennsylvania.
98	Mourning Cloak, *Nymphalis a. antiopa* (Linnaeus, 1758)	Willow, *Salix* Linnaeus sp.	Peale implied that the figured individuals were from Pennsylvania. This species occurs from Alaska southward to central Mexico, and is native to Eurasia, though not all these populations are applicable to the nominotypical subspecies as portrayed.
100	Red Admiral, *Vanessa atalanta rubria* (Fruhstorfer, 1909)	Stinging nettle, *Urtica dioica* Linnaeus	The nominotypical subspecies occurs in Europe, Eurasia, and northern Africa.
101	Painted Lady, *Vanessa cardui* (Linnaeus, 1758)	Probably bull thistle, *Cirsium vulgare* (Savi) Tenore.	
102	American Lady, *Vanessa virginiensis* (Drury, 1773)	Sweet everlasting, *Pseudognaphalium obtusifolium* (Linneaus) Hilliard & B.L. Burtt	It is stated in the published caption that the red ventral coloration is exaggerated, but these markings vary from orange, to pink, to red, and can be quite vivid on fresh specimens. This illustration was figured by Poesch (1961).
103	Common Buckeye, *Junonia c. coenia* Hübner, [1822]	Canada toadflax, *Nuttallanthus canadensis* (Linnaus) D.A. Sutton	The depicted nominotypical subspecies occurs in the eastern United States and Cuba.
104	Top: White Peacock, *Anartia jatrophae guantanamo* Monroe, 1942; Bottom: Cuban Peacock, *Anartia chrysopelea* Hübner, [1831]		The figured specimen of *A. j. guantanamo* was collected by Ramón de la Sagra near Havana, Cuba. This subspecies occurs in Florida, the Bahamas, Cuba, and the Turks & Caicos. The figured specimen of *A. chrysopelea* was taken near Havana, Cuba. The name used by Peale refers to a closely related species that occurs on Hispaniola, *Anartia lytrea* (Godart, 1819).
105	Top: Banded Peacock, *Anartia fatima fatima* (Fabricius, 1793); Bottom: Red Peacock, *Anartia amathea amathea* (Linnaeus, 1758)	Plant unknown (imaginary?)	*Anartia fatima* occurs southward into South America. *Anartia a. amathea* is found from Central America to Argentina, and in the Lesser Antilles.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
106	Top: Florida Purplewing, *Eunica tatila tatilista* (Kaye, 1926); Bottom: Dingy Purplewing, *Eunica monima* (Stoll, 1872)	Plant unidentifiable	The figured specimens of *E. t. tatilista* were collected in Cuba. This subspecies occurs in southern Florida and the Greater Antilles. *Eunica monima* is distributed from the southern United States southward to Venezuela, including the Greater Antilles. The names used by Peale apply to similar South American species: *Myscelia hyperipte* is a junior synonym of *Eunica culvierii* Hubner [1823] and *M. orphyse* refers to *Eunica orphise* (Cramer, 1775).
107	Dirce Beauty, *Colobura dirce wolcotti* Comstock, 1942		The depicted subspecies occurs in the Greater Antilles. The sketches of larva and pupa below the illustration on pg. 112 were likely intended for this drawing. Peale copied those figures from Plate 2 (figs. 3.A and 3.B) of Stoll (1787-1790), which portray the early stages of *Colobura annulata* Willmott, Constantino & J. Hall, 2001 from Suriname (Gernaat et al. 2012). Peale characterized the early stages and mentioned Stoll in his text for *C. dirce.*
108	Top: White-rayed Checkerspot, *Chlosyne ehrenbergii* (Geyer, [1833]); Bottom (figs. 1, 3): Caribbean Banner, *Lucinia sida sida* (Hübner, [1823]); Bottom (fig. 2): Caribbean Banner, *Lucinia sida torrebia* (Ménétrés, 1832)		The figured specimen of *C. ehrenbergii*, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, resides in Peale's collection at ANSP (box 26, no. 6). Two subspecies of *L. sida* appear to be portrayed: the nominotypical subspecies occurs in Cuba, while *L. s. torrebia* is found on Hispaniola. The name used by Peale applies to a related Jamaican species, *Lucinia cadma* (Drury, 1773). Peale evidently also intended to figure a species identified as *Eubagis dyonis* (=*Dynamine dyonis* Geyer, 1837) from a specimen that he collected in "N[ew] Grenada" (Colombia) in 1831 or 1832, but that species (as currently recognized) does not occur in South America.
109	Figs. 1-2: Many-banded Daggerwing, *Marpesia chiron* (Fabricius, 1775); Bottom: Antillian Daggerwing, *Marpesia e. eleuchea* Hübner, 1818		The depicted subspecies *M. e. eleuchea* occurs in the Greater Antilles.
110	Viceroy, *Limenitis a. archippus* (Cramer, 1775)	Willow, *Salix* Linnaeus sp.	This is the predominant subspecies in eastern North America. A female in Peale's collection at ANSP (box 84, specimen 11), collected at Holmesburg (Philadelphia), Pennsylvania, during September 1875, likely served as the model for these figures. The name used by Peale, *Limenitis disippus*, is an amended form of the name *disippe* Godart, 1824 (*Nymphalis*), which is a junior synonym of the name *archippus* (*Papilio*).
112	Adults: Malachite, *Siproeta stelenes biplagiata* (Fruhstorfer, 1907); Early stages: New Beauty, *Colobura annulata* Willmott, Constantino & J. Hall, 2001		The figured adult specimen was collected in Cuba. Peale copied the penciled images of the larva and pupa at the bottom of the page from Plate 2 (figs. 3.A and 3.B) of Stoll (1787-1790), which portray the early stages of *C. annulata* from Suriname (Gernaat et al. 2012). This sketch was intended for the illustration on pg. 107, which portrays *Colobura dirce wolcotti.*
113	Red-spotted Purple, *Limenitis arthemis astyanax* (Fabricius, 1775)	*Vaccinium stamineum* Linnaeus	Two specimens (male and female) in Peale's collection at ANSP (box 37, nos. 17, 18), which he collected in the vicinity of Philadelphia, Pennsylvania, in 1831, undoubtedly served as the models for the figures. This drawing borrows elements from an earlier composition of this species by John Abbot, as portrayed on Plate 10 in Smith & Abbot (1797), a publication cited in Peale's text for this drawing (Fig. 4). Peale also stated that the food plant of this species in the southern United States is *V. stamineum*, clearly in reference to Smith & Abbot (1797). However, he modified the leaves to have toothed margins, which is inconsistent with this plant. The figures of the larva and pupa were probably also based on Abbot's figures in Smith & Abbot (1797).
114	Top: White admiral, *Limenitis a. arthemis* (Drury, 1773); Bottom: Arizona Sister, *Adelpha eulalia* (E. Doubleday, [1848])		The figured specimen of *A. eulalia*, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, resides in Peale's collection at ANSP (box 27, no. 5).

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
115	Top: Iphicleola Sister, *Adelpha iphicleola* (H. Bates, 1864) ssp.; Bottom: Lorquin's Admiral, *Limenitis lorquini* Boisduval, 1852 ssp.		Peale previously included these figures on an unpublished lithograph for *Lepidoptera Americana*, printed in 1836 (ANSP). Although the published caption states that the figured *L. lorquini* is from California, Peale did not indicate its origin. This species is distributed from British Columbia south to Baja California, and east to Montana and Idaho.
116	Male: Karwinski's Beauty, *Smyrna karwinskii* Geyer, [1833]; Female: Blomfild's Beauty, *Smyrna b. blomfildia* (Fabricius, 1781)		The figured male, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, resides in Peale's collection at ANSP (box 26, no. 1). Peale's text for this drawing indicates that the figured female of *S. b. blomfildia* is from Porto Algre, Brazil. This subspecies occurs in South America.
117	Orion Cecropian, *Historis odius odius* (Fabricius, 1775)		The figured specimen was collected near Havana, Cuba.
118	Tailed Cecropian, *Historis acheronta semele* (M. Bates, 1939)		The figured specimens were collected by Ramón de la Sagra near Havana, Cuba. The depicted subspecies occurs in Cuba and on Hispaniola.
119	Silver Emperor, *Doxocopa laure druryi* (Hübner, [1825])	Devilwood, *Osmanthus americanus* (Linnaeus)	The depicted subspecies occurs in Cuba. The plant, which is not a host of this butterfly, was copied from Plate 86 of Michaux (1817-1819).
120	Figs. 1-2: Cuban Leafwing, *Memphis e. echemus* (Doubleday, [1849]); Fig. 3: Hispaniolan Leafwing, *Memphis verticordia* (Hübner, [1831]); Fig. 4: probably Florida Leafwing, *Anaea t. troglodyta* (Fabricius, 1775); Figs. 5-6: Tropical Leafwing, *Anaea aidea* (Guérin-Méneville, [1844])	Plant unidentifiable	The figured specimen of *M. echemus* was collected near Havana, Cuba (this species is endemic to Cuba). The specimen of *M. verticordia* was reportedly captured at "San Domingo" (=Hispaniola, where this species is endemic). The nominotypical subspecies of *A. troglodyta* occurs on Hispaniola, but this species is not found in Central America as indicated in the published caption. A female *A. aidea* in Peale's collection at ANSP (box 28, no. 22), collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, likely served as the model for figures 5 and 6. In the text for this illustration, Peale planned to include a small rendering of the early stages of a related species, *Anaea andria* Scudder 1875, which he traced from figures in Riley (1870). Peale believed this represented the same species as the butterflies shown in figs. 4-6.
121	Glossy Daggerwing, *Marpesia furcula* (Fabricius, 1793) ssp.		The name used by Peale, *Paphia iole* [=*Marpesia iole* (Fabricius, 1782)], is a preoccupied name that was previously employed to define populations of this species with a dorsal purple sheen.
122	Red-striped Leafwing, *Siderone galanthis nemesis* (Illiger, 1801)	Plant unidentifiable	The name used by Peale, *Siderone ide*, is a junior synonym of the name *nemesis* (*Papilio*). The depicted subspecies occurs in Cuba, Puerto Rico, and on Hispaniola.
123	Little Wood-Satyr, *Megisto c. cymela* (Cramer, 1777)	Probably perennial quaking grass, *Briza media* Linnaeus	The name used by Peale, *Neonympha eurytrus*, is generally considered to be a junior synonym of the name *cymela* (*Papilio*). Peale based the larva and pupa on figures drawn by John Abbot in Georgia, as published on Plate 61 in Boisduval & Le Conte (1829-[1837]). Though not documented, this plant may serve as a host.
124	Southern Pearly-eye, *Lethe p. portlandia* (Fabricius, 1781)	Giant cane, *Arundinaria gigantea* (Walter) Mulhlenberg	The figured adults are from Alabama. The larva, pupa, and food plant are based on figures drawn by John Abbot in Georgia, as published on Plate 58 of Boisduval & Le Conte (1829-[1837]). Peale admitted that he copied these figures.
126	Probably Eyed Brown, *Lethe e. eurydice* (Linnaeus, 1763)	Possibly slimstem reedgrass, *Calamagrostis stricta* (Timm) Koeler	The name used by Peale, *Neonympha canthus*, is a junior synonym of the name *eurydice* (*Papilio*). Peale's figures also suggest a similarity with *Lethe a. appalachia* R. Chermock, a species that was not described until 1947. However, the overall appearance agrees with *L. eurydice*. The plant may also suggest *L. eurydice*, as *C. stricta* grows in open wetlands, not forested swamps where *L. appalachia* is found. This grass is not, however, a host of either of these sedge-feeding butterflies.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
127	Adults: Georgia Satyr, *Neonympha areolatus septentrionalis* W. Davis, 1924; Early stages: *Neonympha a. areolatus* (J. E. Smith, 1797)	Indiangrass, *Sorghastrum nutans* (Linnaeus) Nash	The name used by Peale, *Neonympha phocion*, is a preoccupied name that was once used for *N. areolatus*. *Hermeuptychia hermes* (Fabricius, 1775), as mentioned in the published caption, does not occur in the United States as previously believed (Cong & Grishin 2014). Some authors consider *septentrionalis* to represent a subspecies of a recently recognized species, *Neomympha helicta* (Hübner, 1808). The larva and pupa are based on figures drawn by John Abbot in Georgia, as published on Plate 63 of Boisduval & Le Conte (1829-[1837]) and/or the duplicates on Plate 13 of Smith & Abbot (1797). The latter authors portrayed this species in association with *S. nutans*, probably giving Peale the idea to depict this plant as the host.
128	Gemmed Satyr, *Cyllopsis gemma gemma* (Hübner, [1809])	Possibly crabgrass, *Digitaria sanguinalis* (Linnaeus) Scopoli	Although it is indicated in the published caption that these figures do not match *C. gemma*, they are recognizable as this very distinctive species. The larva and pupa were based on figures drawn by John Abbot in Georgia, as published on Plate 62 of Boisduval & Le Conte (1829-[1837]). Though not documented, this plant could serve as a host.
129	Figs. 1-2: Common Alpine, *Erebia epipsodea epipsodea* A. Butler, 1868; Figs. 3-6: Confused Calisto, *Calisto confusa* Lathy, 1899		The name used by Peale, *Erebia blandina*, is a junior synonym of the Old World species *Erebia aethiops* (Esper, 1777). The figured female *E. epipsodea*, reportedly collected in 1841 by Charles Pickering near Mt. Rainier in "Washington Territory," probably corresponds to a female from "Oregon" in Peale's collection at ANSP (box 16, no. 19). The name that Peale used for *C. confusa* refers to a similar Cuban species, *Calisto herophile* Hubner, 1823. The specimens of *C. confusa* were from "the island of Santo Domingo" (=Hispaniola, where this species is endemic).
130	Adults: Common Wood-nymph, *Cercyonis pegala alope* (Fabricius, 1793); Early stages: Common Wood-nymph, *Cercyonis pegala pegala* (Fabricius, 1775)	Possibly Kentucky bluegrass, *Poa pratensis* Linnaeus	The figured adult specimens were captured on the coast of New Jersey. The larva, pupa, and food plant are based on figures drawn by John Abbot in Georgia, as published on Plate 59 of Boisduval & Le Conte (1829-[1837]). These subspecies of *C. pegala* are restricted to the eastern United States, with *C. p. alope* occurring in the northeast and *C. p. pegala* in the southeast.
131	Figs. 1-2: Common Wood-Nymph, *Cercyonis pegala boopis* (Behr, 1864); Fig. 3: Great Basin Wood-Nymph, *Cercyonis sthenele sineocellata* Austin & J. Emmel, 1998 ; Figs. 4-5: Common Wood-Nymph, *Cercyonis pegala ariane* (Boisduval, 1852)		The figured female of *C. p. boopis* was reportedly taken in California. A battered specimen of this subspecies in Peale's collection at ANSP (box 16, no. 8), collected by William Rich in California in 1841, probably served as the model for these figures. The figured "male" (female) specimen of *C. s. sineocellata* was collected in 1841 in the "interior of Washington Territory." A female of this taxon in Peale's collection at ANSP (box 16, no. 7), collected by Charles Pickering in the interior of "Oregon" (Washington), likely served as the model for this figure. The figured specimen of *C. p. ariane* was collected by John K. Townsend on the Columbia River (Oregon or Washington in 1835). Peale associated *C. p. boopis* and *C. s. sineocellata* as the male and female of the same species.
132	Top: Red Satyr, *Megisto rubricata pseudocleophes* L. Miller. 1976; Middle: Jamaican Calisto, *Calisto zangis* (Fabricius, 1775); Bottom: Sugar cane Calisto, *Calisto p. pulchella* Lathy, 1899		The figured *M. r. pseudocleophes*, collected at Guanajuato, Mexico, by John Millington and given to Peale in 1835, resides in Peale's collection at ANSP (box 27, no. 23). This specimen is identified as "*Calisto quadralinea*," a name proposed (but not published) by Peale. *Megisto r. pseudocleophes* occurs in central and southern Mexico. The figured *C. zangis* are from Jamaica, where this is species is endemic.
133	Probably Common Ringlet, *Coenonympha tullia insulana* McDunnough, 1928		The name used by Peale, *Coenonympha california* refers to the subspecies *C. tullia california* Westwood, [1851]. Peale noted that specimens of this butterfly were included in his museum, within Case 27 of Oregon and Rocky Mountain species. This figure does not represent *C. t. california* if the specimen was collected in Oregon or the Rocky Mountains. Peale's box containing "*Coenonympha californica*" is missing from his collection at ANSP, but the specimen was most likely collected in Washington in 1841 by Charles Pickering. The subspecies *C. t. insulana* occurs from southwestern British Columbia to Oregon. Peale previously included these figures on a trial lithograph for Lepidoptera Americana, printed in 1836 (ANSP). On this lithograph, the species was erroneously identified as "*Thecla flavascens*," a name that Peale apparently proposed for a species of Lycaenidae.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
134	Banded Owl-Butterfly, *Caligo atreus dionysos* Fruhstorfer, 1912		Unpublished, hand-colored lithograph originally printed for *Lepidoptera Americana* in 1836. This subspecies occurs in Central America. See lithograph on pg. 158.
135	Atala, *Eumaeus atala* (Poey, 1832)		Peale's box containing a male *E. atala* is missing from ANSP. This is more of a hairstreak than a "blue" as mentioned in the published caption. Rather than being "quite rare" in southern Florida as stated in the caption, this species is locally common in the southeastern part of the state around landscape plantings of its food plants (*Zamia* Linnaeus spp.). This is the only species of Lycaenidae included among this set of Peale's drawings.
136	Urania Moth, *Urania boisduvalii* Guérin, 1829	Cob-nut, *Omphalea triandra* Linnaeus	The figured specimen was collected in Cuba by Felipe Poey. The name used by Peale, *Urania fernandinae*, is a junior synonym of the name *U. boisduvalii*. Peale copied the early stages and plant entirely from a plate that accompanied the original description of *U. fernandinae* by Macleay (1834). This illustration was figured by Foutch (2011).
137	Urania Swallowtail Moth, *Urania fulgens* Walker, 1854	Liliaceae sp.?	Peale collected the figured specimen along the Magdalena River in Colombia, probably during August or September 1832. The plant is not a host, but was added to enhance the composition. This illustration was figured by Poesch (1961).
138	Sloan's Urania, *Urania sloanus* (Cramer, 1776)		The figured specimen from Peale's collection, labeled "Jamaica West Indies," is deposited at ANSP (it was subsequently remounted). It was acquired in 1877 from F. H. Herman Strecker in exchange for an aberrant specimen of *Papilio troilus* (see drawing on pg. 41).
139	Silver-spotted Skipper, *Epargyreus c. clarus* (Cramer, 1775)	American wisteria, *Wisteria frutescens* (Linnaeus) Poiret	Interestingly, Peale does not mention *Wisteria* in his notes for this illustration. See drawing on pg. 175.
140	Wild Indigo Duskywing, *Erynnis baptisiae* (W. Forbes, 1936)	Wild indigo, *Baptisia tinctoria* (Linnaeus) R.Brown	The name used by Peale, *juvenalis*, refers to *Erynnis juvenalis* (Fabricius, 1793), a widespread North American species. This illustration, and the early stages on pgs. 234 and 235, are the earliest known depictions of *E. baptisiae*.
141	Yucca Giant-Skipper, *Megathymus y. yuccae* (Boisduval & Le Conte, [1837])	Probably aloe yucca, *Yucca aloifolia* Linnaeus, or mound-lily yucca, *Yucca gloriosa* Linnaeus	The figured specimens were borrowed in November 1877 from F. H. Herman Strecker (letter dated 19.x.1877, FMNH). Based on the life history of this species published by Riley (1876), Peale mentions both *Y. aloifolia* and *Y. gloriosa* in his text for this illustration. Peale planned to include several small illustrations within the text for this species, all of which were traced from figures in Riley (1876). In fact, it was Riley's publication that prompted Peale to illustrate this species.
142	Cecropia Moth, *Hyalophora cecropia* (Linnaeus, 1758).		This illustration was figured by Foutch (2011).
143	Ailanthus Silkmoth, *Samia c. cynthia* (Drury, 1773)	Tree of heaven, *Ailanthus altissima* (Miller) Swingle	Adults that emerged from these cocoons, collected by G. H. Parker on 16 October 1879 at Philadelphia, Pennsylvania, are in Peale's collection at ANSP (box 79, nos. 4, 5) (emerged 12 June 1880).
144	Figs. 1-3: Grapevine Epimenis Moth, *Psychomorpha epimenis* (Drury, 1782); Figs. 4-6: Eight-spotted Forester Moth, *Alypia octomaculata* (Fabricius, 1775); Bottom: Two-spotted Forester Moth, *Alypiodes bimaculata* (Herrich-Schäffer, 1853)		A specimen of *P. epimenis* in Peale's collection at ANSP (box 21, no. 18), collected by F. E. Melsheimer in York Co., Pennsylvania, may have served as the model for these figures. Peale captured the figured adult specimen of *A. octomaculata* at Brooklyn, New York. The figured male *A. bimaculata*, captured in Mexico and received from Baron Gerolt in 1846, resides in Peale's collection at ANSP (box 17, no. 6). Peale intended to describe this species as "*Agarista geroltii*" in honor Gerolt. This species occurs from the southwestern United States to southern Mexico. Peale considered these species to represent butterflies, not moths.
145	Milkweed Tussock Moth, *Euchaetes egle* (Drury, 1773)	Common milkweed, *Asclepias syriaca* Linnaeus	See drawing on pg. 185, which notes that the figured larva was found at Red Bank, New Jersey.
146	Ornate Bella Moth, *Utetheisa ornatrix* (Linnaeus, 1758)	Probably arrowhead rattlebox, *Crotalaria sagittalis* Linnaeus	The name used by Peale, *Deioeia bella*, is a junior synonym of the name *ornatrix* (*Phalaena*). This illustration is dated 1875 and his notes imply that the figured individuals are from Pennsylvania. His collection at ANSP (box 25) contains many specimens that he collected in 1875 at Holmesburg (Philadelphia), Pennsylvania.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
148	White adults and larva: Unexpected Cycnia Moth, *Cycnia inopinatus* (H. Edwards, 1882); Gray adult: Delicate Cycnia Moth, *Cycnia tenera* (Hübner, 1818)	Milkweed, *Asclepias* Linnaeus sp.	The name used by Peale, *Spilosoma collaris*, refers to a different species, *Cycnia collaris* (Fitch, 1857). The name used in the published caption, *Cycnia antica*, is a junior synonym of the name *tenera* (*Hypercombe*). *Cycnia inopinatus* is found mostly in the eastern United States, while *C. tenera* occurs westward to California and British Columbia. See drawing on pg. 184, which notes that the figured larva was found at Red Bank, New Jersey.
149	Probably Black-waved Flannel Moth, *Lagoa crispata* (Packard, 1864)	Sweet fern, *Comptonia peregrina* (Linnaeus) Coulter, and *Rubus* Linnaeus sp.	See drawing on pg. 224, which notes that these larvae were found in Red Bank, New Jersey. *Comptonia* is not a documented host of this species, but other species of Myricaceae are fed upon.
150	Armyworm Moth, *Mythimna unipuncta* (Haworth, 1809)	Timothy, *Phleum pratense* Linnaeus	At least one adult that resulted from the larvae in these drawings resides in Peale's collection at ANSP (box 76, no. 27), collected at Red Bank, New Jersey (emerged 27 June 1880). In his notes for this drawing, Peale identified the grass as timothy.
151	Pandorus Sphinx Moth, *Eumorpha pandorus* (Hübner, 1821)	Virginia creeper, *Parthenocissus quinquefolia* (Linnaeus) Planchon	The name used by Peale refers to the species *Eumorpha satellitia* (Linnaeus, 1771), which is a Neotropical species. The early stages in this drawing, dated 1880, were derived from Peale's figures on pg. 203, which were rendered in 1833. A pupal exuvia and an adult moth in Peale's collection at ANSP (box 22, nos. 11, 12) are from the same batch of larvae as those portrayed, which produced adults in June 1834. This species is found over much of the eastern United States.
152	Genista Broom Moth, *Uresiphita reversalis* (Guenée, 1854)	Wild indigo, *Baptisia tinctoria* (Linnaeus) R.Brown	Moths that resulted from larvae portrayed in this drawing, collected at Red Bank, New Jersey, are deposited in Peale's collection at ANSP (box 78, nos. 17-34) (emerged July 1880). This species ranges over much of the United States southward into Mexico and the Greater Antilles.
153	Imperial Moth, *Eacles imperialis* (Drury, 1773)	Sweetgum, *Liquidambar styraciflua* Linnaeus	The larvae in this composition are derived from Peale's drawings on pgs. 222 and 223. One of these larvae was found in Washington Heights, New York in September 1879. The other was found in late 1833, probably around Philadelphia, Pennsylvania.
154	Possibly White-marked Tussock Moth, *Orgyia leucostigma* (J. E. Smith, 1797)		The adults are very poor representations, making their identification difficult.
155	Major Datana Moth, *Datana major* Grote & Robinson, 1866	Piedmont staggerbush, *Lyonia mariana* (Linnaeus) D. Don	Hand-colored lithograph, probably created in 1880 (see drawing on pg. 202). The name used by Peale, *Datana ministra*, refers to another species, *Datana ministra* (Drury, 1773). An adult moth in Peale's collection at ANSP (box 22, no. 25), reared in 1833, probably served as the model for the outstretched figure. This species is found over much of the eastern United States. This illustration was figured by [Skinner] (1892).
158	Banded Owl-Butterfly, *Caligo atreus dionysos* Fruhstorfer, 1912		Unpublished lithograph for *Lepidoptera Americana*, printed in 1836. The name used by Peale, *Morpho iris*, is a junior synonym of the name *Morpho atreus* Kollar, 1850. This subspecies occurs in Central America. See lithograph on pg. 134.
159	Top: Tiger Swallowtail, *Papilio glaucus* Linnaeus, 1758. Middle: Elderberry Borer Beetle, *Desmocerus palliatus* (Forster, 1771)		Unpublished hand-colored lithograph.
160	Promethea Moth, *Callosamia promethea* (Drury, 1773)	Sassafras, *Sassifras albidum* (Nuttall) Nees	Published hand-colored lithograph. The plant was derived from Plate 81 of Michaux (1817-1819). Figures from this illustration were copied by J. O. Westwood for Plate 12 of Duncan (1841), which was reproduced for Plate CXVII of Kirby (1897).
162	Promethea Moth, *Callosamia promethea* (Drury, 1773)		Published hand-colored lithograph. The dorsal figure and cocoon were copied by J. O. Westwood for Plate 12 of Duncan (1841), which was reproduced for Plate CXVII of Kirby (1897).

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
163	Regal Moth, *Citheronia regalis* (Fabricius, 1793)	Black gum, *Nyssa sylvatica* Marshall	Unpublished hand-colored lithograph. The plant was copied from Plate 110 of Michaux (1817-1819).
164	Io Moth, *Automeris io* (Fabricius, 1775)	Willow, *Salix* Linnaeus sp.	Published hand-colored lithograph.
165	Monarch, *Danaus p. plexippus* (Linnaeus, 1758)	Swamp milkweed, *Asclepias incarnata* Linnaeus	Published hand-colored lithograph. See drawing on pg. 83.
166	Sleepy Orange, *Abaeis nicippe* (Cramer, 1779)	American senna, *Senna hebecarpa* (Fernald) Irwin & Barneby	Unpublished hand-colored lithograph. See lithograph on pg. 78. Peale mistakenly applied the wrong name to this plate, calling the species "*Xanthidia Lisa*," which refers to *Pyrisitia lisa* (Boisduval & Le Conte, [1830]).
167	Large Maple Spanworm Moth, *Prochoerodes lineola* (Goeze, 1781)	Possibly Canada germander, *Teucrium canadense* Linnaeus	Unpublished hand-colored lithograph. See drawing on pg. 182. The name "*Geometra domestica*" used by Peale was of his own making; no such genus or species name is known. Plants of the mint family (Lamiaceae) are not documented hosts of this moth, but it feeds on a wide variety of plants from many families.
168	Zebra Caterpillar Moth, *Melanchra picta* (Harris, 1841)	American sycamore, *Platanus occidentalis* Linnaeus	Unpublished hand-colored lithograph. See drawing on pg. 187, which notes that the larva was found in 1833 near Kaighn's Point, New Jersey. The name *zebra* as used by Peale refers to the appearance of the larva. Peale's collection at ANSP (box 8, no. 3) contains the adult that was reared from the larva portrayed in this drawing (emerged 2 September 1833). His collection also contains two pupal exuviae that resulted from larva reared at that time (box 8, no. 2; box 20, no. 25), including one wrapped in a sycamore leaf, as depicted at the bottom of this illustration. Although sycamore does not appear to be a previously documented food plant, this evidence suggests that it indeed serves as a host.
170	Buck Moth, *Hemileuca maia* (Drury, 1773)	White oak, *Quercus alba* Linnaeus.	
172	Isabella Tiger Moth, *Pyrrharctia isabella* (J. E. Smith, 1797)		Peale's notes on this drawing indicate that the larva was found at Philadelphia, Pennsylvania, in February 1833. A cocoon in Peale's collection at ANSP (box 3, no. 17), dated 1833, possibly resulted from this larva.
173	Probably Variable Oakleaf Caterpillar Moth, *Lochmaeus manteo* Doubleday, 1841	*Moss* sp.	Peale found the larva on 27 February 1833 "on the wissahicon" (=Wissahickon Creek), a tributary of the Schuylkill River, Philadelphia, Pennsylvania. The larvae were found "at the roots of moss," probably near an actual food plant, which includes various trees and shrubs.
174	Silver-spotted Skipper, *Epargyreus c. clarus* (Cramer, 1775)		The name used by Peale, *Eudamus bathyllus*, refers to the species *Thorybes bathyllus* (J. E. Smith, 1797). The figure and description of the larva most closely agree with *E. clarus*, but the head capsule lacks the yellow-orange eye patches of this species. Peale found the larva in August 1877 on "Wild indigo" at Red Bank, New Jersey. The pupa resulted from a larva found in 1832 at Red Bank, New Jersey, and it was included in the composition on pg. 139. Wild indigo is not a documented food plant, but this butterfly is known to feed on a variety of Fabaceae.
175	Silver-spotted Skipper, *Epargyreus c. clarus* (Cramer, 1775)	American wisteria, *Wisteria frutescens* (Linnaeus) Poiret	See complete composition on pg. 139.
176	Probably Evergreen Bagworm Moth, *Thyridopteryx ephemeraeformis* (Haworth, 1803)		Found in 1833 on apricot (*Prunus armeniaca* Linnaeus), probably in Philadelphia, Pennsylvania. See drawing on pg. 177.
177	Evergreen Bagworm Moth, *Thyridopteryx ephemeraeformis* (Haworth, 1893)	Honeylocust, *Gleditsia triacanthos* (Linnaeus)	The name used by Peale, *Oiketiccus coniferarum*, is a junior synonym of the name *ephemeraeformis* (*Sphinx*). Found in 1833, probably around Philadelphia, Pennsylvania. See drawing on pg. 176.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
178	Corn Earworm Moth, *Helicoverpa zea* (Boddie, 1850)	Corn, *Zea mays* Linnaeus	Found in 1880 at Red Bank, New Jersey.
179	Unknown moth	Moss and liverwort	Found in 1833 "near the the wissahickon," which is a tributary of the Schuylkill River, Philadelphia, Pennsylvania. It does not resemble a species of lichen moth as suggested in the published caption.
180	Elder Shoot Borer Moth, *Achatodes zeae* (Harris, 1841)	Cut-leaved elder, *Sambucus nigra var. laciniata* (Linnaeus) Zabel	Found in 1830 at Philadelphia, Pennsylvania. Peale coined the name "*Aegeria ferruginosa*" for this species, and the specimens of *A. zeae* in his collection at ANSP (box 29, nos. 29-31) are identified as such.
181	Deadwood borer moth, *Scolecocampa liburna* (Geyer, 1837)		Found "under the Bark of a Pine stump" southwest of Kaighn's Point, New Jersey.
182	Large Maple Spanworm Moth, *Prochoerodes lineola* (Goeze, 1781)	Possibly Canada germander, *Teucrium canadense* Linnaeus	See lithograph on pg. 167. Found in 1833, probably around Philadelphia, Pennsylvania. Plants of the mint family (Lamiaceae) are not documented hosts of this moth, but it feeds on a wide variety of plants from many families.
183	Forest Tent Caterpillar Moth, *Malacosoma disstria* Hübner, 1820	Post oak, *Quercus stellata* Wangenheim	The name used by Peale, *Clisiocampa sylvatica*, is a junior synonym of the name *M. disstria*. Found in 1833. In Peale's collection at ANSP (box 3, no. 3) is a cocoon from 1833, possibly resulting from the larva portrayed in this drawing. Oaks are in the genus *Quercus* Linnaeus, not *Fagus* Linnaeus as indicated in the published caption.
184	Unexpected Cycnia Moth, *Cycnia inopinatus* (H. Edwards, 1882)	Milkweed, *Asclepias* Linnaeus sp.	Found in 1879 at Red Bank, New Jersey. The name used in the published caption, *Cycnia antica*, is a junior synonym of the name *tenera* (*Hypercombe*). See completed composition, mistakenly combining two different species, on pg. 148.
185	Milkweed Tussock Moth, *Euchaetes elge* (Drury, 1773)	Common milkweed, *Asclepias syriaca* Linnaeus	Found in 1879 at Red Bank, New Jersey.
186	Top: Spotted Apatelodes Moth, *Apatelodes torrefacta* (J. E. Smith, 1797); Bottom: Banded Tussock Moth, *Halysidota tessellaris* (J. E. Smith, 1797)	Maple, *Acer* Linnaeus sp., or (more likely) northern red oak, *Quercus rubra* Linnaeus	Found in 1879 at Red Bank, New Jersey.
187	Zebra Caterpillar Moth, *Melanchra picta* (Harris, 1841)	American sycamore, *Platanus occidentalis* Linnaeus	See completed composition on pg. 168. Found in 1833 near Kaighn's Point, New Jersey. The name used by Peale, *Colocasia zebra*, refers to the appearance of the larva and is not a valid name. Peale's collection at ANSP (box 8, no. 3) contains the adult that was reared from the larva portrayed in this drawing (emerged 2 September 1833). His collection also contains two pupal exuviae that resulted from larva reared at that time (box 8, no. 2; box 20, no. 25), including one wrapped in a sycamore leaf, as depicted at the bottom of this illustration. Although sycamore does not appear to be a previously documented food plant, this evidence suggests that it indeed serves as a host.
188	Pink-spotted Hawkmoth, *Agrius cingulata* (Fabricius, 1775)	Probably sweet potato, *Ipomoea batatas* (Linnaeus) Lamarck	Found in 1833, probably around Philadelphia, Pennsylvania.
189	Pink-spotted Hawkmoth, *Agrius cingulata* (Fabricius, 1775)	Purple morning-glory, *Ipomoea purpurea* (Linnaeus) Roth.	
190	Smeared Dagger Moth, *Acronicta oblinita* (J. E. Smith, 1797)	Common buttonbush, *Cephalanthus occidentalis* Linnaeus.	
191	Carolina Sphinx Moth, *Manduca sexta* (Linnaeus, 1763)	Irish Potato, *Solanum tuberosum* Linnaeus	The name used by Peale, *Sphinx carolina*, is a junior synonym of the name *S. sexta*. Larva found in 1833, probably around Philadelphia, Pennsylvania.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
192	Greater Black-letter Moth, *Xestia dolosa* Franclemont, 1980	Cabbage, *Brassica oleracea* Linnaeus	In Peale's collection at ANSP (box 22, no. 1) is the adult that was reared from the larva portrayed in this drawing, which was probably found around Philadelphia, Pennsylvania (emerged 26 August 1833).
193	Five-Spotted Hawkmoth, *Manduca quinquemaculata* (Haworth, 1803)	Garden tomato, *Solanum lycopersicum* Linnaeus.	
194	Io Moth, *Automeris io* (Fabricius, 1775)	Wild indigo, *Baptisia tinctoria* (Linnaeus) R.Brown	In Peale's collection at ANSP (box 75, nos. 4-6) are egg shells, cocoons, and an adult that correspond to the larvae mentioned on this drawing, which were found in 1879 at Red Bank, New Jersey.
195	Luna Moth, *Actias luna* (Linnaeus, 1758)	Hickory, *Carya* Nuttall sp.	Found in 1833, probably around Philadelphia, Pennsylvania.
196	Unknown moth	Common ragweed, *Ambrosia artemisiifolia* Linnaeus.	
197	Unknown; no larva shown	Fern sp.	Found in 1877 at Ocean Grove, New Jersey. The cocoon of *Callopistria mollissima* (Guenée, 1852) (the species suggested in the published caption) is typically spun in leaf litter, not on the host as indicated by Peale's drawing and notes.
198	Red-humped Caterpillar Moth, *Schizura concinna* (J. E. Smith, 1797)		Found on apple (*Malus domestica* Borkhausen) according to Peale's notes for this drawing. This species is widespread in North America.
199	Unicorn Caterpillar Moth, *Schizura unicornis* (J. E. Smith, 1797)	Hawthorn, *Crataegus* Linnaeus sp.	
200	Hummingbird Clearwing Moth, *Hemaris thysbe* (Fabricius, 1775)	Blackhaw, *Viburnum prunifolium* Linnaeus	The name used by Peale, *Sesia pelasgus*, is a junior synonym of the name *thysbe* (*Sesia*). Larvae found in 1833, probably around Philadelphia, Pennsylvania. The red lateral line on the green larva is unusual.
201	Hog Sphinx, *Darapsa myron* (Cramer, 1780)	Arrowwood, most likely *Viburnum dentatum* Linnaeus or *V. recognitum* Fernald	Found in 1833, probably around of Philadelphia, Pennsylvania.
202	Piedmont staggerbush, *Lyonia mariana* (Linnaeus) D. Don		Drawn in 1880, a portion of this illustration was copied for the lithograph on pg. 155.
203	Pandorus Sphinx Moth, *Eumorpha pandorus* (Hübner, 1821)	Virginia creeper, *Parthenocissus quinquefolia* (Linnaeus) Planchon	See the completed composition on pg. 151. The name used by Peale, *Philampelus satellitia*, refers to the species currently recognized as *Eumorpha satellitia* (Linnaeus, 1771), which is a Neotropical species. A pupal exuvia and an adult of this species in Peale's collection at ANSP (box 22, nos. 11, 12) are from the same batch of larvae as those portrayed, which produced adults in June 1834.
204	Hog Sphinx, *Darapsa myron* (Cramer, 1780)	River grape, *Vitis riparia* Michaux	Found in 1833, probably around Philadelphia, Pennsylvania.
205	Moth, possibly a species of Catocalinae	Red maple, *Acer rubrum* Linnaeus	Larva (which died) was found in 1833, probably around Philadelphia, Pennsylvania.
206	Unknown moth	Wild indigo, *Baptisia tinctoria* (Linnaeus) R.Brown	Found in 1879 at Ocean Grove, New Jersey.
207	Probably Baltimore Bomolocha Moth, *Hypena baltimoralis* (Guenée)		Found on maple (*Acer* sp.) in 1833, probably around Philadelphia. Pennsylvania.
208	Clear Dagger Moth, *Acronicta clarescens* Guenée, 1852		The name used by Peale, *Acronycta* [sic] *pruni*, is a junior synonym of the name *A. clarescens*. Found in 1879 on apple (*Malus domestica* Borkhausen) at Red Bank, New Jersey.
209	Polyphemus Moth, *Antheraea polyphemus* (Cramer, 1776)	Red maple, *Acer rubrum* Linnaeus	A female in Peale's collection at ANSP (box 7, no. 7) resulted from one of the larvae portrayed in this drawing, which were found in 1833, probably around Philadelphia, Pennsylvania (emerged 7 July 1834).

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
210	Promethea Moth, *Callosamia promethea* (Drury, 1773)		Found in 1833 on tuliptree (*Liriodendron tulipifera* Linnaeus), probably around Philadelphia, Pennsylvania.
211	Mottled Prominent Moth, *Macrurocampa marthesia* (Cramer, [1780])	Blackjack oak, *Quercus marilandica* Münchhausen	Found in 1833, probably around Philadelphia, Pennsylvania.
212	Top: Orange-tipped Oakworm Moth, *Anisota senatoria* (J. E. Smith, 1797); Middle: *A. senatoria* (J. E. Smith, 1797) (young larva; unfinished sketch); Bottom: Probably Yellow-necked Caterpillar Moth, *Datana ministra* (Drury, 1773)	Oak, *Quercus* Linnaeus sp.	Larvae found in 1874 and 1879 at Holmesburg, Pennsylvania, and Red Bank, New Jersey.
213	Top: Orange-tipped Oakworm Moth, *Anisota senatoria* (J. E. Smith, 1797); Bottom: Yellow-necked Caterpillar moth, *Datana ministra* (Drury, 1773)	Scrub oak, *Quercus illicifolia* Wangenheim	Larvae found in 1832, probably at Philadelphia, Pennsylvania, and 1879 at Ocean Gove, New Jersey.
214	Pine Sawfly, *Neodiprion* Rohwer sp.	Pine, *Pinus* Linnaeus sp.	Found in 1877 at Ocean Beach, New Jersey.
215	Probably Yellow-necked Caterpillar Moth, *Datana ministra* (Drury, 1773)	Piedmont staggerbush, *Lyonia mariana* (Linnaeus) D. Don	The name used by Peale refers to a different species, *Datana perspicua* Grote & Robinson, 1865. Found in 1833 near Kaighn's Point, New Jersey. The plant is not identifiable on the drawing, but Peale mentions it in his notes. This drawing is also reproduced on pg. 244 (bottom row, far left).
216	Waved sphinx moth, *Ceratomia undulosa* (Walker, 1856)	Ash, *Fraxinus* Linnaeus sp.	The name used by Peale, *Sphinx cineria*, is a junior synonym of another species, *Sphinx chersis* (Hübner, 1823). Found in 1833, probably around Philadelphia, Pennsylvania.
217	Waved sphinx moth, *Ceratomia undulosa* (Walker, 1856)		The crippled moth that resulted from this larva is in Peale's collection at ANSP (box 78, no. 14) (emerged 8/9 June 1834). Found in 1833 on ash (*Fraxinus* Linnaeus sp.) by "Mr. Robins," probably at Philadelphia, Pennsylvania. This figure is also reproduced on pg. 244 (bottom row, second from left).
218	Pearly Wood-nymph Moth, *Eudryas unio* (Hübner, [1831])	Probably seedbox, *Ludwigia alternifolia* Linnaeus	The name used by Peale refers to a different species, *Eudryas grata* Fabricius, 1793. Two adult moths in Peale's collection at ANSP (box 22, nos. 9, 10) were probably reared from the same batch of larvae portrayed in this drawing. They were found in 1833 at Woodbury, New Jersey.
219	Salt Marsh Moth, *Estigmene acrea* (Drury, 1773)	Broadleaf arrowhead, *Sagittaria latifolia* Willdenow	Found in 1833, probably around Philadelphia, Pennsylvania. *Sagittaria* is not a documented host, but this species is known to feed on a wide variety of plants from many families.
220	Probably Yellow-necked Caterpillar Moth, *Datana ministra* (Drury, 1773) or Spotted Datana Moth, *Datana perspicua* Grote & Robinson, 1865		Found in 1879 at Red Bank, New Jersey.
221	Unknown moth		Found in 1879 at Red Bank, New Jersey.
222	Imperial Moth, *Eacles imperialis* (Drury, 1773)		Found on sweetgum (*Liquidambar styraciflua* Linnaeus) in 1879 at Washington Heights, New York. See completed composition on pg. 153.
223	Imperial Moth, *Eacles imperialis* (Drury, 1773)		Found on white oak (*Quercus alba* Linnaeus) in 1833, probably around Philadelphia, Pennsylvania. See completed composition on pg. 153.
224	Probably Black-waved Flannel Moth, *Lagoa crispata* (Packard, 1864)	Sweet fern, *Comptonia peregrina* (Linnaeus) Coulter, and *Rubus* Linnaeus sp.	Larvae found in 1879 at Red Bank, New Jersey. See drawing on pg. 149. *Comptonia* is not a documented host of this species, but other species of Myricaceae are fed upon.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
225	Crowned Slug Moth, *Isa textula* (Herrich-Schäffer, 1854)	White oak, *Quercus alba* Linnaeus	This illustration is also reproduced on pg. 244 (bottom row, far right).
226	Hoary Edge Skipper, *Achalarus lyciades* (Geyer, 1832)	Plant unidentifiable	The name used by Peale, *Hesperia lycidas*, is a preoccupied name once used for *A. lyciades*. Found in 1879 at Red Bank, New Jersey. See drawing on pg. 232.
227	Probably Locust Twig Borer, *Ecdytolopha insiticiana* Zeller, 1875	Presumably Locust, *Robinia* Linnaeus sp.	Found in 1833 (probably around Philadelphia, Pennsylvania) on "*Robinia viscossissima*," which likely refers to *Robinia viscosa* Ventanat (clammy locust).
228	Copper Underwing Moth, *Amphipyra pyramidoides* Guenée, 1852	Rose, *Rosa* Linnaeus sp.	A cocoon and an adult moth in Peale's collection at ANSP (box 22, nos. 34, 35) resulted from the larva portrayed in this drawing, which was found in 1833, probably around Philadelphia, Pennsylvania.
229	Moth, probably a pyraloid or tortricoid	Presumably wild indigo, *Baptisia tinctoria* (Linnaeus) R.Brown	Peale coined the name "*saltatorius*" for this species. Found on "wild indigo" in 1834, most likely around Philadelphia, Pennsylvania.
230	Western Furcula Moth, *Furcula occidentalis* (Lintner, 1878)	Presumably willow, *Salix* Linnaeus sp.	The name used by Peale, *Phalaena borealis*, refers to the species *Furcula borealis* (Guérin-Méneville, 1844). Though not evident on the figures, Peale's written description most closely matches *F. occidentalis* in referring to a yellow border around the dark saddle markings. The food plant is also consistent with this species. Found on "willow" in 1879 at Red Bank, New Jersey.
231	Black Wedge-spot Moth, *Homophoberia apicosa* (Haworth, 1809)	Presumably *Polygonum* Linnaeus sp.	In Peale's collection is the cocoon and adult moth that resulted from this larva (emerged 8 July 1834). Found in 1834 (probably around Philadelphia, Pennsylvania) on "Asmart," which is a name used for *Polygonum* sp.
232	Common Sootywing, *Pholisora catullus* (Fabriciuis, 1793)	Probably *Amaranthus* Linnaeus sp.	The name used by Peale, *Hesperis lycidas*, is a preoccupied name once used for the species *Achalarus lyciades* (Geyer, 1832). Found in 1879 at Red Bank, New Jersey. Peale identified the food plant as "Tell tale," which refers to a variety of *Coleus* Loureiro. He likely misidentified a species of *Amaranthus* based on its superficial resemblance to *Coleus*.
233	Leaf Tier Moth, *Pococera* Zeller sp.	Pin oak, *Quercus palustris* Muenchhausen	Found in 1834 north of Kensington, New York.
234	Probably Wild Indigo Duskywing, *Erynnis baptisiae* (W. Forbes, 1936)	Wild indigo, *Baptisia tinctoria* (Linnaeus) R.Brown	Found in 1879 at Red Bank, New Jersey. The name used by Peale, *Thanaos juvenalis*, refers to *Erynnis juvenalis* (Fabricius, 1793), a widespread North American species. See the drawing on pg. 235, and the completed composition on pg. 140.
235	Wild Indigo Duskywing, *Erynnis baptisiae* (W. Forbes, 1936)	Wild indigo, *Baptisia tinctoria* (Linnaeus) R.Brown	Found in 1877 at Ocean Grove, New Jersey. The name used by Peale, *Pap. juvenalis*, refers to *Erynnis juvenalis* (Fabricius, 1793), a widespread North American species. See the drawing on pg. 234, and the completed composition on pg. 140.
236	Probably Sweetheart Underwing Moth, *Catocala amatrix* (Hübner, [1813])	Poplar, *Populus* Linnaeus sp.	Found in 1844, probably around Washington, D.C., or Philadelphia, Pennsylvania.
237	White-lined Sphinx Moth, *Hyles lineata* (Fabricius, 1775)		Found in 1836 on grape (*Vitis* Linnaeus sp.) by Robert E. Griffith, Jr. of Philadelphia, Pennsylvania. In Peale's collection at ANSP (box 22, nos. 13, 14) are the pupal exuvia and adult moth that resulted from this larva (emerged 20 August 1836).
238	Possibly *Morpho epistrophus* (Fabricius, 1796)	Possibly *Inga* Miller sp.	The name used by Peale, *Morpho Laertes*, is a junior synonym of the name *epistrophus* (*Papilio*). Peale was in Rio de Janeiro with the Wilkes Expedition when he found this larva in December 1838. Peale personally reared this species, thus the plant probably represents a tropical host. A fresh specimen of *M. epistrophus* at ANSP from Peale's collection, labeled "*Laertes*" from Brazil, may be the specimen he reared.
239	Angle-lined Prominent Moth, *Clostera inclusa* (Hübner, [1831])	Willow, *Salix* Linnaeus sp.	The name used by Peale, *Phalaena anastomosis*, is a junior synonym of the name *inclusa* (*Ichthyura*). Found in 1879 at Red Bank, New Jersey.

Table 1 (cont.)

Page no.	Insect species	Plant species	Notes
240	Red Admiral, *Vanessa atalanta rubria* (Fruhstorfer, 1909)	Probably Canada woodnettle, *Laportia canadensis* (Linnaeus) Weddell	Found in 1875 along Pennypack Creek, Holmesburg (Philadelphia), Pennsylvania.
241	Peppered Moth, *Biston betularia* (Linnaeus, 1758)	Black locust, *Robinia pseudoacacia* Linnaeus	Found in 1880 at Red Bank, New Jersey.
242	Chokecherry, *Prunus virginiana* Linnaeus		Found in 1880 at Red Bank, New Jersey.
243	Impressed Dagger Moth, *Acronicta impressa* Walker, 1856	Birch, *Betula* Linnaeus sp.	Found in 1880 at Red Bank, New Jersey.
244-245	Small reproductions of thirty-two illustrations of early stages, six of which are butterflies: *Papilio polyxenes asterius* (Stoll, 1782), *Papilio t. troilus* Linnaeus, 1758, *Erynnis* Schrank sp., *Colias p. philodice* Godart, 1819, *Speyeria i. idalia* (Drury, 1773), and *Pieris r. rapae* (Linnaeus, 1758). Eight of these drawings were incorporated into Peale's later compositions (see drawings on pgs. 39, 40, 66, 75, 92, 215, 217, and 225).		

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Allopatry and parapatry in hairstreak butterflies (Lycaenidae, Eumaeini) with uniform male sexual structures

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Abstract. An unusual characteristic of the *Electrostrymon guzanta* species complex is that its male primary and secondary sexual structures are uniform. Eumaeine taxonomy is often based on variation of these structures, and the taxonomy of this group is unresolved. Evolutionary changes in sexual structures are often hypothesized to promote reproductive isolation among closely related sympatric species, and the incidence of sympatry in this complex would be predicted to be low. To resolve the taxonomy and to assess the sympatry prediction, individuals of this species complex were partitioned into wing phenotypes based upon 21 qualitative characters, which were coded. We also measured 6 quantitative characters, which were analyzed with logistic regression. To determine the distinctiveness of phenotypes, the coded characters were analyzed with maximum parsimony because it provides the most efficient summary of the data. It also provides a hypothesis of character state evolution. Based on these results, the taxonomy of the *E. guzanta* species complex, including its nomenclature, was updated. *Electrostrymon thurman* Thompson & Robbins, **new species**, is named for high elevation individuals of the species complex from Costa Rica and western Panama (type locality). Chimeric holotypes of *Kisutam simplisis* K. Johnson & Kroenlein, 1993 and *Angulopis strymonotis* K. Johnson & Kroenlein, 1993 are restricted under ICZN article 73.1.5, and the latter name is synonymized with *Electrostrymon joya* (Dognin, 1895), **new synonym**. As predicted, the incidence of sympatry in the *E. guzanta* species complex is low. Three of the four species in the complex—*E. guzanta*, *E. thurman*, and *E. perisus*—are allopatric. The distribution of the fourth member of the species complex, *E. denarius*, overlaps that of *E. guzanta* and that of *E. thurman*, but it occurs at lower elevations (statistically significant). The theory of hybridization parapatry proposes areas of distributional overlap where there is reproductive interference. Data on reproductive interference are yet needed to determine whether this distributional overlap accords with the prediction of parapatry.

Key words: Calycopidina, *Electrostrymon*, hybridization parapatry, *guzanta*, *thurman*, secondary sexual structures.

Introduction

The *Electrostrymon guzanta* (Schaus) species complex (Lepidoptera, Lycaenidae, Eumaeini, Calycopidina) is a primarily montane Neotropical monophyletic lineage (Figs. 1-21, 24-25) that is biologically unusual for eumaeines because males lack secondary structures on the wings and there are no evident interspecific differences in genitalic morphology (Duarte & Robbins 2010). Male secondary sexual structures in insects are postulated to promote species recognition and to contribute to reproductive isolation among sympatric species (e.g., Löfstedt et al. 1991, Symonds & Elgar 2008). Further, interspecific genitalic differences among animals are usually hypothesized to result from sexual selection, which may allow females to select among conspecific males and to reject non-conspecific males (e.g., Eberhard 2010, Simmons 2014). According to this theory, then, we might hypothesize that a lineage with uniform male sexual structures, such as the *E. guzanta* species complex, would be composed of species that are allopatric or parapatric with each other.

The *E. guzanta* species complex possesses highly apomorphic genitalic structures so it is unambiguous which individuals belong to the complex (Duarte & Robbins 2010), but the species level classification of the complex is unresolved. For example, seven specific names have been proposed for this lineage,

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but it is unclear which, if any, apply to individuals from higher elevations in Costa Rica and Panama (Robbins 2004, Robbins et al. 2012a). Since genitalia and male secondary sexual structures cannot be used to distinguish species in this complex, it was suggested that an analysis of wing pattern variation might provide evidence on which to base a species level classification (Robbins et al. 2012a).

In the first part of the paper, we describe and code geographically variable qualitative and quantitative wing pattern traits in the *E. guzanta* species complex. For the qualitative characters, we looked for discrete states that partition the complex into phenotypes. For the variable quantitative characters, we analyzed them with logistic regression. To determine the distinctiveness of the phenotypes, we analyzed the characters with maximum parsimony because it is the most efficient summary of interspecific differences (Farris 1979), regardless of the phylogeny, and because it represents a widely used phylogenetic estimator for morphological characters. These results are the foundation for a species level taxonomy for the *E. guzanta* complex, including the description of a new species. In the second part of the paper, we ask if the species that we recognize are sympatric. In most cases, the answer is simple and straightforward. In one comparison, we use the theory of hybridization parapatry (Key 1981, Bull 1991, Pettengill & Moeller 2012, Werner et al. 2014, Bournez et al. 2015) to interpret the results for those species that occur at overlapping elevations in the same geographic area.

MATERIALS AND METHODS

The results in this paper are based primarily upon 352 museum specimens belonging to the *E. guzanta* species complex. The specimens cited in this study are deposited in the following collections, with abbreviations and museum names from Evenhuis (2015) when available.

BMNH — The Natural History Museum [formerly British Museum (Natural History), London, UK.
CUIC — Cornell University, Ithaca, New York, USA.
ICN — Instituto de Ciencias Naturales de la Universidad Nacional, Universidad Nacional de Colombia, Bogotá, Colombia.
MZFC — Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, México D.F., Mexico.
PMT — Private Collection of Paul M. Thompson, Chantilly, Virginia, USA.
USNM — National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

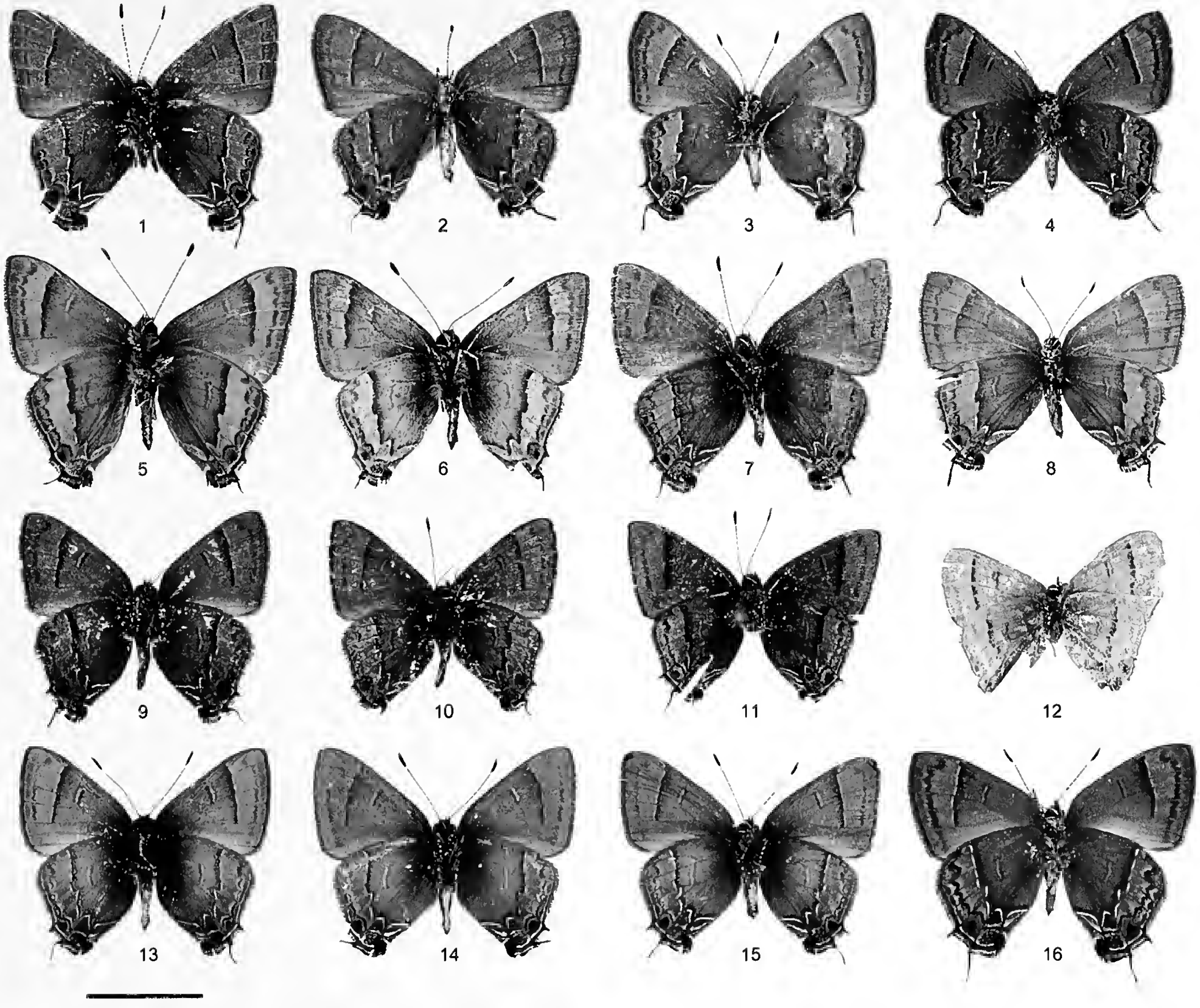
The following abbreviations are used: FW—forewing; HW—hindwing; D—dorsal; V—ventral. Following Klots (1951) and Ehrlich and Ehrlich (1961), the "limbal" part of the wing refers to the area of the ventral wings between the postmedian and submarginal lines. Wing venation follows Comstock (1918). The species names used were identified from their original descriptions and/or from examination of type specimens in the BMNH or USNM. All statistical tests were done with commercially available SAS JMP software.

The preliminary classification of the *E. guzanta* species complex in Robbins (2004) was used as an initial guide in finding variable traits that formed discrete states, which were then used to characterize phenotypes. We specifically looked for characters that might modify the preliminary classification as well as for variable characters that would indicate the affinity of the high elevation specimens from Panama and Costa Rica.

We used digital Vernier calipers to measure quantitative traits in each sex that appeared to vary among phenotypes. It was our original intention to analyze the quantitative data using discriminant analysis, which assumes that variates are normally distributed. However, Shapiro-Wilk and Lilliefors tests showed significant departure from normality in about 20% of the comparisons. For this reason, we analyzed measurements between taxa using logistic regression (Hosmer et al. 2013), which does not assume normality.

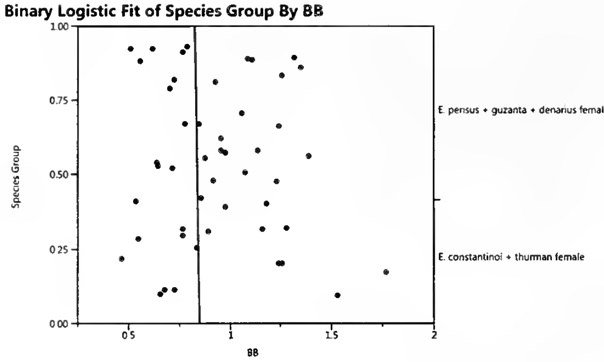
We used multinomial logistic regression to determine the degree to which different quantitative characteristics differentiate groups of taxa. Although oversimplified, a nearly vertical logistic regression line indicates that a character distinguishes two groups of taxa, while an inclined line does not. For groups of taxa that separated via multinomial logistic regression, we performed binary logistic regression to confirm the differentiation. Using the binary model, we considered a character to be distinguishing if the value of McFadden's pseudo-R^2, $R^2(U)$, produced by the logistic regression model exceeded 0.995 (Fig. 22).

To determine differences between phenotypes, we used maximum parsimony optimization in TNT and WinClada software (Nixon 2002, Goloboff et al. 2008). As noted, parsimony optimization provides the most efficient mathematical summary of the information in a data matrix (Farris 1979). Further, the optimized changes in character state are hypothesized evolutionary changes. We used *Electrostrymon constantinoi* (K. Johnson & Kroenlein) as an outgroup because it was the sister to the *E. guzanta* species complex in a previous phylogenetic analysis (Duarte & Robbins 2010).



Figures 1-16. Ventral wing pattern variation in the *E. guzanta* species complex. **1**. *E. guzanta* male (Mexico). **2**. *E. guzanta* male (Mexico). **3**. *E. guzanta* male (Nicaragua). **4**. *E. guzanta* female (Nicaragua). **5**. *E. thurman* male (Panama). **6**. *E. thurman* male (Panama). **7**. *E. thurman* male (Panama). **8**. *E. thurman* female (Panama). **9**. *E. perisus* male (Colombia). **10**. *E. perisus* male (Colombia). **11**. *E. perisus* male (Colombia). **12**. *E. perisus* female (Colombia). **13**. *E. denarius* male (Nicaragua). **14**. *E. denarius* male (Panama). **15**. *E. denarius* male (Panama). **16**. *E. denarius* female (Panama). Scale 1 cm.

Figures 17-21. Dorsal wing pattern variation in *E. denarius*. **17**. Male (Panama). **18**. Male (Panama). **19**. Male (Mexico). **20**. Male (Nicaragua, El Crucero/Las Nubes). **21**. Female (Panama).



```
Whole Model Test
Model              -LogLikelihood        DF     ChiSquare     Prob>ChiSq
Difference              32.601275         1      65.20255        <.0001*
Full                   1.68012e-6
Reduced                 32.601277


RSquare (U)                          1.0000
AICc                                4.26667
8IC                                 7.74241
Observations (or Sum Wgts)               48

Measure                     Training Definition
Entropy RSquare               1.0000 1-Loglike(model)/Loglike(0)
Generalized RSquare           1.0000 (1-(L(0)/L(model))^(2/n))/(1-L(0)^(2/n))
Mean -Log p                   0.0000 ∑ -Log(ρ[j])/n
RMSE                          0.0000 √ ∑(y[j]-ρ[j])²/n
Mean Abs Dev                  0.0000 ∑ |y[j]-ρ[j]|/n
Misclassification Rate        0.0000 ∑ (ρ[j]≠ρMax)/n
N                                 48 n

Parameter Estimates
Term                    Estimate    Std Error    ChiSquare    Prob>ChiSq
Intercept   Unstable   2365.9387    131673.36         0.00        0.9857
88          Unstable   -2799.768     155700.4         0.00        0.9857

For log odds of E. constantinoi + thurman female/E. perisus + guzanta + denarius female
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Figure 22. Binary logistic regression analysis of Character 26 (Table 2) differentiating females of *E. constantinoi* and *E. thurman* from the others.

Based on the results of the wing pattern analyses, we updated the taxonomy and nomenclature of the *E. guzanta* species complex, including the description of a new species according to the requirements of the International Code of Zoological Nomenclature (ICZN 1999). As part of the species description, genitalic morphology follows Klots (1970) as modified for the Eumaeini (Robbins 1991). Other morphological terms follow Snodgrass (1935). Nomenclature is updated and summarized in a list. Labels on the holotype are given verbatim with comments in brackets. Months are reported by their first three letters in English (other than the holotype label). Finally, we note that *E. guzanta* has been recorded from the United States (Texas) (Warren et al. 2004) on the basis of one female specimen and on various adult images (North American Butterfly Association, http://www.naba.org/chapters/nabast/guzanta.html, Butterflies of America, http://www.butterfliesofamerica.com/L/Lycaenidae.htm, accessed 19 May 2015). We address the identification of Texan specimens elsewhere (Thompson & Robbins, in prep.).

Allopatry of species that occur in different countries is a straightforward determination. To assess the hypothesis of elevational parapatry in the *E. guzanta* species complex, we restricted the "elevation study series" to those specimens in which elevation was specifically noted on the data label. We did not include data if elevation was omitted or was given as a range. We plotted the number of localities where each species had been found for each elevation and country. Mexico was restricted because of its large size to the south-central part of the country bounded on the north by the trans-volcanic mountain range (about 19ºN latitude) and on the east by the Isthmus of Tehuantepec (about 95ºW longitude). This area included the states of Michoacán, Morelos, Guerrero, Oaxaca (north of the Isthmus of Tehuantepec), and Veracruz (south of Orizaba). We omitted Nicaraguan specimens. Virtually all Nicaraguan museum specimens of Eumaeini are deposited in BMNH or USNM, but those in BMNH lack elevation data and those in USNM are given as a range of elevations for localities above 1,000 m (Robbins et al. 2012a). We used the nonparametric Wilcoxon (Mann-Whitney) test for independent samples to determine whether there were significant differences in elevation localities for each species in a country because there was no a priori reason to expect the frequency of elevation localities to be normally distributed.

RESULTS AND DISCUSSION

Wing Pattern and Genitalic Variation

Representative ventral wing pattern variation in the *E. guzanta* species complex is illustrated (Figs. 1-16). The dorsal wings of both sexes of *E. guzanta*, *E. thurman*, and *E. perisus* are brown with an orange anal lobe (cf. Figs. 24-25). In contrast, *E. denarius* has orange scaling dorsally, but the amount of orange scaling is sexually dimorphic and geographically variable (Figs. 17-21).

We identified 21 variable wing pattern characters in the *E. guzanta* species complex that had discrete, qualitatively different states (Table 1). Minor variation within each state is noted (Table 1). We measured 6 quantitative characters. One of these distinguished female groupings based upon logistic regression (Character 26 in Table 2, Fig. 22). None of the quantitative characters differentiated male groupings in the logistics regression analysis. However, the mean, standard deviation, and range of

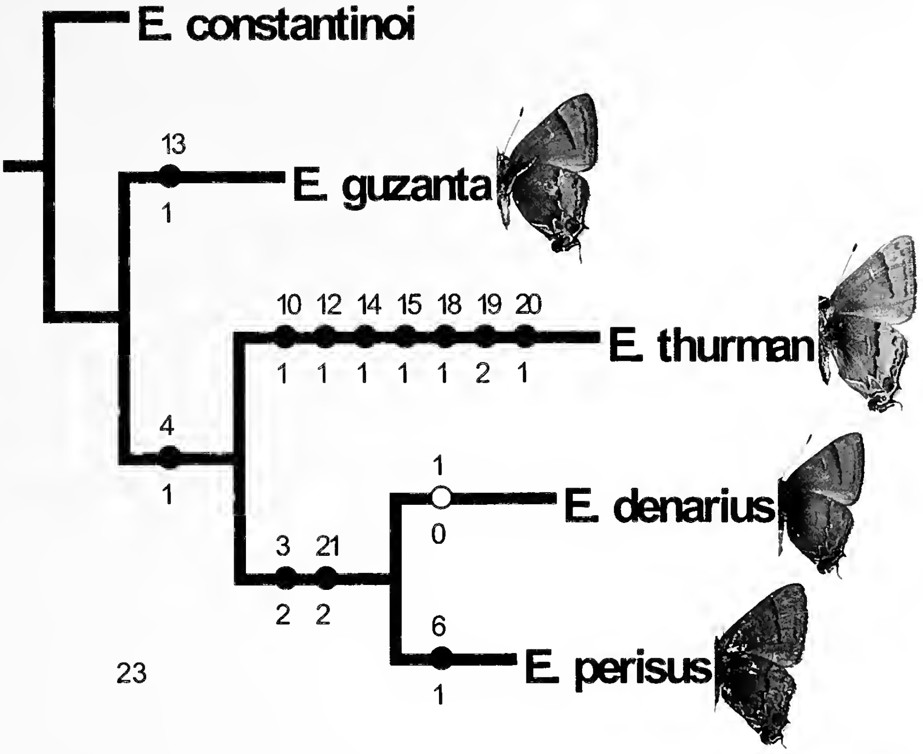


Figure 23. Most parsimonious tree for *E. guzanta* species complex with unambiguous character state changes (CI = 91, RI = 57). Hollow circles represent homoplastic changes.

the quantitative characters in Table 2 may be useful for distinguishing phenotypes when measurements are not in an area of overlap. One ratio in the logistic regression differentiated female groupings in the same way as Character 26 (Table 2), but was not independent of this character.

We assigned individuals to one of four wing pattern phenotypes differentiated by the character states in Tables 1 and 2. The taxonomy and nomenclature section below provides the rationale for the names that we apply to these phenotypes. These phenotypes differ from the previous taxonomy in that (1) high elevation specimens from Costa Rica and Panama represent a phenetically distinct taxon that is also phylogenetically distinct (Fig. 23) and (2) there is geographic variation within *E. denarius* (Figs. 17-20). These discrepancies from the previous classification are addressed in the taxonomy and nomenclature section.

We coded the qualitative characters (Table 1). Based on these data, there was one most parsimonious 33-step equal weight tree (Fig. 23). Further, each implied weight most parsimonious tree with values for the parameter K=1, 10 100, 1000 resulted in one tree, also with the same topology as the most parsimonious equal weight tree. Unambiguous optimization shows where distinguishing character states are hypothesized to have evolved (Fig. 23).

The male and female genitalia of *E. thurman* are illustrated (Figs. 26, 27). We found no evident variation in a comparison of 13 male genitalic preparations among the four wing pattern phenotypes. There was minor intraspecific variation in the shape of the valvae and in the size of the more posterior cornutus, but none of the wing phenotypes could be distinguished by these structures. We also compared six female genitalic preparations. The female genitalia are small and relatively non-descript, and the signa are less conspicuous than they appear in Fig. 27.

TAXONOMY AND NOMENCLATURE

Taxonomic history

Generic placement. The current members of the *E. guzanta* species complex were placed in the adjoining *Thecla endymion* (Fabricius) and *T. cecrops*

Table 1. Qualitative wing pattern characters for distinguishing species in the *E. denarius* species complex. The outgroup is *E. constantinoi*. The number to the right of each character description is its coded state for the parsimony analysis. The term "limbal area" denotes the wing area that lies between the postmedian and submarginal lines.

Char #	Character	*E. constantinoi*		*E. guzanta*		*E. thurman*		*E. denarius*		*E. perisus*	
1	Male dorsal wing color	Brown; with orange suffusion on both wings	0	Brown	1	Brown	1	Brown; with orange suffusion on both wings	0	Brown	1
2	Female dorsal wing color	Brown; with sky-blue suffusion on HW	0	Brown; with faint orange suffusion on both wings	1	Brown	2	Brown; with faint orange suffusion on both wings	1	Brown	2
3	Edges of DHW anal lobe	Brown on outer & inner margins; and females on vein CuA_2	0	Little or no dark brown basally	1	Little or no dark brown basally	1	Entirely surrounded by dark brown	2	Entirely surrounded by dark brown	2
4	Male DHW submarginal white scaling	Anal lobe to Cu2	0	Anal lobe to Cu2	0	White spot adjacent to anal lobe	1	White spot adjacent to anal lobe	1	White spot adjacent to anal lobe	1
5	Female DHW submarginal white scaling	Anal lobe to M1	0	Anal lobe to Cu2	1	White spot adjacent to anal lobe	2	White spot adjacent to anal lobe	2	White spot adjacent to anal lobe	2
6	Width of basal part of VFW postmedian line	Thin	0	Thin	0	Thin	0	Thin	0	Broad	1
7	Color of basal part of VFW postmedian line	Bright orange	0	Brown (or brown with hints of dull orange	1	Brown	1	Brown	1	Brown	1
8	Middle part of VFW postmedian line	Thin	0	Thin	0	Absent	1	Wide	2	Wide	2
9	Faintness of distal (white) part of VFW postmedian line	Not faint	0	Faint	1	Very faint	1	Very faint	1	None or very faint	1
10	Faintness of basal part of VHW postmedian line	Not faint	0	Not faint	0	Faint	1	Not faint	0	Not faint	0
11	Color of basal part of VHW postmedian line	Bright orange	0	Orangish brown	1	Orangish brown	1	Orangish brown	1	Orangish brown	1
12	Color of middle part of VHW postmedian line	Black	0	Black	0	Brown	1	Black	0	Black	0
13	Width of distal part of VHW postmedian line	Thin	0	Broad	1	Thin	0	Thin	0	Thin	0
14	Color of distal part of VHW postmedian line	White	0	White	0	Cream	1	White	0	White	0

Table 1. Cont.

Char #	Character	E. constantinoi		E. guzanta		E. thurman		E. denarius		E. perisus	
15	Color of limbal area of VFW and VHW	Medium brown; (female slightly lighter and male same color as discal area)	0	Medium brown (slightly lighter than discal area)	0	Very light, beige to pale brown (much lighter than discal area)	1	Medium brown (slightly lighter or same color as discal area)	0	Medium brown (slightly lighter than discal area)	0
16	Color of VHW cubital spot	Orange with thin yellow suffusion	0	Red-orange to orange	1	Orange to yellow-orange	2	Yellow to yellow-orange	3	Mostly brown, rarely yellowish-brown	4
17	Size of VHW cubital spot	Medium	0	Large	1	Small	2	Small	2	Small	2
18	Color of basal portion of area between distal border of VHW cubital spot and base of fringe	Brown	0	Brown	0	Cream	1	Brown	0	Brown	0
19	Width of distal portion of area between distal border of VHW cubital spot and base of fringe	Thick	0	Thin	1	None	2	Thin	1	Thin	1
20	Orange ring surrounding VHW anal lobe black spot	No	0	No	0	Yes	1	No	0	No	0
21	VHW submarginal orange markings	Orange spot in cell 2A intrudes broadly into but not across cell Cu2; cell M3 has hints of orange	0	Orange spot in cell 2A extends at least halfway across lunule in cell Cu2; Orange line from vein Cu2 to vein M3 or beyond	1	Orange spot in cell 2A extends at least halfway across lunule in cell Cu2; Orange line from vein Cu2 to vein M3 or beyond	1	None	2	None	2

Table 2. Quantitative wing pattern characters for distinguishing species in the *E. denarius* species complex. The outgroup is *E. constantinoi*. X̄ = sample mean; S = sample standard deviation, R = sample range (minimum, maximum); N = sample size.

Char #	Character	*E. constantinoi*	*E. guzanta*	*E. thurman*	*E. denarius*	*E. perisus*
22	Male FW length (mm)	X̄ = 12.38 S = 0.106 R = 12.30, 12.45 N = 2	X̄ = 13.50 S = 0.920 R = 11.72, 14.83 N = 18	X̄ = 12.52 S = 0.717 R = 11.42, 13.88 N = 16	X̄ = 11.22 S = 0.687 R = 9.51, 12.29 N = 16	X̄ = 12.27 S = 0.770 R = 11.24, 13.31 N =8
23	Female FW length (mm)	X̄ = 12.23 S = 0.443 R = 11.94, 12.74 N = 3	X̄ = 12.79 S = 1.025 R = 11.18, 14.74 N = 21	X̄ = 13.03 S = .744 R = 11.76, 14.35 N =17	X̄ = 12.38 S = 0.833 R = 11.18, 13.48 N = 6	X̄ = 11.02 N =1
24	Male height of VHW cubital spot central black & brown areas (mm)	X̄ = 0.49 S = 0.035 R = 0.46, 0.51 N = 2	X̄ = 1.09 S = 0.164 R = 0.89, 1.45 N = 19	X̄ = 0.72 S = 0.111 R = 0.55, 0.88 N = 15	X̄ = 0.83 S = 0.095 R = 0.68, 1.03 N = 16	X̄ = 1.02 S = 0.084 R = 0.94, 1.13 N = 7
25	Male height of VHW cubital spot & distal white border (mm)	X̄ = 1.75 S = 0. 190 R = 1.62, 1.89 N = 2	X̄ = 2.01 S = 0.192 R = 1.69, 2.26 N = 19	X̄ = 1.70 S = 0.166 R = 1.50, 2.19 N = 15	X̄ = 1.30 S = 0.130 R = 1.08, 1.52 N = 16	X̄ = 1.61 S = 0.152 R = 1.35, 1.77 N = 7
26	Female height of VHW cubital spot central black & brown areas (mm)	X̄ = 0.51 S = 0.045 R = 0.47, 0.56 N = 3	X̄ = 1.16 S = 0.207 R = 0.90, 1.77 N = 20	X̄ = 0.70 S = 0.084 R = 0.54, 0.84 N = 17	X̄ = 1.18 S = 0.238 R = 0.88, 1.53 N = 6	X̄ = 0.86 N = 1
27	Female height of VHW cubital spot & distal white border (mm)	X̄ = 1.86 S = 0.098 R = 1.75, 1.92 N = 3	X̄ = 1.99 S = 0.229 R = 1.58, 2.43 N = 20	X̄ = 1.73 S = 0.210 R = 1.37, 2.21 N = 17	X̄ = 2.02 S = 0.278 R = 1.65, 2.49 N = 6	X̄ = 1.34 N = 1

Table 3. Statistical comparison of the elevations at which different taxa are recorded.

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value	Hodges-Lehmann	Lower CL	Upper CL
E. thurman Panama	*E. perisus* Colombia	-2.25	1.920286	-1.1717	0.2413	-350	.	.
E. thurman Panama	*E. guzanta* Mexico South	-3.0441	3.21746	-0.94612	0.3441	-175	-600	270
E. perisus Colombia	*E. guzanta* Mexico South	1.1765	3.702006	0.31779	0.7506	100	-450	770
E. denarius Panama	*E. denarius* Mexico South	-3.6825	2.393996	-1.53824	0.124	-160	-490	50
E. denarius Panama	*E. denarius* Costa Rica	-1.625	2.340267	-0.69437	0.4875	-135	-550	1130
E. denarius Mexico South	*E. denarius* Costa Rica	0	2.078805	0	1	15	-450	1300
E. guzanta Mexico South	*E. denarius* Mexico South	9.479	3.174156	2.9863	0.0028 *	650	250	1000
E. thurman Panama	*E. denarius* Panama & Costa Rica	8.647436	2.77735	3.113556	0.0018 *	600	200	1080

(Fabricius) species groups (Draudt 1919-1920: 795-797) until Johnson and Kroenlein (1993b: 3-5) named *Pendantus*, noting the distinctive shape of the male genitalia labides in lateral aspect (Fig. 26). In a checklist *Pendantus* was preliminarily synonymized with *Ziegleria* K. Johnson (Robbins 2004) based on the lack of a sclerotized ridge on the lateral edge of the female 8th abdominal tergum. However, a subsequent phylogenetic analysis found that *Pendantus* is a lineage nested within *Electrostrymon* Clench, not within *Ziegleria*, which remains a phylogenetically valid genus (Duarte & Robbins 2010).

***Electrostrymon guzanta* species complex**. Highly autapomorphic male and female genitalic structures characterize the *E. guzanta* species complex (Duarte & Robbins 2010), especially the "rectangular" shape of the male genitalia labides (first noted by Johnson & Kroenlein 1993b). However, Johnson and Kroenlein (1993b) included in *Pendantus* some species, such as *Arzecla sethon* (Godman & Salvin), which lack the male genitalia labides synapomorphy. Conversely, they described new species in other genera that possess the synapomorphy (see nomenclatural list below for specifics). A possible explanation for these seemingly incongruent results is that Johnson and coworkers routinely illustrated adults and genitalia that are not from the same individual, this result being most evident when the sex of the adult and the genitalia were different (cf. Robbins & Lamas 2002 and the results below).

Electrostrymon thurman Thompson & Robbins new species

(Figs. 5-8, 24-29)

ZooBank LSID: urn:lsid:zoobank.org:pub:3F44721B-329C-4D14-BD8B-E8D11E8CBF1C

Diagnosis and Description. *Electrostrymon thurman* is placed in *Electrostrymon* following Duarte and Robbins (2010) because the female genitalia corpus bursae is less than 2 mm long, it possesses vestigial "fan-shaped" signa (Fig. 27), and the male genitalia gnathos lack teeth (Fig. 26).

Electrostrymon thurman is placed in the *E. guzanta* species complex because its male and female genitalia (Figs. 26-27) are indistinguishable from those of *E. guzanta*. Specifically, the unique rectangular posterior shape of the labides (Fig. 26) is a synapomorphy for the *E. guzanta* species complex (Duarte & Robbins 2010).

Analysis of wing pattern variation (including adult size) shows that *E. thurman* is unambiguously distinguished from the other taxa in the *E. guzanta* species complex by Characters 10, 12, 14, 15, 18, 19, and 20 (Table 1, Fig. 23). It is additionally distinguished from *E. denarius* + *E. perisus* by characters 3 and 21 and from *E. guzanta* by characters 4 and 13.

Holotype ♂ (Fig. 24). [off-white label with black ink handwriting] Panama: Chiriquí/Volcán Barú 1800 m/11[Feb]-8 [19]76/G. B. Small. [red label with black printing] Holotype/ *Electrostrymon thurman*/Thompson & Robbins. Deposited USNM.

Paratypes (27♂&8♀, deposited USNM unless noted otherwise). Costa Rica. 2♀ Mount [Volcán] Poás, May. Panamá, Chiriquí. 1♂,1♀ Cerro Punta, 5400 ft, 30 Jun 1965, 2 Jul 1965. 3♂,1♀ Cerro Totuma, 6350 ft, 21 Feb 2012 (PMT). Volcán Barú. 1♀ 5400 ft, 18 Aug 1975; 3♂,1♀ 1700 m, 22 Feb 1977, 23 Feb 1977, 19 Mar 1976, 9 Apr 1979; 11♂&1♀ 1800 m, 1-22 Feb 1976; 8♂ 1800 m, 9 Apr 1979; 1♂ 1800-2000 m, 12 Apr 1979; 1♀ 2300 m, 12 Apr 1979.

Etymology. This species is named for Albert Thurman, in recognition of his four decades of collecting and studying Panamanian Lepidoptera, and of encouraging others to do the same. The name is a noun in apposition.

Female. The sexes of *E. thurman* are associated because they occur at the same localities and have wing patterns that are exceedingly similar. It is sometimes difficult to determine the sex of an individual solely by wing pattern.

Variation. The ventral wing ground color varies from tan to gray to charcoal, as illustrated (Figs. 5-7).

Superficially Similar Species. *Electrostrymon thurman* is most likely to be confused with sympatric individuals of *A. sethon*, but is distinguished by both male and female genitalic characters, as outlined in Duarte and Robbins (2010).

Distribution (Fig. 28). Costa Rica and western Panama.

Habitat. *Electrostrymon thurman* inhabits the Tropical Lower Montane Rain Forest life zone (Holdridge 1967) and is recorded from 1,650-2,300 m elevation (Fig. 29).

Behavior. Males displaying territorial behavior were collected along a mountain road (1,800-2,000 m) on the eastern slopes of Volcán Barú, Chiriquí. Nine males were collected from 10:00-11:30 hours on 9 Apr 1979, and two more from 13:00-14:00 hours on 12 Apr 1979 (vouchers in USNM). In Feb 2012, adult males and females were observed nectaring at flowering trees at the edge of a ridgetop pasture in lower montane forest in the early afternoon on a sunny and windy day (Fig. 29).

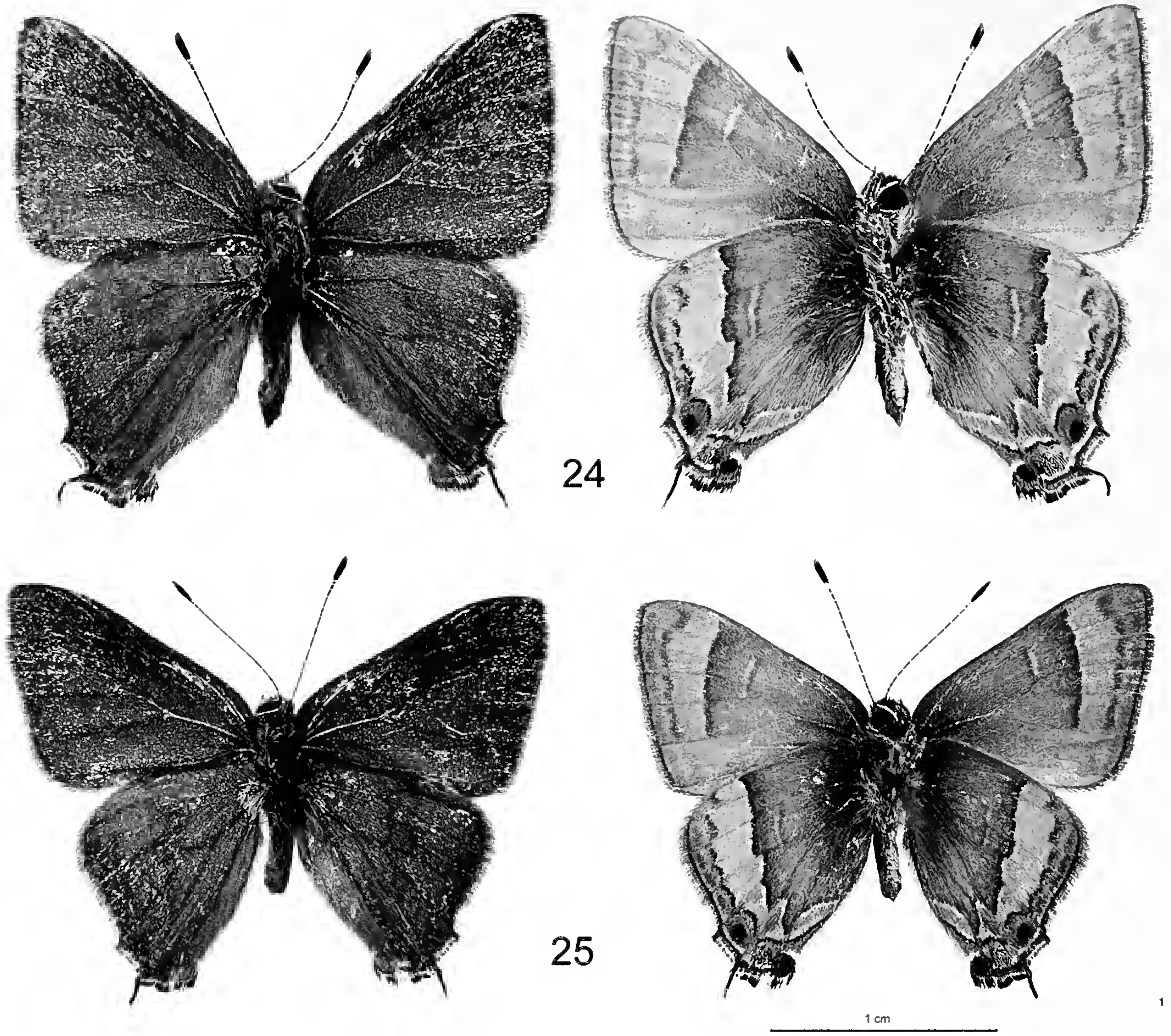
Caterpillar food "plant". Most caterpillar food "plant" records for the Calycopidina, including *Electrostrymon*, are plant detritus (Duarte & Robbins 2010, Robbins et al. 2010). We presume that caterpillars of *E. thurman* also eat plant detritus, at least facultatively.

Recognition as a distinct species. The data in Tables 1 and 2 show that *E. thurman* is phenotypically distinct. The most parsimonious cladogram (Fig. 23) suggests that it is monophyletic and phylogenetically distinct. The traits that it shares with the allopatric *E. guzanta* appear to be symplesiomorphies. The distribution of *E. thurman* overlaps that of *E. denarius*, which is part of its sister lineage. All previously proposed specific names refer to other phenotypes. Treating *E. thurman* as a distinct new species is in accord with these results.

Remarks. The distribution and elevation of *E. thurman* and *Kisutam rosemary* Thompson & Robbins are nearly identical (cf. Thompson & Robbins 2015), as far as is known. Wherever one occurs, the other might be expected. However, the two species have distinctly different biogeographical relationships. Whereas the sister species of *E. thurman* occurs in the South American mountains and Central American lowlands, the sister of *K. rosemary* is endemic to the mountains of northern Central America. They also differ in that *E. thurman* appears to be a common species while *K. rosemary* is uncommon, at least judging by the number of specimens in museum collections.

Geographical variation of *E. denarius*

Individuals of *E. denarius* from El Crucero/ Las Nubes, Managua, Nicaragua (approximately 11º55'16"N, 86º16'32"S) possess more dorsal orange scaling on both wings (Fig. 20) than others of this



Figures 24-25. Types of *E. thurman*, dorsal surface on left. **24**. Male holotype (Panama). **25**. Female paratype (Panama). Scale 1 cm.

species (Figs. 17-19), including the Nicaraguan type of *Thecla calena* Hewitson. El Crucero/Las Nubes is subtropical humid forest at 700–900 m elevation that is located from 18 km SSW to 25 km S of the city of Managua (Robbins et al. 2012a). It is part of a band of subtropical humid forest that occurs semicontinuously in a northwest to southeast direction, especially on low mountains such as Volcán San Cristóbal, Rota, Masaya, and the volcanoes in Lake Nicaragua. More on the geology of this area can be found in Weyl (1980).

The significance of this geographic variant of *E. denarius* cannot be assessed at present. Its ventral wing pattern and genitalia are typical of *E. denarius*. Of the 52 eumaeine species recorded from El Crucero/Las Nubes in Robbins et al. (2012a), *E. denarius* is the only one with a variant wing pattern. In the museum collections we examined, there are no individuals of *E. denarius* from other parts of this band of subtropical humid forest, so we cannot assess variation of the El Crucero/Las Nubes phenotype. In fact, the only other known Nicaraguan specimen of *E. denarius* is the type of *Thecla calena* from Chontales to the east of Lake Nicaragua (Robbins et al. 2012a). Finally, we note that some individuals from Mexico (Fig. 19) also have more dorsal orange suffusion than others, but not as much as those from El Crucero/Las Nubes.

Species synonymies

Godman and Salvin (1887-1901: 77) synonymized *Thecla calena* with *Tmolus denarius*, but then described *Thecla plusios* writing "This is perhaps a doubtful species" because their specimens from Guatemala were in poor condition. In a checklist (Robbins 2004), these names were treated as synonyms. The wing pattern analysis in this paper confirms both synonymies.

Johnson (1992) described *Arases aurantiaca* from a male holotype. The verbal description of its male genitalia is nondescript. The referenced figure of the male genitalia was omitted. It is unclear whether the holotype (figured on the Butterflies of America web site (www.butterfliesofamerica.com/L/Lycaenidae.htm, accessed 19 May 2015) is male or female, based on its wing shape. Robbins (2004) synonymized this species with *E. guzanta*. Regardless of the sex of the holotype, the wing pattern analysis in this paper confirms the synonymy.

Johnson and Kroenlein (1993b) described *Kisutam simplisis* from a female holotype and illustrated her genitalia along with those of *K. syllis* (Godman & Salvin). Comparing these stylized illustrations with those of *Kisutam* genitalia in Duarte and Robbins (2010) and Thompson and Robbins (2015), neither genitalia appears to belong to a species of *Kisutam*. In fact, so far as we are aware, neither would appear to be Calycopidina, unless these illustrations are inaccurate. According to the wing pattern analysis in this paper, the adult holotype female (figured on the Butterflies of America web site (www.butterfliesofamerica.com/L/Lycaenidae.htm, accessed 19 May 2015) is a female of *E. denarius*. Under Article 73.1.5 of the International Code of Zoological Nomenclature (ICZN 1999), we exclude the abdomen from the holotype, clarifying and confirming the synonymy of this species specific name with *E. denarius*, as proposed in Robbins (2004).

Angulopis strymonotis Johnson & Kroenlein was described from a chimeric holotype. The holotype of *A. strymonotis* is described as "male" on p. 20 of the text, but the adult illustrated on figure 13 on plate 5 and its legend (on an unnumbered page) label it as "female". The specimen in the BMNH labelled as holotype lacks a head and an abdomen and is identical to Johnson's figure 13. It is illustrated on the Butterflies of America web site (http://www.butterfliesofamerica.com/L/Lycaenidae.htm, accessed 19 May 2015). The ventral wing pattern of the holotype of *A. strymonotis* is indistinguishable from syntypes of *E. joya* (Dognin) in the BMNH and USNM. The genitalia of the holotype of *A. strymonotis* is described as "male" on page 20 of the text, and figure 2F partially illustrates a male genitalia that appears to belong to the *E. guzanta* species complex. Further, the original description of *A. strymonotis* states that brush organs abut the male genitalia vinculum. Brush organs are present in the *E. guzanta* species complex, but are lacking in *E. joya* (Duarte & Robbins 2010). It would appear that the adult wings and abdomen of the holotype of *A. strymonotis* belong to different sexes and to different species, a chronically occurring problem with Johnson holotypes (cf. Robbins & Lamas 2002). Regardless, under Article 73.1.5 of the International Code of Zoological Nomenclature (ICZN 1999), we exclude the abdomen from the holotype. Consequently, *Angulopis strymonotis* Johnson & Kroenlein, 1993 is a **new synonym** of *Electrostrymon joya* (Dognin, 1895), and the previous synonymy of *A. strymonotis* with *E. perisus* in a checklist (Robbins 2004), which was based on the genitalia, is now invalid.

Nomenclatural list

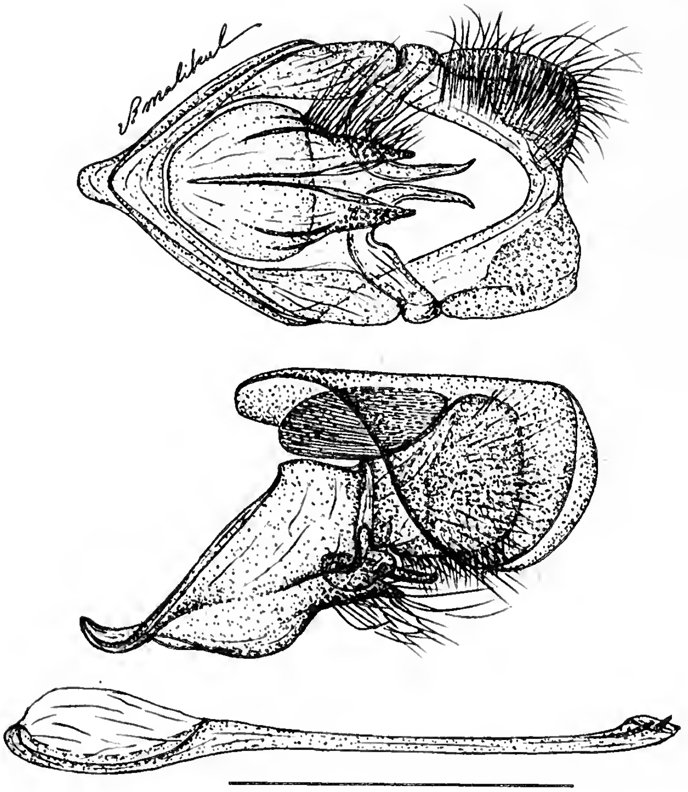
The following classification of the *E. guzanta* species complex is based on the results of the qualitative and quantitative wing pattern analyses in this paper and various nomenclatural issues addressed above. In addition, the nomenclatural status of *Angulopis strymonotis* is now changed so that it is a synonym of *E. joya*.

Electrostrymon guzanta (Schaus, 1902) (*Thecla*), type locality: Mexico (VER)
  aurantiaca (K. Johnson, 1992) (*Arases*), type locality: Mexico (CHIA)
Electrostrymon thurman Thompson & Robbins, **new species**, type locality: Panama
Electrostrymon perisus (H.H. Druce, 1907) (*Thecla*), type locality: Venezuela
Electrostrymon denarius (Butler & H. Druce, 1872 (*Tmolus*), type locality: Costa Rica
  renarius (Butler, 1873) (*Tmolus*), missp.
  calena (Hewitson, 1877) (*Thecla*), type locality: Nicaragua
  plusios (Godman & Salvin, 1887) (*Thecla*), type locality: Mexico (VER)
  simplisis (K. Johnson & Kroenlein, 1993) (*Kisutam*), type locality: Costa Rica, chimeric **holotype restricted** (ICZN, Art. 73.1.5)

Electrostrymon joya (Dognin, 1895) (*Thecla*), type locality: Ecuador
  strymonotis (K. Johnson & Kroenlein, 1993) (*Angulopis*), type locality: Ecuador, chimeric female **holotype restricted** (ICZN, Art. 73.1.5), **new synonym**

Distribution and elevation

Electrostrymon guzanta, *E. thurman*, and *E. perisus* are allopatric. *Electrostrymon guzanta* is recorded from Mexico, Guatemala, El Salvador, and Nicaragua (records from the lowlands of the United States in Texas



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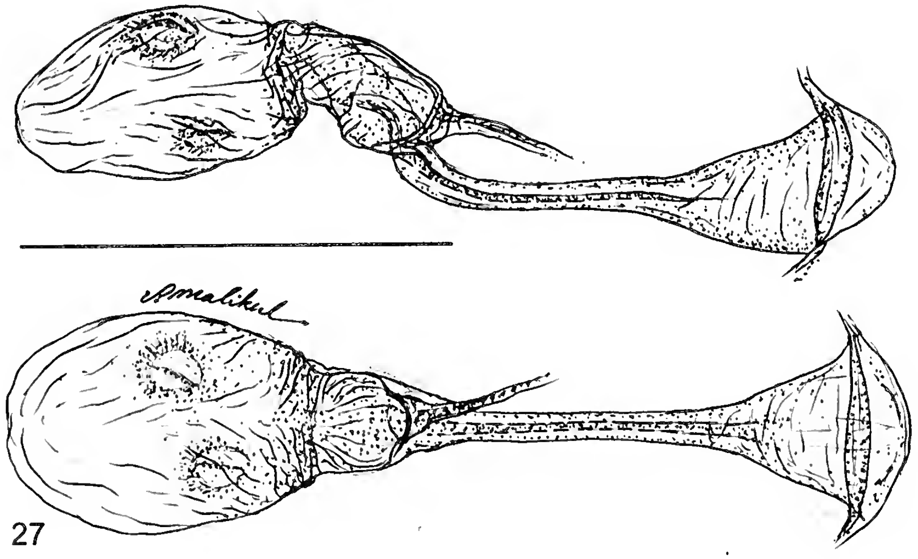

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Figures 26-27. Genitalia of *E. thurman*, posterior of insect to the right. **26**. Male, ventral aspect (top), lateral aspect with 8th tergum (middle), and penis in lateral aspect (bottom). **27**. Female, lateral (top) and dorsal aspects. Scale 1 mm.

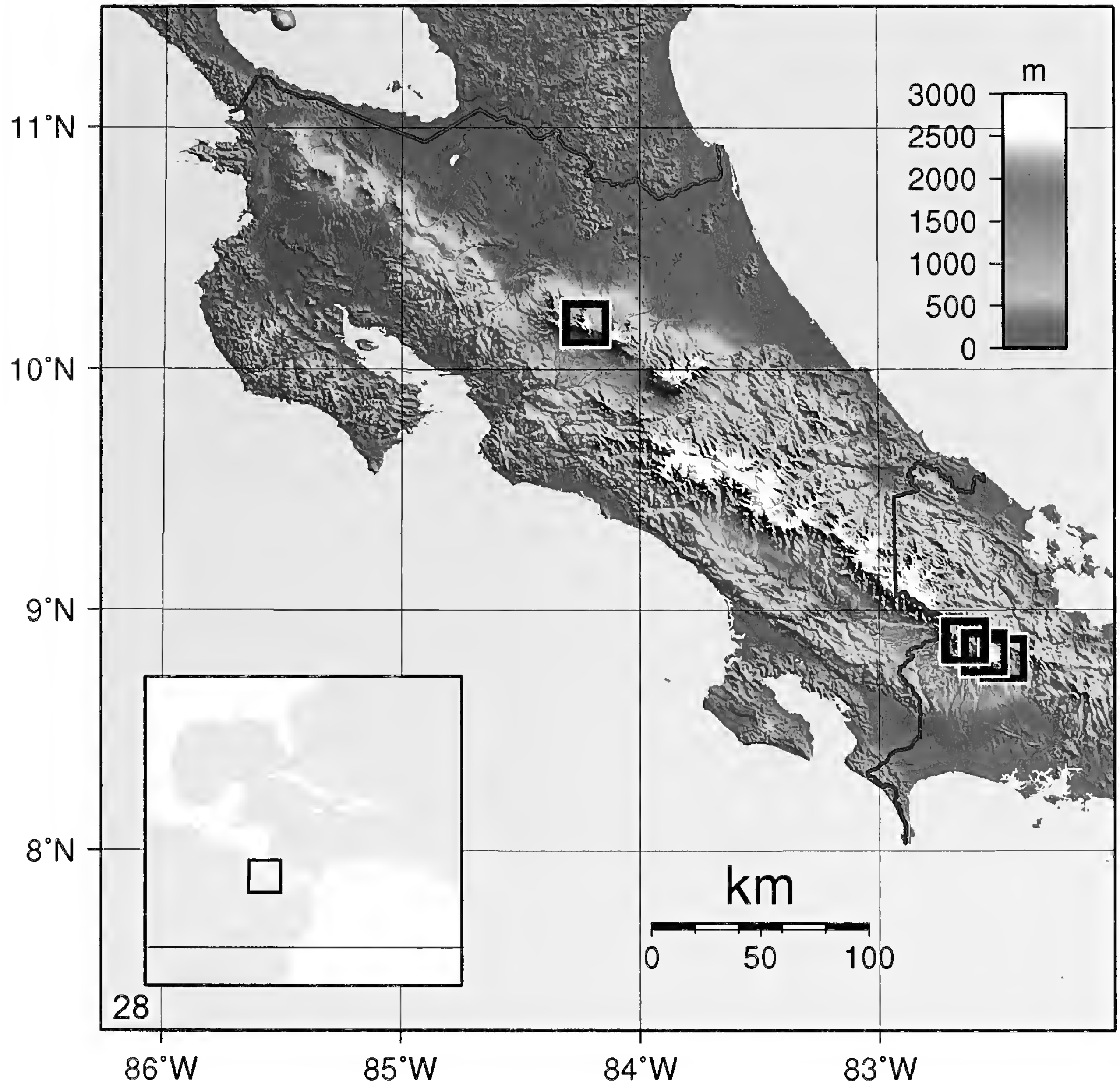


Figure 28. Distribution of *E. thurman*.

are being addressed elsewhere); *E. thurman* from Costa Rica and Panama; and *E. perisus* from Venezuela and northern Colombia. The localities where *E. guzanta*, *E. thurman*, and *E. perisus* occur have elevations that range from 1,350 m to 2,550 m (Fig. 30). There are no statistical differences in mean locality elevation rank in pairwise comparisons among these three species (Table 3). *Electrostrymon guzanta* and *E. thurman* are separated by a gap of lowland habitat in southeastern Nicaragua, and *E. thurman* and *E. perisus* are similarly separated by the lowland Isthmus of Panama. There is no evidence suggesting current dispersal across either of these lowland gaps.

The geographically most widespread species in the *E. guzanta* species complex is *E. denarius*, which is recorded from Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama. Although the southeastern-most specimen of *E. denarius* was found near the Panama-Colombia border, this species is unrecorded from South America. The localities where *E. denarius* occurs have elevations that range from 50 to 1,750 m (Fig. 31). There are no statistical differences in

Figure 29. Cerro Totuma, Chiriquí, Panama (1,950 m elevation). Adult males and females of *E. thurman* were feeding on flowering trees at the edge of this ridgetop pasture.

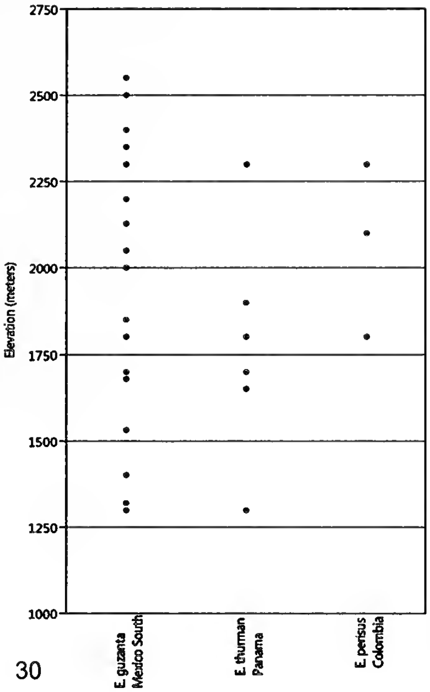
mean locality elevation rank in pairwise comparisons of *E. denarius* in different countries (Table 3).

Electrostrymon denarius occurs at significantly lower elevations than the remainder of the species complex despite elevational overlap from 1,350 to 1,750 m (Fig. 32). The mean locality elevation rank for *E. denarius* in Mexico is significantly lower than that for *E. guzanta* ($p<0.05$, Table 3). The mean locality elevation rank for *E. denarius* in Costa Rica and Panama is significantly lower than that for *E. thurman* ($p<0.05$, Table 3). We could not compare *E. denarius* elevations with those of *E. perisus* because the former is unrecorded in South America.

Allopatry, parapatry, or sympatry?

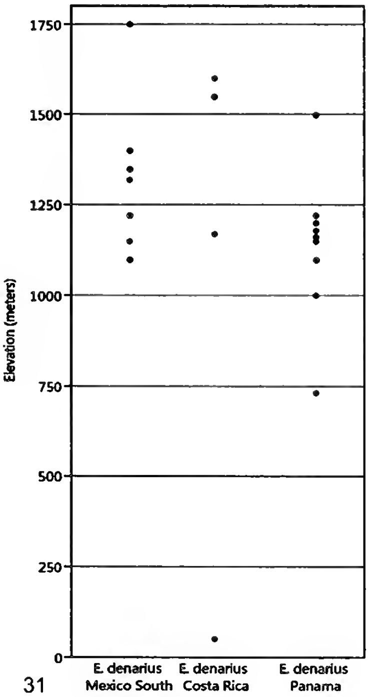
The lack of male secondary sexual organs in Lepidoptera is associated with allopatry in closely related species (Phelan & Baker 1987, Robbins et al. 2012b). Genitalic differences are hypothesized to result from sexual selection driven by female choice (Eberhard 2010, Simmons 2014), which then facilitates sympatry between closely related species following secondary contact. The four members of the *E. guzanta* species complex have uniform genitalia and lack wing secondary sexual structures. In accord with this theory, as already noted, *E. guzanta*, *E. thurman*, and *E. perisus* are allopatric with each other.

The elevational overlap between *E. denarius* and *E. guzanta/E. thurman* (Fig. 32) appears to falsify the predictions that these taxa should be allopatric or parapatric, but supplemental data would be needed to substantiate such a conclusion. Geographic range overlap is a characteristic of parapatric distributions due to reproductive interference (Key 1981, Bull 1991, Pettengill & Moeller 2012, Werner et al. 2014, Bournez et al. 2015). For example, adult insects can disperse to, and survive in, areas with reproductive interference, even if they do not successfully leave offspring.



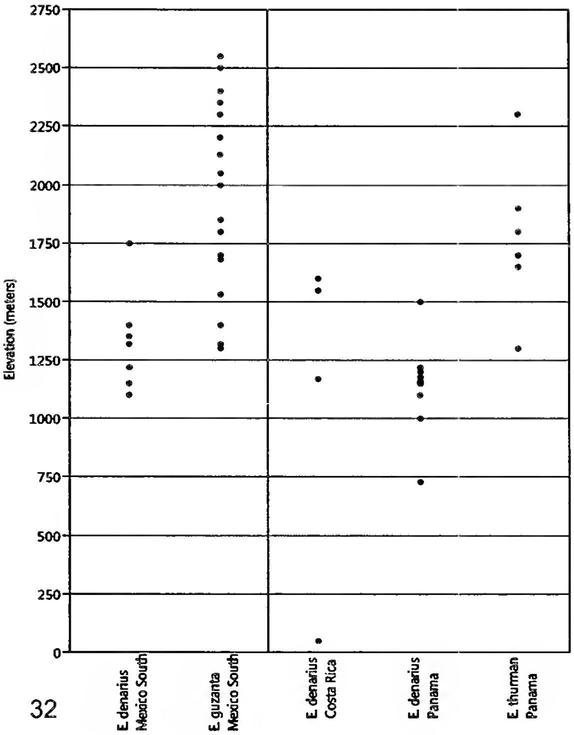
30

Figure 30. Locality elevations at which *E. guzanta, E. thurman,* and *E. perisus* have been found. There is no statistical difference among the species (Table 3).



31

Figure 31. Locality elevations in different countries where *E. denarius* has been found. There is no statistical difference among the countries (Table 3).



32

Figure 32. *Electrostrymon denarius* occurs at lower elevations than *E. guzanta* in Mexico and at lower elevations than *E. thurman* in Costa Rica/Panama (Table 3).

Documentation of reproductive biology is needed to determine whether the distributions of *E. denarius* and *E. guzanta/E. thurman* are parapatric, as predicted.

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EDITOR'S NOTE

The electronic edition of this article has been registered in ZooBank to comply with the requirements of the amended International Code of Zoological Nomenclature (ICZN). This registration makes this work available from its electronic edition. ZooBank is the official registry of Zoological Nomenclature according to the ICZN and works with Life Science Identifiers (LSIDs). The LSID for this article is: urn:lsid:zoobank.org:pub:3F44721B-329C-4D14-BD8B-E8D11E8CBF1C. Registration date: 9 July 2016. This record can be viewed using any standard web browser by clicking on the LSID above.

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A comparison of macro-moth assemblages across three types of lowland forest in Fiji

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Abstract. Although many studies have shown a relationship between forest type and quality on resident lepidopteran assemblages, there appears to be an absence of such studies in Pacific island countries. This study compared nocturnal macro-moth assemblages in a native rainforest, mixed forest and a plantation of exotic trees (mahogany) near Suva, Fiji Islands. Four nightly surveys (4 h from dusk) were performed in each forest type using a mercury vapour light. A total of 491 macro-moths belonging to 92 species in nine families were collected. No statistically significant differences in abundance, species richness and various diversity indices were observed across the different forest types. Endemic species were collected in all three locations, although significantly more endemic individuals were collected in the native forest compared to the exotic plantation. When examining species composition, 'analysis of similarity' (ANOSIM) and non-metric multidimensional scaling suggested that the faunas observed in the mixed forest and the exotic forest might be different, with the fauna in the native forest intermediate between these two. Although we found no major differences in the moth assemblages in these three sites, the results collected provide baseline data for future studies and comparisons with other localities. The results also reinforce previous findings which demonstrate that exotic plantations and semi-degraded forests may still provide useful refuges for endemic insect species of conservation value.

Key words: Ecological monitoring, indicator species, Lepidoptera, South Pacific.

Introduction

Herbivorous insects, such as Lepidoptera, have a close functional relationship with the vegetation they utilize, and hence often respond sensitively to deforestation and subsequent forest regeneration (Hilt 2005). The distribution and quality of plant communities, in terms of host plants for larvae and floral resources for adult insects, can have immediate effects on the abundance and composition of the co-occurring lepidopteran fauna (Robinson 1975; Fisher 2011). Because of their sensitivity to habitat quality, nocturnal moths have long been considered valuable indicators for monitoring the ecological effects of forest change and for providing a surrogate measure of forest 'health' (Willottf 1999; Schulze et al. 2000; Beck et al. 2002; Axmacher et al. 2004, Summerville et al. 2004).

The destruction of native forests remains a serious threat to endemic terrestrial fauna and flora of Pacific islands. Since 1967 an estimated 19% (140,000 ha) of Fiji's forests have been lost, principally due to conversion to commercial agriculture, rural development projects, spread of small settlements and the development of urban growth (Evenhuis & Bickel 2005; Prasad 2010). A comprehensive study of the Macro-Lepidoptera of Fiji was produced by Robinson (1975) and a later checklist provided by Evenhuis (2013), with new species records for Fiji regularly being reported (e.g. Clayton 2002, 2008, 2010, 2011, 2015; Tikoca et al. 2016a). However,

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as far as we can ascertain, in South Pacific islands there have been few, if any, comparisons of moth assemblages among forest types, nor any work utilizing macro-moth communities as indicators of habitat change, habitat degradation or restoration success.

Fiji still contains a wide range of forest types, from pristine native cloud and rain forests to highly managed plantations containing exotic tree species (Prasad 2010; Sue 2010). The aim of this study was to examine the assemblages of nocturnal macro-moths across three secondary lowland forests near Suva, Viti Levu: a native forest, an exotic plantation and a mixed forest containing regeneration of native species after commercial use. The relationships between forest type and macro-moth abundance, species richness, patterns of endemism, and species composition were assessed. In addition, two moth-based 'Forest Quality Indices', as proposed by Kitching et al. (2000), were evaluated for their potential and applicability as conservation tools in a Pacific island setting.

Materials & methods

Study sites

Macro-moth assemblages were compared in three secondary lowland forest types, namely: (i) native forest (Savura), (ii) exotic plantation forest (Mt. Korobaba) and (iii) mixed forest (Colo-i-Suva). The three sites are located on the south-eastern part of Fiji's largest Island, Viti Levu, at elevations < 300 m above sea level (a.s.l). Savura (-18.070, 178.448) consists of 397 ha of native forest located in the province of Naitasiri, 14 km west of Nausori. The site was established as a forest reserve in 1963 and has not been logged since that time. A total of 587 plant species have been recorded from the area, of which 560 (96%) were considered native to Fiji, with 29% considered endemic. The dominant plant families present include Myristicaceae, Cyatheaceae and Clusiaceae (Keppel et al. 2005).

Mahogany (*Swietenia macrophylla*) plantations cover a considerable area of the south-eastern parts of Viti Levu (Tuiwawa et al. 2013). Mt. Korobaba is located 8 km west of Suva (-18.097, 178.388), and was cleared and systematically planted and managed for the mahogany timber trade from the late 1950's to 1970's (Kirkpatrick & Hassall 1985). The sampling sites within Mt. Korobaba were in elevations <200 m a.s.l., in areas which contained mature unlogged mahogany forest with a 90% relative dominance of mahogany.

Colo-i-Suva is located in the province of Naitasiri, 7 km north-west of Suva, (-18.328, 178.274). Sampling sites were within a two and a half square kilometre of tropical rainforest that was set up as a reserve in 1964 (soon after mahogany stands were planted in the area) and established as the Colo-i-Suva forest park in 1970 (Paine 1991). The vegetation at Colo-i-Suva contains a mixture of both exotic timber species and native species at various growth stages in the understorey, and approximately 70 native plant species have been recorded from the site (Tuiwawa & Keppel 2013).

Light trapping and insect identification

Moths were collected using a manual light trapping system, consisting of a 125W mercury vapour lamp powered by a portable generator and a 2 x 2 m white sheet positioned in front of the light source which was spread out and secured onto nearby trees or branches. All moths that landed on the white sheet were collected and placed into jars charged with ethyl acetate as a killing agent. Each sample consisted of the individuals collected in one night in the four hours after dusk.

Previous research comparing light trap efficiency at one of the field sites (Colo-i-Suva) indicated that four nights of sampling would obtain a good proportion (c. 90%) of the estimated moth species present (Tikoca 2016c). Therefore, sampling was carried out on four nights within each site, performed over six nights in October 2012 with two sites being randomly selected for sampling on each occasion.

Specimens were assigned to species level by reference to keys, images and nomenclature provided by Robinson (1975), Holloway (1998), Clayton (2004), CSIRO (2011) and Evenhuis (2013), with family designations as revised by Zahiri et al. (2011). Species were classified as being 'endemic' if they have only been recorded from Fiji. This classification is based on taxa at the species level, and no account is taken of possible endemic sub-species. We accept that any designation of a species as endemic has to be made with some reservations given the incomplete knowledge of occurrences in different island groups in the South Pacific, and the relatively unstable taxonomy in some groups. Individuals of the large genus *Cleora* were not identified to species level and '*Cleora* sp.' was treated as a single taxon. Of the ten species belonging to the genus *Cleora* in Fiji only *C. injectaria* and *C. samoana* are not considered endemic. However, as neither of these species was recorded in this study, '*Cleora* sp.' was considered as an endemic taxonomic unit in our analyses.

Measures of community structure

For each sample, macro-moth abundance (N), species richness (S) and rate of endemism were obtained. Species diversity was defined using the Shannon-Weiner index [$H' = -\Sigma p_i.\log(p_i)$] and evenness index [$J = H'/\log(s)$], where p_i = proportion of individuals consisting of the *i*th species.

Kitching et al. (2000) proposed an index to measure forest quality in terms of the abundance of certain moth families, calculated as: 100 × [Geometridae / (Arctiidae + Noctuidae)]. However, due to taxonomic revisions at family level, Arctiidae and some Noctuidae are now placed in the family Erebidae (Zahiri et al. 2011). Therefore we calculated the Forest Quality Index (FQI) proposed by Kitching (2000) using previous taxonomy, and then a second FQI ('Tikoca FQI') based on current family-wise designations calculated as: 100 × [Geometridae / (Erebidae + Noctuidae)]. Each FQI was calculated for each of the twelve samples separately and also based on the overall catch from each forest using pooled data.

Statistical analysis

All statistical analyses were performed using Minitab (v17, Minitab Inc, USA) and Community Analysis Package (v4, Pisces Conservation Ltd, UK). Forest types were compared using a one way analysis of variance (ANOVA) test with *post-hoc* Tukey's tests used for pairwise comparisons after a significant result. Abundance of moths and species richness data were $\log_{10}$ transformed prior to analysis to help reduce the effects of the relationship between mean and variance (Tikoca 2016c), and prior to ANOVA being performed, homogeneity of variance was verified for all variables examined using Levene's test. Due to a prevalence of zero scores, the abundances of each family at the three sites were compared using a non-parametric Kruskal-Wallis test.

The species-sample matrix obtained was extremely sparse, with 79% of cells equal to zero. Legendre and Gallagher (2001) indicated that, with sparse matrices such as this, principle components analysis on raw data might be inappropriate because samples that actually contain no common species may appear similar due to a prevalence of shared absences. Therefore we compared the compositions of the moth faunas among the three forest types using non-metric multidimensional scaling (NMDS) and 'analysis of similarity' (ANOSIM) using square root transformed data (Community Analysis Package; Henderson & Seaby 2008). For the NMDS, a Bray-Curtis similarity measure was employed and principal components analysis used to give initial positions of the samples. The ANOSIM procedure examines whether samples from within pre-defined groups are more similar in composition than samples from different groups, again using a Bray-Curtis

Table 1. Abundance of individuals and number of species in macro-moth families collected at three forests near Suva, Viti Levu, Fiji, produced by four hours trapping on four separate nights using an MV light.

	Individuals				Species			
	Savura	Colo-i-Suva	Mt Korobaba		Savura	Colo-i-Suva	Mt Korobaba	
Family	Native	Mixed	Exotic	Total	Native	Mixed	Exotic	Total
Cossidae	1	0	0	1	1	0	0	1
Erebidae	99	50	63	212	20	19	21	32
Geometridae	81	39	30	150	9	10	11	21
Limacodidae	7	6	3	16	4	4	2	7
Noctuidae	22	29	13	64	10	15	16	19
Nolidae	2	7	6	15	1	3	4	5
Sphingidae	3	1	1	5	2	2	1	3
Thyrididae	5	3	7	15	2	2	2	3
Uranidae	4	4	5	13	1	1	1	1
Grand Total	224	139	128	491	50	55	48	92
No. of singletons					21	27	24	34
Proportion of Singletons (%)					42.0	49.1	50.0	37.0

Table 2. Abundance and species richness of macro-moths and levels of endemism at three forests near Suva, Viti Levu, Fiji, produced by four hours light trapping (mean ± se; n = 4). Samples with different letter codes (**a** or **b**) were separated by Tukey test at $P < 0.05$.
* - ANOVA performed on $\log_{10}$ transformed data

Site	**Savura**	**Colo-i-Suva**	**Mt Korobaba**		
Forest type	Native	Mixed	Exotic	$F_{2,11}$	P
Abundance (N)	56.0 ± 13.8	34.8 ± 10.4	32.0 ± 9.9	0.86*	0.457
Species richness (S)	20.5 ± 4.2	20.8 ± 6.0	17.2 ± 4.3	0.13*	0.881
Species diversity (H')	2.36 ± 0.23	2.61 ± 0.35	2.54 ± 0.25	0.21	0.815
Evenness (J')	0.80 ± 0.06	0.91 ± 0.01	0.93 ± 0.02	3.39	0.080
Endemic abundance (EN)	37.2 ± 8.0^{a}	14.5 ± 4.4^{ab}	10.0 ± 1.4^{b}	5.06*	0.034
Endemic abundance (EN %)	69.4 ± 6.5	42.5 ± 6.6	40.5 ± 10.4	4.03	0.056
Endemic richness (ES)	7.8 ± 1.1	7.5 ± 2.4	5.2 ± 0.9	0.36*	0.708
Endemic richness (ES %)	40.2 ± 6.1	33.5 ± 7.1	35.2 ± 8.5	0.23	0.799
Site total Kitching FQI	118.6	57.4	40.5	-	-
Site total Tikoca FQI	68.6	49.4	39.5	-	-
Mean sample Kitching FQI	156.8 ± 64.2	54.9 ± 16.0	95.7 ± 68.1	0.87	0.450
Mean sample Tikoca FQI	65.9 ± 6.2	46.3 ± 15.6	94.3 ± 68.6	0.95	0.423

measure of similarity. The test statistic produced, R, ranges from -1 to +1, with +1 indicating all the most similar samples are within groups, and -1 indicating that all the most similar samples are never in the same group. Both of these multivariate procedures were performed three times: on a matrix including the abundance of all species, a matrix including only species with total abundance ≥ 3, and on a sample-by-family matrix.

Results

Moth abundance and diversity

A total of 491 macro-moth individuals belonging to 9 families and 92 species were collected. Three families - Erebidae, Geometridae and Noctuidae - made up the majority of individuals (87%) and species (78%) collected (Table 1; Appendix).

The total number of species collected at each site was similar: 55 species were recorded at Colo-i-Suva, 50 species at Savura and 48 species at Mt. Korobaba. There were no significant differences in abundance among the three sites for any of the families recorded (Kruskal-Wallis tests, $P > 0.180$ in all cases) (Table 1). There were also no statistically significant differences among the three forests in terms of total moth abundance, species richness, species diversity and evenness of moth assemblages (Table 2).

A considerable proportion (c. 35%) of the total catch in each forest type consisted of endemic species, although there were no statistically significant differences among the three forests in terms of numbers of species or proportions of endemic species in the individual collections (Table 2). However, there were clear differences in the abundances of endemic species among the three forests. The exotic forest at Mt Korobaba had significantly fewer endemic individuals than the native forest at Savura, with the mixed forest at Colo-i-Suva being intermediate between these two extremes (Table 2).

Comparison of macro-moth assemblage composition

When comparing the three forests in a pairwise fashion, the ANOSIM procedure identified no significant differences among the moth faunas in the three locations when considering family-level identifications ($R < -0.10$; $P > 0.35$). However, the ANOSIM procedure indicated there was moderate evidence that the moth assemblages in the mixed and exotic forests exhibited some differences when considering all species ($R = 0.19$; $P = 0.07$) and when considering only those species with abundances ≥ 3 ($R = 0.18$; $P = 0.10$). The findings from the ANOSIM were supported by the results of the NMDS (Figure 1), where no obvious clustering of the samples from the three forests occurred when the analysis was based on families (Figure 3c). However, some separation of the groups was observed along NMDS Axis 1 when the analysis was based on species-level identifications, especially between the moth samples taken from the mixed and the exotic forests (Figure 1a,b).

Twenty percent of the total species recorded in this study were found in all three forest types (Figure 2; Appendix). In addition, a further 27% of species were shared by at least two of the sites (Figure 3). However, this indicates that over half of the species recorded (53%) were only found at a single site, and thus may have potential as indicators of certain habitat types. Unfortunately 34 of these 49 site-unique species were represented by singletons and thus could not be considered as indicator species. Similarly, a further six of the site-unique species were only recorded in a single night's trapping and thus exhibited no consistency of capture within that location. Indeed, no species were found that were unique to a single site and occurred in all of the samples taken from that site.

However, based on the results of the NMDS analysis, there appeared some tendency for the abundances of *Ericaea leichardtii* and *Ericaea inangulata* (Erebidae), and less so *Sasunaga oenistis* (Noctuidae) and *Rusicada nigritasis* (Erebidae), to be correlated (rank correlation) with the NMDS Axis 1 score, indicating a positive association with the exotic forest. Also, by examining the raw data, it was found that two endemic taxa, *Cleora* sp and *Calliteara fidjiensis*, made up approximately 50% of the individuals in the native forest at Savura, and so it might be speculated that a high abundance of these taxa may indicate high quality forest in a Fijian setting.

Forest quality indices

The values of the FQI proposed by Kitching *et al.* (2000) and the alternative 'Tikoca FQI' proposed here were highly correlated across the 12 moth samples ($r_s = 0.944$, $P < 0.001$). When considering the FQIs based on the total catch at each site, both FQIs exhibited a similar pattern: the FQIs for the native forest at Savura were considerabley higher that that seen in the exotic forest at Mt Korobaba, with the mixed forest at Colo-i-Suva intermediate between these two (Table 2).

However, there were some discrepancies, and a difference in the ranking of sites, when using FQIs based on the total catch and those based on the sample means (Table 2). These anomolies resulted primarily because some samples consisting of small numbers of individuals (e.g. 10, 14 and 16) produced some extreme FQI values, such as an FQI of 300 for one sample from the exotic forest at Mt Korobaba. This value was given equal weighting when the mean FQI values for Mt Korobaba was calculated (95.7 & 94.3), but the small number of individuals meant the effect of this sample on the pooled FQI estimates (40.5 & 39.5) was much reduced.

DISCUSSION

Moth abundance, diversity and composition

Many previous studies have examined macro-moth community patterns in forests as a response to the state of the forests studied, including logging and recovery regimes (Fisher 2011; Hilt 2005; Willott 1999), natural disturbance (Chaundy 1999), reforestation age (Taki et al. 2010), native and agricultural habitats (e.g. Ricketts et al. 2001), and plantations (Hawes et al. 2009). Often there are clear negative relationships between moth abundance and species richness with increasing habitat degradation and forest disturbance (Hawes et al., 2009; Ricketts et al. 2001). However, only slight differences were found in the abundance and species diversity of the moth faunas in the three different Fijian forests investigated here. The lack of distinctiveness may be due to the forests we examined all being geographically close to each other and in recent years they have all suffered similarly low amounts of disturbance in terms of logging management. Also, this study was performed over a relatively narrow time period. Recent work has identified considerable seasonal fluctuations in Fijian moth populations, and it is possible that clearer differences do occur between forest types at different times of the year (Tikoca et al 2016b).

The proportion of singletons was high for each location (> 40%), and for the total catch (37%), which suggests that, even though the moth sampling regime was based on previous appraisals of suitable sampling effort (Tikoca 2016c), the number of samples used per site was insufficient in this case (Coddington et al. 2009). However, given the various summary statistics used to compare abundance and diversity of the moth assemblages in each forest type, we do not believe that the lack of statistically significant results occurred due to a lack of statistical power, and was more a reflection of the small differences that actually occurred between sites.

Although there are few data on host plant specificity for Fijian moth species, we can assume that endemic moth species primarily utilize native host plants, and that diversity of endemic plants should be associated with high incidence of endemic

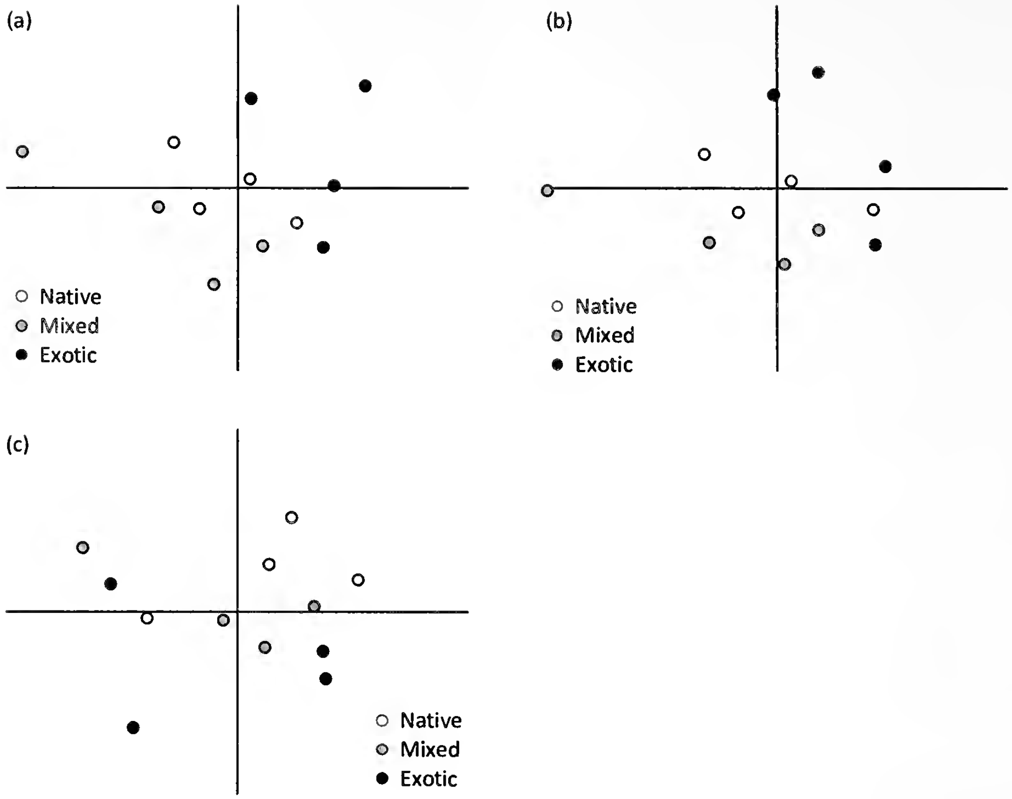

Figure 1. Scatter plots of NMDS Axis 2 versus NMDS Axis 1 scores of twelve macro-moth samples. NMDS was performed on square-root transformed data of moths collected during one nights sampling in a native (Na; Savura), a mixed (Mi; Cool-i-Suva) and an exotic (Ex; Mt Korobaba) forest on Viti Levu, Fiji Islands: (**a**) based on NMDS on data for all species, (**b**) based on NMDS on data for species represented by ≥ 3 individuals and (**c**) based on the abundance of each family in each sample.

moths (Miller & Hammond 2007). This turned out to be the case: Savura had much higher abundance (threefold) of endemic individuals than the other two forests studied, and Savura is also the most floristically diverse forest with the highest degree of indigenous plant species and composition (Keppel et al. 2005). Conspicuous numbers of endemic moths were also recorded at Colo-i-Suva and Mt. Korobaba which suggests that these moth species are finding adequate resources in these habitats. The value of plantations of exotic tree species for providing habitats for native invertebrates has been observed previously (e.g. Pawson et al. 2010, 2011), but until more is known of the specific life history requirements of Fijian endemic moth species no explicit management actions can be taken in order to increase their numbers at these, and other, locations.

In terms of species composition, only 20% of species were found at all three sites, and the multivariate methods suggested there could be dissimilarities in the compositions of the moth assemblages at the different sites. However, this separation was not between the exotic and native forest as might have been predicted, and thus did not indicate any gradient of change in moth assemblages from high quality native forest to low quality exotic plantation, with mixed forest having a fauna intermediate between these two. Although the data obtained suggested that a few species might show some weak associations with certain forest types, we could not identify any strong candidates as indicators of habitat quality or class.

The moth-based Forest Quality Index proposed by Kitching et al. (2000) utilized family-level identifications, and in upland rainforests in Queensland, Australia, FQI values of 98.7 for uncleared remnants, 68.2 for regrowth remnants and 18.6 for 'scramberland' remnants were obtained. The values we obtained using the pooled catches for each site were of similar magnitude: 118.6 for the native forest at Savura, 57.4 for the mixed forest at Colo-i-Suva and 40.5 for the exotic plantation at Mt. Korobaba. The ranking of the sites by these pooled-data FQI scores appeared sensible, in that the FQI ranks matched the sequence of habitat quality we had notionally pre-determined: exotic → mixed → native forest. However, the values we obtained when using the sample averages suggest that these indices can produce some highly anomalous values when sample sizes are small, and might only be of value when a large number of individuals (> 100) has been recorded at each location.

Changes of macro-moth community composition with forest structure over time

The abundance and diversity of macro-moths in Colo-i-Suva revealed an interesting development in this community over the last 50 years or so. One of Robinson's (1975) primary collecting sites in the 1960s and 1970s was Colo-i-Suva, where he identified the dominant species as *Nola fijiensis* (Nolidae), *Progonia micrastis* (Noctuidae), and *Hypenagonnia* spp. (Noctuidae). In the current study, none of these species were encountered at the Colo-i-Suva site at all (although additional collections made by the authors at Colo-i-Suva have since revealed a few occurrences of *Hypenagonnia* spp. but neither of the other two species). The dominant taxa in our collections from Colo-i-Suva were *Cleora* sp. (Geometridae), *Calliteara fidjiensis* (Lymantridae) and *Spodoptera mauritia* (Noctuidae) (Appendix). The Colo-i-Suva area was cleared to aid the mahogany trade from 1950–1960 (Tuiwawa et al. 2012), which means Robinson's collecting was conducted during the late 1960s/70s on a disturbed forest system, and consequently *Nola fijiensis* was described by Robinson (1975) as a species typical of a disturbed lowland forest. The forest at Colo-i-Suva has changed considerably over the last 50 years: the understory of largely native forest plant species has been allowed to develop and remnant mahogany plants have matured. Robinson (1975) suggested that moth faunal composition develops with forest structure and age, and the absence of *N. fijiensis* in Colo-i-Suva during the current study suggests that the recovery of the forest may have caused a shift in macro-moth species composition and the loss of this species.

Conclusions

Although this study showed that the three forest types sustain similar macro-moth communities in terms of abundance and species richness, the major difference identified was the ability of the native forest to sustain higher populations of endemic species than the exotic forest. Over two thirds of the total macro-moths collected in the native forest belonged to endemic species, and this relatively large population of endemic moths in the native forest may be explained by the high frequency of indigenous plant species that presumably support them, although this hypothesis requires further research on host plant usage for confirmation.

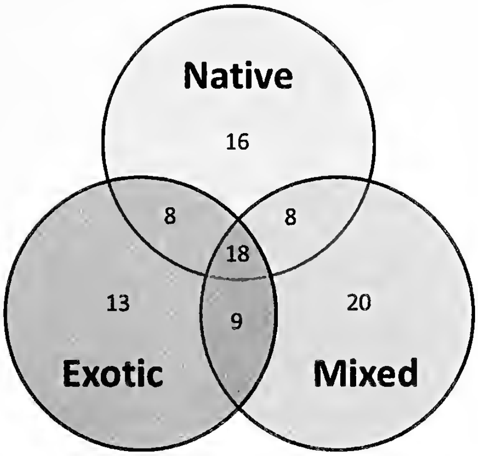

Figure 2. Venn diagram illustrating the number of moth species (total = 92) collected in a native (Savura), a mixed (Cool-i-Suva) and an exotic (Mt Korobaba) forest on Viti Levu, Fiji Islands. The numbers are based on total catches obtained on four sample nights in each forest using a MV-lamp combined with hand collecting of specimens.

With a caveat that sample numbers must be large to avoid anomalous values, the use of forest quality indices appears to have some potential as a tool to compare the quality of Fijian forests in terms of their moth assemblages. Endemic moth species were also found in considerable numbers in both the mixed and exotic forest, and management of these sites to enhance their ability to sustain native invertebrate species should be further explored.

Acknowledgements

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APPENDIX. Species of moths recorded using a mercury vapour lamp for four nights at each of three forest sites near Suva, Fiji Islands, October 2012.

Family	Species	Savura	Colo-i-Suva	Mt. Korobaba
Cossidae	*Acritocera negligens*	1	0	0
Erebidae	*Achaea robinsoni*	1	0	1
	Adetoneura lentiginosa	0	0	1
	Aedia sericea	0	2	0
	Argina astraea	0	3	0
	Asota woodfordi	0	1	0
	Bocana manifestalis	2	0	1
	Calliteara fidjiensis	52	11	2
	Dysgonia duplicata	2	1	0
	Dysgonia prisca	1	2	1
	Ericaea inangulata	3	2	7
	Ericaea leichardtii	10	3	10
	Euchromia vitiensis	1	0	0
	Eudocima fullonia	1	0	0
	Hydrillodes surata	2	7	2
	Hypenagonia emma	3	0	0
	Hypocala deflorata	0	0	4
	Mecodina variata	2	0	1
	Mocis trifasciata	0	0	1
	Neogabara plagiola	0	1	0
	Nyctemera baulus	1	0	0
	Oeonistis delia	6	2	3
	Oxyodes scrobiculata	4	1	13
	Palaeocoleus sypnoides	2	2	1
	Polydesma boarmoides	0	3	5
	Rhesalides curvata	0	2	2
	Rusicada nigritasis	1	0	3
	Rusicada vulpina	0	1	0
	Serodes mediopallens	0	1	2
	Serrodes campana	1	0	0
	Simplicia cornicalis	1	2	1
	Thyas coronate	0	0	1
	Thyas miniacea	3	3	1
Geometridae	*Agathia pisina*	1	0	0
	Anisodes gloria	0	1	0
	Anisodes monetara	5	6	4
	Anisodes niveopuncta	0	0	1
	Anisodes oblivaria	2	1	0
	Bulonga philipsi	6	2	1
	Chlorochaeta cheromata	0	0	1
	Chloroclystis encteta	0	2	0
	Cleora sp.	59	21	14

APPENDIX. Cont.

Family	Species	Savura	Colo-i-Suva	Mt. Korobaba
	Gelasma stuhlmanii	0	0	1
	Gymnoscelis sara	0	1	0
	Horisme chlorodesma	0	3	0
	Mnesiloba eupitheciata	0	0	2
	Nadagara irretracta	0	1	0
	Polyclysta gonycrota	0	0	2
	Pseuderythrolopus bipunctatus	0	1	1
	Pyrrhorachis pyrrhogona	1	0	2
	Thalassodes pilaria	3	0	0
	Thalassodes chloropis	0	0	1
	Thalassodes figurate	1	0	0
	Thalassodes liquescens	3	0	0
Limacodidae	*Beggina albafascia*	0	1	2
	Beggina bicornis	0	1	0
	Beggina mediopunctata	2	0	0
	Beggina minima	2	1	0
	Beggina unicornis	1	0	0
	Beggina zena	0	3	1
	Beggina sp.	2	0	0
Noctuidae	*Aegilia vitiscribens*	0	2	0
	Agrotis ipsilon	0	1	0
	Athetis thoraicica	0	0	3
	Chasmania tibialis	1	1	0
	Chrysodeixis eriosoma	8	1	3
	Condica conducta	0	1	0
	Condica illecta	1	3	2
	Dactyloplusia impulse	0	1	0
	Gyrtonia purpurea	0	1	0
	Leucania venalba	1	0	0
	Leucania yu	1	1	0
	Penicillaria jocosatrix	0	1	0
	Sasunaga oenistis	2	0	3
	Spodoptera litura	0	1	0
	Spodoptera mauritia	4	10	0
	Stictoptera stygia	0	1	1
	Stictoptera vitiensis	1	2	1
	Targalla delatrix	1	0	0
	Tiracola plagiata	2	2	0
Nolidae	*Austrocarea albipicta*	2	0	1
	Barasa triangularis	0	2	1
	Earias flavida	0	4	0
	Maceda mansueta	0	0	1
	Maceda savura	0	1	3

APPENDIX. Cont.

Family	Species	Savura	Colo-i-Suva	Mt. Korobaba
Sphingidae	*Macroglossum godeffroyi*	2	1	0
	Theretra nessus	1	0	0
	Theretra silhetensis	0	0	1
Thyrididae	*Banisia anthina*	0	1	0
	Banisia messoria	4	0	6
	Striglina navigatorum	1	2	1
Uraniidae	*Urapteroides anerces*	4	4	5

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Review of the West Indian *Astraptes xagua* (Lucas) complex (Hesperiidae: Eudaminae) with the description of a new subspecies from the Bahamas

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Abstract. *Astraptes xagua* (Lucas) is one of six species within the genus recorded from Cuba, Hispaniola, and the Bahamas in the West Indies. Although Steinhauser and J.Y. Miller completed a review of *Astraptes* based on morphological characters, the advent of molecular phylogenetic analysis provides further insight into the current status of the *Astraptes xagua* complex. We reinstate *A. christyi* (Sharpe) as a species-level taxon based on the differences in genitalia and *COI* barcodes, and describe a new subspecies, *A. xagua harveyi* Clench, Steinhauser and J. Y. Miller, type locality North Andros Island, Bahamas. Thus, the *A. xagua* complex consists of two species, one of which is divided into two subspecies.

Key words: Bahamas, neotropical, *COI*, genitalia.

Resumen. *Astraptes xagua* (Lucas) es una de las seis especies dentro del género registrado para Cuba, la Española, y las Bahamas en las Indias Occidentales. Aunque Steinhauser y J.Y. Miller completaron un examen de *Astraptes* basado en caracteres morfológicos, el advenimiento del análisis filogenético molecular proporciona información sobre el estado actual de la especies del complejo *Astraptes xagua*. Restablecemos *A. christyi* (Sharpe) como especie basados en las diferencias en los genitales y el *COI*, códigos de barras y describimos una nueva subespecie *A. xagua harveyi* Clench, Steinhauser y J. Y.Miller cuya localidad tipo es el norte de la isla de Andros, en las Bahamas. Así, el complejo *A.xagua* consta de dos especies, una de las cuales se divide en dos subespecies.

Palabras clave: Bahamas, neotropical, *COI*, genitalia.

INTRODUCTION

The genus *Astraptes* Hübner includes some very showy, robust-bodied skippers that are geographically distributed throughout the southern United States, Central and South America in addition to the West Indies with more than 26 species described thus far. This genus is distinguished by the narrow costal fold on the male forewing and the antennae extending along approximately one half of the forewing length with tails on the hindwing absent in the six species present the West Indies. The genus has been reviewed in whole or in part by Lindsey (1925), Williams and Bell (1933), W. H. Evans (1952), and more recently by Pelham (2008), Warren et al. (2009) and Mielke (2005) in addition to Steinhauser (1986, 1989), and Steinhauser and Miller (unpublished ms 2001circa 2004). Although we completed a rigorous analysis of the genus based on morphological treatment, it became obvious that with the number of cryptic species discovered by Herbert et al. (2004) and additional discussions by A. V. Z. Brower (2005) that further analyses would be required for a taxonomic revision.

Astraptes xagua (Lucas) currently includes two formally described subspecies, *A. x. xagua* and *A. xagua christyi* (Sharpe). Another potential subspecies has been known since Donald J. Harvey and subse-

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quently Clench (1977) collected it on North Andros 40 years ago. *Astraptes xagua* is bivoltine in Hispaniola and Cuba with most records in December to January in addition to June and July (Smith et al 1994; Matthews et al. 2012). However, the emergence patterns are variable with the specimens collected on North Andros in August and November and also observed but not collected in May and June. The advent of molecular phylogenetic analysis now provides further insight into the current status of *Astraptes xagua* and associated subspecies. The *Astraptes xagua* complex is reviewed here based on both morphological characters and molecular analysis to further delineate the current taxa.

Materials and methods

Specimens examined in this study are deposited in the collections of the McGuire Center for Lepidoptera and Biodiversity. Additional comparative material was examined from the American Museum of Natural History, Carnegie Museum of Natural History, National Museum of Natural History (Smithsonian Institution), and The Natural History Museum, London.

Male and female genitalia were macerated in 10% KOH, dissected and cleared in 70% ethanol prior to permanent storage in glycerin vials. Terminology for wing venation follows the modified Comstock-Needham system described by L. D. Miller (1970). Forewing length is measured from the base of the wing to the end of the fringe at the apex; width is measured normal to the costa from the fringe at the end of the tornus. Nomenclature for the genitalia follows that of Klots (1956).

Standard COI barcodes (658-bp 5' segment of mitochondrial *cytochrome oxidase subunit I*) were obtained from 14 specimens. DNA was extracted from a single leg and processed in the Grishin lab using Macherey-Nagel (MN) NucleoSpin R tissue kit according to the protocol described (Cong & Grishin 2014). Special primers developed for Eudaminae were used. Newly generated sequences and accompanying data were submitted to GenBank and received accession numbers (KY659594-KY659602). *Astraptes naxos* (Hewitson 1867), a continental species which is distributed in Brazil, was used as the outgroup and for comparative morphological examination of the species currently within the *Astraptes xagua* complex.

Results

Astraptes xagua xagua (Lucas, 1857)
Figures male 1-2; genitalia 13 a-i; female 3-4, genitalia 17
Eudamus xagua Lucas, 1857
= *Goniloba malefida* Herrich-Schaffer, 1862

MALE: Averaged 23.20 x 12.70 mm in five males measured, varying from 22.5 x 12 to 24 x 13 mm.

Dorsal: Forewing with narrow costal fold; ground color black-brown, basal third shiny cerulean blue; no hyaline spots. Hindwing same black-brown as forewing, basal third to half shiny cerulean blue.

Ventral: Forewing ground color black-brown on basal half, especially below cell, in Cu$_2$-2A and as a vague darker postdiscal band beyond and above discal cell; slightly paler brown forewing distad, much paler along anal margin; basal third shiny cerulean blue above Cu$_2$, reaching to origin of Cu$_1$ but does not reach white spots at mid-costa in costal cell; in Sc-R$_1$, this latter spot may be missing. Hindwing: Similar mottled dark brown as forewing, may be slightly darker basally, but otherwise unmarked. Fringes concolorous.

Head, thorax and abdomen black-brown, covered with shiny cerulean blue hair scales and setae above. Palpi black above, pale yellow beneath; pectus pale yellow; legs dark brown, forelegs overscaled whitish on posterior; mid and hind legs overscaled whitish along inner margins. Mid and hind tibiae smooth; mid tibiae with single pair of spurs, hind tibiae with two pairs. Antennae: nudum below, beige shading to gold average 25.0 segments (n=4), range 24 to 26, with five to seven segments on the club.

Genitalia (Figs:13 a-i) similar to *Astraptes naxos* (Figs. 16a-i) but overall smaller and with the following differences: The valvae are asymmetrical but more nearly equal in length as in *fulgerator* and *fulgor*, rather than as in *naxos* and *paros*, based on the material available. The process of the cucullus is spinous with the posterior of cucullus sharply pointed; ampulla is also reduced. There is an elongate lightly sclerotized band ventral to costal margin in *Astraptes x. xagua.* Aedeagus with several internal cornuti similar to a brush and the sclerotized margins with minute spicules.

FEMALE: Similar to male but slightly larger (forewing averaged 27.00 x 14.33 (n=6), range 25.5 x 13.5 to 27.5 x 15), with shiny cerulean blue area somewhat reduced on the dorsal surface. The ventral forewing white costal spots may be absent, but generally enlarged or there may be an additional apical cell spot. The antennal nudum averaged 25.83 segments (n=6), range 23 to 28 segments, with six to eight segments on the club.

Genitalia (Fig. 17 a) with general configuration as in *A. naxos* (Figs. 20 a, b) but slightly reduced in size. Lamella postvaginalis moderately sclerotized with central indentation along posterior margin and a series of erect setae and scales which are longer around the indentation; lamella postvaginalis shades paler toward the lamella antevaginalis; membranous area above the lightly sclerotized bar of the antrum leads to the membranous ductus bursae with the origin of the ductus seminalis dextral; corpus bursae bulbous as opposed to slightly elongate in *naxos* and length of paired signa spicuate and slightly reduced; corpus bursae length approximately one half length of ductus bursae.

Specimens examined. 4♂ 1♀, CUBA: Guantanamo ex colln. Le Moult, A. C. Allyn Acc. 1968-1; genit preps SRS 701, 702; 1♂ CUBA NFD; 1♂ CUBA: GUANTANAMO: 2 km W Yateritas; sea level; 29.vi.1994, L. D. & J. Y. Miller, L. R. Hernandez, sta. 1994-28,

Figures 1-12 (Opposite page). Adult specimens of *Astraptes x. xagua*: 1) ♂ dorsal, 2) ♂ ventral, 3) ♀ dorsal, 4) ♀ ventral (LEP-34276, JYM 7651); 5) *Astraptes xagua harveyi* Holotype ♂ dorsal, 6) Holotype ♂ ventral; 7) Paratype ♀ dorsal, 8) ♀ ventral (LEP-34276); *Astraptes christyi* 9) ♂ dorsal, 10) ♂ ventral; *Astraptes naxos,* 11) ♂ dorsal, 12) ♂ ventral.


1


2


CUBA: SANTIAGO de CUBA
Parque Nac. Gran Piedra, 1100-1200 m
cloud forest; 9.vii.1995; LD & JY Miller,
MJ Simon & LR Hernandez clrs. 1995-12

Allyn Museum
Acc. 1995-14

Allyn Museum Photo
No. 990909-27A,28A

1 cm


3

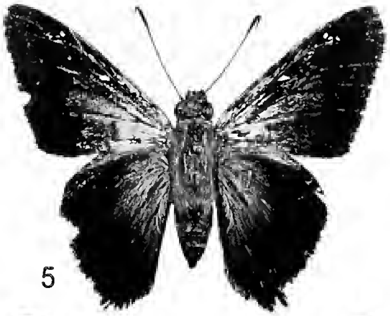

4


CUBA: GUANTANAMO
GTMO Naval Base, site 12,
E. of Sherman Ave.
19.91661, -75.132414
25.I.2012 D. Matthews &
T. Lott

nectaring on *Melochia tomentosa*

GTMO-LEP Inventory
D. Matthews
MGCL Accession
2012-2

MGCL 170980
McGuire Center for Lepidoptera
& Biodiversity, FLMNH, UF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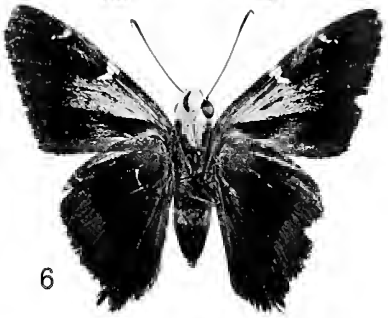

6


NORTH ANDROS:
Nicolls Town
11.viii.1976

BAHAMA IDS
leg. D. Harvey

Photo
11. XI. 74
np rm

[redacted]

HoloType No.
684
Carn. Mus. Ent.

Allyn Museum Photo
No. 990909-17A,18A

[illegible]
Astraptes
xagua harveyi
[illegible] & R. Steinhauser
[illegible]


7


8


DNA voucher
LEP-34276

NORTH ANDROS:
Nicolls Town
15.viii.1976

BAHAMA IDS
leg. D. Harvey

[redacted]

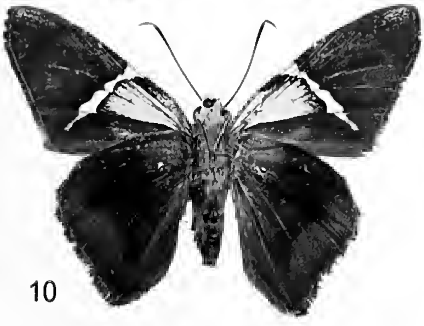
PARATYPE ♀
Euthymele
xagua
harveyi
S. R. Steinhauser

Allyn Museum Photo
No. 990909-19,20A

genitalia vial
M- 7651
Jacqualine Y. Miller

PARATYPE ♀
Astraptes
xagua harveyi
H. Clench, S. R. Steinhauser
J. Y. Miller


9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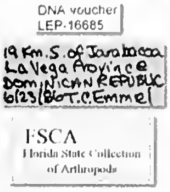
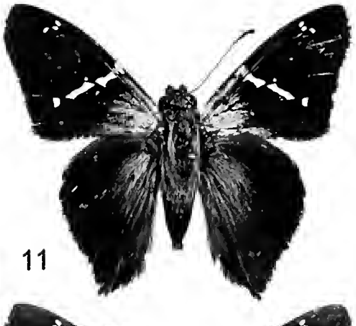

DNA voucher
LEP-16685

19 Km. S. of Jarabacoa
La Vega Province
DomINICAN REPUBLIC
6/23/86 T. C. Emmel

FSCA
Florida State Collection
of Arthropods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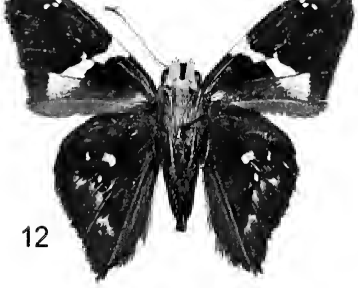
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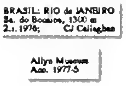
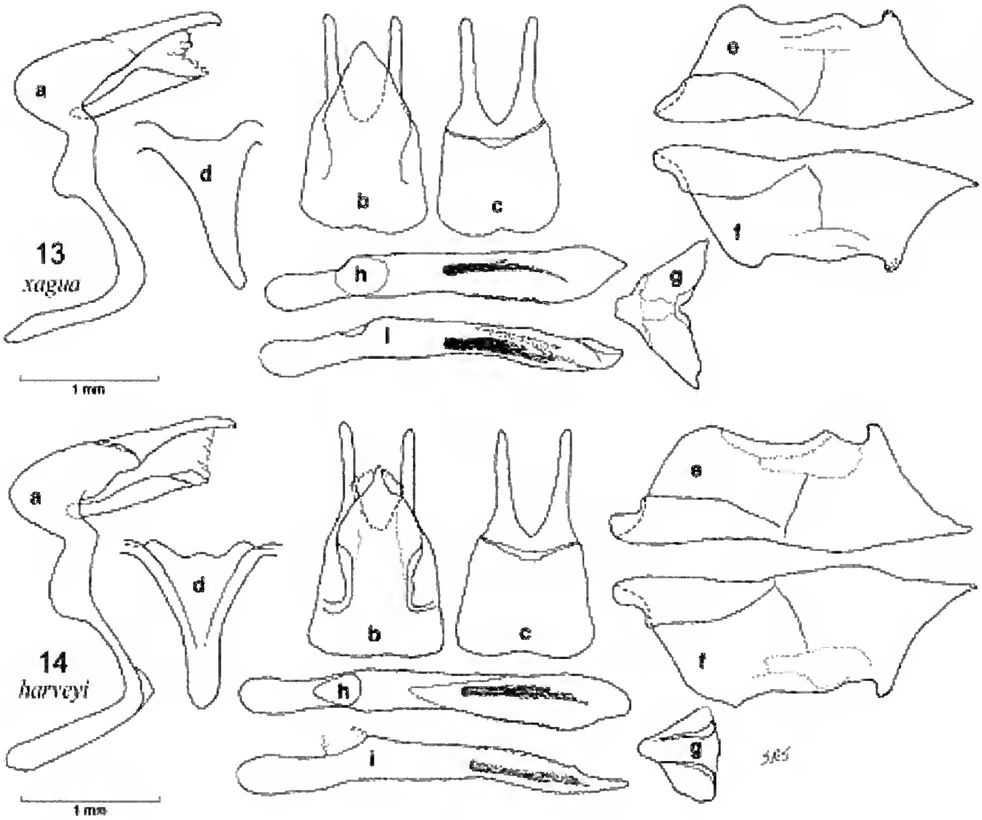

BRASIL: RIO de JANEIRO
Sa. do Bocaino, 1300 m
2.i.1976;   CJ Callaghan

Allyn Museum
Acc. 1977-5



Figures 13-14. (Scale line= 1 mm) 13 a-i) Male genitalia *Astraptes x. xagua* (scale line = 1 mm): *Astraptes xagua xagua* (SRS-701) a – tegumen, uncus and related structures – lateral; b – tegumen, uncus and gnathos – ventral; c – tegumen, uncus – dorsal; d – saccus – ventral; e – juxta – ventral; f – right valva, interior – lateral; g – left valva, interior – lateral; h – penis, cornutus- dorsal; i – penis, cornutus lateral. 14 a-i) Male genitalia *Astraptes xagua harveyi* (PT) (SRS – 1196) a – tegumen, uncus and related structures – lateral; b – tegumen, uncus and gnathos – ventral; c – tegumen, uncus – dorsal; d – saccus – ventral; e – juxta – ventral; f – right valva, interior – lateral; g – left valva, interior – lateral; h – penis, cornutus- dorsal; i – penis, cornutus lateral.view.

Acc. 1994-12; 1♂ CUBA: SANTIAGO DE CUBA: Santa Maria dos Palmas 200m; 8.vii.1995 L. D. & J. Y. Miller, L. R. Hernandez, M. J. Simon; 1♂ CUBA: SANTIAGO DE CUBA: Parque Nac. Gran Piedra; 11-1200 m; cloud forest; 9.vii.1995, L. D. & J. Y. Miller, L. R. Hernandez, M. J. Simon; 1♂ CUBA: GRANMA: El Naranjo, Pico Torquino Nac. Park, 5.vii.1995, L. D. & J. Y. Miller, L. R. Hernandez, M. J. Simon; 2♀ CUBA: Guantanamo: U.S. Naval Base, Site 4, 19.9347, -75.0972, 19.i.2012, J. Toomey & R. Portell (LEP 34273, KY659600); 5♂, 2♀, MGCL 170981 (LEP-10545), 170982; Site 7, vic. Stephens Ave., 19.92296, -75.12894, 23.i.2012, nectaring on *Gliricidium sepium*, D. Matthews, R. Portell, J. Toomey, T. Lott; MGCL170977 (LEP-10542), 170983–170987 (1♂ 170986, LEP-10543, KY659601; 1♂ 170987, LEP10544, KY659602), 170989; Site 11, E of Sherman Ave., nr. Library, 19.91368, -75.139947, 21.i.2012, nectaring on *Bouganvilla*, D. Matthews; 2♀, MGCL 170979, 17980; Site 12, E. of Sherman Ave., 19.91661, -75.132414, 25.i.2012, nectaring on *Melochia tomentosa*, D. Matthews & T. Lott.

Diagnosis: Ground color dorsal wings blackish brown with basal third shiny cerulean blue and no hyaline spots on forewing. Ventral with forewing ground color black-brown on basal half, especially below cell, in Cu$_2$-2A and as a vague darker postdiscal band beyond and above discal cell; basal third shiny cerulean blue above Cu$_2$, reaching to origin of Cu$_1$ but does not reach white spots at mid-costa in costal cell. Hindwing: Similar mottled dark brown as forewing, but otherwise unmarked.

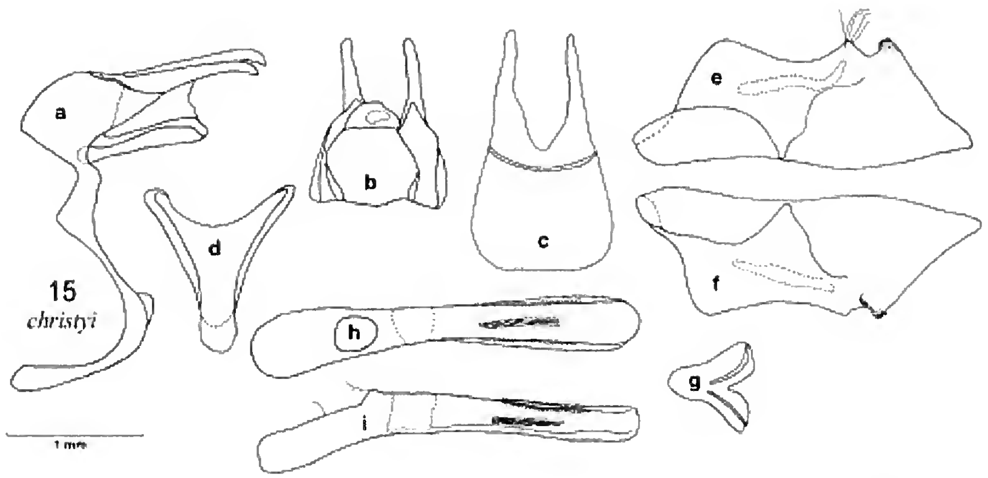
Distribution: *Astraptes x. xagua* is only recorded from Cuba.

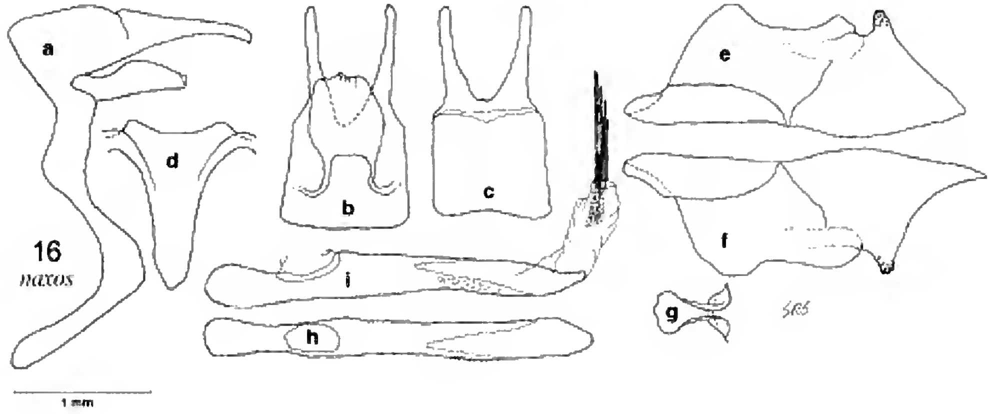
Astraptes xagua harveyi H. Clench, S. R. Steinhauser, J. Y. Miller, sp. nov.

(Figs. 5-6 male HT; 14 a-i male genitalia; Female Paratype 7-8; female genitalia 18 a-b.)

ZooBank LSID: urn:lsid:zoobank.org:act:7690A568-0F9C-401B-8C10-DE8AFBA5A56F

In an unpublished manuscript, "Bahama Butterflies: Hesperiidae" (1979), Harry K. Clench provided the following very brief description of this subspecies (slightly edited here). However, we believe it is sufficient to credit him with its authorship: "This is the only hesperiid in the Bahamas [broadly] marked with bright, iridescent





Figures 15-16. (Scale line= 1 mm) 15 a-i) Male genitalia *Astraptes christyi* (JYM-7649) a – tegumen, uncus and related structures – lateral; b – tegumen, uncus and gnathos – ventral; c – tegumen, uncus – dorsal; d – saccus – ventral; e – juxta – ventral; f – right valva, interior – lateral; g – left valva, interior – lateral; h – penis, cornutus- dorsal; i – penis, cornutus lateral. 16 a-i) male genitalia. *Astraptes naxos* (SRS 1989) a – tegumen, uncus and related structures – lateral; b – tegumen, uncus and gnathos – ventral; c – tegumen, uncus – dorsal; d – saccus – ventral; e – juxta – ventral; f – right valva, interior – lateral; g – left valva, interior – lateral; h – penis, cornutus- dorsal; i – penis, cornutus lateral view.

blue [not green] (on the body, the bases of both wings above, and the base of the forewing below). Its large size (fw length 24-28 mm) and absence of tails will further distinguish it. The three subspecies of *xagua* are remarkably distinct from one another. Nominate *xagua* (Cuba) has no white marks upfw; of them, *x. christyi* (Hispaniola) has a diagonal median band, but no subapical spots; and *x. harveyi* has three or four subapical spots, but only a subcostal spot representing the diagonal band."

We have expanded this description as follows:

MALE: Forewing averaged 24.5 x 13.0 mm (n=3), range 24 x 13 (holotype) to 25 x 13 mm.

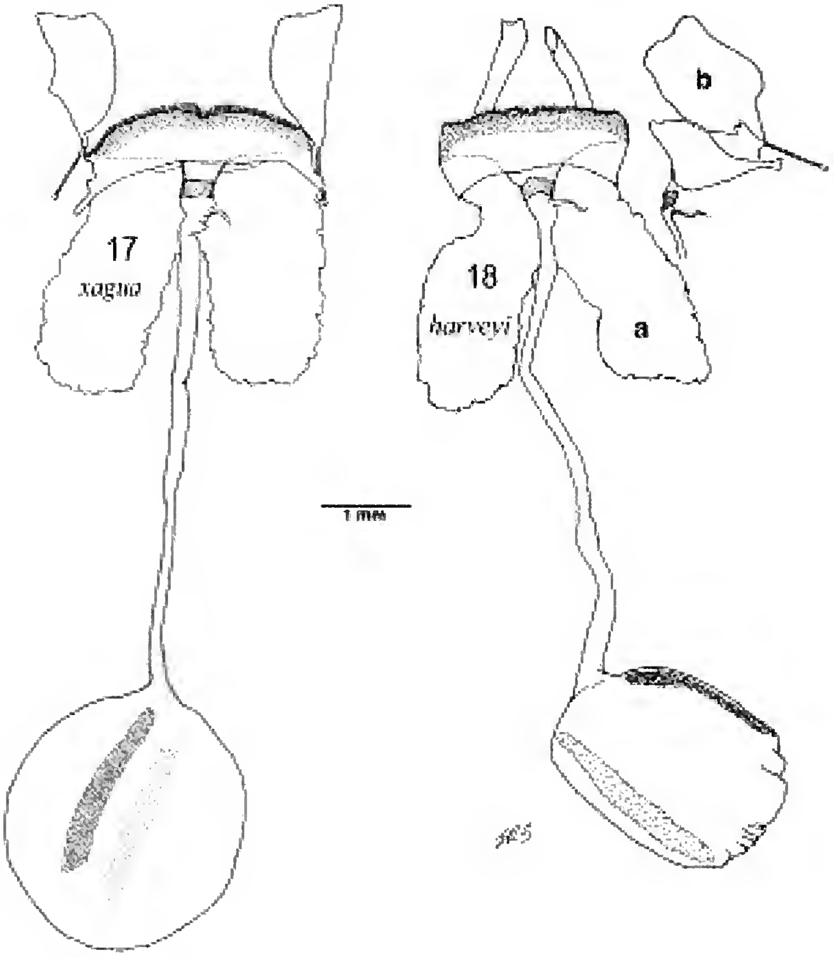
Dorsal: Forewing round color is similar to *A. x. xagua*, but blue area is enlarged to cover nearly half of the forewing and more diffuse distad. There are three to four pre-apical white spots in R_3-R_1, R_4-R_5 and R_5-M_1 in a line directed to midway between apex and mid termen with a single white central hyaline upper cell spot. The basal blue area reaches beyond cell spot, covering about half the wing. Hindwing as in *A. x. xagua*.

Ventral: Forewing slightly paler brown than above, much paler in anal cell, somewhat darker at base in basal nine tenths of Cu_2-2A and bearing a darker brown postdiscal band similar to that of *A. x. christyi*, but more prominent. Basal blue reaches origin of vein M_3, and is present in central Cu_2 -2A. White spots as above with additional opaque pre-apical spot in R_2-R_3, and mid costal opaque spots in costal cell and Sc-R_1 enlarged; lightly overscaled whitish sprinkled with a few shiny blue setae near apex in Cu_2-2A. Hindwing basal two thirds same dark brown basad as in discal area of forewing with an irregular distal margin; outer third distinctly paler brown posteriorad of Rs and may be dentate above 2A. Fringes concolorous.

Head, thorax, legs and abdomen as in *xagua;* antennal nudum 7/21 in holotype, 7/20 in one paratype with complete antennae.

Genitalia: (Figs. 14 a-i) as *A. x. xagua*; the process of the cucullus projects dorsally with few spicules; juxta is reduced and morphologically distinct.

FEMALE: Slightly larger, paratypes measured 27 x 14 and 28.5 x 15 mm (n=2),



Figures 17-18. (Scale line= 1 mm) 17 a) Female genitalia *Astraptes x. xagua* (SRS 702) ventral view, sterigma flattened, 18 a-b) Female genitalia *Astraptes xagua harveyi* (SRS 1197) a) ventral view; b) papilla analis, lateral view.

Dorsal forewing pre-apical white spot in R_2-R_3 and upper cell spot slightly larger. Hindwing as male but rounder. Shiny cerulean blue somewhat paler. Antennal nudum 7/21 and 9/21 in two female paratypes.

Ventral: As in male, but forewing central costal spot enlarged and extends across cell.

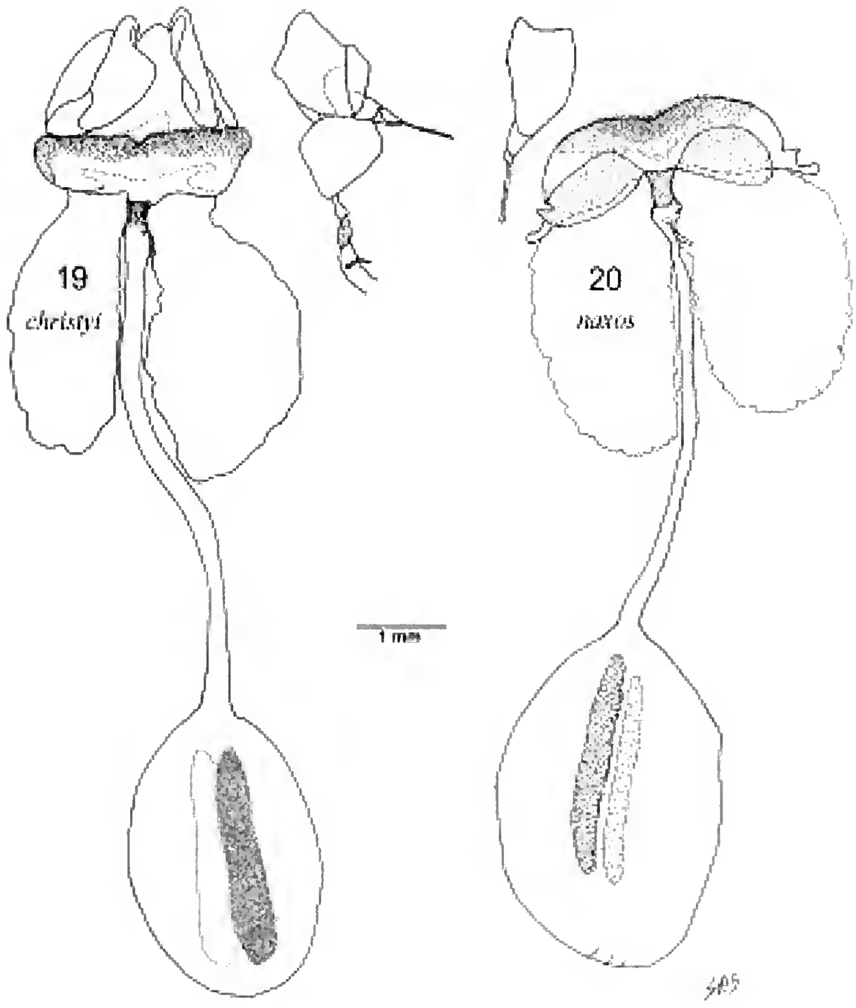
Genitalia (Figs. 18 a-b): As in *A. x. xagua.*

Etymology: The late Harry K. Clench proposed the name, *Astraptes xagua harveyi*, for this striking skipper, after its discoverer, Dr. Donald J. Harvey, but the description was not published before his untimely death in 1979. That omission is corrected here with this posthumous description and publication.

Types: Holotype male from Bahamas: North Andros Island; Nicolls Town; 11.viii.1976; leg D. Harvey, deposited in the Carnegie Museum of Natural History and bearing the following labels: printed and hand printed white label NORTH ANDROS: Nicolls Town 11.viii.1976; printed white label - BAHAMA IDS leg. D. Harvey; printed and hand printed red label- HOLOTYPE No. 684 Carn. Mus. Ent.; printed and hand printed red label- HOLOTYPE (male symbol) Astraptes xagua harveyi H. Clench; printed and hand printed white label - Allyn Museum Photo No. 990909-17 A, 18A. Another red label has been added: Holotype ♂/ *Astraptes/xagua harveyi*/H.Clench, S. R. Steinhauser/J. Y. Miller. There are two male and two female Paratypes: 1♂ Bahamas: North Andros Island; nr. Nicholls Town, 10 August, 1980, leg. J.D. Weintraub (LEP-34272, KY659598), deposited in the Allyn Museum of Entomology (MCGL); 1♂ same data as holotype, 12.viii.1976; 1♀ same data 15.viii.1976, D. Harvey (LEP-34276, KY659599; JYM gen 7651) and 1♀ Bahamas: North Andros Is., Nicolls Town, Sta. 182; 22.xi.1973 leg H.K. Clench (LEP-34149, KY659597; SRS gen 1197); the latter three specimens are deposited in the Carnegie Museum Natural History.

Diagnosis: *A. xagua harveyi* can be easily distinguished from nominate *A. x. xagua* by the presence of the dorsal four white pre-apical forewing spots and the white mid costal across the forewing cell approximately one half distance to cell end. On the ventral surface, the white forewing markings are enlarged and there is a marked difference in the darker rich brown coloration basad with paler brown along the submarginal areas of both wings.

Distribution: Voucher specimens of *Astraptes xagua harveyi* are only known from North Andros Island in the Bahamas thus far, but apparently Clench in his notes observed it on South Andros as well. The type series was only collected in Nicolls Town on North Andros. Despite extensive searches in that location by several collectors (L. D. and J. Y. Miller, M. Simon, G. Goss, R. Rozycki, D. Matthews) in recent years, no further specimens have been observed. In 1994



Figures 19-20. (Scale line= 1 mm) Figs 19 a-b) Female genitalia *Astraptes christyi* (JYM 7648) a) ventral view; b) papilla analis, lateral view. 20 a-b) Female genitalia *Astraptes naxos* (SRS 774) a) ventral view; b) papilla analis, lateral view.

L. D. Miller saw a specimen across from the dense forest at AUTEC (Atlantic Undersea Test and Evaluation Center) on the southern area of N. Andros with another specimen observed by Rick Rozycki in that location in 2012. Mark Simon observed three specimens along a dense xeric tropical forest near Stanyard Creek, but we have not seen this species elsewhere on the island. It has not come to blacklight or mercury vapor light, and we have attempted collecting for it very early in the morning and late at night. We have not observed this species elsewhere in the Bahamas despite our ongoing collecting efforts on other major islands.

Astraptes christyi (Sharpe, 1898), **reinstated status** J. Y. Miller & N. Grishin

(Figs. 9-10 male; male genitalia 15 a-i; female genitalia, 19 a-b)

Telegonus christyi Sharpe, 1898
= *Thymele angustus* Skinner, 1920

MALE: (Figs 9-10) Dorsal: Forewing averaged 26.33 x 13.94 mm (n=9) range 25.5 x 13 to 27 x 14.5 mm (holotype 27 x 14 mm);

Dorsal: forewing similar to *A. xagua*, ground color blackish brown paler on the distal half of forewing with forewing apex more acute; narrow central hyaline white band extending from mid costa at end of costal fold to near tornus in Cu_2-1A, comprising spots in costal cell (often opaque), Sc-R_1 discal cell, Cu_1-Cu_2 and a small triangular spot in Cu_2-1A; no pre-apical spots. Shiny cerulean blue on basal forewing and broader than in *xagua*. Coloration of hindwing dark blackish brown with shiny cerulean blue extends to almost one half of the wing near cell; shape of wing is considerably broader than in *xagua*.

Ventral: Ground color of forewing dark brown at base, paler brown distad; hyaline band broader than above and extends almost to the tornus; basal blue area reaches central band except in costal cell, darker basal area extending posteriorly to anal margin which is sparsely sprinkled with a few cerulean blue scales as in *A. x. harveyi*. Hindwing darker brown at base overscaled faintly with blues scales at base and angled sharply at Rs-M_1, arched basally and then fused to a point in Cu_2-2A; submarginal area paler brown. Fringes concolorous.

Key to the taxa of *Astraptes xagua* complex

UPF plain, without white spots..***xagua***
1' UPF with white spots..**2**
UPF with complete hyaline white transverse band, without pre-apical spots..***christyi***
2'. UPF with white spot mid costa and three pre-apical spots..***xagua harveyi***

Head, thorax, abdomen above as in *xagua*; ventral with fuscous to beige on midthorax to first abdominal segment as opposed dark blackish brown of mesothorax, metathorax, and abdomen in *A. x. xagua* and *A. xagua harveyi*; legs brown with fuscous/beige line along distal margins. Antennal nudum averaged 26.25 segments (n=8), range 25 to 27 with six to seven segments on the club.

Genitalia: (Figs 15 a-i) Uncus similar to *A. x. xagua* but more elongate with anterior margin of tegumen smooth as opposed undulate in *A.christyi*. Valvae asymmetrical with lighter sclerotized bar ventral of costal margin reduced; ampula with elongate setae and process of cucullus spinose; posterior of cucullus blunt as in *A. naxos* as opposed to acute in *A. x. xagua* and *A. xagua harveyi*; interior margin of valvula extending toward the process of the cucullus roughly sclerotized and curved similar to some members of the *fulgerator* complex. Aedeagus with dorsal margins spicuate and number of cornuti markedly reduced.

FEMALE: Coloration and markings as male but slightly larger, forewing averaging 29.40 x 15.30 mm in (n=10) from 28 x 14.5 to 30 x 16 mm

Hindwing more rounded. Antennal nudum averaged 26.33 segments (n=9) range from 25 to 28, with six to seven segments on the club.

Genitalia: (Figs. 18 a-b): General configuration is similar to that of *A. x. xagua* and *A. x harveyi* with the distal margin of postvaginalis more heavily sclerotized shading lighter toward the antevaginalis; postvaginalis with more prominent undulate margin midway on posterior postvaginalis and with erect setae and scales more elongate centrad; corpus bursae more bulbous with signa heavily spicuate similar to those of *A. x. xagua*, *A. xagua harveyi*, and *A. naxos*.

Specimens examined. Dominican Republic: La Vega: Jarabacoa, Pine forest 1800 m. 22.vii.1986, D. Matusik; same but 1♂, 1♀ 21.vii.1986; 1♂ 24.vii.1986; 1♂ 26. vi, 1♂ 30.vi, 1♂ 1.vii.1986; 1♂, 1♀ Dominican Republic: La Vega: Jarabacoa, 18 July 1986, specimen no.530 M ex Gonzalez (♂ LEP-34271, KY659594); 1♂ 19 km S. Jarabacoa, La Vega Province, Dominican Rep., 23.vi.1986, T. C. Emmel; 2♂ 2 km SE Jarabacoa, (Constanza Rd), 1900 Ft. elev.; 1♂ La Vega Prov., Dominican Republic, Dec. 30 1985, T. C. Emmel; 1♂ Rep. Dominicana: La Vega, Jarabacoa (LEP-34274, KY659595) 1♂ 2 km SE Jarabacoa, (Constanza Rd), 1900 Ft. elev.; 1♂ La Vega Prov., Dominican Republic, J. L. Nation; 2♂ 6/22/1986 (♂ LEP-34275, KY659596); 1♂ on Constanza RD 6/24/1986; 1♂ DOMINICAN REPUBLIC, LA VEGA, Jarabacoa 1700 Ft., June 10, 1988, Louis Sanchez; Dominican Republic, Jarabacoa, 2/20/1985, Lowell Harris; DOMINCAN RREPUBLIC: La Vega: vic. Jarabacoa 620 m; 11.1.1987, L. & J. Miller Sta DR-16.

Diagnosis: The following features distinguish *Astraptes christyi* for elevation to species rank: 1) Presence of the transverse white hyaline somewhat opaque band along with the absence of the apical markings, 2) More extensive cerulean blue on forewing and hindwing; 3) The extant and shape of the darker brown area on the hindwing especially the distal margin; 4) Coloration of ventral head, thorax and abdomen from the buff to yellow present on the palpi which extends down the mid-ventral thorax and on first abdominal segment; 5) Male genitalic features include differences in the valvae with the posterior margin of the cullier, process of the cullier, interior margin of the valve and the sparse number of cornuti; 6) Female genitalia indicate a close alignment with *A. xagua* with slight differences on the sterigma. These features in addition to the analyses of *COI* data below indicate sufficient supportive evidence to reinstate *A. christyi* to species status.

Distribution: *Astraptes christyi* was originally described by Emily Sharpe for Dr. Cuthbert Christy in recognition of his field notes and collection efforts of Lepidoptera taken in 1896 on Hispaniola. *Astraptes christyi* is endemic to Hispaniola and thus far has generally been recorded from the Dominican Republic especially in La Vega Province (Schwartz 1989, Smith et al 1994).

COI barcode analysis and morphology of *Astraptes xagua* complex

The dendrogram (Fig. 21) resulting from our analysis of *COI* barcode sequences suggests that *A. xagua harveyi* and nominate *xagua* form a monophyletic group, and *christyi* is more distant from them. Continental Brazilian relative, *naxos,* was used as an outgroup. The Cuban samples (both Santiago and Guantanamo) have essentially identical barcodes with the Bahamian closely aligned to the Cuban group as a separate haplotype. *A. christyi* is separated from *xagua* by 2.5 % and this is supported by a number of morphological characters: presence of the transverse hyaline somewhat opaque band, absence of apical markings, wing shape more acute, increased expanse of blue on the base of the dorsal wings, shape of the outer margin of darker ventral hindwing postdiscal band margin, and coloration of the mid-ventral thorax, in addition to the male genitalia (differences in valvae in the development of process of the cullier, shape of the posterior cullier, and sparse number of cornuti). Nominate *xagua* has no dorsal wing markings whereas *x. harveyi* has prominent preapical spots. The barcodes suggest an accelerated rate of evolution in *x. harveyi* due to some special selection pressure.

There are currently six species of *Astraptes* recorded from the West Indies: *A. talus* (Cramer), *A. anaphus* (Cramer*), A. xagua* (Lucas), *A. cassander* (Fabricius), *A. habana* (Lucas), and *A. jaira* (Butler). *Astraptes talus* and *A. anaphus* are widespread in the West Indies and also found in Central America. *Astraptes cassander* is restricted to Cuba while *A. jaira* is found in Jamaica. *Astraptes habana* and *A. xagua* are restricted to Hispaniola and Cuba with *A. christyi* restricted to Hispaniola. *Astraptes x. harveyi* is only recorded on North and possibly South Andros in the Bahamas. *Astraptes xagua* and its subspecies are essentially the West Indian equivalents of *A. fulgerator, fulgor,* and *naxos* on the continents. Given the

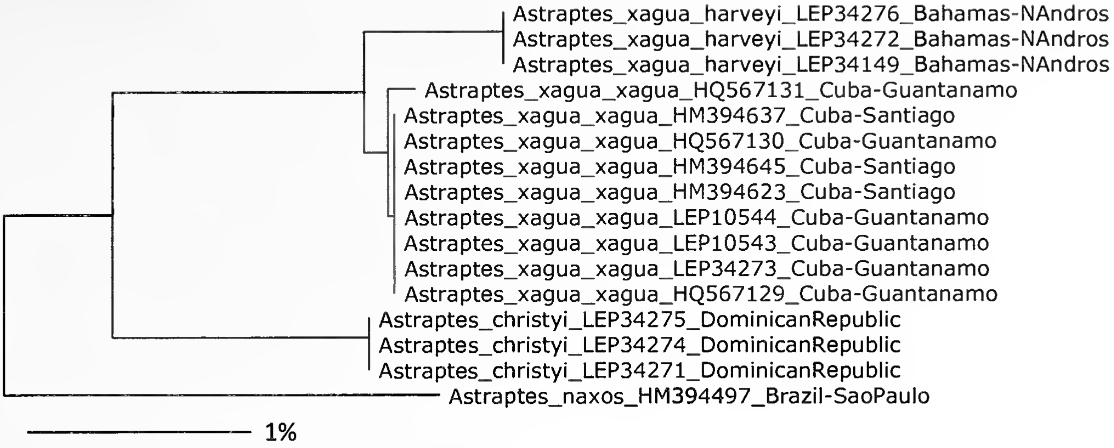


Figure 21. *COI* DNA barcode distances dendrogram for *Astraptes xagua* complex, *A. christyi*, and *A. naxos*. Species name, voucher code and general locality are shown for each specimen. Sequences with voucher codes starting from "LEP" were obtained in this work, others are GenBank accessions. Scale bar shows 1% sequence divergence.

diversity of cryptic species in the genus *Astraptes*, further morphological and molecular studies are required.

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Editor's note

The electronic edition of this article has been registered in ZooBank to comply with the requirements of the amended International Code of Zoological Nomenclature (ICZN). This registration makes this work available from its electronic edition. ZooBank is the official registry of Zoological Nomenclature according to the ICZN and works with Life Science Identifiers (LSIDs). The LSID for this article is: urn:lsid:zoobank.org:pub:369615DC-F4A3-45D5-A45C-DC09A9A28A3E Registration date: 25 March, 2017. This record can be viewed using any standard web browser by clicking on the LSID above.

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Editorial

JRL R.I.P.

I tried to extend the closing of the JRL to volume 50, as this would have been a cleaner number. No such luck, events kept closing in, so here we are at 49 and the end of the line. When Bill Hovanitz developed the idea for the Journal of Research on the Lepidoptera, and established the Lepidoptera Research foundation, Inc to institutionalize the effort in 1962, the future was very different from today. Bill envisioned an open academic platform for good works for understanding ecology and systematics of the Lepidoptera. His timing followed the beginnings of "New Systematics" and "Evolutionary Biology" as real hot items for study and research a couple of decades earlier by the great evolutionary biologists Theodosius Dobzhanski, Ernst Mayr, George Simpson, Sewell Wright and others. Butterflies and moths served well as metaphors and experimental subjects across natural history biology. These insects were charismatic but also structurally highly suited for certain specialties as population ecology and behavior.

Interest in all of nature politically peaked as well, concerns for the environment were worldwide and youth took interest in higher education especially concerned with biodiversity and promoting conservation. Although all groups of living organisms commanded scholastic attention, work with Lepidoptera enjoyed outsized attention. Appropriate Journals covering most fields metastasized. The world of academic publishing burgeoned by providing means of evaluating articles by review processes so comparative ratings became *de rigueur* and competitive styles established to parallel socio economic criteria of the developed world. Science publishing became big business. Robert Maxwell seduced scientists to develop "Big Science" with his publications model.

Systematics and related academic fields reached their zenith in the latter half of the 20th century. Genetic molecular biology was born and rapidly became the hard science base because of its value in providing applications for improving human life. Not to be ignored by all this was the sudden rearing of the ugly head of monetization. Monetization changed everything, for the western capitalistic academic world at least, with its profound relationships still sinking in. The commons and private property were churned together with increasingly hostile social class attitudes set in motion. Most societies reached for a life style never before seen, and in the reaching brought on what seems to be irreversible environmental damage. Our beloved Lepidoptera are declining almost everywhere, in lockstep with most other plants and animals. Whether any of this is reversible remains to be seen. In the meantime we humans are feeling many pressures.

Comforting delusion maintains most. Coming back to the city after apple picking excursion to the countryside a few weeks ago, I suddenly noticed the windshield effect on our car. The many bless the clean glass and absence of annoying bugs. Hello?

So extinctions are a characteristic of the publishing system as well.

I am not as angry about terminating the JRL as for realizing the environment that supported it is disappearing. The citizen scientists burgeon in special arenas (Monarchs), but the intellectual generalists and particularly kids at natural history meetings are clearly on the way out. Facebook and Instagram now provide the dopamine that swallows our goals of sweeter times.

We cannot thank Konrad Fiedler sufficiently for the effort he devoted to preserve and expand the idea of the JRL. In spite of his exemplary work, we were unable to reach a viable subscriber base. He implemented strong review policies and attempts at soliciting manuscripts. Nancy Vannucci was able to support him in processing papers rapidly and professionally. All in spite of providing the services without charge. Both gave far above the call of duty. Nancy worked on the JRL for over ten years. She learned a great deal and contributed much to the entire process of producing the Journal as well as managing reviews, etc. Nancy become highly proficient in language including editorial comment, on top of which she managed all the logistics. She was a great resource and cannot be thanked enough.

All that is left to say now is:

So long JRL, sorry we're leaving the building.

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Cover: Males and females of *Oeneis tanana* Warren & Nakahara, 2016. © Andrew D. Warren 2016. See article above.