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Phylogeny of North America's largest cicada radiation redefines *Tibicinoides* and *Okanagana* (Hemiptera: Auchenorrhyncha: Cicadidae: Tibicininae)

JEFFREY A. COLE[1,2,*], WILL CHATFIELD-TAYLOR[3], ELLIOTT A. SMEDS[4], JOHN R. COOLEY[5], VALORIE A. GONZALEZ[6] & CARESSA WONG[2]

[1]*Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007 USA*
[2]*Division of Natural Sciences, Pasadena City College, 1570 East Colorado Boulevard, Pasadena, CA 91106 USA*
jacole@pasadena.edu; *https://orcid.org/0000-0002-3485-6056*
[3]*Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Canada, K1S 5B6*
williamchatfieldtayl@cmail.carleton.ca, *wchatfieldtaylor@gmail.com;* *https://orcid.org/0000-0001-6509-4317*
[4]*Department of Entomology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94188 USA*
esmeds@calacademy.org; *https://orcid.org/0000-0003-1054-7491*
[5]*Department of Ecology and Evolutionary Biology, University of Connecticut Hartford, 10 Prospect Street, Hartford, CT 06103 USA*
https://orcid.org/0000-0002-3691-2592
[6]*Department of Biochemistry, University of California San Diego, 9500 Gilman Drive, La Jolla, CA 92093 USA*
https://orcid.org/0000-0002-8454-8393
Corresponding author

Abstract

Tibicinoides, with three small endemic California cicada species, has a confusing, intertwined systematic history with *Okanagana* that we unravel here. An ingroup including all species of *Tibicinoides* and the majority (84.7%) of *Okanagana* species were sampled for six gene regions, polarized with *Clidophleps*, *Okanagodes*, *Subpsaltria*, and *Tibicina* outgroups, and subjected to Bayesian phylogenetic analysis. Although the ingroup was monophyletic from all outgroups including *Tibicina*, *Tibicinoides* rendered *Okanagana* paraphyletic among two major ingroup clades. To bring classification into agreement with phylogeny, we redescribe and redefine *Tibicinoides* to include all *Okanagana* species with a hooked uncus in the male genitalia, all of which grouped with the type *T. cupreosparsa* (Uhler, 1889) in the first of these clades: *T. boweni* (Chatfield-Taylor & Cole, 2020) **comb. n.**, *T. catalina* (Davis, 1936) **comb. n.**, *T. hesperia* (Uhler, 1876) **comb. n.**, *T. mercedita* (Davis, 1915), *T. minuta* (Davis, 1915), *T. pallidula* (Davis, 1917a) **comb. n.**, *T. pernix* (Bliven, 1964) **comb. n.**, *T. rubrovenosa* (Davis, 1915) **comb. n.**, *T. simulata* (Davis, 1921) **comb. n.**, *T. striatipes* (Haldeman, 1852) **comb. n.**, *T. uncinata* (Van Duzee, 1915) **comb. n.**, *T. utahensis* (Davis, 1919) **comb. n.**, and *T. vanduzeei* (Distant, 1914) **comb. n.** *Okanagana* is redescribed and restricted to the species of the second major clade which contained the type *O. rimosa* (Say, 1830). We describe two new genera for morphologically distinct orphan lineages: *Chlorocanta* **gen. nov.** for *C. viridis* (Davis, 1918) **comb. n.** and *Hewlettia* **gen. nov.** for *H. nigriviridis* (Davis, 1921) **comb. n.** We recognize *O. rubrobasalis* Davis, 1926 **stat. rev.** as a species and relegate two former species to junior subjective synonyms: *O. noveboracensis* (Emmons, 1854) = *O. canadensis* (Provancher, 1889) and *O. occidentalis* (Walker *in* Lord, 1866) = *O. lurida* Davis, 1919. *Tibicinoides* and *Okanagana* together represent a rapid radiation that presents challenges to phylogenetic analysis including suboptimal outgroups and short internodes.

Key words: California floristic province, rapid radiation, protoperiodical, taxonomy

Introduction

Okanagana Distant, 1905 is the most speciose North American cicada genus, currently containing 59 species in the United States, Canada, and Baja California, México (Chatfield-Taylor & Cole 2020; Sanborn 2014; Sanborn & Heath 2017). The genus is distributed across North America with the greatest diversity found west of the Rocky Mountains (Sanborn & Phillips 2013). *Okanagana* represents a major cicada radiation in North America that is characterized by protoperiodical life cycles (Chatfield-Taylor & Cole 2017), host plant specificity (Watts 1992), endosymbiont (Campbell *et al.* 2015) and parasite (Soper *et al.* 1976) coevolution, and diverse signaler-receiver behavior (Alt & Lakes-Harlan 2018; Cooley 2001; Stölting *et al.* 2002) that is involved in mate recognition (Chatfield-Taylor & Cole 2019). Further study of the ecological and behavioral complexity of this fascinating

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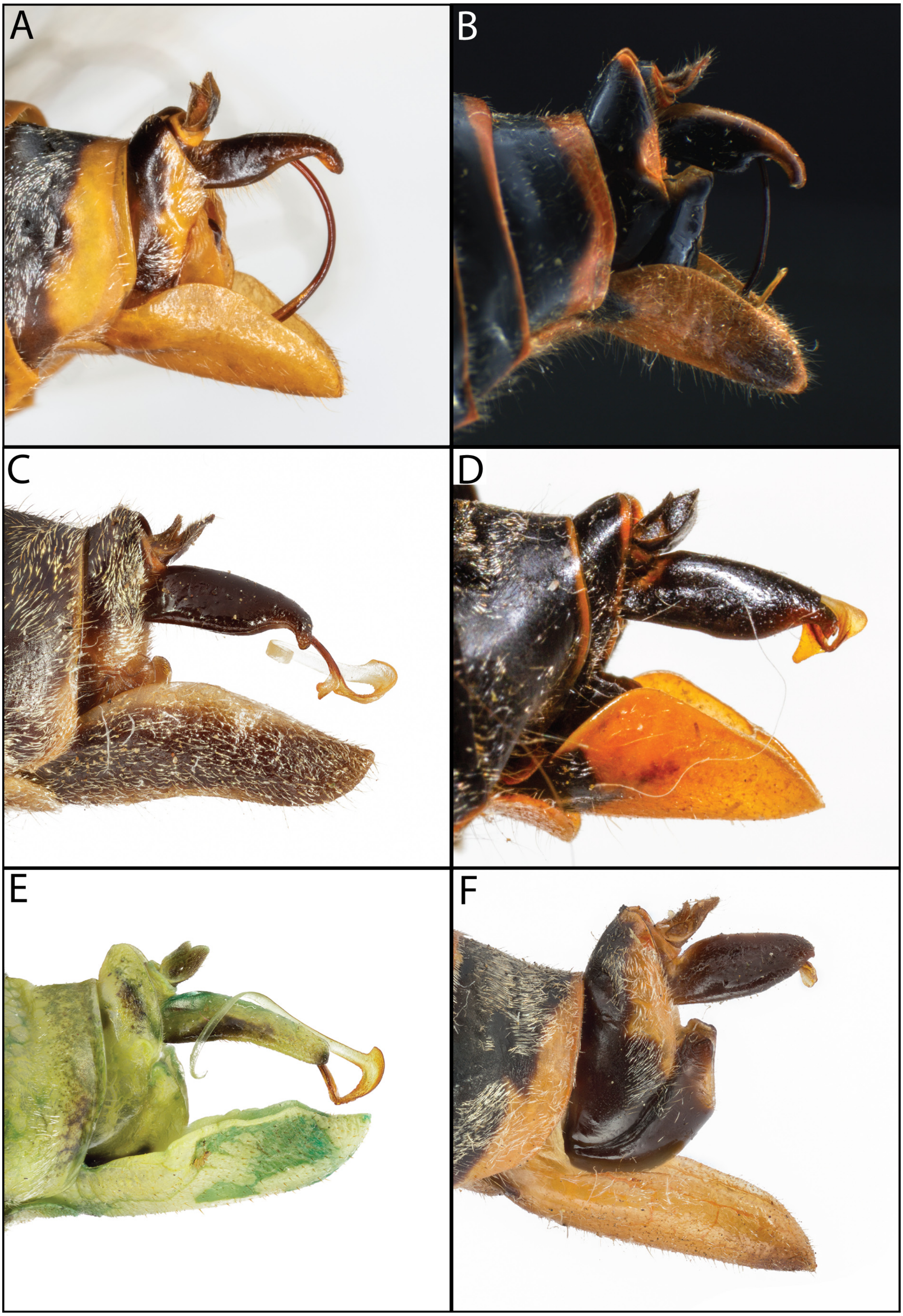


FIGURE 1. Comparative uncus morphology, left lateral view. A. *Clidophleps* sp., B. *Tibicen quadrisignata* (Hagen, 1855) (image credit: A. Sanborn), C. *Tibicinoides cupreosparsa*, type species of *Tibicinoides*, D. *Okanagana simulata*, E. *Okanagana nigriviridis*, F. *Okanagana rimosa*, type species of *Okanagana*.

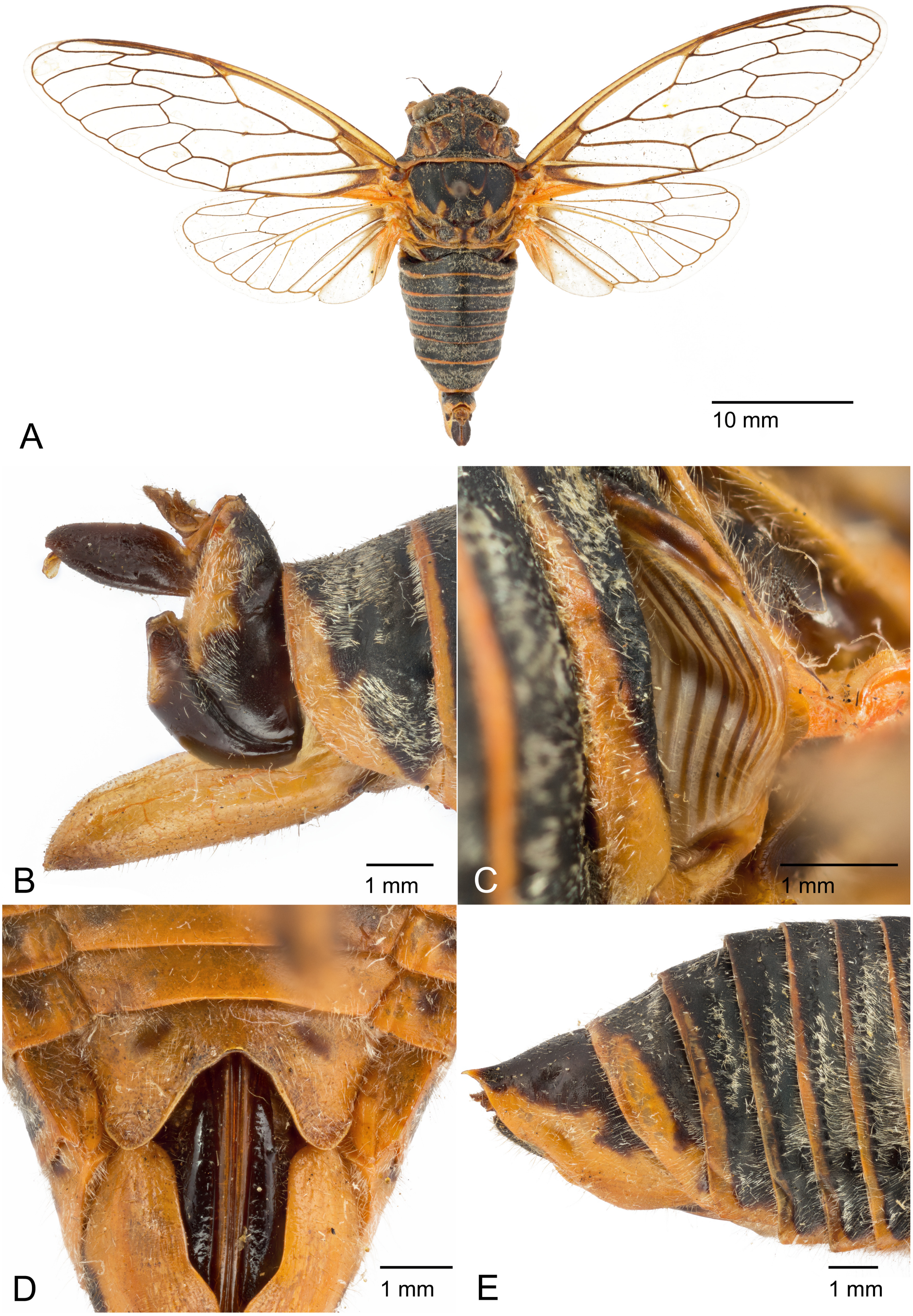


FIGURE 2. *Okanagana rimosa*, type species of the genus *Okanagana*: A. dorsal habitus, B. male genitalia, right lateral view, C. timbal, D. female genitalia, ventral view, and E. female genitalia, right lateral view.

radiation requires improved systematics, not only with respect to the interrelationships of species but also among related genera. *Tibicinoides* Distant, 1914, with three California species (Sanborn 2014; Sanborn & Heath 2017), deserves consideration as a component of this radiation as all but one of the species has at one time or another been classified in *Okanagana*. A well sampled phylogeny of *Okanagana* and related genera has not yet been attempted owing to their diversity and to the difficulty of sampling due to the sporadic protoperiodical adult emergence of many taxa (Chatfield-Taylor & Cole 2017). Phylogenetic studies to date have not included *Tibicinoides*.

The systematic position of *Okanagana* within the subfamily Tibicininae (Sanborn 2014; Sanborn & Heath 2017) is supported by molecular data (Łukasik *et al.* 2019; Marshall *et al.* 2018) as part of a Holarctic clade that also includes *Tibicinoides*, *Clidophleps* Van Duzee, 1915, and *Okanagodes* Davis, 1919 from North America, *Tibicina* Kolenati, 1857 from Europe and North Africa, and *Subpsaltria* Chen, 1943 from China (Marshall *et al.* 2018). When used as an outgroup along with *Clidophleps* and *Okanagodes*, *Okanagana* formed a paraphyletic grade with respect to *Tibicina* (Sueur *et al.* 2007). Of note is the hooked uncus character state (hereafter abbreviated HU) in the male genitalia of nearly all species of the outgroup genera (Fig. 1 A–B; Davis 1919; Luo & Wei 2015a; Simons 1954) save some *Tibicina* (see Hertach 2021).

The genus *Okanagana* was based on *Cicada rimosa* Say, 1830 (Fig. 2; Distant 1905). Apart from striking cryptic coloration in a few host plant-specific species (e.g. *O. nigriviridis* Davis, 1921 and *O. opacipennis* Davis, 1926), *Okanagana* cicadas are rather homogeneous in appearance. From this homogeneity a group of *Okanagana* stands out by virtue of a HU character state (Fig. 1D vs. 1F). HU diagnosed two species groups in early *Okanagana* species keys (Davis 1919; Simons 1954). Given the HU character state in the outgroups, certain *Okanagana* may have lost the HU character state (Fig. 1 E–F), or perhaps there is more than one HU origin. All HU *Okanagana* males also possess two timbal ribs. Except for *O. viridis* Davis, 1918, which has 2 timbal ribs, all other non-HU *Okanagana* have more than 2 timbal ribs (e.g. Fig. 2C with 7 ribs, range 3–11 ribs vs. Fig. 3C; WCT unpublished data).

Tibicinoides has a confusing systematic history (Heath 1978; Metcalf 1963; Sanborn 2014; Sanborn & Heath 2017). Based on the tiny southern California species *Tibicen cupreo-sparsa* Uhler, 1889 (Fig. 3; Distant 1914), *Tibicinoides* was diagnosed from *Okanagana* primarily by the former possessing shorter forewing apical (=marginal) cells (Fig. 3A) than the latter (Fig. 2A; Davis 1919; Distant 1914; Heath 1978; Lawson 1920; Sanborn & Heath 2017; Simons 1954). Four species have at one time or another been classified in *Tibicinoides*: *cupreosparsa* (Fig. 3), *Cicada hesperia* Uhler, 1876, *Okanagana mercedita* Davis, 1915, and *O. minuta* Davis, 1915. Contradictory taxonomic decisions were made in the most recent revision of *Okanagana*, *Tibicinoides*, and *Okanagodes*: *hesperia* was transferred to *Okanagana* based solely on the wing cell character state, but *mercedita* and *minuta* were retained under *Okanagana* despite having short forewing apical cells, accompanied by a note that *cupreosparsa*, *mercedita*, and *minuta* are likely congeneric (Davis 1919). Also worth noting in this revision is that the HU character state grouped *Tibicinoides* with HU *Okanagana* at the first key couplet (Davis 1919). Shortly thereafter, *mercedita* and *minuta* were transferred to *Tibicinoides* (Davis 1927). Simons (1954) used even fewer characters in his key to genera, citing only differences in proportions of forewing cell length, and considered *minuta* to be a synonym of *mercedita*. All four species that have been classified under *Tibicinoides* possess HU (e.g. Figs. 1C, 3B; Davis 1915, 1919; Lawson 1920) and two timbal ribs (e.g. Fig. 3C).

The species-level diversity of *Okanagana* and *Tibicinoides* is reasonably well established with few species descriptions (Bliven 1964; Chatfield-Taylor & Cole 2020; Heath & Sanborn 2007) since the most recent revision (Davis 1919) and a regional California synopsis (Simons 1954). Given the homogeneity of the group, much attention was paid to color pattern varieties in the historical literature. Some varieties were eventually given official taxonomic status as subspecies (e.g. *O. synodica nigra* Davis, 1944) while others (e.g. *O. rubrovenosa* var. *rubida* Davis, 1936) were synonymized (Sanborn 2014; Sanborn & Heath 2017). A few names persist as valid species that likely represent aberrant color patterns. For example, *O. lurida* Davis, 1919 was described from a single male exhibiting a unique color pattern in Washington State, USA (Davis 1919). Color pattern variation and shared geographic ranges among series of specimens later suggested that *O. lurida* and *O. occidentalis* (Walker *in* Lord, 1866) may be conspecific (Davis 1919, 1926, 1936, 1939).

After many years of collecting, including four protoperiodical emergences across California and the western United States since 2003, we establish the first extensively sampled species-level phylogenetic hypothesis for *Okanagana* and related genera. We enact taxonomic changes to reflect phylogeny and show evidence for rapid radiation of *Okanagana* and *Tibicinoides*.

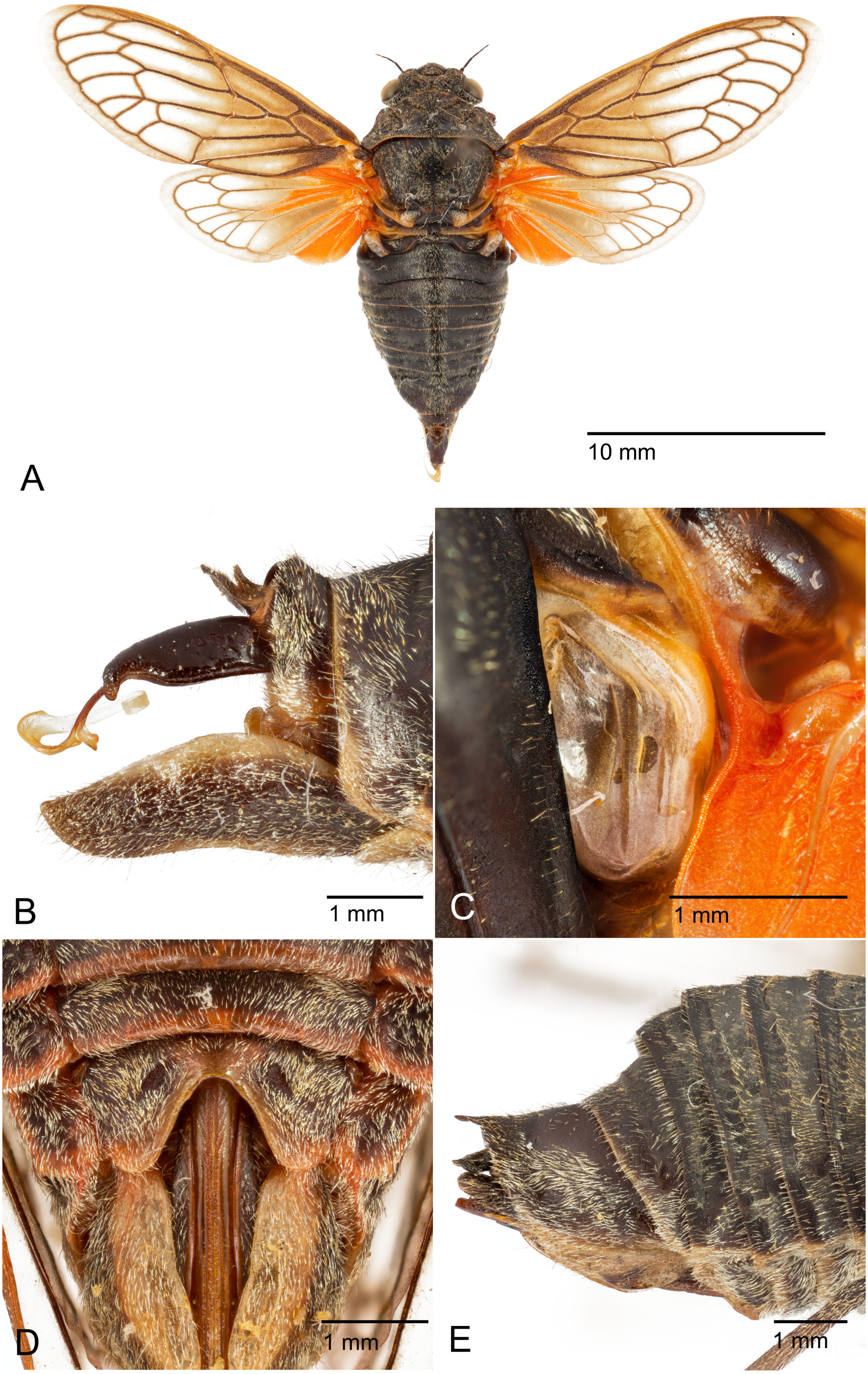


FIGURE 3. *Tibicinoides cupreosparsa*, type species of the genus *Tibicinoides*: A. dorsal habitus, B. male genitalia, right lateral view, C. timbal, D. female genitalia, ventral view, E. female genitalia, right lateral view.

Methods

Taxon sampling. Exemplars for this study were selected from a molecular voucher specimen collection accumulated over field collecting that began in 2003. Ingroup sampling covered 50 of the 59 (84.7%) described *Okanagana* species and all species that are currently or have previously been classified in *Tibicinoides*. Counting total described taxa including subspecies and varieties, ingroup sampling included 53 of 62 (85.4%) currently recognized taxa (Sanborn 2014; Sanborn & Heath 2017). Outgroup sampling consisted of exemplars of related genera (Marshall *et al.* 2018; Sueur *et al.* 2007): *de novo* sequencing of *Okanagodes* and *Clidophleps* from North America and a single *Tibicina* from Greece, and GenBank accessions for *Tibicina* from France (Sueur *et al.* 2007) and *Subpsaltria* from China (Marshall *et al.* 2018: Supp. Table 1). Molecular voucher specimens were accessioned at the Natural History Museum of Los Angeles County (LACM) and the Biodiversity Research Collections at the University of Connecticut.

DNA extraction and gene sampling. DNA was extracted from right middle legs preserved in 95% (JR Cooley (JRC)) or 100% (JA Cole (JAC)) ethanol or, for a few exemplars, legs that were rapidly dried. Extractions (DNeasy Blood and Tissue Kit, Qiagen Inc., Valencia, CA, USA) followed manufacturer protocol for animal tissues except for a prolonged proteinase K digestion for 12–18 h at 56°C (JRC) or overnight at 55°C (JAC), and a final elution step with ddH$_2$O (JRC) or two 50 µl volumes of buffer AE (JAC).

Gene sampling included six common markers used in cicada phylogenetics: an *elongation factor 1 alpha* (*EF1α*) fragment spanning 3 exons and 2 introns, the 5' untranslated region (UTR) plus a portion of the coding region of *acetyltransferase 1* (*ARD1*), a *calmodulin* intron (*CAM*; Buckley *et al.* 2006), *16S rDNA* (*16S)*, the 3' half of *cytochrome oxidase I* (*COI*), and the entire *cytochrome oxidase II* gene plus flanking regions of 5' *tRNA-Leu* and *3' tRNA-Lys* (*COII*). The first three genes are nuclear (hereafter referred to together as nDNA) and the remaining three are mitochondrial (mtDNA). Most genes were amplified with touchdown polymerase chain reaction (PCR) in 25 µl (JRC) or 10 µl (JAC) reaction volumes, during which an initial denaturation at 95°C for 60 s was followed by a variable annealing temperature that dropped -1°C/cycle for 10 cycles, followed by 30 cycles at a fixed annealing temperature. Two custom primer pairs, designed from preliminary mitogenome alignments (Łukasik *et al.* 2019; JAC unpublished data), avoided *COI* pseudogenes (numts): JerryHU with PatHU for *Tibicinoides* and HU *Okanagana*, and JerryTGA with PatTGA for the remaining taxa (Table 1). *ARD1* was amplified using nested PCR, in which a 1:100 dilution of the initial amplicon served as a template for the second PCR reaction. Primers and specific PCR reaction conditions are shown in Table 1.

Most PCR products were Sanger sequenced by commercial providers (Seqtech, Valencia, CA, USA (JRC) or Laragen Inc., Culver City, CA, USA (JAC)) using 10 uM PCR primers. PCR products from 2023 were sequenced with a nanopore sequencer (model MinION Mk1C, Oxford Nanopore Technologies, Oxford, UK) loaded with R9.4.1 flow cells. PCR products in 96 well plates were multiplexed via native barcode expansion (kit EXP-NBD196, Oxford Nanopore Technologies, Oxford, UK), during which unique sequence tags were ligated (kit LSK-109, Oxford Nanopore Technologies, Oxford, UK) onto ~130 ng amplicons according to manufacturer instructions. Nanopore sequencing proceeded for 72 h. Nanopore reads were basecalled and demultiplexed during sequencing in real time with Guppy v. 6.3.8 (available from www.nanoporetech.com) using default quality control settings, 'fast' basecalling, and .fastq file output.

Contig assembly, alignment, and model selection. Forward and reverse Sanger trace files were assembled into contigs and edited manually in Geneious v. 2023.1.2 (www.geneious.com). For nanopore reads native barcode sequence tags, adapters, and primers were trimmed from demultiplexed .fastq files with Cutadapt v. 4.0 (Martin 2011) by searching for primer sequences and trimming primers along with all sequence extending 5' and 3' from primers.

Quality control and contig assembly of protein coding gene nanopore reads were accomplished with ONTbarcoder v. 0.1.9 (Srivathsan 2021). Reads were filtered by product length, proportion of ambiguous bases, and similarity to preliminary nucleotide and amino acid alignment consensus. Reads differing more than 50 bp in length, with ambiguities in 30% or more of positions, or differing more than 10% from alignment consensus were rejected, while those passing quality control were combined into exemplar-specific contigs. Length and amino acid consensus criteria filtered out pseudogenes. Contigs for noncoding DNA were built using NGSpeciesID v. 0.1.3 (Sahlin *et al.* 2021). Subsets of 300 reads ('sample_size 300') were clustered by expected product length, allowing 50–200 bp deviation depending on expected length variability (i.e. intron lengths) under clustering parameters (kmer count 13 and window size 20) that are appropriate for nanopore reads (Sahlin *et al.* 2021). Resulting contigs were polished using Medaka 0.11.5 (available from https://github.com/nanoporetech/medaka) implemented in NGSpeciesID.

TABLE 1. PCR primers and reaction conditions.

Gene	Primer	Primer sequence	Annealing time	Extension conditions	Reference
EF1α	EF1a-F650-ambig	TGCTGCKGGTACTGGTGAAT	15 s	68°C, 75 s	Marshall *et al.* 2018
	EF1-N-1419	ACACCAGTTTCAACTCTGCC			Sueur *et al.* 2007
ARD1	ARD1-1041F	TGGAAAGTGTTTCTGTCACATTTTCG	15 s	68°C, 75 s	Marshall *et al.* 2018
	ARD1-1733R	ATCTCTTTTCATAGCGTATGCGTC			
	ARD1ForShort	CGCTTTGTGAGAGAATTRC			
	ARD1RevShort	GTATGCGTCTTCACCRTCTGC			
CAM	Cal-60-for	AACGAAGTAGATGCCGATGG	45 s	72°C, 150 s	Buckley *et al.* 2006
	Cal-72-rev	GTGTCCTTCATTTTNCKTGCCATCAT			UBC Insect Primer
16S	LR-J-12887	CCGGTCTGAACTCAGATCACGT	15 s	68°C, 75 s	Simon *et al.* 1994
	LR-N-13398	CGCCTGTTTAACAAAAACAT			
COI	JerryTGA	CAACAYYTATTTTGATTTTTTGG	60 s	72°C, 75 s	Sanborn *et al.* 2021
	PatTGA	TTCATTGCACTAATCTGCCATATTA			
	JerryHU	CAACATTTGTTCTGATTCTTTGG			This study
	PatHU	TTCATTGCACTATTCTGCCATATTA			
COII	TL2-J-3033	AATATGGCAGATTAGTGC	60 s	72°C, 75 s	Simon *et al.* 1994
	TGACOII	ATGCTATATCTCCTATAATAGACC			This study
	TK-N-3786	GTTTAAGAGACCATTACTT			Simon *et al.* 1994

Protein coding regions were aligned by amino acid sequence in Geneious. Noncoding *EF1α* introns, *ARD1* UTR, *CAM* introns, and ribosomal *16S* sequences were aligned with the *L-INS-i* algorithm in Mafft v. 7.471 (Katoh *et al.* 2002; Katoh & Standley 2013). Matrix editing and concatenation were accomplished in Mesquite v. 3.61 (Maddison & Maddison 2015). Nucleotide substitution models were parameterized and partitioned with PartitionFinder 2 (Guindon *et al.* 2010; Lanfear *et al.* 2012, 2016).

Phylogenetic analysis. Three phylogenetic matrices were analyzed: (1) three locus nDNA dataset, (2) three locus mtDNA dataset, and (3) concatenated analysis of all six loci. Topologies were rooted with *Clidophleps* and *Okanagodes* exemplars (Marshall *et al.* 2018).

Bayesian consensus trees were estimated with MrBayes version v. 3.2.7a (Huelsenbeck *et al.* 1996; Huelsenbeck & Ronquist 2001; Ronquist *et al.* 2012) run on the UCSD XSEDE supercomputer available at the CIPRES Science Gateway (Miller *et al.* 2010) with the following specifications: all partitions unlinked, all starting topologies equally likely, and four runs of four chains (3 heated and 1 cold chain) each for 3×10^7 generations. Consensus trees were redrawn from visualizations in FigTree v. 1.4.4 (available from http://tree.bio.ed.ac.uk/software/figtree/). Character states were reconstructed with squared change parsimony using the 'Trace Character History' function in Mesquite.

Morphology and songs. Specimens were examined in LACM, at the California Academy of Sciences (CAS), the Snow Entomological Museum (SEMK), the Bohart Museum of Entomology (UCDC), and in the personal collections of JAC, EAS, and WCT. Identification of genera and species was accomplished using dichotomous keys (Davis 1919; Simons 1954) and original descriptions. Morphological terminology followed that of Moulds (2005). Habitus and morphological characters were imaged at CAS (Big Kahuna, Visionary Digital). Digital photo stacks were captured with a DSLR camera (model 5D Mark III, Canon Inc., New York, NY, USA) merged using Zerene Stacker (available at www.zerenesystems.com), and edited in Adobe Lightroom and Photoshop. Song recording and analysis followed established methodology (Chatfield-Taylor & Cole 2019, 2020). The map, generated with ArcGIS v. 10.8.1 (www.esri.com), plotted occurrence data obtained from GBIF (GBIF.org accessed 23 November 2022, GBIF occurrence download at https://doi.org/10.15468/dl.y9cr6b).

Results

Alignment and model selection. Alignment lengths were 917 bp for *EF1α* (423 bp (141 codon) CDS + 494 bp introns), 616 bp for *ARD1* (202 bp UTR + 414 bp (138 codon) CDS), 1809 bp for *CAM*, 519 bp for *16S*, 828 bp (276 codons) for *COI*, and 741 bp (247 codons) for *COII*). Alignments of noncoding regions were repeatable judging from inspection of multiple iterations of algorithmic alignment. Substitution model partition results are shown in Table 2.

TABLE 2. Phylogenetic matrix partitioning schemes resulting from PartitionFinder 2 analysis.

Partition	Model	Gene regions included in partition
Analysis 1: nDNA		
1	K80+Γ	*ARD1* and *EF1α* CDS1st codon positions
2	F81	*ARD1* and *EF1α* CDS 2nd codon positions
3	GTR+Γ	*EF1α* CDS 3rd codon position and introns, *CAM* introns
4	HKY+I	*ARD1* CDS 3rd codon position and UTR
Analysis 2: mtDNA		
1	HKY+I+Γ	*16S*
2	HKY+I+Γ	*COI* and *COII* 1st codon positions, *COII* 2nd codon position
3	GTR+I+Γ	*COI* 2nd codon position
4	HKY+I+Γ	*COI* and *COII* 3rd codon positions
Analysis 3: concatenated matrix		
1	F81+I	*ARD1* and *EF1α* CDS 1st codon positions
2	GTR+Γ	*EF1α* CDS 3rd codon position and introns, *CAM* introns
3	HKY+I+Γ	*ARD1* UTR and CDS 3rd codon position, and *COI* 2nd codon position
4	HKY+I+Γ	*16S*
5	HKY+I+Γ	*COI* 1st codon position, *COII* 1st and 2nd codon positions
6	HKY+I+Γ	*COI* and *COII* 3rd codon positions

Phylogenetic analyses. MCMC runs for all analyses converged below the 2.00×10^{-2} threshold standard deviation of split frequencies (Huelsenbeck & Ronquist 2001): (1) nDNA analysis = 4.28×10^{-3}, (2) mtDNA analysis = 3.14×10^{-3}, and (3) concatenated analysis = 1.90×10^{-3}.

Topologies resulting from analysis of nDNA (Fig. 4) and mtDNA (Fig. 5) found *Subpsaltria* + *Tibicina* sister to the *Okanagana* + *Tibicinoides* ingroup with maximum support (posterior probability = 100%). Two major clades, also well supported, resolved within the ingroup (Figs. 4–5): the first clade contained all *Tibicinoides* together with all HU *Okanagana*, while the second contained most remaining *Okanagana*, including the type species *O. rimosa*. *Tibicinoides* thus rendered *Okanagana* paraphyletic. In addition to the two major clades mentioned previously, two other isolated lineages were found in the ingroup: *O. nigriviridis* and *O. viridis* (Figs. 4–5). Relationships among the four ingroup lineages were unresolved, apart from a weak grouping of *O. nigriviridis* with the HU *Okanagana* + *Tibicinoides* clade by mtDNA (Fig. 5). Apart from the long branches that separated the *Clidophleps* + *Okanagodes* outgroup and a few internodes at the base of the ingroup, branch lengths were generally short, including those that separated the outgroup clade *Subpsaltria* + *Tibicina* from the ingroup, and especially along the backbone of the ingroup (Figs. 4–5).

FIGURE 4. Bayesian consensus trees of nDNA (analysis 1 in Methods: Phylogenetic analysis). Posterior probabilities below 100% are shown along associated branches, all unlabeled branches are 100% posterior probability. Branches are proportional to lengths. Current assignments to genera (Sanborn 2014; Sanborn & Heath 2017) are annotated at the right.

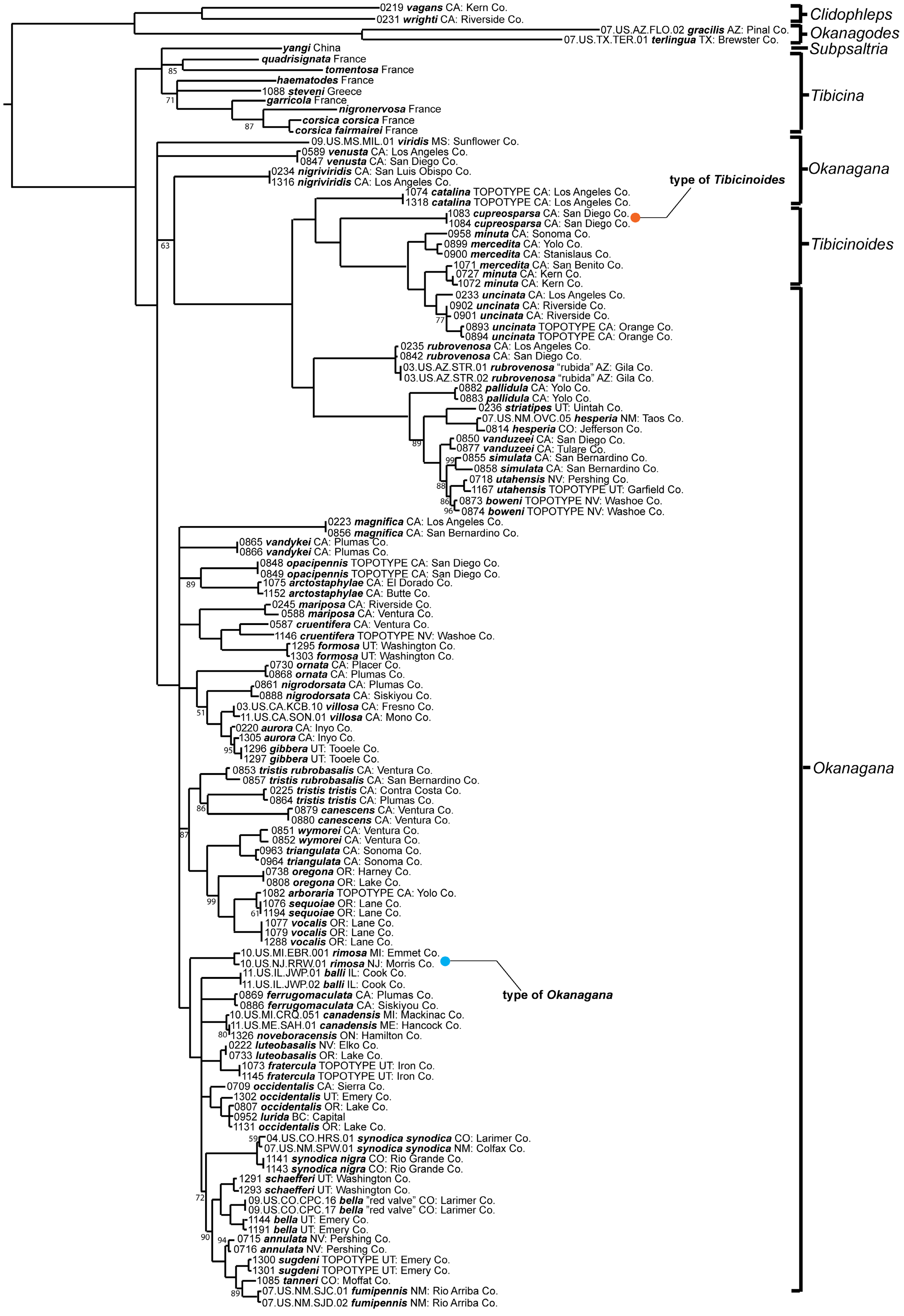


FIGURE 5. Bayesian consensus tree of mtDNA (analysis 2 in Methods: Phylogenetic analysis). Annotations as in Fig. 4.

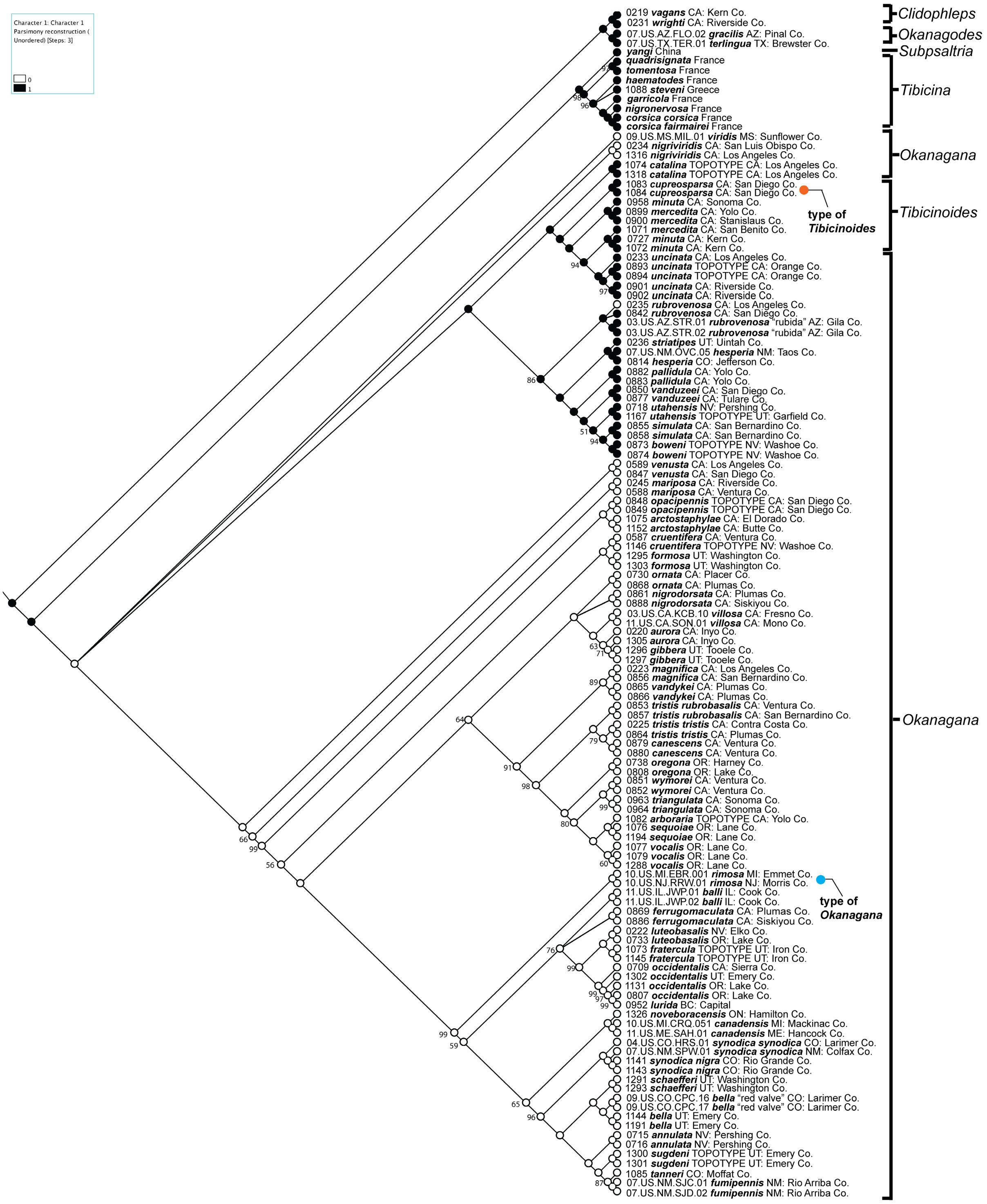


FIGURE 6. Bayesian consensus phylogram of concatenated matrix (analysis 3 in Methods: Phylogenetic analysis). Annotations as in Fig. 4. Parsimony reconstruction of the uncus shape character is shown as black=hooked uncus (HU) and white=uncus without distoventral hook.

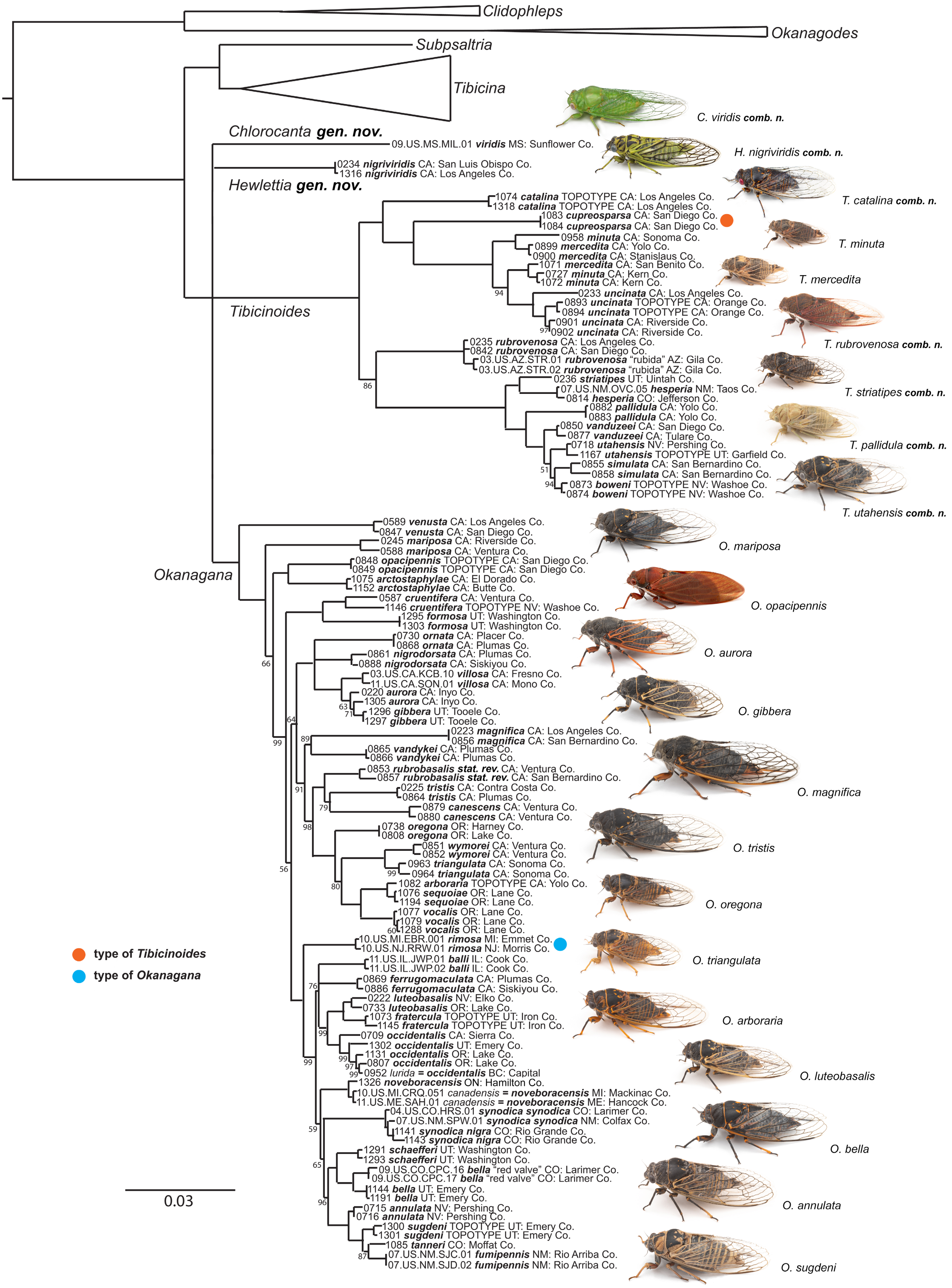


FIGURE 7. Bayesian consensus tree of concatenated matrix (analysis 3) as in Fig. 6 with branches proportional to lengths. Outgroups are cartooned. Concepts of genera as revised in this work appear on relevant branches. Photographed representatives of each genus appear to the right of the tree (Supp. Table 3).

Nodes between subclades in several cases collapsed or were weakly supported (Figs. 4–5); species-level relationships and internodes were poorly resolved in general with nDNA (81.2% of nodes with posterior probability = 100%; Fig. 4) and better resolved with mtDNA (90.3% of nodes with posterior probability = 100%; Fig. 5). nDNA and mtDNA trees were generally concordant where resolution allowed (Figs. 4–5) although limited gene tree discordance was observed, for example the grouping of *O. boweni* with *O. simulata* as shown by nDNA (Fig. 4) and alternatively with *O. utahensis* with mtDNA (Fig. 5).

The concatenated analysis recovered a four lineage polytomy at the base the ingroup (Figs. 6–7) like the nDNA and mtDNA topologies (Figs. 4–5). Parsimony reconstruction of the uncus shape showed an ancestral HU character state that was lost in the common ancestor of the ingroup and then regained in the *Tibicinoides* + HU *Okanagana* clade (Fig. 6).

Notable species-level relationships that were recovered now follow. Multiple exemplars of *T. mercedita* and *T. minuta* were interdigitated regardless of species in a clade that was separated from *T. cupreosparsa* by long branches (Figs. 4–5, 7). A Canadian *O. lurida* exemplar resolved at the crown of a grade of geographically widespread *O. occidentalis* exemplars from California, Utah, and Oregon, USA (Figs. 4–7). *O. noveboracensis* (Emmons, 1854) showed no genetic differentiation from *O. canadensis* (Figs. 5, 7). *O. tristis rubrobasalis* was sister to *O. t. tristis* + *O. canescens* Van Duzee, 1915 (Figs. 5–7).

Systematic treatment. At the genus-group level, we resolved paraphyly of *Okanagana* by redefining *Tibicinoides* to include all ingroup taxa with the HU character state. Redescriptions of *Okanagana* and *Tibicinoides* now follow along with the description of new genera for *O. viridis* and *O. nigriviridis* (Fig. 7).

Okanagana Distant, 1905

Fig. 1 (A. dorsal habitus, B. male genitalia, right lateral view, C. timbal, D. female genitalia, ventral view, E. female genitalia, right lateral view)

Type Species: *Cicada rimosa* Say, 1830

Included Species: *annulata* Davis, 1935, *arboraria* Wymore, 1934, *arctostaphylae* Van Duzee, 1915, *aurantiaca* Davis, 1917b, *aurora* Davis, 1936, *balli* Davis, 1919, *bella* Davis, 1919, *canescens* Van Duzee, 1915, *cruentifera* (Uhler, 1892), *ferrugomaculata* Davis, 1936, *formosa* Davis, 1926, *fratercula* Davis, 1915, *fumipennis* Davis, 1932, *georgi* Heath & Sanborn, 2007, *gibbera* Davis, 1927, *hirsuta** Davis, 1915, *luteobasalis* Davis, 1935, *magnifica* Davis, 1919, *mariposa mariposa* Davis, 1915, *mariposa oregonensis* Davis, 1939, *napa* Davis, 1919, *nigrodorsata* Davis, 1923, *noveboracensis* (Emmons, 1854), *occidentalis* (Walker *in* Lord, 1866), *opacipennis* Davis, 1927, *oregona* Davis, 1916, *orithyia* Bliven, 1964, *ornata* Van Duzee, 1915, *rhadine* Bliven, 1964, *rimosa rimosa* (Say, 1830), *rimosa ohioensis* Davis, 1942, *rubrobasalis* Davis, 1926 **stat. rev.**, *salicicola* Bliven, 1964, *schaefferi* Davis, 1915, *sequoiae* Bliven, 1964, *sperata* Van Duzee, 1935, *sugdeni* Davis, 1938, *synodica synodica* (Say, 1825), *synodica nigra* Davis, 1944, *tanneri* Davis, 1935, *triangulata* Davis, 1915, *tristis* Van Duzee, 1915, *vandykei* Van Duzee, 1915, *venusta* Davis, 1935, *villosa* Davis, 1941, *vocalis* Bliven, 1964, *wymorei* Davis, 1935, *yakimaensis* Davis, 1939.

Etymology: The name is derived from the Syilx Okanagan people(s) or the Okanagan Valley of British Columbia. Feminine.

Distribution: *Okanagana* are found throughout the United States and Canada with a single species, *O. aurantiaca*, endemic to Baja California, México. Species diversity is highest in Southern California (Davis 1917b; Sanborn & Phillips 2013).

Redescription: Males and females are similar to members of the genus *Tibicinoides*. Inter-species body size is highly variable with some intra-specific variation. *Head:* The width of the head and eyes is usually equal to subequal the width of the apical pronotal margin. The clypeus is variably pronounced. The center of the vertex has an epicranial suture; sulcate or not, marked or not. *Thorax*: The pronotal margins are subquadrate to apically constricted with a longitudinal sulcus of varying depth running along the midline. There are two bilateral fissures that run inwards towards the center of the pronotum at an anterior-posterior angle. The humeral and apical angles are distinct or not. The cruciform elevation is located directly anterior to the hind margin of the mesonotum. The anterior lateral sides of the mesonotum may show vestigial stridulatory grooves. The posterior edge of the metanotum is visible. *Wings*: Both fore and hind wings are hyaline, and the basal membranes are variable in color but typically orange. The fore wing length is 2.5–3 times the width, with 8 apical cells. The trapezoidal-shaped radial cell reaches the costal node halfway along length of costa, and the ratio of apical cell to ulnar cell length is approximately 1:1. The hind wing has 6 apical cells with a typical branched CuA vein (Fig. 2A). The wing venation is usually dark, with species-specific exceptions. *Legs*: Metacoxa with a meracanthus with a distinct triangular shape, typically as long or longer than the coxa. Metatibiae with spines, all other tibiae without spines. *Abdomen*: Timbals completely exposed. Timbal membrane with 3–11 long ribs spaced with short ribs (e.g. Fig. 2C). In females there is no vertical gap between tergite VII and tergite VIII and epipleurite VII is usually longer in length compared to epipleurite VI (Fig. 2D–E).

Male Genitalia: Sternite VII in males is variably shaped, covering the base of sternite VIII (=valve). Sternite VIII extends parallel to the length of the body, partially housing the uncus and aedeagus. The uncus has its dorsal and lateral margins variably shaped from parallel to with a bulge. From the dorsal aspect the tip of the uncus is bulbous or not, excavated or not: a species-specific feature. The uncus never has a hooked tip (as in Figs. 1C–D, 3B) though in the lateral aspect there may be a slight point in some species.

Female Genitalia: Sternite VII is variably excavated on its posterior margin, forming a primary notch with a secondary notch in the center of the primary (Fig. 2D). Both excavations are seldom rounded in their entirety, often forming distinct angles between the primary and secondary notch. The secondary notch may be rounded or distinctly V-shaped (if clear). The sides of sternite VII form rounded apical prongs that vary in shape. Both traits are often species-specific.

Diagnosis: The visible posterior margin of the metanotum and the trapezoidal-shaped radial cell that reaches the costal node halfway along length of the costa identify the genus to *Okanagana*, *Tibicinoides*, *Chlorocanta* **gen. nov.**, or *Hewlettia* **gen. nov.**. Males may be identified to genus by the uncovered timbals with more than two long ribs (e.g. Fig. 2C) and an uncus without a distinct ventroapical hook (Fig. 2B).

Most female *Okanagana* can be diagnosed by the absence of a vertical gap between tergite VII and tergite VIII, which gives females a streamlined appearance in the lateral aspect (Fig. 2E) rather than the hump-backed look of female *Tibicinoides* (Fig. 3E). There are some exceptions to this, which can be the result of rough handling during collecting. The diagnosis can be confirmed by looking at the relative lengths of epipleurite VI and VII and the excavation of sternite VII. In *Okanagana* females epipleurite VII is distinctly longer than VI when in *Tibicinoides* they are subequal in length (Fig. 2D). Sternite VII is variably excavated on its posterior margin, forming a primary notch with a secondary notch in the center of the primary (Fig. 2D). In *Okanagana* the primary and secondary notches are seldom completely rounded and often form a distinct angle: *Tibicinoides* females have both the primary and secondary notches rounded and never have distinct angles between the two. In *Okanagana* the notch may also be V-shaped, which is never seen in *Tibicinoides*. As with *Tibicinoides*, the best way to identify females is by gestalt, which becomes easier with increasing familiarity.

This paper describes two additional genera: *Chlorocanta* **gen. nov.** and *Hewlettia* **gen. nov.** Male *Chlorocanta* **gen. nov.** can be separated from *Okanagana* by the presence of an uncus without a hook (Fig. 8B) but only two long timbal ribs on the timbal membrane (Fig. 8E). Females of this genus can be diagnosed by their green color (yellowish when faded); a feature unshared by other *Okanagana* except *O. aurantiaca*, which possesses a black longitudinal dorsal stripe on the abdomen. Male and female *Hewlettia* **gen. nov.** can be distinguished entirely by the green and black patterning across the body and the presence of 5 rather than 6 apical cells on the hind wing (Fig. 9A).

*We include *hirsuta* with *Okanagana* based on examination of a male specimen in the UCDC collection, which lacks HU. The uncus morphology was omitted in the original species description, which was based on a single female specimen (Davis 1915). *T. catalina*, which does possess a HU and for which a male type was available, was initially described as a subspecies of *hirsuta* (Davis 1936), before being elevated to species level by Miller (1985).

Tibicinoides **Distant, 1914**

Fig. 2 (A. dorsal habitus, B. male genitalia, right lateral view, C. timbal, D. female genitalia, ventral view, E. female genitalia, right lateral view)

Type species: *Tibicen cupreo-sparsa* Uhler, 1889

Included species: *boweni* (Chatfield-Taylor & Cole, 2020) **comb. n.**, *catalina* (Davis, 1936) **comb. n.**, *cupreosparsa* (Uhler, 1889), *hesperia* (Uhler, 1876) **comb. n.**, *mercedita* (Davis, 1915), *minuta* (Davis, 1915), *pallidula* (Davis, 1917a) **comb. n.,** *pernix* (Bliven, 1964) **comb. n.**, *rubrovenosa* (Davis, 1915) **comb. n.**, *simulata* (Davis, 1921) **comb. n.**, *striatipes* (Haldeman, 1852) **comb. n.**, *uncinata* (Van Duzee, 1915) **comb. n.**, *utahensis* (Davis, 1919) **comb. n.**, *vanduzeei* (Distant, 1914) **comb. n.**

Etymology: Unknown. Perhaps referencing gestalt similarity (*g. -oides* "likeness") with *Tibicen*, meaning "flute player," a genus established early in cicada systematic history in which the type species was originally described, and in which several other early species were at one time or another classified. Perhaps also refers to similarity with the related European genus *Tibicina*. Neuter.

Distribution: *Tibicinoides* are found in western North America. Their range extends north to Washington state, south into southern Baja California, México, and east into Kansas following shortgrass and sage dominated prairie (Sanborn & Phillips 2013).

Redescription: Body size is highly variable with both inter and intra-specific variation. *Head:* The width of the head and eyes is equal to subequal that of the apical pronotal margin. The clypeus is variably pronounced. The center of the vertex has a deeply sulcate epicranial suture. *Thorax*: The pronotal margins are subquadrate to apically constricted with a longitudinal sulcus of varying depth running down the center. Two bilateral fissures run inwards towards the center of the pronotum at an anterior-posterior angle. The humeral and apical angles of the pronotum are distinct or not. The cruciform elevation is located directly anterior to the hind margin of the mesonotum. The anterior lateral sides of the mesonotum show vestigial stridulatory grooves in both sexes. The metanotum is clearly visible. Most species have the head, pronotum, and mesonotum variably black, brown, and yellow, but with a distinct set of four markings arranged in a trapezoid directly anterior to the cruciform elevation. *Wings*: Both fore and hind wings are hyaline, and the basal membranes are variable in color but typically orange. The fore wing length is 2.4–2.9 times the width, with 8 apical cells. The trapezoidal-shaped radial cell reaches the costal node situated halfway along the length of the costa. The ratio of apical cell to ulnar cell length is subequal in most species but 2:1 in the species of *Tibicinoides* prior to its revision. The hind wing has 6 apical cells with a typical branched cubitus anterior (CuA) vein (Fig. 3A). The wing venation color is variable both within and among species with the base of the wings strongly infuscated or not. *Legs*: Metacoxa with a meracanthus with a distinct triangular shape, typically as long or longer than the coxa. All tibiae are often heavily setose but only the metatibiae have spines. *Abdomen*: In males the timbals are completely exposed with the timbal membrane having two long and two short ribs (Fig. 3C). The majority of female *Tibicinoides* show a distinct vertical gap between tergite VII and tergite VIII, giving them a hump-backed appearance (Fig. 3E), and epipleurite VII is usually subequal in length to epipleurite VI. Tergite VII is angled slightly inward posteriorly, particularly towards the base, causing this appearance. The abdominal sternites can be heavily setose or not, with intra-specific variation in this regard.

Male Genitalia: Sternite VII in males is variably shaped, covering base of sternite VIII. Sternite VIII extends parallel to the length of the body, partially housing the uncus and aedeagus. The uncus is generally straight in the lateral aspect and curves at the tip, forming the characteristic hook of the genus (Fig. 3B). The aedeagus is variable but is often a species-specific shape and is attached to the ventral surface of the uncus.

Female Genitalia: Sternite VII is variably excavated on its posterior margin, forming a primary notch with a secondary notch in the center of the primary (Fig. 3D). Both excavations are rounded in their entirety, forming no distinct angles between the primary and secondary notch (if clear). The sides of sternite VII form rounded apical prongs that vary in shape. Both traits are often species-specific.

Diagnosis: *Tibicinoides* and *Okanagana* are North American cicadas with the hind margin of the metanotum not hidden by the mesonotum, combined with a trapezoidal-shaped radial cell that reaches the costal node situated halfway along length of costa. Diagnosing *Tibicinoides* from other North American cicadas is simple with males but more difficult with females. Males can be differentiated by the combination of an uncus with a distinct hook (Fig. 3B) and exposed timbals with two long and two short timbal ribs (Fig 3C).

Diagnosing females from *Okanagana* by morphology alone is difficult. Phenotypically they are not sexually dimorphic from males making field identification easier if both sexes are present. The hump-backed look of female *Tibicinoides* (Fig. 3E) is seen only rarely in *Okanagana*, which appear much more streamlined in the lateral aspect (Fig. 2E), and this is the most useful feature for in-field diagnosis. This appearance is caused by a distinct vertical gap between tergites VII and VIII with tergite VII being angled inward towards the base. The result is that epipleurite VII is subequal in length to epipleurite VI, and angles inward at a sharper angle relative to epipleurite VI. *Okanagana* lack the inward constriction of tergite VII, causing epipleurite VII to be distinctly longer than epipleurite VI, without a clear difference in angle. Rough handling of the specimen can distort this feature. The primary and secondary notches of sternite VII are both completely rounded with no distinct angles, eliminating the majority of *Okanagana* which often have distinct angles in the primary notch or have the primary or secondary notches V-shaped. However, the best way to identify female *Tibicinoides* is by gestalt, and it becomes easier with more experience. Many species of *Tibicinoides* also have at least a single distinct feature identifying them to the genus.

This paper describes two additional genera; *Chlorocanta* **gen. nov.** and *Hewlettia* **gen. nov.** Males of these two genera can be diagnosed from all *Tibicinoides* by a lack of a hooked uncus (Figs. 8B, 9B). Female *Chlorocanta* **gen. nov.** can be diagnosed from *Tibicinoides* by their green color (yellow when faded) and the almost triangular primary notch with slight bulging to the lateral margins and distinct secondary notch (Fig. 8D), which lacks the consistent rounding of the notch seen in *Tibicinoides*. *Hewlettia* **gen. nov.** females are distinguishable entirely by the green and black patterning across the body and the presence of 5 rather than 6 apical cells on the hind wing (Fig. 9A).

New Genera (Monotypic)

Chlorocanta Chatfield-Taylor, 2023 gen. nov.

Fig. 8 (A. dorsal habitus, B. male genitalia, right lateral view, C. male genitalia, dorsal view, D. female genitalia, ventral view, E. timbal)

Type species: *Okanagana viridis* Davis, 1918, here designated

Included species: *Chlorocanta viridis* (Davis, 1918) **comb. n.**

Type Locality: Holotype male is from O'Reilly, Bolivar County, MS, 10-VII-1917. The holotype is in the American Museum of Natural History (AMNH) and the allotype is located at the Mississippi Entomological Museum, Mississippi State University (Sanborn & Heath 2017).

Etymology: From the Greek *khlōrós,* meaning "pale green", in reference to the uniform green coloration of this genus, and Latin *cantus*, meaning "song" or "singing". Feminine.

Distribution: *Chlorocanta viridis* is found in the southeast United States. It is confined to deciduous forests and may be associated with elm (*Ulmus*; Hill & Marshall 2013). It is also known to come to lights unlike related New World Tibicininae. Its range extends east to near the Mississippi/Alabama border, west to Houston, Texas, north into the southwest corner of Tennessee, and there are several records from southeast Oklahoma.

Description: A medium-sized cicada that is most notable for the bright green coloration on the entire body of both sexes. The type species *C. viridis* was recently treated in detail (under *Okanagana viridis*) by Hill and Marshall (2013) and this description of *Chlorocanta* was aided in part by their paper.

Head: The width of the head across the eyes extends distinctly past apical pronotal margin. The clypeus is weakly produced and rounded, lacking a strong clypeal suture. The vertex has a depression along the midline but lacks a strong epicranial suture. *Thorax*: The lateral pronotal margins are subquadrate with the anterior margin convexly curved and the posterior margin sinuate. The apical angles of the pronotum are pointed and the humeral angles are rounded and not strongly pronounced. The center of the pronotum is broad, without a clear longitudinal sulcus. There are two bilateral fissures on each side of the pronotum that run inwards towards the center of the pronotum at an anterior-posterior angle. The cruciform elevation is located directly anterior to the hind margin of the mesonotum. The mesonotum is unmarked. The posterior edge of the metanotum is visible. *Wings*: Both fore and hind wings are hyaline with green venation. The fore wing length is 2.86–2.99 times the width, with 8 apical cells. The trapezoidal-shaped radial cell reaches the costal node halfway along length of costa, and the ratio of apical cell to ulnar cell length is approximately 1:1. The hind wing has 6 apical cells with a typical branched CuA vein (Fig. 8A). *Legs*: Metacoxa with a meracanthus with a distinct triangular shape, equal in length to the coxa. Metatibiae with spines, all other tibiae without spines. *Abdomen*: In males the timbals are completely exposed with the timbal membrane having two long and two short ribs (Fig. 8C; Hill & Marshall 2013) The tergites are a uniform green and the sternites are a paler yellowish-green compared to the rest of the body.

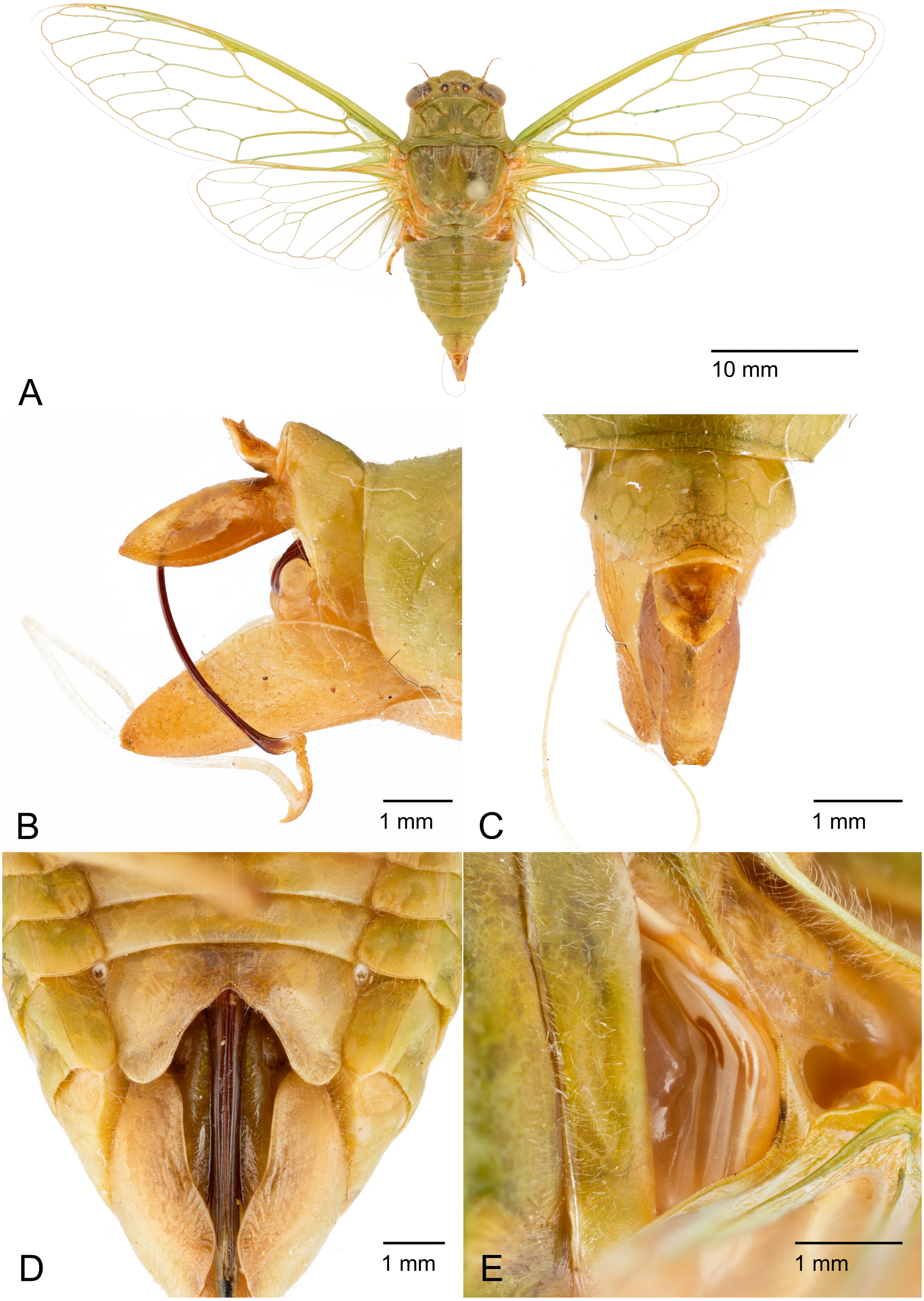


FIGURE 8. *Chlorocanta viridis*. A. male habitus, dorsal view, B. male genitalia, right lateral view, C. male genitalia, dorsal view, D. female genitalia, ventral view, E. timbal.

Male Genitalia: Sternite VII is twice the length of epipleurite VII and flattened at the tip. Sternite VII covers the base of sternite VIII. Sternite VIII is short, triangular, and tapering towards the tip with little curvature. The uncus is not hooked at the tip. The dorsal margin of the uncus is longer than the ventral margin, which curves up to form a distinct point as in many *Okanagana*.

Female Genitalia: Sternite VII has broad, almost triangular primary notch with slight bulging to the lateral margins and, contrary to Davis (1918), has a distinct secondary notch. The sides of sternite VII form rounded apical prongs.

Diagnosis: *Chlorocanta* is a North American cicada with the hind margin of the metanotum not hidden by the mesonotum, combined with a trapezoidal-shaped radial cell that reaches the costal node situated halfway along length of costa, characters that *Chlorocanta* shares with *Okanagana, Tibicinoides,* and *Hewlettia* **gen. nov.** If collection data is available, *Chlorocanta* is the only cicada with the above combination of characters within its range. If sufficiently preserved, the bright green coloration is enough to differentiate this genus from both *Okanagana* and *Tibicinoides*, however specimens of *Chlorocanta* often fade to a paler yellow which may confuse this single diagnostic feature (Hill & Marshall 2013). Male *Chlorocanta* possess two long timbal ribs (Fig. 8E) as in *Tibicinoides* but have an uncus without a hook (Fig. 8B), the combination of which separates male *Chlorocanta* from other related genera. The uncus of *Okanagana* is not hooked (Fig. 2B) and all species have more than two long timbal ribs (Fig. 2C) including *O. aurantiaca*, the only other green *Okanagana* in North America. *Tibicinoides* have two long timbal ribs (Fig. 3C) but the uncus is always hooked (Fig. 3B). *Hewlettia* **gen. nov.** are green but have 5 apical cells in the hind wing (Fig. 9A) as opposed to 6 apical cells in *Chlorocanta* (Fig. 8A), features unique in both sexes of the genus *Hewlettia* **gen. nov.**

While the large size (up to 25 mm; Davis 1918; Hill & Marshall 2013), and green (or faded yellowish color) is enough to diagnose females with reliability, the shape of sternite VII (Fig. 8D) can ensure a diagnosis. The almost triangular primary notch with slight bulging to the lateral margins and distinct secondary notch lacks the consistent rounding of the notch seen in *Tibicinoides* (Fig. 3D) and there are no purely green (or yellowish) *Okanagana* of that size except for *O. aurantiaca*, which may be immediately diagnosed by the presence of a long, black longitudinal stripe on the abdomen.

Hewlettia Smeds, 2023 gen. nov.

Fig. 9 (A. dorsal habitus, B. mesonotum detailing stridulatory grooves, left dorsolateral view, C. female genitalia, ventral view, D. male genitalia, right lateral view, E. male genitalia, dorsal view, F. male genitalia, ventral view)

Type species: *Okanagana nigriviridis* Davis, 1921, here designated.

Included species: *Hewlettia nigriviridis* (Davis, 1921) **comb. n.**

Type Locality: Holotype male and allotype female from USA, California, San Bernardino County, Upland, 1-VII-1920. Types deposited at AMNH with a single male paratype each deposited at Staten Island Institute of Arts and Sciences and the United States National Museum (Sanborn & Heath 2017).

Etymology: Named in honor of Esther Parnell Hewlett (1885–1975), an amateur entomologist and entrepreneur who made her living farming and selling Lepidoptera from Southern California. Between 1918 and 1922 she collected the type series of five cicada species (*Okanagana nigriviridis, rubrobasalis, simulata, Clidophleps wrighti*, and *Platypedia laticapitata)* near her home in Upland, California (Davis 1921, 1926). Feminine.

Distribution: *Hewlettia* is restricted to chamise habitat in the Peninsular, Transverse, and Southern Coast Ranges of California, as far north as San Luis Obispo County and as far south as Ensenada Municipality in Baja California, México.

Description: A medium-sized cicada with narrow wings and a dramatic green and black color pattern. *Head:* The width of the head and eyes is equal or slightly wider than the apical pronotal margin, and wider than the mesonotum. The clypeus is strongly produced. The center of vertex has a deeply sulcate epicranial suture. *Thorax:* The pronotal margins are subquadrate and wider than the mesonotum, with a sharply excavated longitudinal sulcus running along the midline. There are two bilateral fissures that run inwards towards the center of the pronotum at an anterior-posterior angle. Both the humeral and apical angles of the pronotum are rounded. The cruciform elevation is located directly anterior to the hind margin of the mesonotum. The anterior lateral sides of the mesonotum show vestigial stridulatory grooves in both sexes. The posterior edge of the metanotum is clearly visible. *Wings:* Both fore and hind wings are hyaline with blue iridescence, and the basal membranes are greenish white. The fore wing length is approximately 3.1 times the width, with 8 apical cells. The trapezoidal radial cell reaches the costal node halfway along length of the costa. Ulnar cells and cubital cell approximately equal in length. The apical cells are two-thirds to subequal the length of the ulnar cells. The basal cell is opaque and greenish white in color. All fore wing venation except for the costal vein is bordered with black infuscation. The hind wings have 5 apical cells resulting from an unbranched CuA vein (Fig. 9A). The postero-basal joint of the forewing has a curved swelling which contacts the stridulatory files on the mesonotum when at rest, forming a scraper. *Legs:* Metacoxa with the meracanthus reduced and almost lacking a triangular point, shorter than the length of the coxa. All tibiae are setose but only the metatibiae have spines. *Abdomen:* In males the timbals are completely exposed, with the timbal membrane having 5 long and 5 short ribs. In females, the posterior margin of epipleurite VII with sharp posterior projection that nearly covers tergite VIII. The lateral areas of the abdominal sternites, epipleurites, and tergites are covered with fine silvery hairs.

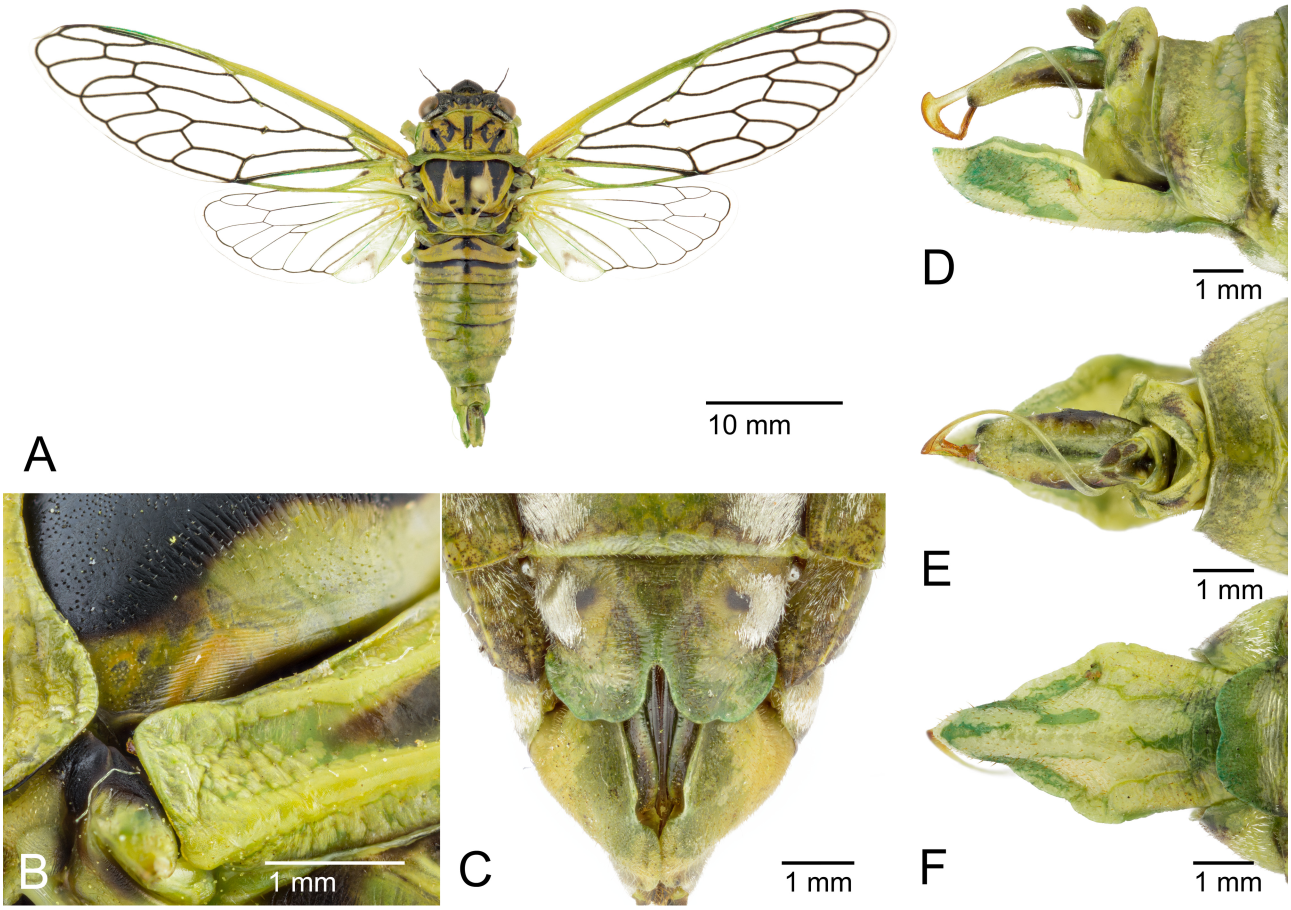


FIGURE 9. *Hewlettia nigriviridis*. A. male habitus, dorsal view, B. female stridulatory ridge, C. female genitalia, ventral view, D. male genitalia, right lateral view, E. male genitalia, dorsal view, F. male sternite VIII, ventral view.

Male genitalia: Sternite VIII extends parallel to the length of the body, partially housing the uncus and aedeagus. The sides of sternite VIII have pronounced lateral angles which taper posteriorly, such that the shape when viewed from below resembles the nib of a fountain pen (Fig. 9F). The uncus has a gentle downward curve in the lateral aspect, with the dorsal and ventral surfaces subparallel (Fig. 9D). In the dorsal aspect, the tip of uncus has a shallow medial notch (Fig. 9E). The aedeagus is long and whip-like, enclosed within a tubular groove in the ventral surface of the uncus.

Female genitalia: The posterior margin of sternite VII is divided by a sharp medial notch that swells out ventrally near its base. The sides of sternite VII form lobes that are broad and flattened posteriorly (Fig. 9C).

Diagnosis: *Hewlettia* can be distinguished from all other North American cicada genera by the combination of uncovered timbals, an exposed metanotum, and an unbranched CuA vein in the hind wing resulting in 5 apical cells (Fig. 9A). The former two characters are shared with *Okanagana*, *Tibicinoides*, and *Chlorocanta* **gen. nov.** In addition to the hind wing venation, the following features distinguish *Hewlettia* from *Okanagana*, *Tibicinoides,* and *Chlorocanta*: the green and black coloration; head including eyes wider than the mesonotum; blue iridescence of the wings; fore wings more than 3 times as long as they are broad; and a reduced meracanthus nearly lacking a conspicuous point. Males may further be distinguished by the pen nib shape of sternite VIII (Fig. 9F), and females by the flattened bilateral lobes on the posterior margin of sternite VII (Fig. 9C).

Synonymy

Okanagana noveboracensis (Emmons, 1854)

Cicada noveboracensis—Emmons, 1854: 152.
Tibicen rimosa—Uhler, 1892: 160 (Incorrect synonymy).
Tibicen noveboracensis—Osborn, 1895: 202 (A revision in status).
Okanagana rimosa—Distant, 1906: 126 (An incorrect synonymy).
Tibicen rimosa noveboracensis—Patch, 1906: 222 (As a subspecies of an incorrect synonymy).
Okanagana novaeboracensis—[sic], Gibson, 1911: 119 (Revised status, incorrect spelling).
Okanagana noveboracensis—Van Duzee, 1915: 38 (Current combination).
Cicada canadensis Provancher, 1889: 213. **New junior subjective synonym**. *
Neotype Locality: USA, New York, Erie County, Buffalo. Deposited at the Carnegie Museum of Natural History (Sanborn 2009).

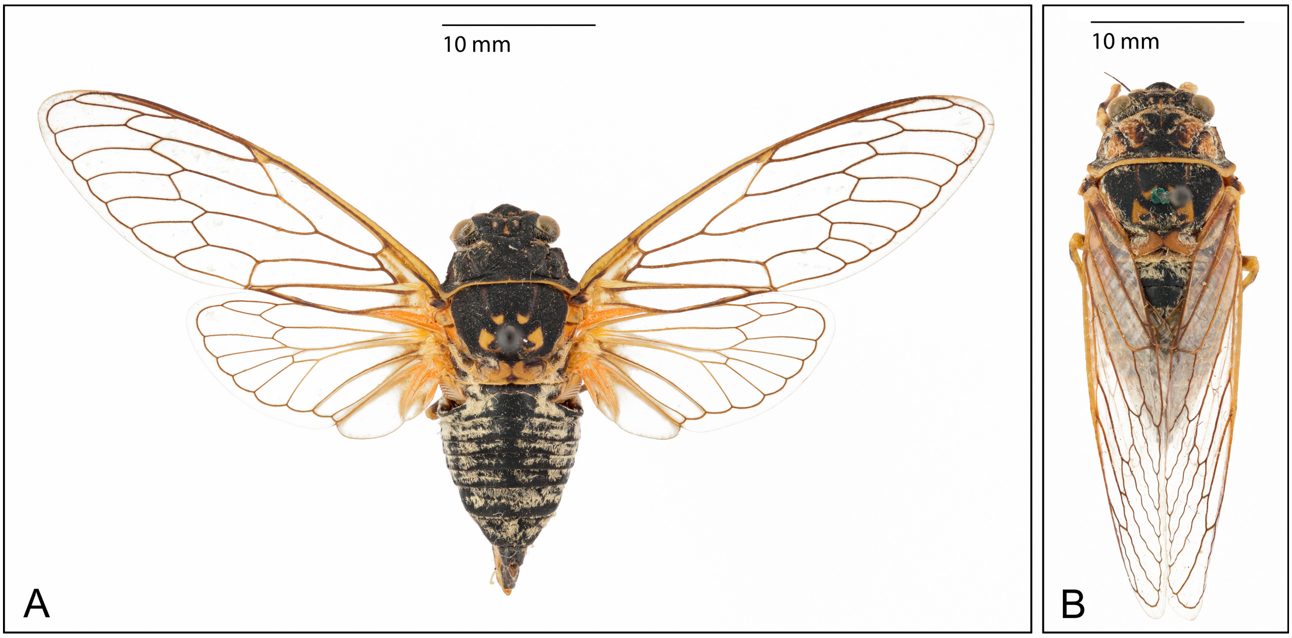


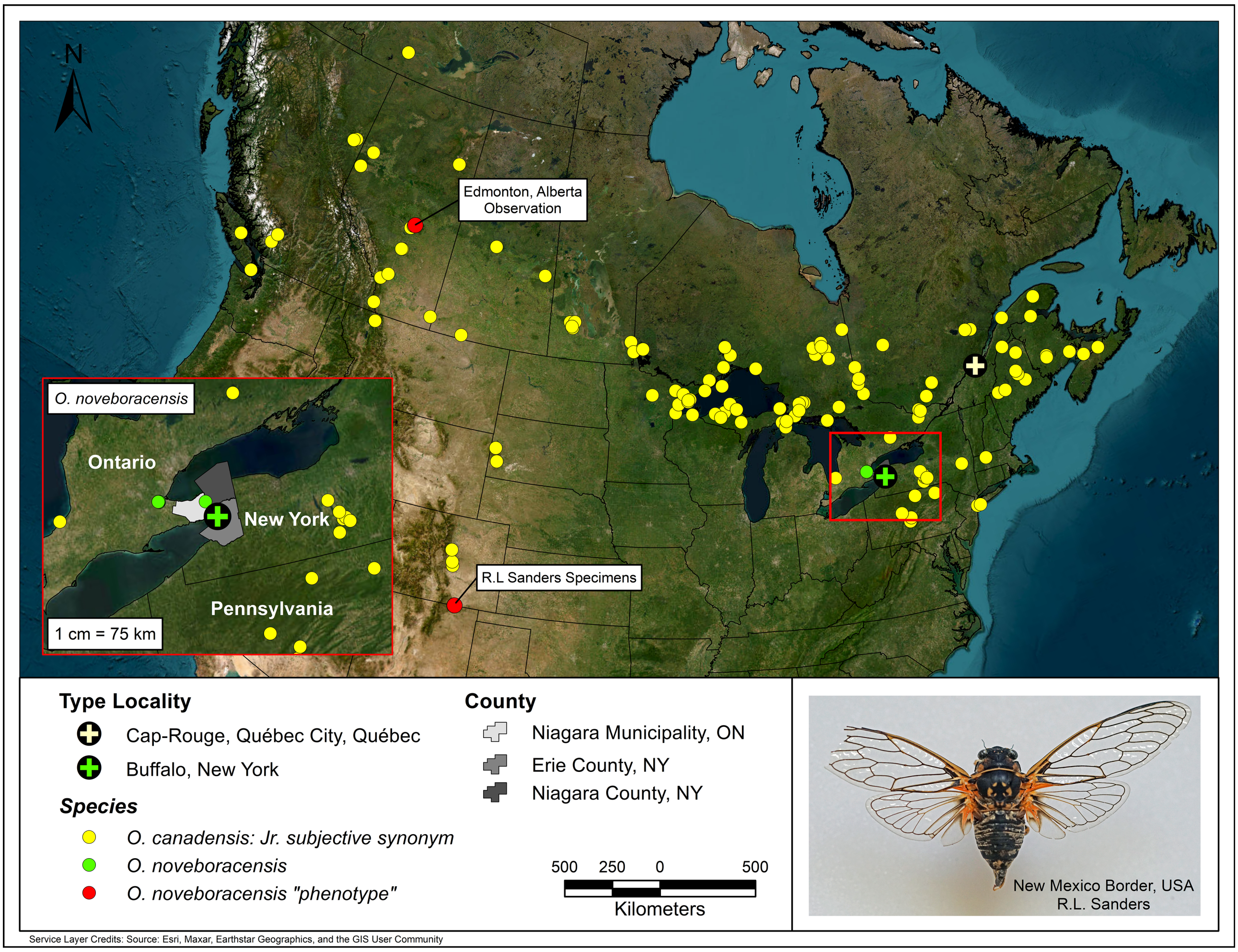
FIGURE 10. Habitus comparison between A. *O. canadensis* and B. *O. noveboracensis*.

Rationale for synonymy: *O. noveboracensis* is a color pattern variant (Fig. 10) that is not genetically differentiated (Figs. 4–5, 7), not geographically localized (Fig. 11), and not bioacoustically distinct (Table 3) from *O. canadensis*. Phylogenetically, *O. noveboracensis* nests within *O. canadensis* with no detected genetic distance (*COI* uncorrected genetic distance 0.00%; Supp. Table 2; Fig. 5). Type *O. noveboracensis* represent a localized population in northeastern North America that is peripatric (Fig. 11) to *O. canadensis* (Sanborn & Phillips 2013) that have the typical color pattern (Fig. 10A). At the opposite extreme of the range in southwestern USA, a pair of specimens obtained from R.L. Sanders north of the New Mexico border share the *O. noveboracensis* color pattern (Fig. 11 inset below right) but are genetically *O. canadensis* (JAC unpublished data). An *O. rimosa*-like species was previously mentioned from the Rocky Mountains (Kondratieff *et al.* 2002) that may also refer to this form of *O. canadensis* given the superficial similarities between *O. rimosa* and *O. noveboracensis* (Sanborn 2009). Bioacoustically, there are no known instances of peripatric species of *Okanagana* that share the same calling song (Chatfield-Taylor & Cole 2019; unpublished data), yet the calls of *O. canadensis* and *O. noveboracensis* are almost identical in syllable rate and overlap in dominant frequency (Table 3). Based on the combined evidence we make *O. canadensis* a **new junior subjective synonym** of *O. noveboracensis.*

TABLE 3. Peak frequency and syllable rate for *O. noveboracensis* and *O. canadensis*, where a syllable refers to a first order grouping of pulses and is used *per* Chatfield-Taylor and Cole (2019).

Species	Peak Frequency (kHz, ± SD)	Syllable Rate (s^{-1}, ± SD)	n	Number of Localities
O. canadensis	9.59 ± 0.64	24.9 ± 1.5	15	7
O. noveboracensis	9.70 ± 0.45	26.3 ± 0.9	13	1

*We are preparing an application to the ICZN, with Joel Kits at the Canadian National Insect Collection, under article 23.9.3 of the Code of Zoological Nomenclature to reverse the precedence of *O. canadensis* (Provancher, 1889) over *O. noveboracensis* (Emmons, 1854), and recommend maintaining the prevailing combination of *O. canadensis* until the Commission has ruled.



Service Layer Credits: Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community

FIGURE 11. Distributions of *O. canadensis* and *O. noveboracensis* showing peripatry. Inset details *O. noveboracensis* type locality. Lower right detail: habitus of *O. noveboracensis*-like phenotype from southwestern extreme of range.

Okanagana occidentalis (Walker *in* Lord, 1866)

Cicada occidentalis—Walker *in* Lord, 1866: 339.
Tibicen occidentalis—Woodworth, 1888: 68 (Incorrect synonymy).
Okanagana occidentalis—Van Duzee, 1915: 44 (Revised status).
Okanagana lurida—Davis, 1919: 192. **New junior subjective synonym**

Type locality: Canada, British Columbia, Chilliwack (Sanborn & Webb 2001). Lectotype deposited in the British Museum of Natural History (Sanborn & Heath 2017).

Rationale for synonymy: *O. lurida* from British Columbia, Canada, resolved at the crown of a paraphyletic grade of multiple samples of *O. occidentalis* (Figs. 4–7) separated by negligible genetic distance (*COI* uncorrected distance 0.00–1.45%; Supp. Table 2). We conclude that *O. lurida* is an uncommon color pattern variant of *O. occidentalis* (Fig. 12). Davis (1926, 1939) remarked upon the similarity between the two species in appearance and on the geographic distribution shared with *O. occidentalis* (Sanborn & Phillips 2013). Examination of numerous specimens of *O. lurida* in SEMK and CAS confirm that this color pattern variant occurs among specimens of *O. occidentalis* from throughout the distribution. Field observations have found *O. lurida* among large numbers of *O. occidentalis* (JAC, pers. obs.). *O. lurida* is therefore made a **junior subjective synonym** of *O. occidentalis*.

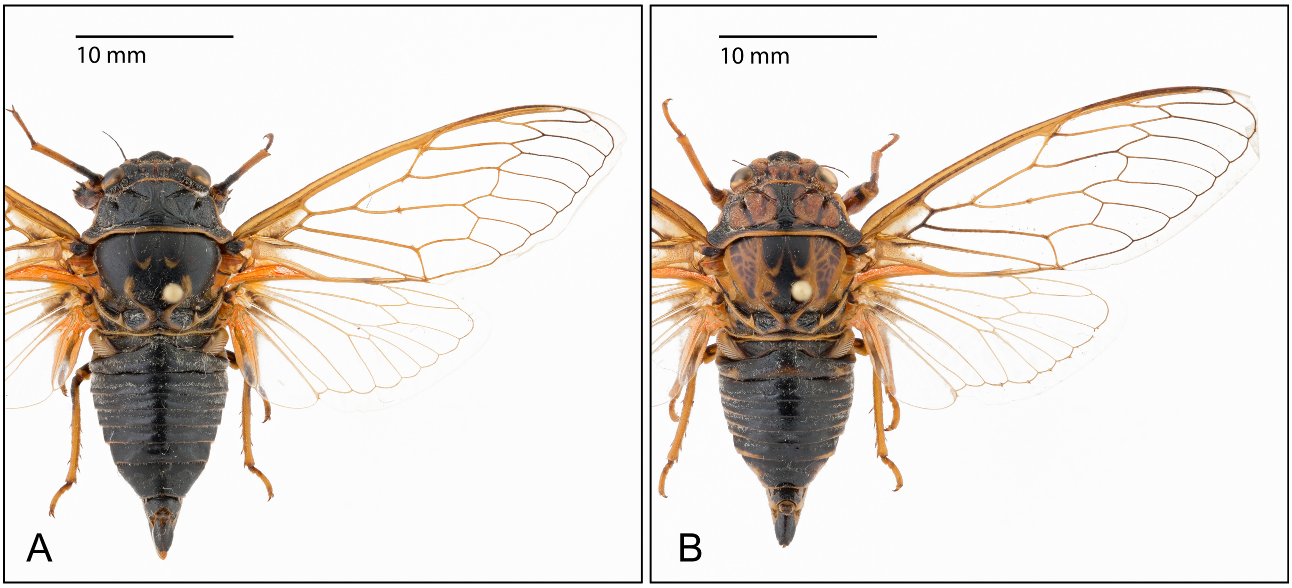


FIGURE 12. Habitus comparison between A. *O. occidentalis* with typical color pattern, and B. *O. occidentalis* collected from the same locality with uncommon *"O. lurida"* color pattern.

New Species

Okanagana rubrobasalis Davis, 1926 stat. rev. = *Okanagana tristis rubrobasalis* Davis, 1926

Okanagana tristis rubrobasalis—Davis, 1926: 184.
Okanagana rubrobasalis—Katō, 1932: 175 (Revised status to species level).
Okanagana tristis rubrobasilis—[sic], Simons, 1954: 178 (Revised status to original combination and spelling error)
Okanagana rubrobasalis **stat. rev.** (Revised to species level as proposed by Katō, 1932).

Type Locality: Holotype: male from Nellie, San Diego Co., CA, 24 June 1918; Allotype from Upland, San Bernardino Co., CA 1 July 1920. Holotype and allotype are deposited at American Museum of Natural History (Sanborn & Heath 2017).

Rationale for status revision: Two fresh specimens were sequenced, including one from near the allotype locality of *O. tristis rubrobasalis* at Upland, San Bernardino Co., California (Davis 1926; Supp. Table 1). Our results found a sister relationship for *O. tristis tristis* + *O. canescens* (Figs. 5–7). Unlike *O. tristis*, this species exhibits a rainfall-mediated protoperiodical phenology (Chatfield-Taylor & Cole 2017) and has a southern distribution that is allopatric from *O. tristis tristis*. There are also measurable, consistent differences in the dominant frequency of their call (unpublished data). The clear genetic separation from *O. tristis tristis* (*COI* uncorrected distance 5.56–5.68%; Supp. Table 2), combined with differing ecology and an allopatric distribution support revising the status of *O. tristis rubrobasalis* to the level of species as *O. rubrobasalis* **stat. rev.** as first proposed by Katō (1932).

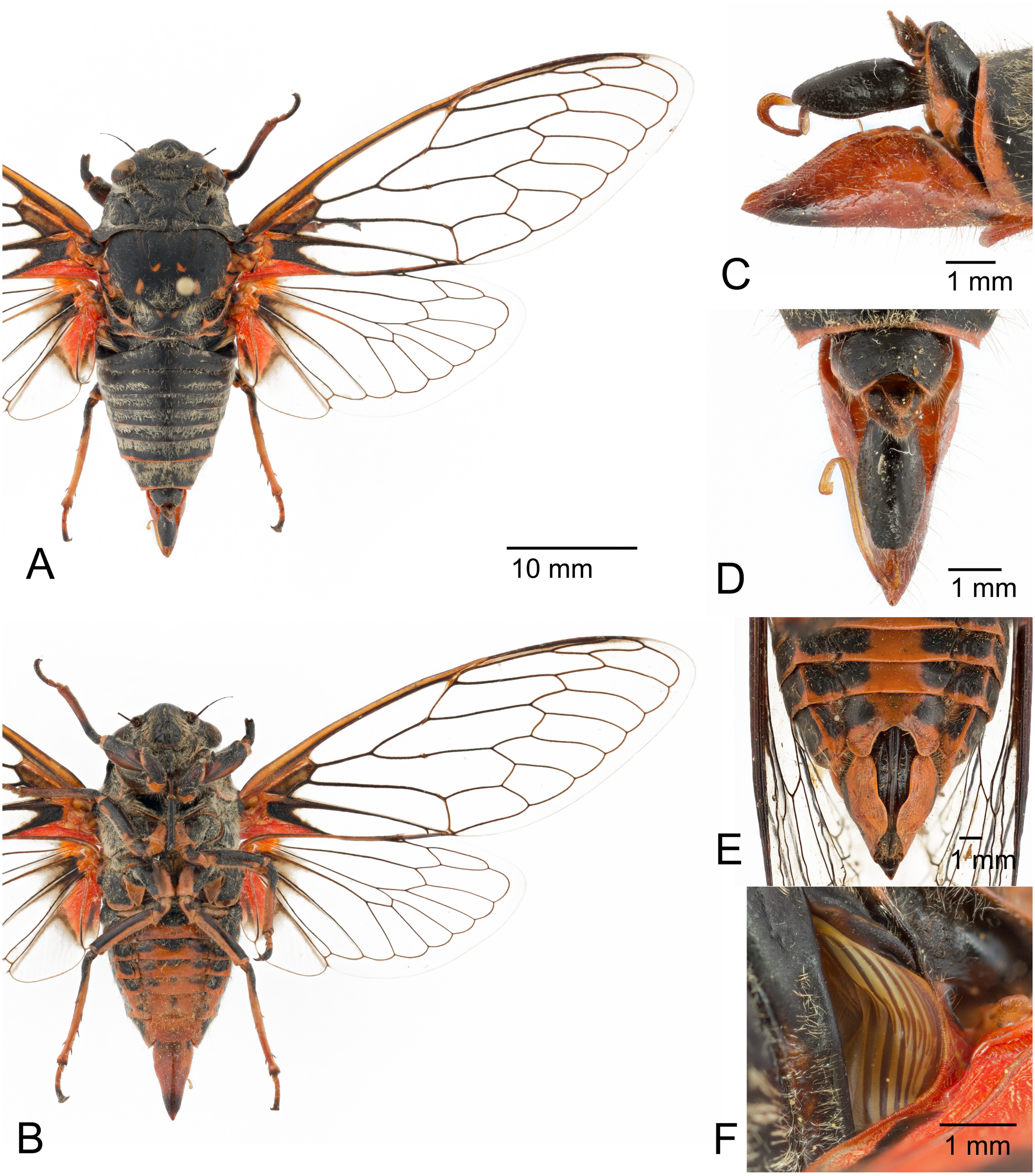


FIGURE 13. *Okanagana rubrobasalis* A. male habitus, dorsal view, B. male habitus, ventral view, C. male genitalia, right lateral view, D. male genitalia, dorsal view, E. female genitalia, ventral view, F. timbal.

Description: *O. rubrobasalis* was originally described as a subspecies of *O. tristis* (Davis 1926). Major separating features from *O. tristis* included the blood-red wing membranes in *O. rubrobasalis* (Fig. 13A, B) compared to pale orange in *O. tristis*, a longer, red sternite VIII (Fig. 13C, D) , broader wings, and the differing geographic distribution (Davis 1926). We here add that the front is strongly pronounced as in *O. cruentifera* rather than like *O. tristis*. The trapezoidal pattern of markings on the mesonotum are red and much less pronounced than the orange markings in typical *O. tristis*. In new specimens (which Davis seldom had) the sternites are also blood red (Figs 13B, E) rather than orange, losing this strong color gradually over time. The tergites are lined with red along their distal margins (Fig. 13A).

Discussion

Phylogenetic analysis. Given the generally short internodes (Figs. 4–5, 7), we hypothesize that *Tibicinoides* and *Okanagana* experienced rapid radiation in their recent evolutionary history (Kodandaramaiah *et al.* 2010; Rothfels *et al.* 2012; Shavit *et al.* 2007). Phylogenetic estimation is challenging for rapid radiations (Kodandaramaiah *et al.* 2010) due to both systematic and stochastic error. The phylogenetic hypotheses presented here were generally robust, especially with species-group resolution, but ingroup backbone relationships were problematic, particularly the base of the ingroup (Figs. 4–5, 7). Low support may come from gene tree incongruence, suboptimal outgroups, and poor phylogenetic signal in the data, which we discuss in turn.

First, incomplete lineage sorting or hybridization may lead to incongruence among gene trees (Joly *et al.* 2009; Meng & Kubatko 2009). Both incomplete lineage sorting and hybridization are expected with young taxa, for which there are several cicada examples (e.g. Banker *et al.* 2017; Marshall *et al.* 2011; Wade *et al.* 2015). Hybridization in particular, detected through mito-nuclear discordance (Gompert *et al.* 2008), may be expected among sympatric lineages that are reproductively isolated through prezygotic barriers such as calling song (e.g. Cole *et al.* 2021; Wade *et al.* 2015). While topological support varied between nDNA and mtDNA datasets (Figs. 4–5), namely poor resolution of the *Okanagana* ingroup with slower-evolving nuclear genes (see Wade *et al.* 2015), mito-nuclear discordance was generally not observed and resolution in concatenated analyses was strong (Figs. 6–7), suggesting little discordance. Our analyses thus appear to have avoided this type of systematic error.

Suboptimal outgroup rooting offers a potential explanation for poorly resolved regions of the topologies. A number and variety of outgroups are desirable for phylogenetic inference (Li *et al.* 2012), and multiple outgroups improve results over single outgroups (Shavit *et al.* 2007), especially when laddered across progressively deeper nodes (Wiley & Lieberman 2011). Outgroup choice for this study was limited by the relative paucity of genera of Tibicininae compared with other subfamilies like Cicadinae (Marshall *et al.* 2018; Sanborn 2014). Our analyses included laddered outgroups from a reasonable sampling of related tibicinine genera that included the close relatives *Subpsaltria* and *Tibicina* (Marshall *et al.* 2018; Sueur *et al.* 2007). Attempts to gather genetic data from aged pinned *Paharia* Distant, 1905 exemplars, which also have HU, were not successful. *Okanagodes* and *Clidophleps* are perhaps too distantly related to the ingroup (Figs. 4–5); long branches between outgroups and the ingroup reduce support as homoplasy accumulates (Rothfels *et al.* 2012; Wheeler 1990) or overwhelm the signal of shorter branches (Rothfels *et al.* 2012). Our analyses therefore effectively received rooting from only one closely related outgroup, *Subpsaltria* + *Tibicina* (Figs. 4–5).

Finally, multiple speciation events that occurred in rapid succession may not allow enough time for synapomorphies to solidify out of plesiomorphic character variation to avoid hard polytomies (Whitfield & Kjer 2008), introducing stochastic error. Short pairwise genetic distances for much of the ingroup, particularly among *Okanagana*, support the occurrence of this phenomenon in our trees (Supp. Table 2). We attempted to correct for systematic error through wide taxon sampling (Parfrey *et al.* 2010); the topologies presented here are indeed large improvements over preliminary analyses (not shown) with reduced taxon sampling. Perhaps multilocus methods are up to the challenge of overcoming the stochastic error. Although increasing the size of the character dataset often helps correct stochastic error this is no guarantee (Philippe *et al.* 2011), especially with rapid radiations (e.g. Gray *et al.* 2020; Scherz *et al.* 2022).

Systematic treatment. Our results provide evidence for the monophyly of a *Tibicinoides* + *Okanagana* ingroup that is sister to an outgroup clade comprised of *Subpsaltria* + *Tibicina* Figs. 4–7). The arrangement of outgroup and ingroup genera agree with subfamily- (Marshall *et al.* 2018) and genus-level (Sueur *et al.* 2007) studies. Doubt as to the monophyly of *Okanagana* with respect to *Tibicina* (Sueur *et al.* 2007) is dispelled.

We define *Tibicinoides* as a natural group by reassigning all HU *Okanagana* to that genus, settling the status of and species assignments to *Okanagana* and *Tibicinoides* per Distant that have been in question since the most recent revision of those genera (Davis 1919). We erect two new genera, *Chlorocanta* and *Hewlettia* (Fig. 7), for orphaned lineages with transitional character states that resolved at the base of the ingroup (Figs. 4–7). Isolated taxa are frequently observed as relict lineages that lie sister to diverse clades (e.g. Simon *et al.* 2019). The lineages we recovered in our analyses are congruent with and explain shared morphology, physiology, and behavior among clades, details of which now follow.

Reconstruction of the evolutionary history of uncus shape given our phylogenetic hypotheses found HU as a plesiomorphic character state. HU was then lost in the most recent common ancestor of the ingroup and regained as a shared derived character of *Tibicinoides* (Fig. 6). We acknowledge that the reconstructed history of the uncus shape character may change as the relationships at the base of the ingroup are resolved and as more genera of the Tibicininae are added to the phylogeny. For now, weak evidence for a *Hewlettia* + *Tibicinoides* clade (Fig. 5) supports the hypothesis that *Tibicinoides* regained the HU character state as the *Hewlettia* uncus lacks a hook. Separate HU origins are supported by comparative morphology of the male genitalia between outgroups and *Tibicinoides* (Fig. 1). The *Tibicinoides* uncus is subcylindrical above and concave below, the hook formed from a distoventral notch formed from a short emargination along each ventrolateral margin (Fig. 1C–D). The uncus of outgroup genera is also concave below and is subcylindrical throughout much of its length, but the hook tends to be formed by a decurved, apical cylindrical constriction and the distoventral emargination tends to be longer and more pronounced (Fig. 1A–B). Uncus character states are uniform within New World genera as redefined in this work: all *Tibicinoides*, *Clidophleps*, and *Okanagodes* possess HU of similar morphologies within their respective genera, and all *Okanagana* have an uncus without a distoventral hook. Although the Old World outgroup *Subpsaltria* and the majority of *Tibicina* species have HU, some *Tibicina* show an uncus without a hook (Hertach 2021), illustrating that this sexual character may vary within genera as well.

The new genera described in this work exhibit transitional character states between the outgroups and the ingroup. *Chlorocanta* combines an uncus without a hook (Fig. 8B), as in *Hewlettia* and *Okanagana*, with two timbal ribs (Fig. 8E) as in *Tibicinoides* (Fig. 3C). *Hewlettia* presents a mosaic of characters across the tibicinine genera. Of note is the presence of a file on the mesonotum (Fig. 8B) and a scraper on the forewing of both sexes, a character shared with both *Clidophleps* and *Subpsaltria* (Luo & Wei 2015b; Varley 1939) but not with *Chlorocanta*, *Okanagana*, or *Tibicinoides.* Despite possessing this character there are no records of *H. nigriviridis* stridulating.

Our contribution to the evolutionary history of the Tibicininae also improves understanding of bioacoustical evolution. *Tibicinoides* and *Okanagana* calls consist of a constant syllable rate (a first order group of pulses per Baker & Chesmore 2020) produced at a consistent dominant frequency (Chatfield-Taylor & Cole 2019). *Tibicinoides* songs are, in some species, characterized by high intraspecific variation in syllable rate (Chatfield-Taylor & Cole 2019; Sanborn *et al.* 2002; unpublished data) while *Okanagana* (Chatfield-Taylor & Cole 2019) and *Tibicina* (Popov 1975; Sueur & Aubin 2003) exhibit low intraspecific variation in syllable rate. Physiologically, *Tibicinoides* timbals use synchronous muscle and activate under neurogenic control, while *Okanagana* timbals have asynchronous muscle fibers that are myogenic (Josephson & Young 1985; JRC unpublished data). Our phylogenetic hypotheses prompt the study of *Chlorocanta* and *Hewlettia* bioacoustics in order to complete the comparative picture. The *Hewlettia* calling song structure is more similar to those of *Chlorocanta, Okanagana*, and *Tibicinoides* rather than to *Clidophleps*, *Subpsaltria*, and *Tibicina* (unpublished data). Thus, *Hewlettia* morphologically and behaviorally bridges *Okanagana* with the Old World relatives *Subpsaltria* and *Tibicina* as well as with the early branching New World *Clidophleps.*

The present work was largely concerned with genus-group systematics. Species level systematics will be handled in forthcoming revisions of *Okanagana* and *Tibicinoides*, but here we begin updating classification in clearcut cases: two color pattern variants (Figs. 10–12) were synonymized and a subspecies (Fig. 13) was reinstated to species rank. Increased population sampling will be required to decide upon the status of several other taxa. For example, populations of *T. mercedita* and *T. minuta* showed no affinity with current classification (Figs. 4–7), but we make no changes pending increased population sampling and analysis of genetics and behavior from topotypes. Several species named by Bliven (1964) are dubious and were largely omitted from consideration in this work pending revision.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper. Supplementary Table 1. Exemplars and GenBank accessions; Supplementary Table 2. Uncorrected *COI* genetic distance matrix from mtDNA dataset (analysis (2) in Methods: Phylogenetic analysis); Supplementary Table 3. Collection data for imaged specimens.