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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 (*Magicalcada* 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 (*Magicalcada* 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).