Spring 4-25-2014

Body Size and Species Richness Changes in Glyptosaurinae (Squamata: Anguidae) Through Climatic Transitions of the North American Cenozoic

Sara ElShafie
University of Nebraska-Lincoln, selshafie@huskers.unl.edu

BODY SIZE AND SPECIES RICHNESS CHANGES IN GLYPTOSAURINAE (SQUAMATA: ANGUIDAE) THROUGH CLIMATIC TRANSITIONS OF THE NORTH AMERICAN CENOZOIC

by

Sara J. ElShafie

A THESIS

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of the Requirements

For the Degree of Master of Science

Major: Earth and Atmospheric Sciences

Under the Supervision of Professor Jason J. Head

Lincoln, Nebraska

April, 2014

BODY SIZE AND SPECIES RICHNESS CHANGES IN

GLYPTOSAURINAE (SQUAMATA: ANGUIDAE)

THROUGH CLIMATIC TRANSITIONS OF THE NORTH AMERICAN CENOZOIC

Sara Joan ElShafie, M.S.

University of Nebraska, 2014

Adviser: Jason J. Head

Poikilothermic vertebrates offer excellent climate proxies based on relationships between environment and measurable variables such as body size and species richness. Relationships of these variables in lizards to environmental transitions over long time scales are poorly understood. Here I show that patterns of body size and species richness in a lizard clade, Glyptosaurinae (Squamata: Anguidae), correspond to known histories of paleotemperatures through the Cenozoic of North America. Glyptosaurines have the richest fossil record among North American Cenozoic lizards and exhibit a wide range of skull sizes. In order to estimate body size for glyptosaurines and other fossil anguids, I collected skull and snout-vent length measurements of extant anguimorph lizards from museum collections, and used these data to model body size from skull length. I used my glyptosaurine body size estimates to calculate mean annual paleotemperatures (MAPT) for the interior of North America through the Paleogene. I also obtained anguid species richness data at NALMA temporal resolution from museum collections and literature. I compared these data to known Paleogene climate histories for the interior of North America using published MAPT proxies derived from terrestrial paleofloras and mammalian fossils.

I found that maximum body size was comparable among the largest glyptosaurines from the early Eocene and the late Eocene, indicating paleotemperatures of about 19 – 20ºC during both intervals. Other terrestrial proxies indicated declines in continental MAPT of about 3 – 8ºC in the middle to late Eocene. This could indicate that overall temperature decreases remained above critical minimum temperatures for efficient metabolism in large lizards, or that some glyptosaurines behaviorally maintained body temperatures above cooler ambient levels in the late Eocene. Minimum MAPTs calculated using glyptosaurine body size estimates showed significant correlation with published continental MAPT proxies from other terrestrial indicators. I also found that glyptosaurine species richness peaked in the Wasatchian, followed by a decline through the remainder of the Paleogene; these patterns coarsely coincide with increases and decreases in continental MAPT.

ACKNOWLEDGEMENTS

I wish to thank my primary adviser, Dr. Jason Head, for his outstanding mentorship and professional training. I also thank my committee members, Dr. David Watkins and Dr. Ross Secord, for technical training and constructive suggestions. For helpful discussions on this project, I also thank my lab mate, Jorge Moreno-Bernal, and Drs. Robert Hunt, Jr., Chris Bell, Sarah Werning, Kevin Padian, Patricia Holroyd, Robert Sullivan, Jacques Gauthier, Hans Larsson, and Bhart-Anjan Bhullar. Drs. Jason Head and Chris Bell also provided access to obscure literature. Thank you to Greg Brown (University of Nebraska State Museum) for preparation of a new *Peltosaurus* specimen (UNSM 12102), without which I would not have had any complete limb material for small fossil anguid lizards.

For museum collections access and assistance, I thank the following individuals: Dr. Jason Head, Dr. Robert Hunt, Jr., Dr. Patricia Freeman, George Corner, Thomas Labedz (UNSM); Dr. Mark Norell, Carl Mehling, David Kizirian (AMNH); Dr. Hans Dieter-Sues, Dr. Matthew Carrano, Michael Brett-Surman (USNM); Alan Resetar, William Simpson (FMNH); Dr. Kevin Padian, Dr. Patricia Holroyd (UCMP); Dr. Carol Spencer, Dr. Jimmy McGuire (MVZ); Dr. Matthew Lamanna, Dr. José Padial, Amy Henrici, Steve Rogers (CM); Dr. Christopher Bell (CJB); Dr. Jacques Gauthier, Dr. Christopher Norris, Daniel Brinkman (YPM); Dr. Jeff Wilson, Dr. Adam Rountrey (UMMP); Toni Culver, Nicole Ridgwell (UCM); Dr. Christian Sidor, Ron Eng (UWBM). I am also grateful to Dr. Andrew Farke (RAM) for the loan of a *Peltosaurus* specimen (RAM 7104).

GRANT INFORMATION

Funding for research and conference travel was provided by the Friends of the Nebraska State Museum, the Nebraska Geological Society, the Society for Vertebrate Paleontology, the Doris O. and Samuel P. Welles Research Fund (UCMP), the Department of Earth and Atmospheric Sciences at the University of Nebraska Lincoln (UNL), and a Layman Award (to Dr. Jason Head, UNL).

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

Figure

CHAPTER 1

INTRODUCTION

The purpose of this research is to investigate relationships of evolutionary histories in lizards to known histories of climate change, and to test the predictive value of lizard body size for estimating minimum mean annual paleotemperatures for continental interiors. Body size and species richness correlate with climate in extant herpetofaunas; proxies derived from these variables in reptiles can therefore predict climate parameters and biotic response to climatic shifts (Scheibe, 1987; Zimmerman and Tracy, 1989; Böhme et al., 2008; Head et al., 2009, 2013). Recent studies have used body size in fossil squamates to infer paleoclimate for continental interiors in South America (Head et al., 2009) and Southeast Asia (Head et al., 2013). No squamate-based proxy exists for paleoclimate in North America, however. Existing proxies for climate in the Cenozoic of North America that are based on terrestrial indicators include morphology of paleofloras (e.g., Gregory and McIntosh, 1996; Wilf, 2000; Wing et al., 2000, 2005; Sandau, 2005); fossil land snail distributions (Evanoff et al., 1992); stable oxygen isotope ratios in *Coryphodon* bone and tooth enamel as well as freshwater gar scale enamel (Fricke and Wing, 2004); and *in vivo* stable oxygen isotope ratios from fossil ungulate tooth enamel, as well as diagenetic stable oxygen and carbon isotope ratios from fossil mammal bone fragments (Zanazzi et al., 2007; see Figure 13). These proxies indicate pronounced increases in mean annual paleotemperatures (MAPT) from the late Paleocene to the early Eocene, followed by potential decreases in the middle to late Eocene

(Evanoff et al., 1992; Sandau, 2005) and early Oligocene (Gregory and McIntosh, 1996; Zanazzi et al., 2007). Marine indicators provide the most continuous and temporally well-resolved climate records (e.g., Zachos et al., 2001, 2008); it is unknown how well these marine models correlate with terrestrial proxies.

This study tests the hypothesis that climatic transitions through the Paleogene in the continental interior of North America were drivers of body size and species richness change in glyptosaurine lizards (Squamata: Anguidae). This study also examines the implications of glyptosaurine body size for understanding climate. Glyptosaurines have a dense fossil record that spans multiple climatic transitions from the late Cretaceous through the Paleogene of North America. Glyptosaurines are most abundant in Paleogene deposits in the Great Plains and Western Interior of the United States (Gilmore, 1928; Meszoely, 1970; Sullivan, 1979; Figure 2). Glyptosaurines exhibit a wide range of body size and include some of the largest known taxa of any lizard clade in the Paleogene record of North America (Sullivan, 1979). Glyptosaurines were nested within extant members of Anguidae (Conrad, 2008), and had comparable head: limb length ratios to extant taxa (see Figures 4, 8). These factors make North American glyptosaurine lizards excellent model taxa for examining the relationship between faunal and environmental change over long timescales.

Body size in glyptosaurine lizards has never been estimated, and no study has previously examined the relationship between body size, species richness, and climate through deep time in any fossil lizard clade. In this study, I examine patterns of species richness and body size change in glyptosaurines and other fossil anguids through the Paleogene of North America in order to determine if 1) patterns of body size change and

2) patterns of species richness change in anguid lizards track known histories of continental climate change in the interior of North America through the Paleogene; 3) MAPT calculated from body size estimates for glyptosaurine lizards compare to previous estimates of MAPT from other terrestrial indicators for the Great Plains and Western Interior of North America.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York; CJB, Christopher J. Bell Lab, Jackson School of Geosciences, Austin; CM, Carnegie Museum of Natural History, Pittsburgh; FAM, Fricke Collection, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; MSU, Michigan State University, Lansing; MVZ, Museum of Vertebrate Zoology, Berkeley; RAM, Raymond M. Alfe Museum of Paleontology, Claremont; SDNHM, San Diego Natural History Museum, San Diego; UCM, University of Colorado Museum, Boulder; UCMP, University of California Museum of Paleontology, Berkeley; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; UNSM, University of Nebraska State Museum, Lincoln; USNM, United States National Museum, Washington, D.C.; UWBM, University of Washington Burke Museum, Seattle; YPM, Yale Peabody Museum, New Haven.

CHAPTER 2

MATERIALS & METHODS

Materials

I examined 114 fossil anguid specimens from museum collections and the literature representing at least 14 genera (including ten glyptosaurine genera; see Appendix 1) spanning the late Cretaceous, Paleogene and early Neogene of North America. I sampled specimens by North American Land Mammal Age (NALMA) because that was the best temporal resolution that I could consistently use in order to sample the glyptosaurine record (except for the early Arikareean, for which all of the specimens date to the base of the Gering Formation, 28.3 Ma; Tedford et al., 1996). All fossil specimens in the dataset include complete or partial cranial material (e.g., Figures 1, 4, 8). I measured lengths of complete skulls (from the anterior tip of the snout to the posterior extent of the quadrate), as well as lengths of individual cranial bones (frontal, parietal, maxilla, mandible, dentary; all measurements were taken in millimeters). Two glyptosaurine specimens also included a complete limb element (Figures 4, 8). No fossil anguids are known from complete skeletal material.

In order to estimate snout-vent length (SVL) from skull length for fossil anguids (see Methods), I measured 126 wet and 39 dry skeletal specimens from museum collections representing six genera of extant anguid lizards (Table 1, Appendix 2). I measured only specimens that included complete skulls and axial columns. In order to estimate SVL from skull length for larger glyptosaurines (see Methods), I also measured

29 wet and 7 dry skeletonized specimens of extant *Heloderma* (Table 2, Appendix 3) from museum collections that included complete skulls and axial columns. For both groups, I measured skull length from anterior snout tip to the posterior extent of the quadrate (dry specimens) or external ear opening (wet specimens).

Methods

Body Size Estimation for Small Anguids

In order to estimate complete skull length for fossil anguid specimens that included only partial cranial material, I used ratios of cranial bones (frontal, parietal, dentary, or mandible) to skull length based on complete skulls from specimens of close taxonomic affinity and/or comparable size (see Appendix 1).

I used anatomical measurements of extant lizards in linear regression models and calculated ratios to generate body size estimates for fossil anguid taxa (Appendices 1, 2, 3, Figure 6). The distribution of skull lengths in my fossil dataset was skewed to the right due to the size of the largest glyptosaurine skulls (Figure 3), so I divided the data into two size classes and used a different method to estimate SVL in each group. For the smaller glyptosaurines, (skull length ≤ 52 mm, the skull length for the largest *Peltosaurus* specimen in the dataset), I used measurements from extant limbed anguid lizards because these groups have similar head: body proportions (Figure 4; see below for methods for skull length > 52 mm). I sampled all extant limbed anguid genera (Table 1, Appendix 2), but omitted *Barisia* and *Sauresia* from the dataset because the average head: femur length ratio for all other genera in the sample combined most closely approximated that of *Peltosaurus* (UNSM 12102; see Figure 4) with these two genera eliminated. Omission of

Barisia and *Sauresia* also produced a dataset with a normal distribution (Figure 5) and a lower standard deviation for head: femur length than resulted from removal of any other genus or genera.

In order to estimate SVL for small fossil anguids, I generated a Reduced Major Axis (RMA) linear regression model in PAST v. 3.1 (Hammer et al., 2001) using the natural logs of head length and SVL in adult extant limbed anguids (with the exception of *Barisia* and *Sauresia*; Figure 6). I used RMA rather than Ordinary Least Squares linear regression in order to account for possible variability in the dependent variable (head length measurements). I also used the natural log of head length and SVL measurements because this gave both variables a normal distribution for the anguid dataset (Figure 5). This regression had a high predictive power and a small range of error for SVL (LN SVL = (0.892 +/- 0.0307)*LN Head Length + (1.81 +/- 0.00906); n = 165 (see Table 1); R = 0.90, R^2 = 0.81, p (uncorr.) << 0.00; Figure 6). I plotted each body size datum at the midpoint of its respective NALMA interval (Figures 9, 10, 11) as a representative value for that time bin (with the exception of early Arikareean data, which all date to about 28.3 Ma; Tedford et al., 1996).

In order to verify that the largest individuals in the extant anguid dataset did not skew the regression model, I generated another regression (Figure 7) omitting the largest 25% of extant anguid taxa (skull length > 26.2 mm) to determine if the relationship for the smaller taxa could accurately predict SVL of the largest extant measured anguid taxon, *Diploglossus millepunctatus* (head length 42 – 47.5 mm). The resulting regression equation successfully estimated SVLs within 1 – 12% of actual values for four specimens of *D. millepunctatus* in the dataset (Regression equation: LN SVL = 0.927*LN Head

Length + 1.72; n = 124; *R* = 0.82, R^2 = 0.68, *p* (uncorr.) << 0.00). This indicates that the first regression (Figure 6) can reliably estimate SVLs for head lengths that fall at or close to the upper end of the range on which the regression was based.

I applied my measurements of skull length for small fossil anguid specimens (skull length ≤ 52 mm, that of the largest measured *Peltosaurus* specimen; see Figure 3) to the equation from the RMA regression (Figure 6) in order to estimate SVL for each fossil specimen from this size class (see Figure 10). Adding or subtracting the corresponding standard error values from the slope and intercept of the RMA equation yielded upper and lower estimates, respectively, for each fossil specimen (Figure 11).

I developed the regression model in Figure 6 based on the assumption that Glyptosaurinae was nested within extant members of Anguidae (i.e., it was not a basal outgroup; Conrad, 2008; Conrad and Norell, 2008). I also assume that head: limb proportions were consistent for all anguid lizards smaller than or comparable in size to *Peltosaurus* (see Figure 3) based on the only specimen from this size group (skull length ≤ 52 mm) that included a complete limb element (*Peltosaurus,* UNSM 12102, Figure 4).

I assume here that all fossil anguids in the smaller size group (skull length ≤ 52 mm) had limbs. It is possible that some small-bodied anguids may have been limbless, however: Gauthier (1982) proposed that *Apodosauriscus* may be an annielline, and Meszoely et al. (1978) assigned *Machaerosaurus* to Anguinae, a clade that includes the extant limbless taxa *Ophisaurus, Anguis,* and *Anniella* (Pianka and Vitt, 2003). No limb material is known for either *Apodosauriscus* or *Machaerosaurus*. I therefore used the regression in Figure 6 to estimate SVL for these and all other small-bodied fossil anguids.

Body Size Estimation for Large Glyptosaurines

The largest fossil anguid lizards (skull length ≥ 53 mm, e.g., *Paraglyptosaurus*; see Figure 3) are all glyptosaurines. The taxa in this size group have skull lengths that are sufficiently larger than the range of skull lengths for other fossil anguids (skull length ≤ 52 mm; Figure 3) and extant anguid lizards (see Appendix 2). Regression models derived from measurements of extant anguids therefore do not provide reasonable estimates of SVL for the larger fossil taxa. I instead used the skull: body ratio of *Heloderma* to estimate SVL for large glyptosaurines because these groups have similar skull: limb proportions (Figure 8). I used the mean head length: SVL ratio for both species of *Heloderma* (*H. suspectum* and *H. horridum*), taken from wet and dry skeletonized specimens (Table 2, Appendix 3). I used this method as an alternative to regression models because the range of skull lengths for the *Heloderma* dataset fell below the range for the largest examined or measured glyptosaurines (see Table 2, Figure 9), which resulted in a large range of error in attempted regression models. Simple ratios for adult *Heloderma* yielded SVL estimates with a small range of error (SVL = Head Length/0.188 (+/- 0.0180), error equals one standard deviation, n = 36 (see Table 2); see Figures 10, 11). I used only specimens of adult *Heloderma* (≥ 230 mm in *H. suspectum*, ≥ 330 mm in *H. horridum*; Beck, 2005) for which I could measure complete skull length and SVL.

Species Richness Estimation

I collected North American species richness data for fossil anguid lizards at NALMA temporal resolution from museum collections, literature (see Appendix 4), and the Paleobiology Database (paleobiodb.org; see Figure 12). I used only occurrences from material that was diagnostic to the species level and excluded indeterminate occurrences (i.e., ‘Anguidae indet.’), as well as indeterminate species of genera for which only one valid species is documented (e.g., ‘*Helodermoides sp.’* = *Helodermoides tuberculatus*; see Sullivan, 1979), in order to get a minimum estimate of species richness for each NALMA interval. I also extended stratigraphic ranges at the generic level between first and last occurrences and included range-through taxa in species counts (see Foote and Raup, 1996). I plotted total species richness for each NALMA at the midpoint of its respective interval (Figure 12) as a representative value for that time bin.

Continental Paleotemperature Proxies

I obtained existing proxies based on terrestrial fossil indicators for the interior of North America through the Cenozoic from literature (Figure 13, Table 3). I collated estimates from leaf margin analyses (Wing and Greenwood, 1993; Gregory and McIntosh, 1996; Wilf, 2000; Wing et al., 2000; Johnson and Ellis, 2002; Sandau, 2005; Pound et al., 2011, 2012); stable isotope ratio analyses of fossil mammal bone and tooth enamel (Fricke and Wing, 2004; Zanazzi et al., 2007), as well as gar scale enamel (Fricke and Wing, 2004); and one proxy based on land snail distributions (Evanoff et al., 1992). All proxy data came from the Great Plains and Western Interior of North America.

I estimated MAPT from glyptosaurine body size using the metabolic scaling equation from Head et al. (2013):

$$MAPT = MAT + 3\alpha 10^{\circ}C*(\log_{10}(SVL_{Fossil}/SVL_{Extant})/\log_{10}Q_{10}),$$

where MAPT is the minimum mean annual paleotemperature required to enable a lizard to reach a given size, SVL_{Fossil} is the maximum estimated SVL for a given fossil glyptosaurine, SVL_{Extant} is the largest verified SVL for a non-captive *Heloderma suspectum* (360 mm; used here because it has the northernmost range of *Heloderma*, which was used in this study to estimate SVL for the largest glyptosaurines; Beck, 2005), MAT is the minimum mean annual temperature from GIS data for the northernmost extent of the range of *H. suspectum* (14ºC; Beck, 2005; Hijmans et al., 2005), α is the metabolic scaling component of 0.33 (Makarieva et al., 2005a), and Q_{10} is a mass-specific metabolic rate. I calculated MAPT using both $Q_{10} = 3$ (observed in *Heloderma* for body temperature increases from 15ºC to 25ºC; Beck, 2005) and $Q_{10} = 2$ (the minimum general observed value for poikilotherms; Schmidt-Nielsen, 1983). I applied the largest estimated glyptosaurine SVL (per NALMA) to this equation for the Tiffanian through the early Arikareean (i.e., SVL ≥ 175 mm). Minimum MAPTs calculated from maximum SVL estimates for fossil anguids from the Lancian through the Torrejonian (SVL < 150 mm) indicated much colder minimum temperatures than have been estimated from other terrestrial proxies for the same intervals. For example, one maximum SVL estimate of 115 mm (indeterminate anguid, Torrejonian) yielded minimum MAPTs values of -2.3 – 3.7 (see Table 4), at least 6ºC lower than contemporary estimates from leaf margin analysis data for the Western Interior (Johnson and Ellis, 2002; see Table 3). The metabolic scaling equation used here (based on Head et al., 2013) indicates minimum temperatures needed to sustain a given body size, and thus estimates low temperatures for smaller lizards. MAPT estimates based on estimated SVLs of < 150 mm were therefore uninformative for this study.

CHAPTER 3

RESULTS

Body Size Change in North American Glyptosaurine Lizards through the Paleogene

The largest glyptosaurines in the early and middle Paleocene ranged in SVL from 72 mm (indeterminate glyptosaurine, Puercan) to 174 mm (*Melanosaurus*, Tiffanian) (Figure 10, Appendix 1.2). Maximum body size exceeded 660 mm by the early Eocene (*Paraglyptosaurus,* Wasatchian), and may have remained at this level through much of the Eocene. Maximum body size reached at least 436 mm in the middle Eocene (*Glyptosaurus,* Uintan), and late Eocene estimates (666 mm, *Helodermoides,* Chadronian) are comparable to those for the early Eocene (Figure 10, Table 4, Appendix 1.2).

The majority of measured Orellan glyptosaurines in this study were specimens of *Peltosaurus* (see Appendix 1.2). Two measured specimens of *Helodermoides* were also referred to the Orellan, but both of these specimens (USNM 13861, 13869; see Appendix 1.2) came from historical collections and did not have precise locality or stratigraphic documentation (the specimen labels indicated the Brule Formation, and an unnamed locality 7-8 miles east of Douglas, WY). It is possible that these specimens actually came from Chadronian deposits; in this case, the present data indicate that the last occurrence of the largest glyptosaurines was in the Chadronian, and that *Peltosaurus* was the only glyptosaurine genus present in the early Oligocene, with a maximum estimated SVL of 207 mm (see Figure 10, Table 4). Maximum body size was < 200 mm in the Whitneyan and early Arikareean (*Peltosaurus*), similar to maximum body size estimates for the middle Paleocene. No lizard fossils comparable in size to the largest glyptosaurines have been recovered from the Neogene record of North America within the recent latitudinal range of fossil glyptosaurine localities (Figure 2).

Body size patterns observed in this study result at least in part from small sample size, and the data may not represent the largest individuals that existed in each NALMA. Given that glyptosaurines have a long stratigraphic record (about 40 myrs; Figure 16) that has been sampled by multiple institutions for over 140 years (e.g., Marsh, 1871, to Smith, 2011), however, these results likely reflect overall patterns of body size change for the history these lizards.

Species Richness in North American Anguid Lizards through the Cenozoic

Glyptosaurines were the most speciose anguid lizards through the Paleogene (Figure 12). Glyptosaurine species richness peaked in the Wasatchian, concurrent with the first occurrence of the largest glyptosaurines (see Figure 10) and increase in continental MAPT relative to Paleocene levels in North America (Figure 13). No more than five contemporary genera occupied the largest size class (skull length > 52 mm) through the Eocene (see Appendix 1).

The glyptosaurine record for the middle Eocene is sparse. Only two anguid specimens assignable to a genus are known from the middle Eocene (Uintan) of North America (YPM PU 11303, *Glyptosaurus sp.,* Uinta County, UT (unpublished), and SDNHM 75932, *Glyptosaurus sylvestris*, San Diego County, CA (Moscato, 2013; see Appendix 1). The paucity of the glyptosaurine record in the Uintan and Duchesnean results at least in part from sampling bias. The museum collections I sampled contain fewer records from these intervals than from other NALMAs: for example, the University of California Museum of Paleontology collections house 30,653 specimens from the Wasatchian, but only 7,094 from the Uintan and 763 from the Duchesnean (ucmpdb.berkeley.edu). I was able to estimate head length for one small Duchesnean specimen (CM 42469, a partial dentary of an indeterminate fossil anguid; see Figures 9, 10, 11), but it is very probable that my data do not represent the maximum body size for this interval.

Only two glyptosaurine genera are known from the late Eocene (*Helodermoides* and *Peltosaurus*; Figures 1, 9, Appendix 1). *Peltosaurus* may be the only diagnostic glyptosaurine in the record for the early Oligocene. This genus represents the last occurrence of Glyptosaurinae in the early Arikareean (at least as recent as 28.3 Ma; Tedford et al., 1996; see Appendix 1), after which anguid species richness remains low through the Neogene compared to numbers reached in the early Eocene (Figure 12).

Patterns of species richness for glyptosaurines do not correlate to those for mammals in the early Paleogene (Figure 12). Alroy (2009) used standardized sample sizes to track mammal species numbers through the Cenozoic and found that the Wasatchian is not more heavily sampled than other NALMAs. Peak anguid species richness in the Wasatchian may therefore indicate greater species numbers for this group in the early Eocene, followed by a decline in species richness through the late Paleogene.

No diagnostic glyptosaurine material has been recovered from the Neogene record of North America or other continents. The last undisputed occurrence of this clade is in the early Arikareean (28.3 Ma; Appendix 1).

Paleogene Temperatures in the Interior of North America

Existing terrestrial proxies for Paleogene temperatures in the Great Plains and Western Interior indicate a marked increase in mean annual paleotemperature (MAPT) from the late Paleocene to the early Eocene, from around 13ºC in the Clarkforkian (late Paleocene; Wing et al., 2000) to over 20ºC in the early Eocene (Wilf, 2000; Johnson and Ellis, 2002; Table 3, Figure 13). Some terrestrial proxies indicate fluctuations through the early Paleogene (e.g., Wilf, 2000; Wing et al., 2000; Fricke and Wing, 2004), but MAPTs remain high in the early Eocene relative to the Paleocene, particularly around the time of the Early Eocene Climatic Optimum (52.0 – 50.0 Ma; Zachos et al., 2001; see Table 3). Fewer proxies are available for the middle Eocene, but one study estimates MAPT of about 16ºC for the Western Interior in the middle Uintan (Sandau, 2005). Terrestrial proxies for the late Eocene indicate that MAPTs may have compared to the middle Eocene at this time (e.g., 16.5ºC; Evanoff et al., 1992) or reached higher levels than in the Uintan (e.g., 21ºC; Zanazzi et al., 2007). MAPTs in the early Oligocene were lower than Eocene temperatures (e.g., about 13ºC; Gregory and McIntosh, 1996; Zanazzi et al., 2007; Table 3, Figure 13).

Minimum MAPTs calculated from maximum SVL estimates in early Eocene glyptosaurines also indicate higher temperatures (19.5 – 22.8ºC in the Wasatchian, 19.6 – 22.9ºC in the Bridgerian) relative to the middle Paleocene (3.7 – 7.5ºC, Tiffanian) and late Paleocene (13.6 – 13.7ºC, Clarkforkian; Table 4, Figure 13). Only two diagnostic glyptosaurines from the middle Eocene (Uintan) were observed in this study (Appendix 1), and these two specimens have almost equivalent estimated SVLs (436 and 435; see Figures 10, 11, Appendix 1.2). In order to compare glyptosaurine minimum MAPT estimates with published estimates from other terrestrial proxies for the Western Interior, only the Uintan specimen from Utah (YPM PU 11303) was used to calculate minimum MAPT for the Uintan; the resulting value was comparable to a published MAPT estimate for the middle Uintan (15.7 – 16.7ºC vs. 16.1ºC; see Sandau, 2003). Uintan MAPTs may have exceeded this level, as the glyptosaurine estimate represents the minimum MAPT required to sustain a lizard with an SVL of 436 mm (see Table 4). Maximum glyptosaurine SVL estimates indicate minimum Chadronian MAPTs that are comparable to estimates for the early Eocene (19.6 – 22.8ºC).

Results of minimum MAPT estimates from maximum glyptosaurine SVL for the Orellan vary depending on whether *Helodermoides* or *Peltosaurus* is taken to represent the largest glyptosaurines from that NALMA. The corresponding estimate for *Helodermoides* (19.6 – 22.8ºC) indicates elevated temperatures comparable to minimum glyptosaurine MAPT estimates for the early and late Eocene, whereas the estimate for *Peltosaurus* indicates much lower minimum MAPTs for the Orellan (6.1 – 9.0ºC), closer to other glyptosaurine estimates for the early Oligocene (Figure 13, Table 4).

Glyptosaurine maximum body size estimates of paleotemperatures indicate minimum MAPTs of 3.8 – 7.6ºC in the Whitneyan, and 5.9 – 8.9ºC in the early Arikareean (28.3 Ma; Tedford et al., 1996; Table 4), comparable to results of other terrestrial indicators for MAPTs in the early Oligocene (around 13ºC; Gregory and McIntosh, 1996; Zanazzi et al., 2007; Table 3). Temperatures may have remained lower in the Neogene compared to the Eocene; one SVL estimate from a Barstovian anguid indicates a minimum MAPT of 3.6 – 7.4ºC in the Great Plains (Table 4), and paleofloral proxies for the late Miocene indicate MAPTs of 12.5 – 14.0ºC in Idaho (Pound et al., 2011, 2012).

CHAPTER 4

DISCUSSION

Body Size – Climate Relationships in Glyptosaurine Lizards

Mass-specific metabolic rate in poikilotherms normally decreases with increased body size, but higher ambient temperatures override this relationship and elevate minimum metabolic rate (Makarieva et al., 2005a). Gigantism has already been correlated with increase in MAPT for a mid-late Paleocene boid snake (Head et al., 2009) and a middle Eocene acrodontan lizard (Head et al., 2013). Existing terrestrial fossil proxies indicate that continental mean annual paleotemperatures (MAPT) in the Great Plains and the Western Interior may have increased from about 12ºC in the Tiffanian to at least 15ºC in the Wasatchian, and possibly exceeded 20ºC by the Early Eocene Climatic Optimum (Wilf, 2000; Wing et al., 2000; Zachos et al., 2001; Johnson and Ellis, 2002; Table 3, Figure 13). Elevated temperatures in the early Eocene relative to the Paleocene coincide with the first occurrence of the largest known glyptosaurine lizards (Figure 10). Minimum MAPTs calculated from maximum estimated SVLs of the largest measured glyptosaurines in the Wasatchian and Bridgerian yield comparatively high temperature estimates (19.5 – 22.9ºC; Tables 4, 6).

Stable isotope proxies from fossil mammal bone and enamel (Zanazzi et al., 2007) indicate Chadronian temperatures as high as 26ºC (Figure 13, Table 3), indicating that maximum glyptosaurine body size continued to track continental MAPT in the late Eocene. This estimate corresponds to minimum MAPTs calculated from maximum glyptosaurine body size in the Chadronian (as high as 24ºC for *Helodermoides*; Figure 13, Table 4). These estimates may reflect active temperatures for large late Eocene glyptosaurines in the interior of North America. Field studies indicate that the large extant helodermatid lizard *Heloderma suspectum,* which is comparable in morphology and body proportion to the large glyptosaurine *Helodermoides* (Figure 8), prefers an ambient temperature range of 28 – 30ºC and is observed to be active at temperatures as low as 17.4ºC (John-Alder et al., 1983; Beck, 2005). It is therefore possible that ambient temperatures in the interior of North America remained above a critical threshold for efficient metabolism in large glyptosaurine lizards prior to the Oligocene.

Estimates of minimum MAPT based on maximum glyptosaurine body size indicate a statistically significant correlation to some published terrestrial proxies for the late Paleocene through the early Oligocene for the interior of North America (regression equation (using *Peltosaurus* estimate for the Orellan): Other Terrestrial MAPT Proxy = 0.664* Glyptosaurine Max SVL MAPT + 6.46; n = 9; $R = 0.94$, $R^2 = 0.88$, p (uncorr.) < 0.00; Figure 14a, Table 6). This relationship is less robust when the maximum estimated SVL of the largest specimen of *Helodermoides* allegedly from the Orellan is used to calculate minimum MAPT for that interval (regression equation: Other Terrestrial MAPT Proxy = 0.663*Glyptosaurine Max SVL MAPT + 5.73; n = 9; $R = 0.78$, $R^2 = 0.61$, p (uncorr.) = 0.013; Figure 14b, Table 6). This is because using the maximum SVL for *Helodermoides* in the Orellan gives an MAPT estimate that is at least 10ºC higher than the estimate from the maximum Orellan SVL of *Peltosaurus*. This indicates that either 1) *Helodermoides* did not have the same physiological relationship with ambient temperature as other glyptosaurines (see section below on Diet and Ecology of

Glyptosaurine Lizards), or 2) the two specimens of *Helodermoides* are outliers (see Figure 11) that may actually have come from Chadronian deposits.

The difference between these Orellan estimates is not as large when *mean* SVL estimates (Figure 11, Table 5) are used to correlate minimum MAPTs derived from glyptosaurine body size to MAPTs from other terrestrial proxies (Figure 15, Table 7). This correlation is robust with or without including the two *Helodermoides* specimens allegedly from the Orellan in the mean SVL value for that NALMA interval (with *Helodermoides* excluded from Orellan mean SVL – regression equation: Other Terrestrial MAPT Proxy = 0.480*Glyptosaurine Mean SVL MAPT + 9.44; n = 9; $R = 0.97$, $R^2 = 0.94$, p (uncorr.) << 0.00; with *Helodermoides* included in Orellan mean SVL – regression equation: Other Terrestrial MAPT Proxy = 0.495*Glyptosaurine Mean SVL MAPT + 9.20; n = 9; $R = 0.98$, $R^2 = 0.96$, p (uncorr.) << 0.00; Figure 15, Table 7).

Early Eocene glyptosaurines demonstrated an increase in body size range, rather than an upward shift of all body sizes, as some smaller glyptosaurine taxa occurred in the Wasatchian and Bridgerian (Figures 10, 11, 16, Appendix 1). The mean SVL estimate calculated for the Wasatchian is much lower than that of the Bridgerian, and the range between the maximum and minimum estimated SVL for this interval is greater than that of any other NALMA (Figure 11). This may be partial artifact of sampling bias, but it is also possible that temperature increase in the early Eocene facilitated *in situ* evolution of some larger glyptosaurine taxa (e.g., *Glyptosaurus, Paraglyptosaurus*). Other contemporary taxa that first occurred in the Paleocene did not appreciably alter their body size range (e.g., *Melanosaurus, Xestops* (which may actually represent a juvenile form of *Melanosaurus* (see Sullivan, 1986)). The largest glyptosaurine SVL estimates (≥ 650 mm) occur only in closely related Eocene and late Oligocene taxa (Glyptosaurini; Figure 16, Appendix 1), indicating that gigantism may have evolved only once in this clade.

Elevated MAPTs may have also caused larger taxa to immigrate into the Great Plains and Western Interior basins. Fossil anguid lizards are only known to occur in western North America prior to the Eocene, but a number of Eocene glyptosaurines are known from other northern continental records (Sullivan, 1979; Conrad and Norell, 2008). For example, *Paraplacosauriops,* a putative sister taxon to *Peltosaurus*, occurs in Europe by the middle Eocene (Augé and Sullivan, 2006; Conrad and Norell, 2008), and *Placosaurus,* thought to be a sister taxon to *Glyptosaurus,* is known from the middle and late Eocene of Europe and Asia (Sullivan and Augé, 2006; Conrad and Norell, 2008). A specimen referable to Glyptosaurinae has also been reported from Wasatchian deposits in Ellesmere Island in northern Canada (Estes and Hutchison, 1980). It is therefore possible that anguid lizards immigrated into or dispersed from the interior of North America during warm intervals in the early Eocene. Relationships of larger North American glyptosaurines from the Eocene to taxa first occurring in the Paleocene imply missing lineages over stratigraphic intervals of at least 6 myrs (Figure 16). The most recent cladistic assessments for the common late Paleogene glyptosaurine *Peltosaurus* require a ghost lineage of about 24 myrs (Conrad, 2008; Conrad and Norell, 2008; Figure 16). Immigration and dispersal may explain some of these missing records for relationships among glyptosaurines found in North America.

Species Richness – Climate Relationships in Glyptosaurine Lizards

Many glyptosaurine species were previously named (see, e.g., Marsh, 1871, 1872; Cope, 1873; Gilmore, 1928) and subsequently revised, synonymized, or negated (e.g., by Meszoely, 1970; Sullivan, 1979, 1989; Estes, 1983), which complicated calculation of species richness for the clade. After reviewing existing literature and sampling almost all major museum collections in the United States, and including range-through taxa in species counts, the present results indicate that glyptosaurines were the most speciose anguids through the Paleogene (Figure 12). Glyptosaurine species richness reached a maximum for the Paleogene in the Wasatchian, concurrent with increased minimum MAPT for the interior of North America inferred from glyptosaurine body size and other terrestrial proxies (Figure 13, Tables 3, 4). This increase in species richness in the early Eocene may have resulted in part from *in situ* evolution, or from immigration of taxa to the Great Plains and intermontane basins of the Western Interior. Species richness data in this study likely reflects some sampling bias, particularly in the middle Eocene, which does not have a robust anguid record (see Figure 10).

Lower glyptosaurine species richness after the Wasatchian (Figure 12) may correspond to aridification in the continental interior. Mean carbon isotope values from late Eocene and early Oligocene fossil ungulates indicate a shift from moist forests to dry, open habitats in the Great Plains (Boardman and Secord, 2013). Paleosols from the Western Interior also indicate a decline in mean annual precipitation (MAP) from the late Eocene to the early Oligocene (Retallack, 2007). Leaf area analyses of Uintan floras indicate a drop in MAP to about 56 cm in the Western Interior (Sandau, 2005) from about 144 cm in the earliest Paleocene (Wing et al., 2005). Decreased temperatures or drying from the late Eocene to the early Oligocene (Evanoff et al., 1992; Zanazzi et al., 2007; Table 3, Figure 13) may have added environmental stress to declining glyptosaurine species numbers. Glyptosaurines were already extinct outside of North America by the end of the Eocene (Sullivan, 1979). Only *Peltosaurus* and possibly *Helodermoides* remained in the early Oligocene (Figure 10; Sullivan, 1979). Cooling and aridification may have led to reduced habitat and food availability, and contributed to the extinction of glyptosaurines by the Neogene.

Diet and Ecology of Glyptosaurine Lizards

Glyptosaurines lack the dentition of an obligate herbivore or carnivore (Gauthier, 1982). Sullivan (1979) described the dental morphology of large early Eocene glyptosaurines (e.g., *Paraglyptosaurus, Arpadosaurus*) as having a “simple obtuse tooth type” with varying degrees of “robustness” (p. 67), and noted that these lizards also had robust mandibles and highly fused skulls. Citing a previous study of lizard tooth morphology (Hotton, 1955), Sullivan (1979) proposed a durophagous diet of terrestrial mollusks for large glyptosaurines. Gauthier (1982) observed that the cranial morphology of large glyptosaurines indicated substantial temporal musculature, but instead concluded that the dental morphology of large glyptosaurines more closely resembles that of recent omnivorous lizards, such as Australian lygosomine scincids, whose body armor is comparable to that of extant anguids.

It is possible that glyptosaurines maintained a specific ecological niche associated with large body size through major environmental transitions in the late Paleogene. Considering the concurrent floral and faunal changes between those intervals (Evanoff et al., 1992; Hutchison, 1992; Alroy, 1996; Boardman and Secord, 2013), it is also possible that these animals changed their ecological habits as new niches became available. Extant *Heloderma* demonstrate a wide range of habits and habitats. *Heloderma suspectum* is found in xeric environments in the southwestern United States, while *Heloderma horridum* inhabits tropical dry forests in Mexico and Central America that receive a large amount of seasonal precipitation (Pianka and Vitt, 2003; Beck, 2005). Both species take shelter and search for prey in existing burrows, but *H. suspectum* is also saxicolous, and *H. horridum* is known to be actively arboreal (Beck, 2005). Anatomically, *H. suspectum* and *H. horridum* are nearly indistinguishable, and they closely resemble large glyptosaurines in cranial morphology and body proportion (i.e., head: humerus length ratio; Figure 8). Indeed, *Helodermoides* was initially thought to be a fossil helodermatid based on its cranial morphology (Douglass, 1903). The ecological lability of *Heloderma* therefore suggests that large glyptosaurines may have exploited multiple niches in order to survive climatic and environmental transitions through the late Eocene and possibly the early Oligocene of North America. It is also possible that climatic shifts in the late Eocene led to the extinction of all large glyptosaurines except *Helodermoides,* and that this taxon alone was able to behaviorally maintain large body size amidst changing conditions.

CHAPTER 5

CONCLUSIONS

1. My results indicate a statistically significant correlation between minimum MAPT estimates based on maximum glyptosaurine body size and published MAPT estimates from other terrestrial proxies in the early Paleogene.
2. The largest glyptosaurines first occurred in the early Eocene of North America, coinciding with marked increase in MAPT from the Paleocene.
3. Equally large glyptosaurines occurred in the Chadronian, and allegedly in the Orellan, during times of possible decrease in MAPT. This may indicate that 1) decreases in MAPT recorded in some proxy data do not represent a climatic shift below critical temperatures needed to maintain large size in glyptosaurine lizards, or 2) large glyptosaurines could behaviorally maintain elevated body sizes over long biological time scales despite decrease in ambient temperature.

REFERENCES

Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127(1): 285-311.

Alroy, J. 2009. Speciation and extinction in the fossil record of North American mammals; pp. 301-323 *in* R. Butlin, J. Bridle, and D. Schluter, (eds.), Speciation and Patterns of Diversity. Cambridge University Press, Cambridge.

Augé, M., and R. M. Sullivan. 2006. A new genus, *Paraplacosauriops* (Squamata, Anguidae, Glyptosaurinae) from the Eocene of France. *Journal of Vertebrate Paleontology* 26(1): 133-137.

Beck, D. D. 2005. Biology of Gila Monsters and Beaded Lizards. Vol. 9. University of California Press, Berkeley. 211 pp.

Boardman, G. S., and R. Secord. 2013. Stable isotope paleoecology of White River ungulates during the Eocene–Oligocene climate transition in northwestern Nebraska. *Palaeogeography, Palaeoclimatology, Palaeoecology* 375: 38-49.

Böhme, M., Ilg, A., Ossig, A., and H. Küchenhoff. 2008. New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe. *Geology* 34(6): 425-428.

Conrad, J. L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History* no. 310: 1-182.

Conrad, J. L., and M. A. Norell. 2008. The braincases of two glyptosaurines (Anguidae, Squamata) and anguid phylogeny. *American Museum Novitates* no. 3613: 24 pp.

Cope, E. D. 1873. Synopses of new Vertebrata from the Tertiary of the Plains. *Palaeontological Bulletin* no. 15: 1-6.

Douglass, E. 1903. New vertebrates from the Montana Tertiary. *Annals of Carnegie Museum* 2(5): 145-199.

Estes, R. 1983. Sauria terrestria, Amphisbaenia. *Handbuch der Paläoherpetologie*, Part 10A. Gustav Fischer Verlag, Stuttgart, xxii + 249 p.

Estes, R. A., and J. H. Hutchison. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology* 30: 325-347.

Evanoff, E., Prothero, D. R., and R. H. Lander. 1992. Eocene-Oligocene climatic change in North America: the White River formation near Douglas, east-central Wyoming. Eocene-Oligocene Biotic and Climatic Evolution. Princeton University Press, Princeton, New Jersey: 116-130.

Foote, M. and D. M. Raup. 1996. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* 22(2): 121-140.

Fricke, H. C., & S. L. Wing. 2004. Oxygen isotope and paleobotanical estimates of temperature and $\delta^{18}O$-latitude gradients over North America during the early Eocene. *Amer. J. Sci.* 304: 612-635.

Gauthier, J. M. 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contributions to Geology, University of Wyoming* 21(1): 7-54.

Gilmore, C. M. 1928. Fossil lizards of North America. *Memoirs of the National Academy of Sciences* 22: 1-201.

Greenwood, D. R., and S. L. Wing. 1995. Eocene continental climates and latitudinal temperature gradients. *Geology* 23(11): 1044-1048.

Gregory, K. M. and W. C. McIntosh. 1996. Paleoclimate and paleoelevation of the Oligocene Pitch-Pinnacle flora, Sawatch Range, Colorado. *GSA Bulletin* 108(5): 545-561.

Hammer, Ø., Harper, D. A. T., and Ryan, P. D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1): 9pp. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Head, J. J., Bloch, J. I., Hastings, A. K., Bourque, J. R., Cadena, E. A., Herrera, F. A., Polly, P. D., and C. A. Jaramillo. 2009. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* 457: 715-718.

Head, J. J., Gunnell, G. F., Holroyd, P. A., Hutchison, J. H., and R. L. Ciochon. 2013. Giant lizards occupied herbivorous mammalian ecospace during the Paleogene greenhouse in Southeast Asia. *Proc. Royal Soc. B* 280: 1-7.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965-1978.

Hotton III, N. 1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. *American Midland Naturalist* 53(1): 88-114.

Hutchison, J. H. 1992. Western North American reptile and amphibian record across the Eocene/Oligocene boundary and its climatic implications. In: *Eocene–Oligocene climatic and biotic* evolution: 451-63.

John-Alder, H. B., Lowe, C. H., and Albert F. Bennett. 1983. Thermal dependence of locomotory energetics and aerobic capacity of the Gila Monster (*Heloderma suspectum*). *Journal of Comparative Physiology* 151(2): 119-126.

Johnson, K., and B. Ellis. 2002. A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary Boundary. *Science* 296: 2379-2383.

Makarieva, A. M., Gorshkov, V. G., and B.-L. Li. 2005a. Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos* 111(3): 425-436.

Makarieva, A. M., Gorshkov, V. G., and B.-L. Li. 2005b. Gigantism, temperature and metabolic rate in terrestrial poikilotherms. *Proceedings of the Royal Society B: Biological Sciences* 272(1578): 2325-2328.

Marsh, O. C. 1871. Notice of some new fossil reptiles from the Cretaceous and Tertiary formations. *American Journal of Science* 1(3): 447-459.

Marsh, O. C. 1872. Preliminary description of new Tertiary reptiles, Parts I and II. *American Journal of Science* 4: 298-309.

Meiri, S. 2008. Evolution and ecology of lizard body sizes. *Glob. Eco. Biogeo.* 17(6): 724-734.

Meszoely, C. A. M. 1970. North American fossil anguid lizards. *Bulletin of the Museum of Comparative Zoology* 139: 87-149.

Meszoely, C. A. M., Estes, R. and H. Haubold. 1978. Eocene anguid lizards from Europe and a revision of the genus Xestops. *Herpetologica* 34(2): 156-166.

Moscato, D. 2013. A glyptosaurine lizard from the Eocene (late Uintan) of San Diego, California, and implications for glyptosaurine evolution and biogeography. Masters Thesis. East Tennessee State University. Department of Geosciences

The Paleobiology Database. www.paleobiodb.org. Accessed February 2013 – March 2014.

Pianka, E. R., and L. J. Vitt. 2003. Lizards: Windows to the evolution of diversity. University of California Press, 333 p.

Pound, M. J., Haywood, A. M., Salzmann, U., Riding, J. B., Lunt, D. J., and S. J. Hunter. 2011. A Tortonian (Late Miocene, 11.61-7.25 Ma) global vegetation reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 300: 29-45.

Pound, M. J., Haywood, A. M., Salzmann, U., and J. B. Riding. 2012. Global vegetation dynamics and latitudinal temperature gradients during the mid to late Miocene (15.97-5.33 Ma). *Earth Science Reviews* 112: 1-22.

Retallack, G. J. 2007. Cenozoic paleoclimate on land in North America. *The Journal of Geology* 115(3): 271-294.

Rowe, T., Cifelli, R. L., Lehman, T. M., and A. Weil. 1992. The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos, Texas. *Journal of Vertebrate Paleontology* 12(4): 472-493.

Sandau, S. D. 2005. The Paleoclimate and Paleoecology of a Uintan (Late Middle Eocene) Flora and Fauna from the Uinta Basin, Utah. Doctoral dissertation, Brigham Young University. Department of Geology.

Scheibe, J. S. 1987. Climate, competition, and the structure of temperature zone lizard communities. *Ecology* 68(5): 1424-1436.

Schwartz-Nielsen, K. 1983. Animal physiology: Adaptation and environment, 3rd ed. Cambridge University Press, New York.

Smith, K. T. 2011. The evolution of mid-latitude faunas during the Eocene: late Eocene lizards of the Medicine Pole Hills reconsidered. *Bulletin of the Peabody Museum of Natural History* 52(1): 3-105.

Sullivan, R. M. 1979. Revision of the Paleogene genus *Glyptosaurus* (Reptilia, Anguidae). *Bulletin of the American Museum of Natural History* 163(1): 1-72.

Sullivan, R. M. 1986. The skull of *Glyptosaurus sylvestris* Marsh, 1871 (Lacertilia: Anguidae). *Journal of Vertebrate Paleontology* 6(1): 28-37.

Sullivan, R. M. 1989. *Proglyptosaurus huerfanensis*, new genus, new species: Glyptosaurine lizard (Squamata: Anguidae) from the early Eocene of Colorado. *American Museum Novitates* no. 2949: 8 pp.

Sullivan, R. M., and M. Augé. 2006. Redescription of the holotype of *Placosaurus rugosus gervais* 1848-1852 (Squamata, Anguidae, Glyptosaurinae) from the Eocene of France and a revision of the genus. *Journal of Vertebrate Paleontology* 26(1): 127-132.

Tedford, R. H., Swinehart, J. B, Swisher III, C. C., Prothero, D. R., King, S. A., and T. E. Tierney. 1996. The Whitneyan-Arikareean Transition in the High Plains; pp. 312-334 *in* D. J. Prothero and R. J. Emry (eds.), The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, New York.

The University of California Museum of Paleontology Specimen Search. ucmpd.berkeley.edu. Accessed October 2013 – April 2014.

Wilf, P. 2000. Late Paleocene – early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. *Bulletin of the Geological Society of America* 112(2): 292-307.

Wing, S. L., and D. R. Greenwood. 1993. Fossils and fossil climate: The case for equable continental interiors in the Eocene. *Philosophical Transactions: Biological Sciences* 341(1297): 243-252.

Wing, S. L., Bao, H., and P. L. Koch. 2000. An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic. Warm Climates in Earth History. Cambridge University Press, Cambridge, 197-237.

Wing, S. L., Harrington, G. J., Smith, F. A., Bloch, J. I., Boyer, D. M., and K. H. Freeman. 2005. Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* 310(5750): 993-996.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science* 292: 686-693.

Zachos, J. C., Dickens, G. R., and R. E. Zeebe. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451(7176): 279-283.

Zanazzi, A., Kohn, M. J., MacFadden, B. J., and D. O. Terry, Jr. 2007. Large temperature drop across the Eocene–Oligocene transition in central North America. *Nature* 445(7128): 639-642.

Zimmerman, L. C. and C. R. Tracy. 1989. Interactions between the environment and ectothermy and herbivory in reptiles. *Physiological Zoology* 62: 374-409.

APPENDIX 1.1. FOSSIL ANGUID LOCALITY DATA

Modern coordinates obtained using the Paleobiology Database and Google Earth. See Figure 2 for locality map.

Collection	**Specimen #**	***Genus***	***Species***	**NALMA**	**Formation**	**Locality**	**Modern Coordinates**
UCMP	46089	*Odaxosaurus*	*piger*	Lancian	Lance Fm	V 5620, Niobrara Co., WY	43.1° N, 104.6° W
UCMP	61414	*Odaxosaurus*	*piger*	Lancian	Lance Fm	V 5620, Lull 2, Niobrara Co., WY	43.1° N, 104.6° W
UCMP	49992	*Odaxosaurus*	*piger*	Lancian	Lance Fm	V 5620, Lull 2, Niobrara Co., WY	43.1° N, 104.6° W
UCMP	46624	*Odaxosaurus*	*piger*	Lancian	Lance Fm	V 5620, Lull 2, Niobrara Co., WY	43.1° N, 104.6° W
UCMP	46037	*Odaxosaurus*	*piger*	Lancian	Lance Fm	V 5620, Lull 2, Niobrara Co., WY	43.1° N, 104.6° W
UCMP	49772	*Odaxosaurus*	*piger*	Lancian	Lance Fm	V 5711, Bushy Tailed Blowout, Niobrara Co., WY	43.2° N, 104.6° W
UCMP	49780	*Odaxosaurus*	*piger*	Lancian	Lance Fm	V 5711, Bushy Tailed Blowout, Niobrara Co., WY	43.2° N, 104.6° W
UCMP	229961	Glyptosaurinae	indet.	Puercan	Tullock Fm	V 74122, Biscuit Springs, Garfield Co., MT	47.6° N, 107.0° W
AMNH	2686	*Machaerosaurus*	*torrejonensis*	Torrejonian	Lebo Fm	Gidley Quarry, Sweetwater Co., MT	45.8° N, 109.8° W
YPM	PU 20574	Anguidae	indet.	Torrejonian	Tongue River Fm	Medicine Rocks, Carter Co. MT	46.0° N 104.5° W
CM	87168	*Odaxosaurus*	*sp*	Torrejonian	Fort Union Fm	Swain Quarry, Dad, WY	41.3° N, 107.7° W
AMNH	FR 2686	*Machaerosaurus*	*torrejonensis*	Torrejonian	Lebo Fm	Gidley Quarry, Sweetgrass Co., MT	45.8° N, 109.8° W
UCMP	114385	Glyptosaurinae	indet.	Tiffanian	Fort Union Fm	V 74158, West Saddle Locality, Fremont Co., CO	38.5° N, 105.4° W

CM	5431	Anguidae	indet	Tiffanian	Fort Union Fm	Saddle Locality, Bison Basin, WY	42.3° N, 108.2° W
CM	5434	Anguidae	indet	Tiffanian	Fort Union Fm	Saddle Locality, Bison Basin, WY	42.3° N, 108.2° W
CM	18728	Anguidae	indet	Tiffanian	Fort Union Fm	Saddle Locality, Bison Basin, WY	42.3° N, 108.2° W
CM	40509	Anguidae	indet	Tiffanian	Fort Union Fm	Ledge Locality, Bison Basin, WY	42.3° N, 108.2° W
CM	69641	Anguidae	indet	Tiffanian	Fort Union Fm	Saddle Locality, Bison Basin, WY	42.3° N, 108.2° W
UCM	98615	*Melanosaurus*	*sp.*	Tiffanian	Debeque Fm	CO (unspecified)	
YPM	PU 20631	*Odaxosaurus*	*sp.*	Tiffanian	Polecat Bench Fm	Cedar Point Quarries, Bighorn Co., WY	44.7° N, 108.4° W
UMMP	77641	*Odaxosaurus*	*piger*	Clarkforkian	Fort Union Fm	FG006, Bighorn Basin, WY	
UMMP	73787	*Melanosaurus*	*maximus*	Clarkforkian	Willwood Fm	SC116, Clarks Fork Basin, Park Co., WY	44.3° N, 109.0° W
UMMP	74618	*Melanosaurus*	*maximus*	Clarkforkian	Willwood Fm	SC164, Clarks Fork Basin, Park Co., WY	44.3° N, 109.0° W
UMMP	74615	*Melanosaurus*	*maximus*	Clarkforkian	Willwood Fm	SC023, Clarks Fork Basin, Park Co., WY	44.3° N, 109.0° W
UMMP	65550	*Melanosaurus*	*maximus*	Clarkforkian	Willwood Fm	SC050, Clarks Fork Basin, Park Co., WY	44.3° N, 109.0° W
UMMP	74616	*Xestops*	*vagans*	Clarkforkian	Willwood Fm	SC081, Clarks Fork Basin, Park Co., WY	44.3° N, 109.0° W
AMNH	7431	*Proglyptosaurus*	*huerfanensis*	Wasatchian	Huerfano Fm	Costillo Pocket, Quarry 1, Gardner, CO	37.8° N, 105.1° W
USNM	18316	*Glyptosaurus*	*sylvestris*	Wasatchian	Wind River Fm (Lost Cabin Mbr)	White Hills, Fremont Co., WY	42.4° N, 108.9° W
USNM	6004*	*Paraglyptosaurus*	*hillsi*	Wasatchian	Huerfano Fm	Muddy Fork of Huerfano River, Huerfano Co., CO	37.8° N, 105.1° W
AMNH	5168	*Melanosaurus*	*maximus*	Wasatchian	Willwood Fm	Clark Fork Basin, Park Co., WY	44.8° N, 109.0° W

UCMP	151761	*Arpadosaurus*	*sp.*	Wasatchian	Wasatch Fm	V 74024, Sweetwater Co., WY	41.7° N, 108.9° W
UCMP	47740	*Gerrhonotus*	*sp.*	Wasatchian	Wasatch Fm	V 5421, Sand Quarry, Moffat Co., CO	40.6° N, 108.1° W
UCMP	215232	*Proxestops*	*sp.*	Wasatchian	Wasatch Fm	V 70243, Sweetwater Co., WY	41.7° N, 108.9° W
UCMP	100118	*Apodosauriscus*	*sp.*	Wasatchian	Wasatch Fm	V 70246, Sweetwater Co., WY	41.7° N, 109.0° W
UCMP	100102	*Proxestops*	*sp.*	Wasatchian	Wasatch Fm	V 70246, Sweetwater Co., WY	41.7° N, 109.0° W
USNM	25826	*Arpadosaurus*	*gazinorum*	Wasatchian	Wasatch Fm	12 miles north of Big Piney, WY	42.7° N, 110.1° W
CM	44836	*Xestops*	*sp.*	Wasatchian	Wind River Fm (Lost Cabin Mbr)	2411: K-6, WY	Not Found
CM	42270	*Paraglyptosaurus*	*sp.*	Wasatchian	Wind River Fm (Lost Cabin Mbr)	3186: K-5, WY	Not Found
CM	42411	*Xestops*	*sp.*	Wasatchian	Wind River Fm (Lysite Mbr)	792: Lysite Rim, WY	Not Found
CM	42179	*Glyptosaurus*	*sylvestris*	Wasatchian	Wind River Fm (Lost Cabin Mbr)	3188: K-5, WY	Not Found
CM	44820	*Glyptosaurus*	*sylvestris*	Wasatchian	Wind River Fm (Lost Cabin Mbr)	2411: K-6, WY	Not Found
YPM	PU 21801	*Melanosaurus*	*maximus*	Wasatchian	Willwood Fm	Little Sand Coulee, Park Co., WY	44.9° N, 109.1° W
UCMP	216000	*Gaultia*	*silvaticus*	Wasatchian	Willwood Fm (Wa0)	V 99019, Bighorn Basin, WY	44.0° N, 107.6° W
UCMP	126000*	*Glyptosaurus*	*sylvestris*	Bridgerian	Bridger Fm	V 81250, Uinta Co., WY	41.2° N, 110.5° W
USNM	16527	*Glyptosaurus*	*sylvestris*	Bridgerian	Bridger Fm	Grizzly Buttes, Bridger Basin, Uinta Co., WY	41.2° N, 110.5° W

USNM	18106	*Glyptosaurus*	*sylvestris*	Bridgerian	Bridger Fm (B Mbr)	Field #47-112, Bridger Basin, WY	41.5° N, 109.8° W
AMNH	FR 6055	*Glyptosaurus*	*sylvestris*	Bridgerian	Bridger Fm	Grizzly Buttes, Bridger Basin, Uinta Co., WY	41.2° N, 110.5° W
AMNH	6054	*Paraglyptosaurus*	*princeps*	Bridgerian	Bridger Fm	Grizzly Buttes, Bridger Basin, Uinta Co., WY	41.2° N, 110.5° W
USNM	12590	*Paraglyptosaurus*	*princeps*	Bridgerian	Bridger Fm	Uinta Co., Bridger Basin, Levitt, WY	41.3° N, 110.3° W
YPM	1072	*Glyptosaurus*	*sylvestris*	Bridgerian	Bridger Fm (B Mbr)	Grizzly Buttes, Bridger Basin, Uinta Co., WY	41.2° N, 110.5° W
USNM	V 16520	*Glyptosaurus*	*sylvestris*	Bridgerian	Bridger Fm	Uinta Co., WY	
YPM	VP 58255	*Glyptosaurus*	*sp.*	Bridgerian	Bridger Fm	Point Gulch, Uinta Co. WY	41.2° N, 110.5° W
YPM	1092	*Glyptosaurus*	*sp*	Bridgerian	Bridger Fm	Bridger Basin, WY (Field No. 474)	
YPM	7601	*Paraglyptosaurus*	*princeps*	Bridgerian	Bridger Fm	Millersville, WY (Field No. 622)	41.4° N, 110.2° W
YPM	7602	*Paraglyptosaurus*	*princeps*	Bridgerian	Bridger Fm	Millersville, WY (Field No. 777)	41.4° N, 110.2° W
SDNHM	75932	*Glyptosaurus*	*sylvestris*	Uintan	Santiago Fm (Mbr C)	Rancho Del Oro, San Diego Co., CA	32.9° N, 117.1° W
YPM	PU 11303	*Glyptosaurus*	*sp.*	Uintan	Uinta Fm (Mbr C)	Kennedy's Hole, Uinta Co., UT	40.1° N, 109.2° W
CM	42469	Anguidae	indet.	Duchesnean	Wagon Bed Fm (Hendry Ranch Mbr)	20: Badwater Locality,Natrona Co., WY	43.2° N, 107.1° W
AMNH	8706	*Helodermoides*	*tuberculatus*	Chadronian	Chadron Fm	Bates Hole, Natrona Co., WY	43.2° N, 107.1° W
UNSM	4511*	*Helodermoides*	*tuberculatus*	Chadronian	Chadron Fm	Dw-107, Sioux Co., NE	42.4° N, 103.8° W
AMNH	6800	*Helodermoides*	*tuberculatus*	Chadronian	Chadron Fm	Badlands, SD	43.8° N, 103.1° W
USNM	529372	*Helodermoides*	*sp.*	Chadronian	Chadron Fm	Flagstaff Rim, Natrona Co., WY	43.2° N, 107.1° W
FAM	8711	*Parophisaurus*	*pawneensis*	Chadronian	Chadron Fm	6 mi from Douglas, Converse Co., WY	42.9° N, 105.2° W

AMNH	8138	*Peltosaurus*	*granulosus*	Chadronian	Chadron Fm	Chadron, NE	42.8° N, 103.0° W
USNM	15607	*Peltosaurus*	*granulosus*	Chadronian	Chadron Fm	Toadstool Park, NE	42.4° N, 103.8° W
CM	51344	*Helodermoides*	*tuberculatus*	Chadronian	Chadron Fm	212: Cameron Springs, WY	
CM	1050	*Helodermoides*	*tuberculatus*	Chadronian	Renova Fm	546: McCartys Mtn, Jefferson Co., MT	45.2° N, 112.6° W
CM	707	*Helodermoides*	*tuberculatus*	Chadronian	Renova Fm	879: 1 mi W of Pipestone Springs, MT	45.9° N, 112.3° W
CM	9975	*Helodermoides*	*tuberculatus*	Chadronian	Renova Fm	547: S of McCartys Mtn, MT	45.2° N, 112.6° W
UNSM	125564	*Helodermoides*	*tuberculatus*	Chadronian	Chadron Fm	Sx-0, Sioux Co., NE	42.4° N, 103.8° W
UNSM	128143a	*Helodermoides*	*tuberculatus*	Chadronian	Chadron Fm	Dw-107, Dawes Co., NE	42.4° N, 103.8° W
UNSM	128143b	*Helodermoides*	*tuberculatus*	Chadronian	Chadron Fm	Dw-107, Dawes Co., NE	42.4° N, 103.8° W
USNM	13869	*Helodermoides*	*tuberculatus*	Orellan	Brule Fm	8 mi E of Douglas, Converse Co., WY	42.9° N, 105.2° W
USNM	13861	*Helodermoides*	*tuberculatus (prev. Glyptosaurus giganteus)*	Orellan	Brule Fm	7 mi E of Douglas, Converse Co., WY	42.9° N, 105.2° W
UNSM	50000	*Parophisaurus*	*pawneensis*	Orellan	Brule (Orella B or C)	Sf-102, Scotts Bluff Co., NE	41.8° N, 103.8° W
FMNH	P 27236	*Parophisaurus*	*pawneensis*	Orellan	Brule (Orella B or C)	Round Top, near Crawford, Dawes Co., NE	42.8° N, 103.1° W
FMNH	P 27235	*Parophisaurus*	*pawneensis*	Orellan	Brule Fm	Harrison, Sioux Co., NE	42.4° N, 103.8° W
UMMP	27179	*Parophisaurus*	*pawneensis*	Orellan	Brule Fm	Jack Casement Ranch, Logan Co., CO	41.0° N, 103.4° W
UMMP	25623	*Parophisaurus*	*pawneensis*	Orellan	Brule Fm	Bill Grimm Ranch, Sioux Co., NE	42.8° N, 103.9° W
MSU	VP 1114	*Parophisaurus*	*pawneensis*	Orellan	Brule Fm	Chimney Canyon Locality, Logan Co., CO	41.0° N, 103.4° W
MSU	VP 1136	*Parophisaurus*	*pawneensis*	Orellan	Brule Fm	Pawnee Buttes Locality, Weld Co., CO	40.8° N, 104.0° W
MSU	VP 1137	*Parophisaurus*	*pawneensis*	Orellan	Brule Fm	Chimney Canyon "Secret" Locality, Logan Co., CO	41.0° N, 103.4° W

AMNH	1652	*Peltosaurus*	*sp.*	Orellan	Brule (Orella B or C)	5 mi S of Scenic, SD	43.5° N, 101.9° W
AMNH	42915	*Peltosaurus*	*sp.*	Orellan	Brule (Orella B or C)	7 mi S of South Heart, ND	46.9° N, 102.8° W
AMNH	8750	*Peltosaurus*	*sp.*	Orellan	Brule (Orella B or C)	West Central Side Red Shirt Table, Shannon Co., SD	43.3° N, 102.5° W
UNSM	84298	*Peltosaurus*	*sp.*	Orellan	Brule (Orella B or C)	Sf-102, Scotts Bluff Co., NE	41.8° N, 103.8° W
UNSM	84302	*Peltosaurus*	*sp.*	Orellan	Brule (Orella D)	Sx-36, Sioux Co., NE	42.4° N, 103.8° W
UNSM	50004	*Peltosaurus*	*sp.*	Orellan	Brule (Orella B or C)	Big Badlands, SD	43.9° N, 102.5° W
UNSM	84297	*Peltosaurus*	*sp.*	Orellan	Brule (Orella B or C)	Big Badlands, SD	43.9° N, 102.5° W
UNSM	84296*	*Peltosaurus*	*sp.*	Orellan	Brule (Orella B)	Sx-38, Sioux Co., NE	42.4° N, 103.8° W
FMNH	UC 1720	*Peltosaurus*	*granulosus*	Orellan	Brule Fm	Harrison, Sioux Co., NE	42.4° N, 103.8° W
FMNH	P 27072	*Peltosaurus*	*granulosus*	Orellan	Brule Fm	Harrison, Sioux Co., NE	42.4° N, 103.8° W
FMNH	PR 1339	*Peltosaurus*	*sp.*	Orellan	Brule (Orella B or C)	Sage Creek, Pennington Co., SD	43.9° N, 102.4° W
AMNH	8759	*Peltosaurus*	*granulosus*	Orellan	(Not given)	B. Parsons Ranch, Siome Co., NE	42.4° N, 103.8° W
RAM	7104	*Peltosaurus*	*granulosus*	Orellan	(Not given)	V 96231, Sioux Co., NE	
CM	425	*Peltosaurus*	*granulosus*	Orellan	Brule (Orella B or C)	323: Prairie Dog Creek, NE	42.4° N, 103.8° W
CM	60405*	*Parophisaurus*	*sp.*	Orellan	Brule Fm (Cedar Creek Mbr)	2147: Pawnee Grasslands, Pawnee Butte, CO	40.8° N, 104.0° W
CM	9771	*Peltosaurus*	*sp.*	Orellan	Brule Fm	393: Slim Buttes, 1/2 mi S of Reva Pass, SD	45.5° N, 103.1° W
UWBM	89169	*Peltosaurus*	*sp*	Orellan	(Not given)	C1266, Shannon Co., SD	43.3° N, 102.5° W

FMNH	UR450	*Peltosaurus*	*sp.*	Orellan	Brule Fm	Sowbelly Canyon, Hat Creek Basin, Sioux Co., NE	42.4° N, 103.8° W
FMNH	UR 453	*Peltosaurus*	*sp.*	Orellan	Brule Fm	Sowbelly Canyon, Hat Creek Basin, Sioux Co., NE	42.4° N, 103.8° W
FMNH	P 12861	*Peltosaurus*	*abbotti*	Whitneyan	Brule Fm	Cottonwood Creek of White River, Shannon Co., SD	43.3° N, 102.5° W
UNSM	133087	*Peltosaurus*	*sp.*	Whitneyan	Brule Fm (Whitney C)	MO-106, Morrill Co., NE	41.7° N, 103.1° W
UCMP	81949	*Peltosaurus*	*sp.*	Whitneyan	Brule Fm (Unit F)	V 68159, Backward Butte, Harding Co., SD	45.6° N, 103.5° W
UNSM	12102*	*Peltosaurus*	*sp.*	Whitneyan	Brule Fm (Whitney A)	Sx-22, Sioux Co., NE	42.4° N, 103.8° W
UNSM	81001	*Peltosaurus*	*sp.*	early Arikareean	Gering Fm (B Mbr)	Mo-160, Lone Skull Quarry, Morrill Co., NE	41.7° N, 103.1° W
UNSM	50003	*Peltosaurus*	*sp.*	early Arikareean	Gering Fm	Bn-102, Banner Co., NE	41.5° N, 103.8° W
UNSM	56069	*Peltosaurus*	*sp.*	early Arikareean	Gering Fm	Mo-108, Morrill Co., NE	41.7° N, 103.1° W
UNSM	125578	*Peltosaurus*	*sp.*	early Arikareean	Gering Fm	Mo-155, Dunlap Ranch Quarry, Morrill Co., NE	41.7° N, 103.1° W
FMNH	PR 851	*Peltosaurus*	*sp.*	early Arikareean	Rosebud Fm (Rockyford Mbr)	Cedar Butte, Mellete Co., SD	43.3° N, 102.5° W
UNSM	85537	Anguidae	indet.	Barstovian	Valentine Fm	Bw-106, Norden Bridge Quarry, Brown Co., NE	42.8° N, 100.0° W
UMMP	V55674	*Gerrhonotus*	*mungerorum*	Clarendonian	Ogallala Fm	UM-K6-59, Wakeeney locality, Trego Co., KS	39.0° N, 99.9° W

APPENDIX 1.2. FOSSIL ANGUID MEASUREMENT DATA

Head lengths in bold indicate estimated measurements; all other head lengths were measured from complete skulls. An asterisk (*) indicates specimens used to calculate skull lengths for incomplete fossil specimens based on ratios between skull length and other cranial elements (i.e., frontal, parietal, dentary, mandible, maxilla). Snout-vent length (SVL) estimates calculated using regression equation in Figure 6. Minimum and maximum SVL estimates indicate one standard error for anguids with skull length ≤ 52 mm; one standard deviation for anguids with skull length > 52 mm (see Methods).

Inst.	**Specimen #**	***Genus***	***Species***	**NALMA**	**Head Length (mm)**	**Estimated SVL (mm)**	**SVL Minimum (mm)**	**SVL Maximum (mm)**
UCMP	46089	*Odaxosaurus*	*piger*	Lancian	**26.51**	113.70	101.89	126.88
UCMP	61414	*Odaxosaurus*	*piger*	Lancian	**28.84**	122.57	109.56	137.13
UCMP	49992	*Odaxosaurus*	*piger*	Lancian	**23.81**	103.31	92.88	114.91
UCMP	46624	*Odaxosaurus*	*piger*	Lancian	**28.04**	119.53	106.93	133.62
UCMP	46037	*Odaxosaurus*	*piger*	Lancian	**22.40**	97.83	88.13	108.61
UCMP	49772	*Odaxosaurus*	*piger*	Lancian	**24.32**	105.28	94.60	117.18
UCMP	49780	*Odaxosaurus*	*piger*	Lancian	**26.89**	115.15	103.14	128.56
UCMP	229961	Glyptosaurinae	indet.	Puercan	**15.95**	72.27	65.78	79.40
AMNH	2686	*Machaerosaurus*	*torrejonensis*	Torrejonian	**20.26**	89.45	80.83	99.00
YPM	PU 20574	Anguidae	indet.	Torrejonian	**26.82**	114.88	102.91	128.25
CM	87168	*Odaxosaurus*	*sp*	Torrejonian	**24.66**	106.59	95.73	118.69
AMNH	FR 2686	*Machaerosaurus*	*torrejonensis*	Torrejonian	**10.97**	51.74	47.64	56.19
UCMP	114385	Glyptosaurinae	indet.	Tiffanian	**18.81**	83.72	75.82	92.45

CM	5431	Anguidae	indet	Tiffanian	**23.11**	100.60	90.53	111.79
CM	5434	Anguidae	indet	Tiffanian	**25.39**	109.40	98.17	121.92
CM	18728	Anguidae	indet	Tiffanian	**26.94**	115.34	103.31	128.78
CM	40509	Anguidae	indet	Tiffanian	**36.26**	150.34	133.44	169.39
CM	69641	Anguidae	indet	Tiffanian	**27.72**	118.32	105.88	132.21
UCM	98615	*Melanosaurus*	*sp.*	Tiffanian	**42.76**	174.16	153.80	197.23
YPM	PU 20631	*Odaxosaurus*	*sp.*	Tiffanian	**33.31**	139.90	124.47	157.23
UMMP	77641	*Odaxosaurus*	*piger*	Clarkforkian	**14.02**	64.38	58.84	70.46
UMMP	73787	*Melanosaurus*	*maximus*	Clarkforkian	**55.89**	297.29	271.31	328.76
UMMP	74618	*Melanosaurus*	*maximus*	Clarkforkian	**65.65**	349.20	318.69	386.18
UMMP	74615	*Melanosaurus*	*maximus*	Clarkforkian	**39.37**	161.36	142.87	182.25
UMMP	65550	*Melanosaurus*	*maximus*	Clarkforkian	**32.38**	136.20	121.30	152.94
UMMP	74616	*Xestops*	*vagans*	Clarkforkian	**41.14**	168.72	149.15	190.85
AMNH	7431	*Proglyptosaurus*	*huerfanensis*	Wasatchian	**78.26**	416.28	379.90	460.35
USNM	18316	*Glyptosaurus*	*sylvestris*	Wasatchian	100.00	531.91	485.44	588.24
USNM	6004*	*Paraglyptosaurus*	*hillsi*	Wasatchian	125.00	664.89	606.80	735.29
AMNH	5168	*Melanosaurus*	*maximus*	Wasatchian	84.12	447.45	408.35	494.82
UCMP	151761	*Arpadosaurus*	*sp.*	Wasatchian	**48.85**	259.84	237.14	287.35
UCMP	47740	*Gerrhonotus*	*sp.*	Wasatchian	**20.44**	90.16	81.44	99.81
UCMP	215232	*Proxestops*	*sp.*	Wasatchian	**18.91**	84.11	76.16	92.89
UCMP	100118	*Apodosauriscus*	*sp.*	Wasatchian	**7.47**	36.73	34.22	39.43
UCMP	100102	*Proxestops*	*sp.*	Wasatchian	**18.41**	82.11	74.41	90.61
USNM	25826	*Arpadosaurus*	*gazinorum*	Wasatchian	**77.56**	412.55	376.50	456.24
CM	44836	*Xestops*	*sp.*	Wasatchian	**33.86**	141.45	125.81	159.04
CM	42270	*Paraglyptosaurus*	*sp.*	Wasatchian	**64.15**	341.22	311.41	377.35
CM	42411	*Xestops*	*sp.*	Wasatchian	**21.61**	94.76	85.45	105.09
CM	42179	*Glyptosaurus*	*sylvestris*	Wasatchian	**93.33**	496.44	453.06	549.00

CM	44820	*Glyptosaurus*	*sylvestris*	Wasatchian	**101.37**	539.20	492.09	596.29
YPM	PU 21801	*Melanosaurus*	*maximus*	Wasatchian	**36.24**	150.25	133.35	169.28
UCMP	216000	*Gaultia*	*silvaticus*	Wasatchian	**48.65**	195.42	171.89	222.18
UCMP	126000*	*Glyptosaurus*	*sylvestris*	Bridgerian	122.09	649.41	592.67	718.18
USNM	16527	*Glyptosaurus*	*sylvestris*	Bridgerian	**78.51**	417.59	381.10	461.80
USNM	18106	*Glyptosaurus*	*sylvestris*	Bridgerian	**101.49**	539.84	492.67	597.00
AMNH	FR 6055	*Glyptosaurus*	*sylvestris*	Bridgerian	**94.02**	500.11	456.41	553.06
AMNH	6054	*Paraglyptosaurus*	*princeps*	Bridgerian	**126.54**	673.09	614.27	744.35
USNM	12590	*Paraglyptosaurus*	*princeps*	Bridgerian	**122.82**	653.30	596.21	722.47
YPM	1072	*Glyptosaurus*	*sylvestris*	Bridgerian	**105.84**	562.98	513.79	622.59
USNM	V 16520	*Glyptosaurus*	*sylvestris*	Bridgerian	**87.78**	466.89	426.09	516.32
YPM	VP 58255	*Glyptosaurus*	*sp.*	Bridgerian	**49.16**	197.23	173.43	224.31
YPM	1092	*Glyptosaurus*	*sp*	Bridgerian	**122.05**	649.19	592.47	717.93
YPM	7601	*Paraglyptosaurus*	*princeps*	Bridgerian	**110.97**	590.24	538.67	652.74
YPM	7602	*Paraglyptosaurus*	*princeps*	Bridgerian	**119.52**	635.76	580.21	703.07
SDNHM	75932	*Glyptosaurus*	*sylvestris*	Uintan	**81.83**	435.25	397.22	481.34
YPM	PU 11303	*Glyptosaurus*	*sp.*	Uintan	**81.98**	436.06	397.96	482.24
CM	42469	Anguidae	indet.	Duchesnean	**29.85**	126.82	113.22	142.06
AMNH	8706	*Helodermoides*	*tuberculatus*	Chadronian	75.70	402.66	367.48	445.29
UNSM	4511*	*Helodermoides*	*tuberculatus*	Chadronian	96.13	511.33	466.65	565.47
AMNH	6800	*Helodermoides*	*tuberculatus*	Chadronian	**97.63**	519.31	473.93	574.29
USNM	529372	*Helodermoides*	*sp.*	Chadronian	**87.25**	464.10	423.54	513.24
FAM	8711	*Parophisaurus*	*pawneensis*	Chadronian	29.17	123.48	110.33	138.18
AMNH	8138	*Peltosaurus*	*granulosus*	Chadronian	37.67	155.70	138.03	175.64
USNM	15607	*Peltosaurus*	*granulosus*	Chadronian	**50.63**	201.67	177.19	229.53
CM	51344	*Helodermoides*	*tuberculatus*	Chadronian	57.15	303.99	277.43	336.18
CM	1050	*Helodermoides*	*tuberculatus*	Chadronian	46.36	246.60	225.05	272.71

CM	707	*Helodermoides*	*tuberculatus*	Chadronian	**63.43**	337.39	307.91	373.12
CM	9975	*Helodermoides*	*tuberculatus*	Chadronian	**67.77**	360.48	328.98	398.65
UNSM	125564	*Helodermoides*	*tuberculatus*	Chadronian	**122.68**	652.57	595.55	721.67
UNSM	128143a	*Helodermoides*	*tuberculatus*	Chadronian	**103.44**	550.24	502.16	608.50
UNSM	128143b	*Helodermoides*	*tuberculatus*	Chadronian	**125.30**	666.49	608.25	737.06
USNM	13869	*Helodermoides*	*tuberculatus*	Orellan	100.56	534.89	488.16	591.53
USNM	13861	*Helodermoides*	*tuberculatus*	Orellan	118.95	632.71	577.43	699.71
UNSM	50000	*Parophisaurus*	*pawneensis*	Orellan	15.03	68.53	62.49	75.16
FMNH	P 27236	*Parophisaurus*	*pawneensis*	Orellan	**42.68**	173.30	153.06	196.21
FMNH	P 27235	*Parophisaurus*	*pawneensis*	Orellan	**27.82**	119.15	106.60	133.17
UMMP	27179	*Parophisaurus*	*pawneensis*	Orellan	22.41	97.92	88.20	108.71
UMMP	25623	*Parophisaurus*	*pawneensis*	Orellan	20.25	89.56	80.92	99.13
MSU	VP 1114	*Parophisaurus*	*pawneensis*	Orellan	18.75	83.39	75.53	92.07
MSU	VP 1136	*Parophisaurus*	*pawneensis*	Orellan	34.53	143.69	127.73	161.65
MSU	VP 1137	*Parophisaurus*	*pawneensis*	Orellan	29.83	126.82	113.22	142.06
AMNH	1652	*Peltosaurus*	*sp.*	Orellan	**34.70**	144.98	128.84	163.15
AMNH	42915	*Peltosaurus*	*sp.*	Orellan	35.02	146.28	129.95	164.66
AMNH	8750	*Peltosaurus*	*sp.*	Orellan	33.70	141.15	125.55	158.69
UNSM	84298	*Peltosaurus*	*sp.*	Orellan	33.72	141.15	125.55	158.69
UNSM	84302	*Peltosaurus*	*sp.*	Orellan	39.92	164.26	145.35	185.64
UNSM	50004	*Peltosaurus*	*sp.*	Orellan	35.56	147.59	131.08	166.18
UNSM	84297	*Peltosaurus*	*sp.*	Orellan	46.14	186.11	163.98	211.24
UNSM	84296*	*Peltosaurus*	*sp.*	Orellan	51.17	205.30	180.27	233.81
FMNH	UC 1720	*Peltosaurus*	*granulosus*	Orellan	**40.42**	165.74	146.61	187.36
FMNH	P 27072	*Peltosaurus*	*granulosus*	Orellan	44.21	179.59	158.42	203.59
FMNH	PR 1339	*Peltosaurus*	*sp.*	Orellan	**43.83**	178.00	157.06	201.72
AMNH	8759	*Peltosaurus*	*granulosus*	Orellan	**27.61**	118.09	105.68	131.95

RAM	7104	*Peltosaurus*	*granulosus*	Orellan	**41.27**	168.72	149.15	190.85
CM	425	*Peltosaurus*	*granulosus*	Orellan	**51.64**	205.30	180.27	233.81
CM	60405*	*Parophisaurus*	*sp.*	Orellan	27.27	117.04	104.78	130.74
CM	9771	*Peltosaurus*	*sp.*	Orellan	49.48	198.11	174.17	225.34
UWBM	89169	*Peltosaurus*	*sp*	Orellan	51.87	207.14	181.83	235.97
FMNH	UR450	*Peltosaurus*	*sp.*	Orellan	**47.48**	191.16	168.27	217.17
FMNH	UR 453	*Peltosaurus*	*sp.*	Orellan	**44.92**	181.20	159.79	205.47
FMNH	P 12861	*Peltosaurus*	*abbotti*	Whitneyan	43.37	176.42	155.72	199.86
UNSM	133087	*Peltosaurus*	*sp.*	Whitneyan	**38.37**	158.12	140.09	178.46
UCMP	81949	*Peltosaurus*	*sp.*	Whitneyan	**28.27**	120.40	107.68	134.62
UNSM	12102*	*Peltosaurus*	*sp.*	Whitneyan	**34.19**	142.66	126.85	160.45
UNSM	81001	*Peltosaurus*	*sp.*	early Arikareean	**50.74**	203.48	178.73	231.66
UNSM	50003	*Peltosaurus*	*sp.*	early Arikareean	36.04	148.91	132.21	167.73
UNSM	56069	*Peltosaurus*	*sp.*	early Arikareean	**47.52**	191.16	168.27	217.17
UNSM	125578	*Peltosaurus*	*sp.*	early Arikareean	**47.68**	191.93	168.92	218.08
FMNH	PR 851	*Peltosaurus*	*sp.*	early Arikareean	**37.36**	154.32	136.84	174.03
UNSM	85537	Anguidae	indet.	Barstovian	**42.71**	173.98	153.64	197.01
UMMP	V55674	*Gerrhonotus*	*mungerorum*	Clarendonian	26.00	111.76	100.21	124.64

APPENDIX 2. EXTANT ANGUID LOCALITY AND MEASUREMENT DATA

All specimens represent adult individuals for which compete skull and snout-vent length (SVL) could be measured. This dataset was used to generate the regression equation in Figure 6.

Collection	**Specimen #**	***Genus***	***Species***	**Dry/ Wet**	**Locality**	**Head Length (mm)**	**SVL (mm)**
AMNH	R-140067	*Abronia*	*campbelli*	Dry	Guatemala	25.37	114.66
USNM	224801	*Abronia*	*taeniata*	Wet	Mexico, Veracruz	25.76	111.00
FMNH	111784	*Abronia*	*graminea*	Wet	Mexico	21.28	87.00
FMNH	111786	*Abronia*	*graminea*	Wet	Mexico	26.40	90.00
FMNH	111773	*Abronia*	*graminea*	Wet	Mexico	25.70	98.00
FMNH	111781	*Abronia*	*graminea*	Wet	Mexico	27.71	92.00
FMNH	111780	*Abronia*	*graminea*	Wet	Mexico	25.66	98.00
FMNH	111775	*Abronia*	*graminea*	Wet	Mexico	25.48	99.00
FMNH	111783	*Abronia*	*graminea*	Wet	Mexico	25.74	89.00
FMNH	111777	*Abronia*	*graminea*	Wet	Mexico	27.29	99.00
FMNH	111778	*Abronia*	*graminea*	Wet	Mexico	24.15	97.00
FMNH	111779	*Abronia*	*graminea*	Wet	Mexico	24.96	104.00
FMNH	106538	*Abronia*	*graminea*	Wet	Mexico	27.78	98.00
USNM	113193	*Abronia*	*gramineus*	Wet	Mexico, Veracruz	23.55	95.00
USNM	148889	*Abronia*	*martindelcampoi*	Wet	Mexico, Guerrero	29.63	112.00
FMNH	105600	*Abronia*	*martindelcampoi*	Wet	Mexico, Guerrero	26.02	105.00

FMNH	38514	*Abronia*	*martindelcampoi*	Wet	Mexico, Guerrero	27.55	101.00
USNM	108310	*Celestus*	*duquesneyi*	Wet	Jamaica, Portland Point	28.60	137.00
USNM	328802	*Celestus*	*darlingtoni*	Wet	Dominican Republic, La Vega	15.01	48.00
USNM	259955	*Celestus*	*curtissi*	Wet	Dominican Republic, Isla Catalina	11.02	63.00
USNM	259954	*Celestus*	*curtissi hylonomus*	Wet	Dominican Republic, La Altagracia	12.34	74.00
USNM	239367	*Celestus*	*curtissi curtissi*	Wet	Haito, Ouest	12.55	67.00
USNM	30189	*Celestus*	*enneagrammus*	Wet	Mexico	13.99	83.00
FMNH	281	*Celestus*	*enneagrammus*	Wet	Guatemala	21.10	93.00
FMNH	70998	*Celestus*	*enneagrammus*	Wet	Mexico, Veracruz	13.22	65.00
FMNH	111100	*Celestus*	*enneagrammus*	Wet	Mexico	10.20	49.00
FMNH	111102	*Celestus*	*enneagrammus*	Wet	Mexico	10.43	52.93
FMNH	111103	*Celestus*	*enneagrammus*	Wet	Mexico	10.60	51.00
USNM	328147	*Celestus*	*barbouri*	Wet	Jamaica, Trelawny	14.67	84.00
FMNH	245494	*Celestus*	*warreni*	Wet	Hispaniola	16.63	75.00
FMNH	101248	*Celestus*	*cyanochloris*	Wet	Costa Rica	15.54	77.00
USNM	259472	*Celestus*	*stenurus*	Dry	Dominican Republic	17.84	76.00
USNM	259471	*Celestus*	*stenurus*	Dry	Dominican Republic	18.62	90.72

USNM	328820	*Celestus*	*stenurus*	Wet	Dominican Republic	23.48	119.00
USNM	259470	*Celestus*	*costatus oreistes*	Dry	Dominican Republic	19.28	87.25
FMNH	13254	*Celestus*	*costatus*	Dry	Haiti, between St. Marc & Gonaive	29.66	164.66
AMNH	51163	*Celestus*	*costatus*	Dry	Dominican Republic	17.19	76.50
FMNH	42187	*Celestus*	*costatus*	Wet	Haiti, Port-au-Prince	15.22	63.00
FMNH	13245	*Celestus*	*costatus*	Wet	Haiti	19.41	100.98
FMNH	13248	*Celestus*	*costatus*	Wet	Haiti	18.85	94.54
FMNH	13242	*Celestus*	*costatus*	Wet	Haiti	22.80	97.08
FMNH	13244	*Celestus*	*costatus*	Wet	Haiti	16.50	75.98
FMNH	13287	*Celestus*	*costatus*	Wet	Haiti	16.39	69.00
USNM	328775	*Celestus*	*costatus*	Wet	Dominican Republic	19.71	101.00
AMNH	R-72358	*Celestus*	*crusculus*	Dry	Jamaica	14.40	81.18
USNM	328164	*Celestus*	*crusculus*	Wet	Jamaica, Trelawny	11.39	65.00
USNM	512240	*Diploglossus*	*nigropunctatus*	Wet	Cuba, Guantanamo	18.54	113.00
USNM	221100	*Diploglossus*	*pleei*	Wet	Puerto Rico, Manati	11.03	83.00
FMNH	211387	*Diploglossus*	*pleei*	Wet	Puerto Rico, San Juan	17.24	99.00
USNM	347178	*Diploglossus*	*bilobatus*	Wet	Panama, Bocas del Toro	10.68	57.50

FMNH	101510	*Diploglossus*	*bilobatus*	Wet	Costa Rica	13.45	70.00
FMNH	152064	*Diploglossus*	*bilobatus*	Wet	Panama	20.76	82.00
USNM	209642	*Diploglossus*	*lessonae*	Wet	Brazil, Pernambuco State	19.99	117.00
FMNH	19249	*Diploglossus*	*millepunctatus*	Wet	Colombia, Malpelo Island	48.33	205.00
FMNH	165517	*Diploglossus*	*millepunctatus*	Wet	Colombia	52.38	195.00
FMNH	165518	*Diploglossus*	*millepunctatus*	Wet	Colombia	57.50	200.00
CJB	2093	*Diploglossus*	*millepunctatus*	Dry	NO DATA	42.12	183.00
FMNH	19248	*Diploglossus*	*millepunctatus*	Dry	Colombia, Malpelo Is.	54.75	239.75
FMNH	12491	*Diploglossus*	*delasagra*	Wet	Cuba, Cienfuegos	13.03	74.00
FMNH	40017	*Diploglossus*	*fasciatus*	Wet	Peru	13.69	51.00
FMNH	236386	*Diploglossus*	*bivattatus*	Wet	Honduras, Yoro	20.26	107.60
FMNH	78137	*Diploglossus*	*monotropis*	Wet	Columbia	34.70	155.00
FMNH	78136	*Diploglossus*	*monotropis*	Wet	Colombia	23.56	137.00
FMNH	60126	*Diploglossus*	*monotropis*	Wet	Panama	40.28	136.00
FMNH	167606	*Diploglossus*	*monotropis*	Wet	Columbia	30.55	157.00
FMNH	165180	*Diploglossus*	*monotropis*	Wet	Columbia	33.76	150.00
FMNH	165179	*Diploglossus*	*monotropis*	Wet	Columbia	26.22	104.00
AMNH	R-154690	*Diploglossus*	*stenurus*	Dry	Haiti	18.72	120.71
USNM	240084	*Elgaria*	*paucicarinata*	Wet	Mexico, Baja California	19.52	101.00
FMNH	1107	*Elgaria*	*coerulea*	Wet	USA, California, Eureka	23.96	95.00

FMNH	1107	*Elgaria*	*coerulea*	Wet	USA, California, Eureka	18.50	88.00
FMNH	2894	*Elgaria*	*coerulea*	Wet	USA, California, Santa Clara Co.	22.44	94.00
AMNH	57821	*Elgaria*	*coerulea*	Dry	NO DATA	34.62	153.94
CJB	1818	*Elgaria*	*coerulea*	Dry	USA, Oregon	18.81	93.00
CJB	2080	*Elgaria*	*coerulea*	Dry	USA, California	21.94	114.00
USNM	313411	*Elgaria*	*coerulea*	Dry	USA, Washington (King, Seattle)	18.57	93.66
FMNH	94873	*Elgaria*	*coerulea principis*	Wet	USA, California	18.77	83.00
FMNH	94874	*Elgaria*	*coerulea principis*	Wet	USA, California	22.75	94.00
FMNH	1219	*Elgaria*	*coerulea palmeri*	Wet	USA, California, Hot Springs	23.73	95.00
FMNH	1219	*Elgaria*	*coerulea palmeri*	Wet	USA, California, Hot Springs	23.24	97.00
FMNH	1219	*Elgaria*	*coerulea palmeri*	Wet	USA, California, Hot Springs	25.88	100.00
FMNH	1219	*Elgaria*	*coerulea palmeri*	Wet	USA, California, Hot Springs	26.22	95.00

FMNH	1219	*Elgaria*	*coerulea palmeri*	Wet	USA, California, Hot Springs	24.70	80.00
FMNH	1219	*Elgaria*	*coerulea palmeri*	Wet	USA, California, Hot Springs	21.46	95.00
USNM	297237	*Elgaria*	*multicarinata*	Wet	USA, California, Monterey	22.38	95.00
FMNH	219675	*Elgaria*	*multicarinata*	Wet	NO DATA	30.74	134.00
FMNH	219678	*Elgaria*	*multicarinata*	Wet	NO DATA	29.32	120.00
CJB	1803	*Elgaria*	*multicarinata*	Dry	USA, Oregon	20.12	92.00
USNM	559828	*Elgaria*	*multicarinata*	Dry	USA, California, Santa Barbara	29.58	124.56
USNM	220196	*Elgaria*	*multicarinata*	Dry	USA, California, Monterey	30.65	132.00
USNM	229771	*Elgaria*	*multicarinata*	Dry	USA, California, Butte	20.25	103.00
USNM	559835	*Elgaria*	*multicarinata*	Dry	USA, California, Santa Barbara	23.38	105.00
USNM	559836	*Elgaria*	*multicarinata*	Dry	USA, California, Santa Barbara	28.98	125.00
USNM	559826	*Elgaria*	*multicarinata*	Dry	USA, California, Santa Barbara	23.98	129.00

FMNH	857	*Elgaria*	*m. multicarinata*	Wet	USA, California, Redwood City	30.07	97.00
FMNH	857	*Elgaria*	*m. multicarinata*	Wet	USA, California, Redwood City	26.41	95.00
FMNH	857	*Elgaria*	*m. multicarinata*	Wet	USA, California, Redwood City	22.94	90.00
FMNH	2895	*Elgaria*	*m. multicarinata*	Wet	USA, California, Santa Clara Co.	23.61	96.00
FMNH	2892	*Elgaria*	*m. multicarinata*	Wet	USA, California, Point Carmel	20.34	85.00
FMNH	1886	*Elgaria*	*multicarinata scincicauda*	Wet	USA, Oregon, Curry Co., Agnes	23.15	112.00
USNM	13783	*Elgaria*	*multicarinata scincicauda*	Dry	USA, California	26.90	126.00
FMNH	130599	*Elgaria*	*multicarinata nana*	Wet	Mexico, Baja California	22.65	92.00
FMNH	130600	*Elgaria*	*multicarinata nana*	Wet	Mexico, Baja California	23.89	90.00
FMNH	130601	*Elgaria*	*multicarinata nana*	Wet	Mexico, Baja California	23.41	90.00

FMNH	23600	*Elgaria*	*multicarinata webbii*	Wet	USA, California	26.14	102.00
FMNH	2813	*Elgaria*	*multicarinata webbii*	Wet	USA, California, Los Angeles	24.52	101.00
FMNH	22652	*Elgaria*	*multicarinata webbii*	Wet	USA, California, Los Angeles	22.37	101.00
FMNH	2497	*Elgaria*	*multicarinata webbii*	Wet	USA, California, Riverside	35.07	132.00
FMNH	23603	*Elgaria*	*multicarinata webbii*	Wet	USA, California	31.42	120.00
AMNH	R-154696	*Elgaria*	*multicarinata webbii*	Dry	USA	19.50	94.45
AMNH	R-110172	*Elgaria*	*multicarinata webbii*	Dry	USA, California, San Diego	33.30	133.87
CJB	1299	*Elgaria*	*multicarinata webbii*	Dry	California	30.22	145.00
CJB	2079	*Elgaria*	*multicarinata webbii*	Dry	California	28.04	136.00
FMNH	130594	*Elgaria*	*cedrosensis*	Wet	Mexico, Baja	17.80	71.00
FMNH	130596	*Elgaria*	*cedrosensis*	Wet	Mexico, Baja	25.08	92.00
FMNH	130595	*Elgaria*	*cedrosensis*	Wet	Mexico, Baja	22.96	87.00
FMNH	130598	*Elgaria*	*cedrosensis*	Wet	Mexico, Baja	25.03	95.00
FMNH	130597	*Elgaria*	*cedrosensis*	Wet	Mexico, Baja	20.91	88.00
FMNH	74773	*Elgaria*	*kingii*	Wet	USA, Arizona	22.80	95.00
FMNH	74772	*Elgaria*	*kingii*	Wet	USA, Arizona	22.70	100.00

FMNH	94875	*Elgaria*	*kingii*	Wet	USA, Arizona	18.06	89.30
FMNH	110347	*Elgaria*	*kingii*	Wet	Mexico	19.97	106.00
FMNH	110346	*Elgaria*	*kingii*	Wet	Mexico	25.77	103.00
USNM	223993	*Elgaria*	*kingi*	Wet	USA, Arizona	19.68	96.00
USNM	292555	*Elgaria*	*kingii*	Dry	USA, Arizona, Cochise Co., Portal	19.47	89.12
USNM	292554	*Elgaria*	*kingii*	Dry	USA, Arizona, Cochise Co., Portal	21.16	102.00
FMNH	213397	*Elgaria*	*sp.*	Dry	NO DATA	20.82	103.82
USNM	113218	*Gerrhonotus*	*liocephalus*	Wet	Mexico, Oaxaca	24.91	121.00
FMNH	99593	*Gerrhonotus*	*liocephalus*	Wet	Mexico	39.13	150.00
FMNH	99594	*Gerrhonotus*	*liocephalus*	Wet	Mexico	40.20	146.00
FMNH	38525	*Gerrhonotus*	*liocephalus*	Wet	Mexico, Guerrero, Chilpancingo	23.35	112.00
AMNH	106732	*Gerrhonotus*	*liocephalus*	Dry	Mexico	18.20	71.10
CJB	2155	*Gerrhonotus*	*liocephalus*	Dry	NO DATA	34.91	154.00
USNM	25085	*Gerrhonotus*	*liocephalus*	Dry	Mexico	23.01	79.00
FMNH	167099	*Gerrhonotus*	*infernalis*	Wet	Mexico, Coahuila	34.83	128.00
USNM	103705	*Gerrhonotus*	*infernalis*	Wet	Mexico, Coahuila	30.96	122.00
FMNH	37538	*Gerrhonotus*	*infernalis*	Wet	USA, Texas, Travis Co.	32.18	127.00

FMNH	130990	*Gerrhonotus*	*infernalis*	Wet	USA, Texas, Hays Co.	25.32	115.00
FMNH	106121	*Gerrhonotus*	*infernalis*	Wet	USA, Texas	30.54	137.00
FMNH	22452	*Gerrhonotus*	*infernalis*	Dry	USA, Texas, Brewster Co.	37.70	163.70
FMNH	38517	*Mesaspis*	*gadovii*	Wet	Mexico, Guerrero	19.52	83.64
FMNH	38521	*Mesaspis*	*gadovii*	Wet	Mexico, Guerrero	22.54	84.00
FMNH	38524	*Mesaspis*	*gadovii*	Wet	Mexico, Guerrero	17.34	75.00
FMNH	38522	*Mesaspis*	*gadovii*	Wet	Mexico, Guerrero	23.09	96.00
FMNH	38518	*Mesaspis*	*gadovii*	Wet	Mexico, Guerrero	18.12	80.00
FMNH	38520	*Mesaspis*	*gadovii*	Wet	Mexico, Guerrero	18.81	91.00
AMNH	90945	*Mesaspis*	*gadovii levigata*	Dry	Mexico	18.04	87.58
AMNH	90944	*Mesaspis*	*gadovii levigata*	Dry	Mexico	25.70	108.22
AMNH	90946	*Mesaspis*	*gadovii levigata*	Dry	Mexico	15.68	83.68
AMNH	90947	*Mesaspis*	*gadovii levigata*	Dry	Mexico	18.51	90.90
AMNH	90948	*Mesaspis*	*gadovii levigata*	Dry	Mexico	23.07	103.17
FMNH	177595	*Mesaspis*	*monticola*	Wet	Costa Rica	12.59	52.00
FMNH	177596	*Mesaspis*	*monticola*	Wet	Costa Rica	12.78	55.00
FMNH	188758	*Mesaspis*	*monticola*	Wet	Costa Rica	18.73	63.00
FMNH	188779	*Mesaspis*	*monticola*	Wet	Costa Rica	18.62	74.00
FMNH	188780	*Mesaspis*	*monticola*	Wet	Costa Rica	15.06	73.00
FMNH	112026	*Mesaspis*	*viridiflava*	Wet	Mexico, Oaxaca	13.90	57.00
FMNH	99025	*Mesaspis*	*viridiflava*	Wet	Mexico, Oaxaca	12.19	53.00

FMNH	99026	*Mesaspis*	*viridiflava*	Wet	Mexico, Oaxaca	9.97	43.00
FMNH	99031	*Mesaspis*	*viridiflava*	Wet	Mexico, Oaxaca	9.89	43.00
FMNH	99023	*Mesaspis*	*viridiflava*	Wet	Mexico, Oaxaca	10.24	40.00
FMNH	68615	*Mesaspis*	*moreletii fulva*	Wet	Guatemala, Jalapa	20.17	77.99
FMNH	64971	*Mesaspis*	*moreletii salvadorensis*	Wet	El Salvador, Santa Ana	19.70	77.00
FMNH	64972	*Mesaspis*	*moreletii salvadorensis*	Wet	El Salvador, Santa Ana	18.01	83.00
AMNH	90980	*Mesaspis*	*moreleti temporalis*	Dry	Mexico	15.65	80.70

APPENDIX 3. EXTANT HELODERMATID LOCALITY AND MEASUREMENT DATA

All specimens represent adult individuals for which compete skull and snout-vent length (SVL) could be measured. Mean head length: SVL ratios from this dataset were used to calculate SVL for large fossil glyptosaurines.

Institution	**Specimen #**	***Genus***	***Species***	**Dry/Wet**	**Head Length (mm)**	**SVL (mm)**
FMNH	22038	*Heloderma*	*horridum*	Dry	70.27	405.27
FMNH	250611	*Heloderma*	*horridum*	Dry	83.51	492.77
FMNH	38532	*Heloderma*	*horridum*	Wet	71.37	345.00
MVZ	70256	*Heloderma*	*horridum*	Wet	64.04	280.00
MVZ	50864	*Heloderma*	*horridum*	Wet	58.37	290.00
MVZ	50865	*Heloderma*	*horridum*	Wet	58.25	267.00
MVZ	50863	*Heloderma*	*horridum*	Wet	58.61	281.00
MVZ	68970	*Heloderma*	*horridum*	Wet	58.32	286.00
CM	112344	*Heloderma*	*horridum*	Dry	81.25	504.25
FMNH	22232	*Heloderma*	*suspectum*	Dry	58.24	322.98
FMNH	229925	*Heloderma*	*suspectum*	Dry	57.56	352.56
FMNH	22249	*Heloderma*	*suspectum*	Dry	57.34	323.19
FMNH	22866	*Heloderma*	*suspectum*	Wet	54.91	255.00
FMNH	25751	*Heloderma*	*suspectum*	Wet	57.86	283.00
FMNH	15096a	*Heloderma*	*suspectum*	Wet	52.74	292.00
FMNH	15096b	*Heloderma*	*suspectum*	Wet	57.52	293.00
FMNH	26141	*Heloderma*	*suspectum*	Wet	55.98	289.00

MVZ	29398	*Heloderma*	*suspectum*	Dry	52.16	320.00
UCMP	223170	*Heloderma*	*suspectum*	Wet	57.83	297.00
UCMP	8177	*Heloderma*	*suspectum*	Wet	58.58	352.00
UCMP	10478	*Heloderma*	*suspectum*	Wet	54.37	285.00
UCMP	241507	*Heloderma*	*suspectum*	Wet	52.73	287.00
UCMP	9189	*Heloderma*	*suspectum*	Wet	61.38	356.00
UCMP	229640	*Heloderma*	*suspectum*	Wet	62.36	335.00
UCMP	10479	*Heloderma*	*suspectum*	Wet	55.09	335.00
CM	21318	*Heloderma*	*suspectum*	Wet	56.73	290.00
CM	S6907	*Heloderma*	*suspectum*	Wet	53.39	265.00
CM	19338	*Heloderma*	*suspectum*	Wet	54.27	306.00
CM	142372	*Heloderma*	*suspectum*	Wet	54.40	295.00
CM	S4828	*Heloderma*	*suspectum*	Wet	52.40	337.00
CM	25220	*Heloderma*	*suspectum*	Wet	52.55	296.00
CM	S4447	*Heloderma*	*suspectum*	Wet	49.24	246.00
CM	29378	*Heloderma*	*suspectum*	Wet	68.50	368.00
CM	29377	*Heloderma*	*suspectum*	Wet	58.60	342.00
CM	S6904	*Heloderma*	*suspectum*	Wet	68.69	333.00
CM	19348	*Heloderma*	*suspectum*	Wet	51.85	266.85

APPENDIX 4. ADDITIONAL REFERENCES FOR ANGUID SPECIES RICHNESS

THROUGH THE CENOZOIC OF NORTH AMERICA

These references were used in addition to some publications from the Reference list (see page 30) to estimate species richness glyptosaurines and all fossil anguid lizards through the Cenozoic of North America (see Figure 12).

NALMA	Reference
Lancian	Gilmore 1928; Estes 1964; Meszoely et al. 1978; Gauthier 1982; Sullivan 1982; Sullivan & Lucas 1996; Lillegraven & Eberle 1999; Estes 1964; Gauthier 1982; Good 1988
Puercan	Gauthier 1982; Sullivan & Lucas 1986; Sullivan 1981, 1982, 1991; Sullivan & Lucas 1996; Hartman 1986, Lillegraven & Eberle 1999; Estes 1964
Torrejonian	Estes 1964, 1976; Gauthier 1982;Good 1988; Sullivan 1981, 1982, 1986; Sullivan & Lucas 1986a; Sullivan 1991; Sullivan & Lucas 1996; Robison 1986
Tiffanian	Gauthier 1982; Gilmore 1942; Estes 1976; Sullivan 1982; Sullivan 1991; Sullivan & Lucas 1996; Meszoely 1970
Clarkforkian	Gauthier 1982; Sullivan 1991; Sullivan & Lucas 1996; Gilmore 1928; Bartels 1983
Wasatchian	Gilmore 1928; Gauthier 1982; McKenna 1960; Gunnel & Bartels 2001; Conrad & Norell 2008; Gingerich 1989; Hutchison 1992; Meszoely 1970; Sullivan 1979; ell & Bartels 2001; Hirsch et al. 1987; Sullivan 1979
Bridgerian	Marsh 1871; Douglass 1908; Gilmore 1928;White 1952; Gunnell & Bartels 2001; Hutchison 1992; Meszoely 1970; Sullivan 1979; Zonneveld et al. 2000
Uintan	Moscato 2013
Duchesnean	Hutchison 1992
Chadronian	Holman 1972; Smith 2006, 2011; Sullivan 1979; Hutchison 1992
Orellan	Douglass 1903, 1908; Gilmore 1928; Meszoely 1970; Sullivan 1979; Sullivan & Holman 1996; Hutchison 1992

Whitneyan	Gilmore 1928; Cook & Cook 1933; Galbreath 1953; Meszoely et al. 1978; Sullivan 1987, 1979; Hutchison 1992; Macdonald 1951
Arikareean	Holman 1981; Hutchison 1992; Meylan 1984; Sullivan & Holman 1996; Hulbert 1992; Robinson & van Devender 1973; Estes 1963
Hemingfordian	Hulbert 1992; Holman 1998, 2003; Robinson & van Devender 1973; Webb 1981; Yatkola 1976
Barstovian	Estes & Tihen 1964; Wellstead 1977, 1981; Holman 1970, 1973, 1976; Holman & Sullivan 1981
Clarendonian	Hulbert 1992; Estes & Tihen 1964; Holman 1970, 1975, 1987; Wilson 1968; Voorhies 1990; Gauthier 1980
Hemphillian	Hulbert 1992
Blancan	Etheridge 1961; Meszoely 1970; Estes 1963; Good 1988; Meylan et al. 2001; Ray 1957
Irvingtonian	Auffenberg 1955; Hulbert 1992; Ray 1957; Meylan 1955; Holman & Winkler 1987; Meylan et al. 2001; Meszoely 1970
Rancholabrean	Gut & Ray 1963; Holman 1987; Meszoely 1970; Hulbert 1992; Ray 1957; Hecht 1963; Etheridge 1960, 1961

TABLE 1. EXTANT ANGUID SPECIMEN TOTALS

Adult extant limbed anguid lizards included in dataset used to generate RMA regression for ln(Head Length) vs. ln(Snout-Vent Length) (SVL), which was used to estimate SVL for some fossil glyptosaurine lizards. Extant anguid specimens were measured at the following museum institutions: AMNH, CJB, FMNH, USNM.

Genus	***Species***	**# Wet Specimens**	**# Dry Skeletonized Specimens**	**Total # Specimens**
Abronia	*campbelli*	0	1	1
Abronia	*taeniata*	1	0	1
Abronia	*graminea*	12	0	12
Abronia	*martindelcampoi*	3	0	3
Genus Total		**16**	**1**	**17**
Celestus	*duquesneyi*	1	0	1
Celestus	*darlingtoni*	1	0	1
Celestus	*curtissi*	3	0	3
Celestus	*enneagrammus*	6	0	6
Celestus	*barbouri*	1	0	1
Celestus	*cyanochloris*	1	0	1
Celestus	*stenurus*	1	2	3
Celestus	*costatus*	7	3	10
Celestus	*crusculus*	1	1	2
Genus Total		**22**	**6**	**28**
Diploglossus	*nigropunctatus*	1	0	1
Diploglossus	*pleei*	2	0	2
Diploglossus	*bilobatus*	3	0	3
Diploglossus	*lessonae*	1	0	1

Diploglossus	*millepunctatus*	3	2	5
Diploglossus	*delasagra*	1	0	1
Diploglossus	*fasciatus*	1	0	1
Diploglossus	*bivattatus*	1	0	1
Diploglossus	*monotropis*	6	0	6
Diploglossus	*stenurus*	0	1	1
Genus Total		**19**	**3**	**22**
Elgaria	*paucicarinata*	1	0	1
Elgaria	*coerulea*	11	4	15
Elgaria	*multicarinata*	18	12	30
Elgaria	*cedrosensis*	5	0	5
Elgaria	*kingii*	6	2	8
Elgaria	*sp.*	0	1	1
Genus Total		**41**	**19**	**60**
Gerrhonotus	*liocephalus*	4	3	7
Gerrhonotus	*infernalis*	5	1	6
Genus Total		**9**	**4**	**13**
Mesaspis	*gadovii*	6	5	11
Mesaspis	*monticola*	5	0	5
Mesaspis	*viridiflava*	5	0	5
Mesaspis	*moreletii*	3	1	4
Genus Total		**19**	**6**	**25**
Total for All Genera		**126**	**39**	**165**

TABLE 2. EXTANT HELODERMATID SPECIMEN TOTALS

Adult extant helodermatid lizards included in dataset used to calculate a ratio for Head Length: Snout-Vent Length in order to estimate (SVL) for large fossil glyptosaurine lizards. Extant helodermatid specimens were measured at the following museum institutions: CM, FMNH, MVZ, UCMP.

Genus	***Species***	**# Wet Specimens**	**# Dry Skeletonized Specimens**	**Total # Specimens**
Heloderma	*suspectum*	23	4	27
Heloderma	*horridum*	6	3	9
Genus Total		**29**	**7**	**36**

TABLE 3. PUBLISHED PALEOGENE TERRESTRIAL MAPT PROXIES

Terrestrial mean annual paleotemperature (MAPT) proxies for the Great Plains and Western Interior of North America for the late Cretaceous through the Paleogene from literature. Reported error indicates one standard deviation, unless otherwise noted (*).

Reference	**Method**	**Time**	**MAPT Estimate (ºC)**
Pound et al. (2012)	Leaf margin analysis	Late Miocene	14 (7.25 – 5.33 Ma) 14 (11.61 – 7.25 Ma)
Pound et al. (2011)	Leaf margin analysis	Late Miocene	12.5 – 14 (11.61 – 7.25 Ma)
Gregory & McIntosh (1996)	Leaf margin analysis	Early Oligocene	12.7 +/- 1.5* (32.9 – 29 Ma)
Zanazzi et al. (2007)	Stable oxygen isotope data from fossil ungulate tooth enamel and stable oxygen and carbon isotope data from fossil mammal bone fragments	Late Eocene, early Oligocene	21.0 +/- 5.05* (late Eocene, 36.0 – 33.7 Ma) 13.1 +/- 4.7* (early Oligocene, 33.7 – 32.0 Ma)
Evanoff et al. (1992)	Land snail distributions	Late Eocene (Chadronian)	16.5
Sandau (2005)	Leaf margin analysis	Middle Eocene (Uintan)	16.1
Wing & Greenwood (1993)	Leaf margin analysis	Late Early Eocene	18.6 +/- 1.0 (49.6 – 48.6 Ma) 18.6 +/- 1.0 (50.8 – 49.8 Ma)
Wilf (2000)	Leaf margin analysis	Early Eocene	19.6 +/- 2.1 (49.8 – 49.6 Ma) 21.3 +/- 2.2 (52.8 Ma) 16.4 +/- 4.4 (53.0 Ma)

Fricke & Wing (2004)	Stable oxygen isotopes from mammal (*Coryphodon*) enamel and bone and gar scale enamel	Early Eocene	18.7 (54.3 Ma) 15.5 (53.8 Ma) 18.3 (53.0 Ma)
Wing et al. (2000)	Leaf margin analysis	Latest Paleocene - Early Eocene	12.9 +/- 2.4 to over 15 +/-2.4 (Clarkforkian) 18.2 +/- 2.3 to 10.8 +/- 3.3 (55.0 – 54.0 Ma) 15.8 +/- 2.2 to 22.2 +/-2.0 (52.7 – 52.9 Ma)
Johnson & Ellis (2002)	Leaf margin analysis	Early Paleocene – Early Eocene	18.5 +/- 3.2 (65.4 Ma) 22.2 +/- 2.0 (64.1 Ma) 11.7 +/- 2.0 (60 – 56.2 Ma) 18.6 +/- 3.3 (55.6 Ma) 21.3 +/- 2.0, 22.2 +/- 2.0 (52.8 Ma)

*Error indicates standard error rather than standard deviation.

TABLE 4. PALEOGENE TEMPERATURES FROM MAXIMUM GLYPTOSAURINE BODY SIZE ESTIMATES

Estimates of minimum mean annual paleotemperature (MAPT) in the interior of North America through the middle and late Paleogene calculated from maximum estimated snout-vent length (SVL) for glyptosaurine lizards (except for the Torrejonian and Barstovian estimates, which come from indeterminate anguid specimens) for each North American Land Mammal Age (NALMA) for which n > 1. MAPT estimates calculated using the metabolic scaling equation from Head et al. (2013; see Methods; Maximum extant SVL (for *Heloderma suspectum*) = 360 mm; Minimum MAT = 14ºC). All specimens come from the Great Plains and Western Interior. Lower and upper SVL estimates calculated using one standard deviation. Lower and upper values for maximum estimated SVL indicate one standard error for anguids with skull length ≤ 52 mm; one standard deviation for anguids with skull length > 52 mm (see Methods). Lower and upper MAPT estimates calculated using lower and upper values for maximum estimated SVL; the value reported for each is the lowest and highest value, respectively, obtained from calculations using Q_{10} values of both 3 and 2 (values calculated using $Q_{10} = 2$ are italicized; $Q_{10} = 3$, in bold). Orellan estimates are given for the largest corresponding specimens of both *Peltosaurus* (*) and *Helodermoides*.

NALMA	**Taxon**	**Maximum SVL estimate (lower, upper) (mm)**	**MAPT estimates for Q_{10} = 3, *2* (ºC)**	**Range for MAPT estimates (ºC)**
Lancian	*Odaxosaurus piger*	123 (110, 137)	*-1.4,* **4.3**	*-3.0,* **5.3**
Torrejonian	Indeterminate anguid	115 (103, 128)	*-2.3,* **3.7**	*-3.9,* **4.7**

Tiffanian	*Melanosaurus maximus*	175 (154, 198)	*3.7,* **7.5**	*1.9*, **8.6**
Clarkforkian	*Melanosaurus maximus*	349 (319, 386)	*13.6*, **13.7**	*12.3, 15.0*
Wasatchian	*Paraglyptosaurus hillsi*	665 (607, 735)	**19.5**, *22.8*	**18.7**, *24.2*
Bridgerian	*Paraglyptosaurus princeps*	673 (614, 744)	**19.6**, *22.9*	**18.8**, *24.4*
Uintan	*Glyptosaurus sp.*	436 (398, 482)	**15.7**, *16.7*	**14.9**, *18.2*
Chadronian	*Helodermoides tuberculatus*	666 (608, 737)	**19.6**, *22.8*	**18.7**, *24.2*
Orellan*	*Peltosaurus sp.*	207 (182, 236)	*6.1,* **9.0**	*4.2,* **10.2**
Orellan	*Helodermoides tuberculatus*	632 (577, 700)	**19.1**, *22.1*	**18.3**, *23.5*
Whitneyan	*Peltosaurus abbotti*	176 (156, 200)	*3.8,* **7.6**	*2.0*, **8.7**
Early Arikareean (28.3 Ma)	*Peltosaurus sp.*	203 (179, 232)	*5.9,* **8.9**	*4.0,* **10.0**
Barstovian	Indeterminate anguid	174 (154, 197)	*3.6,* **7.4**	*1.8,* **8.6**

TABLE 5. PALEOGENE TEMPERATURES FROM MEAN GLYPTOSAURINE BODY SIZE ESTIMATES

Estimates of minimum mean annual paleotemperature (MAPT) in the interior of North America for the late Cretaceous and Paleogene calculated from mean values of snout-vent length (SVL) estimates for glyptosaurine lizards for each North American Land Mammal Age (NALMA) for which n > 1. MAPT estimates calculated using the metabolic scaling equation from Head et al. (2013; see Methods; Maximum extant SVL (for *Heloderma suspectum*) = 360 mm; Minimum MAT = 14ºC). All specimens come from the Great Plains and Western Interior. Lower and upper mean SVL estimates calculated using one standard deviation (stdev). Lower and upper MAPT estimates calculated using range for mean estimated SVL (+/- 1 stdev); the value reported for each is the lowest and highest value, respectively, obtained from calculations using Q_{10} values of both 3 and 2 (values calculated using Q_{10} = 2 are italicized; Q_{10} = 3, in bold). Orellan estimates are given for the largest corresponding specimens of both *Peltosaurus* (*) and *Helodermoides*.

NALMA	**Mean SVL estimate (+/- 1 stdev) (mm)**	**MAPT estimates for Q_{10} = 3, *2* (ºC)**	**Range for MAPT estimates (ºC)**
Lancian	114 (104, 125)	*-2.4,* **3.7**	*-1.2,* **4.4**
Torrejonian	91 (63, 119)	*-5.7*, **1.6**	*-11.0*, **4.0**
Tiffanian	124 (95, 153)	*-1.2,* **4.4**	*-5.1*, **6.3**
Clarkforkian	196 (90, 303)	*5.3*, **8.5**	*-5.1,* **6.3**

Wasatchian	293 (93, 493)	*11.1*, **12.2**	*-5.3, 18.5*
Bridgerian	545 (408, 681)	**17.7**, *19.9*	**15.1**, *23.1*
Uintan	436 (217, 568)	**15.7**, *16.7*	**15.7**, *16.7*
Chadronian	393 (217, 568)	**14.8**, *15.2*	*6.8, 20.5*
Orellan*	151 (112, 191)	*1.6,* **6.2**	*-2.6,* **8.3**
Orellan	181 (63, 300)	*4.2,* **7.8**	*-10.9*, **12.3**
Whitneyan	149 (126, 173)	*1.4,* **6.1**	*-1.0*, **7.4**
Early Arikareean (28.3 Ma)	178 (153, 203)	*3.9,* **7.7**	*1.8,* **8.8**

TABLE 6. TEMPERATURE CORRELATION DATA USING MAXIMUM GLYPTOSAURINE BODY SIZE ESTIMATES

Estimates of minimum mean annual paleotemperature (MAPT) based on maximum estimates of glyptosaurine snout-vent length (SVL) for each North American Land Mammal Age (NALMA) with the most comparable published terrestrial indicators from Table 3. These data were used to generate the reduced major axis regressions in Figure 14. The estimate for the Orellan marked with an asterisk (*) is for the largest measured *Peltosaurus* specimen from that NALMA. The Orellan estimate in parentheses is for the largest *Helodermoides* specimen from that interval.

NALMA	**Glyptosaurine Maximum SVL Estimate (mm)**	**Glyptosaurine MAPT Estimate (ºC) (Q_{10} = 3)**	**Published Terrestrial MAPT Estimate (ºC)**	**Published Proxy Reference (see Table 3)**
Tiffanian	174.85	7.5	11.7	Johnson & Ellis (2002)
Clarkforkian	349.20	13.7	12.9	Wing et al. (2000)
Wasatchian	664.89	19.5	18.7	Fricke & Wing (2004)
Bridgerian	673.09	19.6	19.6	Wilf (2000)
Uintan	436.06	15.7	16.1	Sandau (2005)
Chadronian	666.49	19.6	21.0	Zanazzi et al. (2007)
Orellan	207.14* (632.71)	9.0* (19.1)	13.1	Zanazzi et al. (2007)
Whitneyan	176.42	7.6	12.7	Gregory & McIntosh (1996)
Early Arikareean (30.0-28.0 Ma)	203.48	8.9	12.7	Gregory & McIntosh (1996)

TABLE 7. TEMPERATURE CORRELATION DATA USING MEAN GLYPTOSAURINE BODY SIZE ESTIMATES

Estimates of minimum mean annual paleotemperature (MAPT) based on mean estimates of glyptosaurine snout-vent length (SVL) for each North American Land Mammal Age (NALMA) with the most comparable published terrestrial indicators from Table 3. These data were used to generate the reduced major axis regressions in Figure 15. The estimate for the Orellan marked with an asterisk (*) is the mean SVL with the two *Helodermoides* outliers from this NALMA interval omitted (see Figure 10). The Orellan estimate in parentheses is the mean for the interval when these outliers are included.

NALMA	**Glyptosaurine Mean SVL (mm)**	**Glyptosaurine MAPT Estimate (ºC) (Q_{10} = 3)**	**Published Terrestrial MAPT Estimate (ºC)**	**Published Proxy Reference (see Table 3)**
Tiffanian	123.97	4.4	11.7	Johnson & Ellis (2002)
Clarkforkian	196.19	8.5	12.9	Wing et al. (2000)
Wasatchian	293.22	12.2	15.5	Fricke & Wing (2004)
Bridgerian	544.64	17.7	18.6	Wing & Greenwood (1993)
Uintan	435.66	15.7	16.1	Sandau (2005)
Chadronian	392.57	14.8	16.5	Evanoff et al. (1992)
Orellan	151.45* (181.27)	6.2* (7.8)	13.1	Zanazzi et al. (2007)
Whitneyan	149.40	6.1	12.7	Gregory & McIntosh (1996)
Early Arikareean (30.0-28.0 Ma)	177.96	7.7	12.7	Gregory & McIntosh (1996)

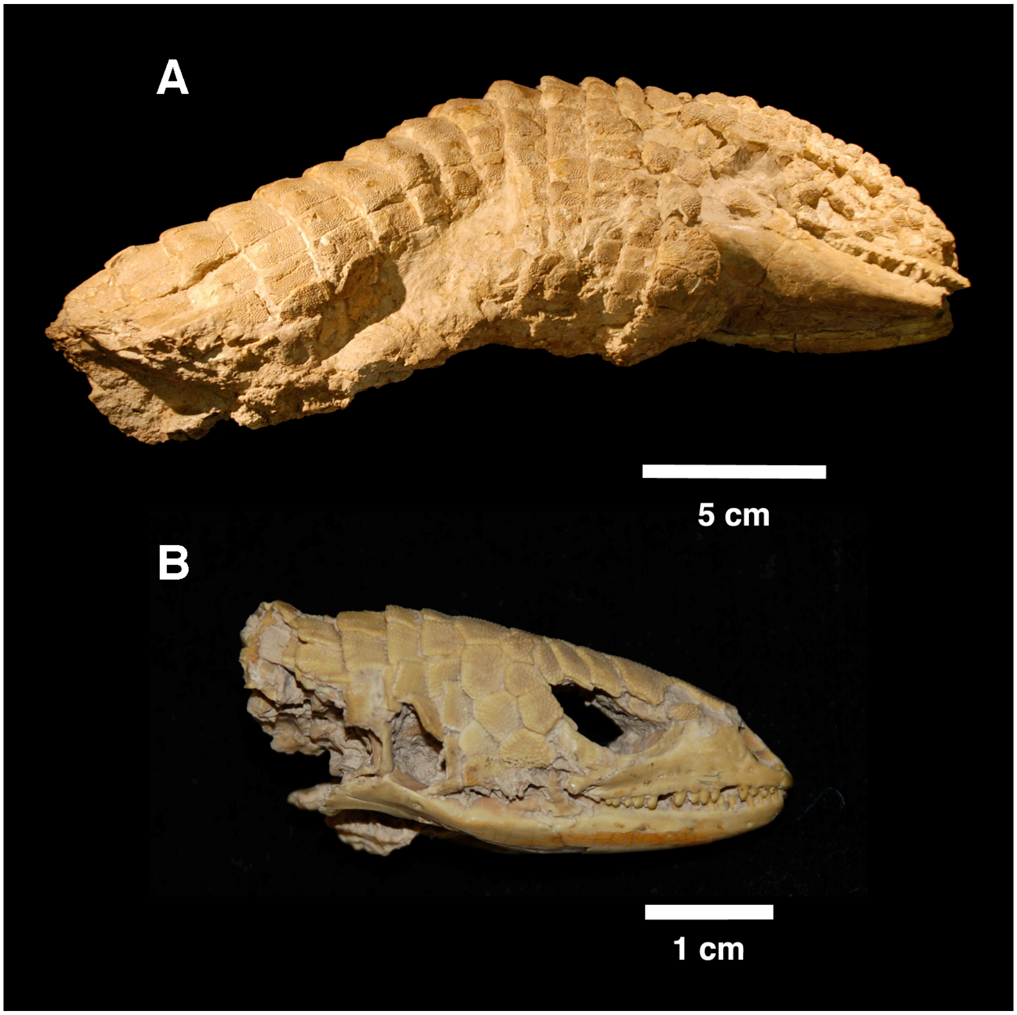


FIGURE 1. (A) *Helodermoides tuberculatus* (USNM 13869) and (B) *Peltosaurus granulosus* (UNSM 84302), the only two glyptosaurine lizards known from the late Eocene and early Oligocene. Both are found in the Great Plains region.

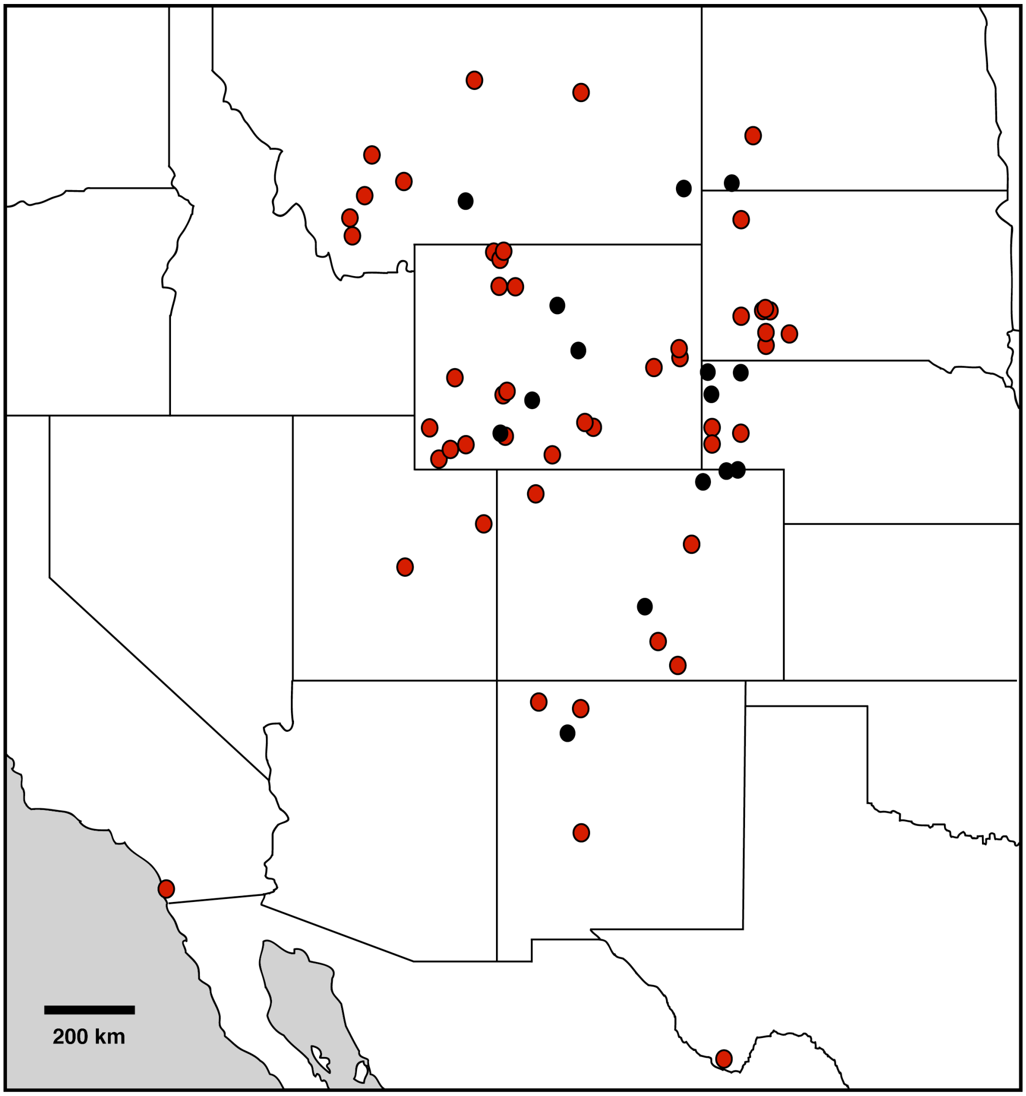


FIGURE 2. Known North American localities for diagnostic late Cretaceous and Paleogene material referred to glyptosaurine (red circles) and other anguid taxa (black circles). Paleogene glyptosaurines primarily occur in the Western Interior basins and western Great Plains, but occurrences in the late Cretaceous of southwestern Texas (Big Bend National Park; Rowe et al., 1992) and the middle Eocene of southern California (San Diego County) indicate that the range of glyptosaurine lizards may have extended across much of the western United States. Locality data obtained from the Paleobiology Database, published literature, and museum collections.

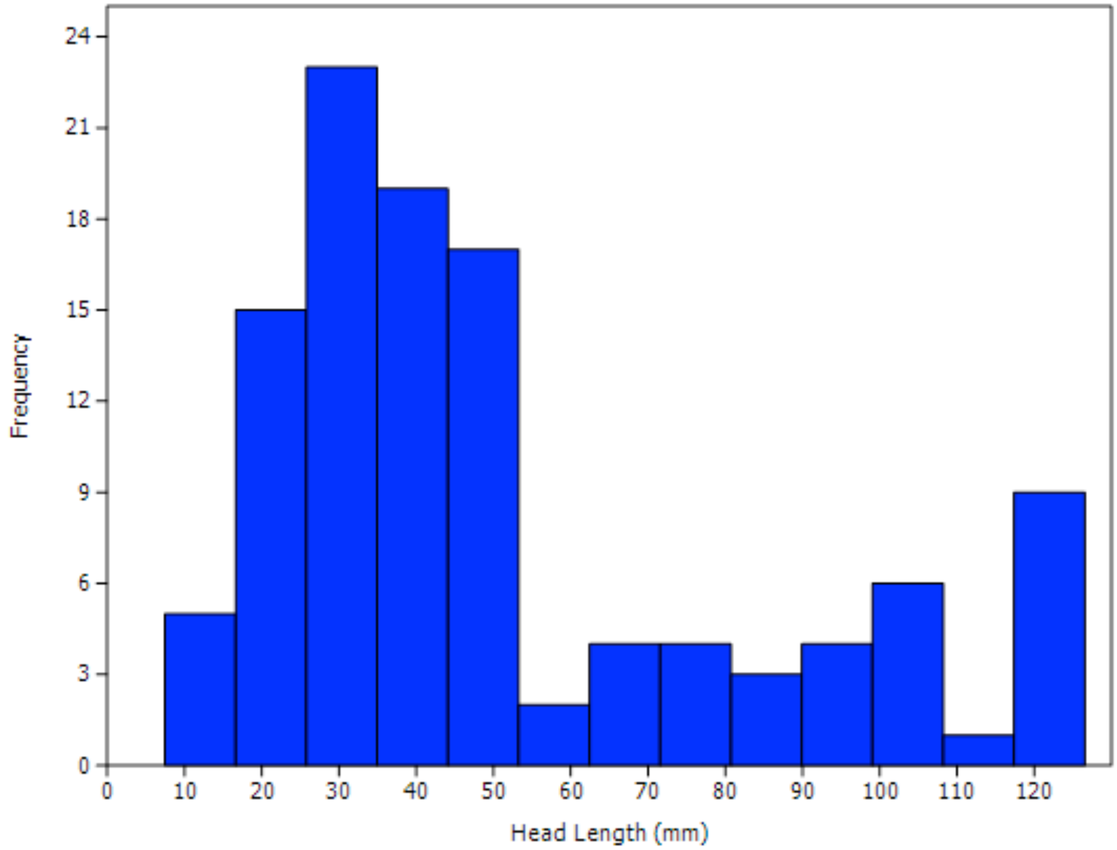


FIGURE 3. Distribution of head length for fossil anguid specimens (n = 114). The data show a bimodal distribution between head lengths of ≤ 52 mm and ≥ 53 mm. All specimens in the latter size class are glyptosaurines. Histogram generated using PAST (v. 3.1; Hammer et al., 2001).

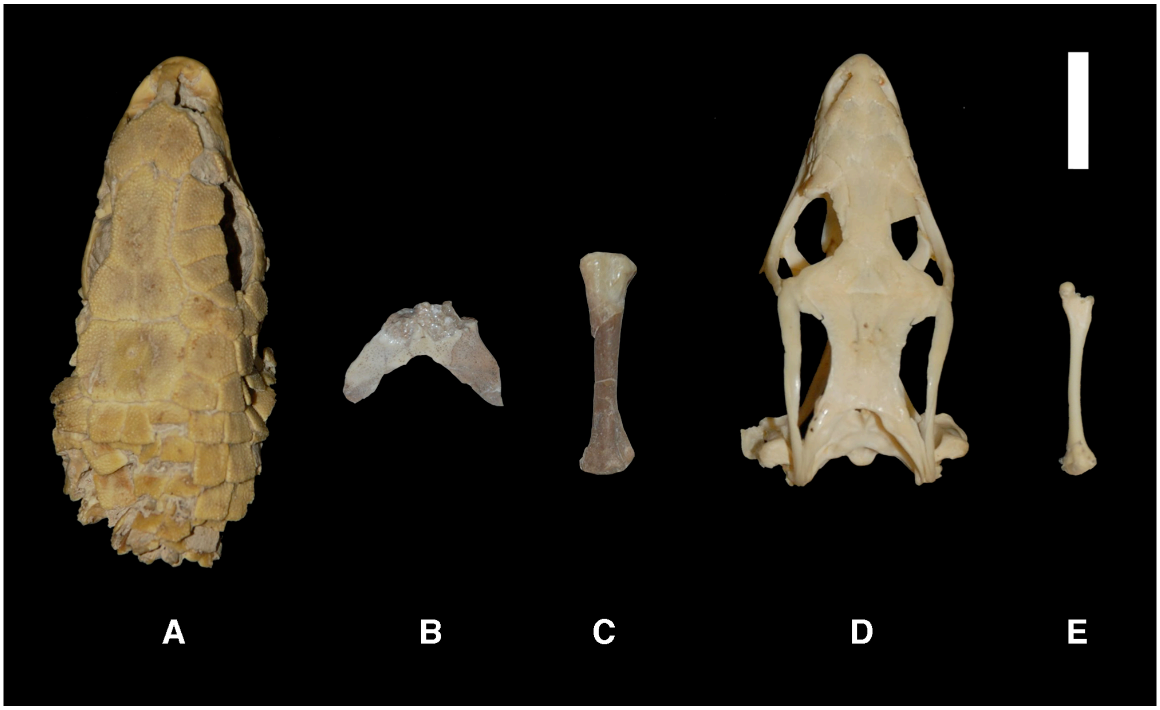
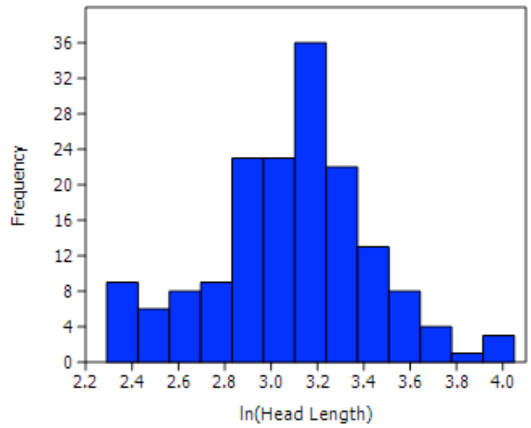
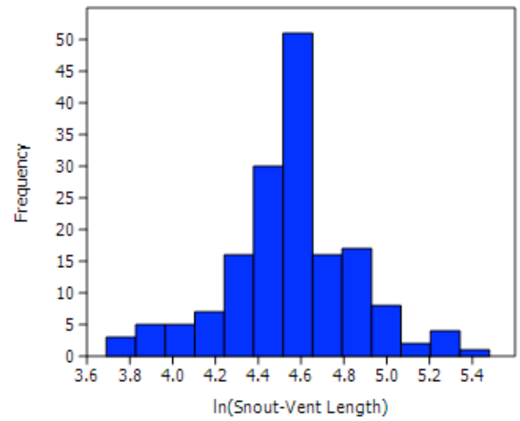


FIGURE 4. (A) Skull of *Peltosaurus granulosus* (UNSM 84302) in dorsal view, (B) posterior parietal fragment of *Peltosaurus granulosus* (UNSM 12102) in dorsal view, (C) left femur of *Peltosaurus granulosus* (UNSM 12102) in lateral view, (D) skull of *Gerrhonotus infernalis* (FMNH 22452) in dorsal view, (E) right femur of *Gerrhonotus infernalis* (FMNH 22452) in anterior view. Skull length of UNSM 12102 was calculated using the ratio of parietal width to skull length based on UNSM 84296 (see Appendix 1). Complete skull length of UNSM 12102 would approximately equal that of UNSM 84302 (A). The head: femur length ratio of UNSM 12102 (1.93; estimated head length = 34.19 mm, femur length = 17.71 mm) is comparable to that of extant limbed anguid lizards such as *Gerrhonotus* (1.95, n = 217). This indicates that glyptosaurines smaller than or comparable to *Peltosaurus* in size had head: body proportions that were similar to these extant anguid lizards. Scale bar = 1 cm.



A.



B.

FIGURE 5. Distributions of natural logs of (A) head length (B) and snout-vent length in extant limbed anguid lizards (excluding *Barisia* and *Sauresia*; n = 165). Both variables have an approximately normal distribution. Original head lengths and snout-vent lengths were measured in millimeters. Histograms generated using PAST (v. 3.1; Hammer et al., 2001).

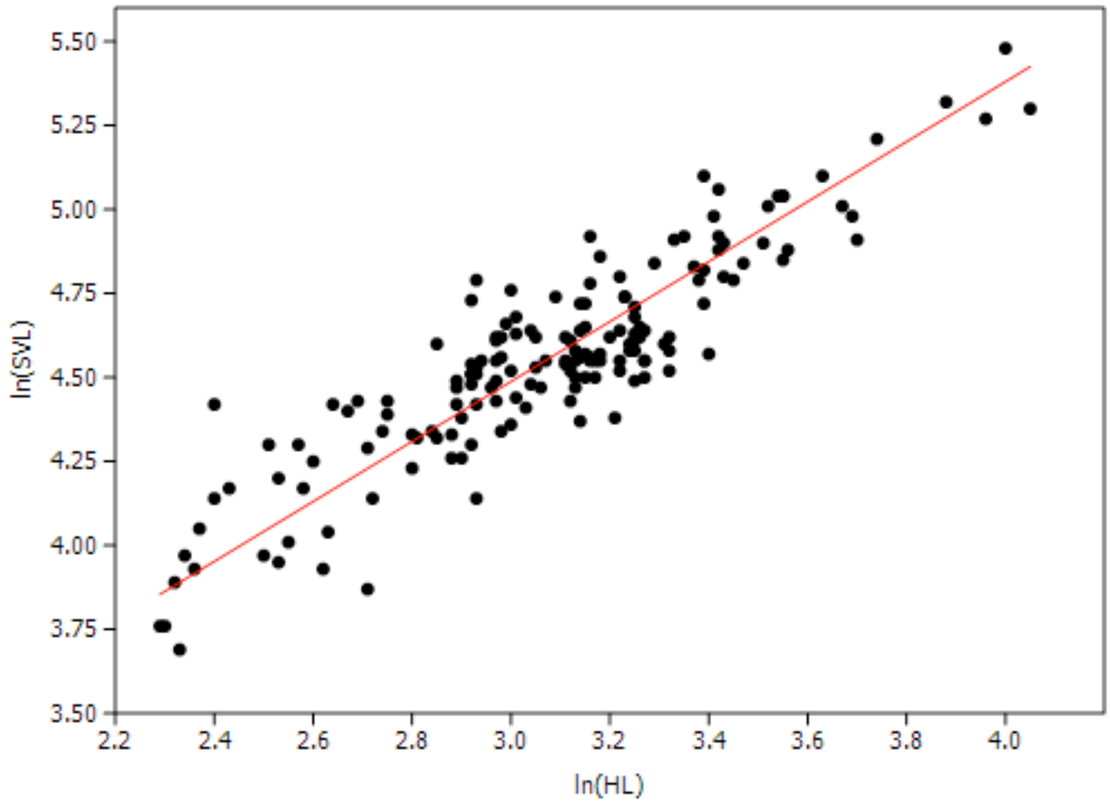


FIGURE 6. Reduced Major Axis linear regression model relating natural logs of head length (HL) to snout-vent length (SVL) for extant limbed adult anguid lizards (excluding *Barisia* and *Sauresia*). I applied skull lengths of small-medium-sized fossil glyptosaurines (skull length ≤ 52 mm) to this regression in order to estimate SVL for those specimens. Regression equation: LN SVL = 0.892*LN Head Length + 1.81; n = 165; $R = 0.90$, $R^2 = 0.81$, p (uncorr.) << 0.00. Regression generated using PAST v. 3.1 (Hammer et al., 2001).

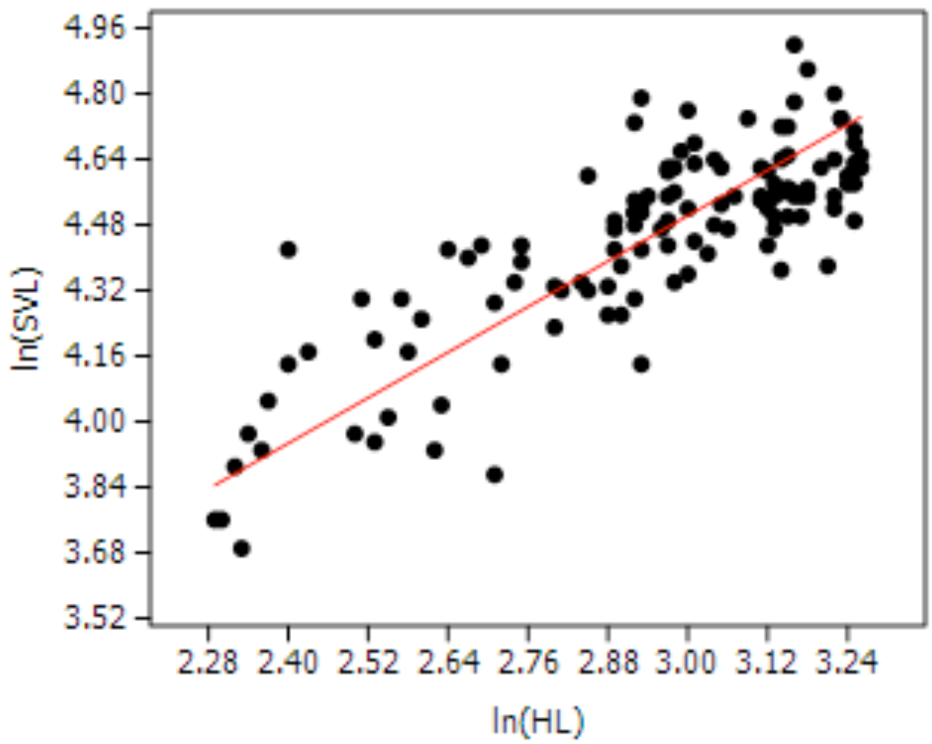


FIGURE 7. Reduced Major Axis linear regression model relating natural logs of head length (HL) to snout-vent length (SVL) for the 75th percentile (HL < 26.2 mm) of the dataset containing measurements from extant limbed anguid lizards (excluding *Barisia* and *Sauresia*). This regression accurately predicted SVL for four specimens of *Diploglossus millepunctatus,* the largest extant anguid measured in this study. This indicates that the largest individuals in the dataset do not bias the slope of the regression equation (Figure 6), which was used to estimate SVL for small-medium fossil glyptosaurines (skull length ≤ 52 mm). Regression equation: LN SVL = 0.927*LN Head Length + 1.72; n = 124; $R = 0.82$, $R^2 = 0.68$, p (uncorr.) << 0.00. Regression generated using PAST v. 3.1 (Hammer et al., 2001).

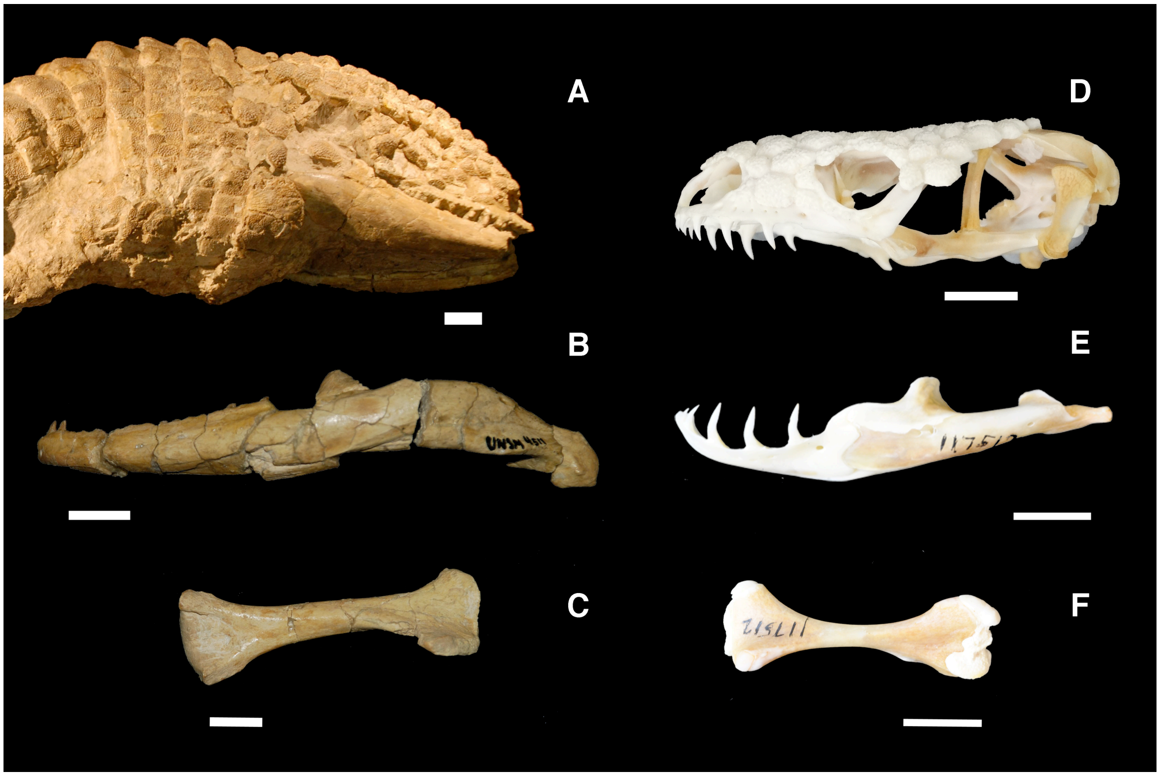


FIGURE 8. (A) Skull and cervical osteoderms of *Helodermoides tuberculatus* (USNM 13869) (B) left mandible in lateral view and (C) right humerus in posterior view of *Helodermoides tuberculatus* (UNSM 4511), (D) anterior skull in left lateral view, (E) left mandible in lateral view, and (F) right humerus in anterior view of *Heloderma suspectum* (UCMP 117512). The mandible: humerus ratio of UNSM 4511 (1.67; head length = 96.13 mm, humerus length = 57.46 mm) is comparable to the mean ratio for *Heloderma* (1.69, n = 49 (37 *H. suspectum,* 13 *H. horridum*)), and differs from the mean ratio for extant limbed anguids (2.48, n = 217, excluding *Barisia* and *Saurisia*). This indicates that large glyptosaurines such as *Helodermoides* had head: body proportions dissimilar to extant limbed anguids but comparable to that of *Heloderma.* Scale bar = 1 cm.

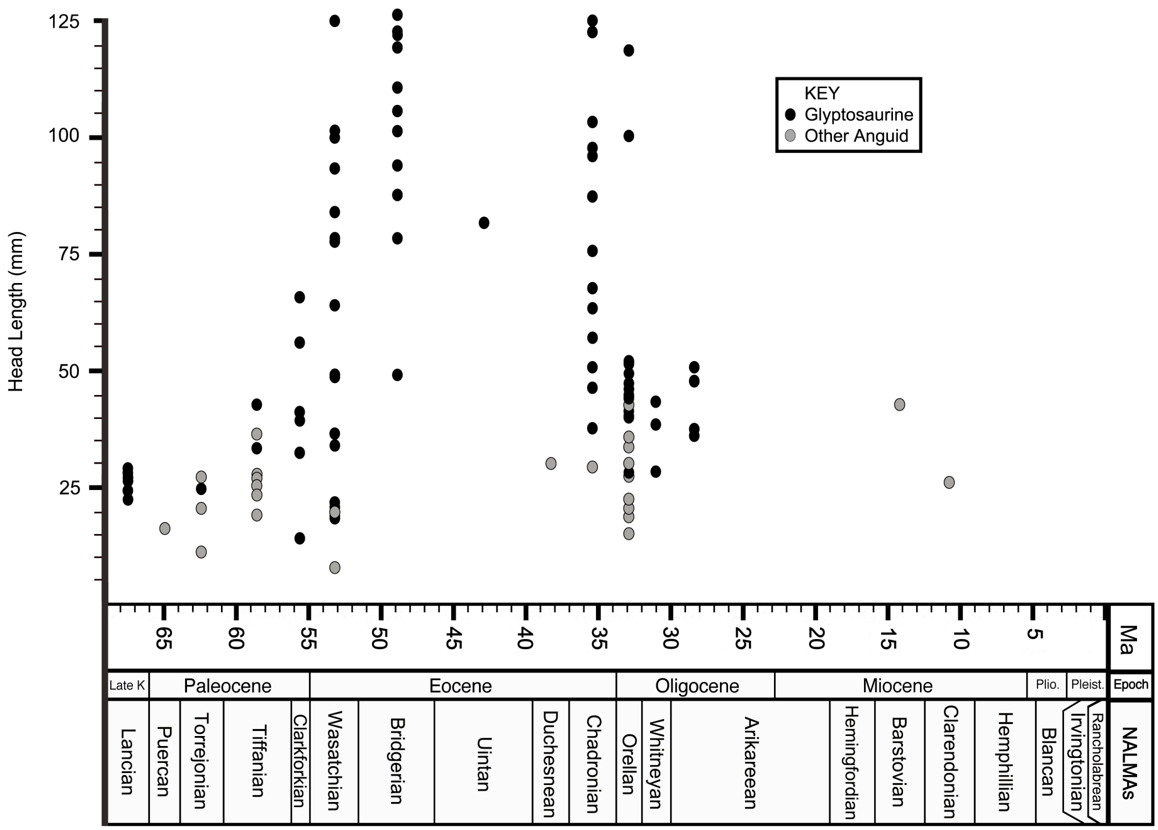


FIGURE 9. Measured and estimated head lengths for glyptosaurines (black circles) and other fossil anguid lizards (grey circles; total n = 114) through the Cenozoic of North America. For fossil specimens that included only partial cranial material, I estimated skull length using ratios of cranial bones (frontal, parietal, dentary, or mandible) to skull length based on complete skulls from specimens of close taxonomic affinity and/or comparable size (see Appendix 1.2). All specimens come from the Great Plains and Western Interior, with the exception of one Uintan glyptosaurine (SDNHM 75932), which was found in San Diego County, CA. Timescale based on Woodburne et al. (2004).

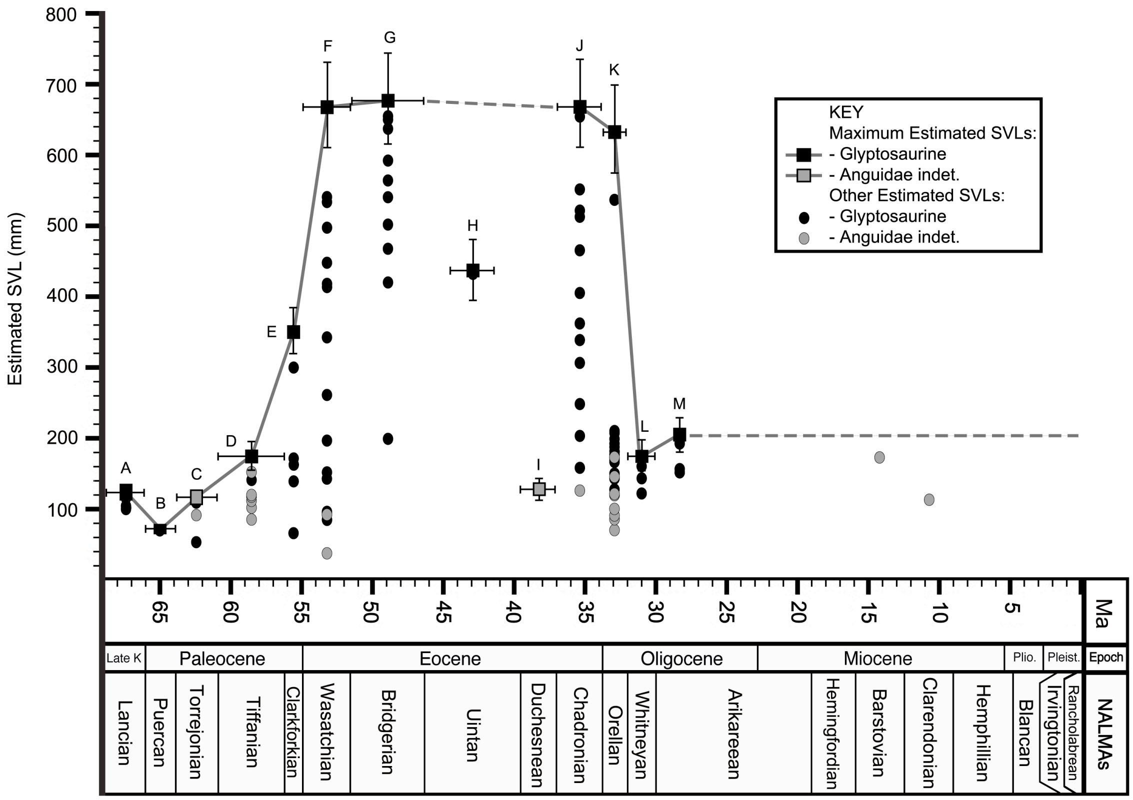


FIGURE 10. Estimated snout-vent lengths (SVL) for glyptosaurines (black circles) and other fossil anguid lizards (grey circles; total n = 114) through the Cenozoic of North America. SVL estimated using linear regression or head: body ratios based on measurements from extant anguimorph lizards (see Methods). Squares indicate maximum estimated SVL for glyptosaurines (black) and other fossil anguids (grey) in each interval. Only a few estimates for the middle Eocene (2 Uintan, 1 Duchesnean) were obtained; dashed line indicates possibility of sustained maximum body size around 670 mm through the late Paleogene. Dashed line to the right indicates the maximum SVL (inferred from extant members) for all fossil lizard taxa found within the known range of late Paleogene anguids (see Appendix 1.1). Vertical error bars on maximum estimates indicate standard error or one standard deviation (for largest taxa, SVL >400 mm; see

Appendix 1.2). Horizontal error bars indicate duration of NALMA interval. All data plotted at midpoint of corresponding NALMA interval. Timescale based on Woodburne et al. (2004). Maximum SVL taxa: (A) *Odaxosaurus piger*, (B) indeterminate glyptosaurine, (C) indeterminate anguid, (D) *Melanosaurus sp.*, (E) *Melanosaurus maximus*, (F) *Paraglyptosaurus hillsi*, (G) *Paraglyptosaurus princeps*, (H) *Glyptosaurus sylvestris*, (I) indeterminate anguid, (J) and (K) *Helodermoides tuberculatus* , (L) *Peltosaurus abbotti*, (M) *Peltosaurus sp.*

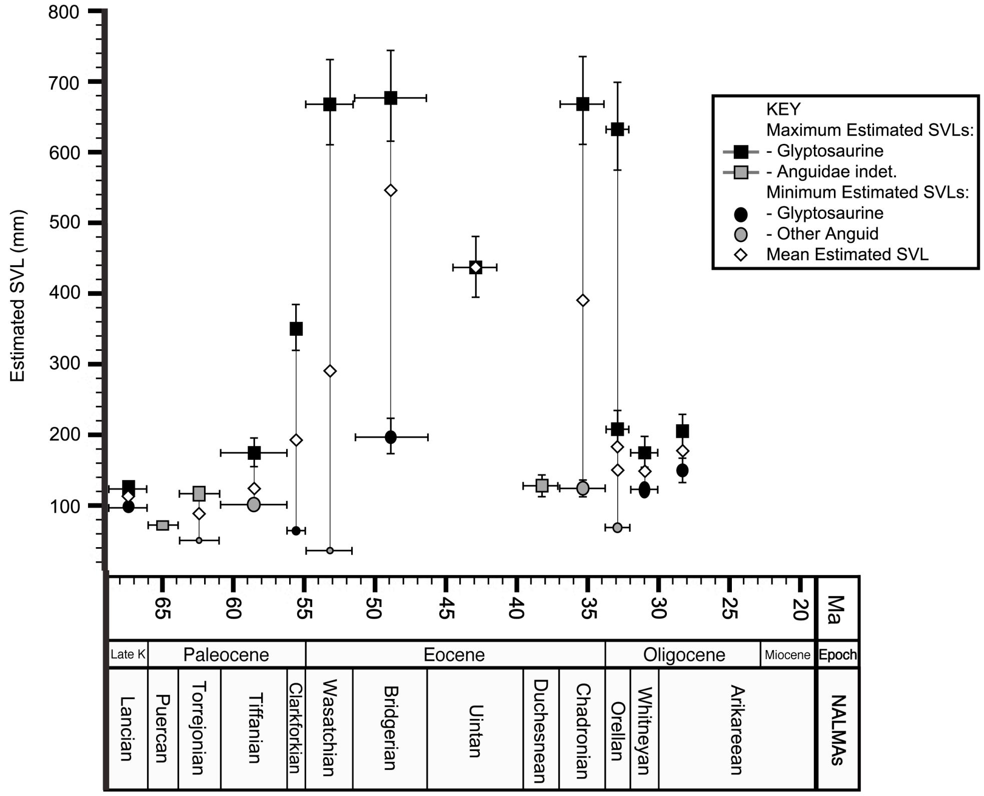


FIGURE 11. Mean, maximum, and minimum estimated snout-vent length (SVL) in anguid lizards for the late Cretaceous and Paleogene of North America. Maximum and minimum SVLs estimated using linear regression or head: body ratios based on measurements from extant anguimorph lizards (see Methods). Mean SVLs calculated as sample mean for all SVL estimates per North American Land Mammal Age (NALMA) interval. Vertical error bars on maximum and minimum SVL estimates indicate standard error or one standard deviation (for largest taxa, SVL >400 mm; see Appendix 1). Horizontal error bars indicate duration of NALMA interval. All data plotted at midpoint of corresponding NALMA interval. Timescale based on Woodburne et al. (2004).

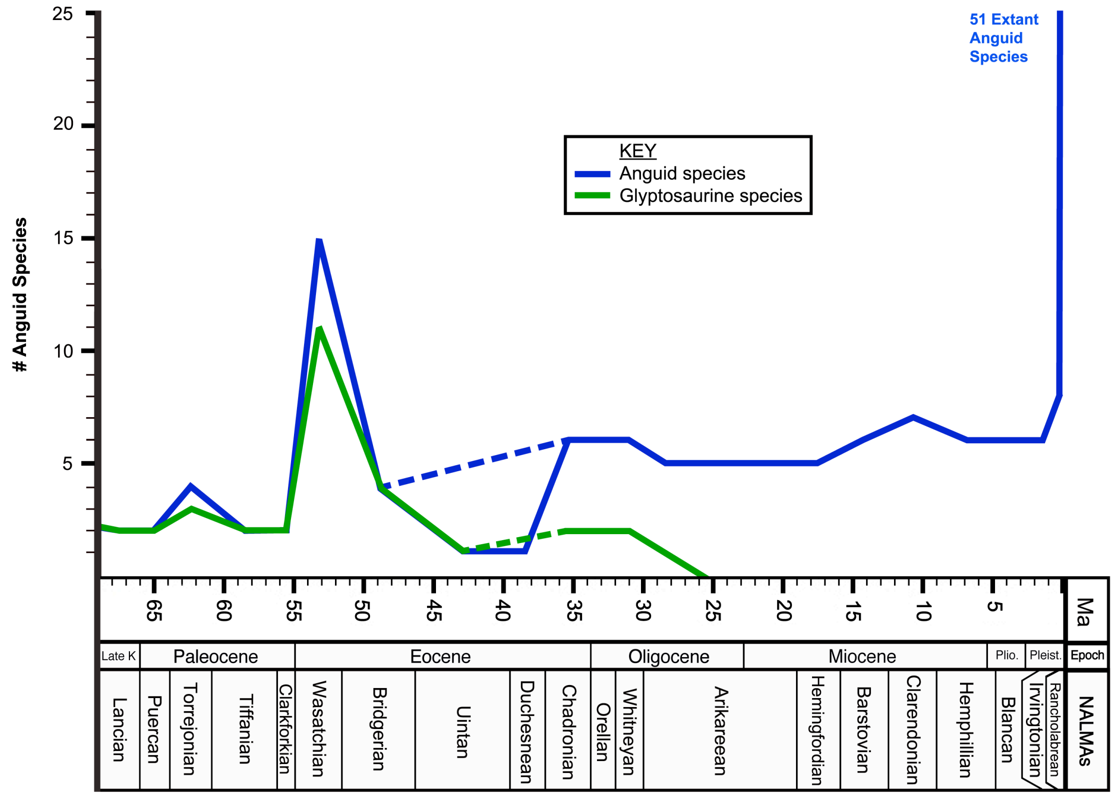


FIGURE 12. Species richness for glyptosaurines (green) and all anguid lizards (blue) through the Cenozoic of North America by North American Land Mammal Age (NALMA). Dashed lines indicate potential minimum species richness for NALMA intervals with very low or missing records. Anguid species sampled from museum collections, literature (see Appendix 4), and the Paleobiology Database. Anguid species counts include range extensions (generic level) between first and last occurrences. All data plotted at midpoint of corresponding NALMA interval.

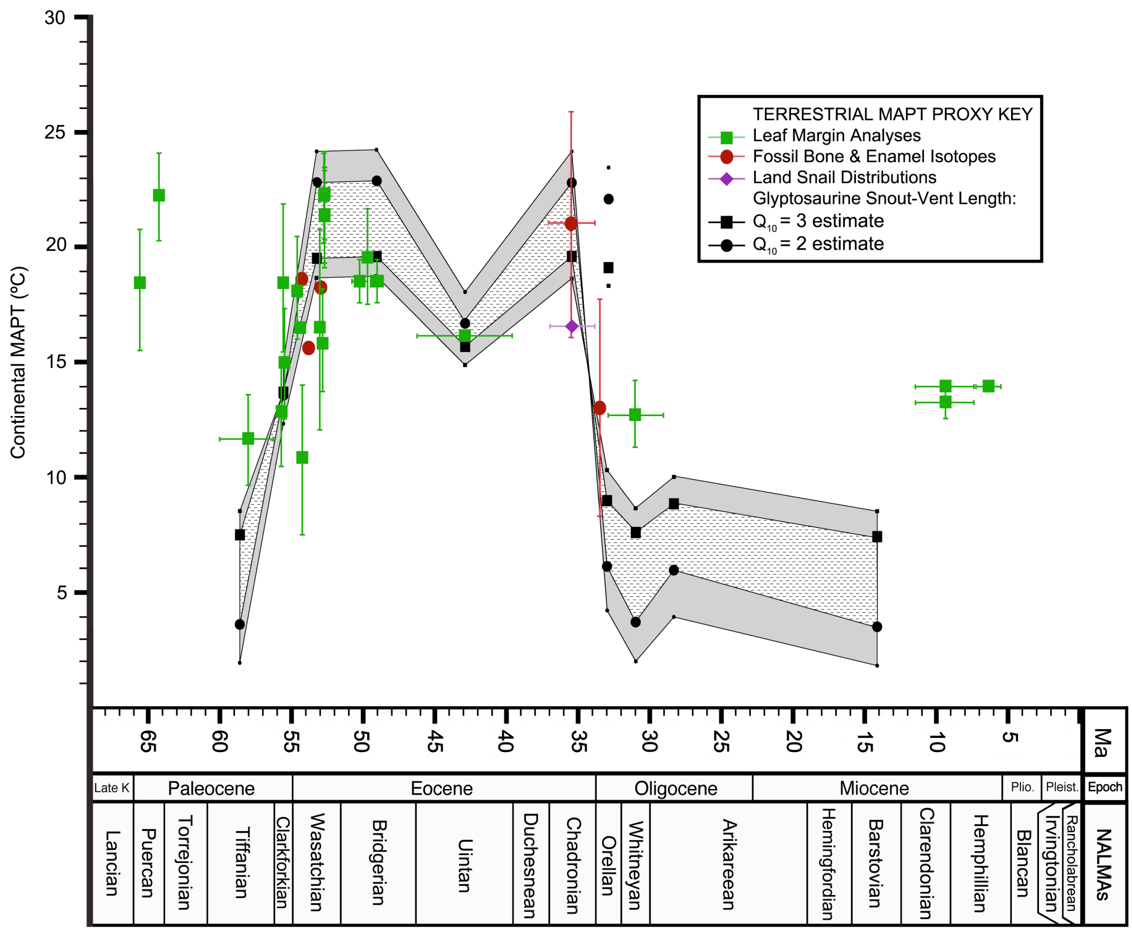
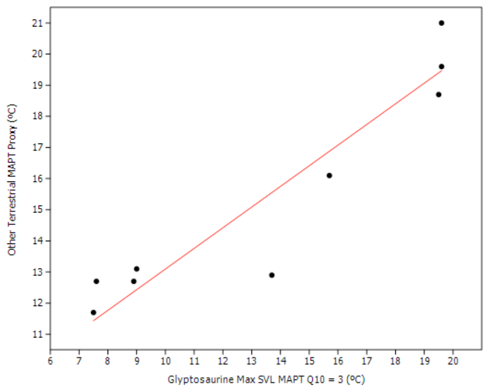
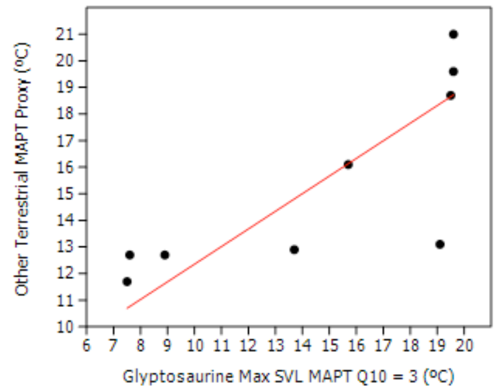


FIGURE 13. Estimates for mean annual paleotemperature (MAPT) based on maximum glyptosaurine snout-vent length estimates (except for the Barstovian estimates, which come from an indeterminate anguid specimen; see Methods, Table 4), as well as existing terrestrial proxies from literature (see Table 3) for MAPT in the interior of North America through the Paleogene by North American Land Mammal Age (NALMA). And estimate from the Barstovian is included for comparison. Dashed areas indicate range between glyptosaurine MAPT estimates using Q_{10} values of 2 (black circles) and 3 (black squares) for the maximum SVL estimate from each NALMA. Grey area indicates range between maximum and minimum glyptosaurine MAPT estimates calculated using maximum and minimum SVL estimates for the largest specimen from each NALMA (see

Appendix 1, Table 4). Orellan estimate is based on the largest corresponding *Peltosaurus* specimen, but estimates for the largest specimen of *Helodermoides* allegedly from the Orellan are also plotted (isolated points). Vertical error bars for existing terrestrial proxies indicate one standard deviation (standard error for late Eocene – early Oligocene isotope and leaf margin analyses). Horizontal error bars indicate duration of NALMA time bin. All data plotted at midpoint of corresponding NALMA interval. All MAPT proxies are based on fossil data from the Great Plains or Western Interior of the United States. See Table 3 for non-lizard proxy references. Timescale based on Woodburne et al. (2004).

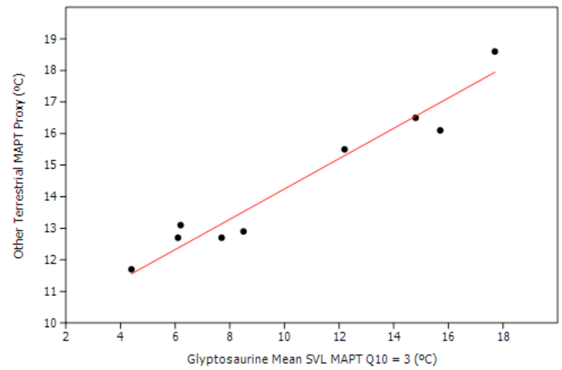


A.

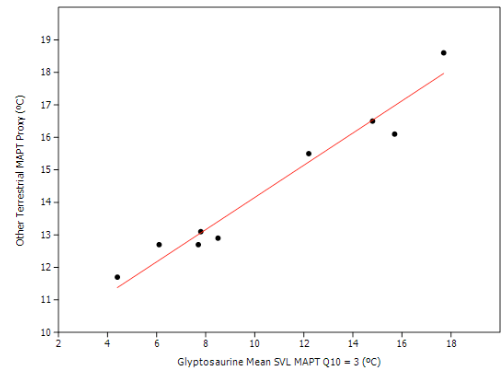


B.

FIGURE 14. Estimates for mean annual paleotemperature (MAPT) for the interior of North America through the middle and late Paleogene based on maximum estimated glyptosaurine snout-vent length (SVL; estimate calculated using $Q_{10} = 3$; horizontal axis) for each North American Land Mammal Age, correlated to comparable estimates from published data based on other terrestrial indicators (vertical axis). See Table 6 for regression data. (A) Orellan maximum SVL estimate based on corresponding largest measured specimen of *Peltosaurus*; regression equation: Other Terrestrial MAPT Proxy = 0.664*Glyptosaurine Max SVL MAPT + 6.46; n = 9; $R = 0.94$, $R^2 = 0.88$, p (uncorr.) < 0.00; (B) Orellan maximum SVL estimate based on corresponding largest measured specimen of *Helodermoides*; regression equation: Other Terrestrial MAPT Proxy = 0.663*Glyptosaurine Max SVL MAPT + 5.73; n = 9; $R = 0.78$, $R^2 = 0.61$, p (uncorr.) = 0.013. Regressions generated using PAST v. 3.1 (Hammer et al., 2001).



A.



B.

FIGURE 15. Estimates for mean annual paleotemperature (MAPT) for the interior of North America through the middle and late Paleogene based on <u>mean</u> of estimated glyptosaurine snout-vent lengths (SVL; estimate calculated using $Q_{10} = 3$; horizontal axis) for each North American Land Mammal Age, correlated to comparable estimates from published data based on other terrestrial indicators (vertical axis). See Table 7 for regression data. (A) Orellan mean SVL estimate with two *Helodermoides* specimens excluded; regression equation: Other Terrestrial MAPT Proxy = 0.480*Glyptosaurine Mean SVL MAPT + 9.44; n = 9; $R = 0.97$, $R^2 = 0.94$, p (uncorr.) << 0.00; (B) Orellan mean SVL estimate with two *Helodermoides* specimens included; regression equation: Other Terrestrial MAPT Proxy = 0.495*Glypto-saurine Mean SVL MAPT + 9.20; n = 9; $R = 0.98$, $R^2 = 0.96$, p (uncorr.) << 0.00. Regressions generated using PAST v. 3.1 (Hammer et al., 2001).

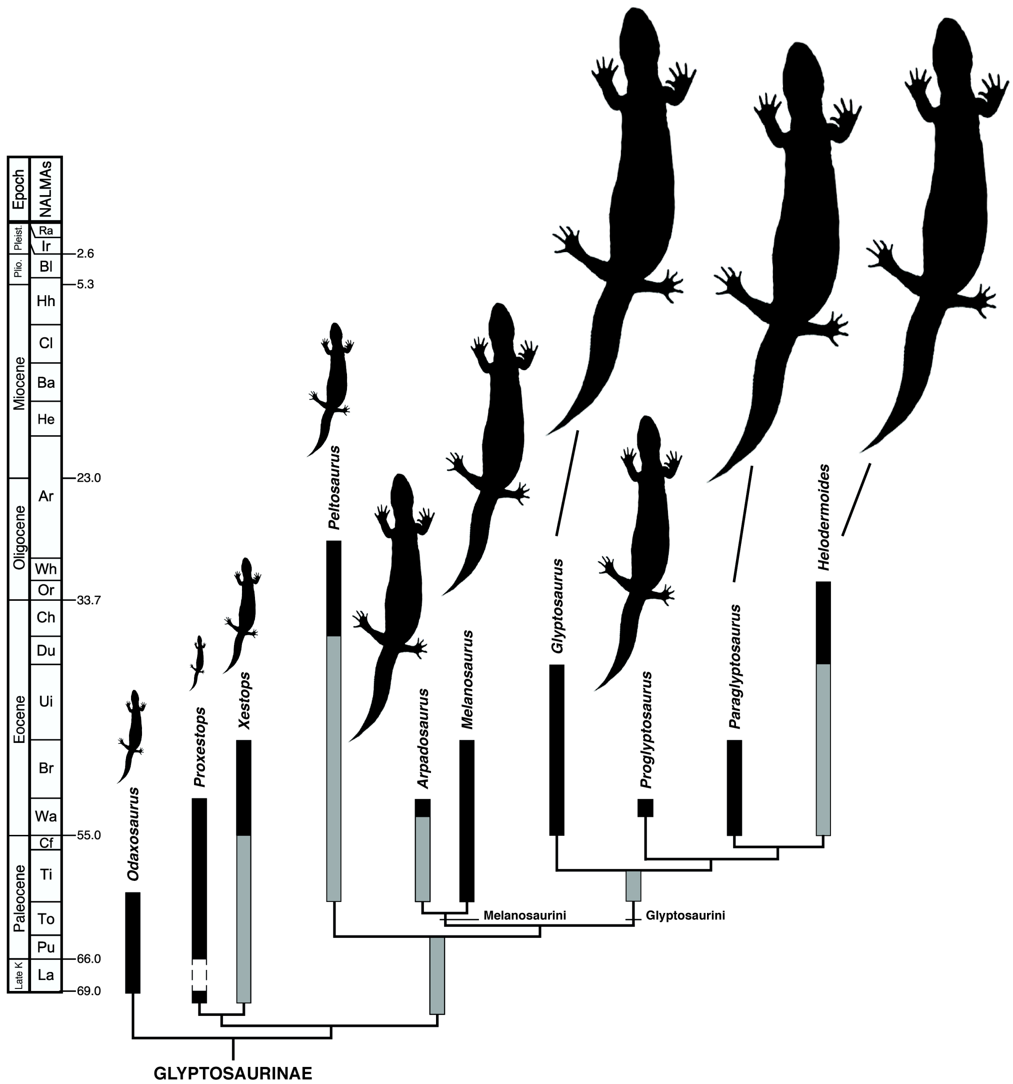


FIGURE 16. Temporal distribution and relationships of glyptosaurine taxa with relative body size illustrated. Black bars indicate known ranges. Grey bars indicate missing lineages as implied by sister taxa. Dashed bar indicates range extended between first occurrence and upper range. Squares indicate single stratigraphic occurrences. Lizard outlines indicate the maximum estimated SVL for the corresponding genus relative to the maximum estimated SVL for all glyptosaurines (*Paraglyptosaurus*, 673 mm). Phylogeny based on Conrad (2008) and Conrad and Norell (2008). Timescale based on Woodburne et al. (2004).