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CONSTRAINING NEOGENE TEMPERATURE AND PRECIPITATION HISTORIES
IN THE CENTRAL GREAT PLAINS USING THE FOSSIL RECORD OF *ALLIGATOR*

by

Evan T. Whiting

A THESIS

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CONSTRAINING NEOGENE TEMPERATURE AND PRECIPITATION HISTORIES
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Evan Tyler Whiting, M.S.

University of Nebraska, 2016

Advisor: Sherilyn C. Fritz

Most amphibians and reptiles (excluding birds) are poikilothermic; their internal body temperature varies with that of their external environment. This makes them useful as climate proxies, especially when linked to geographic distributions of ambient climate. I evaluate the utility of the extant crocodylian genus *Alligator* as a paleoclimate proxy for the Central Great Plains (CGP) using species distribution modeling. *Alligator* is a readily identifiable taxon with a good CGP fossil record during the Neogene (~23–2.6 Ma). *Alligator* first appeared in the CGP in the late Eocene (~37 Ma), was absent during most of the Oligocene, reappeared in the early Miocene (~19 Ma), and was extirpated in the late Miocene (~9–6 Ma). This history of occurrence and extirpation implies substantial climatic and environmental changes through time.

To quantify these changes, I constructed species distribution models for extant American alligators using 19 climatic variables and the Maximum Entropy algorithm. I found that living *Alligator* occupies most of its potential geographic range based on modern climatic parameters and is therefore a useful climate proxy. Driest quarter precipitation is the primary variable constraining *Alligator* distributions, which contrasts with results from other studies suggesting that coldest month mean temperature is the

most important factor. Model results and the fossil distribution of *Alligator* suggest that the CGP witnessed increasing aridity and decreasing temperatures during the late Miocene before the spread of C₄ grasslands; this agrees with several other independent proxy reconstructions. The presence or absence of fossil *Alligator*, used in concert with these other proxies, can therefore help constrain paleoclimatic conditions in the CGP during the Neogene.

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To Eileen

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CHAPTER 1

INTRODUCTION

The Great Plains region covers a large portion of the North American continental interior, occupying much of the vast space between the Appalachian and Rocky Mountain ranges (Jacobs et al., 1999). Within the larger Great Plains region is the Central Great Plains (CGP), which spans several states in the continental USA: Nebraska, Kansas, Oklahoma, and Texas (Fig. 1). The CGP, and specifically Nebraska, possesses one of the longest and most continuous Cenozoic terrestrial geological sequences in the world (Voorhies, 1983). This record spans over 900 meters of stratigraphic section and 30 million years of Earth history, beginning with the Eocene-Oligocene White River Group and continuing to the Pleistocene and recent (Schultz et al., 1961; Diffendal and Voorhies, 1994; Woodburne, 2004).

The Neogene is represented particularly well in the Nebraska record and provides a detailed record of biotic, climatic, and environmental change based on multiple proxies (Table 1; Polly and Head, 2015). These include fossil mammals (Janis, 1989, 1993; MacFadden, 1997; Passey et al., 2002; Fox and Fisher, 2004; Janis et al., 2002, 2004; Strömberg, 2006; Maguire and Stigall, 2009; Fraser and Theodor, 2012; Kita et al., 2014; Polly and Head, 2015), fossil plants and phytoliths (Axelrod, 1985; Leopold and Denton, 1987; Strömberg, 2002, 2004, 2005; Edwards et al., 2010; Pound et al., 2011, 2012;

Strömberg and McInerney, 2011; McInerney et al., 2011), and paleosols (Retallack, 1997, 2001; Fox and Koch, 2003, 2004; Fox et al., 2012).

Fossil ectotherms, the so-called ‘lower’ vertebrates (e.g. most actinopterygian fish, amphibians, and reptiles [excluding birds, which are endothermic]), have been largely ignored by most researchers studying the Neogene of the CGP. However, these animals can contribute a great deal of valuable information about paleoclimates and paleoenvironments. Most ectotherms are poikilothermic and have internal body temperatures that vary depending on the conditions of their external environment. Poikilotherms, therefore, are directly linked to environmental variables, such as ambient temperature, based on their physiologies and functional traits, such as maximum body size (Makarieva et al., 2005a, 2005b; Head et al., 2009, 2013; Polly and Head, 2015).

Fossil poikilotherms are abundant in the Neogene of the CGP, especially in Nebraska. This record includes representatives of several major amphibian and reptile (herpetofauna) clades: anurans and salamanders (Tihen and Chantell, 1963; Estes and Tihen, 1964; Chantell, 1964, 1971; Holman, 1976, 1987; Holman and Sullivan, 1981; Holman and Voorhies, 1985; Joeckel, 1988; Parmley, 1992; Parmley et al., 2015); squamates and chelonians (Estes and Tihen, 1964; Holman, 1976, 1977, 1987; Yatkola, 1976; Holman and Sullivan, 1981; Wellstead, 1982; Holman and Corner, 1985; Joeckel, 1988; Parmley and Holman, 1995; Passey et al., 2002; Parmley and Hunter, 2010); and crocodylians (Mook, 1923, 1946; Schmidt, 1941; Voorhies, 1971; Martin, 1984; Passey et al., 2002; Whiting and Head, 2015). Many of these fossil poikilotherms occur in association with each other spatiotemporally and represent distinct herpetofaunas; these

taxonomic associations slowly changed over time, because of biotic interactions and abiotic environmental change (Jacisin et al., 2015).

The crocodylian fossils curated in the University of Nebraska State Museum (UNSM) collection have never been systematically described or documented, except for a few specimens discussed by Voorhies (1971). In this thesis, I provide the first systematic description of the Miocene crocodylian fossils in the UNSM collection and utilize this newly described record in concert with species distribution modeling of extant American alligators to reconstruct paleoclimate in the CGP during the Miocene epoch of the Neogene period.

CHAPTER 2

MIocene CROCODYLIANS IN THE CENTRAL GREAT PLAINS

Introduction

Crocodylians were present in what is now Nebraska during the Hemingfordian, Barstovian, and Clarendonian North American land mammal ages (NALMAs) of the Miocene epoch, approximately 19–9 million years ago (Ma; Passey et al., 2002; Tedford et al., 2004; Whiting and Head, 2015). They were extirpated from Nebraska and the greater Central Great Plains (CGP) region during the late Miocene (Whiting and Head, 2015); crocodylians last occurred in Nebraska during the Clarendonian (~9 Ma) and in the southern CGP during the Hemphillian (~6 Ma). This was the second major regional extirpation of crocodylians from the Great Plains during the Cenozoic. They were previously extirpated from the region shortly after the end of the Eocene (~34 Ma; Whiting and Hastings, 2015), which coincided with global cooling and regional aridification across the Eocene-Oligocene boundary (e.g. Zachos et al., 1996, 2001, 2008; Zanzari et al., 2007; Liu et al., 2009; Corsini et al., 2011; Boardman and Secord, 2013; Goldner et al., 2014). The apparent absence of crocodylians in the Great Plains during most of the Oligocene implies that regional paleoclimatic and paleoenvironmental conditions in the North American continental interior were unfavorable (Markwick, 1994). Crocodylians reappeared in the CGP in the early Miocene (~19 Ma;

Hemingfordian) and persisted until their subsequent extirpation in the late Miocene (~9–6 Ma).

All complete and/or diagnostic Miocene crocodylian fossils from Nebraska have been referred to the extant genus *Alligator* (Mook, 1923, 1946; Schmidt, 1941; Brochu, 1999), although most of the crocodylian specimens collected from the CGP are too incomplete or fragmentary to be diagnosed to *Alligator* using a strictly apomorphy-based approach. These records (Table 2) include specimens from the Miocene of Nebraska (Voorhies, 1971; Martin, 1984; Whiting and Head, 2015), Kansas (Liggett, 1997), Oklahoma (Savage, 1941; Woodburne, 1959), and Texas (Holman, 1966, 1977). Since *Alligator* is the only crocodylian taxon identified from the continental interior of North America in deposits younger than the middle Eocene (Brochu, 1999; Whiting and Hastings, 2015), it is most likely that all Miocene (and Eocene-Oligocene) crocodylian fossils from the CGP represent this genus (cf. *Alligator*).

The following account provides the first systematic description of all Miocene crocodylian fossils curated at the University of Nebraska State Museum (UNSM), as well as a discussion on the Miocene CGP fossil crocodylian record. Use of the qualifier ‘Cf.’ (confer; comparable to) in taxonomic identifications invokes multiple lines of evidence independent of diagnostic morphology, which is incomplete or lacking in most of the UNSM specimens described herein.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **FHSM**, Sternberg Museum of Natural History, Hays; **FMNH**, Field Museum of

Natural History, Chicago; **OMNH**, Sam Noble Oklahoma Museum of Natural History, Oklahoma City; **SMPSMU**, Shuler Museum of Paleontology, Southern Methodist University, Dallas; **UNSM**, University of Nebraska State Museum, Lincoln.

Terminology and Anatomical Abbreviations—Abbreviations for tooth and alveolus positions follow Hastings et al. (2010). Abbreviations for femoral measurements follow Farlow et al. (2005).

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789

GLOBIDONTA Brochu, 1999

cf. *ALLIGATOR* Cuvier, 1807

Referred Specimens

UNSM 135037: a nearly complete right dentary with alveoli d1-?d15 (alveoli d1 and d?6-d?9, and d?15 are incomplete), nearly complete right splenial, partial anterior right coronoid, two right surangular fragments, a posterior left mandibular fragment including portions of the left surangular, angular, and articular, an anterior left dentary fragment with alveoli d1-d?11 (alveoli d?8 and d?11 are incomplete), anterior left splenial fragment, partial right postorbital with incomplete postorbital bar, partial posterior left maxilla with at least the last five maxillary alveoli, partial left ectopterygoid fragment, left anterior maxilla fragment with at least five alveoli (?m1-m5); ?left ?premaxilla

fragment with alveoli pm?1-pm?4 and lateral border of external naris; two isolated tooth crowns, a partial lumbar vertebra, at least six incomplete keeled dorsal osteoderms, and several unidentifiable associated skeletal fragments.

Locality—*Aletomeryx* Quarry (UNSM Locality Cr-23), Cherry County, Nebraska, USA; Runningwater Formation, lower Miocene (early Hemingfordian).

Description—UNSM 135037 is highlighted by an anterior right mandibular ramus, comprised by the right dentary and splenial, and possibly coronoid (Fig. 2). The ventrum and lateral side of this small specimen are covered by pitting typical in crocodylians. The mandibular symphysis is long, extending for the full length of the dentary alveoli series d1-d7/d8. There are partial teeth in place for several alveoli, including one with an intact crown at position d10. Alveoli d4 and d11 appear to be the largest in the entire preserved dentary tooth row. The nearly complete right splenial enters the mandibular symphysis posteriorly, and possesses an anterior foramen intermandibularis oralis (FIO) opening just posterior to the termination of the symphysis. The splenial is closer to the dentary tooth row posteriorly, where the dentary disappears medially near the termination of the tooth row.

A small, anterior sliver of the right surangular is preserved, attached to the dentary; there is no indication of the presence of a surangular spur, or its relationship to the missing posteriormost dentary tooth row. It appears that the anteriormost border of the external mandibular fenestra is visible, but there is not enough preserved to provide a suggestion of the fenestra's relative size. The anterior part of the right coronoid is preserved where it meets the posterior splenial on the medial side of the mandibular

ramus. This region of the mandibular ramus is somewhat crushed, but it does appear that the foramen intermandibularis medius is open anteriorly and is not completely enclosed by the borders of the anterior coronoid.

The incomplete anterior left dentary (Fig. 3) is similar in morphology to the right. It includes a small portion of the left splenial entering the mandibular symphysis, and an anterior FIO opening. Observation of the left dentary in lateral view suggests a ‘deep’ curvature of the bone between d4 and d10. The first two dentary alveoli appear somewhat procumbent, facing anterodorsally rather than dorsally. The mandibular symphysis is also well-preserved, and extends the length of d1-d7/d8. Partial teeth appear to be in place for all dentary alveoli.

The posterior left mandible fragment (Fig. 3) includes portions of the left surangular, angular, and articular. The retroarticular process is broken posterior to the glenoid fossa. The posterior surface of the articular is slightly damaged, including the opening of the foramen aerum; this foramen is closer to the medial margin of the articular than the lateral margin. The surangular appears to continue to the dorsolateral margin of the glenoid fossa, rather than truncating; truncation is characteristic of *A. mississippiensis* and the late Miocene Nebraska metataxon *A. mefferdi* (Mook, 1946; Brochu, 1999). No part of the external mandibular fenestra is preserved, thereby precluding an assessment of its size or the location of the termination of the surangular-angular suture.

A fragmentary element tentatively referable to a left premaxilla includes the first four premaxillary alveoli and possibly the lateral border of the external naris (Fig. 4). The posteriormost portion of the premaxilla preserves a small suture, possibly for the left

nasal at the posterior border of the external naris. There are partial teeth in place in pm2-pm4; pm1 appears to be an empty alveolus filled with sediment. The great disparity in relative size between pm4 and the other alveoli, as well as the presence of small pits along the surface medial to the tooth row provide support for this bone being a premaxillary fragment.

The left maxillary fragment has a sculptured, convex dorsal surface and a smooth ventral surface medial to the maxillary tooth row (Fig. 4), indicating that this fragment likely belongs to the anterior region of the left maxilla. The large ventral concavity medially adjacent to m1-m3 is likely the occlusion pit for d11, based on direct comparisons to complete extant and fossil *Alligator* skulls. The largest maxillary alveolus is therefore most likely m4, which is the largest maxillary alveolus in all species of *Alligator* and many other alligatorids (Brochu, 1999).

The incomplete posterior left maxilla preserves at least the last five maxillary alveoli, including the ultimate and penultimate alveoli with partial in situ dentition (Fig. 4). The posteriormost two alveoli appear to be equal in size, and are located just anterior to the suture of the maxilla and left ectopterygoid. The ectopterygoid is broken distally to the maxilla; much of it is obscured by sediment, but it appears that the entire maxilla-ectopterygoid suture is intact. The incompleteness of both bones precludes an assessment of the size and shape of the suborbital fenestra.

The right postorbital is relatively complete. There is only a small portion of the anterolateral border of the right supratemporal fenestra, so nothing definitive can be said about the relative size of the fenestra with respect to the size of the skull table. The

sutures with the frontal and right squamosal are present, and the postorbital bar is broken dorsally to any sutures with the corresponding extension from the absent jugal.

The partial vertebra appears to be from the lumbar region, as it has smooth lateral surfaces and no evidence of a ventral hypophysis. The dorsal osteoderms are keeled, suggesting alligatorid affinities. They are very similar to the osteoderms of UNSM 135036, from the same locality (Cr-23).

Discussion—The presence of an anterior FIO opening, coupled with splenial participation in a mandibular symphysis spanning at least seven dentary alveoli, support the notion that this specimen belongs to a basal alligatorine or basal species of *Alligator*, such as *A. prenasalis* or *A. mcgrewi* (Brochu, 1999). The absence of an anterior FIO opening is an autapomorphy for *A. mississippiensis* (Brochu, 1999; Snyder, 2007; Whiting et al., In press). A relatively long mandibular symphysis is reminiscent of basal alligatorines and basal species of the genus *Alligator*; derived species of *Alligator* possess a shorter symphysis, typically extending the length of the first four or five dentary alveoli (Brochu, 1999). A lack of splenial participation in the mandibular symphysis is synapomorphic for derived *Alligator* (Brochu, 1999). The ‘deep’ curvature of the dentary between d4 and d10 is also characteristic of basal alligatorines (Brochu, 1999). UNSM 135037 is referred to Globidonta (Brochu, 1999) based on the following ambiguous synapomorphies: fourth dentary alveolus larger than the third, and alveoli separated; largest maxillary alveolus is the fourth. UNSM is tentatively referred to *Alligator* because of the lack of morphological deviation in the preserved elements from that known for *Alligator*. Since it is from the same locality as the holotype specimen (FMNH P26242) of

Alligator mcgrewi (Schmidt, 1941), and it does not exhibit any morphology different from that species, UNSM 135037 is very likely the same taxon.

UNSM 135036: an anterior left dentary fragment with alveoli d1-d4 (alveoli d3-d4 are incomplete) and a portion of the left mandibular symphysis, an accompanying left dentary fragment with medial sutures for the splenial (missing), at least three indistinct mandibular fragments, a posterior right prefrontal fragment, incomplete proximal right ulna, at least two incomplete thoracic vertebrae and other vertebral fragments, at least nine complete or partial keeled dorsal osteoderms, and some unidentifiable skeletal fragments.

Locality—*Aletomeryx* Quarry (UNSM Locality Cr-23), Cherry County, Nebraska, USA; Runningwater Formation, lower Miocene (early Hemingfordian).

Description—UNSM 135036 includes several different skeletal elements representing a relatively small-bodied individual, similar to UNSM 135037 from the same locality. The anterior left dentary fragment includes the first two alveoli (d2 is occupied by a small tooth) and has the medial remnants of alveoli d3-d4. Despite its incompleteness, it can be determined that d4 is definitely larger than any other alveolus in the preserved dental series. The left mandibular symphysis is partially preserved on the medial portion of the specimen. Another portion of the left dentary is preserved, although it does not connect to the anteriormost piece discussed above. This fragment includes several partial alveoli, a relatively smooth dorsal surface, and the preserved sutures for the missing splenial on its medial surface. The posteriormost portion of the left

mandibular symphysis is barely evident, but the preserved splenial sutures on this fragment indicate that the splenial participated in the mandibular symphysis.

The partial posterior right prefrontal (Fig. 5) displays a smooth lateral surface, which forms a small part of the anteromedial border of the orbit, and sutures with the missing frontal on its medial surface. There is not a great degree of sculpturing, nor is the lateral protuberance very prominent or large. The anterior portion of the prefrontal is missing, prohibiting a determination of its full extent and anterior sutural relationships.

At least two incomplete vertebrae are known from this specimen. One is an anterior thoracic vertebra, with the remnants of a hypophysis on the ventrum of the specimen and diapophyses on the lateral surfaces. The other is a lumbar vertebra, with no evidence of a ventral hypophysis and smooth lateral surfaces. The approximate positions of both vertebrae within the vertebral column cannot be ascertained.

The partial right ulna is expanded proximally, in a similar fashion to most crocodylians, and is missing its distal end (Fig. 5). The dorsal osteoderms are all keeled. Some are more rectangular in shape and may have belonged to the dorsal midline, while others are more oblong and could have been located in a number of different positions on the individual's dorsum.

Discussion—UNSM 135036 is referred to *Globidonta* (Brochu, 1999) based on the following ambiguous synapomorphy: fourth dentary alveolus larger than the third, and alveoli separated. UNSM 135026 is tentatively referred to *Alligator* because of the lack of morphological deviation in the preserved elements from that known for *Alligator*. This specimen, in addition to UNSM 135037, described above, is also from the same

locality as the *A. mcgrewi* holotype; UNSM 135036 may also be attributed to the same taxon because of its similar morphology.

UNSM 135035: a right anterior dentary fragment with alveoli d1-4 (alveoli d1 and d3-d4 are incomplete) and a portion of the right mandibular symphysis.

Locality—Sinclair Quarry 2 of the Lower Snake Creek Beds, Sioux County, Nebraska, USA; Olcott Formation, middle Miocene (early Barstovian).

Description—UNSM 135035 is an anterior right dentary fragment (Fig. 6). Its incompleteness precludes more specific taxonomic identification beyond Globidonta (Brochu, 1999), but several important features are present. All but the anteriormost portion of the right mandibular symphysis is preserved. The mandibular symphysis extends posteriorly beyond at least the fourth dentary alveolus, although breakage prohibits further comment on its full extent. The only complete alveolus is d2; d1 and d3-d4 are incomplete, although their relative sizes can still be determined. The fourth alveolus is the largest of the partially preserved series, followed next in size by d1; d2 and d3 appear to be roughly equal in diameter (~7.8 mm). Small pockmarks characteristic of crocodylian cranial bones are evident on the ventrum of the specimen, while the dorsal surface laterally adjacent to the mandibular symphysis is smooth with only a few small depressions aligned medially to the tooth row (a feature prevalent in most crocodylians).

Discussion—The relative size of this dentary fragment suggests that it belonged to an individual of moderately large body size, much larger than both UNSM 135036 and UNSM 135037. UNSM 135035 is referred to Globidonta (Brochu, 1999) based on the

following ambiguous synapomorphy: fourth dentary alveolus larger than the third, and alveoli separated. UNSM 135035 is tentatively referred to *Alligator* because of the lack of morphological deviation in the preserved elements from that known for *Alligator*. The mandibular symphysis of UNSM 135035 appears to be shorter than those of the two previously described specimens; this evidence, as well as larger size, indicates that UNSM 135035 is likely a more derived and larger species than *A. mcgrewi*.

UNSM 135021: a left anterior dentary fragment with alveoli d1-d7 (alveoli d1 and d7 are incomplete).

Locality—UNSM locality Kx-134, Knox County, Nebraska, USA; ?Fort Randall Formation, middle Miocene (late [middle] Barstovian).

Description—UNSM 135021 is a water-worn left anterior dentary fragment (Fig. 6) from the middle Miocene ?Fort Randall Formation of Nebraska. It is inconclusive as to whether or not the splenial entered the mandibular symphysis, because of a high degree of weathering to the specimen. The ventrum is covered in the typical crocodylian pattern of extensive pitting, and small pits are arranged parallel to the dentary tooth row on the dorsal portion of the specimen. There are seven alveoli preserved, including partial in situ dentition for d3. The fourth dentary alveolus is by far the largest in the series, and is distinctly separate from both d3 and d5. The mandibular symphysis is no more than five dentary alveoli in length.

Discussion—UNSM 135021 is referred to Globidonta (Brochu, 1999) based on the following ambiguous synapomorphy: fourth dentary alveolus larger than the third,

and alveoli separated. UNSM 135021 is tentatively referred to *Alligator* because of the lack of morphological deviation in the preserved elements from that known for *Alligator*. The shorter mandibular symphysis of this specimen (as well as of UNSM 135035) hints at derived alligatorine affinities; short mandibular symphyses are seen only in derived alligatorines, such as derived species of *Alligator*, whereas longer mandibular symphyses are characteristic of basal alligatorines and species of *Alligator* (Brochu, 1999, 2004).

EUSUCHIA (Huxley, 1875)

Insertae sedis

Taxonomic Ambiguity

The morphologically indeterminate specimens described below are also most likely attributable to *Alligator*, primarily because of the spatiotemporal context that the fossils were found in. There is no evidence, morphological or otherwise, to support the referral of these fossils to any other crocodylian taxon.

Referred Specimens

UNSM 85346—a mostly complete vertebra (Fig. 7) from UNSM locality Bw-106, Bridgewater County, Nebraska, USA; Valentine Formation, middle Miocene (late Barstovian). This vertebra likely belongs to the lumbar region, because of its lack of projections on its smooth, lateral surfaces. The neurocentral sutures are not completely fused, suggesting that this individual had not yet attained full maturity (Brochu, 1996).

The specimen is missing the distalmost portions of the transverse processes, and the dorsalmost portion of the neural spine.

UNSM 85347—a small partial caudal vertebra from UNSM locality Bw-106, Bridgewater County, Nebraska, USA; Valentine Formation, middle Miocene (late Barstovian). This specimen is missing much of the dorsal portion, including the zygopophyses, neural spine, and transverse processes. It does, however, possess fully closed neurocentral sutures.

UNSM 135019—a mostly complete cervical vertebra (Fig. 7) from UNSM locality Kx-134, Knox County, Nebraska, USA; ?Fort Randall Formation, middle Miocene (late [middle] Barstovian). There is evidence of a small hypophysis on the ventrum of the centrum, and both the diapophyses and parapophyses are preserved on either lateral side of the specimen. The neural spine is broken, as is the right postzygopophysis. The neurocentral sutures of this vertebra are nearly fused, implying that this individual was approaching ontogenetic maturity (Brochu, 1996).

UNSM 135020—a mostly complete caudal vertebra (Fig. 7) from UNSM locality Kx-133, Knox County, Nebraska, USA; ?Fort Randall Formation, middle Miocene (late [middle] Barstovian). This caudal vertebra is missing most of its neural spine and transverse processes, as well as the left prezygopophysis and right postzygopophysis. There are no neurocentral sutures visible, which implies complete fusion. This individual

may or may not have been ontogenetically mature; neurocentral suture closure occurs in a caudal to cranial pattern in crown crocodylians (Brochu, 1996), so this caudal vertebra would have completely fused prior to the individual reaching full maturity.

UNSM 54112—a partial tooth crown from UNSM locality Kx-134, Knox County, Nebraska, USA; ?Fort Randall Formation, middle Miocene (late [middle] Barstovian). This specimen is missing its distal tip and proximal base, with visible carinae.

UNSM 135016 and 135017—two small, isolated tooth crowns from UNSM locality Cr-114, Cherry County, Nebraska, USA; Valentine Formation, middle Miocene (late Barstovian).

UNSM 135018—a large vertebral centrum (Fig. 7) from UNSM locality Cr-114, Cherry County, Nebraska, USA; Valentine Formation, middle Miocene (late Barstovian). This vertebral centrum is likely from the thoracic or lumbar region of the vertebral column, given its large size and lack of ventral projections. Its neurocentral sutures are barely visible, indicating that this vertebra was nearly fused.

UNSM 135022—two dorsal osteoderm fragments (Fig. 8) from UNSM locality Kx-120, Knox County, Nebraska, USA; Valentine Formation, middle Miocene (late Barstovian). These osteoderm fragments represent relatively large-bodied individuals,

given their size and thickness. The smaller fragment appears to preserve the lateral margin of a potential dorsal midline osteoderm, with a straight border. The larger specimen is very thick, and is roughly rectangular in shape; this suggests that it could be a dorsal midline osteoderm.

UNSM 135000–135014—several dorsal osteoderms and osteoderm fragments (Fig. 8) from UNSM locality Wt-102, Webster County, Nebraska, USA; Valentine Formation, middle Miocene (late Barstovian). Based on their relative sizes and thicknesses, these keeled osteoderms likely represent medium- to large-bodied individuals.

UNSM 135015—an isolated and heavily water-worn right jugal fragment from UNSM locality Wt-102, Webster County, Nebraska, USA; Valentine Formation, middle Miocene (late Barstovian). This right jugal fragment is very rounded, likely due to significant post-depositional fluvial transport as a pebble-sized clast. The lateral surface still maintains its pitted appearance, but the rest of the specimen is smooth and rounded. The postorbital bar is still barely discernible.

UNSM 135023—a single dorsal osteoderm and six partial tooth crowns from UNSM locality Ap-105, Antelope County, Nebraska, USA; Ash Hollow Formation, upper Miocene (medial Clarendonian). The osteoderm is small and flat, albeit the characteristic pockmarked texture. One edge appears smooth and unbroken, while the

other is uneven and broken. Four of the six tooth crowns are very small and blunt, whereas the other two are more distally tapered and are probably caniform teeth. These fossils were originally mentioned by Voorhies (1971) in his description of Miocene crocodylian fossils from Nebraska.

UNSM 135027—a complete right femur (Fig. 9) and partial dorsal osteoderm from UNSM Locality Bw-105, Bridgewater County, Nebraska, USA; Ash Hollow Formation, upper Miocene (late Clarendonian). This complete right femur is ~17 cm in length, with the following additional measurements: Fdw = 39.02 mm; Fdh = 28.48 mm; Fpmn = 20.86; Fpmx = 37.59 mm; Ftr = 55.87 mm. These measurements provide a total body length estimate of ~2.4 m, based on the logarithmic regression equations of Farlow et al. (2005, Table 3). Extant male *Alligator mississippiensis* can reach total body lengths of ~3.5–4.5 m, whereas females typically do not attain a total body length of more than ~3 m (Woodward et al., 1995). Therefore, UNSM 135027 could represent either an immature male, or a female nearing ontogenetic maturity. The partial dorsal osteoderm associated with this femur is broken along its dorsal keel, the presence of which suggests an alligatorid affinity.

UNSM 135026—a partial lumbar vertebra from UNSM Locality Bw-105, Bridgewater County, Nebraska, USA; Ash Hollow Formation, upper Miocene (late Clarendonian). This partial vertebrae is likely from the lumbar region of the vertebral column, given its smooth lateral surfaces and lack of a ventral hypophysis. The

neurocentral suture does not appear to be completely fused, suggesting that this individual had not yet attained full maturity (Brochu, 1996).

UNSM 135024—an isolated caniform tooth from UNSM locality Bw-123, Bridgewater County, Nebraska, USA; Ash Hollow Formation, upper Miocene (late Clarendonian). This tooth includes both the complete crown and much of its root. The enamel on the crown is fully intact, and the carinae are clearly visible.

UNSM 135025—three isolated tooth crowns and a small, incomplete caudal vertebra from UNSM locality Bw-123, Bridgewater County, Nebraska, USA; Ash Hollow Formation, upper Miocene (late Clarendonian). The three tooth crowns are all quite small; one has a small root remnant still attached to it. The caudal vertebra is missing its transverse processes, postzygopophyses, and left prezygopophysis. Given its diminutive size and its centrum's deep concavoconvexity, this vertebra was likely positioned near the end of the caudal vertebrae series.

UNSM 135028—a moderately-sized vertebral centrum (Fig. 7) from UNSM locality Sh-107, Sheridan County, Nebraska, USA; Ash Hollow Formation, upper Miocene (late Clarendonian). This vertebral centrum is relatively large and robust, and is likely from the thoracic or lumbar region of the vertebral column. Its neurocentral sutures are almost entirely fused, indicating that this individual was nearing ontogenetic maturity (Brochu, 1996).

UNSM 135029—a small, isolated tooth crown from UNSM locality Sh-107, Sheridan County, Nebraska, USA; Ash Hollow Formation, upper Miocene (late Clarendonian).

UNSM 135030–135034—five dorsal osteoderms (Fig. 8) from UNSM locality Sh-107, Sheridan County, Nebraska, USA; Ash Hollow Formation, upper Miocene (late Clarendonian). Three of these osteoderms are complete; the other two are broken and fragmentary. All of them possess a dorsal keel.

Miocene Crocodylian Distributions in the Central Great Plains

There is ample evidence to suggest that all of the Miocene UNSM crocodylian fossils belong to the genus *Alligator*, despite the fact that none of them can be assigned to genus or species based on morphological apomorphies alone. As previously stated, there are no crocodylian taxa other than *Alligator* known from the continental interior of North America in deposits younger than the middle Eocene (Brochu, 1999; Whiting and Hastings, 2015). All diagnosable Miocene crocodylian fossils from the CGP have been referred to either the genus or species of *Alligator* (Mook, 1923, 1946; Schmidt, 1941; Brochu, 1999). These include specimens collected from some of the same localities (e.g. *Aletomeryx* Quarry) as morphologically indeterminate UNSM specimens (Table 2). None of the UNSM fossils deviate in morphology from what is known for *Alligator*. These

observations strongly support the assumption that all of the Miocene crocodylian fossils from Nebraska and the CGP belong to the genus *Alligator*.

All known Miocene fossil *Alligator* localities in the CGP are shown in Figure 1 and Table 2. The first Miocene occurrence of *Alligator* in the CGP is in the Runningwater Formation (Hemingford Group) of northwestern Nebraska, which was deposited ~19–17.5 Ma during the Hemingfordian 1 biochron (Tedford et al., 2004). Alligators in the CGP during this time interval were small-bodied and blunt-snouted and belonged to the species *Alligator mcgrewi* (Schmidt, 1941; Brochu, 1999, 2004). The only known localities from which fossils representing this taxon have been recovered are located in the northwestern counties of Nebraska, which is likely, because there are no other deposits of the same age throughout the rest of the state (Burchett and Pabian, 1991). This geological bias prohibits an assessment of the total Hemingfordian 1 distribution of *Alligator* in Nebraska and the CGP, but it was probably much larger than the small geographic area of the Runningwater Formation that is currently exposed.

Alligators next occur in the Sheep Creek and Olcott Formations, which are also part of the Hemingford Group exposed in the northwestern corner of Nebraska (Burchett and Pabian, 1991). These rocks represent or correspond to the Hemingfordian 2 and Barstovian 1 biochrons (~17.5–15 Ma; Tedford et al., 2004), respectively. Alligators from these two formations are rare but appear to have been larger-bodied than their diminutive predecessors in the Runningwater Formation. The most complete specimen from this time interval (~17.5–15 Ma) is the holotype of *Alligator thomsoni* (AMNH 1736; Mook, 1923) from the AMNH Trojan Quarry locality (Skinner et al., 1977). The A.

thomsoni holotype skull is relatively short-snouted (Mook, 1923) but not to the same degree as seen in *A. mcgrewi* (i.e. the skull is almost as wide as it is long; Schmidt, 1941). Mook (1923) appears to have incorrectly referred a paratype mandible (AMNH 1737) to *A. thomsoni* that exhibits morphology closer aligned with *A. mcgrewi*, a more basal species of *Alligator*. Without precise stratigraphic constraints, which were lacking in Mook's (1923) original description, it is impossible to conclude if *A. thomsoni* and *A. mcgrewi* were sympatric (or even the same taxon at different ontogenetic stages) during this time interval.

Barstovian 1 fossil alligators are also known from the Fleming Formation of Texas (Table 2). Isolated crocodylian teeth have been recovered from the Trinity River (Holman, 1966, 1977). This is the southernmost occurrence of *Alligator* in the CGP during the early-middle Miocene and indicates that alligators probably occupied a larger geographic range than only within what is now Nebraska.

Alligator fossils become more abundant in deposits representing the Barstovian 2 biochron (~15–12.5 Ma; Tedford et al., 2004), typified by the Valentine Formation (Ogallala Group) of Nebraska. There are a few fossil *Alligator* specimens in the UNSM collection from the ?Fort Randall Formation ('medial' Barstovian), although there is scant information regarding these biochronologic and geologic units. Alligators in the Valentine Formation occur mainly in the Niobrara River valley in northern Nebraska, which likely indicates that there is an erosional bias preferentially exposing fossils in this region. The presence of *Alligator* fossils at the Wt-102 locality in extreme southern Nebraska suggests that they had a wider distribution during the Barstovian 2 biochron

than just the Niobrara River valley. There are more fossil *Alligator* localities in the Valentine Formation of Nebraska than in any other Miocene geologic unit in the CGP, which is likely attributable to both geological and collecting biases. More Ogallala Group rocks are exposed in Nebraska than any other Neogene geologic unit (Burchett and Pabian, 1991), and these deposits have been exhaustively investigated and collected (e.g. Diffendal and Voorhies, 1994). There was a distinctive ectothermic fauna in Nebraska during this time interval, which included freshwater actinopterygian fish, such as *Ictalurus* sp. (catfish), *Lepisosteus* sp. (gar), and *Amia* sp. (bowfin), alligators, and other herpetofauna characteristic of modern southeastern North America (Voorhies, 1971). This distinctive ectothermic fauna disappeared in the late Miocene, likely because of decreasing temperatures and increasing aridity (Jacisin et al., 2015).

Alligators were still present in Nebraska during the Clarendonian (~12.5–9 Ma), although there is a brief hiatus in the record spanning the Clarendonian 1 biochron. Since there are very few known localities representing this time interval in Nebraska, this is most likely represents a geological or collecting bias (Fig. 10). *Alligator* fossils in the upper Miocene Ash Hollow Formation (upper Ogallala Group) were found at localities representing fluvial riparian settings, such as Pratt Slide (Bw-123 in Table 2). Pratt Slide is notable, because it probably represents a valley-fill and likely had its own localized microclimate and paleoenvironmental conditions (Kita et al., 2014). The most complete *Alligator* fossil from the Clarendonian is the holotype specimen of *Alligator mefferdi* (AMNH 7016; Mook, 1946) from the AMNH George Sawyer Ranch locality in north-central Nebraska. This specimen represents one of the last Miocene occurrences of

Alligator in Nebraska prior to the extirpation of the genus to more southern latitudes during the Hemphillian (~9–6 Ma; Table 2; Fig. 1).

There are no known records of *Alligator* from any fossil localities of Hemphillian age in Nebraska; all Hemphillian *Alligator* localities in the CGP are found in southern Kansas, northern Oklahoma, and northern Texas (Table 2; Fig. 1). These fragmentary (i.e. isolated teeth and osteoderms) records are important for establishing *Alligator* presence and indicate that alligators persisted into the Hemphillian in the southern CGP.

Based on the distributions of fossil alligators in the CGP, it appears that northern Nebraska may have been close to the northern extent of the *Alligator* range during the Miocene. There are no known *Alligator* fossils from north of the Niobrara River valley during any part of the Neogene, and alligators appear to be somewhat rare at many of the Miocene localities in Nebraska. This may be attributable to a sampling bias (Fig. 10). However, it could also indicate that the paleoenvironments that these northern Nebraska localities represent possessed climatic conditions that were closer to the minimum requirements for *Alligator* presence (see Chapter 3). This could also potentially be extended to the late Miocene localities in Kansas, Oklahoma, and Texas, which represent the northern extremes of *Alligator* distributions during the Hemphillian. If this was the case, then it provides an informative perspective on the northernmost extent of climatic regimes conducive to alligators in the CGP during the Miocene, which is very useful for paleoclimate reconstruction.

CHAPTER 3

PALEOCLIMATE RECONSTRUCTION USING FOSSIL *ALLIGATOR***Introduction**

Alligators occupy higher latitudes than any other extant crocodylians (Kellogg, 1929; Lance, 1989, 2003; Thorbjarnarson, 1992) and are better adapted, physiologically and behaviorally, for survival in cooler conditions than other members of Crocodylia (e.g. Smith, 1975; Brisbin et al., 1982; Hagan et al., 1983; Lang, 1987; Asa et al., 1998). Therefore, *Alligator* should not be used as the sole representative for all other extant and extinct crocodylians. Using *Alligator* as a representative for all Neogene fossil crocodylians in the Central Great Plains (CGP), however, is valid, since all of these fossils most likely belong to *Alligator* (see Chapter 2).

American alligators (*Alligator mississippiensis*) tolerate a wide range of climatic conditions within their geographic distribution (Fig. 1), which today includes most of the southeastern USA (Kellogg, 1929; Spotila et al., 1972; Lang, 1987; Lance, 1989; Crocodile Specialist Group, 1996). Experimental and observational studies on thermal tolerances and thermoregulatory behaviors in wild and captive *A. mississippiensis* indicate critical temperature minima and maxima of about 4–8°C and 33–38°C, respectively (Colbert et al., 1946; Coulson and Hernandez, 1964; Brattstrom, 1965; Smith, 1975; Brisbin et al., 1982; Hagan et al., 1983; Asa et al., 1998). These extremes can be plastic, depending on a variety of conditions (Spotila et al., 1972; Smith, 1975;

Lang, 1987). Colbert et al. (1946) suggested a preferred body temperature range of ~32–35°C for wild alligators living in Florida. However, Asa et al. (1998) reported that captive American alligators in Missouri typically avoided temperatures >31°C, had a preferred body temperature range of ~29–31°C, and were tolerant of cooler temperatures (~7–8°C). These differences in populations suggest a possible latitudinal gradient of thermal tolerances and preferences for American alligators (Lang, 1987), which complicates assessments of their exact critical temperature extremes. Alligators are also known to frequently change their daily activity levels and behavioral patterns seasonally, corresponding to differences in seasonal temperatures (Smith, 1975).

Regardless of exact temperature tolerances and preferences, all *Alligator* populations need a permanent source of surface water in order to survive (Colbert et al., 1946; Spotila et al., 1972; Markwick, 1994; Asa et al., 1998). Water acts as a thermal buffer that aids in thermoregulation (Colbert et al., 1946; Spotila et al., 1972; Asa et al., 1998) and is an essential element of the fundamental ecological niche of *Alligator*. Alligators have even been reported to survive freezing conditions by remaining submerged in water slightly warmer than the surrounding air and utilizing a small breathing hole in the frozen surface of a pond (Brisbin et al., 1982; Hagan et al., 1983). This ‘icing response’ (Hagan et al., 1983) could help to explain the persistence of wild alligators in the northernmost reaches of their current range, as well as captive alligators that have been released outside of this range (e.g. Clarke, 1953; Barton, 1955). The latter notably includes an individual that survived in southern Pennsylvania for over five years (Barton, 1955). Based on all of these observations, it is evident that the thermal

tolerances and preferences of modern American alligators are dynamic and dependent on many variables.

The thermal tolerances and preferences of the other extant species of *Alligator*, the critically endangered Chinese Alligator (*Alligator sinensis*), are not fully known (Thorbjarnarson and Wang, 2010). There is a general dearth of life history data on the Chinese Alligator compared with the American Alligator, most likely because of its critically endangered status and rapidly dwindling wild population in Anhui Province (Wang et al., 1998; Thorbjarnarson and Wang, 1999, 2010; Thorbjarnarson et al., 2002; Chen et al., 2003; Zhang et al., 2009). Chinese alligators have been reported to enter hibernation in excavated burrows at temperatures below $\sim 18^{\circ}\text{C}$ and reemerge when temperatures reach $\sim 16^{\circ}\text{C}$ (Chen et al., 2003; Zhang et al., 2009), but no other temperature tolerance data are published. American alligators are much more abundant and easily obtained for research, which is why so much more is known about them compared to their Asiatic relatives. Because of the general lack of physiological thermal tolerance information and greatly reduced range of *A. sinensis*, it is more pertinent to use *A. mississippiensis* for SDMs.

Species Distribution Modeling

Species distribution modeling (SDM), sometimes called ecological/environmental niche or climate envelope modeling by different authors (e.g. Elith and Leathwick, 2009; Peterson and Sobéron, 2012; Sobéron, 2014), is an ecological modeling method used to predict a given organism's geographic distribution with respect to its fundamental (i.e.

Grinnellian) ecological niche, the combination of all the abiotic conditions within which the organism naturally occurs (Grinnell, 1917a, 1917b; Hutchinson, 1957, 1959; Peterson, 2001; Kearney and Porter, 2004; Sobéron, 2007, 2014; Holt, 2009; Sobéron and Nakamura, 2009). The first step in constructing a SDM is compiling species occurrence data, which can be obtained from museum collections, online databases, or direct field observations (Peterson, 2001; Sobéron and Peterson, 2005; Elith et al., 2006; Elith and Leathwick, 2009), and to reference these occurrences with latitude and longitude coordinates. Additionally, environmental parameters must be selected for use in a SDM. These are most commonly derived from global climate data sets generated from long-term (decadal to centennial) weather station records, averaged and interpolated over the Earth's land surface (e.g. New et al., 1999, 2000, 2002; Hijmans et al., 2005; Elith et al., 2006; Kriticos et al., 2012).

Once the species occurrence data and environmental variables have been collected, both datasets can be analyzed with a specialized SDM software program. Some of the most prevalent SDM programs use genetic matching algorithms, such as Genetic Algorithm for Rule-set Prediction (GARP; Stockwell and Noble, 1992; Stockwell and Peters, 1999), the principle of maximum entropy (MaxEnt; Phillips et al., 2004, 2006; Elith et al., 2011), and maximum likelihood analysis (MaxLike; Royle et al., 2012; Fitzpatrick et al., 2013) in order to generate a model prediction of the study organism's geographic distribution with respect to its climate envelope, or fundamental ecological niche (Elith and Leathwick, 2009). Several studies comparing GARP, MaxEnt, MaxLike, and other methods have achieved varying results (Elith et al., 2006; Phillips et al., 2006;

Peterson et al., 2007; Royle et al., 2012; Fitzpatrick et al., 2013). MaxEnt has been shown to generally outperform GARP and several other older programs and methods (Elith et al., 2006; Phillips et al., 2006; Pearson et al., 2007), although it has also been demonstrated to have some weaknesses compared to GARP (Peterson et al., 2007), as well as to newer programs, such as MaxLike (Royle et al., 2012; Fitzpatrick et al., 2013). Peterson et al. (2007) showed that MaxEnt can generate biased results (under- or over-predictions) based on differing probability thresholds and spatial biases in model inputs, whereas GARP was more efficient at predicting the entire distribution of a species beyond the spatial limits of the input data. Despite this, MaxEnt has performed well in generating SDMs for multiple extant organisms, including extant reptiles and amphibians (e.g. Kearney and Porter, 2004; Pearson et al., 2007; Franklin et al., 2008; Watling et al., 2012; Bucklin et al., 2013; Rödder et al., 2013; Frishkoff et al., 2015; Hipsey and Müller, 2015), and has also been used in various paleobiological applications.

The number of applications of SDMs to the fossil record has increased recently, although there are still many important issues to deal with and research avenues that have yet to be thoroughly explored (Svenning et al., 2011; Varela et al., 2011; Franklin et al., 2015). Most paleo-SDM studies have focused on the responses of terrestrial plants and vertebrates to Pleistocene glacial-interglacial cycles (e.g. Carstens and Richards, 2007; Waltari et al., 2007; Banks et al., 2008; Svenning et al., 2008; Waltari and Guralnick, 2009; Lawing and Polly, 2011; Polly and Eronen, 2011; McGuire and Davis, 2013; Rödder et al., 2013; Davis et al., 2014). Others have looked deeper into geologic time, investigating Neogene CGP horses (Maguire and Stigall, 2009) and Paleozoic marine

invertebrates (Stigall Rode and Lieberman, 2005; Stigall and Lieberman, 2006; Stigall, 2012). Time-averaging and taphonomic biases are omnipresent issues plaguing paleo-SDM and paleobiological research in general, inevitably leading to coarseness in spatial, temporal, abundance, and diversity data (e.g. Kowalewski, 1996; Roy et al., 1996; Kowalewski et al., 1998; Eronen et al., 2010a). SDMs and ecometric (i.e. functional trait-based) studies of modern organisms conducted over large geographic scales, however, have generated datasets more comparable to paleobiological evidence, although they often lack detail on finer spatial scales (Eronen et al., 2010a, 2010b, 2010c; Polly, 2010; Polly et al., 2011; Lawing et al., 2012; Polly and Head, 2015).

Researchers have employed fossil crocodylians as qualitative paleoclimate proxies for well over a century (e.g. Owen, 1850, Hibbard, 1960), but Markwick (1994, 1998) was the first to quantitatively assess the climatic controls on modern and fossil crocodylian distributions. Markwick (1994, 1998, 2007), and subsequently, Maguire and Stigall (2009), used a preferred temperature range of 25–35°C for the extant American Alligator to represent the preferred temperature range of all crown group crocodylians (i.e. Crocodylia). Markwick (1994) rationalized this based on the logic that *Alligator* occurs at higher latitudes than any other crocodylian taxon, thus providing a minimum temperature tolerance for the entire clade. This study seeks to further quantify constraints on the climatic parameters of living and fossil alligators in the Miocene CGP based on a SDM of the extant American Alligator in the southeastern USA.

Model Construction

In order to quantify the climatic constraints on the distribution of extant *Alligator* in North America, which can then be applied to the Miocene fossil record of the CGP, I constructed a SDM for the American Alligator. For species occurrence data, I sampled a geographic range map of the American Alligator (*Alligator mississippiensis*) representing the historical distribution of the taxon prior to significant anthropogenic influences, such as hunting and habitat alteration/loss (Crocodile Specialist Group, 1996). I sampled this range map (Fig. 1), available from the International Union for Conservation of Nature (IUCN), with uniform grid points spaced 25 km apart. I then extracted the latitude and longitude coordinates of these grid points using QGIS (QGIS Development Team, 2015). For my environmental parameter input data, I selected the 19 ‘current’ bioclimatic variables (Table 3) commonly used in SDMs, available from the University of California–Davis Worldclim online database (Hijmans et al., 2005). These variables were downloaded at 2.5 arc minute resolution and properly formatted for use with the Maximum Entropy (MaxEnt) modeling algorithm.

MaxEnt is a machine learning algorithm that operates by maximizing the spread of entropy (i.e. minimizing the amount of constraint) across a probability density, π , in a theoretical covariate space defined by the pixels of the study area and parameters of the model features (Phillips et al., 2004, 2006; Elith et al., 2011). The algorithm searches for the probability density (π) under which each feature (i.e. environmental variable) has the same mean by analyzing multiple types of model features (e.g. linear, quadratic) and comparing them to their expected empirical values, each measured by a regularization

constant, β (Phillips et al., 2006). This process allows the program to find the distribution of maximum entropy across the pixels of the study area in covariate space based on the constraints of the model features, which should, in turn, approximate the maximum geographic distribution of the study species based on the actual environmental variables characterizing that physical area (Phillips et al., 2004, 2006; Elith et al., 2011).

MaxEnt uses presence-only data and thus generates an unconditional model of a species' distribution; conditional models incorporate both presence and absence data (Phillips et al., 2006). It is also important to note that MaxEnt does not predict a species' actual likelihood of occurrence; instead, it calculates a habitat suitability index, which indirectly predicts a species' likelihood of occurrence based on the probability that its suitable habitat exists within the predicted geographic distribution (Phillips et al., 2006; Royle et al., 2012; Fitzpatrick et al., 2013). This index is displayed on maps generated for the species' predicted geographic distribution and has a scale ranging from 0–1 (0 indicates a 0% likelihood that a suitable habitat for the species exists based on the input parameters, whereas 1 indicates a 100% likelihood that a suitable habitat is present).

In addition to finding the distribution of maximum entropy and predicting the geographic distribution of the study species, MaxEnt also calculates the raw percentage of each environmental variable's contribution to the model. The program then randomly permutes the data and calculates a second percentage for each variable's contribution (Phillips et al., 2004, 2006). The regularized training gains of the environmental variables can also be subjected to a jackknifing procedure in MaxEnt. Jackknifing is a generalized resampling method frequently used in statistics that aims to estimate variance and/or

reduce bias in one or more datasets (Miller, 1974). A jackknife estimator is obtained by systematically omitting each observation from a sample dataset and calculating the mean of the remaining observations barring the omitted observation (Miller, 1974). In MaxEnt, jackknifing helps determine the importance of each individual variable, by systematically omitting each environmental variable and calculating a jackknife estimator that is then applied to all of the variables. The resulting jackknife scores show how important each individual variable is to the model prediction (Elith et al., 2011).

I conducted my modeling run in MaxEnt using the uniform 25 km grid points that I extracted from the IUCN *A. mississippiensis* range map (Crocodile Specialist Group, 1996) and the 19 bioclimatic variables that I obtained from the WorldClim database (Hijmans et al., 2005). My modeling run was conducted with the default (i.e. auto) model features selected in order to try to minimize potential overfitting of the input data and provide the best estimate for the geographic distribution of *A. mississippiensis* based on the input data. I also selected the jackknifing option to resample my resulting data and analyze each variable's individual importance to my model. Minimum, maximum, and average values for each bioclimatic variable within the resulting predicted model distribution (Table 3) were obtained by selecting and extracting all of the 50 km grid points of Polly (2010) within my predicted model distribution using QGIS and analyzing these points in the program Mathematica.

Model Prediction

Results from MaxEnt indicate that the predicted model distribution generated from the input data (Figs. 11 and 12) is a good approximation of the actual fundamental ecological niche of the American Alligator. This is primarily supported by an area under the receiver operating curve (AUC) value of 0.91. The AUC is a way of evaluating the performance of a model independent of threshold choice, which should allow for direct comparisons between different modeling approaches (Phillips et al., 2006; Elith et al., 2011). There have been some criticisms of the use of the AUC in SDMs (e.g. Allouche et al., 2006; Peterson et al., 2007, 2008; Lobo et al., 2008), but these are not addressed here.

A receiver operating curve (ROC) is defined by a collection of samples representing both positive and negative points, which are ordered by a machine classifier as belonging to different classes, based on a given threshold value (Phillips et al., 2006). In ROC analysis with respect to SDMs, positive points are represented by species presence data, and negative points are represented by species absence data; for unconditional models, randomly chosen background points without presence data are substituted for absence data (Phillips et al., 2004, 2006). Following the classification of positive and negative points, the true positive rate (sensitivity: absence of omission error) and false positive rate ($1 - \text{specificity}$: commission error) can be calculated; when both the true and false positive rates are plotted across all thresholds as the dependent and independent variables, respectively, the ROC is generated (Phillips et al., 2006). The area under this curve, or AUC, is taken to be the probability that all positive and negative points were correctly ordered by the machine classifier, with a completely random value

of 0.5 (50% probability that the classifier correctly ordered all of the positive and negative points around the model threshold) and an ideal value of 1 (100% probability that the classifier correctly ordered all of the positive and negative points around the model threshold); therefore, an AUC value close to 1 signifies a robust model, although the maximum AUC value for a species with a large geographic distribution will be less than 1 because of the unconditional nature of the model (Phillips et al., 2004, 2006).

The numerical and statistical results of the model are collated along with the 19 bioclimatic variables and their abbreviations in Table 3. The raw percent contributions, permuted importance percent contributions, and jackknifed regularized training gains of all 19 bioclimatic variables used are shown in Figure 13. Overall, variable 17 (driest quarter precipitation [DQP]), contributed the most (~58% contribution and permuted ~29% contribution) to the model prediction for *A. mississippiensis*. DQP also had the highest jackknifed regularized training gain (= 1.291) of all 19 variables, which provides further support that it is the most important climatic variable associated with the modern geographic distribution of *Alligator*. DQP values range from ~115–443 mm, with an average value of ~239 mm. In the southeastern USA, where *Alligator* lives today, the dry season typically corresponds to the coldest part of the year. *Alligator* requires the presence of water in order to help buffer its internal body temperature from both hot and cold extremes, so its thermoregulatory efficiency will depend on a source of permanent available surface water. Markwick (1994, 1998) states that precipitation does not necessarily reflect the amount of available surface water in a given area, which is true for some regions. However, because precipitation is such an important contributor to the

amount of available surface water within the southeastern USA (e.g. this region is not a desert with a large permanent river, such as the Nile River example provided by Markwick [1994]), it is reasonable to propose that precipitation approximates the amount of surface water available to alligators.

While they had low raw and permuted importance percent contributions to the model, driest month precipitation (DMP), mean annual precipitation (MAP), and coldest quarter precipitation (CQP) all had high jackknifed regularized training gain values, suggesting that these variables also play a major role in influencing the distribution of *Alligator*. DMP and CQP are autocorrelated with DQP, but MAP is an independent measure. MAP within the modeled *Alligator* distribution ranges from ~720–1840 mm, with an average value of ~1250 mm. This indicates, unsurprisingly, that *Alligator* prefers wetter environments, which allow for more effective thermoregulation under a range of different temperatures and conditions (see above).

Warmest month maximum temperature (WMT_{Max}) had the second greatest raw percent contribution to the model (~11%), but a lower permuted contribution (~3%) than temperature seasonality ($T_{Seasonality}$; ~36%). WMT_{Max} values range from ~22–36°C, with an average value of ~33°C. These values are consistent with the maximum tolerated temperature of *A. mississippiensis* measured experimentally (~33–38°C). *Alligator* cannot occur in areas where the hottest temperatures during the year exceed their critical thermal maximum. Mean annual temperature (MAT) and coldest quarter minimum temperature (CQT_{Min}) did not have large percent contributions to the model prediction but had the next greatest jackknifed regularized training gain values following the precipitation

variables discussed above (DQP>DMP>CQP>MAP). MAT values ranged from ~8–24°C, with an average value of ~16°C. These values show that *Alligator* generally lives in much cooler conditions than previously thought and discredit the continued use of a 25–35°C temperature range proposed by Markwick (1998, 2007) and subsequently used by others (e.g. Maguire and Stigall, 2009) for *Alligator* presence. Instead, *Alligator* presence indicates a MAT range of ~8–24°C, whose upper end member can be extended to ~33°C for WMT_{Max} (see above).

This conclusion differs from that of Markwick (1994, 1998, 2007), who concluded that the coldest month minimum temperature (CMMT; abbreviated as CMT_{Min} herein) is the main climatic variable constraining *Alligator* distributions. A CMT_{Min} value of 5.5°C has been used as the *de facto* limiting climatic factor for ‘crocodilian’ occurrence both in the modern (e.g. Markwick, 2007) and fossil realms (e.g. Shunk et al., 2006), since first proposed by Markwick (1994, 1998). In this MaxEnt analysis, however, CMT_{Min} never contributed substantially to the model prediction (see Fig. 13). The values for CMT_{Min} ranged from -7.9–15.7°C throughout the predicted distribution, with an average value of -0.5°C. This average value is 5° less than the CMT_{Min} value originally put forth by Markwick (1998) and is lower than the measured critical minimum temperature for *A. mississippiensis* (~4–8°C). However, considering the American Alligator’s adaptations to surviving freezing temperatures (see Introduction of Chapter 3), the low CMT_{Min} values predicted by my SDM still fall within the realm of possibility.

The major temperature and precipitation constraints for extant *Alligator* can be approximated using the comprehensive SDM results. The presence of alligators indicates:

(1) MAP amounts ranging from ~720–1840 mm, with >115 mm of precipitation during the dry season; and (2) MATs ranging from ~8–24°C, with temperatures <~33–36°C during the warmest month of the year and ~6.6°C during the coldest quarter of the year. $T_{\text{Seasonality}}$, a unitless measure of temperature variation throughout the year (similar to and often autocorrelated with isothermality, or temperature ‘evenness’), may also play a role in constraining the distribution of *Alligator*, as supported by its large permutation importance percent contribution to the model prediction (~36%). This metric is more difficult to apply to the fossil record, however, because we do not yet have a firm grasp on seasonality in deep time (especially in non-analog paleoenvironments and ecosystems; e.g. Williams and Jackson, 2007; Williams et al., 2007; Fitzpatrick and Hargrove, 2009). Generally, alligators tend to proliferate in areas with lower $T_{\text{Seasonality}}$, because seasonal temperature differences are less extreme.

Figure 11 shows a geographic map of the world overlain with the habitat suitability index for *A. mississippiensis* as predicted by the SDM. As expected, habitat suitability index values are highest in the southeastern USA, where the training data were gathered. Interestingly, though, habitat suitability index values are also high in eastern Asia, in the precise region that *A. sinensis* occupies today in the Anhui Province of China (Thorbjarnarson and Wang, 1999; 2010). The model prediction that a suitable habitat for American alligators exists in China, where Chinese alligators occur today, provides robust support for genus-level ecological niche conservatism. This is further strengthened by a latitudinal reflection of the predicted distribution of suitable *A. mississippiensis* habitats in the southern hemisphere at roughly the same latitudes as *Alligator* occurs in

the northern hemisphere. Figure 12 provides a more detailed perspective of the model predictions in the eastern USA. The model predicts that *Alligator* could theoretically inhabit areas in states north of their current range, most notably including parts of Tennessee, Kentucky, and southernmost Indiana, Ohio, and Pennsylvania. The presence of Mio-Pliocene fossil alligators in eastern Tennessee (Shunk et al., 2006) and historical reports of alligators living outside their ‘normal’ range (e.g. Barton, 1955) may strengthen the model’s somewhat unexpected results. In these northern regions, it is likely that biotic interactions (particularly anthropogenic influences) are limiting the distributions of alligators, even if a suitable habitat exists (based solely on the abiotic bioclimatic variables).

A note of caution with regards to interpreting these results: MaxEnt can overfit the training data to the background environmental parameters (Phillips et al., 2006; Peterson et al., 2007), especially for geographically widespread taxa found across a variety of overlapping climatic regimes (e.g. Franklin et al., 2008). Therefore, these results may be an over-prediction of the maximum habitable area of *A. mississippiensis*, and alligators might not actually be able to occur as far north as the model predicts.

Neogene Central Great Plains Paleoclimate

During the late Neogene (~12.5–3 Ma), the CGP and several other major regions around the world witnessed dramatic changes in climate, vegetation and, consequently, ecosystem structure (Janis, 1989, 1993; Cerling et al., 1993, 1997; MacFadden, 1997; Jacobs et al., 1999; Cerling and Ehleringer, 2000; Janis et al., 2002, 2004; Edwards et al.,

2010; Strömberg and McInerney, 2011). An impressive combination of paleoclimatic and paleoenvironmental proxies for the CGP provides strong evidence for this profound ecosystem shift, but quantitative proxy estimates vary (Table 1).

Prior Reconstructions of Neogene Central Great Plains Paleoclimate

Estimates of MAT and MAP for the CGP during the early Miocene range from $>\sim 17^{\circ}\text{C}$ and $\sim 1000\text{--}1900$ mm, respectively (Axelrod, 1985; Leopold and Denton, 1987; Janis et al., 2004; Fraser and Theodor, 2012; Polly and Head, 2015). By the middle to late Miocene (Barstovian–Clarendonian; $\sim 16\text{--}13$ Ma), MAT and MAP are estimated to have dropped to $<\sim 17^{\circ}\text{C}$ and $\sim 750\text{--}1200$ mm, respectively (Axelrod, 1985; Leopold and Denton, 1987; Retallack, 1997, 2001; Janis et al., 2004; Fox and Koch, 2003, 2004; Pound et al., 2011, 2012; Fox et al., 2012; Fraser and Theodor, 2012; Polly and Head, 2015). Marked changes in the mammalian faunas of the CGP occurred during this interval, including a shift to a more open habitat-adapted ‘Clarendonian chronofauna’ dominated by horses, rather than ruminant artiodactyls (Janis, 1989, 1993; MacFadden, 1997; Janis et al., 2002, 2004; Passey et al., 2002; Tedford et al., 2004). There were also distinct changes in the herpetofaunas; at the end of the Barstovian (~ 12.5 Ma), several key reptile (*Rhineura*, *Gerrhonotus*, *Micrurus*) and amphibian (*Siren*) taxa exited the CGP fossil record, most likely because of changes in regional temperature and precipitation regimes (Jacisin et al., 2015).

The Clarendonian-Hemphillian faunal transition ($\sim 11\text{--}8$ Ma) witnessed even more drastic faunal and floral changes, as well as a large drop in $\delta^{18}\text{O}$ isotopic values throughout the CGP (Passey et al., 2002). MAT is estimated to have decreased to $<\sim 13^{\circ}\text{C}$

during the early Hemphillian (~9–7 Ma; Fox and Koch, 2003, 2004; Pound et al., 2011, 2012), and MAP likely dropped to ~250–1000 mm (Axelrod, 1985; Leopold and Denton, 1987; Retallack, 1997, 2001, 2007; Janis et al., 2004; Fraser and Theodor, 2012; Polly and Head, 2015). C₄ biomass in the CGP increased dramatically at ~6.5 Ma, as evident from pedogenic and biogenic stable $\delta^{13}\text{C}$ isotopic records (Passey et al., 2002; Fox and Koch, 2003, 2004; Fox et al., 2012; Kita et al., 2014). The plant phytolith record also supports an increasing C₄ component and opening of CGP ecosystems, especially from ~8–2 Ma onward (Strömberg, 2002, 2004, 2005; Strömberg and McInerney, 2011; McInerney et al., 2011). Water-stressed C₃ plants and grasses, however, were probably dominant in the floras of the CGP during the Clarendonian–Hemphillian NALMAs, implying increasing regional aridity and/or seasonality during the late Neogene (Passey et al., 2002; Fox and Koch, 2003, 2004; Fox et al., 2012; Kita et al., 2014). C₃ grass (Gramineae/Poaceae) macrofossils have been recovered from several sites in the late Miocene Ash Hollow Formation of Nebraska (Voorhies and Thomasson, 1979; Thomasson, 2005), suggesting that C₃ grasslands may have been quite widespread during the Clarendonian NALMA. This is also supported by the phytolith record (Strömberg, 2002, 2004; Strömberg and McInerney, 2011; McInerney et al., 2011).

By the late Hemphillian NALMA (~6–4 Ma), MAT had likely decreased to ~8–10°C (Fox and Koch, 2003, 2004), and MAP had fallen to ~250–600 mm (Axelrod, 1985; Leopold and Denton, 1987; Retallack, 1997, 2001, 2007). C₄ plants became dominant in the CGP floras at this point, as reflected in the Pliocene floral, faunal, and isotopic records (Passey et al., 2002; Fox and Koch, 2003, 2004; Fox et al., 2012; Kita et al.,

2014; Strömberg, 2002, 2004, 2005; Strömberg and McInerney, 2011; McInerney et al., 2011).

Passey et al. (2002) very briefly mention the disappearance of ‘crocodilians’ from the CGP as an indicator of paleoclimatic and paleoenvironmental change, although they, like Maguire and Stigall (2009), utilized the 25–35°C range presented by Markwick (1994, 1998, 2007) as their paleotemperature constraint. The $\delta^{18}\text{O}$ isotopic results that Passey et al. (2002) obtained suggest cooler conditions in the early Hemphillian, which agrees with the southward extirpation of crocodylians from the CGP, as well as with large-scale climatic trends during the late Miocene (Fig. 14; Zachos et al., 2001, 2008).

Application of *Alligator* Species Distribution Model to Reconstruct Neogene Paleoclimate in the Central Great Plains

The extant *Alligator* SDM and the spatiotemporal distributions of fossil alligators in the CGP can be used to quantitatively constrain the temperature and precipitation histories of the region during the Neogene (Fig. 14). This reconstruction is predicated on the principle of ecological niche conservatism (NC) for the genus *Alligator*. NC states that the fundamental ecological niche of a given taxon is conserved through time (Wiens and Graham, 2005; Wiens et al., 2010; Peterson, 2011; Peterson et al., 1999). The principle has been demonstrated in several clades at the species level and above (e.g. Hawkins et al., 2006; Hadly et al., 2009; Buckley et al., 2010; Kozak and Wiens, 2010; Olalla-Tárraga et al., 2011). Ideally, NC needs to be tested, rather than assumed, for closely related taxa (e.g. Knouft et al., 2006; Losos, 2008). SDMs are a robust method for

the comparison of niches to test for NC in a small number of phylogenetically close taxa (Peterson et al., 1999; Warren et al., 2008; Wiens et al., 2010). Since *Alligator* is only represented by two extant species, this method is the most appropriate. The results of the SDM in this study indicate that the climate envelope of the derived American Alligator is also applicable to the more basal Chinese Alligator. The prediction that *A. mississippiensis* could occupy both the same geographic and climatic space as *A. sinensis* provides robust support for NC in *Alligator*, which can be applied to the fossil record and extinct species of *Alligator* in North America and Asia.

The SDM results provide constraints for several temperature and precipitation variables in the CGP during the Neogene, especially if seasonality was more pronounced in the late Neogene, as some have suggested (Passey et al., 2002; Fox and Koch, 2003, 2004). *Alligator* can occur in locations with a MAT of ~8–25°C, and an average MAT of ~16°C. If MAT decreased to ~8–10°C or lower during the late Miocene (early Hemphillian; ~9–6 Ma), then alligators would likely have started to track their preferred habitat as it moved southwards during this time interval (Fig. 14). This is supported by the distribution of fossil alligators in the CGP: alligators are absent from Nebraska after the Clarendonian and appear further south in Kansas, Oklahoma, and Texas during the early Hemphillian (Fig. 1). *Alligator* also only occupies areas with a MAP of ~750–1900 mm, with an average of ~1250 mm. These new constraints largely agree with the MAP estimates from other proxies; earlier MAP estimates range from as high as ~1900 mm in the early Miocene (when *Alligator* reappeared in the CGP after its Oligocene hiatus) to as low as ~250 mm in the late Miocene (when *Alligator* was extirpated from the CGP). The

SDM-borne constraints generated in this study suggest that MAP fell below 720 mm after ~9 Ma, forcing the extirpation of alligators from Nebraska. The presence of alligators in Kansas, Oklahoma, and Texas suggests that MAP did not fall below 720 mm during the early Hemphillian in the southern CGP. Their absence in the ensuing late Hemphillian implies that the CGP had become too arid and cool by that time, with values below the 720 mm and 8°C MAP and MAT thresholds for *Alligator*, respectively. Isothermality, or temperature ‘evenness’ during the year (Hijmans et al., 2005), also may have decreased below a certain threshold, leading to greater swings in temperature that may be indicative of increased seasonality.

If seasonality did become more prevalent in the CGP during the Late Neogene, *Alligator* could be further utilized as a quantitative proxy, because of its strong relationships to seasonal temperature and precipitation extremes. The SDM indicates that DQP is by far the most important bioclimatic variable governing the distribution of extant *Alligator* in North America, because it contributes ~58% to the model prediction and has the highest jackknifed regularized training gain score (Table 3). If a distinct dry season occurred in the CGP during the late Neogene, and it did not receive sufficient precipitation (>115 mm), then alligators would have struggled to maintain a foothold in the region.

The *Alligator* temperature and precipitation estimates largely complement and supplement the available paleoclimate proxies for the Neogene CGP (Table 1). However, they differ considerably from the MAP estimates generated from hypsodonty indices (Janis et al., 2004; Fraser and Theodor, 2012; Polly and Head, 2015). In general, the

hypso-donty-borne MAP estimates appear to be high; the values for the latest Miocene are still >1000 mm (Janis et al., 2004; Fraser and Theodor, 2012; Polly and Head, 2015), which conflicts with inferences based on the absence of alligators (<720 mm). The evolution of hypso-donty has been shown to lag actual grassland propagation and may be a better proxy for environmental dust and grit than vegetation type (Strömberg, 2002, 2006; Strömberg et al., 2013), although it is still strongly correlated with MAP, which regulates dust production (Damuth and Fortelius, 2001; Fortelius et al., 2002). The *Alligator*-derived climate estimates also differ from Retallack's (1997, 2001, 2007) paleosol MAP proxy estimates, which appear to be too low (<750 mm in the middle Miocene to ~250–500 mm in the late Miocene/early Pliocene). *Alligator* presence suggests a MAP of ~720–1840 mm, and the plant macrofossil record suggests a MAP of ~800–1000 mm during the middle to late Miocene (Axelrod, 1985; Leopold and Denton, 1987; Pound et al., 2011, 2012). MAP fell below ~720 mm in the latest Miocene and earliest Pliocene, but probably not to the ~250–500 mm level estimated by Retallack (1997, 2001, 2007) based on the plant records (Axelrod, 1985; Leopold and Denton, 1987).

It is important to note that there are no known *Alligator* records from north of Nebraska during any part of the Neogene. This distribution of Miocene fossil localities could indicate that Nebraska may have been close to the northern extent of the *Alligator* range during the Miocene and, consequently, the northern extent of the climatic conditions that meet the minimum temperature and precipitation requirements for *Alligator* presence (see above). This may also be the case for late Miocene localities in

Kansas, Oklahoma, and Texas, which represent the northern extremes for *Alligator* during the Hemphillian. If this is correct, then these northernmost extents of climatic conditions conducive to alligators could be used in concert with other proxies to geographically hindcast paleoclimate regimes in the CGP during the Miocene.

Conclusions

Globally during the late Miocene, crocodylians (including *Alligator*) underwent a southward latitudinal range shift concurrent with northern hemisphere glaciation, aridification, and the spread of grassland ecosystems (Mannion et al., 2015). The results derived here based on a SDM for the extant American Alligator enable the quantification of temperature and precipitation constraints on the changing *Alligator* distributions through geologic time. These estimates and the trends they suggest, based on fossil *Alligator* presence and absence, in the CGP during the Neogene agree well with paleoclimate estimates generated from other independent proxies. Therefore, *Alligator* is a useful paleoclimatic indicator that can be used in the future to complement other existing methods of paleoclimatic reconstruction to help constrain temperature and precipitation histories during time intervals for which alligators were present.

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TABLE 1. Published Neogene Central Great Plains Paleoclimatic and Paleoenvironmental Proxies.

*Mean annual temperature (MAT) and mean annual precipitation (MAP) estimate ranges, as well as paleoenvironmental changes, are given from the beginning to the end of the time interval analyzed in each reference or set of references.

Reference(s)	Method(s)	Time Interval	MAT Estimate (°C)	MAP Estimate (mm)	Paleoenvironmental Change
Retallack (1997, 2001, 2007)	Paleosol horizon depth analysis	Middle Miocene–Early Pliocene	—	*750–250	Short-grass prairie transitioned to tall-grass prairie and aridity increased after ~10 Ma
Fox and Koch (2003, 2004); Fox et al. (2012)	Stable carbon and oxygen isotope ratios of pedogenic carbonates	Late Miocene–Early Pliocene	*17–8	—	C ₄ biomass increased significantly at ~6.5 Ma
Strömberg (2002, 2004, 2005); Strömberg and McInerney (2011); McInerney et al. (2011)	Fossil plant phytolith assemblage analysis and stable isotope ratios of phytoliths	Early Miocene–Late Pliocene	—	—	Open or mixed C ₃ woodland savannas transitioned to open C ₄ grasslands with few trees in late Miocene (~8–5 Ma)
Axelrod (1985); Leopold and Denton (1987)	Fossil macroflora assemblage analysis	Early Miocene–Early Pliocene	—	*1000–600	Open or mixed C ₃ woodland savannas transitioned to open C ₄ grasslands with few trees from ~7–5 Ma
Pound et al. (2011, 2012)	Fossil macroflora leaf margin analysis and modeling	Late Miocene	10–15	800–1000	Temperate broadleaved savanna grassland prevalent in late Miocene (~12–7 Ma)

Passey et al. (2002); Fox and Fisher (2004); Kita et al. (2014)	Stable carbon and oxygen isotope ratios of fossil mammal tooth enamel carbonate	Middle Miocene–Early Pliocene	—	—	Water-stressed C ₃ plants and grasslands were common during the late Miocene; C ₄ grasslands expanded in the Hemphillian (~6.5–5 Ma)
Janis (1989, 1993); Janis et al. (2002, 2004); Strömberg (2006); Fraser and Theodor (2012); Polly and Head (2015)	Fossil mammal hypsodonty (tooth crown height) and/or digestive physiology	Early Miocene–Early Pliocene	—	*1800–1000	Wet, open or mixed C ₃ woodland savannas transitioned to drier, open C ₄ grasslands after ~7 Ma
Maguire and Stigall (2009)	Fossil horse ecological niche modeling	Middle Miocene–Early Pliocene	—	—	Vegetation change from cooling and drying caused habitat fragmentation (~9 Ma)
This Study	<i>Alligator</i> species distribution modeling	Early Miocene–Late Miocene	*24–<8	*~1840–<720	Temperature decreased, aridity increased, and dry season became cooler and drier in late Miocene (~9 Ma)

TABLE 2. Miocene Central Great Plains Fossil *Alligator* Occurrence Data.

Approximate NALMA ages for geologic formations and localities were compiled from Tedford et al. (2004), the Paleobiology Database, and the MIOMAP database (Carrasco et al., 2005). Latitude and longitude coordinates for each locality were obtained from the UNSM collection and Google Earth, Paleobiology Database, and/or MIOMAP database.

State	Geologic Formation	Locality	Biochron (NALMA)	Age (~Ma)	Collection(s)	Latitude (°N)	Longitude (°W)
Nebraska	Runningwater	Cr-23 = <i>Aletomeryx</i> Quarry	Hemingfordian 1	19–17.5	AMNH, FMNH, UNSM	42.75	-102.03
Nebraska	Runningwater	Ron Brown Quarry	Hemingfordian 1	19–17.5	AMNH	42.51	-103.72
Nebraska	Sheep Creek	Sx-128	Hemingfordian 2	17.5–16	UNSM	42.17	-103.80
Nebraska	Sheep Creek	Ginn Quarry	Hemingfordian 2	17.5–16	AMNH	42.39	-102.47
Nebraska	Sheep Creek	Thompson Quarry	Hemingfordian 2	17.5–16	AMNH	42.20	-103.78
Nebraska	Olcott	Trojan Quarry	Barstovian 1	16–14.8	AMNH	42.16	-103.72
Nebraska	Olcott	Sinclair Quarry	Barstovian 1	16–14.8	AMNH, UNSM	42.16	-103.73
Texas	Fleming	Trinity River	Barstovian 1	16–14.8	AMNH, SMPSMU	30.40	-95.03
Nebraska	?Fort Randall	Kx-133	Barstovian 2	14.8–12.5	UNSM	42.82	-97.64
Nebraska	?Fort Randall	Kx-134	Barstovian 2	14.8–12.5	UNSM	42.82	-97.66

Nebraska	Valentine	Cr-13	Barstovian 2	14.8–12.5	UNSM	42.83	-100.52
Nebraska	Valentine	Cr-114	Barstovian 2	14.8–12.5	UNSM	42.83	-100.52
Nebraska	Valentine	Kp-101	Barstovian 2	14.8–12.5	UNSM	42.80	-100.05
Nebraska	Valentine	Kx-110	Barstovian 2	14.8–12.5	UNSM	42.83	-97.64
Nebraska	Valentine	Kx-120	Barstovian 2	14.8–12.5	UNSM	42.48	-98.10
Nebraska	Valentine	Kx-168	Barstovian 2	14.8–12.5	UNSM	42.52	-98.19
Nebraska	Valentine	Wt-102	Barstovian 2	14.8–12.5	UNSM	40.03	-98.51
Nebraska	Ash Hollow	Ap-105	Clarendonian 2	12–10	UNSM	42.38	-98.12
Nebraska	Ash Hollow	Kilpatrick Pasture Quarry	Clarendonian 2	12–10	AMNH	42.10	-103.43
Oklahoma	Laverne	Beaver Quarry	Clarendonian 2	12–10	OMNH	36.45	-100.14
Texas	Ogallala	Spade Flats	Clarendonian 2	12–10	AMNH	35.00	-100.80
Nebraska	Ash Hollow	Bw-105	Clarendonian 3	10–9	UNSM	42.67	-99.77
Nebraska	Ash Hollow	Bw-106	Clarendonian 3	10–9	UNSM	42.79	-100.03
Nebraska	Ash Hollow	Bw-123	Clarendonian 3	10–9	UNSM	42.58	-100.10
Nebraska	Ash Hollow	Sh-107	Clarendonian 3	10–9	UNSM	42.80	-102.42

Nebraska	Ash Hollow	George Sawyer Ranch	Clarendonian 3	10–9	AMNH	42.69	-100.85
Kansas	Ogallala	Beckerdite Local Fauna	Hemphillian 2	7.5–6.8	FHSM	37.26	-99.83
Texas	Ogallala	Box T Ranch	Hemphillian 2	7.5–6.8	AMNH	36.10	-100.10
Oklahoma	Ogallala	Optima/Guymon	Hemphillian 3	6.8–5.8	OMNH	36.75	-101.37

TABLE 3. Bioclimatic Variables Used in Species Distribution Modeling and Resulting Numerical and Statistical Data.

Bioclimatic variables, generated by Hijmans et al. (2005), were obtained from the WorldClim online database. Abbreviations for bioclimatic variables shown in this table are used throughout the text. Minimum, maximum, and average values for each variable within my predicted model distribution are denoted in the ‘Min.’, ‘Max.’, and ‘Avg.’ columns, respectively.

Variable	Abbreviation and (Unit)	Contribution to Model (%)	Permutation Importance (%)	Jackknifed Regularized Training Gain	Min. Value	Max. Value	Avg. Value
Mean Annual Temperature	MAT (°C)	5.2	2.1	1.1087	8°C	24.2°C	16.4°C
Mean Diurnal Temperature Range	MDTR (°C)	2.5	0.8	0.7201	7°C	14.7°C	12.8°C
Isothermality	T _{Isothermality}	4.2	8.9	1.0808	31%	38.5%	34%
Temperature Seasonality	T _{Seasonality}	9.5	35.5	0.9538	308.6	929.8	732.6
Warmest Month Maximum Temperature	WMT _{Max} (°C)	10.6	2.6	0.9512	22.5°C	35.9°C	32.5°C
Coldest Month Minimum Temperature	CMT _{Min} (°C)	0	0.8	0.9800	-7.9°C	15.7°C	-0.5°C
Annual Temperature Range	ATR (°C)	0.1	0	0.7254	15.7°C	40.1°C	33°C

Wettest Quarter Mean Temperature	WeQMT (°C)	0	0.1	0.2424	3.8°C	27.7°C	18.6°C
Driest Quarter Mean Temperature	DQMT (°C)	0	0	0.6581	-1.5°C	28.3°C	15.1°C
Warmest Quarter Mean Temperature	WaQMT (°C)	0.1	3.4	0.9236	16.7°C	28.7°C	25.5°C
Coldest Quarter Mean Temperature	CQMT (°C)	0.2	4.3	1.0923	-1.5°C	20°C	6.6°C
Mean Annual Precipitation	MAP (mm)	0.1	1.5	1.1483	720 mm	1841 mm	1249 mm
Wettest Month Precipitation	WMP (mm)	3.4	3.8	1.0886	98 mm	245 mm	143.8 mm
Driest Month Precipitation	DMP (mm)	5.6	3.4	1.2580	30 mm	138 mm	69.7 mm
Precipitation Seasonality	P _{Seasonality}	0	0	0.7656	7%	66%	21.4%
Wettest Quarter Precipitation	WeQP (mm)	0.5	1.2	1.0550	241 mm	646 mm	389.4 mm
Driest Quarter Precipitation	DQP (mm)	57.9	29.1	1.2909	115 mm	443 mm	238.8 mm
Warmest Quarter Precipitation	WaQP (mm)	0	2.5	0.7456	175 mm	612 mm	333.2 mm
Coldest Quarter Precipitation	CQP (mm)	0	0	1.2060	115 mm	467 mm	294.4 mm

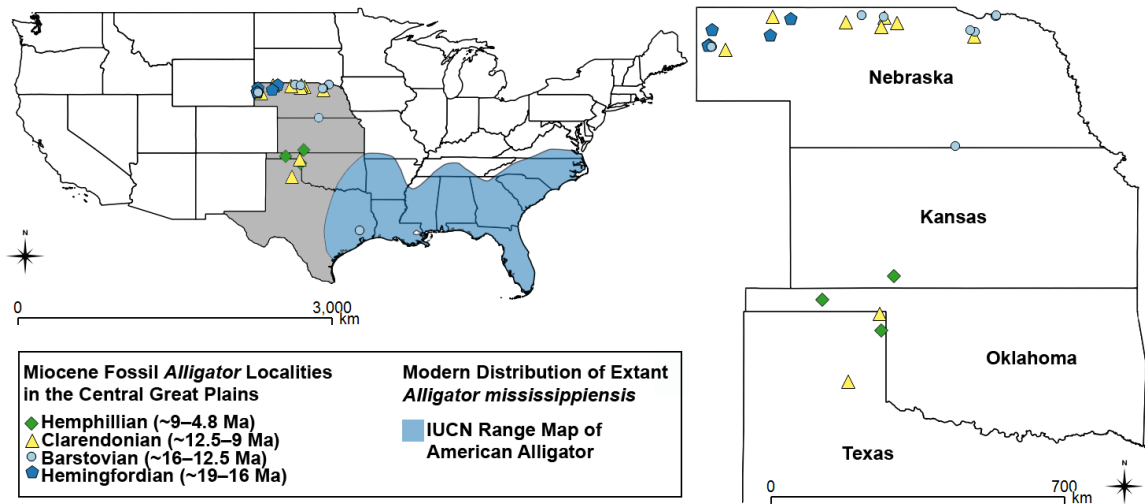


FIGURE 1. Map of the continental USA with the Central Great Plains states (Nebraska, Kansas, Oklahoma, and Texas) shaded in gray and the IUCN American Alligator (*Alligator mississippiensis*) distribution (Crocodile Specialist Group, 1996) shaded in blue. The inset on the right shows the distribution of fossil *Alligator* localities in the Central Great Plains during the Neogene, binned by North American land mammal ages (NALMAs; Tedford et al., 2004).

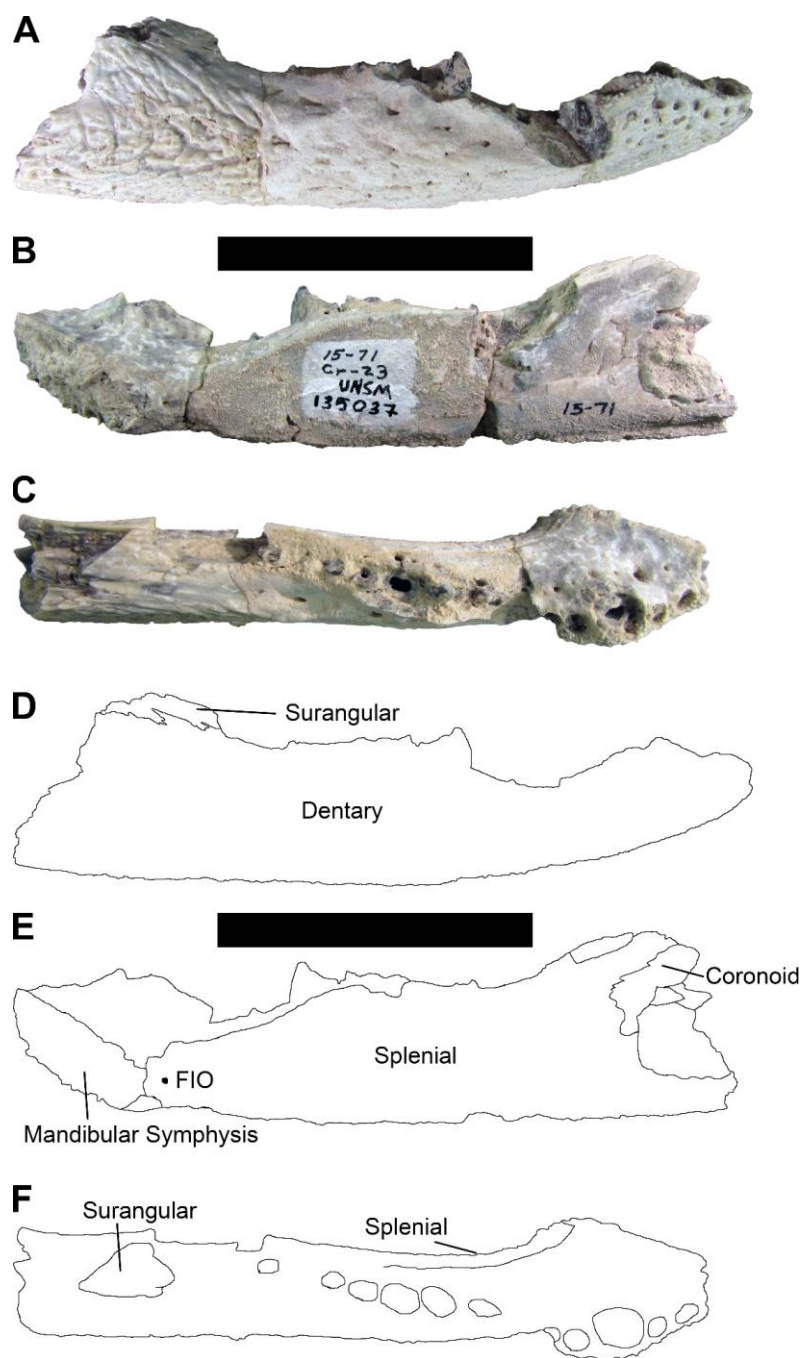


FIGURE 2. UNSM 135037, incomplete right mandible and sketches: (A) lateral aspect; (B) medial aspect; (C) dorsal aspect; (D) sketch of lateral aspect; (E) sketch of medial aspect; (F) sketch of dorsal aspect. Scale bars = 5 cm. **Abbreviations:** FIO, anterior foramen intermandibularis oralis opening.

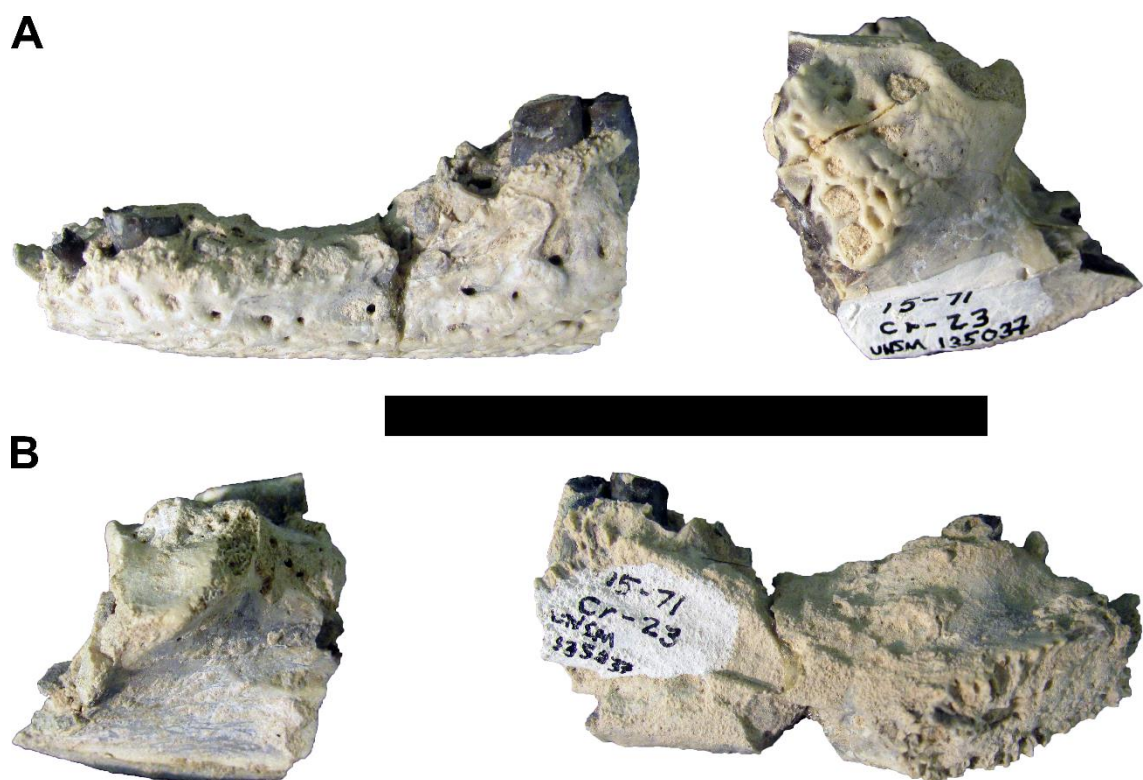


FIGURE 3. UNSM 135037, anterior and posterior left mandibular fragments: (A) lateral aspect; (B) medial aspect. Scale bar = 5 cm.

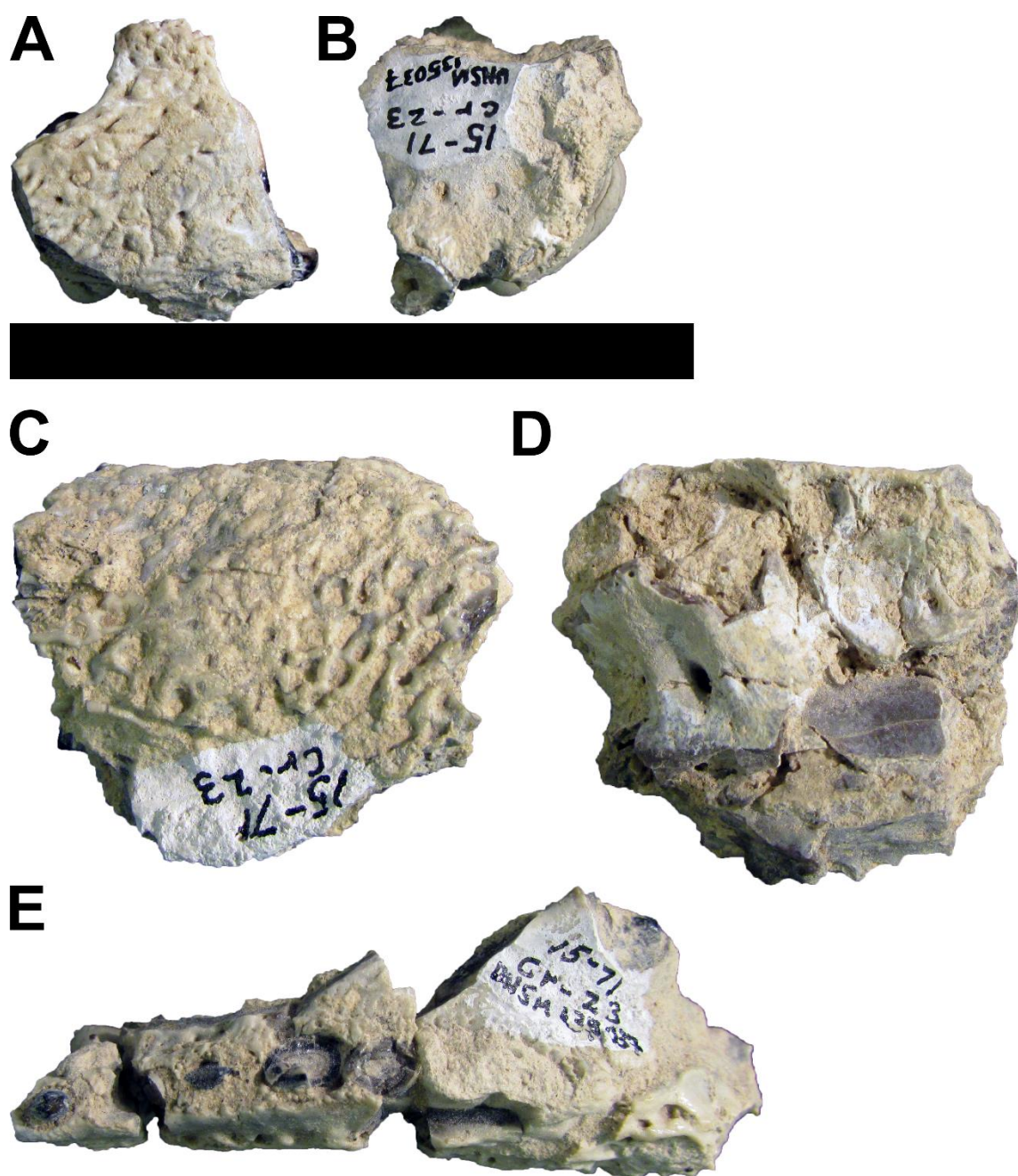


FIGURE 4. UNSM 135037, ?premaxillary and maxillary fragments: partial ?left ?premaxilla in (A) dorsal and (B) ventral aspects; anterior left maxilla fragment in (C) dorsal and (D) ventral aspects; posterior left maxilla fragment with attached partial left ectopterygoid in ventral aspect (E). Scale bar = 5 cm.



FIGURE 5. UNSM 135036, prefrontal and ulna: (A) posterior right prefrontal fragment in dorsal aspect and (B) partial proximal right ulna in ?anterior aspect. Scale bar = 5 cm.

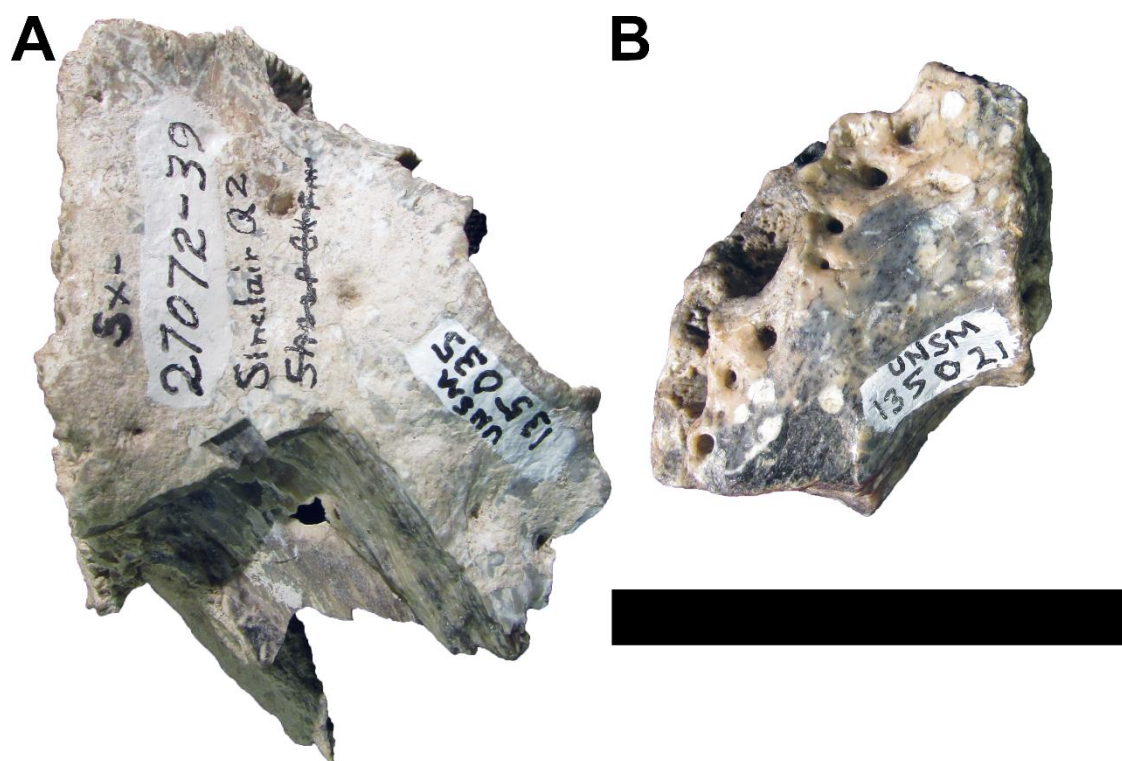


FIGURE 6. Anterior dentary fragments: (A) UNSM 135035, right dentary; (B) UNSM 135021, left dentary. Both are shown in dorsal aspect. Scale bar = 5 cm.

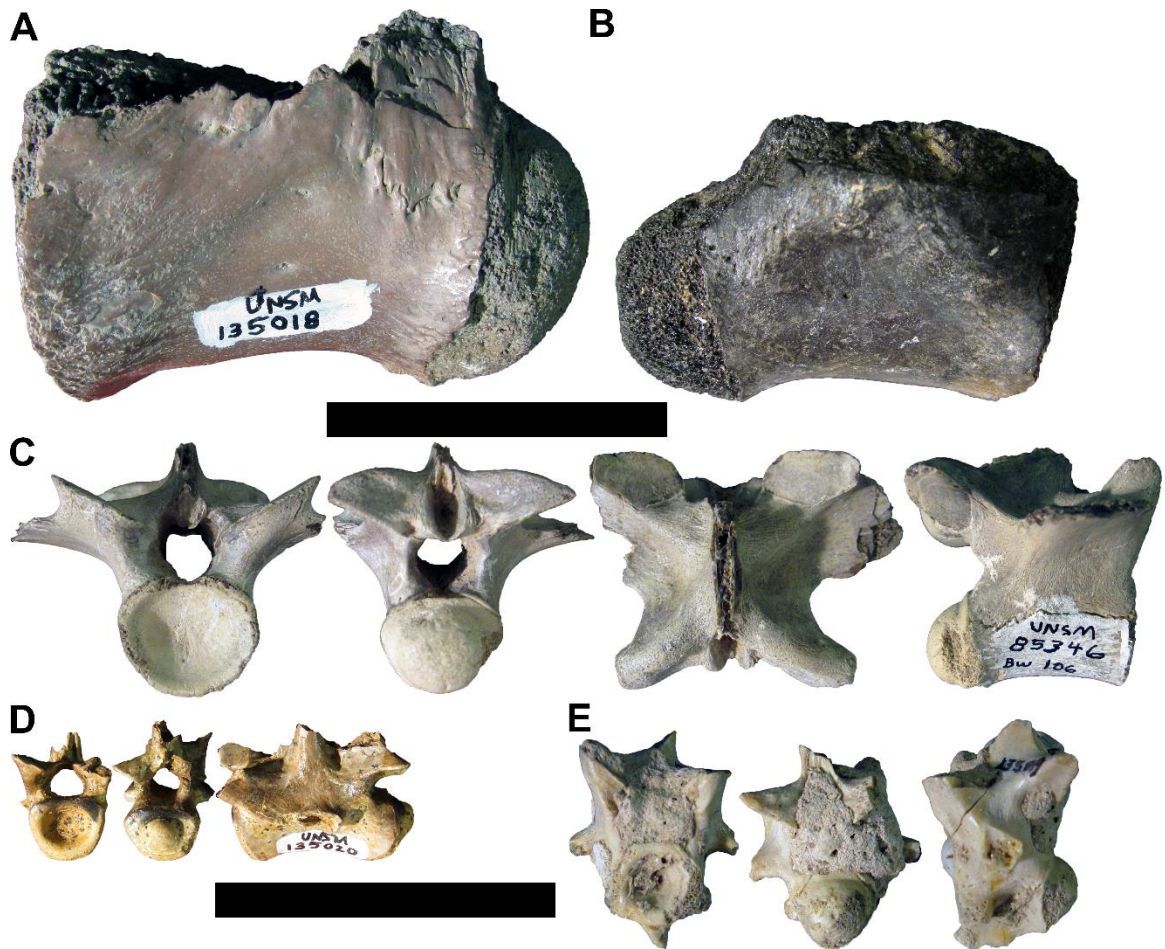


FIGURE 7. Vertebrae: (A) UNSM 135018, vertebral centrum, in left lateral aspect; (B) UNSM 135028, vertebral centrum, in right lateral aspect; (C) UNSM 85346, thoracic vertebra, in anterior, posterior, dorsal, and right lateral aspects; (D) UNSM 135020, caudal vertebra, in anterior, posterior and left lateral aspects; (E) UNSM 135019, cervical vertebra, in anterior, posterior, and left lateral aspects. Scale bars = 5 cm.



FIGURE 8. UNSM 135027, complete right femur: (A) anterior aspect; (B) posterior aspect. Scale bar = 5 cm. Total body length for this individual (~2.4 m) was estimated using measurements from this femur and the equations of Farlow et al. (2005).

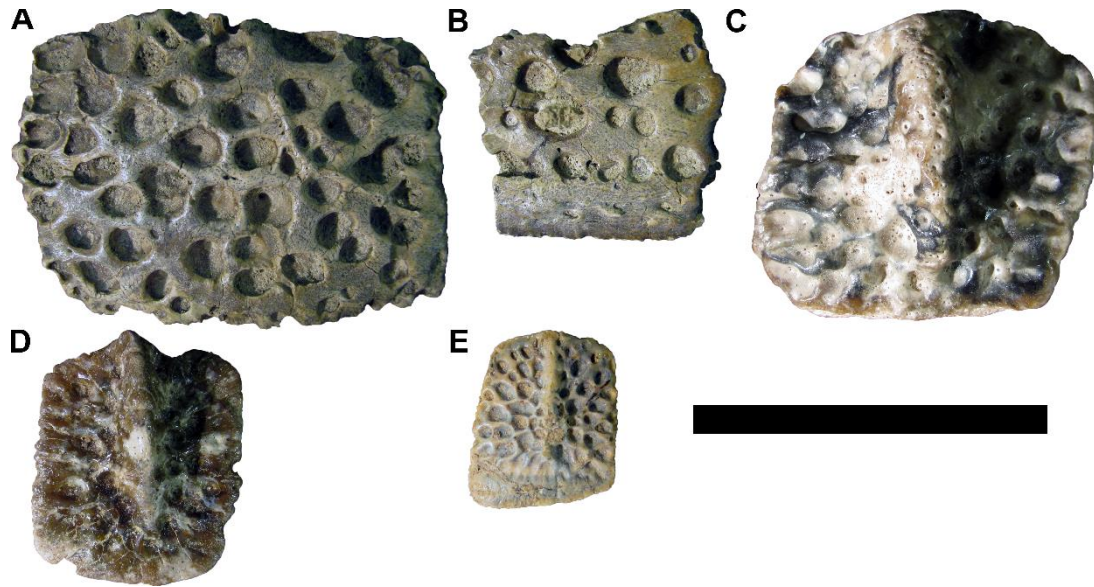


FIGURE 9. Dorsal osteoderms: (A) UNSM 135022, ?midline osteoderm; (B) UNSM 135022, partial ?lateral margin of ?midline osteoderm; (C) UNSM 135003, (D) UNSM 135007, and (E) UNSM 135034, osteoderms of indeterminate position. All osteoderms shown in dorsal aspect. Scale bar = 5 cm.

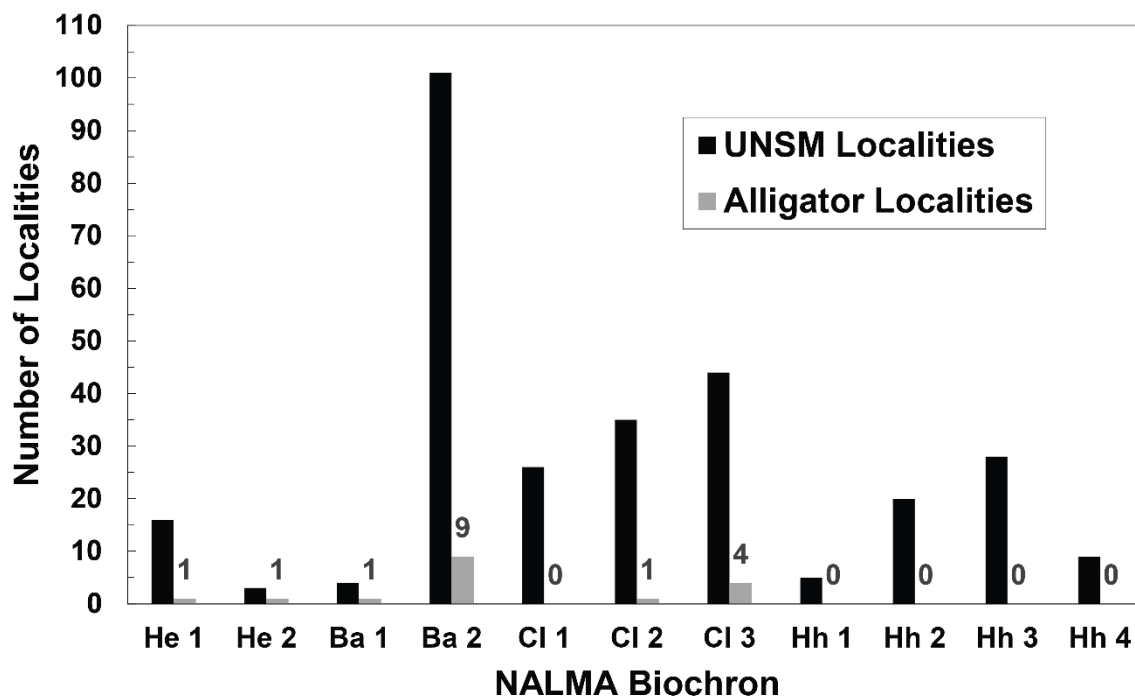


FIGURE 10. Number of UNSM fossil localities binned by NALMA substage/biochron. Numbers above the gray columns indicate the number of UNSM fossil *Alligator* localities for each biochronologic bin. There are larger sample sizes for the late Barstovian and late Clarendonian than any of the other biochrons, indicating a sampling bias. This is reflected by the number of fossil *Alligator* localities, which are greatest during these intervals. **Abbreviations:** He, Hemingfordian; Ba, Barstovian; Cl, Clarendonian; Hh, Hemphillian.

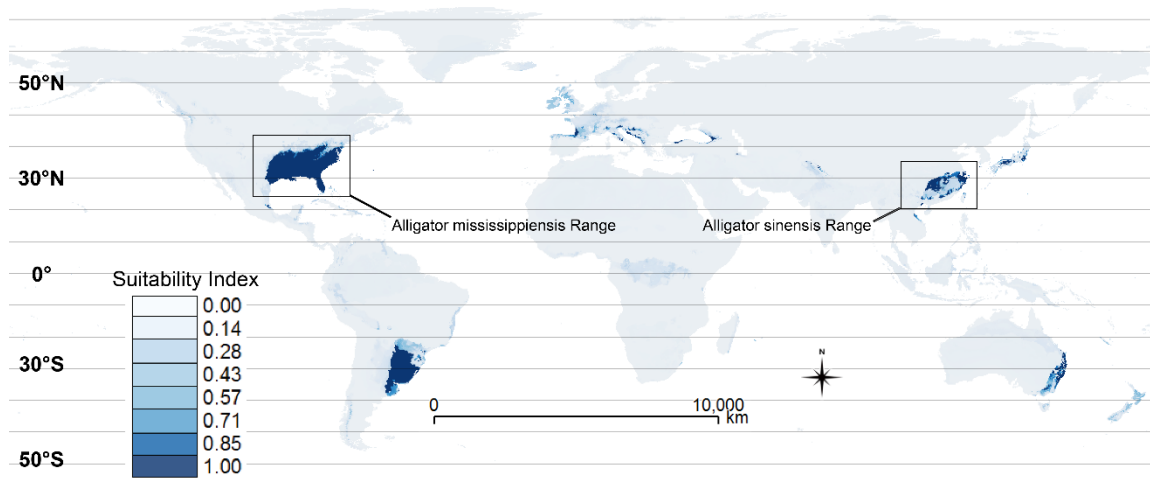


FIGURE 11. MaxEnt *Alligator mississippiensis* predicted world distribution map. Note that the model developed here predicts *A. mississippiensis* to occur where *A. sinensis* occurs today; this provides support for ecological niche conservatism in the genus *Alligator* (see text).

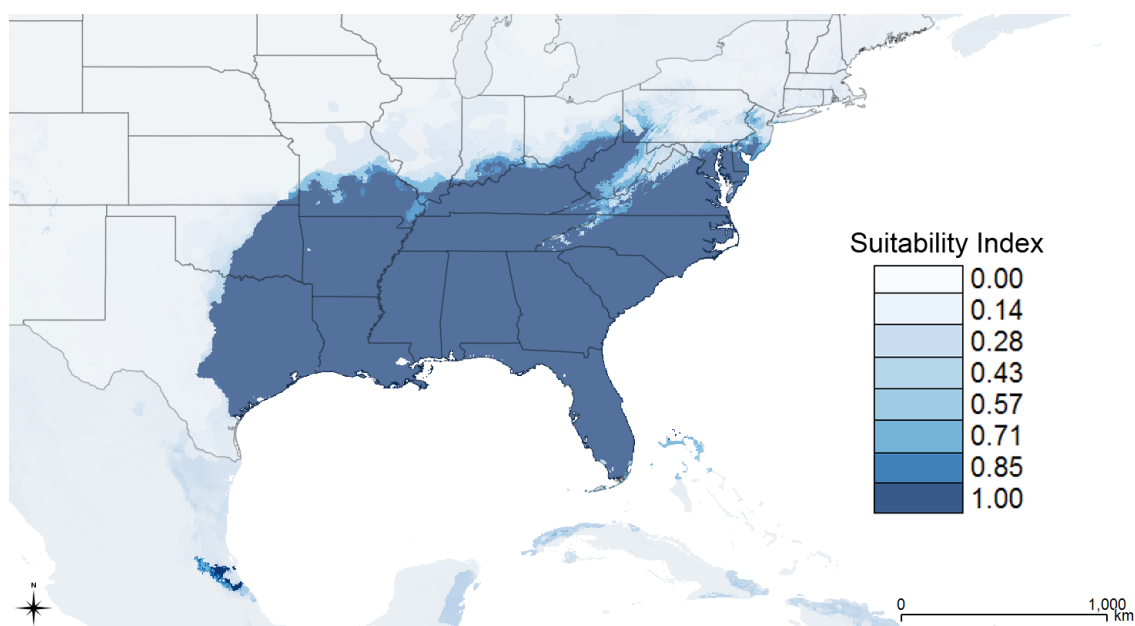


FIGURE 12. MaxEnt *Alligator mississippiensis* predicted USA distribution map.

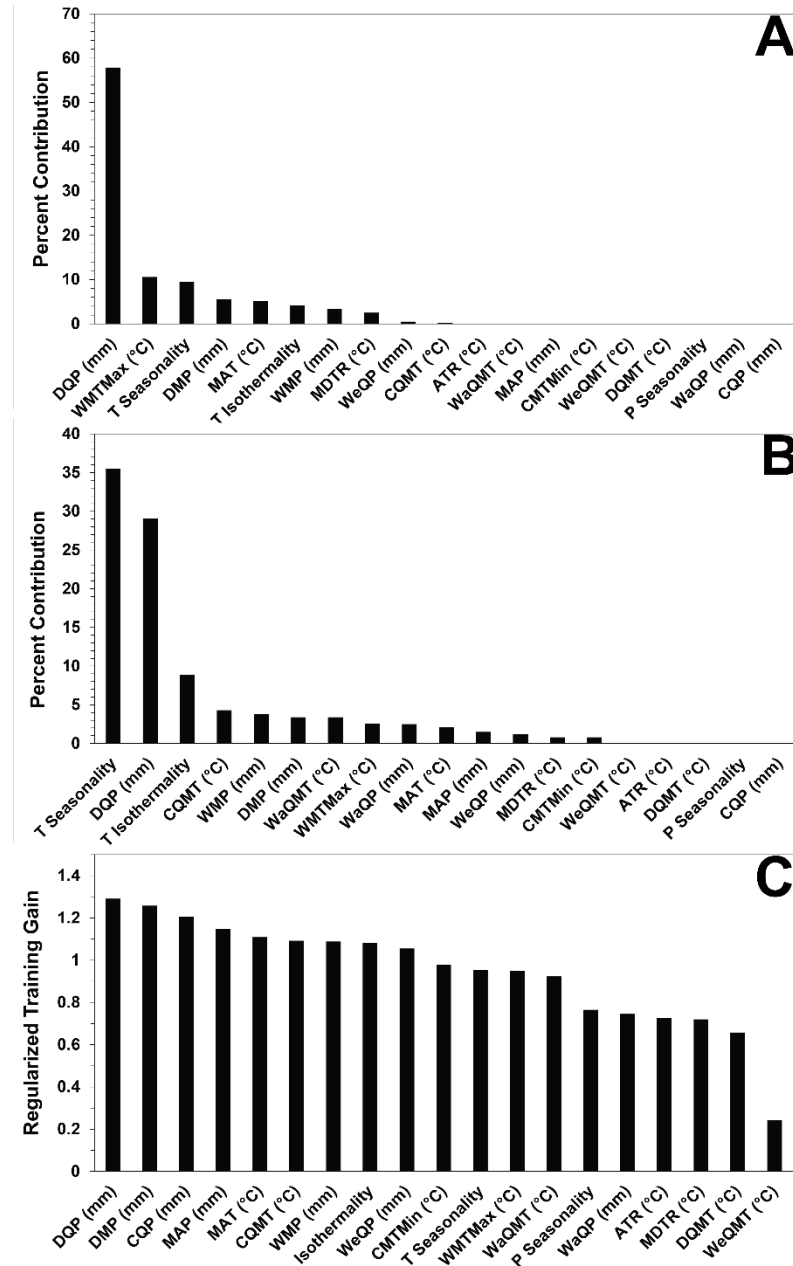


FIGURE 13. MaxEnt modeling results: (A) raw percent contribution of all 19 bioclimatic variables to model prediction; (B) permuted importance percent contribution of all 19 bioclimatic variables to model prediction; (C) jackknifed regularized training gains of all 19 bioclimatic variables used in MaxEnt modeling run. See Table 3 for abbreviations and exact values for all variables.

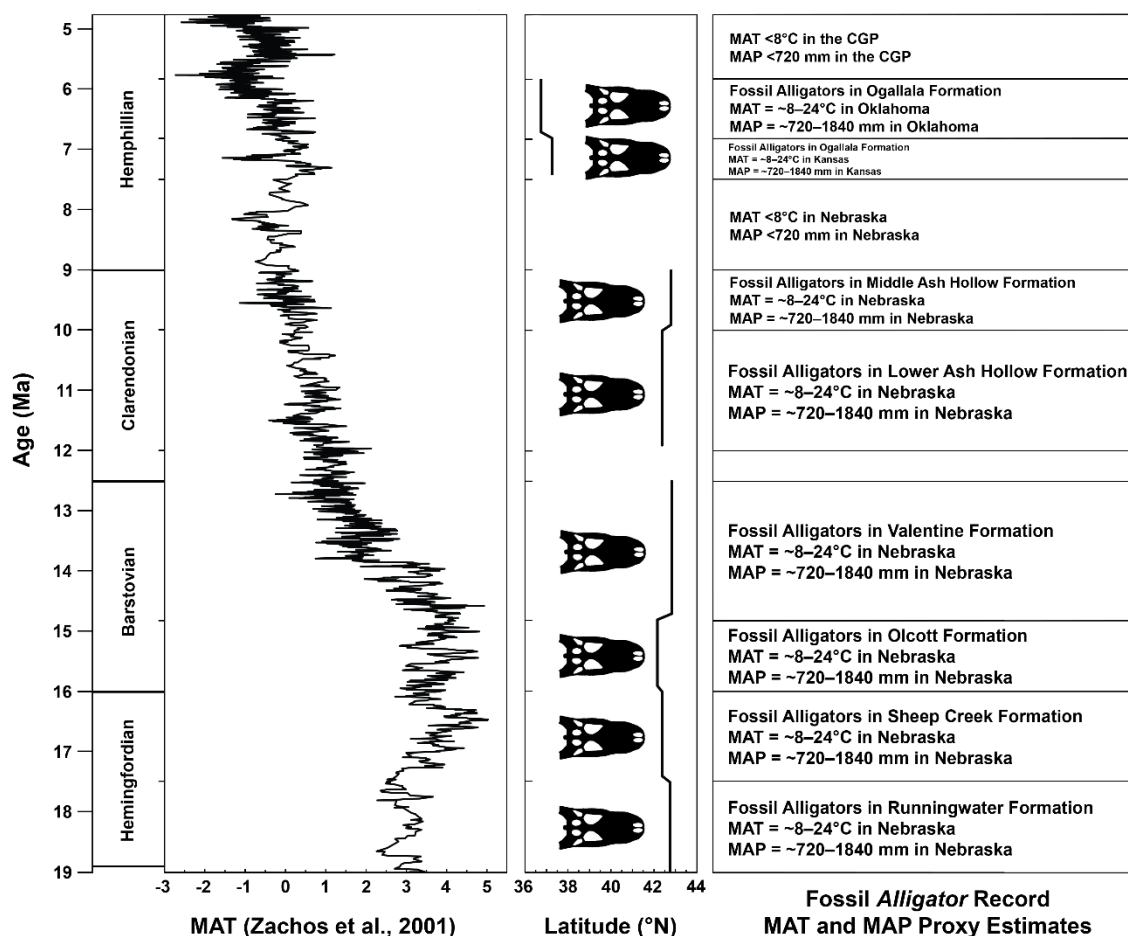


FIGURE 14. Summary of *Alligator* fossil record and paleoclimate proxy estimates during the Neogene of the Central Great Plains. Biochronology follows Tedford et al. (2004). A 5-point running average for global MAT, generated from $\delta^{18}\text{O}$ values in benthic foraminifera, was obtained from Zachos et al. (2001). The northernmost latitude occupied by *Alligator* during the Neogene is shown in the middle column with *Alligator* skull silhouettes indicating intervals from which fossil alligators have been recovered. The column on the far right indicates which geologic formations and CGP states *Alligator* fossils were recovered from, as well as the paleoclimatic constraints (MAT and MAP) generated by the *Alligator mississippiensis* SDM in this study (see text for details).