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

ANDREW D. WARREN¹, SHINICHI NAKAHARA¹, VLADIMIR A. LUKHTANOV²,³, KATHRYN M. DALY⁴, CLIFFORD D. FERRIS⁵, NICK V. GRISHIN⁶, MARTIN CESANEK⁷ AND JONATHAN P. PELHAM⁸

¹McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, 3215 Hull Rd., UF Cultural Plaza, PO Box 112710, Gainesville, Florida, 32611-2710 USA

²Department of Karyosystematics, Zoological Institute of the Russian Academy of Sciences, Universitetskaya nab. 1, 199034 St. Petersburg, Russia

³Department of Entomology, University of Alaska Museum, 907 Yukon Dr., Fairbanks, Alaska, 99775-6960 USA

⁴Howard Hughes Medical Institute and Departments of Biophysics and Biochemistry, University of Texas Southwestern Medical Center, 5323 Harry Hines Blvd., Dallas, Texas 75390-9050 USA

⁵5405 Bill Nye Ave., R.R. 3, Laramie, WY 82070 USA; Research Associate, McGuire Center for Lepidoptera and Biodiversity

⁶Burke Museum of Natural History and Culture, Box 353010, University of Washington, Seattle, Washington 98195-3010 USA

hesperioidea@yahoo.com, snakahara@ufl.edu, lukhtanov@mail.ru, kmdaly@alaska.edu, cdferris@uwyo.edu, grishin@chop.swmed.edu, martin.cesanek@gmail.com, zapjammer@comcast.net

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...
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. tagygete* 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 “tagygete group.” Based on this character, Gross (1970) united *O. bore*, *O. tagygete*, *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. carlyiDyar, 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 genital 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 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’-ATTCAACCAATCATAGATGTTGG-3’) -Ven-m2COIR (reverse, 5’-GGTAACCTGTTCTATCGTGTC3’), and Meg-mCOIF2 (forward, 5’-CCTCGWATATAAYAAGATTGTTG-3’) -sCOIR (reverse, 5’-TAAACTTCTGGATGTCCAAAT-CA-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 approximately two-fifths length of forewing costa, 40 segments shorter than first segment in male, same length in female; antennae segment similar to first and second segments in scale orientation, about three times longer than first segment; third antennal segment claw-like, about three times longer than first antennal segment.

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 setose; 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 irregularly 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 30° angle to horizontal, distal half of valva roughly trapezoidal in lateral view with 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 spines, 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-1): Dorsal forewing ground color dark brown; androconial dark brown undulating band extending from costa, distal to discal cell, fading distally in cell M<sub>4</sub>, curved inwards below M<sub>4</sub> and extending to cell Cu<sub>1</sub>; black ocellus in cell M<sub>4</sub> generally with creamy pupil in center; ocelli in cells M<sub>4</sub> and Cu<sub>1</sub> variably present, smallest in M<sub>4</sub>, 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: dorsal 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<sub>4</sub>, 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<sub>4</sub>, M<sub>3</sub> and M<sub>2</sub>; black ocellus in cell Cu<sub>1</sub> 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 antevaginalis 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 sigilla located at ventral side of corpus bursae, sigilla prominent and parallel to each other, spines of sigilla developed.


J. Res. Lepid.
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 (32♂, 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°14.6’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 of Tok, 1700’, 10-VI-1999, J. L. Harry (1♂, 2♀ MGCL); 12-VI-1999, J. L. Harry (1♀, MGCL); 13-VI-1999, J. L. Harry (2♂, 2♀ 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, 5-VI-1997, C. D. Ferris (1♂, 1♀ MGCL); 14-VI-1997, C. D. Ferris (52♂, 17♀ CDF); 6-VII-1997 C. D. Ferris (2♂, 2♀ MGCL; incl. SN-15-147, SN-15-151); 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-1979, K. W. Philip (1♂ KWP UAM1009532); 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-VI-1999, M. Douglas (5♂, 7♀ MGCL); Tok, 17-VI-1971, L. Jennings (1♂ KWP, UAM1003794); 9-VI-2005, Szymczak (1♂ JPB); Tok Cutoff, 5 mi. S of Tok, Butch Kuth Ave., roadside flowers in open aspen/spruce forest, 13-V-1995, K. W. Philip (11♂, 5♀ KWP, UAM100379326-UAM100379329, UAM100379344-UAM100379346, UAM100379367-UAM100379369, UAM100379384-UAM100379387); 14-VI-1995, K. W. Philip (25♂, 3♀ KWP, UAM100379330-UAM100379345, 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.


**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.

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-VI-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); 24-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 (2♂ MGCL); 0.8 mi. N of Lewes Lake Rd. on Hwy. 2, 2700', 6-VI-1991, J. & F. Preston (6♂, 1♀ MGCL); 14 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.
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 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.](image-url)
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 *COI* 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.

The third barcode cluster includes the Sierra Nevada 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

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; pers. obs. ADW 2015). 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; pers. obs. ADW 2015).

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).

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 8. Habitat of *Oeneis tanana*, 8 miles south of Tok, Alaska, 25 June 2007. Photo by David Shaw.](image-url)
Figure 9. Dendrogram generated from Bayesian analysis of COI barcode sequences from taxa in the bore group of *Oeneis*, with *O. norma* as the outgroup. See text for details of the analysis. Colored groupings identify taxa and populations discussed in the text.
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; Goetheus & 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 Rhodolia 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 Palaearctic region. *Oeneis excavitor* 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 genital 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 genital 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*.

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 include five species-level taxa: *O. chryxus* (including *O. c. ivaldila, 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 Nevada taxon (*O. c. ivaldila 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. c. chryxus* and *O. c. 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 Palearctic 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.

**Acknowledgements**

We are extremely grateful to everyone who has helped make this study possible. Derek Sikes facilitated access to the University of Alaska Museum (Fairbanks, Alaska) where the Kenelm Philip (KWP) collection is currently housed. Derek also provided DNA sequences and assistance with the compilation of distributional data. Luciana Musetti and Riley Gott generously loaned legs for DNA extraction and provided images and data from specimens in the Triplehorn Insect Collection at Ohio State University (Columbus, Ohio). Jim Brock (Tucson, Arizona) provided images and specimen data from his collection. David Shaw (Issaquah, Washington) provided continuous encouragement and habitat photos from near the type locality of *O. tanana*. We also thank Jackie Miller, Debbie Matthews-Lott, Tom Emmel, Jim Schlatcha (MGCL) and John Douglass (Toledo, Ohio) for logistical support and discussions, and Katie Lane and Elena Ortiz (MGCL) for preparing specimens. Thanks to John Calhoun for reviewing an early version of the manuscript, Zdenek Fric for discussions, and Konrad Fiedler and an anonymous reviewer for helpful comments and corrections. Finally, we thank the late Malcolm Douglas, Jack Harry and Kenelm Philip for their decades of fieldwork in western and arctic North America, and for providing the majority of known specimens of *O. tanana*. V. Lukhtanov was supported by state research project no. 01201531195 and RFBR grants 15-29-02553 and 15-04-01581. Funding for the DNA barcoding of the UAM specimens was provided by the United States Fish and Wildlife Service’s Alaska Region NWRS Inventory and Monitoring Initiative.

**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:C3C004C6-9D38-4B99-AF4F-813B1689FCD5. Registration date: March 13, 2016. This record can be viewed using any standard web browser by clicking on the LSID above.

**Literature Cited**


