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Are Miami blues in Cuba? A review of the genus *Cyclargus* Nabokov  
(Lepidoptera: Lycaenidae) with implications for conservation management

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Are Miami blues in Cuba? A review of the genus *Cyclargus* Nabokov  
(Lepidoptera: Lycaenidae) with implications for conservation management

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**Abstract.** We review the genus *Cyclargus* Nabokov (Lepidoptera: Lycaenidae) based on detailed comparative analyses of wing patterns, genitalia, and mitochondrial COI DNA barcode sequences, and suggest that *Cyclargus* is composed of four species: *C. thomasi* (Clench), *C. woodruffi* (W. Comstock and Huntington), *C. ammon* (Lucas), and *C. dominica* (Möschler). The following new subjective synonyms are proposed: *C. erembis* Nabokov **syn. n.** and *C. kathleena* K. Johnson and Matusik **syn. n.** are *C. thomasi noeli* (W. Comstock and Huntington); *C. sorpresus* K. Johnson and Matusik **syn. n.** and *C. shuturn* K. Johnson and Bálint **syn. n.** are *C. ammon*; and *Cyclargus oualiri* Brevignon **syn. n.** is *C. woodruffi*. Additionally, we report the discovery of *C. thomasi noeli* in Cuba (where

this taxon was previously confused with *C. ammon*), report *C. ammon* from Hispaniola for the first time, and document the widespread sympatry of *C. thomasi* and *C. ammon* in the northern Caribbean (including south Florida, Cuba, Cayman Islands, Hispaniola, Lucayan Archipelago). Finally, we provide a provisional synonymic list of *Cyclargus* taxa, which may serve as a taxonomic framework to assist efforts to conserve the Miami blue (*C. thomasi bethunebakeri* (W. Comstock and Huntington)), a taxon listed as “Endangered” under the Endangered Species Act in the United States.

**Key words.** Biodiversity, biogeography, Caribbean Basin, DNA barcodes, Miami blue, morphology, taxonomy, West Indies.

## Introduction

The genus *Cyclargus* Nabokov is one of a few butterfly genera endemic to the northern Caribbean (including south Florida), yet there has never been a consensus on the number of species-level taxa. Nabokov (1945) originally included four species in *Cyclargus*: *C. ammon* (Lucas, 1857), *C. dominica* (Möschler, 1886), *C. thomasi* (Clench, 1941) and *C. woodruffi* (W. Comstock and Huntington, 1943). Three years later, *C. erembi* Nabokov, 1948 was described from Little Cayman Island, based on a single male specimen. Riley (1975) treated *C. ammon*, *C. dominica*, and *C. thomasi* as species-level taxa (yet placed them in *Hemiargus* Hübner), but considered *C. woodruffi* to be a subspecies of *C. thomasi*, and *C. erembi* a subspecies of *C. ammon*. Subsequently, four additional species of *Cyclargus* have been named: *C. kathleena* Johnson and Matusik, 1992 - based on six male specimens from Pedernales Province, Dominican Republic; *C. sorpresus* Johnson and Matusik, 1992 - based on three male specimens from Pedernales Province, Dominican Republic; *C. shuturn* Johnson and Bálint, 1995 - based on a pair of specimens from St. Ann’s Parish, Jamaica; and *C. oualiri* Brévignon, 2002 - based on reared specimens from Guadeloupe. Lamas (2004) recognized all of the recently proposed taxa at the species-level, yet combined *C. thomasi* (including all of its subspecies *sensu* Riley 1975) with *C. ammon*, without justification; this has resulted in considerable taxonomic confusion in the past decade. Warren et al. (2018) followed Lamas (2004) except that *C. ammon* was treated as a full species, resulting in a current list of eight species-level taxa in *Cyclargus*. However, the taxonomic status of the recently described species has never been fully investigated.

*Cyclargus* butterflies have been the focus of recent conservation efforts in Florida, United States, where the Miami blue (*C. thomasi bethunebakeri* (W. Comstock and Huntington, 1943)) is currently listed as “Endangered” under the Endangered Species Act (USFWS 2012). Despite its protected status, many questions remain about the global distribution of the Miami blue, specifically regarding its possible occurrence in Cuba and whether any populations of *C. thomasi* in The Bahamas may be referable to *C. t. bethunebakeri*. Confusion between *C. thomasi* and *C. ammon* has hindered efforts to preserve existing populations of *C. t. bethunebakeri* in Florida, which resulted in the listing of *C. ammon* and the less similar “blue” butterflies *Leptotes cassius* (Cramer, 1775) and *Hemiargus ceraunus* (Fabricius, 1793) as “Threatened” in south Florida under the Endangered Species Act due to similarity of appearance to *C. t. bethunebakeri* (USFWS 2012).

This research was initiated in January, 2012, as a project to inventory the Lepidoptera fauna of the United States Naval Base, Guantánamo Bay (GTMO) in conjunction with ongoing studies of the invertebrate paleofauna (Portell et al. 2008, 2009). Two sampling periods, 18–25 January 2012 and 3–10 October 2013 resulted in the collection of 3,278 specimens (2,727 moths, 551 butterflies) with a total of 59 butterfly species and more than 334 moth species recorded for the base (Matthews et al. 2012). In this publication, label data were given for *Cyclargus ammon* collected from GTMO in January 2012 and specimens collected on the base by R. A. Anderson in 1962 and 1971.

Thirteen additional *Cyclargus* specimens were collected at GTMO in October 2013. In the field, JKT determined these as Miami blues, while DLM countered that the taxon was not known to occur in Cuba. This assertion was based on literature accounts (Alayo and Hernández 1987; Minno and Emmel 1993; Smith et al. 1994; Saarinen 2009), including a recent list of the Cuban fauna (Barro and Núñez 2011). Following preparation of the 2013 material, DLM took a more critical look at all the Cuban specimens previously curated as *Cyclargus ammon* (Lucas, 1857) in the collections of the McGuire Center for Lepidoptera and Biodiversity (MGCL). Dissections of several specimens, both males and females, confirmed

that both *C. ammon* and *C. thomasi* occur on the naval base as well as other locations in Guantánamo Province. Twenty-one specimens of Cuban *C. thomasi* were identified, including three specimens collected at GTMO in October 2013 (Fig. 1–6). The occurrence of *C. thomasi* in Cuba is of special interest because of the decline and local extirpation of the once common Miami blue (Calhoun et al. 2002) despite extensive conservation initiatives (Daniels 2009). Cuban *C. thomasi* could represent an ancestral source of Florida's Miami blues as well as a potential source for future recolonization.

Recent Cuban lists (Barro and Núñez 2011; Núñez and Barro 2012) omit the occurrence of *C. thomasi* there. A literature search revealed that Cuban records for this species were published as early as 2002. Calhoun et al. (2002) mentioned personal communications with L. R. Hernández regarding “an insect similar to *C. thomasi*” and Hernández (2004) subsequently gave a species account of *C. thomasi* from Cuba and Isle of Pines [Isla de la Juventud]. Craves (2004) also published photographs and reported on the occurrence of *C. thomasi*, tentatively identified as *C. thomasi bethunebakeri*, from locations in three Cuban provinces: Matanzas, Ciego de Avila, and Santiago de Cuba. These sources, together with anonymous eye-witness accounts, are mentioned in the Federal Register (USFWS 2012). The presence of a Cuban entity resembling *C. thomasi* was acknowledged, but with no subspecies designation provided.

Previous authors have included partial line drawings of *Cyclargus* genitalia (Nabokov 1945, 1948; Johnson and Matusik 1992; Johnson and Bálint 1995) as part of taxonomic descriptions and revisionary studies. While certain structures are shown in detail, these outline drawings are difficult to interpret in context of the whole genital capsule, the labeling schemes are complicated, and the range of individual variation is not represented. In order to facilitate accurate identifications of *C. thomasi* (Fig. 1–6) and *C. ammon* (Fig. 7–10), better understand the variation of genitalic structures within and between taxa and populations, and designate a subspecific name for Cuban *C. thomasi*, representative comparative material was examined from Florida and the West Indies. Wing maculation patterns were studied and multiple genitalic dissections of *Cyclargus* specimens, detailed below, were prepared. As initial morphological study revealed the need for various taxonomic changes within the genus, we extended the scope of our investigation to include analyses of DNA barcode sequences for more than 100 samples of *Cyclargus*, as well as outgroup samples within the subfamily Polyommatainae.

In an effort to resolve the taxonomy of the genus, we herein provide a review of *Cyclargus*, and present the first genitalia illustrations of Cuban *C. thomasi*. We provide an updated systematic and synonymic list of *Cyclargus*, with revised or confirmed status based on morphological and DNA data. Finally, we discuss the implications of our results for the conservation management of the Miami blue (*C. t. bethunebakeri*).

## Materials and Methods

**Abbreviations.** The following abbreviations and collection codens are used throughout the text: **AME** – Allyn Museum of Entomology (now part of MGCL), **ADW** – Andrew D. Warren Collection, **AMNH** – American Museum of Natural History, New York, NY; **BOA** – Butterflies of America Website (Warren et al. 2018); **CMNH** – Carnegie Museum of Natural History, Pittsburgh, PA; **FLMNH** – Florida Museum of Natural History, University of Florida, FL; **FSCA** – Florida State Collection of Arthropods, Gainesville, FL; **GTMO** – Guantánamo Bay Naval Base, Cuba; **MGCL** – McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL.; **NHMUK** – The Natural History Museum, London, UK.

**Morphological study.** Genitalia were prepared following standard dissection techniques (Robinson 1976). In some males, the left valve was removed to view the mesal (inner surface of the valve). Temporary glycerin slides were made for imaging with all structures returned and permanently stored in plastic genitalia vials pinned adjacent to specimens labeled with corresponding preparation numbers. Structures were photographed at manually selected multiple focal planes with a Zeiss Axiophot transmitted light microscope (40× objective), Axiocam 3.1 camera software, and a KS 400 3.0 digital imaging system. Images were stacked with Zerene Stacker, version 1.04 using the PMax (pyramid maximum contrast) algorithm for male valvae and females and the DMap (depth map algorithm) for whole male genital capsules. General terminology for genitalia follows Klots (1956) and specialized terms for Lycaenidae follow Nabokov (1945).

Nomenclature for adult wing venation and cells (Fig. 11) follows Miller (1970) and Klots (1951). Wing maculation terminology follows Kunte and Tiple (2009), in part. Images of adults were taken with a Cannon EOS 60D camera equipped with a Cannon MP-E 65 mm macro photo lens set at 1× in a reflective funnel illuminated with OttLite® bulbs. Image plates for both pinned adults and genitalic structures were assembled and edited in Adobe Photoshop 5.1.

**Barcode analysis.** Tissue samples (two legs each) were vouchered for DNA extraction of recently collected GTMO and Bahamas specimens (2012-2014) prior to relaxing for pinning. Legs or abdominal tissue were likewise removed from older pinned specimens (1930-2008). General methods for sequencing and analysis of COI barcodes follow Shiraiwa et al. (2014), with *Cyclargus*-specific probes developed for assembling fragmented DNA of older specimens. Sequences and accompanying specimen data were submitted to GenBank and received accession numbers MK124470-MK124543.

**Material examined.** Material was examined from MGCL, FSCA, ADW, NHMUK, AMNH, and CMNH. In addition to Cuban material, primarily from GTMO and Guantánamo Province (see specimens examined), 1,858 *Cyclargus* adults from Florida, The Bahamas, and West Indies, representing all but two described taxa, were examined firsthand, along with type images available on BOA. Male and female specimens (n = 65) were dissected from Cuba, six major islands of The Bahamas, the Cayman Islands, Jamaica, Dominican Republic, Puerto Rico, St. Kitts, and the British Virgin Islands, and included topotypical exemplars of most subspecific taxa.

Partial data and associated specimen and/or genitalia preparation numbers are given in figures and captions. Full data for comparative non-Cuban specimens were captured in an Excel spreadsheet with records corresponding to unique identifier number labels placed on specimens. This information is not included here to safeguard localities of potentially sensitive populations. Complete label data for all Cuban specimens examined are given below. This listing supersedes the data account given for *C. ammon* in Matthews et al. (2012), which erroneously included some *C. thomasi* specimens. Localities on labels are reproduced verbatim, while dates are standardized. Numbers preceded by “Prep.” refer to dissections stored in genitalia vials. Numbers preceded by LEP- refer to DNA vouchers. Numbers preceded by MGCL refer to unique specimen identifiers.

#### Cuban Specimens Examined – *Cyclargus thomasi*

**GUANTÁNAMO:** 2 km E Yateritas Rd., sl, 25.vii.1995, T.W. Turner (1 M) LEP-22376, MGCL 245056; 2 km W Yateritas, sta. 1994-28, sea level, 29.vi.1994, L.D. & J.Y. Miller & L.R. Hernández, Allyn Museum Acc. 1994-12 (1 F) MGCL 245065; Baracoa, Boca de Yumuri, sta. 1994-20, 60-100m, 27.vi.1994, L.D. & J.Y. Miller & L.R. Hernández, AME Acc. 1994-12 (1 M) MGCL 245058; GITMO Bay, US Naval Base 4.x.1962, R.A. Anderson, AME Acc. 1996-19 (1 M) MGCL 245054, Photograph Butterflies of America 2008; same data, (2 F) MGCL 245062, MGCL 245068, Photograph Butterflies of America 2008; Guantánamo Bay, US Naval Base, 14.vii.1971, R.A. Anderson, AME Acc. 1996-19 (1 M) MGCL 245055, Photograph Butterflies of America 2008; same data, (1 M) LEP-22375, MGCL 245052; same data 15.vii.1971 (1 M) MGCL 245053; GITMO. Bay, US Naval Base, 13.vii.1972, R.A. Anderson, Project Photo J.B. Heppner 8261/62, *Cyclargus ammon* (Lucas) det. J.B. Heppner '08 (1 M) MGCL 245747; GTMO Naval Base, vic. Stephens Ave., Site 7b, 19.922061°, -75.129662°, 7.x.2013, D. Matthews, J.Y. Miller, J. Toomey & R. Portell, MGCL Acc. No. 2013-31, (1 M) Prep. DM 1688, MGCL 230736; GTMO Naval Base, Site 15, marsh area nr. Ridge Trail, 19.922776°, -75.13268°, 4.x.2013, D. Matthews, J.Y. Miller, R. Portell, J. Toomey, MGCL Acc. 2013-31, (1 M) Prep. DM 1682, LEP-17798, MGCL 230742; same data, (1 F) Prep. DM 1692, LEP-22349, MGCL 230758; Jauco, Mpio. Maisi, sta. 1994-17, 60-100m, 26.vi.1994, L.D. & J.Y. Miller & L.R. Hernández, AME Acc. 1994-12 (1 M) MGCL 245059; Jauco, Mpio. Maisi, sta. 1995-14, 10.vii.1995, L.D. & J.Y. Miller, M.J. Simon & L.R. Hernández, AME Acc. 1995-14, (1 M) Genitalia Vial no. M-7887, LEP-22377, MGCL 245061; same data, (1 F) Prep. DM 1698, FLMNH-057, MGCL 245066; Juaco, Maisi Municipality, 5m, 25.vii.1995, T.W. Turner (1 M) MGCL 245057; same data (1 F) MGCL 245063; Los Camarones, Minas Amores rd., sta. 1995-18, 12.vii.1995, L.D. & J.Y. Miller, M.J. Simon & L.R. Hernández, AME Acc. 1995-14, (1 M) Prep. DM 1694, MGCL 245060; Pacare, sta. 1994-26, sea level, 29.vi.1994, L.D. & J.Y. Miller & L.R. Hernández, AME Acc. 1994-12, (1 F) Prep. M-7888, MGCL 245067; Puerto Caleta, sta. 1994-18, sea level, 26.vi.1994, L.D. & J.Y. Miller & L.R. Hernández, AME

Acc. 1994-12, (1 F) Prep. DM 1693, MGCL 245064.

### Cuban Specimens Examined – *Cyclargus ammon*

**BARACOA:** Boca de Yumuri, sta. 1994-20, 60-100m, 27.vi.1994, L.D. Miller, J.Y. Miller & L.R. Hernández, (1 M) MGCL 245467; Las Vertientes, sta. 1992-21, 27.vi.1994, L.D. Miller, J.Y. Miller & L.R. Hernández (1 F) MGCL 245500; **GUANTÁNAMO:** 2 km E Yateritas Rd., s.l., 25.vii.1995, T.W. Turner (1 M) MGCL 245469; 2 km E Yaterites, sta. 1994-16, sea level, 26.vi.1994, L.D. Miller, J.Y. Miller & L.R. Hernández (1 M) MGCL 245468; 2 km W Yateritas, sta. 1994-28, sea level, 29.vi.1994, L.D. Miller, J.Y. Miller & L.R. Hernández (2 F) MGCL 245501, MGCL 245502; El Aguacate, NW Cd. Guantánamo, sta. 1994-15, 180m, 25.vi.1994, L.D. Miller, J.Y. Miller & L.R. Hernández (1 M) MGCL 245462; US Naval Base Guantánamo Bay, 15.vii.1971, R.A. Anderson, AME Acc. 1996-19 (1 F) LEP-24409, NVG-15091F05, MGCL 245104; GTMO Naval Base, Site 15, marsh area nr. Ridge trail, 19.922776°, -75.13268°, 22.i.2012, MGCL Acc. 2012-2, D. Matthews & T. Lott, (1 F) LEP-10587, MGCL 171104; same locality, 4.x.2013, MGCL Acc. 2013-31, D. Matthews, J.Y. Miller, R. Portell & J. Toomey (1 F) LEP-17803, MGCL 230744; same data, (2 M) Prep. DM 1678, LEP-17800, MGCL 230739; LEP-17802, MGCL 230741; GTMO Naval Base, Site 17, W of golf course, 19.921906°, -75.132168°, 9.x.2013, MGCL Acc. 2013-31, D. Matthews, J.Y. Miller, R. Portell & J. Toomey, (2 M) LEP-17806, MGCL 230727; Prep. DM 1715, LEP-17801, MGCL 230728; GTMO Naval Base, site 21, E Ridgeline Trail, 19.925023°, -75.128832°, 6.x.2013, MGCL Acc. 2013-31, D. Matthews, J.Y. Miller, R. Portell & J. Toomey (1 F) Prep. DM 1683, MGCL 230737; Juaco, Maisi Municipality, 5 m, 25.vii.1995, T.W. Turner, (1 M) MGCL 245470; Maisi, Mpio Maisi, sta. 1994-22, 20 m, 27.vi.1994, L.D. Miller, J.Y. Miller & L.R. Hernández (4 M) MGCL 245463–245465, MGCL 245466; same data (1 F) MGCL 245499; San Antonio del Sur, sea level, 29.vi.1994, L.D. & J.Y. Miller & L.R. Hernández, sta. 1994-27, Allyn Museum Acc. 1994-12, (1 F) Prep. DM 1697, MGCL 245498; **HAVANA:** “KUBA”, Mira Flores, 20.vii.1989 (2 F) MGCL 245507, MGCL 245508; same data (4 M) MGCL 245486, MGCL 245489, MGCL 245490, MGCL 245492; Havana Country Club, 4.ix.1958, A.C. Allyn Acc. 1969-20 (1 M) MGCL 245461; Havana, Provincia Matanzas, vii.1993, J.G. Filiatrault (10 M) MGCL 245474–245483; same data (2 F) MGCL 245505, MGCL 245506; **MATANZAS:** Varadero, 21.iii.1980, FSCA (2 M) MGCL 245471, MGCL 245472; Cajalbana, 2.vii.2005, Rayner Nunez (1 F) MGCL 245503; Sardinera, x.1991 D.S. Smith (1 M) MGCL 245473; same data (1 F) MGCL 245504; **PROVINCE UNKNOWN:** “KUBA” 5-20.viii.1990 (10 M) MGCL 245484, MGCL 245485, MGCL 245487, MGCL 245488, MGCL 245491, MGCL 245493–245497; same data (2 F) MGCL 245509, MGCL 245510.

## Results

### 1. Results of Morphological Study

#### 1.1. *Cyclargus ammon* vs. *C. thomasi* – Wing Patterns

The following text addresses potentially diagnostic characters only. In addition to the brief original descriptions (Lucas 1857; Clench 1941), more complete descriptions for both *C. ammon* and *C. thomasi* are available in Comstock and Huntington (1943), Nabokov (1945), and Smith et al. (1994). **Dorsally**, both *C. ammon* (Fig. 7, 9, 63–69, 87–93) and *C. thomasi* (Fig. 1, 3, 5, 52–60, 72–81) are distinguished from other Caribbean blues (*Leptotes* Scudder, *Hemiargus* and *Brephidium* Scudder) by the presence of two distinct black submarginal spots at the hindwing tornus in cells  $Cu_2$ -2A and  $Cu_1$ - $Cu_2$ . A single spot is present on *Hemiargus*, multiple spots on *Brephidium*, and no spots or spots only showing through from the undersurface on *Leptotes*. This character alone is not reliable for diagnosing *Cyclargus* and is complicated by the sexual dimorphism exhibited in blues. *Cyclargus* females (Fig. 5, 9, 72–95) have black-bordered fore- and hindwings, and an orange crescent capping the lateral ( $Cu_1$ - $Cu_2$ ) hindwing submarginal spot. *Cyclargus ammon* males (Fig. 7, 63–69) are generally distinguished from *C. thomasi* (Fig. 1, 3, 52–60) dorsally by the presence of peach to orange scales above (proximad of) the  $Cu_1$ - $Cu_2$  spot. The peach to orange scales may be few in number and appear diffuse (e.g., Fig. 65, 68) or form a distinct crescent, which can exceed the diameter of the black spot in height (e.g., Fig. 67). The latter character is subject to variation further addressed below and occasional specimens of *C. thomasi* are found with

some peach scales above the submarginal spot. *Cyclargus ammon* females (Fig. 9, 87–93) differ from those of *C. thomasi* (Fig. 72–81) dorsally in having a more reddish-orange (as opposed to yellow-orange) crescent above the  $Cu_1$ - $Cu_2$  spot, the height of which extends proximally for a distance greater than (up to 2×) the  $Cu_1$ - $Cu_2$  spot diameter. The orange scaling may also extend laterally into the adjacent cells, but is separated by brown-black scaling on the veins. *Cyclargus thomasi* females are further distinguished from *C. ammon* in having the orange crescent separated proximally from adjacent blue scales of the cell by a usually thin border of brown-black scales, whereas in *C. ammon*, the orange and blue scales meet. On *C. thomasi* females, some specimens also have a submarginal suffusion of white scales extending proximally into the blue scaling of cells  $M_1$ - $M_2$  through  $Cu_2$ -2A.

**Ventrally**, males and females of both species are not distinctly dimorphic. On the forewing, there is a distinct postdiscal band (mesial line) of darker gray color than the gray basal ground color and flanked by patches of white scales in each cell  $R_2$ - $R_3$  and  $R_{4+5}$ - $M_1$  to  $Cu_2$ -2A. On *C. ammon* (Fig. 8, 10, 112–119), the line tends to form a contiguous arc from cells  $R_2$ - $R_3$  to  $M_3$ - $Cu_1$ , whereas on *C. thomasi* (Fig. 2, 4, 6, 96–107), these cell sections are more often offset from each other. This character is variable as is the tendency for the  $R_2$ - $R_3$  mesial line spot to be darker than the others, especially on *C. ammon*. Hindwings more reliably differentiate *C. thomasi* (Fig. 2, 4, 6, 124–141) and *C. ammon* (Fig. 8, 10, 145–150), with three principal diagnostic characters. First is the presence of a basal black or gray spot in cell  $Cu_2$ -2A in *C. thomasi* (basal spot three, Fig. 11). This spot is typically darker than the ground color and ringed or flanked by white scales but may be reduced to a few dark scales on worn specimens (and on eastern Bahamas populations, e.g., Fig. 136). This  $Cu_2$ -2A basal spot is consistently absent on *C. ammon*. The second ventral hindwing distinguishing character is the orange crescent above the black (bordered in metallic blue)  $Cu_1$ - $Cu_2$  spot. As on the dorsal hindwing of females, this crescent is reddish orange on *C. ammon* (Fig. 8, 10, 145–150) and yellowish orange on *C. thomasi* (Fig. 2, 4, 6, 124–141). The height of the crescent exceeds the diameter of the  $Cu_1$ - $Cu_2$  spot on *C. ammon* and is equal or less than the spot diameter on *C. thomasi*. Finally, the prominent postdiscal white band of the ventral hindwing forms a smooth arc on *C. thomasi*, whereas on *C. ammon*, the band appears jagged, in part as a result of proportionally longer rectangular sections in cells  $M_1$ - $M_2$  and  $M_2$ - $M_3$  compared to adjacent cells. As will be further discussed, variation in the width of the postdiscal band minimizes the diagnostic utility of this trait in Bahamas populations.

## 1.2. *Cyclargus ammon* vs. *C. thomasi* – Male Genitalia

Diagnostic characters differentiating *C. ammon* and *C. thomasi* occur in basic structural components of the male genitalia as well as more specialized structures unique to Lycaenidae and Polyommatainae. Beginning dorsally, the paired uncus lobes are proportionally similar in both species, however, the falces differ in the relative length of the terminal arm portion, which extends further beyond the humerulus (humped basal portion) in *C. ammon* (Fig. 17) than in *C. thomasi* (Fig. 14). The tegumen of both species is proportionally similar in length, with *C. ammon* having more protruding lateral (basal) lobes (Fig. 16). The vinculum extends laterally as narrow rods from the tegumen base which meet ventrally. The vinculum is proportionally longer in *C. ammon* than in *C. thomasi*.

Centrally, the phallic complex consists of the phallus encased in a subzonal sheath which “folds back” and extends laterally in *C. thomasi* (Fig. 13), and dorsally in *C. ammon* (Fig. 16) at the zone (anellus) as sclerotized alulae with membranous connections to the sagum. The sclerotized distal, suprazonal, portion of the phallus includes a more heavily sclerotized sheath ventrally with a single ventrally projecting subterminal thorn-like process. In *C. thomasi* (Fig. 13) this thorn is large, originates midway between the zone and sheath terminus, and is preceded basally by a distinct concavity. In *C. ammon* (Fig. 16), the thorn is very small and arises near the sheath terminus. In both species, the vesica is basally armed with minute spinules. Larger cornuti were not observed as the vesica was not everted in dissections and cornuti were not visible through the sclerotized phallobase. The phallus terminates basally in paired proximal tabs (apophyses), which flank the ductus ejaculatorius. No consistent differences were noted in the shape or length of the tabs between the two species. Likewise, the phallobase is variously swollen in some individuals of both species. The sagum is evenly sclerotized in *C. thomasi*, with a dense arrangement of multiple rows of terminal spines of graded lengths (Fig. 13). In *C. ammon* (Fig. 16), the sagum is mostly membranous, sclerotized only at a small patch of spines, which though fewer, are generally longer than in *C. thomasi*. Along with membranous connections to the tegumen, the

sagum is supported by both the allulae and a v-shaped sclerotized furca. As in the vinculum, the furca is proportionally longer in *C. ammon* than in *C. thomasi*. The angle of the furca, as well as the ventral midpoint of the vinculum, serve as reinforced attachment points for the valvae.

Valvae are similarly obovate in shape in both *C. ammon* and *C. thomasi*, but with the ventral (mesal) margin more convexly rounded in *C. ammon* (Fig. 16, 38, 39) and the distal portion more acutely tapered in *C. thomasi* (Fig. 13, 22–36). The dorsal (lateral) margin is heavily sclerotized and extends distally into a partly retractable arm or rostellum terminating in a toothed spatulate comb which when retracted, rests on a more membranous recess near the valve apex. In *C. ammon*, the comb is distally convex with the teeth more or less evenly developed (Fig. 38, 39, 50). In *C. thomasi*, the comb is distally truncate, appearing transversely stretched with respect to the long axis of the valve, with the dorsal-most tooth elongated, forming a prominent beak in profile (Fig. 22–36, 43–49). Comb variation is exceptional within *C. thomasi* and is further discussed below.

### 1.3. *Cyclargus ammon* vs. *thomasi* – Female Genitalia

The papillae anales and posterior apophyses are similar in both *C. thomasi* (Fig. 18) and *C. ammon* (Fig. 20), with the apophysis posterioris length exceeding 2× the papilla analis width. In *C. thomasi*, the anterior apophysis is very short, its length less than half the papilla analis width. In *C. ammon*, the anterior apophysis is reduced to a triangular projection of the anterior margin of tergite VIII. In both species the ostium is centrally placed, but there are striking differences between them in sclerotized armature. In *C. ammon*, the ostium is flanked by two elongate sclerites (Fig. 21), and projects beyond sternite VII as a membranous partly extensible tubular structure termed a henia. In *C. thomasi* the henia is a tapered, moderately sclerotized cup-like structure with an acutely rounded posterior lip (Fig. 19). The henia may be partly retracted anterad near the middle of sternite VII or fully extended with only the posterior lip projecting beyond the margin of sternite VII-VIII. Sternite VII is partially sclerotized in both species, often obscuring the view of the henia. In *C. ammon* and *C. thomasi*, the ductus bursae is a separate tubular structure inserted within the henia with the inception of the thin ductus seminalis on the dorsal side of the ductus bursae, basad within the henia. A membranous, plicate “periostial pocket” surrounds the henia as an invagination of the sternite VII-VIII intersegmental membrane (Fig. 18, 20). In *C. thomasi* the pocket usually protrudes anterad on either side of the henia. In *C. ammon*, the pocket is more evenly concave centrally, and with sclerotized plicae. The ductus bursae is slightly longer than the ovate corpus bursae in both species. The corpus bursae of both species has fine spiculations and no signa.

### 1.4. Interspecific and Intraspecific Variation in the Genus *Cyclargus*

#### a. Dorsal Wing Patterns

The dorsal forewings of *Cyclargus* males show little variation between and within species other than the basic ground color and a slight grading of the black terminal margin basad into the blue scales. Ground color of fore- and hindwings is similar. In comparing series of images taken with consistent lighting and magnification (Fig. 52–71), the ground color ranges from deep blue on the 2009 MGCL captive colony specimens of *C. thomasi* (Fig. 52) to pale blue on specimens of *C. thomasi clenchi* (L. Miller, Simon and Harvey, 1992) (Fig. 60). Within the more western populations of *C. thomasi*, the blue color can be a slate blue or more typically have a slight purplish cast. *Cyclargus ammon* and *Cyclargus woodruffi* (W. Comstock and Huntington), likewise vary in ground color, with most specimens also having a purplish cast to the blue (Fig. 88), as opposed to the occasional mazarine (Fig. 87) or cerulean blue. Older, faded specimens are a more muted blue with a brownish gray cast. Specimens exposed to excessive moisture during relaxing and preparation also tend to appear brownish, indicating possible damage to structural elements of blue reflective scales.

There is some variation in the development of the two black submarginal spots of the male dorsal hindwing tornus, with that of cell  $Cu_2-2A$  smaller than that of  $Cu_1-Cu_2$  in some specimens, but no consistent patterns were found within the genus (Fig. 52–71). The “orange” cap above the  $Cu_1-Cu_2$  submarginal spot is often diagnostic in distinguishing between *C. ammon* and *C. thomasi*. This scale cap does, however, vary considerably in development within *C. ammon* populations, ranging from a well-defined elongated crescent (Fig. 67) to just a few scales (Fig. 66) or nearly absent (Fig. 65), and while usually absent on *C. thomasi*, occasional specimens are encountered with a few orange scales

present. In addition to *C. ammon*, these “orange” scales are also normally present on *C. woodruffi* and *C. dominica*. On *C. woodruffi*, they tend to be reddish orange (Fig. 61, 62) while on *C. dominica* they are peach to yellowish orange (Fig. 70, 71).

The dorsal forewings of female *Cyclargus* are variable in the extent of brown/black scaling. As shown for *Chilades pandava pandava* Horsfield (Polyommataini) (Kunte and Tiple 2009), the frequency of these forms may correspond to wet versus dry season. However, both forms may be present at a given time and location, as seen on Mayaguana Island females of *C. thomasi*. As on males, the blue ground color varies, and within *C. woodruffi* of the Lesser Antilles it ranges from the typical blue with a purplish cast to a distinct purple in populations of eastern Puerto Rico and the Virgin Islands.

Dorsal hindwings of *Cyclargus* females exhibit a wide range of variation (Fig. 72–95) both within and between species. The ground color, in addition to blue with purplish hues, may be brown or grayish brown (Fig. 77, 82) and/or include an infusion of white scales in the postdiscal part of each cell (Fig. 83, 95), and/or capping, or flanking the two black submarginal spots of the tornus ( $Cu_1$ - $Cu_2$ ,  $Cu_2$ -2A) (Fig. 84, 94) (these are the ‘praeterterminal marks’ of Nabokov 1945, 1948). The white scaling is most pronounced on *C. dominica* and includes a white ring bordering the medial black submarginal spot ( $Cu_2$ -2A) and a distinct, u-shaped white border on the lateral ( $Cu_1$ - $Cu_2$ ) submarginal spot. The latter character is unique and diagnostic for *C. dominica* (Fig. 94, 95). The shape and length of the orange crescent cap above the  $Cu_1$ - $Cu_2$  submarginal spot varies from less than, to about 2× the spot diameter. Development of the orange crescent, while variable, tends to be most extensive on females of *C. woodruffi* (Fig. 82–86) and *C. ammon* (Fig. 87–93), and although separated by brown scaling on veins, may cross over into the adjacent cells  $M_3$ - $Cu_1$  and  $Cu_2$ -2A (Fig. 82, 91).

### b. Ventral Wing Patterns

As noted, the ventral forewings of males and females do not reliably separate *C. thomasi* and *C. ammon*. The ventral forewing of *C. woodruffi* is, however, distinct from other *Cyclargus* in having the postdiscal band cell spot in  $M_2$ - $M_3$  distinctly elongate (Fig. 108 arrow, 109–111), with the adjacent spots in cells  $M_1$ - $M_2$  and  $M_3$ - $Cu_1$  continuing the postdiscal band from the basal and lateral ends of  $M_2$ - $M_3$ , respectively. *Cyclargus dominica* can be distinguished from *C. woodruffi*, *C. ammon*, and *C. thomasi* in having the white scaling bordering the discal cell-end bar grading and contiguous distad to the margin of the postdiscal band, and not separated from the postdiscal band by darker basal ground scaling (Fig. 120–123).

Patterns of the ventral hindwings (Fig. 124–153) of both males and females are by far the most complex and include diagnostic, though overlapping features of species and subspecies. The hindwing ground color is gray in all species but varies in brightness, hue, and degree of white overscaling in *C. thomasi* and *C. ammon*. In general, ventral hindwings of Bahamas populations of *C. thomasi* are noticeably darker than those from Florida, Cuba, and Hispaniola. Ground color of Bahamas specimens ranges from a brownish gray to a slate gray. In contrast to Bahamas *C. thomasi*, *C. woodruffi*, has a more uniform brownish gray ground color with white overscaling reduced or entirely lacking. In *C. dominica*, the basal ground color is a pale gray-brown, with white overscaling that grades into adjacent bands.

Along with a distinct round black subbasal spot, cell  $Sc+R_1$ -Rs includes a distinct costal spot (Kunte and Tiple 2009) in *C. thomasi*, *C. woodruffi*, and *C. ammon*. These spots are similar in diameter to the submarginal spots of the tornus. The relative distance between the subbasal and costal spot and the alignment of the costal spot with the paler, subtending spot-like element (or macule) of cell  $Rs-M_1$  is variable within populations of *C. thomasi* and *C. ammon*. The costal spot, like the subbasal spots, is confined to the cell space between adjacent veins. On *C. ammon*, the costal spot is occasionally enlarged, appearing oblong, as it is transversely expanded within the cell. Within Crooked Island populations of *C. thomasi*, some specimens have the subbasal and costal spots rimmed in white, but filled with a shade of gray similar or only slightly darker than the ground color, as opposed to black or dark gray (Fig. 136–138). On *C. dominica*, the costal spot is poorly defined and similar to the subtending spot-like element of  $Rs-M_1$ .

The aforementioned subbasal spots are present in cells  $Sc+R_1$ -Rs, the poster half of the discal cell, cell  $Cu_2$ -2A, and the anal cell of *C. thomasi* and *C. woodruffi*. A spot-like element (of the broken discal band) is present in cell 2A-3A (Fig. 11). This element is more distally positioned from the wing base than the subbasal spots but can be easily confused with them when counting spots in the field. The subbasal spot

of  $Cu_2$ -2A (spot 3, Fig. 11) is consistently absent in *C. ammon* and in *C. thomasi* it may be very small in Bahamas populations, and sometimes absent in specimens from the more eastern island banks. On *C. dominica*, all subbasal spots are reduced and form a contiguous narrow subbasal band as opposed to a series of distinct, round, white-rimmed spots (Fig. 151–153). The subbasal spot of the discal cell is interesting in that it remains confined to the posterior part of the cell within what would be cell  $M_2$ - $M_3$  if vein  $M_2$  continued all the way to the wing base. On *C. dominica*, the subbasal band traverses the entire cell, and is composed of two conjoined spot-like elements. On *C. thomasi*, a minute second discal basal spot was noted in the anterior ( $M_1$ - $M_2$ ) part of the discal cell in one wild Florida specimen (Plantation Key) and numerous captive colony vouchers (Fig. 124).

Within the genus, the cell end bar and medial and cubital elements of the discal band form a gray Y-shaped marking, which is similar or darker than the ground color and bordered by a narrow or diffused border of white scales. This Y-mark ranges from narrow and well defined (*C. ammon*, *C. dominica*, western *C. thomasi*) to broad and broken (eastern Lucayan *C. thomasi*, *C. woodruffi*), depending on the extent of white scaling of the adjacent postdiscal band.

The white postdiscal band is broad and well-developed on *C. ammon*, *C. dominica*, and *C. thomasi* of Cuba and Hispaniola, as well as all wild *C. thomasi* Florida specimens examined at MGCL ( $n = 621$ ). On *C. thomasi*, the white postdiscal band elements extend fully to the veins or are slightly contracted from the veins, occasionally taking on a bottle shape with slight mesal constrictions forming 'bottlenecks' (Fig. 130). On *C. thomasi* from The Bahamas, the white elements tend to be reduced, which together with the darker gray ground color, produce a distinct phenotype. Florida 2009 captive colony vouchers examined ( $n = 258$ ) are generally similar to Bahamas material in these characters (Fig. 124).

As on Bahamas *C. thomasi*, the postdiscal band on *C. woodruffi* is distinctly reduced and has a fragmented, jagged appearance, with elements of cells  $M_1$ - $M_2$ ,  $M_2$ - $M_3$ , and  $Cu_1$ - $Cu_2$  being the most developed. As noted, the postdiscal band is well-developed on *C. ammon*, yet individual populations from the Great and Little Bahamas banks include specimens of both phenotypes (well-developed vs. reduced bands). On *C. woodruffi*, *C. dominica*, and especially *C. ammon*, there is a tendency for the postdiscal white elements of  $M_1$ - $M_2$  and  $M_2$ - $M_3$  to appear offset (Fig. 149, 150) from what appears as a smoother arc of the *C. thomasi* postdiscal band. This offset arrangement correlates with the typically larger patch of orange scaling above the black submarginal spot on  $Cu_1$ - $Cu_2$  in these species, particularly females.

As noted above, in both sexes of *C. ammon* and *C. woodruffi*, the extent of the orange cap on the ventral hindwing  $Cu_1$ - $Cu_2$  submarginal spot tends to be greater overall, up to 2× the spot diameter, compared to that of *C. thomasi* and *C. dominica*. Relative size variation in the cap is highest within *C. woodruffi* and Bahamas *C. thomasi*.

Within the Polyommatae, ventral hindwing submarginal spots are frequently rimmed or filled with reflective metallic silver or turquoise markings referred to as scintillae (Nabokov 1945, 1948; Pyle 2002). In *Cyclargus*, the scintillae are usually confined to the inner margins of the black submarginal spots ( $Cu_1$ - $Cu_2$ ,  $Cu_2$ -2A) (Fig. 11), and overlay the black scales. Upon close examination and subsequent removal of individual scales, we found these scales are completely clear with an opalescent sheen. The scales, when placed on top of black, appear metallic turquoise-blue in *C. thomasi*, *C. woodruffi*, and *C. ammon*. This examination was prompted by our observation that the orange cap of the  $Cu_1$ - $Cu_2$  spot in *C. dominica* appears somewhat pink. We found that *C. dominica* is unique within the genus in that the reflective overscaling regularly extends from the  $Cu_1$ - $Cu_2$  black submarginal spot into the central area of the orange cap. These reflective scales appear glossy pink when overlaid on orange scales, and when removed and placed on black, appear violet.

The structural elements of these reflective scales and the gene(s) which regulate scintillae expression within the genus and related taxa may be of interest for future inquiry. Of note is the strikingly unique aberrant phenotype expressed in the majority of specimens preserved from the 2009 MGCL captive colony of *C. t. bethunebakeri* (Fig. 124). These specimens have a well-developed extra scintilla spot (comprised of about 100 reflective scales) within the submarginal macule of cell  $M_3$ - $Cu_1$ . No other *Cyclargus* taxa bear this marking and of the 621 wild Florida Miami blue specimens examined (from throughout its former range dating back to 1930), only two specimens (from Key Largo) were found which have a very faint trace (one or two individual reflective scales) within the  $M_3$ - $Cu_1$  submarginal macule. Unfortunately, no wild-collected specimens from the Bahia Honda Key founding population

were vouchered at MGCL. However, photographs of live adults from Bahia Honda from 2004 are of the wild phenotype, without the extra scintilla spot (Warren et al. 2018).

### c. Male Genitalia

*Cyclargus* male genitalia (Fig. 12–17, 22–51) include numerous diagnostic characters at the species level. Intraspecific variation in specialized structures, however, reduces their utility at the subspecific level. Nabokov (1945) emphasized the development of the sagum in defining Neotropical genera, most notably in *Cyclargus* and *Echinargus* Nabokov. As noted above and illustrated in Figures 13 and 16, the sagum is useful in distinguishing between *C. thomasi* and *C. ammon*, being membranous in the later species with fewer, but well-developed spines. The sagum of *C. woodruffi* is indistinguishable from that of *C. thomasi*, both in shape and sclerotization, with overlapping variation in the development of multiple rows of spines. In *C. dominica*, the sagum is similarly sclerotized, but more elongate, with a ventral ridge and no spines. The latter character may merit further investigation, as Nabokov (1945) indicated serrations in one of two specimens he dissected.

As with the sagum, the shape of the phallus of *C. thomasi* and *C. woodruffi* is similar and both have a large thorn between the zone and apex on the suprazonal sheath. *Cyclargus ammon* is distinct from *C. thomasi* and *C. woodruffi* in having a much smaller thorn, positioned closer to the apex of the suprazonal sheath. In *C. dominica*, this thorn is further reduced and positioned at the sheath apex. Within species, the phallus shape is more or less consistent in the lateral aspect but varies in the stature of the dorsal aspect of the phallobase (Fig. 12, 15). The shape and relative length of proximal tabs is also variable within species, with the basal portion of the tabs variously sclerotized.

Nabokov (1945) was precise in measuring relative lengths and angles of the uncus and falx (Fig. 14, 17) as well as other structures. Unfortunately, intraspecific variation in the relative length of the falx arm to the humerulus, and difficulty in positioning specimens to measure these structures, reduces their utility. Valvae, on the other hand, when removed and slide mounted (Fig. 22–42), can be more easily compared. Overall valve shape is similar in *C. thomasi* (Fig. 22–36), *C. woodruffi* (Fig. 40–42), and *C. dominica* (Fig. 37), with the dorsal rostellum-bearing margin strongly bowed and the apex of the valve terminating in an acute rounded point. The apical margin of the valve is moderately sclerotized and subtended by a membranous depression and shelf-like mentum on which the rostellum rests when retracted. In *C. ammon* (Fig. 38, 39), the dorsal margin of the valve is only slightly bowed, the apex rounded but not acute, and the ventral margin rounded and distinctly bulging. Variation in the thickness of the dorsal margin as well as thickness and curvature of the free portion of the rostellum is especially notable within *C. thomasi* (Fig. 22–36). Valve shape of *C. dominica* is closest to that of *C. woodruffi* (Fig. 40–42), but differs in the shape of the rostellum comb (Fig. 37).

Rostellum combs are diagnostic at the species level but are highly variable in the total number of teeth and development of the dorsal, terminal teeth (Fig. 43–51). In *C. thomasi*, the enlarged, beak-like, dorsal tooth is one of the key species-level characters, but relative length varies within populations and no subspecific-level patterns were found. Further, some specimens possessed differences between combs of the right and left valve of the same individual, as in *C. woodruffi* (Fig. 42 a, b). In general, the combs of *C. woodruffi*, while having a slightly developed dorsal tooth, are distinguished from those of *C. thomasi* by the expanded spatulate ventral portion of the comb (Fig. 40–42, 51), with the rostellum juncture toward the dorsal end of the comb. In contrast, the juncture of the rostellum with combs is more central in *C. thomasi* and *C. ammon* (Fig. 43–50), and ventral in *C. dominica* (Fig. 37). In the latter species, the comb extends from the rostellum at a nearly right angle from the ventral, heel-like, region of the comb.

### d. Female Genitalia

Interspecific differences between female *C. ammon* and *C. thomasi* are noted above. No subspecific-level patterns were found in *C. thomasi*, and variation tends to correspond with overall adult size. In this case, larger females have better developed lateral lobes of the periostial pocket (Fig. 18). Within all species there is some variation in relative lengths of the posterior apophysis and size of the ductus and corpus bursae. Female genitalia of *C. dominica* (not figured) are similar to *C. ammon* in having a reduced, very short anterior apophysis and a membranous henia. While paired ostial sclerites are present in *C. ammon* (Fig. 21), none were found in *C. dominica*. The periostial pocket is more quadrate in *C. dominica* compared to that of *C. ammon*, and lacks the sclerotized plicae seen in *C. ammon*, *C.*

*thomasi*, and *C. woodruffi*. Slight differences were noted in the ostium/henia of *C. woodruffi* compared to that of *C. thomasi*. In both species these form a sclerotized cup (Fig. 19), with that of *C. woodruffi* tending to be more lightly sclerotized. In *C. woodruffi*, a central ostial sclerite is more visible and distally bifid. *Cyclargus woodruffi* was also found to have paired signa appearing as a very minute sclerotized spot on opposite sides of the corpus bursae in some but not all specimens. Examination of additional specimens may reveal population or subspecies-level trends in the presence of the latter character. In general, genital dissections of female *Cyclargus* butterflies are exceedingly difficult because of the delicate nature of the henia. In the practice known as inverted copulation, the henia everts to collect the male spermatophore. In dissections, this mostly membranous structure, like a male vesica, can be extruded, or tucked away inside the ductus bursae. Likewise, the periostial pockets are often everted in dissections and require careful manipulation to discern the original shape and placement relative to Sternite VII.

## 2. Results of COI DNA Barcode Analysis

Mitochondrial COI DNA barcode sequences (657bp) were obtained from more than 100 *Cyclargus* specimens from throughout the range of the genus. Most specimens were *C. thomasi* and *C. ammon*, which show differences of less than 1%. Outgroup taxa [*Hemiargus ceraunus filenus* (Poey) from GTMO and The Bahamas (n = 7), *Leptotes cassius theonus* (Lucas) from GTMO and The Bahamas (n = 4), and *Brephidium exilis isopthalma* (Herrich-Schäffer) from GTMO (n = 4)] showed little intraspecific variation and differ by more than 2% from *Cyclargus* (Fig. 154).

*Cyclargus thomasi* and *C. ammon* from GTMO were found to have the same COI haplotype and cannot be distinguished by COI barcodes. This haplotype, with C in position 1457, is similar to other *C. thomasi* populations, but different from other *C. ammon* populations. The identical barcode suggests introgression between these two species in Cuba at some point in the past. A unique *C. ammon* haplotype, with G at position 1088 and C at 1634, from Florida, Jamaica, and The Bahamas, probably represents an original *C. ammon* haplotype. However, a similar situation was found with one male specimen from North Caicos Island, recognized by genitalia and wing patterns as *C. thomasi* but having the same “ammon” haplotype. In this case, the reverse may have occurred with the loss of *C. thomasi* mitochondria through introgression.

Populations of Bahamas *C. thomasi* have several haplotypes that do not correlate with geography, but represent some common variation within each population. Within the eastern Bahamas, eight different haplotypes were found, including one identical to GTMO specimens. The latter haplotype was also present in Great Inagua (southeastern Bahamas). Of the material sampled from the western Bahamas, one or two haplotypes were found on each island except for South Andros and Long Island with six haplotypes each, four of which are shared. Populations of *C. thomasi* from The Bahamas have been segregated into three subspecies. The status of these designations relative to haplotypes and morphology will be treated further in the discussion.

Our COI dendrogram (Fig. 154) suggests that Cuban *C. thomasi* are most closely related to *C. thomasi* populations on Hispaniola and thus best correspond with the subspecific entity *C. thomasi noeli* (W. Comstock and Huntington, 1943). Sequences from former Florida *C. t. bethunebakeri* populations are closest to those of specimens from North and South Andros, Eleuthera, and Cat Islands in The Bahamas, but represent a unique haplotype with T in position 1463. COI haplotypes of remaining Florida populations restricted to the Marquesas Keys and Boca Grande (Longcore 2013) have yet to be determined.

Sequences obtained from elsewhere in the West Indies were of interest in understanding potential relationships between taxa and resolving taxonomic questions within the genus. COI sequences from the Cayman Islands included numerous *C. ammon* and a two male *C. thomasi*. The first, from Cayman Brac in MGCL, was readily identified by genitalia and wing patterns. The second was revealed when NVG examined and obtained DNA from the holotype of *C. erembis* [NHMUK] from the Little Cayman. This *C. erembis* COI sequence fits within *C. thomasi*, closest to Florida populations. The COI barcode sequence from the holotype of *C. kathleena* from the Dominican Republic was found to be identical with that of *C. thomasi noeli* from the Dominican Republic. From Jamaica, a sequence obtained from St. Ann's Parish (type locality for *C. shuturn*) was identical to the Bahamas and Florida *C. ammon* haplotype. Also from Jamaica, a sequence obtained from the endemic *C. dominica* was unique and found to be closest

to *C. thomasi*, differing by at least four base pairs (0.6%).

We obtained four COI barcode sequences from *Cyclargus thomasi woodruffi* (*sensu* Warren et al. 2018). These include one distinct haplotype from St. Kitts and Barbuda, which differs from Greater Antilles *C. thomasi* and *C. ammon* by about 1%. Based on COI sequence differences, ventral forewing morphology, and male genitalia as discussed above, we consider *C. woodruffi* to be a species-level taxon, although details of its relationship to *C. thomasi noeli* in Puerto Rico remain to be elucidated in greater detail (see below). Barcode sequences from specimens from the British Virgin Islands are unique in having G at position 1160. Adults from the British Virgin Islands are apparently indistinguishable by wing patterns and male genitalia from other *C. woodruffi* populations, thus the significance of this unique haplotype remains to be elucidated.

## Discussion and Conclusions

### 1. Geographic considerations

In this section, we discuss our results in the context of each major island group within the distribution of the genus *Cyclargus*, including taxonomic notes on recently described *Cyclargus* from Hispaniola, Jamaica and Guadeloupe.

#### 1.1 South Florida

*Cyclargus thomasi* and *C. ammon* have occurred in direct sympatry in the Florida Keys. *Cyclargus thomasi* was once widespread in southern peninsular Florida, but is now absent from the peninsula and most of the Florida Keys (Calhoun et al. 2002). Additional colonies of the Miami blue (*C. t. bethunebakeri*) have been located in south Florida since the taxon was first listed as “Endangered” (Longcore 2013), and a captive breeding program has been reestablished at the University of Florida. Based on wing patterns, these individuals are morphologically consistent with previous wild Florida populations prior to 2009, and currently show no predominant aberrations in submarginal spots or an extra scintilla spot within the submarginal macule of cell  $M_3-Cu_1$  (ADW, personal observations).

Our analysis confirms the unique COI haplotype of older Florida populations known as *C. t. bethunebakeri*, which has not been seen in populations of *C. thomasi* from Cuba or the Bahamas, although we have not obtained barcode sequences from the newly discovered Florida populations. While the historical and recent distribution of *C. t. bethunebakeri* (the Miami blue) in south Florida is well-documented (Calhoun et al. 2012), and its larval foodplants are well-known, our understanding of the historical distribution and ecology of *C. ammon* in Florida remains incomplete.

In reviewing specimens in the MGCL collections, a Florida specimen of *C. ammon*, collected on Big Pine Key in 1984, was located in unsorted material. This specimen was mentioned by Minno and Emmel (1993) and Calhoun et al. (2002) as being the earliest potential Florida record; the specimen was, however, not available to them for examination. An earlier specimen, a male collected on Key West by R.A. Anderson, 28 June 1973 [MGCL] is also now identified as *C. ammon*. Based on this, we confirm that *C. ammon* was present in Florida in 1973 and, perhaps, earlier. It was collected periodically since then on Big Pine Key (1984, 1999, 2000 [MGCL]), and at times has been a well-established breeding resident there (Calhoun et al. 2002) where it was sympatric with, and using the same larval foodplant as *C. thomasi*. Jaret Daniels (personal communication 2018) also observed *C. ammon* on Bahia Honda Key occurring sympatrically with *C. thomasi*.

The current status of *C. ammon* in Florida is unknown, although we are unaware of verified reports within the last decade. Given the recent listing of *C. ammon* as “threatened” under the Endangered Species Act due to its similarity to *C. t. bethunebakeri*, collecting of *C. ammon* is prohibited without special permits. Because of this, populations (if present) are unlikely to be detected or confirmed, and the haplotype diversity of any extant populations cannot be readily assessed.

Larval foodplants for *C. t. bethunebakeri* in Florida include *Caesalpinia* L. and *Pithecellobium* Mart. species, as well as *Cardiospermum* L. (balloon vine), where larvae feed concealed within the balloon-

like pods (Minno and Emmel 1993). *Cyclargus ammon* also utilizes *Caesalpinia* as a larval foodplant in Florida, as well as *Vachellia* Wight & Arn. (formerly *Acacia* Mill.) species (Calhoun et al. 2002).

### 1.2. Cuba

Until very recently, travel restrictions have complicated the exchange of scientific information between Cuban and United States scientists. With few exceptions, the exchange of specimens for detailed study and analysis for precise identifications has been restricted by the lack of permits for collection and import/export. Our survey work at GTMO, sanctioned by the Environmental Office, United States Navy Base, Guantánamo Bay, provided a rare opportunity to obtain freshly collected specimens of both *C. thomasi* and *C. ammon* where they occur together. Recently collected material facilitates genetic studies and to our knowledge, no other specimens or genetic material of *C. thomasi* have been collected or exported from Cuba to the United States since 1995. Furthermore, previously collected Cuban material of *C. thomasi* was overlooked and misidentified as *C. ammon* in the MGCL collections.

While COI barcodes were not useful in distinguishing between *C. ammon* and *C. thomasi* at GTMO, the two species are clearly recognizable by wing patterns and genitalic characters. The COI barcode obtained for *C. thomasi* is informative, however, in showing that GTMO *C. thomasi* are closest to *C. thomasi noeli* from Hispaniola. Our designation of Cuban *C. thomasi* as subspecies *noeli* is further supported by wing characters, as detailed in the review of wing pattern variation above. Future studies of *Cyclargus* in Cuba may reveal additional COI haplotypes. Any populations found along the northwestern coast (Havana region) will be of logical interest as these are in close proximity to the remaining Florida populations of *C. thomasi* in the Marquesas Keys and Boca Grande.

Habitats at GTMO range from sea-level marshes and mangroves to dry, tropical, sub-montane scrub hills and ridges reaching 153 m. *Cyclargus* were associated with coastal low elevation areas at GTMO (Sites 7 and 15). While we have not verified larval foodplants for *Cyclargus* species at GTMO, the following potential larval foodplants for *C. thomasi noeli* and *C. ammon* occur there (Areces-Mallea 2010): *Caesalpinia vesicaria* L., *Pithecellobium circinale* (L.) Benth., *P. hystrix* (A. Rich.) Benth., *Vachellia farnesiana* (L.) Wight & Arn., and *V. laeta* R. Br. ex Benth. In addition to these species, we identified *Pithecellobium unguis-cati* (L.) Benth. as the major component of a hedge at GTMO Site 7, which is another likely larval foodplant of *Cyclargus*. These plants were flowering in January 2012 and were a popular nectar source for *Leptotes cassius*, as well as *Electrostrymon angelia* (Hewitson) and *Chlorostrymon maesites* (Herrich-Schäffer). In January 2012, *C. ammon* was found at Site 15 near *Vachellia*, and both *C. ammon* and *C. thomasi* were found actively nectaring at *Vachellia*, again at Site 15, in October 2013.

### 1.3. The Cayman Islands

*Cyclargus ammon* and *C. thomasi* are also sympatric in the Cayman Islands, contrary to previous reports. Miller and Steinhauser (1992) identified 49 *Cyclargus* specimens collected on Grand Cayman and Cayman Brac in October-November, 1990, as *C. ammon erembis*, following Riley's (1975) taxonomic treatment. Recent accounts of Cayman butterflies (Askew 1988; Askew and Stafford 2008) list only one taxon, *C. ammon erembis*, though the latter publication aptly notes taxonomic confusion created by Lamas (2004) in listing all previous subspecies of *C. thomasi* as subspecies of *C. ammon*.

With a newly trained eye, DLM examined Steinhauser's series of Cayman material and found one somewhat worn male specimen with a basal dark spot in cell  $Cu_2-2A$  on the hindwing venter. Genitalia dissection (Fig. 31, 47) revealed this suspect specimen as *C. thomasi*. Going back to earlier literature, Carpenter and Lewis (1943) were the first to publish on Cayman butterflies and recorded 32 males and 21 females of "*Hemiargus ammon* (Lucas)" and four males and one female *Hemiargus catalina* (Fabricius). The latter, actually *C. thomasi*, were misidentified based on an earlier account of Florida and Hispaniola specimens by Bethune-Baker (1916), who identified them as *Hemiargus catalina* (which is now recognized as a synonym of *Leptotes cassius* (Zoological Museum 2018)).

After describing the genus *Cyclargus* in 1945, Nabokov was sent one of the four "*catalina*" specimens reported by Carpenter and Lewis (1943), by G. D. Hale Carpenter. Unfortunately, with only one specimen, a male from Little Cayman, and few other *Cyclargus* for general comparison, Nabokov did not examine enough material to realize the full extent of variation within *C. thomasi* genitalia and

proceeded to describe a new species, *C. erembis*. This description (Nabokov 1948) is extremely detailed as was typical of the author, and includes measurements of numerous structures.

The *C. erembis* holotype [NHMUK] was examined and photographed by NVG. Comparison of the male genitalia illustrations of Nabokov (1948) with that of *C. thomasi* lead us to conclude the *C. erembis* holotype and the MGCL Cayman Brac specimen (Fig. 31, 47) are unquestionably the same species. The contracted white elements of the hindwing postdiscal band and other wing markings are consistent with Cuban and Hispaniolan *C. thomasi noeli*. Furthermore, the COI sequence of the *C. erembis* holotype falls within the range of *C. thomasi*. We thus conclude *C. erembis* is a junior subjective synonym of *C. t. noeli*.

Based on the number of specimens examined (MGCL), *Cyclargus ammon* is apparently much more common in the Cayman Islands than *C. t. noeli*. The apparent dominance of *C. ammon* over *C. thomasi noeli* in the Cayman Islands may have contributed to the oversight of Riley (1975), and subsequently Smith et al. (1994), in treating all Cayman Islands *Cyclargus* as an endemic subspecies of *C. ammon*. Both accounts note the large size and bold hindwing ventral markings of Cayman *C. ammon*. Some Cayman *C. ammon* specimens do possess bold markings. However, equally boldly marked specimens, with exceptionally large black spots (Sc+R<sub>1</sub>-Rs) were also examined from Grand Bahama Island.

Studies of the Cayman butterfly fauna (Askew 1980, 1988) show a flux of species presence, with extinctions and recolonizations, such that the islands together support about 30 species at any one time from a total of 46 recorded. A few of these species are derived from Jamaica but the majority of colonizations are apparently of Cuban origin.

#### 1.4. Jamaica

Two species of *Cyclargus* occur in Jamaica. The first, *C. dominica*, is endemic to the island though widely distributed, and uses *Pithecolobium dulce* (Roxb.) Benth., *Vachellia tortuosa* (L.) Seigler & Ebinger, and *V. macracantha* (Humb. & Bonpl. Ex Willd.) Seigler & Ebinger as larval foodplants (Smith et al. 1994; Turner and Turland 2017). The second species, *C. ammon*, was first reported from the island by Iftner et al. (1993) and was thought to be a recent, but well-established introduction. Subsequently, Johnson and Bálint (1995) obtained Jamaican specimens from J. Shuey and described a new species, *C. shuturn*. K. Johnson and Bálint, based on the holotype male and an “allotype” female from St. Ann’s Parish.

Examination of the *C. shuturn* holotype images available online, images of a female from Trelawny Parish (Warren et al. 2018), along with a male and female specimen in MGCL (St. Ann’s Parish) reveal no differences in wing maculation patterns beyond variation seen in Cuban, Cayman, and Bahamas specimens. The two MGCL St. Ann’s Parish specimens were dissected and no genitalic differences were found between these and *C. ammon* from The Bahamas and Cuba. Furthermore, the COI haplotype sequence obtained from the St. Ann’s Parish male is identical to those of *C. ammon* from The Bahamas (South Andros, Grand Bahama, and Abaco) and Florida (Big Pine Key). Based on the above findings we hereby synonymize *C. shuturn* as a junior subjective synonym of *C. ammon*. Turner and Turland (2017) give a detailed and illustrated account of the life history of this species (as *C. shuturn*) on *Vachellia tortuosa*.

#### 1.5. Hispaniola

While *Cyclargus ammon* has not previously been reported from the island, both it and *C. thomasi* are present on Hispaniola, as explained below. Comstock and Huntington’s (1943) type series of *C. thomasi noeli* includes the holotype male and “allotype” female from St. Marc, Haiti, along with 19 males and 12 females from other locations in Haiti and six males and two females from the Dominican Republic. A male from Mona Island (midway between the east end of the Dominican Republic and Puerto Rico) was also mentioned by Comstock and Huntington, but not explicitly included in the type series.

*Cyclargus kathleena* was described from a male holotype and five male paratypes from localities within Pedernales Province, Dominican Republic; the female was unknown (Johnson and Matusik 1992). We examined the holotype specimen (MGCL) and images of two of the male paratypes (Warren et al. 2018); wing patterns of these specimens (though worn) are indistinguishable from *C. thomasi noeli*.

Genitalia of the *C. kathleena* male holotype have not been located and the abdomen is missing from the specimen. Johnson and Matusik (1992) did not state that the holotype was dissected and there are no labels with Johnson’s dissection numbers provided in the publication, nor a corresponding label

on the holotype [MGCL]. Johnson and Matusik (1992) noted that *C. kathleena* was sympatric with *C. thomasi noeli*, but that it occurred in pine bottom grassland habitat and flew at a different time of day. They differentiated the valvae of *C. kathleena* as being more elongate, the comb margin entire versus serrate, and the phallus thinner than in *C. thomasi*, and provided a stylized illustration. Examination of Johnson's illustrated comb figure for *C. t. noeli* using overlays of scanned figures, shows it to be indistinguishable, tooth by tooth, from the figure of *C. thomasi* by Nabokov (1945) from Great Inagua. The lateral valve figures of *C. t. noeli* and *C. t. thomasi* likewise correspond to Nabokov's figures. As noted in the COI results, the sequence obtained from the *C. kathleena* holotype is identical to that of multiple examples of *C. thomasi noeli* from the Dominican Republic. Based on COI data, wing maculation characters, and our knowledge of variation within *C. thomasi* male genitalia, we treat *C. kathleena* as a junior subjective synonym of *C. thomasi noeli*.

Johnson and Matusik (1992) also described *C. sorpresus* from the Dominican Republic, based on a holotype male and two paratype males from Pedernales Province. The holotype was illustrated in greater detail by Warren et al. (2018). This taxon was differentiated from *C. ammon* in lacking a bold orange dorsal hindwing spot, having a gray subapical patch across the ventral forewing, a more ovate, diminutive comb, a more robust and sigmoid phallus, and a dorsally projecting setate lobe on the lateral valve surface. All of these characters fall within the range of variation seen in *C. ammon* from Cuba, the Cayman Islands, and The Bahamas. In particular, the dorsal orange spot is highly variable, ranging from a distinct large bright orange crescent to just a few peach scales in the same populations. The setate lobe of the valve is present in all *Cyclargus* and its prominence in a lateral aspect depends on the orientation of the valve, whether or not setae are lost in cleaning a dissection, and whether or not the illustrator chooses to include setae (Nabokov 1945 did not). Based on this, and the recently obtained COI barcode sequence from the *C. sorpresus* holotype, which is identical to that of *C. ammon* from The Bahamas and Florida, we treat *C. sorpresus* as a junior subjective synonym of *C. ammon*.

With our treatment of *C. sorpresus* as a synonym of *C. ammon*, we herein report *C. ammon* from Hispaniola for the first time. Further field studies on the island are required to determine the degree of sympatry of the two *Cyclargus* species. Contrary to what we observed for the Cayman Islands, *C. thomasi* appears to far more widespread and common on Hispaniola than *C. ammon*.

### 1.6. The Lucayan Archipelago

The Bahamas and Turks and Caicos islands, together forming the Lucayan Archipelago, support populations of both *C. thomasi* and *C. ammon*, which exhibit a wide range of variation in wing patterns, genitalic morphology, and COI haplotype diversity. The haplotype diversity seen in these smaller islands is likely the result of periodic extinctions followed by recolonizations and intermixing between islands of The Bahamas, between the southern Bahamas, Cuba, and Hispaniola, and historically, between Florida and the Little and Great Bahamas Banks. Gene flow between islands and from neighboring larger land masses is likely facilitated by prevailing trade winds, tropical systems, and expanded land masses during glacial maxima.

*Cyclargus thomasi* of the Lucayan Archipelago has been divided into three subspecies (but see below). From west to east, these are *C. t. thomasi* from islands of the Little and Great Bahamas Banks, *C. t. bahamensis* (Clench, [1943]) from the Crooked and Acklins Islands, Plana Cays, and Ragged Islands, and *C. t. clenchi* (L. Miller, Simon and Harvey, 1992) from Mayaguana, Great and Little Iguana, and the Turks and Caicos banks. No substantial differences or consistent patterns were found in genitalia, with males, for example, having a somewhat variable comb shape, tooth number, and curvature and robustness of the rostellum (Fig. 22, 23, 25, 26, 35, 36) within the Great Bahamas Bank and across the whole archipelago.

However, differences were found between the *C. thomasi* subspecies in wing pattern traits. As detailed in the descriptions of variation, there is a tendency for a darker gray ground color on the ventral wing surfaces (Fig. 133-141) and a reduction in the white postdiscal hindwing band throughout the archipelago, more so in the eastern islands. The most consistent pattern was found in males of Great Inagua and Mayaguana Island, which are a paler blue dorsally (Fig. 59, 60), the hindwing postdiscal band in both males and females is reduced to a chain of small white spots, and the two posterior-most dark basal spots ( $Cu_1$ - $Cu_2$  and  $Cu_2$ -2A) are reduced and sometimes absent (Fig. 139-141). These patterns allow recognition of the populations occurring in the archipelago southwest of the Mayaguana Passage as *C. t. clenchi*.

No consistent wing pattern differences were found between Bahamas Banks (*C. t. thomasi*) vs. Crooked and Acklins Island populations (*C. t. bahamensis*) except that there is a tendency for some but not all individuals of the latter to have paler subbasal and costal spots on the ventral hindwing (Fig. 136–138), which are not darker than the subcostal macule, gray post-discal, or discal cell-end bar. Because of this tendency, we feel it is best not to synonymize *C. t. bahamensis* with *C. t. thomasi* at this time. Study of more material is needed and perhaps a more rigorous statistical approach to diagnoses based on inconsistent traits, such as that outlined by Patten and Unitt (2002). We also recognize that evolution is an ongoing chaotic process, especially in this genus with remarkable phenotypic plasticity. Population segregates (or subspecies) as once described based on a small sample may continue to change in both genotype and phenotype, rendering their designation arbitrary by geographic location only.

An unvouchered literature record for the occurrence of the Miami blue (*C. thomasi bethunebakeri*) on the Bimini Islands, at the western margin of the Great Bahama Bank, apparently originated from Riley (1975) and has been propagated by subsequent authors (e.g., Smith et al. 1994, USFWS 2012). As a result, questions about the global range of the Miami blue persist. We were unable to locate any *Cyclargus* specimens from the Bimini Islands for direct examination. Since *C. t. bethunebakeri* can apparently be identified by its unique COI haplotype, a specific project to collect and sequence specimens from Bimini would likely resolve the identity of any current populations as *C. t. bethunebakeri*, or more likely, *C. t. thomasi*, and further clarify patterns of gene flow. Until specimens are secured from the Bimini Islands, the subspecies-level identity of any *C. thomasi* populations there will remain speculative.

*Cyclargus ammon* is common in The Bahamas, but appears to be restricted to the Little and Great Bahamas Banks. Specimens were examined from Grand Bahama, Great Abaco, Long, North Andros, and South Andros islands. Additionally, literature records include Rum Cay (Smith et al. 1994). The presence of an “ammon” COI haplotype from a North Caicos specimen suggests the species or immigrant hybrid descendants were once established there. We anticipate current range extensions to be found for *C. ammon* as island surveys continue.

As in *C. thomasi*, wing patterns of *C. ammon* are highly variable in The Bahamas in regard to the dorsal orange hindwing spot, width of the hindwing white postdiscal band, and size of ventral hindwing black spots in cell Sc + R<sub>1</sub>-Rs. Variation in the expression of the white postdiscal hindwing band is seen within series of specimens collected at the exact same locality and time including recent collections by JYM and field associates in South Andros and Great Abaco. Although labels on series of older museum specimens of *C. ammon* bear two different subspecific manuscript names by Clench, we found no consistent morphological evidence to support the designation of subspecies.

### 1.7. Puerto Rico

Specimens of both *C. thomasi noeli* and *C. woodruffi* have been examined from Puerto Rico, yet we have not seen *C. ammon* from the island and are unaware of any literature records indicating its presence there. Most Puerto Rican *Cyclargus* specimens examined are from the Stuart Ramos collection (MGCL) and are from the southwestern coastal parts of the main island, as well as Mona Island. In both genitalia and wing patterns, most of these *Cyclargus* concur with our concept of *C. thomasi noeli*. A few specimens, however, are intermediate; male genitalia possess valve combs of *C. thomasi*, while the ventral forewings bear elongate postdiscal band cell spots at M<sub>2</sub>-M<sub>3</sub> as in *C. woodruffi* of the Lesser Antilles. A series of specimens of *C. woodruffi* collected by R. A. Anderson in March 1982 at the eastern end of the island (in what was then the Roosevelt Roads United States Naval Base), are distinctly *C. woodruffi* based on male genitalia (Fig. 41), the forewing elongate spot (Fig. 108), and ventral hindwing ground color and maculation (Fig. 142).

While *C. ammon* and *C. thomasi* appear to be closely related based on COI haplotype analysis, morphological characters of male and female genitalia seem to indicate a closer relationship between *C. thomasi* and *C. woodruffi* (see description of interspecific vs. intraspecific variation). Since both *C. thomasi* and *C. woodruffi* are present on the island, and Puerto Rico is the westernmost range of *C. woodruffi*, this island is of particular interest as a potential hybrid transition zone.

Specimens identified as *C. ammon woodruffi* in a recent book on the butterflies of Puerto Rico (Pérez-Asso et al. 2009) unfortunately do not include locality information. The male illustrated (p. 105) appears to be *C. thomasi noeli*, while the female, though lacking the oblong mark of the second ventral forewing median cell of *C. woodruffi*, shows coloration and ventral hindwing patterns intermediate between *C.*

*thomasi noeli* and *C. woodruffi*.

### 1.8. The Lesser Antilles

Only one *Cyclargus* species, *C. woodruffi*, is known to occur east of Puerto Rico, where it is found in the Leeward Islands of the Lesser Antilles. Smith et al. (1991) reported *C. woodruffi* to be the most common butterfly during surveys (1989-90) of the type locality, Anegada Island. Specimens of *C. woodruffi* in MGCL were examined from the following islands: St. Thomas, St. John, Tortola, Marina Cay, Virgin Gorda, St. Croix, St. Martin, St. Barthelemy, St. Eustatius, Nevis, St. Kitts, Barbuda, and Antigua. Overall, little variation was found in wing patterns and genitalia of the Leeward Islands material examined. Slight variations were found in the elongation of the male combs (Fig. 40, 42, 51), with one of two specimens dissected from Tortola (Fig. 42a, b) similar to Nabokov's (1945) illustration of a male from Tortola, differing only slightly on each valve.

Three different haplotypes were found, with those on St. Kitts and Barbuda being identical. The St. Kitts and Barbuda haplotype differs from *C. thomasi* and *C. ammon* by about 1%. The two other haplotypes found from the Leeward Islands are thus far unique but cluster within *C. thomasi* sequences. At this time, there is not enough evidence to assume these differences are anything other than normal variation, yet the sequences suggest the possibility of past introgression with *C. thomasi*.

Foodplants used by *Cyclargus* in the Lesser Antilles parallel those known for Florida and the Greater Antilles. Catling and Kostiuik (2015) give an account of *C. woodruffi* on St. Kitts and Nevis and illustrate larvae and tending ants from *Cardiospermum* on Nevis. JYM also observed larvae feeding on this plant in 1993 on Nevis (personal observation).

About 70 miles to the south of Nevis is the Island of Guadeloupe, where *C. oualiri* Brevignon was described from specimens reared on *Caesalpinia ciliata* (Wikstr.) Urb. Brévignon (2002) differentiated females of *C. woodruffi* from *C. oualiri* in having almost no blue on the dorsal surface and different ventral wing patterns from *C. woodruffi* from Anegada and Puerto Rico. He also referred to figure 49 in d'Abrera (1995) of specimens (labeled as *C. thomasi*) from the British Virgin Islands (between Anegada and Puerto Rico) as belonging to *C. oualiri*.

Wing patterns of adults figured by Brevignon (2002), as well as the referenced figures in d'Abrera (1995), are consistent with those of *C. woodruffi* examined from other islands. The male genitalia drawings are likewise consistent with *C. woodruffi*, although the male comb is partly obscured in the drawing and the dorsally projecting tooth of the comb appears somewhat enlarged as in *C. thomasi*. Despite the latter character, the ventral forewing of both the male and female illustrated have the distinctive oblong mark of median cell  $M_2$ - $M_3$  characteristic of *C. woodruffi*.

Given our knowledge of variation in *C. woodruffi* across its range, we treat *C. oualiri* as a synonym of *C. woodruffi* at the species level. No Guadeloupe *Cyclargus* specimens were available for firsthand examination or sequencing for this study. Examination of *Cyclargus* adults and genitalia from Guadeloupe, along with further morphological and DNA analyses, may at some point support division of *C. woodruffi* into subspecies.

Surveys and reviews of the fauna of the Windward Islands (extending west to the ABC islands) record species of *Hemiargus*, but as yet no taxa of *Cyclargus* (Smith et al. 1994; Woodruff et al. 1998; Debrot and Miller 2004). The absence of *Cyclargus* on these islands, together with the distribution of the endemic *C. woodruffi* restricted to Puerto Rico and the northeastern Leeward Islands, suggests a lack of viable dispersal routes to and from South America in recent times.

## 2. Current Species Distributions

The current distributions of the four recognized species of *Cyclargus* are summarized in Figure 155. With the exception of *C. dominica*, our studies of museum specimens, together with the synonymy of certain taxa, reveal distributions with ranges more extensive than previously believed. The most wide-ranging species, *C. thomasi*, is now known to occur further north in The Bahamas (Abaco Island) and is confirmed to occur in Cuba and the Cayman Islands. The range of *C. ammon* now extends south to include Jamaica and east to the Dominican Republic, and though still needing clarification with DNA analyses, the range of *C. woodruffi* is extended west to include Mona Island. Although the genus is considered endemic to south Florida and the West Indies, only the Jamaican *C. dominica* is known to

be endemic to a single island.

### 3. Historical Biogeography of *Cyclargus*

Vila et al. (2011) detected a pattern of five separate dispersals of Polyommata into the New World through Beringia. The first southward dispersal of southeast Asian ancestral stock resulted in the present-day Neotropical taxa that form a strongly supported monophyletic group of ten genera, including *Cyclargus*. Divergence of this Neotropical clade from Old World ancestors occurred at 10.7 Ma. Descendants of the first dispersal, except *Echinargus* Nabokov, became extinct in the Nearctic Region, with *Hemiargus* and *Cyclargus* representing secondary colonizations from the south. These findings (Vila et al. 2011) are of particular interest in understanding the historical biogeography of *Cyclargus*. By 20 Ma, the Caribbean and North and South American plates were already near their present location, with the Greater Antilles near their present positions, except with Cuba being divided into five smaller islands, and Hispaniola divided into two (Blakey 2018). This means that by the time ancestral stock of the Caribbean endemic genus *Cyclargus* arrived from Central or South America, an over-water route of at least 160 km (roughly 100 mi) was required for colonization from the Yucatan Peninsula, or between the Lesser Antilles to Puerto Rico if colonizing from South America. Both the Greater and Lesser Antilles changed in size and shape from 10.7 Ma to present, with interglacial rises in sea level, orogeny in the Greater Antilles, and volcanic activity in the Lesser Antilles, yet retained separations from the mainland throughout this period (Blakey 2018). Southern Florida and The Bahamas were likewise subject to changes subsequent to the 10.7 Ma mark, and were for the most part completely submerged until ~2.5 Ma, with the succeeding building and subsidence of carbonate platforms until present (Hine 2013, Shinn and Lidz 2018), so that colonization and diversification of *Cyclargus* in these areas north of the Cuban precursor islands and the Caribbean Plate was only possible from about 1.5 Ma.

Though small, these butterflies have somehow managed to colonize and recolonize islands throughout the past few million years, with trade winds likely promoting westward movement of adults through the Caribbean, and hurricanes promoting westward and northward movement. Although Fabaceae are the ancestral foodplants for the tribe, it is worth noting that balloon vine (*Cardiospermum*) pods remain viable and can float for up to six months in seawater (Gildenhuis et al. 2013). Larvae of former populations of *C. thomasi* in Florida (Minno and Emmel 1993) and extant populations of *C. woodruffi* on Nevis (Catling and Kostiuik 2015) fed concealed within these pods.

### 4. Utility of Barcodes in Blues

While comprehensive genomic studies have yet to be completed to differentiate between *Cyclargus* species, our comparison of *C. thomasi* versus *C. ammon* is yet another example of two morphologically distinct species which differ by much less than 1% difference in COI base-pairs, a mark sometimes considered minimally diagnostic of species-level divergence. Although we cannot positively conclude identical sequences shared between the two species at GTMO are the result of introgression or incomplete lineage sorting (or both), the distribution and frequency of the various haplotypes across the species ranges are suggestive of introgression. Hybridization can be a natural agent in speciation, as in *Heliconius* Kluk (Jiggins et al. 2008), yet the prospect of introgression, especially if undetected in nuclear DNA, is challenging from a conservation management perspective, where the goal is preservation of threatened or endangered taxa and thus their existing genotypes.

Although the differences in the various COI barcodes recovered are minimal, along with revealing the possibility of hybrid introgression, dendrogram branching patterns (Fig. 154), together with geographic and morphological patterns, helped determine the subspecies designation of *C. thomasi* from Cuba and provided support for the species-level status of *C. woodruffi*. With additional sequences, *Cyclargus* barcodes may give further clarity to hybrid transition zones, but appear to offer little in terms of mapping gene flow in The Bahamas.

## 5. Implications for Conservation Management

The precise identity (and even the validity) of the subspecies concept is a concern when federal regulations governing sampling and management are applied at this taxonomic level. While several *Cyclargus thomasi* phenotypes can be recognized, there is some overlap in wing pattern traits, which may also be complicated with seasonal wing pattern variation. Given the extreme phenotypic plasticity within the genus, small populations may be prone to wing pattern changes as a founder effect in both island and captive environments, as we've seen with vouchered MGCL 2009 captive colony Miami blues. The evolution of the unique phenotype in the MGCL captive colony suggests that captive stock should regularly be infused with adults from wild populations to maintain genetic diversity.

Our studies indicate that *C. t. bethunebakeri* of Florida possesses a unique COI barcode haplotype not found in neighboring populations in The Bahamas and Cuba. Thus, the COI barcode serves as a potentially diagnostic character to identify the Miami blue, although additional sequences from Cuba and The Bahamas, and from the newly located populations of *C. t. bethunebakeri* in Florida, would be useful to further test this hypothesis. However, given our current knowledge of COI haplotypes of *C. thomasi* from Cuba and the Bahamas, *C. t. bethunebakeri* (the Miami blue) should provisionally be considered endemic to Florida, with the caveat that the subspecies-level placement of populations in the Bimini Islands, if extant, remains unknown. This implies that populations of *C. thomasi* in Cuba and The Bahamas should not be considered as potential stock for any future captive breeding or reintroduction efforts in Florida.

Given the potential for introgression within the genus and subspecific segregates, genomic studies with fresh material are recommended to establish a baseline for tracing past, present and future genetic changes within the genus. Such studies, together with previous work using microsatellite DNA to study local population dynamics (Saarinen 2009; Saarinen et al. 2009, 2014), may provide critical diagnostic tools for conservation efforts. In addition, immature stages of *Cyclargus* (eggs, larvae, pupae) should be preserved whenever available, so that the immature morphology can be examined for potentially diagnostic characters.

The precinctive status and species-level identification of various *Cardiospermum* species, larval foodplants for some populations of *C. thomasi*, continues to be a subject of debate (Carroll and Loye 2006; Gildenhuis et al. 2013). Since herbarium samples were not vouchered with past collections of *C. t. bethunebakeri* in Florida, it would be of interest to determine the *Cardiospermum* species being used by *C. woodruffi* in Nevis and conduct oviposition/feeding tests with captive Florida stock. As a vine, *Cardiospermum* can grow on power and telephone lines in utility easements and is thus subjected to aggressive management. While management of these plants in Florida likely contributed to the decline of the Miami blue, anything we can learn about their present use in other *Cyclargus* populations may be valuable for future conservation efforts in Florida and the West Indies.

## Summary

Our review of *Cyclargus* has hopefully resolved various taxonomic issues that have hindered identifications and our understanding of taxa within the genus, and may serve as a taxonomic framework to assist future conservation management decisions. Below, we present a provisional synonymic list of *Cyclargus* taxa, recognizing four species-level taxa. We note that these are the same species-level divisions proposed by Nabokov (1945) when *Cyclargus* was described.

## Provisional Synonymic List of *Cyclargus*

*Cyclargus thomasi thomasi* (Clench, 1941)

*Hemiargus catilina thomasi* Clench (1941: 407)

*Cyclargus thomasi bahamensis* (Clench, [1943])

*Hemiargus bahamensis* Clench (1942 [1943]: 57)

*Cyclargus thomasi clenchi* (L. Miller, Simon and Harvey, 1992)

*Hemiargus thomasi clenchi* L. Miller, Simon and Harvey (1992: 14)

- Cyclargus thomasi noeli* (W. Comstock and Huntington, 1943)  
*Hemiargus ammon noëli* W. Comstock and Huntington (1943: 99)  
*Cyclargus erembis* Nabokov (1948: 274) **New Synonym**  
*Cyclargus kathleena* K. Johnson and Matusik (1992: 3) **New Synonym**  
*Cyclargus thomasi bethunebakeri* (W. Comstock and Huntington, 1943)  
*Hemiargus ammon bethune-bakeri* W. Comstock and Huntington (1943: 97)  
*Cyclargus woodruffi* (W. Comstock and Huntington, 1943) **Status Confirmed**  
*Hemiargus ammon woodruffi* W. Comstock and Huntington (1943: 100)  
*Cyclargus oualiri* Brevignon (2002: 97) **New Synonym**  
*Cyclargus ammon* (Lucas, 1857)  
*Lycaena ammon* Lucas (1857: 262)  
*Cyclargus shuturn* K. Johnson and Bálint (1995: 11) **New Synonym**  
*Cyclargus sorpresus* K. Johnson and Matusik (1992: 3) **New Synonym**  
*Cyclargus dominica* (Möschler, 1886)  
*Lycaena dominica* Möschler (1886: 26)

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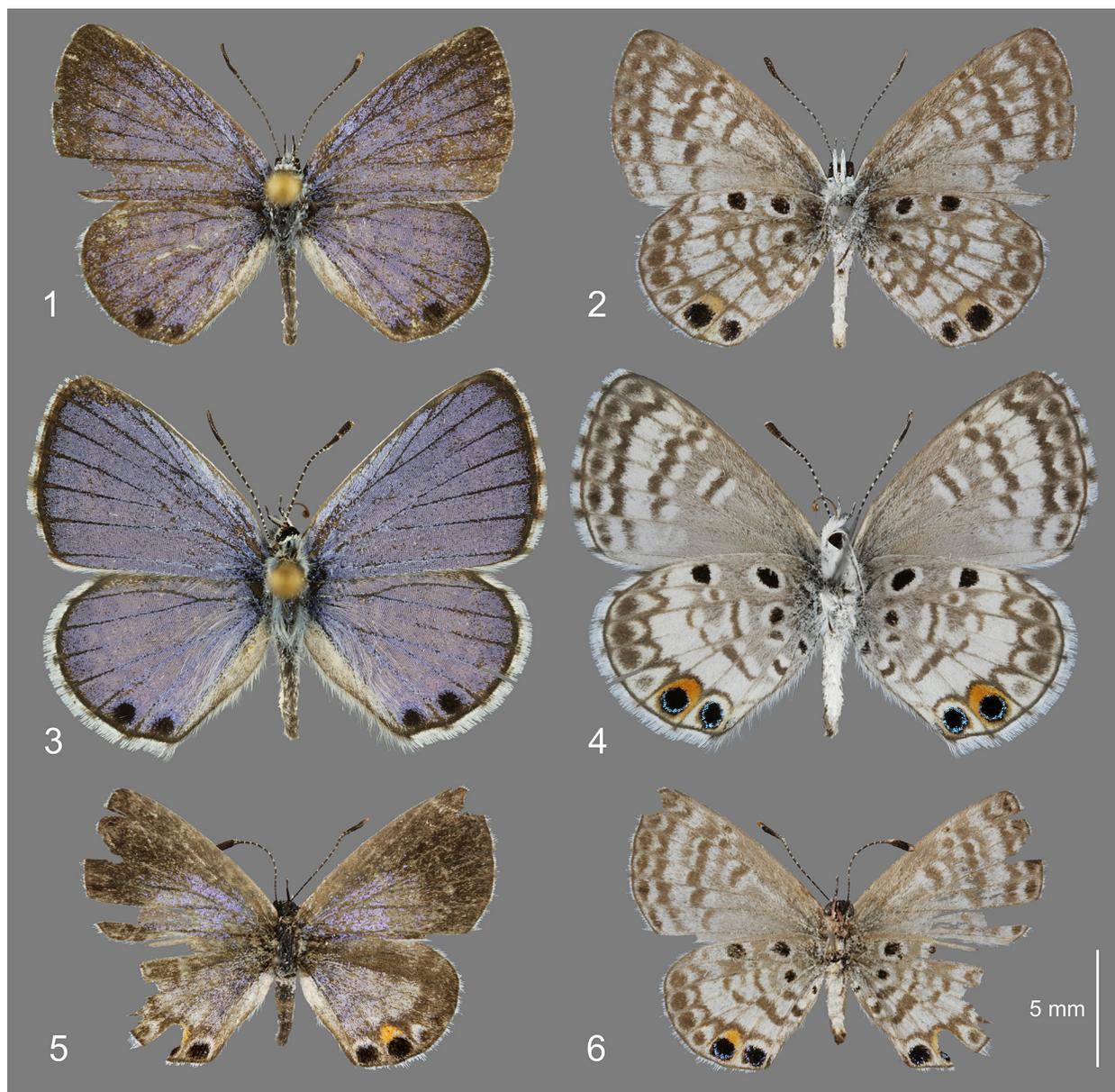
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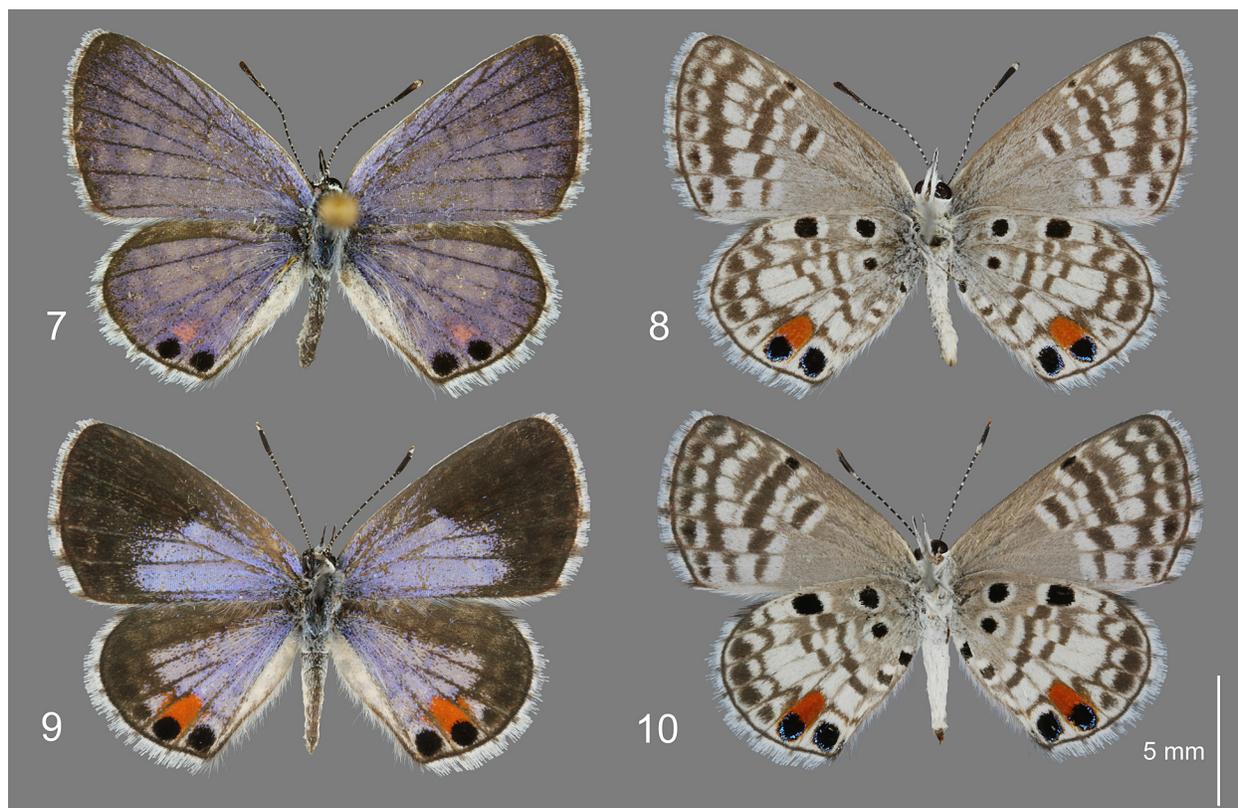
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**Figures 1–6.** *Cyclargus thomasi noeli* collected at GTMO, October 2013. **1)** Male, DM 1682, LEP-17798, dorsal. **2)** Same specimen, ventral. **3)** Male, DM 1688, LEP-17799, dorsal. **4)** Same specimen, ventral. **5)** Female, DM 1692, LEP-22349, dorsal. **6)** Same specimen, ventral.



**Figures 7–10.** *Cyclargus ammon* collected at GTMO, October 2013. **7)** Male, dorsal. **8)** Same specimen, ventral. **9)** Female, dorsal. **10)** Same specimen, ventral.

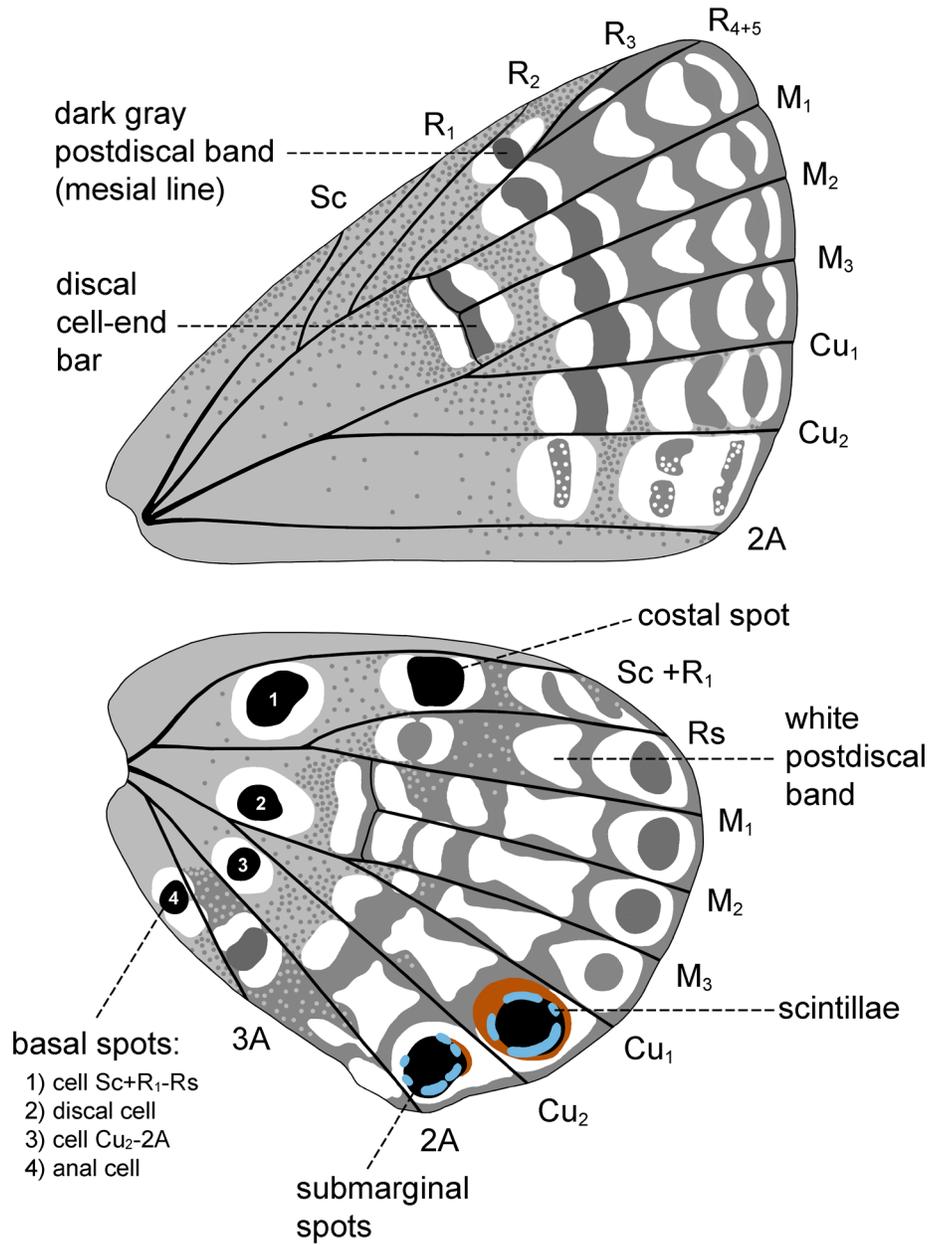
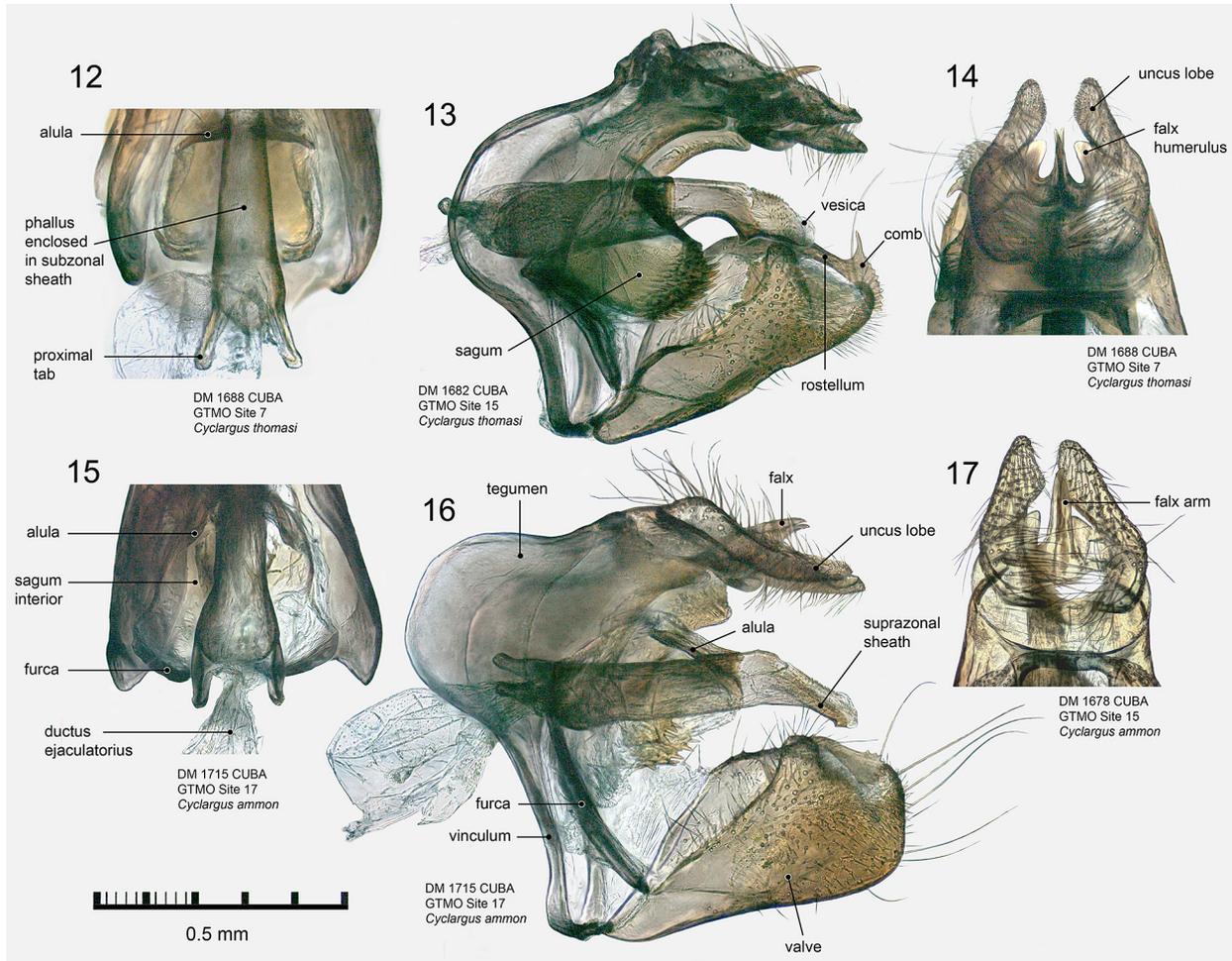
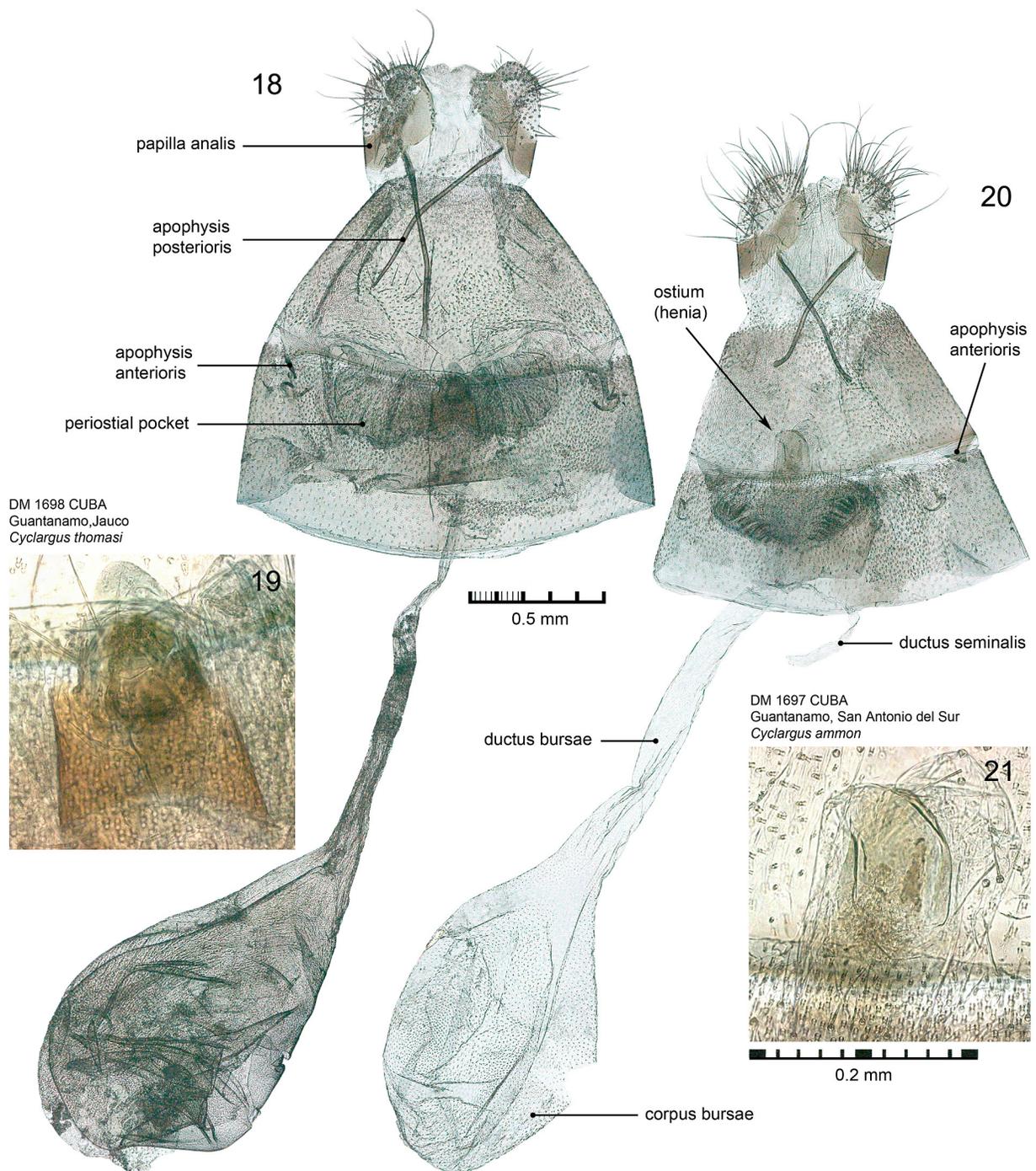


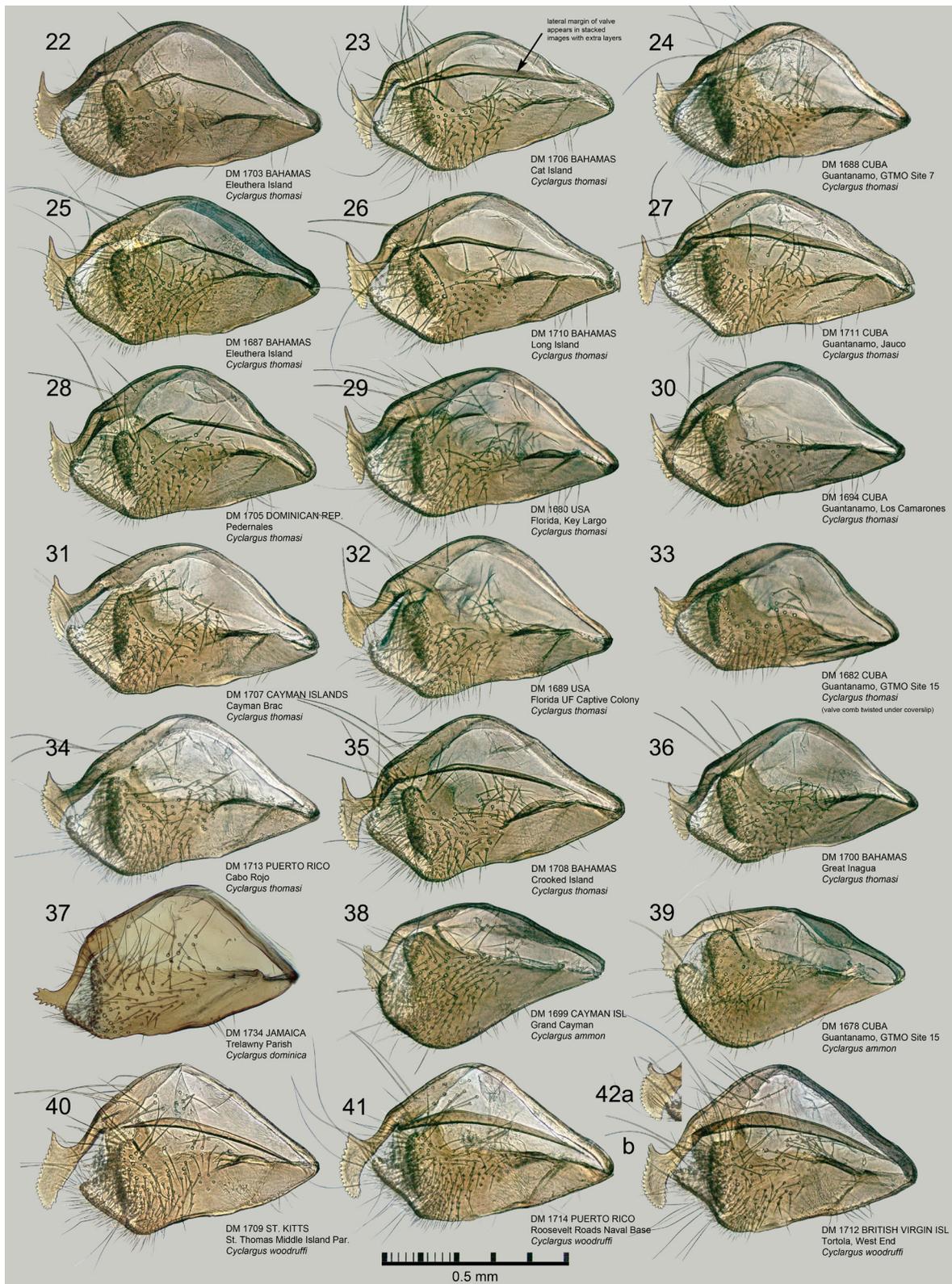
Figure 11. Diagrammatic representation of *Cyclargus* wing venation and maculation elements (fringes excluded).



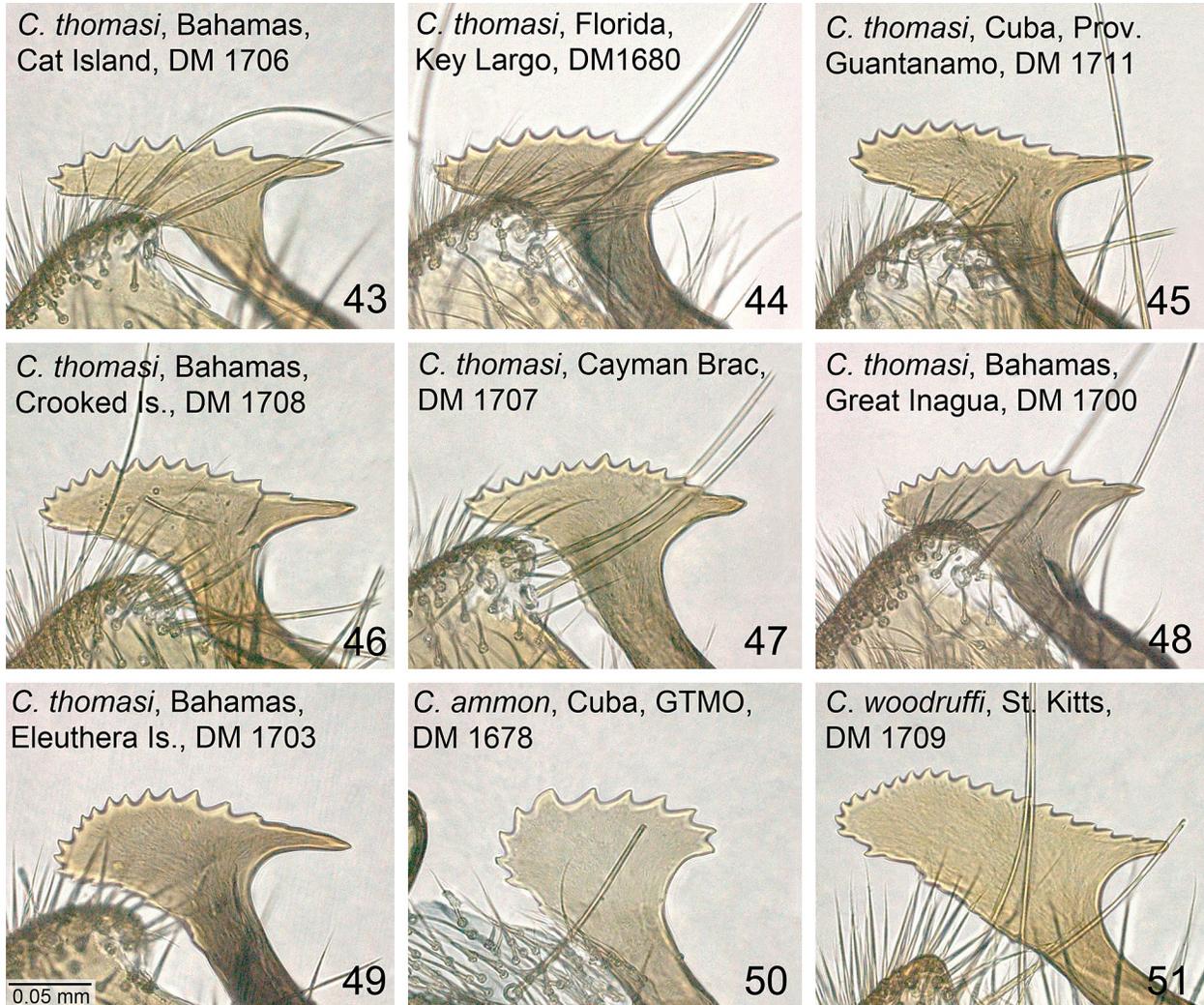
**Figures 12–17.** Male genitalia. **12–14)** *C. thomasi*. **12)** Dorsal view of sagum and phallobase. **13)** Left lateral view of complete genitalia, minus left valve. **14)** Dorsal view of uncus complex. **15–17)** *C. ammon*. **15)** Dorsal view of sagum and phallobase. **16)** Left lateral view of complete genitalia, minus left valve. **17)** Dorsal view of uncus complex.



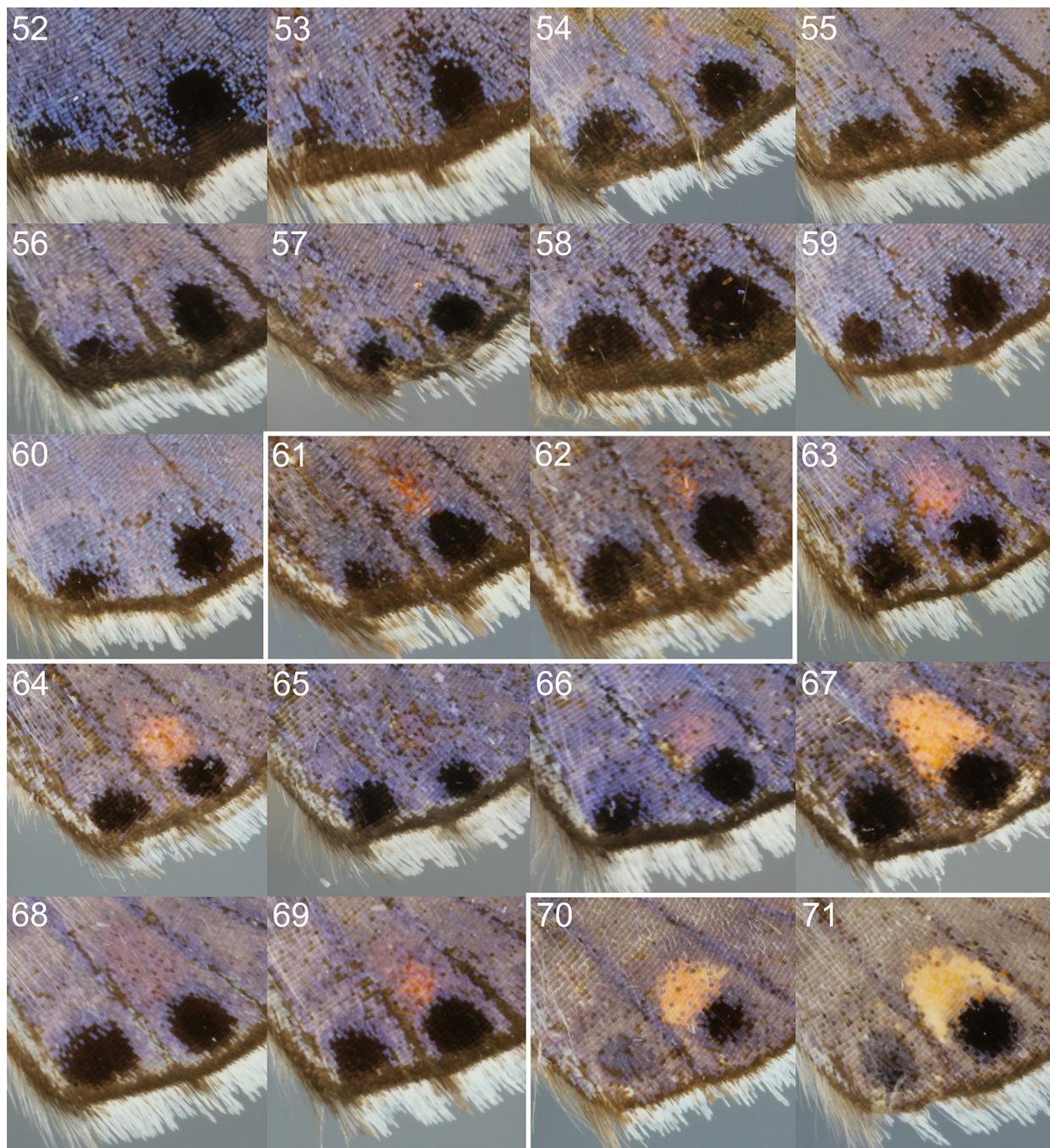
**Figures 18–21.** Female genitalia. 18) *C. thomasi* ventral view. 19) Same specimen, enlargement of henia. 20) *C. ammon* ventral view. 21) Same specimen, enlargement of henia.



**Figures 22–42.** Male valvae, mesal views of left valve, showing shape, variation in rostellum curvature, and terminal comb shape: **22–36)** *C. thomasi*. **37)** *C. dominica*. **38, 39)** *C. ammon*. **40–42)** *C. woodruffi* (42a, b, opposite valve/comb of same specimen). Localities as indicated below images.



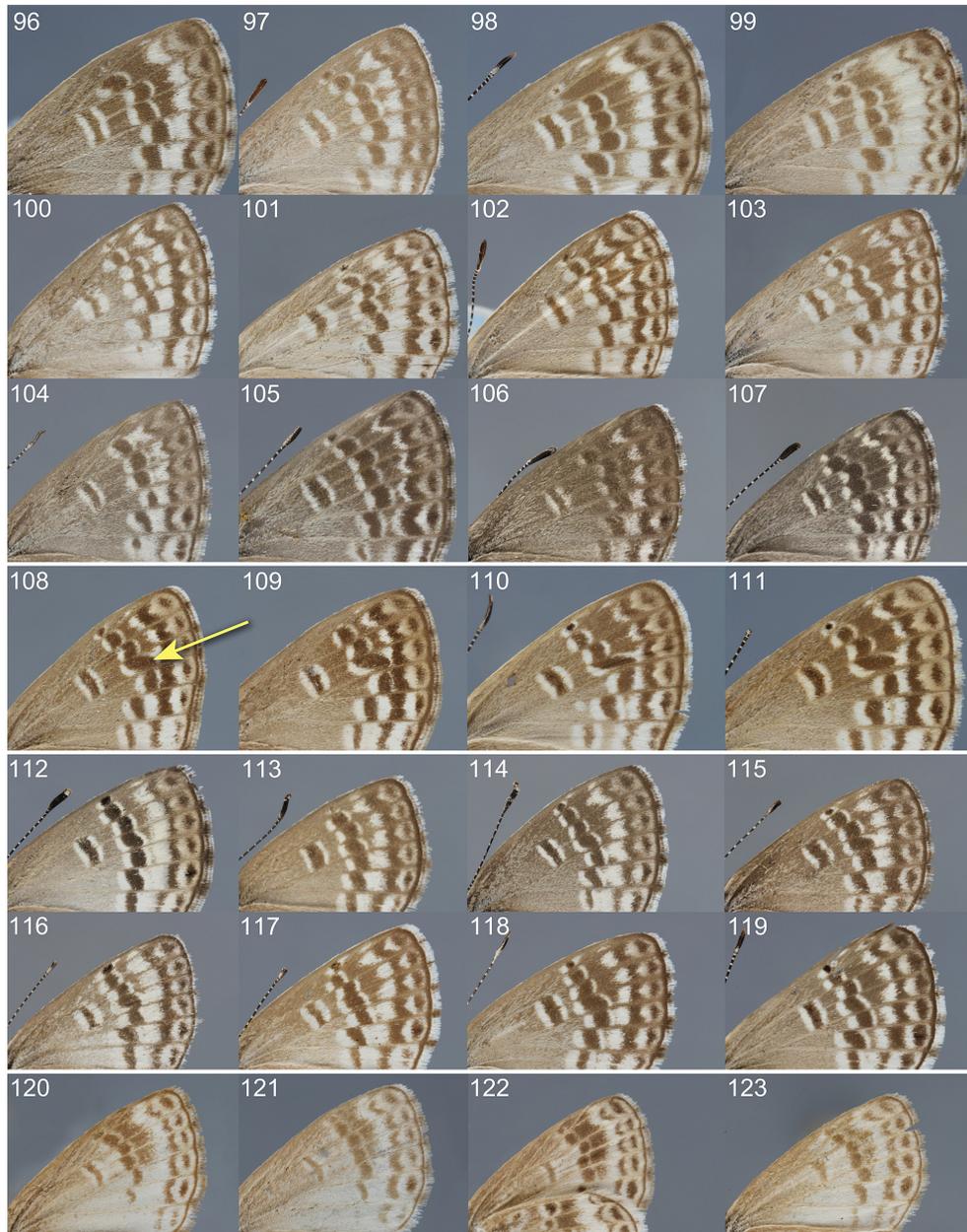
**Figures 43–51.** Enlargements showing detail and variation in rostellum comb shape and tooth arrangement. Localities as indicated above images.



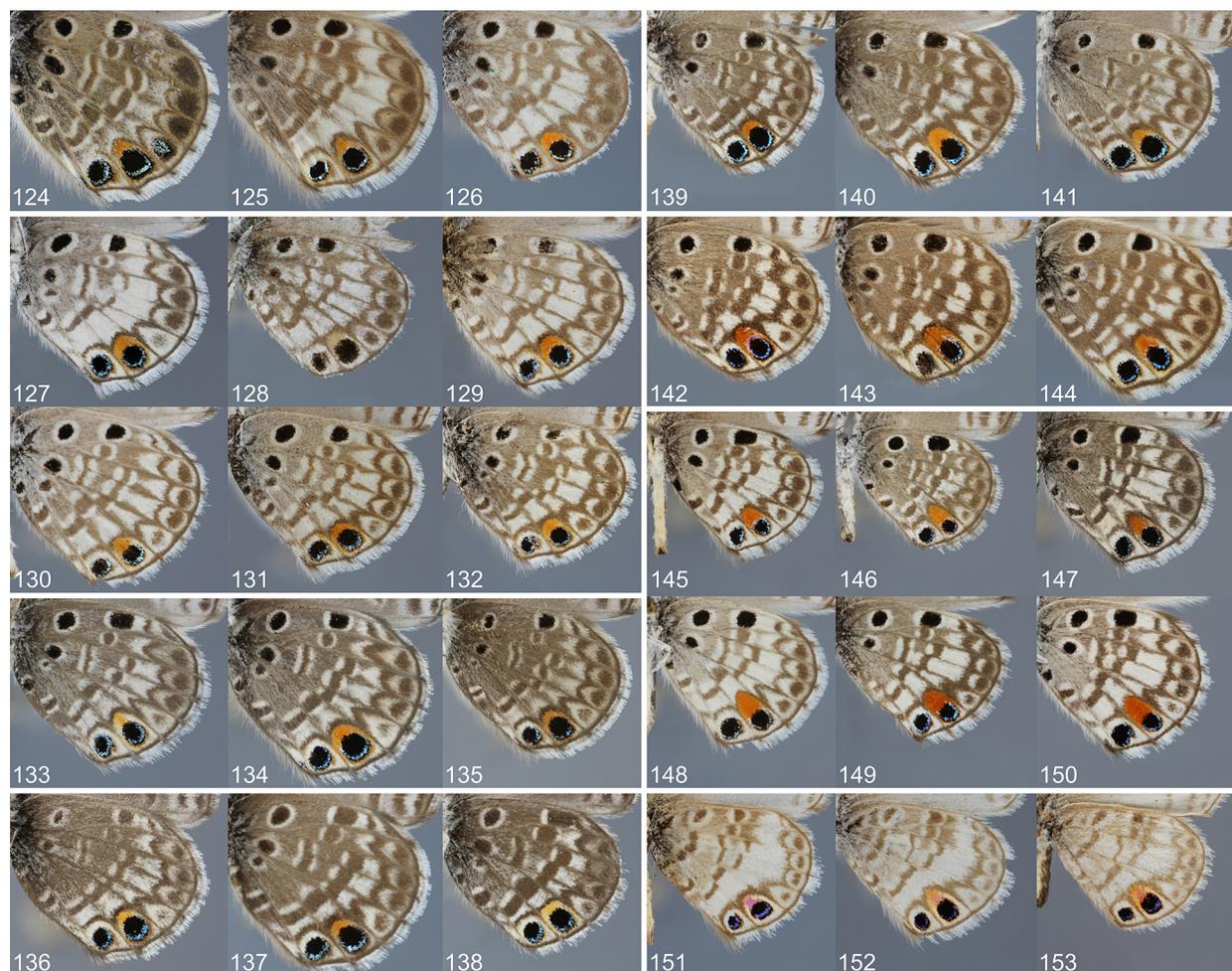
**Figures 52–71.** Male dorsal hindwing ground color and tornal submarginal spots ( $Cu_1$ - $Cu_2$ ,  $Cu_2$ -2A). Species separated by white lines in plate. **52–60)** *C. thomasi*. **52)** Florida: Captive Colony, MGCL 245034. **53)** Florida: Plantation Key, MGCL 245038. **54)** Cuba: Guantánamo: Jauco, MGCL 245061. **55)** Dominican Republic: Pedernales, MGCL 245097. **56)** Bahamas: Long Island, MGCL 236488. **57)** Bahamas: San Salvador Island, MGCL 242239. **58)** Bahamas: Crooked Island, MGCL 245576. **59)** Turks and Caicos Islands: North Caicos, MGCL 245638. **60)** Bahamas: Great Inagua Island, MGCL 245604. **61, 62)** *C. woodruffi*: **61)** Puerto Rico: Ceiba: Roosevelt Roads Naval Station, MGCL 245339. **62)** U.S. Virgin Islands: St. Croix, MGCL 245417. **63–69)** *C. ammon*. **63)** USA: Florida: Big Pine Key, MGCL 245512. **64)** Bahamas: Grand Bahama Island, MGCL 245003. **65)** Bahamas: South Abaco, MGCL 240246. **66)** Bahamas: South Andros Island, MGCL 234818. **67)** South Andros Island, MGCL 234817. **68)** Cuba: province unknown, MGCL 245488. **69)** Cuba: province unknown, MGCL 245488. **70, 71)** *C. dominica*: **70)** Jamaica: Trelawny Parish: Baron Hill, MGCL 245018. **71)** Jamaica: Trelawny Parish: Trelawny, MGCL 245020.



**Figures 72–95.** Variation in *Cyclargus* female dorsal hindwings. Species separated by white lines in plate. **72–81)** *C. thomasi*. **72)** USA: Florida: North Key Largo, MGCL 245045. **73)** USA: Florida: Lower Matacumbe Key, MGCL 245046. **74)** Cuba: Guantánamo: Jauco, MGCL 245066. **75)** Dominican Republic: Semaná: Las Terrenas, MGCL 245151. **76)** Bahamas: Long Island, MGCL 236480. **77)** Bahamas: San Salvador Island, MGCL 242240. **78)** Bahamas: Crooked Island, MGCL 242249. **79)** Bahamas: Mayaguana Island. **80)** Bahamas: Great Inagua Island, MGCL 245614. **81)** Bahamas: Great Inagua Island, MGCL 230970. **82–86)** *C. woodruffi*. **82)** Puerto Rico: Ceiba: Roosevelt Roads Naval Station, MGCL 245342. **83)** St. Maarten, MGCL 245442. **84)** U.S. Virgin Islands: St. Croix, MGCL 245423. **85)** Barbuda, MGCL 245306. **86)** Antigua, MGCL 245338. **87–93)** *C. ammon*. **87)** Bahamas: South Abaco, MGCL 240245. **88)** Bahamas: South Abaco, MGCL 242243. **89)** Bahamas: North Andros Island, MGCL 245684. **90)** Bahamas: North Andros Island, MGCL 230991. **91)** Cayman Islands: Cayman Brac, MGCL 245744. **92)** Cayman Islands: Grand Cayman, MGCL 245746. **93)** Jamaica: Trelawny Parish, MGCL 245756. **94, 95)** *C. dominica*: **94)** Jamaica: Trelawny Parish, MGCL 245025. **95)** Jamaica: Trelawny Parish, MGCL 245027.



**Figures 96–123.** *Cyclargus* ventral forewing patterns. Species separated by white lines in plate. **96–107)** *C. thomasi*. **96)** USA: Florida: Plantation Key, MGCL 245038. **97)** USA: Florida: Captiva Island, MGCL 245035. **98)** USA: Florida: North Key Largo, MGCL 245045. **99)** USA: Florida: Lower Maticumbe Key, MGCL 245046. **100)** Cuba: Guantánamo: Jauco, MGCL 245061. **101)** Cuba: Guantánamo: Jauco, MGCL 245066. **102)** Dominican Republic: Pedernales, MGCL 245097. **103)** Dominican Republic: Monte Cristi, MGCL 245136. **104)** Bahamas: South Andros Island, MGCL 234821. **105)** Bahamas: Long Island, MGCL 236476. **106)** Bahamas: Crooked Island, MGCL 242246. **107)** Bahamas: Crooked Island, MGCL 242249. **108–111)** *C. woodruffi*. **108)** Puerto Rico: Ceiba: Roosevelt Roads Naval Station, MGCL 245339 (arrow indicates elongated  $M_2$ - $M_3$  postdiscal band cell spot). **109)** U.S. Virgin Islands: St. Croix, MGCL 245417. **110)** St. Kitts, MGCL 245222. **111)** Antigua, MGCL 245338. **112–119)** *C. ammon*. **112)** Bahamas, South Abaco, MGCL 240245. **113)** Bahamas: South Abaco, MGCL 242243. **114)** Bahamas: South Andros Island, MGCL 234818. **115)** Bahamas: South Andros, MGCL 234817. **116)** Cuba: Guantánamo: GTMO, MGCL 171104. **117)** Cuba: Guantánamo: GTMO, MGCL 245104. **118)** Cayman Islands: Grand Cayman Island, MGCL 245539. **119)** Cayman Islands: Cayman Brac, MGCL 245744. **120–123)** *C. dominica*. **120)** Jamaica: Trelawny Parish: Baron Hill, MGCL 245018. **121)** Jamaica: Trelawny Parish: Trelawny, MGCL 245020. **122)** Jamaica: Trelawny Parish: Trelawny, MGCL 245027. **123)** Jamaica: Trelawny Parish: Trelawny, MGCL 245025.



**Figures 124–153.** *Cyclargus* male ventral hindwing patterns. Taxa separated by white lines in plate. **124–126)** *C. thomasi bethunebakeri*. **124)** USA: Florida Captive Colony, MGCL 245034, LEP-22360. **125)** USA: Florida: Plantation Key, MGCL 245038, LEP-22365. **126)** USA: Florida: Captiva Island, MGCL 245035, LEP-22361. **127–132)** *C. thomasi noeli*. **127)** Cuba: Guantánamo: GTMO, MGCL 230736, LEP-17799. **128)** Cuba: Guantánamo: GTMO, MGCL 230742, LEP-17798. **129)** Cuba: Guantánamo: Jauco, MGCL 245061, LEP-22377. **130)** Dominican Republic: Puerto Plata, MGCL 245139. **131)** Dominican Republic: Pedernales, MGCL 245097. **132)** Dominican Republic: Pedernales, MGCL 245088. **133–135)** *C. thomasi thomasi*. **133)** Bahamas: South Andros Island, MGCL 234821, LEP-18728. **134)** Bahamas: Long Island, MGCL 236476, LEP-22320. **135)** Bahamas: Great Exuma Island, MGCL 236766, LEP-22334. **136–138)** *C. thomasi bahamensis*. **136)** Bahamas: Crooked Island, MGCL 242245. **137)** Bahamas: Crooked Island, MGCL 245576. **138)** Bahamas: Crooked Island, MGCL 242251. **139–141)** *C. thomasi clenchi*. **139)** Bahamas: Mayaguana Island, MGCL 245586. **140)** Turks and Caicos: North Caicos, MGCL 245638. **141)** Bahamas: Great Inagua Island, MGCL 245604. **142–144)** *C. woodruffi*. **142)** Puerto Rico: Ceiba: Roosevelt Roads Naval Station, MGCL 245339, LEP-22357. **143)** British Virgin Islands: Tortola, MGCL 245372. **144)** St. Kitts, MGCL 245222. **145–150)** *C. ammon*. **145)** USA: Florida: Big Pine Key, MGCL 245512, LEP-22374. **146)** Bahamas: Grand Bahama Island, MGCL 245003, LEP-22387. **147)** Bahamas: South Andros, MGCL 234818, LEP-22385. **148)** Cuba: Province Unknown, MGCL 245488. **149)** Cuba: Province Unknown, MGCL 245491. **150)** Cayman Islands: Grand Cayman, MGCL 245539. **151–153)** *C. dominica*. **151)** Jamaica: Trelawny Parish: Trelawny, MGCL 245025. **152)** Jamaica: Trelawny Parish: Trelawny, MGCL 245020, LEP-24407. **153)** Jamaica: Trelawny Parish: Trelawny, MGCL 245025.

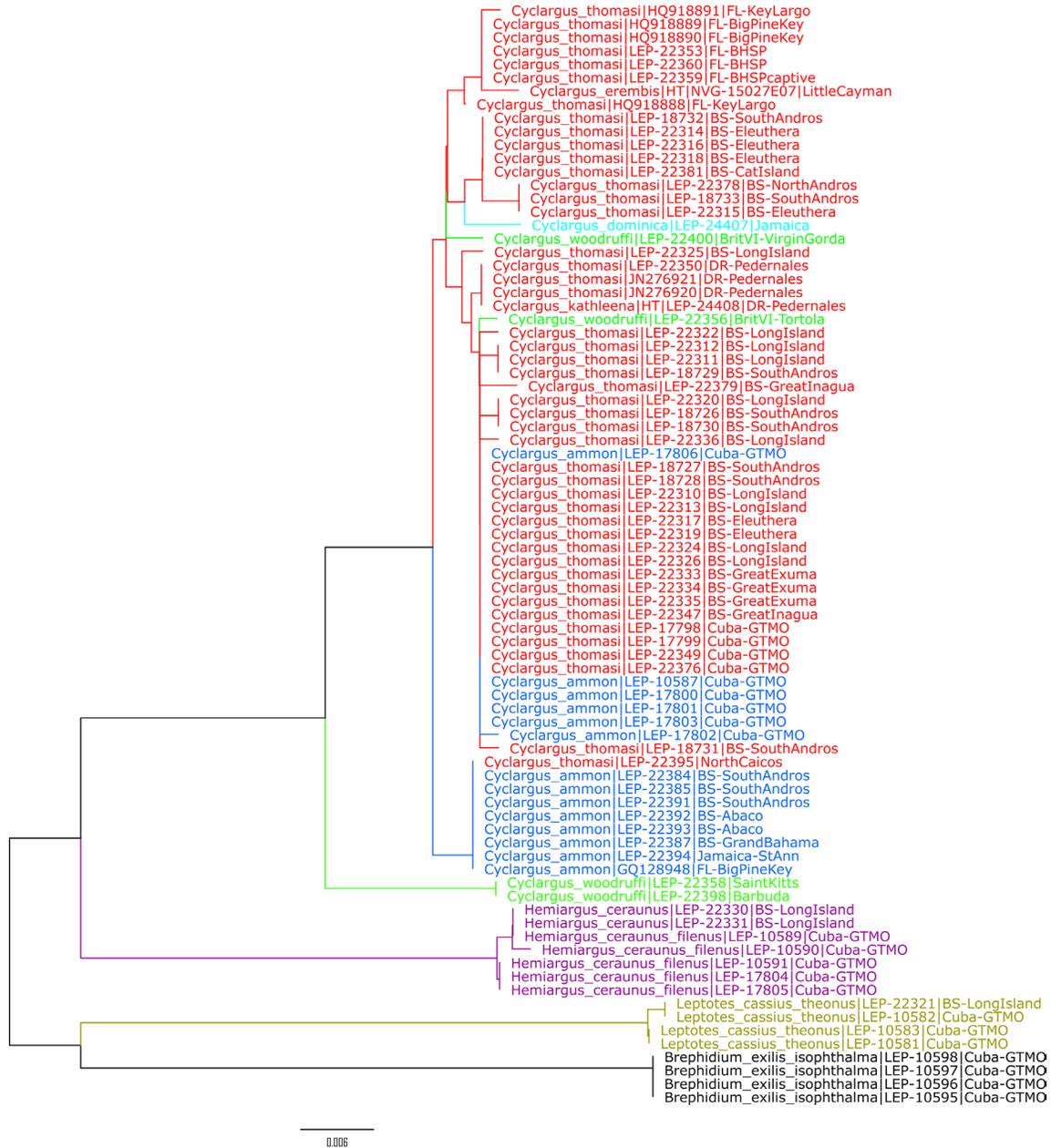


Figure 154. COI dendrogram of *Cyclargus* species and subspecies, with *Hemiargus*, *Leptotes*, and *Brephidium* as outgroups.

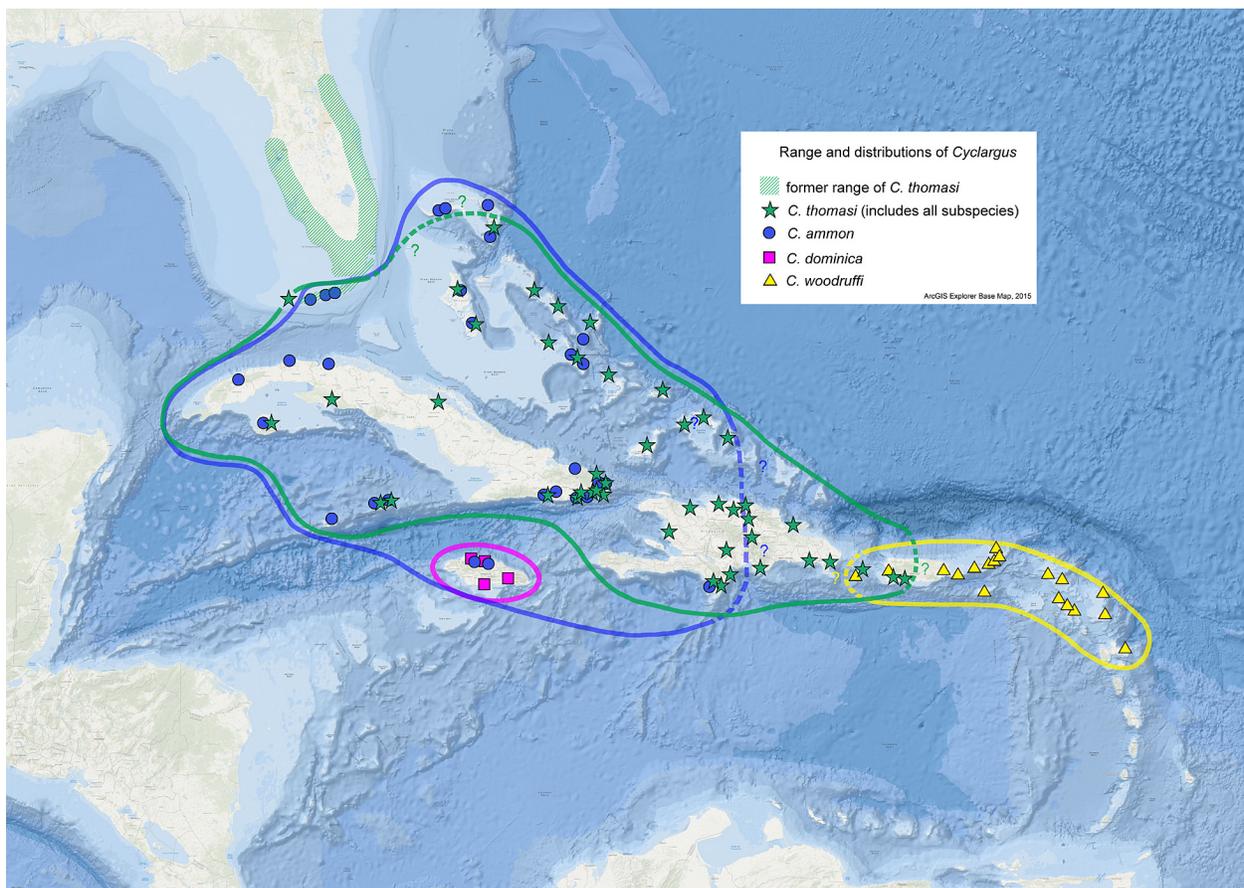


Figure 155. Geographic range and distributions of *Cyclargus* species, with localities of material examined.