


# A phylogenomic perspective on the biogeography of skinks in the *Plestiodon breviostris* group inferred from target enrichment of ultraconserved elements

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## ABSTRACT

**Aim** The aim of our study was to reconstruct ancestral geographic distributions from time-calibrated phylogenies generated from phylogenomic data to answer three broad questions about the biogeography of skinks in the *Plestiodon breviostris* group: (1) Are biogeographic patterns correlated with the formation of the Trans-Mexican Volcanic Belt? (2) Do different methods of phylogenetic estimation result in different topologies? If so, (3) are biogeographic reconstructions impacted by the use of different phylogenetic trees?

**Location** Mexico.

**Methods** We used target enrichment of ultraconserved elements (UCEs) to obtain sequence data from 58 skinks representing 11 of the 13 described species in the group. We estimated time-calibrated phylogenies using concatenated and multi-species coalescent phylogenetic approaches. We used these phylogenies to reconstruct ancestral geographic distributions.

**Results** The final dataset contained 3,282 UCEs from each skink. Samples of each putative species formed well-supported clades in phylogenetic trees. Time-calibrated phylogenies estimated using concatenated and multispecies coalescent methods were generally congruent, but differed in the placement of one basal relationship. Divergences in the *P. breviostris* group were temporally and spatially congruent with the pre-Pleistocene formation of the Trans-Mexican Volcanic Belt. The group most likely colonized the Mexican highlands from east to west during the Late Miocene and Pliocene. Inferences about the early biogeographic history of the group were confounded by the unresolved placement of a key phylogenetic relationship deep in the phylogeny.

**Conclusions** Skinks in the *P. breviostris* group represent another example of a widespread montane Mexican taxon with a long history of pre-Pleistocene diversification associated with the primary formation of the Trans-Mexican Volcanic Belt. This mountain range seems to have been both a cradle of diversification for *P. breviostris* group species and a land bridge facilitating dispersal across the Mexican highlands. Our results highlight the probable existence of new species within the *P. breviostris* complex and suggest that querying a large portion of the genome may be critically important for studying the biogeographic history of these skinks. However, inferred differences between the concatenated and multispecies coalescent phylogenies, and the different biogeographic histories of the *P. breviostris* group reconstructed from these phylogenies, caution that methods of estimating phylogenetic trees used in biogeographic reconstructions need to be carefully considered.

## Keywords

ancestral area, Mexico, phylogenomics, phylogeography, *Plestiodon*, Trans-Mexican Volcanic Belt

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## INTRODUCTION

The Mexican highlands are a complex mosaic of mountain ranges of different ages and origins and are considered a global biodiversity hotspot (Ramamoorthy *et al.*, 1993; Mittermeier *et al.*, 2005). Although the mountainous regions of Mexico have been historically understudied, a number of studies published in the past decade have begun to elucidate the geographic patterns of diversification in wide-ranging montane species (e.g., McCormack *et al.*, 2008; Bryson *et al.*, 2011a, 2012a; Barrera-Guzmán *et al.*, 2012; Ruiz-Sanchez & Specht, 2013; Rodríguez-Gómez & Ornelas, 2015). These and other recent studies suggest that the primary formation of the Trans-Mexican Volcanic Belt between 19 and 3 Ma (Gómez-Tuena *et al.*, 2007) was a key driver of species diversification across the region (McCormack *et al.*, 2008; Bryson *et al.*, 2012a; Mastretta-Yanes *et al.*, 2015). Pleistocene climate change has also played an important role in generating genetic diversity, especially within species (Bryson *et al.*, 2011b, 2014; Barrera-Guzmán *et al.*, 2012; Leaché *et al.*, 2013; Rodríguez-Gómez & Ornelas, 2015; Maldonado-Sánchez *et al.*, 2016).

The historical diversification of species distributed across the Mexican highlands has mostly been inferred from phylogenetic analyses of one or a few genetic loci, usually mitochondrial DNA (mtDNA). However, mtDNA-based studies can be misleading due to stochastic processes that disproportionately affect mtDNA (Funk & Omland, 2003; Edwards & Bensch, 2009), and the low phylogenetic signal in more slowly evolving nuclear genes can limit their phylogenetic utility (Moeller & Townsend, 2011; Lanier *et al.*, 2014). Recent advances in next-generation sequencing of non-model organisms now allow researchers to estimate phylogenies from thousands of loci scattered across the genome (reviewed in Andrews *et al.*, 2016; Toews *et al.*, 2016). Despite this improvement to the field, the most reliable methods for inferring robust phylogenetic trees remain contentious (Liu *et al.*, 2015; Edwards *et al.*, 2016; Springer & Gatesy, 2016). Conceptually different phylogenetic methods can produce incongruent and sometimes strongly conflicting topologies (Edwards *et al.*, 2016). Because phylogenies have become well integrated into historical biogeography (Ree & Sanmartín, 2009; Matzke, 2014), the methods used to estimate phylogenetic trees will have important implications for inferring biogeographic histories.

The widespread distribution of skinks in the *Plestiodon brevirostris* group across the major mountainous regions of Mexico (Fig. 1) makes these lizards an attractive group for examining species diversification in the Mexican highlands. Thirteen species are recognized within the group, including *P. bilineatus*, *P. brevirostris*, *P. colimensis*, *P. copei*, *P. dicei*, *P. dugesii*, *P. indubitus*, *P. lynxe*, *P. nietoi*, *P. ochoterena*, *P. parviauriculatus*, *P. parvulus* and *P. sumichrasti* (Feria-Ortiz *et al.*, 2011; Brandley *et al.*, 2012; Feria-Ortiz & García-Vázquez, 2012). Most of the species are morphologically similar and have long been recognized as part of the *P. brevirostris* group (Tanner, 1958; Dixon, 1969; Robinson, 1979). However, *P. lynxe* and *P. sumichrasti* were recently added to the group based on strong molecular evidence

(Brandley *et al.*, 2012). *Plestiodon sumichrasti* is the only relatively large, stout-bodied species in the group, and together with *P. lynxe* is the only species in the group to possess a light-coloured median dorsal stripe.

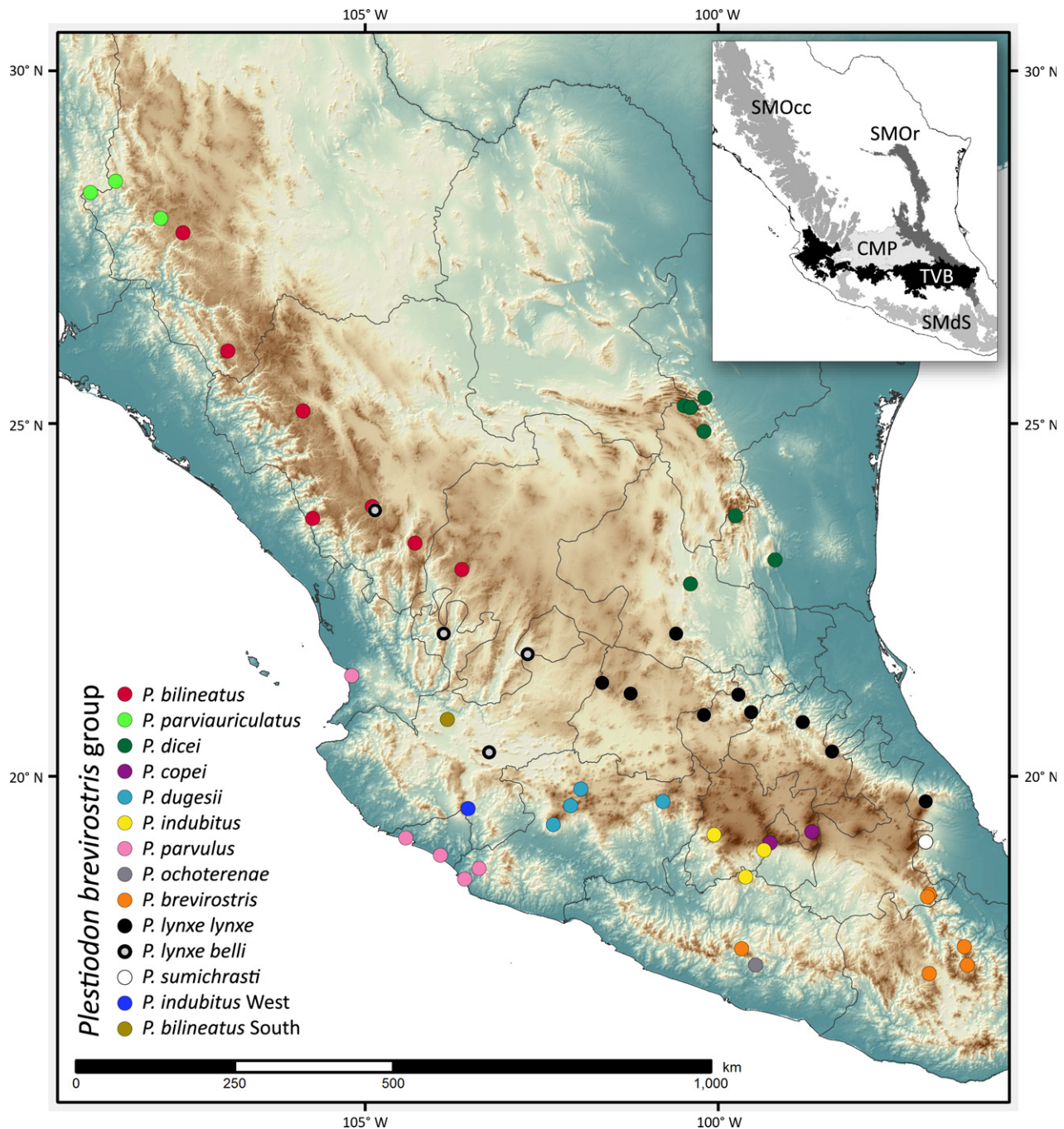
Skinks in the *P. brevirostris* group occupy a variety of habitats across the Mexican highlands and adjacent coastal foothills. Most species inhabit temperate woodlands at mid-to high-elevations within the interior highlands. These include *P. bilineatus* and *P. parviauriculatus* in the Sierra Madre Occidental, *P. dicei* in the northern Sierra Madre Oriental, *P. ochoterena* and *P. nietoi* in the Sierra Madre del Sur, and three species (*P. copei*, *P. dugesii* and *P. indubitus*) in the Trans-Mexican Volcanic Belt. *Plestiodon brevirostris* occurs in the eastern Trans-Mexican Volcanic Belt, the Sierra Madre del Sur and the geographically complex mountainous region near the intersection of the Sierra Madre Oriental, Trans-Mexican Volcanic Belt and Sierra Madre del Sur. Two species in the group, *P. parvulus* and *P. colimensis*, are distributed in tropical dry forests across the western coastal foothills that flank the interior highlands. Distributions of the last remaining and most recently added species in the group are comparatively larger and encompass a wider range of habitats. *Plestiodon lynxe*, comprised of two subspecies, is found in mesquite-grassland and oak forests across the Central Mexican Plateau and temperate woodlands along edges of the Sierra Madre Occidental, Sierra Madre Oriental and Trans-Mexican Volcanic Belt. *Plestiodon sumichrasti* is the only species not endemic to Mexico in the group, and occupies low-elevation tropical and semi-tropical forest east of the southern Sierra Madre Oriental and Sierra Madre del Sur in Mexico and south into northern Honduras.

The systematics of the *P. brevirostris* group have been studied using a combination of mitochondrial and morphological data (Feria-Ortiz *et al.*, 2011) and multilocus data (Brandley *et al.*, 2011, 2012). To date, however, no study has examined the evolutionary history of the group using dense geographic and taxonomic sampling as well as multilocus data. Here we use phylogenomic data from thousands of ultraconserved elements (UCEs) to study the biogeography of skinks in the *P. brevirostris* group. We generate time-calibrated phylogenies using a variety of phylogenetic approaches, and use these phylogenies to reconstruct ancestral geographical distributions. We use these data to answer three broad questions: (1) Are biogeographic patterns correlated with the formation of the Trans-Mexican Volcanic Belt? (2) Do different methods of phylogenetic estimation result in different topologies? If so, (3) are biogeographic reconstructions affected by the use of different phylogenetic trees?

## MATERIALS AND METHODS

### Genetic data

We sequenced 58 skinks representing 11 of the 13 currently recognized species in the *P. brevirostris* group (Feria-Ortiz *et al.*, 2011; Brandley *et al.*, 2012; Feria-Ortiz & García-Vázquez, 2012;



**Figure 1** Localities of skinks in the *Plestiodon brevisrostris* group sampled for this study. Inset shows major mountainous regions of Mexico, including the Sierra Madre Occidental (SMOcc), Sierra Madre Oriental (SMOr), Sierra Madre del Sur (SMdS), Trans-Mexican Volcanic Belt (TVB) and Central Mexican Plateau (CMP). Samples are not colour-coded to match those in Figs 2–4. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

see Fig. 1 and Appendix S1 in Supporting Information). We were unable to include the enigmatic species *P. colimensis* from the coastal foothills of western Mexico and the recently described species *P. nietoi* from the Sierra Madre del Sur (Feria-Ortiz & García-Vázquez, 2012). We also sequenced a population of an undescribed species in the group previously confounded with *P. indubitus* from northern Colima and southern Jalisco (here referred to as '*P. indubitus* West'), and

a morphologically divergent population of *P. bilineatus* from Jalisco ('*P. bilineatus* South') that represents another possibly undescribed species (Feria-Ortiz *et al.*, 2011; Brandley *et al.*, 2012; Feria-Ortiz & García-Vázquez, 2012). We included *P. tetragrammus* as an outgroup (Brandley *et al.*, 2012).

We extracted genomic DNA from tissues using Qiagen DNeasy Blood & Tissue Kits (Qiagen Inc., Valencia, CA, USA) and sent extractions to RAPiD Genomics (Gainesville,

FL, USA) for UCE sequence capture and sequencing. Each pool was enriched using a set of 5,472 custom-designed probes (MYbaits; MYcroarray, Inc., Ann Arbor, MI, USA) targeting 5,060 UCE loci (Faircloth *et al.*, 2012) following an open-source protocol (see [www.ultraconserved.org](http://www.ultraconserved.org) for the full protocol). Pooled libraries were sent to the University of Florida ICBR Facility for 150 bp paired-end sequencing on an Illumina NextSeq500.

### Data assembly

After sequencing, we demultiplexed raw data based on unique sequence tags using CASAVA 1.8.2 (Illumina, Inc., San Diego, CA, USA). We then used TRIMMOMATIC 0.32 (Bolger *et al.*, 2014) to remove low-quality reads, trim low-quality ends and remove adapter sequences from sequences. Cleaned reads were assembled for each individual using the de novo assembler IDBA 1.1 (Peng *et al.*, 2010) run iteratively over k-mer values from 50–90 with a step length of 10. We used PHYLUCE 1.5.0 (Faircloth, 2016) to map assembled reads to probe sequences and then match loci across individuals. Multiple sequence alignment for each locus was completed using MAFFT 7.130 (Katoh & Standley, 2013), and aligned loci were trimmed of long ragged-ends to reduce incomplete data. Datasets were compiled for loci where all individuals were sequenced.

### Phylogenetic analyses and divergence date estimation

We estimated phylogenetic relationships from the concatenated dataset using maximum likelihood (ML) and Bayesian inference (BI) methods. We conducted ML analyses using RAxML 8.1.11 (Stamatakis, 2014) on the CIPRES 3.3 computing cluster (Miller *et al.*, 2010). We partitioned the dataset by UCE locus and ran analyses using the GTRCAT model and 1,000 rapid-bootstrap replicates to assess nodal support. We estimated a time-calibrated Bayesian phylogeny using BEAST 1.8.2 (Drummond *et al.*, 2012). To time-calibrate the tree, we applied two secondary calibration points based on results of a previous biogeographic study on the origins of the genus *Plestiodon* that incorporated three fossil calibrations (Brandley *et al.*, 2011). We calibrated the split between the outgroup and the *P. brevirostris* group using a normal prior with a mean of 18.5 million years ago (Ma) and standard deviation of 2.4 Ma, resulting in a 95% highest probability density (HPD) ranging from 14.5 to 22.5 Ma. The crown node of the *P. brevirostris* group was calibrated using a normal prior with a mean of 13.5 Ma and a standard deviation of 2.1 Ma, resulting in a 95% HPD ranging from 10.1 to 17.0 Ma. We used a GTR+G model of sequence evolution, an uncorrelated lognormal relaxed clock, and a Yule process tree prior, and ran analyses for 40 million generations, retaining trees and parameters every 10,000 steps. Results were displayed in TRACER 1.6 (Rambaut & Drummond, 2007) to confirm acceptable mixing and likelihood stationarity, appropriate burn-in, and effective sample sizes (ESS) above 200 for all estimated

parameters. Parameters associated with the lognormal relaxed clock model failed to converge during preliminary runs, possibly as a result of long isolated branches and substitution rate heterogeneity along these branches (Matari & Blair, 2014; Vanneste *et al.*, 2015). We therefore ran final analyses using a strict clock model. Under the strict clock model, all parameters converged (ESS were all above 1000) and despite using the two different clock models, estimated topologies were identical and divergence dates were within 1 Myr at the base of the tree. We discarded the first 25% of trees as burn-in and summarized the maximum clade credibility tree with median heights using TREEANNOTATOR 1.8.2 (Drummond *et al.*, 2012). The analysis was repeated twice from different starting seeds to confirm adequate mixing and consistent results.

We also analysed a subset of the loci using a Bayesian implementation of the multispecies coalescent in \*BEAST, a part of the BEAST 1.8.2 package. Although computationally intensive, this method takes advantage of the full sequence data to co-estimate gene trees embedded with a shared species tree, compared to other species tree methods that use summary statistics to estimate the species tree, and has been shown to outperform other approaches such as concatenation when branch lengths are short due to a rapid radiation (Ogilvie *et al.*, 2016). We computed the number of parsimony-informative sites in each UCE locus and created a subset of loci having 20 or more parsimony-informative sites. Prior studies have demonstrated improved phylogenetic performance when removing uninformative loci and concentrating on those loci with the highest information content (e.g., O'Neill *et al.*, 2013; Manthey *et al.*, 2016; Meiklejohn *et al.*, 2016). We sampled this reduced dataset by loci, without replacement, to create five resampled datasets, each with 40 loci. Individuals were assigned to 1 of 14 possible lineages based on previous morphological and molecular studies (Feria-Ortiz *et al.*, 2011; Brandley *et al.*, 2012) and the results from concatenation (see Results). To reduce computational burden, we assigned each locus an HKY+G model with empirical base frequency values and a strict clock model with an exponential prior distribution (mean = 1.0). We ran each analyses for  $1 \times 10^9$  generations using a Yule process speciation prior, and sampled the runs every 100,000 generations. Convergence and stationarity were assessed using TRACER, and ESS above 200 were verified for all model parameters associated with the species tree except population sizes. For each subset, we discarded the first 25% of trees as burn-in and summarized the maximum clade credibility tree using TREEANNOTATOR. Each analysis was repeated multiple times from different starting seeds to verify consistent results. We then combined the posterior 25% of trees from each subset using LOGCOMBINER 1.8.2 (Drummond *et al.*, 2012) and summarized the maximum clade credibility tree using TREEANNOTATOR to create a single tree summarizing the posterior estimates of all five \*BEAST runs.

Attempts to time-calibrate each \*BEAST tree using the two calibration points in the concatenated BEAST analyses failed to reach convergence after several billion generations, an unsurprising result given the heavily parameterized models.

We therefore estimated divergence times across the \*BEAST tree of all five subsets using penalized likelihood (Sanderson, 2002) with the *chronos* function of the R package 'ape' (Sanderson, 2002; Paradis *et al.*, 2004; Paradis, 2013). We used the same two calibration points (the split between the outgroup and the *P. brevirostris* group, and the crown node of the *P. brevirostris* group), with upper and lower bounds of 14.5 and 22.5 Ma, and 10.1 and 17.0 Ma respectively.

### Ancestral range estimation

We estimated ancestral ranges using stochastic likelihood-based models of geographic range evolution implemented in the R package 'BioGeoBEARS 0.2.1' (Matzke, 2013). We executed and compared the standard dispersal-extinction-cladogenesis (DEC) model with the DEC+J model, which includes an additional parameter *j* that allows for founder-event speciation by jump dispersal (Matzke, 2014). Founder-event jump dispersal may be important in montane systems where ephemeral woodland corridors allowed dispersal among otherwise isolated mountains during cooler glacial periods (Bryson *et al.*, 2011b). For input trees, we used the maximum clade credibility tree from the concatenated BEAST analysis and the final tree summarizing the posterior estimates of all five \*BEAST runs. We removed all but one specimen in each lineage in the concatenated BEAST tree using the 'drop.tip' function in the 'ape' R package (R Development Core Team, 2014). We assigned each representative sample in the tree to the biogeographic regions spanned by the represented lineage: Sierra Madre Occidental (Occ), northern Sierra Madre Oriental (OrN), southern Sierra Madre Oriental (OrS), Trans-Mexican Volcanic Belt (TVB), Central Mexican Plateau (CMP), Sierra Madre del Sur (SMS), western coastal foothills (WCF) and eastern coastal foothills (ECF). We subdivided the Sierra Madre Oriental into two regions based on geography and phylogeographic breaks across the Cerritos-Arista/Saladan filter barrier in central San Luis Potosí (see Bryson *et al.*, 2012b and references therein). We considered the geologically complex region near the intersection of the Trans-Mexican Volcanic Belt, Sierra Madre Oriental, and Sierra Madre del Sur in southern Puebla and adjacent Veracruz a part of the Sierra Madre Oriental based on strong faunal affinities (Paniagua & Morrone, 2009). We assigned regions to *P. indubitus* West and *P. bilineatus* South based on distributional data in Feria-Ortiz *et al.* (2011). All range sizes were constrained to be composed at most of three regions (the most occupied by any extant lineage). We used likelihood-ratio tests to determine if the DEC model explained the data as well as the DEC+J model.

## RESULTS

### Genetic data

The final data matrix contained 3,282 UCE loci from all 59 skinks for a total length of 1,784,876 aligned base pairs

(bp). Locus length averaged 543 bp (range = 290–876). Each locus contained an average of 38 variable sites (range = 2–180) and 16 informative characters (range = 0–97). Data matrices were deposited in Dryad (doi:10.5061/dryad.21j0n).

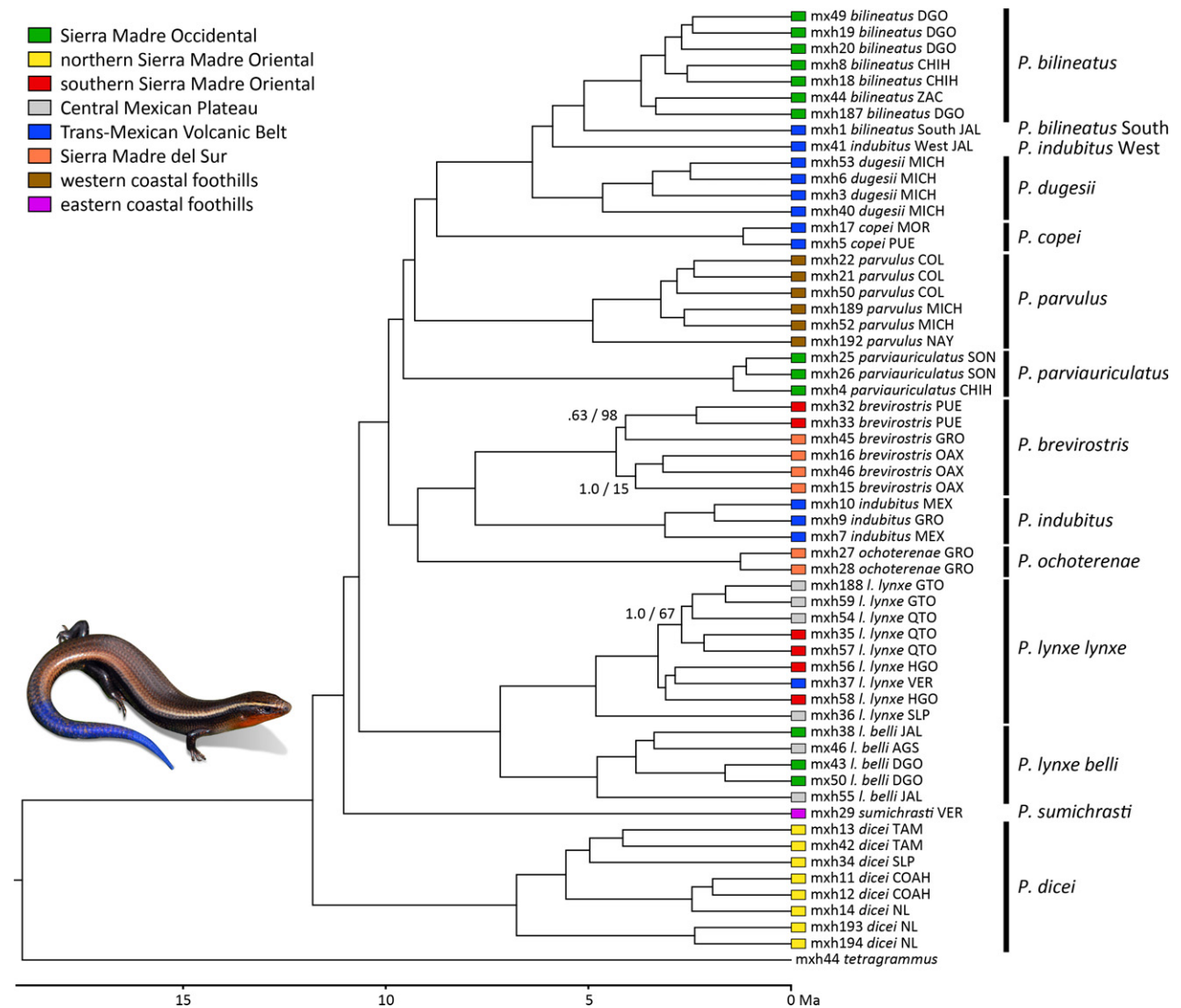
### Phylogenetic analyses and divergence date estimation

Phylogenetic analyses of the concatenated dataset converged on a strongly supported topology (Fig. 2; see Appendix S2 for the ML tree). Samples of each putative species formed well-supported clades. The earliest divergence in the group was between *P. dicei* and the rest of the species, followed by *P. sumichrasti*, and then *P. lynxe*. Samples of each of the two subspecies of *P. lynxe* formed distinct clades. The remaining lineages in the group formed two distinct geographic clades. Lineages from the southern Sierra Madre Oriental, Sierra Madre del Sur and Trans-Mexican Volcanic Belt (*P. brevirostris*, *P. indubitus* and *P. ochoterenae*) formed a clade, and lineages from the Sierra Madre Occidental (*P. bilineatus* and *P. parviauriculatus*), Trans-Mexican Volcanic Belt (*P. indubitus* West, *P. bilineatus* South, *P. dugesi* and *P. copei*), and adjacent western coastal foothills (*P. parvulus*) formed a clade. Early diversification in the group occurred over a relatively short amount of time around 9–12 Ma, based on mean estimates, and estimated species divergences all predated the Pliocene 5 Ma (Fig. 2).

Species trees estimated from the five UCE subsets slightly differed from each other and from the concatenated tree. Differences among trees were not strongly supported, however, and generally involved rearrangements of *P. copei*, *P. parvulus*, *P. parviauriculatus*, *P. sumichrasti* and *P. dicei* (see Appendix S3). The phylogeny reconstructed from all five \*BEAST runs (Fig. 3) was similar to the concatenated tree (Fig. 2) with a single exception: the phylogeny from the species trees weakly supported *P. sumichrasti* as sister to *P. l. lynxe* + *P. l. belli* rather than divergent from *P. l. lynxe* + *P. l. belli* and most of the remaining species in the group. Estimated divergence dates among lineages in both trees were similar, differing by < 2 Myr (Figs 2 & 3, see Appendix S4).

### Ancestral range reconstruction

The DEC+J model provided a significantly better fit to the data for both phylogenies (Table 1). The most probable estimated ancestral areas were similar across internal nodes of the trees (Fig. 4) but differed at several basal nodes, probably as a result of the different phylogenetic placement of *P. sumichrasti* in each tree. The earliest divergence in the group was estimated to occur around 12 Ma in a widespread common ancestor in eastern Mexico distributed across the northern Sierra Madre Oriental + eastern coastal foothills (concatenated phylogeny, Fig. 4a) or northern Sierra Madre Oriental + Trans-Mexican Volcanic Belt + Sierra Madre del



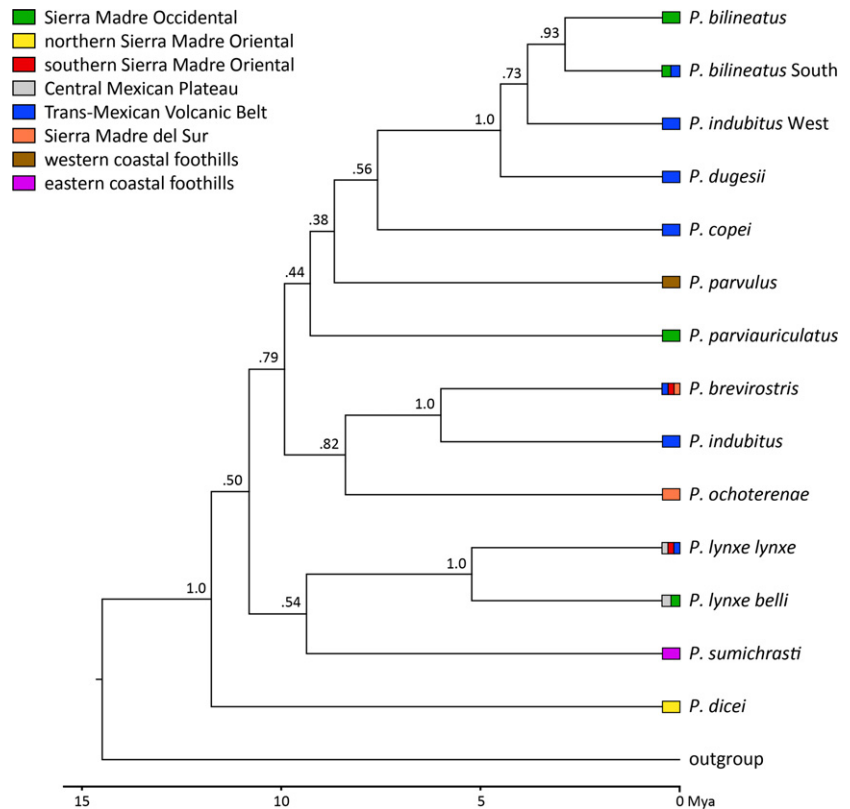
**Figure 2** Time-calibrated phylogeny of skinks in the *Plestiodon brevirostris* group inferred from concatenated UCE loci. Numbers indicate support values (Bayesian posterior probability followed by maximum-likelihood bootstrap) for nodes that received < 0.95 Bayesian posterior probability and 70% bootstrap support. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Sur (species tree phylogeny, Fig. 4b). However, the relative probability for the ancestral areas at this node was low (< 15%), and probabilities between several alternative reconstructions differed by < 5% (see Appendix S4). The next divergence approximately 1 Myr later probably occurred in an ancestor in the eastern coastal foothills (concatenated phylogeny) or Trans-Mexican Volcanic Belt (species tree). Although the relative probability for this reconstruction was higher in the concatenated phylogeny (20%), it was still low in the species tree phylogeny (10%), and probabilities between alternative reconstructions differed by < 5%. Divergences across the rest of the trees (excluding nodes with *P. sumichrasti* and *P. lynxe*) involved ancestors within the Trans-Mexican Volcanic Belt that dispersed once into the Sierra Madre del Sur and western coastal foothills of Mexico, and twice into the Sierra Madre Occidental.

## DISCUSSION

### Biogeography of the *Plestiodon brevirostris* group

The biogeography of skinks in the *P. brevirostris* group highlights the complex evolution of the Mexican highlands biodiversity hotspot. Inferred spatial and temporal patterns of divergences in the *P. brevirostris* group appear strongly correlated with the pre-Pleistocene formation of the Trans-Mexican Volcanic Belt. This mountain range is the youngest in Mexico and has played an important role in the historical diversification of many wide-ranging Mexican highland taxa (Bryson *et al.*, 2012a; Mastretta-Yanes *et al.*, 2015). Periods of uplift between 3–19 Ma created a series of high volcanic mountains and ridges that subdivided most of Mexico (Gómez-Tuena *et al.*, 2007). Based on our estimates,



**Figure 3** Time-calibrated phylogeny of skinks in the *Plestiodon brevirostris* group summarizing five species trees inferred from 40 UCE loci each. Numbers indicate posterior probability support for each node across all trees. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**Table 1** Comparison of dispersal-extinction-cladogenesis (DEC) models with (+J) and without jump dispersal for skinks in the *Plestiodon brevirostris* group. Abbreviations as follows: LnL, log-likelihood; numparams, number of parameters in each model; *d*, dispersal rate; *e*, extinction rate; *j*, founder-event speciation rate; LRT, likelihood-ratio test.

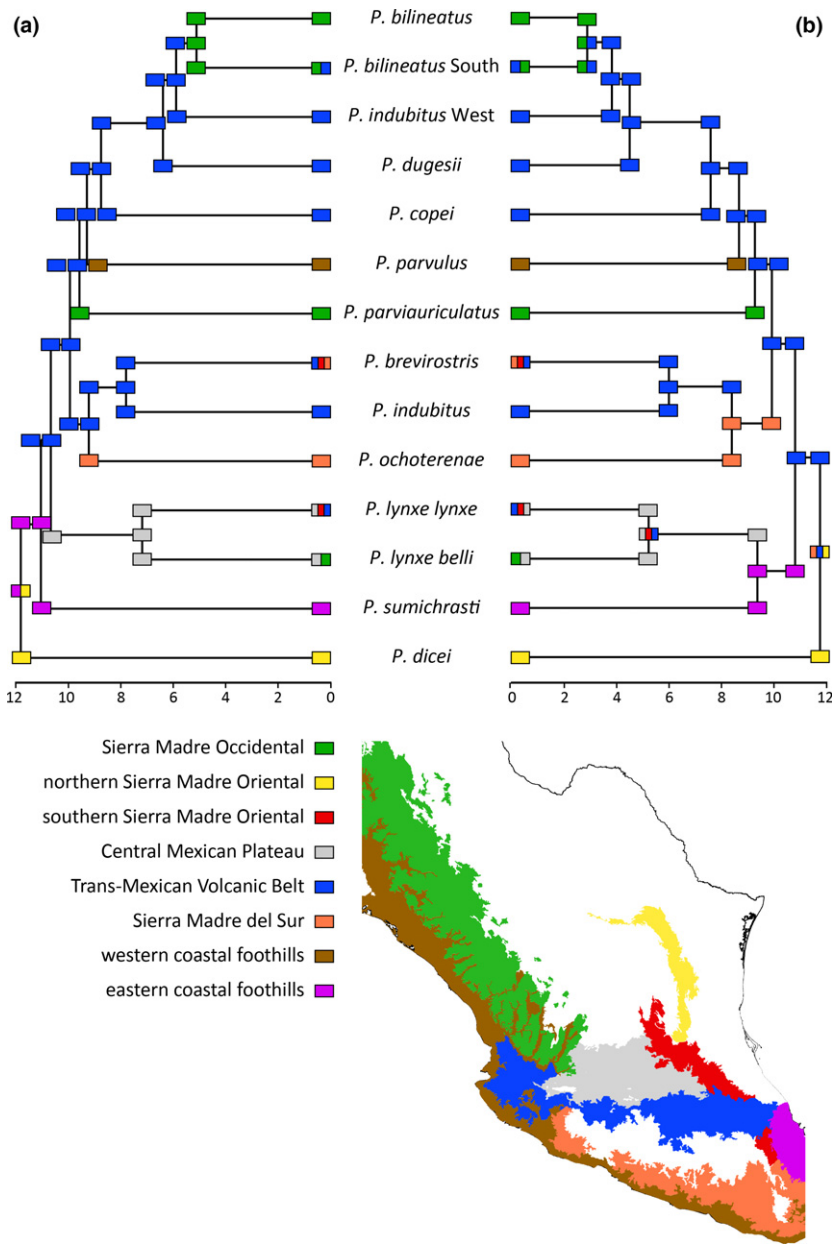
Models	LnL	Numparams	<i>d</i>	<i>e</i>	<i>j</i>	LRT <i>P</i> -value
Concatenated phylogeny						
DEC	-47.15	2	0.012	0.030	0.000	
DEC+J	-41.41	3	0.007	0.000	0.087	0.0007
Species tree						
DEC	-46.38	2	0.014	0.033	0.000	
DEC+J	-41.56	3	0.008	0.000	0.091	0.0019

divergences within the *P. brevirostris* group fall within this same time period and frequently involve ancestors estimated to have occurred in the Trans-Mexican Volcanic Belt (Fig. 2, see Appendix S4). The Trans-Mexican Volcanic Belt appears to have served both as a cradle for *in situ* diversification and as land bridge linking otherwise isolated highland regions in eastern and western Mexico, enabling the dispersal and subsequent diversification of these skinks.

The *P. brevirostris* group appears to have colonized the Mexican highlands from east to west during the Late Miocene and Pliocene. The ancestral origin of the *P. brevirostris* group is uncertain (see Appendix S4) but appears to have been in eastern Mexico. Two of the earliest splits in the group involve species on long branches that occur in the northern Sierra

Madre Oriental (*P. dicei*) and eastern coastal foothills (*P. sumichrasti*). Based on the concatenated phylogeny, the earliest ancestor in the group was probably distributed across both regions (the northern Sierra Madre Oriental and eastern coastal foothills), and at around 10 Ma, dispersed into the Trans-Mexican Volcanic Belt (Fig. 4a). This ancestor then colonized the Central Mexican Plateau. The Sierra Madre del Sur, Sierra Madre Occidental and western coastal foothills were subsequently colonized during multiple dispersal events to each region from ancestors distributed along the Trans-Mexican Volcanic Belt. Biogeographic inferences based on the species tree phylogeny are more complex (Fig. 4b). The earliest ancestor in the *P. brevirostris* group may have been more widespread, and was likely present in the northern Sierra Madre Oriental, Trans-Mexican Volcanic Belt and Sierra Madre del Sur. Estimates suggest the eastern coastal foothills were colonized around 10 Ma, probably from an ancestor in the Trans-Mexican Volcanic Belt. This ancestor in the eastern coastal foothills then colonized the Central Mexican Plateau. This biogeographic scenario – dispersal from the Trans-Mexican Volcanic Belt into the eastern coastal foothills and from there, into the Central Mexican Plateau – is a key difference between the two ancestral area reconstructions based on the concatenated and species tree phylogenies. From the Trans-Mexican Volcanic Belt, ancestors likely dispersed into the Sierra Madre del Sur, Sierra Madre Occidental and western coastal foothills during a relatively short 2-Myr period.

Skinks in the *P. brevirostris* group represent another example of a widespread montane Mexican taxon with a long history of



**Figure 4** Ancestral area estimation for skins in the *Plestiodon brevirostris* group based on the preferred DEC+J model. Ancestral areas were estimated across the (a) time-calibrated phylogeny inferred from concatenated UCE loci and (b) time-calibrated phylogeny summarizing five species trees inferred from 40 UCE loci each. Most probable ancestral range at each node shown. Corner positions represent the geographic range immediately after a cladogenetic event. See Appendix S4 for relative probabilities of all possible ancestral ranges at each node. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

pre-Pleistocene diversification associated with the primary formation of the Trans-Mexican Volcanic Belt (Bryson *et al.*, 2011a, 2012a,b; McCormack *et al.*, 2011; Bryson & Riddle, 2012; Ruiz-Sanchez & Specht, 2013). Interestingly, the specific biogeographic breaks among species in these studies are generally idiosyncratic. Additional phylogeographic studies on highland species with wide distributions across Mexico and subsequent analyses within a comparative framework are clearly needed to fully elucidate shared responses to the evolutionary processes that have contributed to the assembly of this biodiversity hotspot.

**Impacts of phylogeny on biogeographic reconstructions**

Our results clearly demonstrate the sensitivity of biogeographic reconstructions to different guide trees estimated

using different phylogenetic methods. While several biogeographic events are common in both estimates, including colonizations of the Sierra Madre Occidental and western coastal foothills from the Trans-Mexican Volcanic Belt late in the history of the group, ancestral area reconstructions at internal nodes differ. These differences are attributable to the placement of *P. sumichrasti*, which inhabits a different biogeographic region than other species in the *P. brevirostris* group. If this species split from the group shortly after the divergence of *P. dicei*, the earliest ancestor in the group was probably distributed across both the highlands of the northern Sierra Madre Oriental and the lowlands of the eastern coastal foothills (Fig. 4a). This result suggests that the earliest ancestor may have had a relatively broad ecological niche, an important characteristic that may have enabled these skinks to colonize nearly all of the mountainous regions of Mexico. Alternatively,



if *P. sumichrasti* is the sister species to *P. lynxe*, then the earliest ancestor may have been a montane species (Fig. 4b). The shift to a more generalized ecological niche may have occurred later during the evolution of the group. *Plestiodon lynxe* inhabits a variety of habitats including low-elevation mesquite-grassland on the Central Mexican Plateau (Webb, 1968), and along with *P. sumichrasti*, occupy distinctly different habitat types than other species in the *P. brevirostris* group. Both species are also the only two in the group that possess a light-coloured median dorsal stripe, suggestive of a close relationship.

It is important to note that our biogeographic interpretations are based on comparisons between a strongly supported phylogeny of the *P. brevirostris* group estimated from concatenated data (Fig. 2, see Appendix S2) and a weakly supported species tree estimated from subsets of the data (Fig. 3, see Appendix S3). Both of these types of phylogenetic approaches have been heavily debated (e.g., Edwards *et al.*, 2016; Springer & Gatesy, 2016), and researchers have strongly advocated for concatenation-based approaches (Gatesy & Springer, 2014; Springer & Gatesy, 2016) and coalescent-based species tree approaches (Edwards *et al.*, 2016; Linkem *et al.*, 2016). We assume convergence on a similar topology, albeit with weak support, indicates incomplete lineage sorting is not misleading the phylogeny (Leache & Linkem, 2015; Linkem *et al.*, 2016). We utilize our two phylogenies to demonstrate sensitivity of biogeographic reconstructions to different guide trees, but acknowledge that neither might capture the true species history of skinks in the *P. brevirostris* group. Future studies should employ different methods of phylogenetic estimation to test and refine relationships among species in the group.

### Systematics of the *Plestiodon brevirostris* group

Our results based on phylogenetic analyses of over 3,000 genomic loci shed new light on the systematics of the *P. brevirostris* group and highlight potential areas for future taxonomic research. Additional species-level diversity may be present within the group, as proposed previously (Feria-Ortiz *et al.*, 2011; Feria-Ortiz & García-Vázquez, 2012). For example, we found both putative subspecies *P. l. lynxe* and *P. l. belli* to be genetically distinct. Future studies with finer-scale sampling may find that these two subspecies deserve recognition as full species. The phylogenetic position of *P. sumichrasti* is unresolved based on our analyses and also warrants further study. Although individual species trees estimated from the five UCE subsets differed from each other (see Appendix S3), three grouped *P. sumichrasti* together with the two subspecies of *P. lynxe*, as did the phylogeny reconstructed from all five subsets (Fig. 3). This arrangement makes sense based on morphology because it groups together the only *P. brevirostris* group species that possess a light-coloured median dorsal stripe. Future work should analyse additional sequence data from *P. sumichrasti* sampled across its entire distribution to better determine the phylogenetic placement of this enigmatic species. Additional taxonomic

sampling and geographic sampling could also mitigate potential long-branch artefacts (Wiens, 2005; Xi *et al.*, 2012). Finally, we did not include *P. colimensis* and *P. nietoi* in our study. Although the phylogenetic placement of *P. colimensis* is unknown, *P. nietoi* appears to be closely related to *P. brevirostris* and *P. indubitus* from geographically adjacent regions in southeastern Mexico (Feria-Ortiz & García-Vázquez, 2012; Pavón-Vázquez, 2015). We assume the exclusion of *P. colimensis* and *P. nietoi* will have minimal impacts on our biogeographic interpretations. However, this assumption should be fully tested if samples become available in the future.

Assuming only the phylogenetic placement of *P. sumichrasti* is unresolved, our UCE phylogeny differs from previous estimates of phylogenetic relationships among species in the *P. brevirostris* group based on multilocus (Brandley *et al.*, 2011, 2012) and mtDNA (Feria-Ortiz *et al.*, 2011) data. Most notably, *P. ochoterenae* appears to be more closely related to *P. brevirostris* and *P. indubitus* than to *P. copei*, *P. dugesii* and *P. bilineatus* (Brandley *et al.*, 2011, 2012; Feria-Ortiz *et al.*, 2011), a finding more consistent with geography. Topological differences are more dramatic between our phylogeny and mtDNA-based estimates (Feria-Ortiz *et al.*, 2011), although this may be due in part to the large polytomy in the mtDNA tree. Nonetheless, strongly supported differences involving the placement of *P. parviauriculatus*, *P. lynxe*, *P. parvulus* and *P. ochoterenae* suggest caution is warranted when making phylogenetic inferences based on only mtDNA in this group of lizards.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Collection data for skinks.

**Appendix S2** Maximum likelihood phylogeny.

**Appendix S3** Individual species trees.

**Appendix S4** Ancestral areas and divergence dates.

## BIOSKETCH

**Robert W. Bryson Jr.** is interested in the origin and distribution of genetic diversity of species distributed in southwestern North America.

Author contributions: R.W.B., C.J.P.V., A.N.M.O., J.K. and J.E.M. developed the conceptual framework for the project; R.W.B. and A.N.M.O. performed fieldwork and contributed samples; R.W.B. generated the data; R.W.B. and C.W.L. analysed the data; C.J.P.V. provided the taxonomic identifications; and R.W.B. and J.E.M. led the writing.

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