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Phylogeny, biogeography, and display evolution in the tree and brush lizard genus *Urosaurus* (Squamata: Phrynosomatidae)

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ABSTRACT

The brush and tree lizards (*Urosaurus*) are a small clade of phrynosomatid lizards native to western North America. Though not as well known as their diverse sister clade, the spiny lizards (*Sceloporus*), some *Urosaurus* have nonetheless become model organisms in integrative biology. In particular, dramatic phenotypic and behavioral differences associated with specific mating strategies have been exploited to address a range of ecological and evolutionary questions. However, only two phylogenies have been proposed for the group, one of which is pre-cladistic and both based principally on morphological characters that might not provide robust support for relationships within the group. To help provide investigators working on *Urosaurus* with a robust phylogeny in which to frame ecological and evolutionary questions, we establish a molecular phylogeny for the group. We sampled three mitochondrial and three nuclear loci, and estimated phylogenetic relationships within *Urosaurus* using both maximum parsimony (MP) and Bayesian inference (BI), as well as a coalescent-based species tree approach. Finally, we used two methods of ancestral state reconstruction (ASR) to gain insight into the evolution of microhabitat preference and male display signals, traits that have been the focus of studies on *Urosaurus*. All reconstruction methods yield nearly the same ingroup topology that is concordant in most respects with the previous cladistic analysis of the group but with some significant differences; our data suggest the primary divergence in *Urosaurus* occurs between a clade endemic to the Pacific versant of Mexico and the lineages of Baja California and the southwestern US, rather than placing *Urosaurus graciosus* as the basal taxon and linking the Baja and Mexican endemics. We find support for a single transition to a saxicolous lifestyle within the group, and either the independent gain or loss of arboreality. The evolution of throat color patterns (i.e. dewlaps) appears complex, with multiple color morphs likely involving orange reconstructed as ancestral to the group and to most lineages, followed by a single transition to a fixed blue-throated morph in one clade. These results should provide a useful framework for additional comparative work with *Urosaurus*, and establish the phylogenetic context in which *Urosaurus* diversity arose.

1. Introduction

The brush and tree lizards of the genus *Urosaurus* (Squamata: Phrynosomatidae) form a small group of nine species (Wiens, 1993) endemic to the arid and semiarid lands of western United States and Mexico. Species of *Urosaurus* can be found from south of the Isthmus of Tehuantepec in Chiapas, Mexico, to as far north as southwestern Wyoming in the US, and from central and southern Texas to the cape of Baja California, and even a few oceanic islands west of that peninsula (Fig. 1) (Mittleman, 1942; Grismer, 2002; Stebbins, 2003). Brush and tree lizards are easily distinguished from other phyrnosomatid genera by the presence of a distinctive, narrow band of enlarged keeled scales running down the dorsum, and by several other morphological synapomorphies (Mittleman, 1942; Wiens, 1993). As their common name implies, most of these lizards are highly scansorial and spend most of their time on shrubs, trees, or boulders, rather than on the ground (Smith, 1946; Stebbins, 2003).

Though not as widely studied as spiny lizards (*Sceloporus*; Sites et al., 1992), the sister group of *Urosaurus* (Wiens et al., 2010), some brush and tree lizards are nonetheless becoming model organisms of integrative biology because they display extensive morphological and behavioral variation, and are easily manipulated both in captivity and the field (e.g. *Urosaurus graciosus* and *Urosaurus ornatus*). Thus, some *Urosaurus* species, especially *U. ornatus*, have become the focus of a wide range of research, from studies of physiological tradeoffs (French et al., 2007), to the roles of phenotypic plasticity

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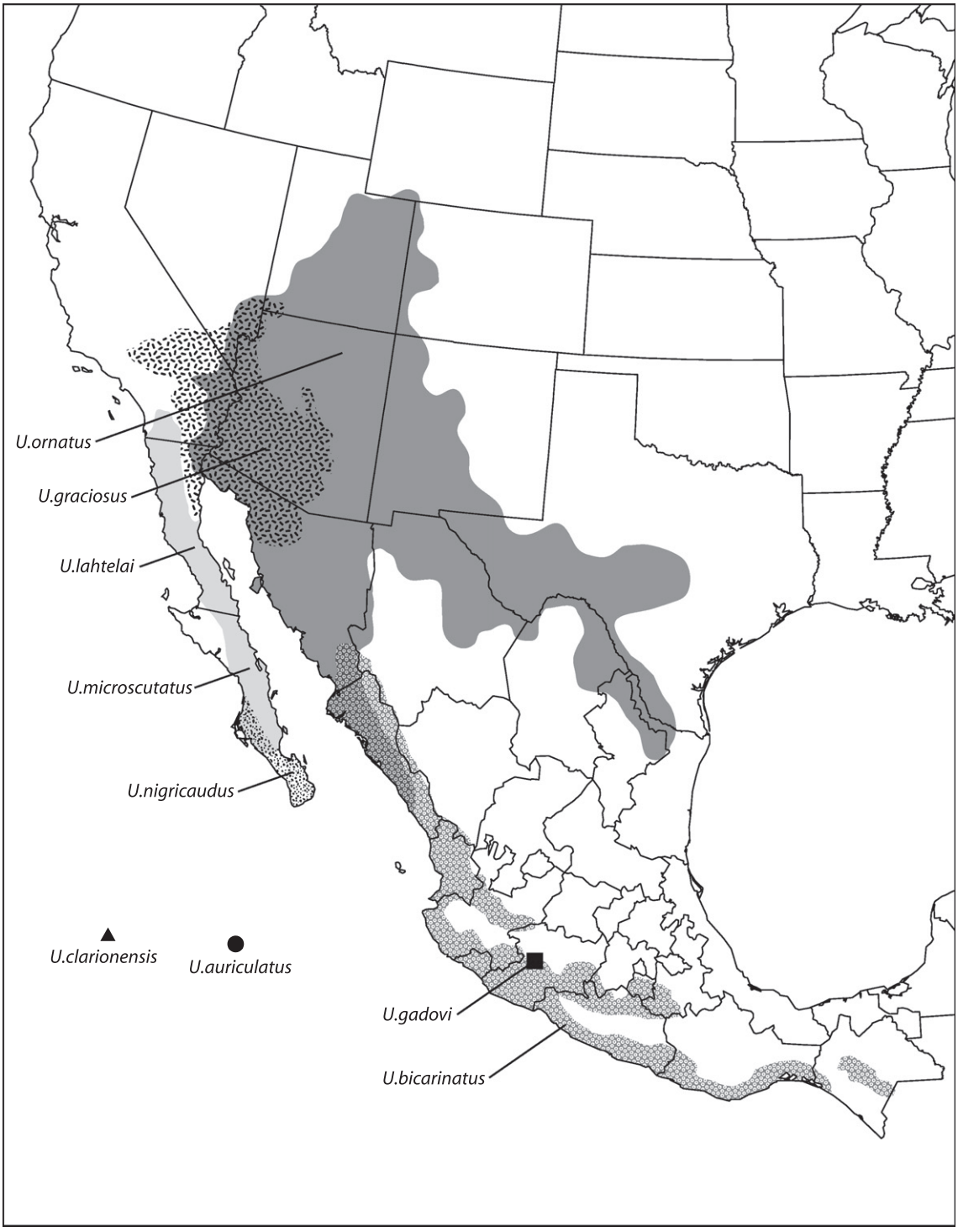

Fig. 1. Geographic distributions of *Urosaurus* species in the western United States and Mexico (after Mittleman, 1942; Wiens, 1993; Grismer, 2002; Stebbins, 2003); see Grismer (2002) for a comprehensive list of insular populations along Baja California.

(Irschick and Meyers, 2007), to understanding mate choice (Hamilton and Sullivan, 2005; McElroy et al., 2007), and the role of the endocrine system in mediating behavior (Moore et al., 1998; Thaker et al., 2009). An exceptional area of research on *Urosaurus* concerns the mechanisms and dynamics of alternative mating strategies exhibited by males with particular throat color morphs (reviewed in Moore et al., 1998). In the model species *U. ornatus*, throat morphs are genetically and hormonally controlled (Hews et al., 1994, 1997; Hews and Moore, 1995) and are associated with various behavioral syndromes (i.e. personalities) such as aggression and boldness or submission and wariness, that influence alternative mating strategies and also correlate with other life history attributes such as anti-predator responses (Thaker et al., 2009). In many *Urosaurus* these throat color morphs vary within and among populations (Thompson and Moore, 1991; Carpenter, 1995), and thus may exhibit the same cyclical fitness dynamics (game theory) as the well-worked model *Uta stansburiana* (Sinervo and Lively, 1996; Zamudio and Sinervo, 2000). In *Uta stansburiana*, the frequency and distribution of these