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A morphological and mtDNA analysis of the badlands tiger beetle, *Cicindela* (*s. str.*) *decemnotata* Say, 1817 (Coleoptera: Carabidae: Cicindelinae) with the description of three new subspecies

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A morphological and mtDNA analysis of the badlands tiger beetle, *Cicindela* (*s. str.*) *decemnotata* Say, 1817 (Coleoptera: Carabidae: Cicindelinae) with the description of three new subspecies

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Abstract. We conducted a morphological and mtDNA analysis of *Cicindela decemnotata* Say (Coleoptera: Carabidae: Cicindelinae) populations from throughout its geographic range to determine the extent of variation within the species and to assess the validity of subspecific names. The morphological study included an analysis of traditional subspecific characters including elytral color and maculations. These results provided evidence for the recognition of four subspecies of *C. decemnotata*, three of which are new: 1. *C. d. decemnotata* Say usually with green to dark green dorsal coloration and complete elytral maculations; it is widely distributed from Canada south to northern New Mexico and west into southern Utah and Idaho; 2. *C. d. meriwetheri* n. ssp. is distinguished by its bright green to green dorsal coloration, elytral maculation characterized by a thin middle band, a lack of humeral maculations, and a small number of genal setae; it has a restricted distribution from eastern Washington north to south central British Columbia; 3. *C. d. bonnevillensis* n. ssp. is distinguished by a combination of green to green-purple dorsal coloration and its greatly reduced elytral maculations; it is restricted to the area of ancient Lake Bonneville in north central Utah; 4. *C. d. montevolans* n. ssp. is distinguished by a predominately red-purple dorsal color and greatly reduced elytral maculations; its distribution is restricted to high elevations of the Bear River Mountains of northeastern Utah and southeastern Idaho. We also analyzed the mitochondrial haplotypes for *cob* and *cox1* genes for one to six individuals from each of the six populations. This molecular analysis indicated recently diverged but discrete groups within *C. decemnotata* that are compatible with the subspecies distinctions postulated from morphology. These shallow molecular divergences within *C. decemnotata* are best explained by rapid phylogenetic radiation in the recent geological past in the wake of postglacial recession.

Introduction

The badlands tiger beetle, *Cicindela* (*s. str.*) *decemnotata* Say (1817) (Coleoptera: Carabidae: Cicindelinae), inhabits sagebrush tracts from the western Great Plains westward to eastern Washington and southern British Columbia south to southern Utah and north to Alaska (Pearson et al. 2006). This medium-sized (9-15 mm) tiger beetle has a spring/fall life cycle with adults emerging from the pupal stage in fall, overwintering and reemerging when suitable spring temperatures permit.

This species was described by Say (1817) from a single female specimen "caught by Mr. Nuttall, on the sandy alluvions of the Missouri, above the confluence of the river Platte", in present day North Dakota (J. Mawdsley, *pers. comm.*). Little was written of this species in early entomological literature, and LeConte (1857) apparently never saw a specimen. Casey (1913) described *C. decemnotata albertina* from two specimens collected in Lethbridge, Alberta, Canada and based this subspecies on differences in color and maculation when "compared with three very good examples of the typical *decemnotata*" (examined, MGK 1992). Harris (1913) described *Cicindela lantzi* from Jefferson Co., Colorado based on a single dark green individual with the humeral lunule and humeral dot connected. Interestingly, he

made no mention of this taxon's relationship to *C. decemnotata* and instead indicated that the elytral maculation was more similar to *C. echo* Casey (= *C.* (*Cicindelidia*) *willistoni echo*, *fide* Freitag 1999) and *C. pseudosenilis* G. Horn (= *C.* (*Cicindelidia*) *willistoni pseudosenilis*, *fide* Freitag 1999) (examined, MCZ Type Database 2010).

In 1988, N. L. Rumpp (in litt.) suggested that populations of *C. decemnotata*, from the Columbia River Basin of eastern Washington represented a distinct subspecies based on their brighter green dorsal coloration, lack of a humeral lunule, and smaller number of genal setae. Rumpp also concluded that populations from Tooele Co., Utah represented yet another distinct subspecies, this one being distinguished by the combination of dark green dorsal coloration with strong blue reflections, blue punctures on the elytra, and maculations reduced to only a very narrow or missing middle band. He considered populations from Logan Canyon, Cache Co., Utah that have primarily red-purple dorsal coloration and reduced elytral maculation to be intergrades between typical *C. decemnotata* and the Tooele Co. form. Leffler (in litt.) concurred with Rumpp's assessment of these populations and provided further discussion of *C. decemnotata* populations from the Pacific Northwest. The most recent publications on the Nearctic tiger beetle fauna recognized *C. decemnotata* as a monotypic species (Freitag 1999; Pearson et al. 2006).

Due to the marked interpopulation variation of *C. decemnotata* and the continual resurfacing of the unpublished subspecific names proposed by Rumpp, CBK and MGK initiated a study of the biogeography of the species to determine if valid subspecies should be recognized. This work coincided with CBK undertaking a study of *C. decemnotata* at the Dugway Proving Ground, a 323,025.75 hectare U.S. Army testing ground in Tooele Co., Utah (Dugway Proving Ground 2012) to determine its distribution and abundance, and possible impacts of base activities. To supplement our morphological studies, MRW conducted molecular studies among various forms of *C. decemnotata*.

Methods

This study included both the analysis of the morphological characters typically used to distinguish tiger beetle species and subspecies and a genetic analysis utilizing mtDNA. Length measurements of pinned specimens were made from the tip of the clypeus to the apex of the elytra. Photographs of pinned specimens were taken with an Olympus® DP 11 digital camera attached to a Wild® M20 compound microscope, processed using Synchroscopy Auto-Montage, and corrected in Adobe Photoshop® CS5. The remaining photographs were taken with various hand held digital SLR or point-and-shoot cameras and modified in Adobe Photoshop® CS5. We compiled an extensive list of locality records for *C. decemnotata* throughout its range, and formatted all in a similar manner with location and date, if available. Collector and GPS coordinates were not included for species listed under "Additional material examined". Records taken from literature sources—where specimens were not examined for this study—are listed as such. Specimens and the associated label data used in this study were borrowed from the following institutions and private collections:

AMNH	—	American Museum of Natural History, New York, New York, USA
BYUC	—	Brigham Young University Collection, Provo, Utah, USA
CBKC	—	C. Barry Knisley Collection, Ashland, Virginia, USA
CID	—	College of Idaho Collection (formerly Albertson College), Caldwell, Idaho, USA
CNC	—	Canadian National Collection, Ottawa, Ontario, Canada
CSUC	—	Colorado State University Collection, Fort Collins, Colorado, USA
DWBC	—	David W. Brzoska Collection, Naples, Florida, USA
JSC	—	Jason Schmidt Collection, Melbourne, Florida, USA
MCZC	—	Museum of Comparative Zoology, Cambridge, Massachusetts, USA
MGKC	—	Michael G. Kippenhan Collection, McMinnville, Oregon, USA
MTEC	—	Montana Entomological Collection, Montana State University, Bozeman, Montana, USA
NHMC	—	Natural History Museum Collection, London, England
NYC	—	Nadeer Youssef Collection, McMinnville, Tennessee, USA

RLHC	—	Ronald L. Huber Collection, Bloomington, Minnesota, USA
SMSC	—	Steven M. Spomer Collection, Lincoln, Nebraska, USA
TLC	—	Todd Lawton Collection, Winnipeg, Manitoba, Canada
TSC	—	Thomas D. Schultz Collection, Granville, Ohio, USA
UIDC	—	University of Idaho Collection, Moscow, Idaho, USA
USUC	—	Utah State University Collection, Logan, Utah, USA
USNM	—	U. S. National Museum, Washington D.C., USA
WSUC	—	Washington State University, Pullman, Washington, USA

Criteria for subspecies. The often considerable morphological variation found within tiger beetle species has resulted in the widespread use of the trinomial system of zoological nomenclature (ICZN 2000). The importance of this category is illustrated by the fact that 45 of the 92 Nearctic species of *Cicindela* (*sensu lato*, *fide* Freitag 1999) have associated subspecies. While the use of subspecies is an integral aspect of tiger beetle taxonomy, applications of subspecies is not universally accepted; Mayr (1969) addressed pertinent concerns of the use of subspecies. In addition, Willis (1967) and Spanton (1988) offered concise, historical outlines of the controversy surrounding the use or need of trinomials for tiger beetles. Here we apply the definition of Mayr (1969): "A subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species". Mayr (1969) points out that a subspecies is a "collective category" and that "sensible use of the category subspecies is still a convenient device for classifying population samples in geographically variable species." Further, Willis (1967) suggested that the valid determination of subspecies could best be determined by the judgment of an expert in the group plus statistical methods. His criteria for a subspecies are: 1. occupy a well-defined geographic area or ecological habitat (zones of intergradation with other subspecies may occur); 2. exhibit a relatively uniform expression of characters within itself; and 3. is readily separated from other subspecies by one and preferably more consistently distinct characters.

To more reliably resolve taxonomic differences, molecular-genetic techniques have been used in conjunction with phylogenetics. The congruence or incongruence between molecular and morphological data is an effective test of species relations (Avise 2000; Barraclough and Vogler 2002; Thiele 1993; Sites and Marshall 2003; Will and Rubinoff 2004). Indeed, morphological traits by themselves have often led to ambiguity, indiscrete variation, or distributional inconsistency (Mayr 1969; Cracraft 1983; Archie 1985; Goldstein and Desalle 2003; Pearson and Vogler 2001; Sites and Marshall 2003; Hebert et al. 2004). In such cases, the tools of molecular genetics can be applied to reduce the ambiguities of naming (sub)specific entities as discretely segregated clusters (gene pools) with similar sequences. As a result, some historically delineated forms have been determined to more likely represent naturally synonymous taxa, allopatric isolates, the extremes of clinal variation, or unnatural groupings of distant relatives (Boyd and Rust 1982; Schultz 1986; Serrano 1988; Vogler and DeSalle 1993; Morgan et al. 2000; Cardoso et al. 2003). Likewise, some (sub)species traditionally thought to be sister lineages have had to be reconsidered after a thorough molecular genetic analysis (Morgan et al. 2000). In this study, mitochondrial DNA analysis was used in conjunction with morphological characters to resolve subspecific relationships within *C. decemnotata.*

Character Analysis in Tiger Beetles

Color, elytral maculation pattern, elytral sculpture, chaetotaxy, aedeagal shape, and labral shape are six of the most commonly used morphological characters for determining the taxonomy of species of tiger beetles. Color and elytral maculation are the most frequently used to differentiate subspecies (Knisley and Schultz 1997; Pearson and Vogler 2001; Pearson et al. 2006). On the basis of our knowledge and experience with tiger beetle taxonomy and preliminary study with *C. decemnotata*, we analyzed all six of these morphological characters for resolving the population differences within this species.

Color. The composition and structure of tiger beetle coloration is due to epicuticular microsculpture and melanin deposits with the uniformity of the microsculpture determining color purity (Schultz and Rankin 1985; Schultz 1986). We considered the dorsal coloration of *C. decemnotata,* especially that of the elytra, a variable, but important character for resolving subspecies. The elytral surface of

C. decemnotata consists of a series of shallow depressions, or "pits", with raised granules. The pits are often darker, or different, in color compared to the intervening areas; however, with the unaided eye these colors often blend to create a single color (Knisley and Schultz 1997). Color can range from bright metallic to dull; in addition, depending on the type and angle of light under which specimens are examined, colors can appear darker or lighter, or even shift hues. As a general pattern, the color of head and pronotum tend to be similar to that of the elytra. The margins of the head, pronotum and thoracic pleurites most often have brighter, contrasting color along their margins as well as in the depressed area between the anterior lobe and disc of the pronotum, while the margin of the elytra occasionally has a shiny, contrasting color (Fig. 11C). The first few abdominal ventrites are often the same, or similar, in color as the adjacent thoracic ventrites and gradually become darker, most often dark blue to purple at the apex. The femora are generally the same color as the thoracic pleurites, but the tibia are a darker, duller color. For consistency, we categorized colors as: green (Fig. 2E, 5F, 9B), dark green (Fig. 4A-C), blue-green (Fig. 1B-C, 5A-E, 7A), blue (Fig. 7B), green-purple (Fig. 3A-B, 3D), purple (Fig. 2B, 3C, 3E-F, 7C), and red-purple (Fig. 1D, 2C-D, 2F, 9A-C). Red-purple is a composite color that often appears brown to the unaided eye with many individuals having strong dark-green areas. Because they were so rare, two others colors, olive green (Fig. 2A) and black (not shown) were not included in the study.

Elytral maculation. The maculations of *C. decemnotata* consist of five primary marks: humeral dot, posthumeral dot, middle band, subapical dot, and apical dot (Fig. 12). Frequently individuals will have the subapical dot and apical dot narrowly connected along the elytral margin and rarely with the humeral dot connected to the posthumeral dot (Fig. 11D). Any or all markings may be absent or reduced. To evaluate differences in maculation pattern among populations we graded specimens (usually 10-20 randomly selected specimens per population, if available) from 34 *C. decemnotata* populations throughout the species' range (Table 1) to determine the mean size of the separate and combined total for marks. For purposes of this calculation, we considered the combined humeral and posthumeral dots as the "humeral lunule", and the subapical and apical dots as the "apical lunule"; the middle band is retained as a single unit. Using a numerical scale to score size, the humeral lunule was ranked on a scale of 0 to 3 (Fig. 13A-D), the middle band on a scale of 0 to 7 (Fig. 14A-H), and the apical lunule on a scale of 0 to 3 (Fig. 15A-D). In this grading system, 0 corresponded with the maculation absent and the respective highest number indicated the largest size maculation for that position. We also graded the thickness of the connection between the subapical dot and apical dot on a scale of 0 to 3 (Fig. 16A-D); a 0 was given if there was no connection or if one of the maculations was missing and 3 if the connection was broad (Fig. 16D). The extent of overlap between the subapical dot and posterior portion of the middle band (foot) (Fig. 17A-D) were similarly graded with 0 if one of the maculations was missing or if there was wide separation and 3 if there was distinct overlap (Fig. 17D). The individual maculations for all individuals in each population were graded according to the above system and a mean value calculated for the population. Then the means of the sum of all maculations were calculated to provide an overall grade for each population (Table 2).

Elytral sculpture. The shallow depressions, or "pits" and associated raised granules are characteristic of the elytral surface of *C. decemnotata*. The granule is most often found on the anterior side of the pit, and often smaller secondary granules can be found intermixed between the pits. The spatial variation of the elytral sculpturing has been used to distinguish several closely related Nearctic species, or subspecies, of *Cicindela* (*sensu lato*, *fide* Freitag 1999) such as *Cicindela nebraskana* Casey and *C. longilabris* Say, C*ylindera t. terricola* (Say) and *Cy. t. cinctipennis* (LeConte), and *Dromochorus belfragei* (Guérin-Méneville) and *D. pruinina* (LeConte) (Pearson et al. 2006).

Body chaetotaxy. While setal patterns are important characters in the identification of tiger beetles from the tribe to species level, they are rarely utilized at the subspecific level. One notable exception is *C. (Cicindelidia) willistoni* LeConte which exhibits marked differences in the number of seta on the vertex of the head (Willis 1967). In *C. decemnotata*, we analyzed two areas that exhibit setal variation—the genae and first antennomere—to determine if these might be used to separate subspecies.

Labrum. The shape of the labrum, including the number of teeth, pigmentation, and number of setae, has been an important character in the determination of tiger beetle species. Although these characters are often reliable for distinguishing taxa from the tribe to genus level, many species groups have similar labral characters, thus the utilization of the labrum as a diagnostic character must be taken on a case by case basis. The labrum of *C. decemnotata* generally has its width approximately twice

its length (Fig. 19A and D), most often with six to eight setae along the anterior margin, and anterior central area projecting further than lateral points with three well developed teeth.

Aedeagus. The male aedeagus, including the composition of the internal components, has been utilized to distinguish species of tiger beetles (Rivalier 1950, 1954), minor variation in shape is unlikely to be useful for subspecific determination.

Molecular Analysis

Selection of Taxa. The genetic analysis in this study included one to six specimens from seven populations representing what we hypothesized were the four subspecies of *C. decemnotata* (Table 1). Notable morphs of *C. decemnotata* unavailable for the genetic analysis included the dark purple individuals from Idaho and the unusual violet (or blue) colored morphs noted by Acorn (2001) from Alberta (Peace River) and the Yukon (Whitehorse). All specimens used in the mtDNA analysis were preserved live by rapid dehydration in ethanol and sent to the laboratory at Randolph-Macon College in Ashland, Virginia where the molecular analysis was conducted and where voucher specimens have been housed.

mtDNA Isolation and Manipulation. Using a DNeasy® Tissue Kit following the manufacturer's instructions, total genomic DNA was extracted from dried and pulverized leg and/or thoracic material. The mitochondrial genes of interest were cytochrome b (*cob*) and cytochrome oxidase subunit I (*cox1*), two genes that have been regularly applied in taxonomic studies of *Cicindela* (Morgan et al. 2000; Boore 2001; Cardoso and Vogler 2005). The primers utilized were CB2 (5'-GAG GAG CAA CTG TAA TTA CTA A-3') and CB4 (5'-AAA AGA AAT TAT CAT TCA GGT TGA AT-3') which amplified a 385bp section of the cytochrome b gene (*cob*) and Pat (5'-TCC AAT GCA CTA ATC TGC CAT ATT A-3') and Jerry (5'-CAA CAT TTA TTT TGA TTT TTT GG-3') which amplified a 769 bp section of the cytochrome oxidase I gene (*cox1*). All PCR experiments were conducted alongside negative controls where water was used in place of extracted DNA; any runs that yielded a band in the negative control were discarded. Cleanup of final PCR products was conducted using a QIAquick® PCR Purification Kit following the manufacturer's (Qiagen Inc.) instructions listed under the QIAquick® PCR Purification using the microcentrifuge protocol. The purified PCR products were sequenced at the MCV-VCU Massey Cancer Center Nucleic Acids Research Facility in Richmond, Virginia.

Sequences were aligned using Bioedit Freeware Version 7.0.4.1 (Hall 1999). All raw sequences produced by the genetic analyzer were tested for appropriate identity through a DNA-DNA BLAST search of the NCBI database. Global Clustal W was conducted for edited sequences of the same source population, and any deviations from the consensus sequence of the population were reassessed to discount or confirm the polymorphism. Using EMBOSS-TRANSEQ sequence analysis tool through the EMBL-EBI database, edited sequences were translated into protein data under invertebrate mitochondrial genetic code. Ambiguous nucleotides were reconciled (where possible) assuming minimal change for peptide sequence and codon usage relative to published sequence data. Functional (and fully contiguous) identities of *cob* and *cox1* translations were confirmed by searching through the NCBI database using Protein-Protein BLAST. Final sequences were deposited into the NCBI database as follows: *C. decemnotata decemnotata* (DQ923385–DQ923386, JN861054-JN861057, JN861068-JN861071), *C. splendida* Hentz and *C. limbalis* Klug (EU723573-EU723596), *C. decemnotata bonnevillensis* (JN861048-JN861053, JN861062-JN861067), *C. decemnotata meriwetheri* (JN861044-JN861045, JN861058-JN861059), and *C. decemnotata montevolans* (JN861046-JN861047, JN861060-JN861061).

Molecular Data Analysis. Sets of rigorously re-edited sequences were truncated to appropriate lengths and aligned using Bioedit Freeware. By convention of this paper, bases 1-385 correspond to *cob*, base assignments 386-1157 correspond to *cox1* to produce unique haplotypes. Haplotype designations by convention of this paper were formulated from the two letter abbreviation for the state or province from which the specimens originated, followed by a dash and the lowest number specimen observed exhibiting the haplotype. In order to ease computation demands for later phylogenetic reconstructions, specimens sharing a haplotype were combined and numbers after the decimal for each haplotype designation represent the total number of specimens observed sharing the haplotype. Pairwise sequence divergences were calculated for all sequences while also accounting for all possible states of ambiguous nucleotides. Populations were examined for the presence of shared haplotypes and fixed nucleotide polymorphisms as diagnostic criteria for ESU status (*sensu* Vogler et al. 1993a; Vogler et al. 1993b; Vogler and DeSalle 1994).

Statistical parsimony analysis of haplotype networks was conducted under TCS Version 1.21, where estimates of the most parsimonious connections of haplotype pairs were calculated to 99% confidence limits that such connections did not involve homoplasious changes (Clement et al. 2000). Haplotype networks were ordered into a hierarchy by repeatedly nesting lower (n-step) groupings of haplotypes into higher (n+1) step groups of haplotypes until the entire haplotype set was incorporated into a single n-step network (Templeton 2004; Templeton et al. 1987; Templeton and Sing 1993). Thereafter, nested geographical clade analysis (NGCA) was conducted in conjunction with Geodis Version 2.4 using 20 million permutations where significant associations of haplotype groups within each n-step network and their geographical distribution were elucidated (Posada et al. 2000). Significant associations represented geographical distribution of hierarchical groupings in a network that was statistically different from a random pattern of no geographical structure. Potential biological causes of these later associations were inferred through the key in Templeton (2004).

All phylogenetic reconstructions were conducted using a concatenated set of *cob* and *cox1* data (1157 nucleotides total) for 23 terminals. Congruence between *cob* and *cox1* was evaluated using a partition homogeneity test (incongruence length difference test; ILD) with PAUP* Version 4.0 Beta 10 (Swofford 2002) using 100 replicate data partitions and heuristic search of 10 random sequence additions and tree bisection-reconnection (TBR) branch swapping (Farris *et al.*1994). The ingroup and outgroup datasets consisted of 14 and 9 terminals respectively. The sister species of *C. denverensis* Casey, *C. limbalis* Klug, *C. splendida* Hentz were selected as outgroup taxa according to phylogenetic hypotheses presented from other analyses (Barraclough and Vogler 2002; Vogler et al. 2005). These outgroup data were either produced prior for other cicindelid phylogenetic analyses at Randolph-Macon College in Ashland, Virginia or were downloaded from the NCBI database (Barraclough et al. 1999; Pons et al. 2004; Vogler and Welsh 1997; Vogler et al. 2005; Woodcock and Knisley 2009). By convention of this paper, sequences published in the NCBI database are marked with REF as their haplotype designation. Maximum Parsimony (MP) based phylogenetic reconstructions were investigated through PAUP* using 2,000 replications of a standard heuristic search with 10 random sequence additions and tree bisection-reconnection (TBR) branch swapping with all characters weighted equally. Branch supports under parsimony criteria were evaluated by nonparametric bootstrap (BP), and third-delete jackknife (JK) calculated to high confidence levels using 10,000 replications. Additional tests performed under MP included constrained-tree topology-dependent permutation tail probability tests (T-PTP; Faith 1991) using 10,000 randomized matrices to generate a null distribution. The T-PTP test statistic (calculated by subtracting minimum tree length under constrained monophyly from minimal unconstrained tree length; ΔL = range of steps; *L = length difference for unpermuted data) may be interpreted as significant support for a specified monophyly (for critical reviews of T-PTP see Carpenter et al. 1998; Faith and Trueman 1996; Swofford et al. 2001).

Complementary phylogenetic analyses using model-based approaches were conducted through maximum likelihood (ML) and Bayesian inference. The best-fit model of nucleotide substitution for Bayesian Inference was identified using the Akaike Information Criterion (AIC) as calculated with Modeltest 3.7 (Posada and Crandall 1998). The favored model was General Time Reversible (GTR; Lanave et al. 1984; Rodríquez et al. 1990) with invariable base frequencies (I). Phylogenetic analyses under maximum likelihood were conducted using GARLI (version 0.96; Zwickl 2006). Analyses under ML were allowed to run for 5,000,000 generations without any premature termination. Branch supports of ML trees were evaluated using 1,000 replicates of nonparametric bootstrap (BP). Phylogenetic analyses by Bayesian inference methodology (BI) were conducted using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). All model parameters were estimated by MrBayes under the metazoan mitochondrial code. Branch support of the best set of trees for the given model of nucleotide substitution was estimated using posterior probabilities (PP). Analyses were initiated with random starting trees and conducted for 13,000,000 generations with four independent Markov Chains. Every 100th generated topology was saved and the first 1,000 generated topologies were excluded from the final 50% majority rule consensus tree.

Results

The results of the analysis of the morphological characters of maculation, genal setae and dorsal coloration along with the genetic analysis, support naming four subspecies of *C. decemnotata*—three of which are newly described here.

Cicindela (*s. str.*) *decemnotata decemnotata* Say

(Fig. 1A-D, 2A-F, 3A-F, 4A-D, 10A-B, 11C-D, 18A-C, 19A-B, 23, 24)

Cicindela decemnotata Say 1817:19. Type locality: "... on the sandy alluvions of the Missouri, above the confluence of the river Platte." Type depository: Presumed destroyed (Mawdsley 1993). Concept based on two specimens labeled: "USA: MT: Yellowstone Co., 15 mi NE Billings, 11-IV-2011, M. Kippenhan" in MCZ.
Cicindela purpurea var. decemnotata Say: Schaupp 1884:90
Cicindela decemnotata Say: Leng 1902:134
Cicindela decemnotata Say: Harris 1911:8
Cicindela decemnotata albertina Casey 1913:24 (synonymy follows Horn 1915:374). Type locality: "Canada (Lethbridge, Alberta)." Type depository: USNM.
Cicindela lantzi Harris 1913:68 (synonymy follows Horn 1915:374). Type locality: "Jefferson, Col." Type depository: MCZ [MCZ Type Database 2010].
Cicindela purpurea decemnotata Say: Horn 1915:374
Cicindela (*s. str*.) *limbalis decemnotata* Say: Rivalier 1954:253.
Cicindela (*s. str*.) *decemnotata* Say: Freitag 1999:21

Identification. *Cicindela d. decemnotata* can be characterized by the following: dorsal coloration exhibiting the full range of color—dark green, green, blue-green, blue, green-purple, purple, red-purple, olive green and black; individuals often have contrasting margins on the head, thorax and elytra which range from bright metallic green to dark green to blue-purple; elytral maculation complete with humeral dot, posthumeral dot, middle band, subapical dot and apical dot; geographic distribution from the western great plains of South Dakota and Nebraska westward to the eastern slope of the Wasatch Range in Utah, south central to eastern Idaho, Montana west of the Continental Divide and southern Canada to Alaska.

Description. Head. Bright metallic green with varying amounts of copper to red-purple to brown on disc; width of eyes greater than pronotum, narrower than elytra, base equal to width of anterior margin of pronotum; frons shallowly rounded towards clypeus, deep and irregularly sculpted rugae in middle with dense, long white setae; clypeus relatively smooth, glabrous; vertex with vermicular rugae in middle bordered by deep, parallel rugae next to interocular plate becoming vermicular and erratic towards occiput; interocular plate with deep parallel rugae, one supraorbital setae; genae with deep parallel rugae, long irregularly spaced long white setae in apical half; labrum unpigmented with anterior margin dark brown, not wider than clypeus, central one-third slightly expanded outward with three well developed teeth, 4 to 9 (most often 6) long white submarginal setae projecting beyond anterior margin; mandibles stout with four teeth and basal molar, outer margin unpigmented, inner margin green, teeth black; maxillary and labial palpi green to dark green, apex of terminal palpomeres testaceous, first labial palpomere black; antennomeres 1-4 metallic green, occasionally with varying amounts of copper to red-brown reflections, antennomere 1 with 3-5 sensory setae on apex and 8-12 long white accessory setae on frontal face, antennomere 2 with 1 accessory setae, antennomere 3 with 2 sensory setae on apex and 4-6 accessory setae on exterior margin, antennomere 4 with 2 sensory setae on apex and 2-4 accessory setae on exterior margin, antennomeres 5-11 black, clothed with small decumbent setae and 2 sensory setae on apex.

Figure 1. *Cicindela d. decemnotata* adult habitus. A. Adult, 15 mi. NE of Billings, Yellowstone Co., MT, 24-IV-2011. B. Male, "CO: Garfield Co., RT 139, 2-VI-1991" (CSUC). C. Male, "WY: Big Horn Co., Lovell LTA, 02-IX-2000" (CSUC). D. Male, "ID: Caribou Co., N. of Canyon Rd., 30-VI-2007" (MGKC). Scale bar = 5mm for B–D.

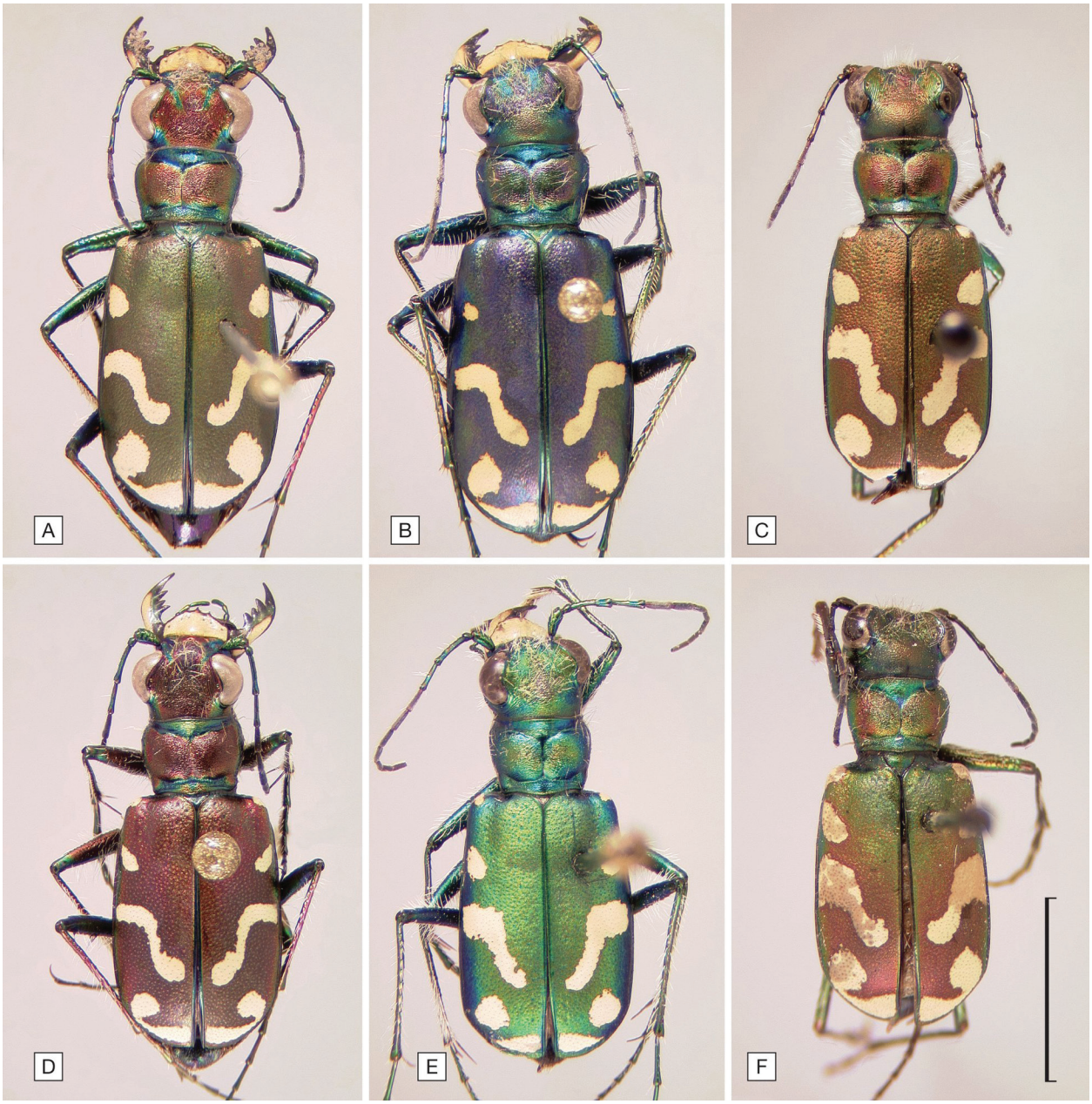

Figure 2. *Cicindela d. decemnotata* adult habitus. A. Female, "MT: Beaverhead Co., Centennial Valley, 3-VI-2007" (MGKC). B. Male, "MT: Broadwater Co., SE of Canyon Ferry Res., 7-V-2007" (MGKC). C. Male, "CO: Larimer Co., Jct 15/88, 14-VI-1992" (CSUC). D. Male, "MT: Beaverhead Co., Centennial Valley, 27-VI-2009" (MGKC). E. Male, "CO: Montezuma Co., Mesa Verde N.P. 8-V-1999" (MGKC). F. Male, "CO: Park Co., Barlow Ranch, VI-1915" (MGKC). Scale bar = 5mm for all.

Thorax. Bright metallic green to dark green to blue to purple along margins, disc with varying amounts of yellow green, copper, red-purple, brown, green, or green blue; pronotum wider than long (ratio 3:2), trapezoidal, widest in anterior third; surface with shallow, vermicular rugae; proepisternum clothed throughout with sparse, long white setae; prosternum surface shallowly, irregularly sculptured, glabrous; mesoepisternum surface irregularly sculpted, sparse setae on basal and posterior margins; mesoepimera surface irregularly sculpted, sparse setae on posterior margins; metaepisternum clothed throughout with sparse, long white accessory setae; metasternum smooth with sparse, long white accessory setae along anterior and lateral margins.

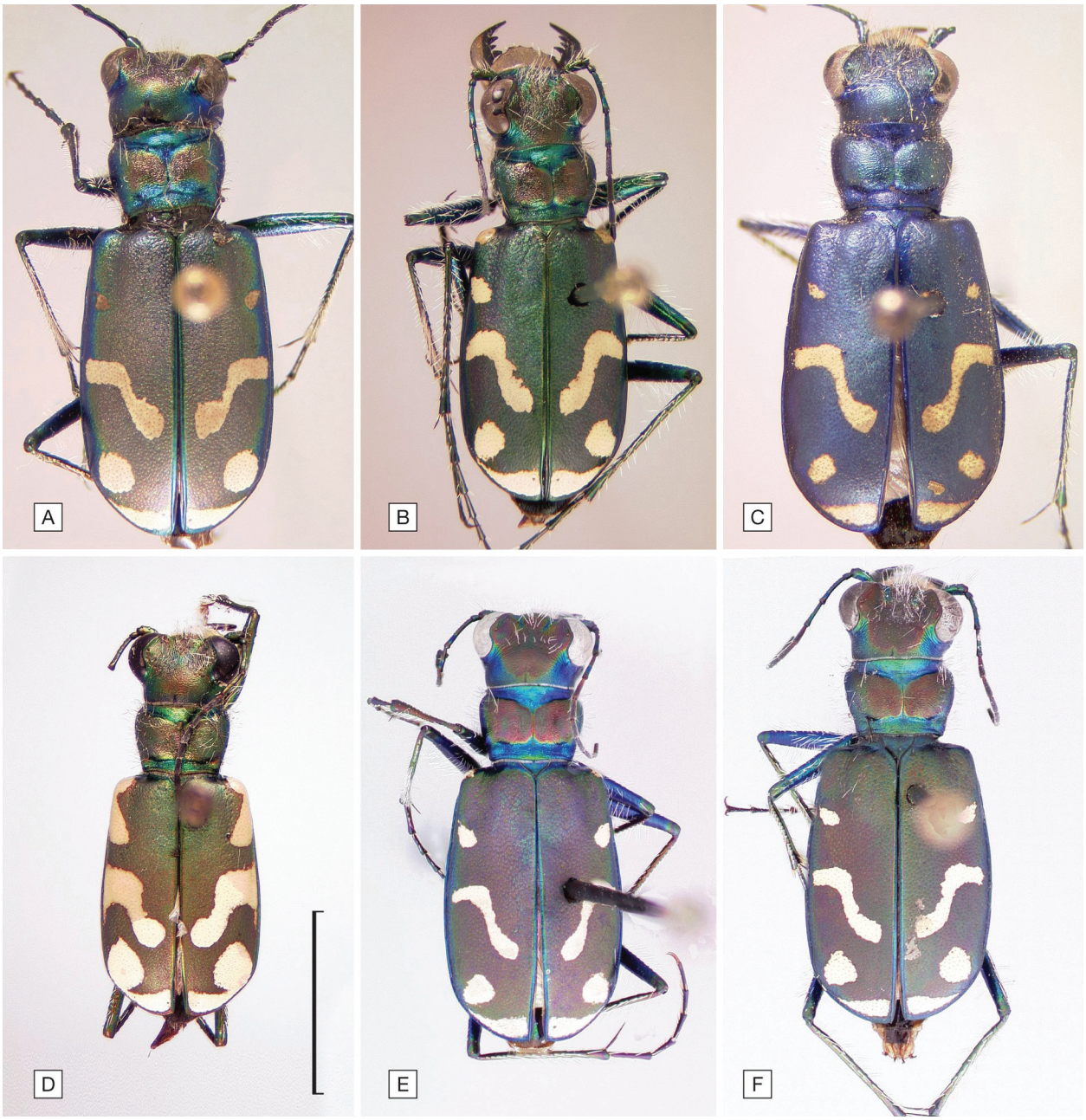

Figure 3. *Cicindela d. decemnotata* adult habitus. A. Female, "CO: Grand Co., RT 36 Lake Granby, 27-V-1994" (CSUC). B. Male, "MT: Yellowstone Co., NE of Billings, 28-IV-2008" (MGKC). C. Female, "MT: Jefferson, June 12, 1924" (MTEC). D. Male," Jefferson, Colo, June 20, 1918" (USNM). E. Female, "Idaho Bonneville Co. Willow Creek Ririe Dam, 5 mi SE Ririe 30-V-1975" (BYUC) F. Female, "6 mi SE Malta, IDA Cassia Co. IV-30-71" (UIDC). Scale bar = 5mm for all.

Elytra. Disc ranging from green with yellow green reflections to dark green to blue-green to blue to green-purple to purple to red-purple to olive-green to black; occasionally with lateral margins bright metallic green to dark green to blue purple; longer than wide (ratio 8:5); humeri rounded, humeral impression shallow but distinct; surface shallowly convex, lateral margins sharply curved downward, posterior margin broadly rounded; sutural spine small, slightly retracted; microserrations small but distinct; scutellum small, triangular; entire elytra surface covered with minute reticulate fovea with larger, shallow depressions with a small, raised granule along anterior edge, depressions and granules irregularly placed; large punctures within humeral impressions; maculation consists of small, rounded

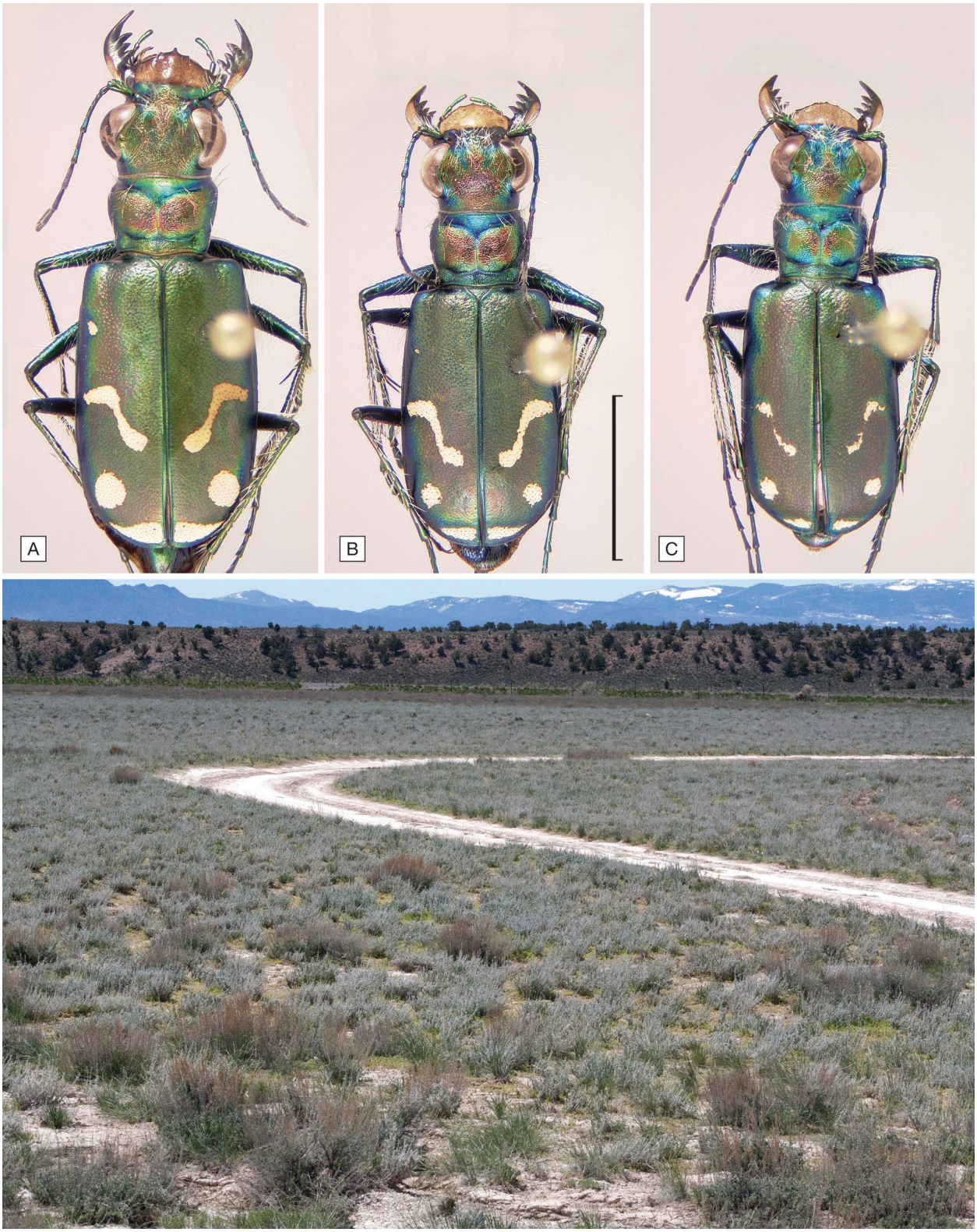

Figure 4. *Cicindela d. decemnotata* adult habitus. A. Female, "UT: Sevier Co., Hwy 50, NW of Salina, 5-V-2011" (MGKC). B. Male, "UT: Sevier Co., Hwy 50, NW of Salina, 5-V-2011" (MGKC). C. Male, "UT: Sevier Co., Hwy 50, NW of Salina, 5-V-2011" (MGKC). D. Habitat: S, Hwy 50, NW of Salina, Sevier Co., UT, 5-V-2011. Scale bar = 5mm for A–C.

humeral dot, larger, oblong ovular posthumeral dot, complete middle band not touching lateral margin, middle band with rounded knee, long transverse arm and well defined rounded foot, large subapical dot, and triangular apical dot; all markings off white in color.

Abdomen. Ventrites green to purple with appressed setae on lateral margin, central area with very sparse appressed setae, posterior margin with widely spaced sensory setae; male pleurite 6 with shallow, broadly rounded indentation along anterior margin; pleurite 7 divided, rounded triangular shape; female pleurite 6 posterior face flat, depressed with short, closely spaced sensory setae.

Legs. Pro- and mesocoxae globose, anterior margin with dense, long white accessory setae; metacoxae triangular with lateral margin elongate, smooth with sparse, long white accessory setae in lateral half, 2 to 3 medium length white accessory setae in central area, 2 medium length sensory setae on apex; pro- and mesotrochanters dark brown, small, triangular shaped with slight green reflections and one, long sensory seta on apex; metatrochanter large, kidney shaped, dark brown, with slight green reflections and one seta, glabrous; femur, tibia and tarsi bright metallic green with varying amounts of yellow-copper to red to brown reflections; femur with rows of long, erect white setae; profemora also with very dense long, erect white setae on anterior face; tibia with rows of long, erect white setae, anterior margin with two long, stout spurs; male tarsomeres expanded, flattened on bottom with dense short white setae creating pads, scattered short erect setae on dorsal and lateral surfaces, apex with medium length erect setae; female tarsomeres 1-5 with short erect evenly spaced setae on ventral surface, scattered short erect setae on dorsal and lateral surfaces, apex with medium length erect setae; claws simple, length less than half length of 5th tarsomere.

Length. MT: Yellowstone Co. male 10.10mm–12.20mm (mean = 11.43mm, n=20), female 11.20mm –13.30mm (mean = 12.29mm, n=20). MT: Beaverhead Co. male 10.90mm–12.20mm (mean = 11.41mm, n=20)., female 11.60mm - 13.20mm (mean=12.19mm, n-14). MT: Broadwater Co. male 11.00mm - 13.90mm (mean = 12.10mm, n=20), female 12.00mm–13.20mm (mean = 12.82, n=11).

Material Examined.

USA: ALASKA: Yukon River, Chester Bluffs 64.50.900, 7. 56. 447 June 2005 (3, NHMC).

COLORADO: Archuleta Co.: Hwy 160 7-8 mi E Hwy 84, 15-IV-1989 (10, DWBC). Upper Piedra R. 26-VII-69 (Kippenhan 1994). E. Fork San Juan River, 10-VI-60, 1-V-61, 9-V-61 (3, RLHC). Garfield Co.: Rt. 139, mm 28, 2-VI-91 (1, CSUC). Grand Co.: Rt. 36, 1 mi S Lake Granby Dam 27-V-94 (1, CSUC). Gunnison Co.: 1 mi W. Doyleville, alkali flat and road cut, 3-VII-1991 (1, CSUC). LaPlata Co.: 12 mi E Durango, Hwy 160, 16-IV-1983, 15-IV-1989, 18-IV-1991, 12-13-V-1984 (120, DWBC). Hwy 160 12 mi SE Durango, 13-V-1970 (Lawton 1972). Larimer Co.: SE Jct. Co. Rd. 15/88, 14-VI-1992 (1, CSUC). Mineral Co.: E Fk. San Juan R., 1-V-61 (Kippenhan 1994). Montezuma Co.: Mesa Verde Nat. Park, West Plateau Area, 8-V-1999 (3, CSUC; 1, MGKC). Park Co.: Barlow Ranch, VI-13 (Kippenhan 1994). Barlow Ranch, 22-IV-13, VI-1913, 27-VI-13, 12-VII (21, USNM). Jefferson, 26-VI-13 (Kippenhan 1994). Jefferson (2, USNM). South Park, 14-VI-15 (Kippenhan 1994). So. Park, 15-VI, 22-VI, 25-VI-13 (5, USNM). 12 mi SE Jefferson, Tarryall Creek, 9000', 7-13-VI- (1, RHLC). Moffat Co.: Browns Park NWR, 17-V-1996 (5, CBKC). 3 mi E. Maybell, E. bank Yampa R., 21-VI-1970 (Willis and Stamatov 1971). 3 mi N Maybell, 23-IX-53 (10, AMNH). 0.2 mi. S Craig Hwy. 13, 25-IV-1987 (6, DWBC). Hwy 13 28.5 mi N Craig, 25-IV-1987 (1, DWBC). Rd. 318 mm19 NW of Maybell, 23-IV-1993 (2, DWBC). 9.6 mi NE Craig, 21-VII (Kippenhan 1994). Dinosaur Nat. Mon., Gates of Lodore, 2-3-VI-91 (Kippenhan 1994). Maybell, 3-V-65 (1, RLHC). Rio Blanco Co.: 2 mi N Garfield Co. line, N Big Foundation Ck, 28-V-1990 (1, CSUC). Routt Co.: Escalante Hills, 28-IX (1, USNM). Weld Co.: Pawnee Nat. Grassland, Co Rd 57, off SR 14, 17-IX-1994 (1, CSUC). 1 mi N Rockport, Hwy 85, 20-V-92 (4, CSUC).

IDAHO: Caribou Co.: N. of Canyon Rd., 30-VI-2007 (3, MGKC). Bannock Co.: Pocatello Ck. (1, BYUC). Pocatello, 4483' (Leffler 1979). Pocatello 28-IX-62 (3, BYUC); 8-X-74 (1, BYUC). North Pocatello (1, BYUC). Downey, 1-X-72 (1, CIDC). Bingham Co.: Buckskin Basin,16-IX-60 (1, UIDC). Blackfoot, 16-IV-57 (1, UIDC). Bonneville Co.: Idaho Falls, N.R.T.S. Id, 17-IV-1967 (1, MGKC). Idaho Falls (3, BYUC), 15-V-79 (1, BYUC). Willow Creek, Rivie Dam (1, BYUC). 1.1 mi. W Swan Valley off Hwy 26, 23-V-1985 (10, DWBC). Butte Co.: 2 mi NW Arco, 10-VI-62 (1, UIDC). 20 mi E. Howe, 27-III-67 (1, UIDC). 6 mi S Howe (1, UIDC). T4N S17, 1527 m 43.30.11;113.01.33 (1, CIDC). Cassia Co.: Idahome Rd, .3 mi W I-84, 23-IV-1987, 22-V-1985 (4, DWBC). 3 mi E. Idahome, 11-IX-65 (1, UIDC). 5 mi NE Malta, 27-III-55 (2, UIDC). 6 mi SE. Malta, 30-IV-71 (10, UIDC). 7 mi SE. Malta (2, UIDC). Oakley, 25-IX-31 (1, USNM).

Clark Co.: Crystal Falls Cave, 6-IX-66 (10, UIDC). Fremont Co.: Targhee Nat. Forest, 12-V-2007 (6, MTEC). Targhee Nat. Forest, 18-V-2007 (5, MGKC). Targhee Nat. Forest, 15-IX-2007 (4, MGKC). 1 mi E of Fog Butte, Hamilton Hill Rd., 25-V-2005 (14, CBKC). Jefferson Co.: 4.5 mi NW Terreton, 11-VI-85 (1, UIDC). Lincoln Co.: Richfield (1, UIDC). 4 mi E. Richfield, 12-IV-58 (2, UIDC). 10.5 mi NE Richfield (3, UIDC). 7 mi NE Richfield, 24-III-78 (1, CIDC). Shoshone (1, UIDC). Nez Perce Co.: Lewiston 5-V-33 (2, USNM). Power Co.: Rockland, 26-V-79 (1, UIDC). Twin Falls Co.: T135, R16E, S30, 30-IX-81 (1, CIDC). Hollister, 11-V-31, 8-VI-35 (2, USNM).

MONTANA: Beaverhead Co.: Centennial Valley, Pitfall Trap, 30-VIII-13-IX-2008 (6, MTEC). Centennial Valley, 25-V-1999 (1, MTEC). Dillon, 20-IV-1936 (9, MTEC). Dillon, 6-VII-1936 (1, MTEC). F&O Ranch, 15-VII-1935 (1, MTEC). Centennial Valley, North Side Rd, 26-V-2007 (35, CBKC; 32, MGKC). North Side Rd., 27-VI-2009, 25-VIII-2009, 16-IX-2009 (13, MGKC) Broadwater Co.: Canyon Ferry Res., SE Side, 28-IV-2007, 7-V-2007, 3-V-2008, 13-V-2011, 1-IX-2007 (49, MGKC). Carbon Co.: Fromberg, 7-V-1918 (1, MTEC). SE Bridger/Bowler, w foothills Pryor Mts., 4850', 6-VI-1998 (1, CSUC). Chouteau Co.: Judith R. Landing at Missouri R./Hwy 236, 24-IV-1995 (1, CSUC). *No local*, 13-IX-1926 (1, MTEC). Fergus Co.: 7 mi S Missouri R. off Hwy 236 (1, JSC). Gallatin Co.: Buffalo Jump State Park, 4-IX-1980 (1, MTEC). *No local*, 13-IV-1922 (1, MTEC). *No local*, 9-V-1924 (1, MTEC). Jefferson Co.: Elkhorn Mts, 1954 (1, USNM). *No local*, 12-VI-1924 (1, MTEC). *No local*, 26-VI-1924 (3, MTEC). Lewis and Clark Co.: Helena, 27-V-07 (1, USNM). Madison Co.: Ruby Res., 9 mi S. Alder, 29-VI-2-VII-1964 (2, MTEC). Sweetwater Basin, Ruby Mts., 25-VI-1989 (1, MTEC). Musselshell Co.: Musselshell, 16-VI-1928 (1, MTEC). 23 mi NW Roundup, US Hwy 87, 2-VI-65 (1, RHLC). Petroleum Co.: 1.5 mi S, 6 mi W Winnett, 25-V-1971 (1, MTEC). Pondera Co.: 8 mi SSE of Shelby, Marias Valley Rd., Co. Line, 30-V (1, MGKC) Powell Co.: Deer Lodge, 5-V-1989 (2, MTEC). Toole Co.: Shelby, 20-VIII-1934 (1, CSUC). 5 mi S of Shelby at I-15, N of Marias R., 27-IV-1995 (1, CSUC). Silver Bow Co.: Butte, 5-VI-1949 (1, USUC). Yellowstone Co.: 37 mi. NE of Billings, 24-IV-2011, 15-V-2010 (8, CSUC; 31, MGKC). 15 mi. NE of Billings, 13-IV-2008, 15-IV-2010, 28-IV-2008, 24-VI-2011 (68, MGKC). Unknown County: Park City, 5-IV-1915 (3, MTEC).

NEBRASKA: Sioux Co.: N of Harrison, IX-2004, 14-V-2006 (2, SMSC; Spomer et al. 2004).

NEW MEXICO: San Miguel Co.: Las Vegas (1, CMNH).

NORTH DAKOTA: Slope Co.: Burning Coal Vein, 2-VI-72, 17-VI-1972 (2, RLHC). Mountrail Co.: 8 mi SW New Town, 12-V-1974 (1, RLHC).

UTAH: Beaver Co.: 4 mi. N. Milford, 6-VI-2011 (4, MGKC). 5 mi N. of Milford, 11-V-78 (1, USNM). Hwy 257, 4 mi N Milford, 26-IX-85 (2, BYUC). Carbon Co.: North Fork Gordon Ck, 12 mi W. Spring Glen, 18-VI-2003, 26-VII-2005 (2, BYUC). Daggett Co.: State line along Green River, 6-VI-92 (2, CBKC). 4.3 mi W state line, 17-V-96 (3, CBKC). Duchesne Co.: Lake Fork, north of Mountain Home, 14-IX-90 (1, BYUC). Garfield Co.: Henderson Canyon viewpoint, 20-V-2005 (15, CBKC). Henderson Canyon Trail, near Henrieville, 16-V-2000 (BYUC). 4 mi S Hatch, 29-VIII-1990 (1, USUC). Millard Co.: Delta, 14-VIII-1948 (1, USUC). Hwy 6 N of jct rt 174, 6-VI-2011 (2, MGKC). Sevier Co.: I-70, 19 mi E Salina, 18-V-1984 (6, DWBC). Hwy 50, mm 53, W of Salina, 17-IV-1993 (12, DWBC). Hwy 50 west of Salina, 5-V-2011 (89, MGKC). 21 mi E Salina, Hwy 70, 19-V-78 (2, RHLC). Uintah Co.: Hwy 40 1.8 mi W Colorado, 24-IV-1987 (9, DWBC). Dinosaur N.M., 25-IV-1987 (1, USUC). Utah Co.: Birdseye, 10-VIII-2005 (1, BYUC). Sevier Co.: Hwy 40 1.8 mi W Colorado, 18-V-1984 (1, DWBC).

WYOMING: Albany Co.: Rt. 30, 1 mi SE Laramie, ORV tracks near highway, 30-VI-1975 (7, CBKC). 1 mi SE Laramie, 7-VI-1977 (10, CBKC). 1 mi SE Laramie, 9-VI-1970 (Willis and Stamatov 1971). 2 mi E Laramie, 7700', 13-IV-2003, 14-V-2003, 2-VI-2003 (5, CSUC). I-80, 8 mi E Laramie, 29-V-1988 (5, DWBC). SE Edge of Laramie, 18-VII-1971 (Lawton and Willis 1974). T15N, R72W, 13-V-73 (CIDC). T15N R73W, 8-IV-70 (2,USNM). 2 mi E Laramie, T16N, R72W, section 31, 7700' (5, CSUC). Big Horn Co.: Lovell LTA-D7, Nat. Guard Training Area, 20-V-2000, 1-VI-2000, 2-IX-2000 (3, CSUC; 1, JSC). 10 mi WSW Emblem, 14-VI-1970 (Willis and Stamatov 1971). Carbon Co.: Hwy 30, 9 mi W Medicine Bow, 20-VI-1986, 22-IV-1994, 26-IV-1987, 26-IV-1992, 10-V-1990, 21-V-1978, 25-V-1985, 25-V-1988, (115, DWBC). Hwy 287, mm 23-22.5, N Rawlins, Soda Lake, 26-V-2006 (22, CBKC). Hwy 30-287, 11 mi W Medicine Bow, 23-VIII-2006 (2, CBKC). 9 mi W. Medicine Bow, N side Hwy 287 (JSC). Crook Co.: 6 mi NE Sundance, 13-VI-1970 (Willis and Stamatov 1971). Fremont Co.: East Fork Lodge, 13-27-VII-1990 (1, CSUC). East Fork Lodge, 7350', 30-V-1988 (1, CSUC). 10 mi S Shoshoni, 16-IV-65, 6-IX-66 (2, RHLC). 1 mi S. Moneta, 17-IX-72 (1, RHLC). Hot Springs Co.: Owl Creek Mts. (3, USNM). Laramie Co.: Cheyenne, V-1889, 20-IV (2, USNM). Cheyenne (1, USUC). SE Jct 15 and 88, dry creek bed (1, CSUC). Natrona Co.: Casper, 4-V-1926 (1, RHLC). Park Co.: Cody, 26-VII-35 (1, USUC). Sublette Co.: Hwy 191, 19 mi. SE

Pinedale, 21-VI-1994 (6, DWBC). Merna, V-41 (1, USNM). Teton Co.: Mammoth Hot Springs (2, USNM). Uinta Co.: Ft. Bridger, 21-VII-49 (4, AMNH). Washakie Co.: Hwy 16, 4.4 mi W Tensleep, 13-VI-1982 (1, DWBC).

CANADA: ALBERTA: 8 mi E. Manyberries 13-V-65, 6-V-66 (7, USNM). North of Hays on Bow River 23-V-2005 (6, TLC). RD875 Bow R. (N - Hays), 19-20-V-1986 (25, DWBC). Hwy 3 Oldman R. (W of Monarch), 28-V-1987 (5, DWBC). Drumhellar, 5-VIII-1974 (1, USUC). Hwy 3, 10.8 mi SW. Ft. MacLeod, 28-V-1997 (8, DWBC). Medicine Hat, 14-IV-23, 3-IV-27, 21-IV-29, 26-IV-30, 26-V-31, 7-IX-29, 21-IX-29, 5-IX-30, IX-65, 17-X-26 (18, USNM). Lost R. Ranch, Milk River, 5-V-65 (2, USNM).

SASKATCHEWAN: Swift Current, 20-VIII-1940 (5, CNC). Willows, 24-VI-1955 (2, CNC). Elbow, 24-VI-1954 (2, CNC). Rock Glen, 2-VIII-1985 (1, CNC). TP8, Rg 2, 17-VIII-1987 (2, CNC).

MANITOBA: VI-37 (2, UIDC).

YUKON: Whitehorse, 4-VIII-1987 (18, CNC). Whitehorse, 14-V-16, 21-V-16, 20-V-23, 22-V-16, 31-V-16 (5, USNM). Whitehorse, Canyon Mt., 10-VIII-1950 (1, CNC). Kluane N.P., 10-VIII-1950 (1, CNC). Upper Yukon River, 14-V-16 (1, USNM).

Variation. This subspecies has a much greater geographical distribution than the others, and as expected, a high degree of interpopulation variation of elytral maculation and dorsal coloration. All but two of the populations examined have a well-developed maculation pattern consisting of a humeral dot, posthumeral dot, middle band, subapical dot and apical dot, with mean overall maculation scores ranging from 7.0 to 17.1, and with most populations having between 14 and 16 in overall maculation scores. Populations with the highest maculation scores are Carbon Co., Wyoming (17.1), Alberta, Canada (17.3) and Garfield Co., Utah (16.6). The geographic distance between these populations and the fact that other heavily maculated populations are scattered throughout the distribution of *C. d decemnotata* indicate that a high overall maculation score appears to be a random occurrence. Harris' type of *C. lantzi* has the humeral dot broadly connected to the posthumeral dot, and is apparently a very rare aberration as we have examined only one other specimen with this character (Fig. 11D). The populations with the lowest total mean maculation scores are from Beaver (7.5) and Sevier (10.8) counties, Utah; both of which are south of the *C. d. bonnevillensis* populations in Tooele Co. and within the area occupied by the ancient Lake Bonneville. These populations may represent intergrades between *C. d. decemnotata* and *C. d. bonnevillensis*, but are assigned to the nominotypical subspecies pending future molecular analysis.

Variation of elytral maculation is well represented in three populations we sampled. The first, a series of 31 specimens collected in the Centennial Valley, Beaverhead Co., Montana on one day, all had well developed posthumeral dots, middle bands, sub apical and apicals dots, but only 26 had humeral dots. The second, a series of 89 specimens collected along Hwy 50, west of Salina, Utah (Fig. 4A-C) on the same day, all had middle bands, sub and apicals dots while only 18 had post humeral dots and none had humeral dots. In this series, two specimens had the middle band reduced to a transverse dash. In the third series of 53 specimens collected along the SE side of Canyon Ferry Res., Broadwater Co., Montana, (Fig. 2B) at various dates, all had middle bands and apicals dots, 52 had subapical and postapical dots and only four had humeral dots.

Despite inter- and intrapopulational variation in color, individual populations tend to exhibit a limited range of variation. For example, most populations from Bannock and Cassia Counties (Fig. 3E-F) have dark purple or dark green dorsal coloration whereas populations along the Utah/Colorado (Fig. 2E) border tend to be brighter green often with secondary coloration of yellow-green. In a series of nine specimens from the Targhee National Forest, Fremont Co., Idaho, all specimens exhibit a deep red-purple dorsal coloration. Acorn (2001) documented a violet or blue-purple colored variety from the Yukon and parts of Alberta, and concluded that this color was a result of specimens being photographed in bright light or an artifact of being dried. Some populations have a mixing of color, often a dull, olive-green (Fig. 2A) on the elytral resulting in a muddy appearance. When present, the contrasting color along the lateral elytral margin varies in width, it is almost always bright green to blue—rarely purple—regardless of the remainder of the elytral color.

Throughout the range of *C. decemnotata*, the labrum demonstrates slight variation in the shape of the anterior margin (Fig 19B), number of setae and less commonly, pigmentation (Fig. 19B). There

is a notable variation in the number of accessory setae on the first antennomere, however, there is no consistent pattern among the various populations.

Distribution. Alaska, Alberta, Colorado, Idaho, Manitoba, Nebraska, New Mexico, North Dakota, Saskatchewan, South Dakota, Utah, Wyoming, Yukon. Two specimens (USNM) collected in 1933 in Lewiston, Nez Pierce Co., Idaho are the only records of this subspecies north of the Snake River Plain in Idaho and are within the range of *C. d. meriwetheri*; further collecting in this area is needed to verify this occurrence of this subspecies in this area.

***Cicindela decemnotata meriwetheri* Knisley and Kippenhan, new subspecies**
(Fig. 5A-F, 6A-C, 18D, 19C, 23)

Cicindela decemnotata Say: Hatch 1938:233
Cicindela d. n. ssp Clifford: Leffler 1979:343

Identification. This subspecies can be recognized by the combination of green dorsal coloration with the lateral margins of the elytra, head and pronotum being bright green to occasionally dark green or blue-green, elytral maculation reduced to middle band, subapical dot, apical dot and occasionally a posthumeral dot; reduced number of setae on the genae (<3); and distribution restricted to the Columbia Basin of central Washington and southern British Columbia.

Description. *Differs from the nominotypical subspecies in*:

Head. Bright green, genae, anterior margins of eyes and clypeus bright green to dark green to blue-green; antennomeres 1-4 with varying amounts of bright green, often with yellow-green reflections; labrum with central area pronounced, central tooth larger than lateral teeth; genae with 0 to 8 setae. Thorax. Margins bright green to dark green, disc bright green, often with yellow-green reflections.

Elytra. Lateral margins bright green to dark green to blue-green transitioning to green in central areas, occasionally with yellow-green reflections; maculation consists of a reduced to complete middle band, subapical dot, apical dot and occasionally a small posthumeral dot. Elytral sculpture with shallow puncture, pronounced primary granules and numerous, small secondary granules.

Abdomen. Dark green to blue-green.

Legs. Femur, tibia and tarsomeres bright green, occasionally with yellow-green reflections.

Length. Grant Co.: male 11.10mm–12.00mm (mean=11.60mm, n=9); female 12.00mm–13.20mm (mean=12.57mm, n=8).

Type Locality. Washington, Grant Co., Grand Coulee Dam Airport, trails through sagebrush.

Type Material. Holotype. Male labeled: "WA, Grant Co., Grand Coulee Airport, Dirt road NW of runway, 47.54.574, 119.05,174, 11,13-IV-08 C.B. Knisley" [typeset white label]. "HOLOTYPE *Cicindela (s. str.) decemnotata meriwetheri* Knisley and Kippenhan" [typeset red label with black border printed on white paper]. Depository: MCZC.

Allotype. Female labeled: "WA, Grant Co., Grand Coulee Airport, Dirt road NW of runway, 47.54.574, 119.05,174, 11, 13-IV-08 C.B. Knisley" [typeset white label]. "ALLOTYPE *Cicindela (s. str.) decemnotata meriwetheri* Knisley and Kippenhan" [typeset red label with black border printed on white paper]. Depository: MCZC.

Paratypes. "USA: WA: Grant County, Grand Coulee Dam Airport, 47°55.23'N • 119°04.98'W, 8-X-2011 M Kippenhan" [typeset white label with black border] (1m, 2ff, CSUC; 1m, 2ff, MGKC). "USA: WA: Grant County, Grand Coulee Dam Airport, 47°55.23'N • 119°04.98'W, 1-X-2009 M Kippenhan" [typeset white label with black border] (1m, 2ff, MGKC). "USA: WA: Grant County, Grand Coulee Dam Airport, 47°55.23'N • 119°04.98'W, 19-III-2010 - 1594', M & S Kippenhan cols." [typeset white label with black border] (1m, AMNH; 1m, MCZ; 4mm, 2ff, MGKC; 1m, MTEC). "USA: WA: Grant County, Grand Coulee Dam Airport, 47°55.23'N • 119°04.9'W, 20-IV-2011 Kippenhan col" [typeset white label with black border] (1f, AMNH; 1f, CSUC; 1m, BYUC; 2mm, 1f, MGKC). "USA: WA: Walla Walla Co.,

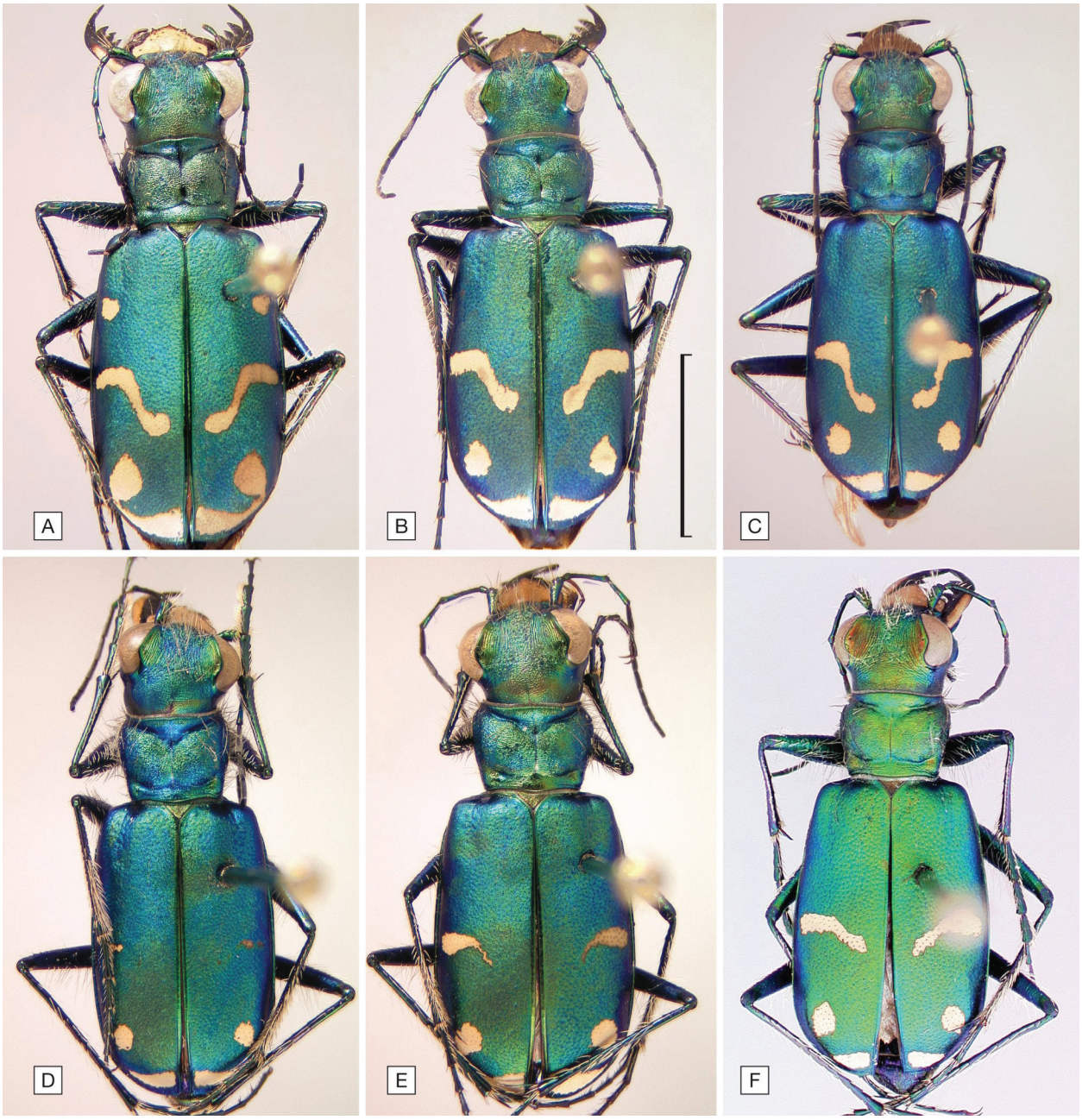

Figure 5. *Cicindela d. meriwetheri* adult habitus. A. Female, "WA: Walla Walla Co., Hwy 12 E of Hwy 730, 3-X-2003" (MGKC). B. Female, "WA: Grant Co., Grand Coulee Airport, 19-III-2010" (MGKC). C. Male, "USA, WA Walla Walla Co., Hy 12-2 mi E Hy 730 (Wallula Jct). 4-X-1991" (DWBC). D. Male, "BC: 5 mi S Penticton, 13-IV-2008" (CBKC). E. Female. "BC: 5 mi S Penticton, 13-IV-2008" (CBKC). F. Male, "BC: 5 mi S Penticton, 13-IV-2008" (CBKC). Scale bar = 5mm for all.

Hwy 12, 2.6 mi. E. junction, HWY 730, clay bank, 46°03.5' N • 118°51.27' W, 3-X-2003 M. Kippenhan" [typeset white label with black border] (1m, CBKC; 1m, 3ff, MGKC). "USA: WA: Walla Walla Co., 24 September 2000, Hwy 12, 2.8 mi. E. Hwy 730, M. Kippenhan col." [typeset white label with black border] (1f, MGKC)."USA: WA: Walla Walla Co., 16 September 2000, Hwy 12, 2.8 mi. E. Hwy 730, M. Kippenhan col." [typeset white label with black border] (1m, 1f, CBKC). "USA - WA - Walla Walla Co., Hy. 12 - 2 m E. - Hy. 730, (Wallula Jct.), D. Brzoska 4-X-1991" [typeset white label] (6mm, 5ff, DWBC)."WA-Walla Walla Co., 2-4mW-Wallula Jct., D. Brzoska 20-IV-1984" [typeset and hand printed white label]

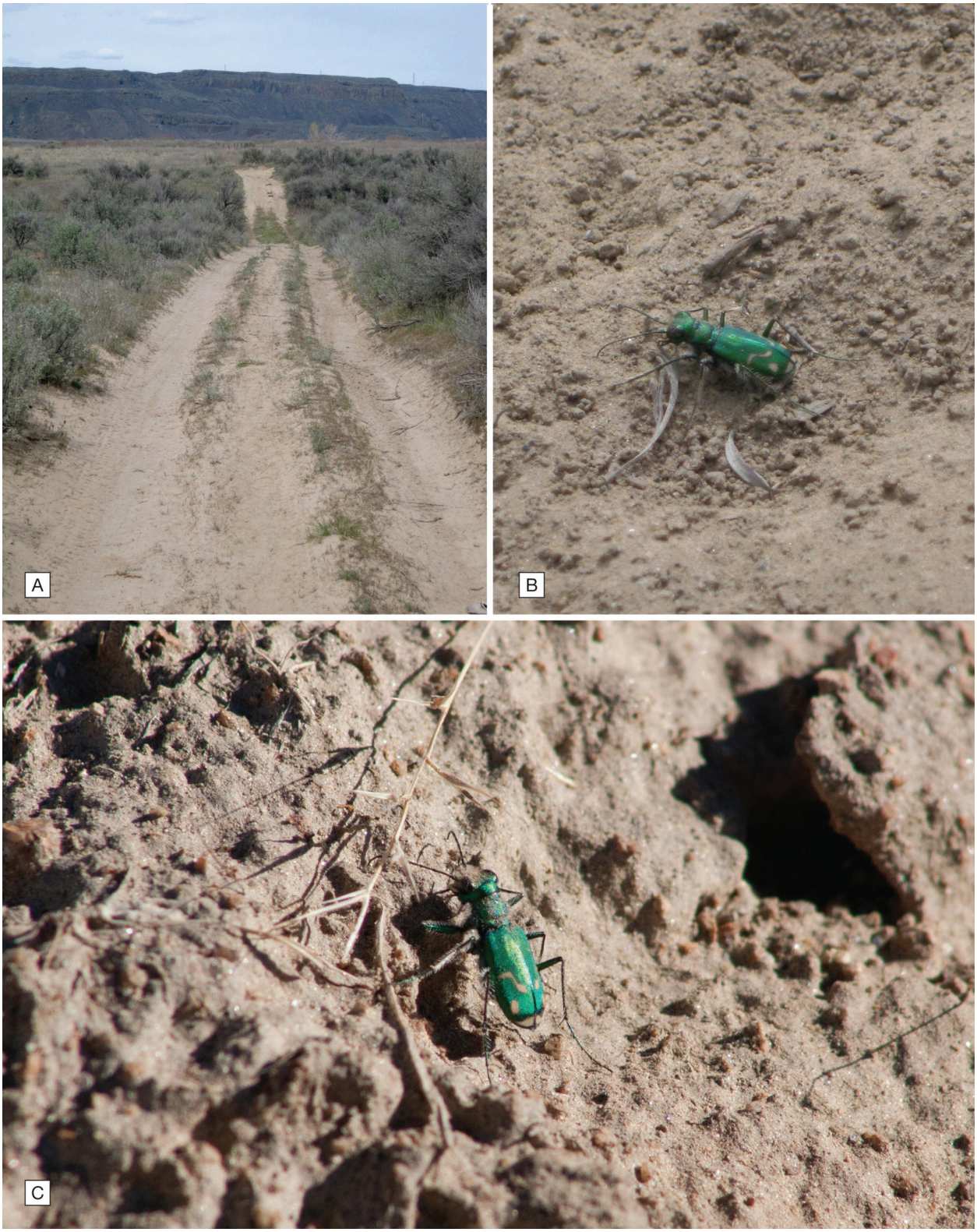

Figure 6. *Cicindela d. meriwetheri*. A. and B. Habitat and adult: Grand Coulee Airport, Grant Co., WA, 19-III-2010. C. Adult: Grand Coulee Airport, Grant Co., Washington, 8-IX-2011.

(3mm, DWBC). "WA- Walla Walla Co., 2-4mW-Wallula Jct., D. Brzoska 21-IV-1987" [typeset and hand printed white label] (1m, CBKC; 3mm, 5ff, DWBC). "USA: WA: Walla Walla Co., Hwy 12, 2.8 mi. E. Hwy 730, 13 Oct 2002, M. Kippenhan c." [typeset white label] (1m, CBKC). "WA, Grant Co., Grand Coulee Airport, Dirt road N,W of runway, 47.54.574, 119.05,174, 11, 13-IV-08, C.B. Knisley [typeset white label] (9mm, 8ff, CBKC). "WASH.:WALLA WALLA Co., 3 mi. E. Wallula Jct., 14 Apr. 1973, D. L. Pearson" [typeset white label] (3mm, USNM). "Touchet, Wash, Mar. 17 1934, HP Lanchester" [typeset white label] (1m, 1f, USNM). "Touchet, Wash, Mar. 10, 1938, HP Lanchester" [typeset white label] (1f, USNM). All paratypes labeled: "PARATYPE, *Cicindela (s. str.) decemnotata meriwetheri* Knisley and Kippenhan" [typeset red label with black border printed on white paper].

Additional Material Examined.

U**SA: WASHINGTON:** Adams Co.: Lind (Leffler and Pearson 1976). Ritzville, 16-IX-62 (1, RLHC) Franklin Co.: Perry (Leffler and Pearson 1976). Ferry Co.: Republic, 15-IX-03 (1, USNM) Lowden, 19-III-36, 14-IV-34, 16-IV-34 (3, USNM). Grant Co.: Black Lake, 9 mi NNE Moses Lake (Leffler and Pearson 1976). Moses Coulee (1, USNM). Okanogan Co.: 2 mi E Tonasket (Leffler and Pearson 1976). Walla Walla Co.: College Place, 20-VII-34 (1, USNM). Touchet, 17-III-34, 27-III-34, 10-III-35, 17-III-35, 1-IV-38, 11-IV-35, 2-IV-34 (25, USNM). 3 mi E Wallula Jct., 14-IV-73 (4, USNM). 2.4 mi. E Wallula Jct., 20-IV-62 (3, USNM). Hwy 12, 2 mi E Hwy 730 (Wallula Jct), 4-X-1991 (15, DWBC). 2-4 mi W Wallula Jct, 20-IV-84 (7, DWBC). Lowden, 19-III-36, 14-IV-34, 16-IV-34 (3, USNM).

CANADA: BRITISH COLUMBIA: Kelowna, 14-VI-32 (1, USNM). Mainland, South and southwest (Wallis 1961). Taylor, 3-VI-1948 (1, CNC). 5 mi. S Penticton, E side of Skaha Lake, 12-IV-2008 (35, CBKC). 5 mi. S Penticton, E side of Skaha Lake, 25-V-2006 (20, TLC).

Variation. The dorsal coloration of this subspecies is homogeneous with almost all individuals being green, often with yellow-green reflections on the dorsal surfaces, especially those from British Columbia. The extent of maculation varies geographically with specimens from Grant Co. and Walla Walla Co., Washington, in the southern part of the distribution, having a complete middle band (Fig. 5A-C) whereas the elytral maculation, especially the middle band, of the British Columbia individuals is reduced (Fig. 5D-F). More collecting is needed in north central Washington to determine if these differences in maculation are clinal in nature. *Cicindela d. meriwetheri* has the fewest number of setae on the genae with most individuals having two or three; however it is not unusual to find individuals with between 0 and two and less often, individuals with as many as seven or eight. Rumpp (in litt.) both utilized and later questioned the taxonomic value of genal setae for subspecific determination; we, however, found this character to be of taxonomic value as this subspecies consistently had fewer setae than other populations (Table 2). Individuals of *C. d. meriwetheri* often have the anterior central area of the labrum projecting further, resulting in a smaller length to width ratio (Fig. 19C).

Distribution. East of the Cascade Mountains in Washington and British Columbia. This species has not been recorded from neighboring Oregon. In September 2000, MGK surveyed several sites in Umatilla Co., Oregon, north west of Milton-Freewater but was unable to locate any adults.

Etymology. This subspecies is dedicated to Meriwether Lewis (1774-1809), leader of the Lewis and Clark Expedition (1804-1806) which was the first American expedition to the Pacific Coast, the final leg of which was along the Columbia River in present day Washington.

Remarks. *Cicindela d. meriwetheri* is the most geographically isolated subspecies. The validity of this isolation is reinforced by the nested geographic haplotype analysis that indicates *C. d. meriwetheri* as the most separately exclusive from all included taxa. This separation could be attributed to long distance colonization possibly coupled with subsequent fragmentation, or past fragmentation followed by range expansion with long-distance movement. Additionally, the closest sister taxon to *C. d. meriwetheri* was *C. d. montevolans* rather than nearest geographically adjacent subspecies *C. d. decemnotata*.

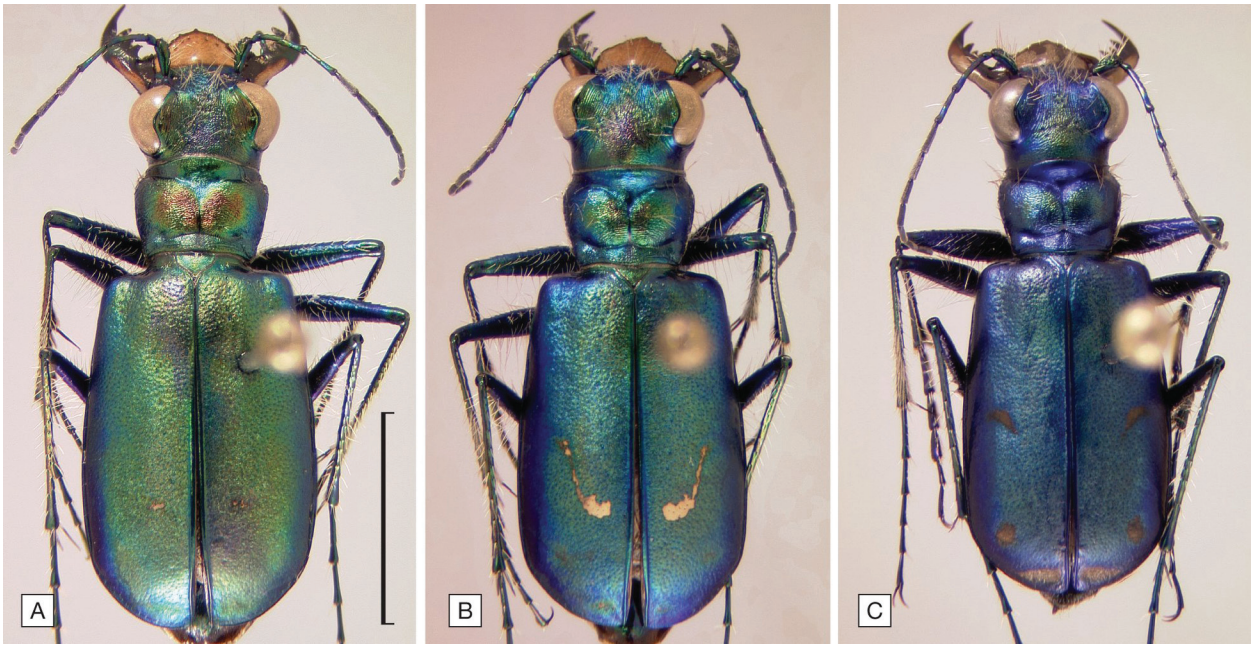

Figure 7. *Cicindela d. bonnevillensis*. A. Female, "UT: Tooele County: Dugway Proving Grounds, 10-V-2009" (MGKC). B. Female, "UT: Tooele County: Dugway Proving Grounds, 10-V-2009" (MGKC). C. Male, "UT: Tooele County: Delle, 9-X-2010" (MGKC). Scale bar = 5mm for all.

cicindela decemnotata bonnevillensis Knisley and Kippenhan, new subspecies
(Fig. 7A-C, 8A-B, 11A, 19D, 23)

Identification. Immediately recognized by the greatly reduced elytral maculation, absence of the humeral and posthumeral dots, green to blue dorsal coloration, largest average length, and distribution restricted to the Tooele Co., Utah.

Description. *Differs from the nominotypical subspecies in*:

Head. Green to blue to blue-purple, specimens with lighter green coloration often have yellow-green reflections.

Thorax. Green to blue to blue-purple, occasionally with yellow-green reflections on disc.

Elytra. Lateral margins dark green to purple, transitioning to green to blue to blue-purple to purple, specimens with lighter green coloration often have yellow-green reflections; elytral maculation consists of a reduced middle band, most often only transverse portion from knee to foot, narrow in width, occasionally absent, subapical dot absent to small, apical dot most often reduced, rarely absent. Elytral sculpture with small, deep punctures with small granules.

Abdomen. Dark green to blue.

Legs. Femur, tibia and tarsomeres green to purple, occasional with yellow-green reflections.

Length. Male 11.50mm–13.10mm (mean=12.47mm, n=12); female 12.20mm–13.90mm (mean=13.00mm, n=12).

Type Locality. Utah, Tooele Co., playa south of Delle.

Type material. Holotype: Male labeled: "UTAH: Tooele County: Delle, 1/4 S., 1/4-1/2 W. of Gas Station. Roads in sagebrush, 40°45.6' N • 112°47.7' W, 31-III-2011 Kippenhan col." [typeset white label with black border]. "HOLOTYPE, *Cicindela decemnotata bonnevillensis* Knisley and Kippenhan" [typeset red label with black border printed on white paper]. Depository: MCZC.

Allotype. Female labeled: "UTAH: Tooele County: Delle, 1/4 S., 1/4-1/2 W. of Gas Station. Roads in sagebrush, 40°45.6' N • 112°47.7' W, 31-III-2011 Kippenhan col. " [typeset white label with black

Figure 8. *Cicindela d. bonnevillensis*. A. and B. Habitat and adults: Delle, Tooele Co., UT, 31-III-2011.

border]. "ALLOTYPE, *Cicindela decemnotata bonnevillensis* Knisley and Kippenhan" [typeset red label with black border printed on white paper]. Depository: MCZC.

Paratypes. "USA: UTAH: Tooele County: Delle, 1/4 S., 1/4-1/2 W. of Gas Station. Roads in sagebrush, 40°45.6' N • 112°47.7' W, 31-III-2011 Kippenhan col." [typeset white label with black border] (1m, 2ff, AMNH; 2mm, CSUC; 1f, MCZC; 13mm, 13ff, MGKC; 1m, 1f, MTEC; 2mm, 1f, USNM). "USA: UTAH: Tooele County: Playa 0.25 mi S. of Delle, 40°45.476' N • 112°47.13' W, 9-IX-2010 M & S Kippenhan" [typeset white label with black border] (1f, AMNH; 1m, CSUC; 1f, MCZC; 1m, 3ff, MGKC; 1f, USNM). "Tooele Co., UT, 15 April 2005, B. Kondratieff, R. Baumann, I-80, Delle" [typeset white label] (2mm, 2ff, CSUC). "Tooele Co., UT, 4 May 2005, J. Schmidt, J. Owens, I-80 Delle Exit, Behind gas station, bare, between sage" [typeset white label] (1f, CSUC). "UT, Tooele Co., Dugway Proving Grd, NW of Wig Mt, 4-X-07, 40.36359; 113.09041, Leg. C. B. Knisley" [typeset white label] (7mm, 8ff, CBKC). "Little Granite Mt.; Tooele Co. Ut., IX-28-1954; J L Eastin, Collector" [typeset and hand printed white labels] (1m, CSUC). " Tooele Co. Ut., IX-27-1954; Little Granite Mt.; J L Eastin, Collector" [typeset and hand printed white labels] (1f, CSUC)."UT, Tooele Co., Dugway Proving Grd, E of Little Granite Mt, 40.11.603,112.48.074, 21-IV-07. C.B. Knisley" [typeset white label] (14mm, 1f, CBKC). "UTAH, Tooele Co., S.E. edge of Dugway Dunes, Dugway Proving Ground, 19 Oct. 1994, R. L. Johnson" [typeset white label] (9mm, 11ff, BYUC). "UT- Toole (sic!) Co., 1/2mW-Delle, D, Brzoska 23-IV-1983" [typeset and hand printed white label] (14mm, 14ff, DWBC). "USA - UT - Tooele Co., I-80 - Delle, D. Brzoska 25-IV-1982" [typeset white label] (1m, 1f, DWBC). All paratypes labeled: "PARATYPE, *Cicindela decemnotata bonnevillensis* Knisley and Kippenhan" [typeset red label with black border printed on white paper].

Additional Material Examined.

USA: UTAH: Tooele Co.: Delle, 1/4 S., 1/4-1/2 W. of Gas Station. 31-III-2011" (20, MGKC). 1/2 mi. S Delle, 11-V-1974 (1, MGKC). Little Granite Mt., 28-IX-1954 (1, MGKC). 1/2 mi E Delle, 23-IV-1983 (6, DWBC). Delle, 7-IX-72 (3, USNM). Dugway Proving Ground (DPG), dunes west of English Village, 18-V-2005 (1, BYUC). DPG, East Dugway dunes 23-II-95 (1, BYUC). DPG, 4 mi NE Camelback Mt., 5,12-IV-54 (2, BYUC). DPG, Flat SW of Camelback Mt., 12-IV-1994 (2, BYUC). DPG, dunes N of Little Davis Mt., 18-V-2005 (2, BYUC). DPG, NE edge Little Davis Mt., 21-III-94 (7, BYUC). DPG, Black Pond, 20-X-1994 (1, BYUC). SW end Cedar Mt., 24-II-1954, 26-X-1953 (2, BYUC), 25-X-1993 (4, BYUC). Granite Peak Foothills, DPG, 27-II-1997 (2, MGKC; 1, BYUC). End Camelback Mt., 27-IV-53 (1, AMNH). Iosepa, 14-X-1933 (1, USUC). 0.5 mi E. Delle, 24-IX-77 (1, UMNH), V-4-53 (1, AMNH; 1, BYUC). Little Granite Mt.(=5 mi Hill. S side of Stark Rd.), just N Davis Mt. Little Granite Mt. 24-II, 5-III, 7-IV, 27-IX-54 (1, BYUC). Skull Valley, 14-IV-36, 3-X-42 (1, RHC), 15-IV-71 (1, AMNH), 14-V-72 (1, AMNH).

Variation. Specimens of this subspecies exhibit greatly reduced elytral maculation. In a series of 62 specimens collected on the same date, five lacked all traces of maculation, 14 had vestiges of the middle band, with most reduced to traces of the foot only, 18 had vestiges of the middle band and subapical dot only, three had vestiges of the middle band and apical dot only, one had only the subapical dot, three had the subapical and apical dots, one had only the apical dot, one had vestiges of the middle band and apical dot, and 15 had the middle band, subapical and apical dots. Only one of 62 specimens had a small posthumeral dot and none had the humeral dot. Collected in late March, this series had two specimens with blue dorsal coloration, the remainder ranged from bright to dark green. This is in contrast to a series of ten specimens collected in October which were dark blue to purple (Fig. 7C) and appeared black when encountered in the field (MGK, pers. observation). Specimens with lighter green dorsal coloration often have faint copper reflection in the basodiscal area in a manner similar to the nominotypical subspecies. Genae setae varied from 7 to 21 but most specimens ranged from 11 to 16.

Distribution. This subspecies occupies the western border of the ancient Lake Bonneville in the western Utah desert in Tooele Co. at lower elevation (<1676m). The type locality is characterized by noticeable deposits of saline, a characteristic not usually encountered with the other subspecies.

Etymology. This subspecies is named in honor of the Pleistocene Lake Bonneville. This lake existed from 32 to 14 thousand years ago and at its peak was 523km long and 217km wide extending south

to Delta and Milford, Utah west to the eastern edge of Nevada and north to south-central Idaho. This ancient lake included present day Great Salt Lake, Sevier Lake and covered most of Utah below 1551m elevation.

Remarks. This subspecies is geographically separated from other subspecies of *C. decemnotata* by the Great Salt Lake to the north, several mountain ranges to the east, and lowland deserts to the west. Populations to the south and southeast of this subspecies, primarily from Beaver, Millard, and Sevier counties have reduced maculations with mean maculation scores intermediate between *C. d. bonnevillensis* and *C. d. decemnotata* in eastern Utah (Fig. 24).

Cicindela decemnotata montevolans Knisley and Kippenhan, new subspecies
(Fig. 9A-D, 11B, 23)

Identification. This subspecies is distinguished by the combination of red-purple dorsal coloration, elytra without contrasting marginal color, and reduced elytral maculation.

Description. *Differs from the nominotypical subspecies in:*

Head. Red-purple to olive-green, genae, anterior margins of eyes and clypeus green to blue-green; antennomeres 1-4 with varying amounts of dark green, occasionally with red reflections.

Thorax. Margins bright green to dark green, disc red-purple to red-purple to olive-green.

Elytra. Coloration red-purple to green to olive-green, lateral margins occasionally bright orange-red to red on red-purple individuals, green on olive-green individuals; red-purple individuals often have varying amounts of green in basodiscal area; maculation consists of remnants of the middle band, occasionally absent, subapical dot, apical dot and occasionally a very small posthumeral dot. Elytral sculpture with small, shallow to deep punctures with medium to small granules, occasionally granules absent.

Abdomen. Dark green to blue-green.

Legs. Femur, tibia and tarsomeres green, often with yellow green to red reflections.

Length. Male 11.70mm–12.50mm (mean=11.90mm, n=10); female 12.30mm–13.50mm (mean=12.90mm, n=6).

Type Locality. Utah, Cache-Rich Co. line at Hwy 89.

Type material. Holotype: Male labeled: "UT, Cache Co., 1.2 mi S Hwy 89 @ Cache-Rich Co. line, 27-VI-05 C.B. Knisley" [typeset white label] "HOLOTYPE *Cicindela (s. str.) decemnotata montevolans* Knisley and Kippenhan" [typeset red label with black border printed on white paper]. Depository: MCZC.

Allotype. Female labeled: "UT, Cache Co., 1.2 mi S Hwy 89 @ Cache-Rich Co. line, 27-VI-05 C.B. Knisley" [typeset white label] "ALLOTYPE *Cicindela (s. str.) decemnotata montevolans* Knisley and Kippenhan" [typeset red label with black border printed on white paper]. Depository: MCZC.

Paratypes. "UT, Cache Co., 1.2 mi S Hwy 89 @ Cache-Rich Co. line, 27-VI-05 C.B. Knisley" [typeset white label] (8mm, 2ff, CBKC; 1m, USNM). "UT, Cache Co./ID, Franklin, Co., Swan Flat Rd. State Line, 41.59.36, 111.29.13; 2544m, 31-VIII-06; Col. C.B. Knisley" (1m, 6ff, CBKC). "USA: UT: Cache County, Swan Flat Rd. .5 mi. N.W., Hwy 89, 7704' camp area, 41°57.44'N • 111°29.25'W, 19-V-2007 M Kippenhan" [typeset white label with black border] (3mm, 2ff, MGKC). "USA: UT: Cache County, Hwy 89 .4 mi. West of, Swan Flat Rd. 7557' trail, 41°57.12'N • 111°29.29'W, 19-V-2007 M Kippenhan" [typeset white label with black border] (3mm, 1ff, MGKC). "USA: UT: Cache County, Swan Flat Rd. .4 mi. N., Hwy 89 8320' dirt road, 41°59.61'N • 111°29.24'W, 19-V-2007 M Kippenhan" [typeset white label with black border] (3mm, MGKC). "USA: UT: Cache Co., Swan Flat Rd. 0.4 mi., W. Hwy 89, Logan Cyn., 41°57.1'N • 111°29.5'W, 19-VI-2010 Kippenhan" [typeset white label with black border] (1f, CSUC; 2m, 1f, MGKC). "USA - UT - Cache Co., Hwy 89 - 1 m E. - Bear, Lake Summit, D. Brzoska 23-V-1992" [typeset white label] (3mm, 3ff, DWBC; 1m, MGKC). "UT- Cache Co., Hwy 89 1m W-Bear L. Summit, D. Brzoska 23-VI-1984" [typeset and hand printed white label] (2ff, AMNH; 1m, CSUC; 7mm, 7ff, DWBC; 1m, MCZC; 1m, 1f, MGKC; 1f, USNM). "UT, Cache Co., Beaver Cr. 7000 ft, VIII-3-1972, G. E. Bohart" [typeset white label] (4mm, USUC)."UTAH Cache Co., Tony Grove, 14 Jul 1982, C. R. Nelson"

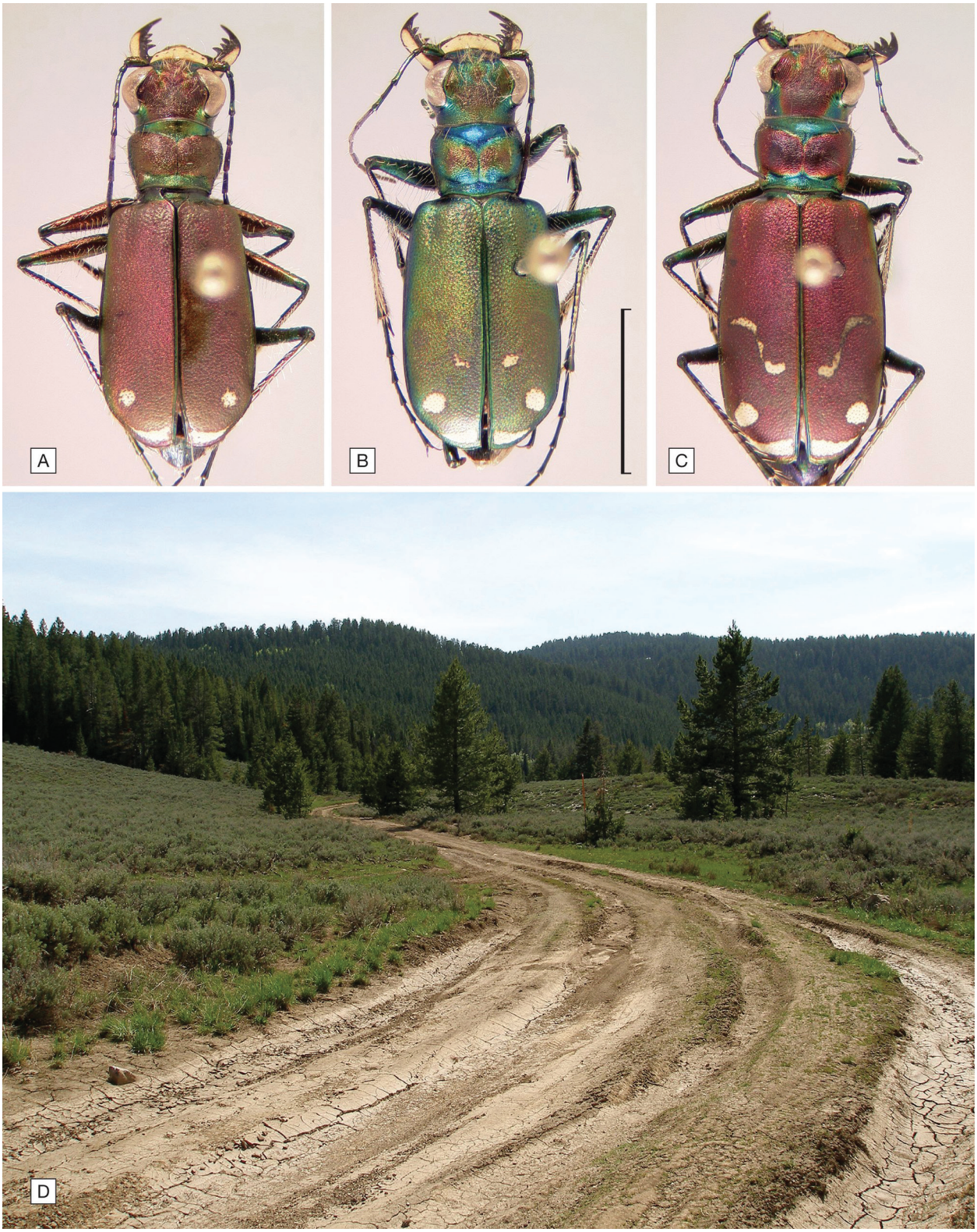

Figure 9. C*icindela d. montevolans*. A. Male, "UT: Cache Co, Swan Flat Rd. W of Hwy 89, 19-V-2007" (MGKC). B. Male, "UT: Cache Co, Swan Flat Rd. W of Hwy 89, 19-V-2007" (MGKC). C. Female, "UT: Cache Co, Swan Flat Rd. W of Hwy 89, 19-V-2007" (MGKC). D. Habitat: south side of Hwy 89 west of Swann Flat Rd, Cache Co., UT, May 2007. Scale bar = 5mm for A–C.

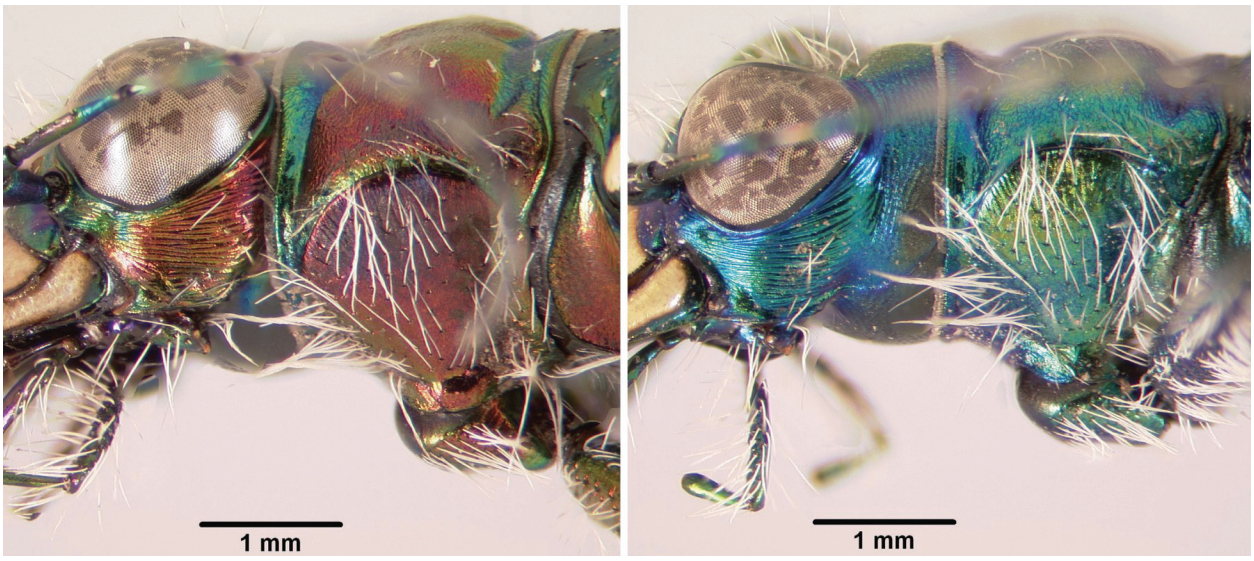

Figure 10. Proepisternal color. A. *Cicindela d. decemnotata*, male, "ID: Freemont Co., Targhee Nat. Forrest, 18-V-2007" (MGKC). B. Cicindela d. decemnotata, male, "MT: Broadwater Co., SE of Canyon Ferry Res., 7-V-2007" (MGKC)

[typeset and hand printed white label] (2ff, BYUC). "Bear Lake Valley, West Side .; G. Lynn Hayward, collector; BYUC 9715" [three typeset white labels] (1f, BYUC). "UT. Cache Co., Franklin Basin, VII-25-71, G. E. Bohart" [typeset white label] (1f, USUC). "UTAH Cache Co, Franklin Basin, 6 July 1972, G. E. Bohart" [typeset white label] (2ff, USUC). "UTAH Cache Co., Franklin Basin, 30 Jul 1982, C.R. NELSON" [typeset white label] (1m, MTEC)."Rich Co. Utah, 9-10-1967, Coll. K.J. Capelle" [typeset and hand printed white label] (1m, USUC). "IDAHO, Liberty Canyon, 11 June 1967; D.L. Parker" [two typeset and hand printed labels] (1m, 3ff, USUC). All paratypes with label: "PARATYPE *Cicindela (s. str.) decemnotata montevolans* Knisley and Kippenhan" [typeset red label with black border printed on white paper].

Additional Material Examined.

USA: UTAH: Box Elder Co.: 4-VII-65 (2, USUC). Cache Co.: . Hwy 89, 1 mi W Bear Lake Summit, 23-VI-1984, 24-VI-1985 (36, DWBC). Logan Canyon, White Pine Trail, 30-VI-1985 (1, CIDC). White Pine Trail, 30-VI-85 (1, NYC). North Logan, VII-81 (2, NYC), Logan Canyon, 16-V-1987 (10, AMNH). Logan Canyon, Tony Grove, 8-V-87 (1, NYC). Allen Canyon, 10-VIII-1961 (1, USUC). Franklin Basin, 25-VI-1971 (13, USUC). Green Canyon, Logan, X-1958 (1, USUC). Logan, 16-VI-1948 (1, USUC). Rich Co.: Limber Pine, 6-X-84 (1, CIDC). Cottonwood Canyon, SW of Laketown, VIII-25; 10-IX-67 (2, USUC).

IDAHO: Bear Lake Co.: Bloomington Lake, 6500' (Leffler 1979). Liberty Canyon, 11-VI-61 (4, USUC).

Variation. For the classification of color, the dorsal coloration of this subspecies is considered red-purple, but the exact hue ranges from red-brown to red-purple. This color combination is a result of a red or dark green base with green punctures. When rotated under artificial light, red-purple individuals exhibits an interesting range of color that often appears either brighter red or purple. This color variation is created by varying amounts of secondary colors, especially in the baso-lateral portions of the elytra. Green individuals (Fig. 9B) are seldom encountered. Interestingly, in a series of seven specimens collected in late August the dorsal coloration is either dark purple-green, dark purple-brown or dark green-purple, but this combination of colors has not been seen in individuals collected in the summer months and may be due to adults emerging in late August and over-wintering, to re-emerge in the following summer. In a comparison to the other subspecies of *C. decemnotata*, the elytra of *C. d. montevolans* often appear duller and may be a result of deeper elytral sculpture. Considering the limited geographic distribution of this subspecies, individuals exhibit considerable variation in the elytral sculpture. Most specimens have small, shallow punctures with small granules; however, individuals

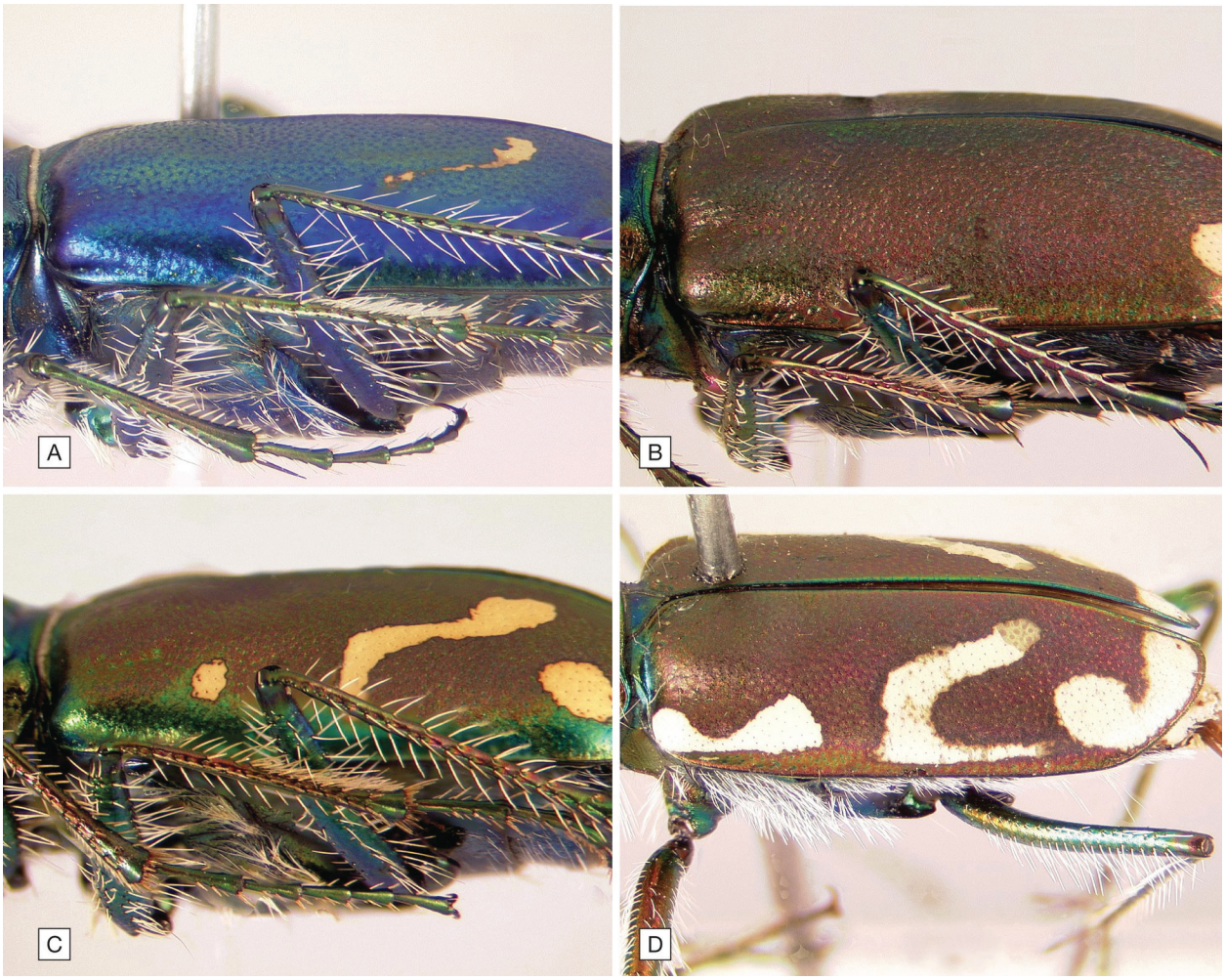

Figure 11. Elytral margin color and maculation. A. *Cicindela d. bonnevillensis*, female, "UT: Tooele County: Dugway Proving Grounds, 10-V-2009" (MGKC). B. *Cicindela d. montevolans*, female, "UT: Cache Co, Swan Flat Rd. W of Hwy 89, 19-VI-2010" (MGKC). *C. Cicindela d. decemnotata*, female,"MT: Broadwater Co., SE side Canyon Ferry Res., 7-V-2007" (MGKC). *D. Cicindela d. decemnotata*, male, "MT: Broadwater Co., Centennial Valley, 27 May 1999" (MGKC).

with larger granules are often present. The elytral maculation of this subspecies is most similar to *C. d. bonnevillensis*. None of the specimens examined has a humeral dot and only two of 16 have a small posthumeral dot. The middle band is most often absent, occasionally being represented by a transverse dash or remnants of the foot, or, if complete, then very thin. The subapical and apical dots are always present, from small to medium in size and most often widely separated. This subspecies is notable in that the number of genal seta is intermediate (mean of 6, range of 2-14) between the nominotypical subspecies and *C. d. meriwetheri* (Table 2).

Distribution. This subspecies occurs only in the Bear River Mountain Range from extreme southeastern Idaho south into northeastern Utah. Most populations are found at over 2,438m in the area of Bear Lake Summit, and as low as 2,072m south of the summit. More collecting is needed, especially in Franklin Co., Idaho and the southern portion of the Bear River Mountain Range to more accurately define its range.

Etymology. The name for this subspecies is derived from the Greek *monte* for mountain and *volans* for flyer, in reference to its high altitude distribution.

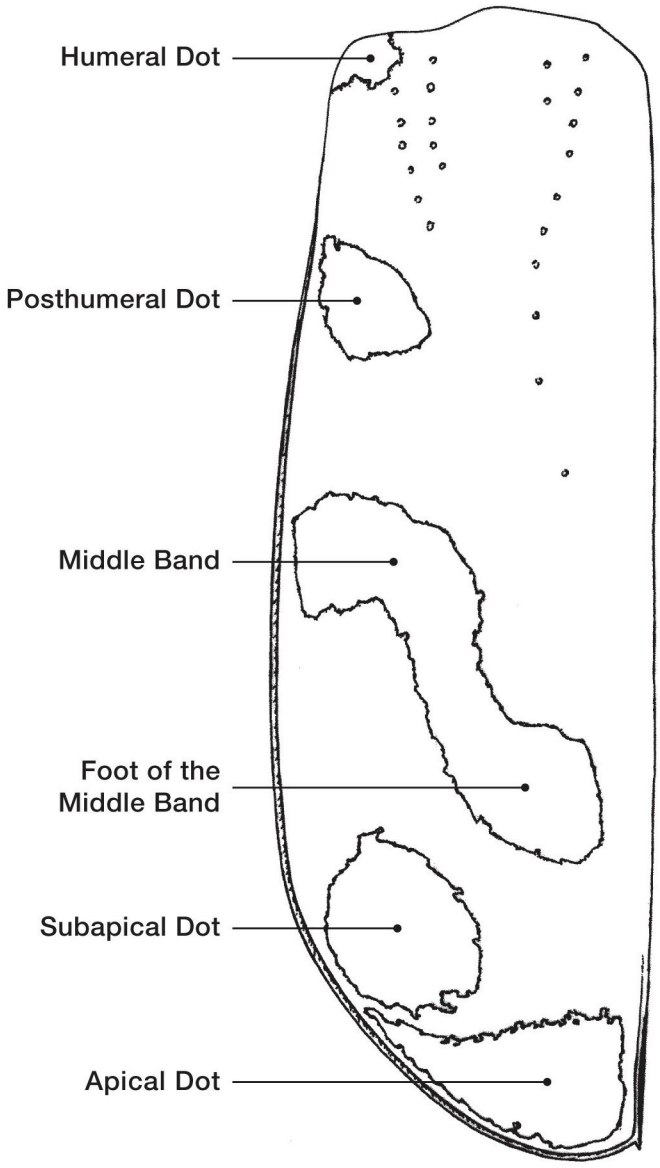

Figure 12. Components of elytral maculation.

Remarks. This subspecies is interesting in the fact that the dorsal coloration of most individuals is similar to select populations of the nominotypical subspecies from Idaho, while the elytral maculation pattern is similar to that of *C. d. bonnevillensis*, and as a result, Rumpp (1988) considered it to be an intergrade population. Based on the isolated high altitude location and the fact that the closest population of *C. d. bonnevillensis* is approximately 175km to the southwest and with the Great Salt Lake providing a barrier between the populations, we consider it to be a distinct subspecies. Three individuals from Caribou Co., Idaho (Fig. 1D) have maculation intermediate between *C. d. decemnotata* and *C. d. montevolans* and may represent an intergrade between the two subspecies. In addition, specimens from Bonneville Co., Idaho are muddy dark green and with thinner elytral maculation and may also represent an intergrade with the nominotypical subspecies.

Results of Molecular analysis

The entire *cob* and *cox1* dataset (23 terminals) of 1157 characters gave 19 variable but parsimony-uninformative autoapomorphic characters (1.64%) and 17 potentially parsimony-informative characters (1.5%). The partition homogeneity test revealed that the *cob* and *cox1* data sets revealed no statistically significant incongruence (P=0.56), and the two genes were combined in one analysis (Bull et al. 1993). Alignments of data matrices were unambiguous as the sequences exhibited no marked variation in amplicon length. Chi-square test of homogeneity of base frequencies for these taxa revealed no significant incongruence between *cob* and *cox1* (Chi-square=2.750533; df=72; P=1.0). The total range of interpopulational pairwise sequence divergence within *C. decemnotata* for the combined *cob* and *cox1* dataset was shallow at 0.2-1.1%. Intraspecific divergence range was not readily correlated to number of haplotypes observed per population or the geographic distance between populations. The range of interspecific pairwise sequence divergence between *C. decemnotata* and the sister species of *C. limbalis* and *C. splendida* for the total dataset was also shallow at 0.3-1.5%.

Genetic analyses revealed that all morphologically defined subspecies within *C. decemnotata* and sister species could be diagnosed either by 1-4 uniquely derived nucleotide polymorphisms (*C. d. montevolans, C. d. meriwetheri,* and the union of *C. limbalis* and *C. splendida*), or a unique combination of nucleotide polymorphisms (*C. d. decemnotata, C. d. bonnevillensis (*Table 3). Statistical parsimony analysis recovered an inferred haplotype nesting design of 13, 6, 3, 2, and 1 nesting groups on the 1-to-5-step hierarchical nesting levels (Fig. 20). Nested Geographic Clade Analyses revealed significant associations for 4 of the 13 total nesting groups. All included taxa coalesced into a single haplotype network at the 5-step level which exhibited significant structure rather than purely random distribution across geographic distance (5-step NGCA Chi-square=1.000; $P<10^{-4}$). Nested Geographic Clade Analy-

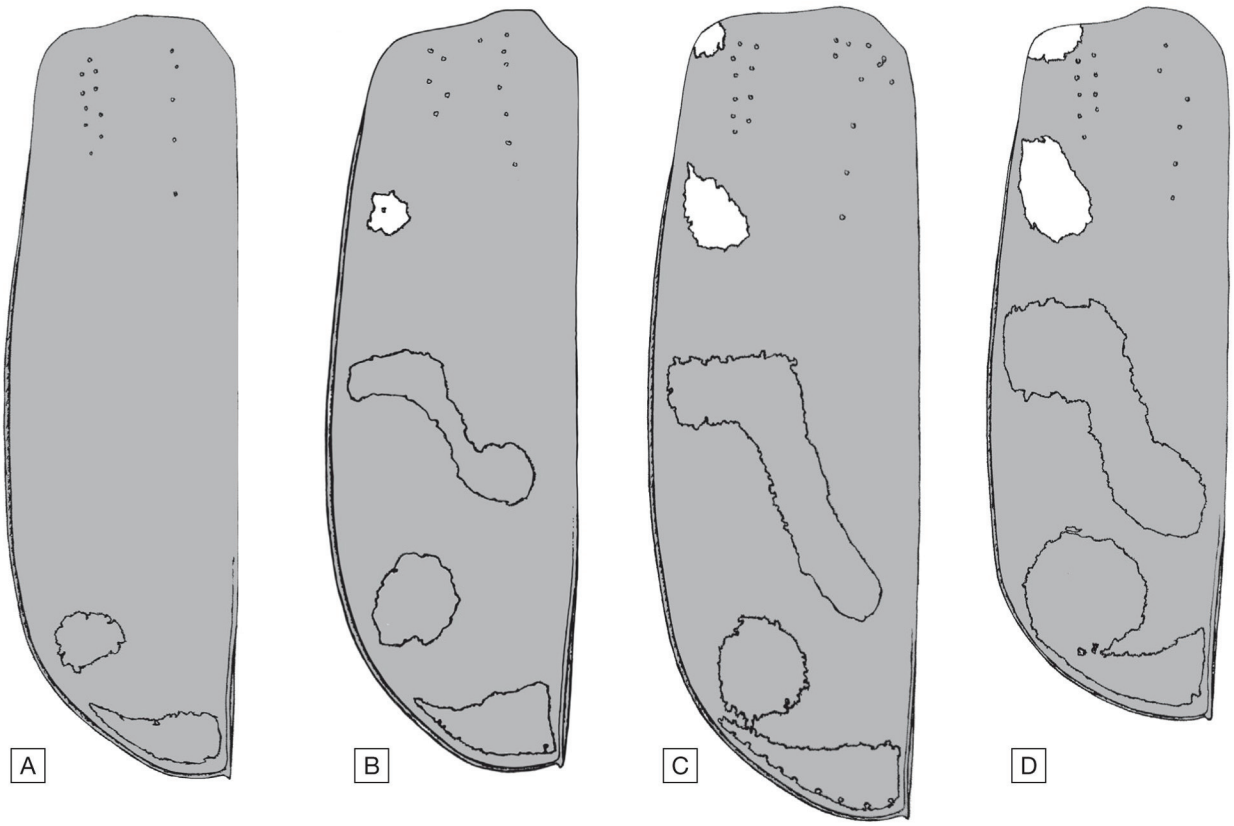

Figure 13. Humeral lunule grading system. 0 to 3 refers to increasing size of humeral lunule: A. 0 (absent). B. 1. C. 2. D. 3 (largest).

sis could attribute this nonrandom separation of groups to long distance colonization possibly coupled with subsequent fragmentation, or past fragmentation followed by range expansion with long-distance movement.

Phylogenetic reconstructions using parsimony criteria, Bayesian inference, and maximum likelihood were extensively congruent; differing mainly in resolution of sister relationships within the groups of sister species and subspecies of *C. decemnotata* (Fig. 21). Parsimony based reconstruction recovered 31 equally parsimonious trees of 42 steps in length with Consistency Index (CI) of 0.857, Retention Index (RI) of 0.875, Rescaled Consistency Index (RC) of 0.750, Homoplasy index (HI) of 0.143, and Goloboff-fit (G-fit) of -15.600 (Fig. 22A). Bayesian Inference recovered a consensus tree of length 47 with best state log likelihood score (ln L) of 1885.94 and parametric CI=0.766, RI=0.771, RC=0.590, HI=0.234, and G-fit= -14.779 (Fig. 21B). Bayesian Inference coalesced by the 100,000th generation. Maximum likelihood reconstruction recovered a best tree with a log likelihood score (ln L) of -1851.0607 and a proportion estimated invariant (invariable) sites (I) of 0.8655. The later ML tree retrieved parsimony scores of length 42 with parametric scores of CI=0.857, RI=0.875, RC=0.750, HI=0.143, and G-fit= -15.600 (Fig. 22C).

Collective comparison of nonparametric bootstrap, jackknife values, and posterior probabilities across all phylogenetic reconstructions recovered variable support for the monophyly of the four subspecies groupings postulated by morphology (Fig. 21). Cladisitic relationships among *C. decemnotata* were not structured by geographic distance alone. Populations of *C. decemnotata* from Utah corresponding to three separate morphosubspecies were recovered in separated clades for all phylogenetic reconstructions and retrieved significant support for reciprocal monophyly under maximum parsimony (T-PTP *L=-6, ΔL=-13 to -57, P=10^{-4}). Likewise, reciprocal monophyly of four separate subspecies of *C. decemnotata* apart from a union of *C. limbalis* and *C. splendida* recovered significant support under maximum parsimony (T-PTP *L=-1, ΔL=-13 to -62, P=10^{-4}).

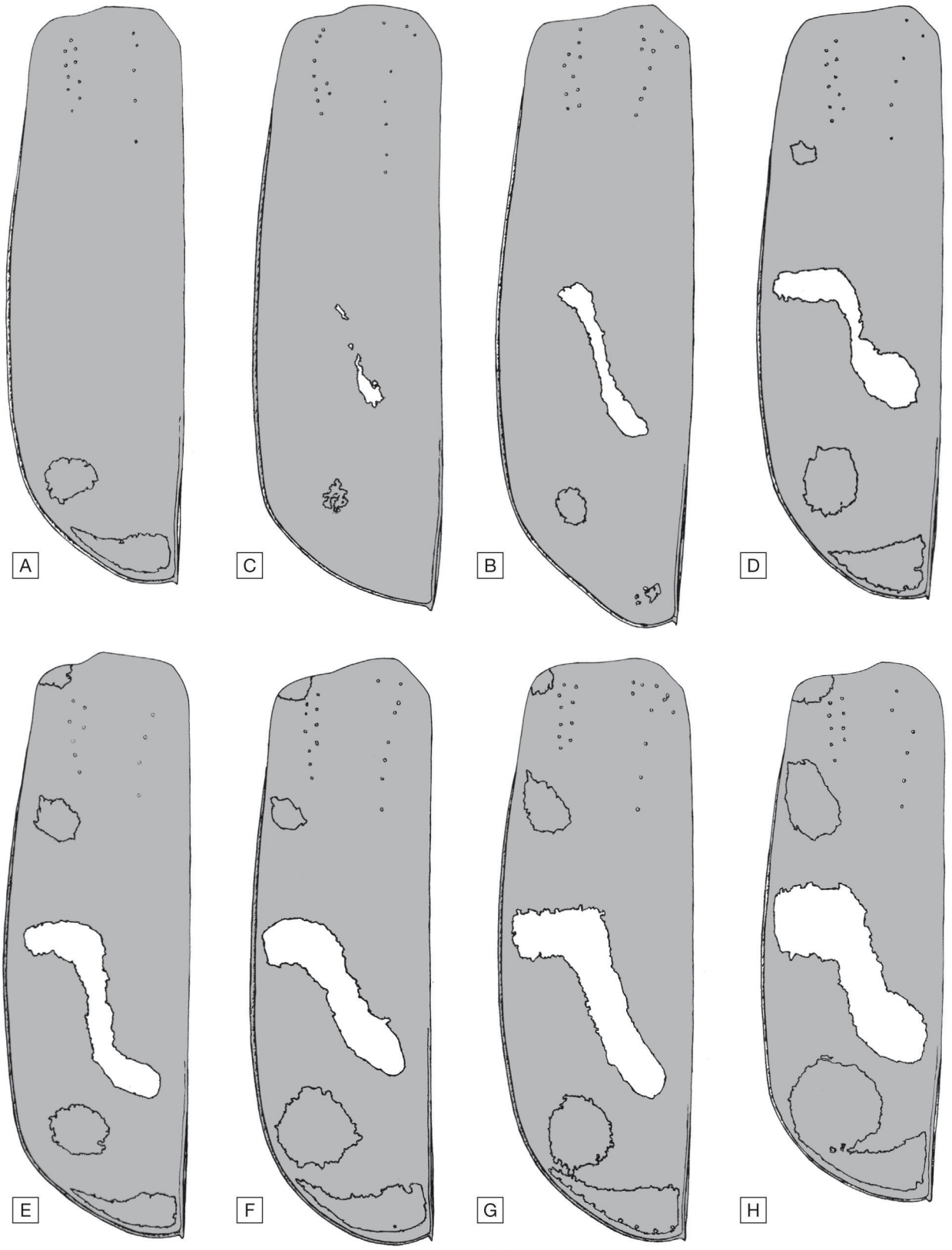

Figure 14. Middle band grading system. 1 to 7 refers to increasing size and completeness of middle band: A. 0 (absent). B. 1. C. 2. D. 3. E. 4. F. 5. G. 6. H. 7 (largest).

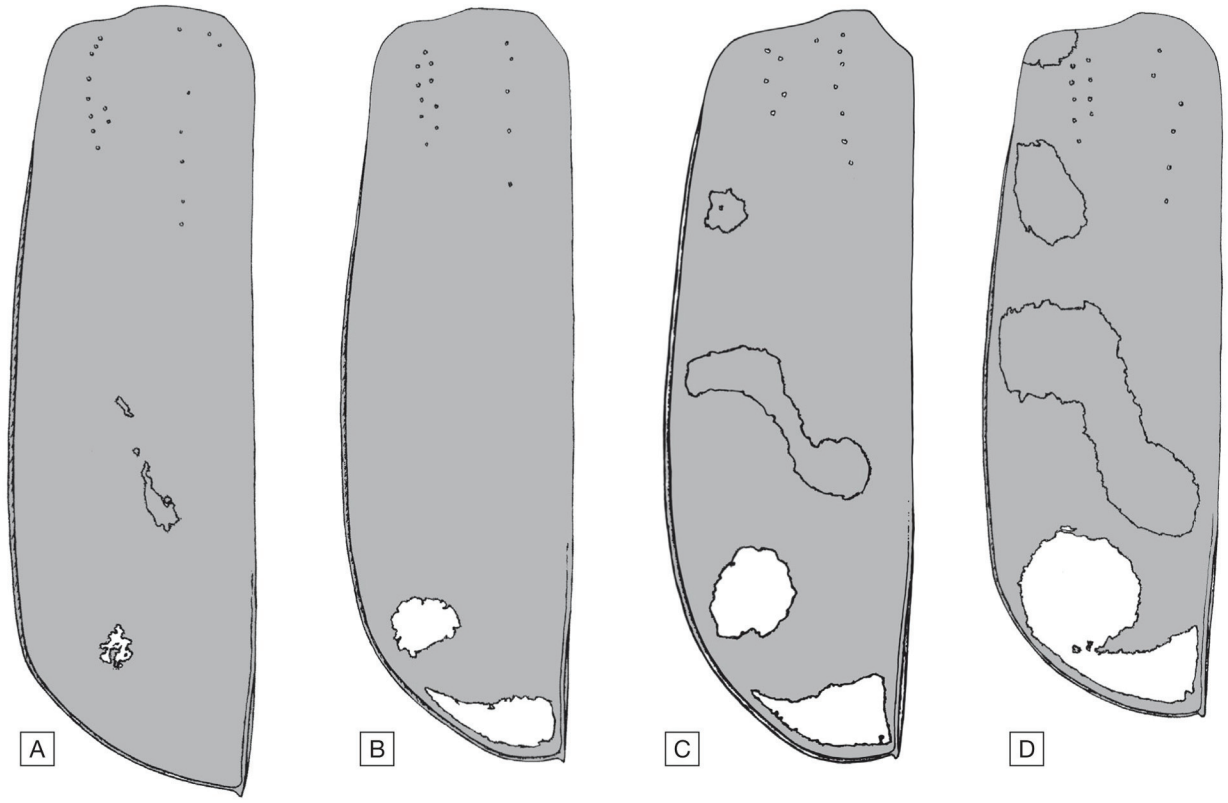

Figure 15. Apical lunule grading system. 0 to 3 refers to increasing size of apical lunule: A. 0 (absent). B. 1. C. 2. D. 3 (largest).

Cicindela d. decemnotata exhibited no nesting using haplotype point of origin in statistical parsimony (Fig. 20). Moreover, *C. d. decemnotata* did not coalesce into an n-step group exclusive from either *C. d. bonnevillensis* or the sister species of *C. splendida* and *C. limbalis.* Haplotypes of nominotypical *C. decemnotata* distributed from Alberta, Wyoming and Utah were aligned together in all phylogenetic reconstructions but without any internal structuring by point of origin (T-PTP *L=-1, ΔL=+6 to -23, *P*=0.052). Similarly, no significant support for internal structure by origin was recovered for nominotypical *C. decemnotata* under maximum parsimony criteria (T-PTP *L=1, ΔL=15 to -49, *P*=0.05941). Monophyly of nominotypical *C. decemnotata* recovered weak branch support (>50) in all phylogenetic reconstructions (Fig. 21). However, constrained-tree topology-dependent permutation tail probability test did recover significant support for reciprocal monophyly of *C. d. decemnotata* from all other included taxa (T-PTP *L=-3, ΔL=-5 to -46, $P=10^{-4}$). Nominotypical *C. decemnotata* could be diagnosed as a plesiospecies from all other included taxa by a unique combination of 8 nucleotide polymorphisms (Olmstead 1995).

Cicindela splendida and *C. limbalis* exhibited no shared haplotypes to any subspecies within *C. decemnotata.* Statistical parsimony analysis retrieved a 2-step nesting group composed of a mixture of *C. splendida* and *C. limbalis* with nominotypical *C. decemnotata* (Fig. 20). Significant associations recovered within this nesting group could be attributed to restricted gene flow or dispersal with some subsequent long distance dispersal (2-step NGCA Chi-square=39.0; $P=3x10^{-4}$). The 3-step nesting group inclusive of *C. splendida* and *C. limbalis,* all nominotypical *C. decemnotata* and *C. d. bonnevillensis* (Fig. 20) could be attributed to long distance colonization possibly coupled with subsequent fragmentation or past fragmentation followed by range expansion with long-distance movement (3-step NGCA Chi-square=1.000; $P=10^{-4}$). Significant support for reciprocal monophyly of *C. splendida* and *C. limbalis* to all *C. decemnotata* was retrieved under maximum parsimony criteria (T-PTP *L=-3, ΔL=-6 to -48, $P=2x10^{-4}$). These sister species to *C. decemnotata*, could be diagnosed (*sensu* Vogler and DeSalle 1994)

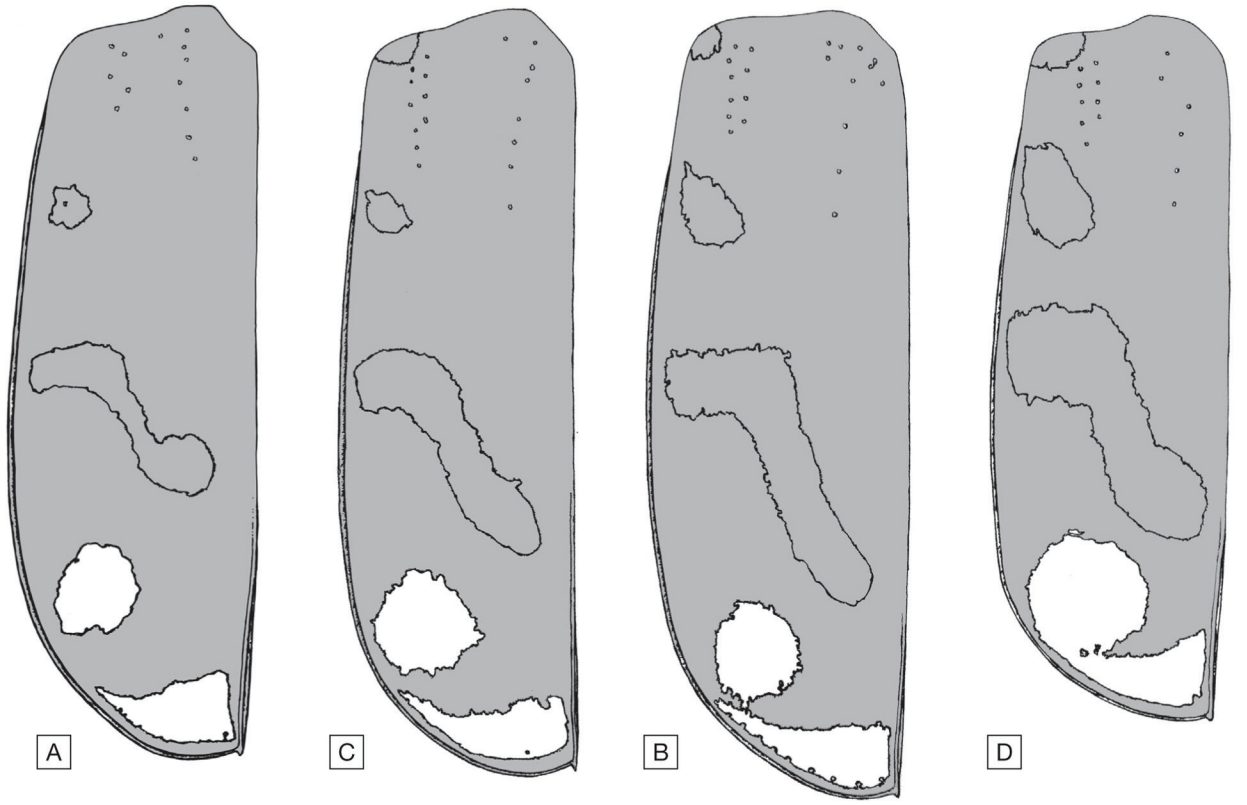

Figure 16. Connection between subapical and apical dots grading system. 0 to 3 refers to connection between sub apical dot and apical dot: A. 0 (widely separate). B. 1 (separate). C. 2 (thin connection). D. 3 (broadly connected).

as an apospecies and separate Evolutionary Significant Unit (ESU) with 1 fixed apomorphic characters state absent from all other sampled taxa (*sensu* Olmstead 1995).

Cicindela d. bonnevillensis formed a cohesive grouping under statistical parsimony at the 2-step level (Fig. 20). The later haplotype network revealed no patterns of geographic distribution significantly different from panmixia under NGCA. Notably, *C. d. bonnevillensis* presented the only example of shared haplotypes between populations sampled in this study. The monophyly of *C. d. bonnevillensis* recovered weak to moderate branch support (>50-53) across all phylogenetic reconstructions (Fig. 21). Additional analyses under maximum parsimony criteria recovered significant support for the reciprocal monophyly of *C. d. bonnevillensis* to all other included taxa was recovered under maximum parsimony criteria (T-PTP *L=-4, ΔL=-12 to -59, $P=10^{-4}$). *Cicindela d. bonnevillensis* could be diagnosed as a plesiospecies from all other included taxa under a unique combination of 8 nucleotide polymorphisms (Olmstead 1995).

Cicindela d. montevolans retained an exclusive haplotype network from all included taxa under the 4-step level of statistical parsimony (Fig. 20). This later haplotype network exhibited significant structure with NGCA and could be attributed to past fragmentation, long distance colonization, or a combination of both processes (4-step NGCA Chi-square=1.000; $P<10^{-4}$). The monophyly of *C. d. montevolans* recovered strong branch supports (92-100) across all phylogenetic reconstructions (Fig. 21). Similarly, maximum parsimony analyses also returned significant support for reciprocal monophyly of *C. d. montevolans* to all other included taxa (T-PTP *L=-2, ΔL=-7 to -51, $P=10^{-4}$). *Cicindela d. montevolans* could be diagnosed as a distinct Evolutionary Significant Unit (ESU) and apospecies through 2 fixed apomorphic characters states absent from all other included taxa (Olmstead 1995; Vogler and DeSalle 1994).

Cicindela d. meriwetheri was exclusive from all included taxa under statistical parsimony to the 5-step level. Significant structure of this haplotype network could be attributed to nonrandom separation of groups to long distance colonization possibly coupled with subsequent fragmentation, or past frag-

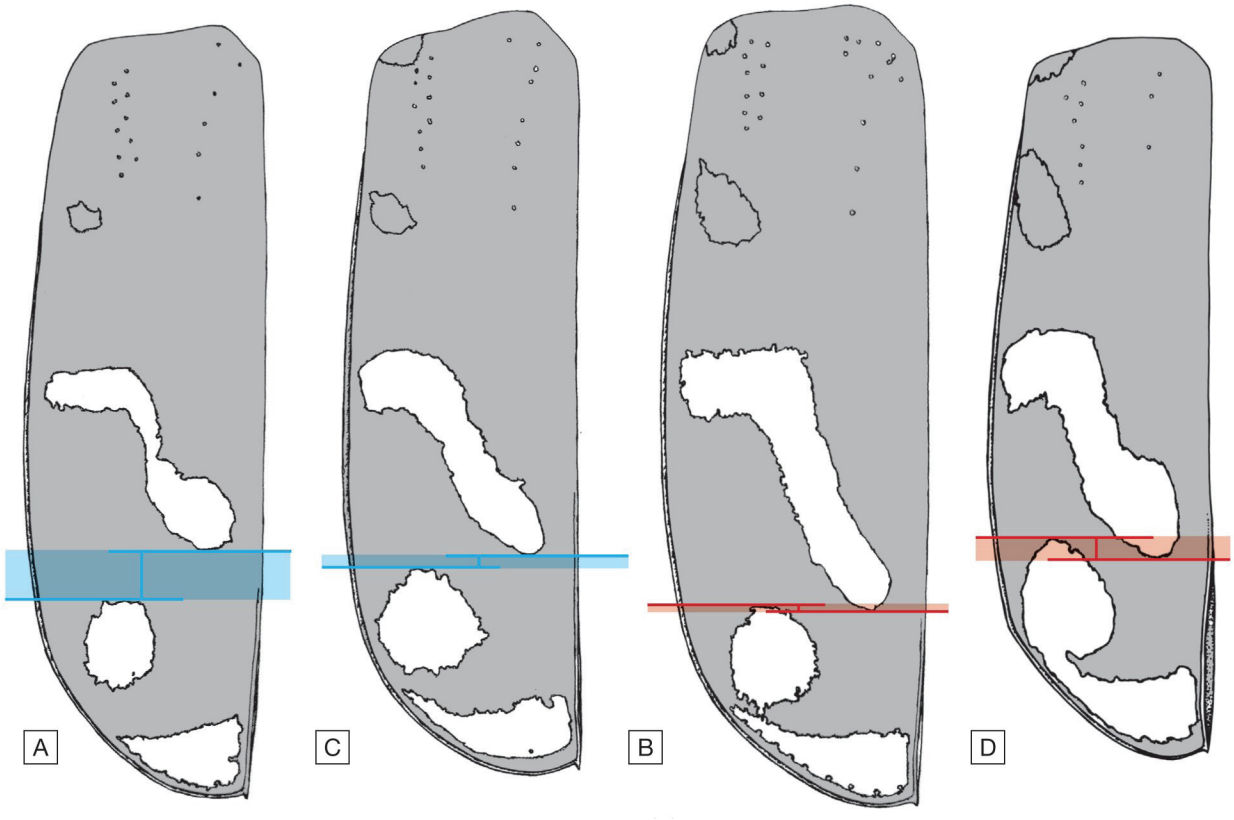

Figure 17. Overlap between middle band and subapical dot grading system. Overlap, or lack of, between apical lunule and post part of middle band; A. 0 (widely separate). B. 1 (separate). C. 2 (narrow overlap). D. 3 (broadly overlapped).

mentation followed by range expansion with long-distance movement (5-step NGCA Chi-square=1.000; $P<10^{-4}$). Notably, the closest haplotype network linkage of *C. d. meriwetheri* to any of the parapatric *C. d. decemnotata* from Alberta was through the 2-step nest inclusive of all *C. d. bonnevillensis*. Strong supports for the monophyly of *C. d. meriwetheri* (branch supports = 97-100) were across all phylogenetic reconstructions (Fig. 21). Additional analyses under maximum parsimony criteria, also retrieved significant support for reciprocal monophyly of *C. d. meriwetheri* against all other included taxa (T-PTP *L=-4, ΔL=-8 to -51, $P=10^{-4}$). *Cicindela d. meriwetheri* could be diagnosed (*sensu* Vogler and DeSalle 1994) as an apospecies and separate Evolutionary Significant Unit (ESU) with 3 fixed apomorphic characters states absent from all other sampled taxa (*sensu* Olmstead 1995).

Discussion

These morphological and molecular analyses illustrate a useful framework for the classification and natural history of *C. decemnotata*. Morphological evidence and collective phylogenetic reconstructions concur in the detection of discrete groups within *C. decemnotata*. Differences in color and microsculpture comparable to those observed in *C. decemnotata* have been used to separate other sister cicindelids to full species; even when the mitochondrial divergences between taxa have not reflected deep partitions (Pearson and Vogler 2001; Vogler et al. 1998). The four defined groupings within *C. decemnotata* are here regarded as subspecies rather than full species on the basis of their collective evidences for reciprocal monophyly, overlapping ranges of intra- and inter-group unweighted pairwise sequence divergence (0.2-1.1%), and short branch lengths relative to phylogenetic relationships recovered between congeneric outgroups. The shallow partitions within *C. decemnotata* are most readily interpreted in the context of a rapid phylogenetic radiation in the recent geological past in the wake of postglacial recession and range expansion across geologically complex terrain (Barraclough and Vogler 2002; Sturmbauer et al.

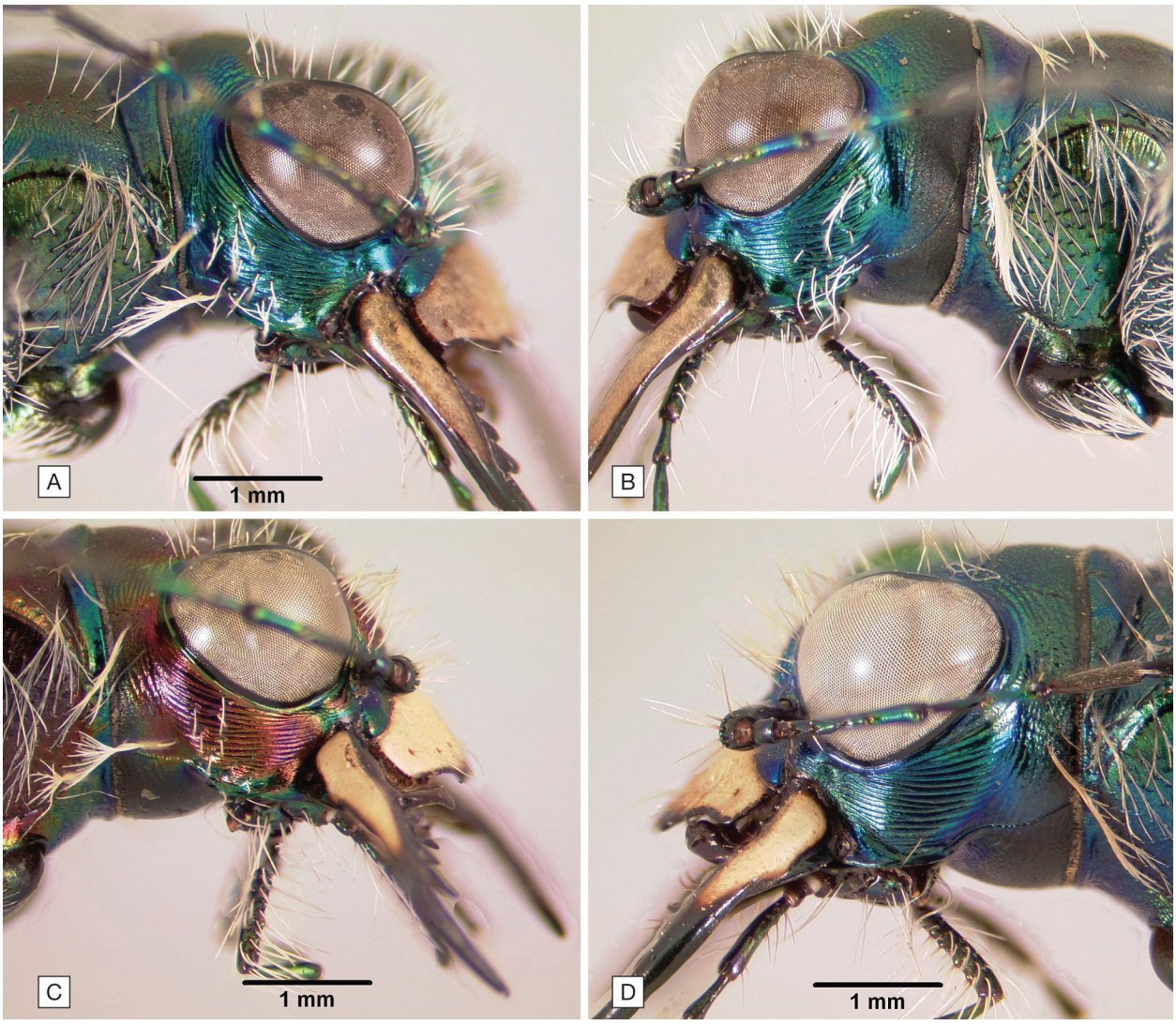

Figure 18. Genal setae. A. and B. *C. d. decemnotata*, male, "MT: Yellowstone Co., NE of Billings, 28-IV-2008" (MGKC). C. *C. d. decemnotata*, male, "MT: Beaverhead Co., Centennial Valley, 12-V-2007" (MGKC). D. *C. d. meriwetheri*, female, "WA: Walla Walla Co., Hwy 12 E of Hwy 730, 3-X-2003" (MGKC).

2003). Other participants in this apparent phylogenetic radiation have included sister species like *C. denverensis*, *C. limbalis*, and *C. splendida* to which *C. decemnotata* is very closely related and recently diverged. Indeed, in such cases of rapid phylogenetic radiation, morphological data may be more appropriate than molecular data for taxonomic delimitation (Tautz et al. 2003).

In the case of *C. decemnotata,* there was collective support for monophyletic groupings corresponding to the four morphologically diagnosed subspecies and shallow hierarchal structure marginally distinguishable from a true polytomy (Vogler et al. 1998). Genetic analyses indicated that all morphologically defined subspecies within *C. decemnotata* and sister species could be diagnosed as apospecies with 1-4 uniquely derived nucleotide polymorphisms (*C. d. montevolans, C.d. meriwetheri,* and the union of *C. limbalis* and *C. splendida*), or as plesiospecies with a unique combination of nucleotide polymorphisms (*C. d. decemnotata, C. d. bonnevillensis*; Table 3; Olmstead 1995). It is expected that the later taxa may yet be diagnosed as apospecies with the inclusion of additional molecular data. Principally, even a single nucleotide polymorphism has been diagnostic in the taxonomic separation of one group from another (Diogo et al. 1999; Goldstein et al. 2003; Sota et al. 2001; Vogler and DeSalle 1994). Three of four morphologically recognized subspecies, namely *Cicindela d. montevolans, C. d. decemnotata,*

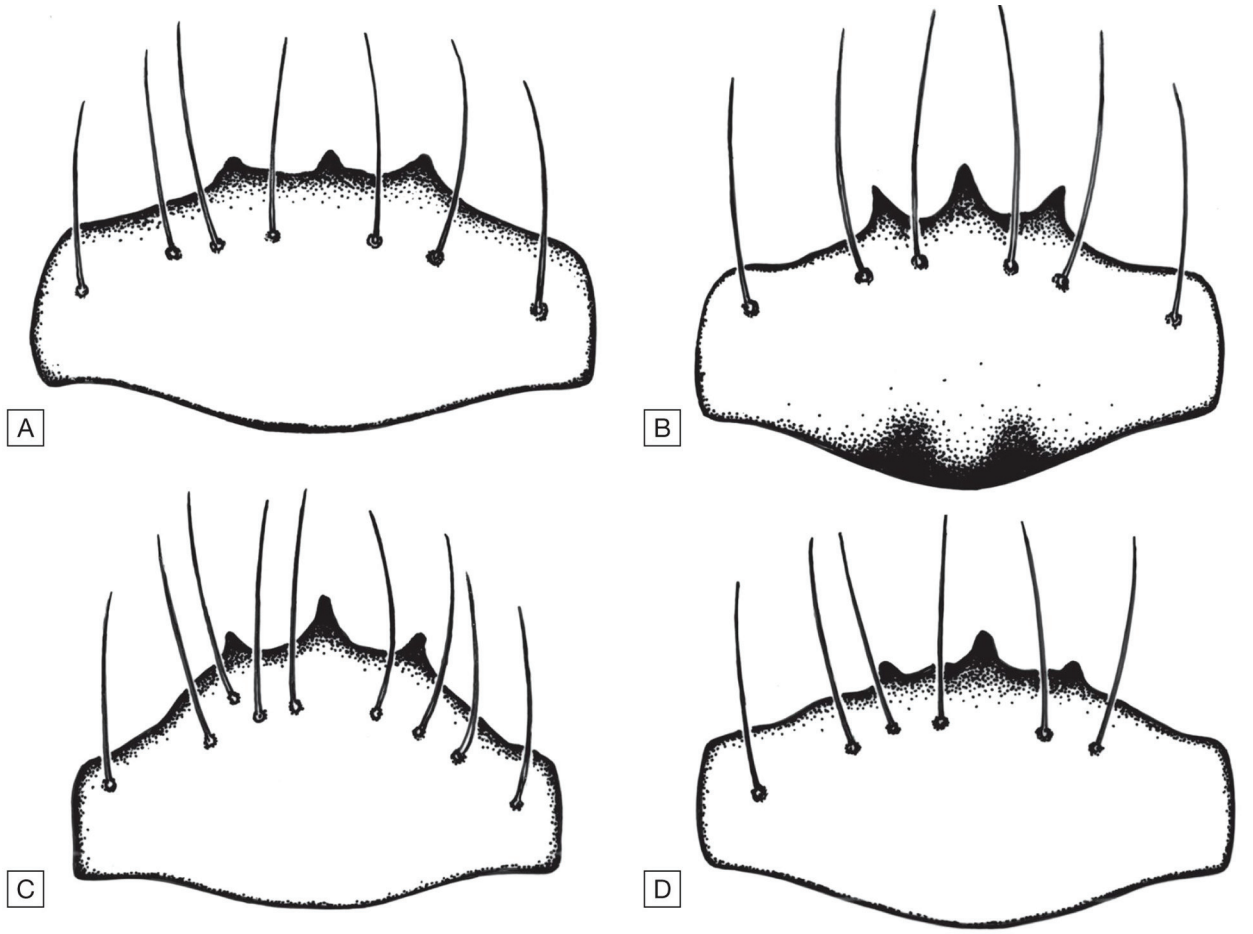

Figure 19. Labrum. A. *C. d. decemnotata*, male, "MT: Yellowstone Co., NE of Billings, 15-IV-2010" (MGKC). B. *C. d. decemnotata*, female, "MT: Beaverhead Co., Centennial Valley, 25-VIII-2009" (MGKC). C. *C. d. meriwetheri*, female, "WA: Walla Walla Co., 24 September 2000 , Hwy 12 2.8 m. E of Hwy 730" (MGKC). D. *C. d. bonnevillensis*, male, "UT: Tooele Co.: Dugway Proving Grounds, 10-V-2009" (MGKC).

and *C. d. meriwetheri*, could be diagnosed (*sensu* Vogler and DeSalle 1994) as separate Evolutionary Significant Units (ESUs) with 2-4 fixed characters states absent from all others within the species.

The variation of territorial ranges observed for *C. decemnotata* subspecies may be interpreted under a model of parapatric (sub)speciation. Geographic ranges of recently split sister species are likely to display asymmetry of range size as a result of the geometry of the landscape and range changes occurring since allopatric speciation events (Barraclough and Vogler 2000). Similarly, while genetic divergences within *C. decemnotata* were very shallow and inference from NGCA indicated widespread gene flow, the inter-haplotypic relationships exhibit significant structure rather than purely random distribution across geographic distance (5-step NGCA Chi-square=1.000; $P<10^{-4}$). Moreover, populations of *C. decemnotata* from Utah corresponding to three separate morphosubspecies occur in separated clades in all phylogenetic reconstructions and with significant support by maximum parsimony for reciprocal monophyly (T-PTP *L=-1, ΔL=-12 to -90, $P=10^{-4}$). Thus, while there is an apparent potential for widespread dispersal of the species across variable terrain, no evidence of intergradation (polyphyly or shared haplotypes) was recovered where two or three subspecies occurred in adjoining ranges. These findings suggest some elements of reproductive isolation operating within *C. decemnotata*. Comparable haplotype fidelity has not been observed among some other recognized cicindelid subspecies. For instance, *C. l. limbata* Say, *C. l. hyperborean* LeConte, and *C. l. nympha* Casey have each been traditionally recognized as a distinct subspecies even while phylogenetic investigation has also revealed multiple shared haplotypes between the adjacent subspecies (Ashworth 2001; Morgan et al. 2000).

It is notable that these data for *C. decemnotata* exhibit marked similarities to the diagnosed evolutionary front in the. *C. maritima* Dejean species group (Vogler et al. 1998). According to current biogeographic models, much of the area now occupied by both *C. decemnotata* and members of the maritima group was covered by an ice shield during the most recent glaciations, and presumably it is only within the last 10,000 years that habitat has opened up for colonization (Pearson and Vogler 2001). Indeed the patterns of rapid range expansion for *C. decemnotata* inferred NGCA from the previous analysis are potentially consistent with postglacial dispersal (Acorn 1992; Morgan et al. 2000). Phylogenetic analysis of the maritima group of species has revealed that pairwise haplotype divergences between species did not exceed 8%, and pairwise haplotype divergences among five species within this group known as the western clade, namely *C. bellissima* Leng, *C. columbica* Hatch, *C. depressula* Casey, *C. limbata* Say, and *C. oregona* LeConte, fell within the low range of 0.5-0.6% (Pearson and Vogler 2001; Vogler et al. 1998). These taxa have been regarded as separate species in that they are allopatrically separated and present distinctive morphologies without intergradation. If a constant rate of molecular change is assumed, then the western species of the maritima group have undergone a rapid phylogenetic radiation in the recent past and the rate of speciation for this clade is accelerated compared to many other cicindelid lineages (Pearson and Vogler 2001). Given that *C. decemnotata* shares a biogeographic range with multiple members of the maritima group (including *C. l. limbata* Say, *C. albissima* Rumpp and, *C. l. nympha* Casey), it seems reasonable to suggest that these two groups may have experienced parallel natural histories. If so, then it stands to reason that the skew between extreme morphological and low genetic divergence in *C. decemnotata* stems from similar (if not the same) causal factors of similar morphological and genetic divergence incongruities within the maritima group; likely, a recent adaptive radiation in the wake of glacial recession (Pearson and Vogler 2001; Vogler et al. 1998). Interestingly, *Cicindela* (*s. str.*) (including both *C. decemnotata* and the maritima group) and *Ellipsoptera* Dokhtouroff, both of which have northerly distributions in the North American continent, displayed more significant departure from the constant speciation rate model than did the other cicindelid clades (Barraclough and Vogler 2002). Other diagnosed phylogenetic radiations sympatric or parapatric to *C. decemnotata* and the maritima group include mustard plants (*Arabis* Linnaeus; Dobes et al. 2004), lilies (*Calochortus* Pursh; Patterson and Givnish 2003), whitefish (*Coregonus* Linnaeus; Fraser and Bernatchez 2001; Pigeon et al. 1997), montane grasshoppers (*Melanoplus* Stål; Knowles 2001), salmonid fishes (Dyke & Prest 1987), western butterflies (*Speyeria* Scudder; Hammond 1991), and chipmunks (*Tamias* Illiger; Good et al. 2003). As with the morphologically diagnosed subspecies of *C. decemnotata*, the North American postglacial fishes exhibit a large suite of morphological characters (including chromatophore patterning) can be used to distinguish members of each group (Streelman and Danley 2003).

Additional molecular genetic analyses of morphologically distinctive forms, such as the dark color of some Idaho populations and the unusual violet (or blue) colored morphs from Peace River, Alberta and the Whitehorse, Yukon (Acorn 2001) may reveal zones of intergradation and other phylogenetically distinct groups. Genetic study of likely sister species, such as polytypic *C. scutellaris* Say and *C. denverensis* may prove useful to further elucidate speciation patterns in this apparent phylogenetic radiation.

Habitat, Co-Occurring Species, Seasonality, and Conservation

Habitat. Pearson et al. (2006) describe the habitat of *C. decemnotata* as "sparsely vegetated grasslands, sagebrush and open brushy areas with clay or gravelly soil at high elevations." Our field experience, along with the examination of historic collection sites indicates that it occurs in a wider range of habitats, soil types, and elevations. This is especially true of *C. d. decemnotata* that is most common along trails and open areas of sagebrush and pine habitats and ranges in elevations over 2438m in Colorado and Wyoming and at latitudes as far north as the Yukon and Alaska. It has been found along highway road cuts, chalky eroded slopes, sandy hills, and the edges of playas and dunes. In 10 sites surveyed in Yellowstone Co., Montana, *C. d. decemnotata* was encountered at only five sites, whereas the associated species *C. purpurea audubonii* LeConte was present at 8 of 10 and *C. denverensis* present at all 10. There were no discernible differences between the 10 sites and the present of *C. decemnotata* at only 5 is still unexplained. In addition, on numerous occasions MGK collected interspecific mating pairs of

C. d. decemnotata and *C. denverensis* at these localities. The spotty distribution of *C. decemnotata* was also noted by Leffler and Pearson (1976) for populations in eastern Washington who stated "...occurs in small isolated areas of what otherwise appears to be extensive and homogeneous habitat."

In south central Montana, *C. d. decemnotata* is allopatric with *C. nebraskana* even though the habitat is identical for both species, whereas the associated species *C. purpurea audubonii* is sympatric with both *C. decemnotata* and *C. nebraskana*. In Washington and British Columbia, *C. d. meriwetheri* is most common on sandy soils along trails or bare areas in sagebrush dominated habitats at lower elevations (usually less than 457m), often with *C. tranquebarica* Herbst. It is interesting to note that in Washington *C. d. meriwetheri* is allopatric with *C. pugetana* even though both species inhabit similar habitat and have similar periods of adult activity. In British Columbia it was found with *C. purpurea audubonii*. *Cicindela d. bonnevillensis* is a Great Basin desert species on silty soils in saltbush flats, the edges of small playas, dirt roads and the stabilized edges of sand hills at elevations near or below 1,524m. It often occurs in the absence of other species or at times with *C. tranquebarica*. *Cicindela d. montevolans* is usually found at elevations at or over 2,438m and is associated with *C. purpurea audubonii* and *C. nebraskana*.

Seasonality. The adults of *C. decemnotata* exhibit a fall-spring adult activity pattern where sexually immature adults emerge from the pupal stage in late summer to early fall and remain active until digging their overwintering burrows in early to mid-October. These adults remerge from late February to early summer (depending on habitat temperatures) to mate and oviposit before dying off. Collection records and our fieldwork indicate that in most locations, adults of *C. d. decemnotata* are most common in April and May and again from late August to October (Fig. 22). In more northern locals, (especially Canada) adults are most often collected in August and seldom before late May. The records for *C. d. meriwetheri* are from April to June and again from September to October indicating a typical fall-spring pattern. Occurring at lower elevations, adults of *C. d. bonnevillensis* emerge in late August before overwintering in October, then reemerge as early as February and typically remain active into May. The seasonality of adults of *C. d. montevolans* deviates from the fall-spring pattern, apparently because of its high elevation distribution. Adults are typically found from late June through late August, a pattern more similar to summer active species. Studies of *C. d. bonnevillensis* at Dugway Proving Ground, Utah indicate that offspring from adults probably take two years to develop through three larval stages prior to emerging as adults. In more northern locations or at high elevations development could take three years.

Conservation. *Cicindela d. decemnotata* is widespread with many known populations. In Montana, an area which has relatively few records for tiger beetles, recent surveys by MGK indicate that additional populations are expected to be discovered. Although there are relatively few known sites for *C. d. meriwetheri* in Washington and British Columbia, there is a considerable amount of suitable habitat and thus the limited number of records can be due more to the lack of surveying rather than actual rarity. *Cicindela d. bonnevillensis* is currently known from less than 20 sites within an approximate 24 x 80 sq. km area of Tooele Co., Utah. Most collection records have been at Delle, Utah along I-80, but recent surveys indicate it is common and widespread within Dugway Proving Ground to the south. The number of actual populations is not known and additional survey work is needed to determine if it might be more widespread in Utah's western desert. However, based on currently known sites, this subspecies should be considered potentially rare and localized. The Cache Co., Utah populations of *C. d. montevolans* may be even more localized within the Bear River Mountain Range with most records coming from the area of Logan Canyon/Bear Lake. Most records are within a 16-32 sq. km area in this high elevation location, but these sites do not at present appear to be threatened by human activity or other factors that could eliminate habitat. Additional surveys are needed in the Bear River Mountain Range to determine the number and distribution of other populations.

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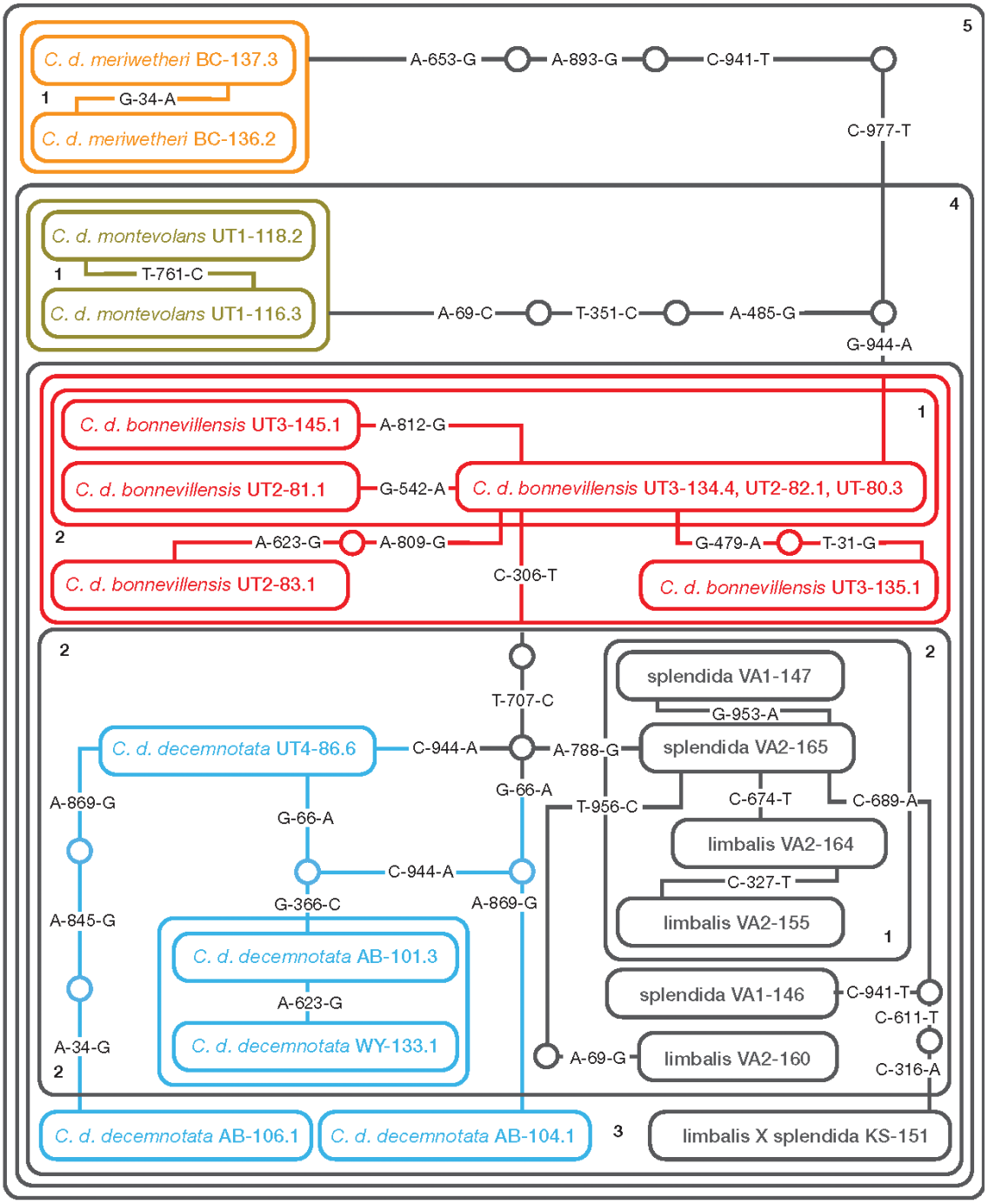

Figure 20. Haplotype networks recovered by statistical parsimony at the 5-step level. Empty circles represent intermediate haplotypes that were not present in the sample, and each bar illustrates a single mutational step relating two haplotypes, and changes of ambiguous significance and marked (*). Taxon names are based on identification by origin and morphology. Bars and taxa are color-coded according to match groups of sister species and subspecies of *C. decemnotata* postulated from morphology.

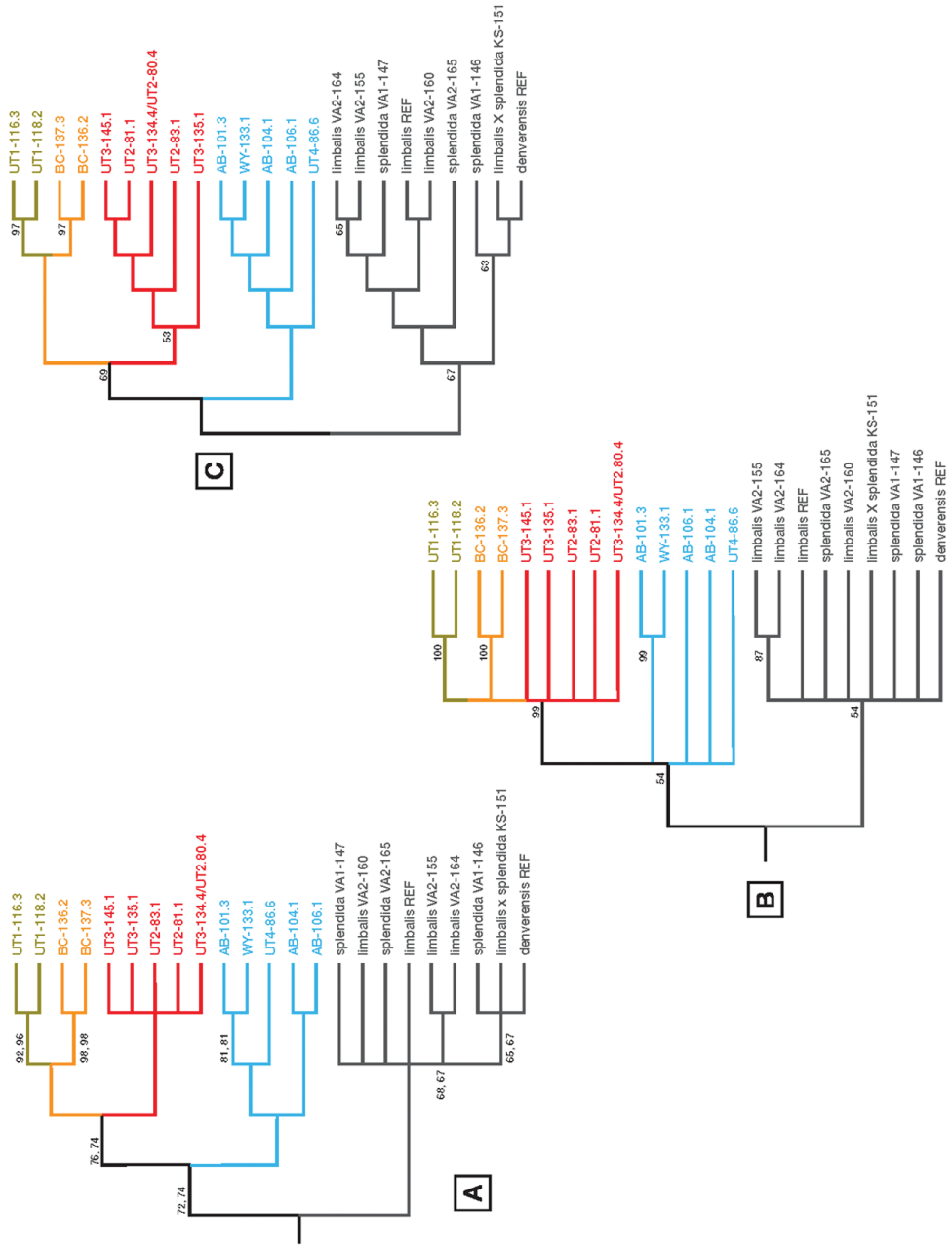

Figure 21. Comparison of congruent tree topologies recovered in phylogenetic reconstruction using maximum parsimony, Bayesian Inference, and Maximum Likelihood. Branches and taxa are color-coded according to match groups of sister species and subspecies of *C. decemnotata* postulated from morphology. Previously published sequences obtained from the NCBI database are marked with REF as their haplotype designation. A. The left cladogram represents one of thirty-one equally parsimonious rooted trees retrieved from unweighted reconstruction under a branch-and-bound search with a combined concatenated cob and cox1 dataset. This tree recovered a length of 42 for 1157 total characters; of which 17 (1.5% total sample) were potentially parsimony informative. Statistical supports >50% are given near their respective nodes in the form of Bootstrap values (BP), and third-delete Jackknife (JK). B. The middle cladogram represents the consensus rooted tree for a combined concatenated cob and cox1 dataset recovered from Bayesian Inference under a General Time Reversible (GTR) model with invariable base frequencies (I). Posterior Probabilities are given near their respective nodes. C. The right cladogram represents the best scoring rooted tree for a combined concatenated cob and cox1 dataset retrieved from maximum likelihood reconstruction under the GTR+I model.

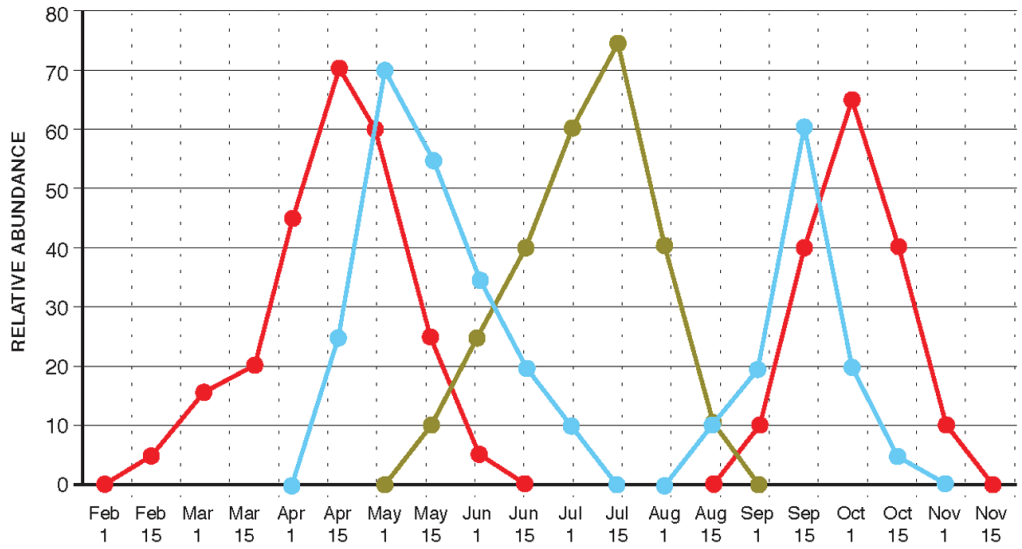

Figure 22. Seasonality of *C. decemnotata* populations based on collection records, *C. d. decemnotata* (blue line), *C. d. bonnevillensis* (red line) and *C. d. montevolans* (olive green line).

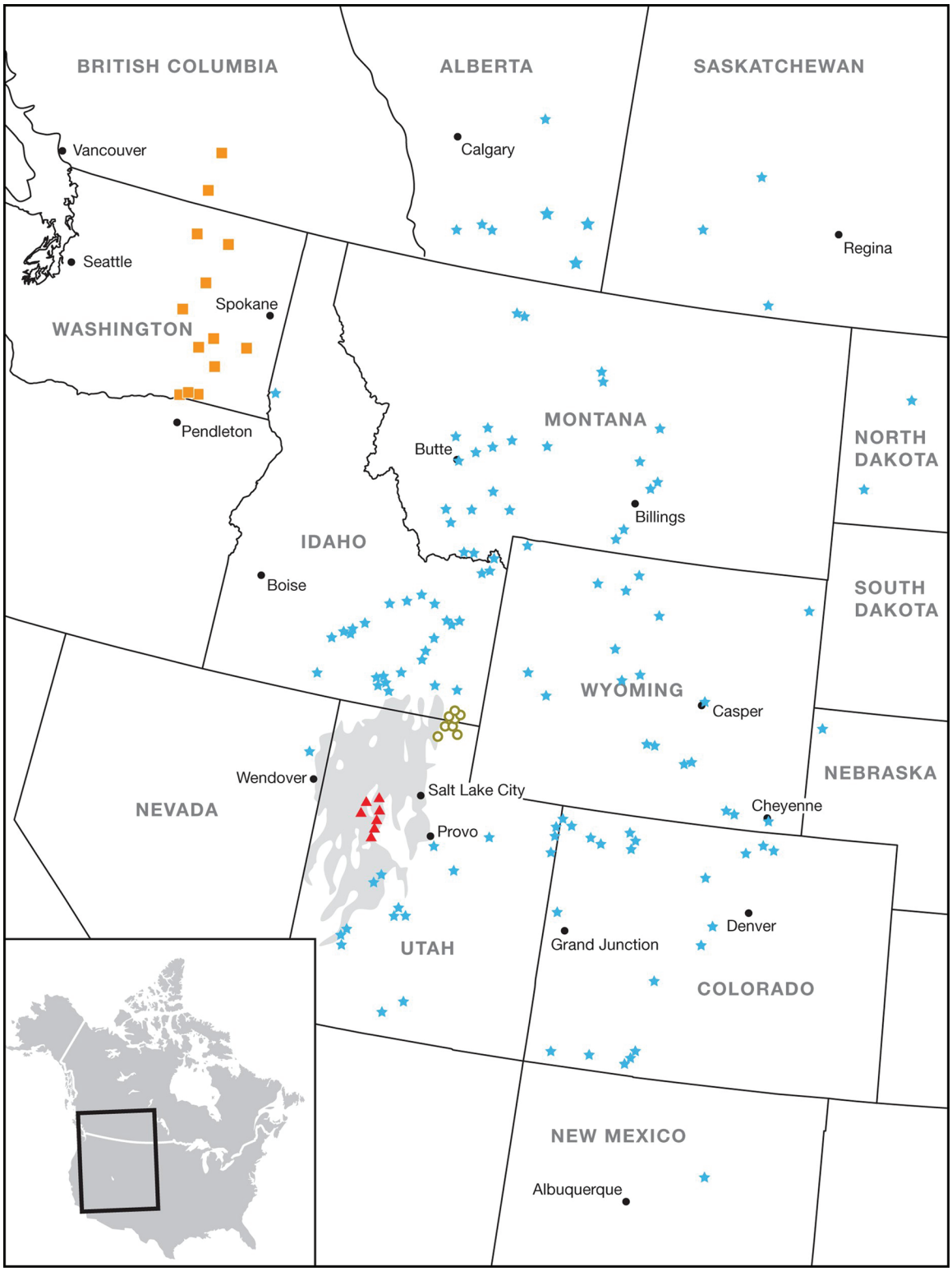

Figure 23. Map of western United States and Canada showing know locals of *C. d. decemnotata* (blue star), *C. d. meriwetheri* (orange square), *C. d. bonnevillensis* (red triangle) and *C. d. montevolans* (olive green outlined circle). Shaded area represents the approximate size and location of Pleistocene Lake Bonneville.

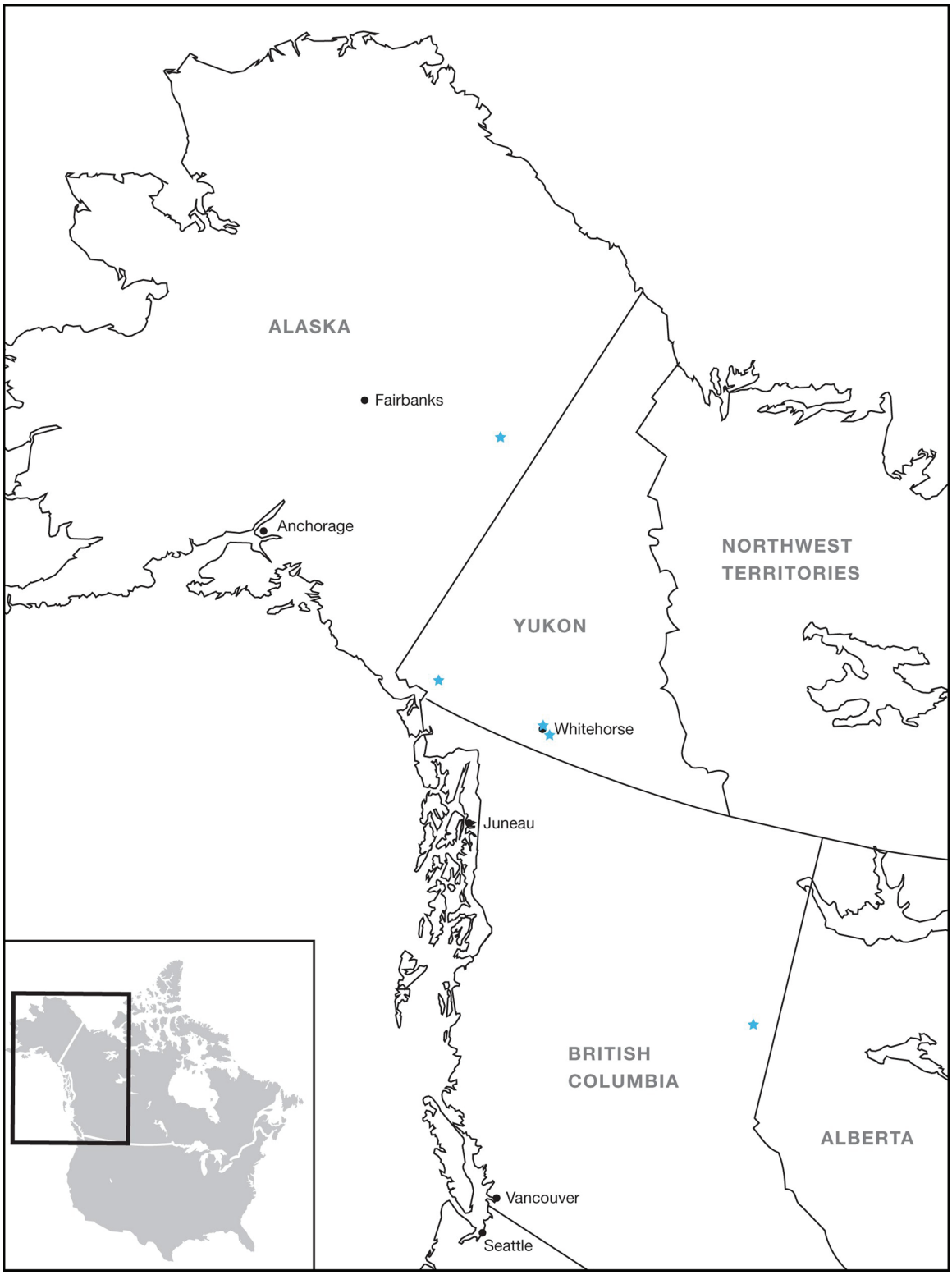

Figure 24. Map of Alaska and northwestern Canada showing know locals of *C. d. decemnotata* (blue star).

Table 1. Origin data for specimens of *C. decemnotata* utilized in the analysis of elytral maculation, genal setae and dorsal coloration.

State-Local	County	Location	Collection
CO01	Moffatt	Brown Park, Green River	CBKC
CO02	Arculeta	Hwy 160, 7-8 mi. west of Hwy 64	DWBC
CO03	La Plata	12 mi. east of Durango	DWBC
ID01	Franklin	Beaver CK and Liberty Cyn	USUC
ID02	Bannock	Pocatello and County	CBKC, BYUC
ID03	Cassia	Malta, Idahome, etc	UIDC, DWBC
ID04	Bonneville	Swan Valley and Idaho Falls	DWBC, BYUC
ID05	Lincoln	Richfield area	UIDC
ID06	Butte, Bingh	*various*	UIDC
ID07	Clark	Crystal Falls	UIDC
ID08	Fremont	Targhee National Forest	MGKC
UT01	Tooele	Dougway Proving Grounds north of Wigg Mt.	CBKC
UT02	Tooele	Delle	MGKC
UT03	Cache	Bear Lake, near ID line	CBKC
UT04	Cache	Cache-Rich Co. Line	DWBC
UT05	Cache	Beaver Ck. and Franklin Basin	USUC
UT06	Box Elder	*unspecified*	USUC
UT07	Sevier	Hwy 50, west of Salina	DWBC
UT08	Beaver	Milford	BYUC
UT09	Uinta	Hwy 40, 1.8 mi. west of CO	DWBC
UT10	Duschene	*various*	BYUC
UT11	Garfield	Henderson Cyn. Overlook	CBKC
MT01	Beaverhead	Centennial Valley	CBKC
MT02	Broadwater	south east side Canyon Ferry Res.	MGKC
MT03	Yellowstone	37 mi. north east of Billings	MGKC
WA01	Grant	Grand Coulee Airport	CBKC
WA02	Walla Walla	Walla Walla	DWBC
WY01	Carbon	9 mi. west of Medicine Bow	DWBC
WY02	Albany	Laramie	CBKC
CN01	BC	Penticton	CBKC
CN02	Yukon	Whitehorse	CNM
CN03	Sask	*various*	CNMC
CN04	Alberta	8 mi. south of Manyberries	USNM
CN05	Alberta	Bow River	TLC

Table 2. Results of analysis of elytral maculation, genal setae, and dorsal color characters in populations of *C. decemnotata*. Key to characters: #=number of specimens. Elytral maculation: Hl=humeral lunule, Mb=middle band; Al=apical lunule; AlCn=connection between apical lunule and anterior spot; OvL= overlap between apical lunule and foot of middle band; Total=sum of previous scores. Genal setae: Left=number setae left side; Right=number setae right side; Average. Color: DG=dark green; G=green; BG=blue-green; B=blue; GP=green-purple; P=purple; RP=red-purple.

State-Local	#	Hl	Mb	Al	AlCn	OvL	Total	Left	Right	Average	DG	G	BG	B	GP	P	R-P
CO01	9	2.2	7.0	3.0	1.4	1.1	**14.7**	13.7	16.5	**15.1**		9					
CO02	12	2.2	6.1	3.0	0.7	1.2	**13.2**	14.6	15.0	**14.8**		12					
CO03	20	2.1	6.7	2.7	1.4	1.2	**14.9**	13.8	14.0	**13.9**		20					
ID01	6	0.5	3.0	2.2	1.0	0.3	**7.0**	6.2	5.2	**5.7**					2	4	
ID02	22	1.9	5.8	2.6	0.8	0.7	**11.8**	11.8	13.5	**12.6**		4			11	7	
ID03	19	2.1	6.3	2.9	0.6	0.4	**12.3**	13.2	14.5	**13.9**		1			6	12	
ID04	11	2.4	6.5	2.9	1.3	1.0	**14.1**	11.9	13.4	**12.7**		4			7		
ID05	7	2.6	6.4	3.4	0.6	0.7	**13.7**	13.3	15.5	**14.4**						7	
ID06	6	2.7	6.7	3.2	0.7	0.8	**15.0**	21.3	22.3	**21.8**		1				5	
ID07	6	3.3	6.3	3.7	1.7	1.2	**16.2**	11.8	12.3	**12.0**						6	
ID08	9	2.5	4.8	2.7	1.1	1.2	**12.3**	9.4	10.8	10.1							9
UT01	26	0	0.4	0.6	0	0	**1**	11.8	13.3	**12.55**		14	8	4			
UT02	32	0	0.1	0.6	0	0	**0.7**	10.1	10.6	**10.35**	15	11	1	4			
UT03	21	0.5	2.5	2.3	0.9	0.2	**6.4**	6.8	6.3	**6.5**		2			7	14	
UT04	20	.25	1.25	1.4	0.5	0.1	**3.5**	6.9	8.1	**7.5**	2						18
UT05	7	0.2	1.6	2	1	0.3	**6.9**	5.7	6.9	**6.3**	3						4
UT06	5	0.0	1.5	1.0	0.0	0.5	**3.0**	3.5	6.5	**5.0**		1		1	3		
UT07	16	0.5	4.9	2.4	1.0	1.0	**9.8**	15.6	15.5	**15.5**	4	11			1		
UT08	2	0.0	4.5	2.0	0.0	0.0	**6.5**	12.5	15.5	**14.0**				2			
UT09	8	2.3	7.1	3.1	1.1	1.3	**14.9**	12.7	12.0	**12.4**		8					
UT10	2	3.0	7.0	3.5	1.0	1.5	**15.8**	13.5	18.5	**16.0**		1			1		
UT11	11	2.5	7.2	3.3	2.1	1.5	**16.6**	12.3	14.6	**13.4**		10			1		
MT01	25	3.0	6.9	3.4	1.9	0.9	**16.1**	12.3	12.7	**12.5**		1			6	18	
MT02	18	1	3.4	1.6	.6	.4	**7**	12.6	12.8	**12.7**	4	11	3				
MT03	15	2.5	5.8	2.5	1.7	1.5	**14**	13	15.6	14.3	8	2			4		1
WA01	20	0.0	5.9	2.8	0.7	0.4	**9.8**	2.2	2.4	**2.3**		19	1				
WA02	21	0.4	5.8	2.3	1.1	1.2	**10.8**	2.8	3.1	**2.9**		18	3				
WY01	15	3.2	6.4	3.4	2.0	2.1	**17.1**	15.2	14.2	**14.7**		15					
WY02	11	2.5	6.8	3.2	2.3	1.7	**16.5**	16.7	17.0	**16.9**	1	6			2	2	
CN01	30	0.0	1.3	1.7	0.1	0.1	**3.2**	1.9	2.4	**2.1**		28	2				
CN02	22	3.0	7.0	3.6	2.1	2.0	**15.7**	11.3	10.7	**11.0**		12			10		
CN03	14	2.4	7	3.4	1.9	1.6	**16.3**	11.4	10.8	**11.1**		13			1		
CN04	8	3.4	7	3.8	1.8	1.3	**17.3**	10.5	10.7	**10.6**		1			6	1	
CN05	11	2.5	6.6	3.0	1.1	1.2	**14.4**	nm	nm	nm		11					

Table 3. Polymorphic nucleotide positions for Cytochrome B (positions 1-411) and Cytochrome Oxidase Subunit I (positions 412-1182) between *C. decemnotata* subspecies and previously published sister species (Woodcock and Knisley 2009). Sequence locations of variable sites are shown in columns; all sites not shown are invariant. Positions diagnostic between subspecies are marked with numerals; other changes reflect intraspecific polymorphism. The "n" and "v" represent transition and transversion mutations respectively.

		0	0	0	0	3	3	3	3	3	3	3	4	4	5	5	6	6	6	6	6	6	7	7	7	8	8	8	8	8	8	9	9	9	9	9	9
		3	3	6	8	0	1	2	5	6	7	8	5	0	2	4	1	2	5	7	8	0	6	8	0	1	4	6	9	4	4	5	5	3	6	7	7
		1	4	6	3	6	8	7	1	6	9	5	0	2	1	3	3	4	9	7	1	8	9	2	5	9	3	1	5	3	6	7	8	9	5	4	7
	C. decemnotata Consesus	T	G	A	G	C	C	T	C	C	A	G	T	G	T	G	A	C	A	T	A	G	A	G	A	G	G	T	A	G	C	T				
I	*C. d. montevolans*	UT1-116.4	*	*	*	A	*	*	*	T	*	*	A	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	G	*	*	*			
		UT1-118.2	*	*	*	A	*	*	*	T	*	*	A	*	*	*	*	*	*	*	*	T	*	*	*	*	*	*	*	G	*	*	*			
II	*C. d. decemnotata*	AB-101.3	*	*	G	*	T	*	*	*	G	*	*	*	*	*	*	*	*	*	*	C	*	*	*	*	*	*	*	G	*	*	*			
		AB-104.1	*	*	G	*	T	*	*	*	*	*	*	*	*	*	*	*	*	*	*	C	*	*	*	*	A	*	*	*	*	*	*			
		AB-106.1	*	A	*	*	T	*	*	*	*	*	*	*	*	*	*	*	*	*	*	C	*	*	*	G	A	*	*	G	*	*	*			
		UT4-86.6	*	*	*	*	T	*	*	*	*	*	*	*	*	*	*	*	*	*	*	C	*	*	*	*	*	*	*	G	*	*	*			
		WY-133.1	*	*	G	*	T	*	*	*	G	*	*	G	*	*	*	*	*	*	*	C	*	*	*	*	*	*	*	G	*	*	*			
III	*C. d. meriwetheri*	BC-136.2	*	A	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	G	*	*	*	*	*	*	*	*	A	C	G	*	*	C		
		BC-137.3	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	G	*	*	*	*	*	*	*	*	A	C	G	*	*	C		
IV	*C. d. bonnevillensis*	UT2-80.3	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
		UT2-81.1	*	*	*	*	*	*	*	*	*	*	*	*	*	A	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
		UT2-82.1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	R	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
		UT2-83.1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	A	*	*	*	*	*	*	G	*	*	*	*	*	*	*	*	*		
		UT3-134.4	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
		UT3-135.1	C	*	*	*	*	*	*	*	*	*	G	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
		UT3-145.1	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	A	*	*	*	*	*	*	*	*	*		
V	*C. splendida*	VA1-146	*	*	*	*	T	*	*	*	*	*	*	*	*	*	*	*	*	*	G	C	*	A	*	*	*	*	*	C	*	*	*			
	C. splendida	VA1-147	*	*	*	*	T	*	*	*	*	*	*	*	*	*	*	*	*	*	*	C	*	A	*	*	*	*	*	*	A	*	*			
	C. limbalis x splendida	KS-151	*	*	*	*	T	A	*	*	*	*	*	*	*	*	C	*	*	*	G	C	*	A	*	*	*	*	*	*	*	*	*			
	C. limbalis	VA2-155	*	*	*	*	T	*	*	*	*	*	*	*	*	*	*	*	*	*	T	*	C	*	A	*	*	*	*	*	*	*	*			
	C. limbalis	VA2-160	*	*	*	A	T	*	*	*	*	*	*	*	*	*	*	*	*	*	*	C	*	A	*	*	*	*	*	*	*	T	*			
	C. limbalis	VA2-164	*	*	*	*	T	*	C	*	*	*	*	*	*	*	*	*	*	*	T	*	C	*	A	*	*	*	*	*	*	*	*			
	C. splendida	VA2-165	*	*	*	*	T	*	*	*	*	*	*	*	*	*	*	*	*	*	*	C	*	A	*	*	*	*	*	*	*	*	*			
Change Type (n/v)		n	n	n	n	v	n	n	v	n	n	v	n	n	v	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n			
Codon Position		1	1	3	3	3	3	3	3	3	3	3	3	3	2	3	3	3	3	3	3	3	3	3	3	2	3	3	3	3	3	3			
Amnino Acid		Y/H	V/I	G	G	N	L	L	P	V	G	L	V/G	R	A	G	L	F	G	V	A	G	S	G	L	K	V	G	M	R	Y	Y			
Diagnostic to Taxon									I				I				III						V				III	III			III			

Table 4. Origin data for specimens used in molecular study including number of sampled individuals per locality (N) and voucher identification numbers (ID nos).

Subspecies	Sample Location	Collector	Number	ID #'s
decemnotata	UT: Garfield Co.	Baumann & Clark	6	86-91
decemnotata	AB: Bow River north of Hays	Lawton	6	101-106
decemnotata	WY: Big Horn Co., Lovell, Nat. Guard Area	Schmidt	1	133
meriwetheri	BC: east side Skaha Lake	T. Lawton	6	136-140
bonnevillensis	UT: Tooele Co., 0.2 mi. S of Delle	Bauman, Clark & Plunkett	2	80-85
bonnevillensis	UT: Tooele Co., Dugway Proving Grounds	Bauman, Clark & Plunkett	9	134,135, 142-145
montevolans	UT: Cache Co., Hwy. 89 at Rich Co. LIne	Knisley & Gowan	6	116-121