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# Phylogenomics of alligator lizards elucidate diversification patterns across the Mexican Transition Zone and support the recognition of a new genus

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Genomic data continue to advance our understanding of species limits and biogeographic patterns. However, there is still no consensus regarding appropriate methods of phylogenomic analysis that make the best use of these heterogeneous data sets. In this study, we used thousands of ultraconserved element (UCE) loci from alligator lizards in the genus *Gerrhonotus* to compare and contrast species trees inferred using multiple contemporary methods and provide a time frame for biological diversification across the Mexican Transition Zone (MTZ). Concatenated maximum likelihood (ML) and Bayesian analyses provided highly congruent results, with differences limited to poorly supported nodes. Similar topologies were inferred from coalescent analyses in Bayesian Phylogenetics and Phylogeography and SVDquartets, albeit with lower support for some nodes. All divergence times fell within the Miocene, linking speciation to local Neogene vicariance and/or global cooling trends following the mid-Miocene Climatic Optimum. We detected a high level of genomic divergence for a morphologically distinct species restricted to the arid mountains of north-eastern Mexico, and erected a new genus to better reflect evolutionary history. In summary, our results further advocate leveraging the strengths and weaknesses of concatenation and coalescent methods, provide evidence for old divergences for alligator lizards, and indicate that the MTZ continues to harbour substantial unrecognized diversity.

ADDITIONAL KEYWORDS: biogeography – coalescence – concatenation – *Gerrhonotus* – phylogenomics.

## INTRODUCTION

The acquisition of genomic data from non-model species continues to fundamentally change how biologists study the evolution of biodiversity (McCormack *et al.*, 2013). These data have helped resolve long-standing phylogenetic questions pertaining to both deep (Crawford *et al.*, 2012, 2015; McCormack *et al.*, 2012; Faircloth *et al.*, 2013) and shallow (Smith *et al.*, 2014) timescales. However, phylogenomic data present new analytical challenges, often requiring a combination of traditional phylogenetic approaches

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(i.e., supermatrix) and coalescent-based methods that explicitly accommodate incomplete lineage sorting (ILS). The combination of alternative methods provides a particularly powerful framework for both species delimitation/discovery and species tree inference in recently diverged groups (Blair *et al.*, 2019). All modern methods have strengths and weaknesses, with likelihood-based coalescent methods taking full advantage of the data and estimating other relevant parameters such as population sizes and divergence times (Ogilvie *et al.*, 2017; Flouri *et al.*, 2018). However, these methods are computationally expensive which can limit their utility for handling data sets with many loci, species or individuals. Two-step summary methods (e.g., ASTRAL) are popular because of speed and relative accuracy (Mirarab *et al.*, 2014). These methods rely on accurate gene trees, which may be problematic when using short loci containing few phylogenetically informative characters (Xi *et al.*, 2015; Meiklejohn *et al.*, 2016). Methods based on site pattern frequencies such as SVDquartets are fast and do not rely on gene trees (Chifman & Kubatko, 2014). However, previous studies suggest that node support may be relatively low compared to other methods and that results may be highly sensitive to the size of the data matrix (Blair *et al.*, 2019). Finally, traditional concatenation remains useful due to speed and the ability to test species monophyly prior to taxonomic assignment, although it may be a statistically inconsistent method of species tree inference under ILS (Kubatko & Degnan, 2007).

The Mexican Transition Zone (MTZ) is defined as the biogeographical region where Neotropical and Nearctic biotas overlap (Morrone, 2010; Halffter & Morrone, 2017). The MTZ broadly encompasses the region extending from the south-western USA to Nicaragua, in which several major biogeographic barriers or zones have been documented including the Sierra Madre Occidental, Sierra Madre Oriental, Trans-Mexican Volcanic Belt, Sierra Madre del Sur, Balsas Basin and Isthmus of Tehuantepec (Mulcahy, 2000; Mulcahy *et al.*, 2006; León-Paniagua *et al.*, 2007; Navarro-Sigüenza *et al.*, 2008; Bryson *et al.*, 2011a, c, 2012a). Numerous phylogenetic and phylogeographic studies focused on Mexican taxa have documented cryptic lineages, both in lowland tropical regions (Devitt, 2006; Zarza *et al.*, 2008; Blair *et al.*, 2015; Ramírez-Reyes *et al.*, 2017) and in the highlands (McCormack *et al.*, 2008, 2011; Bryson *et al.*, 2011a, b, 2012b). Diversification of highland taxa tend to be temporally concordant with both Neogene orogenesis and Pleistocene climate change (McCormack *et al.*, 2011; Bryson *et al.*, 2011b, 2012a; Bryson & Riddle, 2012). In contrast, diversification of Pacific lowland taxa appear older (Devitt, 2006; Blair *et al.*, 2015; Ramírez-Reyes *et al.*, 2017), with divergence in some groups temporally consistent with the formation of the Mexican tropical dry forest (TDF) beginning 30-20 Mya (Becerra, 2005). However, a caveat with these conclusions is that most previous studies were based on either mtDNA only or mtDNA and a small number of nuclear genes, resulting in limited power to estimate relevant evolutionary parameters.

Alligator lizards of the genus *Gerrhonotus* have a distribution spanning much of Mexico (Good, 1994; García-Vázquez *et al.*, 2018a). There are currently nine described species and one undescribed species (García-Vázquez *et al.*, 2018b), several of which are endemic to very small geographic ranges in northern Mexico (García-Vázquez *et al.*, 2018a). Despite previous morphological (Good, 1994) and molecular analyses (Conroy *et al.*, 2005; Pyron *et al.*, 2013; García-Vázquez *et al.*, 2018a), the phylogenetic relationships among species remain incompletely resolved. In particular, the placement of most of the smooth-scaled species (i.e., *Gerrhonotus lugoi*, *Gerrhonotus lazcanoi* and *Gerrhonotus farri*) with respect to their congeners is ambiguous or unknown. In this study, we use genomic data from > 3000 ultraconserved element (UCE) loci to compare and contrast several alternative phylogenetic methods, infer the evolutionary history of *Gerrhonotus*, and provide an updated time frame for diversification throughout the MTZ. We specifically seek to determine if the genomic data are consistent with younger, Pleistocene divergence or older Neogene diversification, the latter of which may be attributed to regional vicariance or global shifts in climate (Zachos *et al.*, 2001).

## MATERIAL AND METHODS

### Taxonomic and genomic sampling

We sequenced 27 alligator lizards representing seven of the nine currently recognized species in the genus *Gerrhonotus* (García-Vázquez *et al.*, 2018a, b), as well as the putative undescribed species from western Mexico [*Gerrhonotus* sp. 'western' (García-Vázquez *et al.*, 2018a)]. For the species with large geographic distributions (*Gerrhonotus infernalis*, *Gerrhonotus liocephalus* and *Gerrhonotus ophiurus*), we included multiple specimens from across the MTZ (Fig. 1; Table 1). We sequenced three of the five smooth-scaled species (*Gerrhonotus lugoi*, *Gerrhonotus parvus* and *Gerrhonotus rhombifer*); *Gerrhonotus farri* and *Gerrhonotus lazcanoi* remain known from only single specimens for which no tissues were available. Because the phylogenetic position of several of the smooth-scaled *Gerrhonotus* remains uncertain (Conroy *et al.*, 2005; García-Vázquez *et al.*, 2018a), we also sequenced multiple individuals of the closely related anguid genera *Abronia* [both arboreal and terrestrial forms

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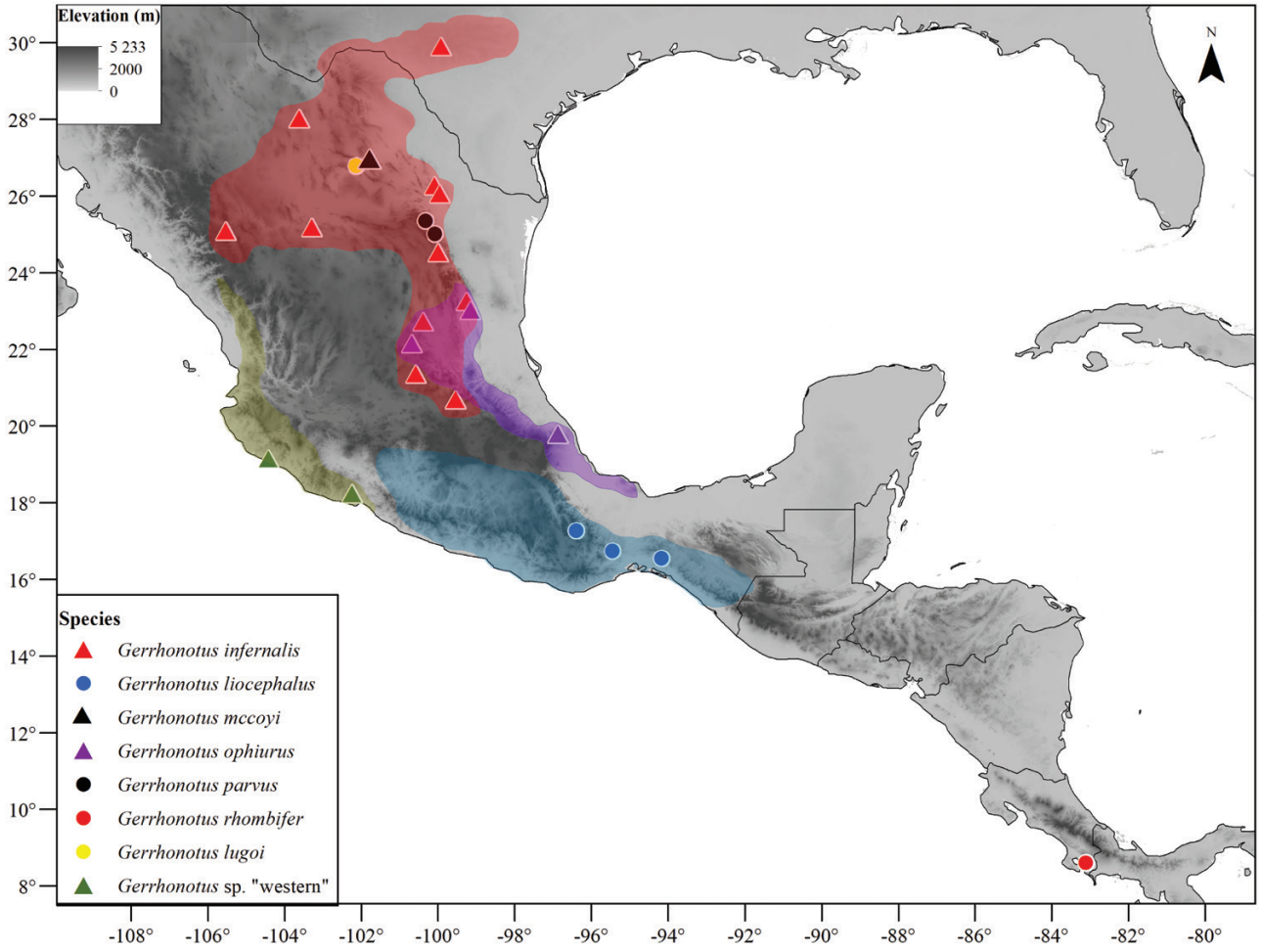


**Figure 1.** Localities of alligator lizards in the genus *Gerrhonotus* sampled for this study. The approximate geographic distributions of *G. infernalis*, *G. liocephalus*, *G. ophiurus* and *G.* sp. 'western' are shaded to illustrate geographic coverage of sampling.

(Gutiérrez-Rodríguez *et al.*, 2021)], and *Barisia*. We sequenced one *Elgaria kingii* to use as an outgroup (Pyron *et al.*, 2013).

We extracted genomic DNA from tissue samples using Qiagen DNeasy Blood & Tissue Kits (Qiagen Inc., Valencia, CA, USA). Aliquots of extracts were shipped to RAPiD Genomics (Gainsville, FL, USA) for UCE library preparation and sequencing. There, 5472 custom-designed probes (MYbaits; MYcroarray, Inc., Ann Arbor, MI, USA) were used to enrich 5060 UCE loci using standard enrichment protocols (Faircloth *et al.*, 2012). Libraries were sequenced on an Illumina HiSeq 3000 (100 paired-end) at the University of Florida Interdisciplinary Center for Biotechnology Research Facility. Data quality filtering and assembly followed previous studies (Bryson *et al.*, 2017). A locus was retained in the final assembly if it was represented by > 75% of individuals.

### Concatenated analysis

We used ExaBayes v.1.5 (Aberer *et al.*, 2014) to infer a Bayesian phylogeny of the concatenated data. The analysis used all 3157 loci and 1 904 599 bp (see Results). ExaBayes is similar to the widely used MrBayes (Ronquist *et al.*, 2012), but is explicitly designed to handle genome-scale data sets due to the high flexibility for parallelization. We implemented four independent runs to determine if individual chains were trapped in local optima. Each chain was run for 1 million generations using default priors for all parameters. Convergence of runs was assessed through the average standard deviation of split frequencies (ASDSF; target < 5%) and through visualization of trace plots and effective sample size (ESS) values (target > 200) in Tracer v.1.6.0 (Rambaut *et al.*, 2014). Upon no indications of lack of convergence, an extended majority rule (MRE) consensus tree

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**Table 1.** Sampling information for all individuals of *Gerrhonotus* and related anguids included in this study.

| Sample number | Species | Tissue number | Locality |
|---|---|---|---|
| *G. rhombifer* MX246 | *Gerrhonotus rhombifer* | UTA uncat | COSTA RICA |
| *G. infernalis* MX134 | *Gerrhonotus infernalis* | PLM 203 | TAMAULIPAS: Reserva el Cielo |
| MXH126GinfNL | *Gerrhonotus infernalis* | JJW 393 | NUEVO LEÓN: La Poza |
| MXH130GinfCOAH | *Gerrhonotus mccoyi* | UOGV 1438 | COAHUILA: Poza Churince, Cuatro Cienegas |
| MXH140GinfNL | *Gerrhonotus infernalis* | RWB 2 | NUEVO LEÓN: 3.5 miles S La Escondida |
| MXH216GinfTX | *Gerrhonotus infernalis* | TJL 2350 | TEXAS: Crockett County |
| *G. infernalis* MX133 | *Gerrhonotus infernalis* | FMQ 3046 | QUERÉTARO: Sierra Gorda |
| *G. infernalis* MX252 | *Gerrhonotus infernalis* | JAC 29285 | DURANGO: Highway 36 W Santiago Papasquiaro |
| *G. infernalis* MX223 | *Gerrhonotus infernalis* | UOGV 1871 | QUERÉTARO: Sierra Gorda |
| MXH136GinfCOAH | *Gerrhonotus infernalis* | RWB 07407 | COAHUILA: Sierra la Concordia |
| MXH139GinfNL | *Gerrhonotus infernalis* | RWB 3 | NUEVO LEÓN: 6.8 miles S Pablillo |
| MXH209GinfCOAH | *Gerrhonotus infernalis* | UOGV 1393 | COAHUILA: Sierra de Jimulco |
| MXH219GlioSLP | *Gerrhonotus infernalis* | RWB 06239 | SAN LUIS POTOSÍ: Las Lagunas |
| MXH212GlioOAX | *Gerrhonotus liocephalus* | RWB 07105 | OAXACA: Ixtlán de Juarez |
| MXH214GlioCHIA | *Gerrhonotus liocephalus* | ANMO 3219 | OAXACA: Cerro Baul |
| MXH220GlioOAX | *Gerrhonotus liocephalus* | JAC 23140 | OAXACA: Mixe, Sta. Maria Guienagati |
| *G. lugoi* MX206 | *Gerrhonotus lugoi* | UANL uncat | COAHUILA: Cuatro Cienegas |
| MXH132GlugCOAH | *Gerrhonotus lugoi* | UOGV 2356 | COAHUILA: Nueva Atalaya, Cuatro Cienegas |
| MXH221GlugCOAH | *Gerrhonotus lugoi* | AMH 345 | COAHUILA: Nueva Atalaya, Cuatro Cienegas |
| MXH127GophSLP | *Gerrhonotus ophiurus* | UANL 6783 | SAN LUIS POTOSÍ: 15 miles E de San Francisco |
| MXH138GophVER | *Gerrhonotus ophiurus* | ANMO 2186 | VERACRUZ: Salvador Diaz Miron, Misantla |
| MXH217GophTAM | *Gerrhonotus ophiurus* | UANL 44 | TAMAULIPAS: Gomez Farias |
| MXH129GparNL | *Gerrhonotus parvus* | UANL 6221 | NUEVO LEÓN: Cañon San Isidro |
| MXH184GparNL | *Gerrhonotus parvus* | UANL 5884 | NUEVO LEÓN: Cañon San Isidro |
| MXH230GparNL | *Gerrhonotus parvus* | UANL 6220 | NUEVO LEÓN: Los Rayones |
| MXH131GlioMICH | *Gerrhonotus* sp. 'western' | ANMO 1097 | MICHOACÁN: Taguazal |
| MXH213GlioCOL | *Gerrhonotus* sp. 'western' | ANMO 1167 | COLIMA: Manzanillo, 2.4 km E La Central |
| MXH226Elki | *Elgaria kingii* | UANL 5700 | CHIHUAHUA: Sierra del Nido |
| MXH232BruMEX | *Barisia rudicollis* | MZFC 12541 | MÉXICO: Valle de Bravo |
| MX339BleCHIH | *Barisia levicollis* | RWB 08110 | CHIHUAHUA: El Zorillo |
| MXH225Abgr | *Abronia graminea* | UANL 6064 | VERACRUZ: Puerto del Aire |
| MXH210Abta | *Abronia taeniata* | ISZ 200 | PUEBLA: Tlatlauquitepec |
| MXH211Mega | *Abronia gadovii* | UOGV 826 | GUERRERO |
| MXH250Mevi | *Abronia viridiflava* | JAC 21525 | OAXACA: Sierra Mixe, W Totontepec |

was generated using the *consense* script (from the ExaBayes package), after a burn-in of 25% of samples. The unrooted consensus tree was subsequently rooted with *E. kingii*. All ExaBayes runs used a total of 64 cores to increase the efficiency of the analysis. We implemented unpartitioned ExaBayes analyses only, as previous partitioned analyses on similar data indicated issues with the estimation of branch lengths (Blair *et al.*, 2019).

We used IQ-TREE v.2.0 (Minh *et al.*, 2020) to infer a maximum likelihood (ML) phylogeny of the full concatenated data. Multiple analyses were performed to assess concordance. We first specified an unpartitioned analysis of all 34 individuals. Because of the size of the alignment, we specified a GTR+R10 substitution model, which relaxes the assumption of gamma distributed rate variation. Support for nodes was determined using both the ultrafast bootstrap (Hoang *et al.*, 2018) and SH-aLRT (Guindon *et al.*, 2010), both with 10 000 replicates. SH-aLRT values > 80% and ultrafast bootstrap values > 95% were indicative of strong support (Guindon *et al.*, 2010; Hoang *et al.*, 2018). Ten independent runs were performed to help minimize the probability of tree searches getting trapped in local optima. Trees were rooted using *E. kingii* (Pyron *et al.*, 2013). We ran analyses with and without sample MX206 to determine the effect of including this individual on the topology. Results indicated that the branch length leading to this sample might be overestimated (although the topology was unaffected), so we took a conservative approach and excluded this sample for all remaining analyses.

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We also ran a third analysis under a GTR+I+G model (ten runs) and used BIC to compare these results to those generated under GTR+R10.

We also performed a partitioned analysis (Chernomor *et al.*, 2016) in IQ-TREE to assess concordance with the unpartitioned analysis. Initial data partitions were defined based on each UCE locus. We then used the *rclusterf 10* command in ModelFinder/IQ-TREE (Kalyaanamoorthy *et al.*, 2017; Lanfear *et al.*, 2017) to determine the best partition strategy for the data, with subsequent tree searches performed on the best partition scheme (i.e., MFP+MERGE command). The MFP+MERGE command is particularly powerful because it simultaneously searches for the best partition scheme and the best model for each partition with a single call to the program. Support for nodes was again determined through ultrafast bootstraps and SH-aLRT (10 000 replicates each). All IQ-TREE analyses utilized up to 16 threads to increase computational efficiency. The best ML tree was subsequently rooted with *E. kingii*.

### Coalescent analysis

We performed two sets of coalescent analyses to assess congruence with the concatenated ML and Bayesian analyses. We first used SVDquartets (Chifman & Kubatko, 2014, 2015) in PAUP* v.4.0a166 (Swofford, 2003) to infer a species tree. We assigned samples to species based on current taxonomy (García-Vázquez *et al.*, 2018a). All quartets were evaluated, and a full species tree was constructed using QFM (Reaz *et al.*, 2014). Support for nodes was assessed through 100 nonparametric bootstrap replicates.

Second, we performed species tree analyses using Bayesian Phylogenetics and Phylogeography (BPP) v.4.1.3 (Yang, 2015; Rannala & Yang, 2017; Flouri *et al.*, 2018). BPP uses the multispecies coalescent model (MSC) in a Bayesian framework to estimate the posterior probabilities of alternative species tree and/or species delimitation hypotheses. Due to the computational requirements of BPP, analyses were restricted to 500 random loci. We used Aliview v.1.17.1 (Larsson, 2014) to remove samples consisting of all missing data from each alignment. Three independent BPP runs were performed to monitor convergence. We used the SVDquartets species tree as the starting tree for all runs, and specified diffuse inverse gamma priors for theta (3, 0.004) and tau (3, 0.05). Each run used a burn-in of 50 000 followed by 100 000 samples with a sampling frequency of 5. The BPP species tree was visualized and manipulated in IcyTree (Vaughan, 2017). We did not utilize summary-based species tree methods (e.g., ASTRAL; (Mirarab *et al.*, 2014)) due to the few phylogenetically informative sites per locus, which often translates to high gene tree error and subsequently poor species trees (Xi *et al.*, 2015; Molloy & Warnow, 2018; but see Chou *et al.*, 2015 for exceptions).

### Divergence time estimation

Divergence times between lineages were estimated using MCMCTREE in PAML v.4.9j (Yang, 2007). Due to the large size of the data set, we used the approximate likelihood method (dos Reis & Yang, 2011), which has performed well with other UCE data (Blair *et al.*, 2019). We pruned the concatenated alignment to one tip per species by selecting individuals with the least amount of missing data. MCMCTREE estimates divergence times on a user-specified tree. Our analyses utilized the ExaBayes topology, and we recognize that results would change slightly if a different topology was specified. We calibrated the root node (i.e. crown Gerrhonotinae) using the oldest fossil information for *Elgaria*, which is dated at approximately 17.5–16.7 Mya (Scarpetta, 2018). As it is possible that the divergence of *Elgaria* from the remaining gerrhonotines is older (Leavitt *et al.*, 2017), we specified soft bounds between 30–17 Mya on the root node. All MCMCTREE analyses used an autocorrelated rates model. We specified gamma priors for kappa (6,2) and alpha (1,1). We used a gamma rate prior of (2,2000), which is diffuse yet appropriate for UCE data. We tested the effect of two different sigma priors [(1,1000) and (1,100)], which controls the amount of rate heterogeneity among branches. For the birth-death parameters we used 0.01, 0.01, 0.1, which creates a uniform prior for node ages. Each run used a burn-in of 4 million iterations, followed by a total of 20 000 samples drawn every 2000 generations. Convergence was assessed both by visualizing ESS values in Tracer (target > 200) and by comparing posterior estimates of node times among runs. We also ran the program without the sequence data (usedata = 0) to compare prior vs. posterior estimates. Time trees were visualized using MCMCtreeR (Puttick, 2019).

## RESULTS

### Concatenated analysis

We successfully generated a total of 3157 UCE loci from 34 samples, representing most species of *Gerrhonotus* and representatives from related genera. One sample (*G. lugoi* MX206) was removed from all analyses due to excessive missing data (> 95%), leaving a total of 33 individuals. The concatenated alignment contained 1 904 599 bp with 185 859 distinct site patterns and 46 429 parsimony informative sites. The proportion of gaps/ambiguous characters per taxon (excluding sample MX206) ranged from 4.06% to 93.95%. BIC favoured a

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GTR+R10 model over GTR+I+G for the unpartitioned analysis (BIC of GTR+R10 = 7110976.7490; BIC of GTR+I+G = 7120146.4229; BIC difference = 9169.6739).

All four independent ExaBayes runs converged to similar posterior distributions. After 1 million generations, the ASDSF was < 1% and ESS values for all parameters were > 200. The MRE consensus Bayesian tree was strongly supported, with virtually all nodes receiving full support (Fig. 2). The genus *Gerrhonotus* was not monophyletic due to the early branching of *G. lugoi*. The three smooth-scaled species (*G. lugoi*, *G. parvus* and *G. rhombifer*) did not form a clade. The recently described *G. mccoyi* was nested within a clade of *G. infernalis*, which was strongly supported. These two species were sister to *G. ophiurus*, all of which were sister to *G. liocephalus*. *Gerrhonotus* (formerly *Coloptychon*) *rhombifer* was placed as an independent lineage sister to *G. liocephalus*+*G. ophiurus*+*G. infernalis*/*mccoyi*. Two western samples from Colima and Michoacán (currently allied to *G. liocephalus*) rooted the base of this clade. The smooth-scaled species *G. parvus* and *G. lugoi* were each monophyletic with strong support. The two *Barisia* species formed a strongly supported clade, as did the four *Abronia* species. The terrestrial *Abronia* species *Abronia viridiflava* was more closely related to the arboreal *Abronia* species *Abronia taeniata* and *Abronia graminea* than to the other terrestrial species *Abronia gadovii*.

The ML analysis also provided strong support for most nodes (Supporting Information, Fig. S1). The branch leading to *G. lugoi* was exceptionally long relative to other branches in the tree, in contrast to the short branch which connected *G. lugoi* to all remaining *Gerrhonotus*; nodal support for this relationship, however, was weak. For the partitioned ML analysis, IQ-TREE/ModelFinder suggested a total of 53 partitions. The partitioned topology was virtually identical to the unpartitioned tree, the only difference being the position of *G. infernalis* MX134. However, support for placement of this sample was ambiguous in both analyses.

### Coalescent analysis

The SVDquartets species tree was similar to the concatenated Bayesian tree, with *G. lugoi* placed as sister to the remaining anguid species (Fig. 3). Similar to the concatenated analyses, terrestrial *Abronia* was not monophyletic. However, in the SVDquartets tree, *A. gadovii* (not *A. viridiflava*) was sister to arboreal *Abronia*. Most nodes in the species tree were supported (bootstrap > 70). However, there was uncertainty in the placement of *G. liocephalus*, *Gerrhonotus* sp. 'western' and *G. rhombifer*. The BPP species tree was topologically identical to the ML trees (Supporting Information, Fig. S2). Most nodes had strong support

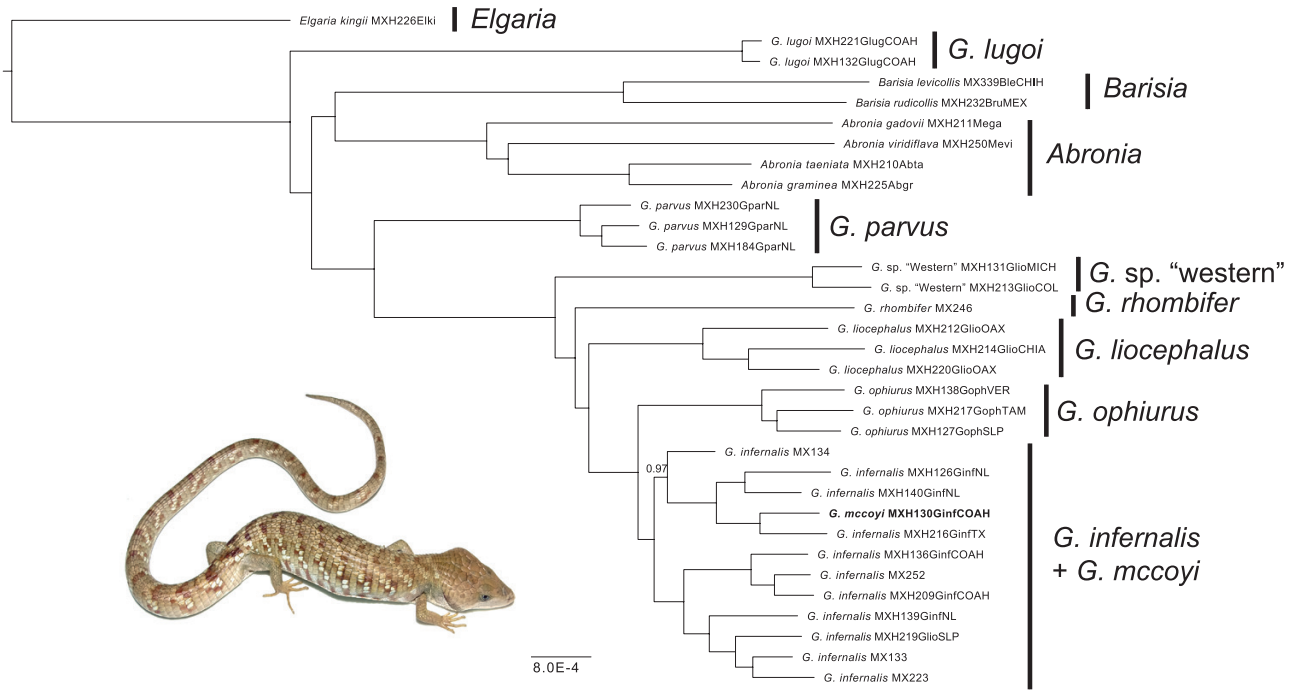


**Figure 2.** Unpartitioned Bayesian extended majority rule (MRE) consensus tree inferred by ExaBayes from the concatenated matrix of 3157 UCE loci (1 904 599 bp). All nodes have full posterior probability, except where indicated. Scale bar represents substitutions per site.

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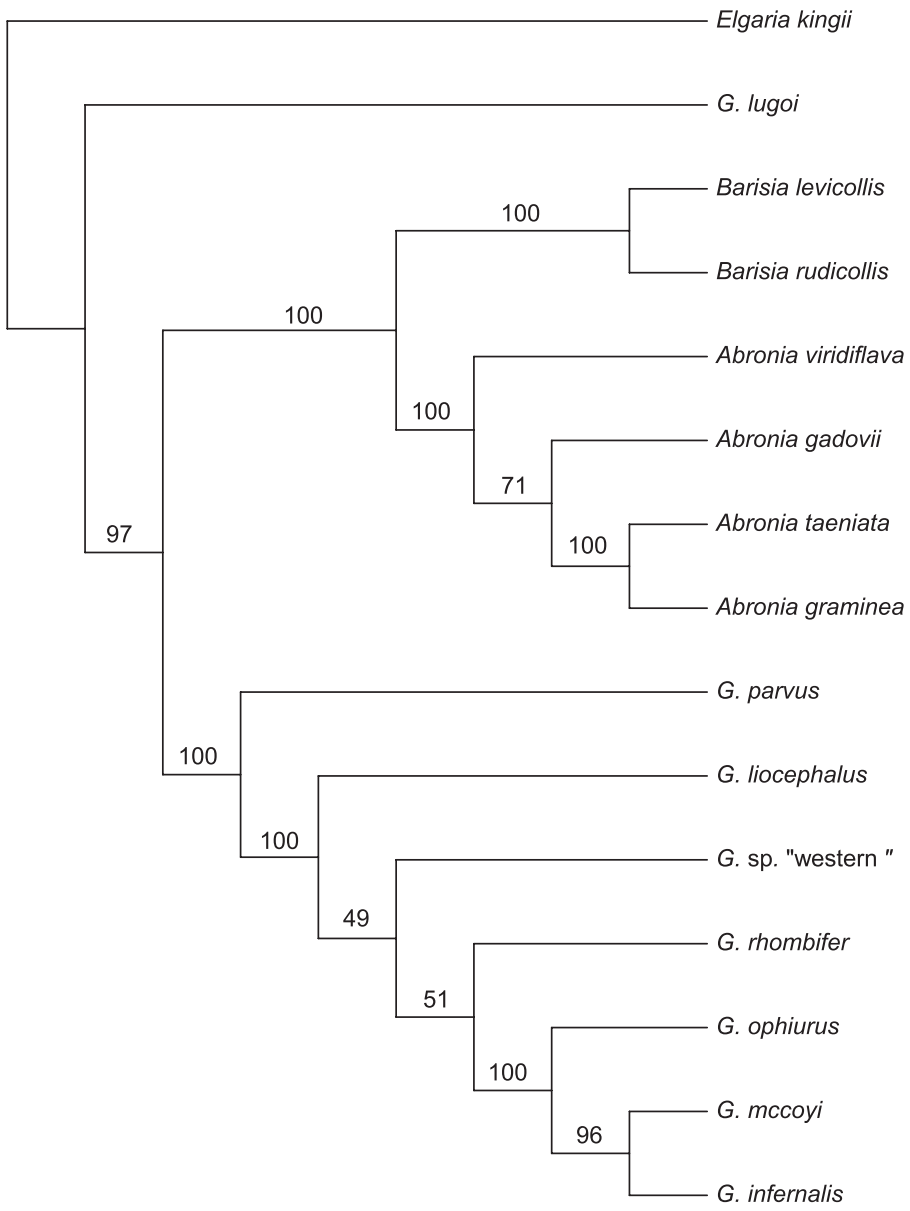


**Figure 3.** SVDquartets species tree of *Gerrhonotus* and related anguids. Numbers at nodes represent bootstrap support values mapped from a bootstrap consensus tree.

(> 0.95), with uncertainty restricted to the placement of *G. liocephalus*, *G. lugoi* and *A. viridiflava*.

### Divergence time estimation

All MCMCTREE runs indicated convergence based on both ESS values and convergence plots (Supporting Information, Fig. S3). The choice of prior for sigma had little influence on posterior estimates. Comparisons of prior and posterior densities indicated that node priors were reasonable, and that the data were informative for estimation of node ages. Nearly all estimated mean divergence times fell within the Miocene (Fig. 4). The divergence of *G. lugoi* from the remaining species occurred during the Oligocene-Miocene transition. No divergences were detected during the Quaternary.

## DISCUSSION

### Phylogenomic inference

The field of phylogenetics is now deeply immersed in the genomics era. Because of the rapid development of new methods to accommodate the large and

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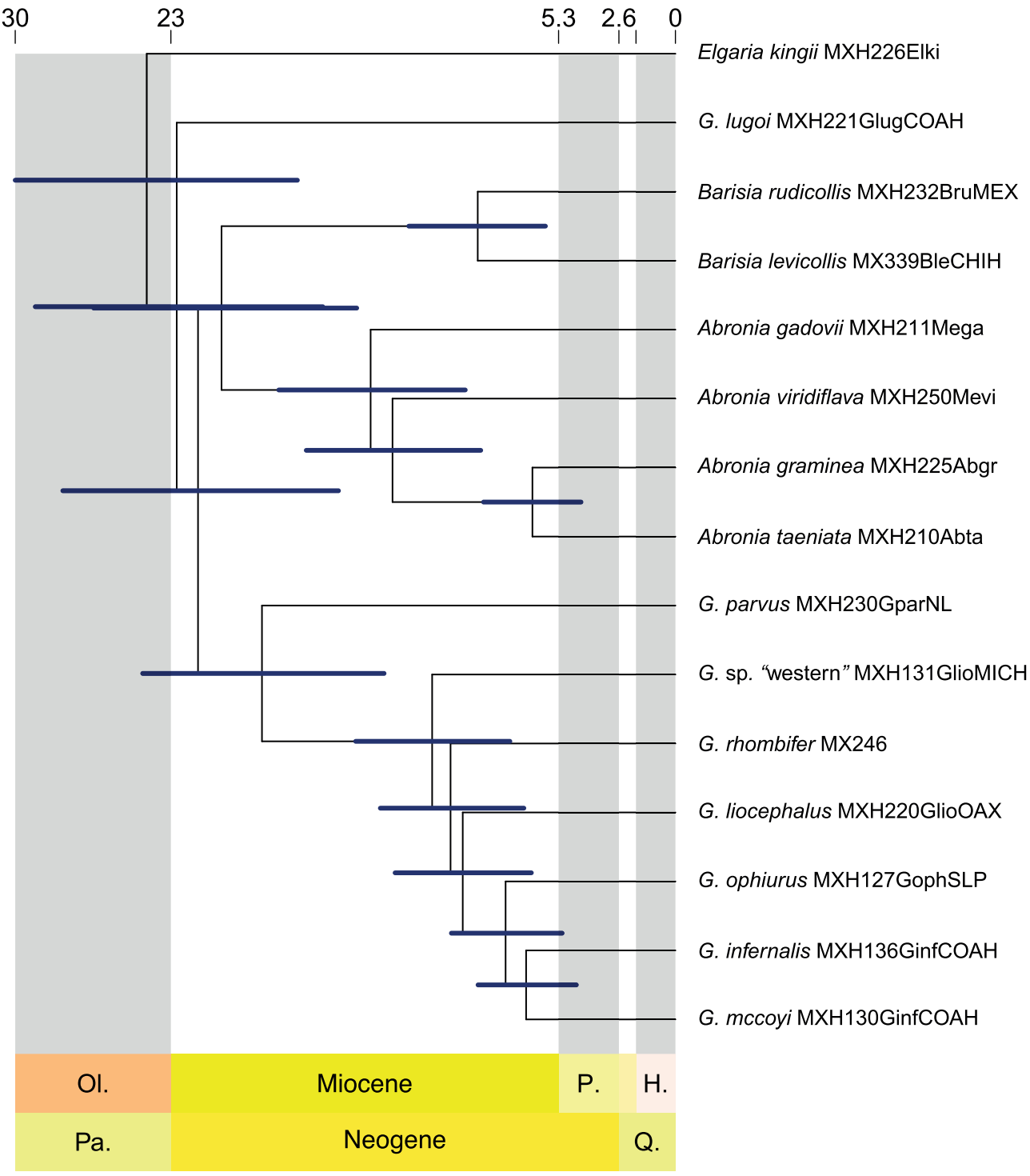


**Figure 4.** Divergence times among gerrhonotine lizards sampled for this study. Horizontal bars at nodes represent 95% highest posterior density (HPD) values. Numbers on top of tree indicate millions of years. H. = Holocene; P. = Pliocene; Ol. = Oligocene; Q. = Quaternary; Pa. = Paleogene.

heterogeneous data being generated, several studies have quantified the performance of both concatenation and newer coalescent methods. In general, it appears that concatenation often performs well for estimating species tree topology, even in instances of low-to-moderate ILS (Mirarab *et al.*,



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2014; Chou *et al.*, 2015; Molloy & Warnow, 2018). These results are encouraging, in part, because concatenation is generally more computationally feasible vs. likelihood-based coalescent methods. Fully Bayesian coalescent methods like BPP are powerful in that they estimate species trees directly from the sequence data (Flouri *et al.*, 2018). However, these methods are computationally expensive and can experience mixing problems in large data sets (e.g., many loci, individuals or species). Gene tree-based coalescent methods (summary methods) like ASTRAL can perform well in cases of high ILS (Mirarab *et al.*, 2014), but the reliance on accurate gene trees may preclude their widespread use on commonly used data such as UCEs and RADseq (Molloy & Warnow, 2018). A primary reason for this limitation is the relatively small number of phylogenetically informative characters in a given locus. RADseq loci are also relatively short (~100–300 bp) and can contain a large quantity of missing data, which can further negatively influence gene tree estimation (Eaton & Ree, 2013). SVDquartets estimates species trees using site pattern frequencies from SNP or multilocus sequence data, does not rely on gene trees and is relatively fast (although bootstrapping can be time consuming). The method has been shown to perform well in simulation (Chou *et al.*, 2015), even in instances of gene flow between sister species (Long & Kubatko, 2018). However, previous analyses of UCE data suggest that the method may be highly sensitive to the size of the concatenated matrix (Blair *et al.*, 2019).

Our concatenation and coalescent analyses of anguid lizards provide several interesting findings. First, there are minor topological differences between the concatenated Bayesian and ML analyses, particularly with respect to the placement of *G. lugoi*. With BI, this species is strongly supported as sister to all gerrhonotine taxa, consistent with some of our coalescent analyses (e.g., SVDquartets), whereas with ML, *G. lugoi* is weakly supported as sister to *Gerrhonotus*, a relationship also inferred with weak support in some coalescent analyses (e.g., BPP).

The alternative topologies recovered in this study highlight the fact that genomic data themselves are not necessarily a panacea for evolutionary inference, and that nuances of the data can lead to meaningful differences in interpretations. Our results also suggest that with real genomic data sets, it may be useful to utilize multiple methods of concatenation instead of relying exclusively on rapid ML methods, as is commonly done. The strong support for nearly every node in our Bayesian tree, combined with the results from previous studies (Blair *et al.*, 2019), suggest that long genomic alignments can lead to fully supported topologies with MCMC techniques. Additional studies should examine this phenomenon more closely using both simulated and empirical data to determine the relative accuracy of the support. Our results are also similar to those in previous studies that find lower support values in trees estimated using the SVDquartets method vs. other techniques such as concatenation, BPP and ASTRAL (Leaché *et al.*, 2015; Blair *et al.*, 2019). This method of phylogenomic inference is relatively new and underexplored, although some data indicate that the method is robust to moderate levels of gene flow (Long & Kubatko, 2018). Finally, the identical BPP and ML topologies inferred in our study provide further evidence that (1) concatenated ML should remain a staple in the phylogeneticist's toolbox, even in cases where ILS is likely; (2) data subsampling remains a viable option for full likelihood-based coalescent methods; and (3) the concatenation-coalescence argument is likely more complex than currently appreciated. The slightly divergent topologies recovered in our study stress the importance of utilizing multiple methods of phylogenomic inference. These results, combined with taxonomic expertise, can help researchers determine the 'preferred' topology for subsequent hypothesis testing. Despite slight discrepancies among some of our analyses, results are highly congruent with other phylogenies using only three genes (García-Vázquez *et al.*, 2018a).

### Biogeography

Several hypotheses have been proposed to explain the timing of biological diversification throughout the MTZ. Pleistocene climate change is often invoked as a catalyst when divergence times of lineages fall within this time frame (Bryson *et al.*, 2011c, b, 2012b; Leaché *et al.*, 2013). Conversely, older geological processes such as the formation and uplift of Mexico's major mountain ranges and the associated climatic and ecological changes (Becerra, 2005; Ferrusquía-Villafranca & González-Guzmán, 2005; Gómez-Tuena *et al.*, 2007; Blair *et al.*, 2015) may explain divergences occurring in the Neogene. All estimated divergence times among gerrhonotine lizards in our analysis fall within the Miocene, supporting the hypothesis of older geological processes shaping diversification patterns at the species level. These results are similar to a previous study of *Gerrhonotus* based on mtDNA and two nuclear loci (García-Vázquez *et al.*, 2018a). Thus, genomic data appear to agree with earlier studies that highlight the relative importance of Neogene processes vs. Quaternary climate change shaping diversification patterns in lineages throughout the MTZ [Bryson *et al.* (2012b, c); Bryson & Riddle (2012); see Myers

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*et al.* (2019) for exceptions]. In addition to regional Neogene vicariance and associated climatic changes resulting from uplift of the Trans-Mexican Volcanic Belt (Gómez-Tuena *et al.*, 2007), a periodic global warming/cooling cycle during the Oligo-Miocene may have also facilitated range expansions and subsequent population isolation, leading to speciation (Zachos *et al.*, 2001). More specifically, our results cannot refute the hypothesis that global warming during the Mid-Miocene Climatic Optimum was correlated with speciation patterns in gerrhonotines. In sum, our study demonstrates how genomic data can help elucidate the history of diversification in biologically rich communities while simultaneously uncovering deep, cryptic lineages that warrant conservation. Our results also suggest caution when interpreting phylogenomic results from a limited number of analyses.

## TAXONOMY

Results from our study are consistent with previous research (Castiglia *et al.*, 2010; García-Vázquez *et al.*, 2018a) that suggests the taxonomy of *Gerrhonotus* is in need of revision. Although we detect some phylogenetic incongruence, all our results suggest that *G. lugoi* is a deeply divergent lineage with origins in the Late Oligocene-Early Miocene. Further, all of our results indicate that the smooth-scaled species do not form a clade, similar to other studies (García-Vázquez *et al.*, 2018a). Our results also provide genomic evidence that *Gerrhonotus* in western Mexico likely represents an undescribed species, as previously posited (Castiglia *et al.*, 2010). The recently described *G. mccoyi* is nested within a clade of *G. infernalis*, consistent with results of a previous study (García-Vázquez *et al.*, 2018a). Despite morphological and ecological differences separating these two species (García-Vázquez *et al.*, 2018b), even genomic data appear to be insufficient to disentangle this probable case of incipient speciation or secondary contact. Our analyses detect relatively deep lineages within *G. infernalis*, corroborating other recent evidence based primarily on mtDNA data (García-Vázquez *et al.*, 2018a). These results support the hypothesis that additional undescribed species may be present in the clade. A thorough phylogeographic study on *G. infernalis* (including *G. mccoyi*) may help clarify the evolutionary history of these taxa, and thus we refrain from making taxonomic changes until more comprehensive sampling can be performed.

The inferred phylogenetic placement and ancient origin of *G. lugoi*, coupled with unique morphological features, provide strong evidence to suggest this taxon should be placed in a new genus to better reflect its evolutionary distinctiveness. We do so below, and provide additional discussion on other smooth-scaled gerrhonotines in the Appendix.

## TAXONOMIC ACCOUNT

*DESERTUM* GARCÍA-VÁZQUEZ, NIETO-MONTES DE OCA & BRYSON JR **GEN. NOV.**

*Type species: Gerrhonotus lugoi* McCoy, 1970.

*ZooBankID:* urn:lsid:zoobank.org:act:B026BBEA-A563-4601-8AA6-3F0D7ECC1F8C.

*Diagnosis and definition:* A small-sized member of the subfamily Gerrhonotinae with postrostral scale single or absent; anterior internasal and frontonasal scales present; supranasal scales separated from postnasal scales and from each other; cantholoreal scale absent; superciliary scales six; primary temporal scales five; subocular scales three; supralabial scales 14–15; dorsal scales smooth; nuchal scale rows 10; longitudinal dorsal scale rows 18–20; transverse dorsal scale rows 56; longitudinal ventral scale rows 14–15; scales on the trailing edges of the limbs granular; and subgranular scales on the leading edges of the shanks absent.

*Comparisons: Desertum* gen. nov. can be distinguished from all other members of Gerrhonotinae, except for some members of *Gerrhonotus* (*G. farri*, *G. parvus* and *G. rhombifer*), by having smooth dorsal scales (dorsal scales keeled in all members of *Abronia*, *Barisia* and *Elgaria*, and in *G. infernalis*, *G. liocephalus*, *G. mccoyi*, *G. ophiurus* and the undescribed species of *Gerrhonotus* from western Mexico). In addition, it can be distinguished from *Elgaria* by the absence of a cantholoreal scale and the presence of anterior internasal scales and granular scales on the trailing edges of the limbs; from *Barisia*, by having a frontonasal scale, more superciliary scales (6–6 vs. 1–3), and supranasal and postnasal scales separated from each other; from terrestrial *Abronia* (formerly *Mesaspis*), by the absence of subgranular scales on the leading edges of the shanks and the presence of more longitudinal ventral scale rows (14–15 vs. 8); and from arboreal *Abronia* by having more nuchal scale rows (10 vs. 6–8) and transverse dorsal scale rows (56 vs. < 40).

*Desertum* gen. nov. may be distinguished from the species of *Gerrhonotus* with smooth dorsal scales as follows: from *G. parvus*, by the absence of a cantholoreal scale and the presence of anterior internasal scales, supranasal scales separated from each other, and more supralabial scales (14–15 vs. 12–13); from *G. farri*, by having more longitudinal dorsal scale rows (18–20 vs. 14), longitudinal ventral scale rows (14–15 vs. 12), subocular scales (3 vs. 2) and primary temporal scales (5 vs. 4); and from *G. rhombifer*, by having fewer

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postrostral scales (0-1 vs. 2) and supranasal scales separated from each other. *Desertum* gen. nov. also has more supralabial scales than any of these species (14–15 vs. 12–13).

*Content: Desertum lugoi* (McCoy, 1970); *D. lazcanoi* (Banda-Leal *et al.*, 2017).

*Etymology:* The generic name comes from the Latin noun '*desertum*', in the nominative singular neuter, meaning 'desert, wilderness, or unfrequented places', in reference to the remote arid habitats inhabited by the species of the genus.

*Distribution and habitat:* This genus is endemic to Mexico, and it is distributed in rocky xerophilic shrubland of the arid mountainous regions of central and southern Coahuila into adjacent Nuevo León at elevations > 730 m a.s.l.

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## DATA AVAILABILITY

Alignments, phylogenetic trees and raw data are available from the Dryad digital repository (Blair *et al.*, 2021).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Unpartitioned maximum likelihood (ML) phylogeny of *Gerrhonotus* and related anguids inferred from the concatenated matrix of 3157 UCE loci (1 904 599 bp) under a GTR+R10 model. Values at nodes represent SH-aLRT/ultrafast bootstrap support (10 000 replicates each).

**Figure S2.** BPP species tree of *Gerrhonotus* and related anguids inferred using 500 UCE loci. Values at nodes represent posterior probability values.

**Figure S3.** Convergence plots from MCMCTREE analyses. Sigma_100 represents posterior mean divergence times estimated from independent runs when using a gamma prior of (1,100) for sigma. Sigma_1000 represents posterior mean divergence times estimated from independent runs when using a gamma prior of (1,1000) for sigma. Values on axes represent millions of years.

## APPENDIX

Only five species of Gerrhonotinae have smooth dorsal scales, three of which are now assigned to the genus *Gerrhonotus*: *G. rhombifer*, *G. parvus* and *G. farri*. The two additional species with smooth dorsal scales are now placed in the genus *Desertum* gen. nov. (*D. lugoi* and *D. lazcanoi*). The degree of keeling of the dorsal scales has long been recognized as an important character to distinguish among species and subspecies of gerrhonotines (Fitch, 1938; Knight & Scudday, 1985). However, our results, and those of other studies (Pyron *et al.*, 2013; García-Vázquez *et al.*, 2018a), clearly show that gerrhonotines with smooth dorsal scales do not form a monophyletic group. *Gerrhonotus rhombifer*, formerly *Coloptychon rhombifer*, is nested within *Gerrhonotus* with keeled scales. *Desertum lugoi*, formerly *Gerrhonotus lugoi*, appears to be more closely related to other gerrhonotines than to *Gerrhonotus*. Although this relationship has received low support in some analyses and studies (García-Vázquez *et al.*, 2018a), in all cases, it is clear that this taxon is highly divergent, and its high genetic and morphological divergence from all other surveyed *Gerrhonotus* justifies its removal from *Gerrhonotus* and transference into a separate new genus in Gerrhonotinae.

*Gerrhonotus parvus* also was markedly divergent genetically and morphologically from all other surveyed *Gerrhonotus*. However, unlike *D. lugoi*, it was consistently recovered as the sister taxon to all remaining *Gerrhonotus* (i.e., *G. parvus* and *G. rhombifer* formed a strongly supported clade with those *Gerrhonotus* of keeled dorsal scales). Thus, although it also is conceivable to recognize *G. parvus* as a distinct genus, we conservatively prefer to retain it in the genus *Gerrhonotus*. This is consistent with previous decisions to tentatively retain *G. parvus* in *Gerrhonotus* (García-Vázquez *et al.*, 2018a).

The two remaining species with smooth dorsal scales (*G. farri* and *D. lazcanoi*) lack molecular data, and therefore their phylogenetic position is unknown. Accordingly, their generic assignment is problematic, and any assignment must be tentative. Because *D. lugoi* and the recently described species *G. lazcanoi* share a unique combination of morphological and coloration characters (Banda-Leal *et al.*, 2017), we tentatively assign *G. lazcanoi* to *Desertum*, an assignment pending corroboration by genetic data. Assignment of *G. farri* is more problematic because it appears to be morphologically intermediate between *Gerrhonotus* (*s.s.*) and *Desertum*; whereas it shares a set of morphological characters with *D. lugoi* (e.g.,

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smooth dorsal scales, rostral-nasal scales contact and supranasal-cantholoreal scales contact (Bryson & Graham, 2010)), it also shares other morphological characters with *G. parvus* and some other species of *Gerrhonotus* (e.g., similar numbers of longitudinal dorsal scale rows, longitudinal ventral scale rows, and subocular and primary temporal scales). Thus, we prefer to tentatively retain *G. farri* in the genus *Gerrhonotus*, an assignment also pending corroboration by genetic data.

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