8-2013

A Glyptosaurine Lizard from the Eocene (late Uintan) of San Diego, California, and Implications for Glyptosaurine Evolution and Biogeography

David Moscato
East Tennessee State University

Recommended Citation

Moscato, David, "A Glyptosaurine Lizard from the Eocene (late Uintan) of San Diego, California, and Implications for Glyptosaurine Evolution and Biogeography" (2013). *Electronic Theses and Dissertations.* Paper 1176. https://dc.etsu.edu/etd/1176

A Glyptosaurine Lizard from the Eocene (late Uintan) of San Diego, California, and Implications for Glyptosaurine Evolution and Biogeography

---

A thesis
presented to
the faculty of the Department of Geosciences
East Tennessee State University
In partial fulfillment
of the requirements for the degree
Master of Science in Geosciences

---

by
David A. Moscato
August 2013

Jim I. Mead, Chair
Blaine W. Schubert
Steven C. Wallace

Keywords: Glyptosaurinae, *Glyptosaurus sylvestris*, San Diego County, Santiago Formation
Uintan, biogeography

ABSTRACT

A Glyptosaurine Lizard from the Eocene (late Uintan) of San Diego, California, and Implications for Glyptosaurine Evolution and Biogeography

by

David Moscato

Glyptosaurine lizards (family Anguidae) are known exclusively from the Paleogene of North America and Eurasia. In North America these lizards are largely restricted to the intermontane basins along the Rocky Mountains, with only sparse, indeterminately-identified skeletal elements known from outside of this region. In this study I describe a new specimen assignable to *G. sylvestris*, notable for being recovered from the late Uintan of the Santiago Formation in southern California, significantly outside the known geographic range of well-preserved glyptosaurine fossils. The presence of *Glyptosaurus* in southern California at a time of widespread geographic change and regional endemism in mammalian faunas, when also considering the results other studies of Eocene lizards, indicates a pattern of evolution for lizards different from the turnovers and regional restrictions observed in mammals. The specimen described here shows features consistent with ontogenetic variation and may help to provide insight into the life history of glyptosaurine lizards.

ACKOWLEDGMENTS

I'm very grateful to Robert Sullivan for introducing me to SDNHM 75932, and to the fascinating family of glyptosaurine lizards, for access to his cast of my main comparative specimen, UCMP 126000, and for helpful advice and critiques during this study. I thank Tom Deméré and Kesler Randall for granting me access to this and other glyptosaurine specimens, and I thank both men, along with Brad Riney, for access to information about the original excavations that recovered this specimen. I thank the staff at the Gray Fossil Site in Tennessee for access to preparatory equipment during fossil preparation of SDNHM 75932, and especially Shawn Haugrud for offering expert advice and assistance during fossil preparation. I thank Sandy Swift for help with photography and figure-making. I thank Carl Mehling for access to the glyptosaurine specimens at the AMNH. I am thankful to Blaine Schubert and Steven Wallace for serving on my thesis committee and offering support and advice. I thank the Don Sunquist Center for Excellence in Paleontology and the ETSU Departments of Geosciences and Biology for financial support during this study. I thank Steven Jasinski for offering plenty of advice, criticism, and frequent and sometimes welcome distractions. I thank Eric Lynch, Leigha King, and all of my other fellow graduate students and colleagues who offered advice, guidance, and company throughout the course of this project and my graduate school years. I am immensely grateful to Jim Mead, for serving as my thesis committee chair, for offering mounds of advice, and for 3 years of guidance, patience, and encouragement.

TABLE OF CONTENTS

Page

Chapter

LIST OF TABLES

Table

LIST OF FIGURES

Figure

CHAPTER 1

INTRODUCTION

The glyptosaurine lizards, subfamily Glyptosaurinae, are an extinct subfamily of squamates belonging to the family Anguidae (Reptilia, Squamata). These lizards are known exclusively from Paleogene strata of North America and Eurasia (65 – 33 Ma) (Estes 1983). In North America glyptosaurines are most common in Eocene (55 – 34 Ma) localities in the intermontane basins of the Rocky Mountains and have been well-studied from these sites. North American glyptosaurines from outside of this region are rare and, when present, are typically fragmentary and unsuitable for detailed description (Schatzinger 1975; Estes and Hutchison 1980; Westgate 1989). In this study I present a previously undescribed glyptosaurine specimen, including well-preserved cranial and post-cranial elements, from the late Uintan Land Mammal Age (LMA) of southern California, approximately 46.2 – 40.4 Ma (middle Eocene). The provenance of this specimen is notable for these important reasons: 1) this site is outside the typically known range of these extinct lizards; 2) this is the first coastal habitat to yield a well-preserved member of the subfamily; and 3) southern California is notable for preserving a unique, endemic mammalian fauna dating to the middle Eocene, one apparently isolated from other parts of the continent by climatic and tectonic factors. For these reasons this specimen presents a unique opportunity to gather vital information about the biogeographic and evolutionary history of these lizards during the Eocene of North America. While other glyptosaurine remains are known from San Diego County, this is the most complete, allowing for comparison with specimens from the Rocky Mountain region.

Taxonomic History

Glyptosaurus was described by Marsh (1871), who named the type species, *G. sylvestris*. Since then the genus has undergone a great deal of taxonomic revision. Meszoely (1970) divided Anguidae into the 3 subfamilies Anguinae, Diploglossinae, and Gerrhonotinae, and placed *Glyptosaurus* in a fourth, extinct subfamily, Glyptosaurinae, consisting at the time of 5 genera: *Glyptosaurus, Peltosaurus, Xestops, Arpadosaurus,* and *Melanosaurus*. In Meszoely's (1970) description, the subfamily was defined in part by the presence of unique tuberculate osteoderms covering the skull and body.

Sullivan (1979) noted that the validity of the North American genus *Glyptosaurus* was questionable and that the genus was in need of revision, and provided a detailed examination of the numerous species in the genus. He divided the genus into 4 genera, naming 2 new genera, *Paraglyptosaurus* and *Eoglyptosaurus*, resurrecting *Helodermoides*, originally named by Douglass (1903), and synonymizing several species of *Glyptosaurus* into the sole species *G. sylvestris*. The remaining species of *Glyptosaurus* were labeled nomina dubia (Sullivan 1979). Sullivan (1979) split the subfamily Glyptosaurinae into 2 tribes, placing the aforementioned 4 genera into the tribe Glyptosaurini and the remaining genera into the paraphyletic tribe "Melanosaurini" (at the time limited to *Peltosaurus, Xestops, Arpadosaurus,* and *Melanosaurus*).

Sullivan (1986) described a newly discovered skull of *G. sylvestris,* leading him to reassess the definition of the taxon. This reassessment was followed by a further analysis of the species *Eoglyptosaurus donohoei* (Sullivan 1989), in which he synonymized the species in part with *G. sylvestris,* and assigned the remaining specimen to a new genus and species, *Proglyptosaurus huerfanensis*. Thus, the genus *Eoglyptosaurus* is considered invalid and has been replaced (in part) by *Proglyptosaurus* in the tribe Glyptosaurini. In addition, while Sullivan

(1979) considered the Eurasian genus *Placosaurus* a nomen dubium, Estes (1983) retained the genus as distinct based on characters of the frontal. The definition of the taxon was later revised (Sullivan and Augé 2006), with the genus being split into 3 distinct species, and later Sullivan et al. (2012) added a fourth, but the genus has been retained as a valid member of the Glyptosaurini. It should be noted that Sullivan and Augé (2006) questioned the validity of the species *Placosaurus mongoliensis,* though they tentatively retained it within the genus, while Conrad and Norell (2008) found *Placosaurus* to be polyphyletic within the tribe Glyptosaurini.

Sullivan (1979) placed 4 genera (mentioned above) into the tribe "Melanosaurini" and noted that the monophyly of this group was questionable, unlike the better-resolved Glyptosaurini. Later, the genus *Proxestops* was added to this tribe (Gauthier 1982; Sullivan 1991). Meszoely et al. (1978) had synonymized the 3 previously named European anguid genera, *Placosauroides, Placosauriops,* and *Paraxestops* with the North American form *Xestops*, but more recently Augé and Sullivan (2006) refuted this, synonymizing *Placosauroides* with *Placosauriops,* and identifying *Placosauriops* and *Paraxestops* alongside *Xestops* as valid members of the "Melanosaurini". This tribe is still considered paraphyletic (Augé and Sullivan 2006).

Smith (2009) named a new glyptosaurine species, *Gaultia silvaticus*, from an earliest Eocene (Wasatchian LMA) fauna in Wyoming. He noted that *Gaultia* shared primitive features with the "melanosaurinid" lizards, namely the plesiomorphically flattened shape of the osteoderms, but also exhibited the derived trait seen in glyptosaurinids of polygonal cranial osteoderms. He thus concluded that *Gaultia* was likely an intermediate between the tribes. Despite being intermediate, *Gaultia* falls into the tribe Glyptosaurini because the tribe is defined by the presence of polygonal cranial osteoderms and is depicted as a glyptosaurinid in Figure 1.1

of the present study, albeit at a basal position within the tribe. Smith (2009) also described another potentially new glyptosaurine lizard, noting that the available material showed distinct differences from known forms, but chose to refrain from formally describing a new taxon until more material is made available. As of this writing the identity of this specimen, called "Glyptosaurinae CG" by Smith (2009), remains unknown, and whether it does in fact represent a new species is yet to be decided.

Smith (2011a) noted that Sullivan (1979) synonymized *Glyptosaurus hillsi* with *Paraglyptosaurus princeps* (the type species of the genus), and later Sullivan (1986) synonymized *P. princeps* with *G. sylvestris*. Based on this, Smith (2011a) suggested that *Paraglyptosaurus* as a genus is technically synonymous with *Glyptosaurus*, and that all species of *"Paraglyptosaurus*" should therefore fall under *Glyptosaurus*. In the same paper Smith (2011a) resurrected *Glyptosaurus hillsi* and named a new species *G. rhodinos*. While the species within the Glyptosaurinae are numerous, their relationships and taxonomic identifications are clearly still in need of revision, but a general description can be provided.

As of this writing the generally accepted phylogeny of the Glyptosaurinae is that the subfamily is split into 2 tribes (Fig. 1.1): the paraphyletic "Melanosaurini" and the better-resolved, monophyletic Glyptosaurini. The "Melanosaurini" includes 6 genera from North America and Europe (*Xestops, Proxestops, Paraplacosauriops, Peltosaurus, Melanosaurus,* and *Arpadosaurus*). The Glyptosaurini traditionally includes 6 genera (*Gaultia, Placosaurus, Proglyptosaurus, Paraglyptosaurus, Glyptosaurus,* and *Helodermoides*), although following Smith (2011a), *"Paraglyptosaurus"* should be synonymized with *Glyptosaurus*. All genera of the tribe Glyptosaurini are known from North America except the European-Asian genus *Placosaurus.* According to the phylogeny presented by Conrad and Norell (2008), Glyptosaurini is split into 2 groups (Fig. 1.1): a) an unresolved polytomy including *Proglyptosaurus, "Paraglyptosaurus", Glyptosaurus,* and *Placosaurus*; and b) a dichotomy comprised of *Helodermoides* and *"Placosaurus*." The validity of *Placosaurus* has come under scrutiny recently. Sullivan and Augé (2006) presented a revision of the genus, reassigning a number of species to other genera, while identifying several other species as nomina dubia, and recognizing only 3 valid species of the genus, *P. rugosus, P. mongoliensis,* and *P. estesi*. Conrad and Norell (2008) found *Placosaurus* to be polyphyletic, with "*P." mongoliensis* and "*P." estesi* falling out as sister to *Helodermoides,* and *P. rugosus* nesting with the polytomy including most of the other glyptosaurinid genera (Fig. 1.1). Sullivan et al. (2012) named a new European species tentatively assigned to *Placosaurus*, ?*Placosaurus ragei*, but this taxon has not been included in any large-scale phylogenetic studies comparable to Conrad and Norell (2008).

The genus *Glyptosaurus*, on which this study focuses, is the eponymous genus of the subfamily and is fairly widespread in North American Eocene fossil deposits. Despite this, little was known about the skull morphology of the taxon until Sullivan (1986) described a beautifully preserved specimen from Wyoming, and cranial remains of the taxon are uncommon still today. Thus, discussion of the well-preserved cranial material presented in this study will be both interesting and valuable to our understanding of these lizards.

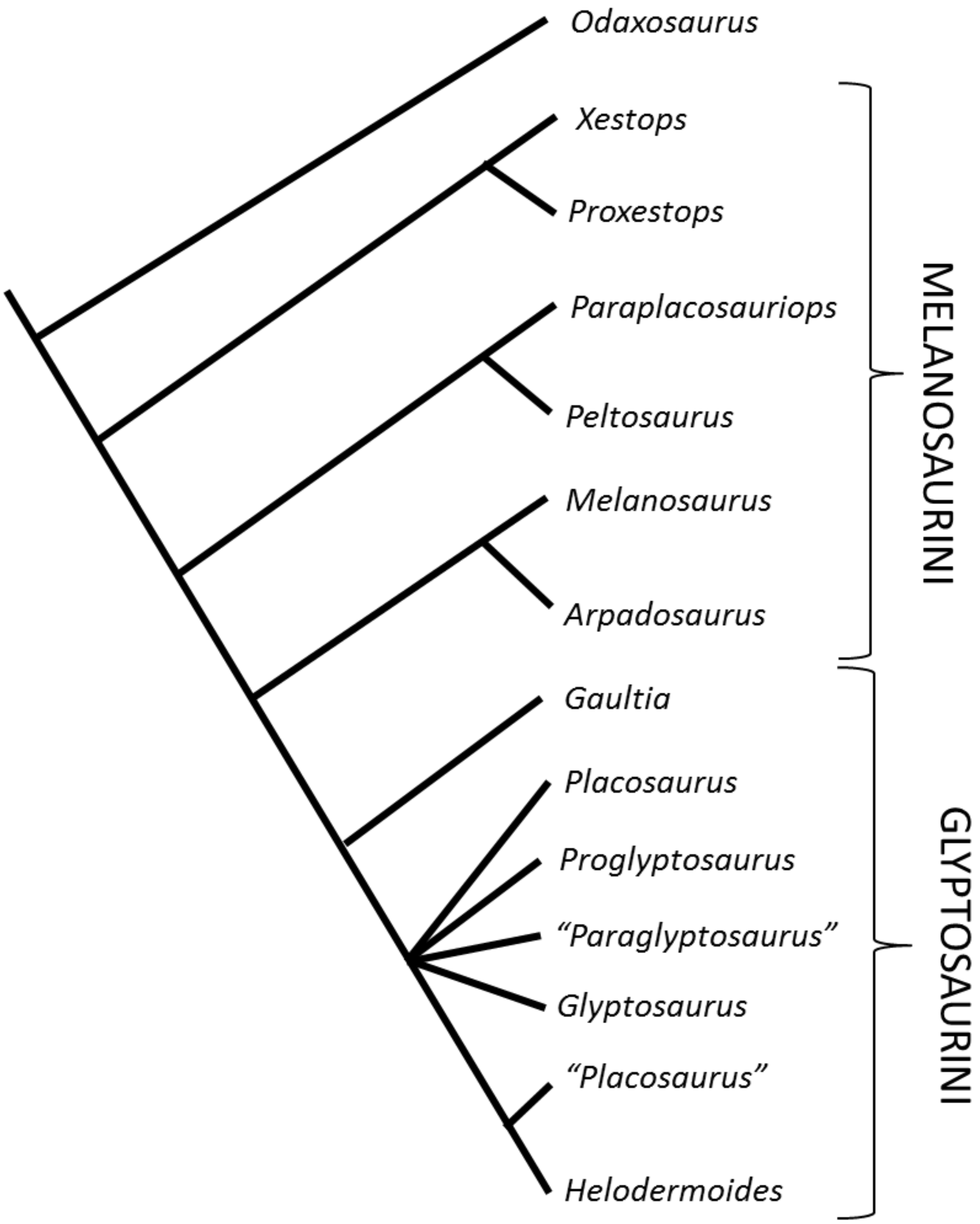

FIGURE 1.1. Phylogenetic relationships within the subfamily Glyptosaurinae, modified from the strict consensus tree presented in Conrad and Norell (2008). The monophyly of the Tribe Glyptosaurini is well-resolved, although relations within the tribe are uncertain, while the "Melanosaurini" is paraphyletic. The Cretaceous form *Odaxosaurus* represents the outgroup (Odaxosaurinae).

Distribution

Glyptosaurine lizards range in age from the Paleocene to the Oligocene and are known from North America, Europe, and Asia, with the majority of species known from the United States (Sullivan 1979; Sullivan and Augé 2006). Within the USA most glyptosaurine fossils are found in the series of intermontane basin regions along the Rocky Mountains in Wyoming, Utah, Colorado, and New Mexico (Fig. 1.2). Indeterminate glyptosaurine remains have been reported from Ellesmere Island in Canada (Estes and Hutchison 1980) and in southern Texas (Westgate 1989), along with fragmentary remains of glyptosaurines that have been noted from southern California (Schatzinger 1975; Golz and Lillegraven 1977). *Glyptosaurus* is known across most of that Rocky Mountain basin region, from Wyoming south to New Mexico.

The majority of glyptosaurine species are known from Eocene strata. The oldest glyptosaurine remains are those of *Proxestops* from the Paleocene (Puercan-Torrejonian LMA) of Montana (Sullivan 1991) and New Mexico (Sullivan and Lucas 1986). The more plesiomorphic *Odaxosaurus*, considered a precursor to the Glyptosaurinae, can be found ranging from Late Cretaceous to Paleocene strata (Sullivan and Lucas 1986; Rowe et al. 1992). The youngest glyptosaurine remains known are of *Helodermoides* dating to the early Oligocene (Orellan LMA) at the latest (Sullivan 1979, Sullivan and Holman 1996) and *Peltosaurus* dating to the late Oligocene (early Arikareean LMA) at the latest (Sullivan and Holman 1996). Holman (1976) had described a species of *Peltosaurus* from the upper Miocene (Orellan LMA) of Nebraska, but this specimen was later reassigned by Wellstead (1982) to *Eumeces* (Scincidae). Other Miocene *Peltosaurus* specimens have been reported in the past (Estes 1983) but have been similarly disputed (Sullivan and Holman 1996). No glyptosaurines are definitively known from younger than the latest Oligocene (Arikareean LMA). The genus *Glyptosaurus* is known exclusively from the early to middle-late Eocene (Wasatchian-Uintan LMA).

The Glyptosaurinae had a Holarctic distribution during the Eocene, appearing in Europe and Asia as well as North America (Estes 1983). Glyptosaurine lizards are known from sites in several European countries, and all are Eocene in age (see Augé and Sullivan 2006 and references therein). The only Asian species of glyptosaurine lizard is *Placosaurus mongoliensis* from middle Eocene Inner Mongolia, originally assigned to *Helodermoides mongoliensis* by Sullivan (1979) and more recently described in detail by Sullivan and Augé (2006).

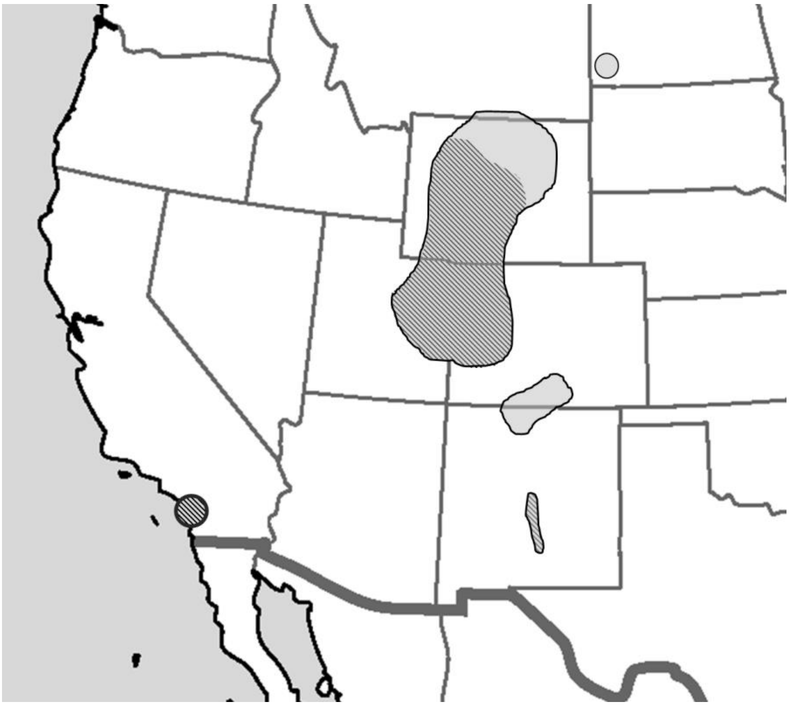

FIGURE 1.2. Main distribution of Glyptosaurinae in the Eocene of North America (modified from Sullivan 1986); though fragmentary, indeterminate remains are known from localities outside of these ranges. Shaded areas indicate the distribution of Glyptosaurinae, while hatchered lines indicate the distribution of *Glyptosaurus*. The circle in the bottom-left indicates the locality of SDNHM 75932 in San Diego as well as nearby Eocene localities yielding additional glyptosaurine remains.

Local Geology

The specimen described in this study (SDNHM 75932) was excavated from the Santiago Formation (Eocene age) in San Diego County California, at a housing project site called Rancho Del Oro. The Santiago Formation in northwestern San Diego County consists of 3 members: A, B and C. Member A is characterized by massive green mudstones and yields little fossil material. Member B consists of fine- to medium-grained marine arkosic sandstones with interbedded claystone and clayey sandstone (Rasmussen et al. 1995) and yields abundant fossil vertebrates (Walsh 1991). Member C is dominated by continental gray-white arkosic sandstones interbedded with green or green-brown siltstones, silty mudstones, and claystones (Wilson 1972). A disconformity separates Members B and C in northwestern San Diego County (Walsh 1991). At Rancho Del Oro the Santiago Formation is represented by Members B and C, which display a regressive sequence; Member B comprises marine shelf sandstones at its lowest exposures and estuarian muddy sandstones and siltstones at its uppermost exposures, while Member C comprises entirely terrestrial arkosic sandstones, siltstones, and mudstones characteristic of a fluvial and floodplain deposition (Rasmussen et al. 1995).

The specimen described here was excavated from Member C at Rancho Del Oro, Village 3, Site 6. The fossil vertebrates that have been recovered from Member C of the Santiago formation are consistent with faunas of the late Uintan and possibly early Duchesnean LMA (Golz and Lillegraven 1977; Walsh 1991). A list of vertebrates recovered from Member C is provided by Golz and Lillegraven (1977), and a brief description of the defining taxa of the late Uintan LMA of southern California is given by Rasmussen et al. (1995). At Rancho Del Oro, Village 3, Site 6, Member C is represented by Unit 4 (a white coarse-grained cross-bedded sandstone) and Unit 3 (comprised of silty, coarse-grained sandstones and massive brown siltstones), which interfingers with Unit 4 above. Unit 3 also preserves an abundance of terrestrial vertebrate remains, particularly in the lower sandstone beds.

The excavation sites at Rancho Del Oro have yielded the remains of numerous important mammal fossils. Rasmussen et al. (1995) described a new specimen of the omomyid primate *Dyseolemur pacificus*; Theodor (1999) described a new species of oreodont, *Protoreodon walshi*; and Colbert (2006) named 2 new species of the new genus *Hesperaletes*, a tapiroid possibly representing the earliest members of the family Tapiridae. Walsh (1991) listed the small mammals from the locality and noted faunal correlation to a number of other local faunas in San Diego County, both in the Santiago Formation and the Sespe Formation. To date, fragmentary glyptosaurine lizard fossils described from southern California have been assigned to 'Glyptosaurinae indet.' (Schatzinger 1975; Golz and Lillegraven 1977). Schatzinger (1975) preliminarily discussed these glyptosaurine remains, describing the fossils as representing at least 2 size morphs, the smaller of which he suggested likely represented *Xestops*, while the larger could represent one of a number of genera. Brattstrom (1955) identified a new species, *Peltosaurus macrodon*, from fragmentary material from the Uintan Sespe Formation in Ventura County; however, Estes (1983) questioned this identification, noting similarities to other glyptosaurine lizards, including *Glyptosaurus*, and labeling *P. macrodon* a nomen dubium. The specimen described in this present study is by far the most complete glyptosaurine lizard described from California or from any North American location outside the Rocky Mountain basinal regions.

CHAPTER 2

MATERIALS AND METHODS

The specimens described here have been archived at the San Diego Natural History Museum (SDNHM) since the original excavation in 1988 and are on loan to the East Tennessee State University for this study. Preparation of SDNHM 75932 took place at the East Tennessee State University and General Shale Brick Natural History Museum at the Gray Fossil Site in Gray, Tennessee, with permission from the SDNHM. This specimen was also associated with other fragmentary material from the same site, SDNHM 75936 and SDNHM 75946, which were both photographed and examined. While SDNHM 75936 consisted entirely of fragmentary elements that were not useful for identification and description here, SDNHM 75946 (an isolated, fragmentary maxilla) did provide diagnostic help and is discussed further below.

Upon discovery and excavation, SDNHM 75932 was entirely encased in a piece of sandstone, approximately 16cm by 12cm, and approximately 5cm thick (Fig. 2.1). The main sandstone section is associated with a number of smaller pieces of sandstone, each with a number of small skeletal elements within, including isolated osteoderms and miscellaneous bone fragments; as small fragmentary remains are not useful for identifying and describing the specimen, and because isolated osteoderms were also present on the main sandstone section, these miscellaneous elements were not examined during this study. The most informative elements of SDNHM 75932, including cranial material and numerous articulated osteoderms, are present in the main slab, where this thesis study is concentrated. Digital photographs were taken to document the state of the specimen before preparation. Pictures were also taken regularly throughout the course of preparation, particularly whenever elements were removed from the slab, so that the original position of each element of the specimen could be referred to in the future.

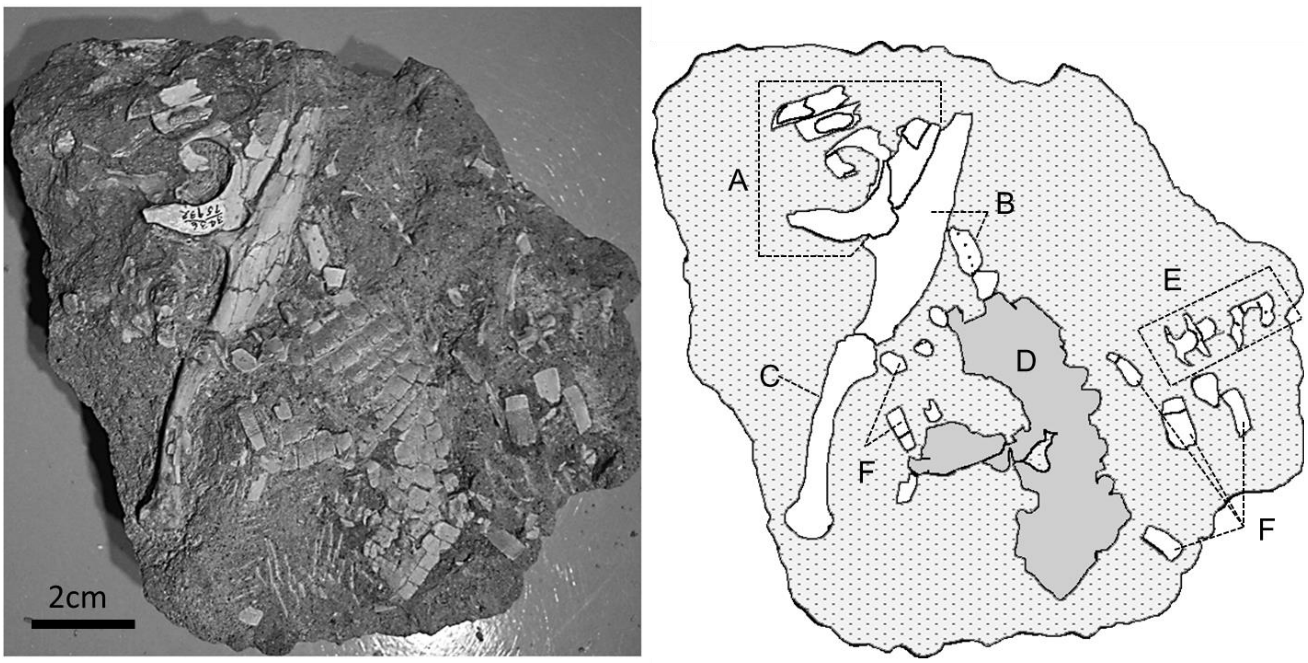

FIGURE 2.1. SDNHM 75932 before preparation. Most of the significant elements are located on the top surface of this sandstone slab and can be seen here. Stippled pattern = matrix. **A**. Associated cranial material, including the right jugal, right maxilla, and other elements of the orbital region. **B**. Nearly complete right mandible and associated dental fragment with foramina. Both were later removed. **C**. Left humerus. This element was later removed in 2 pieces. **D**. Intact osteoderm set (shaded region). This element was left in place on the specimen. **E**. Articulated vertebrae encased in matrix. **F**. Several isolated osteoderms.

Before preparation, it was apparent by cursory examination of the specimen that many of the skeletal elements were located along the top surface of the sandstone slab (Fig. 2.1), yet the sandstone section was thick enough that there existed the possibility that additional elements were encased within the matrix, out of view. To investigate this possibility, SDNHM 75932 was taken to the Mountain States Health Alliance hospital in Johnson City, where a medical CT-scanner was used to provide images of the internal structure of the sandstone block. These images were not high-resolution, as the CT-scanner used was not designed to analyze this type of material, but the scanner was able to detect and display fossil elements within the interior of the slab. These images revealed that the vast majority of skeletal material was located along the top surface, and what few elements lay completely encased in the interior of the sandstone section were small and fragmentary, not critical diagnostic elements and thus deemed unnecessary to target for preparation at the expense of removing semi-articulated elements above.

Preparation on SDNHM 75932 was performed in the fossil preparation lab at the Gray Fossil Site under the guidance and advice of preparator Shawn Haugrud. Excavation of the skeletal elements from the surrounding matrix and removal of matrix from fossil elements was performed using a Micro-Jack 1 and 3 and pin vices. The sediment was relatively soft and unconsolidated, so no additional tools were required. When the fossil was originally excavated and catalogued at SDNHM, chemical consolidants were applied to the fossil, though there is no available record of what consolidants were used (likely glyptal and/or wood glue diluted with water). During the preparation at the Gray Fossil Site, when it was necessary to add further consolidant, Butvar-98 was applied, and when necessary, 91% isopropyl alcohol was applied to dissolve consolidant.

Before preparation of the specimen, the exposed right side of the skull was incomplete, but largely still articulated, exposing most of the lower jaw and the orbit (Fig. 2.1). Other disarticulated elements of the skull were uncovered both underneath and adjacent to these exposed elements. In its in situ position, the left humerus sat behind the exposed right jaw, lying parallel to the orientation of the jaw with the distal end lying against the end of the articular bone of the mandible. Below the skull was a broad contiguous set of articulated osteoderms. Other elements of the skeleton were present scattered in the sediment, including numerous isolated osteoderms, a short column of 5 articulated vertebrae, and fragmentary ribs and distal limb elements (Fig. 2.1).

Each time an element was removed from the matrix, it was set into its own plastic bag and labeled with an identification number. A photograph was then taken, in most cases, of the area where the element had been prior to removal. Most of the elements removed earlier on in preparation were isolated osteoderms. The left humerus, right lower jaw, left jugal, and a fragment of the left maxillary bone, all exposed on the surface of the specimen, were also removed individually during preparation. While in situ, the humerus lay along a plane of weakness in the sediment, and broke along this plane during preparation, and was thus removed in 2 pieces, distal and proximal; these halves have not been glued back together, as it was noted that future study of the bone may in fact be made easier by keeping the distal and proximal halves disarticulated. The remaining cranial material, consisting mostly of orbital elements, was removed as a contiguous piece and separated from the rest of the sandstone section (Fig. 2.2). During preparation of these cranial elements from the matrix, it became clear that these elements were delicate and prone to cracking and fracturing. Because of this, efforts to further prepare these elements were abandoned, and they were consolidated and left in their current exposed state. A fragment of the left mandible was recovered beneath these other cranial elements, but attempts at preparation proved this element to be very delicate as well. Because this piece was fragmentary and preserved little diagnostic characters, it was also left in situ within the sediment.

The large continguous set of osteoderms that covers a large portion of the surface of the specimen (Fig. 2.1D) was left in situ, because removal of these elements would undoubtedly damage the structure, and because the position of these elements in situ is certainly more informative than each osteoderm would be individually. The number of isolated osteoderms recovered from this specimen is more than sufficient to document the morphology of isolated osteoderms, so it was deemed unnecessary to disassemble these associated osteoderms. A set of articulated vertebrae are visible to the right of this set of osteoderms (Fig. 2.1E), as are numerous small elements that appear to represent fragmentary ribs and distal limb material. These elements were not targeted for preparation primarily because they are delicate structures buried deeply within the matrix, and removal would be difficult, with a high probability of damaging the elements. Furthermore, these elements are less crucial for identification and description of this specimen than the more diagnostic elements such as cranial material and osteoderms, upon which preparatory efforts were focused.

Once preparation of SDNHM 75932 was completed, all removed elements were organized into individual containers, numbered, and photographed. Most elements were photographed using a Canon Powershot digital camera. Smaller elements, particularly small cranial osteoderms, were photographed using a specialized microscope camera. Any elements that required reconstruction due to damage sustained either before or during fossil preparation were repaired with the help of equipment and staff at the Gray Fossil Site preparatory lab, using Butvar-76 made with acetone as an adhesive.

As indicated above, SDNHM 75932 is accompanied in the SDNHM collections by 2 associated specimens from Rancho Del Oro Village 3 Site 6. SDNHM 75936 consists of a series of unidentifiable fragments and osteoderms. The fragmentary bones of this specimen are too incomplete or broken to be useful for identification purposes and are not examined in this study. SDNHM 75946 is a single fragmentary maxilla with preserved teeth. No laboratory preparation was needed for this element; it was photographed and examined and is discussed later in this study. Given the similar morphology of the elements of SDNHM 75936 and 75946, as well as their shared provenance with SDNHM 75932, it is assumed that all 3 specimens represent the same taxon, and thus the associated specimens may, where possible, be used to support identification and description of the taxon represented by SDNHM 75932.

Identification and description of SDNHM 75932 was accomplished in part through comparison with other glyptosaurine materials. The author traveled to both the University of Florida in Gainesville, Fl, and the American Museum of Natural History (AMNH) in New York, to examine and photograph fossil glyptosaurine specimens housed in the paleoherpetology collections of these museums. Modern, non-glyptosaurine lizard material from the comparative collections of the East Tennessee State University paleontology collections was also used as reference for examination of SDNHM 75932. The most important comparative specimen used in this study was a cast of UCMP 126000 (*Glyptosaurus sylvestris*), which was loaned to the East Tennessee State University by Dr. Robert M. Sullivan. Direct comparison with this specimen proved essential to the description of SDNHM 75932; this comparison is explored in more detail later in this paper. Identification was also aided by the study of associated material from the Rancho Del Oro site, notably the fragmentary maxilla of SDNHM 75946. The complete list of comparative specimens examined during this study is provided in the Appendix.

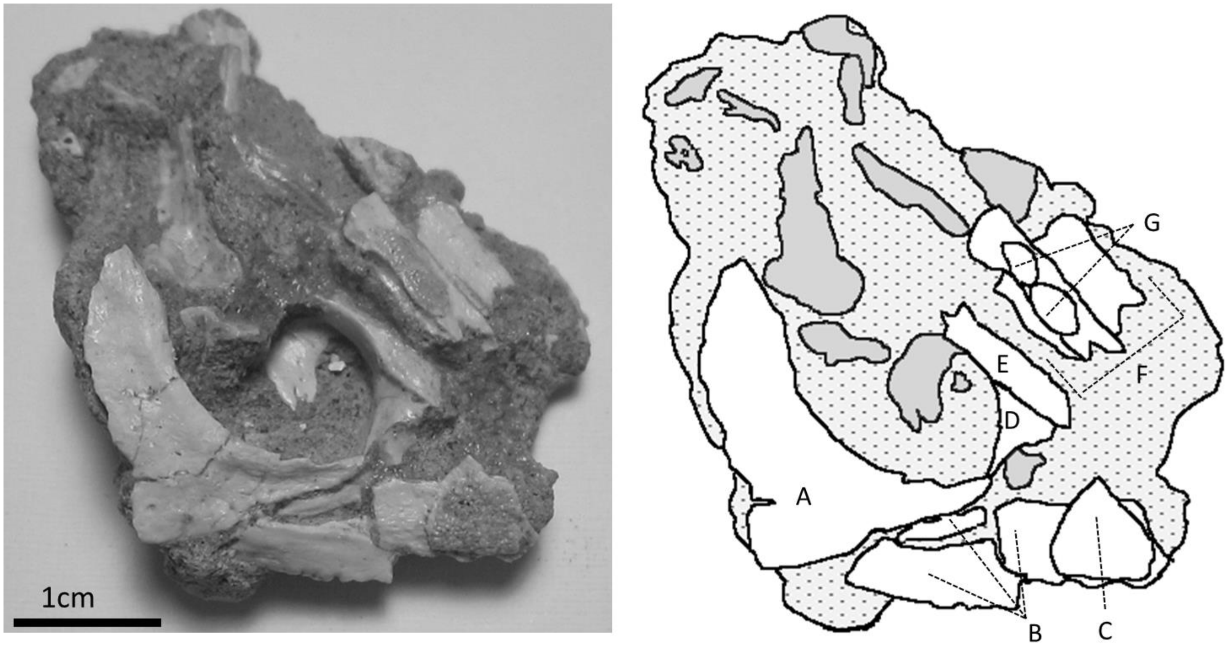

FIGURE 2.2. Partially articulated cranial material surrounding orbit of SDNHM 75932. These elements were removed from the complete slab shown in Figure 2.1 but were left intact as shown here. **A**. Jugal. **B**. Fragmentary maxilla in 3 pieces. **C**. Osteoderm fused to maxilla. **D**. Lacrimal. **E**. Fragmentary postfrontal, **F**. Anterior portion of frontals. **G**. Osteoderms fused to frontal. Shaded areas represent fragmentary cranial bones of unknown identity.

CHAPTER 3

FOSSIL DESCRIPTION AND IDENTIFICATION OF SDNHM 75932

David Moscato

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811

ANGUIMORPHA Fürbringer, 1900

ANGUIDAE Gray, 1925

GLYPTOSAURINAE Marsh, 1872

GLYPTOSAURINI Sullivan, 1979

Glyptosaurus Marsh, 1871

Type Species – *Glyptosaurus sylvestris* Marsh, 1871.

Revised Diagnosis – Sullivan (1986) revised Marsh's (1871) original diagnosis, and described *Glyptosaurus* as differing from all other glyptosaurinids by the: 1) reduction of the pterygoid teeth to a narrow band, as opposed to the broad, ovoid patches of teeth seen in other genera; 2) flattened frontals; 3) broad cranial osteoderms; and 4) concentric rows of tubercles on osteoderms.

Glyptosaurus sylvestris Marsh, 1871

Material – SDNHM 75932 left and right jugal, anterior portion of left and right frontals, partial left maxilla, partial right maxilla, fragmentary orbital elements; nearly complete right lower jaw (including partial dentary, coronoid, surangular, articular), left humerus (broken into halves), five vertebrae, numerous cranial osteoderms (four fused to cranial bone), numerous post-cranial osteoderms (many articulated in contiguous set), fragmentary ribs, fragmentary limb elements. SDNHM 75946 left maxillary fragment, including teeth

Locality and Horizon – Rancho Del Oro, San Diego County, California; Santiago Formation Member C, middle Eocene (late Uintan LMA).

Diagnosis – Same as for genus (see Sullivan, 1986).

MORPHOLOGICAL DESCRIPTION

Osteoderms – Both cranial and post-cranial osteoderms are present in this specimen (Fig. 3.1). Cranial osteoderms are fused to both the left and right maxillae, as well as to the right frontal (Fig. 2.2, 3.2). Glyptosaurine lizards commonly exhibit osteoderm fusion to most of the cranial elements, including the frontals, maxillae, and jugals, as well as many other bones (Sullivan, 1979; 1986). Most of the cranial bones of SDNHM 75932, however, are sparsely covered, or completely lacking osteoderms, indicating a limited degree of fusion between the cranial osteoderms and underlying bone, a feature with interesting implications (see Discussion). Isolated cranial osteoderms are common. The cranial osteoderms are hexagonal in shape, a defining characteristic of the tribe Glyptosaurini. All of these osteoderms have a smooth ventral surface, and a dorsal surface covered in small tubercles. The broad and semi-flattened shape of these cranial osteoderms, along with the arrangement of tubercles in concentric rings along the dorsal surfaces, are characters consistent with *Glyptosaurus, "Paraglyptosaurus,"* and *Placosaurus,* while the cranial osteoderms of *Proglyptosaurus* and *Gaultia* are more apically raised and more apically flattened, respectively, and the cranial osteoderms of *Helodermoides* do not exhibit concentric rings of tubercles (Sullivan, 1979).

Isolated post-cranial osteoderms are ubiquitous in SDNHM 75932. All post-cranial osteoderms are rectangular or somewhat trapezoidal in shape, as is characteristic of Glyptosaurinae. These osteoderms have a smooth ventral surface, and a smooth articulating surface on the anterior portion of the dorsal face, which is otherwise covered in tubercles, also characters shared by all Glyptosaurine lizards (Sullivan, 1979). Articulated post-cranial osteoderms are present in a contiguous set extending away from where the skull was positioned in situ (Fig. 2.1, 3.1). These articulated osteoderms likely covered the neck, or possibly the back, of the individual. Interestingly, there is a cluster of osteoderms located at the middle-to-posterior portion of the articulated osteoderm set that are not rectangular as is expected of post-cranial osteoderms, but instead hexagonal like cranial osteoderms, despite being distant from the skull. It is possible that these unusual osteoderms represent the armor covering a limb joint of the lizard, possibly the underside (‘armpit’) of a limb joint; these atypical osteoderms are located somewhat near to disarticulated limb elements, adding some level of support to this hypothesis.

Maxillae – The maxillae of SDNHM 75932 are represented by two fragments, an anterior fragment of the left maxilla (Fig. 3.2) and a posterior fragment of the right maxilla (Fig. 2.2); the latter is articulated to the right jugal. Both maxillary fragments retain fused osteoderms, but are not completely covered. The left maxillary fragment preserves four mental foramina, one of which is partially obscured by a fused osteoderm. Though the maxilla is a tooth-bearing element in glyptosaurines, teeth are broken and missing on both maxillae of SNHM 75932. However, the shape of the maxillae hint at the characters of this specimen’s dentition. The relatively homodont dentition of *Glyptosaurus* results in a less curved maxilla, compared to the characteristic curvature of the maxilla in the more robust-toothed “*Paraglyptosaurus.”* The maxillae of SDNHM 75932 are consistent with the less curved shape seen in *Glyptosaurus*, and are in fact very similar in shape to those of UCMP 126000.

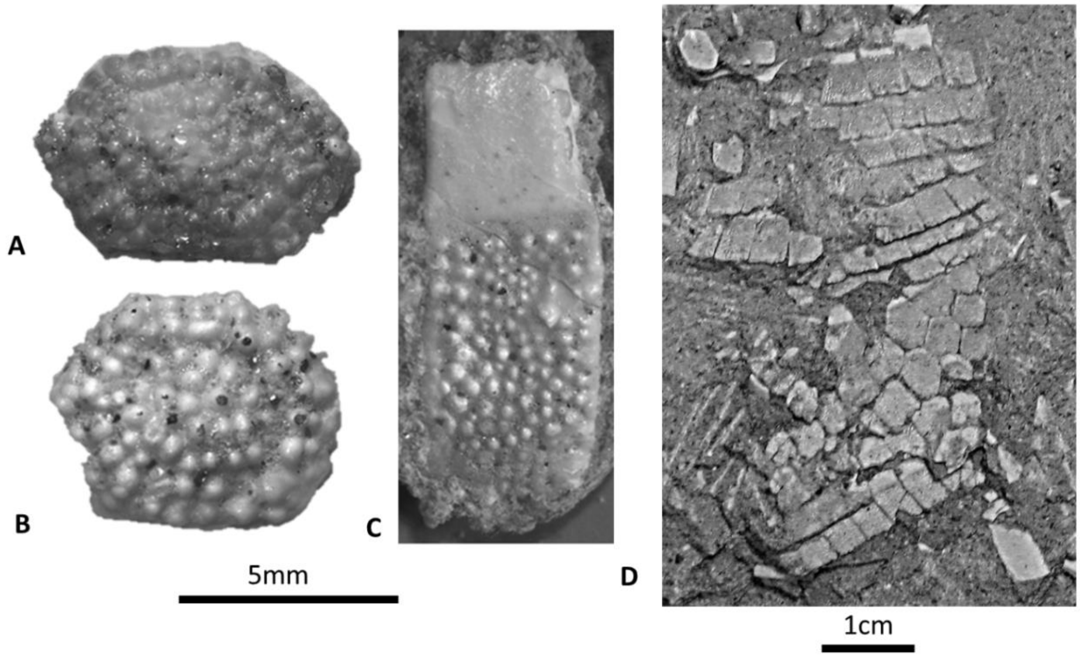

FIGURE 3.1. Osteoderms of SDNHM 75932. **A**., **B**. cranial osteoderms. **C**. Body osteoderm. **D**. articulated osteoderm set.

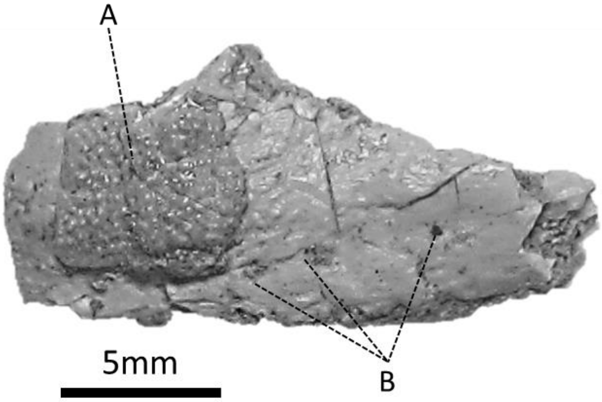

FIGURE 3.2. Anterior left maxillary fragment of SDNHM 75932. Anterior to the left. **A**. fused osteoderm. **B**. mental foramina.

A fragmentary left maxilla is also preserved in SDNHM 75946, an associated specimen from the same site (Fig. 3.3). This element displays fragmentary fused osteoderms, as well as three visible mental foramina, and twelve teeth. The anterior teeth are more slender, pointed and slightly curved than the posterior teeth, which are comparatively obtuse. The teeth preserved in the center of the maxillary length are more densely clustered than those in the anterior or posterior extents. This dentition pattern is consistent with previous specimens of *Glyptosaurus*, in which the teeth are mostly homodont, with slight anterior-posterior differentiation. The posterior teeth are not as exceptionally broad or compressed as seen in certain taxa (notably "*Paraglyptosaurus*"). The maxilla of SDNHM 75946 also exhibits the relatively straight maxillary shape also seen in SDNHM 75932 and UCMP 126000, as opposed to the curved shape exhibited in *"Paraglyptosaurus*." Based on the similar size and shape of this maxilla, and its shared provenance with SDNHM 75932, it is inferred to represent the same taxon, and is used here to lend support to the diagnosis of SDNHM 75932.

Jugals – Both left and right jugals are present and complete. The right jugal remains associated with other bones of the orbital region (Fig. 2.2); most of the ventral border of the right jugal is in articulation with the right maxilla. The ascending process of the jugal should articulate with the postorbital and postorbital, but these elements are missing. The left jugal is isolated and has been removed from the sediment (Fig. 3.4), thus both lateral and medial faces are visible and well-preserved on the left jugal. Both jugals lack fused osteoderms, though both jugals of UMCP 126000 exhibit fused osteoderms over part of their surface.

Prefrontal – The right prefrontal is present among the associated bones of the orbital region (Fig. 2.2), articulating posteroventrally with the lacrimal. While the prefrontal of SDNHM 75932 is obscured partially by matrix and other bones, the visible portion of the bone lacks fused osteoderms, whereas UCMP 126000 exhibits osteoderm fusion on the prefrontal.

Lacrimal – The right lacrimal is preserved among the other bones of the orbital region (Fig. 2.2). The entire anterodorsal border of the lacrimal articulates with the ventral border of the prefrontal, while the posteroventral-most edge of the lacrimal articulates with the anterior-most edge of the jugal.

Frontals – The anterior portion of both articulated frontals are preserved, located anterodorsal to the orbit, partially obscuring the underlying prefrontal (Fig. 2.2E). The frontals are articulated, though the suture line between them is distinct, unlike the more fully fused state seen in other glyptosaurine lizards. Two cranial osteoderms are fused to the surface of the right frontal bone. The frontals of SDNHM 75932 are relatively straight, displaying little of the curvature seen in *Placosaurus* or *Helodermoides*.

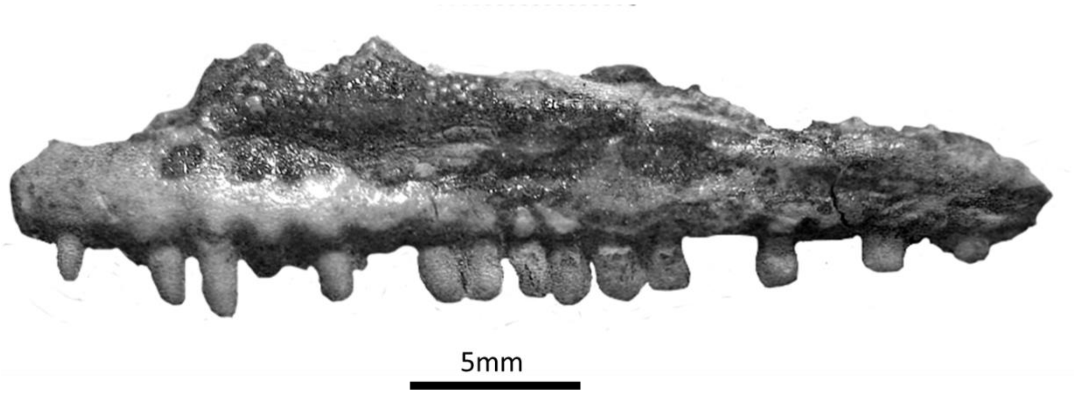

FIGURE 3.3. Fragmentary left maxilla of SDNHM 75946 (associated specimen), displaying dentition. Anterior to the left.

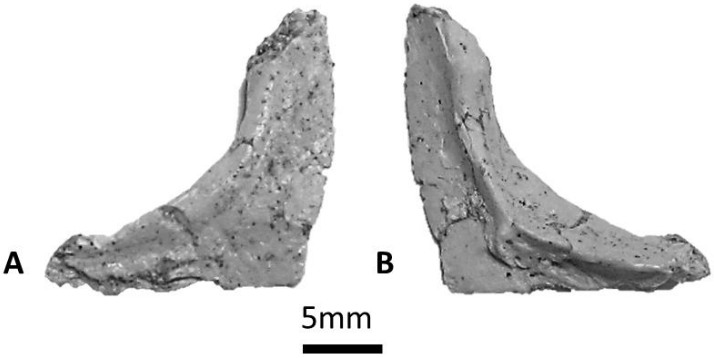

FIGURE 3.4. Left jugal of SDNHM 75932. **A.** lateral view. **B.** medial view. The right jugal can be seen in Fig. 2.2.

Additional Cranial Elements – Numerous fragmentary cranial elements of uncertain identity can be seen surrounding the orbital region in Figure 2.2. These elements are difficult to identify due to being incomplete and/or obscured by the matrix or overlying bone.

Mandibles – The right lower jaw is preserved almost completely, and has been removed from the sediment so that both labial and lingual sides are visible (Fig. 3.5). The coronoid, articular and surangular are preserved well, but the anterior-most portion of the dentary is missing. The lingual face of the dentary is broken and largely absent, and the angular and splenial are both missing, so many lingual features of the mandible are not preserved. The supra-angular foramen is visible near the ventral border of the coronoid, though it is slightly in-filled with sediment. No teeth are preserved because much of the tooth-bearing region of the dentary is absent.

Fragmentary remains of the left mandible were also recovered from SDNHM 75932. A portion of the labial face of the left mandible was recovered beneath the cranial elements of the orbit, though this piece was very brittle and fragmentary, preserving no easily identifiable features. A fragment of the anterior portion of the left dentary was also recovered. This small fragment exhibits four foramina on the labial side, and the dental shelf and tooth alveoli are visible on the lingual side. While no teeth are preserved in this jaw fragment, the alveoli display a straight, somewhat broad shape consistent with the shape of the teeth observed in the maxilla and dentary of other glyptosaurines, including *Glyptosaurus*.

Vertebrae – Five articulated thoracic vertebrae are visible within the sediment to the right of the dorsal osteoderm set (Fig. 2.1E). The ventral face of the centra of these vertebrae can be seen, along with numerous transverse processes. The remaining features of these vertebrae are obscured by sediment, as well as by each other. What features can be seen of these vertebrae are consistent with the vertebrae of other fossil glyptosaurine specimens.

Left humerus – The left humerus is preserved entirely, albeit in two fragments, representing the distal and proximal halves of the element (Fig. 3.6). The proximal end is flattened and broad as in other anguimorphs and many lizards. The proximal epiphyseal end is absent, and the epiphyseal surface is broken. The distal epiphyseal end is present, though the epiphyseal suture is distinctly visible between the epiphyseal end and the diaphysis.

Additional Post-cranial Elements – Nearby the vertebrae, numerous small, fragmentary disarticulated bones are visible which appear to represent distal limb elements and ribs, though these elements are all fragmentary and/or largely obscured by the overlying matrix, preventing more accurate identification. Other small fragmentary elements are present in the matrix, which are so fragmentary that even an approximate identification cannot be made; they likely represent fragments of osteoderms or other post-cranial bones.

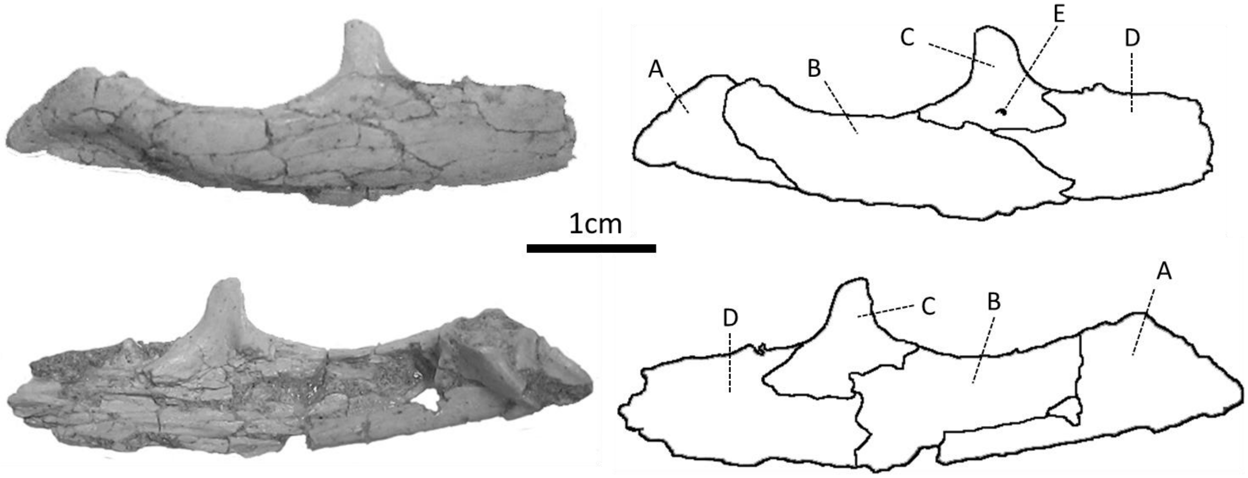

FIGURE 3.5. Right lower jaw of SDNHM 75932 in labial (top, anterior to the right) and lingual (bottom, anterior to the left) views, with outline drawings on the right. **A**. articular. **B**. surangular. **C**. coronid. **D**. dentary (anterior portion absent). **E**. Supra-angular foramen.

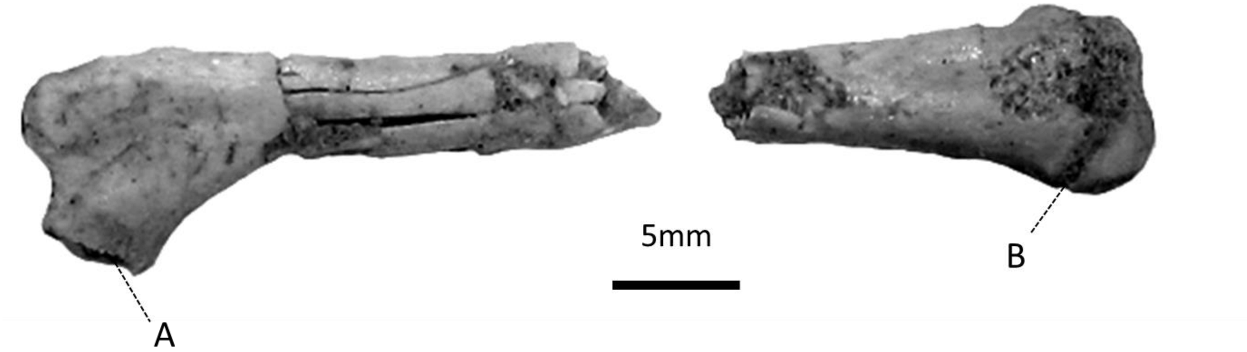

FIGURE 3.6. Left humerus of SDNHM 75932 in proximal (left) and distal (right) fragments. **A**. broken proximal epiphyseal surface. **B**. distal epiphyseal suture.

Comparative Description – SDNHM 75932 is identified as Glyptosaurinae based on the robust rectangular post-cranial osteoderms covered in tubercles. The specimen can be further distinguished from the tribe “Melanosaurini” by its hexagonal cranial osteoderms, a feature characteristic of Glyptosaurini, which contains the genera *Gaultia, Glyptosaurus, “Paraglyptosaurus,” Proglyptosaurus, Helodermoides* and *Placosaurus* (Sullivan, 1979; Smith, 2011a; 2011b).

Gaultia, as described by Smith (2009), is primitive within the tribe Glyptosaurini by the retention of apically flattened osteoderms like those seen in the “melanosaurinids”, though the presence of polygonal cranial osteoderms in *Gaultia* is clearly a characteristic of Glyptosaurini. SDNHM 75932 shows the slightly raised osteoderm shape found in other glyptosaurinids, and thus can be separated from *Gaultia.*

Helodermoides and *Placosaurus* are distinct from all other glyptosaurinid taxa by a distinct curvature of the frontals (Sullivan, 1979; Sullivan and Augé; 2006). These two genera can be distinguished from each other by the fact that the osteoderms of *Helodermoides* do not display tubercles arranged in concentric rings, a feature seen in other glyptosaurinid taxa. SDNHM 75932 displays characteristic concentric rings of tubercles on both cranial and post-cranial osteoderms (Fig. 3.1), as well as straightened frontals (Fig. 2.2), separating it from both *Helodermoides* and *Placosaurus*.

Proglyptosaurus is distinguishable from all other glyptosaurinids by the shape of its cranial osteoderms. Whereas *Gaultia* displays apically flattened cranial osteoderms, and most glyptosaurinids exhibit cranial osteoderms with a slight apical elevation, the cranial osteoderms of *Proglyptosaurus* are distinctly sub-conical in shape. The cranial osteoderms of SDNHM 75932 are consistent with the more flattened state seen in most glyptosaurinids (though, as mentioned above, not as apically flattened as seen in *Gaultia* or "melanosaurinids"), distinguishing it from *Proglyptosaurus*.

Smith (2011a) suggested that *Paraglyptosaurus* (sensu Sullivan, 1979) and *Glyptosaurus* (sensu Sullivan, 1986) should technically be synonymized under *Glyptosaurus*, based on the history of their taxonomic names. Prior to this synonymy, the two genera could be distinguished by their dentition. Whereas the dentition of *Glyptosaurus* (sensu stricto) is plesiomorphically homodont, the posterior teeth of *Paraglyptosaurus* (sensu stricto) are broad, modified for crushing food (Sullivan, 1979). The specialized dentition of *Paraglyptosaurus* (sensu stricto) results in a characteristically curved maxilla, whereas the maxilla of *Glyptosaurus* (sensu stricto) is straighter. Despite their generic synonymy, the defining features of the species within these formerly separate genera remain the same, thus the species formerly assigned to *Paraglyptosaurus* can still be distinguished from *G. sylvestris*, formerly the only species within *Glyptosaurus*. The maxillary fragments preserved in SDNHM 75932 and SDNHM 75946 do not show the curvature seen in "*Paraglyptosaurus.*" Instead they compare very closely with the shape of the maxillae in UCMP 126000. SDNHM 75932 can thus be distinguished from *G. yatkolai* (="*P." yatkolai*) and *G. hillsi* (="*P." princeps*). *G. rhodinos* shares certain features with *G. yatkolai* and *G. hillsi*, namely features of the parietal and longitudinally compressed posterior teeth, which ally it with those genera, and distinguish it from SDNHM 75932 and other glyptosaurines.

SDNHM 75932 can thus be distinguished from all glyptosaurine taxa except for *Glyptosaurus sylvestris.* The cranial elements of SDNHM 75932 compare closely with comparable elements of UCMP 126000, as well as with other *G. sylvestris* specimens; no morphological differences exist between SDNHM 75932 and previous specimens of *G. sylvestris* that would lead me to identify SDNHM 75932 as a new taxon . SDNHM 75932 also displays three of the four characters listed in the revised diagnosis (above) for *G. sylvestris*: 1) flattened frontals; 2) broad cranial osteoderms; and 3) concentric rows of tubercles on osteoderms (the fourth character, pterygoid teeth arranged in a narrow band, cannot be compared as the pterygoids are not preserved in SDNHM 75932). These traits, combined with the straightened shape of the maxilla and longitudinally elongate posterior teeth (as opposed to the compressed form in some species), form a suite of characters that allow identification of SDNHM 75932 to *Glyptosaurus sylvestris.*

Remarks – Sullivan (1986) described the skull of *Glyptosaurus sylvestris* from the plesiotype UCMP 126000, which represents the best known cranial material of *G. sylvestris*, and as such serves as the main comparative specimen for the description of SDNHM 75932. UCMP 126000 was recovered from the Bridgerian LMA (middle Eocene) Bridger Formation in Wyoming (consistent with the common fossil range of *Glyptosaurus,* discussed above). SDNHM 75932 occurs significantly outside this geographic range, representing a noteworthy range extension for the genus and species.

References

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

Smith, K. T. 2009. A new lizard assemblage from the earliest Eocene (Zone Wa0) of the Bighorn Basin, Wyoming, USA: Biogeography during the warmest interval of the Cenozoic. Journal of Systematic Paleontology 7(3):299–358

Smith, K. T. 2011a. The long-term history of dispersal among lizards in the early Eocene: new evidence from a microvertebrate assemblage in the Bighorn Basin of Wyoming, USA. Paleontology 54(6):1243–1270

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

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

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

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

CHAPTER 4

DISCUSSION

Comparison with UCMP 126000

UCMP 126000, from the Bridger Formation of Wyoming, represents the best known skull of *Glyptosaurus sylvestris* (Sullivan 1986). A number of differences are noticeable between the Wyoming specimen UCMP 126000 and the San Diego specimens SDNHM 75932 and 75946, the most obvious being the rarity of fused osteoderms on the cranial bones of the San Diego specimens, in stark contrast to UCMP 126000, which is nearly completely covered with osteoderms. Another notable difference is the size of the specimens: SDNHM 75932 is considerably smaller than UCMP 126000. Interestingly, the size disparity is more drastic when comparing the jaws of the specimens than when comparing the orbital region, which is to say the size difference between the specimens is not isometric. Several measurements were taken to investigate this allometric size disparity (Fig. 4.1). The measurements were limited by the few elements that could be directly compared between the 2 specimens. According to these measurements (Table 4.1), the orbital region of SDNHM 75932 is approximately 80-90% the size of the orbital region of UCMP 126000, while the lower jaws of SDNHM 75932 are less than 60% the size of the lower jaws of UCMP 126000.

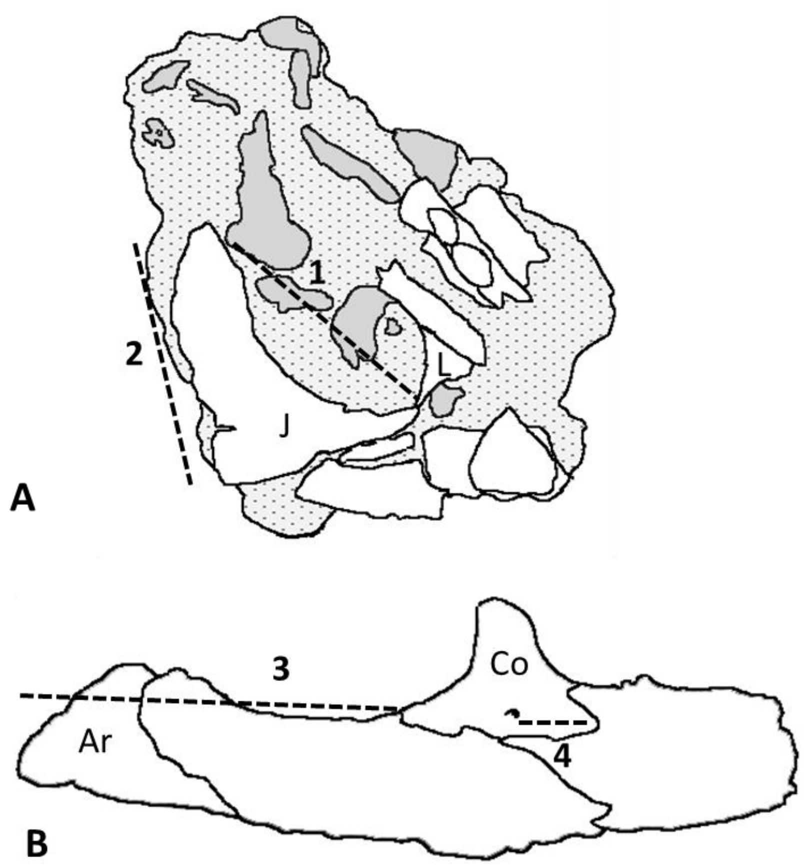

FIGURE 4.1. Measurements listed in Table 4.1, as taken on SDNHM 75932. **A**. Outline of cranial material of SDNHM 75932, as in Figure 2.2. **B**. Outline of right mandible of SDNHM 75932, as in Figure 3.5. Measurements: **1**. Orbital length, length of the orbit at its widest part; **2**. Jugal height, length of the posterior edge of the jugal; **3**. Post. jaw length; distance from labioposterior-most end of right coronoid to posterior end of right articular; **4**. Ant. coronoid length = length of coronoid from supra-angular foramen to labioanterior tip of cornoid. Measurements were chosen based on limited comparable material between the 2 specimens.

TABLE 4.1. Size comparison between SDNHM 75932 and UCMP 126000.

Character	**UCMP 126000**	**SDNHM 75932**	**Ratio SDNHM/UCMP**	**Average Ratio**
Orbit				0.8542
1. Orbital length	24mm	22mm	0.9167	_
2. Jugal height	24mm	19mm	0.7917	_
Lower Jaw				0.5751
3. Post. jaw length	37mm	22mm	0.5946	_
4. Ant. coronoid length	9mm	5mm	0.5556	_

Measurements 1, 2, and 3 were taken on the right-side elements in both specimens, while measurement 4 was taken on the right coronoid of SDNHM 75932 and the left coronoid of UCMP 126000. Measurements are described in detail in Figure 4.1.

These distinctions between these specimens are significant and warrant discussion. A notable difference in body size is often representative of sexual dimorphism in many vertebrates, including lizards, though the other distinctions mentioned above are inconsistent with this explanation. Differences in body size and in the degree of fusion of cranial elements might be argued to indicate a taxonomic distinction between the 2 specimens. Sullivan (1989) listed the size differences of several species of glyptosaurine lizard. It is worth noting that the skull of SDNHM 75932 is significantly smaller than the estimates given by Sullivan (1989) not only for *Glyptosaurus*, but also for "*Paraglyptosaurus"* and *Helodermoides;* SDNHM 75932 is closer in size to *Placosaurus* and *Proglyptosaurus*. Despite these differences, the preserved elements of SDNHM 75932 are similar enough to those of UCMP 126000 that I do not favor identifying them as distinct taxa. I propose instead that these disparities can be explained by ontogeny. Allometric size disparities, lower degree of fusion between skeletal elements, and smaller overall size are all consistent with ontogenetic variation. The relatively large size of the orbital region of SDNHM 75932 in comparison with the rest of the skull is particularly consistent with this being a juvenile specimen.

This hypothesis is supported by a number of previous studies and additional observations. Sullivan (1986) criticized previous authors' usage of frontal fusion as a diagnostic character for glyptosaurines (Sullivan 1979) and suggested that a lower degree of fusion between the frontals (as is evident in SDNHM 75932) is likely to represent ontogenetic variation as opposed to taxonomic differences, a suggestion that has been corroborated by more recent research (Smith 2009). In a study of modern lizard ontogeny, Maisano (2001) found that in many lizards, including *Elgaria* (the only anguid lizard in her study), cranial fusion is not completed until relatively late in the life of the lizard. Fusion of osteoderms to underlying cranial bone has also been shown to be less common in juvenile lizards both in modern and fossil studies (Estes 1983; Barahona and Barbadillo 1998). Further support of the ontogenetic trends of SDNHM 75932 can be found in the low degree of fusion of the epiphyseal surfaces of the humerus of SDNHM 75932. The proximal epiphyseal end is missing, and the distal epiphyseal surface shows a distinct suture (Fig. 3.6), as opposed to adult lizards, where this suture tends to be much more obscure (pers. observation). Maisano (2002) found that in most lizards she studied, epiphyseal fusion of upper limb elements is not complete until the lizard is at least 82% of maximum size (in *Elgaria*, epiphyseal fusion is complete as early as 67% of maximum size). Given the overall morphological similarities between SDNHM 75932 and UCMP126000 and the consistency of these specimens' morphological differences with ontogentic variation, I suggest that SDNHM 75932 represents a juvenile, or at least immature individual of *Glyptosaurus sylvestris*.

The Eocene of North America

The Eocene of North America was a time of dramatic global change. The gradual shift in climate from the greenhouse conditions of the Paleocene to the icehouse world of the Oligocene, as well as the continued uplift of the Rocky Mountains, meant that organisms living in North America, particularly in the western portion of the continent, had to deal with major climatic and tectonic changes. The transition from the Bridgerian and early Uintan LMAs to the later Uintan and Duchesnean LMAs has been fairly well-studied in the western United States (Woodburne 2004; Townsend et al. 2010 and references therein). Most strata of Uintan and similar ages are found in basins of the Rocky Mountain Range, primarily the Wind River, Uinta, Piceance Creek, and Green River Basins (Robinson et al. 2004). Disjunct localities outside of this range occur in the northern Great Plains, up into Saskatchewan and south to New Mexico; western Texas, and Southern California, including the Rancho Del Oro site, described here (Robinson et al. 2004).

Climatic change spurred a floral shift during the middle Eocene. Numerous authors (Woodburne 2004; Townsend et al. 2010) have described the transition in the interior United States from the denser, moist environments of the early Eocene to the drier, more open woodland characteristic of modern flora of the region. In accordance with these climatic and environmental changes, the middle Eocene included major transitions in faunas; evolutionary radiations have been observed in lagomorphs, rodents, primates, artiodactyls, and perissodactyls (Robinson et al. 2004; Woodburne 2004). As mentioned previously, the Eocene is also the time period of the radiation and subsequent diversity of the Glyptosaurinae.

Middle Eocene strata are known in southern California from both San Diego County and

Ventura County, which represent near-sea-level floodplain and deltaic environments (Lillegraven 1980; Walsh 1996). The cooling trend of the time seems to have begun at the coast earlier than in the interior of the continent (Townsend et al. 2010); the middle Eocene environments of southern California were heavily vegetated but dry and possibly semi-arid, and there is evidence of irregular monsoonal conditions (Lillegraven 1980; Woodburne 2004).

One of the marked differences between Bridgerian and early Uintan faunas of North America and later Uintan faunas is the increase in regional endemism in younger strata. Disjunct localities in the intermontane basins of the Rocky Mountains, the northern Great Plains, southern and western Texas, and southern California all yield unique faunal assemblages (Golz and Lillegraven 1977; Storer 1996; Walsh 1996; Townsend et al. 2010). Lillegraven (1979) and Walsh (1996) both noted that the early Uintan faunas of southern California shared many taxa with similarly-aged localities in the interior United States, but that the later Uintan faunas of southern California were distinct both from earlier faunas of the region and from faunas of other late Uintan localities. Lillegraven (1979) attributed this shift toward regional endemism to increasing isolation due to climatic and tectonic barriers. Lillegraven (1980) noted that there was no evidence suggesting the presence of barriers preventing faunal dispersal along the coast of southern California in the middle Eocene, allowing for a stable endemic fauna in the region.

Endemic taxa in middle Eocene southern California have been described by numerous authors (Lillegraven 1979, 1980; Chiment and Korth 1996; Walsh 1996; Colbert 2006) in regard to various segments of the mammalian faunas. Walsh (1991) provided a detailed summary of Eocene mammals from San Diego County, while Robinson et al. (2004) provided an overview of macro- and micro-mammals for the region. Despite the dramatic changes noted during the Eocene in climate, geography, floral and mammalian communities, known Eocene reptiles do not seem to have changed very much between the early and late Eocene (Smith 2011b). Smith (2009) described the dramatic turnover from the lizard communities of the Paleocene to those of the early Eocene; however, Smith (2011b) made the surprising observation that lizard communities of the late Eocene Medicine Pole Hills fossil site in North Dakota are quite consistent with the early Eocene lizard fauna of the Bighorn Basin in Wyoming, described by Smith (2009; 2011a). The author notes that this similarity seems to indicate that climatic transitions during the Eocene were not as drastic as many researchers believe them to have been (Smith 2011b), although I suggest that this effect may also be a sign that reptilian faunas weathered the various changing conditions of the Eocene more resiliently than the plant or mammal communities.

Eocene Biogeography of Glyptosaurinae

Eocene glyptosaurine lizards of both the “Melanosaurini” and Glyptosaurini tribes are found predominantly in the intermontane basins of the Rocky Mountains in North Dakota, Wyoming, Colorado, Utah, and New Mexico (Fig. 1.2), with “melanosaurinids” more commonly occurring in the northern basins, and glyptosaurinids more common in the southern basins. Within Eocene Glyptosaurini, *Gaultia* is known exclusively from Castle Gardens site in Wyoming, dating to the early Wasatchian LMA (Smith, 2011b). *Progylptosaurus* and “*Paraglyptosaurus”* are known from the Huerfano Park and San Juan basins of southern Colorado and northern New Mexico, both occurring in the late Wasatchian. *Helodermoides* is known from late Eocene (Chadronian LMA) strata in southwestern North Dakota (Smith 2006; 2011b), while other occurrences of this taxon are from Oligocene deposits. *Glyptosaurus* (sensu Sullivan 1986) ranges across Wyoming, Utah, and Colorado, with a somewhat disjunct occurrence in the Carthage-La Joya basin in New Mexico, and is temporally wide-ranging, occurring from the late Wasatchian to the late Uintan. SDNHM 75932 thus occurs very late in the known temporal range of *Glyptosaurus*. The presence of *G. sylvestris* in southern California implies a range extension for *G. sylvestris* from the Rocky Mountains west to the California coast. This is the first evidence of the Glyptosaurini tribe, and indeed the subfamily as a whole, extending so far west.

As discussed above, the late Uintan of North America was a time of dramatic regional endemism, with numerous fossil localities across the continent yielding unique faunal assemblages, distinct both from each other and from older faunas (Golz and Lillegraven 1977; Lillegraven 1979; Walsh 1996; Townsend et al. 2010). It seems surprising, therefore, to find *G. sylvestris* occurring in southern California at the end of the Uintan, as well as in similarly-aged and older faunas across the Rocky Mountain basins. All of the aforementioned studies of late-Uintan regional endemism have focused on mammalian faunas; no authors have reported specifically on the presence or absence of such endemism in reptiles. While *G. sylvestris* is the first glyptosaurine species identified from both California and the Rocky Mountains during the Eocene, 3 other lizard genera have been previously identified from both regions: Schatzinger (1975) identified *Tinosaurus, Paleoxantusia,* and *Saniwa* from the San Diego area, all 3 of which have also been identified from the Eocene of the Rocky Mountain range by Smith (2009; 2011a; 2011b). In addition, Smith's (2011b) comparison of early Eocene and late Eocene lizard faunas of the central United States implies that lizard diversity was fairly stable throughout the Eocene, at least in central North America.

In light of these previous studies, along with the present study, it seems reasonable to suggest that *Glyptosaurus*, and perhaps other squamates, did not respond to the tectonic and climatic changes of the middle Eocene to the same extent as the mammals. Certain lizards appear to have retained a high level of diversity as well as wider biogeographic distributions, apparently allowing some of them, including *G. sylvestris*, to maintain a wide range extending from the Rocky Mountains to the west coast. Alternatively, it can also be proposed that the tectonic and climatic barriers established during the late Uintan did, in fact, separate the southern California reptiles from their relatives in the interior basins, as seems to be the case with mammalian faunas. If that is the case, then I would suggest that *G. sylvestris* migrated to California earlier than the late Uintan, and that its presence in southern California during the late Uintan represents a holdover from earlier Eocene faunas. Previous authors have noted the evidence for major glyptosaurine migrations during the Wasatchian. Meszoely et al. (1978) and Sullivan (1979) have suggested that the Glyptosaurinae originated in North America and later migrated to Europe, and glyptosaurine remains from Ellesmere Island in the Canadian Arctic archipelago are known from localities yielding faunas consistent with those of Wasatchian LMA (Estes and Hutchison 1980), implying that this American-European migration may have occurred during this time. These studies imply that the early to middle Eocene was a favorable time for diversification and dispersal of the Glyptosaurinae. I propose that one or more migrations taking place before the onset of widespread regional endemism at the end of the Uintan could be responsible for the presence of glyptosaurine lizards in southern California, even if biogeographic barriers later arose that isolated these lizard populations during the late Uintan.

It remains unclear whether *G. sylvestris* maintained a contiguous range from the Rocky Mountains to the California coast or whether it was present in both places in mutual isolation during the late Uintan. To clarify this, it is prudent to investigate the regions between these regions. Unfortunately, very few Eocene fossil localities exist in these in-between regions, and those that do yield little relevant fossil material. The Elderberry Canyon local fauna of eastern

Nevada dates to the Bridgerian, but the reptile fossils from this site remain unreported (Emry, 1990). Hancock Quarry in northern Utah ranges stratigraphically from the Bridgerian to the Duchesnean LMA (Hanson 1996), and the Turtle Basin local fauna in Utah dates to the Duchesnean (Eaton et al. 1999); both of these sites have yielded fossil remains of turtles and crocodilians, but squamates have not been discovered from either locality. While the absence of lizard fossils at these sites seems conspicuous, and may indeed imply that the *G. sylvestris* in southern California represents a population isolated from those of the Rocky Mountains, it is very difficult to make such an interpretation with confidence given the very small number of localities available for examination.

The Rancho Del Oro site from which SDNHM 75932 and 75946 were recovered represents a fluvial and floodplain depositional environment; the matrix surrounding the specimen featured numerous small mudcracks typical of a floodplain. This environment is consistent with previous fossil remains of glyptosaurines, which are often found in riverine (Estes and Hutchison 1980; Sullivan 1986) or lacustrine environments (Smith 2006). The locality of SDNHM 75932 and 75946 is notable for being a coastal environment, though this is also not unprecedented; the Ellesmere Island locality described by Estes and Hutchison (1980) yields glyptosaurine remains and is also a deltaic/coastal environment. Townsend et al. (2010) noted that middle Eocene southern California was cooler and drier than the interior of the continent at the time. It is worth noting that Sullivan (1986) suggested the more dramatically cooling climate of the late Eocene and Oligocene as the reason for the ultimate extinction of these lizards. If this were true, one would expect to see glyptosaurine lizards disappearing from coastal environments earlier than those in the interior of the continent. SDNHM 75932 and 75946, however, occur at the very end of the known temporal range for *Glyptosaurus*, complicating this hypothesis. It seems that *Glyptosaurus*, and perhaps lizards in general, were not suffering from the cooling trend of the Eocene nearly as much as it might seem intuitive to suggest.

Future Study

Much more remains to be learned about the middle Eocene of southern California. While SDNHM 75932 is the most complete and well-preserved glyptosaurine specimen known from the region, numerous other elements identifiable to Glyptosaurinae have been recovered from fossil localities in the region; in addition to the doubtful *Peltosaurus macrodon* identified by Brattstrom (1955), numerous instances of "Glyptosaurinae indet." have also been reported (Schatzinger 1975; Golz and Lillegraven 1977). Many other specimens remain in the collections of the SDNHM. Future studies should focus on describing and hopefully uncovering more material to further elucidate the status of glyptosaurine lizards in middle Eocene southern California.

SDNHM 75932 also remains important for future study, given the exceptional preservation of the present material. This study focuses largely on cranial material, because these elements are the best know, and thus most diagnostic characters of these lizards, but as more material is found in the future, more detailed comparisons of both crania and post-crania may be more feasible. More comparable glyptosaurine fossil material will also be important for determining patterns of ontogenetic variation in these lizards to further elucidate the possibility of SDNHM 75932 representing an immature individual.

CHAPTER 5

CONCLUSION

Remains of glyptosaurine lizards are fairly common from the Eocene of North America, but the full extent of the distribution of these reptiles remains poorly known. SDNHM 75932, along with SDNHM 74946, represents a fairly well-preserved specimen identifiable to *Glyptosaurus sylvestris* (Reptilia; Anguidae), which shows notable differences from other *Glyptosaurus* fossils that appear to represent ontogenetic variation, implying that SDNHM 75932 represents a juvenile individual. The presence of fossilized remains of *Glyptosaurus sylvestris* from the late Uintan Land Mammal Age (LMA) of San Diego County implies that the tribe Glyptosaurini, in particular the genus *Glyptosaurus*, had a biogeographic distribution distinctly greater than previously recognized. The fact that this taxon was so widely distributed in the late Uintan, at the end of its known temporal range, also implies that these lizards did not experience dramatic turnovers and geographic restrictions as are seen in Eocene mammal faunas. This is consistent with other studies that have shown evidence that Eocene lizard faunas remained fairly constant through the Eocene in the face of climatic and ecologic changes and potentially contradicts the previously suggested hypothesis that glyptosaurine lizards suffered from the cooling trend of the Eocene. The presence of glyptosaurine lizards along the coast during the Uintan might be explained by widespread dispersal earlier in the Eocene, given evidence for Wasatchian-age glyptosaurine migration events. Evidently, lizards (and perhaps other reptiles) were behaving quite differently from mammals during the Eocene. More glyptosaurine fossils remain to be studied from the west coast, and likely from many other locations. Further study of this group of lizards will shed much-needed light on the dynamics of lizard biodiversity and evolution during the Paleogene.

REFERENCES

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

Barahona F, Barbadillo LJ. 1998. Inter- and intraspecific variation in the post-natal skull of some lacertid lizards. Journal of the Zoological Society of London. 245:393–405

Brattstrom BH. 1955. New Snakes and Lizards from the Eocene of California. Journal of Paleontology 29(1):145-149

Chiment JJ, Korth WW. 1996. A New Genus of Eomyid Rodent (Mammalia) from the Eocene (Uintan-Duchesnean) of Southern California. Journal of Vertebrate Paleontology 16(1):116-124

Colbert MW. 2006. *Hesperaletes* (Mammalia: Perissodactyla), a New Tapiroid from the Middle Eocene of Southern California. Journal of Vertebrate Paleontology 26(3):697-711

Conrad JL, Norell MA. 2008. The braincase of two glyptosaurines (Anguidae, Squamata) and anguid phylogeny. American Museum Novitates Number 3613, 24pp.

Douglass E. 1903. New vertebrates from the Montana Tertiary. Annals of the Carnegie Museum 2:145-199

Eaton JG, Hutchison JH, Holroyd PA, Korth WW, Goldstrand PM. 1999. Vertebrates of the Turtle Basin local fauna, middle Eocene, Sevier Plateau, south-central Utah. Utah Geological Survey Miscellaneous Publications 99.1:463–468

Emry RJ. 1990. Mammals of the Bridgerian (middle Eocene) Elderberry Canyon local fauna of eastern Nevada. Geological Society of America Special Papers 243:187–210

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

Estes R, Hutchison JH. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeography, Palaeoclimatology, Palaeoecology 30:325-347

Gauthier JA. 1982. Fossil Xenosauridae and Anguidae from the lower Eocene Wasatch Formation, southcentral Wyoming, and a revision of the Anguoidea. Contributions to Geology, University of Wyoming 21:7-54

Golz DJ, Lillegraven JA. 1977. Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. Contributions to Geology, University of Wyoming 15:43- 65.

Hanson CB. 1996. Stratigraphy and vertebrate faunas of the Bridgerian-Duchesnean Clarno Formation, north-central Oregon. In: Prothero, D. R. and R. J. Emory (Eds.) The terrestrial Eocene-Oligocene transition in North America. Cambridge University Press, Cambridge, pp. 206–239.

Holman JA. 1976. A New *Peltosaurus* (Reptilia, Sauria, Anguidae) from the Upper Miocene of Nebraska. Journal of Herpetology 10(1):41-44

Lillegraven JA. 1979. A biogeographical problem involving comparison of later Eocene terrestrial faunas of western North America; pp. 333-347 in J. Gray and A. J. Boucot (eds.), Historical Biogeography, Plate Tectonics, and the Changing Environment. Oregon State University Press, Corvallis

Lillegraven JA. 1980. Primates from later Eocene rocks of southern California. Journal of Mammalogy 61(2):181-204

Maisano JA. 2001. A survey of state of ossification in neonatal squamates. Herpetological Monographs 15**:** 135-157

Maisano JA. 2002. Terminal fusions of skeletal elements as indicators of maturity in squamates. Journal of Vertebrate Paleontology 22(2):268–275

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

Meszoely CAM. 1970. North American fossil anguid lizards. Bull. Mus. Comp. Zool., 139(2):87-149

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

Rasmussen DT, Shekelle M, Walsh SL, Riney BO. 1995. The dentition of *Dyseolemur*, and comments on the use of the anterior teeth in primate systematics. Journal of Human Evolution 29:301-320

Robinson P, Gunnell GF, Walsh SL, Cyde WC, Storer JE, Stuck RK, Froelich DJ, Ferrusquia-Villafranca I, McKenna MC, 2004. Wasatchian through Duchesnean biochronology. Late

Cretaceous and Cenozoic mammals of North America: Biostratigraphy and Geochronology, pp. 106–154.

Rowe T, Cifelli RL, Lehman TM, Weil A. 1992. The Campanian Terlingua Local Fauna, with a Summary of Other Vertebrates from the Aguja Formation, Trans-Pecos Texas. Journal of Vertebrate Paleontology 12(4):472-493

Schatzinger RA. 1975. Later Eocene (Uintan) lizards from the greater San Diego area, California. Thesis, San Diego State University. 212pp.

Smith KT. 2006. A diverse new assemblage of Late Eocene squamates (Reptilia) from the Chadron Formation of North Dakota, U.S.A. Palaeontologia Electronica 9(2): 44pp.

Smith KT. 2009. A new lizard assemblage from the earliest Eocene (Zone Wa0) of the Bighorn Basin, Wyoming, USA: Biogeography during the warmest interval of the Cenozoic. Journal of Systematic Paleontology 7(3):299–358

Smith KT. 2011a. The long-term history of dispersal among lizards in the early Eocene: new evidence from a microvertebrate assemblage in the Bighorn Basin of Wyoming, USA. Paleontology 54(6):1243–1270

Smith KT. 2011b. The evolution of mid-latitude faunas during the Eocene: Late Eocene lizards of the Medicine Pole Hills reconsidered. Bulletin of the Peabody Museum of Natural History 52(1):3–105

Storer JE. 1996. Eocene–Oligocene faunas of the Cypress Hills Formation, Saskatchewan. In: Prothero, D.R., Emry, R.J. (Eds.), The Terrestrial Eocene–Oligocene Transition in North America. Cambridge University Press, Cambridge, pp. 240–261.

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

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

Sullivan RM. 1989. *Proglyptosaurus huerfanensis*, New Genus, New Species: Glyptosaurine Lizard (Squamata: Anguidae) from the Early Eocene of Colorado. American Museum Novitates Number 2949

Sullivan RM. 1991. Paleocene Caudata and Squamata from Gidley and Silberling Quarries, Montana. Journal of Vertebrate Paleontology 11(3):293-301

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

Sullivan RM, Lucas SG. 1986. Annotated List of Lower Vertebrates from the Paleocene Nacimiento Formation (Puercan-Torrejonian), San Juan Basin, New Mexico. Journal of Herpetology 20(2):202-209

Sullivan RM, Holman JA. 1996. Squamata. In: Prothero, D. R. and R. J. Emory (Eds.) The terrestrial Eocene-Oligocene transition in North America. Cambridge University Press, Cambridge, pp. 354–372

Sullivan RM, Augé M, Wille E, Smith R. 2012. A new glyptosaurine lizard from the earliest Eocene of Dormaal, Belgium. Bulletin de la Société Geologique de France 183(6):627–633

Theodor JM. 1999. Protoreodon walshi, a New Species of Agriochoerid (Oreodonta, Artiodactyla, Mammalia) from the Late Uintan of San Diego County, California. Journal of Paleontology 73(6):1179-1190

Townsend KEB, Rasmussen DT, Murphey PC, Evanoff E. 2010. Middle Eocene habitat shifts in the North American western interior: A case study. Palaeogeography, Palaeoclimatology, Palaeoecology 297:144-158

Walsh SL. 1991. Eocene mammal faunas of San Diego County; pp. 161-178 in P. L. Abbott and J. A. May (eds.), Eocene Geologic History San Diego Region. Society of Economic Paleontologists and Mineralogists, Pacific Section, v. 68.

Walsh SL. 1996. Middle Eocene mammalian faunas of San Diego County, California. In: Prothero, D. R. and R. J. Emory (Eds.) The terrestrial Eocene-Oligocene transition in North America. Cambridge University Press, Cambridge, pp. 75–119

Wellstead CF. 1982. Taxonomic Re-Assignment of the Miocene Lizard, Peltosaurus minimus, from Nebraska. Copeia 1982(3):549-553

Westgate JW. 1989. Lower vertebrates from an estuarine facies of the Middle Eocene Laredo Formation (Claiborne Group), Webb County, Texas. Journal of Vertebrate Paleontology 9(3):282-294

Wilson KL. 1972. Eocene and related geology of a portion of the San Luis Rey and Encinitas quadrangles, San Diego County, California. M.Sc. Thesis, University of California, Riverside.

Woodburne M., 2004. Global events and the North American mammalian biochronology. In: Woodburne, M.O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, pp. 315–343.

APPENDIX

List of Comparative Specimens

TABLE A.1. List of lizard specimens used for comparison in this study. Abbreviations: AMNH, American Museum of Natural History in New York, New York; ETSU, East Tennessee State University Vertebrate Paleontology Collection in Johnson City, Tennessee.

Taxon	**Specimen number**	**Collection**
Family Anguidae		
Subfamily Glyptosaurinae		
Tribe “Melanosaurini”		
Arpadosaurus sp.	AMNH 2103	AMNH, New York
Melanosaurus maximus	AMNH 1616	AMNH, New York
Melanosaurus maximus	AMNH 6167	AMNH, New York
Melanosaurus sp.	AMNH 26200	AMNH, New York
Peltosaurus granulosus	AMNH 8138	AMNH, New York
Peltosaurus sp.	AMNH 2987	AMNH, New York
Peltosaurus sp.	AMNH 1652	AMNH, New York
Peltosaurus sp.	AMNH 2682	AMNH, New York
Peltosaurus sp.	AMNH 26266	AMNH, New York
Peltosaurus sp.	AMNH 2672	AMNH, New York
Peltosaurus sp.	AMNH 2673	AMNH, New York
Peltosaurus sp.	FAM 42915	AMNH, New York
Peltosaurus sp.	UF 191778	University of Florida
Peltosaurus sp.	UF 201899	University of Florida
Peltosaurus sp.	UF 207602	University of Florida
Peltosaurus sp.	UF 207603	University of Florida
Peltosaurus sp.	UF 209732	University of Florida
Peltosaurus sp.	UF 216739	University of Florida
cf. *Peltosaurus* sp.	NE 006	University of Florida
Proxestops siberlingi	AMNH 2688	AMNH, New York
Xestops vagans	AMNH 3819 (type)	AMNH, New York
Xestops sp.	AMNH 3834	AMNH, New York
cf. *Xestops* sp.	AMNH 7585	AMNH, New York
Tribe Glyptosaurini		
Eoglyptosaurus huerfanensis (=*Proglyptosaurus huerfanensis*)	AMNH 7431	AMNH, New York
Glyptosaurus hillsi (=*G. sylvestris*)	AMNH 1617	AMNH, New York

Glyptosaurus sylvestris (also labeled *G. princeps*)	AMNH 5113	AMNH, New York
Glyptosaurus sylvestris	UCMP 126000	From Dr. Bob Sullivan
Glyptosaurus sylvestris	UF 2675	University of Florida
cf. *Glyptosaurus sylvestris*	UF 2293	University of Florida
Glyptosaurus sp.	AMNH 2242	AMNH, New York
Glyptosaurus sp.	UF 2292	University of Florida
Glyptosaurus sp.	UF 200642	University of Florida
Helodermoides mongoliensis	AMNH 6669 (type)	AMNH, New York
Helodermoides tuberculatus	AMNH 1611	AMNH, New York
Helodermoides tuberculatus	AMNH 6800	AMNH, New York
Helodermoides tuberculatus	FAM 8694	AMNH, New York
Helodermoides tuberculatus	FAM 8695	AMNH, New York
Helodermoides tuberculatus	FAM 8697	AMNH, New York
Helodermoides tuberculatus	AMNH 8698	AMNH, New York
Helodermoides tuberculatus	FAM 8706	AMNH, New York
Helodermoides tuberculatus	FAM 8720	AMNH, New York
Helodermoides tuberculatus	FAM 8729	AMNH, New York
Helodermoides tuberculatus	FAM 10161	AMNH, New York
Helodermoides tuberculatus	AMNH 11311	AMNH, New York
Helodermoides tuberculatus	Cast of AMNH 11311	ETSU
Helodermoides sp.	FAM 8748	AMNH, New York
Helodermoides sp.	UF 209489	University of Florida
Paraglyptosaurus princeps	AMNH 1614 Some elements labeled 1615	AMNH, New York
Paraglyptosaurus princeps	AMNH 1619	AMNH, New York
Paraglyptosaurus princeps	AMNH 6055	AMNH, New York
Paraglyptosaurus princeps	AMNH 7455	AMNH, New York
cf. *Paraglyptosaurus princeps*	AMNH 7598	AMNH, New York
cf. *Paraglyptosaurus princeps*	AMNH 7599	AMNH, New York
Paraglyptosaurus yatkolai	AMNH 2600	AMNH, New York
Paraglyptosaurus yatkolai	AMNH 5181	AMNH, New York
Placosaurus sp. (previously labeled *Glyptosaurus*)	AMNH 3099	AMNH, New York
Subfamily Odaxosaurinae		
Odaxosaurus piger	AMNH 12060	AMNH, New York
Odaxosaurus sp.	AMNH 11041	AMNH, New York
Subfamily Diploglossinae		
Diploglossus pleii	AMNH 7695	AMNH, New York

Family Varanidae		
Varanus prasinus	JIM 1393	ETSU
Varanus similis	JIM 0929	ETSU
Family Helodermatidae		
Heloderma suspectum	ETVP 7089	ETSU

VITA

DAVID A. MOSCATO

Personal Data: Date of Birth: September 13, 1988.

Place of Birth: Mineola, New York

Marital Status: Single

Education: Wantagh High School, Wantagh, New York

B.S. Geobiology, Pennsylvania State University, State College, Pennsylvania, 2010

M.S. Geosciences, East Tennessee State University, Johnson City, Tennessee, 2013

Professional Experience: 2011. Fossil excavation at Gray Fossil Site, East Tennessee State University with Dr. Steven Wallace

2011-2012. Specimen preparation and organization in East Tennessee State University Vertebrate Paleontology Lab

2010-2012. Teaching Assistant, Department of Geosciences, East Tennessee State University.

2010-2012. Designed, wrote, and taught several original laboratory exercises for introductory geology courses (GEOL 1041: Physical Geology and GEOL 1051: Historical Geology).

	2010, 2009, 2007. Fossil excavation and screen-washing at Parker’s Pit Cave in Black Hills, South Dakota with Dr. Russell Graham of Pennsylvania State University.
	2010. Research assistant for Dr. Russell Graham at the Pennsylvania State Earth and Mineral Sciences Museum.
	2009. Fossil excavation at Garden Park, Colorado with Virginia Tidwell of the Denver Museum of Nature and Science.
Publications:	**Moscato, D. A.**, Jasinski, S. E. 2012. First Record of Fossil Chelydridae and Trionychidae from the Pleistocene of Sonora Mexico. Journal of Vertebrate Paleontology Vol. 32 (Supplemental) 146A
	Moscato, D. A., Wallace, S. 2011. Analysis of Variation in Snake Vertebrae using Geometric Morphometrics. Journal of Vertebrate Paleontology Vol. 31 (Supplemental) 162A
	Moscato, D. A., Graham, R. 2010. Paleoecology of Late Pleistocene Snakes and Salamanders from Parker’s Pit Cave in the Black Hills, SD. Journal of Vertebrate Paleontology Vol. 30 (Supplemental) 137A
Honors and Awards:	2011 National Science Foundation East Asia and Pacific Summer Institutes (EAPSI) Grant to conduct research at the Institute of Vertebrate Paleontology and Paleoanthropology

(IVPP) in Beijing with Dr. ChangZhu Jin, studing fossil reptiles from China.

2012 ETSU Graduate Studies Excellence in Teaching Award $250

2011 Student Research and Travel Grant, East Tennessee State University Department of Geology $200

2011, 2010 Student Research and Travel Grant, East Tennessee State University Department of Biology $300, $300

2011, 2010, Student Research and Travel Grant, Don Sundquist Center of Excellence in Paleontology $200, $200

2010 American Quaternary Association (AMQUA) Student Travel Grant $300