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Abstract.—Middle-American knob scaled lizards of the genus *Xenosaurus* are viviparous lizards characterized by flattened bodies, peculiar knob-like scales, and extreme specialization to a crevice-dwelling ecology. Species within this rarely seen and enigmatic genus are distributed throughout much of Mexico and Guatemala. *Xenosaurus* is the sole surviving genus of the ancient family Xenosauridae and little is known about the origins and biogeographic history of members of the group. To address this deficit, we estimated divergence times across *Xenosaurus* under the fossilized birth–death model, including published ddRADseq data, morphological data for six extant and three fossil relatives to genus *Xenosaurus*, and fossil occurrence data for the three fossil relatives. Crown *Xenosaurus* was estimated to be 35 million years old, considerably younger than the stem age of the family, implying high rates of extinction. The distribution of *Xenosaurus* populations across Mexico and the location of the three fossil relatives in western North America suggest a Nearctic origin with a north to southeast direction of range evolution in *Xenosaurus*. To test this hypothesis, we performed a Bayesian biogeographic analysis under the Dispersal Extinction Cladogenesis (DEC) model, in order to estimate the historical ranges and patterns of dispersal across the genus. The results of the biogeographic analysis supported this historical north to southeast movement. In conjunction with our diversification estimates, our DEC results suggest that climatic events such as cooling during the Miocene and Pliocene may have shaped the divergence and current distributions in *Xenosaurus*.

Efforts to resolve the phylogeny of Anguimorphs, much like those directed toward Squamates as a whole, have been complicated by conflicts between morphological and molecular hypotheses. However, advances in the production and analysis of molecular data, in conjunction with morphological data, have enabled researchers to disentangle many of the unresolved questions about evolutionary history (Gauthier et al., 2012; Losos et al., 2012; Reeder et al., 2015; Burbrink et al., 2020). Strides have been made in understanding the origins of Middle American knob-scaled lizards of the genus *Xenosaurus*, an ancient and enigmatic Anguimorph lineage.

Xenosaurus is a peculiar genus of crevice-dwelling lizards, occurring in sparse populations across northeastern Mexico, the Atlantic and Pacific versants of central Mexico, and Western Guatemala (Ballinger et al., 1995; Nieto-Montes de Oca et al., 2017). Members of *Xenosaurus* are characterized by their knob-like scalation and flattened appearance. The flat bodies and heads of *Xenosaurus* are likely adaptations to crevice dwelling, allowing the lizards to fit in-between the cracks of cliff faces and boulder piles (Lemos-Espinal et al., 2003). *Xenosaurus* are extreme specialists in these cracks, inhabiting the same crevice for most of their life span with few, if any, excursions to the outside. Efforts to catalogue the distribution and diversity of the genus have proved challenging because of the rarity with which *Xenosaurus* are encountered (King and Thompson, 1968; Ballinger et al., 2000).

Recent work utilizing molecular species delimitation approaches and sampling new localities revealed that species diversity in *Xenosaurus* was greater than previously understood. Findings suggested the presence of ≥18 distinct species of *Xenosaurus*—a large increase from the then 8 described species (Nieto-Montes de Oca et al., 2017). In addition to resolving questions of species limits, Nieto-Montes de Oca et al. (2017) utilized a robust genome-wide molecular data set to produce the first complete phylogeny of *Xenosaurus*. The phylogeny, including all known species, provides an enhanced understanding of diversity and relationships in *Xenosaurus*. However, the origins of the genus are still obscured by the fact that *Xenosaurus* represents the lone living genus of Xenosauridae, an ancient family of now mostly extinct lizards.

Xenosauridae, one of the six Anguimorph families, is believed to be an old family, having emerged 100 million years ago (mya). Morphology-based studies have suggested Xenosauridae to be sister to Helodermatidae or all other Anguimorphs (Bhullar, 2011). However, more recent molecular and combined evidence analyses show the family to be most closely related to Anguidae (Conrad et al., 2011). Despite some previous uncertainty over the identity of the sister lineage to Xenosauridae, the timing of the divergence is consistently supported to be old, having occurred during the Cretaceous (Burbrink et al., 2020). Given its old age and lone genus, Xenosauridae represents a peculiar family with an evolutionary history that has likely been strongly shaped by extinction. The timing and source of extinction across the family is not entirely known, but the biogeography of *Xenosaurus* and its fossil relatives provide potential insights into the origins of these lizards.

Despite the current Middle American distribution of *Xenosaurus*, fossilized xenosaurids provide evidence of a Nearctic origin for Xenosauridae. The closest fossil relative to *Xenosaurus* has been shown to be *Exostinus serratus*, described by Cope (1873) from cranial elements pulled from the Middle Oligocene White River formation of Colorado (Bhullar, 2010). More distantly related fossilized xenosaurids include *Exostinus lancensis* from the late Cretaceous of Wyoming and Montana, described by Gilmore (1928) and Estes (1964), and *Restes rugosus* from the late Paleocene of Wyoming, described by Gilmore (1941) and Estes (1965). Remnants of what could be *E. lancensis* have been found even as far north as the western interior of Canada (Bhullar, 2011). The current distribution of the genus *Xenosaurus*, with isolated populations following a north to
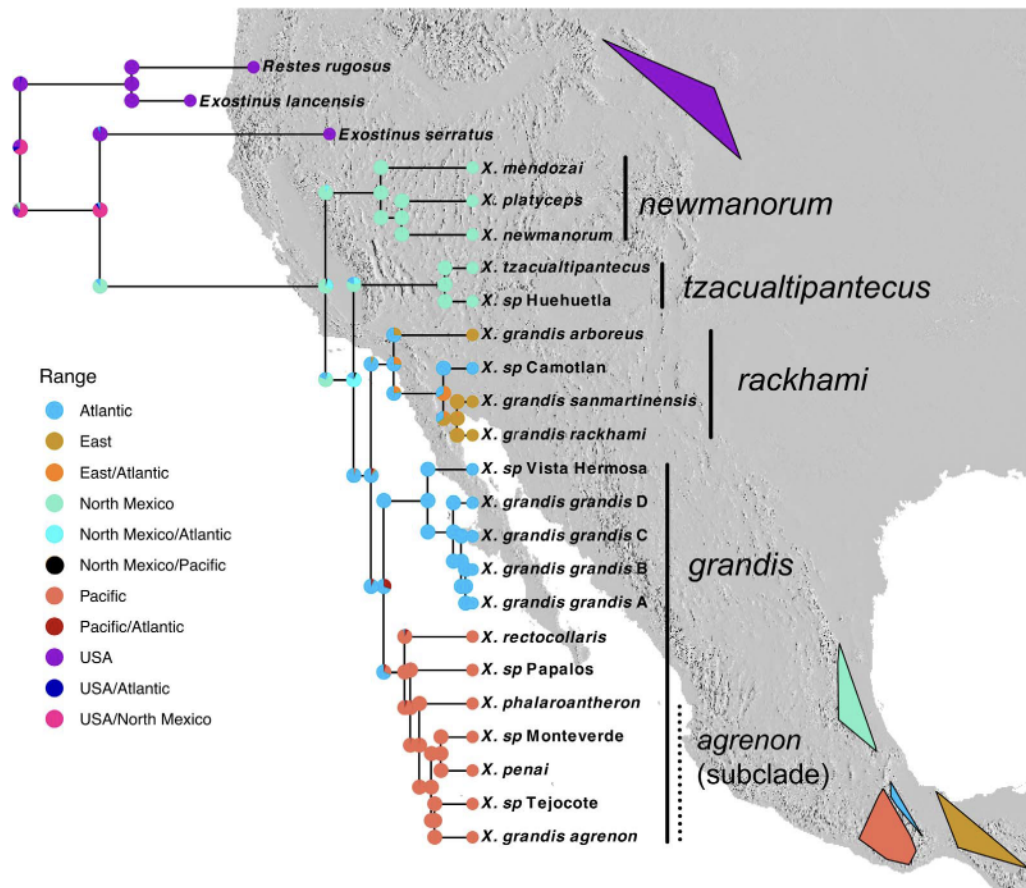
FIG. 1. Dispersal Extinction Cladogenesis biogeographic analysis of genus *Xenosaurus* and related fossil taxa. Current and ancestral ranges are indicated by the color of nodes and tips, corresponding to the accompanying key and to the range polygons given on the map. At nodes, pie charts reflect the uncertainty in estimation of ancestral ranges, with the proportion of the pie occupied by a single color reflecting the posterior probability of the corresponding range at that node. In the analysis, a maximum of two states could be occupied at once. The members of the four *Xenosaurus* clades and the *agrenon* subclade are indicated.

southeast trajectory, lends some support to how a Nearctic migration may have unfolded.

Four geographically distinct clades of *Xenosaurus* have been identified: the *newmanorum*, *tzacualtipantecus*, *grandis*, and *rackhami* clades (Nieto-Montes de Oca et al., 2017). The *newmanorum* and *tzacualtipantecus* clades are the two northernmost clades, found along the Atlantic slopes of Mexico's northeastern Sierra Madre Oriental mountain range, and the clades closest to the root of *Xenosaurus*. The clades are restricted to north of the Mexican Transvolcanic Belt, also known as the Sierra Nevada in Mexico. The *grandis* clade is split between the Atlantic slopes of the Mexican Transvolcanic belt, in the case of the *grandis major* clade, and the Pacific slopes of the Sierra Madre del Sur, in the case of the *agrenon* subclade. The *rackhami* clade is the most southern of the four clades and spans from west of the Isthmus of Tehuantepec in Oaxaca east into Guatemala. The ranges of the four *Xenosaurus* clades are shown in Figure 1. The north to southeast distribution of the four clades, with the earliest diverging clades, *newmanorum* and *tzacualtipantecus*, being the northernmost and the more nested clades following a south to southeast trajectory, provides evidence for a north to southward dispersal in the clade's history.

The separation of geographically close distributions such as *newmanorum* and *tzacualtipantecus* clades, in the absence of clear geological barriers to movement between populations, suggest

climatic events as potential shapers of the current distribution of *Xenosaurus* (Nieto-Montes de Oca et al., 2017). The mesic- and cloud forest–dwelling members of the *rackhami* clade distributed west, north, and east of the Isthmus of Tehuantepec are isolated from one another by the drier lowlands of the Isthmus. Such an arrangement could be explained by a once large distribution of cloud forests during the cooler and wetter Pleistocene, allowing for expansion of a *rackhami* ancestor and subsequent fragmentation of the population at the close of the Pleistocene (Toledo, 1982; Campbell, 1984). The Nearctic migration of xenosaurids into Mexico followed by subsequent speciation events, geographical and climatic in nature, is a promising start to elucidating the origins of present *Xenosaurus*. However, much of the evolutionary history of *Xenosaurus*, like the lizards themselves, has remained elusive to researchers.

In this study we set out to further elucidate the history of the genus by providing insights into the timing of divergence events and the nature of the expansion of *Xenosaurus* across Middle America. We produced a time-calibrated phylogeny for the genus *Xenosaurus* and its three North American xenosaurid fossil relatives through a combined approach, incorporating molecular, morphological, and fossil data. A Bayesian tip-dating approach was taken, allowing fossil taxa to inform divergence time estimates by calibrating the phylogeny while also inferring the placement of these taxa as part of the analysis. We then used this tree to perform a biogeographic analysis to estimate the

ancestral ranges of *Xenosaurus*, including the Nearctic localities of fossil taxa and current localities of taxa in Mexico and Guatemala.

MATERIALS AND METHODS

Phylogenetic Inference.—In our analysis, we combined published double digest restriction site-associated DNA (ddRAD) sequencing molecular data from Nieto-Montes de Oca et al. (2017) and morphological data from Bhullar (2011). The molecular data of Nieto-Montes de Oca et al. (2017) consisted of 4,077 loci for 21 representatives of *Xenosaurus*. The data set was 161,476 characters in length and consisted of 50 total *Xenosaurus* individuals. The morphological data from Bhullar (2011) was a 274-character data set for 6 extant *Xenosaurus*, 3 fossilized members of Xenosauridae, 9 extant Anguimorphs, and 2 extinct fossilized Anguimorphs.

From the molecular data set produced by Nieto-Montes de Oca et al. (2017), we selected one individual from each *Xenosaurus* species, subspecies, and each of the four *X. grandis grandis* clades (Table S1). The final molecular data set used in all analyses was 151,764 characters in length for a total of 21 taxa. The reduced taxa and character number had a minimal effect on the agreement between the relationships reported by Nieto-Montes de Oca et al. (2017) and those produced in our analysis, with only the placement of *X.* sp. Tejocote differing slightly. However, this relationship differs only in the resolution of nodes that are poorly supported in both analyses.

From the original morphological data set produced by Bhullar (2011), we included the six extant *Xenosaurus* and the three fossilized xenosaurids, *Exostinus lancensis*, *E. serratus*, and *Restes rugosus*. The identities of the six extant *Xenosaurus* are indicated in Table S1. We removed characters 64 and 147 from the data set because the original coding of these characters included letters that could not be correctly parsed in some preliminary analyses. Removal of these two characters had no effect on agreement between the topologies of the original Bhullar (2011) analysis trees and our analysis trees.

Phylogenetic inference analyses were performed under the nonclock, strict clock, and relaxed clock models as implemented in MrBayes v3.2.6 (Ronquist et al., 2012b). All MrBayes analyses were run on the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway (Miller et al., 2010). The molecular data were partitioned according to the best fit scheme produced by PartitionFinder, under the Bayesian information criterion (BIC) and using the rcluster search option, with each individual ddRAD locus treated as a starting partition (Lanfear et al., 2014, 2016; Stamatakis, 2014). The best scheme partitioned the molecular data set into 68 partitions, with the morphological data occupying the 69th partition. The nst=mixed option in MrBayes was used for each molecular partition to model average over all subsets of the General Time Reversible model, and morphological data were modeled under the *Mk* model with coding set to variable (Lewis, 2001; Huelsenbeck et al., 2004; Ronquist et al., 2012b). Rate heterogeneity among sites was accounted for in molecular and morphological partitions using a discretized Γ distribution. Nonclock analyses were run for 20 million (M) generations, sampling every 5,000 generations. For all MrBayes analyses, Tracer v1.7 was used to assess convergence both visually, by looking at the trace, and quantitatively through the effective sample size (ESS) values of parameters (Rambaut et al., 2018). The MrBayes default burn-in of 25% was used for all analyses.

Divergence Dating.—We performed divergence dating analyses under the fossilized birth–death tree prior treating fossils as terminal taxa. To determine appropriate settings for the clock rate prior, we performed a strict clock analysis with the topology fixed to the results of the initial nonclock analysis for 20 M generations, sampling every 5,000 generations. Following the recommendations of Ronquist et al. (2012a), we set a lognormal prior on the clock rate with the mean set to the tree height of the strict clock analysis divided by the mean age calibration of the root node of the tree and set the standard deviation so that the upper 95% estimate of tree height divided by the mean age calibration of the root is one standard deviation from the mean of the lognormal distribution. We used the independent gamma rates (IGR) clock model (Lepage et al., 2007) and set the prior on the increase in variance of the IGR clock to the value calculated using the R script provided by Ronquist et al. (2012a).

The ages of the terminal fossils used to calibrate divergence times were drawn from a uniform distribution, with bounds corresponding to the minimum and maximum age of the fossils. The three fossil taxa and their estimated ages were *Exostinus lancensis* (61.7–70.6 mya), *Restes rugosus* (46.2–56.8 mya), and the closest fossil relative to genus *Xenosaurus*, *Exostinus serratus* (33.3–33.9 mya) using dates from the Paleobiology Database (https://fossilworks.org, last accessed April 2019). MrBayes requires that the root of the tree be calibrated, and we did so by using an offset exponential distribution with a lower bound of 61.7 mya, based on the age of the oldest fossil (*Exostinus lancensis*), and a mean of 85 mya. Sampling of extant lineages was treated as random; however, the sampling fraction was set to 1 because our data set includes all known members of *Xenosaurus*, and so the choice of prior on sampling of extant lineages has no impact. Divergence dating analyses were run for 150 M generations, sampling every 30,000 generations, with 4 independent runs each with 1 cold and 3 incrementally heated chains.

We note that a recent method has been developed that allows for integration of the multispecies coalescent with tip-dated analyses, which we did not use here (fossilized birth–death multispecies coalescent model, FBD-MSC; Ogilvie et al., 2022). This method can be particularly useful in avoiding upward biases in divergence date estimates when populations are large, thus leading to high degrees of incomplete lineage sorting. We do not expect this to be a major issue for *Xenosaurus* given expected small population sizes as a result of the restricted ranges of species within the group. Furthermore, from a practical standpoint, our data set includes >4,000 loci, making it a less than ideal candidate for the FBD-MSC model, which the authors state they expect will be applied to data sets of fewer than 1,000 loci (Ogilvie et al., 2022).

Biogeography.—We performed ancestral range reconstruction of *Xenosaurus* and its fossil relatives under the Dispersal Extinction Cladogenesis (DEC) model (Ree et al., 2005; Ree and Smith, 2008) in RevBayes v1.1.1 (Höhna et al., 2014, 2016). The tree topology and branch lengths were fixed to the consensus phylogeny including all compatible groups from our divergence dating analysis. *Xenosaurus* taxa were assigned to four areas in Mexico and Central America based on the sampling localities reported by Nieto-Montes de Oca et al. (2017): 1) northern Mexico (N), 2) eastern Mexico and Guatemala (E), 3) the mid-Pacific coast (P), and 4) the mid-Atlantic coast of Mexico (A). The fossil taxa were assigned to the United States (U). Localities for each taxon are listed in Table S1. Ancestral nodes were allowed to occupy a maximum of two areas at once, which is the maximum number
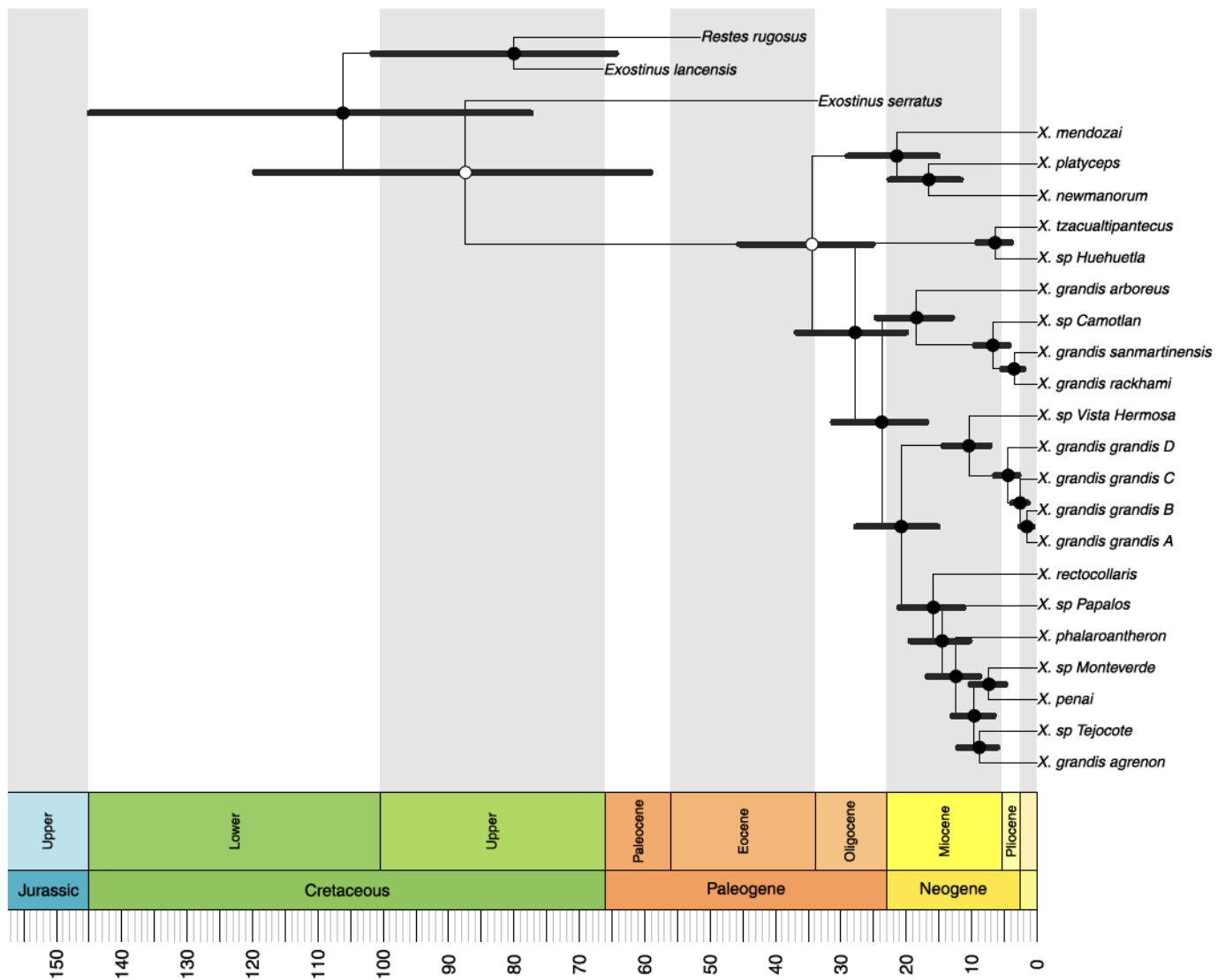
Fɪɢ. 2.   Tip-dated MrBayes phylogeny of genus *Xenosaurus* and Xenosauridae fossil relatives. Node color indicates the posterior probabilities (PP): black: PP ≥ 0.95 and white: PP < 0.75 (no nodes have 0.95 > PP > 0.75). Node bars represent the 95% highest posterior density intervals of divergence dates. Time in the horizontal access is given in millions of years ago (mya) and terminates in the Quaternary, which has been left unlabeled for clarity of presentation.

of areas occupied by terminal lineages. Relative distance was used to weight transitions between areas, with a transition between each adjacent area adding one "step" of distance and assuming that transitions between nonadjacent areas crossed the minimum number of intervening areas. We ran the RevBayes biogeographic analysis for 5,000 generations, sampling every 10 generations with a 25% burn-in.

Rᴇsᴜʟᴛs

The tip-dated phylogeny of Xenosauridae, including all known extant and extinct members of the family, is shown in Figure 2. All evolutionary relationships between members of extant *Xenosaurus* are well-supported with posterior probabilities (PP) of 1. The placement of *Exostinus serratus* relative to genus *Xenosaurus* showed poor support with a PP of 0.37 along with the relationship between *Exostinus lancensis* and *Restes rugosus*, which had a PP of 0.65. However, the relationships were also poorly supported in Bhullar's (2011) original morphological analysis. We estimated the origin of stem

Xenosauridae to have occurred 106 mya, during the lower Cretaceous, with a 95% highest posterior density interval (HPD) of 145–80 mya. Our analysis indicates genus *Xenosaurus* to be much younger, emerging during the Paleogene 34 mya with a 95% HPD of 45–25 mya, with most speciation events occurring during the late Miocene and Pliocene.

Our ancestral range reconstruction infers a north to southeast pattern of dispersal (Fig. 1) and suggests the ancestor of Xenosauridae occupied North America and Northern Mexico. Crown *Xenosaurus* is estimated to have ancestrally occupied Northern Mexico with subsequent dispersal events toward the southeast as the genus diversified. Most of these southeastward dispersal events occurred relatively recently during the Miocene.

Dɪsᴄᴜssɪᴏɴ

We provide the first divergence time estimates for the Xenosauridae (*Xenosaurus* + *Restes* + *Exostinus*) recovering a stem age of 106 mya, somewhat older than the age of the

oldest fossil relative to *Xenosaurus*, *E. lancensis*, which is estimated to be between 61.7 and 70.6 mya. Our divergence time estimates are consistent with studies estimating an initial divergence of Xenosauridae from its sister group in the early to mid-Cretaceous (e.g., Zheng and Wiens, 2016; Burbrink et al., 2020).

Our estimate of the crown age of *Xenosaurus* at 34 mya is young compared with the 106-mya stem age of the family Xenosauridae. The large time gap and the presence of xenosaurid fossils in western North America, far outside of the distributions of all extant members of the clade, suggests that extinction has had a strong influence in shaping the modern diversity and distribution of the clade. This is not an uncommon finding in ancient lizard clades. The family Corytophanidae is currently restricted to the Neotropics, but fossils have been found in North America and Europe (Conrad, 2015), and fossils from Agamidae, now entirely absent from the Americas, have been found in Brazil (Simões et al., 2015), demonstrating the key role for fossils in inferring biogeographic patterns in deep time. In the case of Corytophanidae, it is hypothesized that the family originated from Laurasia and moved to the current distribution following post-Eocene cooling at high latitudes (Conrad, 2015). Xenosauridae similarly seemingly originated in the Nearctic and are currently restricted to the Neotropics, likely having experienced a similar pattern of dispersal with cooling leading to the extinction of higher latitude xenosaurids. This timing is also consistent with our estimated age of Central American crown *Xenosaurus* in the very late Eocene.

Within the genus *Xenosaurus*, we found the majority of diversification occurred within the past 25 million years. In the case of the *grandis* clade and the *agrenon* subclade, fragmentation of mesic forests is believed to have played a major role in diversification. As described by Nieto-Montes de Oca et al. (2017), mesic forest species such as *X. g. grandis* and *X.* sp. Vista Hermosa are separated by the course of the Papaloapan River in northern Oaxaca. On the clade level, the split between the *rackhami* clade and the *grandis* clade could have arisen as a result of the dry lowlands across the Isthmus of Tehuantepec that separate the high-elevation forest habitats of the two clades. The expansion of mesic forests into the lowlands during a period of climatic cooling, followed by subsequent fragmentation resulting from warming, could explain the speciation of the clades and diversification in their current distributions (Toledo, 1982; Campbell, 1984; Nieto-Montes de Oca et al., 2017). The period of climatic cooling, based on our estimates for the divergence and diversification of the *rackhami* and *grandis* clades, is likely to have occurred during the Miocene and Pliocene, within the past 15 million years. Our estimate is earlier than previous hypotheses, such as that by Nieto-Montes de Oca (2017) that suggests cooling and warming occurred during the Pleistocene in the past 2.6 million years. We have focused on climatic factors, following previous literature and because, as described by Nieto-Montes de Oca (2017), in most cases, there are no obvious geological barriers between lineages, and areas of seemingly suitable habitat near occupied habitat are often devoid of *Xenosaurus*. However, it remains possible that currently unknown microhabitat preferences could be important for the diversification of Xenosauridae. Further work into the biology of these lizards and the timing of these climatic events will help to elucidate the accuracy of our time estimates and biogeographic hypothesis for the genus *Xenosaurus*.

Conclusions

In our ancestral range reconstruction using a tip-dated phylogeny, we found support for the Nearctic origin of *Xenosaurus* with fossil taxa occupying the northernmost range and extant taxa having dispersed along a southeast trajectory (Fig. 1). The inference of this biogeographic pattern would have been impossible without the inclusion of fossil taxa present in regions well outside the current range of living *Xenosaurus*. Our estimates of the timing of divergences within *Xenosaurus* are earlier than has been previously hypothesized, suggesting that climatic changes preceding Pleistocene glacial cycles may have been responsible for diversification within this group. As new populations and species of these secretive and poorly known lizards continue to be discovered, we will gain further insight into the processes that have structured diversification in this group.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at http://dx.doi.org/10.1670/21-068.S1.