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A new species of *Okanagana* from the Walker Lane region of Nevada and California (Hemiptera: Auchenorrhyncha: Cicadidae)

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Abstract

Okanagana boweni **sp. n.** is described from the western margin of the Great Basin of North America. The new species is diagnosed from allopatric *O. simulata* Davis and sympatric *O. utahensis* Davis using morphological, bioacoustical, and molecular characters. The distribution of this new species coincides with the Walker Lane region that lies along the border of California and Nevada, USA. Based on geography, bioacoustics, morphology, and molecular phylogenetics, we hypothesize that *O. boweni* **sp. n.** is the allopatric sister species of *O. simulata*.

Key words: bioacoustics, cicadas, allopatry, reproductive isolation, Lake Lahontan, Great Basin

Introduction

Of the 186 cicada species known in North America north of México (Sanborn & Heath 2017), 57 species (31%) belong to the genus *Okanagana*, with the majority of those species found in the western portion of the continent (Sanborn & Heath 2017; Sanborn & Phillips 2013). Apart from regional faunas (Colorado: Kondratieff *et al.* 2002; California: Simons 1954), faunal catalogues (Sanborn 2014; Sanborn & Heath 2017) and the addition of *O. georgi* Heath & Sanborn from Arizona (Heath & Sanborn 2007), *Okanagana* systematics remains in the era of William T. Davis one century ago, who published numerous original descriptions (bibliography in Sanborn 2014) and a synopsis of the genus (Davis 1919). Among the many species described by Davis were *O. simulata* Davis: a large, heavy bodied, black cicada with the type locality at Upland, San Bernardino County, southern California (Davis 1921; Sanborn & Heath 2017) and *O. utahensis* Davis, a widespread inhabitant of habitats containing Great Basin sagebrush (*Artemisia tridentata* Nutt.) (Sanborn *et al.* 2002).

The discovery of new *Okanagana* species is expected given the broad geographic range and the diversity of the genus, especially in the Great Basin (Sanborn & Phillips 2013) which includes some of the most remote localities in the contiguous United States (Rentz 1973). Within this morphologically homogeneous group are species that are widespread (Sanborn & Phillips 2013) and common (Beamer & Beamer 1930; Kondratieff *et al.* 2002) in western North America. Widespread, common species may be undersampled (see Cole & Chatfield-Taylor 2012), especially by naturalists and collectors seeking diversity, and once carefully examined may consist of numerous valid species (e.g. Popple & Walter 2010; Price *et al.* 2007; Sueur & Puissant 2007; Wang *et al.* 2014; Weissman & Gray 2019). Bioacoustical (e.g. Cole 2008; Costa *et al.* 2017; Hertach *et al.* 2016) and molecular techniques that reveal morphologically cryptic species (Bickford *et al.* 2006) will be particularly effective for species discovery in *Okanagana*. The calling songs of *Okanagana* tend to be diagnostic and may facilitate mate recognition in sympatry (Chatfield-Taylor & Cole 2019). Species tend to form in allopatry, however (Coyne & Orr 2004), so in cases of recent allopatric speciation songs may not have diverged significantly (e.g. Liu *et al.* 2019; Popple *et al.* 2008).

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Methods

Morphology. The majority of the specimens examined for this work were collected by the authors during ongoing fieldwork throughout the western United States from 2008-2019. Specimens were examined from the Natural History Museum of Los Angeles County (LACM), the Snow Entomological Museum, University of Kansas (SEMK), the California Academy of Sciences (CAS), and the Cornell University Insect Collection (CUIC; Supp. Table 1).

The uncus of adult males was extruded by immersing the tip of the abdomen in boiling water for a few minutes. Images of male terminalia are depth compositions made with a digital microscope (model VHX-6000, Keyence Corp., Itasca, IL) with a 10 x objective set to 50 x magnification and were exported as .tif files. Female terminalia were imaged using a digital SLR camera (model 7D with MP-E 65 mm macro photo lens and Speedlite 600EX-RT flash, Canon USA Inc., Long Island, NY). Habitus photographs were taken with a digital camera (model TG-5, Olympus Inc., Center Valley, PA) set to microscope mode with image stacking. Measurements were made with a digital 0-6 inch Vernier caliper (Sangabery, Guangdong, China) with body length measured from the frons to the pygidium in males. The species description (see Results) combines characters from the holotype and paratypes to account for strong color pattern variation and slight morphological variation.

Bioacoustics. Calling songs were recorded in the field with a digital PCM recorder (model PCM-D50, Sony Corp., New York, NY) set to a 96 kHz sampling rate and bit depth 16. The frequency range of this equipment (flat response to 40 kHz) encompassed the entire frequency output of the calling songs of these cicadas. Temperatures were measured in the vicinity of singing males with a digital thermal sensor (model Trail Pilot 2, Highgear USA, Inc., Fletcher, NC). Songs were analyzed in Audacity v. 2.3.3 (available from www.audacityteam.org). Syllable rates were measured from syllable counts in 0.5 s oscillogram windows. We define a syllable as the unit of sound output from one contraction of the timbal and all of its ribs (*sensu* Chatfield-Taylor & Cole 2019). Peak frequencies were calculated using a fast Fourier transformation in a Hanning window of size 512. RavenLite v. 2.0 (available from ravensoundsoftware.com) was used to visualize .wav files. Sing-fly behavior is common in these cicadas; thus, we did not collect accompanying voucher specimens for all recordings (Supp. Table 2), but correct assignments were nonetheless possible as recordings were either from populations where the new species was the only *Okanagana* singing (e.g. the type locality) or, if multiple *Okanagana* species were calling at a locality, visual confirmation was made of the calling individual. Statistical song analysis was performed in R (available from www.r-project.org). First, each song character was compared individually between species using ANCOVA, with ambient temperature as a covariate. Second, song characters were tested simultaneously with species identity and population (locality) as predictor variables in MANOVA tests.

Distribution. Museum specimens were georeferenced using Google Earth Pro v. 7.3.2 (available from www.google.com/earth). Specimen records and biogeographic regions were plotted with ArcMap v. 10.1 (ESRI 2012). The polygon that outlines the Walker Lane region was digitized from Carlson *et al.* (2013).

Molecular phylogenetics. We selected a set of taxa that represent relatives of the new species plus described related species based on preliminary phylogenetic analyses with a collection of over 300 tibicinine DNA vouchers (Cole and Chatfield-Taylor, unpublished). All molecular voucher specimens are deposited at LACM. DNA was extracted from middle legs preserved in 100% ethanol using a commercially available extraction kit (DNEasy Blood and Tissue Kit, Qiagen Inc, Valencia, CA). Extractions followed the manufacturer protocol for tissues except for an overnight proteinase K digestion at 55°C and a final elution step that consisted of two 50 µl volumes. Three gene regions were polymerase chain reaction (PCR) amplified: the entire mitochondrial *16S rDNA* gene (*16S*), a fragment of *elongation factor 1 alpha* (*EF1*α) that spanned 3 exons and 2 introns (Marshall *et al.* 2018), and the 5' untranslated region (UTR) plus a portion of the coding region of *acetyltransferase 1* (*ARD1*; Owen *et al.* 2015). Identical touchdown PCR profiles amplified each gene region as follows: initial denaturation for 5 min at 95°C, 10 cycles of 60 s denaturation at 95°C, 15 s annealing that began at 55°C and dropped 1°C/cycle to end at 45°C, 75 s extension at 68°C, 30 cycles as before except with a fixed 45°C annealing temperature, and a final 7 min extension at 72°C. *ARD1* amplification utilized nested PCR, in which a 1:100 dilution of the initial amplicon served as a template for the second PCR reaction. PCR products were sequenced in both directions using the PCR primers by a commercial service (Laragen Inc., Culver City, CA, USA).

Trace files were brought into Geneious v. 3.6 (www.geneious.com) for contig assembly and editing. *EF1*α exons and *ARD1* CDS were aligned by amino acid sequence in Geneious. Noncoding *16S*, *ARD1* UTR, and *EF1*α introns 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 handled in Mesquite v. 3.61 (Maddison & Maddison 2015). Indels for all noncoding regions were coded into a standard categorical matrix where 1 = presence of a nucleotide and 0 = gap at a given position in the sequence. Data partitioning and nucleotide substitution model selection were accomplished with PartitionFinder v. 2.0 (Lanfear *et al.* 2012, 2016). Phylogenetic analysis was performed with MrBayes v. 3.2.7 (Huelsenbeck & Ronquist 2001; Ronquist *et al.* 2012; Ronquist & Huelsenbeck 2003) with the following specifications: indels coded as restriction data with variable coding, all partitions unlinked, all starting topologies considered equally likely, and four runs of four chains (3 heated and 1 cold chain) each for 3 x 10^7 generations. Phylogenetic trees were visualized in FigTree v. 1.4.4 (available from http://tree.bio.ed.ac.uk/software/figtree/).

Results

Okanagana boweni Chatfield-Taylor and Cole, new species

Table 1 (measurements), Table 2 (song statistics), Table 3 (molecular vouchers), Fig. 1 (habitus), Fig. 2 (male timbal), Fig. 3 (male terminalia), Fig. 4 (female terminalia), Fig. 5 (calling song), Fig. 6 (geographic distribution), Fig. 7 (phylogenetic hypothesis). Zoobank ID: 9C190D25-DE35-406D-AC4C-803AF864F25C

Type material. HOLOTYPE: 1 male, USA, NV, Washoe Co., Pyramid Lake, Tamarack Beach, 39.91333°N, 119.54083°W, 1134 m, 10-VII-2019, JA Cole, J Bailey, W Chatfield-Taylor, JF Eguizabal leg., ex tamarisk, rabbitbrush, recording WCT3737, barcode JAC000000230, deposited at LACM, LACM ENT 456101.

PARATYPES: 1 female, same data as holotype, LACM; 1 male, same data as holotype, CAS; 1 male, 1 female, same data as holotype, DNA extractions SING0873, SING0874, LACM; 3 males, same data as holotype, SEMK; 1 male, USA, CA, Inyo Co., Lone Pine Campground, 7 miles west of Lone Pine on Whitney Portal Road, 36.5977°N, 118.1838°W, 1785 m, 9-VII-2008, JA Cole leg., ex *Artemisia tridentata*, DNA extraction SING0246, LACM; 1 male, same data as previous, CAS; 2 males, same data, SEMK; 1 male, CA, Inyo Co., Lone Pine 15 mi. S, 36.3981°N, 118.0256°W, 1129 m, 18-VI-1969, PM Jump leg., LACM; 1 male, CA, Inyo Co., Lone Pine Cp. Gr., 36.5971°N, 118.1769°W, 1744 m, 28-VI-1970, DS Verity leg., LACM; 1 male, CA, Inyo Co., Tinemaha Rd. 2 mi. E US395 nr. Independence, 36.8563°N, 118.2145°W, 1165 m, 28-V-1978, N Lee leg., LACM; 5 males, CA, Lassen Co., Doyle 4.5 mi. S, 39.9792°N, 120.0622°W, 1219 m, 15-VI-1969, RR Snelling & RA Snelling leg., LACM (Supp. Table 1).

Description. Head width narrower than front of pronotum. Deep median groove in yellow triangle at base of epicranium continues between lateral ocelli to form the epicranial suture. Front strongly produced with a median sulcus. Frons hirsute with deep frontocylpeal suture. Supra-antennal plates orange (Fig. 1).

Lateral margins of pronotum distinctly subparallel with broad posterior margin entire, giving a quadrate aspect. Humeral angles broadly rounded, anterior angles acute. Pronotum completely bordered with yellow. Rugose ridges lateral to pronotal midline marked with variable amounts of brown or yellow. Anterior half of pronotum with strongly sulcate broad longitudinal yellow line. Mesonotum black, with broad yellow posterior margin and cruciform elevation partly (holotype) to completely (paratypes) yellow. Four yellow spots form a semicircle with yellow marks at base of each wing. Size and shape of mesonotal markings variable (extensive in holotype). Metanotum bordered by yellow that is interrupted by black anterior to timbals (Figs. 1, 2).

Forewings with yellow costa turning black and slightly fuscous past the node. Venation variegated with yellow to marginal cells (holotype) or mostly black (some paratypes). Posterior margin of membrane gently curved, wing tip rounded (feature visible only on spread, intact specimens). Basal cell opaque, varying from black (holotype) to yellow (some paratypes). Hind wings lightly fuscous at base. Wing membranes orange. Meso- and metasternum hairy, marked with black and yellow. Profemora striped black and yellow, other legs variably marked (Fig. 1).

Tergum sparsely hairy, shining black, with posterior margin of last two tergites variably bordered with yellow (Fig. 1). Male timbals with 2 major and 2 minor ribs (Fig. 2). Sternites yellow with extensive variable black markings edging posterior margins; in holotype, yellow markings are narrow at the center and broaden laterally, giving the impression of a central longitudinal black stripe bordered by two yellow stripes on the abdominal venter. The 7th abdominal sternite hourglass-shaped, medially constricted with rounded apical margins (Fig. 1).

Uncus in dorsal view diamond-shaped, formed from straight lateral margins that widen for one half to two thirds of the length and then converge towards the apex (Fig. 3 shows typical condition). In lateral view, upper surface with distinct curvature, not parallel with respect to lower surface. Hook forms abruptly after short and deep posteroventral excavation. Aedeagus elongated, attached at an angle perpendicular to the plane of the uncus with posterior edge distinctly incurved to varying degrees. Male valve roughly triangular with posterior edge slightly curved. Female with apical prongs on 7th abdominal sternite broad and rounded with a wide, faint secondary notch (Fig. 4).

Diagnosis. *Okanagana boweni* is a large-bodied species most similar to allopatric *O. simulata* in body size and habitus but to sympatric *O. utahensis* in color pattern (Fig. 1). Diagnosis of museum specimens may be accomplished by a suite of characters, some of which are visible on spread specimens with pulled genitalia and others on unprepared specimens.

In unprepared specimens a character combination is necessary for diagnosis of the three similar species. A quadrate pronotum with parallel lateral margins separates *O. boweni* and *O. simulata* from *O. utahensis*, which has an anteriorly constricted pronotum, and a broad longitudinal yellow sulcus on the anterior half of the pronotum separates *O. boweni* and *O. utahensis* from *O. simulata*, in which the sulcus is barely indicated and faintly marked (Fig. 1). Thus, *O. boweni* possesses both a quadrate pronotum with a broad yellow longitudinal sulcus. Less reliable diagnostic characters include the semicircle of mesonotal markings, which tend to be more extensive in *O. boweni* and *O. utahensis* compared with those of *O. simulata*, the head width narrower than the anterior margin of the pronotum in *O. boweni* but subequal in *O. simulata*, and the posterior pronotal margin appearing complete in *O. boweni* but incomplete in *O. simulata* due to a darkened median constriction in the latter (Fig. 1).

On prepared specimens the uncus and aedeagus are valuable characters for diagnosing the two species (Fig. 3). Uncus shape should be used in conjunction with other characters due to intraspecific variation that is found generally throughout *Okanagana* (WCT pers. obs.). In dorsal view, the uncus of *O. boweni* has parallel lateral margins that converge towards the apex with a distinct angle that begins at one half to two thirds of its length, compared with the gradually and smoothly curved lateral margins of *O. simulata* and *O. utahensis*. When exposed in lateral view, the aedeagus is a singular character that diagnoses *O. boweni* from both *O. simulata* and *O. utahensis.* The posterior edge of the aedeagus is long and incurved in *O. boweni*, forms an acute angle in *O. simulata*, and is uniformly straight and short in *O. utahensis* with its posterior margin situated perpendicular to the plane of the uncus (Fig. 3).

Female *O. boweni* may be diagnosed by the lack of the deep secondary notch on the 7th abdominal sternite found in *O. simulata* and to a lesser extent in *O. utahensis* females (Fig. 4). For *O. utahensis* without clearly indicated secondary notches, diagnosis may require examination of pronotal shape or the condition of the longitudinal sulcus (Fig. 1).

O. boweni is sympatric with *O. utahensis* but can be diagnosed from the latter in the field by the larger body size (Table 1) and quadrate aspect of the pronotum of *O. boweni*, in contrast with the smaller body size and trapezoidal aspect lent by the anterior convergence of the lateral pronotal margins in *O. utahensis* (Fig. 1). The morphology of the male (Fig. 3) and female (Fig. 4) terminalia are also diagnostic.

TABLE 1. Average measurements from examined series and holotype measurements for *O. boweni* **sp. n.**, *O. simulata*, and *O. utahensis* (Davis 1919; Davis 1921). Holotype measurements follow the colon. Specimens that are not spread reduce the sample size for wingspan measurement below body size characters. See Supplementary Table 1 for specimen level data. *One specimen not measured due to preservation in alcohol.

Species	Body length	Expanse of forewings	Width of head across eyes
O. boweni **sp. n.** (n=19)*	26.9 ± 1.5: 29.0	69.8 ± 2.5 (n=6): 65.3	8.8 ± 0.3: 8.5
O. simulata (n=11)	26.0 ± 0.9: 27	73.6 ± 2.1 (n=8): 75	8.7 ± 0.3: 9
O. utahensis (n=12)	23.3 ± 1.2: 24.5	61.7 ± 2.1 (n=3): 60	7.7 ± 0.4: 8

Bioacoustics. The male calling song of *O. boweni* is a continuous train of syllables with a single dominant frequency that is similar to the calls of both *O. simulata* and *O. utahensis* (Table 2; Fig. 5; see Chatfield-Taylor & Cole 2019). Amplitude modulation at a rate of 7.82 ± 0.47 s^{-1} (n = 4) may elaborate the song structure (Fig. 5), and when this occurs a wavering quality is imparted to the song as it oscillates in loudness. Amplitude modulations often began or became more pronounced when males were disturbed or approached, behavior that was also observed in *O. simulata* and *O. utahensis* (JAC, pers. obs.).

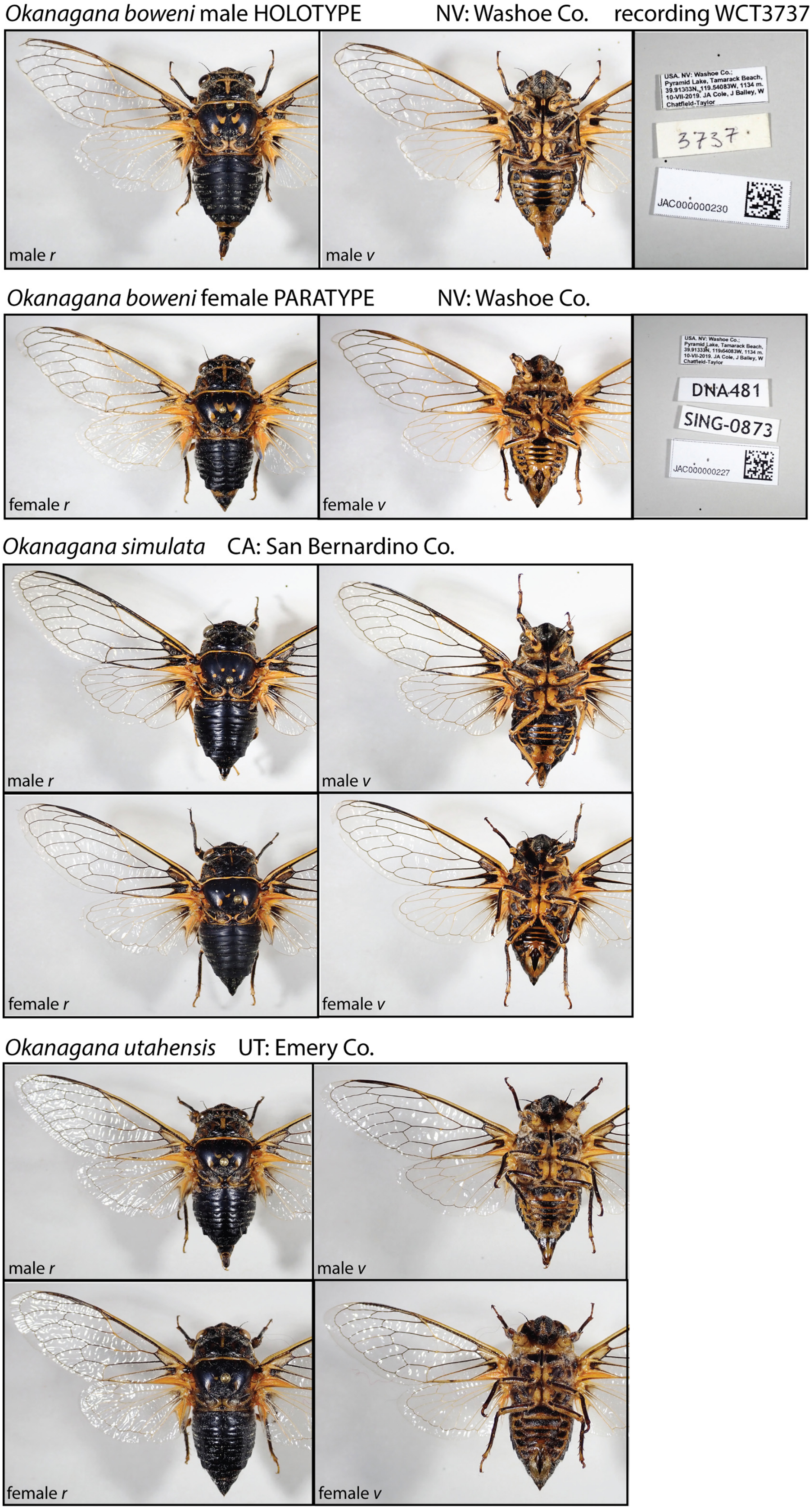

FIGURE 1. Dorsal (left column *r*) and ventral (right column *v*) habitus of *Okanagana boweni* **sp. n.** (top row), *O. simulata* (middle row) and *O. utahensis* (bottom row).

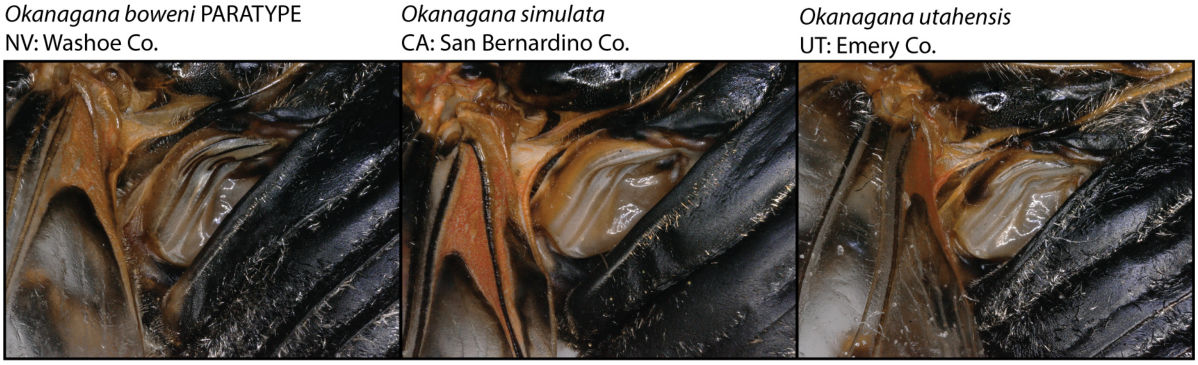

FIGURE 2. Male timbals of *Okanagana boweni* **sp. n.** (left), *O. simulata* (middle) and *O. utahensis* (right), left dorsolateral view.

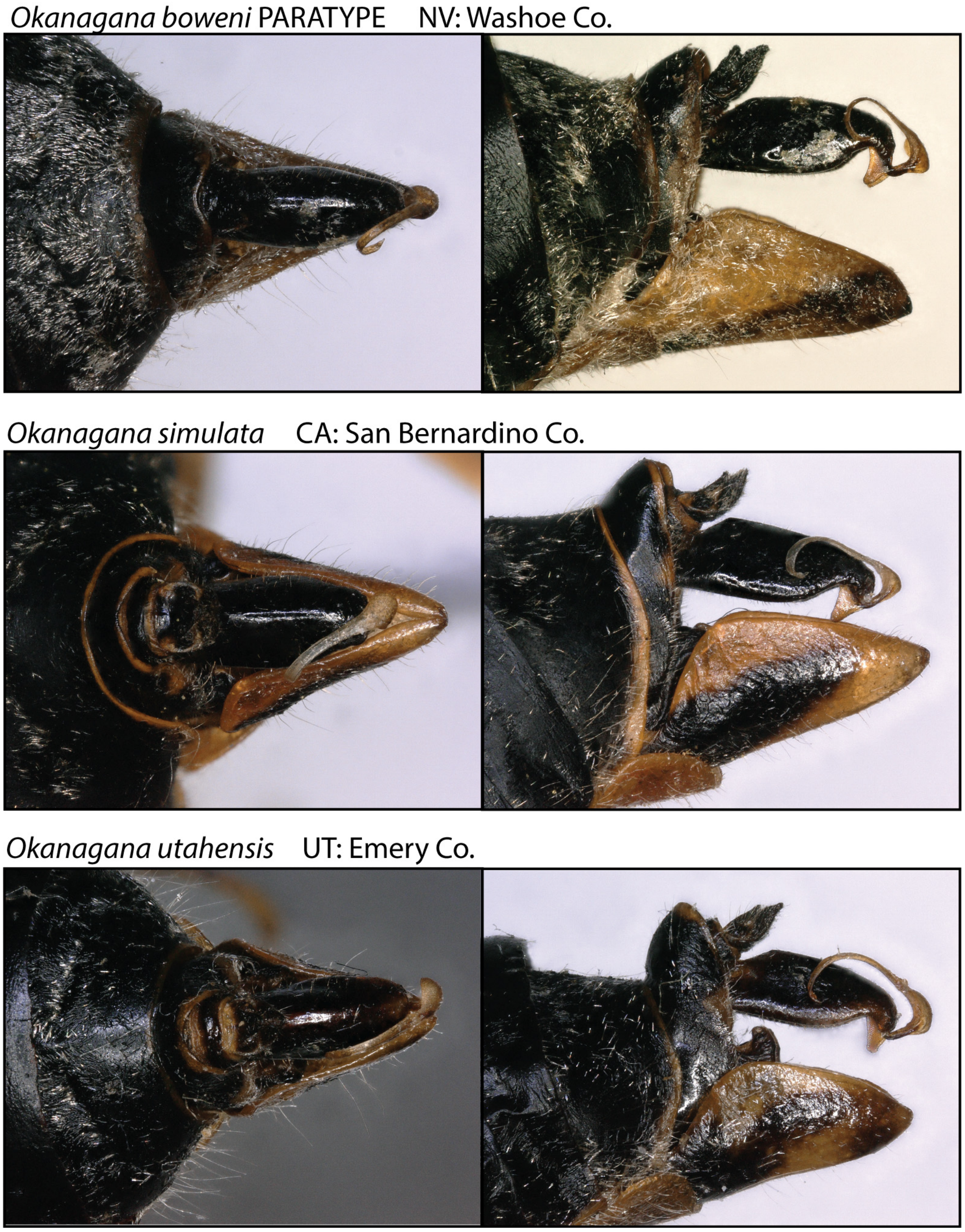

FIGURE 3. Male terminalia of *Okanagana boweni* sp. n. (top row), *O. simulata* (middle row), and *O. utahensis* (bottom row), in dorsal view (left column) and left lateral view (right column).

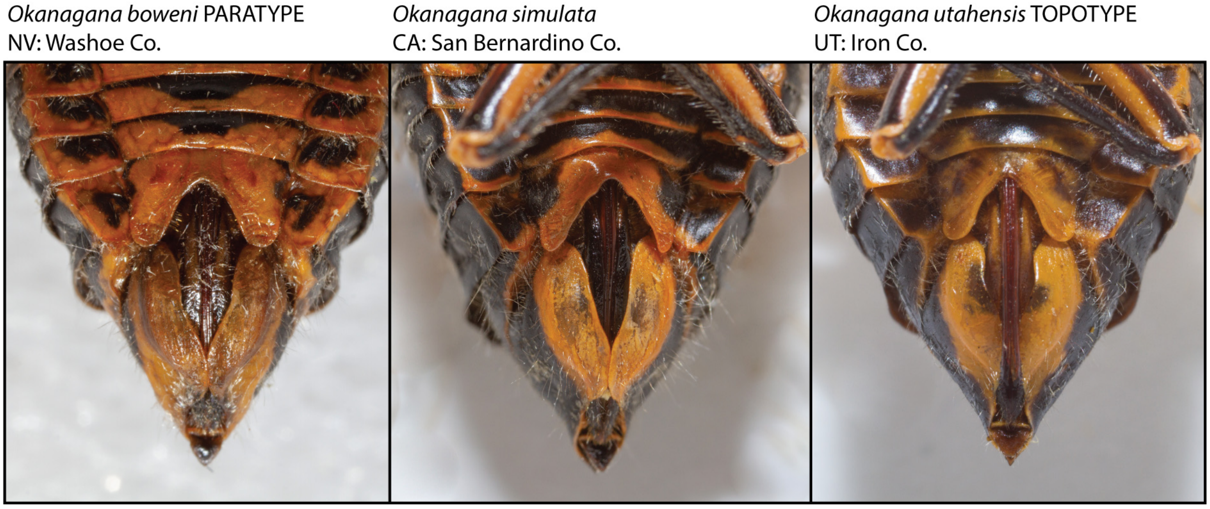

FIGURE 4. Female terminalia of *Okanagana boweni* **sp. n.** (left), *O. simulata* (middle) and *O. utahensis* (right), ventral view.

TABLE 2. Song characteristics of *O. boweni* **sp. n.**, *O. simulata*, and a sympatric population of *O. utahensis* at the *O. boweni* **sp. n.** type locality. Song characters measured from the *O. boweni* **sp. n.** holotype follow the colon.

Species	Syllable rate (s^{-1})	Peak frequency (kHz)
O. boweni **sp. n.** (n = 8)	179.5 ± 5.9: 180.2	7.89 ± 0.54: 8.36
Lone Pine (n = 3)	174.7 ± 3.2	7.67 ± 0.6
Tamarack Beach type locality (n = 5)	182.4 ± 5.4	8.0 ± 0.5
O. simulata (n = 7)	188.1 ± 3.4	7.92 ± 0.3
O. utahensis (n = 6)	362.1 ± 63.7	8.46 ± 0.38

Neither syllable rate (ANCOVA, $P = 0.111$) nor peak frequency ($P = 0.653$) varied with temperature. Songs differed significantly between species (MANOVA, $P = 4.74\text{x}10^{-4}$) but not between *O. boweni* populations ($P = 0.543$). Of the three species, *O. utahensis* was most divergent in song, but songs of *O. boweni* and *O. simulata* also differed significantly ($P = 5.2\text{x}10^{-3}$), differences that were again not explained by population ($P = 9.08\text{x}10^{-2}$). Per the methodology of Chatfield-Taylor and Cole (2019), the calls of *O. boweni* and *O. simulata* were separated by 0.09 standard deviations (SD) in parameter space while separation between *O. boweni* and *O. utahensis* ranged from 0.85 to 2 SD.

Distribution. The distribution extends from the southern extent of the Owens Valley in eastern California north to Pyramid Lake, Nevada (Fig. 6). This distribution coincides with a geologically defined region of major transform faulting (Carlson *et al.* 2013; Wesnousky 2005) that has been termed the Walker Lane (Locke *et al.* 1940). The Walker Lane extends from the Garlock Fault at the southeastern corner of the Sierra Nevada and Tehachapi Range, which forms the northern border of the Mojave Desert, northeast to the Pyramid Lake Block in Nevada, and northwest to the Northern California Shear Zone that borders the Modoc Plateau in northeastern California (Carlson *et al.* 2013; Smith 1962; Stewart 1988).

Etymology. The species is named after Charles Bowen, a naturalist from Belize who kindled the senior author's interest in the biological sciences.

Seasonal occurrence. Available records indicate activity from late spring (28 May, N. Lee, LACM) through midsummer (10 July, holotype, LACM).

Habitat and notes. Habitat at the type locality is primarily alkali flats dominated by sages in the Tridentate group (*Artemisia* spp.) and tamarisk (*Tamarix* sp.; J. Bailey, pers. comm.). At the type locality males called from tamarisk and other available vegetation in their open habitat as they engaged in sing-fly behavior, while females were found exclusively on *Artemisia tridentata*. Besides *O. boweni*, we observed three other hooked uncus species in association with *Artemisia tridentata* during our 2019 field season: *O. simulata*, *O. utahensis*, and *O. vanduzeei* Distant. Hooked uncus taxa have been associated previously with *Artemisia* (Davis 1919; Kondratieff *et al.* 2002; Sanborn *et al.* 2002).

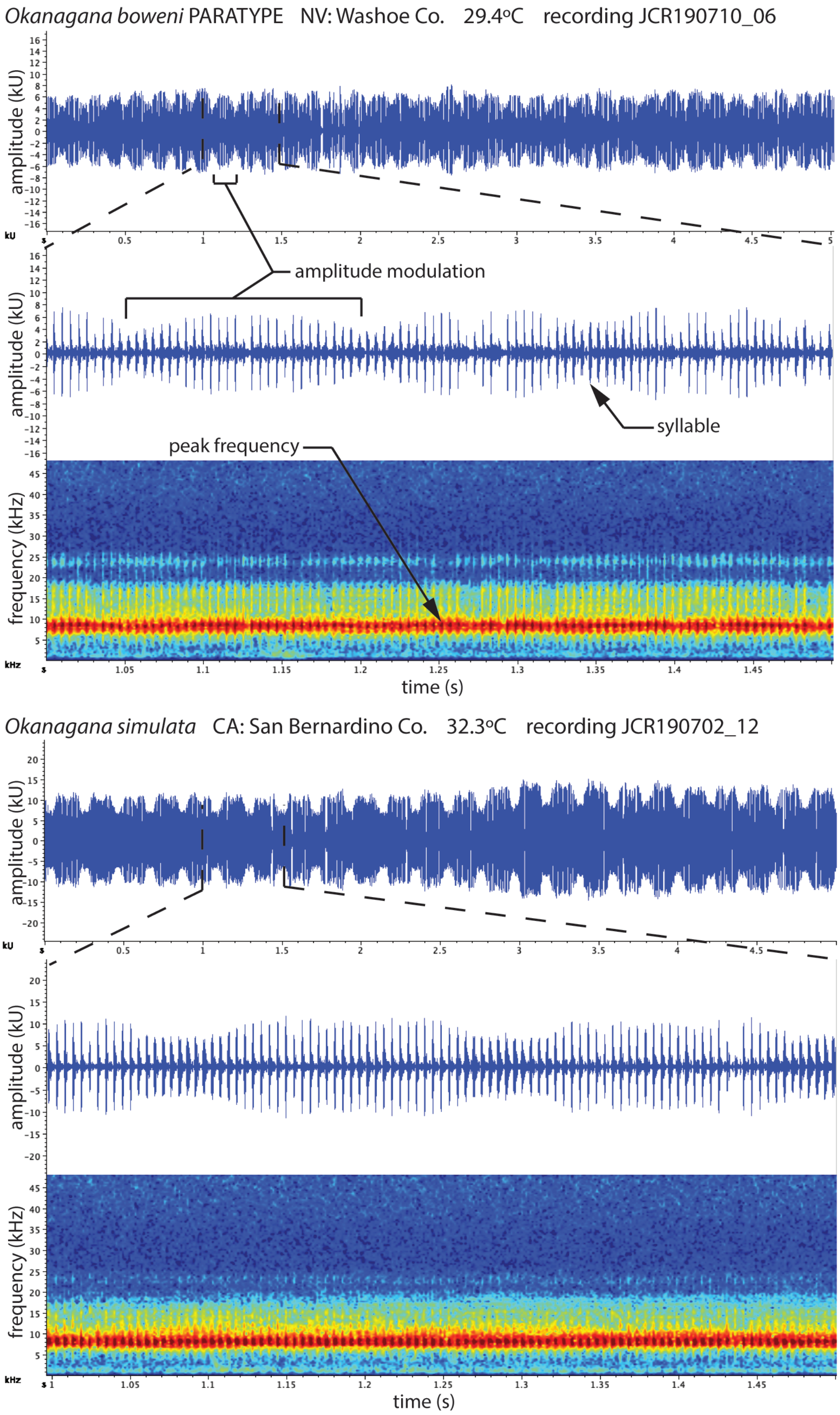

FIGURE 5. Calling songs of *Okanagana boweni* **sp. n.** (above) and *O. simulata* (below). The songs are shown as 5 s oscillogram windows (top) that are zoomed to 0.5 s oscillogram (middle) and spectrogram (bottom) windows. Song characters are illustrated.

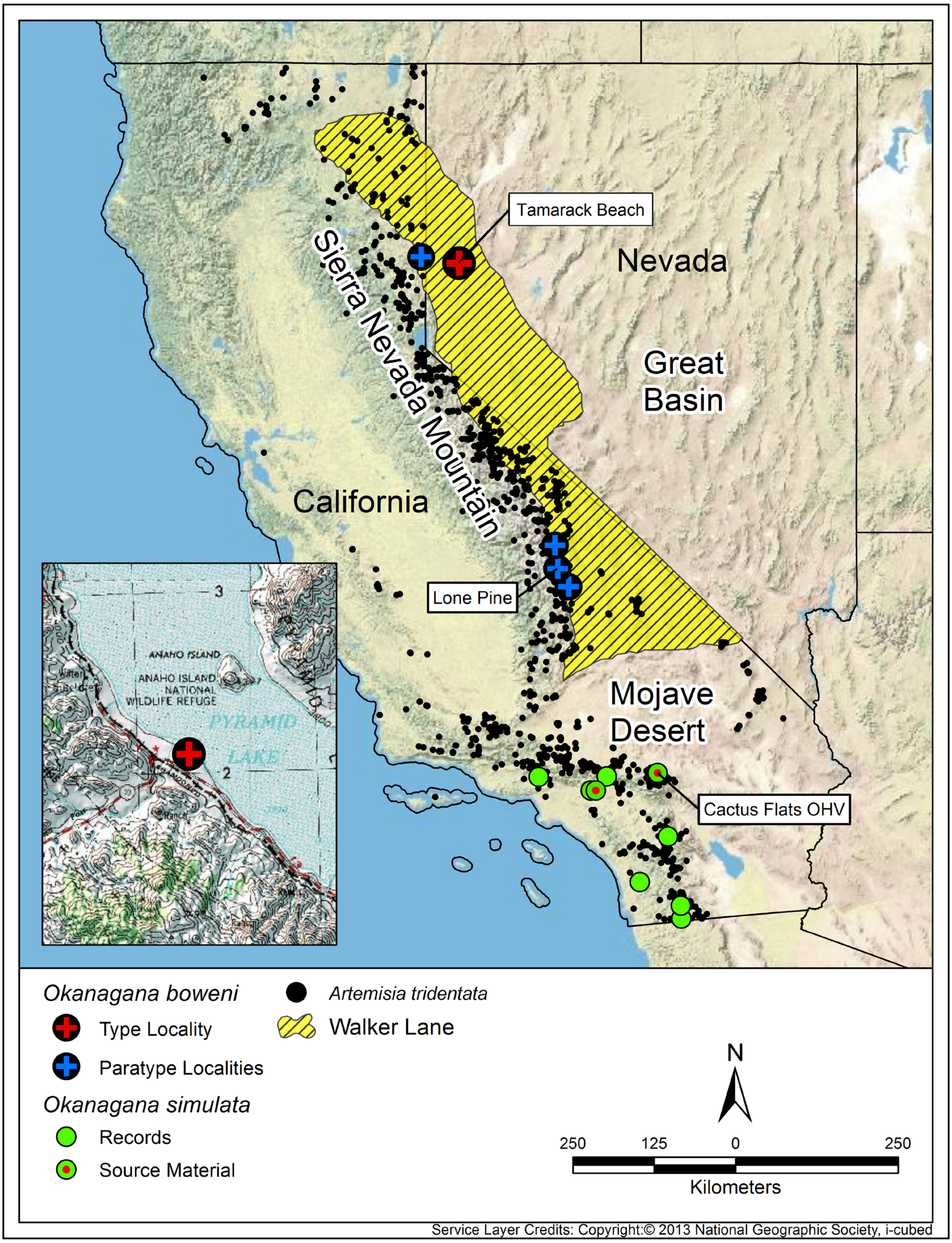

FIGURE 6. Geographic distributions of *Okanagana boweni* **sp. n.** and *Okanagana simulata*, and the California range of their hypothesized host plant *Artemisia tridentata* (data provided by the participants of the Consortium of California Herbaria ucjeps.berkeley.edu/consortium/). The yellow hatched polygon outlines the Walker Lane region (Carlson *et al.* 2013). The inset details the type locality.

TABLE 3. Exemplars used in phylogenetic analysis with GenBank accessions.

species	specimen barcode	extraction	locality	collection date	collectors	*16S* accession	*ARD1* accession	*EF1α* accession
Okanagana boweni **sp.n.** PARATYPE	n/a	SING0246	USA. CA: Inyo Co.; 36.5977 N 118.1838 W, 1785 m	9-VII-2008	JA Cole	MT872648	-	MT948164
Okanagana boweni **sp.n.** PARATYPE	JAC0227	SING0873	USA. NV: Washoe Co.; 39.91333 N 119.54083 W, 1134 m	10-VII-2019	JA Cole, J Bailey, W Chatfield-Taylor, JF Eguizabal	MT872649	MT948152	MT948165
Okanagana boweni **sp.n.** PARATYPE	JAC0228	SING0874	USA. NV: Washoe Co.; 39.91333 N 119.54083 W, 1134 m	10-VII-2019	JA Cole, J Bailey, W Chatfield-Taylor, JF Eguizabal	MT872650	MT948153	MT948166
Okanagana hesperia TOPOTYPE	n/a	SING0641	USA. CO: Jefferson Co.; 39.65004 N 105.18261 W, 1761 m	28-VI-2016	JA Cole	MT872651	MT948154	MT948167
Okanagana pallidula	JAC0243	SING0883	USA. CA: Yolo Co.; 38.57111 N 121.71417 W, 6 m	22-VII-2019	JA Cole	MT872652	MT948155	MT948168
Okanagana rubrovenosa	JAC0241	SING0842	USA. CA: San Diego Co.; 32.75194 N 116.49361 W, 945 m	20-VI-2019	JA Cole, J Bailey	MT872647	MT948151	MT948163
Okanagana simulata	JAC0232	SING0855	USA. CA: San Bernardino Co.; 34.28316 N 116.80694 W, 2079 m	2-VII-2019	JA Cole, SA Downing	MT872653	MT948156	MT948169
Okanagana simulata	JAC0233	SING0858	USA. CA: San Bernardino Co.; 34.28316 N 116.80694 W, 2079 m	5-VII-2019	JA Cole, W Chatfield-Taylor	MT872654	MT948157	MT948170
Okanagana striatipes	n/a	SING0236	USA. UT: Sevier Co.; 38.5288 N 112.2694 W, 1771 m	26-VI-2007	JA Cole	MT872655	MT948158	MT948171
Okanagana utahensis	JAC0237	SING0871	USA. NV: Washoe Co.; 39.86833 N 119.63861 W, 1277 m	10-VII-2019	JA Cole, J Bailey, W Chatfield-Taylor, JF Eguizabal	MT872656	MT948159	MT948172
Okanagana utahensis	JAC0239	SING0872	USA. NV: Washoe Co.; 39.86833 N 119.63861 W, 1277 m	10-VII-2019	JA Cole, J Bailey, W Chatfield-Taylor, JF Eguizabal	MT872657	MT948160	MT948173
Okanagana vanduzeei TOPOTYPE	JAC0421	SING0840	USA. CA: San Diego Co.; 32.67889 N 116.84028 W, 280 m	20-VI-2019	JA Cole, J Bailey	MT872658	MT948161	MT948174
Okanagana vanduzeei TOPOTYPE	JAC0247	SING0841	USA. CA: San Diego Co.; 32.67889 N 116.84028 W, 280 m	20-VI-2019	JA Cole, J Bailey	MT872659	MT948162	MT948175

Molecular phylogenetics. Alignment lengths were 510 bp for *16S*, 198 bp for *ARD1* UTR, 414 bp for *ARD1* CDS, 423 bp for *EF1α* exons, 305 bp for *EF1α* introns, and 1013 indel characters. PartitionFinder returned two partitions: 1) the HKY+I model applied to a partition consisting of the 3rd codon positions of coding regions and all noncoding regions, and 2) the F81 model applied to all first and second codon positions. The standard deviation of split frequencies was 3.63×10^{-3}, which indicated significant convergence of Markov chains.

A *utahensis* - *vanduzeei* clade resolved sister to a *boweni* - *simulata* clade (Fig. 7) with strong support (posterior probability 98%). Whereas the former pair were reciprocally monophyletic, *O. simulata* rendered *O. boweni* paraphyletic. A relatively long branch separated *O. simulata* from *O. boweni*.

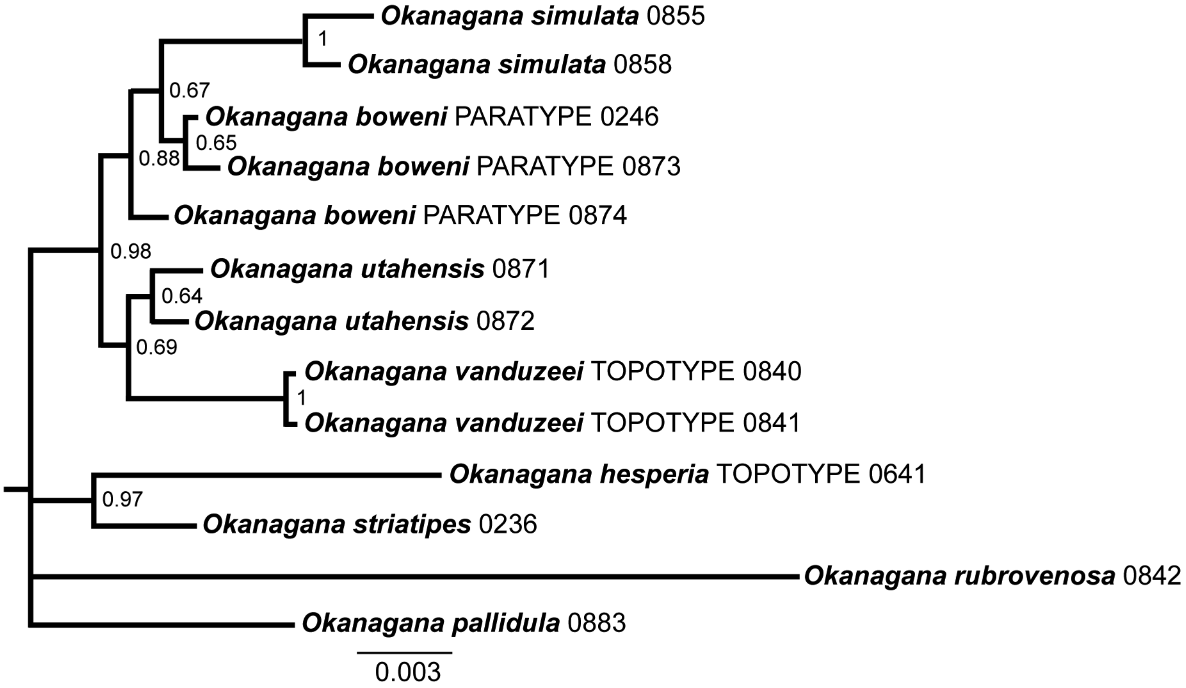

FIGURE 7. Phylogenetic hypothesis for *Okanagana boweni* **sp. n.** and relatives.

Discussion

Systematics that advances causal understanding is consistent with the overall goal of science (Fitzhugh 2013). Speciation is a continuous process that may be divided into initiation, strengthening, and completion phases, thus it is pertinent to consider the phase and the forces that are causing divergence in any empirical case (Butlin 2008). Species hypotheses are invoked to explain differential fixation of characters among individuals due to lineage splitting and reproductive isolation (Fitzhugh 2013), whereas subspecies hypotheses explain cases in which tokogeneny and widespread gene flow persist among individuals. Subspecies ranks have been applied to several recently described cicada taxa (Hertach *et al.* 2016; Marshall & Hill 2017; Popple 2013) in which recent tokogenetic processes were evident in the forms of hybrid songs and/or contemporary gene flow at contact zones.

Recent, rapid divergences are challenging to resolve and require integrative systematic approaches (e.g. Hertach *et al.* 2016) as we have employed here, and it is reasonable to expect from such studies that not all character sets will be congruent. Here, a paraphyletic evolutionary history (Fig. 7) contrasts with cohesive geographic, behavioral, and morphological units. Our decision is to erect *Okanagana boweni* as a new species rather than as a subspecies due to a geography that makes current and future gene flow unlikely, and due to the fixation of multiple characters without intermediates. In more than a decade of fieldwork we have not found intermediates between *O. boweni* and *O. simulata*, and the geography precludes the existence of contact zones. We invite further testing of our species hypothesis and now enumerate the evidence that prompted our designation.

Strong reproductive isolation that satisfies the biological species concept may be inferred from a geography of strict allopatry: *O. boweni* inhabits the Walker Lane region east of the Sierra Nevada and *O. simulata* is found in cismontane southern California (Fig. 6). The southern border of the Walker Lane is the Garlock Fault, to the south of which lies the Mojave Desert, a formidable biogeographical barrier that is unsuitable for and uninhabited by *Okanagana* (Sanborn & Phillips 2013). Furthermore, the host plant of both species, *Artemisia tridentata*, is absent from the Mojave and is found only along the high elevation fringes of the desert (Fig. 6; data provided by the participants of the Consortium of California Herbaria ucjeps.berkeley.edu/consortium/). This barrier likely maintains contemporary reproductive isolation that will persist into the future.

To our knowledge the Walker Lane has not explicitly been correlated with biogeography except for a study of aquatic snails (Hershler *et al.* 1999). The Walker Lane is, however, a subset of the Lake Lahontan system, which has shaped the evolution and distributions of numerous Great Basin organisms (e.g. Kippenhan 2005; Rentz 1973; Riddle *et al.* 2014; Smith *et al.* 1994). The Walker Lane region is characterized by tectonic activity, the grabens of which bear alkali flats that are exposed after inundated sunken land has dried since the Pleistocene (Wesnousky 2005) exposing the alkali flat habitat (Adams & Wesnousky 1998; Benson 1978) with which *O. boweni* is associated. Vicariance due to the geographic evolution of the western Lake Lahontan region would date divergence between the middle and late Pleistocene (Adams & Wesnousky 1998).

The first fixed character we consider is calling song. Sympatric species are predicted to have distinct mating signals (Alexander 1962; Walker 1974), a pattern that holds true for a diversity of *Okanagana*; indeed, sympatric *O. boweni* and *O. utahensis* show song divergence that exceeds a plateau that delineates effective acoustical mate recognition within a multidimensional song parameter space (Chatfield-Taylor & Cole 2019). *Okanagana utahensis* inhabits a wide geographic range and is acoustically distinct from another sympatric relative within that range (Sanborn *et al.* 2002). In contrast, recently evolved allopatric species often have non-significant or marginally significant song divergence (Lukhtanov 2011; examples in cicadas include Sanborn & Phillips 2010, 2011; Simões *et al.* 2000). We show significant song differences between *O. boweni* and *O. simulata*, however, that are comparable in magnitude (Chatfield-Taylor & Cole 2019) to those that separate *O. hesperia* (Uhler) and *O. striatipes* (Haldeman), established allopatric species for which we recovered a sister relationship (Fig. 7). Considering that calling songs may evolve rapidly in cicadas (Marshall *et al.* 2009, 2011), the evolution of incipient premating isolation may place *O. boweni* in the strengthening stage of speciation (Butlin 2008) despite being a young lineage geologically speaking. Regarding paraphyly, *O. boweni* and *O. simulata* behavior may be diverging at a pace that is beyond the resolution of the molecular markers we employed, and genomic approaches may resolve the paraphyly (e.g. Gray *et al.* 2020; Huang *et al.* 2020).

Second, we consider morphology. This new species is part of a substantial radiation of *Okanagana* in which males have a hooked uncus (Davis 1919), a group that is the subject of revisionary systematics (Chatfield-Taylor & Cole, unpublished). Fixed differences in uncus and aedeagus morphology (Fig. 3) may confer physical or tactile reproductive isolation (reviewed in Masly 2012). Between sympatric *O. boweni* and *O. utahensis*, genital morphology may represent a second prezygotic barrier should song recognition fail. The consistent differences we found in genital morphology between our allopatric species pair are at least as great as those found between our sympatric species pair; thus, genitalia may help isolate *O. boweni* and *O. simulata* in a hypothetical scenario of contact, even if song divergence is not sufficient. Genitalia more likely serve as an isolating barrier between taxa with and without a hooked uncus and may help explain sympatric coexistence of species with similar songs. At the Cactus Flats OHV site, San Bernardino County, California, *O. simulata* was sympatric with five other species, of which *O. magnifica* Davis and *O. tristis rubrobasalis* are situated close in song parameter space, potentially jeopardizing mate recognition in lieu of a secondary isolating feature such as genital morphology (Rentz 1972; Usami *et al.* 2006).

Finally, we consider ecology via an hypothesis of color pattern evolution for background matching, a rapidly evolving naturally selected character (e.g. Steiner *et al.* 2007). *Artemisia tridentata* is a wide-ranging plant species that occurs in numerous biogeographic zones (data provided by the participants of the Consortium of California Herbaria ucjeps.berkeley.edu/consortium/). The bright background of alkali flat habitats, owing to high reflectance, contrasts with the darker, less reflective background of more densely vegetated chaparral or pinyon-juniper habitats. Natural selection for background matching may have thus driven the evolution of more extensive pale coloration in *O. boweni* within alkali flats, and a more melanistic color pattern in chapparal and pinyon-juniper inhabiting *O. simulata*. The natural selection benefit of appropriate background matching is emphasized by the shared pale color pattern of sympatric non-sister species *O. boweni* and *O. utahensis*.

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supplementary

Supplementary file will be available on the DOI landing page of this paper.