I Need [Morpho]Space: Determining the Affinity of Fossil Xantusiid Jaws with Implications for Post-KPg Squamate Diversity

Selena Ann Martinez

Adviser: Roxanne Armfield

April 27th, 2022

A Senior Thesis presented to the faculty of the Department of Earth & Planetary Sciences, Yale University, in partial fulfillment of the Bachelor's Degree.

Abstract

Xantusiidae (night lizards) is a lizard clade native to the southwestern United States and Baja California, Cuba, and Central America. There are three extant clades, *Cricosaura typica* (Cuban night lizard), *Xantusia* (desert night lizard), and *Lepidophyma* (tropical night lizard), and multiple fossil members have been identified. Xantusiids are well-known for their microhabitat specialization (inhabiting rock crevices, living in decaying plants), and this specialization has implications for their survival, and resultant speciation, of the Cretaceous-Paleogene Mass Extinction Event. *"Palaeoxantusia"* is a wastebasket taxon of Paleogene pan-xantusiids, though there is debate regarding the species of these fossils. Further uncovering the diversity of *"Palaeoxantusia"* is important for understanding why this clade was so successful following the extinction. Two-dimensional (2D) geometric morphometrics was used to determine intra- versus interspecies variation among *Xantusiidae*. This method was tested on extant xantusiids and then applied to fossil specimens. Individuals were found to cluster by clade, and by fossil or extant status, except in the case of outliers, such as *Xantusia riversiana,* and the species complex *Xantusia vigilis*. Fossil and extant taxa occupy separate morphospaces, suggesting that these animals may have occupied disparate ecological niches in life. Fossil xantusiids and the extant clade *Lepidophyma* were found to show morphologies consistent with generalist ecology. The modern clade *Xantusia* was shown to possess specialized morphologies that may be suited for their crevice-dwelling ecologies.

Introduction

Xantusiidae, known commonly as night lizards, is a clade of small-bodied lizards endemic to southwestern North America and Baja California, Cuba, and Central America (Estes et al., 1988; Noonan et al., 2013). Xantusiids have long been described as a 'secretive' species due to their microhabitat specialization – their ability and preference to seek shelter in protected structures – and their elusive behavior (Bezy et al., 2020). Xantusiids have a paedomorphic appearance compared to other four-legged squamate taxa (Noonan et al., 2013). Although they are active during the day, xantusiids show higher levels of nighttime activity than is typical for most diurnal reptiles (Vicario et al., 2003). Xantusiid microhabitat specialization (dwelling in rock crevices, beneath fallen trees and decaying plants) may have implications for their persistence and diversification in the aftermath of the Cretaceous-Paleogene (K-Pg) Mass Extinction (Robertson et al., 2004).
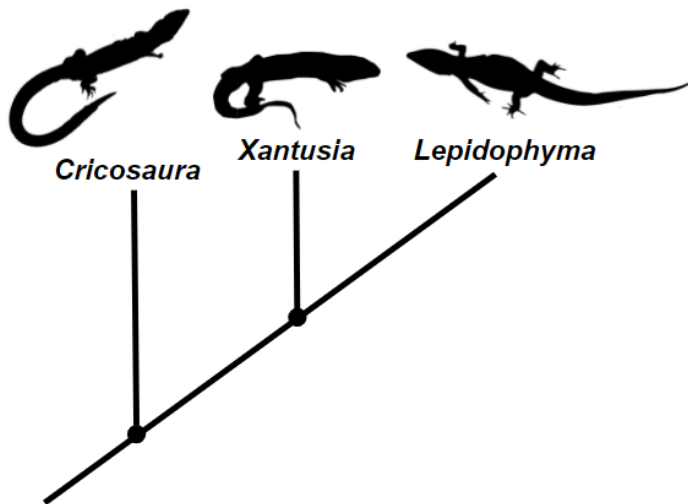

Figure 1: Phylogenetic placement of clades within crown Xantusiidae.

There are three extant clades within crown *Xantusiidae*: *Cricosaura typica*, *Lepidophyma,* and *Xantusia* (Savage, 1963, 1964). The sole living representative of the sister to all other xantusiids, *Cricosaura typica* (in Peters, 1863)*,* inhabits the southernmost coast of Cuba (Peters, 1863; Vicario et al., 2003; Noonan et al., 2013). *Cricosaura typica* is the smallest extant night lizard and is the only oviparous member of *Xantusiidae* (Bezy, 2019). The tropical night lizards (*Lepidophyma*) are restricted to the woodlands and rainforests of Mexico and Central America (Bezy, 2019). They have been found in a variety of microhabitats, including rocks, logs, tree stumps, forest litter, rock crevices, caves, and human dwellings (Bezy, 2019). There are 20 recognized species of *Lepidophyma,* and several Eocene stem fossils have been identified including *Palepidophyma* paradisa and *P. lilliputiana* (Smith and Gauthier, 2013) and *Lepidophyma arizeloglyphum* (Langebartel, 1953). The northern night lizards (*Xantusia*) inhabit the southwestern United States, Baja California, and the Channel Islands (Sinclair et al., 2004). *Xantusia* has been documented living in rock crevices, under rocks on the ground, within various species of yucca, agave, and other desert plants, and tree logs (Bezy, 2019). *Xantusia riversiana* is the only insular member of this clade and has marked phenotypic differences from mainland

species.

Figure 2: Distribution of living Xantusiidae.

The ecology of *Xantusia* is varied, especially when comparing insular and mainland species, though their specialization for microhabitats is a shared feature among taxa (Van Denburgh, 1895; Noonan et al., 2013). Xantusiids are often found to be 'locally abundant', which is to say that they tend to live in small, isolated populations composed of several to many individuals, often possessing morphologies modified to suit their preferred habitats (Zweifel and Lowe, 1966; Bezy, 2019). The northern night lizards (*Xantusia*) are known for living beneath decayed plants or within rock-crevice microhabitats, and for their elusive behavior, except for the island night lizard (*X. riversiana*), which has been described as ground-dwelling. Fallen Joshua trees (*Yucca brevifolia*) are particularly favored as shelter and foraging grounds for *Xantusia vigilis* (Van Denburgh, 1895; Bezy, 1982). The Cuban night lizard (*Cricosaura typica*) lives beneath rocks of varying sizes with leaf-litter and soil below (Barbour, 1914). Tropical night lizards (*Lepidophyma*) can be found seeking cover in a variety of microhabitats, including: rocks, tree

stumps and logs, forest litter, caves, and man-made architecture including archaeological ruins (Bezy and Camarillo-Rangel, 2002; Bezy, 2019).

The reproductive ecology of *Xantusiidae* is unique among squamates. Night lizards grow very slowly, reach reproductive maturity late compared to other lizards, and produce relatively small litters (Mautz, 1979). The most unique aspect of night lizard reproductive ecology is the unisexuality of certain populations of *Lepidophyma* (tropical night lizards). Populations of all-female parthenogenic lizards have been observed and described in Central America (Telford and Campbell, 1970). Although further exploration of the reproductive ecology of night lizards is beyond the scope of this paper, their growth histories may have played a significant role in their ability to survive in the climatic turmoil of the K-Pg Mass Extinction.

Species of *Xantusia* that inhabit rock crevices tend to have larger body sizes overall (e.g., *Xantusia arizonae, X. bezyi, X. bolsonae,* and *X. henshawi*), though their bodies tend to be flattened, likely a specialization for this microhabitat (Bezy, 1989). Rock-dwelling species have a longer fourth toe and hind leg, as well as a longer and broader head than yucca-dwelling species (Bezy, 1989). The island night lizard, *Xantusia riversiana*, is markedly different from mainland members of the same clade. *X. riversiana* tends to be far larger than its mainland relatives and, possibly due to its larger body size, produces larger litters than mainland night lizards (Fellers and Drost, 1991). *X. riversiana's* large size relative to other night lizards may be due to insular gigantism (Bezy, 1989). This conclusion, however, is entirely dependent upon judgment of the ancestral body size for these clades. Bezy (1989) assumes that the small size of mainland species is primitive (hence, island gigantism for *X. riversiana*). Given the larger size of the outgroups *Lepidophyma* and *Palaeoxantusia*, however, it is more likely that the mainland species are dwarfs. In this case, the diminutive *Cricosaura typica* must be an insular dwarf.

The total clade, *Pan-Xantusiidae*, is first reported from the Early Cretaceous of Mexico (e.g.,

Tepexisaurus tepexii; Gauthier et al., 2012). Pan-xantusiids, including *Contogeniidae*, are

remarkably rare in well-sampled Late Cretaceous micro-vertebrate localities in the North

American Western Interior but go on to become one of the most common lizards during the

Paleogene (e.g., Schatzinger, 1980; Estes, 1983; Nydam and Fitzpatrick, 2009; Makádi and

Nydam, 2015). This uptick in pan-xantusiid diversity post-K-Pg has been attributed to increases

in post-extinction niche availability and lack of competitors and predators, though further

examination of Paleogene specimens, aptly called "*Palaeoxantusia"*, is necessary to uncover

how speciose *Pan-Xantusiidae* is before and after the end-Cretaceous (Longrich et al., 2012).
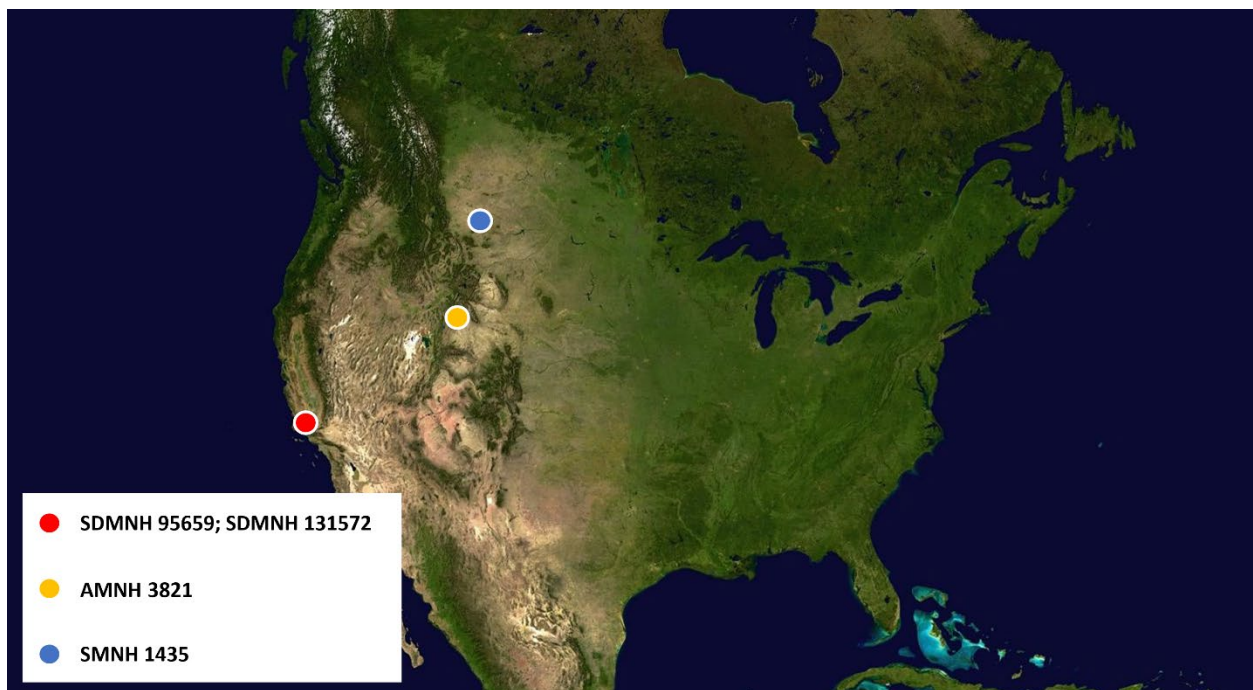

Figure 3: Distribution of fossil specimens used in analysis.

"*Palaeoxantusia*" is a wastebasket taxon of Paleogene pan-xantusiids (Hecht, 1959; Holman, 1972). These extinct species are known from fossil deposits in the North American Western Interior, though the majority of these fossils are fragmentary (Estes, 1976; Sullivan, 1982). "*Palaeoxantusia*" is abundant from Middle Paleocene through Late Eocene (Sullivan, 1982), and most specimens are represented by tooth-bearing maxillary and especially dentary bones, the densest and most durable bones in the skeleton (Green and Holman, 1977). Jaw material is thus preferentially preserved and, as a result, is overrepresented in the fossil record (Woolley et al., 2022).

Catactegenys solaster, represented by a few isolated elements from the Aguja Formation (late Campanian) of Texas, has been suggested to be a potential stem-xantusiid (Nydam et al., 2013). However, that question turns in part on how different authors use the same name, viz., *Xantusiidae*, rather than being entirely a matter of conflicting data. *C. solaster* displays several apomorphies shared by both contogeniids and xantusiids (see Nydam and Fitzpatrick, 2009; Nydam, 2013), and is accordingly referable to *Pan-Xantusiidae*. However, *C. solaster* also shares a few distinctive contogeniid apomorphies as well as one apomorphy shared with xantusiids (Nydam, 2013; Nydam et al., 2013). Despite this character discordance, there are no apomorphies supporting that *C. solaster* is part of (crown) *Xantusiidae* proper, though it is certainly a stem xantusiid (i.e., part of *Pan-Xantusiidae*). Thus, crown xantusiids have yet to be found in well-sampled Late Cretaceous deposits from the North American Western Interior. Nevertheless, unambiguous contogeniids are known, if rare, from the Maastrichtian (e.g., Nydam and Fitzpatrick, 2009), and because *C. solaster* is in any case a stem xantusiid, then pan-xantusiids, if not crown xantusiids, extend back into the Late Cretaceous (Nydam et al., 2013).

Gauthier et al. (2012) argued that *Tepexisaurus tepexii*, from Albian deposits of the Tlayua Formation in Mexico, extends the xantusiid stem deep into the Cretaceous. Nydam (2013) implied that Reynoso and Callison (2000) would dispute that assignment as they only referred to *T. tepexii* as a 'scincoid' rather than a xantusiid. Once again, this reflects ambiguity in the meaning of taxon names, in this instance *Scincoidea.* Because Gauthier et al. (2012) inferred that *Tepexisaurus tepexii* is a stem-xantusiid, that species, along with contogeniids (sensu Nydam and Fitzpatrick, 2009) and *Catactegenys solaster*, would also be 'scincoids', namely, parts of the least inclusive lizard taxon containing all living xantusiids, cordylids, and scincids. Both Reynoso and Callison (2000) and Gauthier et al. (2012) agree of that point; the former authors only indicated that *T. tepexii* is a scincoid while the latter authors went further in specifying which scincoid clade it belonged to; they do not post alternative hypotheses of relationship. Genuine alternative, if poorly supported, hypotheses of relationships for *T. tepexii* based on morphology were offered in Conrad (2008) and Simões et al. (2018), though consideration of their data is beyond the scope of this paper.

The Cretaceous-Paleogene (K-Pg) extinction eliminated more than 75% of species in existence (Alvarez et al., 1980), and 85% of lizard species in the North American Western Interior (Longrich et al., 2012). This mass extinction was triggered by a bolide impact that generated apocalyptic conditions on Earth, complete with global darkness, isolated instances of extreme surface heating, resource depletion, and an impact winter (Hull and Darroch, 2013; Hull, 2015). The unique behaviors and life-history strategies of *Xantusiidae*, and perhaps even the contogeniids that survived this event (Nydam and Fitzpatrick, 2009), may have positioned them for success in the wake of the K-Pg event (Noonan et al., 2013; Smith and Gauthier, 2013). Resolving relationships of "*Palaeoxantusia*", a wastebasket of potentially near-crown and basal-

crown pan-xantusiids from the Paleogene, is central to understanding the survival and subsequent radiation of *Xantusiidae*.

This paper aims to reveal more of the diversity among "*Palaeoxantusia*" emerging from the K-Pg boundary using two-dimensional geometric morphometrics as a method of distinguishing among species of xantusiid lizard.

Materials and Methods

Morphometric Methods

Morphometrics is a quantitative method of evaluating overall shape comparisons (Rohlf, 1990; Zelditch et al., 2004). Anatomical identification of apomorphies is the traditional processes by which paleontologists assign specimens to clades. Apomorphic identification often relies on overall similarity to refer isolated elements to the same species. The morphology of fossils is normally the only avenue through which an identification can be made. Skeletal morphology is an apt indicator of a fossil specimen's affinity. This is also the case for extant taxa, though determining the species is made easier by the availability of molecular data, observable behaviors, and soft tissues (Guha and Kashyap, 2006; Auliya and Koch, 2020). In the past, qualitative assessment of fossil morphology was the method of choice for species assignment, but sometimes led to unreliable, biased specimen identifications (Zelditch et al., 2004). Morphometrics provides a better method of avoiding the bias of human observation by using quantitative tools to evaluate shape and, in turn, morphological differences. This thesis seeks to determine whether species of fossil xantusiids can be identified based on fragmentary lower jaws alone, which are far and away the most common lizard fossils. Morphometric methods were used to quantify intra- versus interspecies variation among *Xantusiidae*. Morphological disparity can be used as a measure of biodiversity, and a high diversity of morphologies can indicate high ecological flexibility and tolerance (Roy and Foote, 1997). Disparate microhabitat specialization is already documented among *Xantusiidae*, but a systematic analysis of morphological disparity among extant taxa as well as fossil assemblages has yet to be undertaken.

11

Geometric morphometrics. Geometric morphometrics is a branch of morphometrics that uses geometric coordinates rather than linear variables in shape comparison. These coordinates are transformed into shape variables that can be analyzed using standard multivariate statistical processes (Lawing and Polly, 2010). Where linear morphometrics uses one-dimensional data for morphological analysis, geometric morphometrics can utilize either two-dimensional (2D) or three-dimensional (3D) coordinates for shape comparison (Buser et al., 2018). 2D measurements are taken from photographs of specimens, and 3D measurements typically use 3D reconstructed CT data for landmark placement. Both 2D and 3D geometric morphometrics can capture common patterns across taxa (Zelditch et al., 2004). 3D morphometrics, however, is more computationally and labor intensive. While 3D morphometrics is able to "capture more data" with respect to 3D structures with significant relief (Cardini and Chiapelli, 2020), this was not a necessary requirement for this analysis, because the dentary can effectively be modelled as a flat, low-relief 2D structure (Cardini, 2014). In light of this, and due to the additional labor requirements, the use of 3D morphometrics was rejected, in favor of 2D morphometrics. I used landmark-based morphometrics to delimit species among previously described and currently undescribed specimens. This analysis was restricted to the lower jaw of xantusiid specimens, the most durable, and therefore most abundant, element in the lizard fossil record.

Principal Components Analysis

Principal component analysis (PCA) is a method that allows the transformation of a large set of variables to a smaller set of dimensions. These new dimensions present most of the variation within a dataset (Zelditch et al., 2004; Mitteroecker and Gunz, 2009). Morphometric variables are expected to be correlated because the features they describe are biologically linked. This produces a multivariate system with complex patterns of variation. PCA is a multivariate

technique that simplifies these patterns and creates new variables that are independent, linear combinations of the original morphometric variables (Zelditch et al., 2004). Once I obtained the principal component values, I created plots (PC1 v. PC2) that illustrate the morphospace occupied by the specimens (Figs. 7, 8, and 9). I focused on PC1 and PC2 because they represent the majority of variation in data across all the analyses run for this project (>60% of total shape variation). The analyses were performed using the program MorphoJ (Klingenberg, 2011) and IBM SPSS Statistics Software (IBM Corp). The PCAs were conducted to see if there was any initial morphospatial difference between and among clades of *Xantusiidae*. Dominant characters were inferred by observing how morphologies differ along the extremes of a PC axis.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, New York, U.S.A.; **LACM**, Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A.; **SDMNH**, San Diego Museum of Natural History, San Diego, California, U.S.A.; **SMNH**, Saskatchewan Museum of Natural History, Regina, Saskatchewan, Canada; **UAZ**, University of Arizona Museum of Natural History, Tucson, Arizona, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **YPM**, Yale Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

Taxon Selection

Extant. Extant taxa were selected based on availability in online repositories and in the Yale Peabody Museum herpetology collections. Modern *Xantusiidae* is a relatively small clade, with approximately 34 living species (Bezy, 2019). 28 specimens were obtained for use in this analysis, 20 specimens of which were used in the final analyses. 18 distinct xantusiid species were assembled, representing over half of the clade diversity. This sample is representative of the three night lizard clades and their distributions across North America and the Caribbean.

Extant Specimens		
Specimen Number	**Taxon**	**Clade**
USNM 547842	*Cricosaura typica*	*Cricosaura*
LACM 128570	*Lepidophyma flavimaculatum*	*Lepidophyma*
LACM 106770	*Lepidophyma gaigeae*	*Lepidophyma*
LACM 143367	*Lepidophyma lowei*	*Lepidophyma*
LACM 136359	*Lepidophyma smithii*	*Lepidophyma*
LACM 136365	*Lepidophyma sylvaticum*	*Lepidophyma*
LACM 136352	*Lepidophyma tuxtlae*	*Lepidophyma*
LACM 134503	*Xantusia bezyi*	*Xantusia*
LACM 136793	*Xantusia bolsonae*	*Xantusia*
LACM 2014	*Xantusia extorris*	*Xantusia*
LACM 101237	*Xantusia gilberti*	*Xantusia*
LACM 100716	*Xantusia henshawi*	*Xantusia*
UAZ 17386	*Xantusia magdalena*	*Xantusia*
LACM 108770	*Xantusia riversiana*	*Xantusia*
LACM 127128	*Xantusia riversiana*	*Xantusia*
LACM 144221	*Xantusia sanchezi*	*Xantusia*
UAZ 17345	*Xantusia sonora*	*Xantusia*
LACM 123671	*Xantusia vigilis*	*Xantusia*
LACM 134509	*Xantusia vigilis*	*Xantusia*
UCMHerp 40825	*Xantusia wigginsi*	*Xantusia*

Table 1: Extant specimens of Xantusiidae *used.*

Fossil Specimens		
Specimen Number	**Taxon**	**Age**
AMNH 3821	*Palaeoxantusia fera*	Eocene (Bridgerian)
AMNH 15917	Unknown	Paleocene (Torrejonian)
AMNH 16156	*"Palaeoxantusia"*	Paleocene (Torrejonian)
SDMNH 95659	*Palaeoxantusia kyrentos*	Eocene
SDMNH 131572	*"Palaeoxantusia"*	Eocene
SMNH 1493.C (SASKC)	*Palaeoxantusia hechti = Palaeoxantusia borealis*	Data not available
SMNH 1435	*Palaeoxantusia hechti = Palaeoxantusia borealis*	Oligocene
UCMP 104758	*Palaeoxantusia alleni*	Eocene
UCMP 109835	Unknown	Eocene
YPM VPPU 16724	*Socognathus brachyodon*	Cretaceous (Lancian)
YPM VPPU 16725	Unknown (*Palaeosyops sp.*)	Eocene (Bridgerian)
YPM VPPU 17506b	*Palaeoxantusia fera*	Eocene (Bridgerian)
YPM VPPU 17506c	*Palaeoxantusia fera*	Eocene (Bridgerian)

Table 2: Extinct specimens of Xantusiidae *used.*

Extinct. Extinct taxa were selected based on availability in the Yale Peabody Museum Vertebrate Paleontology collections, the quality of their preservation, and the type of bones (mandible) preserved. 13 specimens were obtained for use in this analysis, five specimens of which were used in the final analyses.

CT Scanning and Generation of 3D Models

Micro-computer tomography (CT) images of xantusiids lower jaws were the primary source of data for this study. Specimens including lower jaw material were scanned at high resolution at the Yale Chemical and Biophysical Instrumentation Center (CBIC) by Marilyn Fox using a Nikon XTH 225 ST MicroCT Scanner. The resulting digital radiographs were converted into 8-bit TIFF image stacks using Nikon CT Pro3D. Specimens other than those represented in the Yale Peabody Museum collections (YPM) were obtained from the online CT image repository MorphoSource. I rendered these datasets in three dimensions using VG Studio version 3.5.2 (Volume Graphics, 2021). I isolated the lower jaws from the skulls and appendicular skeleton for

all specimens and exported them as surface mesh files (.stl) for landmarking in tpsDig (Rohlf, 2006).

Landmarking

Landmarks were placed on surface mesh files (.stl) of fossil and extant lower jaws using tpsDig (Rohlf, 2006). These landmarks were chosen as they can be readily identified across all specimens, extant and fossil. While the functional relevance of many of the selected landmarks was noted, this analysis is more concerned with the taxonomic question of distinguishing species of *Xantusiidae*.

In extant taxa, 12 fixed landmarks were placed at equivalent points on the surface of surface mesh files. 12 landmarks were chosen because the number of landmarks cannot exceed the number of specimens used in an analysis. In morphometrics, it is best practice to proceed with the least number of landmarks required to produce a biologically informative result. If too few landmarks are selected, the analysis fails to be informative. If too many landmarks are selected, the variation returned by the analysis may reflect oversaturation of the data as opposed to the actual shape variation present. There are four types of landmarks: Type I (the intersection of two tissues), Type II (maximum/minimum points), Type III (defined with respect to the location of other landmarks), and semi-landmarks (a series of landmarks at regular intervals that define a curve) (Barbeito-Andrés et al., 2012). On the mandible, five Type 1 and seven Type II landmarks were plotted. Type I landmarks have the lowest placement error with respect to replication on other specimens. Type II, Type III, and semi-landmarks have higher placement errors than Type I landmarks. Type I landmarks were chosen due to low error, and semi-landmarks were avoided due to high error.

| Landmarks	Type	Location on dentary
1	II	Anteriormost point on dentary
2	II	Most dorsal point of curvature on the coronoid process
3	II	Most posteroventral point of the lower point of the outline of the jaw
4	II	Most anterodorsal point of curvature on the coronoid process
5	II	Most posterodorsal point of curvature of the coronoid process
6	II	Anteriormost point of maximum curvature on the suture between the dentary and the coronoid
7	I	Posteriormost intersection between the coronoid and the surangular
8	I	Most dorsal point of suture between the dentary and the coronoid
9	I	Contact/intersection of coronoid, dentary, and surangular
10	I	Contact/intersection of dentary, surangular, and articular
11	II	Point at most posterior tip of articular
12	I	Ventralmost point of contact between the articular and dentary

Table 3: Landmarks used in extant specimen analysis.
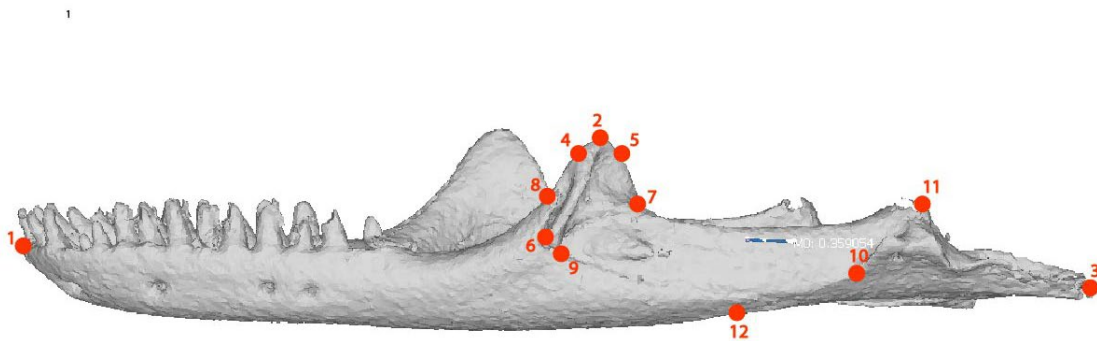
Figure 4: Left mandible in lateral view (X. vigilis).

For the fossil taxa, many landmarks were missing due to inadequate preservation. Some studies have tried to estimate where the missing landmarks are (Gray et al., 2017), but landmark estimations were not made in this study. Unfortunately, the reconstruction of landmarks is biased and can be inaccurate as it is highly dependent on the prior assumptions of researchers (Mitteroecker and Gunz, 2009). Due to the limited nature of the fossil record and the incomplete nature of the specimens available, four landmarks were used in the fossil analysis, as well as in the analysis that combined both extant and fossil specimens. Five specimens could be used in the fossil-only analysis, and 20 were used in the extant and fossil combined analysis. For the fossil-only analysis, one Type I and three Type II landmarks were plotted on the mandible. Only the right side of mandible was considered in this analysis; while this was feasible with fossil taxa, the sample size was limited as a result.

Landmarks	Type	Location on dentary
1	I	Anteriormost point of maximum curvature on the suture between the dentary and the coronoid
2	II	Most posterior point of tooth cusp
3	II	Midpoint of tooth cusp
4	II	Most anterior point of tooth cusp

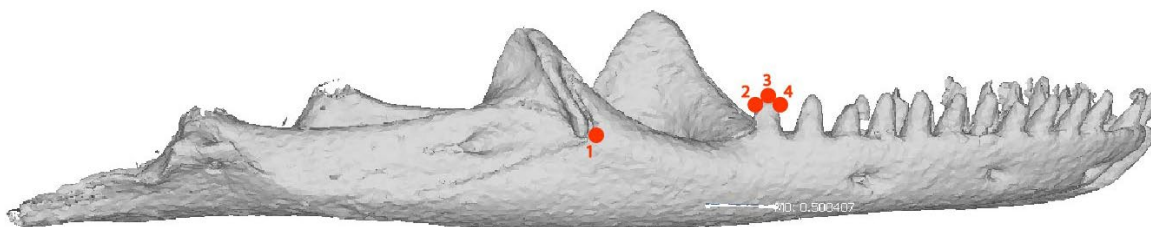Table 4: Landmarks used in fossil and fossil + extant analyses.

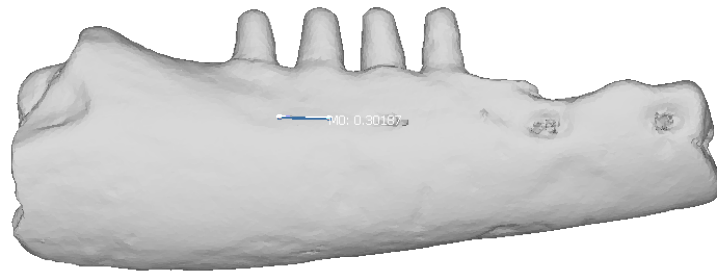Figure 5: Right mandible in lateral view (X. vigilis).

18

Figure 6: Image of fossil specimen AMNH 3821 Palaeoxantusia fera.

Previous morphometric analyses of lizard lower jaws have shown that this method is effective at distinguishing between species of extant taxa for the following squamate groups: *Agamidae* ((Diong and Lim, 1998), *Lacertidae* (Capula et al., 2009), *Liolaemidae* (Minoli et al., 2016), *Pareidae* (Wang et al., 2020), and *Scincidae* (Hollenshead, 2011). Because this study is interested in exploring the hidden diversity of extinct species, it is necessary to perform these initial analyses among extant xantusiids to illustrate the effectiveness of the method with respect to *Xantusiidae* and to indicate the viability of employing this method on extinct taxa.

Morphometric Analysis/Shape Analysis

Shape analysis. This analysis was conducted on two data sets: one data set containing all the extant specimens and one data set containing all the fossil specimens. To align the data, I ran a Procrustes superimposition using the programs MorphoJ and IBM SPSS Statistics Software. The Procrustes superimposition was used to scale the landmark sets and to eliminate the shape differences attributed to absolute shape size, orientation, and translation (Gray et al., 2017).

Results

Geometric Morphometrics

Extant analysis. PC1, which accounts for 43.20% of total shape variation in the mandible, fails to demonstrate a substantial separation between the three clades of *Xantusiidae* (Tab. 5, Fig. 7). Five out of six species of *Lepidophyma* plot on the left side of the PC1 axis, and 10 out of 13 species of *Xantusia* plots on the right side of the PC1 axis. Only one individual within *Lepidophyma* (*Lepidophyma smithii*) falls within the *Xantusia* hull. PC2 summarizes 18.14% of total mandible shape variation and reveals a separation between *Xantusia* and *Lepidophyma*. *Xantusia* occupies the morphospace at the top half of the PC2 axis, and *Lepidophyma* occupies the bottom half of the PC2 axis. Overall, *Xantusia* occupies the largest amount of morphospace. The clade *Cricosaura typica* plots consistently in the center of the morphospace occupied by *Xantusia* but it represents a single specimen, the only one that could be obtained for this analysis and is an underestimate of *Cricosaura* morphotype. Taxonomic groups appear to cluster morphologically on the PC2 axis. PC3 summarizes 14.63% of variation, and PC4 and beyond account for less than 25% of the variation combined.

Principal Component Analysis (PCA): Extant		
PC	Eigenvalues	% Variance
1	0.00277794	43.204
2	0.00116625	18.138
3	0.00094090	14.633
4	0.00045939	7.145
5	0.00033980	5.285
6	0.00020277	3.154
7	0.00017031	2.649
8	0.00011824	1.839
9	0.00008352	1.299
10	0.00007221	1.123
11	0.00003506	0.545
12	0.00002367	0.368
13	0.00002125	0.331
14	0.00000903	0.140
15	0.00000495	0.077
16	0.00000333	0.052
17	0.00000085	0.013
18	0.00000027	0.004
19	0.00000005	0.001

Table 5: Table of principal component values, eigenvalues, and percent variance values from the principal component analysis of extant xantusiids.
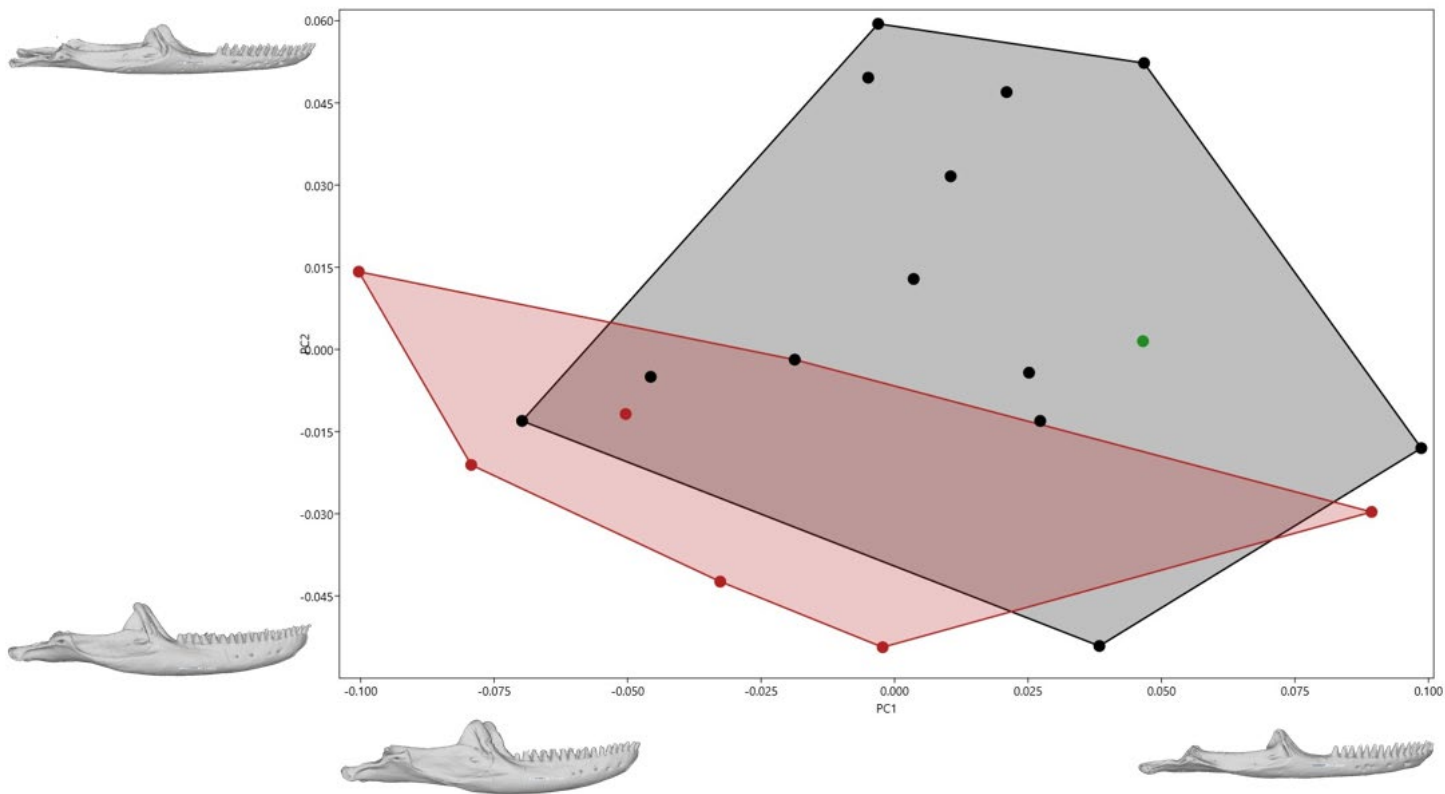
*Figure 7: Plot of principal components 1 and 2 for the extant xantusiid geometric morphometric dataset. Convex hulls outline the extent of each clade's morphospace. Different clades are represented using different colors for each clade. (Xantusia = **Black**; Lepidophyma = **Red**; Cricosaura = **Green**). Images of lower jaws along PC axes represent those at maximum and minimum scores in respective PC axes to illustrate shape changes associated with PC axes (lateral view).*

Fossil analysis. The first two PC axes summarize over 99% of the total shape variation of the mandible (Tab. 6). PC3 and beyond account for less than 1% of shape variance. PC1, which summarizes 76.80% of total shape variation in the mandible, demonstrates separation among all but two of the five fossil specimens. PC2 accounts for 22.35% of total shape mandible variation and shows separation between the five specimens. The two specimens of the species *Palaeoxantusia borealis* (SMNH 1435 and SMNH 1493.C/SASKC) plot in two distinct positions in the morphospace. *Palaeoxantusia borealis* (SMNH 1493.C/SASKC) plots in the middle of the morphospace, whereas *Palaeoxantusia borealis* (SMNH 1435), which allegedly belongs to the same species, falls in the extremes of both the PC1 and PC2 axes. Specimens AMNH 3821 (*Palaeoxantusia fera*) and SDMNH 131572 ("*Palaeoxantusia" sp.*) plot relatively close to each other on both the PC1 and PC2 axes.

Principal Component Analysis (PCA): Fossil

PC	Eigenvalues	% Variance
1	0.00595760	76.802
2	0.00173385	22.352
3	0.00006549	0.844
4	0.00000014	0.002

Table 6: Tables of principal component values, eigenvalues, and percent variance values from the principal component analysis of fossil xantusiids.
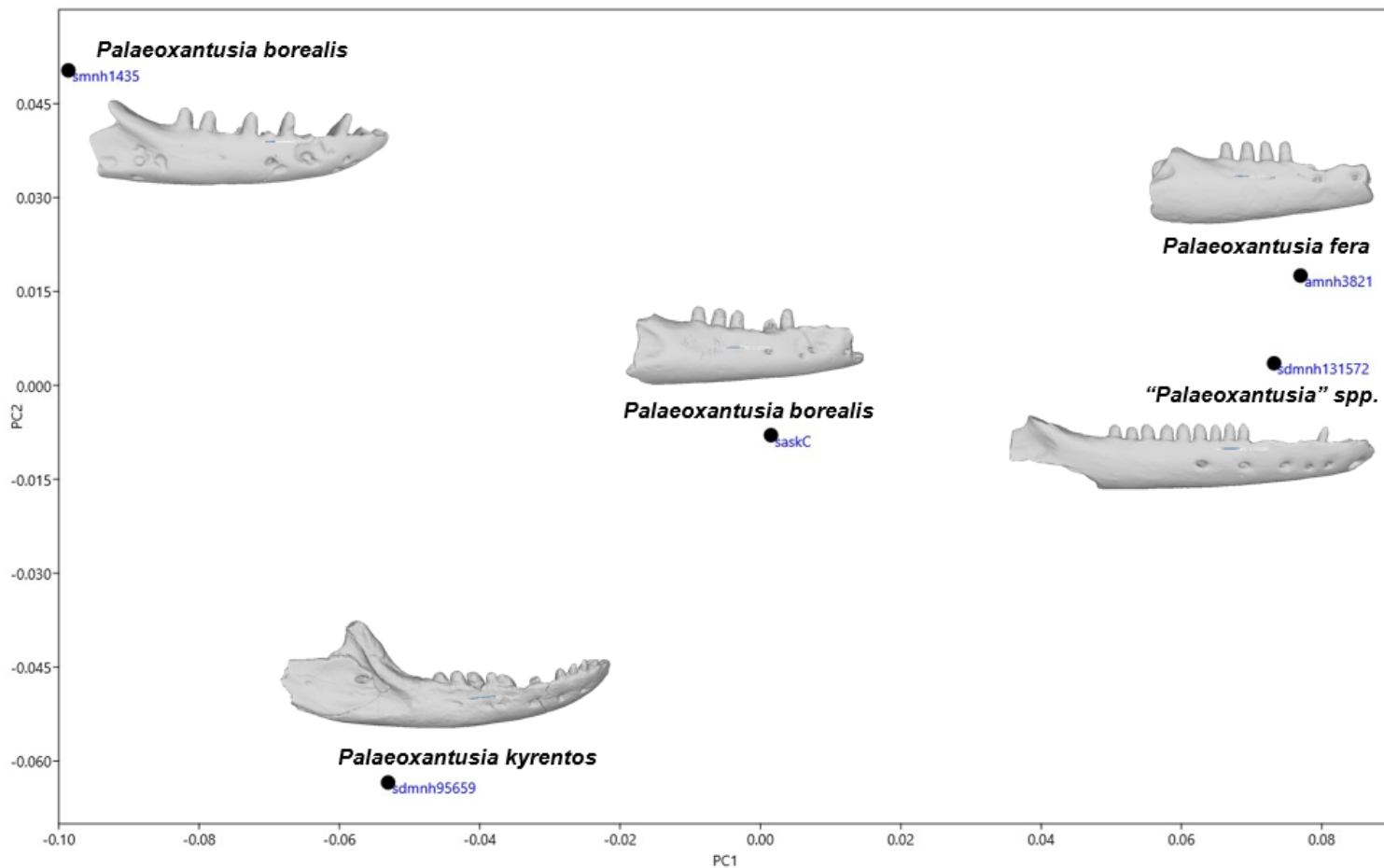

Figure 8: Plot of principal components 1 and 2 for the fossil xantusiid geometric morphometric dataset. Points are labeled by specimen number. CT scan renderings are displayed next to their respective specimens.

Principal Component Analysis (PCA): Extant + Fossil		
PC	Eigenvalues	% Variance
1	0.00205904	63.545
2	0.00100539	31.028
3	0.00014076	4.344
4	0.00003511	1.083

Table 7: Tables of principal component values, eigenvalues, and percent variance values from the principal component analysis of extant and fossil xantusiids.
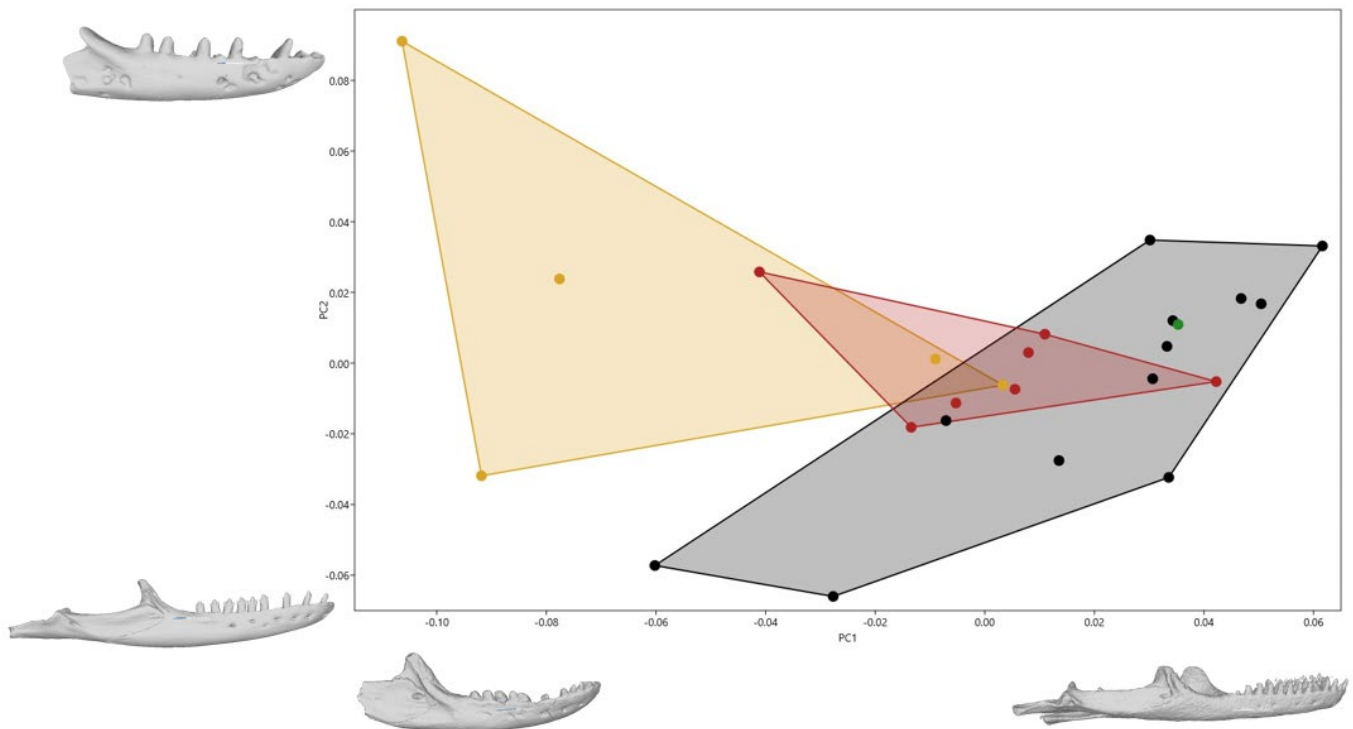

*Figure 9: Plot of principal components 1 and 2 for the extant and fossil xantusiid geometric morphometric dataset. Convex hulls outline the extent of each clade's morphospace. Different clades are represented using different colors. (Xantusia = **Black**; Lepidophyma = **Red**; Cricosaura = **Green**; Palaeoxantusia = **Yellow**). Shapes along PC axes represent those at maximum and minimum scores in respective PC axes to illustrate shape changes associated with PC axes (lateral view).*

Combined extant and fossil analysis. The first two PC axes summarize 94.57% of the total shape variation of the mandible (Tab. 7). PC3 and beyond account for 5.43% of variance. PC1, which accounts for 63.55% of total shape variation in the mandible, demonstrates substantial separation between crown *Xantusiidae* and *Palaeoxantusia*. PC2 summarizes 31.03% of total mandible shape variation, but it does not appear to reveal a substantial separation between crown *Xantusiidae* and *Palaeoxantusia*. *Palaeoxantusia* and *Xantusia* occupy the largest amount of morphospace. The *Lepidophyma* convex hull plots in the middle of the morphospace. *Cricosaura* plots consistently within the *Xantusia* hull, but as mentioned above, this is an underestimate of the clade's morphospace. Taxonomic groups appear to cluster morphologically. However, there appears to be more variation across both axes in *Palaeoxantusia* than within any other clade.

The PCA plot for PC1 versus PC2 was rendered using the age of the specimens (Modern v. Fossil) as the category for convex hulls (Fig. 9). The fossil convex hull plots in the left side of the morphospace, and the modern convex hull plots in the right side of the morphospace. The two groups overlap in the center of the morphospace, with 1 modern specimen (*Lepidophyma flavimaculatum*) plotting in the fossil morphospace and 2 fossil specimens (AMNH 3821 and SDMNH 131572) plotting in the modern morphospace. Overall, there is a separation between Fossil and Extant taxa visible on PC1. The clades *Xantusia* and *Cricosaura typica* plot on the right side of the PC1 axis, but the tropical night lizards (*Lepidophyma*) and the insular species *Xantusia riversiana* plot in the middle of the PC1 axis, intermediate between the Extant and Fossil hulls.
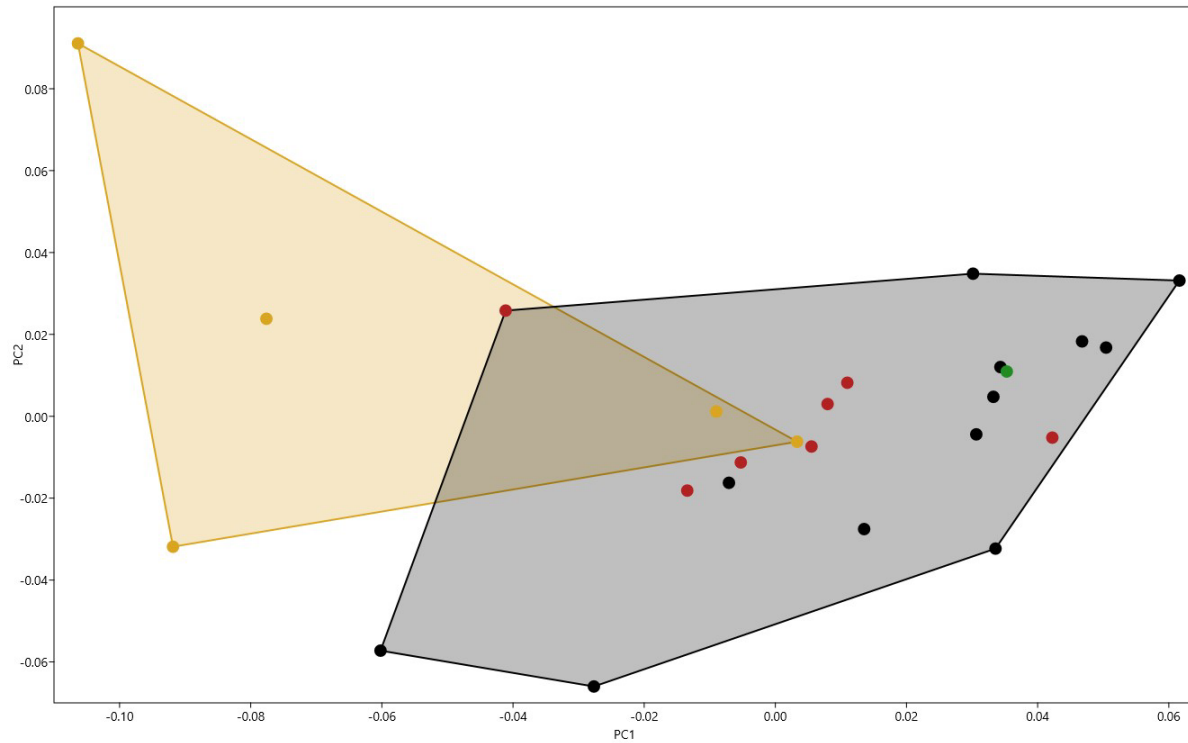
Figure 10: Plot of principal components 1 and 2 for the extant and fossil xantusiid geometric morphometric dataset. Convex hulls outline the extent of age group's (Modern v. Fossil) morphospace. Different groups are represented using different colors. (Fossil = Yellow and Modern = Black). Different clades are represented using different color points. (Xantusia = Black; Lepidophyma = Red; Cricosaura = Green; Palaeoxantusia = Yellow).

Discussion

The results of the morphometrics analysis demonstrate that *Pan-Xantusiidae* is likely more speciose previously thought, with implications for extinction survival and post-KPg radiation.

Morphometrics

Extant analysis.

PC1 is likely driven by the length of the articular and the distance between the coronoid and the posterior tip of the articular. PC2 is likely driven by the size of the coronoid and the distance between the coronoid and the anterior tip of the articular. Generally, *Xantusia* plot in the upper half of the PC2 axis, meaning that they typically possess a shorter coronoid. Gauthier (*pers. comm*.) has suggested that, instead of *Xantusia riversiana* being an example of insular gigantism, the mainland species of Xantusia (all save for *X. riversiana*) are examples of dwarfism. *Lepidophyma* and *X. riversiana* tend to be larger than the mainland *Xantusia* and are shown on this plot as having taller coronoids, illustrating a robustness in these specimens that is lacking in mainland *Xantusia*. Most of the mainland *Xantusia* (*Xantusia vigilis, X. sonora, X. magdalena, X. bolsonae,* and *X. bezyi*) plot together in a morphospace that is separate from that occupied by *Lepidophyma* and *X. riversiana*. These differences in morphospace can be attributed to their differing ecologies. Mainland *Xantusia* exhibits the microhabitat specialization for which the clade is well-known (living in rock crevices and within decaying and dead plants), but *Lepidophyma* and *X. riversiana* present more generalist terrestrial ecologies and do not necessarily show morphologies highly suited for one microhabitat or another.

Saxicolous, crevice-dwelling species (e.g., *Xantusia henshawi*) plot on the far-right end of the PC1 axis and on the lower end of the PC2 axis. Increasing the length of the articular creates an

28

elongate skull, characteristic of these crevice-dwelling species. As mentioned above, night lizards inhabiting rock crevices typically show flattened, elongate skulls compared to more terrestrial generalist night lizard species. These morphologies are likely more conducive to the small, enclosed nature of the crevices. Individuals of the same extant species do not necessarily plot within the same region of morphospace. Some specimens that belong to the same species occupy similar regions of the morphospace (*Xantusia riversiana;* see Fig. 7). However, two specimens of the species *Xantusia vigilis* plot in distinctly separate places in morphospace, and thus these specimens are morphologically distinct from each other. Previous work has suggested the existence of numerous cryptic subclades at the species level within *Xantusia*, and, more specifically, has shown morphological differences between different populations of *Xantusia vigilis* in Southern California (Leavitt et al., 2007). Diversity at the subspecies level may be why the two specimens of *Xantusia vigilis* (LACM 134509 and LACM 123671) occupy two separate areas of morphospace.

The results of this analysis show that geometric morphometrics can be used to distinguish between the *Lepidophyma* and *Xantusia* clades of night lizard, due in most part to mainlaid *Xantusia's* morphological differences. Flattened, elongate skulls (signaled by plotting far to the right on PC1 and plotting low on PC2) are consistently indicative of crevice-dwelling species (*Xantusia henshawi*). Individuals with taller coronoids and more robust articulars tend to belong to *Lepidophyma* or to the insular *Xantusia riversiana*.

Fossil analysis.

It is less clear what drives PC1 than PC2. PC2 is likely driven by the distance between the last tooth in the tooth row and the anterior most point of maximum curvature on the suture between the dentary and the coronoid, as evidenced by the two specimens that sit at the extremes of the PC2 axis (SDMNH 95659 and SMNH 1435).

The patterns detected in the extant analysis can be used to infer the affiliations of fossil specimens. The specimens SMNH 1435 (holotype) and SMNH 1493.C are both identified as *Palaeoxantusia borealis* (Holman, 1972) on the museum labels (the former identified by Holman and the latter unknown). However, in this analysis, these specimens occupy substantially different points in the morphospace, reflecting differences in dentary lengths between the specimens (Fig. 8). As mentioned above, crevice-dwelling species tend to have more elongate jaws, so this difference in morphology (longer dentary in SMNH 1493.C) may indicate this ecology. In the extant-only analysis, individuals of the same species occupy the same or nearly the same positions in the morphospace (Fig. 7). Thus, this analysis suggests that specimens SMNH 1435 and SMNH 1493.C belong to the different species. Multiple lizard species are known from the Cypress Hills Formation of Saskatchewan (Holman, 1972), and multiple species of Palaeoxantusia have been found to have coexisted in other localities (Schatzinger, 1980). Specimens AMNH 3821 (*Palaeoxantusia fera*) and SDMNH 131572 (*Palaeoxantusia sp.*) are located near each other on both the PC1 and PC2 axes of the PCA plot (Fig. 8). Thus AMNH 3821 and SDMNH 131572 presumably represent the same species of stem-xantusiid, likely *Palaeoxantusia fera*.

Combined extant and fossil analysis.

In this analysis, it is also less clear what drives PC1 than PC2. PC2 is likely driven by dentition shape as evidenced by the morphology of the two taxa that fall at the extremes (the fossil specimen SMNH 1435 and LACM 108770, the Island Night Lizard *Xantusia riversiana*). Three of the four landmarks used in the combined extant and fossil analysis were placed on the last tooth in the tooth row. The dentitions of SMNH 1435 and LACM 108770 (*Xantusia riversiana*) differ, the former possesses a unicuspid tooth with a flattened cusp, whereas the latter possesses a tricuspid tooth. As the PC2 axis increases, there is a decrease in the number of cusps and in the pointedness of the tooth. Teeth are preferentially preserved in the fossil record, so if PC2 is driven by dentition shape, even some of the most fragmentary of fossils should be identifiable

.

This analysis also revealed that fossil and modern xantusiids occupy distinctly different areas in morphospace. Modern xantusiids exhibit a wide range of ecologies, including crevice-dwelling, saxicoline, terrestrial, and arboreal. Based on their limited morphospace relative to modern xantusiids, stem-xantusiids may have lacked the same variety of niche occupation. Tooth complexity decreases as PC2 increases. The fossil SMNH 1435 possesses unicuspid teeth (low complexity) which can be indicative of an omnivorous generalist diet (Martinez et al., 2021). *Xantusia riversiana*, on the other hand, possesses tricuspid teeth which seem better adapted for cracking the exoskeletons of small invertebrates (Martinez et al., 2021). Generalists tend to be more successful during and immediately after mass extinctions – they can exploit more resources than their specialized counterparts – and, as a result, tend to be the progenitors of clades. If the fossil SMNH 1435 (and others like it) is considered a dietary generalist, then its assignment (*Palaeoxantusia borealis*) as a basal xantusiid aligns with the common hypothesis of generalists as the originators of clades.

Rock crevices and caves were probably advantageous microhabitats in avoiding the environmental turmoil of the end-Cretaceous extinction., and terrestrial and arboreal microhabitats were likely inhospitable during this time. These results show clear morphological differences, and, due to the link between morphology and ecology, I infer that these two groups (stem and modern xantusiids) occupied different niches. These differences are so great that I can confidently infer that the niches available during the K-Pg extinction were different to present. Further, based on the ecological and climatic upheaval associated with the K-Pg extinction, it is likely that the stem group were limited in their niche options, compared to modern xantusiids.

General overview.

This analysis showed that geometric morphometrics is effective in separating xantusiids by ecology and by clade. This method is useful in delimiting species, although this task becomes more complicated in the case of species complexes like *Xantusia vigilis*. As mentioned earlier, Palaeoxantusia is a wastebasket taxon; while this research was unable to fully disentangle this clade, I was, however, able to assign one previously unnamed specimen to a species, and I challenge the prior species assignments of specimens. Further research with a larger sample size, particularly more fossil xantusiids, is necessary to analyze and interpret intra-species morphological disparity. Another useful analysis may be looking at multiple individuals from each species to determine how much intra-species variation occurs between clades.

Xantusiid Cretaceous Diversity and Post-KPg Speciation

Even though the sample size of stem-xantusiids investigated in this thesis is limited, the morphometric analysis conducted clearly shows that there are likely errors in the assignment of these specimens to species. Research into extant *Xantusiidae* has shown that this clade is likely more speciose than current estimates suggest (Leavitt et al, 2007). Past work has focused on the molecular evidence for higher levels of night lizard diversity (Hedges et al., 1991), but the present study demonstrates morphological disparity among and within species of xantusiids.

Xantusiids are notable for their microhabitat specialization, particularly saxicolous, crevice-dwelling species like *Xantusia henshawi*, *X. sanchezi*, and *Lepidophyma gaigeae*. Field et al. (2018) revealed how K-Pg global forest collapse aligned with a mass extinction of arboreal bird species and linked this to the post-K-Pg radiation of crown arboreal birds. Essentially, if an animal's niche disappears, that animal faces a higher risk of extinction due to loss of habitat and resources. Modern night lizards seek shelter in rock crevices, caves, and decaying plants. If Cretaceous xantusiids exhibited similar ecologies, their persistence and radiation following the K-Pg extinction may have been contingent on their ability to seek refuge in microhabitats such as rocks and caves that were not damaged or decreased by extraterrestrial impact and climatic consequences.

No fossil xantusiids plot in the region of morphospace (far right PC1, bottom PC2) associated with highly specialized crevice dwellers like *Xantusia henshawi*. This may indicate that, while K-Pg xantusiids were small enough to inhabit microhabitats, they had yet to acquire the specialized morphologies associated with these environments. Although, it is possible that the fauna of such microhabitats was not preserved and were not featured in the present study's small

sample. For example, fossil xantusiids lack the elongate dentary that saxicolous xantusiids possess. The morphology of these basal xantusiids may offer a snapshot of the clade prior to the microhabitat specialization for which it is so widely known.

Possible Shortcomings and Future Directions

This analysis runs the risk of overestimating the appropriateness of imposing methods used on modern taxa onto extinct ones and the validity of results. While related, these specimens represent animals with over 60 million years of evolutionary change between them which may impact the viability of these analyses. Additionally, the small sample size for the fossil analysis limits the inferences that can be made. The sample size reduces the number of landmarks that can be placed on the specimen and four landmarks may not represent all the taxonomically important data.

One interesting avenue of research that was not pursued in this study is the attempt to correlate extinct morphologies with extant microhabitat specializations. Species of xantusiid that inhabit rock crevices, like *Xanusia henshawi* (the granite night lizard), exhibit phenotypic adaptations to such habitats (e.g., flattened bodies). Identifying the specific morphologies, especially osteological correlates which may be observable in the fossil record, that correspond to these microhabitats in extant species and comparing these morphologies against extinct ones would further explain what role microhabitat specialization played in the survival and abundance of night lizards post-K-Pg. One significant limitation, however, is the lack of complete fossil specimens. Yet another compelling area of future research is the role of anthropogenically-sourced materials as possible microhabitats for night lizards. The current climate crisis (which is human-induced) may reduce the amount of vegetation available for xantusiids to inhabit, causing

34

them to seek out alternative shelter. Tropical night lizards, for example, are documented as living in archaeological ruins in Central America (Bezy, 2019).

Acknowledgements

References

Alvarez, L. W., W. Alvarez, F. Asaro, and H. V. Michel. 1980. Extraterrestrial cause for the

    Cretaceous-Tertiary extinction. Experimental results and theoretical interpretation, Science,

    208, 1095-1108.

Auliya, M. A., and A. P. Koch. 2020. Visual Identification Guide for the Monitor Lizard Species

    of the World (Genus Varanus). 7-200.

Barbeito-Andrés, J., M. Anzelmo, F. Ventrice, and M. L. Sardi. 2012. Measurement error of 3D

    cranial landmarks of an ontogenetic sample using Computed Tomography. Journal of Oral

    Biology and Craniofacial Research, **2**, 77-82.

Barbour, T. 1914. A contribution to the zoogeography of the West Indies, with special reference

    to amphibians and reptiles. Memoirs of the Museum of Comparative Zoology, **44**, 209-359.

Bezy, R. L. 1982. *Xantusia vigilis*, Baird Desert Night Lizard. Catalogue of American

    Amphibians and Reptiles, 302.1-302.3.

Bezy, R. L. 1989. Night lizards: the evolution of habitat specialists. Terra, **28**, 29-34.

Bezy, R. L., D. H. Leavitt, M. D. Robinson, and K. Bolles. 2020. Biogeography of night lizards

    (*Xantusia*) in Arizona. Sonoran Herpetologist, **33**, 28-40.

Bezy, R.L., and J.L. Camarillo-Rangel. 2002. Systematics of Xantusiid lizards of the genus

    Lepidophyma. Contributions in Science, Natural History Museum, Los Angeles County,

    493, 1-41.

Bezy, R. L. 2019. Night lizards: Field memoirs and a summary of the *Xantusiidae*. Rodeo, NM:

    ECO Herpetological Wear & Publishing.

Buser, T. J., B. L. Sidlauskas, and A. P. Summers. 2018. 2D or not 2D? Testing the utility of 2D

    vs. 3D landmark data in geometric morphometrics of the Sculpin subfamily *Oligocottinae*

    (Pisces; Cottoidea). The Anatomical Record, **301**, 806–818.

Capula, M., S. Chiantini, L. Luiselli, and A. Loy. 2009. Size and shape in Mediterranean insular lizards: patterns of variation in *Podarcis raffonei, P. sicula* and *P. wagleriana* (Reptilia: Squamata: Lacertidae). Aldrovandia, **5**, 217–227.

Cardini, A., and M. Chiapelli. 2020. How flat can a horse be? Exploring 2D approximations of 3D crania in equids. Zoology, **139**, 1–15.

Cardinia, A. 2014. Missing the third dimension in geometric morphometrics: how to assess if 2D images really are a good proxy for 3D structures. Hystrix, the Italian Journal of Mammalogy, **25**, 73–81.

Conrad, J. L. 2008. Phylogeny and systematics of squamata (reptilia) based on morphology. Bulletin of the American Museum of Natural History, 1–182.

Diong, C. H., and S. S. L. Lim. 1998. Taxonomic review and morphometric description of *Bronchocela cristatella* (Kuhl, 1820) (Squamata: Agamidae) with notes on other species in the genus. The Raffles Bulletin of Zoology, **46**, 345-359.

Estes, R. 1976. Middle Paleocene Lower Vertebrates from the Tongue River Formation, Southeastern Montana. Journal of Paleontology, **50**, 500-520.

Estes, Richard. 1983. Sauria Terrestria, Amphisbaenia. Handbuch der Palaoherpetologie, Part 10A. Gustav Fischer Verlag, Stuttgart.

Estes, R., K. de Queiroz, and J.A. Gauthier. 1988. Phylogenetic relationships within Squamata. In R. Estes and G.K. Pregill (editors), Phylogenetic relationships of the lizard families, essays commemorating Charles L. Camp: 119–281. Stanford, CA: Stanford University PressFellers,

G. M., and C. A. Drost. 1991. *Xantusia riversiana*, Cope Island Night Lizard. Catalogue of American Amphibians and Reptiles, 518.1-518.4.

Field, D. J., A. Bercovici, J. S. Berv, R. Dunn, D. E. Fastovsky, T. R. Lyson, V. Vajda, and J. A. Gauthier. 2018. Early evolution of modern birds structures by global forest collapse at the End-Cretaceous Mass Extinction. Current Biology, **28**, 1825-1831.

Gauthier, J. A., M. Kearney, J. A. Maisano, O. Rieppel, and A. D. B. Behlke. 2012. Assembling the squamate tree of life: Perspectives from the phenotype and the fossil record. Bulletin of the Peabody Museum of Natural History, **53**, 3-308.

Gray, J. A., M. C. McDowell, M. N. Hutchinson, and M. E. H. Jones. 2017. Geometric morphometrics provides an alternative approach for interpreting the affinity of fossil lizard jaws. Journal of Herpetology, **51**, 375-382.

Green, M., and J. A. Holman. 1977. A Late Tertiary stream channel fauna from South Bijou Hill, South Dakota. Journal of Vertebrate Paleontology, **51**, 543-547.

Guha, S., and V. K. Kashyap. 2006. Molecular identification of lizard by RAPD & FINS of mitochondrial 16s rRNA gene. Legal Medicine, **8**, 5-10.

Hecht, M. K. 1959. Amphibians and reptiles. In P. McGrew (ed.), The geology and paleontology of the Elk Mountain and Tabernacle Butte Area, Wyoming. American Museum of Natural History Bulletin, **117**, 130-146.

Hedges, S. B., R. L. Bezy, and L. R. Maxson. 1991. Phylogenetic relationships and biogeography of xantusiid lizards, inferred from mitochondrial DNA sequences. Molecular Biology and Evolution, **8**, 767–780.

Hollenshead, M. G. 2011. Geometric morphometric analysis of cranial variation in the *Egernia depressa* (Reptilia: Squamata: Scincidae) species complex. Records of the Western Australian Museum, **26**, 138–153.

Holman, J. A. 1972. Herpetofauna of the Calf Creek local fauna (Lower Oligocene: Cypress

　　Hills Formation) of Saskatchewan. Canadian Journal of Earth Sciences, **9**, 1612–1613.

Hull, P. 2015. Life in the aftermath of mass extinctions. Current Biology, **25**, R941–R952.

Hull, P. M., and S. A. F. Darroch. 2013. Mass extinctions and the structure and function of

　　ecosystems. The Paleontological Society Papers, **19**, 115–156.

IBM Corp. Released 2020. IBM SPSS Statistics for Windows, Version 27.0. Armonk, NY: IBM

　　Corp.

Langebartel, Dave A. 1953. The reptiles and amphibians. In Hatt, Robert T., Faunal and

　　archaeological researches in Yucatan caves. Cranbrook Institute of Science Bulletin, **33**, 97-

　　108.

Lawing, A. M., and P. D. Polly. 2010. Geometric morphometrics: recent applications to the study

　　of evolution and development. Journal of Zoology, **280**, 1–7.

Leavitt, D. H., R. L. Bezy, K. A. Crandall, and J. W. Sites Jr. 2007. Multi-locus DNA sequence

　　data reveal a history of deep cryptic vicariance and habitat-driven convergence in the desert

　　night lizard *Xantusia vigilis* species complex (Squamata: Xantusiidae). Molecular Ecology,

　　16, 4455–4481.

Longrich, N. R., B.-A. S. Bhullar, and J. A. Gauthier. 2012. Mass extinction of lizards and

　　snakes at the Cretaceous–Paleogene boundary. Proceedings of the National Academy of

　　Sciences, **109**, 21396–21401.

Makádi, L., and R. L. Nydam. 2015. A new durophagous scincomorphan lizard genus from the

　　Late Cretaceous Iharkút locality (Hungary, Bakony Mts). Palaontologische Zeitschrift, **89**,

　　925–941.

Martinez, S. A., K.M. Jenkins, B.-A. S. Bhullar. 2021. Dental morphology of Procolophonidae and implications for Permo-Triassic post-extinction recovery [abstract]. In: Society of Vertebrate Paleontology 81st Annual Meeting Program and Abstracts.

Mautz, W. J. 1979. The metabolism of reclusive lizards, the *Xantusiidae*. Copeia, **1979**, 577–584.

Minoli, I., M. Morando, and L. J. Avila. 2016. Sexual dimorphism and interspecific head variation in the *Liolaemus melanops* complex (Squamata: Liolaemini) based on geometric morphometrics. Herpetological Journal, **26**, 225-235.

Mitteroecker, P., and P. Gunz. 2009. Advances in Geometric Morphometrics. Evolutionary Biology, **35**, 235-247.

Noonan, B. P., J. B. Pramuk, R. L. Bezy, E. A. Sinclair, K. de Queiroz, and J. W. Sites Jr. 2013. Phylogenetic relationships within the lizard clade Xantusiidae: Using trees and divergence times to address evolutionary questions at multiple levels. Molecular Phylogenetics and Evolution, **69**, 109–122.

Nydam, R. L. 2013. Squamates from the Jurassic and Cretaceous of North America. Palaeobiodiversity and Palaeoenvironments, **93**, 535–565.

Nydam, R. L., and B. M. Fitzpatrick. 2009. The occurrence of contogenys-like lizards in the late cretaceous and early tertiary of the western interior of the U.S.A. Journal of Vertebrate Paleontology, **29**, 677–701.

Nydam, R. L., T. B. Rowe, and R. L. Cifelli. 2013. Lizards and snakes of the Terlingua Local Fauna (late Campanian), Aguja Formation, Texas, with comments on the distribution of paracontemporaneous squamates throughout the Western Interior of North America. Journal of Vertebrate Paleontology, **33**, 1081–1099.

Peters, W. 1863. Über eine neue von Hrn. Dr. Gundlach auf Cuba entdeckte Sauriergattung,

    Cricosaura typica Gundlach et Peters. Monatsberiche der Königlichen Akademie der

    Wissenschaften Berlin*, **1863***, 362-370.

Reynoso, V.-H., and G. Callison. 2000. A new scincomorph lizard from the Early Cretaceous of

    Puebla, México. Zoological Journal of the Linnean Society, **130**, 183-212.

Robertson, D. S., M. C. McKenna, O. B. Toon, S. Hope, and J. A. Lillegraven. 2004. Survival in

    the first hours of the Cenozoic. Geological Society of America Bulletin, **116**, 760.

Rohlf, F. J. 1990. Morphometrics. Annual Review of Ecology and Systematics, **21**, 299–316.

Rohlf, F. J. 2006. tpsDig, Digitize Landmarks and Outlines, Version 2.05. Stony Brook, NY:

    Department of Ecology and Evolution, State University of New York.

Roy, K., and M. Foote. 1997. Morphological approaches to measuring biodiversity. Trends in

    Ecology & Evolution, **12**, 277–281.

Savage, J. M. 1963. Studies on the lizard family *Xantusiidae* IV. The Genera. Los Angeles

    County Museum Contributions in Science, **71**, 1-38.

Savage, J. M. 1964. Studies on the lizard family *Xantusiidae*. V. The Cuban Night Lizard,

    Cricosaura typica Gundlach and Peters. Copeia, **1964**, 536–542.

Schatzinger, R. A. 1980. New species of *Palaeoxantusia* (Reptilia: Sauria) from the Uintan

    (Eocene) of San Diego Co., California. Journal of Vertebrate Paleontology, **54**, 460–471.

Simões, T. R., M. W. Caldwell, M. Tałanda, M. Bernardi, A. Palci, O. Vernygora, F. Bernardini,

    L. Mancini, and R. L. Nydam. 2018. The origin of squamates revealed by a Middle Triassic

    lizard from the Italian Alps. Nature, **557**, 706–709.

Sinclair, E. A., R. L. Bezy, K. Bolles, J. L. Camarillo, K. A. Crandall, and J. W. Sites. 2004.

    Testing species boundaries in an ancient species complex with deep phylogeographic

    history: genus *Xantusia* (Squamata: Xantusiidae). The American Naturalist, **164**, 396–414.

Smith, K. T., and J. A. Gauthier. 2013. Early Eocene lizards of the Wasatch Formation near

    Bitter Creek, Wyoming: Diversity and paleoenvironment during an interval of global

    warming. Bulletin of the Peabody Museum of Natural History, **54**, 135–230.

Sullivan, R. M. 1982. Fossil lizards from Swain Quarry "Fort Union Formation," Middle

    Paleocene (Torrejonian), Carbon County, Wyoming. Journal of Paleontology, **56**, 996–

    1010.

Telford, S. R., and H. W. Campbell. 1970. Ecological observations on an all-female population

    of the lizard *Lepidophyma flavimaculatum* (*Xantusiidae*) in Panamá. Copeia, **1970**, 379–

    381.

Van Denburgh, J. The species of the genus *Xantusia*. Proceedings of the California Academy of

    Science, **5**, 523-534.

Vicario, S., A. Caccone, and J. Gauthier. 2003. Xantusiid "night" lizards: a puzzling

    phylogenetic problem revisited using likelihood-based Bayesian methods on mtDNA

    sequences. Molecular Phylogenetics and Evolution, **26**, 243–261.

Volume Graphics. 2021. VGStudio Max 3.5.2. Heidelberg, Germany.

Wang, P., J. Che, Q. Liu, K. Li, J. Q. Jin, K. Jiang, L. Shi, and P. Guo. 2020. A revised

    taxonomy of Asian snail-eating snakes *Pareas* (Squamata, Pareidae): evidence from

    morphological comparison and molecular phylogeny. ZooKeys, **939**, 45–64.

Woolley, C. H., J. R. Thompson, Y. H. Wu, D. J. Bottjer, and N. D. Smith. 2022. A biased fossil

    record can preserve reliable phylogenetic signal. Paleobiology, **2022**, 1-16.

Zelditch, M. L., D. L. Swiderski, H. D. Sheets, and W. L. Fink. 2004. Geometric morphometrics

for biologists: A primer: 1-21. Waltham, MA: Elsevier Academic Press.

Zweifel, R. G., and C. H. Lowe. 1966. The ecology of a population of *Xantusia vigilis*, the desert

night lizard. American Museum Novitates, **2247**, 1–58.

.