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Molecular phylogenetics, diversification, and systematics of *Tibicen* Latreille 1825 and allied cicadas of the tribe Cryptotympanini, with three new genera and emphasis on species from the USA and Canada (Hemiptera: Auchenorrhyncha: Cicadidae)

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Abstract

North America has a diverse cicada fauna with multiple genera from all three Cicadidae subfamilies, yet molecular phylogenetic analyses have been completed only for the well-studied periodical cicadas (*Magicicada* Davis). The genus *Tibicen* Latreille, a large group of charismatic species, is in need of such work because morphological patterns suggest multiple groups with complicated relationships to other genera in the tribe Cryptotympanini. In this paper we present a molecular phylogenetic analysis, based on mitochondrial and nuclear DNA, of 35 of the 38 extant USA species and subspecies of the genus *Tibicen* together with their North American tribal allies (*Cornuplura* Davis, *Cacama* Davis), selected *Tibicen* species from Eurasia, and representatives of other Eurasian and Pacific cryptotympanine genera. This tree shows that *Tibicen* contains several well-supported clades, one predominating in eastern and central North America and related to *Cryptotympana* Stål and *Raiateana* Boulard, another in western North America related to *Cacama* and *Cornuplura*, and at least two clades in Eurasia. We also present a morphological cladistic analysis of *Tibicen* and its close allies based on 27 characters. Character states identified in the cladistic analysis define three new genera, two for North American taxa (*Hadoa* gen. n. and *Neotibicen* gen. n.) including several Mexican species, and one for Asian species (*Subsolanus* gen. n.). Using relaxed molecular clocks and literature-derived mtDNA rate estimates, we estimate the timeframe of diversification of *Tibicen* clades and find that intergeneric divergence has occurred since the late Eocene, with most extant species within the former *Tibicen* originating after the mid-Miocene. We review patterns of ecology, behavior, and geography among *Tibicen* clades in light of the phylogenetic results and note that the study of these insects is still in its early stages. Some Mexican species formerly placed in *Tibicen* are here transferred to *Diceroprocta*, following refinement of the definition of that genus.

Key words: evolution, molecular genetics, cladistics, molecular clock, biogeography, disjunction, annual cicada, numt, Cicadinae

Introduction

Cicadas (Auchenorrhyncha: Cicadidae) are large, xylem-feeding insects known for their long underground juvenile life stages and the loud, species-specific songs made by males during their brief aboveground adult lives. North America has a diverse cicada fauna that includes multiple genera from each of the three cicada subfamilies (Cicadettinae, Tibicininae [=Tettigadinae], and Cicadinae—see Moulds 2005). While the extraordinary periodical cicadas (*Magicicada* Davis, seven spp.) have been extensively studied for nearly two centuries, including molecular and morphological systematic analyses (Marlatt 1907; Simon 1979;1983; Sota *et al.* 2013; Williams & Simon 1995), the 185 non-periodical species and subspecies north of Mexico have received only sporadic attention and little to no phylogenetic analysis beyond alpha taxonomy and a role as outgroups in other studies (e.g., Moulds 2005; Sueur *et al.* 2007).

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TABLE 1. Life history of USA cryptotympanine cicada species, summarized mainly from Sanborn and Phillips (2013), Sanborn and Heath (2012), publications of W. T. Davis, and observations of the authors (esp. song characterizations). Taxa with asterisks were not collected in time for this study. Taxonomic authorities are given in the Appendix; *Tibicen tibicen* = *Tibicen chloromerus* (Walker), and *Tibicen pronotalis walkeri* = *Tibicen walkeri* (Metcalf) (see Hill & Marshall 2009). New assignments refer to genera described in the Results section. Recordings of the songs of most USA cryptotympanine species can be found at *www.insectsingers.com*.

Genus	**Species**	**New genus (see Results)**	**Distribution**	**Habitat, hostplants**	**Song description**	**Miscellaneous**
Cacama	*californica**	Unchanged	S CA, NV	Upl. woodland, *Opuntia*	Unknown to this study	Similar to *variegata*
Cacama	*collinaplaga**	Unchanged	TX	Des. grassland, *Opuntia*	Resonant oscillating whine	No red/orange at wing bases
Cacama	*crepitans**	Unchanged	S CA	Upl. woodland, *Opuntia,* sage	Unknown to this study	Localized distribution
Cacama	*moorei*	Unchanged	AZ, NV	Sonoran Des., *Opuntia*	Resonant oscillating whine	Compare to *collinaplaga*
Cacama	*valvata*	Unchanged	SW USA, Mex.	Des., chaparral, *Opuntia*	Resonant oscillating whine	Most widespread *Cacama*
Cacama	*variegata**	Unchanged	TX	Des. grassland, *Opuntia*	Unknown to this study	Most evenly rounded forewings
Cornuplura	*nigroalbata*	Unchanged	SW AZ, Mex.	Des. mountains, *Quercus*	Continuous, oscillating whine	Santa Cruz Co., AZ
Tibicen	*auletes*	*Neotibicen*	E USA, Can.	Forest, *Hardwoods, Quercus*	Slow harsh drr-drr-drr	Largest USA species
Tibicen	*auriferus*	*Neotibicen*	C USA	Prairie, shrubs/grasses	Brassy whine	Similar to *davisi*
Tibicen	*bifidus*	*Hadoa*	SW USA	Des. grasslands, *Yucca, Artemisia*	Brassy buzz	Bifurcate uncus, see *simplex*
Tibicen	*canicularis*	*Neotibicen*	NE/NC USA, Can.	Woodland, conifers, hardwoods	Sharp whine	For some, the "Dog-day Cicada"
Tibicen	*chiricahua*	*Hadoa*	AZ, NM, Mex.	Woodland, *Pinus, Juniperus*	Smooth resonant drone	Compare to *neomexicensis*
Tibicen	*chisosensis**	*Hadoa*	S TX, Mex.	Mtn. woodland, pinyon pine?	Unknown to this study	Only in Chisos Mtns in USA
Tibicen	*cultriformis*	*Neotibicen*	AZ, NM, Mex.	Rip. woodland, *Salix*, *Populus*	Rapid staccato pulses	Related to east-central *Tibicen*
Tibicen	*davisi davisi*	*Neotibicen*	SE USA	Woodland, conifers	Brassy whine	See *auriferus* and *canicularis*
Tibicen	*davisi harnedi*	*Neotibicen*	SC USA	Woodland	Brassy whine	No black stripe on ventral abd.
Tibicen	*dealbatus*	*Neotibicen*	G. Plains	Prairie, hardwoods	Droning zzh-zzh-zzh	Song same as *pronotalis*
Tibicen	*dorsatus*	*Neotibicen*	C USA	Prairie, shrubs/grasses	Tractor-like rattle	Similar to *tremulus*
Tibicen	*duryi*	*Hadoa*	SW USA, Mex.	Mtn. woodland, chaparral, *Pinus*	Complicated warbling buzz	Locally abundant
Tibicen	*figuratus*	*Neotibicen*	SE USA	Woodland, conifers	Rough ding-ding-ding	Calls infrequently
Tibicen	*inauditus*	*Hadoa*	SW USA	Des. woodland/grassland	High-pitched trilling buzz	Smallest USA *Tibicen?*
Tibicen	*latifasciatus*	*Neotibicen*	Coastal NJ-SC/FL	Woodland, cedar	Wee-ooo oscillation	White lateral marks on abdomen
Tibicen	*linnei*	*Neotibicen*	E USA, Can.	Woodland, hardwoods	Maraca-like oscillating buzz	Similar to *pruinosus*
Tibicen	*longioperculus*	*Hadoa*	SE AZ	Des. woodland, *Juniperus*	Brassy buzz	Unusually long opercula
Tibicen	*lyricen engelhardti**	*Neotibicen*	Appalachian Mts.	Woodland, hardwoods	Watery, resonant drone	Very dark coloration
Tibicen	*lyricen lyricen*	*Neotibicen*	E USA, Can.	Woodland, hardwoods	Watery, resonant drone	Common *Tibicen* of the east
Tibicen	*lyricen virescens*	*Neotibicen*	SE USA	Woodland, hardwoods	Watery, resonant drone	Greener form of *lyricen*
Tibicen	*neomexicensis*	*Hadoa*	AZ, NM	Woodland, *Pinus*, *Juniperus*	Pulsed resonant drone	Compare to *chiricahua*
Tibicen	*parallelus*	*Hadoa*	AZ, NM, Mex.	Des. habitats, *Quercus*, *Juniperus*	Oscillating whine, then static	NM type location isolated
Tibicen	*pronotalis*	*Neotibicen*	N G. Plains	Rip. woodland, *Salix, Populus?*	Droning zzh-zzh-zzh	Pronotal mark inconsistent
Tibicen	*pronotalis walkeri*	*Neotibicen*	C USA	Rip. woodland, *Populus,* hardwoods	Droning zzh-zzh-zzh	Song same as *dealbatus*
Tibicen	*pruinosus fulvus**	*Neotibicen*	SE KS, NE OK	Open woodland, hardwoods	Wee-ooo oscillation	Local color variant
Tibicen	*pruinosus pruinosus*	*Neotibicen*	C USA	Open woodland, hardwoods	Wee-ooo oscillation	*The* midwestern *Tibicen*
Tibicen	*resh*	*Neotibicen*	SC USA, Mex.	Open, rip. woodland, hardwoods	Fast harsh drr-drr-drr	Named for mesonotal marks
Tibicen	*resonans*	*Neotibicen*	SE USA	Woodland, conifers	Fast harsh dee-dee-dee	Large-bodied
Tibicen	*robinsonianus*	*Neotibicen*	EC USA	Woodland, hardwoods, *Juniperus*	Slow (ca. 1/s) repeated rasps	High in canopy
Tibicen	*similaris*	*Neotibicen*	SE USA	Woodland, conifers, hardwoods	Rattle w sudden acceleration	Unusual clacking rattle
Tibicen	*simplex*	*Hadoa*	AZ, Mex.	Desert, *Yucca*	Brassy whine	Like *bifidus* but simple uncus
Tibicen	*superbus*	*Neotibicen*	SC USA	Open woodland, hardwoods	Sputtery, rapid cha-cha-cha	Green with sputtery song
Tibicen	*texanus*	*Hadoa*	TX, OK, NM	Open woodland, *Quercus*, *Juniperus*	Brassy buzz	Attractive color pattern
Tibicen	*tibicen australis*	*Neotibicen*	SE USA	Woodland, hardwoods	Clacky warbling buzz	Greener form of *tibicen*
Tibicen	*tibicen tibicen*	*Neotibicen*	E USA, Can.	Swampy woodland, hardwoods	Clacky warbling buzz	Long opercula, waxy
Tibicen	*townsendii*	*Hadoa*	SW USA	Desert, *Yucca*	Whining buzz	Similar to *bifida/simplex*
Tibicen	*tremulus*	*Neotibicen*	C USA	Prairie, sage, *Yucca*	Tractor-like rattle	Similar to *dorsatus*
Tibicen	*winnemanna*	*Neotibicen*	E USA	Woodland, hardwoods	Wee-ooo oscillation	Costa not as bent as *pruinosus*

One of the largest North American groups in need of phylogenetic study is the genus *Tibicen* Latreille and its allies (Sanborn & Heath 2012; Sanborn & Phillips 2013). With 38 USA species and subspecies (Table 1), *Tibicen* extends from the Atlantic to Arizona, north into Canada, and south into Mexico and Central America (Sanborn 2010). Substantial numbers of *Tibicen* species are found across Eurasia as well, although some of these are commonly referenced under the genus *Lyristes* Horváth (Sanborn 2013; 2014a p. 116) (see below). *Tibicen* belongs to the tribe Cryptotympanini Handlirsch, which in addition to other world genera includes the southwestern North American *Cacama* Davis ("cactus dodgers"—see Davis 1919; Sanborn *et al.* 2011) and *Cornuplura* Davis (see Sanborn & Phillips 2012).

Like most cryptotympanine cicadas, *Tibicen* are large and charismatic insects, and the males become especially active in hot weather, hence the common name "Dog Day Cicada" informally used for *Tibicen canicularis* (Harris, 1841). Cicada songs allow identification of most species in the field, even many that are morphologically cryptic (e.g., Alexander *et al.* 1972; Cole 2008). In the USA, *Tibicen* species are found in a wide range of habitats from western intermountain deserts to prairie to humid deciduous forests. They are active as adults mainly in summer from June to September in the eastern and central states (e.g., Beamer 1928 p. 173; Walker 2000) and from spring in the western states. Life cycle lengths for *Tibicen* species are unknown but probably involve multiple juvenile years underground, as observed in cicadas with known life cycles (Campbell *et al.* 2015; Karban 1986). Unlike the periodical cicadas, which can damage fruit and nursery crops, *Tibicen* species are rarely of economic significance (e.g., Wilson 1930). Distributions, habitat associations, and song characteristics for all of the cryptotympanine species north of Mexico are summarized in Table 1 and reviewed further in Sanborn and Phillips (2013). Life history information is also summarized in the publications of Beamer (1928), Myers (1929), and Heath (1978).

Tibicen is of additional interest for a phylogenetic study because its North American members exhibit patterns of morphology and ecology that suggest deeper divisions and potentially complex relationships with other cryptotympanine genera, and a "lack of diagnostic characters" has inhibited progress (Heath 1978 p. 190). Davis (1930) proposed three geographically correlated subgroups based on morphology (Davis 1930; see also Heath 1978), and Heath (1978, p. 204) proposed two invasions of North America by lineages containing *Tibicen* species. However, slightly different arrangements have been proposed based on unpublished molecular data (Sanborn & Heath 2012). Fukuda *et al.* (2006) used mtDNA sequences to identify a relationship between *Tibicen japonicus* (Kato, 1925) from Japan and two species of *Cryptotympana* Stål, but no other *Tibicen* species were examined. Relationships to other world Cryptotympanini remain unknown, although Davis (1930) suggested a connection between western North America *Tibicen* and *Tibicen plebejus* (Scopoli, 1763).

In this paper, we examine the phylogenetic relationships of North American *Tibicen* found north of Mexico using genetic data, conduct a cladistic examination of morphological traits in order to identify new genera, explore the varied relationships of the North American *Tibicen* species to allied *Tibicen* and other cryptotympanine genera, and approximate the timeframe of divergence of the group. We also discuss the ecological and behavioral attributes of the North American species in light of our phylogenetic findings. The new genera are described in the Results and applied through the remainder of the paper.

The status of the genus *Tibicen* Latreille, and its potential priority over *Lyristes* (both potentially claiming the type *Cicada plebeja* Scopoli, 1763), is currently being considered by the ICZN in recently resurrected Case 239 (Boulard & Puissant 2014; Hamilton 2014; Marshall & Hill 2014; Sanborn 2014a). While *Tibicen* has been overwhelmingly applied in North America, some Eurasian species (notably *plebeja*) have been more commonly referenced under *Lyristes* in recent decades. For this paper, we follow the catalogue of Sanborn (2013) and use *Tibicen* pending the decision by the Commission.

Methods

Background and taxon sampling. North American *Tibicen* north of Mexico. Thirty-five of the 38 described species and subspecies of North American *Tibicen* found in the USA and Canada were collected for this project. Some of these taxa extend to Mexico (Table 1). One USA species, *T. chisosensis* Davis, 1934 is found only in the Chisos Mountains in southern Texas and Mexico (Sanborn 2007) and we were unable to obtain material in time for this study. Two subspecies were also not included, *T. pruinosus fulvus* Beamer, 1924 and *T. lyricen engelhardti* (Davis, 1910). Specimen collection data and taxonomic authorities are given in the Appendix. Most of the USA specimens were collected by KH and DM, and when possible the male songs were recorded. Example recordings can be found at *insectsingers.com* and *cicadamania.com*. For most of these species, 2–4 specimens were sequenced in order to sample intraspecific geographic-genetic variation.

Through the efforts of collaborators (see Acknowledgements), we were able to include the type of *Tibicen* (*plebejus*) and its relative *T. gemellus* (see Boulard 1988). In addition, three Asian species were included—*T. bihamatus* (de Motschulsky, 1861), *T. japonicus* (Kato, 1925), and *T. kyushyuensis* (Kato, 1926). Nineteen additional species-level *Tibicen* taxa are found only in Eurasia and 13 in Mexico (Sanborn 2007). Note that *T. bermudianus* (Verrill, 1902) from Bermuda, morphologically and acoustically similar to *T. lyricen* (see Moore 1993), is believed to be extinct (Procter & Fleming 1999), and *T. occidentis* (Walker, 1850) from Chile has been removed from the genus and tribe (Sanborn 2014b). All of the specimens used in this study are housed at the University of Connecticut (Biological Collections Facility or C. Simon laboratory) or in the collection of Max Moulds, Australian Museum.

Allied cryptotympanine genera and outgroups. The tribe Cryptotympanini was recently redefined by Moulds (2005). Twenty cryptotympanine genera are currently catalogued by Sanborn (2013), four of which are found in North America: *Tibicen*, *Cacama*, *Cornuplura*, and *Diceroprocta* Stål. An ongoing family-level molecular study of cicadas (Marshall, Hill, Wade, Owen, Moulds, Simon in prep.) suggests that a redefined concept will be necessary for Cryptotympanini and that *Diceroprocta*, *Oriallela* Metcalf, and the Australian genera will need to be removed. Based on this work we selected the following genera to be represented along with *Tibicen* in the molecular and cladistic analyses: *Cacama*, *Chremistica* Stål, *Cornuplura*, *Cryptotympana*, *Raiateana* Boulard, *Salvazana* Distant, and *Tacua* Amyot & Audinet-Serville. *Cryptotympana* is a very large genus (Hayashi 1987a;b), but we were able to sample five species, including the type *C. atrata* (Fabricius, 1775). Unfortunately, the type species of *Cacama* and *Cornuplura* are found only in Mexico and were not sampled. Six species of *Chremistica* were included. We were unable to obtain specimens of *Antankaria* Distant, *Heteropsaltria* Jacobi, and *Nggeliana* Boulard for molecular analysis.

Lastly, two more distant outgroups from the subfamily Cicadinae—*Platypleura takasagona* Matsumura, 1917 and *Yanga andriana* (Distant, 1899) (tribe Platypleurini Schmidt), were included in order to root the tree. These were also chosen based on the family-level preliminary analyses.

Specimen collection. Upon collection, either the entire specimen or some specimen tissue (1–3 legs) was frozen in 100% ethanol in individually labeled containers. In a few cases, a leg was removed from a dried, pinned specimen for DNA extraction. Most specimens and their associated tissue samples, recordings, or photographs were given an eleven-character collection code—two digits for the year, two letters for the country, two letters for the state/district, three letters for the location, and two digits for the individual specimen number (see Appendix). For most specimens collected by collaborators (see below), the original codes were used. Bodies of specimens with tissue separately preserved were pinned and deposited in the authors' collection at the University of Connecticut. One exception, specimen number 09.US.CT.AUL.EB1, was a sample of eggs from an eggnest deposited by a female *Tibicen auletes*.

Male songs were recorded in the field using one of several digital recorder/condenser microphone combinations, often together with a Sony (Park Ridge, NJ, USA) PBR330 parabolic reflector. Recorders used included the Sony TCD-D8 (2002 and 2003 only), Marantz (Mahwah, NJ, USA) PMD660, Marantz PMD670, and the Zoom (Ronkonkoma, NY, USA) H4 (in 2012 only), while the microphones used included the Sennheiser (Old Lyme, CT, USA) ME66 short shot gun and a Sennheiser ME62 omnidirectional. The latter microphones were used with the Sennheiser K6 power module, and both have frequency responses up to 18 kHz. All songs were digitized at either 44.1 kHz or 48 kHz.

DNA extraction, amplification and sequencing. DNA was extracted from leg muscle using a Qiagen DNeasy Blood and Tissue Kit (Qiagen Inc., Valencia, California, USA) following the manufacturers' instructions but with a proteinase K digestion time of 18h at 54°C. Standard polymerase chain reaction (PCR) methods were used to amplify two portions of DNA using an Ex Taq^{TM} kit (Takara Bio Inc., Otsu, Shiga, Japan): approximately 800 bp of the nuclear elongation factor 1 α (EF-1α gene using the primers EF1-PA-f650ambig (Lee & Hill 2010) and EF-N-1419 (Sueur *et al.* 2007) and an annealing temperature of 58°C, and approximately 1500 bp of the mitochondrial cytochrome oxidase subunit I (COI) gene. COI was amplified using either (1) primers C1-J-1490 (Folmer *et al.* 1994) and TL2-N-3014 (Simon *et al.* 1994) and an annealing temperature of 45°C, yielding the entire segment, or (2) in two sections with TibCOIRev (5' CCTCTTTCYTGHGTAATAATGTRTG 3' and C1-J-

1490 at an annealing temperature of 45°C for the first half and C1-J-2195 (Simon *et al.* 1994) with TL2-N-3014 at an annealing temperature of 56°C. An additional primer, TibCOI_INTREV (5' TAYCARTGAAYAAATCTDCC 3'), was occasionally used in the sequencing phase below when the longer segment was amplified in PCR, in order to improve resolution of the middle region. These alternatives were used as necessary to amplify some problematic individuals exhibiting double-peaked chromatograms indicating possible numts (nuclear copies of mitochondrial DNA), which are often observed in studies using the barcoding region of COI (Buhay 2009). Some true mitochondrial copies were also obtained with the TOPO TA Cloning Kit (Life Technologies, Grand Island, NY, USA). PCR products were visualised on a 1% agarose gel (BP1356-500 agarose Fisher Scientific, Pittsburgh, PA, USA) prior to clean up and purified using ExoSAP-IT (USB Corp., Cleveland, Ohio, USA). EF-1α PCRs that amplified two bands were separated on a 1.5% agarose gel, cut out and purified using the Clontech Extract II kit (Clontech, Mountain View, California, USA).

Purified PCR products were cycle sequenced in both directions using a standard cycle sequencing protocol (with Bigdye v1.1, Applied Biosystems, Foster City, California, USA), and then sequenced on an ABI 3100 capillary sequencer with ABI Prism Sequencing Analysis 3.7 software (Applied Biosystems). All DNA fragments were sequenced in both the 5' and 3' directions. Sequencher (Gene Codes Corporation, Ann Arbor, Michigan, USA) software was used to edit the raw sequence data, and the final alignment was performed by eye in MacClade 4.0 (Maddison & Maddison 2000). Rare polymorphic sites within nuclear DNA were coded as ambiguities. Uncorrected pairwise sequence divergences were calculated using Paup* v4.0b (Swofford 1998).

DNA data processing and model selection. The mitochondrial DNA was divided *a priori* into subsets corresponding to the three codon-positions. For the nuclear EF-1α data, the coding and noncoding sites were grouped into separate subsets (keeping the small amount of coding data in one subset). Finally, a subset of binary indel characters was constructed from the insertion-deletion patterns of the aligned noncoding EF-1α data, using SeqState v1.0 (Müller 2005) and the "simple" coding scheme of Simmons and Ochoterena (2000). This data-partition model was compared with various simpler schemes using the "greedy" search algorithm of PartitionFinder (Lanfear *et al.* 2012), with all models evaluated for the maximum-likelihood runs, and with the "mrbayes" model set chosen for the MrBayes and BEAST analyses (see below). This yielded a partition scheme for the analysis using combined mtDNA and EF-1α data. For analyses of the mtDNA and EF-1α separately, and for analyses of the pared-down taxon set used in the BEAST analysis (see below), PartitionFinder was run using the corresponding subsets from above to check for any changes in the partition scheme.

PartitionFinder also selected a best-fitting nucleotide substitution model for each data subset using the AIC. Gamma distributions were estimated with four rate categories. Indels were modeled using the Mkv model (Lewis 2001). DNA data were tested for nucleotide bias using Paup* v4.0, both whole genes and individual partition sets as necessary following the PartitionFinder results.

Molecular phylogenetic analyses. Maximum-likelihood (ML) analyses of mtDNA only, EF-1α data only, and EF-1α + mtDNA combined were conducted using Garli v2.0 (Zwickl 2006). Heuristic searches to find ML trees were conducted on a Macintosh Macbook Pro, while bootstrapping analyses were conducted on the Univ. of California CIPRES biocomputing cluster. To search for best ML trees, the following settings were used: *genthreshfortopoterm* = 10^6, *scorethreshforterm*=10^{-2}, *significanttopochange*=10^{-2}, *collapsebranches*=1, *linkmodels*=0, *subsetspecificrates*=1. For each ML analysis, ten heuristic searches were conducted (*searchreps*=10). Default settings were used for all other Garli options. Two hundred bootstrap replicates were completed for each analysis using the above settings, except that five heuristic searches were conducted for each replicate.

A phylogenetic tree for each analysis was also estimated using MrBayes v3.2.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003), in order to provide an independent estimate of topology. For each analysis, four (default) chains were run until the average standard deviation of split frequencies dropped below 0.01, after which the first 25% of the samples were used as burnin (*stoprule*=yes, *stopval*=0.01). All model parameters were separately estimated (unlinked) across partitions, including the relative partition rates (*ratepr=variable)*. The prior on branch lengths was set to *unconstrained:exponential(100)*, an exponential distribution with a mean of 0.01 substitutions/site. Samples were taken every 10,000 generations. Default settings (e.g., two independent runs per analysis, four chains per run) were used otherwise.

Morphological and cladistic analysis. Data for 27 characters were derived from adult morphology (one head, five thorax, one foreleg, five wing, one abdomen, and 14 genitalic characters) (Table 2). Character terminology follows Moulds (2005). Eighteen characters are binary and nine are multistate (Table 3). The multistate characters were treated as unordered, and character polarity was determined using the outgroup species *Chremistica ochracea* (Walker, 1850), with more distantly related Asian species from the molecular analysis excluded from the morphological study. Neither character weighting nor successive weighting was employed. Figure 1 illustrates the ten states for character #21, the shape of the uncus.

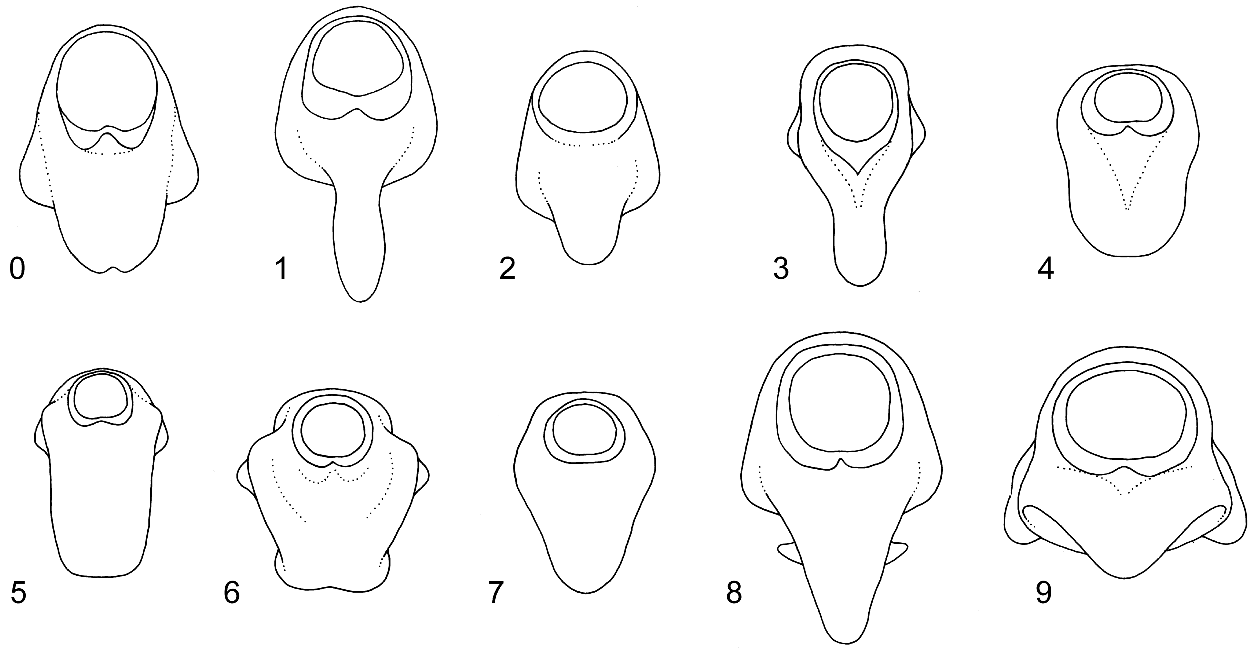

FIGURE 1. Character states used for the uncus, character #21 (see Table 2).

Heuristic parsimony trees were prepared using Hennig86 and CLADOS version 1.2 (Nixon 1992) with TBR + RAS=10 and the MULPARS option, and parsimony bootstrap support was assessed with PAUP* version 4.0b10 using default parameters and 1,000 pseudoreplicates (Swofford 1998). Character numbers were adjusted to begin at '1', rather than the 'zero' default used in the first two programs.

TABLE 2. Morphological character descriptions.

1. Head size: (0) wide, wider than thorax between wings; (1) about as wide or narrower than thorax between wings.
2. Cruciform elevation: (0) very wide, much wider than long; (1) narrow, about as wide as long.
3. Cruciform elevation: (0) depressed diminishingly between anterior arms to extremities of anterior arms; (1) depressed between anterior arms only adjacent to body of cruciform elevation.
4. Basisternum 3: (0) flat, undeveloped; (1) very slightly raised; (2) bulbous; (3) bulbous and protruding distally beyond base of hind coxae.
5. Opercula of male: (0) short, terminating at about rim of tympanal cavity; (1) protruding past rim of tympanal cavity.
6. Fore leg femoral primary spine: (0) erect; (1) lying flat, prostrate.
7. Wing margin: (0) medium width; (1) very broad, on hind wing wider than any of apical cells 3, 4 or 5.
8. Fore wing vein M before branching: (0) very long, approximately half length of discal cell; (1) shorter than half length of discal cell.
9. Fore wing vein M_{1+2} where forming margin of discal cell: (0) shorter or about as long as one other inner margin vein of discal cell; (1) extremely long, far longer than the other two veins combined.
10. Hind wing apical cells: (0) six; (1) five.
    NOTE: Species normally with 5 hind wing apical cells usually have a small number of individuals with 4 or even 6 apical cells (usually only in one wing); such species are considered to have 5 apical cells and those minority individuals with 4 or 6 are regarded as abnormal.
11. Hind wing 2nd cubital cell width at distal end: (0) greater than 1st *anal* cell; (1) less than 1st *anal* cell.
    Note: Some species with these cells about equal have some individuals with the cubital larger than the anal and some vice versa; such species are scored as '?'.
12. Timbal covers, basal part of inner margin: (0) convex; (1) concave.
13. Sternite VIII: (0) U-shaped in cross-section, much less than maximum width of sternite VII; (1) V-shaped in cross-section,

much less than maximum width of sternite VII; (2) V-shaped in cross-section, as wide as or almost as wide as maximum width of sternite VII.

14. Pygofer shape in ventral view: (0) more or less parallel-sided; (1) tapering towards top and bottom, coffin-shaped; (2) considerably broadened towards the top, tending triangular in shape.
15. Pygofer dorsal beak: (0) well developed, acute and spine-like; (1) absent or poorly developed, with basal portion broadly rounded.
16. Pygofer distal shoulder: (0) straight or turned inwards; (1) turned outwards.
17. Pygofer distal shoulder: (0) undeveloped; (1) moderately developed, broad and rounded.
18. Upper pygofer lobe: (0) moderately developed, broadly rounded, projecting; (1) absent or barely developed; (2) strongly developed into a long linear spine; (3) an ill-defined, broadly rounded, internal and lightly sclerotized lobe.
19. Pygofer basal lobe in lateral view: (0) moderate length and apically rounded; (1) very long (at least 4x longer than wide), apically pointed; (2) moderate, pointed; (3) moderate, bi-lobed.
20. Pygofer basal lobe in lateral view: (0) tucked inside, hidden; (1) exposed, either tight against pygofer margin or entirely exposed.
21. Uncal overall shape in dorsal view: (0) very short and broad, about as long as wide, tending triangular; (1) long, finger-like; (2) short, broad and laterally lobed outwards at base in dorsal view, tapering to a rounded apex; (3) short, broad at base, tapering to a distal finger-like extension with a rounded apex; (4) long, broad, wide at base but thereafter less so, arched in cross-section, apex bluntly rounded; (5) long, broad, tending parallel-sided throughout its length, arched in cross-section, apex straight in dorsal view; (6) short, very broad at base, tapering to an expanded apex that is laterally lobed, the large rounded lateral lobes down-turned; (7) short, very broad at base, tapering evenly to rounded apex; (8) short, wide at base, tapering to a distal finger-like extension bearing a pair of large ventral spikes subapically; (9) short, about as long as wide, arched in cross-section, tending triangular.
22. Aedeagal restraint: (0) by a pair of sclerotized swellings at ventral base of uncus; (1) by tubular encapsulation prior to ventral surface of uncus.
23. Aedeagal basal plate in lateral view: (0) straight, aligned with basal portion of theca; (1) distal half or so strongly bent downwards away from alignment of basal portion of theca.
24. Thecal apex: (0) without ventral subapical thorn; (1) with ventral subapical thorn.
25. Theca apex: (0) parallel-sided or almost so, sclerotized, with apical serrations on rim; (1) flared and lightly sclerotized, sometimes in part heavily sclerotized; (2) flared and not sclerotized; (3) parallel-sided and not sclerotized apically.
26. Theca distal half: (0) evenly curved downwards in an arc; (1) curved downwards but kinked near base of curve; (2) straight or weakly curved upwards with apical portion slightly down-turned.
27. Uncus: (0) simple; (1) bifurcate at the extremity; (2) deeply cleft.

Divergence-time analysis. Few fossils are known from the tribe Cryptotympanini, and none can yet be unambiguously assigned to a node in our trees although a family-level review is underway. Therefore, literature-derived clock estimates for the mitochondrial COI gene were used to approximate a timeframe for the cryptotympanine radiation in a Bayesian relaxed-clock analysis conducted in BEAST v2.1.2 (Drummond *et al.* 2006; Drummond & Rambaut 2007). BEAST was used to estimate the phylogeny from the DNA dataset (minus indels) with the substitution rate for the mtDNA partition guided by a COI clock prior encompassing a range of slow to fast literature estimates (from 0.007 to 0.0175 substitutions/site/my, see Marshall *et al.* 2015). This procedure scales the tree according to the amount of mtDNA evolution reconstructed while fitting the likelihood model. However, phylogenetic signal for the scale of molecular substitution can be poor at large genetic distances (Brown *et al.* 2010; Marshall 2010; Marshall *et al.* 2015), and the pairwise uncorrected mtDNA distances in our cryptotympanine dataset approached 20% (see branch lengths in Fig. 3 for model-corrected distances). As a result, we removed the most distant outgroups (*Platypleura*, *Yanga*, *Chremistica*, *Salvazana*, *Tacua*) from the divergence time analysis and calibrated the remaining tree with the method of "relative-time scaling" used by Marshall *et al.* (2015) for the cicada tribe Cicadettini. In this procedure, a younger, well-sampled focal clade is chosen and its root age estimated using relaxed molecular clock analysis of the corresponding data subset as described above, while the full tree is estimated in a separate, uncalibrated BEAST analysis (i.e., with all gene rates estimated relative to one another). The node ages and confidence intervals in the larger tree are then scaled *post hoc* to the estimated root age of the focal clade. In our case, we selected the large subclade containing the eastern and central USA *Tibicen* species.

The divergence time analysis was run with the mtDNA combined into a single partition (as opposed to partitioned by codon-position) to accommodate published whole-gene clock rates. Substitution models for the whole-gene partition scheme were selected using Partitionfinder (Lanfear *et al.* 2012); gamma distributions were estimated with four categories. Other BEAST settings were as shown in Marshall *et al.* (2015). BEAST was run until effective sample sizes for most parameters exceeded 200 as indicated by Tracer v1.5 (Rambaut & Drummond 2007). Convergence was accelerated by assuming the monophyly of well-supported major clades from the MrBayes analyses.

Table 3. Morphological character matrix. Character names and state descriptions are given in Table 2. Taxonomic authorities are given in the Appendix, and new generic assignments of the USA species are summarized in Table 1.

	00000 00001 11111 11112 22222 22 12345 67890 12345 67890 12345 67
Chremistica ochracea	00000 00000 00000 00000 00000 00
Cacama valvata	11011 01001 10110 00100 00111 00
Cacama moorei	11011 01001 10110 00100 00111 00
Cornuplura nigroalbata	00011 01000 10110 00200 00112 02
Cryptotympana atrata	00130 00110 00010 00100 30102 10
Cryptotympana holsti	00130 00110 00010 00100 30102 10
Cryptotympana takasagona	00130 00100 00010 00100 30102 10
Raiateana kuruduadua	00020 00100 00010 01100 30100 10
Tibicen auletes	00020 00100 00020 11301 61100 20
Tibicen auriferus	00021 00100 00000 01321 51102 00
Tibicen bifidus	11011 01000 10110 00101 10101 01
Tibicen bihamatus	01021 10100 11101 01101 40100 10
Tibicen canicularis	00020 00100 00000 01301 51102 10
Tibicen chiricahua	11010 01000 ?0110 00101 10101 00
Tibicen cultriformis	00020 00100 00201 01311 71100 20
Tibicen davisi davisi	00021 00100 00100 01321 51102 10
Tibicen dealbatus	00020 00100 00201 01301 71100 10
Tibicen dorsatus	00020 00100 00201 01301 71100 20
Tibicen duryi	10011 00000 10110 00101 20102 00
Tibicen figuratus	00020 00100 00201 01301 71100 10
Tibicen inauditus	10010 00000 10110 00101 20102 00
Tibicen kyushyuensis	01020 10100 11111 01101 40100 10
Tibicen latifasciatus	00021 00100 00000 01301 51102 10
Tibicen linnei	00021 00100 00000 01301 51102 10
Tibicen longioperculus	10011 00000 10110 00101 10102 00
Tibicen lyricen lyricen	00021 00100 00000 01301 51102 10
Tibicen lyricen virescens	00021 00100 00000 01301 51102 10
Tibicen neomexicensis	11010 01100 10110 00101 10101 00
Tibicen parallelus	00011 00000 ?0110 00101 20101 00
Tibicen plebejus	00020 00100 00010 00100 90102 10
Tibicen pronotalis walkeri	00020 00100 00201 01301 71100 10
Tibicen pronotalis pronotalis	00020 00100 00201 01301 71100 10
Tibicen pruinosus pruinosus	00020 00100 00000 01301 51102 10
Tibicen resh	00020 00100 00221 11301 61100 20
Tibicen resonans	00020 00100 00021 11301 61100 20
Tibicen robinsonianus	00020 00100 00000 01301 51102 10
Tibicen tibicen australis	00021 00100 00000 01301 51102 10
Tibicen tibicen tibicen	00021 00100 00000 01301 51102 10
Tibicen similaris	00021 00100 00100 00331 81102 10
Tibicen superbus	00021 00100 00000 01321 51102 00
Tibicen texanus	10010 00000 10110 00101 20102 00
Tibicen tremulus	00020 00100 00201 01301 71100 20
Tibicen townsendii	10011 01100 10110 00101 20101 ?0
Tibicen winnemanna	00020 00100 00000 01301 51102 10

Results

Generic descriptions. Three new genera are proposed here based on the molecular and morphological results given below, one for the mainly eastern and central North American *Tibicen* species, one for a mainly western

North American clade, and one for certain Asian species. We list their descriptions immediately so that the new combinations can be used consistently for the remainder of the paper and in the figures. In addition, we discuss the definition of *Tibicen* Latreille used in this paper.

Neotibicen gen. n., Hill and Moulds

Type species: *Cicada canicularis* Harris, 1841

Included species: *auriferus* (Say, 1825) comb. n., *auletes* (Germar, 1834) comb. n., *bermudianus* (Verrill, 1902) comb. n., *canicularis* (Harris, 1841) comb. n., *cultriformis* (Davis, 1915) comb. n., *davisi davisi* (Smith & Grossbeck, 1907) comb. n., *davisi harnedi* (Davis, 1918) comb. n., *dealbatus* (Davis, 1915) comb. n., *dorsatus* (Say, 1825) comb. n., *figuratus* (Walker, 1858) comb. n., *latifasciatus* (Davis, 1915) comb. n., *linnei* (Smith & Grossbeck,1907) comb. n., *lyricen engelhardti* (Davis, 1910) comb. n., *lyricen lyricen* (De Geer, 1773) comb. n., *lyricen virescens* (Davis, 1935) comb. n., *pronotalis pronotalis* (Davis, 1938) comb. n., *pronotalis walkeri* (Metcalf, 1955) comb. n., *pruinosus fulvus* (Beamer, 1924) comb. n., *pruinosus pruinosus* (Say, 1825) comb. n., *resh* (Haldeman, 1852) comb. n., *resonans* (Walker, 1850) comb. n., *robinsonianus* (Davis, 1922) comb. n., *similaris* (Smith & Grossbeck, 1907) comb. n., *superbus* (Fitch, 1855) comb. n., *tibicen australis* (Davis, 1912) comb. n., *tibicen tibicen* (Linnaeus, 1758) (= *Tibicen chloromerus* Say) comb. n., *tremulus* (Cole, 2008) comb. n., *winnemanna* (Davis, 1912) comb. n.

Etymology. Combination of the Greek prefix *neo* meaning new and the Latin word *tibicen* meaning a flute player; masculine.

Distribution. Generally from the Rocky Mountains east to the Atlantic Coast, extending into southern Canada and northern Mexico. *Neotibicen cultriformis* extends much farther into the southwest and is the only *Neotibicen* species to reach Arizona. The species from Bermuda (*N. bermudianus*) has been reported extinct (Procter & Fleming 1999).

Diagnosis. Medium to large cicadas with robust bodies, variable in body color between species but mostly a mixture of black with green or dull yellow. *Head* including eyes wide, as wide or wider than mesonotum between wings; vertex with distance between supra-antennal plate and eye about equal to or greater than length of antennal plate. *Thorax* with pronotal collar width at dorsal midline equal to or less than maximum diameter of eyes; paranota moderately ampliate, no mid lateral tooth; cruciform elevation depressed diminishingly between anterior arms to extremities of anterior arms; basisternum 3 bulbous. *Fore wings* hyaline; with 8 apical cells; subapical cells absent; ulnar cell 3 angled to radial cell; basal cell broad, tending to be rounded; vein CuA weakly bowed so that cubital cell no larger than medial cell; veins M and CuA widely separated at basal cell; stem of vein M shorter than half length of discal cell; vein M_{1+2} where forming margin of discal cell shorter or about as long as one other inner margin vein of discal cell; vein RA_1 aligned closely with Sc for its length and not diverging in subapical region; veins CuP and 1A fused in part; infuscations either present or absent, if present then overlaying veins at bases of apical cells 2 and 3; wing outer margin developed for its total length, never reduced to be contiguous with ambient vein. *Hind wings* with 6 apical cells; no infuscation on ambient vein; width of 1st cubital cell at distal end about equal to 2nd cubital cell or just a little larger; 2nd cubital cell width at distal end greater than 1st anal cell; anal lobe broad with vein 3A curved, long, separated from wing margin; veins RP and M fused basally; wing margin of medium width, not excessively broad. *Male opercula* passing rim of tympanal cavity (only just passing in some species, very long in others); overlapping. *Fore leg* femoral primary spine erect. *Male abdomen* in cross-section with sides of tergites straight or weakly convex, epipleurites reflexed to ventral surface; tergites 2 and 3 enlarged, about twice as wide as tergites 3–7; sternites IV–VII in cross-section convex; sternite VIII either V-shaped or U-shaped in cross-section, as wide as or less than maximum width of sternite VII; timbal covers present, very slightly domed, fully rounded dorsally and extending to metathorax and tightly closed, lower margin extending anteriorly from or very near auditory capsule, meeting but not overlapping opercula; timbal ribs robust; basal dome very large; timbals extended below wing bases.

Male genitalia. *Pygofer* in ventral view either parallel-sided or broadened towards the top; pygofer with distal shoulders broad, rounded (but barely developed in *similaris*); upper pygofer lobes ill-defined, broadly rounded, internal and lightly sclerotized; basal lobes undivided, moderately developed, in lateral view exposed, either tight against pygofer margin or entirely exposed, of moderate length and apically rounded, pointed or bi-lobed; dorsal beak either absent, poorly developed or well developed and a part of chitinized pygofer. *Uncus* dominant; undivided, considerably variable in shape and size, either long or short; lacking accessory spines (claspers). *Aedeagus* restrained by tubular encapsulation on ventral surface of uncus; basal plate in lateral view with distal half or so strongly bent downwards away from alignment of basal portion of theca; in dorsal view apical arms short, base broad and long with midline deeply furrowed; ventral rib completely fused with basal plate; junction between theca and basal plate rigid, without a 'hinge'; thecal shaft recurved basally through 180° or more, J shaped; distal half of thecal shaft either straight, curved downwards and usually kinked near base or weakly curved upwards with apical portion slightly downturned; pseudoparameres absent; thecal apex flared or parallel-sided; thecal subapical cerci absent; flabellum absent; conjunctival claws absent; vesica retractable, vesical opening apical on theca. *Male reproductive system* unknown. *Female reproductive system* ditrysian; length of accessory glands unknown.

Distinguishing features. *Neotibicen* differs from all other cicada genera in having the following combination of attributes: male basisternum 3 is very bulbous; male timbal covers are fully rounded dorsally, extending to the metathorax and tightly closing the timbal cavity; male tergites 2 and 3 are enlarged, about twice as wide as each of tergites 3–7; aedeagal basal plate in lateral view shows the distal half or more strongly bent downwards through about 90 degrees; and the aedeagus is restrained by tubular encapsulation prior to the ventral surface of the uncus.

Hadoa gen. n. Moulds

Type species: *Tibicen duryi* Davis, 1917

Included species: *bifida* (Davis, 1916) comb. n., *chihuahuaensis* (Sanborn, 2007) comb. n., *chiricahua* (Davis, 1923) comb. n., *chisosensis* (Davis, 1934) comb. n., *distanti* (Metcalfe, 1963) comb. n., *duryi* (Davis, 1917) comb. n., *fusca* (Davis, 1934) comb. n., *hidalgoensis* (Davis, 1941) comb. n., *inaudita* (Davis, 1917) comb. n., *longiopercula* (Davis, 1926) comb. n., *minor* (Davis, 1934) comb. n., *montezuma* (Distant, 1881) comb. n., *neomexicensis* (Stucky, 2013) comb. n., *paralleloides* (Davis, 1934) comb. n., *parallela* (Davis, 1923) comb. n., *robusta* (Distant, 1881) comb. n., *sugdeni* (Davis, 1941) comb. n., *texana* (Metcalf, 1963) comb. n., *townsendii* (Uhler, 1905) comb. n.

Etymology. Derived from a Western Apache word for “sing”; feminine.

Distribution. Throughout the southwestern USA (Arizona to Texas and the central Rocky Mountains) and Mexico.

Diagnosis. Large cicadas with robust bodies, variable in body colour between species but mostly a mixture of black and dull yellow. *Head* including eyes about as wide as (slightly wider in *parallela*) or narrower than thorax between wings; vertex with distance between supra-antennal plate and eye about equal to or slightly less than length of antennal plate. *Thorax*: pronotal collar width at dorsal midline equal to or less than maximum diameter of eyes; paranota moderately ampliate, no mid lateral tooth; cruciform elevation depressed diminishingly between anterior arms to extremities of anterior arms; basisternum 3 only very slightly raised, not bulbous. *Fore wings* hyaline; with 8 apical cells; subapical cells absent; ulnar cell 3 angled to radial cell; basal cell broad, tending to be rounded; vein CuA weakly bowed so that cubital cell no larger than medial cell; veins M and CuA widely separated at basal cell; stem of vein M very long (approximately half length of discal cell) except in *neomexicensis* and *townsendii* where it is shorter; vein M_{1+2} where forming margin of discal cell shorter or about as long as one other inner margin vein of discal cell; vein RA_1 aligned closely with Sc for its length and not diverging in subapical region; veins CuP and 1A fused in part; infuscations either present or absent, if present overlaying veins at bases of apical cells 2 and 3; wing outer margin developed for its total length, never reduced to be contiguous with ambient vein. *Hind wings* with 6 apical cells; no infuscation on ambient vein; width of 1st cubital cell at distal end about equal to 2nd cubital cell or just a little larger; 2nd cubital cell width at distal end *usually* less than 1st anal cell; anal lobe broad with vein 3A curved, long, separated from wing margin; veins RP and M fused basally; wing margin of medium width or very broad (wider than any of apical cells 3, 4 or 5). *Male opercula* either terminating at about rim of tympanal cavity or extending beyond; overlapping. *Fore leg* femoral primary spine erect. *Male abdomen* in cross-section with sides of tergites straight or weakly convex, epipleurites reflexed to ventral surface; tergites 2 and 3 enlarged, wider than tergites 3–7; sternites IV–VII in cross-section convex; sternite VIII V-shaped in cross-section, much less than maximum width of sternite VII; timbal covers present, very slightly domed, fully rounded dorsally and extending to metathorax and tightly closed, lower margin extending anteriorly from or very near auditory capsule, meeting but not overlapping opercula; timbal ribs robust; basal dome very large; timbals extended below wing bases.

Male genitalia. *Pygofer* in ventral view tapering towards top and bottom, coffin-shaped; pygofer with distal shoulders undeveloped, either straight or turned inwards; upper pygofer lobes absent or barely developed; basal lobes undivided, moderately developed, in lateral view exposed, either tight against pygofer margin or entirely exposed, of moderate length and apically rounded; dorsal beak well developed, acute. *Uncus* dominant; undivided (except in *H. bifida* which is apically bifurcate), either long and finger-like or short and broad tapering to a rounded apex and laterally lobed outwardly at base; subapically without ornamentation; lacking accessory spines (claspers). *Aedeagus* restrained by a pair of lightly sclerotized swellings at ventral base of uncus; basal plate in lateral view with distal half or so strongly bent downwards away from alignment of basal portion of theca; in dorsal view apical arms short, base broad and long with midline deeply furrowed; ventral rib completely fused with basal plate; junction between theca and basal plate rigid, without a 'hinge'; thecal shaft recurved basally through 180° or more, J shaped; distal half of thecal shaft evenly curved downwards in an arc; pseudoparameres absent; thecal apex flared and either sclerotized or not sclerotized; thecal subapical cerci absent; flabellum absent; conjunctival claws absent; vesica retractable, vesical opening apical on theca. *Male reproductive system* unknown. *Female reproductive system* ditrysian; length of accessory glands unknown.

Distinguishing features. *Hadoa* is closely allied to *Cornuplura* and *Cacama*. It differs from *Cornuplura* in having the male upper pygofer lobe absent or barely developed—in *Cornuplura* this is strongly developed into a long linear spine. It differs from *Cacama* in having 6 hind wing apical cells instead of 5. *Hadoa* differs from *Neotibicen*, with which it is partially sympatric in North America, in having male basisternum 3 only very slightly raised (almost flat), while in *Neotibicen* it is distinctly bulbous.

Hadoa differs from all other cicada genera in having the following combination of attributes: the distance between the supra-antennal plate and the eye is about equal to or slightly less than the length of the antennal plate; male timbal covers are fully rounded dorsally, extending to the metathorax and tightly closing the timbal cavity; male abdominal tergites 2 and 3 are each much larger than any one of 4–7; male basisternum 3 is a little swollen; and the upper pygofer lobe is absent or barely developed.

***Subsolanus* gen. n. Moulds**

Type species: *Cicada bihamatus* de Motschulsky, 1861

Included species. *atrofasciatus* (Kirkaldy, 1909) comb. n. (sensu *Cicada sinensis* Distant, 1890), *bihamatus* (de Motschulsky, 1861) comb. n., *chujoi* (Esaki, 1935) comb. n., *esakii* (Kato, 1958) comb. n., *flammatus* (Distant, 1892) comb. n., *flavomarginatus* (Hayashi, 1977) comb. n., *intermedius* (Mori, 1931) comb. n., *jai* (Ouchi, 1938) comb. n., *japonicus* (Kato, 1925) comb. n., *kyushyuensis* (Kato, 1926) comb. n., *leechi* (Distant, 1890) comb. n., *pekinensis* (Haupt, 1924) comb. n., *slocumi* (Chen, 1943) comb. n., *tsaopaonensis* (Chen, 1943) comb. n.

We were unable to examine all Eurasian species and there may be other species currently placed in *Tibicen* or *Lyristes* that belong here.

Etymology. From the Latin *Coriolanus* meaning the East, or the Orient and referring to the distribution of this genus; masculine.

Distribution. China, Taiwan, Russia and Japan.

Diagnosis. Medium to large cicadas with robust bodies, with all species having velvety black coloration with pale yellow to orange markings and a central (rounded) W-shaped marking on mesonotum. *Head* including eyes wide, as wide or wider than mesonotum between wings; vertex with distance between supra-antennal plate and eye about equal to length of antennal plate. *Thorax* with pronotal collar width at dorsal midline less than maximum diameter of eyes; paranota moderately ampliate, no mid lateral tooth; cruciform elevation depressed diminishingly between anterior arms to extremities of anterior arms; basisternum 3 bulbous but not protruding distally beyond base of hind coxae. *Fore wings* hyaline; with 8 apical cells; subapical cells absent; ulnar cell 3 angled to radial cell; basal cell broad, tending to be rounded; vein CuA weakly bowed so that cubital cell no larger than medial cell;

veins M and CuA widely separated at basal cell; stem of vein M shorter than half length of discal cell; vein M_{1+2} where forming margin of discal cell shorter or about as long as one other inner margin vein of discal cell; vein RA_1 aligned closely with Sc for its length and not diverging in subapical region; veins CuP and 1A fused in part; infuscations either present or absent, if present overlaying veins at bases of apical cells 2 and 3 and sometimes elsewhere; wing outer margin developed for its total length, never reduced to be contiguous with ambient vein. *Hind wings* with 6 apical cells; no infuscation on ambient vein; width of 1st cubital cell at distal end about equal to 2nd cubital cell or just a little larger; 2nd cubital cell width at distal end less than 1st anal cell; anal lobe broad with vein 3A curved, long, separated from wing margin; veins RP and M fused basally; wing margin of medium width, not excessively broad. *Male opercula* either terminating at about rim of tympanal cavity (posterior margin of 2nd sternite) or extending beyond; overlapping or contiguous basally. *Fore leg* femoral primary spine lying flat, prostrate. *Male abdomen* in cross-section with sides of tergites straight or weakly convex, epipleurites reflexed to ventral surface; tergites 2 and 3 enlarged, along dorsal midline each much wider than any of tergites 3–7; sternites IV–VII in cross-section convex; sternite VIII V-shaped in cross-section, less than maximum width of sternite VII; timbal covers present, very slightly domed, with basal part of inner margin a little concave, otherwise extending to metathorax and tightly closed, with lower margin extending anteriorly from or very near auditory capsule, meeting but not overlapping opercula; timbal ribs robust; basal dome very large; timbals extended below wing bases.

Male genitalia. *Pygofer* in ventral view either more or less parallel-sided or tapering towards top and bottom; pygofer with distal shoulders broad, rounded; upper pygofer lobes absent or barely developed; basal lobes undivided, moderately developed but very short, in lateral view tight against pygofer margin with apical portion not exposed in most cases, of moderate length and apically rounded; dorsal beak absent or poorly developed, with basal portion broadly rounded. *Uncus* dominant; undivided, long and broad (stout), without ornamentation; lacking accessory spines (claspers); apically half bent inward (at more than 100 degrees). *Aedeagus* restrained by a pair of sclerotized swellings at ventral base of uncus; basal plate in lateral view with distal half or so strongly bent downwards away from alignment of basal portion of theca; in dorsal view apical arms short, base broad and long with midline deeply furrowed; ventral rib completely fused with basal plate; junction between theca and basal plate rigid, without a 'hinge'; thecal shaft recurved basally through 180° or more, J- shaped; distal half of thecal shaft evenly curved downwards in an arc and usually kinked near base; pseudoparameres absent; thecal apex parallel-sided or almost so, sclerotized; thecal subapical cerci absent; flabellum absent; conjunctival claws absent; vesica retractable, vesical opening apical on theca. *Male reproductive system* unknown. *Female reproductive system* unknown.

Distinguishing features. *Subsolanus* is distinguished from *Tibicen, Neotibicen* and *Hadoa* by the basal part of the inner margin of the timbal covers that is broadly concave and by the fore leg femoral primary spines that often lie flat, prostrate (but in some species are obliquely erect). *Subsolanus* differs from all other genera by having the combination of the above features plus having the timbal covers tightly closing the timbal cavity, the pygofer dorsal beak absent or poorly developed, and the 2nd cubital cell width at distal end less than the 1st anal cell width.

Tibicen Latreille 1825

Tibicen as defined in this paper (based on *T. plebejus*) differs from the allied new genera described here (all the species of which were previously placed in either *Tibicen* or *Lyristes*) in having the fore leg femoral primary spines erect, the basal part of the inner margin of the timbal covers straight or convex, basisternum 3 bulbous, the uncus in dorsal view short (about as long as wide), and the pygofer basal lobe tucked inside and hidden in lateral view.

Key to genera of species previously in *Tibicen* based on males

1. Fore leg femoral primary spines usually lying flat, prostrate, but sometimes obliquely erect; basal part of inner margin of timbal covers slightly concave . . . . ***Subsolanus* gen. n.**
\- Fore leg femoral primary spines erect; anterior dorsal margin of timbal covers straight or convex 2
2. Basisternum 3 bulbous 3
\- Basisternum 3 only very slightly raised, almost flat . . . . ***Hadoa* gen. n.**
3. Male opercula protruding past rim of tympanal cavity . . . . ***Neotibicen* gen. n.**

-	Male opercula short, terminating at about rim of tympanal cavity	4
4.	Uncus in dorsal view short, about as long as wide; pygofer basal lobe tucked inside, hidden in lateral view. Females indistinguishable	***Tibicen* Latreille**
-	Uncus in lateral view either short and tapering towards apex or long being much longer than wide; pygofer basal lobe partly exposed in lateral view	***Neotibicen* gen. n.**

DNA extraction, amplification and sequencing. The edited sequence lengths were 1467 bp of COI mtDNA and 783 bp of EF-1α, which included 405 bp of coding region and 378 bp of intron. The intron region contained 103 indel characters that were coded by Seqstate. All sequences have been deposited in Genbank with accession numbers KR674147-KR674245 for COI and KR705752-KR705866 for EF-1α. Note that in the following sections all assignments of species to the new genera *Hadoa*, *Neotibicen*, and *Subsolanus* are new combinations.

Several species amplified numts as well as the COI mtDNA fragment. We initially amplified two overlapping smaller portions of COI of approximately 800 bp each, however we found that we would often amplify numt sequences in one or both of these smaller fragments. By amplifying ca. 1500 bp at once we were able to eliminate many of the numt sequences. For a limited number of taxa (03.US.MA.MAR.01 *Neotibicen canicularis*, 05.US.LA.SFF.01 *N. pruinosus pruinosus*, and 07.US.MO.WSP.01 *N. robinsonianus*), COI was eventually obtained via cloning. We were unable to obtain COI for any specimens of *N. winnemanna*, *N. latifasciatus, N. linnei,* and *Hadoa duryi* Davis, 1917.

Model selection and data partitioning. PartitionFinder confirmed a five-subset partition scheme for the likelihood-based phylogenetic analyses (Garli and MrBayes), with the mitochondrial codon-positions each handled separately and the EF-1α intron sites separated from the exon sites. For the divergence-time analyses, a three-subset partition was confirmed. The partition schemes and the specific substitution models proposed by PartitionFinder for each data subset are shown in Table 4.

TABLE 4. Partition schemes and molecular substitution models for DNA data subsets.

	DATA SUBSET					
ANALYSIS	mt-all	mt1pos	mt2pos	mt3pos	efcoding	efintron
Garli ML	N/A	GTR+I+G	TIM+I+G	K81uf+G	TrN+I+G	TVM+G
MrBayes	N/A	GTR+I+G	GTR+I+G	HKY+G	HKY+I+G	GTR+G
BEAST main analyses	GTR+I+G	N/A	N/A	N/A	K80+I	GTR+G
BEAST *Neotibicen* clade only	GTR+G	N/A	N/A	N/A	K80+I	HKY+G

Tests for base-composition bias in Paup* were nonsignificant (P = 1.0) for the mtDNA dataset as a whole, for the separate first- and second-codon-position mtDNA subsets, and for the EF-1α data subsets. The test was significant for the 3rd position mtDNA data subset ($P < 10^{-8}$). Consequently, a Garli ML analysis was run without the mtDNA third-codon-position sites to check for any well-supported differences in the resulting tree.

Molecular phylogenetic results, intergeneric level. Combined data. In the combined molecular tree (Fig. 2), North American taxa formerly placed within the genus *Tibicen* form two major clades separated by other cryptotympanine genera. The first of the two clades, strongly supported by a 97% ML bootstrap percentage (BP) and 1.0 posterior probability (PP), contains the new genus *Neotibicen*. This "east-central North America" clade is strongly supported (BP 100, PP 1.0) as sister to a clade containing the Asia-Pacific *Cryptotympana* and *Raiateana* species, although the order of divergence of the latter two genera remains unclear. A second major North American clade (BP 99, PP 1.0) contains the ten western *Hadoa* species plus *Cacama* and *Cornuplura* (which both extend into Mexico). Diverging at the same point in the tree as these two large clades, but with an uncertain order, are well-supported clades containing the new Asian genus *Subsolanus* and a clade pairing *Tibicen gemellus* with *T. plebejus*. Weakly supported as sister to all of these, is a well-supported (BP 91, PP 1.0) clade containing most of the sampled *Chremistica* species as well as *Salvazana mirabilis* Distant, 1913. *Tacua speciosa* (Illiger, 1800) and *Chremistica ochracea* group as the most distant ingroup clade, but with no bootstrap support.

The five included *Cryptotympana* species form a strongly-supported monophyletic group. Relationships within the *Cryptotympana* clade and the distant *Chremistica* + *Salvazana* and *C. ochracea* + *Tacua* ingroup clades are otherwise only weakly resolved and are not considered further in this paper.

Single-gene analyses. Phylogenetic patterns are broadly similar when the mitochondrial data (Fig. 3) and the nuclear-gene data (Fig. 4) are analyzed independently. The mtDNA tree supports all of the major clades discussed above with BP > 80 and PP 1.0, including the *Neotibicen* group, its relationship to *Cryptotympana*/*Raiateana*, and the large clade containing *Hadoa* species plus *Cacama* and *Cornuplura*. In the EF-1α tree, divergence levels are low and support levels are weaker overall, but the major clades are concordant with the mtDNA and combined-data trees and still supported with BP 70 or higher and PP=1.0. No well-supported generic-level discordance exists between the mtDNA and EF-1α trees. Notably, *Hadoa parallela* and *Cacama* split off as a weakly supported monophyletic clade at the base of the western group in the mtDNA tree, while *Cacama* is alone as the first lineage to branch off in the EF-1α tree, again with weak support only. EF-1α could be sequenced from only one Japanese *Tibicen* species, so the clade was necessarily monotypic in that tree.

Molecular phylogenetic results, North American intrageneric relationships. New genus *Hadoa*. Other than *Hadoa parallela*, the species of this new genus form one large well-supported group (BP 90 BP, PP 1.0) that is sister to *Cornuplura nigroalbata* (Davis, 1936) (Fig. 2) in the combined-data molecular tree. *Hadoa bifida* and *H. simplex*, originally described at subspecific rank, are found together at the top of the tree, with a sister-group relationship to *H. longiopercula*. *Hadoa chiricahua* and *H. neomexicensis* (recently distinguished from *H. chiricahua*) reconstruct as sister taxa, and together they share a sister-clade relationship to the *H. longiopercula* + *H. simplex* + *H. bifida* clade. The two deepest splits in the group lead to *H. townsendii* and a well-supported clade (BP 96, PP 1.0) containing *H. texana*, *H. inaudita*, and *H. duryi*, although the order of these two lineages is only weakly resolved. The position of *H. parallela* is not clearly resolved, with some conflict apparent between the nuclear and mtDNA data.

New genus *Neotibicen*. The large *Neotibicen* clade contains two well-supported subgroups. One of these contains ten large-bodied species and subspecies that are mainly distributed in the central USA. In this clade in the combined-data molecular tree, *N. tremulus* and *N. cultriformis* are sister species (BP 99, PP 1.0), as well as *N. auletes* and *N. resh* with moderate support (BP 81, PP 1.0). *N. pronotalis pronotalis*, *N. pronotalis walkeri*, and *N. dealbatus* form a well-supported clade (BP 97, PP 1.0). At a deeper level, the *N. pronotalis* + *dealbatus* and *N. cultriformis* + *N. tremulus* clades are united with *N. dorsatus* in a larger grouping (BP 90, PP 1.0). Support for additional relationships, such as a greater *N. auletes* + *N. resh* + *N. resonans* clade, is only moderate (BP 81, PP 0.98). Relationships within this clade in the separate mtDNA and EF-1α trees were generally concordant with these results but with weaker support, with the exception of *Neotibicen auletes* which was sister to *N. resh* in the combined tree but sister to *N. resonans* in the mtDNA-only tree.

The remaining 17 *Neotibicen* species and subspecies have relatively poor phylogenetic resolution due to missing mtDNA data from species where numt amplification was problematic. However, strong support exists for a *Neotibicen tibicen tibicen* + *N. tibicen australis* clade (BP 100, PP 1.0) and a clade containing *N. auriferus*, *N. superbus*, and the two *N. davisi* subspecies (BP 98, PP 1.0). Weak support suggests a clade uniting *N. linnei* and *N. robinsonianus* (BP 63, PP 1.0) and a larger clade containing *N. canicularis*, *N. pruinosus*, *N. winnemanna*, *N. robinsonianus*, *N. latifasciatus*, and the *N. lyricen* subspecies (BP 69, PP 1.0). All of the well-supported relationships found within this broader clade in the combined-data analysis are either present in the separate mtDNA and EF-1α trees or unresolved. No well-supported conflict is evident.

Combined data with third codon positions removed. Three well-supported differences were observed when the third-position mtDNA data were removed in a separate ML analysis. First, *Neotibicen figuratus* joined *N. auletes*, *N. resh*, and *N. resonans* at the base of the central *Neotibicen* clade, with their branching order unresolved. Second, 63% BP support was found for *Raiateana* as the sister lineage to *Neotibicen*. Third, in the western North American clade, *Hadoa longiopercula* was weakly supported as sister to the *H. bifida* + *H. simplex* clade.

Morphological cladistic results. Heuristic parsimony analysis of the included cryptotympanine species, using *Chremistica ochracea* as the outgroup, yielded one most parsimonious tree (Fig. 5). The morphological tree contains broadly similar groups to those in the combined-data molecular tree, including a *Hadoa* + *Cacama* + *Cornuplura* clade (BP=88%), a *Neotibicen* clade (BP=58%), and a clade containing Japanese *Subsolanus* species (BP=92%). Bootstrap support beyond these clades is poor or below 50%, and the phylogenetic positions of *Cryptotympana*, *Tibicen*, *Subsolanus*, and *Raiateana* between the western and eastern North American clades are only weakly supported. Fig. 6 shows dorsal and ventral photos of the USA species examined, plus one representative each of *Cornuplura* and *Cacama*, with all taxa assigned to the new genera supported by the cladistic analysis.

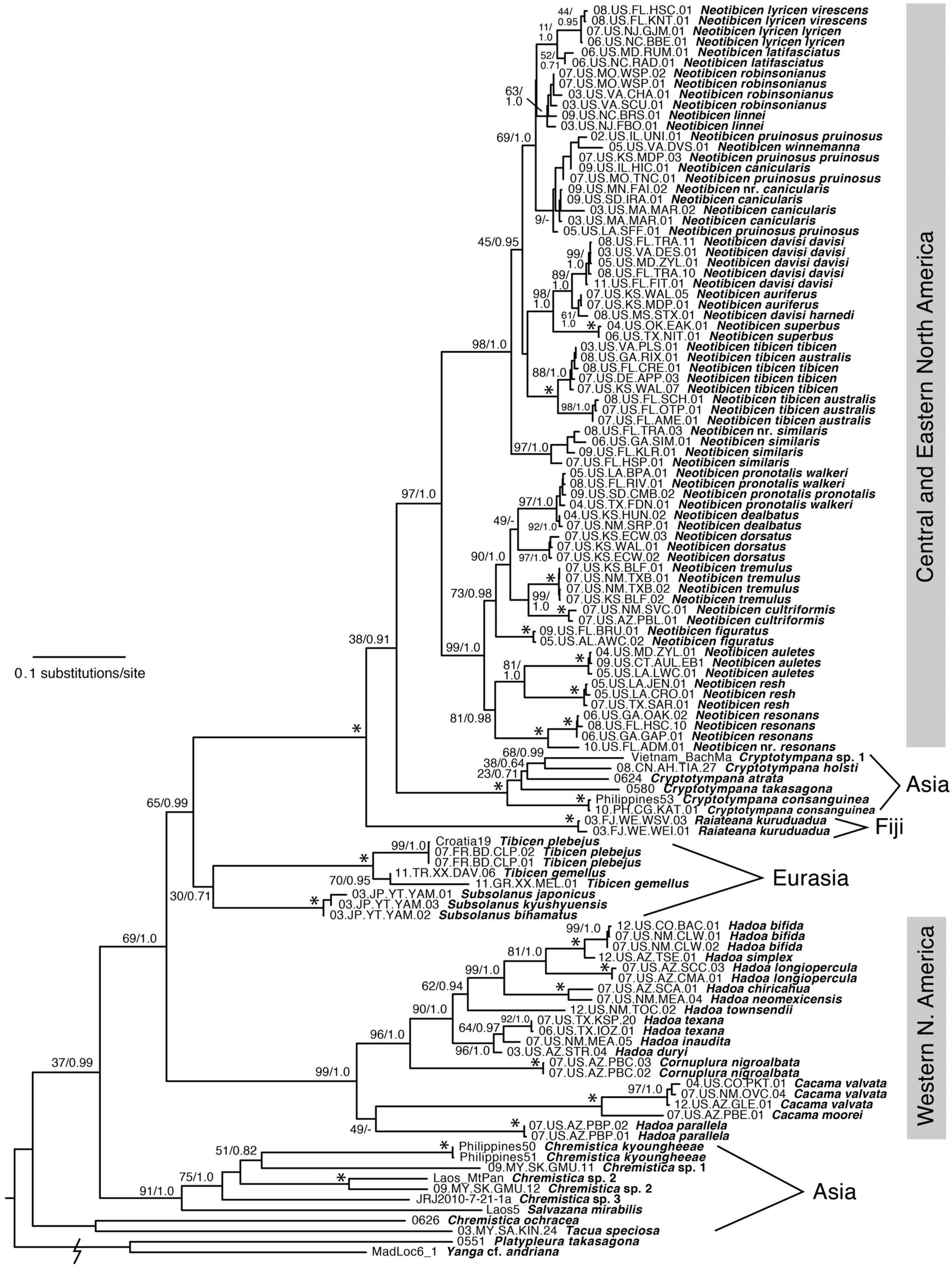

FIGURE 2. Maximum-likelihood phylogeny of North American cryptotympanine cicada species (mainly from USA and Canada) and selected world relatives based on a combined nuclear DNA + mtDNA dataset. Support values show maximum-likelihood percentages followed by posterior probabilities from a separate Bayesian analysis (asterisks indicate 100/1.0). Note that 0.2 substitutions/site was removed from the outgroup branch for presentation purposes. All taxa listed under the new genera *Hadoa*, *Neotibicen* and *Subsolanus* are comb. n. Codes refer to specimens listed in the Appendix.

FIGURE 3. Cryptotympanini tree based on maximum-likelihood analysis of mtDNA alone. Support values shown are maximum-likelihood bootstrap percentages and Bayesian posterior probabilities from a separate analysis. Note that 0.2 substitutions/site was removed from the outgroup branch for presentation purposes. All taxa listed under the new genera *Hadoa*, *Neotibicen* and *Subsolanus* are comb. n.

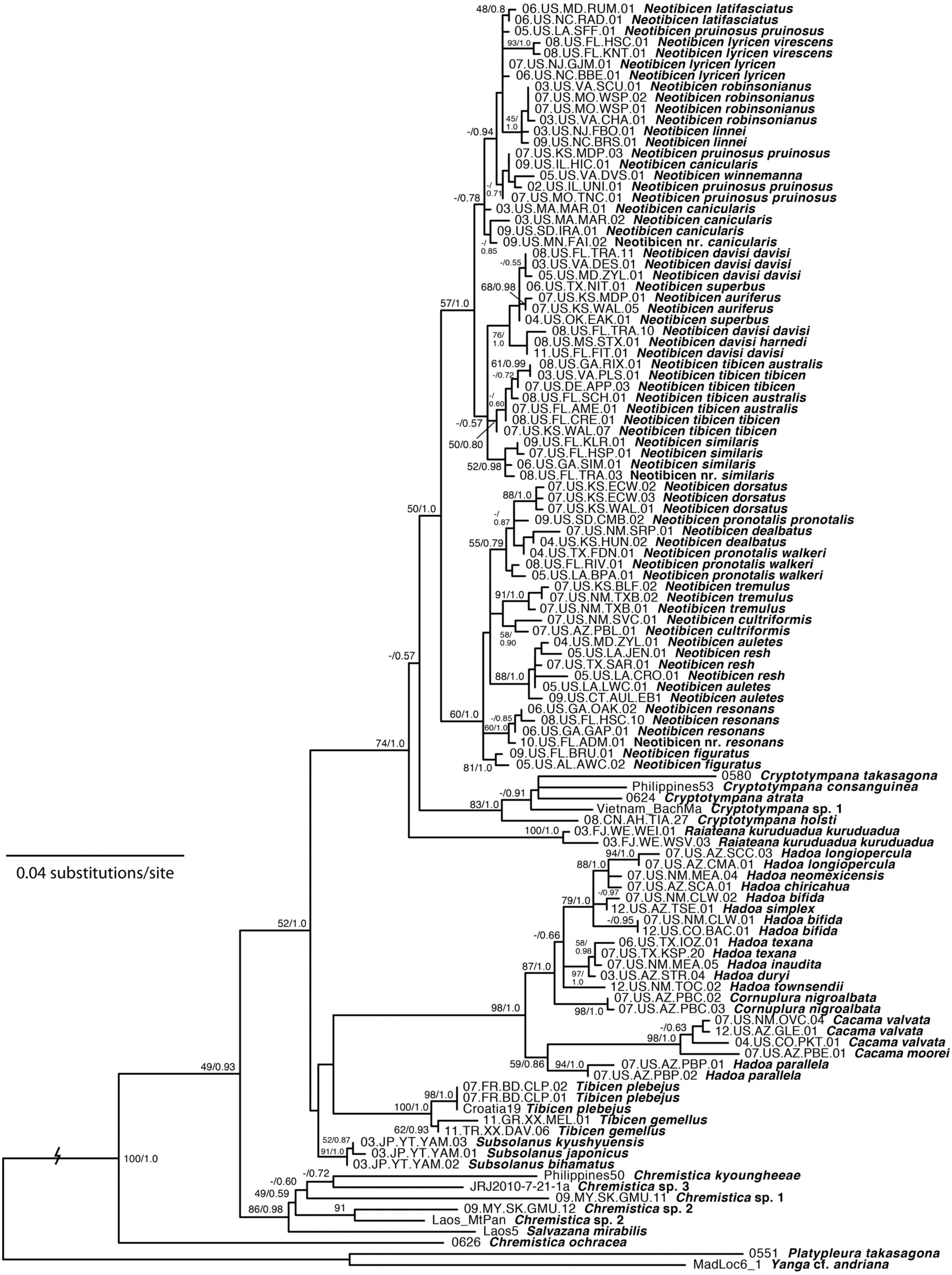

FIGURE 4. Cryptotympanini tree based on maximum-likelihood analysis of nuclear EF-1α data alone. Support values shown are maximum-likelihood bootstrap percentages and Bayesian posterior probabilities from a separate analysis. Note that 0.16 substitutions/site was removed from the outgroup branch for presentation purposes. All taxa listed under the new genera *Hadoa*, *Neotibicen* and *Subsolanus* are comb. n.

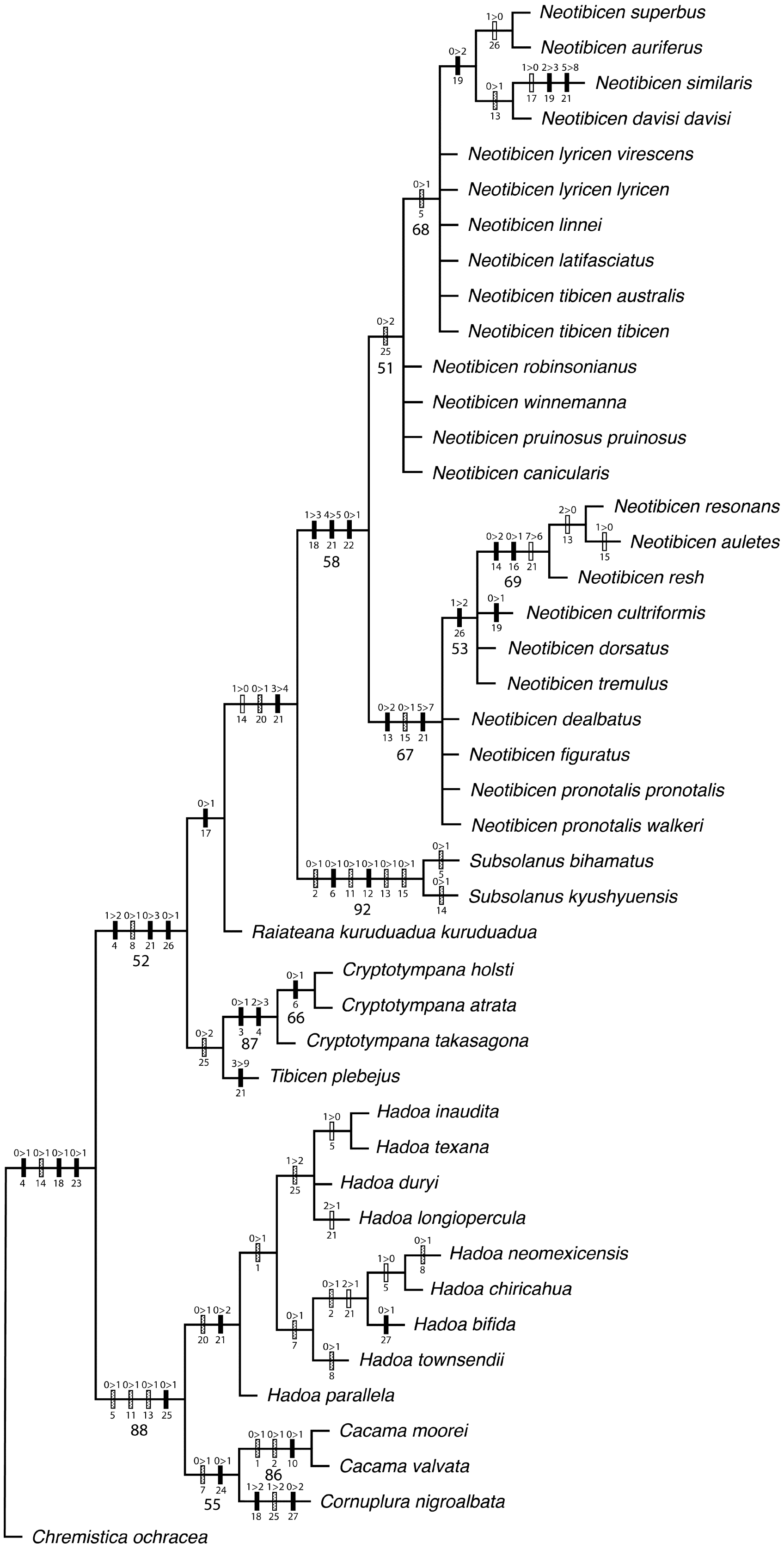

FIGURE 5. The most parsimonious tree (length 71, CI 64, RI 90) from the morphological cladistic analysis of the characters given in Tables 2 and 3. Numbers at nodes are bootstrap values greater than 50%. Character transformations shown at nodes: black bars = non-homoplasious forward change; grey bars = homoplasious forward change; white bars = reversal (whether homoplasious or not). The most distantly related Asian taxa were excluded from this analysis. All taxa listed under the new genera *Hadoa*, *Neotibicen* and *Subsolanus* are comb. n.

FIGURE 6. Dorsal and ventral-posterior (inset) photographs of the described North American cryptotympanine cicada species and subspecies included in this study (minus *Neotibicen davisi harnedi* and *Cacama moorei*), in alphabetical order by genus and then species. All taxa listed under the new genera *Hadoa* and *Neotibicen* are comb. n. Scale bar shows approximately 1 cm. Specimen codes refer to the Appendix, which also includes the earlier taxonomic assignments.

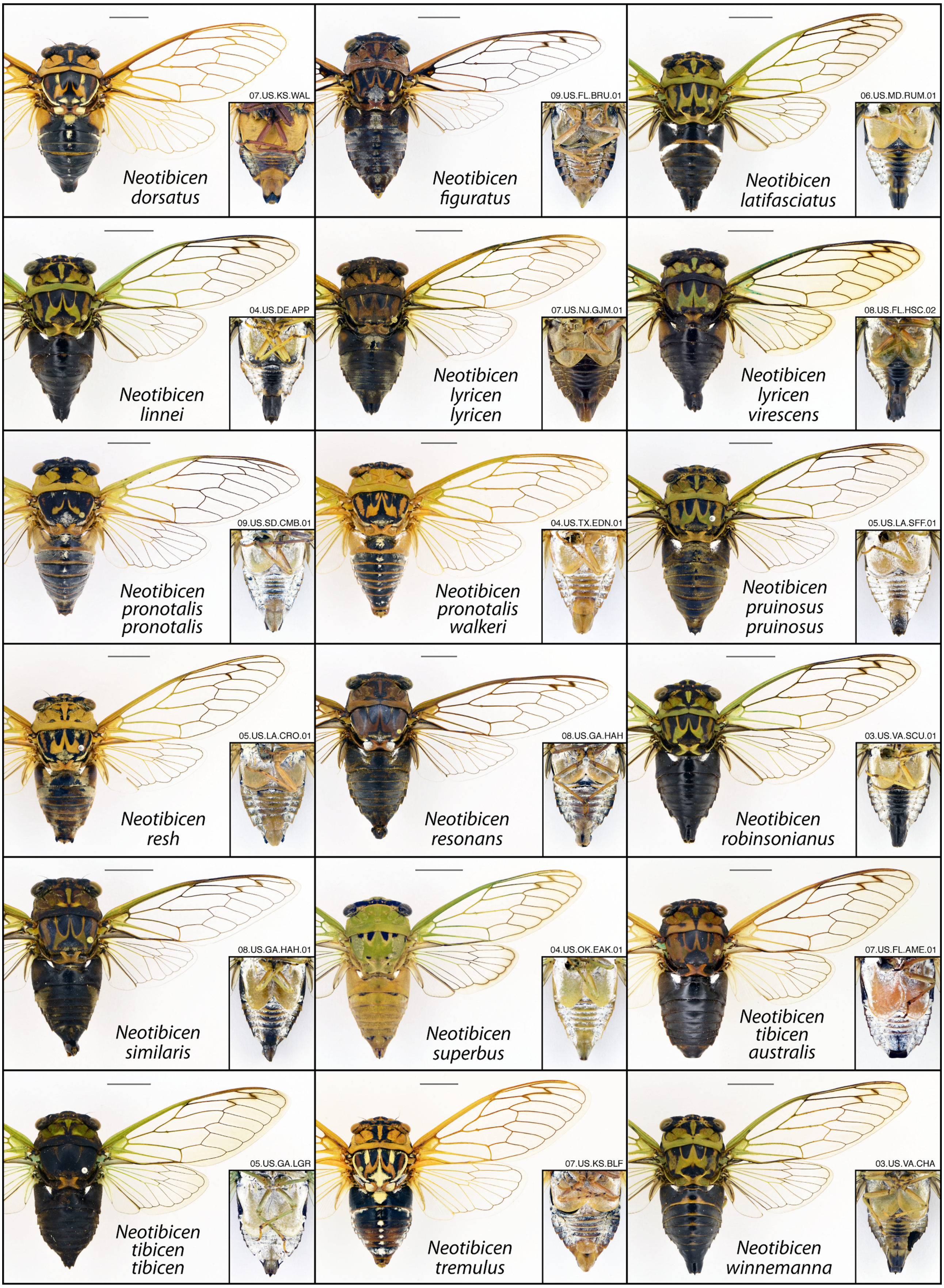

FIGURE 6. (Continued)

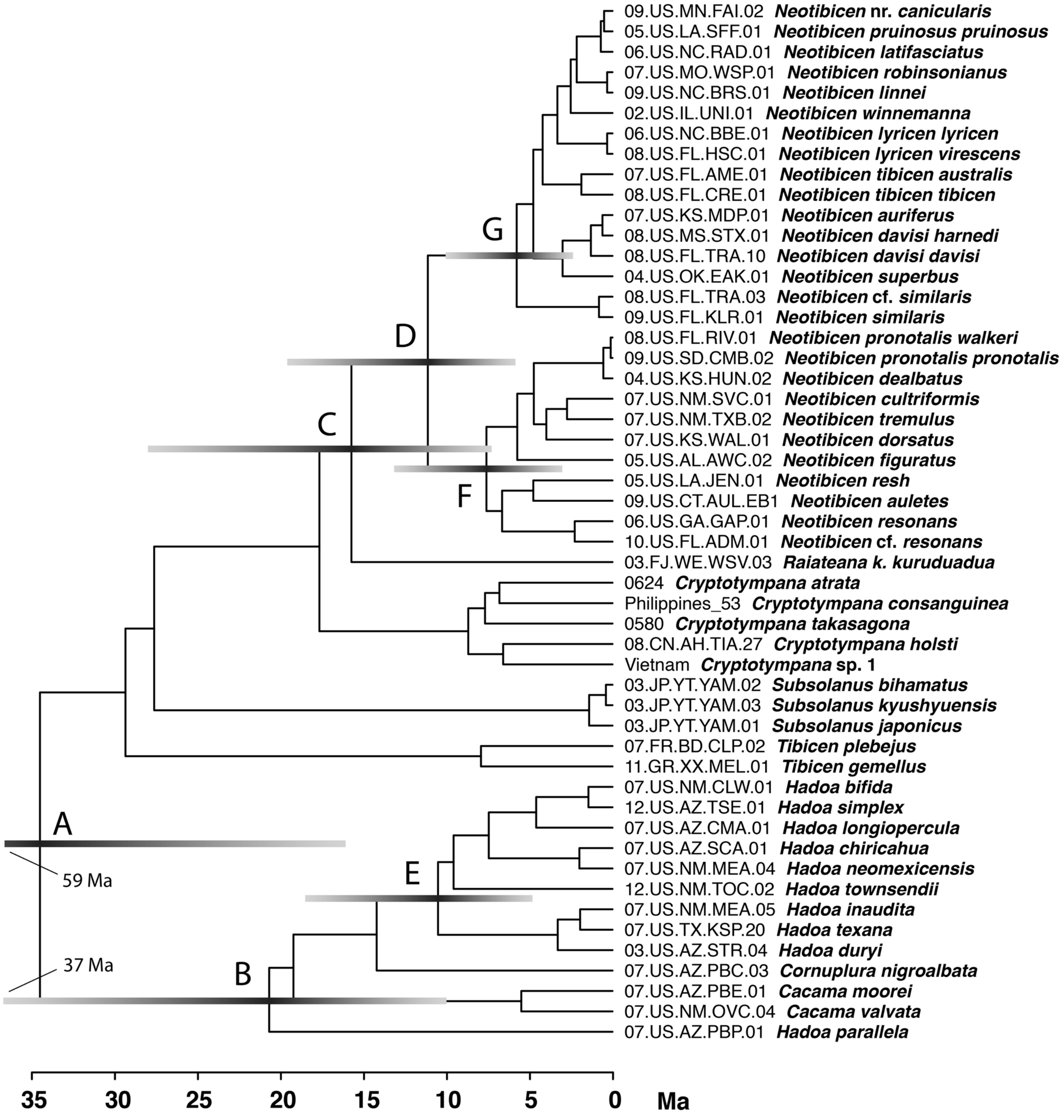

FIGURE 7. Relaxed-clock chronogram of North American cryptotympanine cicada species (mainly from USA and Canada) and selected world relatives. The tree shows the median age estimates, and the gradient bars show the 95% confidence intervals of focal nodes. The chronogram was calibrated using literature-derived molecular clock estimates for the mtDNA cytochrome oxidase I gene. Lettered nodes correspond to the most recent common ancestors of A) all ingroup taxa, B) western North American Cryptotympanini, C) *Raiateana* (Fiji) + *Neotibicen* (eastern+central North American Cryptotympanini), D) *Neotibicen* alone, E) the large monophyletic subgroup of *Hadoa*, F) the large-bodied *Neotibicen* subclade, and G) the green-and-black subclade of *Neotibicen*. All taxa listed under the new genera *Hadoa*, *Neotibicen* and *Subsolanus* are comb. n.

Divergence-time analysis. Relaxed-clock analysis of the focal *Neotibicen* clade under the literature-based COI clock prior yielded a median root age of 11.1 Ma (95% HPD range 5.7–19.8 Ma) for the most recent common ancestor of this genus. *Post-hoc* scaling of the uncalibrated tribe-level chronogram (which had *Platypleura*, *Yanga*, *Chremistica*, *Salvazana*, and *Tacua* excluded) placed the median estimates for the generic-level divergences (including *Cryptotympana*, *Raiateana*, *Cacama*, and *Cornuplura*) in the Oligocene to mid-Miocene period (34 to 14 Ma, Fig. 7). Median ages of most species-level lineages fell within the past ten million years.

Discussion

Phylogenetic relationships of cryptotympanine species. Trees based on molecular (Figs. 2–4) and morphological data (Fig. 5) show several clades containing formerly-*Tibicen* species that are partly separated by other described genera: (1) a large clade mainly from east-central North America (*Neotibicen* gen. n.), allied in the molecular tree to *Raiateana* and a monophyletic *Cryptotympana* from the Asia-Pacific region, (2) Eurasian *Tibicen* and *Subsolanus* gen. n., and (3) a clade containing *Hadoa* gen. n. and the *Cacama* and *Cornuplura* species. Other cryptotympanine genera, mainly from Asia, are more distantly related. Morphological analysis identifies characters for defining three new genera that are well-separated from the disputed type species of *Tibicen*, *T. plebejus*. These genera have been named and described above; note again that all species referenced under these genera below are new combinations.

The existence of two main North American lineages containing formerly-*Tibicen* species is consistent with Heath's (1978 p. 204) hypothesis of two invasions of the continent by these cicadas. The phylogenetic position of the *Neotibicen* clade (Figs. 2, 3) suggests Asian ancestry for this group, although this remains tentative because many *Tibicen* species have not been sampled. Disjunctions between eastern North America and eastern Asia have been observed in a variety of plants and animals and have been attributed to processes operating in the middle to late Tertiary (Manos and Meireles 2015; Wen 1999; Wen 2001). The geographic ancestry of the *Hadoa* + *Cacama* + *Cornuplura* clade is less clear because it is supported by a long branch, which suggests either inadequate taxon sampling or extinction, both of which can mislead biogeographic inference.

Davis (1930) discussed three groups of *Tibicen* species in the United States: a western group containing species with parallel-sided abdomens and black-and-orange coloration, an eastern North American group containing generally black-and-green species, and a mainly central group containing larger-bodied and more fulvous species (see also Heath 1978). The first of these corresponds to *Hadoa*, and the latter two are resolved here within *Neotibicen*. Sanborn and Phillips (2013) refer to finding the same three groups, using an unpublished molecular data set and an unspecified taxon set.

Few phylogenetic hypotheses have been offered for USA cryptotympanine cicadas other than the three clades discussed above and the implied monophyly of *Cacama* and *Cornuplura* (the latter untested here). Our molecular results (Figs. 2–4) confirmed sister-group relationships for some subspecies pairs (see *Neotibicen lyricen*, *N. pronotalis*) but revealed more complicated situations for others—one of the four *N. tibicen australis* individuals clustered with its sister taxon *N. tibicen tibicen* in the mtDNA tree, and *N. davisi harnedi* shares a sister-group relationship to *N. auriferus* rather than *N. davisi davisi*. The lack of a sister-group relationship between *N. dorsatus* and *N. tremulus* is unexpected, given that one was described from within the other (Cole 2008). Although the position of *harnedi* conflicts with the taxonomy, the connection between *N. davisi* and *N. auriferus* does confirm a prediction made by Davis (1918).

Additional work is needed to resolve the section of the *Neotibicen* clade containing *N. canicularis*, *N. latifasciatus*, *N. linnei*, *N. lyricen*, *N. pruinosus*, *N. robinsonianus*, and *N. winnemanna*. We could not amplify the true mitochondrial copy in some of these species (see Appendix), and the nuclear marker alone is not informative enough to establish the relationships of these morphologically similar species. Despite their apparently close genetic relationships, many of the *Neotibicen* species are broadly sympatric (Davis 1922), suggesting an intriguing history of diversification.

Ecology and geography. The distributions of the *Neotibicen* and *Hadoa* + *Cacama* + *Cornuplura* clades coincide with a transition between eastern (mesic-adapted) and western (xeric-adapted) North American flora and fauna, which occurs roughly at the 100th meridian. Within each clade the species vary widely in ecology (Table 1) (Heath 1978; Sanborn & Phillips 2013), although recently diverged species sets tend to be similar. Overall, most species inhabit trees, with both deciduous- and coniferous-forest taxa present in both groups. Arboreal habits are most common in *Neotibicen* and least common in the *Hadoa* and *Cacama* species. Both clades contain species adapted to other vegetation types such as grasses (*N. auriferus*) (Beamer 1928), prairie shrubs (e.g., *N. dorsatus*) and cactus (*Cacama* spp.) (Sanborn *et al.* 2011). *N. tibicen* [=*T. chloromerus* (Walker, 1850)] is linked to swampy forest habitat (Bunker *et al.* 2007; Moore 1966). The lone eastern clade representative found in the west, *Neotibicen cultriformis*, inhabits gallery forests. Specific hostplants are poorly known overall, but some species have close associations with particular plant genera (e.g., *Opuntia* for *Cacama* spp., *Yucca* L. for *Hadoa bifida*, *H. simplex* and *H. townsendii*, and *Juniperus* L. for *Neotibicen latifasciatus*).

Strong geographic associations of deep-level cicada clades are common. Genera from the subfamily Tibicininae Distant (*Okanagana* Distant and allies—102 USA species and subspecies) are dominant in the western mountain states, especially California, but only one species, *Okanagana viridis* Davis, 1918, reaches the lowland southeastern USA (Hill & Marshall 2013). In contrast, *Neotibicen* is diverse in the east yet does not reach the Pacific coast or California, which contains more cicada species than any other American state (see also Davis 1930; Heath 1978; Sanborn & Phillips 2013). Ongoing family-level analyses (in prep.) will offer the chance to explore these complex biogeographic relationships and implied historical hypotheses (e.g., Heath 1978 p. 202–207) in light of Cenozoic geological and climatic history.

Timing of diversification. Relaxed-clock phylogenetic analyses calibrated with an insect mtDNA clock prior (Fig. 7) suggest that all North American cryptotympanine diversification occurred during the Cenozoic era (< 65 Ma), with median dates for the intergeneric splits occurring from the early Oligocene (ca. 34 Ma) and with most extant species appearing from the late-Miocene (< 10 Ma, Fig. 7). Median dates for the most recent common ancestors of *Neotibicen* and the main *Hadoa* clade were 11 and 10 Ma, respectively—both following the mid-Miocene climatic optimum (Zachos *et al.* 2001). The date range for the *Neotibicen* common ancestor is broadly consistent with the likely origin of this genus via eastward dispersal across the Bering land bridge (as suggested by Heath 1978): because *Neotibicen* contains temperate species, the ancestor would not likely have been able to cross after about 10 Ma, when boreal habitats became established there (Sanmartín 2001). The broader western clade (*Cacama* + *Cornuplura* + *Hadoa*) appears to have begun diversifying earlier (ca. 21 Ma), consistent with a prediction by Heath (1978 p. 204) that this clade invaded North America earlier than the ancestor of the eastern species. Only the closest species pairs dated to Pleistocene divergence times (2.6 Ma–10 ka), including all taxa currently described as subspecies.

The oldest fossil currently placed in *Tibicen* is *T. grandiosa* (Scudder 1892) from the Florissant shale formation in Colorado (late Eocene, ca. 34 Ma). *T. grandiosa* is a hindwing only, but it does exhibit a morphological trait (character 11 from Tables 2 and 3) that appears on the cladogram on the long stem supporting the *Hadoa* + *Cacama* + *Cornuplura* clade (Fig. 5). The age estimates for the root of the cryptotympanine chronogram do not conflict with this potential fossil placement. Note that the Paleocene-age fossil *Davispia bearcreekensis* Cooper, initially compared to *Tibicen* (Cooper 1941), is more likely related to *Okanagana* (unpublished data). The oldest proposed cicada fossils are from the late Cretaceous (Poinar & Kritsky 2012).

Songs, genetic divergence, and species. Because cicada songs are used by males to attract mates, they are always species-specific for sympatric and synchronic species (Alexander *et al.* 1972). With practice, songs of cryptotympanine cicadas are generally recognizable by ear, a feature that allows field identification and rapid collection of distribution data. Behavior associated with singing in cryptotympanine species ranges from alternation of short calling bouts with flights—as in *Cacama valvata* (Uhler, 1888), *Neotibicen tibicen*, and *Magicicada* (Cooley & Marshall 2001)—to stationary advertisement (*Neotibicen pronotalis*, *Cornuplura nigroalbata*, *Hadoa duryi*) similar to that documented in *Okanagana* (Cooley 2001). Beamer (1928) stated that *N. pronotalis walkeri* is the most persistent singer of all of the Kansas Cicadidae. Many species can be stimulated into singing by playbacks of conspecific song, a feature that can be exploited to reveal silent males in field surveys (Stucky 2012).

Few detailed analyses have been made of cryptotympanine songs (for a rare example see Ohya 2004), which often contain complex frequency-modulation and lack the discrete elements that have facilitated interspecific comparisons in other groups (e.g., Marshall *et al.* 2011; Popple 2013). Measurement of frequency-based characters requires samples of high-quality recordings in numbers sufficient for careful study (e.g., Sueur & Aubin 2003). At this stage, phylogenetic signal in the form of similar but field-distinguishable songs is apparent between some closely related species-pairs with Pliocene (5.3-2.6 Ma) or younger divergences, including *Neotibicen auriferus*/*N. davisi*, *Hadoa texana*/*H. inaudita*, and *H. chiricahua*/*H. neomexicensis* (Stucky 2013). Overall structural similarities are apparent among the large-bodied *Neotibicen* species and among the western cryptotympanine genera, suggesting that detailed study of these songs in a phylogenetic context would be fruitful.

In North American cryptotympanine cicadas, exceptions to the rule of species-specificity in song occur in the most recently diverged and often allo- or parapatric taxon sets (see Sanborn & Phillips 2013 for detailed distributions), several of which are currently described as subspecies and/or appear to have diverged in the Pleistocene (*N. tibicen* subspecies, *N. lyricen* subspecies, *N. pruinosus*/*N. winnemanna*/*N. latifasciatus*, *N. pronotalis*/*N. dealbatus*). These species groups tend to have model-corrected mtDNA (COI) divergences below approximately 0.03 substitutions/site/my (Fig. 3), which was identified as an approximate threshold for song-distinctiveness in New Zealand *Kikihia* Dugdale (Marshall *et al.* 2011). However, some of the western species (e.g., *Hadoa townsendii*, *H. bifida*, and *H. simplex*) have songs that are similar despite much larger mtDNA distances. The moderate genetic distance between *Neotibicen dorsatus* and *N. tremulus* is also unexpected, as well as their nonsister relationship, given their similarities in song and morphology (Cole 2008).

Refinement of *Diceroprocta* and exclusion of species from *Tibicen*. Although preliminary molecular data indicate that *Diceroprocta* and *Tibicen* (including the new genera named here) are not especially closely related within the subfamily Cicadinae (Marshall, Hill, Wade, Owen, Moulds, Simon in prep.), many species have been moved between these genera historically. Five species are here removed from *Tibicen* and placed in *Diceroprocta: Diceroprocta bimaculatus* (Sanborn, 2010) comb. n., *Diceroprocta heathi* (Sanborn, 2010) comb. n., *Diceroprocta nigriventris* (Walker, 1858) comb. n., *Diceroprocta oleacea* (Distant, 1891) comb. n., and *Diceroprocta sublaqeatus* (Uhler, 1903) comb. n. The first two of these species possess the following attributes found in *Diceroprocta* as defined by Sanborn (2012) (a) the uncus is bifurcate; (b) the position of crossvein r on vein RP is such that the distance between r and r-m is about equal to the distance from r to the ambient vein; (c) the margin of female sternite VII is sinuate; and (d) the male pygofer has acute lateral lobes (= distal shoulders). However, Sanborn (2007) points out that these attributes show some variation and are not necessary definitive. We add the following attributes defining *Diceroprocta*: (a) the vertex of the head is elongated so that the distance between the supra-antennal plate and the eye is greater than length of the antennal plate; (b) the hind wing anal lobe is always narrow; (c) the lateral margins of the male opercula overlap the ventral margins of the timbal covers; (d) the uncus of the male genitalia carries a pair of projecting finger-like lobes at its base dorsally; and (e) the theca has the vesica extruded and ornamented. In addition, in most *Diceroprocta* species, the section of vein RA_2 that is proximal to crossvein r is considerably greater than 1/3rd the length of the distal section, while in *Neotibicen* the proximal section is less than 1/3rd the length of the distal section (this character varies in *Hadoa* and *Cacama*). Finally, in many *Diceroprocta* species, but very rarely in *Neotibicen* and *Hadoa*, the thin cell formed by RA_1 and SC slightly widens distally. Although color patterns are rarely applied in generic diagnoses, we also note that, when comparing *Diceroprocta* to *Neotibicen* and *Hadoa*, the pronotal collar in *Diceroprocta* is usually boldly colored, standing out against the background color of the dorsum (whether light or dark), and it is never interrupted with black color medially.

All the above attributes found generally in *Diceroprocta* are present in *Diceroprocta heathi* and *D. bimaculatus*. Further, (1) no species of *Tibicen* or its allies possesses the distinctive pair of projecting finger-like lobes on the uncus at its base dorsally; (2) the lateral margins of the male opercula do not overlap the ventral margin of the timbal covers but the reverse is the norm with the timbal covers overlapping the opercula; and (3) the theca of *Tibicen* does not have an ornamented vesica. *Diceroprocta heathi* and *D. bimaculatus* also lack the swollen male basisternite 3.

The three remaining species being transferred here were examined by photographs of the types and from published illustrations. All three species possess the forewing vein RP bifurcation and RA_1 cell widening of *Diceroprocta*, as well as the pronotal collar coloration described above.

Future directions. North American cicada biology has a long history even apart from the literature on *Magicicada*, which dates to Gov. William Bradford of Plymouth Colony in 1633 (Kritsky 2004). Several of the eastern species were described by the earliest systematists of the modern era, including *Cicada tibicen* by Linnaeus (Sanborn 2008). Because of this long history, the identities of a few species remain unclear, and we are particularly indebted to the early 20th century work by William T. Davis that contributed many North American species and generic descriptions (see also Heath 1978; Sanborn & Heath 2012) and sorted out problems caused by incomplete descriptions and lost types (Sanborn & Heath 2012). New species continue to be discovered (Cole 2008; Stucky 2013) and at least three remain to be described (Hill and Marshall unpublished observations). Beyond taxonomy and Davis' papers, the biology of the non-periodical USA species has been studied only sporadically, with a few notable exceptions including Beamer's (1928) detailed life history work on Kansas cicadas and many state-level papers (reviewed in Sanborn *et al.* 2008), most of which are focused on distributions. Hostplant associations have been only anecdotally documented in most cases and life-cycle lengths remain unknown for most species, although one recent paper experimentally examined links between ecological parameters and emergence phenology in *Neotibicen dealbatus* (Smith *et al.* 2006). Little is known about the physiology (e.g., Hennig *et al.* 1994) or reproductive biology (communication, mating, oviposition) of the annual species, in contrast to *Magicicada* and other cicada groups around the world. One exception is the substantial literature on thermal adaptations of cicadas (e.g., Heath *et al.* 1971; Sanborn 2002;2004; Toolson 1987; Toolson *et al.* 1994). Hopefully, new interest in the biology and history of these insects will be stimulated by Sanborn and Heath's recent book on the cicadas of North America north of Mexico (Sanborn & Heath 2012), the first detailed published distributions of those taxa (Sanborn & Phillips 2013), a new catalogue of the Cicadidae (Sanborn 2013), the increasing availability of species-specific songs online (e.g., *insectsingers.com*), an extensive online bibliography of the Cicadidae (McNary 2014), and by the phylogenetic results of this study.

This study has yielded the first comprehensive phylogenetic information on the USA cryptotympanine cicada species and placed them in the context of a large Northern Hemisphere radiation. We have dated the diversification of these cicadas to the late Cenozoic era and found that most extant species originated in the late Miocene, Pliocene, and Pleistocene epochs, a period during which world climate became progressively cooler and drier (Zachos *et al.* 2001), and our trees suggest that at least one of the two cryptotympanine clades arrived in North America from Asia. We have established new genera that will facilitate the discussion of the history and biology of morphologically and ecologically distinguishable clades. Finally, we have published sample recordings online that can facilitate rapid collection of distributional data and detection of range changes (e.g., Bunker *et al.* 2007; Marshall *et al.* 1996; Stucky 2012). An important next step will be to integrate molecular data from additional species from Mexico and Central America, while also sampling more species from Asia. Family-level studies in preparation, which will better integrate the available fossil information, will further test the molecular-clock-based results and sharpen our picture of the global history of these charismatic insects.

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References

Alexander, R.D., Pace, A.E. & Otte, D. (1972) The singing insects of Michigan. *Great Lakes Entomologist*, 5, 33–69.

Beamer, R.H. (1928) Studies on the biology of Kansas Cicadidae. *University of Kansas Science Bulletin*, 18, 155–263.

Boulard, M. (1988) Les *Lyristes* d'Asie Mineure (Hom. Cicadidae). I. Sur deux formes éthospécifiques syntopiques et description de deux espéces nouvelles. *L'Entomologiste*, 44, 153–167.

Boulard, M. & Puissant, S. (2014) Comments on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 71, 119–131.

Brown, J.M., Hedtke, S.M., Lemmon, A.R. & Lemmon, E.M. (2010) When trees grow too long: investigating the causes of highly inaccurate Bayesian branch-length estimates. *Systematic Biology*, 59, 145–61. http://dx.doi.org/10.1093/sysbio/syp081

Buhay, J.E. (2009) "COI-like" sequences are becoming problematic in molecular systematic and DNA barcoding studies. *Journal of Crustacean Biology*, 29, 96–110.

http://dx.doi.org/10.1651/08-3020.1

Bunker, G.J., Neckermann, M.L. & Cooley, J.R. (2007) New northern records of *Tibicen chloromera* (Hemiptera: Cicadidae) in Connecticut. *Transactions of the American Entomological Society*, 133, 357–361.
http://dx.doi.org/10.3157/0002-8320-133.3.357

Campbell, M.A., Van Leuven, J.T., Meister, R.C., Carey, K.M., Simon, C. & McCutcheon, J.P. (2015) Genome expansion via lineage splitting and genome reduction in the cicada endosymbiont *Hodgkinia*. *Proceedings of the National Academy of Sciences of the United States of America*. [early view]
http://dx.doi.org/10.1073/pnas.1421386112

Cole, J.A. (2008) A new cryptic species of cicada resembling *Tibicen dorsatus* revealed by calling song (Hemiptera: Auchenorrhyncha: Cicadidae). *Annals of the Entomological Society of America*, 101, 815–823.
http://dx.doi.org/10.1093/aesa/101.5.815

Cooley, J.R. (2001) Long-range acoustical signals, phonotaxis, and risk in the sexual pair-forming behaviors of *Okanagana canadensis* and *O. rimosa* (Hemiptera: Cicadidae). *Annals of the Entomological Society of America*, 94, 755–760.
http://dx.doi.org/10.1603/0013-8746(2001)094[0755:LRASPA]2.0.CO;2

Cooley, J.R. & Marshall, D.C. (2001) Sexual signaling in periodical cicadas, *Magicicada* spp. (Hemiptera: Cicadidae). *Behaviour*, 138, 827–855.
http://dx.doi.org/10.1163/156853901753172674

Cooper, K.W. (1941) *Davispia bearcreekensis* Cooper, a new cicada from the Paleocene, with a brief review of the fossil Cicadidae. *American Journal of Science*, 239, 286–304.
http://dx.doi.org/10.2475/ajs.239.4.286

Davis, W.T. (1918) Mississippi cicadas, with a key to the species of the southeastern United States. *Journal of the New York Entomological Society*, 26, 141–155.

Davis, W.T. (1919) Cicadas of the genus *Cacama*, with description of several new species. *Journal of the New York Entomological Society*, 27, 68–79.

Davis, W.T. (1922) An annotated list of the cicadas of Virgina with description of a new species. *Journal of the New York Entomological Society*, 30, 36–52.

Davis, W.T. (1930) The distribution of cicadas in the United States with description of new species. *Journal of the New York Entomological Society*, 38, 53–72.

Distant, W.L. (1904) Rhynchotal notes.-XXVII. *Annals and Magazine of Natural History*, 14, 329–336.
http://dx.doi.org/10.1080/03745480409443017

Drummond, A.J., Ho, S.Y., Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biology*, 4, e88.
http://dx.doi.org/10.1371/journal.pbio.0040088

Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7, 214.
http://dx.doi.org/10.1186/1471-2148-7-214

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–297.

Fukuda, H., Takegawa, Y. & Taketo, A. (2006) Comparison of mitochondrial DNA sequences among Japanese cicadas, with special reference to three Tibicenine species. *Memoirs of Fukui University of Technology*, 36, 163–170.

Hamilton, K.G.A. (2014) Comment on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 71, 179–180.

Hayashi, M. (1987a) A revision of the genus *Cryptotympana* (Homoptera: Cicadidae). Part I. *Bulletin of the Kitakyushu Museum of Natural History*, 6, 119–212.

Hayashi, M. (1987b) A revision of the genus *Cryptotympana* (Homoptera: Cicadidae). Part II. *Bulletin of the Kitakyushu Museum of Natural History*, 7, 1–109.

Heath, J.E., Hanegan, J.L., Wilkin, P.J. & Heath, M.S. (1971) Adaptation of the thermal responses of insects. *American Zoologist*, 11, 145–156.
http://dx.doi.org/10.1093/icb/11.1.147

Heath, M.S. (1978) *Genera of American cicadas north of Mexico. Doctoral Thesis.* University of Florida, Gainesville, 231 pp.

Hennig, R.M., Weber, T., Huber, F., Kleindienst, H.-U. & Popov, A.V. (1994) Function of the tensor muscle in the cicada *Tibicen linnei*. *Journal of Experimental Biology*, 187, 33–44.

Hill, K.B.R. & Marshall, D.C. (2009) Confirmation of the cicada *Tibicen pronotalis walkeri* stat. nov. (= *T. walkeri*, Hemiptera: Cicadidae) in Florida: finding singing insects through their songs. *Zootaxa*, 2125, 63–66.

Hill, K.B.R. & Marshall, D.C. (2013) The song, morphology, habitat, and distribution of the elusive North American cicada *Okanagana viridis* (Auchenorrhyncha: Cicadidae). *Annals of the Entomological Society of America*, 106, 598–603.
http://dx.doi.org/10.1603/AN13072

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
http://dx.doi.org/10.1093/bioinformatics/17.8.754

Karban, R. (1986) Prolonged development in cicadas. *In:* Taylor, F. & Karban, R. (Eds.), *The evolution of insect life cycles*. Springer, New York, pp. 222–235.

Kritsky, G. (2004) *Periodical cicadas: the plague and the puzzle*. Indiana Academy of Science, Indianapolis, Indiana, 148 pp.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701. http://dx.doi.org/10.1093/molbev/mss020

Lee, Y.J. & Hill, K.B.R. (2010) Systematic revision of the genus *Psithyristria* Stål (Hemiptera: Cicadidae) with seven new species and a molecular phylogeny of the genus and higher taxa. *Systematic Entomology*, 35, 277–305. http://dx.doi.org/10.1111/j.1365-3113.2009.00509.x

Lewis, P.O. (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50, 913–925. http://dx.doi.org/10.1080/106351501753462876

Maddison, D.R. & Maddison, W.P. (2000) *MacClade 4: Analysis of phylogeny and character evolution.* Sinauer Associates, Sunderland, Massachusetts, 492 pp.

Manos, P.S. & Meireles, J.E. (2015) Biogeographic analysis of the woody plants of the southern Appalachians: Implications for the origins of a regional flora. *American Journal of Botany*, 102, 780–104. http://dx.doi.org/10.3732/ajb.1400530

Marlatt, C.L. (1907) The periodical cicada. *Bulletin of the United States Department of Agriculture Bureau of Entomology*, 71, 1–181.

Marshall, D.C. (2010) Cryptic failure of partitioned Bayesian phylogenetic analyses: lost in the land of long trees. *Systematic Biology*, 59, 108–17. http://dx.doi.org/10.1093/sysbio/syp080

Marshall, D.C., Cooley, J.R., Alexander, R.D. & Moore, T.E. (1996) New records of Michigan Cicadidae (Homoptera), with notes on the use of songs to monitor range changes. *Great Lakes Entomologist*, 29, 165–169.

Marshall, D.C. & Hill, K.B.R. (2014) Comments on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 71, 103–107.

Marshall, D.C., Hill, K.B.R., Cooley, J.R. & Simon, C. (2011) Hybridization, mitochondrial DNA taxonomy, and prediction of the early stages of reproductive isolation: Lessons from New Zealand cicadas of the genus *Kikihia*. *Systematic Biology*, 60, 482–502. http://dx.doi.org/10.1093/sysbio/syr017

Marshall, D.C., Hill, K.B.R., Moulds, M.S., Vanderpool, D., Cooley, J.R., Mohagan, A. & Simon, C. (2015) Inflation of molecular clock rates and dates: Biogeography, molecular phylogenetics, and diversification of a global cicada radiation from Australasia (Hemiptera: Cicadidae: Cicadettini). *Systematic Biology*. [in review]

McNary, T. (2014) Bibliography of the Cicadoidea. Available from: http://www.tmcnary.com/CicadaBibliography.htm (accessed 26 August 2014)

Moore, T.E. (1966) The cicadas of Michigan (Homoptera: Cicadidae). *Papers of the Michigan Academy of Science Arts and Letters*, 51, 75–96.

Moore, T.E. (1993) Acoustic signals and speciation in cicadas (Insecta: Homoptera: Cicadidae). *In:* Lees, D.R. & Edwards, D. (Eds.), *Evolutionary Patterns and Processes*. Academic Press, London, pp. 269–284.

Moulds, M.S. (2005) An Appraisal of the Higher Classification of Cicadas (Hemiptera: Cicadoidea) with Special Reference to the Australian Fauna. *Records of the Australian Museum*, 57, 375–446. http://dx.doi.org/10.3853/j.0067-1975.57.2005.1447

Müller, K. (2005) SeqState: Primer design and sequence statistics for phylogenetic DNA data sets. *Applied Bioinformatics*, 4, 65–69. http://dx.doi.org/10.2165/00822942-200504010-00008

Myers, J.G. (1929) *Insect singers: a natural history of the cicadas*. George Routledge and Sons, London, 304 pp.

Nixon, K.C. (1992) *Clados version 1.2. Computer program and reference manual.* Trumansburg, New York. [unkown pagination]

Ohya, E. (2004) Identification of *Tibicen* cicada species by a Principal Components Analysis of their songs. *Anais da Academia Brasileira da Ciências*, 76, 441–4. http://dx.doi.org/10.1590/s0001-37652004000200038

Poinar, G. & Kritsky, G. (2012) Morphological conservatism in the foreleg structure of cicada hatchlings, *Burmacicada protera* n. gen., n. sp. in Burmese amber, *Dominicicada youngi* n. gen., n. sp. in Dominican amber and the extant *Magicicada septendecim* (L.) (Hemiptera: Cicadidae). *Historical Biology*, 24, 461–466. http://dx.doi.org/10.1080/08912963.2011.603421

Popple, L.W. (2013) A revision of the *Pauropsalta annulata* Goding & Froggatt species group (Hemiptera: Cicadidae) based on morphology, calling songs and ecology, with investigations into calling song structure, molecular phylogenetic relationships and a case of hybridisation between two subspecies. *Zootaxa*, 3730, 1–102. http://dx.doi.org/10.11646/zootaxa.3730.1.1

Procter, D. & Fleming, L.V. (1999) Biodiversity: the UK overseas territories. Joint Nature Conservation Committee, Peterborough, 131 pp.

Rambaut, A. & Drummond, A.J. (2007) Tracer v1.5. Available from: http://evolve.zoo.ox.ac.uk/ (accessed 2 December 2009)

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
http://dx.doi.org/10.1093/bioinformatics/btg180

Sanborn, A.F. (2002) Cicada thermoregulation. *Denisia*, 4, 455–470.

Sanborn, A.F. (2004) Thermoregulation and endothermy in the large western cicada *Tibicen cultriformis* (Hemiptera: Cicadidae). *Journal of Thermal Biology*, 29, 97–101.
http://dx.doi.org/10.1016/j.jtherbio.2003.11.007

Sanborn, A.F. (2007) New species, new records and checklist of cicadas from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Zootaxa*, 1651, 1–42.

Sanborn, A.F. (2008) The identity of *Cicada tibicen* Linné [= *Tibicen chloromerus* (Walker, 1850)] (Hemiptera: Cicadoidea: Cicadidae). *Entomological News*, 119, 227–231.
http://dx.doi.org/10.3157/0013-872X(2008)119[227:TIOCTL]2.0.CO;2

Sanborn, A.F. (2010) Two new species and new records of cicadas from Central America (Hemiptera: Cicadomorpha: Cicadidae). *Studies on Neotropical Fauna and Environment*, 45, 67–76.
http://dx.doi.org/10.1080/01650521003778814

Sanborn, A.F. (2013) *Catalogue of the Cicadoidea (Hemiptera: Auchenorrhyncha). With contributions to the bibliography by Martin H. Villet.* Academic Press, San Diego, 1001 pp.

Sanborn, A.F. (2014a) Comments on *Tibicina* Amyot, 1847 and *Lyristes* Horváth, 1926 (Insecta, Hemiptera, Homoptera): proposed conservation by the suppression of *Tibicen* Berthold, 1827 [?Latreille, 1825], and concerning the type species of *Cicada* Linnaeus, 1758. *Bulletin of Zoological Nomenclature*, 71, 108–118.

Sanborn, A.F. (2014b) A new genus and new tribe of cicada from South America (Hemiptera: Cicadoidea: Cicadidae) with a note on the taxonomic position of *Ahomana* Distant, 1905. *Proceedings of the Entomological Society of Washington*, 116, 339–348.

Sanborn, A.F. & Heath, M.S. (2012) *The cicadas (Hemiptera: Cicadoidea: Cicadidae) of North America north of Mexico*. Entomological Society of America, Lanham, MD, 227 pp.

Sanborn, A.F., Heath, M.S., Phillips, P.K. & Heath, J.E. (2011) The genus *Cacama* Distant, 1904 (Hemiptera: Cicadidae) with the description of three new species. *Zootaxa*, 2897, 35–50.

Sanborn, A.F. & Phillips, P. (2013) Biogeography of the cicadas (Hemiptera: Cicadidae) of North America, north of Mexico. *Diversity*, 5, 166–239.
http://dx.doi.org/10.3390/d5020166

Sanborn, A.F. & Phillips, P.K. (2012) Ecology, acoustic behavior, and morphology of the cicada *Cornuplura nigroalbata* (Hemiptera: Cicadoidea: Cicadidae). *Annals of the Entomological Society of America*, 105, 879–883.
http://dx.doi.org/10.1603/AN12064

Sanborn, A.F., Phillips, P.K. & Gillis, P. (2008) The cicadas of Florida (Hemiptera: Cicadoidea: Cicadidae). *Zootaxa*, 1916, 1–43.

Sanmartín, I. (2001) Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, 73, 345–390.
http://dx.doi.org/10.1111/j.1095-8312.2001.tb01368.x

Scudder, S.H. (1892) Some insects of special interest from Florissant, Colorado and other points in the Tertiaries of Colorado and Utah. *Bulletin of the United States Geological Survey*, 93, 1–5.

Simmons, M.P. & Ochoterena, H. (2000) Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology*, 49, 369–381.
http://dx.doi.org/10.1093/sysbio/49.2.369

Simon, C. (1979) Evolution of periodical cicadas: phylogenetic inferences based on allozymic data. *Systematic Zoology*, 28, 22–39.
http://dx.doi.org/10.2307/2412996

Simon, C. (1983) Morphological differentiation in wing venation among broods of 13- and 17-year periodical cicadas *Magicicada*. *Evolution*, 37, 104–115.
http://dx.doi.org/10.2307/2408179

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved PCR primers. *Annals of the Entomological Society of America*, 87, 651–701.
http://dx.doi.org/10.1093/aesa/87.6.651

Smith, D.M., Kelley, J.F. & Finch, D.M. (2006) Cicada emergence in southwestern riparian forest: influences of wildfire and vegetation composition. *Ecological Applications*, 16, 1608–1618.
http://dx.doi.org/10.1890/1051-0761(2006)016[1608:CEISRF]2.0.CO;2

Sota, T., Yamamoto, S., Cooley, J.R., Hill, K.B.R., Simon, C. & Yoshimura, J. (2013) Independent divergence of 13- and 17-yr life cycles among three periodical cicada lineages. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 6919–6924.
http://dx.doi.org/10.1073/pnas.1220060110

Stucky, B. (2012) First record of the cicada *Tibicen pruinosus* in Colorado, with a key to Colorado species of *Tibicen* (Hemiptera: Cicadidae). *Western North American Naturalist*, 72, 100–104.
http://dx.doi.org/10.3398/064.072.0113

Stucky, B. (2013) Morphology, bioacoustics, and ecology of *Tibicen neomexicensis* sp. n., a new species of cicada from the Sacramento Mountains in New Mexico, U.S.A. (Hemiptera, Cicadidae, *Tibicen*). *ZooKeys*, 337, 49–71.
http://dx.doi.org/10.3897/zookeys.337.5950

Sueur, J. & Aubin, T. (2003) Specificity of cicada calling songs in the genus *Tibicina* (Hemiptera: Cicadidae). *Systematic Entomology*, 28, 481–492.
http://dx.doi.org/10.1046/j.1365-3113.2003.00222.x

Sueur, J., Vanderpool, D., Simon, C., Ouvrard, D. & Bourgoin, T. (2007) Molecular phylogeny of the genus *Tibicina* (Hemiptera, Cicadidae): rapid radiation and acoustic behaviour. *Biological Journal of the Linnean Society*, 91, 611–626.
http://dx.doi.org/10.1111/j.1095-8312.2007.00823.x

Swofford, D.L. (1998) *PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Version 4.* Sinauer Associates, Sunderland, Massachusetts.

Toolson, E.C. (1987) Water profligacy as an adaptation to hot deserts: water loss rates and evaporative cooling in the Sonoran Desert cicada, *Diceroprocta apache* (Homoptera: Cicadidae). *Physiological Zoology*, 60, 379–385.

Toolson, E.C., Ashby, P.D., Howard, R.W. & Stanley-Samuelson, D.W. (1994) Eicosanoids mediate control of thermoregulatory sweating in the cicada, *Tibicen dealbatus*. *Journal of Comparative Physiology B*, 164, 278–285.
http://dx.doi.org/10.1007/BF00346443

Walker, F. (1850) *List of specimens of Homopterous insects in the collection of the British Museum*. British Museum Trustees, London, 260 pp.

Walker, T.J. (2000) Seasonal occurrence of cicadas in Alachua County, Florida. Available from: http://entnemdept.ifas.ufl.edu/walker/buzz/c700fl2.htm (accessed 25 August 2014)

Wen, J. (1999) Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics*, 30, 421–455.
http://dx.doi.org/10.1146/annurev.ecolsys.30.1.421

Wen, J. (2001) Evolution of eastern Asian–eastern North American biogeographic disjunctions: a few additional issues. *International Journal of Plant Sciences*, 162, S117–S122.
http://dx.doi.org/10.1086/322940

Williams, K.S. & Simon, C. (1995) The ecology, behavior, and evolution of periodical cicadas. *Annual Review of Entomology*, 40, 269–295.
http://dx.doi.org/10.1146/annurev.en.40.010195.001413

Wilson, J.W. (1930) *Tibicen davisii* Smith and Grosbeck (Cicadidae) a new pest of economic importance. *Florida Entomologist*, 14, 61–65.
http://dx.doi.org/10.2307/3492389

Zachos, J., Pagani, M., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292, 689–693.
http://dx.doi.org/10.1126/science.1059412

Zwickl, D.J. (2006) *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Doctoral Thesis.* The University of Texas, Austin, TX, 115 pp.

APPENDIX. Taxonomic, locality, and sequencing data, with specimens sorted by sample code for reference to Figs. 2-4. “CI” is cytochrome oxidase I, “EF” is a segment of EF-1α, and S and E refer to “start” and “end” sections. Rec=Recorded. Codes with asterisks correspond to cicadas illustrated in Fig. 6 that were not sequenced. New generic assignments for USA species are shown in Table 1 and in the Results section; some Mexican species are assigned new genera in the paper as well.

Code	Genus	Species	Species reference	Country	Location	Lat.	Lon.	Date	Rec.	5′ CI	3′ CI	S EF	E EF
02.US.IL.UNI.01	*Tibicen*	*pruinosus pruinosus*	(Say, 1825)	USA	IL, Champagne-Urbana, GPS estim.	40.099	-88.230	26-Jun-2002	No	–	–	X	X
02.US.MD.ZYL*	*Tibicen*	*auletes*	(Germar, 1834)	USA	MD, St Mary’s Co., Ridge	38.121	-76.364	2002	No				
03.FJ.WE.WEI.01	*Raiateana*	*kuruduadua kuruduadua*	(Distant, 1881)	Fiji	Viti Levu, S of Korovou	-17.560	177.947	27-Jan-2003	No	X	X	X	X
03.FJ.WE.WSV.03	*Raiateana*	*kuruduadua kuruduadua*	(Distant, 1881)	Fiji	Viti Levu, SE of Vatukacevaceva	-17.429	178.107	28-Jan-2003	Site	X	X	X	X
03.JP.YT.YAM.01	*Tibicen*	*japonicus*	(Kato, 1925)	Japan	Yamagata Prefecture, Honshu	–	–	Aug-2003	No	–	–	X	X
03.JP.YT.YAM.02	*Tibicen*	*bihamatus*	(de Motschul., 1861)	Japan	Yamagata Prefecture, Honshu	–	–	Aug-2003	No	–	X	X	X
03.JP.YT.YAM.03	*Tibicen*	*kyushyuensis*	(Kato, 1926)	Japan	Yamagata Prefecture, Honshu	–	–	Aug-2003	No	–	–	X	X
03.MY.SA.KIN.24	*Tacua*	*speciosa*	(Illiger, 1800)	Malaysia	Kinabalu National Park	6.006	116.543	3-Apr-2003	No	X	X	X	PT
03.US.AZ.STR.04	*Tibicen*	*duryi*	Davis, 1917	USA	AZ, Gila Co., nr. Strawberry	34.422	-111.512	29-Jun-2003	Yes	–	–	X	X
03.US.MA.MAR.01	*Tibicen*	*canicularis*	(Harris, 1841)	USA	MA, Barnstable Co., Marconi (GPS est.)	41.900	-69.967	7-Sep-2003	Site	X	X	X	X
03.US.MA.MAR.02	*Tibicen*	*canicularis*	(Harris, 1841)	USA	MA, Barnstable Co., Marconi (GPS est.)	41.900	-69.967	7-Sep-2003	No	–	–	X	X
03.US.NJ.FBO.01	*Tibicen*	*linnei*	(Sm. & Grossb., 1907)	USA	NJ, Monmouth Co., Freehold Boro	40.266	-74.281	26-Aug-2003	Yes	–	–	X	X
03.US.VA.CHA*	*Tibicen*	*winnemanna*	(Davis, 1912)	USA	VA, Albemarle Co., Charlottesville	38.010	-78.476	17-Aug-2003	No				
03.US.VA.CHA.01	*Tibicen*	*winnemanna*	(Davis, 1912)	USA	VA, Albemarle Co., Charlottesville	38.010	-78.476	17-Aug-2003	No	–	–	X	X
03.US.VA.DES.01	*Tibicen*	*davisi davisi*	(Sm. & Grossb., 1907)	USA	VA, Suffolk City Co., Great Dismal Swp	36.641	-76.576	15-Aug-2003	No	X	X	X	X
03.US.VA.PIS.01	*Tibicen*	*tibicen tibicen*	(Linnaeus, 1758)	USA	VA, Bedford Co., E of Bedford	37.301	-79.369	15-Aug-2003	No	–	–	X	X
03.US.VA.SCU.01	*Tibicen*	*robinsonianus*	(Davis, 1922)	USA	VA, Culpeper Co., S of Culpeper	38.445	-77.991	17-Aug-2003	No	–	X	X	X
04.US.CO.PKT.01	*Cacama*	*valvata*	(Uhler, 1888)	USA	CO, Otero Co., Sth of La Junta (GPS est.)	37.658	-103.648	4-Jul-2004	Site	X	X	X	X
04.US.DE.APP*	*Tibicen*	*linnei*	(Sm. & Grossb., 1907)	USA	DE, Kent Co., S of Dover	38.752	-75.893	28-Aug-2004	Site				
04.US.KS.HUN.01*	*Tibicen*	*dealbatus*	(Davis, 1915)	USA	KS, Clark Co., W of Ashland	37.195	-99.853	5-Jul-2004	Yes				
04.US.KS.HUN.02	*Tibicen*	*dealbatus*	(Davis, 1915)	USA	KS, Clark Co., W of Ashland	37.195	-99.853	5-Jul-2004	Site	X	X	X	X
04.US.MD.ZYL.01	*Tibicen*	*auletes*	(Germar, 1834)	USA	MD, St Mary’s Co., Ridge	38.121	-76.364	2004	No	X	X	X	X
04.US.OK.EAK.01	*Tibicen*	*superbus*	(Fitch, 1855)	USA	OK, Caddo Co., E. of Eakly	35.291	-98.523	6-Jul-2004	Site	X	X	X	X
04.US.TX.EDN.01	*Tibicen*	*pronotalis walkeri*	Metcalf, 1955	USA	TX, Jackson Co., N of Edna	29.022	-96.560	10-Jul-2004	Site	X	X	X	X
05.US.AL.AWC.02	*Tibicen*	*figuratus*	(Walker, 1858)	USA	AL, Chambers Co., AL Welcome Ctr	32.839	-85.198	21-Aug-2005	Site	X	X	X	X
05.US.GA.LGR*	*Tibicen*	*tibicen tibicen*	(Linnaeus, 1758)	USA	GA, Troupe Co., SW of La Grange	32.876	-85.150	21-Aug-2005	No				
05.US.LA.BPA.01	*Tibicen*	*pronotalis walkeri*	Metcalf, 1955	USA	LA, St Martin Pa., W of Henderson	30.320	-91.830	24-Aug-2005	No	X	X	X	X
05.US.LA.CRO.01	*Tibicen*	*resh*	(Haldeman, 1852)	USA	LA, Acadia Pa., nr Crowley	30.234	-92.385	23-Aug-2005	No	X	X	X	X
05.US.LA.JEN.01	*Tibicen*	*resh*	(Haldeman, 1852)	USA	LA, Acadia Pa., E of Jennings	30.237	-92.610	13-Jun-2005	No	X	X	X	X
05.US.LA.LWC.01	*Tibicen*	*auletes*	(Germar, 1834)	USA	LA, St Tammany Pa., LA Welcome Ctr	30.300	-89.711	23-Aug-2005	No	X	X	X	X
05.US.LA.SFF.01	*Tibicen*	*pruinosus pruinosus*	(Say, 1825)	USA	LA, St Landry Pa., SE of Washington	30.586	-92.035	23-Aug-2005	Site	X	X	X	X
05.US.MD.ZYL.01	*Tibicen*	*davisi davisi*	(Sm. & Grossb., 1907)	USA	MD, St Mary’s Co., Ridge	38.121	-76.364	19-Aug-2005	Site	X	X	X	X

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APPENDIX. (Continued)

										5’	3’	S	E
Code	Genus	Species	Species reference	Country	Location	Lat.	Lon.	Date	Rec.	CI	CI	EF	EF
05.US.VA.DVS.01	*Tibicen*	*winnemanna*	(Davis, 1912)	USA	VA, Boutetourt Co., S side of Daleville	37.393	-79.907	20-Aug-2005	No	–	–	X	X
0551	*Platypleura*	*takasagona*	Matsumura, 1917	Taiwan	Hsichih City. Mt. Uchihshan	–	–	4-Jun-2003	No	X	X	X	X
0580	*Cryptotympana*	*takasagona*	Kato, 1925	Taiwan	Taipei City. Ta-an Chu.	–	–	9-Jun-2003	No	X	X	X	X
06.US.GA.GAP.01	*Tibicen*	*resonans*	(Walker, 1850)	USA	GA, Tattnall Co., Gordonia-Altamaha SP	32.082	-82.123	24-Jul-2006	Yes	X	X	X	X
06.US.GA.OAK.02	*Tibicen*	*resonans*	(Walker, 1850)	USA	GA, Emanuel Co., Oak Park	32.402	-82.304	16-Jul-2006	Site	X	X	X	X
06.US.GA.SIM.01	*Tibicen*	*similaris*	(Sm. & Grossb., 1907)	USA	GA, Toombs Co., ENE of Vidalia	32.258	-82.246	25-Jul-2006	Site	X	X	X	X
06.US.MD.RUM.01	*Tibicen*	*latifasciatus*	(Davis, 1915)	USA	MD, Somerset Co., Rumbly	38.093	-75.856	7-Sep-2006	Yes	–	–	X	X
06.US.NC.BBE.01	*Tibicen*	*lyricen lyricen*	(De Geer, 1773)	USA	NC, Carteret Co., W of Emerald Isle	34.666	-77.032	3-Sep-2006	No	X	X	X	X
06.US.NC.BWC*	*Tibicen*	*davisi davisi*	(Sm. & Grossb., 1907)	USA	NC, Carteret Co., W of Atlantic Beach	34.694	-76.826	4-Sep-2006	No				
06.US.NC.RAD.01	*Tibicen*	*latifasciatus*	(Davis, 1915)	USA	NC, Carteret Co., W of Beaufort	34.722	-76.671	3-Sep-2006	Yes	–	–	X	X
06.US.TX.IOZ.01	*Tibicen*	*texanus*	Metcalf, 1963	USA	TX, Kerr Co., NW of Kerrville	30.121	-99.207	8-Jun-2006	Yes	X	X	X	X
06.US.TX.NIT.01	*Tibicen*	*superbus*	(Fitch, 1855)	USA	TX, US77 S of Waxahachie	32.215	-96.881	6-Jun-2006	Site	X	X	X	X
0624	*Cryptotympana*	*atrata*	(Fabricius, 1775)	Taiwan	Taoyuan Hsiang. Chuwei Port	–	–	4-Jun-2003	No	X	X	X	X
0626	*Chremistica*	*ochracea*	(Walker, 1850)	Taiwan	Pingtung Hsien, Manchou Hsiang	–	–	8-Jul-2003	No	X	–	X	X
07.FR.BD.CLP.01	*Tibicen*	*plebejus*	(Scopoli, 1763)	France	Cuges Les Pins. GPS estimated	43.275	5.700	9-Jul-2007	No	X	X	X	X
07.FR.BD.CLP.02	*Tibicen*	*plebejus*	(Scopoli, 1763)	France	Cuges Les Pins. GPS estimated	43.275	5.700	9-Jul-2007	No	X	X	X	X
07.US.AZ.CMA.01	*Tibicen*	*longioperculus*	Davis, 1926	USA	AZ, Cochise Co., Rustler Park	31.928	-109.256	27-Jun-2007	Site	X	X	X	X
07.US.AZ.PBC*	*Cornuplura*	*nigroalbata*	(Davis, 1936)	USA	AZ, Santa Cruz Co., Pena Blanca RA	31.394	-111.090	24-Jun-2007	Site				
07.US.AZ.PBC.02	*Cornuplura*	*nigroalbata*	(Davis, 1936)	USA	AZ, Santa Cruz Co., Pena Blanca RA	31.394	-111.090	24-Jun-2007	Site	X	X	X	X
07.US.AZ.PBC.03	*Cornuplura*	*nigroalbata*	(Davis, 1936)	USA	AZ, Santa Cruz Co., Pena Blanca RA	31.394	-111.090	24-Jun-2007	Site	X	X	X	X
07.US.AZ.PBE.01	*Cacama*	*moorei*	S&H in Sanb. *et al.*, 2011	USA	AZ, Santa Cruz Co., Pena Blanca RA	31.390	-111.117	25-Jun-2007	No	X	X	X	X
07.US.AZ.PBL.01	*Tibicen*	*cultriformis*	(Davis, 1915)	USA	AZ, Santa Cruz Co., Pena Blanca Lake	31.400	-111.091	2-Sep-2007	Yes	X	X	X	X
07.US.AZ.PBL.03*	*Tibicen*	*cultriformis*	(Davis, 1915)	USA	AZ, Santa Cruz Co., Pena Blanca Lake	31.400	-111.091	2-Sep-2007	Site				
07.US.AZ.PBP.01	*Tibicen*	*parallelus*	Davis, 1923	USA	AZ, Santa Cruz Co., Pena Blanca RA	31.389	-111.100	2-Sep-2007	Yes	X	X	X	X
07.US.AZ.PBP.02	*Tibicen*	*parallelus*	Davis, 1923	USA	AZ, Santa Cruz Co., Pena Blanca RA	31.389	-111.100	2-Sep-2007	Yes	X	X	X	X
07.US.AZ.SCA.01	*Tibicen*	*chiricahua*	Davis, 1923	USA	AZ, Cochise Co., Sunnyside Canyon	31.425	-110.417	25-Jun-2007	Yes	X	X	X	X
07.US.AZ.SCC*	*Tibicien*	*chiricahua*	Davis, 1923	USA	AZ, Cochise Co., Sunnyside Canyon	31.430	-110.406	26-Jun-2007	Site				
07.US.AZ.SCC.01*	*Tibicen*	*duryi*	Davis, 1917	USA	AZ, Cochise Co., Sunnyside Canyon	31.430	-110.406	26-Jun-2007	Yes				
07.US.AZ.SCC.03	*Tibicen*	*longioperculus*	Davis, 1926	USA	AZ, Cochise Co., Sunnyside Canyon	31.430	-110.406	26-Jun-2007	Site	X	X	X	X
07.US.DE.APP.03	*Tibicen*	*tibicen tibicen*	(Linnaeus, 1758)	USA	DE, Kent Co., S of Dover	38.752	-75.893	26-Aug-2007	Site	X	X	X	X
07.US.FL.AME.01	*Tibicen*	*tibicen australis*	(Davis, 1912)	USA	FL, Nassau Co., N of Jacksonville	30.630	-81.477	28-Aug-2007	Site	X	X	X	X
07.US.FL.HSP.01	*Tibicen*	*similaris*	Sm. & Grossb., 1907	USA	FL, Alachua Co., High Springs	29.876	-82.539	29-Aug-2007	No	X	X	X	X
07.US.FL.OTP.01	*Tibicen*	*tibicen australis*	Davis, 1912	USA	FL, Alachua Co., Gainesville	29.681	-82.279	28-Aug-2007	No	X	X	–	–
07.US.KS.BLF*	*Tibicen*	*tremulus*	Cole, 2008	USA	KS, Comanche Co., Protection	37.192	-99.501	5-Sep-2007	Site				
07.US.KS.BLF.01	*Tibicen*	*tremulus*	Cole, 2008	USA	KS, Comanche Co., Protection	37.192	-99.501	5-Sep-2007	Yes	X	X	–	–
07.US.KS.BLF.02	*Tibicen*	*tremulus*	Cole, 2008	USA	KS, Comanche Co., Protection	37.192	-99.501	5-Sep-2007	Site	X	X	X	X
07.US.KS.ECW.02	*Tibicen*	*dorsatus*	(Say, 1825)	USA	KS, Barber Co., E of Coldwater	37.281	-98.864	5-Sep-2007	No	X	X	X	X

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APPENDIX. (Continued)

Code	Genus	Species	Species reference	Country	Location	Lat.	Lon.	Date	Rec.	5’ CI	3’ CI	S EF	E EF
07.US.KS.ECW.03	*Tibicen*	*dorsatus*	(Say, 1825)	USA	KS, Barber Co., E of Coldwater	37.281	-98.864	5-Sep-2007	No	–	–	X	X
07.US.KS.MDP.01	*Tibicen*	*auriferus*	(Say, 1825)	USA	KS, Meade Co., Meade	37.285	-100.327	5-Sep-2007	Yes	X	X	X	X
07.US.KS.MDP.03	*Tibicen*	*pruinosus pruinosus*	(Say, 1825)	USA	KS, Meade Co., Meade	37.285	-100.327	5-Sep-2007	Site	–	–	X	X
07.US.KS.WAL*	*Tibicen*	*dorsatus*	(Say, 1825)	USA	KS, Montgomery Co., Coffeyville	37.032	-95.645	6-Sep-2007	Site				
07.US.KS.WAL.01	*Tibicen*	*dorsatus*	(Say, 1825)	USA	KS, Montgomery Co., Coffeyville	37.032	-95.645	6-Sep-2007	Yes	X	X	X	X
07.US.KS.WAL.05	*Tibicen*	*auriferus*	(Say, 1825)	USA	KS, Montgomery Co., Coffeyville	37.032	-95.645	6-Sep-2007	Site	X	X	X	X
07.US.KS.WAL.07	*Tibicen*	*tibicen tibicen*	(Linnaeus, 1758)	USA	KS, Montgomery Co., Coffeyville	37.032	-95.645	6-Sep-2007	Site	X	X	X	X
07.US.MO.TNC.01	*Tibicen*	*pruinosus pruinosus*	(Say, 1825)	USA	MO, Ripley Co., Doniphan	36.622	-90.835	7-Sep-2007	No	–	–	X	X
07.US.MO.WSP.01	*Tibicen*	*robinsonianus*	Davis, 1922	USA	MO, Washington Co., SW of De Soto	38.078	-90.683	7-Sep-2007	Site	X	X	X	X
07.US.MO.WSP.02	*Tibicen*	*robinsonianus*	Davis, 1922	USA	MO, Washington Co., SW of De Soto	38.078	-90.683	7-Sep-2007	Site	–	–	X	X
07.US.NJ.GJM.01	*Tibicen*	*lyricen lyricen*	(De Geer, 1773)	USA	NJ, Salem Co., SE of Quinton	39.510	-75.381	1-Jul-2007	No	X	X	X	X
07.US.NM.CLW.01	*Tibicen*	*bifidus*	(Davis, 1916)	USA	NM, Union Co., SW of Clayton	36.433	-103.230	19-Jun-2007	Site	X	X	X	X
07.US.NM.CLW.02	*Tibicen*	*bifidus*	(Davis, 1916)	USA	NM, Union Co., SW of Clayton	36.433	-103.230	19-Jun-2007	Site	X	X	X	X
07.US.NM.MEA.04	*Tibicen*	*neomexicensis*	Stucky, 2013	USA	NM, Otero Co., E of Mayhill	32.921	-105.425	28-Jun-2007	Yes	X	X	X	X
07.US.NM.MEA.05	*Tibicen*	*inauditus*	Davis, 1917	USA	NM, Otero Co., E of Mayhill	32.921	-105.425	28-Jun-2007	Yes	X	X	X	X
07.US.NM.OVC.04	*Cacama*	*valvata*	(Uhler, 1888)	USA	NM, Taos Co., Orilla Verde RA	36.321	-105.753	20-Jun-2007	Site	X	X	X	X
07.US.NM.SRP.01	*Tibicen*	*dealbatus*	(Davis, 1915)	USA	NM, Guadelupe Co., Santa Rosa	34.939	-104.691	4-Sep-2007	Yes	X	X	X	X
07.US.NM.SVC.01	*Tibicen*	*cultriformis*	(Davis, 1915)	USA	NM, Grant Co., Silver City.	32.787	-108.254	3-Sep-2007	No	X	X	X	X
07.US.NM.TXB.01	*Tibicen*	*tremulus*	Cole, 2008	USA	NM, Quay Co., US54 at NM/TX line	35.651	-103.042	4-Sep-2007	Yes	X	X	X	X
07.US.NM.TXB.02	*Tibicen*	*tremulus*	Cole, 2008	USA	NM, Quay Co., US54 at NM/TX line	35.651	-103.042	4-Sep-2007	Site	X	X	X	X
07.US.TX.KSP.20	*Tibicen*	*texanus*	Metcalf, 1963	USA	TX, Kerr Co. Kerrville	30.007	-99.127	30-Jun-2007	Yes	X	X	X	X
07.US.TX.SAR.01	*Tibicen*	*resh*	(Haldeman, 1852)	USA	TX, Guadalupe Co., E of San Antonio	29.617	-97.805	30-Aug-2007	No	X	X	X	X
08.CN.AH.TIA.27	*Cryptotympana*	*holsti*	Distant, 1904	China	Tiantou, Yuexi County	–	–	15-Jun-2008	No	X	X	X	X
08.US.FL.CRE.01	*Tibicen*	*tibicen tibicen*	(Linnaeus, 1758)	USA	FL, Okaloosa Co., W of Crestview	30.753	-86.619	22-Jul-2008	No	X	X	X	X
08.US.FL.HSC.01	*Tibicen*	*lyricen virescens*	Davis, 1935	USA	FL, Alachua Co., High Springs	29.874	-82.547	24-Jul-2008	No	X	X	X	X
08.US.FL.HSC.02*	*Tibicen*	*lyricen virescens*	Davis, 1935	USA	FL, Alachua Co., High Springs	29.874	-82.547	24-Jul-2008	No				
08.US.FL.HSC.10	*Tibicen*	*resonans*	(Walker, 1850)	USA	FL, Alachua Co., High Springs	29.874	-82.547	1-Sep-2008	No	X	X	X	X
08.US.FL.KNT.01	*Tibicen*	*lyricen virescens*	Davis, 1935	USA	FL, Hillsborough Co, S of Knights	28.028	-82.155	1-Sep-2008	No	X	X	X	X
08.US.FL.RIV.01	*Tibicen*	*pronotalis walkeri*	Metcalf, 1955	USA	FL, Jackson Co. E of Bascom	30.947	-85.007	5-Sep-2008	Site	X	X	X	X
08.US.FL.SCH.01	*Tibicen*	*tibicen australis*	Davis, 1912	USA	FL, Orange Co. S. of Chuluota	28.599	-81.125	7-Jul-2008	No	X	X	X	X
08.US.FL.TRA.03	*Tibicen*	nr. *similaris*	(Sm. & Grossb., 1907)	USA	FL, Leon Co., Tallahassee	30.485	-84.386	20-Jul-2008	Yes	X	X	X	X
08.US.FL.TRA.10	*Tibicen*	*davisi davisi*	(Sm. & Grossb., 1907)	USA	FL, Leon Co., Tallahassee	30.485	-84.386	4-Sep-2008	No	X	X	X	X
08.US.FL.TRA.11	*Tibicen*	*davisi davisi*	(Sm. & Grossb., 1907)	USA	FL, Leon Co., Tallahassee	30.485	-84.386	4-Sep-2008	No	X	X	X	X
08.US.GA.HAH*	*Tibicen*	*resonans*	(Walker, 1850)	USA	GA, Lowndes Co., Hahira	30.992	-83.387	24-Jul-2008	No				
08.US.GA.HAH.01*	*Tibicen*	*similaris*	(Sm. & Grossb., 1907)	USA	GA, Lowndes Co., Hahira	30.992	-83.387	24-Jul-2008	No				
08.US.GA.RIX.01	*Tibicen*	*tibicen australis*	(Davis, 1912)	USA	GA, Stewart Co., W of Richland	32.068	-84.712	4-Sep-2008	No	X	X	X	X

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APPENDIX. (Continued)

Code	Genus	Species	Species reference	Country	Location	Lat.	Lon.	Date	Rec.	5′ CI	3′ CI	S EF	E EF
08.US.MS.STX.01	*Tibicen*	*davisi harnedi*	Davis, 1918	USA	MS, Rankin Co, Jackson	32.268	-90.136	7-Sep-2008	Site	X	X	X	X
09.MY.SK.GMU.11	*Chremistica*	sp. 1	–	Malaysia	Sarawak, Gunung Mulu NP	4.042	114.813	2009	No	X	X	X	X
09.MY.SK.GMU.12	*Chremistica*	sp. 2	–	Malaysia	Sarawak, Gunung Mulu NP	4.042	114.813	2009	No	X	X	X	X
09.US.CT.AUL.EB1	*Tibicen*	*auletes*	(Germar, 1834)	USA	CT, Wallingford	–	–	Aug-2009	N/A	X	X	X	X
09.US.FL.BRU.01	*Tibicen*	*figuratus*	(Walker, 1858)	USA	FL, Gainesville	29.626	-82.330	17-Sep-2009	No	X	X	X	X
09.US.FL.KLR.01	*Tibicen*	*similaris*	(Sm. & Grossb., 1907)	USA	FL, Karick Lake South RA	30.891	-86.646	15-Sep-2009	No	X	X	X	X
09.US.IL.HIC.01	*Tibicen*	*canicularis*	(Harris, 1841)	USA	IL, Will Co., E of Joliet	41.510	-87.925	2-Sep-2009	Yes	–	–	X	X
09.US.MN.FAI.02	*Tibicen*	nr. *canicularis*	(Harris, 1841)	USA	MN, Fairmont	43.635	-94.448	6-Sep-2009	Yes	X	X	X	X
09.US.NC.BRS.01	*Tibicen*	*linnei*	(Sm. & Grossb., 1907)	USA	NC, Wake Co., Garner	35.720	-78.641	10-Sep-2009	No	–	–	X	X
09.US.SD.CMB.01*	*Tibicen*	*pronotalis pronotalis*	Davis, 1938	USA	SD, Chamberlain	43.816	-99.326	4-Sep-2009	Yes				
09.US.SD.CMB.02	*Tibicen*	*pronotalis pronotalis*	Davis, 1938	USA	SD, Chamberlain	43.816	-99.326	4-Sep-2009	Site	–	–	X	X
09.US.SD.IRA.01	*Tibicen*	*canicularis*	(Harris, 1841)	USA	SD, Brookings Co., S. of Brookings	44.155	-96.756	5-Sep-2009	Site	–	–	X	X
10.PH.CG.KAT.01	*Cryptotympana*	*consanguinea*	Distant, 1916	Philippines	Camiguin Province, Mambajao Mun.	9.216	124.720	27-Jun-2010	No	X	X	–	–
10.US.FL.ADM.01	*Tibicen*	nr. *resonans*	Walker, 1850	USA	FL, Orange Co, Altamonte Springs	28.667	-81.361	10-Aug-2010	No	X	X	X	X
11.GR.XX.MEL.01	*Tibicen*	*gemellus*	(Boulard, 1988)	Greece	Island Ikaria, Pezi, Mt Melissa	37.565	26.051	14-Jul-2011	No	X	X	X	X
11.TR.XX.DAV.06	*Tibicen*	*gemellus*	(Boulard, 1988)	Turkey	Aydim, Kusadasi, Davutlar	37.728	27.308	24-Jun-2011	No	–	–	X	X
11.US.FL.FIT.01	*Tibicen*	*davisi davisi*	(Sm. & Grossb., 1907)	USA	FL, W of Crystal River	28.910	-82.681	22-Sep-2011	No	X	X	X	X
12.US.AZ.GLE.01	*Cacama*	*valvata*	(Uhler, 1888)	USA	AZ, W of Gleeson	31.730	-109.843	12-Jun-2012	No	X	X	X	X
12.US.AZ.TSE.01	*Tibicen*	*simplex*	Davis, 1941	USA	AZ, E. of Tombstone	31.741	-109.968	17-Jun-2012	Yes	X	X	X	X
12.US.CO.BAC.01	*Tibicen*	*bifidus*	(Davis, 1916)	USA	CO, Baca Co. SW of Springfield. GPS est.	37.279	-102.924	14-Jun-2012	Yes	X	X	X	X
12.US.NM.TOC*	*Tibicen*	*townsendii*	(Uhler, 1905)	USA	NM, E. of Truth or Consequences	33.129	-107.118	15-Jun-2012	Site				
12.US.NM.TOC.02	*Tibicen*	*townsendii*	(Uhler, 1905)	USA	NM, E. of Truth or Consequences	33.129	-107.118	15-Jun-2012	Yes	X	X	X	X
Croatia19	*Tibicen*	*plebejus*	(Scopoli, 1763)	Croatia	Pirovik, Cela. GPS estimated	15.667	43.817	11-Jul-2003	No	X	X	X	X
JRJ2010-7-21-1a	*Chremistica*	sp. 3	–	Philippines	Murcia, Brgy. Minoyan, Negros	10.508	123.107	21-Jul-2010	No	X	X	X	X
Laos_MtPan	*Chremistica*	sp. 2	–	Laos	Mt. Pan	–	–	2003	No	X	–	X	X
Laos5	*Salvazana*	*mirabilis*	Distant, 1913	Laos		–	–		No	X	–	X	X
MadLoc6_1	*Yanga*	*andriana*	(Distant, 1899)	Madagascar		–	–		No	X	X	X	X
Philippines50	*Chremistica*	*kyoungheeae*	Lee, 2010	Philippines	Mindanao	–	–	2007-9	No	X	X	X	X
Philippines51	*Chremistica*	*kyoungheeae*	Lee, 2010	Philippines	Mindanao	–	–	2007-9	No	X	X	–	–
Philippines53	*Cryptotympana*	*consanguinea*	Distant, 1916	Philippines	Mindanao	–	–	2008-9	No	X	X	X	X
Vietnam_BachMa	*Cryptotympana*	sp. 1	–	Vietnam	Bach Ma	–	–	2003	No	X	X	X	X