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

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

by

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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 – 20°C during both intervals. Other terrestrial proxies indicated declines in continental MAPT of about 3 – 8°C 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.
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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) MA PT calculated from body size estimates for glyptosaurine lizards compare to previous estimates of MA PT from other terrestrial indicators for the Great Plains and Western Interior of North America.

Institutional Abbreviations

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).
Length + 1.72; n = 124; R = 0.82, R² = 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 \( \geq 53 \) 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 \( \leq 52 \) 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* (\( \geq 230 \) mm in *H. suspectum*, \( \geq 330 \) 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):

\[
\text{MAPT} = \text{MAT} + 3a10^\circ\text{C}*(\log_{10}(\text{SVL}_{\text{Fossil}}/\text{SVL}_{\text{Extant}})/\log_{10}Q_{10}),
\]

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* (14°C; 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 15°C to 25°C; 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 6°C 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 Arikarean (*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 13°C in the Clarkforkian (late Paleocene; Wing et al., 2000) to over 20°C 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 16°C 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., 16.5°C; Evanoff et al., 1992) or reached higher levels than in the Uintan (e.g., 21°C; Zanazzi et al., 2007). MAPTs in the early Oligocene were lower than Eocene temperatures (e.g., about 13°C; 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 – 22.8°C in the Wasatchian, 19.6 – 22.9°C in the Bridgerian) relative to the middle Paleocene (3.7 – 7.5°C, Tiffanian) and late Paleocene (13.6 – 13.7°C, 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 – 14.0°C 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 24°C 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 – 30°C and is observed to be active at temperatures as low as 17.4°C (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 10°C 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 ($\geq 650$
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.
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


Cope, E. D. 1873. Synopses of new Vertebrata from the Tertiary of the Plains. 


APPENDIX 1.1. FOSSIL ANGUID LOCALITY DATA

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

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<td>Wasatchian</td>
<td>Wasatch Fm</td>
<td>V 5421, Sand Quarry, Moffat Co., CO</td>
<td>40.6° N, 108.1° W</td>
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<td>UCMP</td>
<td>215232</td>
<td>Proxestops sp.</td>
<td>Wasatchian</td>
<td>Wasatch Fm</td>
<td>V 70243, Sweetwater Co., WY</td>
<td>41.7° N, 108.9° W</td>
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<td>UCMP</td>
<td>100118</td>
<td>Apodosauriscus sp.</td>
<td>Wasatchian</td>
<td>Wasatch Fm</td>
<td>V 70246, Sweetwater Co., WY</td>
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<td>100102</td>
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<td>USNM</td>
<td>25826</td>
<td>Arpadosaurus gadinorum</td>
<td>Wasatchian</td>
<td>Wasatch Fm</td>
<td>12 miles north of Big Piney, WY</td>
<td>42.7° N, 110.1° W</td>
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<td>CM</td>
<td>44836</td>
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<td>Wind River Fm (Lost Cabin Mbr)</td>
<td>2411: K-6, WY</td>
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<td>CM</td>
<td>42270</td>
<td>Paraglyptosaurus sp.</td>
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<td>3186: K-5, WY</td>
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<td>CM</td>
<td>42411</td>
<td>Xestops sp.</td>
<td>Wasatchian</td>
<td>Wind River Fm (Lysite Mbr)</td>
<td>792: Lysite Rim, WY</td>
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<td>42179</td>
<td>Glyptosaurus sylvestris</td>
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<td>3188: K-5, WY</td>
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<td>Wasatchian</td>
<td>Wind River Fm (Lost Cabin Mbr)</td>
<td>2411: K-6, WY</td>
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<td>YPM</td>
<td>PU 21801</td>
<td>Melanosaurus maximus</td>
<td>Wasatchian</td>
<td>Willwood Fm</td>
<td>Little Sand Coulee, Park Co., WY</td>
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<td>216000</td>
<td>Gautlia silvaticus</td>
<td>Wasatchian</td>
<td>Willwood Fm (Wa0)</td>
<td>V 99019, Bighorn Basin, WY</td>
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<td>126000*</td>
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<td>Bridgerian</td>
<td>Bridger Fm</td>
<td>V 81250, Uinta Co., WY</td>
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<td>USNM</td>
<td>16527</td>
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<td>Bridgerian</td>
<td>Bridger Fm</td>
<td>Grizzly Buttes, Bridger Basin, Uinta Co., WY</td>
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<td>Specimen No.</td>
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<td>Species</td>
<td>Age</td>
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<td>Field #47-112, Bridger Basin, WY</td>
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<td>Uinta Co., Bridger Basin, Levitt, WY</td>
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<td>Bridger Fm (B Mbr)</td>
<td>Grizzly Buttes, Bridger Basin, Uinta Co., WY</td>
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<td>Uinta Co., WY</td>
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<td>Point Gulch, Uinta Co., WY</td>
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<td>princeps</td>
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<td>Bridger Fm</td>
<td>Millersville, WY (Field No. 622)</td>
<td>41.4° N, 110.2° W</td>
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<td>princeps</td>
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<td>Bridger Fm</td>
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<td>75932</td>
<td>Glyptosaurus</td>
<td>sylvestris</td>
<td>Uintan</td>
<td>Santiago Fm (Mbr C)</td>
<td>Rancho Del Oro, San Diego Co., CA</td>
<td>32.9° N, 117.1° W</td>
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<td>Glyptosaurus</td>
<td>sp.</td>
<td>Uintan</td>
<td>Uinta Fm (Mbr C)</td>
<td>Kennedy’s Hole, Uinta Co., UT</td>
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<td>CM</td>
<td>42469</td>
<td>Anguidae</td>
<td>indet.</td>
<td>Duchesnean</td>
<td>Wagon Bed Fm (Hendry Ranch Mbr)</td>
<td>20: Badwater Locality, Natrona Co., WY</td>
<td>43.2° N, 107.1° W</td>
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<td>AMNH</td>
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<td>Helodermoides</td>
<td>tuberculatus</td>
<td>Chadronian</td>
<td>Chadron Fm</td>
<td>Bates Hole, Natrona Co., WY</td>
<td>43.2° N, 107.1° W</td>
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<tr>
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<td>Helodermoides</td>
<td>tuberculatus</td>
<td>Chadronian</td>
<td>Chadron Fm</td>
<td>Dw-107, Sioux Co., NE</td>
<td>42.4° N, 103.8° W</td>
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<td>tuberculatus</td>
<td>Chadronian</td>
<td>Chadron Fm</td>
<td>Badlands, SD</td>
<td>43.8° N, 103.1° W</td>
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<td>sp.</td>
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<td>Chadron Fm</td>
<td>Flagstaff Rim, Natrona Co., WY</td>
<td>43.2° N, 107.1° W</td>
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<td>FAM</td>
<td>8711</td>
<td>Parophisaurus</td>
<td>pawneensis</td>
<td>Chadronian</td>
<td>Chadron Fm</td>
<td>6 mi from Douglas, Converse Co., WY</td>
<td>42.9° N, 105.2° W</td>
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<td>Institution</td>
<td>Specimen No.</td>
<td>Species</td>
<td>Subspecies</td>
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<td>State, County, NE/Miles of Site</td>
<td>Latitude, Longitude</td>
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<td>Chadronian</td>
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<td>Chadron, NE</td>
<td>42.8° N, 103.0° W</td>
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<td>granulosus</td>
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<td>Toadstool Park, NE</td>
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<td>51344</td>
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<td>212: Cameron Springs, WY</td>
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<td>tuberculatus</td>
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<td>Renova Fm</td>
<td>546: McCartys Mtn, Jefferson Co., MT</td>
<td>45.2° N, 112.6° W</td>
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<td>Chadronian</td>
<td>Renova Fm</td>
<td>879: 1 mi W of Pipestone Springs, MT</td>
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<td>Chadronian</td>
<td>Renova Fm</td>
<td>547: S of McCartys Mtn, MT</td>
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<td>Sx-0, Sioux Co., NE</td>
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<td>Chadronian</td>
<td>Chadron Fm</td>
<td>Dw-107, Dawes Co., NE</td>
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<td>tuberculatus</td>
<td>Chadronian</td>
<td>Chadron Fm</td>
<td>Dw-107, Dawes Co., NE</td>
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<td>13869</td>
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<td>tuberculatus</td>
<td>Orellan</td>
<td>Brule Fm</td>
<td>8 mi E of Douglas, Converse Co., WY</td>
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<tr>
<td>UNSM</td>
<td>13861</td>
<td>Helodermoides</td>
<td>tuberculatus (prev. Glyptosaurus giganteus)</td>
<td>Orellan</td>
<td>Brule Fm</td>
<td>7 mi E of Douglas, Converse Co., WY</td>
<td>42.9° N, 105.2° W</td>
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<td>Parophisaurus</td>
<td>pawneensis</td>
<td>Orellan</td>
<td>Brule (Orella B or C)</td>
<td>SF-102, Scotts Bluff Co., NE</td>
<td>41.8° N, 103.8° W</td>
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<td>Parophisaurus</td>
<td>pawneensis</td>
<td>Orellan</td>
<td>Brule (Orella B or C)</td>
<td>Round Top, near Crawford, Dawes Co., NE</td>
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<td>pawneensis</td>
<td>Orellan</td>
<td>Brule Fm</td>
<td>Harrison, Sioux Co., NE</td>
<td>42.4° N, 103.8° W</td>
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<td>pawneensis</td>
<td>Orellan</td>
<td>Brule Fm</td>
<td>Jack Casement Ranch, Logan Co., CO</td>
<td>41.0° N, 103.4° W</td>
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<td>Brule Fm</td>
<td>Bill Grimm Ranch, Sioux Co., NE</td>
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<td>Brule Fm</td>
<td>Chimney Canyon Locality, Logan Co., CO</td>
<td>41.0° N, 103.4° W</td>
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<td>Brule Fm</td>
<td>Pawnee Buttes Locality, Weld Co., CO</td>
<td>40.8° N, 104.0° W</td>
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<td>Orellan</td>
<td>Brule Fm</td>
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<td>Genus</td>
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<td>1652</td>
<td>Peltosaurus</td>
<td>sp.</td>
<td>Orellan Brule (Orella B or C)</td>
<td>5 mi S of Scenic, SD</td>
<td>43.5° N, 101.9° W</td>
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<td>Peltosaurus</td>
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<td>7 mi S of South Heart, ND</td>
<td>46.9° N, 102.8° W</td>
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<td>AMNH</td>
<td>8750</td>
<td>Peltosaurus</td>
<td>sp.</td>
<td>Orellan Brule (Orella B or C)</td>
<td>West Central Side Red Shirt Table, Shannon Co., SD</td>
<td>43.3° N, 102.5° W</td>
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<td>84298</td>
<td>Peltosaurus</td>
<td>sp.</td>
<td>Orellan Brule (Orella B or C)</td>
<td>Sf-102, Scotts Bluff Co., NE</td>
<td>41.8° N, 103.8° W</td>
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<td>Peltosaurus</td>
<td>sp.</td>
<td>Orellan Brule (Orella D)</td>
<td>Sx-36, Sioux Co., NE</td>
<td>42.4° N, 103.8° W</td>
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<td>50004</td>
<td>Peltosaurus</td>
<td>sp.</td>
<td>Orellan Brule (Orella B or C)</td>
<td>Big Badlands, SD</td>
<td>43.9° N, 102.5° W</td>
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<td>UNSM</td>
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<td>sp.</td>
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<td>Big Badlands, SD</td>
<td>43.9° N, 102.5° W</td>
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<td>84296*</td>
<td>Peltosaurus</td>
<td>sp.</td>
<td>Orellan Brule (Orella B)</td>
<td>Sx-38, Sioux Co., NE</td>
<td>42.4° N, 103.8° W</td>
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<td>UC 1720</td>
<td>Peltosaurus</td>
<td>granulosus</td>
<td>Orellan Brule Fm</td>
<td>Harrison, Sioux Co., NE</td>
<td>42.4° N, 103.8° W</td>
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<td>P 27072</td>
<td>Peltosaurus</td>
<td>granulosus</td>
<td>Orellan Brule Fm</td>
<td>Harrison, Sioux Co., NE</td>
<td>42.4° N, 103.8° W</td>
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<td>PR 1339</td>
<td>Peltosaurus</td>
<td>sp.</td>
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<td>Sage Creek, Pennington Co., SD</td>
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<td>granulosus</td>
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<td>B. Parsons Ranch, Siome Co., NE</td>
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<td>granulosus</td>
<td>Orellan (Not given)</td>
<td>V 96231, Sioux Co., NE</td>
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<td>Peltosaurus</td>
<td>granulosus</td>
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<td>323: Prairie Dog Creek, NE</td>
<td>42.4° N, 103.8° W</td>
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<td>CM</td>
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<td>Parophisaurus</td>
<td>sp.</td>
<td>Orellan Brule Fm (Cedar Creek Mbr)</td>
<td>2147: Pawnee Grasslands, Pawnee Butte, CO</td>
<td>40.8° N, 104.0° W</td>
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<td>CM</td>
<td>9771</td>
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<td>sp.</td>
<td>Orellan Brule Fm</td>
<td>393: Slim Buttes, 1/2 mi S of Reva Pass, SD</td>
<td>45.5° N, 103.1° W</td>
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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).

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APPENDIX 2. EXTANT ANGUID LOCALITY AND MEASUREMENT DATA

All specimens represent adult individuals for which complete skull and snout-vent length (SVL) could be measured.

This dataset was used to generate the regression equation in Figure 6.

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APPENDIX 3. EXTANT HELODERMATID LOCALITY AND MEASUREMENT DATA

All specimens represent adult individuals for which complete 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.

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<tr>
<th>Institution</th>
<th>Specimen #</th>
<th>Genus</th>
<th>Species</th>
<th>Dry/Wet</th>
<th>Head Length (mm)</th>
<th>SVL (mm)</th>
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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 of glyptosaurines and all fossil anguid lizards through the Cenozoic of North America (see Figure 12).

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<th>NALMA</th>
<th>Reference</th>
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<td>Marsh 1871; Douglass 1908; Gilmore 1928; White 1952; Gunnell &amp; Bartels 2001; Hutchison 1992; Meszoely 1970; Sullivan 1979; Zonneveld et al. 2000</td>
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<td>Whitneyan</td>
<td>Gilmore 1928; Cook &amp; Cook 1933; Galbreath 1953; Meszoely et al. 1978;</td>
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<td>Sullivan 1987, 1979; Hutchison 1992; Macdonald 1951</td>
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<td>1992; Robinson &amp; van Devender 1973; Estes 1963</td>
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<td>1981; Yatkola 1976</td>
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<td>&amp; Sullivan 1981</td>
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<td>1987; Meylan et al. 2001; Meszoely 1970</td>
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<td>1963; Etheridge 1960, 1961</td>
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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.

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<th>Genus</th>
<th>Species</th>
<th># Wet Specimens</th>
<th># Dry Skeletonized Specimens</th>
<th>Total # Specimens</th>
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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.

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<th>Genus</th>
<th>Species</th>
<th># Wet Specimens</th>
<th># Dry Skeletonized Specimens</th>
<th>Total # Specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heloderma</td>
<td>suspectum</td>
<td>23</td>
<td>4</td>
<td>27</td>
</tr>
<tr>
<td>Heloderma</td>
<td>horridum</td>
<td>6</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>Genus Total</td>
<td></td>
<td>29</td>
<td>7</td>
<td>36</td>
</tr>
</tbody>
</table>
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 (*).

<table>
<thead>
<tr>
<th>Reference</th>
<th>Method</th>
<th>Time</th>
<th>MAPT Estimate (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pound et al. (2012)</td>
<td>Leaf margin analysis</td>
<td>Late Miocene</td>
<td>14 (7.25 – 5.33 Ma) 14 (11.61 – 7.25 Ma)</td>
</tr>
<tr>
<td>Pound et al. (2011)</td>
<td>Leaf margin analysis</td>
<td>Late Miocene</td>
<td>12.5 – 14 (11.61 – 7.25 Ma)</td>
</tr>
<tr>
<td>Gregory &amp; McIntosh (1996)</td>
<td>Leaf margin analysis</td>
<td>Early Oligocene</td>
<td>12.7 +/- 1.5* (32.9 – 29 Ma)</td>
</tr>
<tr>
<td>Zanazzi et al. (2007)</td>
<td>Stable oxygen isotope data from fossil ungulate tooth enamel and stable oxygen and carbon isotope data from fossil mammal bone fragments</td>
<td>Late Eocene, early Oligocene</td>
<td>21.0 +/- 5.05* (late Eocene, 36.0 – 33.7 Ma) 13.1 +/- 4.7* (early Oligocene, 33.7 – 32.0 Ma)</td>
</tr>
<tr>
<td>Evanoff et al. (1992)</td>
<td>Land snail distributions</td>
<td>Late Eocene (Chadronian)</td>
<td>16.5</td>
</tr>
<tr>
<td>Sandau (2005)</td>
<td>Leaf margin analysis</td>
<td>Middle Eocene (Uintan)</td>
<td>16.1</td>
</tr>
<tr>
<td>Wing &amp; Greenwood (1993)</td>
<td>Leaf margin analysis</td>
<td>Late Early Eocene</td>
<td>18.6 +/- 1.0 (49.6 – 48.6 Ma) 18.6 +/- 1.0 (50.8 – 49.8 Ma)</td>
</tr>
<tr>
<td>Wilf (2000)</td>
<td>Leaf margin analysis</td>
<td>Early Eocene</td>
<td>19.6 +/- 2.1 (49.8 – 49.6 Ma) 21.3 +/- 2.2 (52.8 Ma) 16.4 +/- 4.4 (53.0 Ma)</td>
</tr>
<tr>
<td>Source</td>
<td>Methodology</td>
<td>Time Period</td>
<td>Results</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-------------------------------------------------------</td>
<td>---------------------------------</td>
<td>-------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Fricke &amp; Wing (2004)</td>
<td>Stable oxygen isotopes from mammal (<em>Coryphodon</em>) enamel and bone and gar scale enamel</td>
<td>Early Eocene</td>
<td>18.7 (54.3 Ma) 15.5 (53.8 Ma) 18.3 (53.0 Ma)</td>
</tr>
<tr>
<td>Wing et al. (2000)</td>
<td>Leaf margin analysis</td>
<td>Latest Paleocene - Early Eocene</td>
<td>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)</td>
</tr>
<tr>
<td>Johnson &amp; Ellis (2002)</td>
<td>Leaf margin analysis</td>
<td>Early Paleocene – Early Eocene</td>
<td>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)</td>
</tr>
</tbody>
</table>

*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 = 14°C). 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.

<table>
<thead>
<tr>
<th>NALMA</th>
<th>Taxon</th>
<th>Maximum SVL estimate (lower, upper) (mm)</th>
<th>MAPT estimates for Q_{10} = 3, 2 (°C)</th>
<th>Range for MAPT estimates (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lancian</td>
<td><em>Odaxosaurus piger</em></td>
<td>123 (110, 137)</td>
<td>-1.4, <strong>4.3</strong></td>
<td>-3.0, <strong>5.3</strong></td>
</tr>
<tr>
<td>Torrejonian</td>
<td>Indeterminate anguid</td>
<td>115 (103, 128)</td>
<td>-2.3, <strong>3.7</strong></td>
<td>-3.9, <strong>4.7</strong></td>
</tr>
<tr>
<td>Time Period</td>
<td>Genus</td>
<td>Specimen</td>
<td>Length</td>
<td>Width</td>
</tr>
<tr>
<td>------------------</td>
<td>----------------------</td>
<td>----------</td>
<td>--------</td>
<td>-------</td>
</tr>
<tr>
<td>Tiffanian</td>
<td><em>Melanosaurus maximus</em></td>
<td>175 (154, 198)</td>
<td>3.7, 7.5</td>
<td>1.9, 8.6</td>
</tr>
<tr>
<td>Clarkforkian</td>
<td><em>Melanosaurus maximus</em></td>
<td>349 (319, 386)</td>
<td>13.6, 13.7</td>
<td>12.3, 15.0</td>
</tr>
<tr>
<td>Wasatchian</td>
<td><em>Paraglyptosaurus hillsi</em></td>
<td>665 (607, 735)</td>
<td>19.5, 22.8</td>
<td>18.7, 24.2</td>
</tr>
<tr>
<td>Bridgerian</td>
<td><em>Paraglyptosaurus princeps</em></td>
<td>673 (614, 744)</td>
<td>19.6, 22.9</td>
<td>18.8, 24.4</td>
</tr>
<tr>
<td>Uintan</td>
<td><em>Glyptosaurus sp.</em></td>
<td>436 (398, 482)</td>
<td>15.7, 16.7</td>
<td>14.9, 18.2</td>
</tr>
<tr>
<td>Chadronian</td>
<td><em>Helodermoides tuberculatus</em></td>
<td>666 (608, 737)</td>
<td>19.6, 22.8</td>
<td>18.7, 24.2</td>
</tr>
<tr>
<td>Orellan*</td>
<td><em>Peltosaurus sp.</em></td>
<td>207 (182, 236)</td>
<td>6.1, 9.0</td>
<td>4.2, 10.2</td>
</tr>
<tr>
<td>Orellan</td>
<td><em>Helodermoides tuberculatus</em></td>
<td>632 (577, 700)</td>
<td>19.1, 22.1</td>
<td>18.3, 23.5</td>
</tr>
<tr>
<td>Whitneyan</td>
<td><em>Peltosaurus abbotti</em></td>
<td>176 (156, 200)</td>
<td>3.8, 7.6</td>
<td>2.0, 8.7</td>
</tr>
<tr>
<td>Early Arikareean (28.3 Ma)</td>
<td><em>Peltosaurus sp.</em></td>
<td>203 (179, 232)</td>
<td>5.9, 8.9</td>
<td>4.0, 10.0</td>
</tr>
<tr>
<td>Barstovian</td>
<td>Indeterminate anguid</td>
<td>174 (154, 197)</td>
<td>3.6, 7.4</td>
<td>1.8, 8.6</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>NALMA</th>
<th>Mean SVL estimate (+/- 1 stdev) (mm)</th>
<th>MAPT estimates for Q_{10} = 3, 2 (ºC)</th>
<th>Range for MAPT estimates (ºC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lancian</td>
<td>114 (104, 125)</td>
<td>-2.4, 3.7</td>
<td>-1.2, 4.4</td>
</tr>
<tr>
<td>Torrejonian</td>
<td>91 (63, 119)</td>
<td>-5.7, 1.6</td>
<td>-11.0, 4.0</td>
</tr>
<tr>
<td>Tiffanian</td>
<td>124 (95, 153)</td>
<td>-1.2, 4.4</td>
<td>-5.1, 6.3</td>
</tr>
<tr>
<td>Clarkforkian</td>
<td>196 (90, 303)</td>
<td>5.3, 8.5</td>
<td>-5.1, 6.3</td>
</tr>
<tr>
<td>Epoch</td>
<td>N</td>
<td>X</td>
<td>Y</td>
</tr>
<tr>
<td>-----------------------</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td>Wasatchian</td>
<td>293</td>
<td>93</td>
<td>493</td>
</tr>
<tr>
<td>Bridgerian</td>
<td>545</td>
<td>408</td>
<td>681</td>
</tr>
<tr>
<td>Uintan</td>
<td>436</td>
<td>217</td>
<td>568</td>
</tr>
<tr>
<td>Chadronian</td>
<td>393</td>
<td>217</td>
<td>568</td>
</tr>
<tr>
<td>Orellan*</td>
<td>151</td>
<td>112</td>
<td>191</td>
</tr>
<tr>
<td>Orellan</td>
<td>181</td>
<td>63</td>
<td>300</td>
</tr>
<tr>
<td>Whitneyan</td>
<td>149</td>
<td>126</td>
<td>173</td>
</tr>
<tr>
<td>Early Arikareean</td>
<td>178</td>
<td>153</td>
<td>203</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>NALMA</th>
<th>Glyptosaurus Maximum SVL Estimate (mm)</th>
<th>Glyptosaurus MAPT Estimate (°C) (Q₁₀ = 3)</th>
<th>Published Terrestrial MAPT Estimate (°C)</th>
<th>Published Proxy Reference (see Table 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiffanian</td>
<td>174.85</td>
<td>7.5</td>
<td>11.7</td>
<td>Johnson &amp; Ellis (2002)</td>
</tr>
<tr>
<td>Clarkforkian</td>
<td>349.20</td>
<td>13.7</td>
<td>12.9</td>
<td>Wing et al. (2000)</td>
</tr>
<tr>
<td>Wasatchian</td>
<td>664.89</td>
<td>19.5</td>
<td>18.7</td>
<td>Fricke &amp; Wing (2004)</td>
</tr>
<tr>
<td>Bridgerian</td>
<td>673.09</td>
<td>19.6</td>
<td>19.6</td>
<td>Wilf (2000)</td>
</tr>
<tr>
<td>Uintan</td>
<td>436.06</td>
<td>15.7</td>
<td>16.1</td>
<td>Sandau (2005)</td>
</tr>
<tr>
<td>Chadronian</td>
<td>666.49</td>
<td>19.6</td>
<td>21.0</td>
<td>Zanazzi et al. (2007)</td>
</tr>
<tr>
<td>Orellan</td>
<td>207.14* (632.71)</td>
<td>9.0* (19.1)</td>
<td>13.1</td>
<td>Zanazzi et al. (2007)</td>
</tr>
<tr>
<td>Whitneyan</td>
<td>176.42</td>
<td>7.6</td>
<td>12.7</td>
<td>Gregory &amp; McIntosh (1996)</td>
</tr>
<tr>
<td>Early Arikareean (30.0-28.0 Ma)</td>
<td>203.48</td>
<td>8.9</td>
<td>12.7</td>
<td>Gregory &amp; McIntosh (1996)</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>NALMA</th>
<th>Glyptosaurine Mean SVL (mm)</th>
<th>Glyptosaurine MAPT Estimate (ºC) (Q₁₀ = 3)</th>
<th>Published Terrestrial MAPT Estimate (ºC)</th>
<th>Published Proxy Reference (see Table 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiffanian</td>
<td>123.97</td>
<td>4.4</td>
<td>11.7</td>
<td>Johnson &amp; Ellis (2002)</td>
</tr>
<tr>
<td>Clarkforkian</td>
<td>196.19</td>
<td>8.5</td>
<td>12.9</td>
<td>Wing et al. (2000)</td>
</tr>
<tr>
<td>Wasatchian</td>
<td>293.22</td>
<td>12.2</td>
<td>15.5</td>
<td>Fricke &amp; Wing (2004)</td>
</tr>
<tr>
<td>Bridgerian</td>
<td>544.64</td>
<td>17.7</td>
<td>18.6</td>
<td>Wing &amp; Greenwood (1993)</td>
</tr>
<tr>
<td>Uintan</td>
<td>435.66</td>
<td>15.7</td>
<td>16.1</td>
<td>Sandau (2005)</td>
</tr>
<tr>
<td>Chadronian</td>
<td>392.57</td>
<td>14.8</td>
<td>16.5</td>
<td>Evanoff et al. (1992)</td>
</tr>
<tr>
<td>Orellan</td>
<td>151.45* (181.27)</td>
<td>6.2* (7.8)</td>
<td>13.1</td>
<td>Zanazzi et al. (2007)</td>
</tr>
<tr>
<td>Whitneyan</td>
<td>149.40</td>
<td>6.1</td>
<td>12.7</td>
<td>Gregory &amp; McIntosh (1996)</td>
</tr>
<tr>
<td>Early Arikareean</td>
<td>177.96</td>
<td>7.7</td>
<td>12.7</td>
<td>Gregory &amp; McIntosh (1996)</td>
</tr>
<tr>
<td>(30.0-28.0 Ma)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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.

USNM 13869 specimen/photograph copyright Smithsonian Institution 2014, all rights reserved.
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.
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: $\ln SVL = 0.927*\ln Head Length + 1.72$; $n = 124; R = 0.82, R^2 = 0.68, p \text{ (uncorr.)} << 0.00$. 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.

USNM 13869 specimen/photograph copyright Smithsonian Institution 2014, all rights reserved.
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). An 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).
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).
FIGURE 15. Estimates for mean annual paleotemperature (MAPT) for the interior of North America through the middle and late Paleogene based on mean 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*Glyptosaurine 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).