



Molecular systematics and historical biogeography of tree boas (*Corallus* spp.)

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ABSTRACT

Inferring the evolutionary and biogeographic history of taxa occurring in a particular region is one way to determine the processes by which the biodiversity of that region originated. Tree boas of the genus *Corallus* are an ancient clade and occur throughout Central and South America and the Lesser Antilles, making it an excellent group for investigating Neotropical biogeography. Using sequenced portions of two mitochondrial and three nuclear loci for individuals of all recognized species of *Corallus*, we infer phylogenetic relationships, present the first molecular analysis of the phylogenetic placement of the enigmatic *C. cropanii*, develop a time-calibrated phylogeny, and explore the biogeographic history of the genus. We found that *Corallus* diversified within mainland South America, via over-water dispersals to the Lesser Antilles and Central America, and via the traditionally recognized Panamanian land bridge. Divergence time estimates reject the South American Caribbean-Track as a general biogeographic model for *Corallus* and implicate a role for events during the Oligocene and Miocene in diversification such as marine incursions and the uplift of the Andes. Our findings also suggest that recognition of the island endemic species, *C. grenadensis* and *C. cookii*, is questionable as they are nested within the widely distributed species, *C. hortulanus*. Our results highlight the importance of using widespread taxa when forming and testing biogeographic hypotheses in complex regions and further illustrate the difficulty of forming broadly applicable hypotheses regarding patterns of diversification in the Neotropical region.

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1. Introduction

Inferring the evolutionary history of a group in a particular region is one way to elucidate the processes by which the fauna of that region originated (Crisp et al., 2011; Riddle, 2009). In particular, comparing the evolutionary histories of multiple codistributed lineages allows one to formulate general biogeographic hypotheses that can be further tested and refined with additional

taxa (Castoe et al., 2009; Daza et al., 2009). Extreme geological and environmental complexity as well as areas of high richness, high endemism, and multiple major biogeographic provinces (Udvardy, 1975) make the Neotropical region particularly interesting to biogeographers (Beheregaray, 2008; Graham, 1997). However, complex interactions among multiple factors have also precluded a consensus regarding the ecological and historical processes that have generated observed patterns of diversity. Although several broad biogeographic hypotheses have been proposed, the evolutionary history of most Neotropical taxa remains poorly understood and thus, the generality of these hypotheses remains untested in many clades (Beheregaray, 2008).

Multiple historical events have played a role in biological diversification in South America, but four major ones are of primary importance and have received the most attention (Rull, 2011).

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First, marine incursions from the Pacific and Caribbean covered large tracts of Amazonia with huge lakes and swamps during the Tertiary, isolating lineages in upland areas such as the Brazilian and Guianan shields (Haffer, 2008; Webb, 1995). Second, the Andean uplift during the Miocene created a major continental barrier to dispersal while also providing new montane habitat and opportunities for colonization and diversification (Haffer, 2008; Rull, 2011). Third, contraction of forests during Pleistocene climatic fluctuations is thought to have isolated populations of forest-adapted taxa in refugia, which subsequently led to speciation (Haffer, 1969, 2008; Vanzolini, 1970). Finally, closure of the Panamanian Isthmus provided a dispersal route between North and South America which has been coined the “Great American Biotic Interchange-GABI” (Lessa et al., 1997; Simpson, 1940). The GABI was first recognized by Wallace (1876) and has since been identified as important in structuring biogeographic patterns in multiple taxa including birds, mammals, and invertebrates (Johnson and Weckstein, 2011; Lessa et al., 1997; Zeh et al., 2003); however divergences in many squamate taxa that span both sides of the Panamanian Isthmus predate its formation (Castoe et al., 2009; Daza et al., 2009, 2010). Among these events, the formation of Pleistocene refugia has received the most attention and debate, whereas the closure of the Panamanian Isthmus is the only event for which the timing is precisely dated (Rull, 2011).

The genus *Corallus* is a member of the subfamily Boinae, a group with clear Gondwanan origins (Noonan and Chippindale, 2006). Currently, eight species are recognized based on morphology or in some cases morphology and molecular data: *C. annulatus* (*sensu lato*, but see taxon sampling in Materials and Methods), *C. batesii*, *C. caninus*, *C. cookii*, *C. cropanii*, *C. grenadensis*, *C. hortulanus*, and *C. ruschenbergerii* (Henderson et al., 2009). Four species are endemic to South America, including the rare and enigmatic *C. cropanii*, which is only known from four specimens (three existing) and whose taxonomic placement has been of great interest (Kluge, 1991; Machado-Filho et al., 2011). Two species are distributed in both Central and South America (*C. annulatus* and *C. ruschenbergerii*), and two species are endemic to the Lesser Antilles (*C. cookii* and *C. grenadensis*) (Henderson, 2002; Henderson et al., 2009). Phylogenetic relationships have been explored using morphology (Kluge, 1991; Henderson, 1997, 2002; Henderson and Hedges, 1995; Henderson et al., 2009) and molecular phylogeographic analyses have been conducted on individual species (Vidal et al., 2005). However, a time-calibrated phylogeny for all members of the genus,

which could be used to test both spatial and temporal components of biogeographic hypotheses, is not presently available.

Here, we use DNA sequence data from two mitochondrial and three nuclear genes of all species of *Corallus* to infer their phylogenetic relationships. We then reconstruct the biogeographic history of the group by integrating divergence times of species, as estimated by relaxed-clock divergence dating methods, with ancestral area analyses that account for dispersal and extinction to infer the biogeographic history of the group. Finally, we use our results to evaluate the potential roles of major Neotropical biogeographic events (e.g., marine incursions, Andean uplift, Pleistocene refugia, and Panamanian Isthmus) in the diversification of *Corallus*.

2. Materials and methods

2.1. Taxon sampling

We used 20 specimens of *Corallus* including all species from 18 localities across the distribution of the genus (Fig. 1, S1). We did not have access to tissue samples from specimens positively identified as *C. batesii* and available sequence data were restricted to cytochrome-*b* (*cyt-b*) from two individuals. Our Ecuadorian sample of *C. annulatus* could not be definitively classified as either *C. annulatus* or *C. blomeri*, and as there is no question whether these species are sister and we are not addressing the validity of *C. blomeri*, we treat *C. annulatus* herein as including both *C. annulatus* and *C. blomeri*. Tissue samples were collected by us, obtained through museum loans, or donated by private individuals from personal tissue collections. For phylogenetic analyses, we included sequences from GenBank for additional boid taxa and *Cylindrophis* for use as outgroups. These outgroup taxa were also included in divergence dating analysis in order to provide external nodes on which we could place prior age information based on the fossil record. A detailed list of specimens, including voucher numbers and GenBank accession numbers, is provided in Supplementary Information (S1).

2.2. Laboratory methods

We extracted total genomic DNA from liver tissue, muscle tissue, or shed skins either stored frozen or in ethanol using Qiagen DNeasy kits (tissue protocol). We amplified the complete

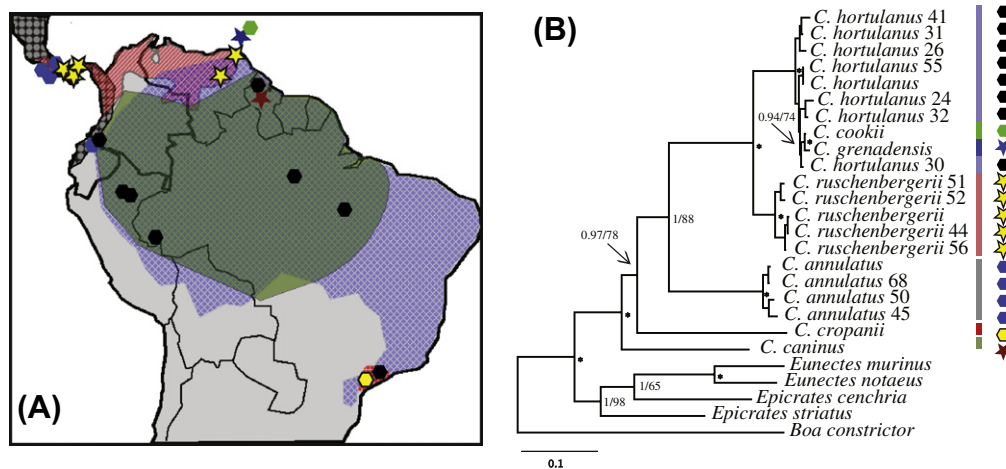


Fig. 1. (A) Map of Central and South America showing approximate distributions and sampling localities of *Corallus* species used in this study. (B) Phylogenetic estimate of relationships of the genus *Corallus* based on Bayesian Inference in the program Mr. Bayes. Tree topology was identical in both BI and ML inference. Node numbers indicate Bayesian posterior probability and ML bootstrap values (PP/ML). Nodes labeled with an asterisk (*) had a posterior probability of 1 and a bootstrap value of 100%. Vertical colored bars correspond to colors in distribution map whereas symbols to the right of the bars correspond to sample localities on the map. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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