The early history of character evolution in alligatoroids

Adam Patrick Cossette

University of Iowa

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THE EARLY HISTORY OF CHARACTER EVOLUTION IN ALLIGATOROIDS

by

Adam Patrick Cossette

A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Geoscience in the Graduate College of The University of Iowa

August 2018

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CERTIFICATE OF APPROVAL

PH.D. THESIS

This is to certify that the Ph.D. thesis of

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ABSTRACT

This project seeks to explore, name, and describe some of the earliest known members of Alligatoroidea. Explorations of *Bottosaurus harlani* and *Deinosuchus* reveal that early in their evolutionary history alligatoroids had attained bauplans that are highly divergent from the ancestral condition in both body size and morphology.

*Bottosaurus harlani* preserves aspects of the skull table – including constricted supratemporal fenestrae, a linear frontoparietal suture, and a large trapezoidal dorsal supraoccipital exposure – that are similar to those of caimans. Optimal trees from phylogenetic analysis recover *B. harlani* in three different positions; as a sister either to the modern dwarf caimans (*Paleosuchus*), or either living species of *Paleosuchus*. That a substantial stratigraphic gap separates *B. harlani* from both species of *Paleosuchus*, which first appears in the Miocene, along with low character and nodal support raises questions about this relationship. However, should the relationships recovered here be true, *Bottosaurus harlani* would be the oldest known caiman. The taxon indicates that morphologies common to modern caimans date to the earliest record of the clade.

In addition to the enigmatic *B. harlani*, the Campanian giant *Deinosuchus* was re-evaluated as part of this project. Recent consensus has been that the three named species of *Deinosuchus* (*D. hatcheri*, *D. riograndensis*, and *D. rugosus*) represent a single, widely ranging species. Newly-collected material from the Big Bend region of western Texas and increased sampling of the lineage from throughout North America allowed for a review of species-level systematics of *Deinosuchus* and helped refine its phylogenetic placement among crocodylians.
*Deinosuchus* from western and eastern North America can be consistently differentiated and represent different species.

As a result of the lack of diagnostic characters in the very incomplete holotype specimen, the name *Deinosuchus* is restricted to *D. hatcheri*. To encompass specimens formerly included in *Deinosuchus* a new genus, *Deinosuchoides*, is erected. In addition to naming a new genus, the holotype specimen for *Deinosuchus rugosus* is determined to be undiagnostic to species level and is therefore a nomen dubium. A new species, *Deinosuchoides schwimmeri*, is erected upon a cranial specimen from Mississippi.

The snout of *Deinosuchoides* is very long and wide. Almost invariably, crocodylian snouts are either long or wide, but not both. In addition to the unusually long and wide snout, the skull table of this taxon bears hallmarks found in species of other long-snouted taxa such as *Tomistoma* and *Gavialis*.

To explore the variability of the crocodylian skull table a morphometric analysis was conducted with the inclusion of fossil taxa. As the skull table is robust and likely to be recovered in the paleontological record this element was an ideal fit for a morphometric study. In addition to establishing the morphospace occupation of fossil taxa, the morphometric analysis found considerable overlap in morphospace between Alligatoroidea and Crocodyloidea – the overlap between these groups may be the product of shared ancestry. Additionally, similarities exist in the ecologies of these groups as evidenced by shared snout shape categories. This project finds association between skull table shape and snout length. As such, plotting isolated skull tables in morphospace, may indicate snout length and thus ecology of fossil taxa.

When landmarks representing the supratemporal fenestrae are included in the analysis Gavialoidea is broadly separated from the other groups in morphospace. It has been long
hypothesized that the size of the supratemporal fenestrae reflect the length of the snout as a result of jaw musculature attaching to their medial margins. However, this relationship is not as straightforward as previously hypothesized; the snouts of the crocodyloids *Tomistoma* and *Euthecodon* may exceed the length of the snout in gavialoids but their supratemporal fenestrae are proportionally smaller. This study suggests that a phylogenetic constraint on the size of the supratemporal fenestrae may be present in crocodyloids.

In addition to exploring morphospace occupation, allometric trajectories of all extant taxa with available ontogenetic sequences were explored. The smallest extant taxa (*O. tetraspis*, *P. palpebrosus*, and *P. trigonatus*) demonstrate allometric trajectories that plot alongside the juveniles of the other taxa in this analysis. This may suggest that the small sizes of the skull tables in these species were achieved through paedomorphosis, or the maintenance of juvenile morphologies into adulthood.
PUBLIC ABSTRACT

Alligatoroidea is a group of crocodylians including *Alligator mississippiensis* Daudin 1802 and all species closer to it than to *Crocodylus niloticus* Laurenti 1768 or *Gavialis gangeticus* (Gmelin 1798). The group has a diverse fossil record extending back to the Campanian and ranged into the mid to high paleolatitudes of present day North America, Europe, and Asia. Here, the earliest alligatoroids are explored to help understand the relationships of species both within and outside of the group. As part of this project the enigmatic *Bottosaurus harlani* and one of the largest known crocodylians, the 10 meter giant *Deinosuchus*, are explored and new species are named. This work explores the dramatic changes in body types, size, and continental habitation of the group.

Additionally, a portion of the crocodylian skull is studied through geometric morphometrics allowing for a preliminary quantification of shapes and an exploration of feeding ecology in fossil forms. Similarities in the structure of the skull were discovered and evolutionary constraints on the possible shapes were uncovered.
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INTRODUCTION

This project explores the evolutionary history and phylogenetic relationships of the earliest alligatoroids. This work helps establish the extreme morphological diversity present early in the group’s history. Historical diversity exceeds extant diversity in measures of body size and skull shape. Yet, it is these extant groups who have experienced the largest share of scholarship and tend to predominate the characters used in phylogenetic analyses of Alligatoroidea. Here the author seeks to qualify the morphological diversity of the earliest members of the clade through increased character sampling for these phylogenetically basal taxa. This work also helps to establish the number of species of the giant Campanian alligatoroid *Deinosuchus* and suggests that current analyses of Caimaninae may be diagnosing the group on the basis of shared ancestral character states.

There are eight recognized extant alligatoroid species that form the crown-group Alligatoridae (the last common ancestor of *Alligator mississippiensis* and *Caiman crocodilus* and all of its descendants): two species of alligatorine (*Alligator mississippiensis* Daudin 1802 in the United States and *Alligator sinensis* Fauvel 1879 in China) and six species of Latin American (and primarily South American) caimanine; the spectacled caiman (*Caiman crocodylus* Linnaeus 1758), broad-snouted caiman (*Caiman latirostris* Daudin 1802), yacare caiman (*Caiman yacare* Daudin 1802), black caiman (*Melanosuchus niger* Spix 1825), Cuvier’s dwarf caiman (*Paleosuchus palpebrosus* Cuvier 1807), and smooth-fronted caiman (*Paleosuchus trigonatus* Schneider 1801). Genetic and morphometric analyses suggest that some caimanine “species” are cryptic species complexes subject to future species-level subdivision (Amato and Gatesy, 1994; Venegas-Anaya et al., 2008; Escobedo et al., 2011; Okamoto et al., 2015).
The group was historically much more diverse than present, with extinct taxa extending into the Campanian (Erickson, 1972; Williamson, 1996; Brochu, 1999). In Laurasia, they were most diverse from the late Paleocene through the middle Eocene, and their range extended into the Canadian Arctic and throughout Western Europe (Berg, 1966; Estes, 1980; Markwick, 1998; Brochu, 2004, 2010; Martin et al., 2014; Eberle et al., 2014). Their South American Paleogene record is poor, but they were highly diverse and morphologically disparate there in the Miocene (e.g., Langston, 1965; Aguilera et al., 2006; Riff et al., 2010; Bona et al., 2012; Hastings et al., 2013; Scheyer et al., 2013; Salas-Gismondi et al., 2015). Crown alligatorids are also known from the Eocene of East Asia (Martin et al., 2014; Skutschas et al., 2014), but their relationships to other alligatoroid lineages are unclear. The basal most alligatoroid appears to be *Leidyosuchus canadensis* Lambe 1907 from the Campanian of Alberta (Brochu, 1997, 1999; Wu et al., 2001).

The name *Leidyosuchus* has been broadly applied to many eusuchians from the Late Cretaceous through Eocene of North America (Lucas and Sullivan, 1986; Brochu, 1997). Authors such as Brochu (1997) and Wu et al. (2001) maintain that the sole representative of *Leidyosuchus* is *L. canadensis* and the group is polyphyletic. *Leidyosuchus canadensis* is the type species for the genus and consists of skull and mandible fragments (Lambe, 1907), though more complete cranial and postcranial material was subsequently found (Sternberg, 1932; Wu et al., 2001).

An assemblage of extinct crocodylians from the Paleocene to middle Miocene of the Northern Hemisphere have been assigned to the genus *Diplocynodon* Paumel 1847. These have, at times, been argued to be closely related to *Leidyosuchus* (e.g. Lambe, 1907; Rauhe and Rossmann, 1995), though phylogenetic analyses typically link a monophyletic *Diplocynodon* limited to European forms with other alligatoroids, to the exclusion of *Leidyosuchus* and
erstwhile North American “Diplocynodon”, pertaining to non-alligatoroid lineages (Brochu, 1997, 1999; Delfino and Smith, 2012; Martin et al., 2014). In Europe, well-known forms date from the late Paleocene to the Miocene (Berg, 1966; Buscalioni et al., 1992; Martin, 2010; Martin et al., 2014). Notwithstanding the abundance of information known about Diplocynodon, a world-wide analysis including all known species has not been conducted and monophyly of the group has been questioned (Buscalioni et al., 1992). Analyses of Diplocynodon systematics have historically focused primarily on dental occlusion and alveolar morphology (Brochu, 1999). A feature used to identify Diplocynodon, and the basis for its name, are two pseudocanine teeth on the mandible. However, this feature may be plesiomorphic at a broader level within Crocodyliformes and requires further analysis (Norell, 1988; Brochu, 1999).

*Allognathosuchus* Mook 1921 has been applied to an assemblage of blunt snouted alligatoroids with enlarged back teeth from the Paleocene and Eocene of the Northern Hemisphere (Mook, 1921; Simpson, 1930; Wassersug and Hecht, 1967; Sullivan et al., 1988; Rauhe and Rossman, 1995; Brochu, 2004; Lucas and Sullivan, 2004). The genus originally included two species, *Crocodilus polyodon* (Cope 1873) and *Crocodilus heterodon* (Cope 1872), the former from the middle Eocene Bridger Formation and the latter from the early Eocene Wasatch Formation. Isolated teeth have been used to extend the range of the group into the Cretaceous (Lucas, 1992). This assertion must be viewed skeptically as many early globidontans share similar tooth morphology in the form of globular posterior dentary teeth (Figure 4).

 Constituents of the *Allognathosuchus* assemblage are morphologically similar, yet the group may not be monophyletic. Many holotypes are fragmentary and some names may be undiagnosable (Lucas, 1992; Brochu, 1999). *Allognathosuchus polyodon* is an alligatorid more closely related to Alligator than to Caiman (i.e. an alligatorine), but other species attributed to
Allognathosuchus may be more distantly related to alligatorines or basal globitontans (Brochu, 1999, 2004). Other alligatoroids share large, bulbous posterior teeth with Allognathosuchus. These include Late Cretaceous Brachychampsia Gilmore 1911 and Stangerochampsia Wu et al. 1996, Paleocene Navajosuchus Simpson 1930, and basal species of Alligator (Brochu, 2004). Including all members of the clade in a phylogenetic analysis will be important to address the monophyly of the group.

Bottosaurus is an alligatoroid from the Late Cretaceous and early Paleocene of North America. It is found primarily in marine sediments of the United States’ eastern seaboard and Gulf of Mexico. There are currently two named species of Bottosaurus, B. harlani (Meyer 1832) and Bottosaurus tuberculatus Cope, 1870. Bottosaurus is diagnosed by the presence of tribodont teeth with dorsoventrally wrinkled enamel and mesiodistal carinae. Unlike other alligatoroids with enlarged posterior teeth, the posterior teeth of Bottosaurus harlani are mediolaterally compressed.

Only fragmentary mandibular and postcranial material has been referred to Bottosaurus in the literature, but more complete material referable to B. harlani from New Jersey is known. Cranial and postcranial elements attributed Bottosaurus harlani Meyer, 1832, are described from the Rowan Fossil Quarry, a Cretaceous–Paleogene locality in Mantua Township, New Jersey, USA. This specimen (NJSM 11265) represents the most complete individual attributable to the species and includes significant postcranial elements not found in other specimens. Posterior elements of the skull are described for the first time and the species is placed into a phylogenetic context.

Deinosuchus is a lineage of giant (≥10 m) Late Cretaceous crocodylians from North America. These were the largest semiaquatic predators in their environments and are known to
have fed on dinosaurs. Fossils have been found in units of Campanian age from Coahuila, northern Mexico to Montana in the west and Mississippi to New Jersey in the east. Three species have been named – *D. hatcheri* and *D. riograndensis* from the western interior and *D. rugosus* from the Atlantic coastal plain – and recent consensus has been that all three represent a single widely-ranging species. Here the author seeks to challenge this hypothesis through a holistic re-analysis of all known *Deinosuchus* material.

The author studied newly-collected material from the Big Bend region of western Texas and increased sampling of the lineage from throughout North America to review species-level systematics of *Deinosuchus* and help refine its phylogenetic placement among crocodylians. *Deinosuchus* from western and eastern North America are consistently differentiated and represent different species. Western specimens have inflated, deeply ornamented dorsal osteoderms whose keels are largely obliterated whereas eastern specimens of a similar size have reduced inflation. Additional differences are manifest in the premaxilla - eastern specimens have deep occlusal marks posterior to the junction of the first and second premaxillary teeth – western specimens have very deep premaxillae with premaxillary fenestration.

Morphological and molecular analyses strongly support monophyly of crown-group alligatoroids (the clade Alligatoridae) with alligators (Alligatorinae) being the sister group to the caimans (Caimaninae) (Figure 5) (Brochu, 1999; Densmore and White. 1991; Norell, 1988, 1989; Oaks, 2011). However, many fossil alligatoroids have not been subjected to phylogenetic analyses (Brochu, 1999). As a result, our understanding of basal alligatoroid phylogenetics and systematics is fragmentary.

To address our incomplete understanding of Alligatoroidea, all known stem alligatoroid taxa are subjected to phylogenetic analysis. In concert with increased taxon sampling, new
characters are described to clarify relationships within the clade. This task is challenging, as fossils of freshwater eusuchians with conservative morphologies are often found as isolated and fragmentary elements. In addition, many characters used in morphological analyses are sourced from the derived morphologies of crown Alligatoridae. Basal members of Alligatoroidea, temporally near the divergence of the ancestral alligatoroid, share similar plesiomorphic morphologies complicating parsimony analyses.

This project consists of viewing all published stem alligatoroid taxa. New characters and character states are be created to encompass the morphological diversity of stem taxa that are not adequately described by characters obtained from more derived species. New characters gleaned from as yet poorly known taxa, such as the new specimen of *Bottosaurus* described as part of this project, will help establish relationships within Alligatoroidea and broadly inform relationships among the major crocodylian clades.

The phylogenetic work was initiated through viewing fossil alligatoroids at museums and coding characters for each specimen. Taxa analyzed include all extant alligatorids and basal alligatoroids. The extant specimens provide the author with a sense of variation found in modern specimens that may be applied to the understanding of variation in fossil species. Sampling outside of Alligatoroidea consisted of looking at basal brevirostrians, crocodyloids, gavialoids, and immediate outgroups to crown Crocodylia.

In addition to describing early alligatoroid taxa, a morphometric analysis was conducted as part of this dissertation. The dorsal portion of the adult crocodylian skull, posterior to the orbits, is always flat and is referred to as the skull table (Mook, 1921). This structure is found in all crocodylians and appears to be part of a trend leading to overall flattening of the skull in Crocodylia (Langston, 1973). The skull table is a synapomorphy of Crocodyliformes and appears
in no other semiaquatic predator. Yet, little work has been done focusing on the shape of the skull table.

Of particular interest to the author is the robust nature of the skull table; it is likely to be recovered in the fossil record. Yet, a morphometric analysis has not been conducted on the skull table with the inclusion of fossils. In addition to comparisons amongst taxa, comparisons of allometric change within taxa are explored in this study to elucidate patterns of convergence, divergence, and parallelism among Crocodylian taxa.

**Institutional Abbreviations**

Specimens were viewed, coded, and measured from the following institutions: Alabama Museum of Natural History (ALMNH), American Museum of Natural History (AMNH), Bristol City Museum (BSP), Academy of Natural Sciences of Philadelphia (ANSP), Carnegie Museum (CM), Denver Museum of Natural History (DMNH), East Tennessee State University (ETVP), Field Museum of Natural History (FMNH), Hessisches Landesmuseum Darmstadt (HLMD), Kenya National Museums (KNM), Museum of Comparative Zoology (MCZ), Mississippi Museum of Natural Science (MMNS), Muséum National d'Histoire Naturelle Paris (MNHN), Natural History Museum London (NHM), New Jersey State Museum (NJSM), Peabody Museum Harvard University (PMHU), Texas Memorial Museum (TMM), Römisch Germanisches Museum (RGM), Royal Tyrell Museum of Paleontology (RTMP), South Dakota School of Mines (SDSM), Senckenburg Museum Frankfurt (SMF), Science Museum of Minnesota (SMM), University of Florida (UF), United States National Museum (USNM), Yale Peabody Museum (YPM).
CHAPTER 1
A NEW SPECIMEN OF THE ALLIGATOROID BOTTOSAURUS HARLANI AND THE
EARLY HISTORY OF CHARACTER EVOLUTION IN ALLIGATORIDS

Introduction

Among alligatoroid crocodylians, diversity of caimanine alligatorids is three times greater
than that of their sister group, the alligatorines. There are six recognized extant caimanine
species: the common or spectacled caiman (*Caiman crocodilus*), the yacaré (*Caiman yacare*), the
broad-snouted caiman (*Caiman latirostris*), the black caiman (*Melanosuchus niger*), and two
species of dwarf or smooth-fronted caiman (*Paleosuchus palpebrosus* and *Paleosuchus
trigonatus*). Some appear to be cryptic species complexes and their diversity is likely greater than
currently recognized (Amato & Gatesy, 1994; Venegas-Anaya et al., 2008; Escobedo-Galvan et
al., 2011, 2015).

The Central American range of *Caiman crocodilus* may be attributed to a comparatively
recent range extension (Estes & Báez, 1985; Vanzolini & Heyer, 1985; Venegas-Anaya et al.,
2008). Otherwise, all living caimanine species are South American. Alligatorines and outgroups
to Alligatoridae, are Laurasian (Norell et al., 1994; Brochu, 1999, 2011; Martin, 2007). If this
distribution is the product of vicariance we would expect an alligatorine-caimanine divergence
by the end of the Jurassic as tectonic processes separated North and South America. However,
the fossil record is inconsistent with this hypothesis; the earliest known alligatorines are from the
early Paleocene (Simpson, 1930; Mook, 1942). Molecular divergence estimates are broadly
consistent with fossil first appearances and suggest an alligatorine-caimanine divergence
proximal to the Cretaceous–Paleogene boundary (Hass et al., 1992; Roos et al., 2007; Oaks, 2011).

A single dispersal event from North America to South America seems sufficient to explain the current distribution of caimanines. However, when the fossil record is included the biogeographic patterns of the clade become murky. There are reports of North American caimans (Busbey, 1989; Brochu, 2010). *Orthogenysuchus olseni* (Mook 1924) and *Tsoabichi greenriverensis* (Brochu 2010), both from the lower Eocene of Wyoming, are unrelated in phylogenetic analyses. Multiple dispersals between South America and North America are likely.

Much of the caimanine fossil record is from Miocene or younger sediments, and many of the fossils are highly derived and not referable to any extant lineage (Salas-Gismondi et al., 2015; Scheyer et al., 2013; Scheyer and Delfino, 2016). The Paleogene record in South America is sparse and dominated by incompletely known forms (e.g., Simpson, 1937; Bona, 2007; Brochu, 2011; Pinheiro et al., 2013).

Fossils of uppermost Cretaceous to lower Paleocene age have been referred to *Bottosaurus harlani* Meyer, 1832, but only fragmentary mandibular and postcranial material has been reported in the literature. More complete material referable to *B. harlani* from the Cretaceous–Paleogene of New Jersey is known. Here we describe a fairly complete *B. harlani* specimen (NJSM 11265) recovered from the Hornerstown Formation of New Jersey. NJSM 11265 preserves portions of the snout and posterior skull as well as the majority of the lower jaw. Postcranial material includes portions of all limbs and limb girdles as well as numerous osteoderms and vertebrae. This specimen represents a remarkable opportunity to understand new morphological traits in the species and evaluate the status of fragmentary specimens attributed to *Bottosaurus*. 
Phylogenetic analyses including NJSM 11265 support a caimanine affinity for *B. harlani* and reveal a complex biogeographic and evolutionary history within Caimaninae. These relationships have several implications. First, *Paleosuchus* may be on a branch with a very long ghost lineage. Second, some characters currently used to diagnose Caimaninae may apply to more inclusive clades. Should this be the case, our understanding of the characters diagnosing the clade will have to be reconsidered and the phylogenetic relationships of ingroup taxa will have to be re-evaluated.

This paper has three objectives: first, to describe NJSM 11265 and, in the process, more fully describe the holotype; second, to assess the number of species attributable to *Bottosaurus*; and third, to explore its phylogenetic and biogeographic relationships and potential implications for the diagnosis of Caimaninae.

**Previous Work**

The remains of *Bottosaurus harlani* have been reported from throughout the Upper Cretaceous and lower Paleogene marginal marine sediments of western New Jersey, USA. The type specimens, ANSP 9226 + 9227 and ANSP 9174 (Fig. 2), were discovered years before their first description in 1824 and comprise a partial right dentary containing 11 alveoli and three teeth, an incomplete right angular apparently from the same jaw, and a single tooth (Harlan, 1824; Spamer and Daeschler, 1995). The partial angular (ANSP 9227) preserves the posterior angle of the lower jaw and the floor of the mandibular fossa but additional morphology cannot be determined. The dentary (ANSP 9227) maintains posterior portions of the mandibular symphysis but interpretation of morphology is hindered by poor preservation. Tooth positions cannot be determined beyond rough number of preserved alveoli. The loose tooth (ANSP 9174) is globular,
low crowned, robustly built, and likely from the mid-posterior of the dental arcade. In occlusal view it shows slight labiolingual compression, preserves apical striations of the enamel, and bears mesial and distal carinae. The specimens are dark, greenish-brown and very heavy for their size. The fossils, like others from the New Jersey green sands, are infiltrated with pyrite and prone to deterioration.

Unfortunately, through poor record keeping and the passing of time, it is impossible to determine the type specimen’s exact provenience. Harlan (1824) provided a coarse description stating that the fossil was found by Samuel Wetherill three miles from White Hill, New Jersey. This description likely refers to the White Hill Mansion, a property in Fieldsboro, Burlington County, New Jersey.

Harlan (1824) noted that the *B. harlani* type specimen shared morphological affinities with crocodiles and alligators to the exclusion of gavials. He stated that the uniqueness of the specimen, especially the robust proportions of the lower jaw and the distinctive blunt teeth, was sufficient to erect a new species, which was named *Crocodylus harlani* by Meyer (1832). Harlan, presumably unfamiliar with Meyer’s work, later designated the specimen *Crocodylus macrorhyncus* Harlan, 1835. The name proposed by Harlan is the name most commonly encountered in the systematic literature of the 19th century. In 1849 Agassiz proposed a new genus, *Bottosaurus*, based upon the Harlan type material (Academy of Natural Sciences of Philadelphia, 1849). Leidy (1865: Fig. 2, E-G) figured and re-described the Harlan type material. Leidy was the first to suggest in the literature that *Crocodylus macrorhyncus* is a junior objective synonym of *Bottosaurus harlani*.

Mook (1925) figured three *B. harlani* teeth. Of these, two are reportedly from the Burlington County Lyceum of Natural History, and one is from the Academy of Natural
Sciences, Philadelphia. The two teeth from the Burlington County Lyceum are now housed at ANSP (ANSP 9208, ANSP 9175; personal observation). This is intriguing because all collections from the Burlington County Lyceum were moved to the New Jersey State Museum in the early to mid-twentieth century (Parris, personal communication, 2015). Leidy (1865) noted that the teeth had been borrowed from the Burlington County Lyceum for examination. It would seem that the teeth were never returned.

The lectotype specimen, ANSP 9226 + 9227, as originally described by Harlan, comprised an angular and a dentary with three intact teeth. But by 1865, when the dentary was figured by Leidy, only one tooth remained. Presently, the tooth has deteriorated beyond a point where its morphology may be understood. How the dentary (ANSP 9227) became so disfigured is unknown but fossils from the Hornerstown Formation are subject to pyrite disease and begin to decay upon exposure to air (Harlan, 1824; Leidy, 1865; Spamer and Daeschler, 1995).

As the teeth – unusually for a crocodylian – are diagnostic for the species, the diagnosability of the dentary in its current state is questionable. Further, the other type specimen, a partial right angular (ANSP 9226), does not preserve diagnostic morphological characters. However, Leidy (1865) figured the types and provided adequate descriptions of their morphology and the teeth that diagnose the species.

Almost nothing has been said about *B. harlani* since the turn of the 20th century. Upper Cretaceous and Paleocene fossils from elsewhere in North America have been referred to *Bottosaurus* (e.g., Erickson, 1998; Schwimmer et al., 2015). Some named species have been recognized as nomina dubia or misidentified. *Bottosaurus perrugosus*, from the Lance Formation of Wyoming, was named by Cope (1873) and later designated a nomen dubium by Norell et al. (1994) on the basis that the holotype cannot be distinguished from several named species of
alligatoroids. *Bottosaurus belgicus* was erected upon a single tooth (Woodward, 1891) and later referred to *Carinodens*, a genus of mosasaur (Thurmond, 1969; Kuypers et al., 1998).

**Geological Setting of the New Material**

The new specimen of *Bottosaurus harlani*, NJSM 11265, was collected in 1961 by Lukenda, Markewicz, and assistants from the Rowan Fossil Quarry (formerly known as the Inversand Quarry) (Fig. 1). The quarry was an open-pit glauconitic sand mine located in Mantua Township, Gloucester County, New Jersey, USA. It preserves exposures of the uppermost Navesink and basal Hornerstown formations (Olsson et al., 2002). As such, faunal change across the Cretaceous-Paleogene boundary is recorded (Gallagher, 1991, 2002; Olsson et al., 2002).

![FIGURE 1. A, map of the United States showing the location of New Jersey. B, map of New Jersey showing Cretaceous–Paleogene strata and the Rowan Fossil Quarry. Modified from Obasi et al., 2011.](image-url)
The Upper Cretaceous and lower Paleogene deposits of New Jersey are highly fossiliferous (Conrad, 1869; Morton, 1829; Olson and Parris, 1987; Vanuxem, 1829). The Hornerstown Formation, and particularly its Main Fossiliferous Layer (MFL), is well sampled but poorly understood. The formation contains Upper Cretaceous invertebrate and vertebrate fossils near its base but upsection contains Danian invertebrates (Wiest et al., 2016). Within the formation the MFL is 20-30 cm thick and contains a high concentration of vertebrate and invertebrate fossils.

The origin and dating of the MFL are debated (Obasi et al., 2011). It may reflect Cretaceous fossils reworked into Paleogene sediments (Landman et al., 2007), lag deposits resulting in a condensed section consisting of mixed Cretaceous and Paleogene fossils (Kennedy and Cobban, 1996), pronounced bioturbation at the Cretaceous-Paleogene boundary (Gallagher, 1993), or a period of accelerated extinction (Gallagher, 2003). Numerical dating has proven difficult and age estimates have been variable (Gallagher and Parris, 1996; Olsson et al., 2002). Recent workers suggest that the MFL is a mass death assemblage brought on by the Cretaceous–Paleogene extinction event as evidenced by the presence of shocked quartz and an iridium anomaly preserved at the base of the MFL in some sections (Miller et al., 2010; Obasi et al., 2011).

Outstanding preservation of fossils is not uncommon in the glauconite deposits of the Hornerstown Formation (Olson and Parris, 1987). The glauconite is hypothesized to be autochthonous and the depositional environment calm. Further, the Hornerstown Formation contains little terrestrial material and shows scant evidence of current induced disturbances (Olson and Parris, 1987). Although some actualistic taphonomic evidence exists to suggest that
decay in low energy settings does not always guarantee a high degree of articulation (Syme and Salisbury, 2014), the sum of these factors led to preservation of delicate body fossils and left many vertebrate skeletons intact (Olson and Parris, 1987; Obasi et al. 2011). The interpretation of the MFL as an entirely reworked deposit is inconsistent with the presence of complete and partial vertebrate skeletons (Olsson et al., 2002). This is especially true when the MFL is compared to other concentrations of vertebrate fossils in the New Jersey coastal plain (Gallagher, 1993).

**Anatomical Abbreviations**

alv, alveoli; an, angular; ar, articular; cn, cranial nerve; d, dentary; ect, ectopterygoid; emf, external mandibular fenestra; en, external naris; eo, exoccipital; f, frontal; fa, foramen aëreum; fic, foramen intermandibularis caudalis; fm, foramen magnum; foc, foramen of otic capsule; itf, infratemporal fenestra; j, jugal; jp, jugal process; lf, lingual foramen; m, maxilla; mg, Meckelian groove; mpl, maxillary palatal lamina; ms, mandibular symphysis; mjf, medial jugal foramen; n, nasal; o, orbit; pa, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; pos, preotic sinus; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; soc, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; stf, supratemporal fenestra.

**Systematic Paleontology of Bottosaurus harlani**

CROCODYLIA Gmelin, 1789, sensu Benton and Clark, 1988

ALLIGATORIDAE Cuvier, 1807, sensu Norell et al., 1994

*BOTTOSAURUS* Agassiz, 1849

*BOTTOSAURUS HARLANI* Meyer, 1832
Lectotype—ANSP 9226 + 9227, angular bone and dentary fragment; paralectotype ANSP 9174, an isolated tooth (Fig. 2).

Etymology—Meaning of generic name was not originally specified. Bottosaurus is likely a corruption of boto (Latin for button) and sauros (Greek for lizard). The boto prefix likely describes the blunt, button-like teeth seen in material referred to the taxon. The specific epithet honors Richard Harlan, an early American paleontologist.

Referred Specimens—NJSM 11265, partial skull and jaws with associated postcranial skeleton; AMNH 2395, a partial left dentary, 8 loose teeth, vertebral fragments, and a single osteoderm; AMNH 2397, lower jaw fragments, four loose teeth; YPM 325, an isolated tooth; YPM 56140, a partial frontal with associated prefrontals; YPM 274, premaxillae, 12 isolated teeth, lower jaw fragments, fragment of ischium, and a right tibia.

Diagnosis—Tribodont teeth with mesiodistally oriented carinae. Premaxillary teeth circular in cross-section with low apices. Posterior dentary teeth mediolaterally compressed. Distinct U-shaped depression on the frontal at the point of the greatest mediolateral constriction between the orbits. Shares constricted supratemporal fenestrae, linear frontoparietal suture, and large trapezoidal dorsal supraoccipital exposure with most caimans. Medial jugal foramen elliptical in shape and large in size. Osteoderms bear a pronounced parasagittal keel. The combination of these features diagnoses the taxon and separates it from other alligatoroid and eusuchian taxa.

Occurrence—Upper Maastrichtian and lower Danian, New Jersey, USA. ANSP-9226, ANSP-9227, ANSP-9174: Three miles from White Hill Mansion, Fieldsboro, Burlington County, New Jersey. NJSM-11265: Rowan Fossil Quarry, Mantua Township, Gloucester County, New
Jersey, USA. Uppermost Cretaceous to lowermost Paleocene, Main Fossiliferous Layer, Hornerstown Formation.


**Description**

Cranial morphology is best preserved in NJSM 11265 (Figs. 3, 4, 5), however, all referred specimens are included in the description.

Skull—ANSP 9206 preserves the mediadorsal portion of a partial left premaxilla. Preserved portions of the external naris suggest that it was roughly oval and its anteroposterior length was greater than its width. The lateral narial margin is gently inflated. It cannot be
determined if the nasals contributed to the external narial margin. Posterolateral to the external naris is an anteroposteriorly oriented depression bordered by similarly oriented ridges. The dorsal premaxillary process is short and forms a point at a nearly right angle; sutural scars are preserved but the elements they contacted in life cannot be determined.

A pair of associated premaxillae (YPM 274) (Figs. 3B-C) are located in collections of the Yale Peabody Museum. They were found associated with postdentary specimens closely resembling those of NJSM 11265, and we tentatively refer this material to Bottosaurus harlani. The premaxilla forms the majority of the external narial margin. Lateral to the midline the external narial margin is inflated. The lowest portion of the narial margin is at the midline when viewed from an anterior perspective. The external naris opens anterodorsally. Premaxillae contain four teeth. A pit is present on the premaxilla where, in life, the fourth tooth of the dentary would have occluded into. The incisive foramen is situated far from the premaxillary toothrow and although some bone is missing along its margins, the foramen is large.

The maxillae are poorly preserved. A portion of the left maxilla preserves the anterior margin of the suborbital fenestra. The anterior margin of the fenestra is constricted; the maxilla forms a sizeable portion of the medial margin. The left maxillary fragment preserves the lingual margins of four alveoli. The posteriormost three alveoli are narrowly separated from the anterior portion of the suborbital fenestra by the maxillary palatal lamina. The right fragment is from the posterior of the ventrolateral portion of the maxilla and comprises part of the lateral margin of the upper jaws. The curvature of the fragment suggests a blunt snout in this species.
The anterior rami of the jugals are dorsoventrally deep. The jugomaxillary suture is mediolaterally oriented and approximately straight. The lacrimojugal suture is short. An ascending ramus, confluent with the lateral jugal surface, forms the ventrolateral portion of the postorbital bar. The medial jugal foramen is particularly large (Fig. 6). The medialmost margins are damaged (no evidence of crushing) in both left and right jugals but remaining margins suggest an elliptical foramen approximately 2 centimeters in length from anterior to posterior and a width of nearly a centimeter. The posterior ramus is circular in cross-section at its midpoint and forms the ventral margin of the infratemporal fenestra. Starting approximately halfway along its body the posterior portion of the ramus flattens mediolaterally and tapers to a tip.

The prefrontal forms the anteromedial margin of the orbit. YPM 56140 best preserves the prefrontals and suggests that they continue anteriorly beyond the greatest extent of the frontal. In NJSM 11265, near the medialmost extent of the orbital margin, the prefrontal and frontal form a complex suture in the shape of a tongue and groove joint; a posterior extension of the prefrontal fits into an indentation on the frontal. In YPM 56140 the tongue and groove joint is much less pronounced and occurs nearer the mid-line of the skull. Anterior to the complex sutural zone, the frontal and prefrontal contact forms a simple linear suture. There is a pronounced ridge on the prefrontals paralleling the orbital margin.

The prefrontals are separated by the frontals and nasals. The prefrontal pillars

are best preserved in YPM 56140, and the dorsalmost portion and medial process of the pillar are both expanded anteroposteriorly.

The anterior process of the frontal is long, slender, and tapers to an acute point. The length of the anterior process of the frontal and the shape of the preserved orbital margin suggests that the frontal extended anterior to the orbits. Medial to the complex suture with the prefrontals, the frontal bears a deep, U-shaped depression at the point of maximal constriction between the orbits (Figs. 4, 9). The lateral margins of the frontal, bounding the U-shaped depression, are confluent with the prefrontal ridge paralleling the orbital margin. Posterior to the U-shaped depression, its lateral margins adjacent to the orbits are upturned. Posterolateral margins contact the postorbitals. The posterior margin of the frontal forms a linear frontoparietal suture. The frontal, with participation from the anteriormost portions of the postorbital and parietal, forms a depression anteromedial to the supratemporal fenestrae. The ventral side of the frontal preserves a midline groove 0.5 cm in width for the olfactory tract.

The anterior edge of the postorbital, forming the posterior orbital margin, is upturned and is confluent with the ridge on the lateral margin of the frontal. When viewed dorsally, the shape of the postorbital is boomerang-like in outline with the convex angle on the anterior side and the concave angle on the posterior side. The anterior margin of the supratemporal fenestra is bounded by the postorbital; the anterior margin of the supratemporal fenestra is angular with the vertex forming a concave angle on the posterior margin of the postorbital. Internally, the dorsal portion of the anterolateral wall of the supratemporal fenestra is formed by the postorbital. Sutural contact with the parietal is made midway along the anterior wall of the fenestra.

The lateral squamosal margin is gently upturned at its posteriormost extent. The posterior squamosal margin is also upturned and is confluent with the upturned portion of the lateral
squamosal margin; the result is a shallow depression on the squamosal at the posterolateral corner of the skull table. The posterior portion of the squamosal is laterally expanded, creating a skull table that is trapezoidal in shape with the posterior portion being considerably wider than the anterior.

The external otic aperture is a dorsoventrally compressed oval, and the squamosal forms the posterodorsal margin. The squamosal makes contact with the quadrate ramus from the posteriormost margin of the otic aperture to the posteriormost extent of the squamosal.

The linear frontoparietal suture is excluded from the supratemporal fenestrae. The parietal substantially contacts the postorbital within the supratemporal fenestra and bears a modest constriction where it forms the gently upturned medialmost margin of the fenestra. Within the supratemporal fenestra the dorsolateral margin of the parietal overhangs the fenestra leaving a ledge dorsally and a fossa ventral to the ledge. The parietal reaches the posterior margin of the skull table through lateral projections that surround the supraoccipital.

Dorsally, the supraoccipital is large and trapezoidal in shape. It is substantially exposed on the skull table. The anteriormost portion of the supraoccipital on the skull table is indented causing the posterior margin to have a gently upturned appearance. The upturned portion of the supraoccipital is confluent with the moderately upturned posterior margin of the squamosals. In posterior view, the lateral margins of the supraoccipital as exposed on the occipital surface are poorly preserved. The remaining portions suggest that the outline was shaped like a cut diamond. The supraoccipital is excluded from the foramen magnum by medial processes of the exoccipitals.

The quadratojugal forms the posterior margin of the infratemporal fenestra. Because of its incomplete preservation, it is not possible to determine its anterior and posterior extent. It is
unlikely that the quadratojugal contacted the squamosal, but whether it excluded the quadrate from the infratemporal fenestra is unclear.

The quadrate forms the ventral and posterior margins of the external otic aperture; the element forming the anterior margin cannot be determined due to poor preservation. An oval foramen for a preotic sinus penetrates the quadrate anterolateral to the external otic aperture. The position of the foramen aëreum is difficult to determine, but a small foramen on the mediodorsal surface of each quadrate may indicate its position. These foramina are proximal to the ascending quadrate ramus. If they are indeed the remnants of the foramina aërea, their position is unprecedented among eusuchians. Ventrally, a central depression extends the length of the quadrate. The lateral hemicondyle is dorsoventrally more expansive than the medial hemicondyle.

The maxillary ramus of the ectopterygoid forms the posterolateral margin of the suborbital fenestra. Posterior to the maxillary ramus, the anterior pterygoidal ramus is gently curved and forms the concave posterolateral margin of the suborbital fenestra. The posterior portion of the pterygoidal ramus of the ectopterygoid forms the ventrolateral surface of the pterygoid wings.

The anterior portions of the pterygoids are best preserved; the posterior and lateral portions are missing. The pterygoids are separate bones sutured along the sagittal plane anterior to the internal choanae. The anterior margin of the internal choanae is well preserved and demonstrates that the pterygoids alone surrounded the aperture.

The lateral braincase wall is poorly preserved, and only portions of the laterosphenoids remain. Dorsomedial margins of the preserved elements are strongly bowed laterally, making
room for the pallium. When viewed ventrally, a foramen for the otic capsule (Fig. 12B) is exposed by the missing anteroventral portions of the laterosphenoids.

The dorsolateral margin of the foramen magnum is formed by the exoccipitals. The posterior surfaces of the paroccipital processes are poorly preserved. Lateral to the foramen magnum are two foramina corresponding to the passage for branches of cranial nerve XII. The vagus foramen for passage of the jugular vein and cranial nerves IX-XI is lateral to the passages for cranial nerve XII, though only the medial margin for either is preserved. The descending process of the exoccipital, opening for the carotid artery, and basisphenoid are not preserved.

Mandible—The lower jaw is best preserved in NJSM 11265, and the lateral portion of the right dentary is the most complete element (Fig. 5). The mandibular symphysis is not preserved. There are spaces for 15 alveoli; the tooth positions preserved are unclear, but because the anteriormost preserved alveolus is large, it is likely that alveoli 4 through 18 are represented and each ramus had 18 teeth in life. Alveoli 12-14 of the right jaw preserve intact teeth. The dentary forms the anterodorsal margins of the external mandibular fenestra. Sutural scars on the angular indicate a ‘V’ shaped process of the dentary continuing posteriorly ventral to the anterior portion of the fenestra.

The right splenial is poorly preserved and the left is missing. Sutural scars on the angular suggest that the splenial extended to approximately the same posterior extent as the external mandibular fenestra. Sutural scars on the holotype dentary suggest that the splenial closely approached the mandibular symphysis, but did not actually contribute to it. The anterior tip of the splenial passed dorsal to the Meckelian groove. Coronoids are not preserved.

In lateral view the ventral margin of the angular is convex. Preservation is poor at the anterior and posterior extents of the element, and it is unknown if the angular continued to the
posterior tip of the retroarticular process. The anterior margin is indicated by sutural scars on the
dentary. The angular extends anteriorly to the level of the fifteenth dentary alveolus.

Both surangulars are present but anterior portions are poorly preserved. Sutural scars on
the dentary suggest that two anterior processes of the surangular were present in life and they
were subequal; the dorsal process was longest, the ventral process was almost as long. It is
unknown if the dorsal process contributed to the lateral margins of the posterior dentary alveoli.
The posterior and dorsal margins of the external mandibular fenestra are formed by the
surangular. The lingual foramen for the articular artery and alveolar nerve perforates the
surangular alone and does not lie on the surangular-articular suture. A concavity on the
dorsomedial surface of the surangular spans the surangular-articular sutural contact posteriorly to
slightly over mid-length anteriorly. A small central ridge is present anterior to the anterolateral
margin of the glenoid fossa and contributes to the upturned anterolateral and lateral margins of
the glenoid fossa. The lateral surface of the glenoid fossa is formed by the surangular. Although
poorly preserved, posterior attenuation of the surangular on the preserved part of the
retroarticular process strongly suggests that the surangular did not extend to the posteriormost
extent of the process.

When viewed dorsally, the posterior and medial margins of the articulars are poorly
preserved. Overall shape suggests that the posterodorsally projecting retroarticular process was
triangular in dorsal view. The medial margins of both articulars are damaged, but it is likely that
they expanded medially in proximity to the glenoid fossa, which is oriented anterodorsally and
divided into two sulci separated by a modest crest extending from the anterodorsal angle of the
articular. We do not know which sulcus was largest. No specimen preserves the foramen aëreum
of the articular. The descending articular process is triangular in lateral view and has a concave anterior surface.

Dentition—Tooth morphology is well represented by YPM 274 (Fig. 3C), AMNH 2395 (Fig. 10F), and to a lesser degree, NJSM 11265 (Fig. 5D). Premaxillary teeth are nearly circular in cross-section and bear crowns that are unusually short for their width. The posterior teeth of the dentary are mediolaterally compressed in cross-section. The crowns of the anterior teeth are more conical than those of the posterior teeth. The teeth become progressively more blunt and robust mesiodistally along the tooth row. All teeth display wrinkled enamel with basoapically aligned striations and mesial and distal carinae. Apices of unworn teeth are sharply pointed in the posterior portion of the dental series.

Postcranial Skeleton—NJSM 11265 preserves associated postcranial material (Fig. 7). Vertebrae are procoelous. Numerous cervical and dorsal vertebrae are preserved; sacral and caudal regions are not presently known. The left side coracoid and scapula are present, the latter of which has a moderately narrow dorsal blade, robust deltoid crest, and mediolaterally wide body. The deltopectoral crest of the humerus is robust and is concave proximally. Left and right proximal ulnae are preserved. Four metacarpals and a right radiale are preserved. The ilium has a reduced anterior process and a narrow posterior blade with an indented dorsal border. The femur is sigmoidal in shape and preserves depressions for the caudofemoralis musculature anterior and posterior to the fourth trochanter. Left and right proximal ischia are preserved. All osteoderms are dorsoventrally deep and bear a prominent parasagittal keel. Many osteoderms are square in dorsal view and are presumably from the dorsal shield. A number of osteoderms are round in dorsal view suggesting they may be from the nuchal shield.
**Referral of Material to *Bottosaurus harlani***

A number of specimens (AMNH 2395, AMNH 2397, NJSM 11265, YPM 274) may be referred to *B. harlani* based on a combination of diagnostic dental characters. These specimens possess posterior dentary teeth similar to the paralectotype specimen, ANSP 9174, an isolated posterior tooth. The teeth are mediolaterally compressed in cross-section, display wrinkled enamel with basoapically aligned striations, and mesial and distal carinae. The apices of unworn posterior teeth are sharply pointed.

Additionally, the lectotype specimen, ANSP 9227, bears a tooth whose crown has since been destroyed. Figures and descriptions made prior to loss of the crown indicate that the tooth, from the sixth to eighth position in the dentary, was nearly circular in cross-section, possessed a crown that was slightly taller than it was wide, displayed wrinkled enamel with basoapically aligned striations, and had pronounced mesial and distal carinae. Loose teeth from AMNH 2395 and YPM 274 preserve the same morphology and proportions as the mid-jaw tooth from the lectotype.

Two specimens are tentatively referred to *B. harlani* but cannot be directly compared to the type specimens. Their referral was determined via comparison with more complete specimens referable to *B. harlani*. YPM 325, an isolated tooth, resembles the lectotype in every way but the crown is much longer than it is wide. It has tentatively been assigned to *B. harlani* and resembles teeth from AMNH 2395 and YPM 274. YPM 56140, a partial frontal with associated prefrontals, was tentatively referred to *B. harlani* via comparison to NJSM 11265. Both YPM 56140 and NJSM 11265 bear distinct U-shaped depressions on the frontal at the point of greatest interorbital constriction. As they cannot be directly compared to the type specimens, the identity of YPM 325 and YPM 56140 are subject to further confirmation.
Validity of *Bottosaurus tuberculatus*

Cope published on *Bottosaurus* material from the Hornerstown Formation in his manuscript *Synopsis of the extinct Batrachia, Reptilia and Aves of North America*, printed in three parts between 1869 and 1870. In the first part of the synopsis, printed in 1869, Cope attributes crocodylian material found in Burlington County, New Jersey as belonging to *B. harlani* (Cope, 1869). A year later Cope designated a new species, *Bottosaurus tuberculatus* Cope 1870, and assigned syntypes (ANS 9233; Cope, 1869-1870).

The new species was erected in part upon the material previously referred to *B. harlani* in part one of the synopsis. The change in the specific epithet is manifest in the notes associated with the type material (Spamer and Daeschler, 1995). The note, handwritten by Cope, shows the earliest name associated with the specimens as *Bottosaurus harlani*. The specific epithet was subsequently crossed out and changed to *Bottosaurus tuberculatus* (personal observation, Spamer and Daeschler, 1995).

The *B. tuberculatus* syntype material as published by Cope, ANSP 9233 (Fig. 8), consisted of twenty-seven dorsal, lumbar, sacral, and caudal vertebrae, as well as a mostly intact pelvic girdle and hindlimbs, and about fifty pieces of cranial fragments and osteoderms (Cope, 1870). Of the original material, only 35 fragments remain (Gillette, 1978; Spamer and Daeschler, 1995). It currently comprises a partial frontal, the anterior margin of which is missing, several dentary fragments, four jugal fragments, a partial surangular and articular, eight partial dorsal ribs, two vertebrae that lack neural arches, and two osteoderms. The remains are small relative to other known material assigned to *Bottosaurus*. Shared elements between ANSP 9233 and NJSM 11265 suggest that ANSP 9233 was approximately 1/3 smaller in size. The small size of ANSP
and vertebrae missing their neural arches (suggestive of unfused neurocentral sutures) indicates an immature individual.

The fate of the missing pieces was thought to be unknown, but we believe they are housed in the collections of the American Museum of Natural History. The specimen, AMNH 1411 (Fig. 8), represents a mature individual and matches the material thought to have been missing from ANSP. It is unknown how the syntype specimens were separated (Daeschler, personal communication, 2016; Mehling, personal communication, 2016).

A further complication in determining the synonymy of *B. harlani* and *B. tuberculatus* relates to the lack of adequate figures for *B. tuberculatus*. Of the many pieces seen by Cope, only two vertebrae were figured (Fig. 8; Cope, 1869-1870). The vertebrae are not diagnostic at the species level, resemble those of NJSM 11265, and according to Cope (1869-1870) may be easily confused with those of the basal gavialoid *Thoracosaurus*.

Although the ANSP dentary fragments resemble *B. harlani* in overall proportions, the *B. tuberculatus* syntype material does not preserve autapomorphic characters diagnostic at the species level. As a result, *B. tuberculatus* cannot be distinguished as a separate species from *B. harlani*. Moreover, it is missing important features found in the *B. harlani* holotype and NJSM 11265. The *B. tuberculatus* type does not share the U-shaped depression at the point of greatest interorbital constriction as is found on the frontal of specimens referred to *B. harlani* (Fig. 9), nor does it share the enlarged medial jugal foramen also seen on newly referred specimens. Ornamentation of cranial elements is prominent in the ANSP syntype material, but virtually absent among known *B. harlani* specimens.

Postcranial elements shared between *B. harlani* and the AMNH *B. tuberculatus* (AMNH 1411) bear close resemblance to one another and cannot be distinguished as belonging to
separate species. Femora and ischia are similar in proportions and the ilia bear narrow, indented dorsal margins. Vertebral elements shared between the specimens are similar in proportions and morphology. Osteoderms preserve unusually large, robust keels in the same manner as *B. harlani*.

The osteoderms comprising part of the ANSP *B. tuberculatus* type specimen are roughly square in shape and do not bear a keel. The absence of a marked keel is inconsistent with *B. harlani*, but *Borealosuchus* and *Thoracosaurus* – both found in the Hornerstown Formation – have unkeeled osteoderms. Parasagittal osteoderms from *Borealosuchus* and *Thoracosaurus* are rectangular, but osteoderms lateral to these are square (Troxell, 1925; Brochu et al., 2012). It is likely that the ANSP material represents one of these taxa.


The AMNH material cannot be distinguished from *B. harlani* and might be referable to that species, but the syntype series as a whole belongs to multiple species, some of which may not be alligatoroid; it lacks features that diagnose *Bottosaurus*; and none of it is diagnosable to the level of species. *Bottosaurus tuberculatus* should therefore be considered a nomen dubium.
Discussion

In living crocodylians, prey capture is accomplished primarily by the conical anterior teeth and processed by the less acutely pointed posterior teeth (Erickson et al. 2012). As a result of their differential prey acquisition and processing functions, anterior and posterior teeth may vary in morphology. In _B. harlani_, premaxillary teeth are conical, nearly circular in cross-section, robustly built, and low crowned for their width (Fig. 3C). In lateral view, the posterior teeth of the dentary resemble those of a basal globidontan but with unworn apices that abruptly taper to a point (Fig. 10). The result is a tooth with a mesiodistal length that exceeds its height and an apex that culminates in a point. When viewed dorsally, the posterior teeth are labiolingually compressed, resembling those of modern smooth-fronted caimans (_Paleosuchus_ spp.) and dwarf crocodiles (_Osteolaemus_ spp.). These features, although not unique among crocodylians, are combined in _B. harlani_ to produce a unique dental morphology.

Historically, it was believed that crocodyliform tooth morphology was conservative; but less variation is present in extant species relative to the fossil record (Ősi, 2014). Unlike many crocodylians, the teeth of _B. harlani_ are diagnostic. The large, blunt teeth suggest adaptation for crushing hard prey items. Crowns of the posterior teeth are generally lower and more robust than their anterior counterparts. Due to their close proximity to the cranial adductor muscles and the jaw joint, greater forces would be applied to the posterior teeth relative to their anterior counterparts (Erickson et al., 2012; Ősi, 2014). Tooth shape in _B. harlani_ may thus have served as a mechanical adaptation to aid in crushing prey items before swallowing.
Throughout the tooth row, the teeth preserve apical wrinkling of the enamel. This character was suggested by Erickson (1998) as diagnostic for the species, but wrinkled enamel is widespread among fossil crocodyliforms (e.g., Buscalioni et al., 2001; Prasad and Lapparent de Broin, 2002; Turner and Calvo, 2005; Karl et al., 2006; Martin and Buffetaut, 2008; Ösi and Weishampel, 2009; Andrade et al., 2010; Gupta and Kumar, 2013; Ösi, 2014; personal observation). It was also said to be diagnostic for the giant alligatoroid
Deinosuchus rugosus (Schwimmer, 2002). It is unknown if the wrinkling functions as a mechanical adaptation.

Like the teeth, the jaws and snout of Bottosaurus are divergent from a generalist crocodylian bauplan. The mandibular rami are anteroposteriorly short, circular in cross-section, and very robust. Their great thickness in relation to their length is notable. Preserved maxillary and dentary material suggests an animal with a very blunt snout similar to the modern broad-snouted caiman, Caiman latirostris Daudin, 1801, in overall proportions.

The combination of a robust jaw, blunt snout, and bulbous teeth, in conjunction with data retrieved from the geological/depositional setting of the Rowan Fossil Quarry, suggests that B. harlani was as a continental or near-shore durophagous predator. Although its remains are found in nearshore marine sediments it is unknown if Hornerstown Formation B. harlani lived in continental fluvial settings. It may be that upon death specimens were subsequently washed into the sea. Evidence from stable isotopes suggests that NJSM 11265 could not osmoregulate in saline waters (Wheatley, 2010) and therefore could not have spent extended periods in the ocean.

Harlan (1824) proposed that the species was a specialized consumer of mollusks. This interpretation was adopted by later workers (Case, 1925; Abel, 1928; Källin, 1933, 1936, 1939; Carpenter and Lindsey, 1980). Whether B. harlani was ecologically specialized remains unknown and preferred prey items cannot be discerned; many hard bodied taxa are found in the MFL and turtle fossils are commonly found in sediments containing B. harlani (Harlan, 1824; Gallagher, 1993; Obasi et al. 2011). Recently, B. harlani tooth morphology has been used as evidence of chelonivory (Wheatley, 2010).

Teeth resembling those of B. harlani are found in species of the fossil alligatoroid Brachychampsia, whose ecology has been compared to that of Crocodylus rhombifer (Cuvier
a regular consumer of turtles, to suggest that it was a turtle specialist (Carpenter and Lindsey, 1980). Further ecological comparisons may be made with the blunt snouts and comparatively bulbous teeth of the broad snouted caiman (*Caiman latirostris*) and Chinese alligator (*Alligator sinensis*). Both are regular consumers of mollusks (Erickson et al., 2012) and bear similarities to *B. harlani*. The robust morphology of the snout and teeth in these species ensures greater structural rigidity relative to taxa with longirostrine snouts and more gracile teeth (Erickson et al., 2012). However, that *B. harlani* was a generalist cannot be dismissed, as snout shape is phylogenetically conserved among alligatoroids and not always indicative of present diet and ecology (Piras et al., 2014).

### Phylogenetic Analysis

Methods – The matrix used in this analysis is based on that of Brochu (2013) and Hastings et al. (2013, 2016). Invariant characters were excluded. We added *Bottosaurus harlani* and a new character. Codings for *Culebrasuchus* and *Centenariosuchus* were modified from those of Hastings et al. (2013, 2016) following direct observation of specimens. As such, the matrix in this analysis includes 107 morphological characters and 43 ingroup taxa (Appendix 1).

The following character (107) was added: Frontal lacks (0) or bears (1) a U-shaped depression at the point of maximum constriction between the orbits. Many crocodylians have a crescentic crest between the orbits; this is why *Caiman crocodilus* is often called the “spectacled caiman”. The crest extends from one prefrontal, across the anterior process of the frontal, to the other prefrontal, and although it extends posteriorly between the orbits, it does not extend to the narrowest part of the frontal. The condition in *B. harlani* is different – it circumscribes a deep
depression separating the orbital region from the dorsal surface of the snout, and it extends to the point of maximum interorbital constriction.

A maximum parsimony analysis using TNT v.1.0 (Goloboff, Farris & Nixon, 2008) was conducted. Matrices were managed in Mesquite v.3.04 (Maddison and Maddison, 2015). Traditional heuristic searches performing 1000 replicates of Wagner trees (using random addition sequences) were conducted and followed by the tree bisection reconnection swapping algorithm (holding 10 trees per replicate). Collapsing rules were not applied for the reconstructions. Multistate characters were treated as unordered and characters were equally weighted.

Nodal support was assessed with bootstrapping (Efron, 1979; Felsenstein, 1985) and calculation of Bremer support (Bremer, 1988; Bremer, 1994). Bootstrapping and Bremer support analyses were calculated using TNT (Goloboff, Farris & Nixon, 2008). The topologies obtained during the bootstrap replicates are summarized using GC frequencies (Goloboff et al., 2003).

Results

Maximum parsimony analysis recovered 489 equally optimal trees (tree length = 236, consistency index with uninformative characters removed = 0.54, retention index = 0.80). YPM 274 was attributed to Deinosuchus, but it bears the diagnostic dentition of B. harlani. Given the uncertainty over our referral of this material to B. harlani, we ran the phylogenetic analysis both with and without information from this material. The addition of premaxillary characters derived from YPM 274 increases tree length by one step with no effect on topology. The strict and Adams consensus trees derived from them are broadly consistent with previous results using similar datasets (Fig. 11) (Brochu, 1999, 2004, 2010; Martin, 2007, 2010; Delfino, Martin &
Buffetaut, 2008, Delfino et al., 2008). Crown alligatorids form two primary lineages, one including *Alligator* along with its North American and Eurasian relatives, and the other including the extant caimans and their North American and neotropical relatives. *Leidyosuchus* and Diplocynodontinae are the basalmost alligatoroids in this analysis.

The strict consensus tree recovers a monophyletic Globidonta with Cretaceous globidontans (*Stangerochampsa, Albertochampsa*, and *Brachychampsa*) forming a basal polytomy with alligatorines and caimanines. Shortest trees recover Cretaceous globidontans in two positions, as sister to Caimaninae or sister to Alligatorinae. Trees are one step longer when Cretaceous globidontans are moved outside crown Alligatoridae.

Topology within Alligatoridae is largely consistent with previous analyses (Brochu, 1999, 2004, 2010; Hastings, 2013, 2016; Martin, 2007, 2010), albeit with less resolution, and Caimaninae is recovered with a topology similar to that of Brochu (2010). Resolution is low at the base of Caimaninae because of the labile nature of *Necrosuchus ionensis*, a species known primarily from postcranial and mandibular material.

Adding *Gnatusuchus pebasensis* (Salas-Gismondi et al., 2015), a short snouted caimanine from the middle Miocene Pebas formation of Peru, to the analysis recovers 3000 shortest trees (tree length = 250, consistency index with uninformative characters removed = 0.52, retention index = 0.79). *Gnatusuchus* is recovered at the base of Caimaninae (as demonstrated by Salas-Gismondi et al., 2015) but with decreased resolution relative to its exclusion. Basal caimans form a larger polytomy than before with the inclusion of *Culebrasuchus mesoamericanus*, and *Eocaiman cavernensis*. In addition, neither species of *Paleosuchus* nor *Bottosaurus harlani* form a clade within the basal polytomy. Owing to the decreased resolution and lack of traditionally recovered clades *Gnatusuchus pebasensis* was excluded from the main analysis.
FIGURE 11. Alligatoroid phylogenetic relationships supported by analyses in this study. A, strict consensus of optimal trees for Alligatoroidea and Borealsuchus sternbergii outgroup (tree length = 236, CI excluding uninformative characters = 0.54, RI = 0.80). B, strict consensus of optimal trees for Caimaninae. Numbers above nodes indicate Bremer support, numbers below nodes indicate bootstrap GC values.
Depending on topology within Globidonta, two or three character states unambiguously diagnose Caimaninae: the splenials do not meet at the midline and their anterior tips pass dorsal to the Meckelian groove; the frontoparietal suture is linear between the supratemporal fenestrae; and supraoccipital exposure on the dorsal skull table is large and excludes the parietal from reaching the posterior edge of the skull table. All shortest trees include the first two character states. A subset of the trees, which recover Cretaceous globidontans as sister to Caimaninae, include the third character state.

Traditionally, and in the current analysis, homoplastic characters have been used to diagnose Caimaninae. Two of the three characters diagnosing Caimaninae are shared with other taxa in this analysis. The splenials do not meet at the midline in *Diplocynodon* (save *D. remensis*) and derived species of *Alligator*. The frontoparietal suture is linear in several alligatoroids, including diplocynodontines, *Arambourgia*, and in the last common ancestor of *A. thomsoni, A. mississippiensis*, and *A. mefferdi*.

Its linear frontoparietal suture partly explains inclusion of *Bottosaurus harlani* within Caimaninae in this analysis. Its large dorsal supraoccipital exposure is also caiman-like, but it does not exclude the parietal from the posterior edge of the skull table as is diagnostic for Caimaninae. The condition of the splenial symphysis is uncoded as the anteriormost extent of the splenial is not preserved, but sutural scars on the holotype suggest that the splenial reached the symphysis but did not touch the other splenial. When the condition of the anterior splenial is coded in this analysis neither tree length nor topology are affected.

This analysis recovers a clade including *Bottosaurus* and *Paleosuchus*, but with limited character support. The *Paleosuchus + Bottosaurus* clade is unambiguously diagnosed by the compression of the posterior teeth and alveoli of the maxilla and dentary in cross-section. This is
also shared with the alligatorines *Procaimanoidea utahensis*, *Procaimanoidea kayi*, and *Arambourgia gaudryi* from the Eocene of Wyoming, and France respectively. The posterior teeth of *Paleosuchus* are not especially similar to those of *B. harlani* except for their labiolingual compression; those of *Paleosuchus* have more acute apices and do not look bulbous in lateral view.

*Paleosuchus* and *Bottosaurus* share similar skull table morphologies. The surface is planar, and the lateral sides of the table are nearly vertical. Supraoccipital exposure is large, but the parietal is not excluded from the posterior margin of the table as is found in *Caiman*. Unlike *Paleosuchus*, *B. harlani* bears constricted, but nevertheless open supratemporal fenestrae at maturity. The supratemporal fenestrae are open in *Paleosuchus* at hatching, but they close relatively early in posthatching development.


An enlarged dorsal supraoccipital exposure that does not separate the parietal and squamosals is also found in *Tsoabichi* from the lower Eocene of Wyoming (Brochu, 2010). A subset of the shortest trees in this analysis recovers *Tsoabichi* as closely related to the clade
including *Paleosuchus* and *Bottosaurus* based on this shared character. Brochu (2010) found the *Tsoabichi – Paleosuchus* relationship to be problematic for reasons manifest here. In this analysis and that of Brochu (2010), expression of the supraoccipital on the skull table is treated as an unordered character with four states. However, a transformational series could be inferred in which the character state for the supraoccipital contacting the squamosals is derived from one in which the parietals contact the squamosals. If an evolutionary gradient is present, the conditions in *Bottosaurus, Paleosuchus* and *Tsoabichi* could be a reversal or retained plesiomorphy. Further, the supraoccipital tends to be triangular in dorsal view in *Paleosuchus* and *Tsoabichi*, but trapezoidal in *Caiman/Melanosuchus* and *Bottosaurus* (Fig. 12) (Brochu, 2010).

The unexpected phylogenetic placement of the Upper Cretaceous – Paleocene *Bottosaurus* close to *Paleosuchus*, which is first known from the Miocene, could reflect a true relationship or be the product of convergent evolution. Nodal support for *Bottosaurus + Paleosuchus* is low (Fig. 10). The combination of a large stratigraphic gap and low character and nodal support suggest that the phylogenetic relationship recovered in this analysis is unlikely. Further analyses with more complete *B. harlani* material may lead to a phylogenetic placement outside Caimaninae.

**Biogeography**

Although its position is ambiguously supported, based on this analysis, *Bottosaurus harlani* establishes the presence of a North American caiman in the uppermost Cretaceous or lowermost Paleogene. The oldest unambiguous alligatorine, *Navajosuchus mooki* Simpson 1930, is from the lower Paleocene of New Mexico. This establishes representatives of the sister groups
within Alligatoridae by the lower Paleocene. The fossil first appearances agree with molecular data which suggest a divergence between *Alligator* and *Caiman* near the Cretaceous – Paleogene boundary (Hass et al., 1992; Roos et al., 2007; Oaks, 2011). However, the presence of a derived caiman early in the uppermost Cretaceous or lowermost Paleogene suggests a more complicated biogeographic history than previously hypothesized.

Early caimanine history is poorly understood. A basal caiman in this analysis, Paleocene *Eocaiman cavernensis* Simpson, 1933, is the oldest South American caiman known from relatively complete cranial remains. Other Paleocene caimanines from South America – *Eocaiman paleocenicus* Bona, 2007, *Eocaiman itaboraiensis* Pinheiro et al., 2013, *Necrosuchus ionensis* Simpson, 1937, and *Notocaiman stomeri* Rusconi, 1937 – are known from substantially less complete material. Later well-preserved caimanines do not appear until the Miocene, by which time they are among the most bizarre crocodyliforms known (Price, 1964; Langston, 1966).

South America was isolated for much of the Cenozoic. Relative to crocodylids, alligatorids do not possess physiological adaptations to process excess salt and dispersal capacity of caimanines is thought to have been limited (Taplin and Grigg, 1989). Restriction of the clade to South America would be expected and extant caimans, save a single species (*Caiman crocodilus*), conform to this prediction. Neogene range extensions, postdating the closure of the Isthmus of Panama, result in a natural population of *Caiman crocodilus* extending into southern Mexico (Estes and Baéz, 1985; Venegas-Anaya et al., 2008; Brochu and Carbot-Chanona, 2015) and recent introductions in the Antilles and Florida (Ross, 1998). But evidence indicates that caimanines were present in North America prior to transamerican contact. Fossils from the Upper Cretaceous–Paleocene interval of New Jersey (discussed herein) and the Paleocene and
Eocene of Texas may be referable to Caimaninae (Westgate, 1989; Busbey, 1989; Brochu, 1996).

The presence of caimans in South America by the Paleocene suggests the crossing of marine barriers. That caimanines and alligatorines are both present by the lower Paleocene suggests a divergence during the Late Cretaceous. The separation of North and South America predates the Cretaceous; if vicariance is invoked to explain the distribution of alligatorids considerable range extensions are required. Some authors have proposed a short-lived Late Cretaceous land bridge between North and South America (Lucas and Hunt, 1989; Krause et al., 1992) but marine dispersal in proximity to the Cretaceous – Paleogene boundary interval is the likely explanation for the presence of caimanines in South America.

An exclusively South American clade is predicted if the South American caimans represent a single dispersal event. Resolving *Bottosaurus harlani* as the sister taxon to *Paleosuchus* complicates biogeographic reconstructions for Caimaninae and requires additional dispersal events. If *Bottosaurus* is a close relative of South American *Paleosuchus* and North American *Tsoabichi*, two dispersal scenarios are possible. First, the last common ancestor of the *Tsoabichi* + *Bottosaurus* + *Paleosuchus* clade may have dispersed to North America prior to the K-Pg with the last common ancestor of *Paleosuchus* making a later back-dispersal to South America. A second explanation would involve independent back dispersals of *Tsoabichi* and *Bottosaurus* into North America.

**Diagnosis of Caimaninae**

The character state uniting *Paleosuchus* + *Bottosaurus* in this analysis – labiolingually compressed posterior teeth – is nebulous in its current definition. Compression in the crocodylian
dental arcade often lies on a continuum and is present in varying degrees among distantly related species. Other alligatoroids, especially basal globidontans, show various levels of labiolingual compression of the posterior teeth. A quantitative method, such as a ratio of length to width, might be preferable to the currently-used qualitative paradigm. This effort will do well to alleviate the confusion about what it means to have compressed posterior teeth while increasing replicability in coding the character in matrices.

Historically, taxa outside Alligatoroidea have been allied with the crown group based on characters with a complex phylogenetic history. Paralligatorids and hylaeochampsids, for example, share many cranial features with alligatorids currently thought to have been independently derived (e.g., Ösi, 2014; Turner, 2015).

Incompleteness is also a potential issue. Many basal alligatoroids and early caimanines are poorly preserved, allowing only a fraction of the characters used in current phylogenetic analyses to be assessed. Addition of very incomplete taxa to existing crocodylian matrices has generally caused a loss of resolution without fundamentally changing topology (e.g., Brochu, 1997; Delfino et al., 2007), and most simulation studies agree that fragmentarily known ingroup taxa have a stronger impact on resolving power than accuracy, but they can also impact accuracy in some circumstances (e.g., Huelsenbeck, 1991; Wiens, 1998, 2003).

To address this problem, all known stem alligatoroid taxa must be subjected to phylogenetic analysis. In concert with increased taxon sampling, new characters must be described to clarify relationships within the clade. This task will be challenging, as fossils of freshwater eusuchians with conservative morphologies are often found as isolated and fragmentary bones. In addition, many characters currently used in morphological analyses are sourced from the derived morphologies of crown alligatorids. Molecular phylogenies place the
Alligatorinae-Caimaninae split between 71 and 64 mya (Müller and Reisz, 2005; Oaks, 2011). Basal alligatoroids temporally near the origin of Alligatoridae share similar plesiomorphic morphologies, complicating parsimony analyses. It is these basal members, such as *Bottosaurus*, that warrant additional scholarship and whose morphologies should be the source of morphological characters in future matrices.

Understanding the evolutionary history of early neosuchians, and basal forms within the three crown clades bears on the reconstruction of the ancestral condition for Crocodylia and establishes character state polarity. It is possible that the characters diagnosing more inclusive groups within Crocodylia are homoplastic with older, more basal forms. This would have the potential to unite taxa separated by tens of millions of years such as *Bottosaurus* and *Paleosuchus*.
CHAPTER 2
A SYSTEMATIC REVIEW OF THE GIANT ALLIGATOROID DEINOSUCHUS FROM
THE CAMPANIAN OF NORTH AMERICA AND ITS IMPLICATIONS FOR THE
RELATIONSHIPS AT THE ROOT OF CROCODYLIA

Introduction

Alligatorids are the dominant clade of New World crocodylians; six or more living species of caimanines and one species of alligatorine, opposed to three living species of true crocodiles, are currently recognized (Trutnau and Sommerland, 2006; Grigg and Kirshner, 2015). The oldest known crocodylians are alligatoroids (Brachychampsa, Deinosuchus, Leidyosuchus) from the Campanian of North America; suggesting that the crocodylian fauna of the continent has long been dominated by the clade (Lambe, 1907; Gilmore, 1911; Williamson, 1996; Wu et al., 1996).

During the Campanian Age of the Late Cretaceous North America was divided in two by the Western Interior Seaway. Along the extensive wetlands bordering the coasts lived Deinosuchus, the “terror crocodile.” Fossils referred to species of Deinosuchus have been discovered in ten US states (New Jersey, North Carolina, Georgia, Alabama, Mississippi, Texas, New Mexico, Utah, Wyoming, Montana) and Coahuila, Mexico (Fig. 13). This aquatic ambush predator was the largest carnivore in its ecosystem with some specimens approaching 10 meters (Erickson and Brochu, 1999). Species of Deinosuchus are longer and heavier than its predatory competitors and is known to have fed upon dinosaurs (Schwimmer, 2010).

Species of Deinosuchus share morphology diagnostic of Alligatoroidea but preserve a number of highly derived features in an ancient member of the lineage. As such its phylogenetic
relationships have proven enigmatic. Previously published analyses have recovered species of *Deinosuchus* in a poorly resolved position at the base of Alligatoroidea (Brochu, 1999). Here the authors provide new characters and a reevaluation the three named species of *Deinosuchus*.

FIGURE 13. Map of *Deinosuchus* and *Deinosuchoides* localities in the United States of America and Mexico.

Recently, a number of authors have suggested that *Deinosuchus* is monospecific (Schwimmer, 2002; Lucas, 2006; Irmis et al., 2013) and that the name should be restricted to *D. hatcheri* as it is the first published species bearing the name *Deinosuchus* (Irmis et al., 2013). Additional issues arise as the generic name holder, *D. hatcheri*, is based upon a type that has become undiagnostic with discovery of additional species attributable to *Deinosuchus*. 

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Here the author demonstrates that a more complete understanding of the clade reveals that *D. hatcheri* and *D. rugosus* are based on type specimens that cannot be differentiated to the level of species. A new genus is named to encompass *D. riograndensis* and some specimens historically attributed to *D. rugosus*. Additionally, a new species is named for a number of specimens that have been placed in *D. rugosus*.

Although the name *Deinosuchus* is historically important to professional systematists and the public alike, it is taxonomically most stable to restrict the name *Deinosuchus* to *D. hatcheri* and to name a new genus based on the most complete specimen of *D. riograndensis*, a species with several individuals known from its type locality. It is possible that sometime in the near future additional, diagnostic specimens will be found in the type locality of *D. hatcheri* allowing for a reevaluation of the members of the genus.

**History of the Deinosuchus Type Material**

*Deinosuchus hatcheri*

Currently, there are three recognized species of *Deinosuchus* but their type specimens present numerous problems to the systematist. The generic name holder, *Deinosuchus hatcheri* Holland, 1909 was found in the Judith River Formation of Fergus County, Montana. The holotype specimen, CM 963, consisted of two vertebrae, a pubis, one atlantal rib, one first dorsal rib, numerous osteoderms, and several hundred fragments of bones that cannot be identified to element (Figs. 2-4). Subsequently, the atlantal rib, pubis, and most of the unidentified fragments have been lost. Diagnostic characters consist of massive osteoderms with inflated keels, a pubis that is straighter and less deeply excavated posteriorly than extant crocodylians, dorsal-most
extents of dorsal spines transversely broad, and postzygapophyses nearly on the same plane as the transverse processes (Holland, 1909). Knowledge of crocodilian morphology has increased since the publication of the Holland specimen; accordingly, diagnostic characters were tested against an expanded sample of extinct and living taxa.

Characters diagnosing *D. hatcheri* are shared with specimens referable to other species of *Deinosuchus*. Specimens from Texas and the western interior bear massive, inflated dorsal osteoderms and specimens referable to *Deinosuchus* from Texas and Alabama (TMM 43632-1, TMM 43620-1, ALMNH 1002) preserve dorsal vertebrae whose postzygapophyses are nearly on

the same plane as the transverse processes and bear a transversely broad terminal dorsal spine (Fig. 17). TMM 43620-1 and ALMNH 1002 preserve pubes that bear diagnostic characters in common with the *D. hatcheri* holotype specimen (Fig. 18).

The *D. hatcheri* type was diagnostic when it was named. Subsequent discovery of more complete material attributable to other species of *Deinosuchus* has rendered the *D. hatcheri* type undiagnostic to species level as it cannot be distinguished from *D. riograndensis* or *D. rugosus*. To date no additional specimens of *D. hatcheri* have been found in its type locality.

Characters diagnosing *Deinosuchus hatcheri* are shared with other species of *Deinosuchus*. Additionally, the incomplete nature of the type specimen causes more problems because even though the authors have determined there to be multiple morphotypes that can be differentiated from one another the type species for the genus hinders the assignment of specimens to species other than *Deinosuchus hatcheri*. To ensure taxonomic stability, the name *Deinosuchus* should be restricted to *Deinosuchus hatcheri* and a new genus should be named to encompass those specimens assigned to other species of *Deinosuchus*.

**Deinosuchus rugosus**

Initially, the *Deinosuchus rugosus* (Emmons, 1858) type material was referred to *Polyptchodon*, a name commonly used during the 19th century for the Late Cretaceous crocodylian fauna of Southern England, and whose type specimen was subsequently determined to be a pliosaur (Schwimmer, 2002). Later, Cope (1871) assigned the material to “Thecachampsa” a junior synonym of *Crocodylus* and Hay (1902) reassigned the specimen as “Crocodylus” *rugosus*. The current generic assignment was provided by Baird and Horner (1979) who reevaluated the Emmons type material determining it to be a species of *Deinosuchus*.

Emmons (1858) published figures of two teeth attributed to a new species, “*Polyptchodon*” *rugosus*. Although not explicitly stated, these teeth are the syntypes of *D. rugosus*. Currently, USNM PAL 535447, a single tooth, forms the type specimen of *D. rugosus* (Fig. 19). The location of the second tooth forming the type series is unknown.

The type material was discovered in a Miocene marl bed near Elizabethtown, Bladen County, North Carolina in 1852-1853 (Emmons, 1858). The specific epithet refers to the thick, vertically striated enamel of the teeth used by Emmons to diagnose the species. More complete
eastern Deinosuchus material indicates that the teeth comprising the type specimen are likely from the mid-jaw region. Reference to other species of Deinosuchus indicates that the teeth are not diagnostic to the level of species nor to the level of higher taxa.

Figure 17. Comparison of dorsal vertebrae. A, Deinosuchus hatcheri, CM 963, posterior view. B, Deinosuchoides riograndensis, TMM 43620-1, posterior view. C, Deinosuchoides schwimmeri, ALMNH 1002, posterior view. Scale equals 5 cm

Although recovered in a Miocene marl bed, stratigraphic placement of the holotype specimen is complicated as the teeth were likely reworked from the Middle Campanian Black Creek Formation (Miller, 1967; Baird and Horner, 1979, Schwimmer, 2002). The type locality has yielded other very incomplete specimens which are often found reworked into geologically younger strata. Here, the authors, in agreement with Irmis et al. (2013), assert that the uncertain
stratigraphic placement of the type, undiagnostic morphology, and lack of more complete material from the type locality renders *D. rugosis* a nomen dubium.

**Deinosuchus riograndensis**

_Deinosuchus riograndensis_ (Colbert and Bird, 1954) was named upon a mostly incomplete skull, lower jaw, dorsal vertebra, right scapula, superior portion of a right ilium, osteoderms, and other indeterminate fragments from the Campanian age Aguja Formation of Big Bend National Park, Brewster County, Texas. Issues arise with the original generic assignment of the specimen – _Phobosuchus_ (Nopsca, 1924) is named for a polyphyletic assemblage of South American crocodylians. Colbert and Bird (1954) diagnosed the species on the basis of its large size, robust teeth, inflated osteoderms, and large premaxillary fenestrae lateral to the external naris. Save the premaxillary fenestration, these features do not adequately differentiate _D. riograndensis_ from the types of _D. hatcheri_ or _D. rugosus_.

Preservation of the holotype, as all of the Texas _Deinosuchus_, is via calcium carbonate salts; opposed to the eastern _Deinosuchus_ specimens which are preserved via calcium phosphate salts (Schwimmer, 2002). As such, they are prone to extensive cracking; morphology and sutural
contacts can be obscure. In many specimens, otherwise adequately preserved and mostly free of cracks, sutures are hard to see. The large size of all specimens and relative obscurity of sutural marks may indicate maturity; in late ontogenetic stages bones are fully co-ossified and morphology present in the form of sutural contacts may be lost.

Anatomical Abbreviations

an, angular; ar, articular; bo, basioccipital; cn, cranial nerve; cq, cranioquadrate passage; cr, cavichoncal recess; d, dentary; ect, ectopterygoid; emf, external mandibular fenestra; en, external naris; eo, exoccipital; f, frontal; fae, foramen aereum; fcp, foramen caroticum posterius; fm, foramen magnum; itf, infratemporal fenestra; j, jugal; jp, jugal process; mx, maxilla; mjf, medial jugal foramen; n, nasal; o, orbit; og, ophthalmic groove; pa, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; pot, prootic; pt, pterygoid; ptf, post-temporal fenestra; q, quadrate; qj, quadratojugal; sa, surangular; soc, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; stf, supratemporal fenestra.

Systematic Paleontology of Deinosuchus hatcheri

CROCODYLIA Gmelin, 1789, sensu Benton and Clark, 1988

ALLIGATOROIDEA Gray, 1844

DEINOSUCHUS HATCHERI Holland, 1909

Holotype—CM 963, two vertebrae, cervical rib, dorsal rib, fragments of dorsal ribs, pubis, 27 complete or nearly complete osteoderms, several dozen fragments likely from the vertebrae, ribs, and skull (Figs. 2-4).
Occurrence— Judith River Formation, middle Campanian, Late Cretaceous, three miles west of Nolan and Archer’s ranch along the Willow Creek, Fergus County, Montana, USA.

Referable specimens— None

Diagnosis— “Great size, exceeding that of any other representative of the Crocodilia thus far described from North America. Scutes massive and possessing great vertical height in comparison with their breadth, many of the smaller scutes being almost hemispherical, and some of the smallest subglobose. Pubis straighter and less deeply excavated posteriorly than in recent crocodilia. Extremities of dorsal spines of vertebrae broad transversely and thickened for attachements, much more than in existing genera. The postzygapophyses of the vertebrae more nearly on the same plane as the transverse processes and not looking outwardly as much as in other crocodiles” (Holland, 1909).

Description— Some elements indicated by Holland (1909) are missing. Historically the atlantal rib, pubis, and several hundred indeterminate fragments were preserved. Missing elements were coded into the matrix using figures from Holland (1909). Currently, the atlantal rib, pubis, and most of the indeterminate fragments are missing. The collections manager at CM (Amy Henrici) indicates that they were lost long ago.

The most striking feature of the specimen is its incredible size. Preserved elements shared with other species of *Deinosuchus* may be compared to indicate relative sizes. Osteoderms and vertebrae indicate that CM 963 is the largest known specimen of *Deinosuchus*, although some of the largest *D. riograndensis* specimens approach its immense size.

Two very large dorsal vertebrae are preserved; they are procoelous and preserve long transverse and dorsal processes. The dorsal processes end in a dorsally flat, mediolaterally
expanded tuberosity, likely for the attachment of epaxial musculature. As indicated by Holland (1909), the postzygapophyses are nearly on the same plane as the transverse processes.

The most complete vertebra was determined by Holland (1909) to be the seventh in the dorsal series. However, its position cannot be known with certainty. The element is nearly complete save the right transverse process. The left transverse process bears attachment sites for the dorsal ribs and establishes the identity of the vertebra as belonging to the dorsal series. The dorsal process is very long and ends in a large flattened tuberosity. The less complete of the two vertebrae was uncertainly assigned by Holland (1909) as the last vertebra of the lumbar series. This vertebra preserves a left transverse process, the right side is missing. Both the transverse and dorsal processes are shorter than those of the dorsal vertebra. In addition, the transverse process is narrow relative to the dorsal vertebra. The extremity of the dorsal process is largely incomplete but proportions of preserved bone indicate that it was mediolaterally expanded.

A complete left dorsal rib is preserved. Additionally, one midshaft, three proximal, and four distal rib fragments are present; they likely represent dorsal ribs.

There are 27 nearly complete osteoderms and another 10 in various states of completeness. Elements of the nuchal, dorsal, and sacrocaudal shields are preserved. Most osteoderms are deeply pitted with inflated parasagittal keels resulting in an osteoderm that is lumpy in appearance when viewed anteriorly or posteriorly. Some osteoderms, presumably from the nuchal shield are subglobose; a few are nearly spherical. Pitting is highly reduced in these elements with one preserving no pitting whatsoever. Striations that intersect at 45-degree angles, and approximate the shape of a chevron, cover the ventral surfaces; this morphology is especially evident in dorsal shield osteoderms. The striations are presumably for the attachment of epaxial muscles. A few osteoderms show indentations of their margins, presumably where a neighboring
osteoderm would have fit into. These osteoderms are tentatively identified as belonging to the lateral margin of the dorsal shield.

**Systematic Paleontology of Deinosuchoides**

CROCODYLIA Gmelin, 1789, sensu Benton and Clark, 1988

ALLIGATOROIDEA Gray, 1844

**DEINOSUCHOIDES**, gen. nov.

Type Species—*Deinosuchus riograndensis* Colbert and Bird, 1954.

Included Species—*Deinosuchoides riograndensis, Deinosuchoides schwimmeri*.

Etymology—*Deinosuchoides*, meaning *Deinosuchus*-like; in reference to the resemblance of the new taxon to *Deinosuchus*.

**Systematic Paleontology of Deinosuchoides riograndensis**

CROCODYLIA Gmelin, 1789, sensu Benton and Clark, 1988

ALLIGATOROIDEA Gray, 1844

**DEINOSUCHOIDES**, gen. nov.

**DEINOSUCHOIDES RIOGRANDENSIS**, sp. nov.

Holotype—AMNH 3073 (Figs. 8-12), premaxillae and part of a right maxilla, portions of the left articular, angular, and surangular, right and left splenials and dentaries, six loose teeth, one dorsal vertebra (possibly the twelfth vertebra of the presacral series), right scapula, a possible portion of a right ilium, as well as osteoderms and other indeterminate fragments.

Referable specimens—NMMNH P-30064, TMM 40571-1 (Fig. 28), TMM 43538-1, TMM 43620-1 (Figs. 25-26, 31-33), TMM 43632-1 (Figs. 29-30, 34-37).
Diagnosis—“A eusuchian crocodile of tremendous size, the lower jaw being about 1800 mm (approximately 6 feet) in length. The bones of the skull and jaw are heavy and the teeth are robust. In each premaxilla there is a large fenestra lateral to the external narial opening – a distinctive feature not seen in any other known crocodilian. The single known vertebra is strongly procoelous. The broad scapula indicates that the limbs may have been comparatively heavy. Scutes very heavy” (Colbert and Bird, 1954).

Amended Diagnosis—Bulbous premaxillae bear large, dorsally displaced, fenestrae anterolateral to external naris; naris opens posterodorsally and is wider than long; shallow occlusal marks present on the premaxilla between the first and second alveoli and lingual to the third and fourth alveoli; premaxillary-maxillary notch is posteromedial to the fifth premaxillary tooth; anterior margin of suborbital fenestra acute and extends to the posterior margin of the 12th maxillary alveolus from the end of the toothrow; ophthalmic groove trends anteroposteriorly; osteoderms are very large and bear inflated keels.

Occurrence—Campanian, Late Cretaceous, Aguja Formation west of Glenn Spring, Big Bend National Park, Brewster County, Texas, USA.

Description—Deinosuchoides riograndensis AMNH 3073, this specimen represents a very large alligatoroid from the Campanian age Aguja Formation of the Big Bend region of Texas. It was discovered in 1940 by an expedition of the American Museum of Natural History and excavated by Barnum Brown and Roland Bird.

Many bones are adequately preserved but others such as the premaxillae are composed of many cracked pieces held together by plaster. Oftentimes, bones which are proximal to one another, such as the articualr and surangular, do not fit together. The intervening bone is missing either as a product of the fossil preparation process or due to tectonics and weathering.
The premaxillae are very large and particularly deep relative to their length and width (Fig. 20). AMNH 3073 has the largest and most bulbous premaxillae of all specimens referred to species of *Deinosuchoides*. The elements do not fit together. The edges of the premaxillae, especially along the dorsal midline and the dorsal premaxillary processes, are smooth and indicate that the polished edges were likely created via preparation of the specimen.


The anterior and anterolateral margins of the external naris are formed by the premaxillae. The narial margins are smooth; considerable breakage and reconstruction is present
in the area. Preserved portions of the narial margins on the premaxillae and the maxillary fragment suggest that the external naris opened posterodorsally. Laterally, the dorsal processes of the premaxilla would have wrapped around the posterior of the dome-like anteriormost snout. However, as isolated elements this interpretation is dependent on how the premaxillae are posed; comparisons to more complete specimens may be made. The dorsal processes are short relative to the large size of the premaxillae. Their posterior extent comes to a blunt point when viewed from a lateral aspect. Colbert and Bird (1954) described the dorsal processes of the premaxillae as “…barely reaching back to the level of the space between the first and second maxillary teeth, for which reason they embrace only the anterior border of the external nares.” Additional *D. riograndensis* specimens from Texas agree with this assertion but at the time of their description this could not be verified; the right premaxilla does not fit with the maxillary fragment as there is bone missing between the elements.

Unprecedented among eusuchians is the presence of a large fenestra anterolateral to the external naris. The extreme depth of the premaxillae and the dorsal placement of the fenestrae suggest that they were not for receiving the first dentary tooth as is found in modern forms such as *Caiman crocodilus*. This feature is preserved in both premaxillae but the margins of the fenestrae are incomplete; in life they were likely smaller than what is currently preserved. The fenestrae lead to an internal hollow space within the premaxillae. The anterior wall of the premaxilla bears a dorsoventrally-oriented structure extending from the roof of the element to the middle of the anterior wall. The structure sends a 3 cm shelf-like projection posteriorly into the hollow of the premaxilla. There are large bumps on the floor of the premaxillary cavity where the roots of the premaxillary teeth would have been encased in bone. The bone forming the floor of the external naris is not preserved; the incisive foramen is missing.
Each premaxilla preserves five closely spaced alveoli; a single tooth is preserved. Alveoli 1-3 get progressively larger from mesial to distal, the third and fourth are large, and the fifth is the smallest among the premaxillary arcade. The largest alveolus in the left premaxilla is the third but the third and fourth are approximately the same size on the right side. There is a pronounced difference in the amount of bone separating the third and fourth alveoli among the premaxillae; more intervening bone is present on the left side. It is unknown if these differences are pathologic, taphonomic, or the result of preparation. The fifth position of the left element preserves a partially broken crown of an erupting tooth. Posterior to the fifth alveolus is a large notch for receiving the third and fourth dentary teeth as is found in the basal alligatoroid *Leidyosuchus canadensis*.

The anterior portion of the right maxilla has been preserved (Fig. 21). Its lateral margin is complete; the medial margin is damaged. Intervening bone is missing between the right premaxillary and maxillary fragments. However, the outline of their margins in dorsal and lateral views suggests that they were nearly contiguous. The anterior end of the maxillary fragment bears a large dorsal inflation. Medial to the inflation the bone has been destroyed; preserved portions indicate that the maxilla forms part of the posterior floor and the posterolateral margin of the external naris.

Six alveoli and part of a seventh are preserved on the maxillary fragment. The identities of the alveoli are unknown but comparison to TMM 43620-1, a nearly complete *D. riograndensis* skull from the Aguja Formation, suggests that the fragment preserves maxillary alveoli 1-7. Alveoli in positions 3, 4 and, 6 bear teeth. The tooth in the third alveolus is very large and robust, it is anteroposteriorly compressed and bears a lengthwise groove on its distal side where the maxillary tooth to its posterior would have contacted it. The fourth and sixth
alveoli contain partially erupted teeth. The maxilla is expanded laterally in the region of the first to seventh alveoli. Lingual to the sixth alveolus are anterior and posterior indentations for receiving the teeth of the lower jaw. The animal would have had an overbite in this region.

Colbert and Bird (1954) suggest that a fragment of the right nasal is attached to the maxillary fragment and that the nasals were broad. The author cannot locate the nasal fragment, no sutural marks are present. When viewed from a posterior aspect, the maxillary fragment preserves the opening to the maxillary portion of the cavichoncal recess – a moderately deep, u-
shaped indentation is present on the ventral surface of the posterolateral margin of the maxillary fragment. Colbert and Bird (1954) suggest that this indentation is the anterior-most margin of the suborbital fenestra usually encountered in crocodylians. However, when viewed ventrally the anterior margins of most crocodilian suborbital fenestrae give way to an open space occupied by the adductor muscles. But in AMNH 3073 the anterior of the proposed suborbital fenestra has a bony floor. This feature is not related to the suborbital fenestra due to its unusual morphology and its extreme anterior placement. It is more likely a portion of the cavichoncal recess.

The anterior-most portions of the dentaries are preserved (Fig. 22). The right dentary preserves alveoli 1-7. Alveoli 1-6 are complete and bear teeth. The floor of the first alveolus along with the deeper walls of its posterior are preserved. Superiorly the first tooth curves toward the midline, likely as a result of deformation during burial; preserved alveolar margins suggest that in life the tooth projected somewhat laterally away from the midline. Along the midline existed a space separating the first teeth of the two dentary halves; these teeth would have occluded with the premaxilla behind the space for the first and second premaxillary teeth. The alveoli for teeth 3-4 are confluent on the right side, the teeth themselves lie next to one another with moderate and slight anteroposterior compression of tooth 3 and 4 respectively. This condition is not present on the left side where the alveoli are widely spaced and no teeth are present. Differences in morphology may be a product of taphonomy or pathology. When present, enamel on the teeth is thick. The right fragment preserves the mandibular symphysis which extends posteriorly to the space between the fourth and fifth dentary teeth when viewed dorsally.

The left dentary fragment has spaces for 7 alveoli, the posterior portion of the seventh alveolus is missing. Teeth are present in alveoli 3, 6 and 7. The left fragment shows that the splenial reaches the symphysis but does not touch its counterpart. The two dentaries are not
connected at the mandibular symphysis and when viewed from a medial aspect the symphysis contains an anterior projection of the splenial that extends for no more than one alveolus length (stops before the position of the third alveolus). The left side suggests a splenial that thins dorsoventrally as it proceeds to its anterior-most extent. The splenial is not present or the sutures have been obliterated on the right side.

A large left dentary fragment preserves two teeth. Curvature of the lateral side of the fragment suggests that it came from mid-jaw region of the mandible. The medial portion is not preserved. The fragment is contiguous with the left dentary fragment containing the symphysis. There are large, deep pits on the lateral side for the passage of nerves and blood vessels. No discernable alveoli are present save one which bears a tooth that is missing its crown, is nearly round in cross-section, and has very thick enamel. Deep in the jaw, posteroventral to the erupted tooth, is a developing tooth. Colbert and Bird (1954) suggest that nine alveoli are preserved on the left side of the mandible but there is no evidence for discernable alveoli beyond the anterior portion of the seventh in the anterior fragment and a single alveoli in the mid-jaw fragment.

Both angulares are maintained (Fig. 23). Medially, the mandibular fossa and the posterior margin of the foramen intermandibularis caudalis are preserved. The mandibular fossa is extensive for the accommodation of a presumably large adductor mandibulae to close the massive jaws. The lateral side of the left angular preserves sutural scars where the element likely contacted the splenial which itself may have extended posteriorly to the anterior margin of the foramen intermandibularis caudalis.

A portion of the left posterior mandible preserves the surangular (Fig. 23). At the point of the glenoid fossa there is a lateral expansion of the surangular producing a swelling along the dorsolateral portion of the posterior jaw. An anteroposteriorly oriented groove is present on the
dorsal side, it is confluent with the swelled region of the surangular. This portion of the element does not make contact with the articular fragment bearing the posterior wall of the glenoid fossa. The ascending ramus of the left surangular is preserved and fits into a groove on the lateral side of the left articular.

A partial left articular preserves the retroarticular process and the posterior wall of the glenoid fossa; anteroventral portions of the articular are not preserved (Fig. 23). The ridge forming the posterior wall of the glenoid fossa does not bear signs of the foramen aereum. Although incompletely preserved, sutural scars on the lateral side of the articular suggest that the surangular and angular may have extended to the dorsal-most tip of the retroarticular process.

Six loose teeth are preserved (Fig. 23) but it is of note that seven teeth are figured by Colbert and Bird (1954). Associated notes from the AMNH reconstruction suggest that they are left dentary teeth 2, 3, 5, and 6 as well as right dentary teeth 2 and 8 but this suggestion cannot be verified. The best preserved teeth demonstrate modest mesiodistal carinae. Distal to the second and third teeth, crowns get progressively lower and less dagger-like. The dagger-like and low crowned teeth likely functioned for holding (or tearing) and crushing respectively.

Postcranial elements consist of a single dorsal vertebra, right scapula, a possible portion of a superior right ilium, as well as osteoderms (Fig. 24). Colbert and Bird (1954) suggest that the strongly procoelous dorsal vertebra is the twelfth or thirteenth in the presacral series as both rib articulations are present on the transverse process, articular surfaces on the centrum are absent, and the centrum has a keel. The vertebra is well preserved save the right transverse process and dorsal process which are missing. The left transverse process has been displaced by crushing and is bent superiorly where it contacts the intersection of the left pedicle and lamina. The scapula is shorter than expected for such a large animal and is very robust. The articular end of the element is less flared and constriction of the neck is reduced relative to extant alligatorids. The result of this morphology is an articular end that gently grades into the inferior blade of the element. The margins of the inferior two thirds of the blade are nearly parallel. The superior third
of the blade is strongly flared. A partial right ilium demonstrates that the element was very robust.


**TMM 43620-1 and associated material from Texas**

This specimen (Figs. 13-17) represents a very large individual from the Big Bend region of western Texas. It is similar in size to the AMNH holotype specimen and is the most complete
cranial specimen known for any species of *Deinosuchoides*. Preservation is via calcium-carbonate salts (Schwimmer, 2002); much cracking is present and sutures are difficult to discern.

Premaxillae are preserved. Although some dorsoventral crushing is present, the amount of compressed bone in the region suggests that they were as bulbous as the AMNH holotype specimen (Fig. 15). When viewed laterally, the premaxillary region is the deepest portion of the anterior snout. The anterior margin of the external naris, formed by the premaxilla, would have been situated dorsally relative to the posterior margin formed by the maxilla and nasals; the external naris opens posterodorsally and is wider than it is long. Premaxillary fenestrae are preserved. Relative to the AMNH holotype specimen, they are more proximal to the toothrow. This variation in morphology is likely due to crushing. The dorsal processes of the premaxillae are poorly preserved. However, the anterodorsal maxilla preserves marks where it made contact with the dorsal processes of the premaxillae, and indicates that the processes are short and extend to the posterior margin of the naris. The dorsolateral margin of the external naris is formed by the premaxilla.

Ventrally, the premaxillae preserve five alveoli per side – the first two alveolar positions are small and nearly equal in size, the third position is the largest, the fourth position is nearly as large as the third, and the fifth is the smallest among the premaxillary dental arcade. All premaxillary teeth are preserved but the crowns are missing. The first and second premaxillary alveoli are separated by occlusal marks that are likely formed by contact with the first dentary tooth. These features are relatively shallow and are nearly equal to the diameter of the alveoli they separate. Very shallow occlusal marks are present medial to the junction of the third and fourth alveoli; they were likely formed by the second dentary tooth. TMM 40571-1 (Fig. 28), a smaller individual from the same unit may demonstrate a similar morphology. The incisive
foramen is small, mediolaterally thin, shaped like a teardrop, and extends anteroposteriorly from the fourth premaxillary alveolus to the posterior of the premaxillary-maxillary notch. Ventrally, the premaxilla is mediolaterally constricted at the point of the notch. The posterior premaxillary


margin on the ventral surface of the snout is suggested by faint sutures and separation of bone – it extends to the anterior margin of the third maxillary tooth.

A large notch for receiving the third and fourth dentary teeth is present at the point of premaxillary-maxillary contact. The effect of this morphology is a mediolateral constriction of the snout at the juncture of the premaxilla and maxilla. The anterior and medial margins as well
as the anterior roof of the notch are composed of the premaxilla. The posterior margin and roof is formed by the maxilla. The third and fourth dentary teeth would have occluded into this notch; tooth crowns would have been covered by the roof of the notch formed by the maxilla.

Nasals are present, they are broad along the length of the snout. Margins are obscured at points but general outline is confidently determined. As preserved, the anterior nasals end in a blunt point along the midline where they contribute to the posterior margin of the external naris; it is unknown if they continued anteriorly to bisect the naris. Laterally, the anterior nasals expand and form the posterolateral margin of the external naris. TMM 40571-1 appears to share this morphology. At mid-snout, deformation of the right side has caused the medial maxillary margin to fold over the lateral margins of the nasals. Tentatively it is interpreted that the posterior extent of the nasals separate the anterior processes of the prefrontals from contacting the frontals; sutures are faint and cross-cut by many cracks.

Within the external naris, the lateral walls are formed by the maxilla. In dorsal view, the outline of the maxilla demonstrates pronounced mediolateral constriction at the first maxillary tooth, immediately behind the notch for receiving the third and fourth dentary teeth. Conversely, there are two associated areas of mediolateral expansion along the toothrow. The first corresponds to the area between first and seventh alveoli and the second corresponds to the area between the tenth and fourteenth alveoli. In the expanded regions the diameter of the teeth get larger from the anterior-most alveolus to the alveoli at the mid-point of the swelling and then get progressively smaller toward the posterior.

There are 23 teeth in the maxillary toothrow; including the 5 premaxillary teeth there are 28 teeth per side of the upper jaw. The largest maxillary tooth is in the fourth position; the fifth maxillary tooth is nearly as large. Lingual to the maxillary toothrow are depressions caused by
the occlusion of the dentary toothrow; the animal had an overbite. The posterodorsal portion of the maxilla bears two posterior projections; the first separates the anterior-most jugal from the lacrimal and the second separates the anterior lacrimal from the nasals. In palatal view the maxilla terminates anterior to the lower temporal bar.

The left suborbital fenestra is preserved; its posterior margin is missing. The anterior-most, anteromedial, and much of the lateral margin is formed by the maxilla. The anterior margin ends in an acute point roughly equal to the posterior margin of the 12th maxillary alveolus from the end of the toothrow. Although some breakage is present along the medial margin of the fenestra the anterior margin appears to be smooth and unbroken. TMM 43632-1 (Fig. 29) also preserves the anterior margin of the suborbital fenestra. Although much cracking is present, the reconstruction indicates that the anterior margin may not have been as acute as suggested by TMM 43620-1. As the toothrow is incomplete in this specimen, the anterior extent of the fenestra cannot be determined. TMM 43538-1 demonstrates that posterior processes of the maxilla extend along the lateral margins of the palate and form much of the medial margin of the fenestra.

Palatines, save the posterior-most margins, are preserved. Additionally, TMM 43538-1 preserves an anterior left palatine. Extensive cracking obscures their morphology. The palatines appear to form the anterior and medial margins of the suborbital fenestrae; the medial margin of the left suborbital fenestra, formed by the lateral portion of the palatine, is incomplete. The sides of the elements appear to be parallel as they proceed posteriorly. It is unlikely they produced a shelf extending into the suborbital fenestra, this character was left as uncoded.

TMM 43620-1 does not preserve pterygoids or ectopterygoids but TMM 43632-1 (Fig. 29), a very large individual from the same unit, does. Right and left ectopterygoids are preserved, the left is complete. The posterior flange of a right pterygoid is preserved. The elements are extremely robust. Sutural marks on the right pterygoid suggest that the ectopterygoid did not
extend to the posterior tip of the lateral pterygoid flange. The pterygoid ramus of the ectopterygoid is bowed; the posterolateral margin of the suborbital fenestra formed by the ectopterygoid would have been concave. TMM 40571-1 demonstrates that the maxilla broadly separates the ectopterygoid from contacting the maxillary toothrow.

The lacrimals are complete when information from both sides is accounted for. The anterior-most portions of both lacrimals are obscured due to cracking but likely extended anteriorly to a point roughly equal to the jugals; the anterior extent of the lacrimals is much greater than that of the frontal and prefrontals. The medial and lateral margins are linear for much of their length. The posteromedial margin makes a lateral excursion starting just posterior to the anterior extent of the frontal to the orbital margin. Along this length the lacrimal makes broad contact with the lateral margin of the prefrontal. The posterior extent of the lacrimal forms the anterior margin of the orbit. A dorsoventrally oriented, v-shaped notch is present on the lacrimal along the anterior border of the orbit.

In dorsal view, the margins of the anterior prefrontals are obscured. The most likely position of the sutures is indicated. The anterior extent of the prefrontals ends in a moderately blunt point near the snout’s midline. Dorsoventrally oriented swellings are present on the prefrontal and form the medial orbital margin. The swelling of the prefrontal forms the anterolateral extent of a continuous ridge that forms the medial margin of the orbit. Ventrally, the dorsal-most prefrontal pillars are preserved; the medial processes of the pillars are anteroposteriorly expanded. Anterior to the pillars lie anteroposteriorly oriented elliptical recesses of the prefrontal.

The left jugal is preserved in its entirety, the right jugal is largely un.preserved. The anterior maxillojugal suture trends anteromedially from the lateral margin of the posterior snout towards the midline where it ends in a point. When viewed laterally, the anterior ramus is widest immediately rostral to the orbit. The jugal forms a dorsoventral inflation along the lateral margin of the orbit. The ventral and ventromedial portions of the postorbital bar are formed by the jugal. The bar is relatively robust and is inset from the jugal. When viewed from an anterior aspect the
bar is L-shaped and bows toward the midline at the mid-point of its body. The lower temporal bar is formed by the posterior ramus of the jugal. The posterior portion of the ramus flattens dorsoventrally. Its posterior-most portion of the left jugal is missing; a plaster reconstruction is in its place. Remaining margins suggest that the posteriormost portion of the ramus likely tapered into a point lateral to the lateral condyle of the quadrate. When viewed ventrally, the medial jugal foramen cannot be located due to poor preservation and the presence of matrix.

The anterior frontal appears to terminate in a broad sutural contact with the nasals. The anterior extent of the frontal and prefrontals are not equal; the prefrontals are longer. The lateral edges of the anterior process of the frontal are linear. The medial margin of the left prefrontal is broken, leaving the left lateral portion of the frontal looking asymmetrical relative to the right. The lateral edge of the frontal, forming the medial margin of the orbit, is upturned and confluent with the upturned portion of the prefrontal. The frontoparietal suture is curved; the concave side faces anteriorly. The lateral extent of the frontoparietal suture participates in the supratemporal fenestrae where it meets the frontal-postorbital suture. The skull broke almost directly along the suture leaving it exposed? If looking laterally at the orbits can see a clean break between the frontal and postorbital on the right side.

Skull table and otic region sutures are obscured on the right side but obvious on the left. The skull table, extending from the anterior margins of the orbits to the posterior-most margin of the skull, slopes ventrally toward the sagittal axis. The frontals, parietals, and supraoccipital form the midline furrow. The lateral margins of these elements are raised relative to the midline. Elements forming the lateral margins of the skull table, the postorbital and squamosal, are in a single plane dorsal to the midline furrow. The effect of this morphology is a skull table whose midline is dorsoventrally shallower than that of the lateral margins.
The postorbital is boomerang shaped; its anterolateral corner approximates a ninety degree angle. The element forms the posterior margins of the orbits and the anterolateral margins of the large supratemporal fenestrae. Along the dorsal angle of the infratemporal fenestra the postorbital contacts the quadratojugal. Much of the postorbital bar is formed by the postorbital; the postorbital process of the postorbital extends along the dorsolateral face of the bar. Although broken on the right side, the anterolateral side of the post-orbital, just ventral to the skull table, bears a shallow pit-like indentation with postorbital foramina allowing for the passage of postorbital blood vessels. The anteroventral portion of the postorbital, when viewed laterally, bears an anteroposteriorly oriented groove near the suture with the anterior projection of the squamosal; posterovernteral to the groove on the postorbital is a confluent groove on the squamosal. In life a muscular ear flap would attach to the groove.

Dorsally, the parietal is hourglass shaped between the supratemporal fenestrae. A constriction is present at the point of the medial margin of the supratemporal fenestra – which is formed entirely of the parietal. The parietal sends a ventral process into the supratemporal fenestra. However, sutural margins are difficult to interpret and appear to differ between the sides. The parietal sends posterior processes to each side of the supraoccipital and reaches the posterior margin of the skull table. When viewed from a posterior aspect, the parietal comprises the dorsomedial margin of the left post-temporal fenestra which is preserved in its entirety.

The supraoccipital is incompletely preserved; the posterior portion of the element is missing. However, other specimens (TMM 43538-1, TMM 43632-1) from the same unit completely preserve the supraoccipital (Fig. 30). The element is broadly exposed on the dorsal skull table; its length is abbreviated. The result is a half-moon shaped exposure that culminates in a blunt point at its anterior extent. When viewed posteriorly, the supraoccipital is shaped like a
cut diamond gemstone; its dorsolateral extent on the posterior skull forms the ventromedial margin of the post-temporal fenestra. Posteriorly, the body of the supraoccipital bears mediolaterally trending indentations. The indentations are separated by a dorsoventrally oriented medial ridge.

The squamosal forms the posterolateral corner of the skull table. The postorbital-squamosal suture is concave when viewed dorsally and is located at the midpoint of the lateral margin of the supratemporal fenestra. The parietal-squamosal suture trends anteromedially from the posterior margin of the skull table and intersects the supratemporal fenestra at the midpoint of its posterior margin. Along the posterior wall of the supratemporal fenestra the parietal-squamosal suture makes a lateral excursion and intersects the anterior opening of the posttemporal fenestra within the supratemporal fenestra. Laterally, the squamosal forms the roof of the otic aperture and the dorsalmost margin of the infratemporal fenestra. The dorsal and ventral rims of the squamosal groove flare anteriorly. The posterolateral ramus of the squamosal is short and lies on top of the lateral extent of the paroccipital process of the exoccipital. When viewed posteriorly the squamosal forms the dorsolateral margin of the post-temporal fenestra.

The left quadratojugal is preserved but the posteriormost extent has been reconstructed out of clay; the right quadratojugal is missing. The dorsal exposure of the quadratojugal is approximately twice as wide as the ventral exposure. The quadratojugal forms the posterior margin of the infratemporal fenestra. The suture joining the jugal and quadratojugal lies at the posterior angle of the infratemporal fenestra. TMM 43538-1 demonstrates that a quadratojugal spine projects into the infratemporal fenestra along the posterior wall between the posterior and superior angles. A dorsal process of the quadratojugal reaches the dorsal corner of the infratemporal fenestra and contacts the squamosal.

The left quadrate is mostly complete. Like the left quadratojugal, the posteriormost extent has been reconstructed. The quadrate forms the floor of the otic aperture and the ventral portion of the anterior wall along the external auditory meatus. Ventrally, the quadrate bears modest crests for the attachment of the m. posterior adductor mandibulae, they are oriented...
anteroposteriorly along its body. The dorsalmost portions of the quadrate underlying the skull table are preserved but the ventral portions in this area have been lost. Although incompletely preserved, the anterodorsalmost extent of the left quadrate underlying the supratemporal fenestra approaches the capitate process of the laterosphenoid; the elements may have made contact in life. Along the lateral braincase wall the quadrate forms the posterior roof of the trigeminal foramen. TMM 43632-1 preserves an incomplete ventromedial portion the quadrate. The quadrate forms the floor of the cranioquadrate passage and recess. TMM 43632-1 preserves the hemicondyles; the medial hemicondyle is smaller than its lateral counterpart (Fig. 29).

The laterosphenoids are incompletely preserved in TMM 43620-1; ventralmost portions are missing. The laterosphenoid forms the anterior margin of the trigeminal foramen. TMM 43632-1 also preserves dorsal portions, less bone is missing relative to TMM 43620-1, but sutures separating braincase elements are obscured. A pronounced anteroposteriorly trending ophthalmic groove is present on the laterosphenoid anterior to the roof of the trigeminal foramen.

The exoccipital forms the ventrolateral margin of the post-temporal fenestra. Posteriorly, the paroccipital process of the exoccipital is laterally expansive and dorsoventrally wide. The lateral-most extension of the paroccipital process lies ventral to the posterior squamosal prong and makes extensive contact with the quadrate. When the posterior skull is viewed laterally, the exoccipital sends an extension of the paroccipital process into the otic aperture; a thin process contacts the external auditory meatus near its posteroventral corner. Ventrally, the roof of the cranioquadrate recess is preserved on the posterolateral exoccipital. The ventralmost portion along the midline preserves the roof of the foramen magnum. When viewed from a ventral aspect this region is posteriorly expanded.
TMM 43632-1 preserves the ventral exoccipital. The robust ventral process of the element terminates dorsal to the basioccipital tubera and preserves openings for cranial nerves and blood vessels. Four depressions, likely representing in-filled foramina for the passage of cranial nerves, are present per side of the ventral process of the exoccipital. The dorsal-most depression, presumably for the passage of cranial nerve XII, is lateral to the foramen magnum and is separated from the other depressions by a short distance. The other depressions are separated by mediolaterally trending ridges. The dorsal-most and deepest of the contiguous depressions is roughly triangular in shape, is lateral to the ventral margin of the foramen magnum, has what appear to be small foramina inside its margins, and conveyed branches of cranial nerves IX, X, and XI as well as the jugular vein. Below is the smallest depression, whose sides are nearly parallel and is bordered by pronounced mediolaterally trending ridges. The function of this depression is unknown. The ventral-most opening is nearly the same size as the dorsal-most opening but is very shallow. No obvious foramina are present within its borders, its function is unknown.

TMM 43620-1 does not preserve a basioccipital but TMM 43538-1 and TMM 43632-1 do. Preservation is best in TMM 43632-1 (Fig. 30). The element forms the floor of the foramen magnum. Ventral to the occipital condyle, the external surface of the basioccipital is posteriorly oriented. Along the midline, directly below the condyle, lies a relatively large foramen representing the external manifestation of the median eustachian canal. Ventral to the midline foramen, an acute ridge separates dorsoventrally trending depressions of the posterior basioccipital tubera. The edges of the ventral and ventrolateral basioccipital tubera have been chipped away; the external openings of the medial and lateral eustachian foramina are missing. A pronounced wing-like ridge lies lateral to the ventralmost occipital condyle. The ridge trends
dorsoventrally and is expanded anteroposteriorly resulting in a structure that projects outward from the posterolateral surface of the basioccipital tubera. TMM 43632-1 likely preserves the posteroventral basisphenoid but sutures are obscured and morphology cannot be determined.

Complete lower jaws are preserved for TMM 43620-1 (Fig. 31); they are broken at the mandibular symphysis but the left side is largely intact and shows little to no evidence of deformation. The jaw is robustly built and nearly 1.5 meters in length. The mandibular symphysis is short and does not extend posteriorly beyond the fourth dentary alveoli. Posterior to the mandibular symphysis, the mid-jaw alveoli gradually curve medially. The anterior-most alveoli lateral to the mandibular symphysis are oriented sub-parallel to one another. When viewed laterally, the dentary forms the anterior margin of the mandibular fenestra. Two posterior projections of the dentary are present. The dorsal-most of the two projects between the anterior processes of the surangular while the ventral projects into the anterior angular. The dorsal projection bears the anterior portion of a longitudinal depression that is confluent with the surangular that forms the posterior portion of this depression.

The third and fourth dentary alveoli are confluent; their shared margin is oval in shape and is raised relative to the body of the anterior dentary. Anterior teeth appear to project somewhat more buccally than teeth to their posterior. The left jaw preserves a complete lower toothrow; there are spaces for 23 alveoli. The posteriormost alveoli are incompletely preserved on the right side. The right dentary preserves teeth in alveoli 2, 4, 12, 13, 15 and a posterior alveolus of unknown identity. Teeth are present in alveoli 1 and 4 on the left side; the first tooth is complete, the fourth tooth is missing its crown. The first tooth projects anterodorsally and would have occluded into a space between the first and second teeth of the premaxilla. Although
missing in both dentaries, the margin of the third alveolus suggests that the third tooth was the largest in the lower jaw; the fourth dentary tooth was nearly as large as the third. Teeth are large in two regions of the lower jaw. Anteriorly, the third and fourth alveoli are large, in the mid-jaw the eleventh and twelfth alveoli are large. The twelfth and fifteenth teeth have depressions on the medial sides near the base of the crown. These depressions were likely caused by resorption as a replacement tooth grew under the affected teeth. As the maxilla preserves evidence of an overbite in this region the depressions were not caused by occlusion of the upper jaw dentition.

The left splenial is nearly complete. Anteriorly, it tapers along the body of the lower jaw where it reaches the mandibular symphysis but does not touch its counterpart. The splenial overlays the medial side of the jaw anteriorly until the space between dentary alveoli 11 and 12 where it laps onto the dorsal side of the jaw and follows the toothrow medially. The posterodorsal portion of the element extends past the toothrow and continues to the anterodorsal margin of the coronoid. The splenial bounds the anterior half of the foramen intermandibularis medius. Due to poor preservation in this region the participation of the splenial in the foramen intermandibularis caudalis is unknown; remaining portions suggest that it may have formed the anterior margin.

The coronoid is preserved; the anterior margin is somewhat damaged. The superior margin of the element slopes anteriorly. The coronoid bounds the posterior half of the foramen intermandibularis medius and forms the dorsal margin of the foramen intermandibularis caudalis. The coronoid sends two short, blunt projections anterior to the foramen intermandibularis caudalis. They are positioned dorsal and ventral to the foramen.

The surangular sends a process anteriorly along the medial margin of the 23rd alveolus. The anterior processes of the surangular are incompletely preserved on both sides of the lower jaw. The dorsalmost of the anterior processes is preserved on the left side, the anterior-most ventral process is missing. Sutural marks on the dentary suggest that they were equal to subequal – this is confirmed by TMM 40571-1 which preserves the anterior processes. The notch between the two anterior projections bears a foramen. This structure is the posterior-most feature in a lengthwise groove that trends anteriorly along the dentary to the space between the 17th and 18th alveolus. The surangular forms the dorsal and posterior margins of the external mandibular fenestra. The lateral wall of the glenoid fossa is formed by the surangular. Posteriorly, sutural
marks on the articular indicate that the surangular extended to the dorsal tip of the retroarticular process.

When viewed medially, the angular forms the posterior and ventral margins of the foramen intermandibularis caudalis. The dorsal margin is also formed by the angular which sends an acute process toward the anterior margin of the foramen. The angular-surangular suture makes broad contact with the external mandibular fenestra along its ventral margin. Posteriorly, the angular continues to the dorsal tip of the retroarticular process.

The articular forms the ventral margin of the external mandibular fenestra. The glenoid fossa, save the lateral wall, is formed by the articular. The retroarticular process is relatively short but broad. TMM 43620-1 preserves a medially-shifted depression on the articular posterior to the glenoid fossa that may represent remnants of the foramen aerum. Unfortunately, no specimens referable to this species preserve structures that may be confidently identified as the articular foramen aerum. Along the point of contact with the medial surangular and angular there is cracking and matrix present; no other specimens adequately preserve this area and characters representing this region’s morphology were not coded.

TMM 43620-1 preserves portions of the axial skeleton and both limb girdles. Numerous osteoderms are present and some are in association (Fig. 32). All have inflated keels and lumpy, deeply pockmarked ornamentation. An axial rib is present but missing both rib heads. The tuberculum is wide and the dorsal tip is acute. A large dorsal rib is preserved, the rib head is missing. Three phalanges of unknown identity are preserved. Four vertebrae from the dorsal series are preserved. These vertebrae are likely from the lumbar region as the long transverse processes do not bear articular surfaces for rib capitula. The vertebrae were discovered in association and proportions suggest that they were contiguous in series. When present, dorsal-
most neural spines demonstrate a mediolateral swelling for the attachment of epaxial musculature.

Preserved forelimb and girdle elements consist of a coracoid, radius, ulna, and humerus (Fig. 33) The left coracoid is preserved and demonstrates that the blade of the element flared ventrally. A foramen is present immediately anterior to the posterolaterally flaring glenoid fossa. A right humerus and left radius and ulna are preserved. The distal epiphysis of the ulna is complete.

TMM 43620-1 hindlimb girdle elements consist of an ilium and pubis (Fig. 33). The anterodorsal portion of the right ilium is maintained but is poorly preserved. The left pubis is preserved; its blade flares anteriorly. The shaft is broadly curved to the anterior but cracking is present at the juncture of the blade and shaft; extent of curvature may be taphonomic.

TMM 43632-1 expands our understanding of *D. riograndensis* postcranial material (Figs. 22-25) A left femur is preserved; a portion of the mid-shaft is missing. The proximal epiphysis is bulbous and nearly featureless. The lateral condyle of the distal epiphysis is much larger and anteroposteriorly more expansive than the medial counterpart. A distal end of an unknown carpal or tarsal is preserved. Fragments of dorsal and cervical ribs are preserved. A single metatarsal is preserved, the distal epiphysis is missing. Fifteen vertebrae are preserved; four cervical and eleven dorsal. The cervical vertebrae possess relatively short ventral keels.

Referral of Material to *Deinosuchus riograndensis*

In addition to the holotype specimen AMNH 3073, four additional specimens are known from the Big Bend region of west Texas. These specimens preserve numerous elements that may or may not be referable to what is preserved by the holotype. TMM 43620-1 may be referred to *D. riograndensis* on the basis of the preservation of the bulbous premaxillae with associated premaxillary fenestration, shallow occlusal marks present on the premaxilla between the first and second alveoli and lingual to the third and fourth alveoli, and large, inflated osteoderms.

TMM 40571-1 cannot be referred to *D. riograndensis* via comparison to apomorphies preserved by the holotype specimen – although difficult to verify, it may preserve some of the ventral margin of the left premaxillary fenestra. However, this specimen shares the same locality and proportions of the holotype and other specimens referable to the species. Although poorly preserved, a premaxillary fragment may possess a shallow occlusal mark lingual to the third and fourth premaxillary alveoli as is found in the holotype and the most complete specimen referable to *D. riograndensis*. Additionally this specimen demonstrates that the maxilla broadly separates
the ectopterygoid from contacting the maxillary toothrow. Two swellings of the maxillary toothrow are preserved; the first swelling is between maxillary alveoli one and seven and the second is between the tenth and fourteenth alveoli. The first swelling agrees with preserved portions of the holotype. Although incompletely, it is likely that this specimen preserves a premaxillary-maxillary notch on the left side. Like TMM 43620-1 the nasals are broad and swell anteriorly to form the posterior margin of the external naris. Although having underwent extensive preparation and reconstruction, the lower jaw resembles that of TMM 43620-1 in proportions and has the same amount of alveoli. Additionally, an anterior projection of the surangular extends along the medial border of the posteriormost alveolus as is found in TMM 43620-1.

TMM 43538-1 represents the right half of a skull from an individual that is slightly smaller than TMM 43620-1. It is from the Big Bend region of West Texas. This specimen does not preserve any apomorphies found in the *D. riograndensis* holotype specimen but elements in common with the holotype and specimens referable to *D. riograndensis* are of similar proportions and morphologies. Although incomplete, proportions and outline of the skull table, supratemporal fenestrae, otic region, and posterior skull are in broad agreement with TMM 43620-1. Medial and anteromedial margins of the orbits are slightly upturned as is found in TMM 43620-1.

TMM 43632-1 represents a very large individual from the Big Bend region of West Texas. It preserves a posterior skull and skull table, portions of the upper and lower jaw, and numerous limb and axial skeleton elements. It shares inflated osteoderms with the *D. riograndensis* holotype specimen. Additionally, a bulbous left premaxilla is preserved which maintains the ventral margin of the premaxillary fenestra and the portion of the premaxillary-
maxillary notch formed by the premaxilla. Ventrally, the premaxilla preserves parts of five premaxillary alveoli. Proportions of the skull table and supratemporal fenestrae match that of TMM 43620-1.

**Systematic Paleontology of Deinosuchus rugosus**

CROCODYLIA Gmelin, 1789, sensu Benton and Clark, 1988

ALLIGATOROIDEA Gray, 1844

*DEINOSUCHUS RUGOSUS* Emmons, 1858

Holotype— USNM PAL 535447, one tooth (Fig. 19).

Referable specimens— none

Diagnosis— “Teeth thick and conical, and slightly curved; transverse section circular or round; enamel traversed longitudinally by numerous rugose cracks, the strongest of which reach the apex; no trenchant edges or carinae proper” (Emmons, 1858).

Occurrence— Miocene marl bed, likely washed out of the middle Campanian, Late Cretaceous, Black Creek Formation along the Cape Fear River, Elizabethtown, Bladen County, North Carolina, USA.

**Systematic Paleontology of Deinosuchoides schwimmeri**

CROCODYLIA Gmelin, 1789, sensu Benton and Clark, 1988

ALLIGATOROIDEA Gray, 1844

*DEINOSUCHOIDES SCHWIMMERI*, sp. nov.

Holotype— MMNS VP-256 (Figs. 26-28)

Referable specimens— ALMNH 1002, TMM 45973-1
Diagnosis—Deep occlusal marks present on the premaxilla between the first and second alveoli and lingual to the third and fourth alveoli; premaxillary-maxillary notch is lateral to the fifth premaxillary tooth; angular, posterior to external mandibular fenestra, is dorsoventrally expanded so as to form a hump on the dorsal margin; anterior margin of suborbital fenestra blunt and extends no further than the tenth maxillary alveolus from the end of the toothrow; ophthalmic groove trends dorsoventrally.

Occurrence—Early to middle Campanian, Late Cretaceous, Coffee Sand Formation, along Tulip Creek near Tupelo, Lee County, Mississippi, USA.

Etymology—The specific epithet is named in honor of David R. Schwimmer for his tireless work on *Deinosuchus*.

Description—This specimen represents a beautifully preserved posterior skull and partial lower jaw (Figs. 26-28) from the Coffee Sand Formation of Lee County, Mississippi. The right side of the skull preserves a greater number of complete elements and clearer sutural contacts than the left side. The skull table, extending from the orbits to the posterior margin of the skull, slopes ventrally toward the sagittal axis forming a furrow. The furrow is formed by the frontals, parietals, and supraoccipital and whose lateral margins are raised relative to the midline. The lateral margins of the skull table and those elements contributing to it, the postorbitals and squamosals, are in a single plane dorsal to the midline. The midline is doroventrally shallower than that of the lateral margins.

Posterior nasals are preserved. They widen posteriorly and make broad contact with the anterior margin of the frontal. The nasals send posterior processes that bound the anterior projection of the prefrontal so that the projection does not contact the nasals or lacrimals.
The anterior maxilla, along with the rest of the anterior snout, is missing. Posteriorly, the maxilla sends a short, acute posterior process between the lacrimal and nasal and a blunt process between the lacrimal and jugal. A posterolateral process of the maxilla separates the anterolateral jugal from contacting the lateral margin of the snout. Ventrally, the maxilla preserves spaces for 13 posterior alveoli. Assigning tooth positions from the posterior, teeth, minus their crowns, are in positions 3-6 and 8-13. The teeth get smaller in diameter moving posteriorly along the toothrow. Preserved portions indicate that dentine and enamel are thick; posterior teeth have very small pulp cavities. The maxillary foramen for the palatine ramus of cranial nerve V is relatively small and is situated medial to the junction of the twelfth and thirteenth alveoli from the posterior. The maxilla separates the ectopterygoid from contacting the posterior toothrow. The maxilla forms the anterior, anteromedial, and anterolateral margins of the anteroposteriorly expansive suborbital fenestrae. The right suborbital fenestra is better preserved than the left; its posterior margins are missing. Anteriorly, the fenestra ends in a blunt point approximately in line with the junction of the tenth and eleventh alveoli from the posterior. The maxilla sends a posterior process into the lateral palatine along the medial margin of the suborbital fenestra where it extends to in-line with the eighth alveolus from the posterior.

Ventrally, the anterior right palatine is preserved. The maxillopalatine suture is nearly linear and is mediolaterally oriented; the sutural contact is complex. Preserved portions indicate that the palatines contributed to the medial margins of the suborbital fenestrae.

Dorsal portions of the ectopterygoids are preserved; ventral portions have been lost. Ventrally, at the juncture of the postorbital bar and the jugal, the ectopterygoid sends a blunt, broadly curved, process medially along the ventral base of the bar. The jugal face of the element is separated from the ventrolateral margin of the skull by a short distance. Anteriorly, the

maxillary face of the element sends a process forward parallel to the posterior maxillary toothrow and ends in an acute point at the anterior margin of the sixth maxillary tooth from the posterior. The ectopterygoid is separated from the posterior toothrow by the maxilla.

The jugals are long and broad. The maxillojugal suture trends anteromedially from the lateral margin of the posterior snout towards the midline. The anterior extent of the jugal is nearly as long as the lacrimal and ends in a blunt point. An alternative interpretation indicated by cracks on the dorsal surface of the posterior snout is that the jugal does not approach the anterior extent of the lacrimal and ends in a broadly curved sutural contact with the maxilla. The jugolacrimal suture is nearly linear. The anterior ramus of the jugal is widest immediately anterior to the orbit. The jugal forms the lateral margin of the orbit whose edge is upturned. The ventral portion of the postorbital bar is formed by the jugal; the bar is inset from the lateral jugal surface. The bar is relatively robust and when viewed from an anterior aspect the bar is L-shaped and at the mid-point of its body bows toward the midline of the skull. When viewed ventrally, the medial jugal foramen cannot be located due to poor preservation but a small unrelated foramen is present posterior to the confluence of the posttemporal bar and the lower temporal bar. The lower temporal bar is formed by the posterior ramus of the jugal. Posteriorly, the jugal tapers into a point where it meets the quadratojugal at a suture that trends posterolaterally from the posterolateral corner of the infratemporal fenestra to the lateral margin of the skull.

Both lacrimals are preserved, the right element demonstrates clear sutural contacts. The anterior lacrimal ends in a blunt point. Sutural contacts with the jugals, nasals and prefrontals are broad, nearly linear, and trend anteroposteriorly. The lacrimal extends slightly further to the anterior, and much further to the anterior, than the jugal and prefrontal respectively. The posterior lacrimal is somewhat mediolaterally constricted compared to the anterior. A
dorsoventrally oriented, v-shaped notch is present along the anterior margin of the orbit which is formed by the lacrimal.

Prefrontals are preserved; the anterior margins end in an acute point bounded anteriorly by the nasals. The prefrontals exceed the frontal in their anterior extent. Along much of its length the prefrontofrontal suture is anteroposteriorly oriented and nearly linear; at the posterior-most extent the suture forms a nearly right angle and trends mediolaterally to the medial margin of the orbit. The prefrontal forms the upturned anteromedial margin of the orbit. Ventrally, the dorsal prefrontal pillars are maintained; they are expanded anteroposteriorly. Anterolateral to the pillars lie anteroposteriorly oriented elliptical recesses of the prefrontal.

Anteriorly, the frontal ends in a blunt point where it contacts the nasals. The lateral edges of the anterior process of the frontal are linear. Posteriorly, the frontal forms the upturned medial margin of the orbit which is confluent with the upturned anteromedial margin formed by the prefrontal. The frontal contacts the postorbital anteriorly at the posteromedial corner of the orbit. The frontoparietal suture is curved; the concave side faces anteriorly. Posterolaterally, processes of the frontal form part of the anterior margin of the supratemporal fenestrae. When viewed internally, the projection that forms the anterior margin also forms the anterior wall of the fenestra and prevents the parietal from contacting the postorbital.

The anterior margin of the orbits are telescoped. The prefrontals, lacrimal, and jugals contribute to this morphology. The gently upturned medial margins formed by the frontal are confluent with the telescoped anterior margin formed by the prefrontal, lacrimal, and jugal. The result is that the anterior and medial margins of the orbit are cup-like and are formed in part by contributions of the frontal, prefrontal, lacrimal, and jugal.
The postorbital forms the posterior margins of the orbits and the anterolateral margins of the large supratemporal fenestrae. The postorbital-squamosal suture intersects the supratemporal fenestra along the midpoint of the lateral margin. The postorbital contacts the quadrate and the quadratojugal along the dorsal angle of the infratemporal fenestra. The postorbital process is moderately inset from the anterolateral margin of the skull table and extends along the dorsolateral face of the postorbital bar forming much of the structure. When viewed laterally, the anteroventral portion of the postorbital bears an anteroposteriorly oriented groove near the suture with the anterior projection of the squamosal. This groove is confluent with a groove on the squamosal and in life formed the attachment site for the muscular ear flap.

The parietal is hourglass shaped. Dorsally, the element forms the medial margins of the supratemporal fenestrae and within the fenestrae the medial walls. The anterior margin of the parietal enters the supratemporal fenestrae via lateral processes; these processes form the anteromedial walls of the fenestrae. Lateral to the supraoccipital, the parietal reaches the posterior margin of the skull table via posterior processes. Sutural contact with the squamosals are nearly linear and trend posterolaterally from the posterior margin of the supratemporal fenestrae to the posterior skull table. Along the posterior wall of the supratemporal fenestrae the parietal-squamosal suture makes a lateral excursion where it intersects the medial margin of the temporal canal. When viewed from a posterior aspect, the parietal-squamosal suture intersects the post-temporal fenestrae midway along the dorsal margin. The parietal comprises the dorsomedial margins of the post-temporal fenestrae.

The squamosal forms the posterolateral corner of the skull table. The posterolateral margins of the supratemporal fenestrae are formed by the element. Within the fenestra the squamosal forms the posterolateral wall. All margins, save the medial, of the temporal canal are
formed by the element. Laterally, the squamosal forms the roof of the otic aperture, the posterior margin of the external auditory meatus, and the dorsal-most margin of the infratemporal fenestra. The dorsal and ventral rims of the squamosal groove, for attachment of the external ear valve musculature, flare anteriorly then slightly contract at their anteriormost extent. The posterolateral ramus of the squamosal is relatively short. The ventral portion of the posterolateral ramus of the squamosal lies on top of the lateral extent of the paroccipital process of the exoccipital. When viewed from a posterior aspect, the squamosal forms much of the dorsal margin of the post-temporal fenestra.

The supraoccipital is shaped like a half moon; the breadth of the element exposed on the dorsal skull table greatly exceeds the length. A blunt point is present at its anterior extent. When viewed posteriorly, the supraoccipital is shaped like a cut diamond gemstone whose dorsal margin is ventrally indented. Posteriorly, the medial margins of the post-temporal fenestrae are formed by the dorsolateral margins of the element. The posterior body of the supraoccipital bears mediolaterally trending indentations separated by a medial ridge which extends from the dorsal skull table to the ventral margin of the element.

The exoccipitals are complete and form the ventral margin and floor of the posttemporal fenestra; the floor of the fenestra is visible when the skull is viewed dorsally. Anteriorly, very little of the element is preserved on the lateral braincase; ventral portions are missing. The paroccipital process is wide and makes extensive contact with the quadrate. The element extends further laterally than the posterior squamosal prong which sits on top of the paroccipital process of the exoccipital. Ventrally, and somewhat medial to the lateralmost extent of the paroccipital process, the exoccipital forms the roof of the cranioquadrate recess, the floor of the recess is formed by the quadrate. The dorsal and lateral margins of the foramen magnum are formed by
the exoccipitals. Lateral to the occipital condyle, the element preserves openings for cranial nerves and blood vessels. These features are clearest on the left side. Three openings are preserved, they are separated by slight ridges. The dorsal and ventral foramina are roughly the same size and are deeper than the opening in the middle position. The dorsal foramen, lateral to the dorsal-most occipital condyle, bears foramina within its margins but the identities of the cranial nerves and blood vessels that passed through the foramina are unknown. The middle and ventral depressions bear no obvious foramina within their margins, their function is unknown.

The dorsal basioccipital remains but ventral portions have been lost. The floor of the foramen magnum is formed by the element. The occipital condyle is formed by the basioccipital; some breakage is present on the right ventral margin of the condyle. The dorsal occipital condyle has a slight ventral dip when viewed laterally.

Much of the anterior and ventral laterosphenoids are missing. Sutures separating braincase elements are difficult to discern. The anterior margin of the trigeminal foramen is formed by the element. Laterally, the capitate process is oriented anteroposteriorly toward the midline. The laterosphenoid makes a robust contact with the quadrate ventral to the postorbital. The element preserves the ophthalmic groove which trends dorsally as it moves from the trigeminal foramen to the anterior.

Quadratojugals are preserved, the right side is complete. The posterior margin of the infratemporal fenestra is formed by the element. The jugoquadratojugal suture is linear and intersects the posterior angle of the infratemporal fenestra anteriorly. The element preserves a quadratojugal spine that projects into the infratemporal fenestra along the posterior wall between the posterior and superior angles. A dorsal process of the element reaches the dorsal corner of the infratemporal fenestra where it contacts the squamosal.

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Quadrates are preserved, the right side is complete. Dorsally, the element forms the floor of the otic aperture. The ventral and anterior walls of the external auditory meatus are formed by the quadrate. The squamosal-quadrate suture extends to the posterodorsal corner of the external auditory meatus. Posteroventrally, modest crests for the attachment of the posterior adductor mandibulae muscles are present, they are oriented anteroposteriorly along the posterior ramus. The anterodorsalmost extent of the quadrate, ventral to the supratemporal fenestra, makes contact with the capitate process of the laterosphenoid. The ventral process of the quadrate is significant and forms much of the lateral braincase wall. The posterior half of the trigeminal foramen is formed by the quadrate. The floor of the craniocaudal recess is formed by the quadrate. The medial hemicondyle is incompletely preserved; it is unknown which hemicondyle was larger in the species. The quadrate foramen aerum could not be located.

A partial jaw is preserved (Fig. 40). Portions of the left dentary, splenial, surangular, angular, and articular are preserved along with a more complete right articular and right coronoid. The splenial is very fragmentary; no characters were coded for the element. The posteriormost dentary maintains the anterior, anterodorsal, and anteroventral margins of the external mandibular fenestra. All margins of the fenestra are chipped but proportions and contribution of elements is clear. Posteroventrally, the dentary stops anterior to the external mandibular fenestra but possible sutural marks on the angular attest to the dentary extending along the ventral margin of the external mandibular fenestra.

The surangular is poorly preserved; anteriorly, medially, and posterodorsally much bone is missing making description difficult. The posterodorsal margin of the external mandibular fenestra is formed by the element. The surangular-angular suture contacts the external mandibular fenestra along its ventral margin. Sutural marks on the right articular suggests that
the surangular formed the lateral margin of the glenoid fossa. Characters near the juncture of the surangular, angular, and articular were not coded due to poor preservation. Sutural marks on the retroarticular process suggest that the surangular reached the dorsal tip of the articular. The angular is incompletely preserved; the anterior and posterior-most margins are missing. The element forms the posteroventral margin of the fenestra. To the posterior of the fenestra the element expands dorsoventrally such that the dorsal margin has a pronounced hump when viewed laterally. Sutural marks on the articular suggest that the posterior margin of the angular extended to the dorsal tip of the retroarticular process. Although incompletely preserved, the angular forms the posterior and ventral margins of the foramen intermandibularis caudalis. The angular appears to send a process to the anterior and possibly formed part of the dorsal margin as well. Posterior to the foramen the angular becomes dorsoventrally more expansive resulting and a hump-like morphology of the dorsal margin on the medial side of the element.

A right coronoid is preserved; the anterior margin is damaged in places. The element appears to form the posterior margin of the foramen intermandibularis medius. As it is disassociated from the jaw its contribution to the margins of the foramen intermandibularis caudalis is unknown. Although disassociated, the superior margin of the element appears to slope anteriorly, this character was left uncoded in the matrix.

The left jaw fragment preserves a fragment of the ventral articular. A right articular is present but is disassociated from other jaw elements. The left fragment does not preserve any codable morphology. The right fragment preserves the glenoid fossa and the retroarticular process. A depression likely representing the foramen aerum of the articular is inset from the lingual margin of the posterodorsally projecting retroarticular process.

Five partial loose teeth are associated with MMNS VP-256. Enamel is thick. Three are small posterior teeth, one of which preserves a complete crown which is roughly conical and short-crowned. Two are larger anterior dentary or maxillary teeth, one preserves a tall conical crown. The largest and most complete of the crowns demonstrates a slight carina on the mesial and distal sides.

**TMM 45973-1**

This specimen consists of a complete snout and lower jaw (Figs. 29-30) and represents a relatively large individual from the lower Campanian Mooreville Formation of Lowndes County, Alabama, USA. The specimen was found on the west bank of the Alabama River approximately 200 meters upstream from the ACE Lock and Dam. Surficial bone is deteriorating from pyrite disease; a grey powdery substance has replaced fossilized bone in affected areas. The bone has two textures: one is powdery, light tan in color, and feels slightly rough to the touch; the other texture is dark tan in color and smooth to the touch. Powdery tan areas obscure sutures likely as a result of pyrite disease. The posterior of the snout near the right orbit and along the posterolateral margin of the left side has been reconstructed with a dark tan clay. The skull has experienced dorsoventral crushing. Reconstruction efforts were made to separate the palatal portions from the roof of the snout but palatal elements are largely in a single plane. Some of the 3D morphology is obscured but spatial relationships are maintained. The anterior portion of the snout bearing the premaxillae is in a poor state of preservation. The anteroventral portion bearing the premaxillary
alveoli suggests that the anterior snout was moderately deep; it is not likely that the depth equaled that of *D. riograndensis*.


The sutural contacts between the nasals and other elements are clearest in the anterior snout. The anterior nasals are laterally expanded and form the posterior margin of the external naris. Along the midline the nasals project into the posterior naris. There is evidence of broken
bone, in life the projection may have extended further forward but proportions suggest that it would not have extended far enough to bisect the large external naris. Preserved margins suggest that the naris was very wide.

The premaxilla is preserved but the anterior portion is disassociated from the rest of the skull; dorsal margins are largely destroyed. The premaxilla has five alveoli per side. The left side preserves five alveoli with five broken teeth. The right side of the element preserves alveolar positions one, two, and the anterior margin of the fourth; the first position bears a broken tooth. Where the third alveolus is predicted to be, there is bone overgrowth or the products of pyrite disease. Proportions of the teeth can be determined from the left side. Teeth in positions one and two are small, teeth in positions three and four are large, the fifth tooth is small. Among the premaxillary teeth, the third tooth is the largest and the fifth is the smallest. Posterior to the space between the first and second teeth there is a groove produced by the occlusion of the first dentary tooth with the premaxilla. A second groove is present between the third and fourth premaxillary teeth. This groove was likely produced by occlusion with the second dentary tooth. Posterior to the fourth alveolus and posteromedial to the fifth is a large groove for receiving the third and fourth dentary teeth. When viewed from the anterior, the mesial and distal-most premaxillary toothrow is dorsally displaced relative to the third and fourth premaxillary teeth. The effect is a ventral bulge of the premaxilla at the point of the third and fourth alveoli. Posterolateral margins of the element are preserved. Sutures with the maxilla are mediolaterally oriented and trend anteriorly toward the midline. The anterior extent of the posteroventral element may bear remnants of the incisive foramen.

The maxilla is preserved, the right side is nearly complete save its ventral surface. Due to pyrite disease and the powdery texture of surficial bone, sutures on the dorsal side of the snout
are very difficult to determine. The anteriormost maxilla is missing; the element’s contribution in the external naris is unknown. There are 28 teeth in the upper jaw, 23 maxillary, 5 premaxillary. The right side has the best preservation of the toothrow and comparison to MMNS VP-256 suggests that the posteriormost alveoli are preserved. The animal had an overbite in life as suggested by occlusal marks lingual to the maxillary toothrow. Posterodorsally, the maxilla sends a posterior process between the anterior processes of the lacrimal and jugal; additional processes separating posterior snout elements are impossible to determine.

Two mediolateral expansions along the maxillary toothrow are present. The first occurs in the area between the first and seventh alveoli and the second corresponds to the area between the tenth and fourteenth alveoli. The former expansion is pronounced and the latter is minimal. In the anterior part of the first expansion the diameter of the teeth get larger from the anteriormost alveolus to the alveoli at the mid-point of the swelling and then get progressively smaller toward the posterior. Whether the posterior region also does this is not obvious. The fourth maxillary alveolus is the largest, the fifth appears to have been nearly as large. Suborbital fenestrae are large. Their posterior margins are missing; the anterior margin extends as a blunt point to the ninth alveolus from the end of the maxillary toothrow. The maxilla forms the anterior margin and much of the medial and lateral margins. The maxilla sends a posterior process separating the palatines from the anteromedial margin of the fenestra.

The sutures uniting the left and right palatines are present between the suborbital fenestrae. The skull is dorsoventrally compressed in this area and the posterior-most margins of the element are missing. Much of the anterior palatines are obscured or missing. The palatines make up part of the medial margins of the suborbital fenestrae.

The dorsal side of the posterior snout is poorly preserved; much bone is missing and remaining bone is affected by pyrite disease. Some regions are reconstructed from clay. The sutural contacts between the lacrimals and maxilla are clear on the right side. The lacrimals are long and wide. Their anterior extent ends in an acute point beyond the anterior-most extent of the jugal. The sutural contact with the broad jugal is nearly linear. The jugal is best preserved on the right side and ends in a blunt point.
The ectopterygoids are preserved, the right element is more complete. The maxillary face of the ectopterygoid extends along the maxilla to an acute point medial to the anterior margin of the fifth alveolus from the posterior. The maxillary face is broadly separated from the posterior toothrow by the maxilla. Posterior to the maxillary face a fraction of the jugal face of the ectopterygoid is preserved.

A complete right mandible is preserved (Fig. 42); the jaw has been twisted during burial, elements have been offset. Along the lingual margin of the jaw, pyrite disease has caused fossilized bone to be replaced by iron sulfide minerals. The number of teeth in the lower jaw is unknown; the posterior toothrow is very fragmentary.

The dentary is fragmentary in its anterior and posterior extents. Anteriorly, the mandibular symphysis is missing along its medial margin; the lingual margins of some anterior teeth are preserved. It is impossible to determine whether the third and fourth dentary alveoli were confluent. Dorsoventral crushing is present at the point of the external mandibular fenestra; it is likely that the dentary contributed to the anterior and dorsal margins of the fenestra.

A disassociated, partial splenial is present. The lateral side of the element preserves the Meckelian groove. No characters were coded for the element.

The surangular is preserved. The anterior processes of the surangular are subequal. A process of the surangular extends anteriorly along the medial margin of the final alveolus; the anterior-most tip of the process is missing. The surangular-angular suture passes broadly along the ventral margin of the external mandibular fenestra. Although crushed, it appears that the surangular forms the posterodorsal margin of the external mandibular fenestra. The lateral margin of the glenoid fossa is composed of the surangular, the articular forms the remaining margins of the fossa. Characters near the juncture of the surangular, angular, and articular were
not coded due to poor preservation. Sutural marks on the retroarticular process of the articular suggest that the surangular and angular reached the tip of the retroarticular process.

The angular is preserved but some crushing is present anteriorly. The element likely forms the posteroventral margin of the external mandibular fenestra. Posterior to the fenestra, the element expands dorsoventrally; the dorsal margin has a pronounced hump when viewed laterally. The posterior margin of the angular extended to the dorsal tip of the retroarticular process as evidenced from sutures on the articular. The entire ventral margin, and part of the posterior margin of the foramen intermandibularis caudalis are preserved, they are formed by the angular. Posterior to the foramen, the medial side of the angular becomes dorsoventrally expansive.

A nearly complete articular is preserved. The element preserves the glenoid fossa and the retroarticular process. The foramen aerum of the articular cannot be located. Poor preservation and pyrite disease makes morphology of the medial jaw, where the articular, surangular, and angular meet impossible to code.

**ALMNH 1002**

This specimen is tentatively assigned to *D. schwimmeri* and represents the most complete postcranial skeleton attributable to the species. The specimen represents a small, immature individual from the lower Campanian Mooreville Formation near West Greene, Greene County, Alabama, USA. Hind limbs, vertebrae, chevrons, and numerous osteoderms are preserved.

Hind limbs and limb girdles are mostly complete. Left and right ilia are present. The iliac anterior process is virtually absent and the dorsal margin of the iliac blade is rounded with modest dorsal indentation. The supraacetabular crest is narrow. Fragmentary pubes are present,
blades fare anteriorly. Shafts are short and curve to the anterior. Ischia are complete. The limbs are represented by both femora, complete left tibia and fibula, and a distal right tibia and fibula. A left astragalus and calcaneum, and two tarsals of unknown identity are present. Metatarsals I-III and V are present on the right side, the left side preserves metatarsals I-IV. Six phalanges are preserved, it is unknown which limb(s) they are from.

Numerous posterior vertebrae are preserved from the dorsal through caudal series. Some neural arches are fully coossified with the vertebral centra indicating that this specimen represents a nearly mature individual. Nine dorsal vertebrae, both sacral vertebrae, and seventeen caudal vertebrae are preserved. The anterior sacral rib capitulum projects anteriorly of the tuberculum and is visible in dorsal view.

Numerous osteoderms are preserved representing most parts of the dorsal and nuchal shields. Dorsal surfaces are deeply pitted. Smaller osteoderms, presumably from the nuchal shield, are oval in shape and bear inflated keels. Larger osteoderms, likely from the dorsal shield, are rectangular in shape. Some are nearly flat in anterior or posterior view with small keels. Others bear inflated keels.

**Referral of Material to Deinosuchoides schwimmeri**

TMM 45973-1 is from the lower Campanian Mooreville Formation of Lowndes County, Alabama, USA. This specimen was found in a similar geologic context to the holotype specimen from the Coffee Sand Formation of Lee County, Mississippi, USA. The Mooreville Formation is a facies equivalent of the contemporaneous Coffee Sand Formation (Cushing et al., 1964). In addition to their similar proportions, size, and geologic context, TMM 45973-1 may be referred to *D. schwimmeri* based on a similar angular morphology. Like the holotype, the angular of
TMM 45973-1, posterior to the external mandibular fenestra, is dorsoventrally expanded so as to form a hump on the dorsal margin. Additionally, the anterior margin of the suborbital fenestra is blunt in both the holotype specimen and TMM 45973-1; it extends no further than the tenth maxillary alveolus from the end of the toothrow.

ALMNH 1002 does not share elements with the holotype and thus cannot be definitively referred to *D. schwimmeri*. This specimen has been tentatively referred to the species based on size and geologic context; both ALMNH 1002 and the holotype specimen are from the Mooreville Formation. Some osteoderms preserve keels that are inflated.

**Comparisons**

**Opening of external naris**

The direction in which the external naris opens was left uncoded for *D. schwimmeri*. Orienting the premaxillary and maxillary elements attributed to AMNH 3073 suggests that the external naris opened posterodorsally. However, this is based on the assumption that the elements, which are not articulated or contiguous, are oriented as they would be in life. The anterior snout of TMM 43620-1 has been dorsoventrally crushed but overall proportions suggest that the external naris projected posterodorsally. No complete anterior snout is known for *D. schwimmeri* specimens but a posterior narial margin is known for TMM 45973-1, a specimen recovered from Alabama.

Among other large bodied alligatoroids (e.g. *Mourasuchus* and *Purussaurus*) large external nares are common. The large external naris found in species of *Deinosuchus* is shared with most species of *Purussaurus* and *Mourasuchus amazonensis* but is achieved in different
ways. Species such as Purussaurus mirandai Aguilera, Riff, and Bocquentin-Villaneuva, 2006, and Purussaurus brasiliensis Barbosa-Rodrigues, 1892, have external nares that are much longer than they are wide, such that the posterior extent of the narial aperture approaches the orbits. The external naris in species of Deinosuchoides is wider than it is long and resembles Mourasuchus amazonensis Price, 1964, in its proportions. Unlike M. amazonensis, in which the premaxilla forms the entirety of the narial aperture, the nasals contribute to the posterior margin of the external naris in species of Deinosuchoides. Additionally there is considerably more bone separating the external naris from the margins of the snout producing the more robust morphology found in species of Deinosuchoides.

**Supratemporal fenestrae**

The supratemporal fenestrae of Deinosuchoides are large relative to extant alligatoroids and occupy much of the skull table. Large supratemporal fenestrae appear to be common to many basal taxa and are found in fossil taxa such as Leidyosuchus canadensis, species of Borealosuchus, Bernissartia fagesii and gavialoids. Additionally, enlarged supratemporal fenestrae are associated with longirostran species both in the modern and fossil records. The increased thickness of elements surrounding the supratemporal fenestrae is of note in species of Deinosuchoides. Most species with large supratemporal fenestrae generally achieve this morphology through decreased skeletal robusticity surrounding the structure.

**Occlusal marks on the premaxilla**

On the left premaxilla of the D. riograndensis holotype, lingual to the space separating the third and fourth alveoli, is a small depression caused by the occlusion of the second dentary
tooth. TMM 43620-1, a \textit{D. riograndensis} specimen of similar size to the holotype shows the development of a similarly shallow depression. A \textit{D. schwimmeri} specimen from Alabama (TMM 45973-1) demonstrates an occlusal mark in the form of a deep groove (Fig. 44).

![Figure 43](image)


The development of a deep groove would be expected in the large \textit{D. riograndensis} specimens if due to wear through ontogeny. However, TMM 45973-1 represents a smaller individual relative to the \textit{D. riograndensis} specimens from Texas. The very deep occlusal mark in this \textit{D. schwimmeri} specimen is not likely the end-member of a transformational process such as is found in mature \textit{Caiman crocodilus} where repeated occlusion of the fourth dentary tooth on the maxilla initially forms a pit and over time transitions to a groove.
There are additional differences in occlusal patterns between the species in the form of the pits present posterior to the juncture of the first and second premaxillary teeth. There are shallow occlusal marks between the first and second teeth in AMNH 3073 and TMM 43620-1, two *D. riograndensis* specimens of similar size from Texas. TMM 45973-1, a *D. schwimmeri* specimen from Alabama demonstrates very deep occlusal marks posterior to the space between the second and third alveoli. Ontogeny cannot account for the differences in occlusal morphology.

**Premaxillary-maxillary notch**

The position of the fifth premaxillary tooth relative to the premaxillary-maxillary notch differs between *D. riograndensis* and *D. schwimmeri*. The notch is posteromedial to the fifth premaxillary tooth in *D. riograndensis*. Only the anterior margin of the notch is preserved for *D. schwimmeri* but differences in morphology are evident; the anterior margin of the notch is lateral to the fifth premaxillary tooth.

The premaxillary-maxillary notch found in species of *Deinosuchoides* is not likely to be due to wear from prolonged occlusion as many specimens are presumably full grown. The notch is more like that of *Leidyosuchus canadensis* or species of *Diplocynodon* and *Borealosuchus*. In these species the notch is present throughout ontogeny. This condition is in opposition to a similar but unrelated morphology found in *Caiman crocodilus* where the fourth dentary tooth occludes into a pit on the upper jaw before it transitions through ontogeny to an open notch.
Premaxillary fenestrae

The premaxillary fenestrae appear to be autapomorphic for *D. riograndensis*. Complete premaxillae are known for *D. riograndensis* but not *D. schwimmeri*. Portions of the ventral and ventrolateral margins of the fenestra may be preserved by additional *D. riograndensis* specimens, TMM 40571-1 and TMM 43632-1 respectively. When complete, the anterior premaxillae in these specimens bear large fenestrae that are wider than they are tall. It cannot be determined whether specimens of *D. schwimmeri* have this feature as this area is not preserved in any referred specimen.

The holotype of *D. riograndensis*, AMNH 3073, possesses premaxillary material that is very bulbous. The premaxillae belonging to TMM 43620-1, an animal approaching the size of the holotype specimen, are dorsoventrally compressed due to burial. The amount of compressed bone in the region suggests that it its proportions were nearly as bulbous as the holotype material.

*Mourasuchus amazonensis*, also has large fenestrae present on the premaxilla; they are wider than they are long and are slightly inset from the premaxillary toothrow. The fenestrae are approximately the diameter of an anterior dentary tooth in the species. Although the fenestrae are situated somewhat dorsally on the premaxilla, the anterior snout is not particularly deep. They were likely formed by the occlusion of the dentary teeth on the roof of the premaxilla. Other species of *Mourasuchus* are known to have one or more foramina per side of the premaxilla for receiving the anterior dentary teeth (Cidade et al., 2017).

The function of the very large premaxillary fenestrae in *D. riograndensis* is unknown. It is unlikely that they are for receiving enlarged first dentary teeth; the anterior dentary teeth would have to reach unprecedented lengths and diameters for a crocodilian to form these
fenestrae. Extant species bearing holes in the premaxilla for the occlusion of dentary teeth demonstrate that the fenestrae are approximately the same diameter as the occluding teeth. This is evident as the formation of the fenestrae are products of continued occlusion against the premaxillary surface over ontogeny. In species of *Deinosuchoides* the fenestrae are many times the diameter of the anterior dentary teeth and are situated far more dorsally than any known species. The hypothesis that they were formed by occlusion must be discounted and an alternative hypothesis must be presented.

The fenestrae could have functioned as a means to lighten the anterior snout. The mass of the bone forming the very deep anterior snout is considerable. Large fenestrae could be an adaptation to the increased mass in this area. However, the anterior snout functions as a means by which to capture prey, and the prey consumed by the taxon was presumably very large. It would seem that large fenestrae at the tip of the snout would be selected against if they dramatically weakened the anterior snout. Yet the effect of this morphology does not seem to hinder the geographic and geologically widespread occurrence of species of *Deinosuchus*. An additional hypothesis may be forwarded that the fenestrae were for supporting soft tissues. But there is no evidence in the form of accessory growths of bone in the region or neurovascular foramina in the area around the fenestral margins.

**Mediolateral expansion of maxilla**

The mediolateral expansion of the lateral margin of the maxilla varies between specimens of *D. riograndensis* and *D. schwimmeri* in two ways: first, the posterior expansion of the maxilla is less pronounced in *D. schwimmeri*, second, the diameter of the teeth in the second region of expansion show less variability for *D. schwimmeri* relative to *D. riograndensis*. 
Both TMM 43620-1 (*D. riograndensis*) and TMM 45973-1 (*D. schwimmeri*) have complete maxillary toothrows. Additional specimens of *D. schwimmeri* (MMNS VP-256) and *D. riograndensis* (TMM 40571-1) possess the posteriormost fourteen alveoli and first fifteen maxillary alveoli respectively. Comparison to TMM 45973-1 indicates that approximately sixty percent of the maxillary is toothrow preserved in MMNS VP-256 with no deformation. TMM 40571-1 appears to show slight deformation of the preserved toothrow – posterior alveoli are oriented slightly laterally rather than ventrally.

*Deinosuchoides schwimmeri* and *D. riograndensis* specimens, preserving the entire maxillary toothrow, have a mediolaterally-oriented anterior expansion of the maxilla between the first and seventh alveoli and a second expansion between the tenth and fourteenth alveoli. The species differ in the second region of expansion – it is less pronounced in specimens referable to *D. schwimmeri*. In the expanded regions of specimens referable to *D. riograndensis* the diameter of the teeth get larger from the anterior-most alveolus to the alveoli at the mid-point of the swelling and then get progressively smaller toward the posterior. This is only true for the first region of expansion in specimens referable to *D. schwimmeri*, the posterior expansion does not show obvious differences in tooth diameter. The *D. schwimmeri* holotype specimen, although missing the first alveolus of the swelling, agrees with the *D. schwimmeri* specimen from Alabama (TMM 45973-1), teeth of this region are of a similar diameter relative to specimens referable to *D. riograndensis*.

**Skull table**

The skull table of *Deinosuchoides* is reminiscent of gavialoids, *Bernissartia fagesii*, *Leidyosuchus canadensis*, and species of *Borealosuchus* but preserves a combination of
morphological characters not found in these taxa. Lateral margins of the skull table are nearly parallel and are oftentimes constricted anterior to the squamosal rami. The anterolateral corners of the skull table are angular in dorsal outline. Additionally, the taxa share similarly shaped, proportionally large supratemporal fenestrae. Unique among alligatoroids, the skull tables of specimens referred to Deinosuchoides have lateral margins which are higher relative to the midline so that a deep furrow is present along the sagittal axis.

**Foramina for cranial nerves on the exoccipital**

Specimens preserving ventral exoccipitals bear foramina or depressions lateral to the occipital condyle but proportions vary between specimens referable to *D. riograndensis* and *D. schwimmeri*. TMM 43632-1, a *D. riograndensis* specimen from Texas has dorsal foramina, lateral to the foramen magnum and separated from the other depressions by a short distance, that are not found in MMNS VP-256, a *D. schwimmeri* specimen from Mississippi. This is likely due to differential preservation in the area and not as a product of divergent evolution between the forms. In the *D. riograndensis* specimen this dorsalmost foramen is likely for the passage of cranial nerve XII.

In both *D. riograndensis* and *D. schwimmeri*, lateral to the occipital condyle, lie three depressions separated by a series of ridges. The deepest depression in TMM 43632-1 (*D. riograndensis*) and MMNS VP-256 (*D. schwimmeri*) is the dorsalmost of three. It is roughly triangular in shape in *D. riograndensis* but is more oval in *D. schwimmeri*. In both species this depression bears foramina within its margins presumably for the passage of cranial nerves and blood vessels. In *D. riograndensis* the middle foramen is much smaller than the dorsal and ventral foramina, is trough-like and elongate, and has roughly parallel sides. In *D. schwimmeri*
the middle foramen is only slightly smaller than the other foramina, is oval in shape, and is separated from the other two by slight ridges. In both species the ventralmost opening is nearly the same size as the dorsalmost opening but is very shallow. No obvious foramina are present within its borders, the function of this depression is unknown.

The morphology of the three depressions lateral to the occipital condyle is unique to species of *Deinosuchoides*. As evidenced by the foramina within its borders, the dorsal-most depression is for the passage of cranial nerves and blood vessels but the functions of the depressions ventral to it are unknown. The prominence of the ridges separating the depressions, a lack of foramina within the borders of the middle and ventral structures, and shallow depth of the depressions indicate that their likely function may not have been for the conveyance of cranial nerves and blood vessels but rather for the attachment of epaxial muscles.

**Ophthalmic groove**

A trough emanates anterodorsally from the foramen ovale and whose path trends towards the orbits. This combination of factors leads the authors to conclude that the trough corresponds to the path of the ophthalmic branch of the trigeminal nerve. Although this structure is variably present in other species of Crocodyloids it is more pronounced in species of *Deinosuchoides*, likely as a result of the large size of the taxon and the need to convey proportionally larger neurovascular bundles.

The directionality of the groove varies between those specimens preserving the area. In TMM 43620-1 and TMM 43632-1, specimens referred to *D. riograndensis*, the groove is roughly anteroposteriorly trending whereas in the *D. schwimmeri* holotype specimen (MMNS
VP-256) the groove is more dorsoventrally oriented. The functional significance of this variation is unknown.

**Suborbital fenestrae**

Colbert and Bird (1954) suggest an extreme anterior extent of the suborbital fenestra in the *D. riograndensis* holotype (AMNH 3073). Upon inspection, the feature was misidentified as the anterior margin of the suborbital fenestra; it is most likely part of the cavichoncal recess as the specimen does not preserve the suborbital fenestrae. TMM 43620-1 is the only *D. riograndensis* specimen to adequately preserve the suborbital fenestrae. The anterior margin is acute and extends to the posterior margin of the 12th maxillary alveolus from the end of the toothrow. As reconstructed, an additional *D. riograndensis* specimen from Texas (TMM 46320-1) preserves a blunt anterior margin of the fenestra. The specimen is extensively cracked and has been subject to considerable preparation and reconstruction with plaster or clay. It is unknown to which alveolus the structure extended to in this specimen. The *D. schwimmeri* holotype (MMNS VP-256) preserves a suborbital fenestra whose anterior margin is blunt and extends to the 10th alveolus from the end of the toothrow. Additionally, TMM 45973-1, a *D. schwimmeri* specimen from Alabama preserves a relatively complete right suborbital fenestra; the anterior margin is blunt and extends to the juncture of the 9th and 10th alveolus from the end of the maxillary toothrow.

MMNS VP-256 and TMM 45973-1 are similarly sized *D. schwimmeri* specimens. The anterior margins are blunt and the extents of the suborbital fenestrae are similar. TMM 43620-1, a large *D. riograndensis* specimen from Texas demonstrates an extent that exceeds that of the *D. schwimmeri* specimens and an anterior margin that is acute. The extent of the margins may be
affected by size with larger individuals having relatively larger fenestrae as a product of allometric scaling. However, differences in the morphology of the anterior margin of the fenestra are not likely due to the effects of scaling.

Confluence of third and fourth dentary teeth within the alveoli

Species of *Deinosuchoides* are diagnosed, in part, by the confluence of the third and fourth dentary alveoli. This feature is shared with the basal alligatoroids *Leidyosuchus canadensis* and species of *Diplocynodontines*. The confluence of the alveoli differentiates it from contemporaneous *Brachychampsa montana*.

The *D. riograndensis* holotype specimen, AMNH 3073, shows individual variability in degree of the placement of the third and fourth dentary teeth within the confluent alveoli. A wide space is present between the third and fourth dentary teeth of the left side but their counterparts on the right are confluent; no signs of pathology are present. TMM 43620-1, a specimen referable to *D. riograndensis*, preserves both anterior dentaries, the third and fourth dentary teeth do not have a space between them.

Dentary and External Mandibular Fenestra

TMM 43620-1 and MMNS VP-256, *D. riograndensis* and *D. schwimmeri* respectively, are the only specimens to preserve relatively complete external mandibular fenestrae. Although some breakage is present along the anterior margin of the fenestra, the structure appears to be relatively larger in the MMNS specimen compared with the TMM specimen. The difference in size is pronounced in light of the TMM specimen being from a much larger individual. It would appear that *D. riograndensis* has proportionally smaller external mandibular fenestrae. Whether
this difference in size is found in all ontogenetic stages is unknown. Alternatively, as the animal
grows, bone overgrowth could diminish the size of the external mandibular fenestrae over
ontogeny.

The contribution of the dentary to the margin of the external mandibular fenestra may
differ between MMNS VP-256 and TMM 43620-1. In the MMNS specimen the posterior
dentary may have extended further to the posterior relative to the TMM specimen. In the MMNS
specimen the dentary may stop anterior to the external mandibular fenestra. However, possible
sutural marks on the angular would suggest that the dentary extended along the ventral margin of
the fenestra. This would differ from the TMM specimen in which the angular forms the
anteroventral margin of the fenestra. Should the interpretation of sutural marks on the angular in
the region of the anteroventral margin of the external mandibular fenestra prove to be false then
the MMNS and TMM specimens would share similar morphologies.

Dorsal margin of the angular

The dorsal margin of the angular has a pronounced hump posterior to the external
mandibular fenestra in *D. schwimmeri*. TMM 43620-1 the only *D. riograndensis* specimen with
an intact posterior jaw suggests that the dorsal margin of the angular, posterior to the external
mandibular fenestra, was moderately inflated but not to the same degree as *D. schwimmeri*.

Vertebrae

Holland (1909) includes characters derived from vertebrae in his diagnosis of *D.
hatcheri*. It is stated that the species is differentiated from other crocodylians by an expansion of
the terminal dorsal processes of the dorsal vertebrae and postzygapophyses residing nearly on the
same plane as the transverse processes. Specimens referable to both *D. riograndensis* (TMM 43632-1, TMM 43620-1) and tentatively to *D. schwimmeri* (ALMNH 1002) bear vertebral morphology similar to that described by Holland as diagnostic of *D. hatcheri* (Fig. 17). A specimen of *D. riograndensis* (TMM 43632-1) maintains a dorsal vertebra that preserves a left postzygapophysis and a partial left transverse process; they are nearly in the same plane. An additional specimen of *D. riograndensis* (TMM 43620-1) preserves a mostly complete dorsal vertebra whose postzygapophysis and transverse process are nearly on the same plane and bears a transversely broad terminal dorsal spine. When viewed from a posterior aspect, the specimen looks nearly identical to Fig. 3 of Holland (1909). Additionally, ALMNH 1002 preserves a dorsal vertebrae whose postzygapophyses are nearly on the same plane as the transverse processes and bears a dorsal spine whose terminal end is transversely expanded.

Colbert and Bird (1954) compared the vertebrae associated with the *D. riograndensis* and *D. hatcheri* holotypes. The vertebrae are comparable in size, shape of the articular surfaces and centra, and both possessed relatively high neural arches. They stated that enough similarities are present to conclude that the holotype specimens are at the least members of the same genus.

**Osteoderms**

*Deinosuchoides riograndensis* bears osteoderms which are irregular and lumpy; keels are inflated. In opposition to this condition, *D. schwimmeri* osteoderms are often thinner and more regular in shape; the keels of some osteoderms are well defined (Fig. 43). Dorsal surfaces are deeply pitted in both species. Depth and irregularity of pitting tends to be size dependent. *D. hatcheri* from Montana exceeds *D. riograndensis* from Texas in size, likewise, the depth and irregularity of the pitted surfaces in *D. hatcheri* exceeds *D. riograndensis*. Schwimmer (2002)
makes an argument for the differences between eastern and western specimens being due to allometric changes in morphology. To reduce the effects of allometry Schwimmer compared what he believed to be the largest eastern osteoderms to small western osteoderms and found little difference between the taxa. However compelling, it cannot be known whether the osteoderms under comparison were from the same region of the body – large eastern nuchal osteoderms are relatively lumpy in appearance.

Perceived similarities, or differences, in morphology could be due to the position of the body in which the osteoderm resided or due to allometry; positive allometry is expected for an element forming a functional part of the dorsal musculature. It should be noted that variability in osteoderm shape, size, and pronouncement of the keel is only found in eastern specimens.
Deinosuchoides riograndensis osteoderms are invariably lumpy, thick, and bear inflated keels no matter the size or placement within the dermis.

A D. schwimmeri specimen from Alabama attributed to a young adult (ALMNH 1002) preserves dorsal osteoderms that approach the size of the large eastern osteoderm used in Schwimmer’s figure. This specimen’s osteoderms are thin, deeply pitted, and preserve a pronounced keel. Dorsal osteoderms matching this description, save the deep pits, are unknown for western specimens. The authors also sought to reduce the effects of size when comparing osteoderms of eastern and western species of Deinosuchoides. To do so, dorsal osteoderms of nearly the same size were compared. NCSM 14952, a dorsal osteoderm from the D. rugosus type locality in North Carolina measures approximately 13 cm wide. When compared to TMM 43620-1, a specimen from the type locality of D. riograndensis and possessing similarly sized osteoderms to the North Carolina specimen, it is clear that the osteoderms of Texas Deinosuchoides are considerably lumpier in appearance and bear keels that are inflated to a greater degree.

Comparison with Leidyosuchus

Species of Deinosuchoides are contemporaneous with the basal alligatoroid Leidyosuchus canadensis. The taxa are known to have co-occurred in Campanian units from New Mexico to Montana. Owing to their basal position within Alligatoroidea, both taxa share numerous ancestral characters but the forms are consistently differentiated based on size and divergent morphologies; isolated cranial elements are not likely to be confused.

The anterior snout differs between the taxa. The naris is circular and is confluent with the dorsal surface of the anterior snout in L. canadensis. Conversely, in species of Deinosuchoides,
the external naris is wider than it is long and the anterior snout is distinctly bulbous. Species of *Deinosuchoides* and *L. canadensis* share swellings of the lateral margins of the anterior maxilla. Many eusuchians bear these swellings but the morphology is pronounced in species of *Deinosuchoides* and *L. canadensis*. In *L. canadensis* the swellings are in the region of the first to seventh maxillary alveoli with a constriction at the juncture of the seventh and eighth maxillary alveoli. Species of *Deinosuchoides* bear swellings from the first to the sixth maxillary alveoli with a constriction at the juncture of the sixth and seventh alveoli. Additionally, the anteriormost portion of the swelling is more pronounced in *L. canadensis* owing to the extreme constriction of the snout at the premaxillary-maxillary notch.

The presence of a premaxillary-maxillary notch is ancestral for Crocodylia. Species of *Deinosuchoides* and *L. canadensis* have premaxillary-maxillary notches for receiving enlarged dentary teeth housed in the confluent third and fourth dentary alveoli. However, the formation of the notches differ. In *L. canadensis* the notch is formed primarily by the premaxilla, the maxilla only participates in forming the posteriormost portion of the notch. In species of *Deinosuchoides* the premaxilla and maxilla are nearer to equal in their contribution to the notch. The most obvious difference is the presence of a roof covering the medial portion of the notch in species of *Deinosuchoides*; the dentary teeth occluding into the notch would have been at least partially covered by the upper jaw. The effect of this morphology is a less pronounced notch, when viewed dorsally, compared to *L. canadensis*.

The taxa are divergent in multiple lower jaw characters. *L. canadensis* retains many plesiomorphies whereas many character states are derived in species of *Deinosuchoides*. The coronoid differs; in species of *Deinosuchoides* the superior margin of the element slopes anteriorly whereas in *L. canadensis* it retains the plesiomorphic condition and is nearly
horizontal. Additionally, there are considerable differences in the area of the external mandibular fenestra. *L. canadensis* preserves a large fenestra; the dorsal margin of the angular demonstrates a discrete concavity and the angular-surangular suture contacts the external mandibular fenestra at the posterior angle. The fenestra in *D. riograndensis* is present as a narrow slit. In *D. schwimmeri* the fenestral opening is considerably larger but neither species possesses a discrete fenestral concavity on the dorsal margin of the angular; likewise, the angular-surangular suture passes broadly along the ventral margin of the fenestra.

The skull tables share some superficial similarities such as relatively large fenestrae in both forms. However, upon closer scrutiny the tables are divergent. The skull table surface is planar in *L. canadensis* but slopes ventrally toward the sagittal axis in species of *Deinosuchoides*. Anterior to the skull table the shapes of the orbits differ. In *L. canadensis* the orbital margins are flush with the dorsal surface of the skull but in species of *Deinosuchoides* the anterior margins of the orbit are telescoped; the midpoint of the anterior-most margin is ventrally depressed so as to resemble a notch. The result of the differences in orbit and skull table contours are pronounced; *L. canadensis* is not considerably differentiated from expectations for an ancestral eusuchian, whereas *Deinosuchoides* demonstrates a suite of morphological features that are divergent from any known eusuchian. Ventrally, the skull table demonstrates additional divergent morphologies for both forms; the postorbital contacts the quadratojugal, but not the quadrate, medially in *L. canadensis* whereas the postorbital contacts the quadrate and quadratojugal at the dorsal angle of the infratemporal fenestra in species of *Deinosuchoides*.

Great differences in morphology are present along the lateral margins of the posterior skull. The jugal forms the posterior angle of the infratemporal fenestra in *L. canadensis* but the quadratojugal-jugal suture lies at the posterior angle of the fenestra in species of *Deinosuchoides*. 
Additionally, the quadratojugal bears a long anterior process along the lower temporal bar in *L. canadensis* but bears no process in species of *Deinosuchoides*. The area surrounding the external auditory meatus preserves multiple differences. The dorsal and ventral rims of the squamosal groove for the external ear valve musculature are parallel in *L. canadensis* but flare anteriorly in species of *Deinosuchoides*. The squamosal-quadrate suture extends dorsally along the posterior margin of the external auditory meatus in *L. canadensis* but extends only to the posteroventral corner of the external auditory meatus in species of *Deinosuchoides*. The ventral side of the posterior skull demonstrates that the maxilla sends a broad shelf medially into the suborbital fenestra in *L. canadensis* but not species of *Deinosuchoides*.

Additional differences are manifest in the osteoderms. The dorsal osteoderms are derived in species of *Deinosuchoides*; they are lumpy in appearance, have inflated keels, and are rectangular in shape when viewed dorsally. In *L. canadensis*; dorsal osteoderms are flat, obviously keeled, and are roughly square in dorsal view.

**Comparison with species of Diplocynodon**

The oldest species attributable to *Diplocynodon* is from the Paleocene of Europe (Hua, 2004; Martin et al., 2014) but the clade must extend at least as far as the Campanian. Recent phylogenetic analyses have recovered a close relationship to *L. canadensis*, species of *Deinosuchoides*, and basal globidontans implying that the origin of the clade is North American (Brochu, 1999; Delfino and Smith, 2012; Martin, 2014). Owing to their phylogenetic affinities, species of *Diplocynodon* and *Deinosuchoides* share similar morphologies but are divergent in meaningful ways.
The development of a notch at the premaxillary-maxillary juncture differs among species of *Diplocynodon* with a spectrum of morphologies present. Some species such as *D. remensis* possess the plesiomorphic condition of a fully developed notch whereas others such as *D. deponiae* show no development of a notch. Species of *Deinosuchoides* fall somewhere between these endmembers with the full development of a notch but a slight roof formed by the maxilla over the medialmost portion of the feature. Proportions of elements contributing to the notch differ among the species of *Diplocynodon*. In *D. remensis* the notch is formed primarily by the maxilla with the premaxilla only forming the anterior margin of the notch. The notch in *D. hantonensis* is formed primarily by the premaxilla with the maxilla contributing to the posterior margin. Again, species of *Deinosuchoides* lie between these endmembers with the premaxilla and maxilla contributing evenly in the construction of the notch.

Aspects of the dentary and maxilla are shared. Both taxa have confluent third and fourth alveoli with associated large third and fourth dentary teeth. Additionally, enlarged fourth and fifth maxillary teeth are shared between the taxa. It is unknown if the fourth and fifth maxillary teeth of species of *Deinosuchoides* protruded ventrally along the labial margin of the dentary to the extent of that which is found in species of *Diplocynodon*. The holotype specimen of *D. riograndensis*, AMNH 3073, bears a very long fifth maxillary tooth indicating that it may share the protruding overbite formed by the fourth and fifth maxillary teeth found in species of *Diplocynodon*. Further, the enlarged third and fourth dentary teeth, housed in confluent alveoli, are shared.

Species of *Deinosuchoides* and *Diplocynodon* share swellings of the anterior maxillary toothrow. Many eusuchians bear swellings of the anterior maxillary margins but this morphology is pronounced in species of *Deinosuchoides* and *Diplocynodon*. Some species of *Diplocynodon*
demonstrate a constriction of the maxilla present at the seventh alveolus in *D. hantonensis* and *D. darwini*, and between the sixth and seventh in *D. deponiae* – the latter is shared with *Deinosuchoides* which shows a constriction between the sixth and seventh alveoli.

**Comparison with species of Borealosuchus**

Morphological similarities are shared between species of the Campanian alligatoroid *Deinosuchoides* and species of *Borealosuchus* from the Late Cretaceous through Eocene of North America. Similarities are likely the result of retained plesiomorphies or convergence.

Species of both genera bear premaxillary-maxillary notches. Additionally, species such as *Borealosuchus formidabilis* have elongated rostrums with lengthened posterior snout elements. The long jugals and prefrontals of this species are reminiscent of species of *Deinosuchoides*. The elongated rostrums of these species are achieved, in part, by the elongation of posterior snout elements. The taxa can be differentiated via morphology of the prefrontals. In species of *Borealosuchus* the prefrontals are nearly as long as the lacrimals whereas in species of *Deinosuchoides* the lacrimals are nearly twice the length of the prefrontals. *Borealosuchus formidabilis*, which bears a relatively long snout, shares enlarged supratemporal fenestrae with species of *Deinosuchoides*.

Additional similarities are manifest in the shape of the skull table; *B. formidabilis*, *B. acudentatus*, *B. sternbergii*, *B. wilsoni* and species of *Deinosuchoides* have mediolaterally expanded and anteroposteriorly abbreviated skull tables whose lateral margins are nearly parallel. However, the supratemporal fenestrae of species of *Deinosuchoides* are comparatively much larger than those of many species of *Borealosuchus*, save *B. sternbergii* and *B.
acudentatus. As a result of the enlargement of the supratemporal fenestrae the parietal is mediolaterally constricted in of species of Deinosuchoides, B. sternbergii, and B. acudentatus.

**Comparison with Gavialis gangeticus**

Morphological similarities are shared between species of Deinosuchoides and gavialoids such as Gavialis gangeticus. However, similarities are products of retained plesiomorphies or convergent evolution.

Aspects of the skull table and supratemporal fenestrae are shared between the taxa. Both bear very large supratemporal fenestrae whose dermal bones do not overhang the fenestral rim. Expansion of the fenestrae in both forms is primarily accomplished by the mediolateral constriction of the parietal. The expansion of the fenestrae may be a functional consequence of the elongation of the snout. Plesiomorphically, in both forms, the parietal and squamosal are widely separated by the quadrate on the posterior wall of the fenestra. In both forms the postorbitals are mediolaterally expanded resulting in a skull table whose anterolateral margins are as wide, or wider, than the posterolateral margins with a mediolateral constriction of the mid-skull table in outline.

Differences in skull table morphology are manifest in the posterior skull table, otic region, and slopes of the skull table surface. The posterior skull table in G. gangeticus and species of Deinosuchoides does not overhang the posttemporal fenestrae. The result is the exposure of the posttemporal fenestrae when viewed from a dorsal aspect. Additionally, differences are manifest in the exposure of the supraoccipital on the dorsal skull table. In G. gangeticus the supraoccipital is exposed as a thin wedge whose length exceeds its width whereas
in species of *Deinosuchoides* the exposure of the supraoccipital is mediolaterally wide but anteroposteriorly abbreviated.

The slope of the skull table differs between species of *Deinosuchoides* and all known gavialoid species. When viewed from a posterior aspect, the skull table of *G. gangeticus* slopes ventrally away from the sagittal axis toward the lateral margin whereas in species of *Deinosuchoides* the skull table slopes ventrally from the lateral margin toward the sagittal axis.

Additionally, the taxa share character states in the otic region; the postorbital-squamosal suture is oriented ventrally to the skull table, and the dorsal and ventral rims of the squamosal groove for external ear valve musculature are parallel.

The postorbital bars of species of *Deinosuchoides* and gavialoids are robust. However, adjusting for size, it is more robust in *G. gangeticus* relative to *Deinosuchoides*. In both taxa the bar is more or less flush with the lateral surface of the jugal. Differing between the species is the shape of the body of the postorbital bar. When viewed from an anterior aspect the bar is nearly straight in *G. gangeticus* whereas in species of *Deinosuchoides* the bar is medially indented approximately midway along the bar – the result is an L-shaped structure when viewed anteriorly.

The posterior skull differs between the taxa. Species of *Deinosuchoides* demonstrate a verticalized posterior skull whereas in gavialoids it does not. The basioccipital, ventral to the occipital condyle, faces posteriorly in species of *Deinosuchoides* preserving the region whereas in *G. gangeticus* it faces posteroventrally. The rami of the quadrate forming the upper portion of the jaw joint also differ. In species of *Deinosuchoides* they are much longer relative to *G. gangeticus* where they are anteroposteriorly abbreviated.
Salas-Gismondi et al. (2016) found multiple independent acquisitions of telescoped orbits in gavialoid history. Convergence on a similar but unrelated morphology is present in species of *Deinosuchoides*. It is unknown if the related morphologies are adaptations to similar environmental conditions, feeding strategies, or otherwise.

Throughout ontogeny *G. gangeticus* bears a telescoped orbital morphology whose margins form large cups for the soft tissues of the eye. The constriction of the snout immediately anterior to the orbits makes the morphology ever more conspicuous. *Gavialis gangeticus* bears orbits that are fully telescoped along all margins with skull table, anterior snout, and postorbital bar elements contributing. Conversely, in species of *Deinosuchoides*, only the anterior margins of the orbits, formed by the prefrontals, lacrimals, and jugals form the telescoped orbital morphology. Common to both taxa are ventral indentations of the anteriormost orbit formed by the lacrimals. This morphology may be due to a functional constraint relating to field of vision – without the indentation objects directly ahead may be obscured. In addition to the indentation of the anterior orbital margin, *G. gangeticus* bears an additional indentation formed by the jugal at the posteroventral corner of the orbital margin.

Both species of *Deinosuchoides* and *G. gangeticus* bear the longirostran condition in which the snout anterior to the orbits accounts for 70% (or more) of total skull length (Busbey, 1995). In *G. gangeticus* the snout is tubular and formed primarily by the maxilla and premaxilla with minimal contributions by the nasals. In species of *Deinosuchoides* the snout is flattened with considerable contributions of the frontals, prefrontals, lacrimals, and jugals. Longirostrin in species of *Deinosuchus* is primarily due to the elongation of posterior snout elements – the maxilla, nasals, and premaxillae are similar in proportion to what is expected for a mesorostral form such as *Alligator mississippiensis*. 

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Comparison with Tomistomines

Species of Deinosuchoides share some superficial similarities with species of tomistomines. Proportions of the skull table and supratemporal fenestrae are shared between the taxa. Both bear large supratemporal fenestrae likely as an adaptation to longirostry. The skull table surface of D. riograndensis and D. schwimmeri slope ventrally toward the midline; the lateral elements are planar. This morphology is shared with the tomistomines Gavialosuchus eggenburgensis, Kentasuchus spenceri, and Maroccosuchus zennaroi. However similar, the morphologies may be differentiated between the taxa. In D. riograndensis and D. schwimmeri the midline furrow is wide; it is very deep relative to the lateral skull table. In Kentasuchus spenceri and Gavialosuchus eggenburgensis the midline furrow is narrow but in Maroccosuchus zennaroi the furrow is wider, yet not as wide as in D. riograndensis and D. schwimmeri. In the tomistomine species the furrow is shallow relative to the lateral edges of the skull table. In D. riograndensis, D. schwimmeri, and Maroccosuchus zennaroi the lateral skull table bears wide planar surfaces formed by the postorbitals and squamosals. Differences are evident between the three taxa; the medial margins of the supratemporal fenestrae in D. riograndensis and D. schwimmeri are confluent with the midline furrow whereas in Maroccosuchus zennaroi the medial edges of the supratemporal fenestrae form a ridge that is raised dorsally relative to the narrow midline furrow.

Neosuchian species co-occurring with Deinosuchus

In the west, along the shores of the Western Interior Seaway, Deinosuchus and species of Deinosuchoides lived alongside a number of neosuchian and crocodylian species. Remains of Deinosuchus have been found in the Fruitland and Kirtland formations of the San Juan Basin,
New Mexico. These formations contain a diverse crocodylian fauna including *Brachychampsa montana*, “*Leidyosuchus*” (or *Borealosuchus*) and the goniopholid *Denazinosuchus kirtlandicus* (Lucas et al., 2006). In the Aguja Formation of the Big Bend region of west Texas *D. riograndensis* remains have been found alongside *Denazinosuchus kirtlandicus*, but 60 km to the south in the Aguja Formation of Coahuila, Mexico *D. riograndensis* is the sole crocodylian species (Rowe et al., 1992; Rivera-Sylva et al., 2011). The Kaiparowits Formation of Utah preserves a diverse fauna but apomorphy based analyses have limited some taxa historically believed to be found in the formation. *Brachychampsa, Leidyosuchus* or *Borealosuchus*, as many as four alligatoroids of unknown affinities, and a possible goniopholid or pholidosaurid in addition to *D. hatcheri* have been reported in the literature (Wiersma et al., 2004; Irmis et al., 2013). The Mesaverde Formation of Wyoming preserves *Deinosuchus, Leidyosuchus* or *Borealosuchus*, and *Brachychampsa montana* (Breithaupt, 1985). The Judith River Formation of Montana preserves remains of *D. hatcheri* along with *Leidyosuchus* or *Borealosuchus*, and *Brachychampsa montana* (Holland, 1909; Sahni, 1972).

“*Deinosuchus rugosus*” from the Atlantic Coastal Plain have been found alongside a similarly diverse neosuchian and crocodylian fauna. The Marshalltown Formation of New Jersey preserves “*D. rugosus*”, cf. *Brachychampsa*, and cf. *Borealosuchus* (Gallagher et al., 1986; Gallagher, 1993). The Bladen and Black Creek formations of North Carolina, the latter being the type locality for “*D. rugosus*”, contains an unknown species of *Borealosuchus* in addition to “*D. rugosus*” (Baird and Horner, 1979; Crane, 2011). The upper Blufftown Formation at Hannahatchee Creek, Georgia has yielded remains of “*D. rugosus*, *Thoracosaurus neoesariensis* (de Kay, 1842), and *Borealosuchus* sp. (Schwimmer, 1986; Schwimmer, 2002).
The Mooreville Formation of Mississippi and Alabama yields remains of *D. schwimmeri* and *Leidyosuchus* or *Borealosuchus* (Parris et al., 1997; Schwimmer, 2002). The Coffee Formation of Mississippi yields remains of *D. schwimmeri* and *Leidyosuchus* or *Borealosuchus* (Manning, 2006).

Morphological differences in snout and tooth shape as well as size would have effectively partitioned the neosuchian faunas. No neosuchian contemporary possessed the extreme size of *Deinosuchoides* nor the duck-faced snout morphology of the taxon. These adaptations allowed it to consume items far in excess of contemporary species’ prey acquisition tolerances.

Species of *Deinosuchoides* would have competed with medium to large sized Theropods for tetrapod prey items. Gallagher (1993) reported on theropod teeth displaying evidence of exposure to gastric fluids from a likely crocodylian predator in the Atlantic Coastal Plain of New Jersey. It would seem that in the east *D. schwimmeri* was consuming theropods in addition to competing with them for prey.

**Phylogenetic Analysis**

**Matrix**

The matrix used in this analysis follows after Brochu (2011). Changes have been made to the matrix including the addition of *Deinosuchoides riograndensis* and *Deinosuchoides schwimmeri* as well as the addition of new character states. Invariable characters among in-group taxa are excluded from this analysis. The matrix contains 162 morphological characters and 82 ingroup taxa. *Bernissartia fagesii* is used as an outgroup to root the trees. Codings are presented in Appendix 2.
New characters and character states were added to this matrix, as discussed below:

47(5): Splenial reaches mandibular symphysis but does not touch other splenial

72(2): Naris projects posterodorsally.

117(3): Anterior margins of orbit telescoped.

135(2): Skull table surface slopes ventrally toward sagittal axis at maturity, lateral elements planar.

160: Dorsal shield osteoderms planar, exclusive of keel (0) or osteoderms robust, keel inflated (1).

161: Floor of post-temporal fenestrae not visible in dorsal view (0) or visible in dorsal view (1) at maturity.

162: Midmaxillary constriction not present (0) or present between maxillary teeth 5 and 6 (1), 6 and 7 (2), 7 and 8 (3), or 8 and 9 (4).

Methods

A maximum parsimony analysis using TNT v.1.5 was conducted (Goloboff, Farris & Nixon, 2008). Matrices were managed in Mesquite v.3.04 (Maddison and Maddison, 2015). Traditional heuristic searches performing 1000 replicates of Wagner trees (using random addition sequences) were conducted and followed by the tree bisection reconnection swapping algorithm (holding 10 trees per replicate). Collapsing rules and character weighting were not applied for the reconstructions. Multistate characters were treated as unordered.

Character support of the nodes present in the most parsimonious trees was calculated using two different methods. The first method is bootstrapping applied to character resampling (Efron, 1979; Felsenstein, 1985). The second method is Bremer support (Bremer, 1988; Bremer,
1994). TNT v.1.5 was used to calculate Bootstrapping and Bremer supports (Goloboff, Farris & Nixon, 2008). GC frequencies were used to summarize the topologies obtained during the bootstrap replicates (Goloboff et al., 2003).

**Results**

Multiple analyses were completed. Maximum parsimony analysis of the full taxon matrix recovers 2870 shortest trees (tree length = 584, consistency index with uninformative characters removed = 0.38, retention index = 0.82). *Deinosuchoides riograndensis* and *Deinosuchoides schwimmeri* are recovered as sister taxa (Fig. 45). Additionally, the clade is included in a basal polytomy with *Leidyosuchus canadensis*, a taxon commonly recovered as the basal-most alligatoroid (Brochu, 2010, 2011; Martin, 2014; Hastings et al., 2016), Diplocynodontinae, and a clade including Cretaceous globidontans and Alligatoridae.

In this analysis crown alligatorids form two primary lineages, one including *Alligator* and its North American and Eurasian relatives, and the other including the living caimans and their North American and neotropical relatives. Strict consensus trees recover a monophyletic Globidonta. Cretaceous globidontans (*Stangerochampsia, Albertoichampsia*, and *Brachychampsia*) are the sister group to Caimaninae. Tree length increases by one step if Cretaceous globidontans are moved outside of crown Alligatoridae. Cretaceous globidontans are united with Caimaninae due to the angular not extending dorsally beyond the anterior end of the foramen intermandibularis caudalis; the anterior tip of the angular is very blunt.
FIGURE 45 (opposite page). Phylogenetic tree of Crocodylia showing the placement of *Deinosuchoides riograndensis* and *Deinosuchoides schwimmeri*.

This analysis diagnoses Alligatoroidea with the following character states; 54(1) – anterior processes of the surangular are equal to subequal, 63(1) – foramen aerum of articular set in from margin of retroarticular process, 82(0) – all dentary teeth occlude lingual to maxillary teeth, 102(1) – the quadratojugal spine is high, between posterior and superior angles of infratemporal fenestra, 112(1) – anterior tip of frontal forms broad, complex sutural contact with the nasals, 121(1) – quadratojugal spine high, between posterior and superior angles of infratemporal fenestra, 153(1) – quadrate foramen aerum on dorsal surface.

*Deinosuchoides* is unambiguously diagnosed by eleven character states; 42(0) – dentary symphysis extends to fourth or fifth alveolus, 47(5) – splenial reaches mandibular symphysis but does not touch its counterpart, 53(1) – angular-surangular suture passes broadly along ventral margin of external mandibular fenestra late in ontogeny, 56(1) – external mandibular fenestra present as narrow slit, no discrete fenestral concavity on angular dorsal margin, 114(0) – postorbital bar massive, 117(3) – anterior margin of orbit telescoped, 122(2) – quadratojugal-jugal suture lies at posterior angle of infratemporal fenestra, 124(1) – quadratojugal bears modest process, or none at all, along lower temporal bar, 126(0) – postorbital-squamosal suture oriented ventrally, 127(1) – squamosal groove flares anteriorly, and 135(2) – skull table surface slopes ventrally toward sagittal axis at maturity. Three of the states are autapomorphic for the genus: 47(5), 117(3), and 135(2).

Character state 42(0), dentary symphysis extends to fourth or fifth alveolus is shared with alligatoroids and crocodyloids alike. Within Alligatoroidea, all species of *Diplocynodon*, save *D. deponiae*, and large clades within Alligatorinae and Caimaninae share the character state with
species of *Deinosuchus*. Within Crocodyloidea species of *Osteolaemus* and *Crocodylus* share the state with species of *Deinosuchus*. Character state 53(1), angular-surangular suture passes broadly along ventral margin of external mandibular fenestra late in ontogeny is shared with Crocodylinae, *Eogavialis africanus*, and Caimaninae, save the basalmost member *Culebrasuchus mesoamericanus*. Character state 56(1) external mandibular fenestra present as narrow slit, no discrete fenestral concavity on angular dorsal margin is shared with *Borealosuchus threeensis*, *Borealosuchus wilsoni*, *Thoracosaurus neocesariensis*, and *Thoracosaurus macrorhynchus*. Character state 114(0), postorbital bar massive is shared with Gavialoidea. Character state 124(1) quadratojugal bears modest process, or none at all, along lower temporal bar, is shared with Crocodylidae and *Centenariosuchus gilmorei*. Character state 126(0), postorbital-squamosal suture oriented ventrally to skull table, is shared with *Diplocynodon tormis*, *Diplocynodon remensis*, *Euthecodon brumpti*, *Euthecodon arambourgii*, and *Gavialis gangeticus*. Character state 127(1), dorsal and ventral rims of squamosal groove for external ear valve musculature flares anteriorly, is shared with Gavialoidea. These characters are largely variable within and among the major clades of Crocodylia and may be a product of functional constraints, ecology, or otherwise, rather than phylogenetic history.

The sister group relationship for *D. riograndensis* and *D. schwimmeri* is robustly supported by bootstrap and Bremer supports alike (bootstrap = 99 percent of replicates, decay index = 6). Traditionally, Alligatoroidea is also robustly supported (Brochu, 1999) but this analysis found that only 12 percent of bootstrap replicates support the clade (decay index = 2). Removal of the two species of *Deinosuchoides* from the analysis decreases tree length but increases the number of most parsimonious trees (4640 shortest trees, tree length = 512, consistency index with uninformative characters removed = 0.41, retention index = 0.84).
Additionally, the removal of both species of *Deinosuchoides* and *D. hatcheri* increases bootstrap support of Alligatoroidea to 17 percent but has no effect on Bremer supports. Likewise, support increases for basal nodes within the clade but more nested nodes are largely unaffected. Removal of species of *Deinosuchoides* and *D. hatcheri* likely removes conflicts arising from homoplasy and explains the increased support for basal nodes.

Removal of both species of *Deinosuchoides* from the full analysis recovers 5290 shortest trees. Tree length is decreased but C.I., R.I., and strict consensus tree topology are unaffected (tree length = 563, consistency index with uninformative characters removed = 0.39, retention index = 0.83). Topologically, the tree resembles most published analyses of Alligatoroidea which do not include species *Deinosuchoides* (e.g. Brochu, 1999; Martin, 2010). *Leidyosuchus canadensis* is recovered as the basalmost alligatoroid and one node crownward Diplocynodontinae forms a sister group relationship with Cretaceous globidontans and Alligatoridae.

Two additional analyses were performed. The first removed all species of *Borealosuchus*, except *B. sternbergii* (4420 shortest trees, tree length = 571, consistency index with uninformative characters removed = 39, retention index = 83). This dataset sees improved resolution with the polytomy at the base of Alligatoroidea removed. Relationships of basal alligatoroids under these conditions match those of previous authors (e.g. Brochu, 1999; Martin et al., 2014). The second dataset removed all species of *Borealosuchus* (4480 shortest trees, tree length = 559, consistency index with uninformative characters removed = 40, retention index = 83). In this analysis *L. canadensis* is the basalmost alligatoroid. *Deinosuchoides*, Diplocynodontinae, and a clade including Cretaceous globidontans and Alligatoridae form a polytomy one node crownward of the base of Alligatoroidea. Support of Alligatoroidea is equal
for both of the additional analyses (bootstrap = 12 percent of replicates, decay index = 1) and are comparable to the full analysis including all species of *Borealosuchus*.

**Discussion**

Species of *Deinosuchoides* bear highly derived, oftentimes divergent, morphologies in a geologically old member of Alligatoroidea. In addition to a number of autapomorphies for the genus, convergent evolution with long snouted forms is evident. As such homoplasy is introduced into the dataset and resolution at the base of Alligatoroidea is reduced.

Interestingly, five homoplastic character states, 53(1), 56(1), 114(0) 126(0), and 127(1), are shared with gavialoids and one, 126(0), is shared with species of *Euthecodon*. These taxa, along with species of *Deinosuchoides*, are longirostrine. Character states shared among the taxa are located on the skull table and otic area; these regions are known to be functionally constrained by the demands of longirostry (Iordansky, 1973; Langston, 1973; Busby, 1995). Additionally, convergent evolution is evidenced by similar shapes and proportions of osteological elements and sutural contacts of the skull table and otic regions. Although these taxa are distantly related, their ecologies seem to have produced similar functional morphologies related to their longirostry.

Removal of all, or most, species of *Borealosuchus* leads to better resolution at the base of Alligatoroidea relative to the full analysis but causes *Deinosuchoides* and Diplocynodon to form a polytomy with Alligatoridae + basal globidontans. Increased resolution in the restricted analysis is due to the removal of homoplasy. Much of the homoplasy results from retained ancestral character states in species of *Borealosuchus* and *Deinosuchoides*. Shared ancestral character states are particularly concentrated in the skull table and otic regions.
In addition to the shared ancestral character states, many morphological features are shared between the roughly contemporaneous species of *Borealosuchus* and *Deinosuchoides* due to convergence. Shared derived character states are concentrated in the lower jaw. Character state 42(0), dentary symphysis extends to fourth or fifth alveolus, is shared with *B. threeensis*, *B. acutidentatus*, and *B. wilsoni*. Character state 53(1), angular-surangular suture passes broadly along ventral margin of external mandibular fenestra late in ontogeny, is shared with *B. threeensis*. Character state 56(1), external mandibular fenestra present as narrow slit, no discrete fenestral concavity on angular dorsal margin, is shared with *B. threeensis*, *B. acutidentatus*, and *B. wilsoni*. Character state 64(0), surangular extends to posterior end of retroarticular process, is shared with all species of *Borealosuchus* in this analysis.

Interestingly, *B. sternbergii* does not group with the rest of the *Borealosuchus* clade. It is found one node crownward forming a sister group relationship with Planocrainiids + Pristichampsids and Brevirostres (*B. sternbergii* (Planocrainiids + Pristichampsids (Brevirostres))). Additionally, *B. sternbergii* has a stronger effect on the topology at the base of Alligatoroidea relative to other species of *Borealosuchus*. Exclusion of the taxon leads to decreased resolution. However, additional complications arise with the addition of more species of *Borealosuchus* – resolution at the base of Alligatoroidea is greatly decreased as a result of homoplasy.

**Premaxillary fenestrae**

The functional significance of the premaxillary fenestrae in *D. riograndensis* is unknown. It is possible that they were a means by which to lighten the long, wide, robust snout. However, an additional hole placed at the extreme tip of the snout would presumably form a weaker architecture than otherwise but no specimens preserve evidence of breakage and healing in this
region. Alternatively, fenestrae in this region of the snout are often for receiving the anterior dentary teeth. This hypothesis must be discounted as the anterior dentary teeth are not long enough to project through the fenestrae nor wide enough to form such expansive fenestration due to progressive wear.

In the *D. riograndensis* holotype specimen, the anterior wall of the premaxilla bears a dorsoventrally-oriented structure extending from the roof of the element to the middle of the anterior wall. The structure sends a 3 cm shelf-like projection posteriorly into the hollow of the premaxilla. This structure, and possibly associated soft tissues, may have served as a means to partition the anterior snout as it separates the cavichoncal cavity lateral to the naris from the external naris itself.

**Gigantism and thermoregulation**

The differences in size between the species of *Deinosuchoides* may be due to non-taxonomic reasons. It is possible that better environmental conditions and more abundant prey existed in the west and led to the attainment of larger body sizes in *D. riograndensis*. Large-scale studies of the stratigraphic and paleontological records could provide evidence in support of this hypothesis. Conversely, *D. riograndensis* may have lived longer relative to *D. schwimmeri* allowing for continued growth (see Erickson and Brochu, 1999). A study involving the sectioning of osteological elements and counting growth rings among both species may provide an answer.

The large external naris of species of *Deinosuchoides* is shared with other very large alligatoroid taxa such as *Purussaurus brasiliensis, Purussaurus mirandai,* and *Mourasuchus amazonensis*. The expanded external nares in these taxa has been hypothesized as a
thermoregulatory adaptation as gigantism in crocodylians suggests higher, more stable body temperatures and an increased risk of overheating (Moreno-Bernal, 2007). Additionally, the large nares have been implicated in stress-dissipation associated with the presumably immense bite forces produced by these large bodied taxa (Aureliano et al., 2015).

In addition to the thermoregulatory benefits of an enlarged external naris, enlarged supratemporal fenestrae have also been hypothesized as being adaptations to help regulate body temperature in large bodied alligatoroids. The tissues surrounding the supratemporal fenestrae are highly vascularized. Enlargement of these structures, as suggested for *Mourasuchus* (Holliday & Gardner, 2012; Bona et al., 2013), may indicate enhanced vascularization and heat dissipating function. Additional studies regarding this feature in species of *Deinosuchoides* are warranted.

**Adaptations for longirostry**

Species of *Deinosuchoides* share a number of homoplastic character states, 53(1), 126(0), and 127(1), with gavialoids and one, 126(0), with species of *Euthodon*; taxa commonly reconstructed as specialized piscivores. These taxa, along with species of *Deinosuchoides*, possess the longirostrine snout condition. The character states shared between these taxa are on the skull table and otic area, regions are known to be functionally constrained by the demands of longirostry (Iordansky, 1973; Langston, 1973; Busby, 1995; Holliday & Witmer, 2007).

Additionally, convergent evolution is evidenced by similar shapes and proportions of osteological elements and sutural contacts of the skull table and otic regions. Although these taxa are distantly related, their ecologies seem to have produced similar functional morphologies related to their longirostry. It is of note that these taxa, relative to *Deinosuchoides*, are markedly
different in the width and depth of the snout and that species of *Deinosuchoides* are reconstructed as generalist predators capable of taking down, and consuming, very large tetrapod prey. It would seem that the most important factor leading to the convergent morphologies of the skull table and otic area is not the prey type, depth, or width of the snout but rather the length.

Enlarged supratemporal fenestrae have also been considered adaptations for seizing fast moving, active prey (Langston, 1973). M. adductor mandibulae externus profundus inserts on the supratemporal fenestrae of extant crocodylians (Iordansky, 1973; Holliday & Witmer, 2007). The relatively larger supratemporal fenestrae of longirostrine crocodylians are related to the enlargement of the muscle in these taxa (Holliday & Witmer, 2007). The enlargement of the supratemporal fenestrae in species of *Deinosuchoides*, which possess broad, longirostrine snouts, may be related to the enlargement of M. adductor mandibulae externus profundus. The result would be increased speed and strength of jaw closure.

**Geologic ages of *Deinosuchus***

*Deinosuchus* and *Deinosuchoides* specimens are widely distributed in Campanian strata of the United States and Northern Mexico. Ages for eastern and western specimens differ (for a thorough discussion of locality ages see Schwimmer, 2002). The beds containing *Deinosuchus* and *Deinosuchoides* fossils have not been subject to radiometric dating but several units that are both geographically and stratigraphically close have been (Schwimmer, 2002). The type locality of *D. hatcheri* (Judith River Formation of Fergus County, Montana) has been constrained to 80.5 ± 0.15 – 79.5 ± 0.6 million years via stratigraphic correlation to units subject to numerical dating (Hicks et al., 1995; Obradovich, 1993). The oldest occurrence is represented by “*D. rugosus*” in the Blufftown Formation along the Georgia-Alabama border. This unit has been correlated to
units dated at approximately 82 million years (Schwimmer, 2002). The type locality of *D. riograndensis* (the Big Bend region of western Texas) has been suggested via correlation to be younger than the oldest “*D. rugosus*” occurrence but with considerable overlap with younger eastern specimens. This overlap suggests the possibility of interbreeding between *D. riograndensis* and “*D. rugosus*”.

Eastern and western populations of *Deinosuchoides* were separated by lengthy expanses of salt water. During the Campanian the Western Interior Seaway cut North America in two. Minimum distances of hundreds of kilometers between the eastern and western shores have been predicted for this interval (Ostresh, 1990; Schwimmer, 2002). As extant alligatoroids are intolerant of prolonged exposure to saline waters (Taplin, 1988; Mazzoti and Dunson, 1984) it is predicted that their extinct relatives could not effectively osmoregulate in saline waters either (Taplin and Grigg, 1989). As such, dispersal via marine routes is impossible.

Unlike extant alligatoroids, and predictions for their fossil relatives, limited evidence has been produced suggesting that specimens referable to *Deinosuchus* may have been able to tolerate some exposure to saline waters. In this case dispersal via marine routes as is found in extant crocodyloids and gavialoids, and suggested for their extinct relatives, would be possible. Through stable isotope analysis of carbon and oxygen from tooth enamel Wheatley (2010) explored marine and freshwater habitat use in a number of fossil crocodylians including *Deinosuchus*. As *Deinosuchus* remains are sometimes found in marine depositional environments they may have ingested marine resources (i.e. prey and water) (Wheatley, 2010).

Wheatley’s results suggest that *Deinosuchus* consumed large amounts of seawater but these results do not necessarily suggest crossing of marine barriers or saltwater tolerance. Should *Deinosuchus* be able to osmoregulate in saline environments an argument can be made that other
early alligatoroids were saltwater tolerant and that the physiological adaptation was lost in the ancestor of extant alligatorids. However, as *Deinosuchus* was one of the largest crocodylians to have lived, it is possible that it could withstand relatively larger volumes of seawater without possessing anatomical adaptations such as lingual glands for the excretion of salt (Wheatley, 2010). Nonetheless, consumption of saltwater in an organism with no means of processing the excess salt found in seawater is unexpected behavior.

Few *Deinosuchus* remains have been found in sediments representing deep water environments. This is not likely due to limited preservation as deep continental shelf deposits of the Late Cretaceous are typically chalk (Schwimmer, 2002). These deep water deposits are less likely to be disturbed as they are beneath wave base. Preservation potential is high in these environments yet occurrences of *Deinosuchus* in deeper marine deposits are rare. It is possible that *Deinosuchus* did not, or did not regularly, venture into open waters and those specimens recovered in deep water deposits were transported out to sea after the animal died. Taxa unable to swim (dinosaurs for example) have been recovered in marine chalks (Langston, 1960; Schwimmer et al., 1993; Schwimmer, 2002) suggesting that postmortem transportation is relatively common.

Although there is some stratigraphic overlap between *D. rugosus* and *D. riogrindensis* the morphological differences separating the species indicates that they were not interbreeding. Additional differences in size may suggest species level separation. Should *Deinosuchus* be salt water intolerant like modern alligatoroids, the vast distances separating the eastern and western shores of the Western Interior Seaway would have provided an insurmountable barrier for the exchange of genetic information between the species.
Conclusions

Due to the lack of diagnostic characters in the very incomplete holotype specimen, the name *Deinosuchus* is restricted to *D. hatcheri* to promote nomenclatural stability. A new genus, *Deinosuchoides*, is erected to encompass specimens formerly included in *Deinosuchus*. Additionally, as the holotype specimen for *Deinosuchus rugosus* is undiagnostic to species level the species is determined to be a nomen dubium. A new species, *Deinosuchoides schwimmeri*, is erected upon a cranial specimen from Mississippi.

A phylogenetic analysis finds *D. riograndensis* and *D. schwimmeri* to be sister taxa. Species of *Deinosuchoides* are included in a polytomy with *Deinosuchus hatcheri* when the latter’s very incomplete holotype specimen is included in the analysis. A single character state unites the species of *Deinosuchoides* and *D. hatcheri*. An additional eleven character states unite the *Deinosuchoides* clade.

The species of *Deinosuchoides* can be differentiated by osteodermal, braincase, maxillary, and premaxillary morphology in addition to differences in size and geologic age. Further, the species of *Deinosuchoides* are separated geographically by the Western Interior Seaway with *D. riograndensis* found on the western shores and *D. schwimmeri* on the eastern shores and along the Atlantic coast.

*Deinosuchus* and *Deinosuchoides* are some of the largest crocodylians known. They were the top predators in their environments and are known to have fed on dinosaurs. This work reinforces the identity of the “terror croc” as an alligatoroid.
CHAPTER 3
A MORPHOMETRIC ANALYSIS OF THE CROCODYLIAN SKULL TABLE;
TRACKING ALLOMETRY AND PREDICTING ECOLOGY

Introduction

The crocodylian skull is an osteological structure in which many character states are significantly modified from the ancestral archosaur (Iordansky, 1973). As such, the skull of extant crocodylians must be viewed through the lens of historical modifications. The dorsal portion of the adult crocodylian skull, posterior to the orbits, is always flat and is referred to as the skull table (Mook, 1921). Skull tables are a synapomorphy of Crocodyliformes and appear to be part of a trend leading to overall flattening of the skull in Crocodylia (Langston, 1973). No other semiaquatic predator has evolved a skull table to elevate the eyes and ears above the waterline. Yet, little work has been done focusing on the shape of the skull table; similarities and differences among taxa have not been adequately quantified.

The skull table forms a broad, flat surface on the dorsalmost posterior skull of crocodyliforms and the earliest record of this feature extends to the “protosuchians” of the Jurassic (Langston, 1973; Busby, 1995). These basal crocodyliform taxa such as Orthosuchus stormbergi Nash, 1968 and Protosuchus richardsoni Brown, 1933 are reconstructed as semiaquatic predators who possessed limbs capable of an efficient high walking gait while on land.

Specializations of the crocodylian skull are connected to the position of sensory organs on top of the head (Richardson et al. 2002). Fenestration (i.e. supratemporal fenestrae) allows the masticatory muscles to pass through and attach to the skull table. As a result, the jaws articulate caudally and allow for a very wide gape. These features have been achieved through the
dorsoventral flattening of the skull roof to form the skull table, the migration of the orbits and postorbital bars medially, the presence of two pairs of temporal fenestration, and the caudal placement of the quadrate and its articulation with the articular bone of the lower jaw (Richardson et al. 2002). Dorsoventral flattening of the posterior skull, resulting in the crocodylian skull table, allows for the dorsal positioning of the eyes and ears above the waterline and ensures a low profile to maintain the element of surprise needed by a semiaquatic ambush predator.

The skull table is integral to the attachment of jaw musculature. Musculus adductor mandibulae externus profundus originates on the ventrolateral parietal within the supratemporal fenestrae. This muscle is usually small and semicircular in cross-section in members of Brevirostres (Alligatoroidea + Crocodyloidea) but is larger and circular in cross-section in long snouted forms such as gavialoids (Holliday and Witmer, 2007). As a result of the differences in cross-sectional area of m. adductor mandibulae externus profundus, the supratemporal fenestrae are generally larger in long-snouted forms (Iordansky, 1973).

The skull table is robust and likely to be recovered in the fossil record. However, a morphometric analysis has not been conducted on the skull table with the inclusion of fossils. Additionally, previous studies have not analyzed information contained in the outline of the skull table and have quantified the shape of the supratemporal fenestrae with no more than two datapoints (Sadlier, 2009; Piras et al., 2010).

In addition to comparisons amongst taxa, comparisons of allometric change within taxa are explored in this study. Although crocodylians are an excellent clade for studying morphological changes throughout ontogeny, few studies of the crocodylian skull have focused on morphological change over the life of the animal. Crocodylian body mass increases 1000 to

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5000 fold during development and is associated with significant change in cranial morphology (Grenard, 1991; Sadlier, 2009; Watanabe, 2012). Cranial morphology exhibits profound disparity which is particularly evident in the rostrum. As a result much work has focused there (Watanabe, 2012). Until now, the skull table has been excluded from a thorough analysis – its shape must be quantified to elucidate ecological trends and to inform phylogenetic analyses. Additionally, clades may be recognized using skull table characters not currently included in phylogenetic character matrices. The impact of fossil data compared with analyses limited to more complete, but also more derived, living species can be compared.

**Materials and Methods**

This study employs geometric morphometrics, rather than traditional morphometric analysis, in that it uses geometric coordinates instead of linear measurements. Advantages of geometric morphometrics over traditional morphometrics are legion; results can be presented graphically rather than through tables of numbers, data are easily collected from digital photographs, and size is mathematically removed from the analysis to focus purely on shape. Traditional morphometric methods mix size and shape; the size of the animal affects all measurements. The result is that the primary morphometric difference between two taxa is size rather than shape (Zelditch, Swiderski, and Sheets, 2012).

Pictures and figures of dorsal skull tables form the basis for the plotting of two dimensional landmarks in this analysis. Digital images are preferred by the author as they expand the sample size available for the analysis; some specimens cannot be seen first-hand due to time and monetary constraints. Additionally, procrustean geometric morphometrics has relied heavily on two dimensional images to study three dimensional structures such as crocodylian skulls.
This process is simple and low cost, allowing for large datasets without the need to visit numerous collections or to purchase expensive equipment. Additionally, the need for three dimensional measurements of the skull table is negated as it is an element whose morphology is in a single plane in virtually all crocodylians. Further, it has been determined that two dimensional measurements can equal three dimensional landmarks in a procrustean analysis (Cardini, 2014).

For the analyses, two dimensional landmarks are digitized on images of crocodylian skull tables using TPSDig (Rohlf, 2014). All data analyses are performed in the software environment R (v. 3.5.0) (R Core Team, 2018) and centroid size is used as a measure of specimen size. The centroid size of a 2D shape is defined by the square root of the sum of the square distances of each landmark to the center of the form (Zelditch, Swiderski, and Sheets, 2012), as such it is a measure of size that is mathematically independent of shape. Variation in shape between the specimens is extracted using generalized least-squares Procrustes super-imposition and is performed on four separate analyses; an outline analysis, an outline analysis including information from the supratemporal fenestrae (STF), an analysis exploring the allometric trajectories of skull table outlines, and a final analysis that looks at the allometric trajectories of skull table outlines with additional landmarks covering the morphology of the supratemporal fenestrae.

In a geometric morphometric analysis landmarks are quantified as Cartesian coordinates that are used to represent shape. At least three landmarks are required in a geometric morphometric analysis. Zelditch, Swiderski, and Sheets (2012) describe four criteria for choosing an appropriate landmark scheme; the landmarks must represent homologous anatomical loci, they must provide adequate coverage of the morphology, can be found reliably in all
specimens, and do not switch positions relative to one another. In addition to landmarks, sliding semilandmarks are used in this analysis. Semilandmarks are placed between two defined endpoints; landmarks are used as the endpoints in this analysis to provide anchors and make the shape models more intelligible. The semilandmarks are then evenly spaced between the landmarks using a computer algorithm. The algorithm then moves the semilandmarks iteratively along the outline of the skull table to ensure that its shape is adequately covered (Bookstein, 1997).

For the skull table outline analysis four landmarks are placed along the margins of the skull table (Fig. 46). Using this landmark scheme the entirety of the skull table’s outline is preserved. Three of the four landmarks are placed at sutures and one is placed at the posterior midline. The first landmark is located at the sutural contact between the frontal and the postorbital; landmark two is placed at the postorbital-squamosal contact; landmark three is placed at the posteriormost extent of the squamosal; and landmark four denotes the posterior midline of the skull table. Sliding semi-landmarks are placed between the landmarks. This landmark scheme ensures that the entire outline of the skull table is adequately covered.

The parietal-squamosal suture, along the posterior margin of the skull table, is not selected as a landmark point because the parietal is excluded from the posterior-most margin of the skull table by the supraoccipital in some caimanine species. Further, the parietal-supraoccipital suture is not selected as a landmark point because the supraoccipital is not exposed on the dorsal skull table in some species. The positions of the landmarks are chosen because they are homologous to all crocodylian skulls and may be placed accurately for all specimens. The first landmark serves as a non-arbitrary anteriormost extent of the skull table posterior to the orbits; the second landmark represents the anterolateral corner of the skull table;
the third landmark represents the posterolateral extent of the structure; the fourth landmark represents the posteriormost midline of the skull table.

All sliding semi-landmarks are placed at equal distances between their respective landmarks and their densities are tailored to the amount of observed shape change in a region. For example, semi-landmark densities are greatest between landmarks 1-2 and 3-4 (20 semi-landmarks respectively) because the skull table in most taxa show strong curvature in these regions. Semi-landmark placement is relatively less dense between landmarks 2 and 3 (15 semi-landmarks) due to the skull table outline being more or less straight in this region.

For the outline analysis including information from the supratemporal fenestrae, a second set of four landmarks are placed at the margins of the fenestrae (Fig. 46). The additional landmarks quantify the shape of the supratemporal fenestrae as well as shape change and their migration during ontogeny. This landmark scheme was chosen for the supratemporal fenestrae as it is homologous across the taxa sampled and encompasses the length and width of the structure. The first landmark is placed at the parietal-squamosal suture which is invariably
along the posterior margin of the fenestra. The second landmark is placed at the postorbital-squamosal suture along the lateral margin of the fenestra. The third and fourth landmarks are placed at the anteriormost and medialmost margins of the fenestra respectively.

The number of specimens sampled dictates the maximum number of landmarks in an analysis (Adams, 2014). The total of 59 datapoints (4 landmarks and 55 semi-landmarks) does not exceed the aforementioned convention as the outline analysis includes 240 specimens (specimens listed in Appendix 3). The outline analysis including information from the supratemporal fenestrae has 63 datapoints (8 landmarks and 55 semi-landmarks) and 238 specimens.

Allometry is explored through two additional datasets; one for the outline, and a second including both the outline and the supratemporal fenestrae. The skull table outline analysis uses a reduced sample size of 165 specimens. The outline + supratemporal fenestrae analysis uses 164 specimens. These analyses employ the same landmark schemes as used in the above analyses. For the datasets exploring allometric trends over ontogeny some species had to be excluded as the author did not have access to a complete ontogenetic sequence (for a table of specimens see Appendix 3).

Procrustes superimposition is used to analyze variation in shape as it minimizes the differences between landmark configurations among specimens. This method takes all specimens in the analysis and standardizes them by rescaling and rotating them into a common orientation using leastsquares fitting (Rohlf and Slice, 1990). Alignment of the specimens in the digital images does not matter in the comparison of the datasets due to this method (Drake and Klingenberg, 2008). Procrustes superimposition also centers the landmark data from each specimen, scales them to the same size, and rotates them into the same orientation. After the
landmarks have been superimposed the similarities and differences in their shape can be analyzed (Zelditch, Swiderski, and Sheets, 2012).

Although skulls are bilaterally symmetrical, the total shape variation contains a component of asymmetry (Klingenberg et al. 2002). However, this study does not consider asymmetry and only considers the symmetric component of variation; only one side of the skull will be analyzed. As many fossils are incompletely preserved, this method allows for the expansion of the dataset as only one side of the skull table must be perfect in order to be included in this analysis.

Principal component analyses (PCA) were completed using the geomorph package in R (Adams and Otárola-Castillo, 2013). Principle component analysis forms the basis for comparison of similarity and difference among the taxa in this analysis – similarity and difference are graphically displayed as simple scatter plots. Additionally, the axes of a PCA plot are the principle components (PCs) and will be ordered by the amount of variation in shape they represent with the first PC representing the most variation in shape, the second PC representing the second most variation in shape, and so on (Zelditch, Swiderski, and Sheets, 2012). Additionally, each point on a PCA plot represents the shape of a single specimen and similarity in morphospace between two points may be measured by their proximity to one another. A PCA plot may also be referred to as a morphospace as each point on the plot represents a different shape (or configuration of landmarks) (Zelditch, Swiderski, and Sheets, 2012).

Upon the completion of PCA, eigenvalues, eigenvectors, and scores are output by R. Eigenvalues represent the variance on each PC axis, eigenvectors detail the major axes of the data, and scores indicate the location of data points on each PC axis. The calculation of eigenvalues and eigenvectors of the covariance matrix finds the major axes of the data and the
variation among them. Later statistical analysis is completed using the information contained in the scores (Zelditch, Swiderski, and Sheets, 2012).

In this analysis the visualization of shape change along a principle component axis is aided by the use of deformation grids. Deformation grids are deformed rectangular grids that illustrate shape differences between two landmark configurations (Bookstein, 1989). They are calculated for the positive-most and negative-most values along each PC helping visualize shape change along the axis. This visualization of shape differences, and change, is the aim of geometric morphometrics and is a great strength relative to traditional morphometrics. The thin-plate spline algorithm in R automatically generates deformation grids along with eigenvalue, eigenvector, and scores data (Adams and Otárola-Castillo, 2013).

Each species is assigned categorical variables (define groups and are unordered) depending on its phylogenetic relationships and snout length. To test for the association between skull table shape and phylogeny, phylogenetic relationships are determined via literature searches and the author’s phylogenetic analyses. Snout length categories are quantified for each taxon after Busby (1995) in order to test for the association of skull table shape on snout length.

Multivariate analysis of variance (MANOVA) is then performed on the categorical factors (groups of taxa, snout length). MANOVA is the most common method in geometric morphometrics to test for the association between shape and some other variable. This method tests for differences between the means of each group in the analysis with the null hypothesis being that the means are equal for all groups. A p-value is used by this method to test for the overall difference between groups along each significant PC and is based on the proportion of variance measured within a group compared to the variance between groups.
In order to determine how different each group is from one another, pairwise comparisons using t-tests are utilized. Significance was statistically evaluated using a permutation test that randomizes the group assignments of each taxon 999 times and recalculates the distances between each group. The null hypothesis for this method is that the distances between each group are not different from one another. Therefore, if the distances between the groups of randomly assigned species are larger than the actual calculated distances at a rate of less than 0.05 then the p-values may be considered significant.

Before running MANOVA the data were subjected to a Shapiro-Wilk test to determine if the assumptions of MANOVA are met by the data (independent random sampling, data normally distributed). Interpretation of the p-value generated by a Shapiro-Wilk test is straightforward; the null hypothesis that the data are normally distributed is rejected if the p-value is less than 0.05.

The contribution of allometry is explored. Allometry is defined as shape change correlated with size change (Gould, 1966; Mosimann, 1970). Comparisons of allometric trajectories among species are often used to identify evolutionary changes in the size-shape relationship across taxa (Bookstein et al., 2003; Piras et al., 2010; Adams, 2014). Methods developed by Adams and Nisri (2010) and Piras et al. (2010) to analyze ontogenetic allometry are utilized by this study. The observed allometric trajectory for each species is estimated using regression coefficients generated by regressions of shape on size. Residuals from the regressions are then permuted among species. The data is then randomized and regression coefficients are generated. Differences between the randomized allometric trajectories are estimated. Next, the observed differences between allometric trajectories are compared to a random distribution of trajectories produced by 999 iterations obtained via permutations of the residuals as before.
Visualizing ontogenetic allometry in this analysis is after Piras et al. (2010). Principle components analysis is used to generate a set of Procrustes shape variables which are then examined for patterns of variation. In the graphs of Piras et al. (2010) shape is visualized along the first three PC axes. Size is included in the plots by scaling specimens proportional to their centroid size – this allows for the incorporation of allometry into the plot. Allometric trajectories are then visualized through the use of predicted shapes along a regression line.

To test for instances of convergence, parallelism, and divergence among the ontogenetic trajectories the procedure of Adams and Nistri (2010) is used. Procrustes distances between shapes among species at the smallest and largest comparable sizes are compared. Pairwise distances between the smallest comparable specimens for each species are calculated then summed (D_{juv}). This procedure was also done for the largest comparable specimens from each species (D_{adult}). Subtracting D_{adult} from D_{juv} provides a test statistic. This test statistic, if positive, indicates that adults are closer one another than juveniles are to one another in morphospace, a negative number indicates the opposite. This test statistic is statistically evaluated via a permutation procedure that randomizes the sizes relative to each specimen and then recalculates the test statistic 999 times. P-values are considered significant if the randomized test statistic is larger than the observed test statistic at a rate of less than 0.05 against the null hypothesis that the adult and juvenile distributions are not different.

Evidence for ontogenetic convergence is present if the shape distance between two species under comparison is smaller at adult stages than at juvenile stages. If the distance is the same at juvenile and adult stages then evidence is present for parallelism. Lastly, if the distance between adults is larger than that of the juvenile forms then evidence for divergence is present.
Results

In all analyses the first five principle component axes (PCs) explain more than 5% of the total variance (eigenvalues for all PCs presented in Appendix 3). For the outline analysis, the cumulative proportion of variance accounted for by the first five PCs is 80.858% (PC1=31.419%, PC2=24.976%, PC3=10.904%, PC4=7.414%, PC5=6.139%). For the outline analysis with the addition of supratemporal fenestrae landmarks, the cumulative proportion of variance accounted for by the first five PCs is 76.062% (PC1=27.084%, PC2=19.814%, PC3=16.403%, PC4=7.713%, PC5=5.047%).

Interpretation of the principle component axes for the outline analysis are straightforward (Fig. 47). The first PC represents the length of the posterior prong of the squamosal. Positive values indicate a short posterior projection of the squamosal and negative values indicate a long posterior projection. The second PC describes the morphology of the anterolateral corner of the skull table. Positive values of the second PC indicate a mediolaterally restricted anterior margin whose anterolateral corner, formed by the postorbital, is abbreviated and whose angle is obtuse. Negative values of the second PC indicate a mediolaterally expansive anterior margin with an anterolateral corner whose morphology forms a knob-like projection when viewed dorsally and whose angle is acute. The third PC (not pictured) describes the posterior margin with positive values demonstrating an anteriorly concave margin whose midline is posteriorly displaced and negative values demonstrating a posteriorly convex margin whose midline is anteriorly displaced.

For the outline analysis, *Borealosuchus* is separated from the other taxa along the first PC and occupies the negative extremes of the axis (Fig. 47). Whereas there is considerable overlap for all other groups along the first PC. The most positive and negative values along the first PC
are filled by a hatchling *Alligator mississippiensis* and species of *Borealosuchus* respectively. Positive values along this axis indicate a short posterior prong of the squamosal and negative values indicate a long posterior prong. Variance along the first PC is greatest for Alligatoroidea – followed closely by Crocodyloidea – and lowest for *Borealosuchus* (Fig. 48).

**FIGURE 47.** Plot of morphospace resulting from the principle component analysis of the outline dataset. Deformation grids show the shapes represented by the positive and negative extremes of each axis.
The second PC demonstrates considerable overlap for all groups. Along the second PC Gavialoidea and *Borealosuchus* are the most restricted groups in morphospace (Fig. 48). The third PC (not pictured) separates Gavialoidea from the other taxa – the taxon occupies the most positive region of the axis due to the concavity of its posterior margin. For the outline analyses Crocodyloidea occupies the widest range of morphospace (Fig. 48).

The most positive and negative values along the second PC belong to species of *Crocodylus* (especially *C. niloticus* and *C. johnstoni*) and species of *Gavialis* and *Borealosuchus* respectively. Positive values indicate an anterior corner that is mediolaterally abbreviated and whose angle is obtuse whereas negative values correspond to an anterolateral corner that is mediolaterally expansive and whose angle is acute.

The most positive values along the third PC are occupied by gavialoids who demonstrate an anteriorly concave posterior margin and whose midline is posteriorly displaced. The most negative values along this axis are occupied by *Tsoabichi greenriverensis* and a specimen of *Melanosuchus niger* whose posterior margins are posteriorly convex and whose midline is anteriorly displaced.

With the inclusion of information from the supratemporal region all PC axes incorporate outline morphology described above with additional information encompassing the morphology of the supratemporal fenestrae (Fig. 49). The first PC encompasses the symmetry of the supratemporal fenestrae with positive values demonstrating landmarks that are nearly equidistant from one another and whose fenestrae are centered in the middle of each half of the skull table.
Negative values of the first PC indicate a fenestral opening that is mediolaterally constricted and whose axis trends anterolaterally from posterior to anterior.

The second PC indicates the size of the fenestral opening relative to the dorsal skull table with positive values representing relatively larger fenestrae and negative values representing smaller. The most negative values along this PC indicate fenestrae that are completely closed. Interpretation of the third PC axis is not straightforward.
FIGURE 49 (opposite page). Plot of morphospace resulting from the principle component analysis of the outline + supratemporal fenestrae dataset. Deformation grids show the shapes represented by the positive and negative extremes of each axis.

There is still overlap among the groups along the first PC axis (Fig. 49). The positive extreme along the first PC is occupied by a very large *Crocodylus porosus* specimen. This taxon demonstrates relatively symmetrical supratemporal fenestrae whose landmarks are approximately equidistant from one another. The most negative value along this PC is occupied by an *Alligator mississippiensis* hatchling whose supratemporal fenestrae are present as narrow slits, with landmarks 6 and 7 + 5 and 8, lying in close proximity to one another and whose medial and lateral fenestral margins trend anterolaterally from posterior to anterior. Along the first PC variance is greatest for Alligatoroidea and smallest for *Borealosuchus* (Fig. 50).

The second PC separates Gavialoidea, which occupies the most positive values in morphospace along this axis, from the other taxa. The most positive values along the second PC are occupied by species of *Gavialis* whose supratemporal fenestrae occupy the largest proportion of the skull table relative to other taxa. Species of *Paleosuchus* occupy the most negative values along the second PC and whose supratemporal fenestrae are entirely closed. Variance is greatest for Alligatoroidea and smallest for *Borealosuchus* and Gavialoidea (Fig. 50).

The third PC (not pictured) is difficult to interpret and demonstrates overlap among the taxa. Gavialoidea and *Borealosuchus* occupy negative values in morphospace whereas most crocodyloids occupy positive values. Crocodyloidea is dispersed among positive and negative values and occupies a larger portion of morphospace than the other taxa (Fig. 50).

Upon completion of Shapiro-Wilk tests for the outline and outline + STF analyses, p-values for the first three principle components are in excess of the 0.05 threshold and therefore the null hypothesis of normally distributed data cannot be rejected. MANOVA was conducted to
FIGURE 50 (opposite page). Boxplots of variance for each taxon along the first three principle component axes for the outline + supratemporal fenestrae analysis. A. PC1. B. PC2. C. PC3.

FIGURE 51. Morphospace occupation of non-hatchlings in this analysis organized by snout-shape categories.

test if means are significantly different among the groups (PCs 1-5 are significant for all datasets). High F-statistics (outline F=16.082, df=239) (outline + STF F=17.264, df=237), with associated p-values of less than 0.001, indicate significant differences among the groups for all analyses. This suggests that the null hypothesis - means are equal among groups - may be rejected.

To determine where the differences lie between the taxa, pairwise comparisons using t-tests with pooled standard deviation are conducted. P-values below the 0.05 threshold indicate that the null hypothesis of equal means – between the two groups in each comparison – may be
rejected. Significant differences in group means exist between all groups for the outline analysis and outline + STF analysis.

MANOVA completed as part of this analysis suggests that there is a significant association between snout length and skull table shape for PCs 1-3 and 5. P-values do not exceed 0.05 for these PCs indicating that snout shape categories are significantly separated from one another in morphospace (Fig. 51). Skull tables of the long snouted forms generally plot in the lower left, medium in the upper center, and short in the lower right side of the morphospace with some overlap between the categories.

FIGURE 52. Allometric trajectories for the outline analysis. Tick marks along the principle component axes represent increments of 0.01. The horizontal axis, vertical axis, and axis pointing up and to the right represent the first, second, and third principle components respectively.
For the skull table outline analysis the graph of allometric trajectories (Fig. 52) indicates that the outline is more similar for juveniles than for adults. All trajectories start in a limited region of morphospace along the right side of the graph and radiate toward the left. Allometric trajectories for the outline + STF analysis (Fig. 53) demonstrate that juvenile morphology occupies the lower half of the morphospace. Later ontogenetic stages generally plot to the upper left of the juvenile morphologies. Relative to the outline only analysis juvenile morphologies occupy a larger portion of morphospace. Adult morphologies, save *G. gangeticus*, *O. tetraspis*, *P. palpebrosus*, and *P. trigonatus*, converge upon a similar portion of morphospace. As with the outline analysis, adults of the smallest taxa (*O. tetraspis*, *P. palpebrosus*, and *P. trigonatus*) do not diverge substantially from their juvenile counterparts and occupy a region of morphospace separate from other taxa.

There is considerable intraspecific shape change over ontogeny as evidenced by the graphs of allometric trajectories for the outline (Fig. 52) and outline + STF datasets (Fig. 53). Tests for statistical significance indicate that convergence, divergence, and parallelism are present among the outlines of Crocodylian skull tables (see Appendix 3 for distances and p-values). Including information from the supratemporal fenestrae indicates that statistical support for divergence is considerably more common among the skull tables of various crocodylian species (see Appendix 3 for distances and p-value tables) than is convergence or parallelism.
Discussion

The outline analysis shows that Crocodyloidea occupies a greater proportion of morphospace relative to other taxa with Alligatoroidea occupying the next largest proportion (Fig. 47). Borealosuchus occupies the most restricted morphospace in this analysis. Morphospace occupation of Gavialoidea is also restricted. Although the sample sizes for Borealosuchus and Gavialoidea are small relative to Crocodyloidea and Alligatoroidea their pattern of restricted morphospace occupation is likely biological in nature and reflects the limited skull table morphologies of the taxa.

Species belonging to Crocodyloidea and Alligatoroidea encompass multiple snout length categories, and as evidenced from the MANOVA analysis of skull table shape on snout length, there is a significant association between snout length and skull table shape. Crocodyloids in this analysis represent mesorostrine and longirostran morphologies whereas alligatoroids represent brevirostran, mesorostrine, and duck-faced longirostran morphologies. Whereas, Borealosuchus and gavialoids represent relatively narrow-snouted mesorostrine, and longirostran morphologies respectively. The restricted occupation of skull table morphospace may reflect the restricted snout shape categories in these taxa.

Interestingly, the duck-faced longirostran alligatoroid Deinosuchoides schwimmeri occupies a portion of morphospace near Borealosuchus and Gavialoidea, two groups with variably long, narrow snouts. This suggests that snout length may have a larger effect on skull table outline morphology than snout width. When the skull tables are compared between these taxa similarities are evident. Supratemporal fenestrae are large to house enlarged m. adductor mandibulae externus profundus, anterior corners of the skull table project anterolaterally and form an acute angle, and posterior squamosal prongs are relatively long.
The outline + STF analysis indicates that Alligatoroidea occupies the largest proportion of morphospace. This is due to the effect of *Paleosuchus*, a taxon with closed supratemporal fenestrae, at the negative-most extreme of the second PC axis. The exclusion of the taxon results in a morphospace occupation that is similar to Crocodyloidea. As with the full analysis *Borealosuchus* and Gavialoidea occupy the most restricted portions of morphospace.

Gavialoidea is broadly separated from the other taxa along the second PC axis. This is due to the proportionally large supratemporal fenestrae relative to the other taxa. Interestingly, species of *Tomistoma* and *Euthecodon*, which have very long and narrow snouts are separated from Gavialoidea – but occupy the most positive portions of morphospace among crocodyloids. This suggests that there may be some phylogenetic constraints on the size of the supratemporal fenestrae in crocodyloids.

*Gavialis gangeticus* occupies restricted portions of morphospace, separate from other taxa, in the outline + STF analysis, and the two analyses of allometry. This highly derived, yet phylogenetically basal, taxon shares similarities to a number of distantly related longirostran taxa such as species of *Euthecodon* and *Tomistoma*. However, *G. gangeticus* achieves its skull table morphologies in a manner that diverges from other taxa in this analysis.

Allometric trajectories indicate that skull table outline is conserved among juveniles – specimens at the smallest size categories are found in a similar region of morphospace. Juveniles generally share skull tables that are nearly rectangular in outline; lateral and posterior margins are straight, anterolateral and posterolateral corners form nearly right angles, and the posterior squamosal prong is short.

Interestingly, in both the outline and outline + STF analyses, adults of the smallest extant species (*Osteolaemus tetraspis*, *Paleosuchus palpebrosus*, and *Paleosuchus trigonatus*) do not
diverge substantially from their juvenile shapes, and the juvenile shapes of larger species. This is especially evident in the outline analysis where adults occupy a restricted morphospace along with juveniles of other taxa. This could indicate an instance of paedomorphosis in which juvenile morphologies are maintained into adulthood for the smallest taxa.

For the outline analysis, convergence between *O. tetraspis* and *P. palpebrosus* is statistically significant (Appendix 3). Interestingly, the skull table morphologies of the sister taxa, *P. palpebrosus* and *P. trigonatus*, are divergent, yet they plot closely in morphospace and in plots of allometric trajectories. Both species of *Paleosuchus* are represented by few specimens in this analysis with large gaps in the ontogenetic sequence. Unfortunately, tests for significance are hindered by the lack of specimens of comparable size.

Additionally, the allometric trajectories of the outline analysis found statistical convergence between the two relatively slender snouted crocodylids *C. intermedius* and *C. johnstoni*. Although these taxa are not considered to be closely related, their convergent morphologies may indicate similar ecologies.

The allometric trajectories from the outline + STF analysis indicate that *C. johnstoni* and *C. mindorensis* are divergent from the other taxa (Fig. 53), yet the adult forms of these species converge upon one another in morphospace. These Indo-Pacific taxa are considered to be closely related (Brochu et al., 2010) and their similarity to one another is likely the product of shared phylogenetic history.

In addition to quantifying the shape and ontogenetic trajectories of crocodylian skull tables, this study may provide an indirect hypothesis of snout length. Snout length is an important predictor of crocodylian ecology as the snout is the primary means by which the animal interacts with its world. As such the skull is considered to be phylogenetically plastic
among crocodylians (Brochu, 2001). Additionally, snout length is a means by which crocodylians partition themselves in an ecosystem allowing for relatively closely related species, with different snout lengths, to coexist (i.e. *Crocodylus niloticus*, *Osteolaemus tetraspis*, and *Mecistops cataphractus* in West Africa) (Brochu, 2001). Further, snout length varies ontogenetically and serves to ecologically partition animals within the same species (Mook, 1921; Dodson, 1975; Webb and Messel, 1987; Hall and Portier, 1994, Busbey, 1995; Brochu, 2001).

That many crocodylian fossils are incomplete or distorted, characterizing snout shape – and thus predictions of ecology – may be impossible. Phylogenetic bracketing may inform on snout length but oftentimes this method has shortcomings; mapping snout shape over phylogeny reveals that shape among crocodylians is labile and similar morphologies have arisen independently multiple times (Kälin, 1955; Langston, 1973; Busbey, 1995; Russell and Wu, 1997; Brochu, 2001). Insights from the readily fossilized, and oftentimes undistorted, skull table sheds light on the probable shape of the snout giving insights to the ecology of the animal. This is especially true for the relative size of the supratemporal fenestrae compared to the rest of the skull table. Taxa with relatively large supratemporal fenestrae plot in the positive-most values of the first PC in the outline + STF analysis.

**Conclusions**

In this analysis there is considerable overlap in morphospace between Alligatoroidea and Crocodyloidea whereas *Borealosuchus* and Gavialoidea are restricted in their occupation of morphospace. The overlap between Alligatoroidea and Crocodyloidea may be the product of
sharing a more recent common ancestor than the other two groups. Additionally, similarities exist in the ecologies of these groups as evidenced by shared snout shape categories.

With the inclusion of landmarks representing the supratemporal fenestrae, Gavialoidea is broadly separated from the other groups as a result of having proportionally massive supratemporal fenestrae. Although species of the crocodyloids *Tomistoma* and *Euthedon* approach or exceed the length of the snout in gavialoids their supratemporal fenestrae are proportionally smaller. This suggests that there is a phylogenetic constraint on the size of the supratemporal fenestrae in crocodyloids regardless of snout length.

Allometric trajectories of the smallest extant taxa (*O. tetraspis*, *P. palpebrosus*, *P. trigonatus*) plot alongside the juveniles of the other taxa in this analysis. This may indicate that paedomorphosis is present in the skull table outline of these small taxa whose diminutive size may have been achieved via maintenance of juvenile morphologies through ontogeny. This provides future avenues of study for the author who will focus on morphometric analyses of diverse skull regions, full skulls, and postcrania to determine allometric trajectories relative to reconstructions of ancestral character states at nodes in the phylogeny of Crocodylia.

Current understanding of crocodylian behavior is limited. The biological implications of skull table shape, other than raising the eyes and ears above the waterline, are largely unknown. Shape likely plays a role in hydrodynamics, species recognition, and biomechanical adaptations. This study sets the foundations for the quantification of skull table shape in Crocodylia. This information, combined with observations of extant taxa in the field, will form the basis for functional and behavioral comparisons of skull tables among crocodylians.
CHAPTER 4
SUMMARY OF PROJECT

This project sought to explore, name, and describe some of the earliest known members of Alligatoroidea. Explorations of *Bottosaurus harlani*, *Deinosuchus hatcheri*, *Deinosuchoides schwimmeri*, and *Deinosuchoides riograndensis* reveal that early in their evolutionary history alligatoroids had attained bauplans that are highly divergent from the ancestral alligatoroid in both body size and morphology.

*Bottosaurus harlani* preserves aspects of the skull table – including constricted supratemporal fenestrae, a linear frontoparietal suture, and a large trapezoidal dorsal supraoccipital exposure – that are similar to those of caimans. *Bottosaurus harlani* is included within Caimaninae due to its possession of a linear frontoparietal suture between the supratemporal fenestrae.

Optimal trees from phylogenetic analysis recover *B. harlani* in three different positions; as a sister either to the modern dwarf caimans (*Paleosuchus*), or either living species of *Paleosuchus*. That a substantial stratigraphic gap separates *B. harlani* from both species of *Paleosuchus*, which first appears in the Miocene, along with low character and nodal support raises questions about this relationship. The phylogenetic placement of *B. harlani* may reflect an incomplete knowledge of the taxon and further study might support placement outside of Caimaninae. More complete analyses of *B. harlani* and other Cretaceous–Paleogene alligatoroids will help illuminate the relationships among these forms and their living relatives.

Should the relationships recovered here be true, *Bottosaurus harlani* would be the oldest known caiman. The taxon indicates that morphologies common to modern caimans date to the
earliest record of the clade. Additionally, the presence of a caiman (*B. harlani*), proximal to the Cretaceous-Paleogene boundary, in addition to the oldest unambiguous alligatorine (*N. mooki*) from the lower Paleocene establishes representatives of the sister groups within Alligatoridae by the lower Paleocene. The presence of *B. harlani* agrees with molecular data which indicate a divergence between *Alligator* and *Caiman* near the Cretaceous – Paleogene boundary.

The presence of *B. harlani*, a derived caiman, in the uppermost Cretaceous suggests that the biogeographic history of Alligatoroidea is more complicated than previously suggested. Modern caimans are all South American yet South America was isolated from North America for much of the Cenozoic. To explain the presence of caimans in South America by the Paleocene marine barriers must have been crossed and physiological adaptations to excrete excess salt must have arisen in the clade.

Although extant alligatorids are intolerant of salt water, basal alligatoroids may not have been. Dispersal via marine routes as is found in Crocodyloidea and Gavialoidea could have been possible. Through stable isotope analysis of carbon and oxygen from tooth enamel Wheatley (2010) explored marine and freshwater habitat use in a number of fossil crocodylians including alligatoroids – *Bottosaurus* and *Deinosuchus* are part of this analysis. Their remains are recovered in marginal marine depositional environments and they may have ingested marine resources (i.e. prey and water) (Wheatley, 2010). The results suggest that *Deinosuchus* consumed large amounts of seawater but *Bottosaurus* did not. Should *Deinosuchus* be able to osmoregulate in saline environments an argument can be made that early alligatoroids could tolerate salt water and that the physiological adaptation was lost in alligatorids. *Deinosuchus* was one of the largest crocodylians to have ever lived, so it also possible that it was able to withstand relatively larger volumes of seawater without possessing lingual glands for the excretion of salt (Wheatley,
2010). Nonetheless, consumption of saltwater in an organism with no means of processing the excess salt found in seawater is unexpected behavior.

In addition to the enigmatic *B. harlani*, the Campanian giant *Deinosuchus* was re-evaluated as part of this project. Recent consensus has been that the three named species of *Deinosuchus* (*D. hatcheri*, *D. riograndensis*, and *D. rugosus*) represent a single, widely ranging species. This hypothesis was challenged and changes to the taxonomy of the genus were made.

Newly-collected material from the Big Bend region of western Texas and increased sampling of the lineage from throughout North America allowed for a review of species-level systematics of *Deinosuchus* and helped refine its phylogenetic placement among crocodylians. *Deinosuchus* from western and eastern North America can be consistently differentiated and represent different species.

As a result of the lack of diagnostic characters in the very incomplete holotype specimen, the name *Deinosuchus* is restricted to *D. hatcheri*. To encompass specimens formerly included in *Deinosuchus* a new genus, *Deinosuchoides*, is erected. In addition to naming a new genus, the holotype specimen for *Deinosuchus rugosus* is determined to be undiagnostic to species level and is determined to be a nomen dubium. A new species, *Deinosuchoides schwimmeri*, is erected upon a cranial specimen from Mississippi.

The snout of *Deinosuchoides* is very long and wide. Almost invariably, crocodylian snouts are either long or wide, but not both. Wide snouts are relatively common for Alligatoroidea but long snouts are extremely rare. Lengthening of the snout in *Deinosuchoides* was achieved by the lengthening of posterior snout elements. In addition to the unusually long and wide snout, the skull table of this taxon bears hallmarks found in species of other long-snouted taxa such as *Tomistoma* and *Gavialis*. 
To explore the variability of the crocodylian skull table a morphometric analysis was conducted with the inclusion of fossil taxa. As the skull table is robust and likely to be recovered in the paleontological record this element was an ideal fit for a morphometric study. When *Deinosuchoides* is plotted in morphospace it is recovered between species of *Borealosuchus* and *Gavialoidea*, two taxa with long slender snouts. This likely indicates that skull table morphology reflects, in part the length of the snout. As such, plotting isolated skull tables in morphospace, may indicate snout length and thus ecology of fossil taxa.

In addition to establishing the morphospace occupation of fossil taxa, the morphometric analysis found considerable overlap in morphospace between Alligatoroidea and Crocodyloidea – the overlap between these groups may be the product of shared ancestry. Additionally, similarities exist in the ecologies of these groups as evidenced by shared snout shape categories.

When landmarks representing the supratemporal fenestrae are included in the analysis Gavialoidea is broadly separated from the other groups in morphospace. This was primarily the result of having supratemporal fenestrae that occupy a larger proportion of the skull table relative to other taxa. It has been long hypothesized that the size of the supratemporal fenestrae reflect the length of the snout as a result of jaw musculature attaching to their medial margins. However, this relationship is not as straightforward as previously hypothesized; the snouts of the crocodyloids *Tomistoma* and *Euthecodon* may exceed the length of the snout in gavialoids but their supratemporal fenestrae are proportionally smaller. This study suggests that a phylogenetic constraint on the size of the supratemporal fenestrae may be present in crocodyloids.

In addition to exploring morphospace occupation, allometric trajectories of all extant taxa with available ontogenetic sequences were explored. The smallest extant taxa (*O. tetraspis*, *P. palpebrosus*, and *P. trigonatus*) demonstrate allometric trajectories that plot alongside the
juveniles of the other taxa in this analysis. This may suggest that the small sizes of the skull tables in these species were achieved through paedomorphosis, or the maintenance of juvenile morphologies into adulthood.

Through the exploration of the diverse morphologies of basal alligatoroids and analyses of skull table morphology future avenues of study have been presented. This work should focus on the coding and description of new alligatoroid species to elucidate evolutionary trends at the base of the clade. Studies presented herein show that re-evaluation of previously described species may produce fruitful results in light of an expanded knowledge of character evolution within the clade.
APPENDIX 1.

List of characters and character matrix used in the phylogenetic analysis of *Bottosaurus harlani*.

Some codings are based on the literature, namely Brochu, 2010. All others are based on direct observation of specimens.

1. Ventral tubercle of proatlas more than one-half (0) or no more than one half (1) the width of the dorsal crest.

2. Proatlas with prominent anterior process (0) or lacks anterior process (1).

3. Proatlas has tall dorsal keel (0) or lacks tall dorsal keel; dorsal side smooth (1).

4. Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1).

5. Atlantal ribs without (0) or with (1) very thin medial laminae at anterior end.

6. Atlantal ribs lack (0) or possess (1) large articular facets at anterior ends for each other.

7. Anterior half of axis neural spine oriented horizontally (0) or slopes anteriorly (1).

8. Axis neural spine crested (0) or not crested (1).

9. Axial hypapophysis located toward the center of centrum (0) or toward the anterior end of centrum (1).
(10) Hypophyseal keels present on eleventh vertebra behind atlas (0), twelfth vertebra behind atlas (1), or tenth vertebra behind atlas (2).

(11) Third cervical vertebra (first postaxial) with prominent hypophysis (0) or lacks prominent hypophysis (1).

(12) Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel; minimal dorsal flare at maturity (1).

(13) Deltoid crest of scapula very thin at maturity, with sharp margin (0) or very wide at maturity, with broad margin (1).

(14) Scapulocoracoid synchondrosis closes very late in ontogeny (0) or relatively early in ontogeny (1).

(15) Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa, and tapering anteriorly (1).

(16) Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1).

(17) Interclavicle flat along length, without dorsoventral flexure (0) or with moderate dorsoventral flexure (1) or with severe dorsoventral flexure (2).

(18) Anterior end of interclavicle flat (0) or rodlike (1).
(19) Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation ("wasp-waisted;" 2) or narrow, with dorsal indentation (3) or rounded with smooth border; posterior tip of blade very deep (4).

(20) Dorsal osteoderms not keeled (0) or keeled (1).

(21) Dorsal midline osteoderms rectangular (0) or nearly square (1).

(22) Four (0), six (1), eight (2), or ten (3) contiguous dorsal osteoderms per row at maturity.

(23) Nuchal shield grades continuously into dorsal shield (0) or differentiated from dorsal shield; four nuchal osteoderms (1) or differentiated from dorsal shield; six nuchal osteoderms with four central and two lateral (2) or differentiated from dorsal shield; eight nuchal osteoderms in two parallel rows (3).

(24) Ventral armor absent (0) or single ventral osteoderms (1) or paired ventral ossifications that suture together (2).

(25) Anterior margin of dorsal midline osteoderms with anterior process (0) or smooth, without process (1).

(26) Ventral scales have (0) or lack (1) follicle gland pores.

(27) Ventral collar scales not enlarged relative to other ventral scales (0) or in a single enlarged row (1) or in two parallel enlarged rows (2).

(28) Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0) or fourth alveolus larger than third, and alveoli are separated (1).
(29) Dentary symphysis extends to fourth or fifth alveolus (0) or sixth through eighth alveolus (1) or behind eighth alveolus (2)

(30) Dentary gently curved (0), deeply curved (1), or linear (2) between fourth and tenth alveoli.

(31) Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) 13 or 14 and a series behind it, (2) 11 or 12, or (3) no differentiation, or (4) behind 14

(32) Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1).

(33) Mandibular ramus of cranial nerve V exits splenial anteriorly only (0) or splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1) or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2).

(34) Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0) or splenial excluded from mandibular symphysis; anterior tip of splenial passes ventral to Meckelian groove (1) or splenial excluded from mandibular symphysis; anterior tip of splenial passes dorsal to Meckelian groove (2) or deep splenial symphysis, longer than five dentary alveoli; splenial forms wide "V" within symphysis (3) or deep splenial symphysis, longer than five dentary alveoli; splenial constricted within symphysis and forms narrow "V" (4), splenial excluded from mandibular symphysis; anterior tip of splenial passes ventral to Meckelian groove.
(35) Coronoid bounds posterior half of foramen intermandibularis medius (0) or completely surrounds foramen intermandibularis medius at maturity (1) or obliterates foramen intermandibularis medius at maturity (2).

(36) Superior edge of coronoid slopes strongly anteriorly (0) or almost horizontal (1).

(37) Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1).

(38) Coronoid imperforate (0) or with perforation posterior to foramen intermandibularis medius (1).

(39) Angular-surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1).

(40) Surangular with spur bordering the dentary toothrow lingually for at least one alveolus length (0) or lacking such spur (1).

(41) External mandibular fenestra absent (0) or present as narrow slit, no discrete fenestral concavity on angular dorsal margin (1) or present with discrete concavity on angular dorsal margin (2) or present and very large; most of foramen intermandibularis caudalis visible in lateral view (3).

(42) Surangular-dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0) or at posterodorsal corner (1).
(43)  Angular extends dorsally toward or beyond anterior end of foramen intermandibularis caudalis; anterior tip acute (0) or does not extend dorsally beyond anterior end of foramen intermandibularis caudalis; anterior tip very blunt (1).

(44)  Surangular-angular suture lingually meets articular at ventral tip (0) or dorsal to tip (1).

(45)  Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1).

(46)  Articular-surangular suture simple (0) or articular bears anterior lamina dorsal to lingual foramen (1) or articular bears anterior lamina ventral to lingual foramen (2) or bears laminae above and below foramen (3)

(47)  Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0) or perforates surangular/angular suture (1).

(48)  Surangular extends to posterior end of retroarticular process (0) or pinched off anterior to tip of retroarticular process (1).

(49)  Surangular-articular suture oriented anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa.

(50)  Sulcus between articular and surangular (0) or articular flush against surangular (1).

(51)  Dorsal projection of hyoid cornu narrow, with parallel sides (0) or flared (1).

(52)  Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or posterior teeth laterally compressed (1), or all teeth compressed (2)
(53) Naris projects anterodorsally (0) or dorsally (1).

(54) External naris bisected by nasals (0) or nasals contact external naris, but do not bisect it (1) or nasals excluded, at least externally, from naris; nasals and premaxillae still in contact (2) or nasals and premaxillae not in contact (3).

(55) Naris circular or keyhole-shaped (0) or wider than long (1) or anteroposteriorly long and prominently teardrop-shaped (2)

(56) Premaxillary surface lateral to naris smooth (0) or with deep notch lateral to naris (1).

(57) Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny.

(58) Incisive foramen small, less than half the greatest width of premaxillae (0) or large, more than half the greatest width of premaxillae (1) or large, and intersects premaxillary-maxillary suture (2).

(59) Incisive foramen completely situated far from premaxillary toothrow, at the level of the second or third alveolus (0) or abuts premaxillary toothrow (1) or projects between first premaxillary teeth (2).

(60) Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0) or long, extending beyond third maxillary alveolus (1).

(61) Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1). (Norell, 1988, character 29.)
(62) All dentary teeth occlude lingual to maxillary teeth (0) or occlusion pit between 7th and 8th maxillary teeth; all other dentary teeth occlude lingally (1) or dentary teeth occlude in line with maxillary toothrow (2).

(63) Largest maxillary alveolus is #3 (0), #5 (1), #4 (2), #4 and #5 are same size (3), #6 (4), or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6).

(64) Canthi rostrali absent or very modest (0) or very prominent (1) at maturity.

(65) Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary-maxillary suture (1).

(66) Medial jugal foramen small (0) or very large (1).

(67) Maxillary foramen for palatine ramus of cranial nerve V small or not present (0) or very large (1).

(68) Ectopterygoid abuts maxillary tooth row (0) or maxilla broadly separates ectopterygoid from maxillary tooth row (1).

(69) Maxilla terminates in palatal view anterior to lower temporal bar (0) or comprises part of

(70) Medial process of prefrontal pillar expanded dorsoventrally (0) or anteroposteriorly (1).

(71) Prefrontal pillar solid (0) or with large pneumatic recess (1).

(72) Maxilla has linear medial margin adjacent to suborbital fenestra (0) or bears broad shelf extending into fenestra, making lateral margin concave (1)
(73) Anterior face of palatine process rounded or pointed anteriorly (0) or notched anteriorly (1).

(74) Lateral edges of palatines smooth anteriorly (0) or with lateral process projecting from palatines into suborbital fenestrae (1).

(75) Pterygoid ramus of ectopterygoid straight, posterolateral margin of suborbital fenestra linear (0) or ramus bowed, posterolateral margin of fenestra concave (1)

(76) Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing "shelf" (1).

(77) Choana projects posteroventrally (0) or anteroventrally (1) at maturity.

(78) Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0) or pushed inward anterolateral to choanal aperture (1) or pushed inward around choana to form "neck" surrounding aperture (2) or everted from flat surface to form "neck" surrounding aperture (3).

(79) Posterior rim of internal choana not deeply notched (0) or deeply notched (1).

(80) Internal choana not septate (0) or with septum that remains recessed within choana (1) or with septum that projects out of choana (2).

(81) Ectopterygoid-pterygoid flexure disappears during ontogeny (0) or remains throughout ontogeny (1).
(82) Lacrimal makes broad contact with nasal; no posterior process of maxilla (0) or maxilla with posterior process within lacrimal (1) or maxilla with posterior process between lacrimal and prefrontal (2).

(83) Prefrontals separated by frontals and nasals (0) or prefrontals meet medially (1).

(84) Lacrimal longer than prefrontal (0), or prefrontal longer than lacrimal (1), or lacrimal and prefrontal both elongate and nearly the same length (2).

(85) Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1).

(86) Margin of orbit flush with skull surface (0) or dorsal edges of orbits upturned (1) or orbital margin telescoped (2).

(87) Palpebral forms from single ossification (0) or from multiple ossifications (1).

(88) Quadratojugal spine prominent at maturity (0) or greatly reduced or absent at maturity (1).

(89) Postorbital neither contacts quadrate nor quadratojugal medially (0) or contacts quadratojugal, but not quadrate, medially (1) or contacts quadrate and quadratojugal at dorsal angle of infratemporal fenestra (2) or contacts quadratojugal with significant descending process (3).

(90) Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra; quadrate participates in fenestra (1).
(91)  Postorbital-squamosal suture oriented ventrally (0) or passes medially (1) ventral to skull table.

(92)  Squamosal-quadrate suture extends dorsally along posterior margin of external auditory meatus (0) or extends only to posteroventral corner of external auditory meatus (1).

(93)  Posterior margin of otic aperture smooth (0) or bowed (1).

(94)  Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0) or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2).

(95)  Frontoparietal suture concavoconvex (0) or linear (1) between supratemporal fenestrae.

(96)  Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity (1) or supratemporal fenestra closes during ontogeny (2).

(97)  Medial parietal wall of supratemporal fenestra imperforate (0) or bearing foramina (1).

(98)  Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0) or parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1) or parietal and squamosal meet along posterior wall of supratemporal fenestra (2).

(99)  Posterolateral margin of squamosal horizontal or nearly so (0) or upturned to form a discrete "horn" (1)
(100) Mature skull table with broad curvature; short posterolateral squamosal rami along paroccipital process (0) or with nearly horizontal sides; significant posterolateral squamosal rami along paroccipital process (1).

(101) Supraoccipital exposure on dorsal skull table small (0), absent (1), large (2), or large such that parietal is excluded from posterior edge of table (3).

(102) Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1).

(103) Laterosphenoid bridge comprised entirely of laterosphenoid (0) or with ascending process of palatine (1).

(104) Significant ventral quadrate process on lateral braincase wall (0) or quadrate-pterygoid suture linear from basisphenoid exposure to trigeminal foramen (1).

(105) Exoccipitals terminate dorsal to basioccipital tubera (0) or send robust process ventrally and participate in basioccipital tubera (1) or send slender process ventrally to basioccipital tubera (2).

(106) Quadrate with small, ventrally-reflected medial hemicondyle (0) or with small medial hemicondyle; dorsal notch for foramen aerum (1) or with prominent dorsal projection between hemicondyles (2) or with expanded medial hemicondyle (3).

(107) Frontal lacks (0) or bears (1) a u-shaped depression at the point of maximum constriction between the orbits.
Character-taxon matrix used in the phylogenetic analysis of *Bottosaurus harlani*.

*Borealosuchus sternbergii*

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0000000111?1000000000???0??01020000000020000000000000200000001300100?000111000
01000000?010?00000000100?0000
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*Leidyosuchus canadensis*

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????0???1??00001??011??11??010?0000000?2000000101?001000000003000010010111000001
000000?01010100000010000010
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*Diplocynodon ratelii*

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????0???0??000?10040??21??0002101???012000001101?0120000012300101?00001110001
000000??101010001010001010
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*Diplocynodon hantoniensis*

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1000000?110?0101001010?010
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*Diplocynodon muelleri*

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?????????????01??1??410??21??0002??2????0120??100100?0120000012300101?00111100000
000?0?1?0?1001010???010
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*Diplocynodon tormis*

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????????????????1???10??21??0?021?1????0?2?00????1???0120000012300101?0001110000?0
0000?11000101001010???010
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204
Diplocynodon darwini
100100010?0000?1??4101121??01020010??00?20000110100020000?0103000???0000111?00
10000?0?110?1101001010???010

Baryphracta deponiae
10??0???0???1??410??21????02??0????0?20??0??10??01??00??01030???????001?1000?00
00?0?110???0110?010????10

Stangerochampsia mccabei
???10?011?00000100001??11??11010100??01211000010??0110002?110200001??000011100
1020010?120??1100020101??010

Albertochampsia langstoni
?????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
01?0?0??11020??01??00001110010200?0????110002010???000

Brachychampsia montana
11010011??0?0001000103111??1101101????0120?000010100110002?110100001?0010011100
1020010?120?111000101200010

Brachychampsia sealeyi
????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
01?0?????100?????2????10

Alligator sinensis
110110111011011001121111110000120?00013000001101?010010000102000011010001110
010101110120112000201110010
Alligator mississippiensis

110100[0or1]1100110110011121011010001120100013000101101001001000010200001110000
111001010111012011121002011110010

Alligator mefferdi

????????????????????11??????10000120100013000101101001001002000?1?10000?110010
10111?120?11210020111?0010

Alligator thomsoni

????????????????????11??????100001201000110001001000102000011100?1????1
0111?12011?210020111??01?

Alligator olseni

????0???1??10011??111??????1010010????10100010001010100000101001000102001?101111010
10111?120?1120002011??0010

Alligator mcgrewi

100000011?0001110111????1?1100010100000000101010010010000100100000110010000001
1010110120?11200020111?0010

Alligator prenasalis

100?0???1?000011?0112111??1101010????0120000011010000100010200000111100011100
1010110?120?11200020101?0010

Ceratosuchus burdoshi

????????????????????????????????1111??0????0?20??00??01?0010?01?010200??1?0????0????1???0
?0?????????00?11??010
Hassiacosuchus haupti
01?0??????000?1????11?11??11?10?0????0?20??0??101?00100????010?0????0?0??????10
0?0?120?1120002011??010

Allognathosuchus polyodon
????????????????????????????1111010????0?21??00?1?1?001000??01020????000?0?11001??0
1?0??????2000?01????10

Navajosuchus mooki
????0??????0?11110111??11110?0????0?20??00?10??001001?01020?0?1?0??0?110010
10010??2??112?002010???010

Wannaganosuchus brachymanus
????0?1????000?100011????1??11110?0????0?200?00??0??0110000??102?0??1?0100?????01?1
01?0??????1200??010???010

Procaimanoidea kayi
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101100?20?1120002011??010

Procaimanoidea utahensis
01?0?120?112000?010???010

Arambourgia gaudryi
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Necrosuchus ionensis

Tsoabichi greenriverensis

Eocaiman cavernensis

Othogenysuchus olsoni

Purussaurus neivensis

Mourasuchus atopus

Caiman yacare
Caiman crocodilus
1111001010010110011112211100211210101020110200011011000000112000011010001110
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Caiman latirostris
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Caiman lutescens
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Melanosuchus fisheri
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Melanosuchus niger
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Paleosuchus trigonatus
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Paleosuchus palpebrosus
101111011100011121311132112100212221111?20110000?1111001000102000011001101110
1110001112111211?2012100210
Culebrasuchus mesoamericanus

Centenariosuchus gilmorei

Bottosaurus harlani
APPENDIX 2.

List of characters and character matrix used in the phylogenetic analysis of

*Deinosuchus/Deinosuchoides.*

Some codings are based on the literature, namely Brochu, 2010. All others are based on direct observation of specimens.

1. Ventral tubercle of proatlas more than one-half (0) or no more than one half (1) the width of the dorsal crest.

2. Fused proatlas boomerang-shaped (0), strap-shaped (1), or massive and block-shaped (2).

3. Proatlas with prominent anterior process (0) or lacks anterior process (1).

4. Proatlas has tall dorsal keel (0) or lacks tall dorsal keel; dorsal side smooth (1).

5. Atlas intercentrum wedge-shaped in lateral view, with insignificant parapophyseal processes (0), or plate-shaped in lateral view, with prominent parapophyseal processes at maturity (1).

6. Dorsal margin of atlantal rib generally smooth with modest dorsal process (0) or with prominent process (1).

7. Atlantal ribs without (0) or with (1) very thin medial laminae at anterior end.

8. Atlantal ribs lack (0) or possess (1) large articular facets at anterior ends for each other.
(9) Axial rib tuberculum wide, with broad dorsal tip (0) or narrow, with acute dorsal tip (1).

(10) Anterior half of axis neural spine oriented horizontally (0) or slopes anteriorly (1).

(11) Axis neural spine crested (0) or not crested (1).

(12) Posterior half of axis neural spine wide (0) or narrow (1).

(13) Axis neural arch lacks (0) or possesses (1) a lateral process ("diapophysis").

(14) Axial hypapophysis located toward the center of centrum (0) or toward the anterior end of centrum (1).

(15) Axial hypapophysis without (0) or with (1) deep fork.

(16) Hypapophyseal keels present on eleventh vertebra behind atlas (0), twelfth vertebra behind atlas (1), or tenth vertebra behind atlas (2).

(17) Third cervical vertebra (first postaxial) with prominent hypapophysis (0) or lacks prominent hypapophysis (1).

(18) Neural spine on third cervical long, dorsal tip at least half the length of the centrum without the cotyle (0) or short, dorsal tip acute and less than half the length of the centrum without the cotyle (1).

(19) Anterior sacral rib capitulum projects far anteriorly of tuberculum and is broadly visible in dorsal view (0), or anterior margins of tuberculum and capitulum nearly in same plane, and capitulum largely obscured dorsally (1).
(20) Scapular blade flares dorsally at maturity (0) or sides of scapular blade subparallel; minimal dorsal flare at maturity (1).

(21) Deltoid crest of scapula very thin at maturity, with sharp margin (0) or very wide at maturity, with broad margin (1).

(22) Scapulocoracoid synchondrosis closes very late in ontogeny (0) or relatively early in ontogeny (1).

(23) Scapulocoracoid facet anterior to glenoid fossa uniformly narrow (0) or broad immediately anterior to glenoid fossa, and tapering anteriorly (1).

(24) Proximal edge of deltopectoral crest emerges smoothly from proximal end of humerus and is not obviously concave (0) or emerges abruptly from proximal end of humerus and is obviously concave (1).

(25) M. teres major and M. dorsalis scapulae insert separately on humerus; scars can be distinguished dorsal to deltopectoral crest (0) or insert with common tendon; single insertion scar (1).

(26) Olecranon process of ulna narrow and subangular (0) or wide and rounded (1).

(27) Interclavicle flat along length, without dorsoventral flexure (0) or with moderate dorsoventral flexure (1) or with severe dorsoventral flexure (2).

(28) Anterior end of interclavicle flat (0) or rodlike (1).

(29) Iliac anterior process prominent (0) or virtually absent (1).
(30) Dorsal margin of iliac blade rounded with smooth border (0) or rounded, with modest dorsal indentation (1) or rounded, with strong dorsal indentation ("wasp-waisted;" 2) or narrow, with dorsal indentation (3) or rounded with smooth border; posterior tip of blade very deep (4).

(31) Supraacetabular crest narrow (0) or broad (1).

(32) Dorsal osteoderms not keeled (0) or keeled (1)

(33) Dorsal midline osteoderms rectangular (0) or nearly square (1).

(34) Four (0), six (1), eight (2), or ten (3) contiguous dorsal osteoderms per row at maturity.

(35) Nuchal shield grades continuously into dorsal shield (0) or differentiated from dorsal shield; four nuchal osteoderms (1) or differentiated from dorsal shield; six nuchal osteoderms with four central and two lateral (2) or differentiated from dorsal shield; eight nuchal osteoderms in two parallel rows (3).

(36) Ventral armor absent (0) or single ventral osteoderms (1) or paired ventral ossifications that suture together (2).

(37) Anterior margin of dorsal midline osteoderms with anterior process (0) or smooth, without process (1).

(38) Ventral scales have (0) or lack (1) follicle gland pores.

(39) Ventral collar scales not enlarged relative to other ventral scales (0) or in a single enlarged row (1) or in two parallel enlarged rows (2).
(40) Median pelvic keel scales form two parallel rows along most of tail length (0) or form a single row along tail (1) or merge with lateral keel scales (2).

(41) Alveoli for dentary teeth 3 and 4 nearly same size and confluent (0) or fourth alveolus larger than third, and alveoli are separated (1).

(42) Dentary symphysis extends to fourth or fifth alveolus (0) or sixth through eighth alveolus (1) or behind eighth alveolus (2).

(43) Dentary gently curved (0), deeply curved (1), or linear (2) between fourth and tenth alveoli.

(44) Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) 13 or 14 and a series behind it, (2) 11 or 12, or (3) no differentiation, or (4) behind 14.

(45) Splenial with anterior perforation for mandibular ramus of cranial nerve V (0) or lacks anterior perforation for mandibular ramus of cranial nerve V (1).

(46) Mandibular ramus of cranial nerve V exits splenial anteriorly only (0) or splenial has singular perforation for mandibular ramus of cranial nerve V posteriorly (1) or splenial has double perforation for mandibular ramus of cranial nerve V posteriorly (2).

(47) Splenial participates in mandibular symphysis; splenial symphysis adjacent to no more than five dentary alveoli (0) or splenial excluded from mandibular symphysis; anterior tip of splenial passes ventral to Meckelian groove (1) or splenial excluded from mandibular symphysis; anterior tip of splenial passes dorsal to Meckelian groove (2) or deep splenial symphysis, longer than five dentary alveoli; splenial forms wide "V" within symphysis (3) or deep splenial.
symphysis, longer than five dentary alveoli; splenial constricted within symphysis and forms narrow "V" (4), or splenial reaches mandibular symphysis but does not touch its counterpart (5).

(48) Coronoid bounds posterior half of foramen intermandibularis medius (0) or completely surrounds foramen intermandibularis medius at maturity (1) or obliterates foramen intermandibularis medius at maturity (2).

(49) Superior edge of coronoid slopes strongly anteriorly (0) or almost horizontal (1).

(50) Inferior process of coronoid laps strongly over inner surface of Meckelian fossa (0) or remains largely on medial surface of mandible (1).

(51) Coronoid imperforate (0) or with perforation posterior to foramen intermandibularis medius (1).

(52) Process of splenial separates angular and coronoid (0) or no splenial process between angular and coronoid (1).

(53) Angular-surangular suture contacts external mandibular fenestra at posterior angle at maturity (0) or passes broadly along ventral margin of external mandibular fenestra late in ontogeny (1).

(54) Anterior processes of surangular unequal (0) or subequal to equal (1).

(55) Surangular with spur bordering the dentary toothrow lingually for at least one alveolus length (0) or lacking such spur (1).
(56) External mandibular fenestra absent (0) or present as narrow slit, no discrete fenestral concavity on angular dorsal margin (1) or present with discrete concavity on angular dorsal margin (2) or present and very large; most of foramen intermandibularis caudalis visible in lateral view (3).

(57) Surangular-dentary suture intersects external mandibular fenestra anterior to posterodorsal corner (0) or at posterodorsal corner (1).

(58) Angular extends dorsally toward or beyond anterior end of foramen intermandibularis caudalis; anterior tip acute (0) or does not extend dorsally beyond anterior end of foramen intermandibularis caudalis; anterior tip very blunt (1).

(59) Surangular-angular suture lingually meets articular at ventral tip (0) or dorsal to tip (1).

(60) Surangular continues to dorsal tip of lateral wall of glenoid fossa (0) or truncated and not continuing dorsally (1).

(61) Articular-surangular suture simple (0) or articular bears anterior lamina dorsal to lingual foramen (1) or articular bears anterior lamina ventral to lingual foramen (2) or bears laminae above and below foramen (3)

(62) Lingual foramen for articular artery and alveolar nerve perforates surangular entirely (0) or perforates surangular/angular suture (1).

(63) Foramen aerum at extreme lingual margin of retroarticular process (0) or set in from margin of retroarticular process (1).
(64) Surangular extends to posterior end of retroarticular process (0) or pinched off anterior to tip of retroarticular process (1).

(65) Surangular-articular suture oriented anteroposteriorly (0) or bowed strongly laterally (1) within glenoid fossa.

(66) Sulcus between articular and surangular (0) or articular flush against surangular (1).

(67) Dorsal projection of hyoid cornu flat (0) or rodlike (1).

(68) Dorsal projection of hyoid cornu narrow, with parallel sides (0) or flared (1).

(69) Lingual osmoregulatory pores small (0) or large (1).

(70) Teeth and alveoli of maxilla and/or dentary circular in cross-section (0), or posterior teeth laterally compressed (1), or all teeth compressed (2)

(71) Maxillary and dentary teeth with smooth carinae (0) or serrated (1).

(72) Naris projects anterodorsally (0) or dorsally (1) or posterodorsally (2)

(73) External naris bisected by nasals (0) or nasals contact external naris, but do not bisect it (1) or nasals excluded, at least externally, from naris; nasals and premaxillae still in contact (2) or nasals and premaxillae not in contact (3).

(74) Naris circular or keyhole-shaped (0) or wider than long (1) or anteroposteriorly long and prominently teardrop-shaped (2)
(75) External naris (0) opens flush with dorsal surface of premaxillae or (1) circumscribed by thin crest.

(76) Premaxillary surface lateral to naris smooth (0) or with deep notch lateral to naris (1).

(77) Premaxilla has five teeth (0) or four teeth (1) early in posthatching ontogeny.

(78) Incisive foramen small, less than half the greatest width of premaxillae (0) or large, more than half the greatest width of premaxillae (1) or large, and intersects premaxillary-maxillary suture (2).

(79) Incisive foramen completely situated far from premaxillary toothrow, at the level of the second or third alveolus (0) or abuts premaxillary toothrow (1) or projects between first premaxillary teeth (2).

(80) Dorsal premaxillary processes short, not extending beyond third maxillary alveolus (0) or long, extending beyond third maxillary alveolus (1).

(81) Dentary tooth 4 occludes in notch between premaxilla and maxilla early in ontogeny (0) or occludes in a pit between premaxilla and maxilla; no notch early in ontogeny (1). (Norell, 1988, character 29.)

(82) All dentary teeth occlude lingual to maxillary teeth (0) or occlusion pit between 7th and 8th maxillary teeth; all other dentary teeth occlude lingally (1) or dentary teeth occlude in line with maxillary toothrow (2).
(83) Largest maxillary alveolus is #3 (0), #5 (1), #4 (2), #4 and #5 are same size (3), #6 (4), or maxillary teeth homodont (5), or maxillary alveoli gradually increase in diameter posteriorly toward penultimate alveolus (6).

(84) Dorsal surface of rostrum curves smoothly (0) or bears medial dorsal boss (1).

(85) Canthi rostrali absent or very modest (0) or very prominent (1) at maturity.

(86) Preorbital ridges absent or very modest (0) or very prominent (1) at maturity.

(87) Vomer entirely obscured by premaxilla and maxilla (0) or exposed on palate at premaxillary-maxillary suture (1).

(88) Surface of maxilla within narial canal imperforate (0) or with a linear array of pits (1).

(89) Medial jugal foramen small (0) or very large (1).

(90) Ectopterygoid abuts maxillary tooth row (0) or maxilla broadly separates ectopterygoid from maxillary tooth row (1).

(91) Dorsal half of prefrontal pillar narrow (0) or expanded anteroposteriorly (1).

(92) Medial process of prefrontal pillar expanded dorsoventrally (0) or anteroposteriorly (1).

(93) Prefrontal pillar solid (0) or with large pneumatic recess (1).

(94) Medial process of prefrontal pillar wide (0) or constricted (1) at base.
(95) Maxilla has linear medial margin adjacent to suborbital fenestra (0) or bears broad shelf extending into fenestra, making lateral margin concave (1).

(96) Anterior face of palatine process rounded or pointed anteriorly (0) or notched anteriorly (1).

(97) Anterior ectopterygoid process tapers to a point (0) or forked (1).

(98) Palatine process extends (0) or does not extend (1) significantly beyond anterior end of suborbital fenestra.

(99) Palatine process generally broad anteriorly (0) or in form of thin wedge (1).

(100) Lateral edges of palatines smooth anteriorly (0) or with lateral process projecting from palatines into suborbital fenestrae (1).

(101) Palatine-pterygoid suture nearly at (0) or far from (1) posterior angle of suborbital fenestra.

(102) Pterygoid ramus of ectopterygoid straight, posterolateral margin of suborbital fenestra linear (0) or ramus bowed, posterolateral margin of fenestra concave (1).

(103) Lateral edges of palatines parallel posteriorly (0) or flare posteriorly, producing "shelf" (1).

(104) Choana projects posterovertrally (0) or anteroventrally (1) at maturity.
(105) Pterygoid surface lateral and anterior to internal choana flush with choanal margin (0) or pushed inward anterolateral to choanal aperture (1) or pushed inward around choana to form "neck" surrounding aperture (2) or everted from flat surface to form "neck" surrounding aperture (3).

(106) Posterior rim of internal choana not deeply notched (0) or deeply notched (1).

(107) Internal choana not septate (0) or with septum that remains recessed within choana (1) or with septum that projects out of choana (2).

(108) Ectopterygoid-pterygoid flexure disappears during ontogeny (0) or remains throughout ontogeny (1).

(109) Lacrimal makes broad contact with nasal; no posterior process of maxilla (0) or maxilla with posterior process within lacrimal (1) or maxilla with posterior process between lacrimal and prefrontal (2).

(110) Prefrontals separated by frontals and nasals (0) or prefrontals meet medially (1).

(111) Lacrimal longer than prefrontal (0), or prefrontal longer than lacrimal (1), or lacrimal and prefrontal both elongate and nearly the same length (2).

(112) Anterior tip of frontal forms simple acute point (0) or broad, complex sutural contact with the nasals (1), or blunt point (2)

(113) Ectopterygoid extends along medial face of postorbital bar (0) or stops abruptly ventral to postorbital bar (1).
(114) Postorbital bar massive (0) or slender (1).

(115) Postorbital bar bears process that is prominent, dorsoventrally broad, and divisible into two "spines" (0) or bears process that is short and generally not prominent (1).

(116) Ventral margin of postorbital bar flush with lateral jugal surface (0) or inset from lateral jugal surface (1).

(117) Margin of orbit flush with skull surface (0) or dorsal edges of orbits upturned (1) or all orbital margins telescoped (2) or anterior margin of orbit telescoped (3).

(118) Ventrolateral margin of orbit circular (0) or with prominent notch (1).

(119) Palpebral forms from single ossification (0) or from multiple ossifications (1).

(120) Quadratojugal spine prominent at maturity (0) or greatly reduced or absent at maturity (1).

(121) Quadratojugal spine low, near posterior angle of infratemporal fenestra (0) or high, between posterior and superior angles of infratemporal fenestra (1).

(122) Quadratojugal forms posterior angle of infratemporal fenestra (0) or jugal forms posterior angle of infratemporal fenestra (1) or quadratojugal-jugal suture lies at posterior angle of infratemporal fenestra (2).

(123) Postorbital neither contacts quadrate nor quadratojugal medially (0) or contacts quadratojugal, but not quadrate, medially (1) or contacts quadrate and quadratojugal at dorsal
angle of infratemporal fenestra (2) or contacts quadratojugal with significant descending process (3).

(124) Quadratojugal bears long anterior process along lower temporal bar (0) or bears modest process, or none at all, along lower temporal bar (1).

(125) Quadratojugal extends to superior angle of infratemporal fenestra (0) or does not extend to superior angle of infratemporal fenestra; quadrate participates in fenestra (1).

(126) Postorbital-squamosal suture oriented ventrally (0) or passes medially (1) ventral to skull table.

(127) Dorsal and ventral rims of squamosal groove for external ear valve musculature parallel (0) or squamosal groove flares anteriorly (1).

(128) Squamosal-quadrate suture extends dorsally along posterior margin of external auditory meatus (0) or extends only to posteroventral corner of external auditory meatus (1).

(129) Posterior margin of otic aperture smooth (0) or bowed (1).

(130) Frontoparietal suture deeply within supratemporal fenestra; frontal prevents broad contact between postorbital and parietal (0) or suture makes modest entry into supratemporal fenestra at maturity; postorbital and parietal in broad contact (1) or suture on skull table entirely (2).

(131) Frontoparietal suture concavoconvex (0) or linear (1) between supratemporal fenestrae.
(132) Supratemporal fenestra with fossa; dermal bones of skull roof do not overhang rim at maturity (0) or dermal bones of skull roof overhang rim of supratemporal fenestra near maturity (1) or supratemporal fenestra closes during ontogeny (2).

(133) Medial parietal wall of supratemporal fenestra imperforate (0) or bearing foramina (1).

(134) Parietal and squamosal widely separated by quadrate on posterior wall of supratemporal fenestra (0) or parietal and squamosal approach each other on posterior wall of supratemporal fenestra without actually making contact (1) or parietal and squamosal meet along posterior wall of supratemporal fenestra (2).

(135) Skull table surface slopes ventrally away from sagittal axis (0) or planar (1) or slopes ventrally toward sagittal axis, lateral elements planar (2) at maturity.

(136) Posterolateral margin of squamosal horizontal or nearly so (0) or upturned to form a discrete "horn" (1).

(137) Squamosal does not extend (0) or extends (1) ventrolaterally to lateral extent of paraoccipital process.

(138) Supraoccipital exposure on dorsal skull table small (0), absent (1), large (2), or large such that parietal is excluded from posterior edge of table (3).

(139) Anterior foramen for palatine ramus of cranial nerve VII ventrolateral (0) or ventral (1) to basisphenoid rostrum.
(140) Sulcus on anterior braincase wall lateral to basisphenoid rostrum (0) or braincase wall lateral to basisphenoid rostrum smooth; no sulcus (1).

(141) Basisphenoid not exposed extensively (0) or exposed extensively (1) on braincase wall anterior to trigeminal foramen

(142) Extensive exposure of prootic on external braincase wall (0) or prootic largely obscured by quadrate and laterosphenoid externally (1).

(143) Laterosphenoid bridge comprised entirely of laterosphenoid (0) or with ascending process of palatine (1).

(144) Capitate process of laterosphenoid oriented laterally (0) or anteroposteriorly (1) toward midline.

(145) Parietal with recess communicating with pneumatic system (0) or solid, without recess (1).

(146) Significant ventral quadrate process on lateral braincase wall (0) or quadrate-pterygoid suture linear from basisphenoid exposure to trigeminal foramen (1).

(147) Lateral carotid foramen opens lateral (0) or dorsal (1) to basisphenoid at maturity.

(148) Posterior pterygoid processes tall and prominent (0) or small and project posteroventrally (1) or small and project posteriorly (2).

(149) Basisphenoid thin (0) or anteroposteriorly wide (1) ventral to basioccipital.
(150) Basisphenoid not broadly exposed ventral to basioccipital at maturity; pterygoid short ventral to median eustachian opening (0) or basisphenoid exposed as broad sheet ventral to basioccipital at maturity; pterygoid tall ventral to median eustachian opening (1).

(151) Lateral eustachian canals open dorsal (0) or lateral (1) to medial eustachian canal.

(152) Exoccipitals terminate dorsal to basioccipital tubera (0) or send robust process ventrally and participate in basioccipital tubera (1) or send slender process ventrally to basioccipital tubera (2).

(153) Quadrate foramen aerum on mediodorsal angle (0) or on dorsal surface (1) of quadrate.

(154) Quadrate foramen aereum is small (0), comparatively large (1), or absent (2) at maturity.

(155) Quadrate with small, ventrally-reflected medial hemicondyle (0) or with small medial hemicondyle; dorsal notch for foramen aerum (1) or with prominent dorsal projection between hemicondyles (2) or with expanded medial hemicondyle (3).

(156) Iris (0) greenish/yellowish or (1) brown

(157) Two or more (0) or one (1) row of postoccipital osteoderms

(158) Fewer than eight (0) or eight to 14 (1) or more than 14 (2) paired midline scale rows

(159) Palatine-maxillary suture intersects suborbital fenestra at its anteromedial margin (0) or nearly at its anteriormost limit (1)

(160) Osteoderms planar, exclusive of keel (0) or osteoderms robust, keel inflated (1)
(161) Floor of post-temporal fenestrae not visible in dorsal view (0) or visible in dorsal view (1)

(162) Midmaxillary constriction not present (0) or present between maxillary teeth 5 and 6 (1) or 6 and 7 (2) or 7 and 8 (3) or 8 and 9 (4).
Character-taxon matrix used in the phylogenetic analysis of *Deinosuchus* and *Deinosuchoides*.

Bernissartia fagesii

Borealosuchus sternbergii

Borealosuchus threeensis

Borealosuchus formidabilis

Borealosuchus wilsoni

Borealosuchus acutidentatus

Pristichampsus vorax

Pristichampsus geiseltalensis

Planocrania hengdongensis
Planocrania datangensis

Eothoracosaurus mississippiensis

Thoracosaurus neocesariensis

Thoracosaurus macrorhynchus

Eosuchus minor

Eosuchus lerichei

Eogavialis africanus

Gavialis gangeticus

Leidyosuchus canadensis
Deinosuchus hatcheri

Deinosuchoides riograndensis

Deinosuchoides schwimmeri

Diplocynodon ratelii

Diplocynodon hantoniensis

Diplocynodon muelleri

Diplocynodon monsvialensis

Diplocynodon tormis

Diplocynodon darwini

Diplocynodon remensis
Diplocynodon deponiae

Stangerochampsa mccabei

Albertochampsa langstoni

Brachychampsa montana

Brachychampsa sealeyi

Alligator sinensis

Alligator mississippiensis

Alligator mefferdi

Alligator thomsoni

Alligator olseni
Necrosuchus ionensis

Tsoabichi greenriverensis

Eocaiman cavernensis

Purussaurus neivensis

Mourasuchus atopus

Caiman yacare

Caiman crocodilus

Caiman latirostris

UCMP lutescens
Melanosuchus fisheri

Paleosuchus trigonatus

Paleosuchus palpebrosus

Culebrasuchus mesoamericanus

Centenariosuchus gilmorei

Mecistops cataphractus

Crocodylus niloticus

Crocodylus rhombifer
Crocodylus acutus
00100000110101110011112012011021010100010120001110011100001100000
1002110001101101000&100011000010100001110000111000011100001000011101101100100
030120003

Crocodylus moreletii
0010000011010100011001112012011120110110021010100010120001110011100001100000
1002110001101101000&100011000010100001110000111000011100001000011101101100100
030120003

Crocodylus intermedius
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030120003

Crocodylus palustris
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Crocodylus siamensis
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Crocodylus novaeguineae
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030120003

Crocodylus porosus
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Crocodylus novaeguineae
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030120003

Crocodylus raninus
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030120003

Crocodylus mindorensis
1110000010010101110011120120111201101110021010100010120001110011100001100000
1002110001101101000&100011000010100001110000111000011100001000011101101100100
030120003
Crocodylus johnstoni

Crocodylus palaeindicus

Osteolaemus tetraspis

Osteolaemus osborni

Euthecodon brumpti

Euthecodon arambourgii

Tomistoma schlegelii

Tomistoma lusitanica
**APPENDIX 3.**

Table A1. Eigenvalues for each PC of the outline analysis.

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An additional 68 PC axes accounting for 0.444% of total variance in the outline analysis are omitted for brevity.

Table A2. Eigenvalues for each PC of the outline + STF analysis.

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| C     | 0.03 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | x   |
|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|----|
| s     | 0.03 | 0.057| 0.050| 0.02 | 0.00 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | x   |
|       | 300  | 91   | 5081 | 419  | 796 | 262 | 228 | 169 | 684 | 606 | 228 | 154 | 113 | 9    | 567 | 91  | 989 | 61  | 5067 | 449 | 345 | 08  | 777 | 557 |
| M     | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | x   |
| c     | 503  | 263  | 157  | 157  | 3   | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | x   |
|       | 503  | 263  | 157  | 157  | 3   | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | 9    | x   |
| O     | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | x   |
| t     | 705  | 459  | 028  | 028  | 2   | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | x   |
|       | 705  | 459  | 028  | 028  | 2   | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | 2    | x   |
| T     | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | x   |
| s     | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | x   |
|       | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | 090  | 12   | x   |
| G     | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | x   |
| g     | 369  | 479  | 367  | 479  | 369  | 479  | 369  | 479  | 369  | 479  | 369  | 479  | 369  | 479  | 369  | 479  | 369  | 479  | 369  | 479  | 369  | 479  | 369  | 479  | x   |


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