Cretaceous Dinosaurs And The World They Lived In: A New Species Of Ornithischian Dinosaur From The Early Cretaceous (Aptian) Of Texas, Reconstruction Of The Brain Endocast And Inner Ear Of Malawisaurus Dixeyi, And Reconstruction Of The Paleoclimate And Paleoenvironment of Cretaceous Terrestrial Formations In Texas And Oklahoma Using Pedogenic Minerals

Kate Andrzejewski
Southern Methodist University, kruoff@smu.edu

Follow this and additional works at: https://scholar.smu.edu/hum_sci_earthsciences_etds

Part of the Geochemistry Commons, Paleobiology Commons, Paleontology Commons, and the Soil Science Commons

Recommended Citation
Andrzejewski, Kate, "Cretaceous Dinosaurs And The World They Lived In: A New Species Of Ornithischian Dinosaur From The Early Cretaceous (Aptian) Of Texas, Reconstruction Of The Brain Endocast And Inner Ear Of Malawisaurus Dixeyi, And Reconstruction Of The Paleoclimate And Paleoenvironment of Cretaceous Terrestrial Formations In Texas And Oklahoma Using Pedogenic Minerals" (2018). Earth Sciences Theses and Dissertations. 2.
https://scholar.smu.edu/hum_sci_earthsciences_etds/2

This Dissertation is brought to you for free and open access by the Earth Sciences at SMU Scholar. It has been accepted for inclusion in Earth Sciences Theses and Dissertations by an authorized administrator of SMU Scholar. For more information, please visit http://digitalrepository.smu.edu.
CRETACEOUS DINOSAURS AND THE WORLD THEY LIVED IN:
A NEW SPECIES OF ORNITHISCHIAN DINOSAUR FROM THE EARLY CRETACEOUS
(APTIAN) OF TEXAS, RECONSTRUCTION OF THE BRAIN ENDOCAST AND INNER
EAR OF MALAWISAURUS DIXEYI, AND RECONSTRUCTION OF THE PALEOCLIMATE
AND PALEOENVIRONMENT OF CRETACEOUS TERRESTRIAL FORMATIONS IN
TEXAS AND OKLAHOMA USING PEDOGENIC MINERALS

Approved by:

___________________________________
Dr. Louis L. Jacobs
Professor

___________________________________
Dr. Thomas Adams
Curator of Paleontology and Geology
Witte Museum

___________________________________
Dr. Anthony Fiorillo
Vice President of Research and Collections
Perot Museum of Nature and Science

___________________________________
Dr. Neil Tabor
Professor

___________________________________
Dr. Dale A. Winkler
Research Professor
CRETACEOUS DINOSAURS AND THE WORLD THEY LIVED IN:
A NEW SPECIES OF ORNITHISCHIAN DINOSAUR FROM THE EARLY CRETACEOUS
(APTIAN) OF TEXAS, RECONSTRUCTION OF THE BRAIN ENDOCAST AND INNER
EAR OF *MALAWISAURUS DIXEYI*, AND RECONSTRUCTION OF THE PALEOCLIMATE
AND PALEOENVIRONMENT OF CRETACEOUS TERRESTRIAL FORMATIONS IN
TEXAS AND OKLAHOMA USING PEDOGENIC MINERALS

A Dissertation Presented to the Graduate Faculty of

Dedman College
Southern Methodist University

in
Partial Fulfillment of the Requirements
for the degree of
Doctor of Philosophy

with a
Major in Earth Sciences

by
Kate Andrzejewski

B.S., Geology, University of Kansas, 2014
B.S., Ecology and Evolutionary Biology, University of Kansas, 2014

May 19, 2018
ACKNOWLEDGMENTS

First, I thank my advisor Dr. Louis Jacobs whose support and guidance over these past four years has allowed me to achieve a lifelong dream. Thank you for the countless hours spent in the field, reading manuscripts, and providing sage advice.

Second, I thank my committee members Dr. Dale Winkler, Dr. Neil Tabor, Dr. Anthony Fiorillo, and Dr. Thomas Adams. Thank you for your assistance, time, and encouragement. Your feedback and advice were instrumental in completing these projects.

I also thank the faculty and staff at SMU whose encouragement and support continued to cultivate my curiosity and passion for geology. Special thanks to Mike Polcyn for his assistance in computer imaging and endless stimulating conversations. Also, special thanks to Dr. Timothy Myers for his patience and countless hours spent imparting his infinite knowledge of laboratory processes. I would also like to thank Dr. Ian Richards and Dr. Kurt Ferguson for providing access to their lab and for their support with stable isotope extractions. Thanks to Dr. Yapp and Dr. Rosenau for their assistance in isotope theory and calculations. Thanks to Dr. Sadler for his assistance in statistical calculations and methods. Furthermore, I would like to thank my fellow graduate students at SMU for the friendships and memories created over the last four years. I would especially like to thank my office mate Matt Clemens whose assistance and comical wit have been crucial during my time at SMU and Julia McIntosh who provided assistance in the field.
I would like to thank the following institutions for providing access to their facilities and support in various research objectives: the University of Texas for access to their High Resolution X-ray CT facility and the University of Texas A&M, specifically Dr. Andrew Mott, for access and support to the Electron Microprobe laboratory.

I would like to thank the following for providing access to study localities and fossil collections: the Army Corps of Engineers, especially James Burger for providing access to the Proctor Lake fossil locality, Karen Morton for providing access to the fossil collection at the Perot Museum of Nature and Science, staff at the Fort Worth Museum of Science and History for providing access to their collections, Dr. Ronald Tykoski for access to the North Texas Antlers Formation fossil locality, Mr. Cross for providing access to his private land in Oklahoma, Mr. Dean for providing access to his private land in Oklahoma, Mr. Jones for providing continued access to the Jones Ranch fossil locality, and Dr. Christopher Noto for access and field assistance to the Arlington Archosaur fossil locality.

Funding for this research was generously provided by the Dallas Paleontological Society, the Institute for the Study of Earth and Man at Southern Methodist University, and the American Association of Petroleum Geologists.

Finally, I would like to thank my family whose unwavering love and support has allowed me to pursue my dreams. Words can never capture the depth of my love and gratitude. To all of my grandparents, aunts, uncles, and cousins who have encouraged me every step of the way. To my parents, Tim and Nancy Ruoff, who taught me to chase my dreams and have lovingly sacrificed so much, that those dreams may be realized. To my brother and lifelong partner in crime, Josh, thank you for all of your support. To my husband and love of my life, Kolbe, I could never have completed this journey without you.
Cretaceous Dinosaurs And The World They Lived In:
A New Species Of Ornithischian Dinosaur From The Early Cretaceous
(Aptian) Of Texas, Reconstruction Of The Brain Endocast And Inner
Ear Of Malawisaurus Dixeyi, And Reconstruction Of The Paleoclimate
And Paleoenvironment Of Cretaceous Terrestrial Formations In
Texas And Oklahoma Using Pedogenic Minerals

Advisor: Professor Louis L. Jacobs

Doctor of Philosophy conferred May 19, 2018
Dissertation completed April 18, 2018

Material from over thirty individuals of a new ornithopod, represented by nearly every
skeletal element, was recovered from the Proctor Lake locality in the Twin Mountains Formation
(Aptian) of north-central Texas. This material includes various ontogenetic stages, providing
insight into the growth patterns of this species. The new ornithopod, Convolosaurus marri gen.
et sp. nov., is recovered basal to Iguanodontia, but more derived than Hypsilophodon foxii. The
presence and morphology of 4 premaxillary teeth along with a combination of both basal and
derived characters distinguish this taxon from all other ornithopods. Basal characters present in
C. marri including the presence of premaxillary teeth, the shape of the dentary teeth, and position
of the pterygoid wing on the quadrate, whereas the presence of opisthocoelous cervical
vertebrae, large proximal caudal neural spines, and curved maxillary tooth roots suggest C. marri
is more derived than 80% of the basal neornithischians included in this analysis.

A braincase of the Cretaceous titanosaurian sauropod Malawisaurus dixeyi, complete
except for the olfactory region, was CT scanned and a 3D rendering of the endocast and inner ear
was generated. Cranial nerves appear in the same configuration as in other sauropods, including
derived features that appear to characterize titanosaurians, specifically, an abducens nerve canal that passes lateral to the pituitary fossa rather than entering it. Furthermore, the hypoglossal nerve exits the skull via a single foramen, consistent with most titanosaurians, while other saurischians, including the basal titanosauriform, *Giraffatitan*, contain multiple rootlets. The size of the vestibular labyrinth is smaller than *Giraffatitan*, but larger than most derived titanosaurians. Similar to *Giraffatitan*, the anterior semicircular canal is larger than the posterior semicircular canal. This contrasts with more derived titanosaurians that contain subequal anterior and posterior semicircular canals, congruent with the interpretation of *Malawisaurus* as a basal titanosaurian. Measurements of the humerus of *Malawisaurus* provide a body mass estimate of 4.7 metric tons. Comparison of body mass to radius of the semicircular canals of the vestibular labyrinth reveal that *Malawisaurus* fits the allometric relationship found in previous studies of extant mammals and *Giraffatitan brancai*. As in *Giraffatitan*, the anterior semicircular is significantly larger than is predicted by the allometric relationship suggesting greater sensitivity and slower pitch movements of the head.

The clay mineralogy, chemistry, and stable oxygen and hydrogen-isotope compositions were measured from 11 phyllosilicate samples representing Cretaceous paleosol profiles which span the Early to Late Cretaceous boundary in north-central Texas and southern Oklahoma. The samples consist of mineralogical mixtures of illite, smectite, and kaolinite. Samples from the Antlers Formation (Albian) in southern Oklahoma and the Woodbine Formation (Cenomanian) are dominated by kaolinite, while the remaining samples are dominated by smectite and illite. Chemical data is used to estimate paleoprecipitation for each locality using the CALMAG weathering index. Chemical and mineralogical data are used in conjunction with published thermodynamic data to calculate unique hydrogen and oxygen isotope fractionation factors for
each sample. Paleotemperature is then estimated by measuring the hydrogen and oxygen-isotope compositions for each sample and applying the calculated fractionation factors.

The estimated paleoprecipitation ranges from 268 to 1486 mm/yr with two marked increases in precipitation in the Oklahoma Antlers Formation (Albian) localities and Woodbine Formation (Cenomanian) localities. The δD values of the phyllosilicate mixtures range from -50‰ to -67‰. The δ¹⁸O values of phyllosilicate mixtures range from 18.5‰ to 21.7‰. Assuming the phyllosilicates preserve a record of isotopic equilibrium with Cretaceous meteoric waters, the measured hydrogen and oxygen-isotope values correspond to phyllosilicate crystallization temperatures ranging from 26 ± 3°C to 31 ± °C. Cooler temperatures correspond to periods with markedly higher precipitation estimates which also correlate with the presence of extensive shallow seas upon the Texas craton.
# TABLE OF CONTENTS

LIST OF FIGURES .................................................................................................................. xii

LIST OF TABLES .................................................................................................................. xiv

CHAPTER 1 .............................................................................................................................. 1

  1.1 Introduction ....................................................................................................................... 1

CHAPTER 2 .............................................................................................................................. 3

  2.1 Introduction ....................................................................................................................... 3

  2.2 Systematic Paleontology .................................................................................................. 8

  2.3 Cranial Description ......................................................................................................... 10

  2.4 Postcranial Description ................................................................................................. 30

  2.5 Ontogeny ......................................................................................................................... 61

  2.6 Phylogenetic Analysis ..................................................................................................... 69

  2.7 Discussion ....................................................................................................................... 72

  2.8 Conclusions ................................................................................................................... 73

CHAPTER 3 .............................................................................................................................. 74

  3.1 Introduction ....................................................................................................................... 74

  3.2 Materials and Methods ................................................................................................. 75

  3.3 Osteology ......................................................................................................................... 76

  3.4 Cranial Endocast ............................................................................................................ 78
CHAPTER 4

4.1 Introduction ........................................................................................................... 87
4.2 Geologic Setting .................................................................................................. 89
4.3 Materials and Methods ....................................................................................... 93
4.4 Phyllosilicate oxygen and hydrogen isotope fractionation factors ................ 96
4.5 Stable isotope composition of paleosol phyllosilicates and paleoenvironmental proxies ......................................................................................................................... 97
4.6 Paleosol Morphology ......................................................................................... 99
4.7 Clay Mineralogy and Chemical Composition of Paleosol B Horizons ........ 101
4.8 Major-Element Chemistry and Paleoprecipitation Estimates ....................... 107
4.9 Calculation of oxygen and hydrogen fractionation factors of naturally occurring phyllosilicates ................................................................................................. 110
4.10 Calculation of phyllosilicate crystallization temperature .................................. 111
4.11 Meteoric waters and phyllosilicate surface domain arrays ................................ 115
4.12 Assessment of diagenesis .................................................................................. 119
4.13 Paleoclimatic of Early-Late Cretaceous of north-central Texas and southern Oklahoma with possible implications ................................................................. 119
4.14 Comparison to regional paleoclimatic trends across the Early to Late Cretaceous boundary .......................................................... 121

4.15 Conclusions ........................................................................................................ 123

APPENDIX 1 ............................................................................................................. 126

APPENDIX 2 ............................................................................................................. 128

APPENDIX 3 ............................................................................................................. 129

APPENDIX 4 ............................................................................................................. 151

APPENDIX 5 ............................................................................................................. 164

APPENDIX 6 ............................................................................................................. 165

APPENDIX 7 ............................................................................................................. 171

APPENDIX 8 ............................................................................................................. 172

APPENDIX 9 ............................................................................................................. 175

BIBLIOGRAPHY .................................................................................................... 180
LIST OF FIGURES

Figure 2.1 Map of Study Area ................................................................. 5
Figure 2.2 Articulated Specimens ............................................................ 6
Figure 2.3 Modified Stratigraphic Column of Proctor Lake fossil locality ............ 7
Figure 2.4 Premaxilla from specimen SMU 72316 .................................................. 11
Figure 2.5 SMU 72834 Skull ........................................................................ 12
Figure 2.6 SMU 74749 and SMU 72316 cranium .................................................. 14
Figure 2.7 SMU 72834 partial cranium .............................................................. 16
Figure 2.8 SMU 74678 cranium ...................................................................... 19
Figure 2.9 Occipital region of SMU 72834 .......................................................... 24
Figure 2.10 SMU 72316 maxillary and dentary teeth .......................................... 30
Figure 2.11 SMU 75621-1 axis and third cervical vertebra .................................... 32
Figure 2.12 SMU 72834 cervical vertebrae ....................................................... 34
Figure 2.13 SMU 72316 dorsal vertebrae ........................................................... 36
Figure 2.14 SMU 72316 pelvic girdle ............................................................... 38
Figure 2.15 Caudal vertebrae ........................................................................... 39
Figure 2.16 Ossified tendons in the caudal region ............................................... 41
Figure 2.17 SMU 72834 scapula and coracoid; SMU 75564 humerus ..................... 44
Figure 2.18 SMU 70456 left manus .................................................................. 47
Figure 2.19 SMU 77617 left ilium .................................................................... 49
LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Skeletal measurements of <em>C. marri</em> sp. nov. (in mm)</td>
<td>37</td>
</tr>
<tr>
<td>2.2</td>
<td>K-means and hierarchical clustering statistics produced by femora study</td>
<td>67</td>
</tr>
<tr>
<td>3.1</td>
<td>Measurements of associated humerus and body mass estimate of <em>M. dixeyi</em></td>
<td>84</td>
</tr>
<tr>
<td>3.2</td>
<td>Measurements of semicircular canals from the braincase of <em>M. dixeyi</em></td>
<td>84</td>
</tr>
<tr>
<td>4.1</td>
<td>Electron microprobe and x-ray diffraction data for &lt;0.2µm size fraction of</td>
<td>106</td>
</tr>
<tr>
<td></td>
<td>phyllosilicates</td>
<td></td>
</tr>
<tr>
<td>4.2</td>
<td>Calculated chemical formulae for end-member 2:1 phyllosilicates in phyllosilicate mixtures</td>
<td>107</td>
</tr>
<tr>
<td>4.3</td>
<td>X-ray fluorescence data and mean annual precipitation estimates</td>
<td>109</td>
</tr>
<tr>
<td>4.4</td>
<td>Measured phyllosilicate oxygen and hydrogen-isotope compositions, oxygen and hydrogen isotope fractionation equations, and calculated phyllosilicate crystallization temperatures</td>
<td>113</td>
</tr>
</tbody>
</table>
This is dedicated to my family, whose love and support has carried me through and allowed me to thrive during this project.
CHAPTER 1

INTRODUCTION

This dissertation is comprised of three projects focusing on dinosaur fauna of the Cretaceous and reconstructing the paleoenvironment and paleoclimate of the Cretaceous. The first project describes and analyzes the phylogenetic position of a new ornithischian dinosaur from the Early Cretaceous (Aptian) of Texas. This new ornithopod is represented by at least 32 individuals recovered from Proctor Lake, Texas. The individuals recovered from the fossil locality range in size and presumably ontogenetic age. The abundance of fossil material found at the Proctor Lake locality allows for analyses of ontogenetic change and population dynamics of this new ornithopod.

The second project reconstructs the endocast and inner ear of *Malawisaurus dixeyi* using CT scans and imaging software. Unique characters are identified from the reconstruction and are used to evaluate the phylogenetic position of *Malawisaurus dixeyi* within sauropod phylogeny. This reconstruction is also used to examine physiological and behavioral aspects of *Malawisaurus* including estimates of body mass, habitual head orientation, and sensitivity of the vestibular organ.

The third and final project focuses on reconstructing the paleoenvironment and paleoclimate of seven localities that span the Early to Late Cretaceous boundary of north-central Texas and southern Oklahoma. Significant changes including the rise of dominance of
angiosperms and nearly a complete faunal turnover occurs across the Early to Late Cretaceous interval of this region. This study aims to quantify paleoclimate and paleoenvironmental changes across this boundary in an effort to understand their potential impact on changes in floral and faunal composition. This is accomplished by describing paleosols found in terrestrial formations and analyzing pedogenic minerals collected from each locality. Analyses of the mineralogy, chemical composition, and oxygen and hydrogen isotope composition of these pedogenic minerals produces estimates of paleoprecipitation and paleotemperature. These estimates are compared to regional studies of paleoclimate change across the Early to Late Cretaceous interval of the Western Interior of the United States.
CHAPTER 2

A NEW SPECIES OF ORNITHISCHIAN DINOSAUR FROM THE EARLY CRETACEOUS
(APTIAN) OF TEXAS

2.1 Introduction

Vertebrate fossils were first discovered and collected from Proctor Lake, Texas in May 1985 (Fig 2.1). At least 32 individuals of a single species of ornithopod, including three larger articulated individuals and mass accumulations of partially articulated smaller individuals were recovered (Fig 2.2). Initial studies suggested that the mass accumulations of smaller individuals occur in depressions reflecting a nesting site, although no egg shell has been recovered (Winkler and Murry, 1989), and that these groupings may have represented precocious flocks. The purpose here is to describe and name the Proctor Lake ornithopod and to determine its evolutionary position through phylogenetic analysis.

The Proctor Lake locality sits stratigraphically low in the Twin Mountains Formation, the lowest of the three formations in the Trinity Group in this area (Twin Mountains, Glen Rose, Paluxy). Although the age of the Twin Mountains Formation is not tightly constrained, its unconformable base is assumed to be no older than the Aptian stage (≤ 126 Ma) and the base of the overlying Glen Rose Formation is biostratigraphically correlated with the Aptian-Albian
boundary (113 Ma) (Young 1967; Winkler et al., 1990; Jacobs and Winkler, 1998). The Twin Mountains sequence includes transitional marine facies representing the earliest Cretaceous transgressions upon the Texas craton (Young, 1986), prior to the Albian Glen Rose transgression and the late Albian completion of the Western Interior Seaway. The basal portion of the Twin Mountains Formation consists primarily of conglomerates and sandstones and the upper portion comprises thinly interbedded sands and mudstones (Fig 2.3; Winkler and Murry 1989), interpreted as fluvial flood-basin facies. The fossil-bearing strata at Proctor Lake that produced the ornithopod described here are 2m of reddish muds and sands from the lower portion of the Twin Mountains Formation (Winkler and Murry, 1989; Winkler et al., 1988, 1990). These sediments contain horizons with carbonate nodules, root-mottling, and mud cracks indicative of vertic paleosols.

Vertebrate fossils occur throughout the Twin Mountains Formation (Winkler et al., 1990). Other archosaur taxa recovered from the lower part of the formation with the Proctor Lake ornithopod include a crocodyliform, *Wannchampsus kirpachi* (Adams 2014), and a single tooth of a dromaeosaur. The upper portion of the Twin Mountains contains a variety of fauna, including the crocodyliform *Paluxysuchus newmani* (Adams, 2013), sauropod remains at the Jones Ranch site (Winkler and Rose, 2006; Winkler et al., 2012), the theropod *Acrocanthosaurus atokensis* (Harris, 1998), and the ornithopod *Tenontosaurus dossi* (Winkler et al., 1997).
Fig 2.1. Satellite image of Proctor Lake, Texas located in Comanche County (green) (ArcGIS 10.5).
Fig 2.2. Articulated specimens

(A) SMU 70456, articulated subadult individual on display at the Proctor Lake Corps of Engineers Office. Scale arrow equals 10cm. (B) Composite skeleton on display at the Perot Museum of Nature and Science. Scale bar equals 10cm. (C) SMU 75379 and SMU 75380, partial articulated skeletons found stacked on one another. Scale bar equals 5cm.
**Fig 2.3.** Stratigraphic section of Twin Mountains Formation exposed at Proctor Lake (modified from Winkler and Murry, 1989).
2.2 Systematic Paleontology

DINOSAURIA Owen, 1842

ORNITHISCHIA Seeley, 1887

NEORNITHISCHIA Cooper, 1985

CERAPODA Sereno, 1986

ORNITHOPODA Marsh, 1881

Convulosaurus marri gen. et sp. nov.

Etymology: The generic name Convulosaurus translates from Latin meaning “flocking lizard” referring to clusters of juvenile specimens. The species name marri is in honor of Dr. Ray H. Marr who produced the Society of Vertebrate Paleontology videos “We are SVP” and “About the SVP Logo” posted on the SVP website (vertpaleo.org), and who is a strong proponent of students at Southern Methodist University.

Holotype: SMU 72834, a skull and partial articulated skeleton with 9 cervical vertebrae; 15 dorsal vertebrae; 6 sacral vertebrae; 23 caudal vertebrae; right and partial left scapula; right and partial left coracoids; left and partial right humeri; left ulna; left radius; partial left manus; articulated pelvis including the left and right ilia, proximal left and right ischia, partial prepubic rods; proximal and distal ends of the left and right femora and the mid-part of the left shaft; proximal left and right tibiae; and proximal left fibula. The type specimen, SMU 72834, is the
largest individual in the sample measuring approximately 2.5-3m in length; however, this
skeleton does not represent a full grown adult, thus the adult size of this species is unknown.

**Diagnosis:** The presence of four premaxillary teeth with dorsoventrally oriented groove
on the buccal surface distinguishes *Convoloaurus marri* gen. et sp. nov. from all other
ornithopods. Further, it can be distinguished from other basal ornithopods by a unique
combination of primitive and derived character states. Primitive character states include the
presence of premaxillary teeth and two supraorbitals that extend across the entire orbit. Derived
color character states include: curved maxillary tooth roots; opisthocoelous cervical vertebrae; sacral
neural spines twice the height of the sacral centra; proximal caudal neural spines 1.5 times the
height of the centrum; expanded ischial ‘foot’; shallow intercondylar groove on the anterior
surface of the femur; and a laterally compressed prepubic process.

**Referred Specimens:** SMU 70254, left manus; SMU 70444, partial skull; SMU 70456,
articulated skeleton; SMU 70534, articulated left hindlimb; SMU 70635, partial right maxilla;
SMU 71510, right surangular; SMU 71631, right quadratojugal; SMU 71690, left astragalus;
SMU 71854, right scapula; SMU 72316, partial skull, articulated pelvic girdle and vertebral
column, partial left hindlimb; SMU 72534, left calcaneum; SMU 72541, left distal femur; SMU
73170, articulated left pes; SMU 73171, right pes; SMU 74087, partial skull; SMU 74093, right
femur and tibia; SMU 74104, partial left pubis; SMU 74119, distal left ischium; SMU 74124, left
scapula; SMU 74131, cervical vertebrae; SMU 74576, articulated caudal vertebrae with ossified
tendons; SMU 74663, skull and partial skeleton; SMU 74670, articulated caudal vertebrae with
ossified tendons; SMU 74664, left and right scapula; SMU 74665, partial right hindlimb; SMU
74678, partial skull; SMU 74749, skull and partial skeleton; SMU 75379, partial skull; SMU
75380, right premaxilla; SMU 75564, partial skeleton; SMU 75621-1, axis; SMU 75621-2, third
cervical vertebra; SMU 75636, partial left pubis; SMU 77617, partial skeleton. Although these specimens vary in size, they are taken to represent a single species because of consistency in growth rate based on femora measurements and similar overall skeletal morphology.

Locality: Proctor Lake (SMU 001), Comanche County, Texas, Twin Mountains Formation, Early Cretaceous (Aptian).

2.3 Cranial Description

Seven partially articulated specimens and four disarticulated elements were used for skull description. SMU 72834 is the largest and presumably most mature skull. The remaining specimens are significantly smaller and presumably represent younger individuals. Elements that are clearly preserved are described below. Elements that are not preserved or are difficult to interpret based on preservation include the ectopterygoid, parasphenoid, laterosphenoid, coronoid, articular, palatine, vomer, and prearticular.

Premaxilla. SMU 72316 and the type specimen SMU 72834 contain partial, unfused premaxillae (Fig 2.4, 2.5). The premaxilla forms the anterodorsal portion of the narial opening. The dorsal processes of the premaxillae overlap and wedge between the anterior ends of the nasals. The lateral surface of the oral margins is slightly flared and the ventral margin of the premaxilla is ventrally deflected compared to the maxillary tooth row. The posterolateral process of the premaxilla does not contact the lacrimal; however, the left side of SMU 74749 preserves the maxilla rising as a thin sheet that overlaps the posterolateral process of the premaxilla and can contact the nasals making character 7 in the character matrix a problematic character to score.
The anterodorsal surface of the premaxilla is rugose, containing 3 to 5 small foramina. This region of the premaxilla likely supported a rhamphotheca (Sereno 1991). The lateral surface of the premaxilla from SMU 72316 and SMU 75380 contains a foramen that is larger relative to the small foramina on the anterodorsal surface. This larger foramen pierces the premaxilla and is clearly visible in medial view. The anterior tip of the premaxilla contains a short edentulous
region and there is a diastema between the maxillary and premaxillary tooth row. The premaxillae from SMU 72316, SMU 70444, SMU 74087, and SMU 75380 contain 4 premaxillary teeth. These specimens range in size with the anterior-posterior tooth row length of the premaxilla ranging from 11mm to 25mm; therefore, it is unlikely that the number of premaxillary teeth changed during its life.

Fig 2.5. SMU 72834 skull. (A) SMU 72834, skull in right lateral view. (B) Illustration of SMU 72834, in right lateral view (David Baker). Abbreviations: D-dentary, L-lacrimal, MX-maxilla, PMX-premaxilla, QJ-quadratojugal. Scale bar equals 5 cm.

Maxilla. The maxilla forms the ventral and anterior margins of the antorbital fenestra. In lateral view the anterior end tapers to a rugose point forming the premaxillary process of the maxilla. Just posterior to the premaxillary process a short anterolateral process that inserted into
the premaxilla is present in SMU 70635 and SMU 74749 (Fig 2.6). The process is more prominent on the larger specimen SMU 70635. This process is also present in *Haya griva* (Makovicky et al., 2011), *Orodromeus makelai* (Scheetz, 1999), and *Zephyrosaurus schaffi* (Sues, 1980); however, it is more pronounced in these taxa than in the Proctor Lake taxon. A significant foramen at the posteroventral corner of the antorbital fossa is observed in SMU 70635 and SMU 74749. Dorsal to the antorbital fossa the maxilla ascends as a thin sheet, curving posteriorly to contact the lacrimal, forming the anterior margin of the antorbital fenestra. The posterior margin of the maxilla contacts the jugal forming a butt joint. A maxillary fenestra is lacking in the Proctor Lake taxon, distinguishing it from *Hypsilophodon foxii* (Galton, 1974) and *Haya griva* (Makovicky et al., 2011).

The lateroventral portion of the maxilla is rod-like, bearing 8 tooth positions in SMU 74749 and 10 tooth positions in SMU 70635 and SMU 72316 (Fig 2.6). The difference in tooth positions can be attributed to ontogenetic stage as SMU 74749 is smaller and presumably younger than the other two specimens. A prominent anteroposterior ridge runs along the lateral surface of the maxilla. The maxillary teeth in the type specimen, SMU 72834, become increasing medially inset from anterior to posterior as this ridge become more prominent. Ventral to the ridge and above the tooth row are replacement foramina, which are seen in all neornithischians.
Fig 2.6. SMU 74749 and SMU 72316 cranial material. (A) SMU 74749, cranium in right lateral view. (B) Outline drawing of identifiable bone contacts on the right side of SMU 74749 cranium. (C) SMU 72316, cranium in right lateral view. (D). Outline drawing of identifiable bone contacts on the right side of SMU 72316 cranium. Abbreviations: D-dentary, F-frontal, J-jugal, L-lacrimal, MX-maxilla, N-nasal, PF-prefrontal, PMX-premaxilla. Scale bar equals 5cm.

Nasal. In SMU 72316 (Fig 2.6) and SMU 74087 partial nasals are preserved contacting the premaxilla and anterior portions of the maxilla. The nasals are thin bones that are roughly
triangular, domed, and have a slight midline depression as in most ornithopods. The anterior end is embayed by the narial opening with medial and lateral anterior projections overlapped by the dorsal and lateral premaxillary processes. The anterior portion of the nasals form the dorsal and posterior corner of the narial opening. The dorsal processes of the premaxillae divide the anterior portion of the nasals and slightly overlap the medial portion of the nasals which is the condition present in *Hypsilophodon foxii* (Galton 1974), but absent in *Haya griva* (Makovicky et al., 2011) and *Jeholosaurus shangyuanensis* (Barrett and Han, 2009). The nasals come into medial contact posterior to separation by the dorsal premaxillary processes at one third to one half of their length. The nasals broaden posteriorly then taper to rounded or slightly pointed ends that lap onto the frontals. A slight notch separates the posterior ends of the nasals. The anterior frontals thin dramatically toward their contact with the nasals, well anterior to the posterior notch for the prefrontals. The posterolateral surface of the nasal is overlapped by the prefrontal. Foramina in the nasals are lacking as in *Hypsilophodon foxii* (Galton, 1974) and *Parksosaurus warreni* (Galton, 1973) whereas foramina are present in *Haya griva* (Makovicky et al., 2011), *Jeholosaurus shangyuanensis* (Barrett & Han, 2009), and *Thescelosaurus neglectus* (Boyd, 2014).

**Parietal.** Partial parietals are preserved in the type specimen (SMU 72834, (Fig 2.7) and in SMU 70456. The type specimen contains portions of the parietals which reveal lateral surfaces that are anteroposteriorly concave and transversely thin. In dorsal view the parietals slightly overlap the frontals. The medial process of the parietal contacts and is slightly overlapped by the frontals. A ridge is present on each parietal beginning at about the midpoint of the anterior edge. These ridges curve and converge posteriorly at the midline, following the lateral outline of the parietals, to form a weak crest. The anterolateral corners bear strong sutural ridges where they
articulate with the frontals and postorbitals. The parietals are completely fused and posteriorly enclose the dorsal surface of the supraoccipital.

Fig 2.7. SMU 72834 partial cranium. (A) SMU 72834, posterior cranium in right lateral view. (B) SMU 72834, posterior cranium in posterior view. (C) SMU 72834, posterior cranium in dorsal view. (D) Outline drawing of dorsal view of SMU 72834. Abbreviations: BSP proc-basipterygoid process, F-frontal, P-parietal, PO-postorbital, SO-supraorbital, SQ-squamosal, Q-quadrate. Scale bar equals 5cm.

**Frontal.** The frontals are anteroposteriorly longer than they are wide and form the majority of the dorsal margin of the orbits as seen in basal ornithopods *Hypsilophodon foxii*
(Galton, 1974) and *Parksosaurus warreni* (Galton, 1973). The frontals are arched over the orbit and the orbital margins are rugose as is noted in *Haya griva* (Makovicky et al., 2011) and *Zephyrosaurus schaffi* (Sues, 1980). The anterolateral surface of SMU 72834 (Fig 2.7), SMU 70456, and SMU 74087 contain a deep notch where the frontal articulates with the prefrontal. The posterolateral corner contains a groove that extends ventrolaterally where it articulates with the postorbital in a series of pronounced interlocking projections.

The posterior end of the frontal curves slightly downward and articulates with the parietals, forming a triple junction between the frontal, postorbital, and parietal. The suture between the parietals and frontals is straight with the posterior end of the frontals projecting a slight bump into the parietals. The ventral surface contains a concave hour glass shape depression, which becomes wider and deeper in the posterior end. This is outlined by ridges created by the ventrolateral concavities of the orbits. The maximum thickness of the frontals varies amongst specimens. Measured at the posterior limit of the orbit, the thickness of the frontals ranges from 3.5mm (maximum width across the frontals 22.3mm) to 17.3mm (maximum width across the frontals 59.7mm) with an average of 10.7mm amongst 10 specimens. This could possibly be a result of ontogenetic stage or could be a sexually dimorphic feature.

**Jugal.** The jugals are poorly preserved in four specimens, mostly preserving only the anterior portion. The concave dorsal margin of the jugal forms the ventral margin of the orbit. It does not possess a pronounced jugal boss or ornamentation; however, SMU 74749 has several small foramina concentrated along lateral portions of the jugal (Fig 2.6). The maxilla and lacrimal exclude the anterior process of the jugal from the antorbital fenestra in SMU 74749 as is seen in *Hypsilophodon foxii* (Galton, 1974). The anterior process of the jugal inserts into the maxilla, but the anterodorsal tip of the jugal barely contacts the posterodorsal corner of the
lacrimal. Medially the surface of the jugal is smooth. The posterior end rises dorsally and the posterodorsal end contacts the posteroventral edge of the postorbital forming an elongate scarf joint. The jugal flares dorsoventrally toward the posterior, joining the quadratojugal to broadly contact the quadrate.

*Quadratojugal.* SMU 71631 and SMU 74678 (Fig 2.8) represent the most pristine quadratojugals of the Proctor Lake sample. SMU 71631 is not articulated within a skull limiting its descriptive value, but it does appear to maintain its original contact with a partial jugal. SMU 74678 is articulated within a partial skull. The quadratojugal is subtriangular in lateral view and ‘plate-like’. The posterior end of the jugal significantly overlaps the anterior margin of the quadratojugal. A foramen pierces the center of the quadratojugal. Little can be determined from this specimen about the contribution of the quadratojugal to the infratemporal fenestra as the quadrate appears to have shifted. The contact between the quadratojugal and quadrate is preserved in SMU 74678 and quadrates preserved in SMU 75379 and SMU 74087 have concave anterolateral surfaces, which indicate the quadratojugal overlapped a significant portion of the quadrate shaft. A similar contact is seen in *Jeholosaurus shangyuanensis* (Barret and Han, 2009), *Orodromeus makelai* (Scheetz, 1999), *Changchunsaurus parvus* (Jin et al., 2010), and *Parksosaurus warreni* (Galton, 1973), but differs from *Hypsilophodon foxii* (Galton, 1974) in which it does not extensively overlap the quadrate shaft.

*Quadrate.* Two specimens contain complete quadrates; however, they are semi-articulated and some contact surfaces are obscured. The quadrate consists of a vertical columnar shaft that bows anteriorly and has two thin sheets of bone extending anteriorly and anteromedially. The anterolaterally extending sheet is the moderately developed jugal wing, which begins a short distance below the dorsal head of the quadrate and extends to its ventral
end. The quadratojugal significantly overlaps the lower quadrate. The pterygoid wing extends anteromedially beginning from the dorsal head of the quadrate. The sheet expands medially but then begins to taper ventrally ending well above the distal condyles of the quadrate. The pterygoid wing is extensively overlapped by the pterygoid in SMU 72834. The lower third of the quadrate shaft is mediolaterally compressed and ends with equal distal condyles. The upper portion of the quadrate shaft is mediolaterally compressed with the head of the quadrate extending posterodorsally between the prequadrate and postquadrate processes of the squamosal.

Fig 2.8. SMU 74678 cranium. (A) SMU 74678, posterior skull in right lateral view. This specimen contains two supraorbitals which are not fused to the frontal. (B) Outline drawing of right side of SMU 74678 posterior skull. Abbreviations: F-frontal, J-jugal, L-lacrimal, N-nasal, P-parietal, PF-prefrontal, PO-postorbital, Q-quadrate, QJ- quadratojugal, SOB-supraorbital, SQ-squamosal. Scale bar equals 5cm.
Squamosal. A partial right squamosal is preserved in the type specimen SMU 72834 (Fig 2.7) and in SMU 74678 (Fig 2.8). The main body of the squamosal forms the posterolateral margin of the supratemporal fenestra. Four processes then extend from the main portion, although only three are complete enough to describe. The postorbital process extends anteriorly; however, the anterior end is incomplete. Its dorsal surface contacts the ventral surface of the postorbital forming the dorsal margin of the infratemporal fenestra. Two processes extend from the dorsolateral corner of the main body: the prequadratic and postquadratic processes. In posterior view the postquadratic process forms a subtriangular tab that extends towards the lateral surface of the skull. It then contacts the posterior end of the quadrate head. The prequadratic process contacts the anterodorsal margin of the quadrate and extends anteroventrally.

Lacrimal. Two partial lacrimals are represented in SMU 74749 (Fig 2.6) and SMU 74678 (Fig 2.8). Both demonstrate the lacrimal excluding the premaxilla from the antorbital fenestra, forming the posterodorsal and dorsal margins. The posterior edge of the lacrimal forms part of the anterior margin of the orbit. The lateral surface is convex and is dorsal to both the jugal and maxilla similar to the condition in Hypsilophodon foxii (Galton, 1974). The tip of the posteroventral process of the lacrimal barely contacts the anterior tip of the jugal. The posterodorsal corner of the lacrimal fits into the anteroventral corner of the prefrontal. The dorsal surface of the lacrimal contacts the ventral surface of the nasals.

Prefrontal. The prefrontal is preserved in SMU 74678 (Fig 2.8), forming the anterodorsal corner of the orbit. Its posterovoventral surface articulates with a well-defined fossa on the frontal and its anterior portion overlaps the nasal. The anteroventral corner contacts the lacrimal. Its
dorsal surface is slightly convex and the lateral surface is slightly concave. The thick anterior corner contains suture ridges forming an articulation surface for the supraorbital.

**Supraorbital.** Four specimens contain partial supraorbitals; however, SMU 74678 (Fig 2.8) is the only specimen that preserves two supraorbitals or palpebrals, the second being much shorter and located at the posterodorsal corner of the orbit. The supraorbitals are free of the orbital margin and project across a significant portion of the orbit, as seen in *Agilisaurus louderbacki* (Peng, 1992) and *Thescelosaurus neglectus* (Boyd, 2014). It is a slender rod that is slightly wider than it is tall with a sharp lateral edge. The anterior end expands mediolaterally and its anteromedial surface articulates with the prefrontal. The supraorbital then tapers posteriorly ending in a subtriangular point at the posterior end of the orbit.

The accessory supraorbital is approximately half the length of the primary supraorbital. It is proportionally larger than the accessory supraorbital seen in *Agilisaurus louderbacki* (Peng, 1992), but is similar in proportion to the condition in *Thescelosaurus neglectus* (Boyd, 2014). It tapers anteriorly along its entire length, ending in a rounded point. The dorsal surface is slightly concave towards the anterior end, possibly serving as an articulation surface for the primary supraorbital. The ventral surface is slightly concave. Its lateral surface is a sharp edge similar to the primary supraorbital whereas the medial surface is fairly flat. The accessory supraorbital is disarticulated in SMU 74678, thus the exact articulation is unknown. Its anterior end likely contacted the posterior end of the primary supraorbital and then articulated with the posterior margin of postorbital.

**Postorbital.** The anterior of the postorbital forms the posterodorsal corner of the orbit as it articulates with the posterolateral corner of the frontal (Fig 2.7). The orbital margin is smooth unlike the orbital margin formed by the frontals. The anterodorsal corner of the postorbital
articulates to the frontal and parietal forming a triple junction consisting of pronounced
terlocking projections as in *Hypsilophodon foxii* (Galton, 1974), *Zephyrosaurus schaffi* (Sues
1980), and *Orodromeus makelai* (Scheetz, 1999). The postorbital splits into two distinct
processes directed ventrally and posteriorly that occur in the same plane. The ventral process
tapers to a point and is anteriorly concave forming part of the anterodorsal margin of the
infratemporal fenestra. This ventral process contacts the posterodorsal surface of the jugal
forming the anterior margin of the infratemporal fenestra. The relatively thin posterior process of
the postorbital also tapers to a point and is dorsoventrally concave forming the anterolateral
margin of the supratemporal fenestra. This is overlapped onto the squamosal, but the contact is
not well preserved in the specimens being described.

The medial surface of the postorbital has a continuation of the ridge from the frontals and
a ridge that continues from the parietals. These two ridges run dorsoventrally and meet at the
ventral process forming a more prominent ridge. This creates a synovial socket just ventral to the
junction of the ridges where the head of the laterosphenoid articulated. This socket extends onto
parts of the parietal and frontal as it occurs at the triple junction of these bones as is common for
small ornithopods.

*Pterygoid.* The type specimen (SMU 72834) contains the dorsal portion of the right
pterygoid (Fig 2.7). It comprises a thin sheet that overlaps the pterygoid process of the quadrate
and angles medially. The medial margin is concave and articulates with the posterolateral margin
of the basipterygoid process of the basisphenoid.

*Supraoccipital.* The base of the supraoccipital forms part of the dorsal boundary of the
foramen magnum, but it is restricted by the medial process of the exoccipital. The posterior
surface is triangular and narrows dorsally as it is wedged between the parietal wings. In SMU
72834, the anterodorsal end of the supraoccipital is straight rather than pointed (Fig 2.9). The posterior surface contains a median ridge that runs the entire length of the surface as seen in other basal ornithischians such as *Hypsilophodon foxii* (Galton, 1974). The supraoccipital sweeps anteriorly under the parietal wings where it likely contacts the laterosphenoid; however, this contact is not present in SMU 72834 as the laterosphenoid is missing. The opisthotic is sutured to the posterolateral corner of the supraoccipital with a wide square contact. The prootic is sutured along the arched ventral edge of the supraoccipital. This sutural junction is excavated medially to form the fossa subarcuata which housed the floccular lobes of the cerebellum (Galton, 1974).
**Fig 2.9.** Occipital region of SMU 72834. (A) SMU 72834, occipital region in ventral view. (B) Outline drawing of SMU 72834, occipital region in ventral view. Abbreviations: BO-basioccipital, EO-exoccipital, OP-opisthotic, P-parietal, SO-supraoccipital. Scale bar equals 5cm.

*Exoccipital and Opisthotic.* The exoccipital forms the ventrolateral border of the foramen magnum and its medial surface forms part of the occipital condyle. Its ventral surface is then strongly sutured to the basioccipital. The opisthotic forms the lateral wall of the foramen magnum. Most of the anterior surface of the opisthotic is sutured to the supraoccipital and its median anterior corner is sutured to the prootic. The ventral surface of the opisthotic is strongly sutured to the basioccipital. The fenestra ovalis, middle ear cavity, internal auditory meatus, and the jugular foramen are situated between the junction with the opisthotic, prootic, and basioccipital. The lateral extent and paroccipital process of the opisthotic fused with the
exoccipital is incomplete in SMU 72834. SMU 71695 and SMU 71504 contain distal portions of the paroccipital process revealing a laterally compressed bone that curves ventrally and is pendent shaped.

*Basioccipital.* The dorsal surface of the basioccipital forms the posteroventral floor of the braincase. The exoccipital and opisthotic are sutured to its dorsal surface at the posterolateral corners. The basioccipital forms most of the occipital condyle with a bulbous smooth articular surface posteriorly. A ventral keel extends along the ventral midline, which branches in the posterior half to create a large foramen that penetrates dorsally into the basioccipital; however, it does not appear to penetrate the floor of the braincase. In ventral view the anterior end of the basioccipital forms a ‘V-shape’ which creates an anterolateral contact surface with the basisphenoid. This distinguishes it from *Hypsilophodon foxii* (Galton, 1974) whose basioccipital and basisphenoid are fused.

*Prootic.* The type specimen (SMU 72834) contains distal portions of the right prootic, which forms part of the lateral wall of the braincase. The dorsal surface is dorsoventrally convex and articulates posteriorly with the supraoccipital. The posterior end of the prootic tapers to a subtriangular process and is sutured to the opisthotic. Ventrally it is sutured to the basioccipital posteriorly and to the basisphenoid anteriorly. The fenestra ovalis is situated between the junction of the prootic, opisthotic, and basioccipital. Dorsomedially near the suture with the supraoccipital the shallow fossa subarcuata is preserved. The prootic likely contacted the laterosphenoid; however, this is not preserved in the available specimens.

*Basisphenoid.* Only the type specimen (SMU 72834) contains portions of the basisphenoid. This includes two small pieces revealing the posterodorsal region of the basisphenoid, which articulates with the posterior surface of the prootic and the anterior margin
of the basioccipital. These two pieces are concave in lateral view, but little else can be described. A separate piece contains portions of the right basipterygoid process of the basisphenoid, which articulates with the pterygoid. The piece is triangular in cross section and its dorsal surface is concave. The anterior surface are slightly convex and the posteroventral surface reveals two bifurcating ridges that form a subtriangular depression.

*Predentary.* A well preserved predentary is articulated in SMU 70444. The length of the predentary is approximately the same length as the premaxilla. The oral margin is smooth. The predentary has posterolateral processes and a posteroventral process. Together they form the articulation surface for the dentary creating a ‘u-shaped’ sulcus. The posterolateral process extends laterally fitting into the anterodorsal margin of the dentary. The posteroventral process runs connects to the ventral surface of the predentaries and extends farther than the posterolateral processes. The single posteroventral process is not bifurcated. The lateral surface of the predentary contains one prominent foramen and four smaller foramina which are concentrated toward the anterior margin. A shallow groove extends posteriorly beginning near the anterior tip and runs along the lateral surface through the lateral foramen. This groove ends near the posterolateral process. A similar groove is present in *Hypsilophodon foxii* (Galton, 1974) and *Thescelosaurus neglectus* (Boyd, 2014), but in the Proctor Lake ornithopod is not as prominent as the groove present in *Changchunsaurus parvus* (Jin et al., 2010) and *Jeholosaurus shangyuanensis* (Barret & Han, 2009). In ventral view the anterior end of the predentary is rounded distinguishing it from neornithischians *Jeholosaurus shangyuanensis* (Barret & Han, 2009), *Thescelosaurus neglectus* (Boyd, 2014), *Changchunsaurus parvus* (Jin et al., 2010), and *Hypsilophodon foxii* (Galton, 1974) who all display sharply pointed anterior ends.
**Dentary:** The right dentary on the type specimen (SMU 72834) contains 7 teeth (Fig 2.5), but based on spacing could accommodate up to 10 teeth. The tooth row of SMU 70444 measures 39mm and contains 8 dentary teeth, whereas the dentary of SMU 74087 measures 52mm and contains 11 tooth positions, indicating ontogenetic variation in tooth count. A lateral ridge begins at the anterior end of the dentary and becomes more pronounced as it continues posteriorly. Alveoli occur dorsal to the lateral ridge and become moderately inset posteriorly as the lateral ridge becomes more prominent. The most anterior alveoli are smaller and begin directly posterior to the contact with the predentary. A row of replacement foramina lies ventral to the tooth row on the lateral surface of the dentary.

In dorsal and ventral view, the rostral portion of the dentaries turn medially, converging to form a spout-shaped symphysis. The anterior end of the dentary tapers into a rugose process with three foramina that inserts into the predentary. Beginning anteriorly at the predentary articular surface the, Meckelian groove runs along the ventromedial margin of the dentary. The groove widens and deepens as it continues posteriorly to become covered by the splenial. The posterodorsal margin of the dentary forms the anterior portion of the coronoid process. This process rises dorsally and curves posteriorly. The posterior end of the tooth row in SMU 70444 and SMU 72834 is medial to the coronoid process. The posterior margin of the dentary contacts the surangular and the coronoid contacts the dentary medially.

**Splenial.** The splenial is visible in the type specimen SMU 72834 and forms the anteromedial section of the mandible. The ventral margin is anteroposteriorly convex. The splenial tapers both anteriorly and posteriorly forming subtriangular shaped ends. The anterior margin is medial to the dentary and the posterior margin is positioned medial to the angular.
Angular. The angular is a thin sheet that in lateral view comprises the posteroventral portion of the mandible. The ventral margin is anteroposteriorly convex. The anterior limit is positioned medial to the dentary and is overlapped medially by the splenial. The posterior margin of the angular is overlapped by the surangular. The contact with the articular and prearticular are obscured.

Surangular: None of the specimens contain a complete surangular but several key features are preserved. The anterior margin of the surangular contacts the dentary. The ventral margin contacts the angular. A foramen is present on the lateral surface at the contact between the surangular and dentary. The posteroventral portion of the surangular tapers ventrally, but upturns dorsally at its termination to form the retroarticular process. This process bears a foramen on the posterolateral surface in SMU 75379 and SMU 71510.

Premaxillary dentition. Four premaxillary teeth are preserved in each premaxilla of SMU 70444, SMU 74087, SMU 72316 (Fig 2.4), and SMU 75380. The anterior posterior tooth row length of the smallest of these premaxilla, SMU 75380, measures 11mm, and the largest, SMU 72316, measures 25mm. The specimens are fragmentary, but the tooth count is clearly four despite their varying size and presumably ontogenetic stage. The presence of four premaxillary teeth distinguishes this taxon from other basal ornithischians. The crown of the premaxillary teeth are mediolaterally compressed and the pointed crown recurves posteriorly. The anterior and posterior edges of the crown bear denticles similar to Hypsilophodon foxii (Galton, 1974). The denticles extend farther toward the base of the crown on the posterior edge that the anterior. The denticles are weaker or absent on the anterior edge. Buccal and lingual surfaces of the crown are evenly enameled and ornamented with fine ridges similar to Hypsilophodon foxii (Galton, 1974) and Thescelosaurus neglectus (Boyd, 2014). The buccal surface of the crown possesses a
shallow groove that runs toward the base, separating the tooth surface into two lobes. This feature is unique to the Proctor Lake taxon. The bases of the premaxillary teeth are slightly constricted and the roots are circular in cross section.

Maxillary dentition. The tooth row length of SMU 74749 measures 38mm and contains 8 maxillary tooth positions. The tooth row length of type specimen (SMU 72834), SMU 70635, SMU 72316 measure 87mm, 59mm, and 60mm respectively and each bear 10 maxillary tooth positions which are inset medially. The tooth count clearly varies with ontogenetic stage as SMU 74749 is significantly smaller compared to the other two specimens. The maxillary teeth are slightly obliquely aligned with the anterior tooth slightly overlapping onto the buccal surface of its posterior neighbor. The maxillary crowns are laterally compressed, forming a spade-like shape with denticulate margins (Fig 2.10). The apex of the maxillary crown is distinctly asymmetric in buccal view with the apex being offset posteriorly. Enamel is primarily restricted to the buccal side of the maxillary crown. Numerous ridges are present on the enameled buccal surface which are confluent with the denticles and extend to the base of the crown. These ridges are of equal prominence. Margins of the maxillary crown contain up to 17 denticles, but have only 6-7 ridges, thus the number of ridges varies and not all denticles are supported by ridges. The maxillary crown tapers to the root where its base swells slightly forming a cingulum. Maxillary tooth roots are curved medially in anteroposterior view distinguishing the Proctor Lake ornithopod from Hypsilophodon foxii (Galton, 1974).

Dentary dentition. Five specimens contain in situ dentary teeth, thus the exact number and variation of the dentary teeth within the dentary is unknown. The type specimen SMU 72834 contains 7 teeth, but based on spacing could have held up to 11. The right dentary of SMU 74087 measures 52.2mm in length and contains in situ teeth, tooth roots, and aveoli suggesting 11 teeth.
were present. A smaller and presumably younger individual, SMU 70444, contain 8 teeth with the tooth row measuring 39mm, again showing variance in tooth count due to ontogenetic stage. The dentary crowns are similar in morphology to the maxillary teeth as they are laterally compressed with a spade-like shape, denticulate margins, and a cingulum at the base of the crown (Fig 2.10). However, in dentary teeth the enamel and ridges are restricted to the lingual side of the tooth, which contains a prominent apical ridge that runs down the center of the crown toward the base. Six or seven secondary ridges extend from the margins of the crown to its base; however, as in the maxillary teeth there are fewer ridges than denticles present on the crown, similar to *Hypsilophodon foxii* (Galton, 1974). Margins of the dentary crown contain up to 14 denticles. The dentary crowns are symmetrical with the apex occurring at the center of the crown. The roots of the dentary teeth are also curved medially in anteroposterior view.

![Fig 2.10. SMU 72316 Maxillary and dentary teeth. (A) SMU 72316, maxillary tooth lateral view. (B) SMU 72316, maxillary tooth medial view. (C) SMU 72316, dentary tooth medial view. (D). SMU 72316, dentary tooth lateral view. Scale bar equals 1cm.](image)
2.4 Postcranial Description

*Proatlas and Atlas.* The type specimen (SMU 72384) may preserve the proatlas and atlas; however, if present they are obscured from view and cannot be examined as further mechanical preparation would lead to destruction of the type skull.

*Axis.* SMU 75621-1(Fig 2.11) and the type specimen (SMU 72834) reveal a centrum that is longer than it is wide and is ventrolaterally concave with a moderate keel on its ventral surface. Anteriorly an oval intercentrum is present and a shallow depression is present posteriorly. The dorsal surface of the neural arch is laterally compressed forming a well-developed neural spine. The neural arch is exaggerated in the axis, extending posterodorsally over the third cervical vertebra. This extension contains well-developed postzygapophyses, which articulate with the prezygapophyses of the third cervical vertebra. The prezygapophyses of the axis are less developed, but articulate with the atlas. The diapophysis is small and occurs along the suture between the centrum and neural arch. The parapophysis is absent or not preserved in the available specimens.
Fig 2.11. SMU 75621-1 axis and third cervical vertebra. Axis and third cervical vertebrae in left lateral view. Scale bar equals 1cm.

*Fig 2.11. SMU 75621-1 axis and third cervical vertebra. Axis and third cervical vertebrae in left lateral view. Scale bar equals 1cm.*

*Cervical Vertebrae.* The type specimen (SMU 72834) contains 9 cervical vertebrae (including the atlas and axis) although the atlas is obscured by the skull (Fig 2.12). The cervical centra are opisthocoelus with an oval anterior face and D-shaped posterior face. The ventral surface of the centra are strongly concave with a sharp ventral keel that broadens to a T-shape in progressively posterior cervical vertebrae. The neurocentral suture is visible in all the cervical vertebrae. It intersects the paraphysis on the anterolateral surface. Beginning with the axis, the
diapophyses progressively increase in lateral length and migrate anterodorsally along the prezygapophyses.

The neural spine in post-axial cervical vertebrae rises on the posterior end of the dorsal surface slightly anterior of the postzygapophyses. The spines become progressively taller and more pronounced in succeeding vertebrae with the sharp anterior edge migrating anteriorly. The prezygapophyses on anterior cervicals are short paddle shaped extensions with a broad articular surface, but become progressively smaller and more spike shaped along the cervical column. The postzygapophyses that can be observed are larger than the prezygapophyses. The zygapophyses rise and become larger posteriorly. The dorsal surface of the centra is relatively flat, but becomes increasingly excavated in posterior vertebrae as the neural spine and zygapophyses increase in size. The four cervical ribs preserved in SMU 74749 show progressively longer ribs proceeding posteriorly.
Fig 2.12. SMU 72834 cervical vertebrae. (A) Dorsal view of cervical vertebrae 4-9. (B) Left lateral view of cervical vertebrae 4-9. (C) Ventral view of cervical vertebrae 4-9. Abbreviations: d-diapophysis, ns-neural spine, p-parapophysis, prz-prezygapophyses, poz-postzygapophyses. Scale bar equals 5cm.
Dorsal Vertebrae. The type specimen (SMU 72834) preserves 15 dorsal vertebrae. SMU 72316 contains 8 articulated dorsal vertebrae representing the posterior dorsal vertebrae as they articulate to the sacrum (Fig 2.13). SMU 70456 contains 11 articulated dorsal vertebrae with associated ribs although several anterior vertebrae are missing. The ventral surface of the most anterior centra are sharply keeled with ventrolaterally concave surfaces. Posteriorly the keel diminishes becoming a smooth rounded surface. The centra become medially wider and more robust posteriorly (Table 2.1). The anterior faces of the first eight centra are smaller than the posterior faces and are taller than they are wide. The anterior faces of the centra become progressively wider in succeeding vertebrae until the last dorsal vertebra which has equally sized anterior and posterior faces. The dorsal centra are amphicoelous and contain muscle insertion scars along the edges of the anterior and posterior margins, especially along the ventral surface. From anterior to posterior the dorsal ribs become progressively shorter.

Sacral Vertebrae. The type specimen (SMU 72834), SMU 72316, and SMU 70456 contain articulated sacra. SMU 72316 has the best-preserved sacrum, including 6 sacral vertebrae in articulation with dorsal and caudal vertebrae (Fig 2.14). The first two sacral centra are fused; however, the remaining four are separate. The posterior end of centrum 6 is slightly expanded and is concave receiving the anterior end of the first caudal vertebra. The sacral neural spines are greater than twice the height of the sacral centra distinguishing this taxon from Hypsilophodon foxii (Galton, 1974).
Fig 2.13. SMU 72316 dorsal vertebrae. (A) Left lateral view of 7 posterior most dorsal vertebrae. (B) Ventral view of 7 posterior most dorsal vertebrae. Scale bar equals 3cm.
<table>
<thead>
<tr>
<th>Element</th>
<th>SMU 72834</th>
<th>SMU 72316</th>
<th>SMU 70534</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cervical 4- Centrum L x W</td>
<td>41 x 35</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Cervical 7- Centrum L x W</td>
<td>38 x 33</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Dorsal 10- Centrum L x W</td>
<td>38 x 36</td>
<td>31 x 26</td>
<td>—</td>
</tr>
<tr>
<td>Sacrum- L</td>
<td>228</td>
<td>158</td>
<td>—</td>
</tr>
<tr>
<td>Caudal 1- Centrum L x W</td>
<td>33 x 35</td>
<td>27 x 30</td>
<td>—</td>
</tr>
<tr>
<td>Caudal 10- Centrum L x W</td>
<td>48 x 37</td>
<td>41 x 32</td>
<td>—</td>
</tr>
<tr>
<td>Caudal 20- Centrum L x W</td>
<td>—</td>
<td>42 x 18</td>
<td>—</td>
</tr>
<tr>
<td>Caudal 30- Centrum L x W</td>
<td>—</td>
<td>36 x 14</td>
<td>—</td>
</tr>
<tr>
<td>Scapula- L</td>
<td>239 (rt)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Coracoid- Ht. (dor./vent.) x W (pr)</td>
<td>88 x 71 (rt)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Humerus- L x prox. W</td>
<td>221 x 63 (lt)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Ulna- L</td>
<td>182 (lt)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Radius- L</td>
<td>169 (lt)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Femur- L x prox. W x dist. W</td>
<td>316* x 70 x 85 (rt)</td>
<td>282* x — x 76.5 (lt)</td>
<td>—</td>
</tr>
<tr>
<td>Tibia- L x prox. W x dist. W</td>
<td>362* x 94 x — (lt)</td>
<td>314* x 80.4 x — (lt)</td>
<td>345 x 68 x 94 (lt)</td>
</tr>
<tr>
<td>Fibula- L</td>
<td>—</td>
<td>—</td>
<td>301 (lt)</td>
</tr>
<tr>
<td>Metatarsal I- L</td>
<td>—</td>
<td>—</td>
<td>72 (lt)</td>
</tr>
<tr>
<td>Metatarsal II- L</td>
<td>—</td>
<td>—</td>
<td>121</td>
</tr>
<tr>
<td>Metatarsal III- L</td>
<td>—</td>
<td>—</td>
<td>143</td>
</tr>
<tr>
<td>Metatarsal IV- L</td>
<td>—</td>
<td>—</td>
<td>112</td>
</tr>
<tr>
<td>Metatarsal V- L</td>
<td>—</td>
<td>—</td>
<td>52</td>
</tr>
</tbody>
</table>

* Estimated

Table 2.1. Skeletal measurements of C. marri, sp. nov. (in mm). Left and right are indicated along with estimated position of the vertebrae.
Caudal Vertebrae. A nearly complete caudal series is preserved in SMU 72316, containing 43 articulated vertebrae. The type specimen (SMU 72834) preserves a partial caudal series, containing 23 caudal vertebrae. Proceeding posteriorly the height and width of the centra decrease as their length increases (Fig 2.15; Table 2.1). This trend gradually occurs in caudal
vertebrae 1-30 at which point the length of the vertebrae begins to decrease at the most distal portions of the caudal series. Anterior centra are ventrolaterally concave; however, this becomes less prominent in succeeding posterior centra, creating a transition from rounded ventral surfaces to more flat ventral surfaces by caudal vertebra 10.

Fig 2.15. Caudal vertebrae. (A) SMU 70456, proximal caudal vertebra in left lateral view. (B) SMU 72316, distal caudal vertebrae (#32-34) in left lateral view. Scale bar equals 3cm.
Caudal vertebra 10 is the first in the series without caudal ribs. The transverse processes attach at the neurocentral suture and are fused in SMU 72316. The length of the transverse processes of the anterior caudals are approximately equal to the height of the neural spine. The longest caudal rib is found on caudal vertebra 5. The longest caudal ribs preserved are slightly longer than the width of the centra. The first caudal rib sweeps posteriorly, but proceeding ribs extend straight laterally. The prezygapophyses become progressively thinner in posterior vertebrae, but maintain approximately constant length.

The neural spines of the first 9 caudal vertebrae are situated on the posterior half of the centra and slightly recline posteriorly or are nearly vertical. They slightly increase in height from caudals 1-9, but all of them are greater than 1.5 times the height of their respective proximal caudal centra. Posterior to caudal vertebra 9 the neural spines decrease in height and become progressively wider at their base. Caudal vertebra 29 contains the most posterior preserved neural spine although it seems likely that neural spines were present, but not preserved in more posterior vertebra. Although the caudal series is not complete in SMU 72316, *C. marri* probably did not contain an elongate tail with more than 59 caudal vertebrae given the size and morphology of the last preserved caudal vertebra in the series, distinguishing it from *Tenontosaurus* (Winkler et al. 1997). The chevrons are round in cross section and taper to a point. Articulated chevrons present in caudals 8-26 become progressively shorter. The shaft of the chevrons become laterally compressed and oval in cross section. The distal portion of the chevrons becomes expanded in lateral view and wider than the proximal articular surface.

**Ossified tendons.** Ossified tendons are preserved in SMU 70456, SMU 72316, SMU 74610, and SMU 74576 (Fig 2.16). This includes tendons along the dorsal, sacral and caudal sections of the vertebral column. Preserved tendons in the dorsal section are prominently
displayed in SMU 70456. Individual tendons extend the length of two dorsal vertebrae. The tendons run parallel to each other and not in the rhomboidal lattice-like arrangement present in more derived iguanodonts (Norman, 2004). As many as nine tendons are preserved parallel to one another on one side of a single dorsal vertebrae. Additional tendons may have been lost through preservation and possibly preparation. Tendons preserved in the sacral section have the same arrangement as those in the dorsal section although fewer tendons are visible and are slightly thicker.

Fig 2.16. Ossified tendons in the caudal region. (A) SMU 74670, caudal vertebrae with ossified tendons preserved in right lateral view. (B) Outline drawing of SMU 74670, caudal vertebrae and ossified tendons. (C) SMU 72316, articulated caudal vertebrae (#16-26) with ossified tendons preserved in left lateral view. Abbreviations: ns-neural spine. Scale bar equals 5cm.
SMU 72316 contains ossified tendons in the caudal region. Caudals 9-16 contain parallel paraxial and hypaxial tendons. Three to four parallel tendons occur in this section with individual tendons extending the length of 2 centra. Along caudals 16-43, as many as 8 tendons lie parallel. SMU 74670 contains 5 vertebrae in the range of caudals 10-15 based on vertebral size and morphology. This section preserves as many as 18 tendons running parallel along the length of a single centrum. Epaxial and hypaxial tendons extend from the dorsal surface of the neural spine to the ventral surface of the chevrons.

*Sternal Plates.* No sternal plates have been recovered from the Proctor Lake locality. Due to the phylogenetic distribution of sternal plates that are found in neornithischian taxa the absence of sternal plates probably represents preservational bias rather than the absence of these bones form the Proctor Lake taxon.

*Scapula.* The scapula is slightly longer than the humerus in larger specimens including the type specimen (SMU 72834) where the scapula is 17mm longer than the humerus; however, the scapula and humerus are approximately equal in smaller individuals including SMU 74664 where the humerus and scapula both measure 75mm in length. The scapula is a short, broad, blade shaped element with a length approximately 6 times that of its minimum width. The blade strongly expands distally with a distal width two and half times that of the neck width. The interlocking projections on the articular surface form a tight suture with the coracoid; however, the scapula and coracoid are not fused in any of the specimens. The low, broad scapular spine is less pronounced than the sharp scapular spines found in specimens of *Orodromeus makelai* (Scheetz, 1999) and *Oryctodromeus cubicularis* (Varricchio et al., 2007).

The medial surface of the scapular blade of the type specimen (SMU 72834, Fig 2.17) and a smaller specimen (SMU 71854) contains a shallow depression near the glenoid region that
extends laterally approximately halfway along the scapula. Its edge forms a prominent ridge along the anterior medial surface of the scapula. The dorsal and ventral edges of the scapula are round at the anterior end but become progressively thinner and sharper towards the posterior. The scapular blade becomes progressively thinner distally. The distal end of the scapular blade is expanded posteriorly forming a smooth and thin flaring crescent shaped end.

Coracoid. The coracoid is thicker at the scapular articular surface than more distally (Fig 2.17). The circular coracoid foramen on the lateral surface is located close to the posterior margin. On the medial surface the coracoid foramen is shifted proximally and is oval shaped with a well-marked groove extending onto the scapula. This character has been noted in *Hypsilophodon foxii* (Galton, 1974), but is uncommon in basal ornithischians. In lateral view the coracoid is taller than wide in all specimens. The medial surface is concave; the lateral surface is slightly convex.

Humerus. The Proctor Lake taxon humerus is similar to other basal ornithischians. The best preserved humerus (SMU 75564) is from a larger sized individual measuring 175mm (Fig 2.17) as preserved specimens range from 67-221mm. The distal shaft of the humerus is straight and circular in cross section. In lateral view the dorsal half of the humerus curves posteriorly beginning at the deltopectoral crest. The deltopectoral crest has a prominent groove running dorsoventrally along the anterior surface. The coronoid fossa is wider and more pronounced than the olecranon fossa. The medial condyle is round in ventral view and the lateral condyle is slightly larger with a tapered extension on the anterolateral corner.
Fig 2.17. SMU 72834 scapula and coracoid. SMU 75564 humerus. (A) SMU 72834, right scapula in lateral view. (B) SMU 72834, right scapula in medial view. (C) SMU 72834, right scapula in dorsal view. (D) SMU 72834, right coracoid in medial view. (E) SMU 72834, right
coracoid in lateral view. (F) SMU 75564, right humerus in posterior view. (G) SMU 75564, right humerus in lateral view. (H) SMU 75564, right humerus in medial view. Abbreviations: cofo-coracoid foramen, sc spine-scapular spine, delt-p.c.-delta pectoral crest, fos-fossa, r. cond.-radius condyle, u cond.-ulna condyle. Scale bar equals 5 cm.

Twelve complete or nearly complete humeri of range from 67mm to 221mm in length and presumably represent different ontogenetic ages allowing for a close inspection of ontogenetic change. The head of the humerus is more bulbous in larger individuals. The distal shaft of the humerus of smaller specimens is more oval in cross section becoming circular in larger individuals. The shafts are more twisted in larger individuals. A fossa is present on the medial surface of SMU 75564 opposite the deltapectoral crest. A shallow fossa is present on the larger type specimen (SMU 72834) as well, but is not as clearly defined.

_Ulna_. The ulna is longer than the radius and the shaft is slightly bowed and medially concave. The cross-sectional shape of the shaft is oval. The lateral surface is round, but the medial surface is significantly flatter, especially the proximal and distal ends. The olecranon process is moderately developed with a concave radial articular surface on its proximolateral surface. The proximal end is triangular with the lateral half being larger than the medial half due to the presence of the olecranon process. The distal end of the ulna is slightly expanded and crescentic shaped.

_Radius_. The radius is approximately 90% the length of the ulna (Table 2.1). The proximal end is oval with a slightly concave articular surface for the humerus. The distal end is rounded with a smaller maximum diameter than the proximal end. Distinct ridges along the distal shaft impart a rounded “D” shape to the distal condyle. This differs from the flattened distal radius observed in _Tenontosaurus_ (Winkler et al., 1997).
Carpals. SMU 70456 contains a complete left manus articulated to the radius and ulna; however, the carpels are damaged weathering limiting their description (Fig 2.18). A small round carpal is present distal to the ulnare. The ulnare is larger than the radiale and intermedium; however, descriptions on the exact shape cannot be given based on the available material.

Metacarpals. The articulated left manus of SMU 70456 contains 5 metacarpals with metacarpal III being the longest (Fig 2.18). The shape of metacarpals I, II, III, and IV is similar as each have expanded proximal and distal ends with the proximal end being larger. A shallow intercondylar groove is present on the ventral surface of the metacarpals.

Phalanges. The articulated left manus of SMU 70456 preserves a phalangeal formula of 2-3-4-2-1 (Fig 2.18). The unguals of digits I-III are claw like with pointed tips. The ungual of digit IV is significantly reduced. SMU 70254 contains a partial articulated left manus which shows digit III with only 3 phalanges, instead of four. Primitive taxa including Hypsilophodon foxii (Galton, 1974), Orodromeus makelai (Scheetz, 1999), and Thescelosaurus neglectus contain four phalanges on digit III whereas more derived taxa including Tenontosaurus tilleti (Forster, 1990) have three or fewer phalanges on digit III. The correct phalangeal formula for the Proctor Lake taxon, with noted polymorphism for digit III, is 2-3-(3,4)-2-1.
Fig 2.18. SMU 70456 left manus. Left manus (SMU 70456) in dorsal view. Abbreviations: R-radius, U-ulna. Scale bar equals 5 cm.
Ilium. The dorsal edge of the ilium is a uniform thin blade anteriorly, but it thickens posteriorly. The sharp dorsal margin of SMU 70456 is straight, however a smaller partial ilium SMU 77617 (Fig 2.19) shows a sinuous dorsal margin. The pubic peduncle is transversely compressed and is shorter in length than the ischial peduncle. The pubic peduncle curves anteroventrally and tapers distally. The pubic peduncle is triangular in cross sections with a flat posterior surface for the acetabulum. The medial surface of the pubic peduncle contains a concave articular surface where the first sacral rib articulated to the ilium.

The lateral surface of the ilium is slightly concave. The ischial peduncle is robust and rounded forming the posterodorsal margin of the acetabulum. The round lateral boss of the ilium forms part of the synovial contact for the head of the femur. The ilium tapers posterior to the ischial peduncle as the ventral margin migrates dorsally ending with a squared posterior margin. A modest brevis shelf on the ilium extends medially posterior to the ischial peduncle. The anterior process tapers to a thin blade and deflects ventrolaterally. The medial margin is slightly concave with a weak ventral ridge.
Fig 2.19. SMU 77617 left ilium. (A) Left ilium (SMU 77617) in lateral view. (B) Left ilium in medial view. (C) Left ilium in dorsal view. Abbreviations: acet.-acetabulum, ant. proc.- anterior process, isp- ischial peduncle, pp- pubic peduncle. Scale bar equals 5 cm.

*Ischium.* A complete ischium preserved in SMU 74119 shows a flat elongated blade with a proximal region separated by a constricted shaft (Fig 2.20). The iliac peduncle is slightly thicker than the pubic peduncle and curves dorsomedially. The pubic peduncle is flatter and larger than the iliac peduncle expanding anteroventrally with a slightly concave lateral surface. The obturator process falls in the proximal 1/3 of the shaft and curves ventromedially forming a
concave articular surface for the rod-like pubis. In dorsal view the proximal half of the ischium is medially concave and the distal half is straight. The dorsal margin is rounded proximally, but progressively sharpens posteriorly. The ventral margin is sharp to the expanded flat distal surface. The lateral surface of the distal half of the ischium is slightly concave and expands medially. The distal end of the ischium is laterally expanded to form an ischial “foot” with a rounded and rugose posterior end, but not flared as *Tenontosaurus*.

*Pubis.* No complete pubis has been recovered; however, SMU 74679, SMU 74104, SMU 72316, and SMU 75636 contain partial pubes (Fig 2.20). The prepubic process is straight in the smaller individual (SMU 75636), but curves dorsally in the larger specimen SMU 72316 similar to *Tenontosaurus* (Winkler et al., 1997). The prepubic process is laterally compressed anteriorly with a tab-shaped end that extends beyond the distal end of the preacetabular process of the ilium, distinguishing it from *Hypsilophodon foxii* (Galton, 1974). The obturator region of the larger specimens SMU 72834 and SMU 72316 and the smaller SMU 75636 has an open foramen. However, the obturator region in SMU 74104 has a closed foramen. Individual variation in the obturator foramen has been noted in *Hypsilophodon foxii* (Galton, 1974) and *Orodromeus makelai* (Scheetz, 1999). The postpubic process is straight and rod-shaped progressively tapering and becoming laterally compressed distally. The dorsal portion of the main body of the pubis is robust and rounded. The articular surface for the ilium is slightly concave.
**Fig 2.20.** Ischium and pubis. (A) SMU 74119, right ischium in lateral view. (B) SMU 74119, right ischium in medial view. (C) SMU 74119, right ischium in ventral view. (D) SMU 74679, left partial pubis in lateral view. (E) SMU 72316, left partial pubis. (F) SMU 75636, left partial pubis. Abbreviations: ip- iliac peduncle, obt. proc.- obturator process, open fo-open foramen, pp-pubic peduncle, prepubic proc.-prepubic process. Scale bar 5 cm.

**Femur.** Femur length ranges from 51mm to 315mm, capturing a range of ontogenetic size classes. The shaft of the femur is straight and twists slightly in the posterior half such that the lateral surface is more anteriorly facing (Fig 2.21). In lateral view the femur is bowed anteriorly along its length. The lesser trochanter on the anteromedial edge is subtriangular at its dorsal
margin. The greater trochanter is separated from the lesser trochanter by a narrow v-shaped groove. The lateral surface of the greater trochanter is fairly flat, but its dorsal margin is a rounded crest. The head is angled approximately 20 degrees from the transverse plane extending the dorsal margin of the femoral head beyond the greater trochanter. The posterior face of the femoral head is concave with a strong depression running diagonally across its surface to the neck of the femur.

The fourth trochanter is located on the medial margin of the proximal half of the femur. It consists of a triangular blade that extends posteroventrally and has a thick ventral edge that thins posteriorly. The fourth trochanter is larger more prominent in larger specimens. A shallow depression occurs on the medial surface of the femoral shaft posterior to the femoral neck and extending to the base of the fourth trochanter. Galton (1974) identified this as the insertion for the M. caudifemoralis longus. The minimum circumference of the femoral shaft is just distal to the fourth trochanter. The cross section is circular in smaller individuals, but subtriangular in larger individuals. The shaft expands distally towards the condyles. The medial condyle is rounded and more robust than the lateral condyle. The lateral condyle tapers posterolaterally forming a ‘teardrop’ shape in ventral view that extends posteriorly more than the medial condyle. Posteriorly the condyles are separated by a deep intercondylar groove. Anteriorly a shallow distal extensor groove separates the condyles. The extensor groove is more pronounced in larger specimens.
Fig 2.21. Femora. (A) SMU 74665, right femur in posterior view. (B) SMU 74665, right femur in medial view. (C) SMU 74665, right femur in anterior view. (D) SMU 72451, left femur ventral view. (E) SMU 70456, left femur ventral view. Abbreviations: gr. troch.- greater trochanter, lc-lateral condyle, les. troch.- lesser trochanter, mc-medial condyle, 4th troch.- fourth trochanter. Scale bar 5 cm.
Tibia. The tibia in SMU 71836 is approximately equal in length to the femur measuring 100mm compared to the femur measuring 99mm. In larger specimens including SMU 74093 and SMU 74670 the tibia is approximately 15-20% larger than the femur. In all specimens the tibia has a narrower shaft than the femur. In anterior view the shaft of the tibia is sigmoidal as the lateral edge is slightly concave proximally and slightly convex distally. The medial edge is slightly convex proximally and concave distally (Fig 2.22). Proximally the tibia has a dual-lobed lateral condyle and a smaller medial condyle. The anterior condyle of the dual-lobed lateral condyle forms the articulation surface for the fibula, and the posterior condyle forms a slight ridge extending a short distance along the shaft. The small cnemial crest is rounded and extends anterolaterally along the shaft for a short distance.

In cross section the tibia is roughly triangular in shape with rounded corners in the proximal half. The distal half contains a pointed corner created by a sharp lateral edge which begins at the outer malleolus. The posterior surface of the distal end contains attachment and muscle scars as seen in Hypsilophodon foxii (Galton, 1974), Zephyrosaurus schaffi (Sues, 1980), and Orodromeus makelai (Scheetz, 1999). Attachment scars found on the posterior surface of the lateral edge represent the distal articulation surface for the fibula. There is a very shallow ligament groove on the anterior surface of the distal end which forms the articular surface of the ascending process of the astragalus and separates the malleoli. In ventral view the inner malleolus is slightly anteroposteriorly expanded and the outer malleolus is compressed anteroposteriorly and contains a sharp lateral edge.
Fig 2.22. Hind limb. (A) SMU 72316, left hind limb in lateral view. (B) SMU 72316, left hind limb in medial view. (C) SMU 72316, left hind limb in posterior view. (D) SMU 77617, right tibia, fibula, astragalus, calcaneum in lateral view. (E) SMU 77617, right tibia, fibula, astragalus, calcaneum in posterior view. (F) SMU 77617, right tibia, fibula, astragalus, calcaneum in medial view. (G) SMU 77617, right tibia in anterior view. Abbreviations: As- astragalus, Ca-
Calcaneum, cnem. c- cnemial crest, Fem-femur, Fib- fibula, lc-lateral condyle, mc-medial condyle, Tib-tibia, 4th troch.- fourth trochanter. Scale bar 5 cm.

**Fibula.** A thick neck supports the proximal end of the fibula which then tapers distally to a thin fibular shaft. The diameter of the shaft decreases distally which is also marked by a change in cross sectional shape. The shaft of the proximal third of the fibula is D-shaped in cross section with a flat medial surface. This transitions into a circular rod shaped shaft in the middle third of the fibula which transition again into a D-shape in the distal third as the posterior surface becomes flat creating an articulation surface with the outer malleolus of the tibia. The distal end of the fibula has as a swollen bulge with a flat ventral surface that articulates with the calcaneum.

**Astragalus.** Several astragali are preserved; however, the ascending process on the larger specimens is often missing, thus smaller specimens are used in the description. SMU 71690 represents a complete left astragalus. In ventral view the astragalus caps the ventral surface of the medial malleolus of the tibia and small portions of the lateral malleolus. The astragalus then curves and extends dorsally over the anterior surface of the medial malleolus of the tibia. This ascending process of the astragalus extends dorsolaterally ending in a tooth-like projection similar to *Hypsilophodon foxii* (Galton, 1974). On the dorsal surface just below the tooth like projection is a fossa or small notch which is not present in *Hypsilophodon foxii* (Galton, 1974). The medial surface of the astragalus is concave forming the articulation surface with the calcaneum.

**Calcaneum.** SMU 72534 represents a complete calcaneum for this taxon. The posteromedial surface of the calcaneum articulates to the corner and anterior surface of the lateral malleolus of the tibia. The dorsal surface is concave creating a cup which articulates with
the distal end of the fibula. A slight notch is located on the medial surface which articulates with the tooth-like projection of the ascending process of the astragalus. The lateral surface of the calcaneum is also strongly concave. The anterior surface is smooth and convex creating a bulge. The main articulation surface for the astragalus is fairly flat but does have slight bumps which interlock with one another.

**Medial distal tarsal.** SMU 70534 contains an articulated left hind limb including articulated medial and lateral distal tarsals. The medial distal tarsal is a square blocky bone with rounded corners and edges except for a sharp medial edge. The dorsal surface is irregularly concave in the center, but convex dorsomedially. Dorsolaterally it forms an articulation surface with the astragalus. The posteroventral surface articulates with the proximal end of metatarsals II and III. The depression formed by a beveled ventromedial corner observed in *Hypsilophodon foxii* (Galton, 1974) is not observed in the Proctor Lake taxon. Its lateral edge is slightly concave forming an articular surface with the lateral distal tarsal.

**Lateral distal tarsal.** The lateral distal tarsal is wedge-shaped bone as its anterior end is relatively thin and posteriorly expands dorsoventrally. Its dorsal surface is concave forming an articular surface with the calcaneum. The medial surface is slightly convex articulating with the astragalus. The ventral surface is also slightly convex articulating with the concave dorsal surface of metatarsal IV. Metatarsal V likely articulated with the ventral surface of the lateral distal tarsal; however, it is disarticulated in SMU 70534.

**Metatarsals.** SMU 70534 and SMU 77636 (Fig 2.23) are semi-articulated left feet and SMU 73170 is a smaller articulated left foot. The proximal end of the metatarsals is expanded anteroposteriorly in metatarsals I and II, whereas the distal ends are expanded mediolaterally giving them a slightly twisted appearance. Metatarsal I is approximately half the length of
metatarsal III with a concave medial surface (Table 2.1). The shaft of metatarsal I is laterally compressed, but distally expands to form a robust distal condyle. At midshaft it is elliptical in cross section and distal portions of the shaft are triangular in cross section. The anterior surface of metatarsal I is concave with a sharp edge in the proximal half that extends and widens in the distal half. The posterior surface also has a sharp edge in the proximal half that flattens becoming slightly concave in the distal half of the metatarsal. The flattened lateral surface of metatarsal I articulates to the posteromedial surface of metatarsal II. The distal end of metatarsal I is comprised of a robust condyle with no trochlea.

Metatarsal II is slightly shorter than metatarsal III and equal in length to metatarsal IV. The proximal half is laterally compressed with a triangular cross section, whereas the distal half is strongly compressed anteroposteriorly creating an elliptical cross sectional shape. In anterior view the medial side is slightly concave and the lateral side is straight. The medial surface of metatarsal II is flat to slightly convex. The anterior surface is fairly flat with a slight depression in the distal portions which extends into the intercondylar groove. The lateral surface is flat and articulates to the medial surface of metatarsal III. The distal end of metatarsal II is comprised of two condyles, the medial condyle being slightly larger than the lateral. The outer surface of each condyle is marked by ligament pits, but the medial pit is more prominent.
Metatarsal III is the longest metatarsal and is similar in morphology to metatarsal II, but its proximal half is less laterally compressed and the distal portion is anteroposteriorly compressed. Its medial surface is broad and flat on the proximal end, but it then becomes rounded and thinner distally. The dorsal surface is slightly sigmoidal. The anterior surface is
fairly flat with a shallow extensor groove in the distal portion that forms an intercondylar groove on the distal end. The posterior surface is slightly convex in the proximal half and distally forms a flat surface that also contains a shallow extensor groove. The lateral surface is flat and broad in the proximal half, but this surface becomes rounded in the distal half. The distal end consists of two condyles the medial being more robust but the lateral extends slightly farther. The outer surface of each condyle is marked by ligament pits, but the medial pit is more prominent.

Metatarsal IV is equal in length to metatarsal II and has the widest proximal end of any metatarsal which is triangular in dorsal view. In anterior view the medial edge is slightly concave and the lateral edge is flat. The lateral side has a prominent rounded ridge that diminishes distally forming a flat surface. The anterior surface is flat to slightly convex. The distal end consists of a single condyle that contains a shallow extensor groove on the posterior surface and a ligament pit on its lateral surface. The ventral surface of metatarsal IV is slightly rounded.

Metatarsal V is a reduced splint found articulated to the posterolateral side of metatarsal IV. SMU 70534 contains metatarsal V; however, it is not in its original articulation. Based on articulation in other basal ornithischians it likely articulated to the posterior surface of the lateral distal tarsal. Metatarsal V is approximately 34% the length of metatarsal III in this specimen. No phalanges were found associated with metatarsal V.

Phalanges. The phalangeal formula for the pes of this taxon is 2-3-4-5-0 (Fig 2.23). The first phalanx of each digit are the longest with each proceeding phalanx becoming progressively smaller until the ungual. The proximal end of each phalanx is concave and the distal end contains two condyles with prominent extensor grooves on the dorsal and ventral surface as well as defined collateral ligament pits. Deep grooves mark both the anteromedial and anterolateral surface of the unguals. Claw like unguals are present in digits I-IV and are longer than they are
wide with flattened but proximodistally curved ventral surfaces. The unguals of the larger and presumably ontogenetically older SMU 70534 are proportionally wider than the unguals of the smaller and presumably younger individual SMU 73170 and SMU 73171.

### 2.5 Ontogeny

The Proctor Lake fossil locality contains a minimum of 32 individuals ranging in size and ontogenetic stages. For example, femur length ranges from 51mm to 315mm and tibia length ranges from an estimated 64mm to 376mm. Nineteen complete femora were used to estimate femur length for an additional 26 incomplete femora based on linear regression models developed for proximal and distal width of the femora (Fig 2.24; Appendix 1). The strength of this model supports that the individuals recovered from Proctor Lake locality experienced similar growth rates and represent the same species. The Proctor Lake locality is dominated by smaller and ontogenetically younger individuals with few larger individuals, supporting that the Proctor Lake locality could possibly be a nesting site (Fig 2.25). The femora size distribution indicates a higher mortality rate in younger individuals corresponding to results from Woodward et al. (2015) analyzing population dynamics of the hadrosaurid dinosaur *Maiasaura peeblesorum*. This result seems plausible considering younger and weaker individuals may have been selectively targeted during crisis scenarios such as drought. No evidence appears in the taphonomic or skeletal analyses to suggest these individuals died as a result of predation.

Four of the fossil localities at Proctor Lake contain clusters of individuals which are partially articulated; however, the average size of individuals in each cluster ranges (Fig 2.26). The clusters at sites BMQ and 3BS are semi-articulated individuals, many of which are superimposed (Winkler and Murry, 1989). There is no preferred orientation of bones or separation by size or density which suggests these clusters indicate behavioral aspects of the
individuals rather than post depositional sorting by fluvial events (Winkler and Murry, 1989). At site BMQ a minimum of 6 individuals are clustered with an average femora length of 68mm. Femora from a cluster of 8 individuals recovered from 3BS average 97mm in length. The femora of 3 individuals clustered at site 2DU average a length of 139mm and femora from 3 individuals clustered at 1B7 average 244mm. Individuals preserved at sites BMQ and 3BS preserve younger ontogenetic features including approximately equal femur and tibia lengths and fewer dentary teeth (Appendix 2). Individuals preserved at sites 2DU and 1B7 preserve more developed features including larger tibia relative to the femur, larger scapula relative to the humerus, and increased number of maxillary and dentary teeth (Appendix 2). This indicates individuals grouped together after hatching and may have flocked together for protection from predators (Winkler and Murry, 1989; Horner, 1982).
Fig. 2.24. Graph of Femur length distribution from Proctor Lake fossil locality. Graph displaying femur length against proximal width in centimeters. Nineteen complete femora were used to create a linear regression which was then used to estimate the length of 26 additional partial femora. Measurements listed in Appendix 1.
Fig. 2.25. Histogram of femur length distribution from Proctor Lake fossil locality. Graph displaying range of femoral length of 32 individuals recovered from the Proctor Lake locality.
A total of 45 complete and incomplete femora have been collected from the Proctor Lake fossil locality. The length of incomplete femora was calculated using the above regressions. Hierarchical and k-means clustering analyses conducted in the statistical program R recovers 9 clusters of femora size (Fig 2.27). This is supported by a global peak in Cubic Clustering Criterion (CCC) and a peak in the pseudo F in both hierarchical and k-means clustering at 9 clusters (Table 2.2). There is also a dip in the pseudo $t^2$ value at 9 clusters in the hierarchical
cluster analysis (Table 2.2). Together these statistics provide strong support for 9 size classes present at the Proctor Lake locality. This result contrasts histological studies conducted by Horner et al., (2000) on the hadrosaurid dinosaur *Maiasaura* *peeblesorum* which identified 6 size classes based on changes in histologic structure.

Fig. 2.27. K-means clustering analysis with 9 recovered clusters based on femora size. Graphs displaying 9 recovered clusters from K-mean clustering analyses based on femora length, proximal width, and distal width.
Table 2.2. K-means and hierarchical clustering statistics produced by femora study. Left: Hierarchical Clustering Criterion; Right: K-Means Clustering Criterion with highlighted peak pseudo F value.

Histological analysis of four femora recovered from the Proctor Lake locality was conducted by Winkler (1994) in an effort to determine the ontogenetic stage and growth rate of this taxon. Studies of bone histology has been employed to understand the growth of several ornithischian species including *Dryosaurus lettotvorbecki*, *Orodromeus makelai*, *Dryosaurus altus*, *Tenontosaurus tilletii*, and *Maiasaura peeblesorum* (Chinsamy, 1995; Horner et al., 2009; Horner et al., 2000; Woodward et al., 2015). In extant vertebrates LAG’s represent temporary arrested growth and have been shown to have annual periodicity (Peabody, 1961; Castanet et al.,
This concept has been applied extensively to the fossil record including the aforementioned ornithischian taxa to estimate ontogenetic age of individuals. Histological analysis conducted on a large femur recovered from Proctor Lake did not reveal any LAG’s (lines of arrested growth), although secondary osteons are present (Winkler, 1994).

The absence of LAG’s in one of the largest femora recovered from the Proctor Lake locality would suggest the individuals recovered are less than a year old. However, given the size distribution of femora recovered and correlated with differences observed in limb proportions and tooth count, it seems unlikely that the individuals are all less than a year old. This is also supported by the tibia size distribution recovered by Woodward et al. (2015) for the hadrosaurid Maiasaura, which recovered a high concentration of juvenile individuals followed by low concentrations of sub adult and adult individuals all of whom were at least 2 years old. If similar population dynamics are assumed for the Proctor Lake locality, the larger individuals recovered represent sub adult or adult ontogenetic stages. The lack of LAG’s could be due to preservational bias as many elements experienced significant weathering before burial and subsequently underwent replacement and diagenesis.

Similarly, histological analyses of Dryosaurus lettonvorbecki, Dryosaurus altus, and an Early Cretaceous unnamed hypsilophodontid recovered from Australia did not observe LAG’s in the largest sampled elements (Chinsamy, 1995; Chinsamy et al., 1998; Horner et al., 2009). Chinsamy (1995) suggested the lack of LAG’s in Dryosaurus lettonvorbecki reflects an indeterminate growth pattern, differing from many ornithischian taxa. Given the phylogenetic distribution of determinate growth patterns in closely related taxa, Horner et al. (2009) argued that the lack of LAG’s in Dryosaurus lettonvorbecki and Dryosaurus altus reflected an absence
of adult specimens, which could have implications for their positioning within ornithischian phylogeny.

2.6 Phylogenetic Analysis

Morphological characters of *C. marri*, were scored using a modified matrix from Baron et al. (2016) which expanded on datasets compiled by Butler et al. (2007), Butler (2010), Butler et al. (2011), Han et al. (2012), Ösi et al. (2012), and Barrett et al. (2014) (Appendix 3,4). Modifications included adding 5 additional characters (#228, #229, #230, #231, #232 (Scheetz 1999), one new character (#233: presence of medial groove on buccal surface of premaxillary teeth), rescoring 11 characters for *T. dossi* (Appendix 5), and adding *C. marri*. As in previous analyses, five unstable ‘wild card’ taxa including *Yandusaurus*, *Anabisetia*, *Echinodon*, *Yueosaurus*, and *Koreanosaurus* were excluded from the final data set creating a matrix of 50 taxa and 233 characters. The matrix was compiled and edited using Mesquite v.2.74 (Maddison & Maddison, 2009). The matrix was analyzed using TNT 1.5 (Goloboff and Catalano, 2016) with all characters being treated as unordered except characters #112, #135, #137, #138, and #174 following previous studies (Butler et al 2011; Han et al. 2012; Ösi et al. 2012; Barrett et al. 2014; Baron et al. 2016). The search was run using 1000 replications of Wagner trees (with random addition sequence) followed by a tree bisection reconnection (TBR) swapping algorithm (holding 10 trees per replicate). Zero-length branches were collapsed on all recovered most parsimonious trees. Bootstrap and bremer support was also calculated using TNT.

The analysis of the modified matrix retained 96 most parsimonious trees with a best score of 607. The strict consensus tree recovers *C. marri* as more derived than *Hypsilophodon foxii*, but basal to Iguanodontia (Fig 2.28). Apomorphies recovered for *C. marri* include the presence of four premaxillary teeth (112:2), opisthocoelous cervical vertebrae (134: 1); convergently
present in *Agilisaurus louderbacki* (Peng, 1992) and Iguanodontia, an expanded ischial ‘foot’ (182:1); convergently present in *Heterodontosaurus tucki* (Crompton and Charig, 1962) and members of Iguanodontia, and the presence of a medial groove on the buccal surface of the premaxillary teeth (233:1). The monophyletic group consisting of *C. marri* and all taxa more derived than *Hypsilophodon foxii* (Galton, 1974) is unambiguously united in possessing curved maxillary tooth roots (230: 1), sacral neural spines at least twice the height of the sacral centra (144: 1 and 2), and proximal caudal spines at least 1.5 times the height of the caudal centra (142: 1; convergently present in Stegosauria). Iguanodontia is supported unambiguously by possessing diamond shaped maxillary and dentary crowns (115: 2), the absence of cingulum on the maxillary and dentary teeth (123:1); convergently present in *Heterodontosaurus tucki* (Crompton and Charig, 1962), and a laterally inflated medial condyle which partial covers the opening of the flexor (intercondylar) groove of the femur (204: 1).
Fig 2.28. Strict consensus tree produced from phylogenetic analysis. Strict consensus tree of 96 most parsimonious trees recovered from phylogenetic analysis. Bootstrap support values >50% listed beneath nodes.
2.7 Discussion

Ornithopods are a diverse group with numerous character reversals and parallelisms which makes the interpretation of their evolution difficult. The phylogeny of basal ornithischians in particular is poorly resolved and relationships are weakly supported as evidence by recent studies (Boyd, 2015; Baron et al., 2016). This can be attributed in part to the fragmentary nature of many of the taxa making the discovery of the nearly complete taxa *C. marri* crucial to aid in the understanding of ornithischian phylogeny. The genus *Convolosaurus* is clearly unique and defined by the apomorphies described above. *C. marri* is temporally and geographically similar to *Tenontosaurus*, and the two are similar in morphology. However, in addition to the aforementioned apomorphies *C. marri* can be distinguished from *Tenontosaurus* by the presence of two supraorbital bones, narrow and elongate frontals, a predentary with a smooth oral margin, proximally positioned fourth trochanter on the femur, fully open posterior intercondylar groove of the femur, and the absence of an elongate tail. Furthermore, the manus phalangeal formula of *C. marri* (2-3-4-2-1) differs from that of *Tenontosaurus tilletti* (2-3-3-1?-1?; Forster, 1990), however, the count for *Tenontosaurus dossi* is unknown.

The nearly complete nature of the material recovered from Proctor Lake preserves informative characters shedding new light on their distributions in ornithischian phylogeny. For example, the presence of two supraorbital bones that extend across the entire orbit was thought to be a unique character of *Agilisaurus louderbacki* and *Thescelosaurus neglectus* which previous studies indicated represented a primitive trait, recovering *Thescelosaurus neglectus* basal to *H. foxii* (Boyd 2015), however this is clearly present in *C. marri* which was recovered more derived than *H. foxii*. This character is often not preserved, thus its presence in *C. marri* provides more information about its distribution in basal ornithischians.
2.8 Conclusions

The Proctor Lake fossil locality contains a wealth of specimens providing not only nearly complete individual specimens, but also insight into ontogeny and population structure. The femoral length distribution of 32 individuals from the Proctor Lake locality indicates a high mortality rate among the smallest and presumably youngest individuals. Taphonomic clusters of individuals of varying sizes suggest individuals flocked together long after hatching perhaps for protection against predators. The specimens recovered from Proctor Lake reveal a new species of basal ornithopod with a unique set of both basal and derived characters. Characters including an expanded ischial foot, curved maxillary tooth roots, and opisthocoelus cervical vertebrae position *C. marri* as more derived than most basal ornithischians including *H. foxii* (Galton, 1974), but characters such as the presence of premaxillary teeth, shape of the frontals, and the position of the pterygoid wing on the quadrate position *C. marri* basal to Iguanodontians. Thus, this new species provides crucial information and support into the evolution of basal neornithischians.
CHAPTER 3

RECONSTRUCTION OF THE BRAIN ENDOCAST AND INNER EAR OF MALAWISAURUS DIXEYI

3.1 Introduction

Cretaceous titanosaurid material recovered from Malawi, Africa, was first described by Haughton (1928) and named Gigantosaurus dixeyi due to presumed similarity to specimens collected in Tanzania that were referred to as Gigantosaurus (Fraas, 1908). However, the generic name ‘Gigantosaurus’ was preoccupied and was replaced with the generic name Tornieria by Sternfeld (1911) and G. dixeyi from Malawi became known as Tornieria dixeyi without further justification. The generic name Tornieria was later changed to Janenschia by Wild (1991). Because the taxon from Malawi is distinct from the titanosaurid genus Janenschia, which was recovered from Jurassic beds in Tanzania, a new generic name, Malawisaurus, was erected by Jacobs et al. (1993) to accommodate the titanosaurid species from Malawi.

First described by Haughton (1928), Malawisaurus dixeyi was later redescribed by Jacobs et al. (1993) and Gomani (2005) after field expeditions by the Malawi Dinosaur Project (MDP) in 1987, 1989, 1990, and 1992 recovered new fossil material in the same Dinosaur Beds near
Mwakasyunguti, Karonga District, northern Malawi. The Dinosaur Beds are estimated to be Early Cretaceous (Aptian) age based on biochronology (Colin and Jacobs, 1990) and regional proximity to carbonatites to the north and south of the study area dated to 123± 3 to 111± 13.1Ma using K-Ar dating methods (Pentel’kov and Voronovsky, 1979; Eby et al., 1995); however, Le Loeuff et al. (2012) argues the Dinosaur Beds of Malawi could be Late Cretaceous in age based on the vertebrate assemblage and suggest more evidence is needed to accurately date these sites. Field expeditions by the Malawi Dinosaur Project recovered a nearly complete basicranium, Mal-202-1, of *Malawisaurus dixeyi* and associated elements including parietals, ectopterygoid, quadrate, cervical vertebrae, and post cranial elements (Gomani, 2005). The goal of this study is to offer a detailed description of the braincase, digital reconstructions of the endocast, and inner ear based on CT scanning as well as estimate the body mass of *Malawisaurus dixeyi*, and to compare these data to other sauropods to test the phylogenetic position of *Malawisaurus* among titanosaurs.

### 3.2 Materials and Method

To produce a three-dimensional reconstruction of the endocast and inner ear, the specimen, Mal 202-1, was scanned at the University of Texas High Resolution X-ray CT facility using a voltage of 200kV and a current of 0.12mA producing 1707 slices with a voxel size of 70.6µm. Data from the scan were imported into Amira v 4.2 for analysis and visualization. The model was then imported into MeshLab where a laplacian smoothing algorithm was applied. Final rendering was completed in LightWave.

Measurements of the semicircular canals were conducted in Amira v 4.2 following protocols from Spoor and Zonneveld (1995). Radii of the semicircular canals of the vestibular labyrinth was quantified by the radius of curvature, or half the average of the arc height and
width (Spoor et al., 2002). Body mass of Malawisaurus was calculated using the following regression from Campione and Evans (2012), based on the circumference of the humerus, Mal-221, found associated with the basicranium:

$$\log(BM) = 2.6861 \times \log(C_H) - 0.1438$$

where BM is body mass in grams and C_H is circumference of the humerus in mm.

### 3.3 Osteology

The bones surrounding the brain of *Malawisaurus* (Mal-202-1) are well preserved, but with anterior portions missing from the frontals and parietals (Fig 3.1). Bones present are completely ossified and sutures are indistinct both optically and in CT data, suggesting the specimen represents a subadult or adult individual. The braincase is exceptionally well preserved, but with a small amount of shear, the left side shifted slightly anterior relative to the right, allowing for observation of the internal structure of the endocranial cavity.

The supraoccipital forms the dorsal margin of the foramen magnum and bears a prominent nuchal crest that reaches maximum prominence at the dorsal edge, which presumably would contact the parietal as observed in *Giraffatitan* (Janensch, 1935). The wings of the supraoccipital flank the nuchal crest and are concave forming bilateral depressions. The exoccipital and opisthotic are co-ossified into a single complex (otoccipital), which forms the lateral margin of the foramen magnum. The otoccipitals form large anteroposteriorly flattened wing-like paroccipital processes that curve ventrally. A ventrally directed depression for the quadrate articulation lies on the posterolateral surface of the paroccipital processes. The otoccipital contains the mediolaterally narrow and elongate metotic foramen (=vagal, jugular
The metotic foramen served as a passageway for the glossopharyngeal, vagus, and accessory nerves (cranial nerves IX-XI).

Fig 3.1. Braincase of *Malawisaurus dixeyi*. (A) lateral view; (B) lateral view with endocast; (C) posterior view. Abbreviations: BO, basioccipital; BP, basipterygoid process; BT, basal tuber; CAR, canal for cerebral carotid artery; FO, fenestra ovalis; LABYR, labyrinth; LS, laterosphenoid; OC, occipital condyle; PFO, pituitary fossa; PP, paroccipital process; SO, supraoccipital; SPHA, canal for sphenopalatine artery; III, oculomotor nerve; IV, trochlear nerve; V, trigeminal nerve; VI, abducens nerve; VII, facial nerve; IX-XI, shared canal for glossopharyngeal, vagus, and spinal accessory nerves; XII, hypoglossal nerve. Scale bar equals 10cm.
The foramen magnum is ovoid, taller (28mm) than wide (20mm), and slightly narrower than the occipital condyle, (30mm). With the basicranium oriented with the supraoccipital aligned vertically, the occipital condyle faces posterointrally, consistent with evidence from the inner ear suggesting a habitual head posture near horizontal or with a slightly downturned muzzle, similar to the condition seen in *Camarasaurus* (Sereno et al., 2007). The basal tubera of the basioccipital is linked to the condylar region by two thick ridges that outline the subcondylar recess, as in *Sarmientosaurus* (Martínez et al., 2016), *Muyelensaurus* (Calvo et al., 2007), and the Uzbekistan titanosaur CCMGE 628/12457 (Sues et al., 2015).

Beneath the ridge of the basal tubera, the canals for the cerebral carotid arteries enter the braincase near the base of the basipterygoid processes. The bases of the basipterygoid processes are closely spaced. The basipterygoid processes are parallel as in *Sarmientosaurus* and *Muyelensaurus*, unlike the condition observed in *Camarasaurus* (Witmer et al., 2008), *Giraffatitan*, and *Jainosaurus* (Wilson et al., 2009), in which the processes diverge widely.

### 3.4 Cranial Endocast

The braincase of *M. dixeyi* is well preserved with little distortion allowing for great resolution of the internal anatomy. The digitally reconstructed endocast lacks the olfactory and cerebral regions (Fig 3.2). Characteristic traits of sauropods observed in the endocast include the presence of a well-defined and large pituitary fossa and the lack of distinction of gross regions of the brain, presumably obscured by the presence of overlying thick meninges and extensive venous sinuses in life (Hopson, 1979; Witmer et al., 2008; Knoll et al., 2012, 2013; Paulina Carabajal, 2012).
Fig 3.2. Cranial endocast and vestibular labyrinth of *Malawisaurus dixeyi*. (A) left lateral view; (B) caudal view; (C) ventral view; (D) dorsal view; Dashed line represents reconstruction of full endocast based on the endocast of *Sarmientosaurus*. Endocast represented by purple coloring;
cranial nerves by yellow coloring; vestibular labyrinth by pink coloring; carotid artery by red coloring. Scale bar equals 5cm.

The caudal dural expansion, a prominent venous feature of sauropods (Witmer et al., 2008; Knoll et al., 2012), is not preserved in this specimen, although based on the sharp posterior-anterior rise on the dorsal surface of the endocast, it likely had this feature. A median canal connects the pituitary space with the braincase cavity between the trigeminal and abducens nerve. This is observed in basal taxa including *Spinophorosaurus* (Knoll et al., 2012) and more derived sauropod taxa including *Camarasaurus* (Witmer et al., 2008) and *Jainosaurus* (ISI R162; unpublished Witmer Lab data). It has been proposed that this canal served as a passage for the basilar artery (Paulina Carabaja, 2012) or is of venous origin (Sues et al., 2015). The canals for the cerebral carotid arteries enter the posteroventral margin of the pituitary fossa. The pituitary fossa is similar to most sauropods in lacking a ventral median canal representing the craniopharyngeal canal present in the unnamed Uzbekistan titanosaur (Sues et al., 2015).

### 3.5 Cranial Nerves

The cranial nerves have a similar arrangement compared to other sauropods. The trigeminal nerve (V) is the largest of the cranial nerves and exits caudal to the infundibular region via a single foramen. The endocast shows little evidence for the division of the trigeminal nerve into the ophthalmic (V₁), maxillary (V₂), and mandibular (V₃) branches as observed in *Sarmientosaurus* (Martínez et al., 2016); however, Gomani (2005) noted anterior and posterior grooves that exit ventral to the canal and are visible on the CT scans presented here. These grooves may have held maxillary and mandibular branches. The abducens nerve (VI) originates ventral to the trigeminal nerve and extends lateral to the pituitary fossa rather than entering it, which is a derived character state for titanosaurids (Paulina Carabaja, 2012; Knoll et al., 2013; Martínez et al., 2016). The facial nerve (VII) originates posterior to the abducens and trigeminal
nerves and passes ventrolaterally. A large opening posterior to the vestibular labyrinth serves as the passageway for cranial nerves IX-XI. The hypoglossal nerve (XII) exits via one foramen, consistent with most titanosaurids; however, Sarmientosaurus (Martínez et al., 2016), Jainosaurus (Wilson et al., 2009), and Pitekunsaurus (Filippi and Garrido, 2008) contain multiple rootlets.

3.6 Inner Ear

The vestibular labyrinth of M. dixeyi is intermediate in size compared to the large labyrinth of Giraffititan and the smaller sizes in advanced titanosaurids such as Jainosaurus (Fig 3.3; 3.4). The rostral (anterior) semicircular canal is larger and is elevated dorsally compared to the caudal (posterior) semicircular canal. This supports M. dixeyi as a basal titanosaur as more advanced titanosaurids have approximately equal caudal (posterior) and rostral (anterior) semicircular canals. The lateral semicircular canal has the smallest diameter of the three, consistent with most sauropods; however, the lateral semicircular canal of M. dixeyi is longer and slender in comparison to the lateral semicircular canal of other sauropods. The angle between the rostral (anterior) and caudal (posterior) semicircular canals is nearly orthogonal and similar to most titanosaurids except Sarmientosaurus.

3.7 Body Mass and Semicircular Dimensions

Using a regression from Campione and Evans (2012), the body mass of M. dixeyi was estimated to be 4.73 metric tons based on the circumference of the humerus, Mal-221, found associated with the basicranium (Table 3.1). Measurements for the radii of the semicircular canals is shown in Table 3.2. Comparison of the measured radii of the semicircular canals and the predicted radii based on a regression of body mass from Clarke (2005) reveal a pattern similar to Giraffititan brancai (Janensch, 1914) (Fig 3.5). The caudal (posterior) semicircular canal falls within the 95% confidence interval of predicted size, but the lateral semicircular canal...
is smaller than the predicted size. The rostral (anterior) semicircular canal is significantly larger than the predicted size.

**Fig 3.3.** Left vestibular labyrinth of *Malawisaurus dixeyi*. (A) lateral view; (B) posterior view; (C) dorsal view. Abbreviations: C, cochlea; CRC, crus commune; CSC caudal (posterior) semicircular canal; FP, fenestra perilymphatica; FV fenestra vestibuli; LSC, lateral semicircular canal; RSC, rostral (anterior) semicircular canal; VE, vestibule of inner ear. Scale bar equals 2cm.
Fig 3.4. Comparison of left vestibular labyrinth of sauropod dinosaurs (modified from Martinez et al. 2016). (A) Diplodocus longus; (B) Camarasaurus lentus; (C) Giraffatitan brancai; (D) Malawisaurus dixeyi; (E) Sarmientosaurus musacchioi; (F) Unnamed derived titanosaur from Uzbekistan (CCMGE 628/12457); (G) Jainosaurus septentrionalis. Scale bar equals 2cm.
<table>
<thead>
<tr>
<th>Specimen Number</th>
<th>Humerus Length (mm)</th>
<th>Humerus Circumference (mm)</th>
<th>Predicted mass (grams)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mal-316</td>
<td>730</td>
<td>345.5</td>
<td>4731285.6</td>
</tr>
</tbody>
</table>

**Table 3.1.** Measurements of associated humerus and body mass estimate of *Malawisaurus dixeyi* based upon the regression from Campione and Evans (2012).

<table>
<thead>
<tr>
<th>Semicircular Canal</th>
<th>Diameter (mm)</th>
<th>Semicircular Canal</th>
<th>Diameter (mm)</th>
<th>Semicircular Canal</th>
<th>Diameter (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anterior Left</td>
<td>15.18</td>
<td>Posterior Left</td>
<td>11.46</td>
<td>Lateral Left</td>
<td>8.35</td>
</tr>
<tr>
<td></td>
<td>14.19</td>
<td></td>
<td>11.05</td>
<td></td>
<td>9.35</td>
</tr>
<tr>
<td></td>
<td>16.75</td>
<td></td>
<td>11.03</td>
<td></td>
<td>10.20</td>
</tr>
<tr>
<td></td>
<td>14.13</td>
<td></td>
<td>12.36</td>
<td></td>
<td>9.40</td>
</tr>
<tr>
<td></td>
<td>16.25</td>
<td></td>
<td>11.11</td>
<td></td>
<td>8.99</td>
</tr>
<tr>
<td>Anterior Right</td>
<td>16.02</td>
<td>Posterior Right</td>
<td>11.09</td>
<td>Lateral Right</td>
<td>8.36</td>
</tr>
<tr>
<td></td>
<td>15.58</td>
<td></td>
<td>11.16</td>
<td></td>
<td>10.10</td>
</tr>
<tr>
<td></td>
<td>14.85</td>
<td></td>
<td>12.32</td>
<td></td>
<td>10.07</td>
</tr>
<tr>
<td></td>
<td>15.68</td>
<td></td>
<td>11.01</td>
<td></td>
<td>9.35</td>
</tr>
<tr>
<td></td>
<td>14.99</td>
<td></td>
<td>11.20</td>
<td></td>
<td>9.32</td>
</tr>
<tr>
<td>Average Anterior</td>
<td>15.36</td>
<td>Average Posterior</td>
<td>11.38</td>
<td>Average Lateral</td>
<td>9.35</td>
</tr>
<tr>
<td>diameter (mm)</td>
<td></td>
<td>diameter (mm)</td>
<td></td>
<td>diameter (mm)</td>
<td></td>
</tr>
<tr>
<td>Average Anterior</td>
<td>7.68</td>
<td>Average Posterior</td>
<td>5.69</td>
<td>Average Lateral</td>
<td>4.67</td>
</tr>
<tr>
<td>radius (mm)</td>
<td></td>
<td>radius (mm)</td>
<td></td>
<td>radius (mm)</td>
<td></td>
</tr>
</tbody>
</table>

**Table 3.2.** Measurements of semicircular canals from the braincase of *Malawisaurus dixeyi.*
3.8 Discussion

The lateral semicircular canal of *M. dixeyi* is longer and slender compared to most sauropod taxa. This condition is similar to *Sarmientosaurus* and may indicate increased sensitivity in the mediolateral plane emphasizing lateral scanning movements of the head and eyes (Martínez et al., 2016). The angle between the semicircular canals of *M. dixeyi* is nearly orthogonal. A study by Berlin et al. 2013 concluded that deviations from orthogonality of the
semicircular canals in mammals was negatively correlated with vestibular sensitivity. Furthermore, a study conducted by Malinzak et al. (2011; 2012) found mammals with the greatest deviations from canal orthogonality experienced slower head rotations during locomotion. Together this suggests *Malawisaurus* may have experienced higher angular head velocities during locomotion and increased vestibular sensitivity compared to *Sarmientosaurus*. Furthermore, the rostral (anterior) semicircular canal of *M. dixeyi* is larger than the predicted size based on regression from Clarke (2005), which may indicate greater sensitivity. This condition supports behaviors including slower pitch movements of the head (Clarke, 2005).

3.9 Conclusions

CT scans of the braincase of *Malawisaurus dixeyi* recovered from the Dinosaur Beds of Malawi reveal insights into the paleoneuroanatomy and physiology of a basal titanosaur. The derived character state of an abducens nerve canal that passes lateral to rather than entering the pituitary fossa places *Malawisaurus dixeyi* within Titanosauria. The disproportionate size of the semicircular canals of the vestibular labyrinth with a larger rostral (anterior) semicircular canal than caudal (posterior) semicircular canal supports *M. dixeyi* as a basal titanosaur as derived titanosaur exhibit subequal semicircular canals. Body mass estimates based on circumference of the humerus are similar to estimates calculated using the radius of the semicircular canals with the caudal (posterior) semicircular canal falling within the predicted mass of 4.73 metric tons. This study has revealed the potential for imaging software in identifying important characters and new insight into physiology and behavior of extinct taxa.
CHAPTER 4

RECONSTRUCTION OF THE PALEOCLIMATE AND PALEOENVIRONMENT OF CRETACEOUS TERRESTRIAL FORMATIONS IN TEXAS AND OKLAHOMA USING PEDOGENIC MINERALS

4.1 Introduction

Lower Cretaceous terrestrial deposits in Texas and Oklahoma reveal a relatively stable faunal composition of archosaurs and mammals including sauropods, basal iguanodontians, crocodilyforms, triconodontids, and primitive tribosphenids (Jacobs and Winkler, 1998; Winkler et al, 1990, 2015). Approximately 11 million years after the last record of the Trinity fauna, deposits of the Upper Cretaceous Woodbine Formation (Cenomanian) reveal dramatic changes in both fauna and flora. This includes the rise of dominance of angiosperms, the first appearance of snakes and maursupial taxa in the Late Cretaceous, and first appearance of hardrosaurid dinosaur fauna (Jacobs and Winkler, 1998; Winkler et al., 2015). The fauna from the Woodbine Formation is consistently more derived and, with the exception of possibly two taxa *Bernissartia* and *Paracimexomys*, represents a complete faunal turnover among archosaurs and mammals. This change involving high levels of extinction and origination, rapid evolutionary diversification, and the rise of angiosperms likely represents a combination of abiotic and biotic factors as it correlates with the completion of the Western Interior Seaway (Jacobs and Winkler, 1998; Winkler et al., 2015).
Due to its paleontological significance, this study aims to describe the paleoenvironment and paleoclimatic conditions of Lower and Upper Cretaceous strata associated with several fossil localities in an effort to understand the potential impact of climatic and environmental change on fauna and flora compositions across the Early to Late Cretaceous boundary. This is accomplished by qualitative descriptions of paleosols and quantitative analyses to estimate paleoprecipitation and paleotemperature. These results are compared to previous studies using paleopedological and paleobotanical evidence within the Western Interior of the United States, which suggests a temporal regional trend in moisture availability from arid conditions in the Aptian and Early Albian to more humid conditions in the Late Albian and Cenomanian (Mack, 1992; Retallack, 2009).

Here previous interpretations are tested using geochemical weathering indices in paleosols developed by Nordt and Driese (2010) to estimate mean annual precipitation (MAP) for 7 localities spanning the Early to Late Cretaceous transition in north-central Texas and southern Oklahoma and, in doing so provide the first quantitative estimates of Early Cretaceous climate in this region. Mean annual temperature (MAT) is estimated using mineralogic, chemical, and oxygen-and hydrogen-isotope compositions of 2:1 phyllosilicate and kaolinite mixtures from paleosol profiles at these localities following methods established by Tabor and Montañez (2005). These data are then compared to previous studies including quantitative climate models developed for the Early to Late Cretaceous of the Western Interior of North America (Parrish and Curtis, 1982; Parrish et al., 1982; Parrish et al., 1984; Barron and Washington 1982; Barron et al., 1985; Poulsen et al., 2007).
4.2 Geologic Setting

Seven localities were sampled for this study, spanning the Early to Late Cretaceous (Aptian-Cenomanian) interval of north-central Texas and southern Oklahoma. Placing these localities in stratigraphic position is difficult as this section includes transgressions and regressions of the Western Interior Seaway with interfingering of facies. Previous research is used to construct the stratigraphic column (Fig 4.1) to place each locality in a stratigraphic framework; however, due to lack of absolute constraints the age of specific localities is poorly constrained.

The earliest Cretaceous deposits in north-central Texas are those of the Twin Mountains Formation, which lies unconformably above Pennsylvanian and Permian strata. The Glen Rose Formation overlies the Twin Mountains and contains ammonite faunas used to define the Aptian/Albian boundary (Scott, 1940; Young, 1967, 1974, 1986). Paleomagnetic studies indicate normal polarity within the Twin Mountains Formation which correlates to a long normal quiet zone during the Aptian and Albian stages (Winkler et al., 1988; Harland et al., 1982). Thus, the combination of the overlying biostratigraphic marker in the Glen Rose Formation and paleomagnetic data indicates the Twin Mountains Formation is Aptian in age. Exposures of the formation have been interpreted as a meander-belt fluvial system with the upper portion transitioning into marginal marine settings (Hall, 1976).
Fig 4.1. Study area and regional stratigraphic column. (A) Map displays the regional geology of the study area. Paleosols were described and bulk sediment samples were collected at each numbered locality. Locality correlates to site localities listed with collected samples. (B) Lithostratigraphic units spanning the Early to Late Cretaceous interval of north-central Texas and southern Oklahoma. Numbers correlate to the site numbers seen in Fig 4.1 (A). Green color represents terrestrial settings while blue is dominated by marine deposits. (Modified from Jacobs and Winkler, 1998).

Paleosols were identified in the Twin Mountains Formation at two fossil localities: Proctor Lake and Jones Ranch. Paleosols at the Proctor Lake locality were first discovered
during excavation of an unnamed “hypsilophodontid” dinosaur in Proctor Lake, Texas. The site lies approximately 35 meters below the Glen Rose Formation and 17 meters above the Pennsylvanian contact placing it in the lower Twin Mountains Formation (Winkler and Murry, 1989). Exposures of the Twin Mountains Formation at the Jones Ranch fossil locality contain extensive plant and vertebrate fossils. The Jones Ranch locality lies approximately 10 meters below the Glen Rose Formation and is stratigraphically higher in the Twin Mountains Formation than the Proctor Lake locality. The Jones Ranch locality is correlated to the Upper Aptian, near the Aptian-Albian boundary as the Glen Rose Formation thins to the north (~113 MYA) (Winkler and Rose, 2006).

The Twin Mountains and Paluxy Formations are separated by the Glen Rose Formation in the southern part of the study area. To the north the Glen Rose Formation pinches out. The Antlers Formation is the lateral equivalent of the Trinity Group beginning at the Glen Rose pinch out. This formation contains claystone layers with unconsolidated sandstone lenses and carbonate concretions. The vertebrate fauna of the Antlers Formation is similar to that of the Twin Mountains and Paluxy Formations (Nydam & Cifelli, 2002). It is interpreted to represent fluvial, deltaic, and strandplain settings (Hobday et al., 1981; Winkler et al. 1990).

Three paleosol localities were sampled within the Antlers Formation: one in north-central Texas and two in southern Oklahoma. Precise stratigraphic positions of localities within the Antlers is difficult to determine because of the absence of the Glen Rose as a marker. The two localities in Oklahoma are stratigraphically consistent with sections measured at fossil locality OMNH V706, which is considered to be in the middle of the formation, approximately 87 meters above the base (Cifelli et al., 1997). Stable carbon isotope ratios from fossil plants at this site are consistent with those from the middle of the Glen Rose Formation, considered Early Albian in
The Woodbine formation in north-central Texas comprises near shore continental and shallow marine depositional systems including fluvial, deltaic and shelf deposits (Dodge, 1952; Oliver 1971; Main, 2005). Two localities were sampled from the uppermost Woodbine Formation: the Arlington Archosaur site, which produced theropods, ornithopods, hadrosaurs, and crocodiles (Noto et al., 2012) The presence of *C. tarrantense* constrains the age to the Cenomanian, approximately 90-100mya (Kennedy & Cobban, 1990).

The Arlington Archosaur Site is a 2 meter section of peat containing fossils remains of crocodiles and turtles followed by a fossil rich horizon with remains of ornithopods and theropods. Within this section are three distinct paleosols with charcoal, burnt stumps, and roots. Main (2009) interpreted the section to represent a deltaic plain with three wildfire events. The second Woodbine locality sampled in this study is the Acme Brick Bit located approximately 25 miles north of the Arlington Archosaur site. Outcrop exposed by excavation of a brick pit reveals similar sedimentary features consistent with a deltaic plain setting. The section contains an 85 centimeter section of dark, organic rich muds identified as two stacked paleosols. To date no vertebrate fossil material has been recovered from the Acme Brick Pit site. Given the lack of absolute age constraints or marker beds the two localities from the Woodbine are assigned equivalent ages for this study.

The Cretaceous strata that are the subject of this study have undergone a shallow burial history not likely to have exceeded 1500m. (Kier et al., 1976). This is supported by Tabor and
Montañez (2005) who report a relatively shallow burial history west of the study area, in the Eastern Midland Basin of Texas. Their study indicates phyllosilicate samples collected from Pennsylvanian and Permian strata in the Eastern Midland Basin retain original isotopic compositions and suggest they have not been diagenetically altered by burial depth and temperature (Tabor and Montañez, 2005).

4.3 Materials and Methods

This study documents and describes paleosols from 7 localities in north-central Texas and southern Oklahoma. These descriptions include observations of color, grain size, mottling, root abundance, ped structure, abundance and morphology of carbonate accumulations, and slickenside development (Tabor et al., 2017). Each paleosol was classified following the taxonomic framework proposed by Mack et al. (1993) and bulk matrix samples were collected from selected B horizons for elemental and stable isotopic analysis. Abrupt changes in color or grain size aligned in a single horizon were used to define paleosol tops and paleosol bases were defined as the lowest occurrence of unaltered parent material; typically indicated by partial preservation to relict sedimentary structures (Tabor et al., 2017).

Bulk sediment samples were disaggregated in deionized water and centrifuged to isolate the <0.2 μm fraction, regarded to be dominated by pedogenic clays in paleosol profiles (Stern et al., 1997; Tabor et al. 2002; Vitali et al., 2002; Tabor and Montañez 2005; Meyers et al., 2012; Rosenau and Tabor, 2013). The <0.2 μm size fraction was then treated with the following procedures to remove non-phyllosilicate material: (1) 10% acetic acid solution for at least 24 hours to remove calcite (Savin and Epstein, 1970; Lawrence and Taylor, 1971), (2) sodium citrate-bicarbonate-dithionite solution to remove secondary iron oxy-hydroxides, and (3) 30% H₂O₂ solution to remove organic matter.
Clay mineralogy of the treated <0.2 μm size fraction was determined using X-ray diffraction (XRD) analysis. Oriented aggregates were prepared and transferred to glass slides, using the following treatments for each sample: (1) potassium saturation at room temperature, (2) magnesium saturation at room temperature, (3) magnesium saturation followed by glycerol solvation at room temperature, and (4) potassium saturation and heating at 500°C for at least two hours. XRD step-scan analyses of each treatment were conducted in the Roy. M Huffington Department of Earth Sciences at Southern Methodist University (SMU: Dallas, TX) using a Rigaku Ultima III X-ray diffractometer with a step scan of 0.05° over a spectrum of 2°-30° 2θ. Relative abundance of clay minerals in each sample was determined using the area of the background-subtracted intensities of the 001 peak for glycerol-solvated samples (17-20 Å for smectite, 9.9-10.1 Å for illite, 7.1-7.2 Å for kaolinite).

Samples of the <0.2 μm size fraction were then split into three aliquots for chemical and stable isotope analysis. The first aliquot of the <0.2 μm fraction was prepared as a pressed powder pellet using 0.25 μm polished hardened steel dies and coated with ~150-Å layer of high-purity carbon in a carbon evaporator. The pressed pellets were analyzed for major and minor elemental composition using a Cameca SXFive electron microprobe housed at the Texas A&M Materials Characterization Facility.

The second aliquot of the <0.2 μm fraction was analyzed for stable oxygen isotope composition following methods of Clayton and Mayeda (1963). Samples were heated overnight in Nickel-rod bombs connected to the gas extraction line at 100-150°C to remove sorbed and interlayer water. Samples were then reacted with BrF₅ at ~560°C overnight to produce O₂ gas. The O₂ gas was converted to CO₂ using heated graphite rods in high-vacuum glass extraction lines. The CO₂ gas was cryogenically captured and measured on a Finnigan MAT 252 isotope...
ratio mass spectrometer (IRMS) operating in dual inlet mode at Roy M. Huffington Department of Earth Sciences at Southern Methodist University. Repeated oxygen isotope analyses of 3 samples yield an analytical uncertainty of 0.3‰.

The third aliquot of the <0.2 µm fraction was analyzed for stable hydrogen isotope composition following the methods of Savin and Epstein (1970) at the extraction laboratory at Roy M. Huffington Department of Earth Sciences at SMU. Samples were initially outgassed at 150°C for a minimum of 1 hour under closed-system condition in 0.16 bar of O₂ gas to remove sorbed and interlayer water as well as any recalcitrant organic matter not destroyed by previous H₂O₂ treatment. The samples were then dehydroxylated at 850°C under closed-system conditions in 0.16 bar of O₂ gas. The low- and high-temperature water fractions were then quantitatively converted to H₂ gas by passage over depleted uranium metal at ~760°C as two separate fractions. H₂ gas yields were measured on a mercury manometer with an uncertainty of ± 1 µmol, and the δD values of H₂ were measured on a Finnigan MAT 252 IRMS operating in dual inlet mode at SMU. Replicate hydrogen isotope analyses of phyllosilicate samples yield an analytical uncertainty of ±4‰. The oxygen and hydrogen isotopic composition of the <0.2 µm fraction are reported in conventional delta notation (δ) in parts per thousand (‰) relative to the Vienna Standard Mean Ocean Water (V-SMOW; Gonfiantini, 1984). The resulting data were used to estimate paleotemperature using equations established by Savin and Epstein (1970) and Tabor and Montañez (2005).

Bulk sediment samples from each locality were prepared for X-ray fluorescence (XRF) analysis. Samples were dry sieved to remove the >1.68 mm size fraction and the remaining <1.68 mm fraction was powdered with a mortar and pestle. The sediment was then fused with lithium metaborate and tetraborate flux and analyzed for major elemental composition with a
Thermo-Fisher ARL PerformX wavelength-dispersive XRF spectrometer at the Roy M. Huffington Department of Earth Sciences at SMU. Results are reported as oxide weight percents, normalized to their molecular weights. The resulting data were used to estimate paleoprecipitation using the calcium magnesium weathering index (CALMAG) developed by Nordt and Driese (2010).

4.4 Phyllosilicate oxygen and hydrogen isotope fractionation factors

Sheppard and Gilg (1996) proposed the following oxygen and hydrogen isotope fractionation equations between kaolinite and water after revisions to existing empirical and experimental data, which are applied to this study:

\[
1000 \ln^{18} \alpha_{\text{kaolinite-water}} = 2.76 \times 10^6 / T^2 - 6.75
\]

\[
1000 \ln^{D} \alpha_{\text{kaolinite-water}} = -2.2 \times 10^6 / T^2 - 7.7
\]

Where \(^{18}\alpha\) and \(^{D}\alpha\) are the oxygen and hydrogen isotope fractionation factors between kaolinite and water, respectively, and T is temperature in degrees Kelvin.

There is currently a lack of accurately determined oxygen isotope fractionation factors for most 2:1 phyllosilicate minerals mainly due to the difficulty involved in isolating pure end-members from naturally occurring phyllosilicate mixtures and the highly variable chemical composition of naturally occurring 2:1 phyllosilicates that form in low temperature environments, significantly impacting 2:1 phyllosilicate-water oxygen and hydrogen isotope fractionation (Savin and Epstein, 1970; Lawrence and Taylor 1971, 1972). Savin and Lee (1988) proposed the bond-model technique, providing an alternative approach for determining the oxygen isotope fractionation among phyllosilicate minerals and water. This model considers phyllosilicate oxygen isotope fractionation to depend solely on the element to which the oxygen
is bonded in the crystal lattice rather than the physical structure of the mineral. As a result, the oxygen isotopic fractionation between phyllosilicates and water may be expressed as the weighted sum of oxygen isotope fractionation values of the different oxygen-sharing bonds in a particular mineral (Savin and Lee, 1988). This bond-model method of Savin and Lee (1988) is applied to this study to calculate mixed-layer 2:1 phyllosilicate-water oxygen isotope fractionation factors (Table 4.4).

For similar reasons the hydrogen isotope fractionation factors for 2:1 phyllosilicates are also poorly constrained (Yeh, 1980; Capuano, 1992; Sheppard and Gilg, 1996). Results from Gilg and Sheppard (1995) show that the hydrogen isotope fractionation factor of the naturally occurring 2:1 phyllosilicate smectite is largely controlled by its octahedral cation chemistry. With this knowledge, Tabor and Montañez (2005) proposed the following equation to calculate hydrogen isotope fractionation factors for naturally occurring smectites that encompass a range of chemical compositions:

$$\ln^{1000} D_{\alpha} = -2.2 * 10^6/T^2 - 7.7 + (2X_{Al} - 4X_{Mg} - 68X_{Fe})$$

where $X_{Al}$, $X_{Mg}$, and $X_{Fe}$ are the mole fractions of aluminum, magnesium, and iron present in the octahedral layer of the 2:1 phyllosilicate mineral. This equation is used in this study to calculate the hydrogen isotope fractionation factors of mixed layer 2:1 phyllosilicates (Table 4.4).

4.5 Stable isotope composition of paleosol phyllosilicates as paleoenvironmental proxies

The phyllosilicates collected from paleosols can contain a variety of components including pedogenic clays, detrital and burial authigenic clays, and diagenetically altered pedogenic clays. In order for chemical and stable isotope compositions of paleosol
phyllosilicates to provide accurate paleotemperature estimates the following conditions are required:

1). phyllosilicates analyzed from a paleosol are authigenic,

2). phyllosilicates crystallized in isotopic equilibrium with soil water,

3). the phyllosilicates have not been diagenetically altered since the time of formation,

4). knowledge of the relationship between the oxygen and hydrogen isotope compositions of soil-water, and

5). phyllosilicates crystallized in a water-dominated system.

Condition 1 is accomplished by isolating the <0.2µm size fraction, regarded as dominated by pedogenic clays in paleosol profiles (Stern et al., 1997; Tabor et al. 2002; Vitali et al., 2002; Tabor and Montañez 2005). Conditions 4 and 5 have likely been constant for well-developed soils throughout geologic history given the processes that govern the global meteoric water line (Craig, 1961; Rozanski et al., 1993; Yapp, 2000) and the low solubility of silicate minerals (Stumm and Morgan, 1981; Gregory, 1991). Conditions 2 and 3 are specific to each sample and require further scrutiny. One possibility is that the phyllosilicates have been chemically and isotopically altered during burial and lithification (i.e., diagenesis). Several methods are applied and discussed below to discount this scenario. The possibility also exists that the authigenic phyllosilicates collected from each paleosol may be composed of several different fractions crystallized under different climate regimes throughout the development of the soil. This scenario cannot be ruled out by current methods, thus the phyllosilicate crystallization temperatures, and soil-water $\delta^{18}$O estimates determined from the phyllosilicate $\delta^{18}$O and $\delta$D
values, are considered to represent the average paleoenvironmental conditions that persisted throughout active pedogenesis.

4.6 Paleosol Morphology

Paleosol profiles were described and classified at each locality using the framework provided by Mack et al. (1993). The profile from the Proctor Lake locality (Aptian) contained dark red (2.5 YR 3/4, 3/6) stacked B horizons, classified as calcic Vertisols. The clay rich B horizons contain prismatic peds that coarsen upwards through the profile. Pedogenic carbonate nodules were recovered in lower parts of the profile, but the calcareous matrix is highly reactive throughout the profile. Infill dikes ~6cm in diameter cross cut the entire profile (Fig 4.2) and vermicular mottles ~6cm in diameter are found in the lower parts of the profile. The profile from Jones Ranch (Aptian) contained grey (7.5YR 6/1, 7/1) clay rich B horizons, classified as calcic vertisols. Peds were angular to blocky in structure, averaging 2-4cm. The calcite matrix was highly reactive throughout the profile and rhizoliths were noted.
The paleosol profiles described from two localities in the southern Oklahoma Antlers Formation (Albian) were identified as calcic Vertisols. The red (10YR 4/4) B horizons contained wedge-shaped peds 5-7cm across with slickensides clearly present on the outer surfaces of the peds and collectively defining arcuate slickenplanes at depth within the profile. Pedogenic carbonate nodules up to 5cm in diameter were found concentrated in the lower portion of the profiles and decreased in size upwards through the profile (Fig 4.2). The matrix of the profiles was very calcareous throughout. Coarse (~3cm), common and prominent vermicular mottles occur in lower portion of the profiles. The profile described from the Antlers Formation fossil
locality in north-central Texas was classified as a calcic Vertisol. Stage II and III carbonates were noted in the lower portion of the profile. The middle of the profile contained a clay rich B horizon with medium angular/blocky peds (2-4cm across) and stage I carbonates. The calcareous matrix was highly reactive throughout the profile.

The paleosol profile described at the Arlington Archosaur Site (AAS) from the Woodbine Formation (Cenomanian) was classified as a gleyed Vertisol. The dark grey (7.5YR 4/0) B horizons contained wedge-shaped peds 5-7cm across with slickensides clearly present upon the outer surfaces of the peds and collectively defining arcuate slickenplanes at depth within the profile. Concentrations of organic material including charcoal and plant matter were noted throughout the section associated with this profile. The paleosol profile from the Acme Brick Pit locality in the Woodbine Formation also classified as a gleyed Vertisol containing wedge-shaped peds 3-5cm across as described from AAS (Fig 4.2). Both the Acme Brick Pit and AAS localities contain B horizons that are clay- and organic-rich throughout the profile, although the Acme Brick Pit paleosol was notably thinner, approximately 85cm, than the paleosol profile that was described and collected from the AAS locality measuring approximately 2 meters.

4.7 Clay Mineralogy and Chemical Composition of Paleosol B Horizons

XRD analysis conducted on 20 selected paleosol B-horizon matrix samples contain clay mineral assemblages comprising of various amounts of illite, smectite, and kaolinite (Fig 4.3; Appendix 6, 7). Samples collected from the Proctor Lake locality (Aptian) are dominated by illite with an average of 88% per sample. The remainder of the clay in the Proctor Lake paleosol samples consists of kaolinite. The Jones Ranch locality (Aptian) is a mixture of illite and smectite with little kaolinite (Fig 4.3; Appendix 7). Samples collected from localities in Oklahoma from the Antlers Formation (Albian) are dominated by kaolinite with an average of
60% per sample (Fig 4.3; Appendix 7). The remainder of the clay in samples from the Oklahoma Antlers Formation sites consists of illite, except for one sample containing smectite (Fig 4.3; Appendix 7). Samples collected from the Antlers Formation in north-central Texas are dominated by smectite with an average of 78% per sample. The remaining clay is illite with no kaolinite present. Samples from the Woodbine Formation (Cenomanian) are dominated by kaolinite averaging 72% per sample. The Arlington Archosaur Site also contains illite and the samples from the Acme Brick Pit contain both illite and smectite. XRD analysis reveals stratigraphic variation in clay mineralogy through the Lower-Upper Cretaceous interval in north-central Texas and southern Oklahoma (Fig 4.4). Most notable amongst these changes is the lack of smectite in the lower Twin Mountains Formation at the Proctor Lake locality. Secondly, kaolinite percentages increase in the Oklahoma Antlers Formation (Albian) localities and the Texas Woodbine Formation (Cenomanian).
Figure 4.3. X-ray diffraction analyses. Stratigraphically ordered XRD patterns of Mg-saturated and glycerol-solvated clays in the <0.2µm size fraction from the Lower to Upper Cretaceous of Texas and Oklahoma. Paleosols from the Lower Cretaceous Twin Mountains Formation (dark green) are dominated by illite/mica peak (10 Å) and smectite (001; 18.5 Å). Paleosols from the Antlers Formation (light green) contain a mixture of kaolinite (001; 7 Å) and illite. Paleosols from the Upper Cretaceous Woodbine Formation (blue) are dominated by kaolinite.
Fig 4.4. Clay abundance measured from the <0.2µm clay fractions of paleosol B-horizons in Lower and Upper Cretaceous localities from Texas and Oklahoma. Blue represents measured kaolinite percentage, orange represents measured illite percentage, and grey represents measured smectite percentages.

Illite is the the dominant phyllosilicate in four samples selected for hydrogen and oxygen isotope analysis. Illite is often attributed to deposition as a detrital phase or a product of diagenesis (Southard and Miller, 1966; Yemane et al., 1996), but it can also form through mineralogic transformations in soil profiles (Wilson, 1999). Studies of Mesozoic paleosols by Vitali et al. (2002) and Gilg (2000) present evidence for isotopic equilibrium of illites with paleo-meteoric waters that may have been facilitated through transformation and dissolution processes. Comparable to other 2:1 phyllosilicates, the oxygen and hydrogen isotope
fractionation factors are expected to vary due to varying chemical compositions of illite. Thus, the bond-model approach of Savin and Lee (1988) and hydrogen isotope fractionation factor equation of Tabor and Montañez (2005) are used in this study to calculate the oxygen and hydrogen isotope fractionation factors for illite in the mixtures of 2:1 phyllosilicates and kaolinite.

The chemical composition of end-member 2:1 phyllosilicates were calculated using oxide wt. % data collected from the Cameca SXFive electron microprobe from the <0.2µm size fraction (Table 4.1). The wt. % kaolinite of each sample was taken into account based on results from X-ray diffraction spectra. There are differences in the relative proportions of Al$_2$O$_3$ and SiO$_2$ in the crystal structure of kaolinite and 2:1 phyllosilicates, thus it is necessary to consider the different mole fraction contributions of Al and Si from those samples that are mixtures of kaolinite and 2:1 phyllosilicate minerals. The mole fraction of Al$_2$O$_3$ and SiO$_2$ within mineralogical mixtures of each sample were calculated from wt. % oxide data in Table 4.1. Estimated mole fraction of Al and Si contributed from kaolinite were subtracted from the phyllosilicate mixtures to calculate an end-member 2:1 phyllosilicate chemical formula for each sample that was analyzed for oxygen and hydrogen isotopes (Table 4.2).
<table>
<thead>
<tr>
<th>Sample</th>
<th>Stage</th>
<th>Formation</th>
<th>Paleosol Type</th>
<th>Na2O</th>
<th>MgO</th>
<th>Al2O3</th>
<th>SiO2</th>
<th>K2O</th>
<th>CaO</th>
<th>Fe2O3</th>
<th>TiO2</th>
<th>Total</th>
<th>Mineralogyb</th>
<th>Smectite (wt.%a)</th>
<th>Kaolinite (wt.%a)</th>
<th>Illite (wt.%a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AAS2</td>
<td>Cenomanian</td>
<td>Woodbine</td>
<td>gleyed Vertisol</td>
<td>1.05</td>
<td>1.02</td>
<td>31.02</td>
<td>51.62</td>
<td>2.29</td>
<td>0.07</td>
<td>2.57</td>
<td>1.34</td>
<td>90.95</td>
<td>K, I</td>
<td>0</td>
<td>71</td>
<td>29</td>
</tr>
<tr>
<td>15CS717-21</td>
<td>Cenomanian</td>
<td>Woodbine</td>
<td>gleyed Vertisol</td>
<td>1.03</td>
<td>1.05</td>
<td>30.74</td>
<td>51.71</td>
<td>2.20</td>
<td>0.09</td>
<td>2.51</td>
<td>1.08</td>
<td>90.39</td>
<td>K, I</td>
<td>0</td>
<td>69</td>
<td>31</td>
</tr>
<tr>
<td>ABP</td>
<td>Cenomanian</td>
<td>Woodbine</td>
<td>gleyed Vertisol</td>
<td>0.92</td>
<td>0.83</td>
<td>33.93</td>
<td>51.89</td>
<td>1.08</td>
<td>0.06</td>
<td>2.76</td>
<td>0.81</td>
<td>92.27</td>
<td>K, Sm, I</td>
<td>22</td>
<td>72</td>
<td>6</td>
</tr>
<tr>
<td>RNT-6</td>
<td>Albian</td>
<td>Antlers</td>
<td>calcic Vertisol</td>
<td>1.40</td>
<td>3.16</td>
<td>23.55</td>
<td>58.51</td>
<td>3.37</td>
<td>0.08</td>
<td>5.46</td>
<td>1.04</td>
<td>96.60</td>
<td>Sm, I</td>
<td>77</td>
<td>1</td>
<td>22</td>
</tr>
<tr>
<td>RNT-5</td>
<td>Albian</td>
<td>Antlers</td>
<td>calcic Vertisol</td>
<td>1.40</td>
<td>3.05</td>
<td>23.30</td>
<td>58.29</td>
<td>3.33</td>
<td>0.05</td>
<td>5.30</td>
<td>1.03</td>
<td>95.77</td>
<td>Sm, I</td>
<td>81</td>
<td>1</td>
<td>18</td>
</tr>
<tr>
<td>JR-3</td>
<td>Aptian</td>
<td>Twin Mountains</td>
<td>calcic Vertisol</td>
<td>1.31</td>
<td>3.45</td>
<td>21.99</td>
<td>57.99</td>
<td>2.26</td>
<td>0.08</td>
<td>3.81</td>
<td>0.65</td>
<td>91.56</td>
<td>I, Sm</td>
<td>40</td>
<td>1</td>
<td>59</td>
</tr>
<tr>
<td>JR-2-40</td>
<td>Aptian</td>
<td>Twin Mountains</td>
<td>calcic Vertisol</td>
<td>1.26</td>
<td>3.51</td>
<td>23.20</td>
<td>59.12</td>
<td>3.14</td>
<td>0.23</td>
<td>4.01</td>
<td>1.44</td>
<td>95.94</td>
<td>Sm, I</td>
<td>58</td>
<td>6</td>
<td>36</td>
</tr>
<tr>
<td>PL-4</td>
<td>Aptian</td>
<td>Twin Mountains</td>
<td>calcic Vertisol</td>
<td>1.19</td>
<td>3.18</td>
<td>24.27</td>
<td>52.75</td>
<td>4.80</td>
<td>0.35</td>
<td>4.57</td>
<td>0.33</td>
<td>91.44</td>
<td>I, K</td>
<td>0</td>
<td>14</td>
<td>86</td>
</tr>
<tr>
<td>PL-1</td>
<td>Aptian</td>
<td>Twin Mountains</td>
<td>calcic Vertisol</td>
<td>1.29</td>
<td>3.10</td>
<td>24.32</td>
<td>55.29</td>
<td>4.71</td>
<td>0.22</td>
<td>5.02</td>
<td>0.32</td>
<td>94.30</td>
<td>I, K</td>
<td>0</td>
<td>13</td>
<td>87</td>
</tr>
<tr>
<td>Oklahoma</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dean-2</td>
<td>Albian</td>
<td>Antlers</td>
<td>calcic Vertisol</td>
<td>1.28</td>
<td>1.80</td>
<td>29.18</td>
<td>53.99</td>
<td>3.24</td>
<td>0.04</td>
<td>5.36</td>
<td>0.82</td>
<td>95.73</td>
<td>K, I</td>
<td>0</td>
<td>72</td>
<td>28</td>
</tr>
<tr>
<td>Cross-A2</td>
<td>Albian</td>
<td>Antlers</td>
<td>calcic Vertisol</td>
<td>1.25</td>
<td>2.05</td>
<td>28.40</td>
<td>51.38</td>
<td>3.24</td>
<td>0.09</td>
<td>5.48</td>
<td>0.51</td>
<td>92.39</td>
<td>K, I</td>
<td>0</td>
<td>71</td>
<td>29</td>
</tr>
</tbody>
</table>

Table 4.1. Electron microprobe and X-ray diffraction data for the <0.2μm size fraction of phyllosilicates

a Classification scheme of Mack et al. (1993)
b Clay mineralogy of the <0.2μm phyllosilicate size fraction organized in relative order of abundance; K=kaolinite; I=illite; Sm=Smectite
Table 4.2. Calculated chemical formulae for end-member 2:1 phyllosilicates in phyllosilicate mixtures\(^a\).

\(^a\) Chemical formulae were calculated from the oxide data reported in Table, based on the presence of twelve oxygen atoms and two hydrogen atoms in each unit-cell (Moore and Reynolds, 1997).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Formation</th>
<th>Chemical Formulae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texas</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AAS2</td>
<td>Woodbine</td>
<td>((K_{0.45}Na_{0.31}Ca_{0.01})(Al_{1.47}Fe_{0.30}Mg_{0.23}Ti_{0.15})(Si_{2.86}Al_{1.14})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>15CS717-21</td>
<td>Woodbine</td>
<td>((K_{0.42}Na_{0.30}Ca_{0.01})(Al_{1.51}Fe_{0.28}Mg_{0.24}Ti_{0.12})(Si_{2.93}Al_{1.07})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>ABP</td>
<td>Woodbine</td>
<td>((K_{0.21}Na_{0.28}Ca_{0.01})(Al_{1.69}Fe_{0.32}Mg_{0.19}Ti_{0.10})(Si_{2.67}Al_{1.33})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>RNT-6</td>
<td>Antlers</td>
<td>((K_{0.27}Na_{0.17}Ca_{0.05})(Al_{1.44}Fe_{0.26}Mg_{0.30}Ti_{0.05})(Si_{3.67}Al_{1.33})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>RNT-5</td>
<td>Antlers</td>
<td>((K_{0.27}Na_{0.17})(Al_{1.44}Fe_{0.25}Mg_{0.29}Ti_{0.05})(Si_{3.70}Al_{0.30})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>JR-3</td>
<td>Twin Mountains</td>
<td>((K_{0.19}Na_{0.17}Ca_{0.02})(Al_{1.56}Fe_{0.19}Mg_{0.34}Ti_{0.03})(Si_{3.80}Al_{0.20})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>JR-2-40</td>
<td>Twin Mountains</td>
<td>((K_{0.27}Na_{0.16}Ca_{0.02})(Al_{1.42}Fe_{0.20}Mg_{0.35}Ti_{0.07})(Si_{3.72}Al_{0.28})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>PL-4</td>
<td>Twin Mountains</td>
<td>((K_{0.47}Na_{0.18}Ca_{0.03})(Al_{1.46}Fe_{0.26}Mg_{0.36}Ti_{0.02})(Si_{3.52}Al_{0.48})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>PL-1</td>
<td>Twin Mountains</td>
<td>((K_{0.44}Na_{0.19}Ca_{0.02})(Al_{1.46}Fe_{0.28}Mg_{0.34}Ti_{0.02})(Si_{3.58}Al_{0.42})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>Oklahoma</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dean-2</td>
<td>Antlers</td>
<td>((K_{0.67}Na_{0.40}Ca_{0.01})(Al_{1.04}Fe_{0.65}Mg_{0.43}Ti_{0.01})(Si_{2.92}Al_{1.08})O_{10}(OH)_{2})</td>
</tr>
<tr>
<td>Cross-A2</td>
<td>Antlers</td>
<td>((K_{0.69}Na_{0.40}Ca_{0.02})(Al_{0.93}Fe_{0.68}Mg_{0.51}Ti_{0.06})(Si_{2.78}Al_{1.22})O_{10}(OH)_{2})</td>
</tr>
</tbody>
</table>

4.8 Major-Element Chemistry and Paleoprecipitation Estimates from Paleosol B Horizons

Elemental data collected from 15 samples selected for XRF analysis are listed in Table 4.3, which lists oxides used for calculation of the CALMAG indices. Weight percent Al\(_2\)O\(_3\) ranges between 5.1 and 19.0%, CaO between 0.1 and 6.0%, and MgO 0.8 to 5.7% respectively.

The CALMAG proxy was developed by Nordt and Driese (2010) as a weathering index specifically for samples collected from paleosol profiles with vertic features. All paleosols described in this study exhibit vertic features. Therefore, the CALMAG index was applied to the
samples. CALMAG values were calculated using the equation proposed by Nordt and Driese (2010):

$$\text{CALMAG} = \frac{\text{Al}_2\text{O}_3}{\text{Al}_2\text{O}_3 + \text{MgO} + \text{CaO}} \times 100$$

where $\text{Al}_2\text{O}_3$, CaO, and MgO are molar proportions. CALMAG values from the 15 samples range between 31 and 84.7 with an average of 57.4 (Table 4.3). The CIA-K proxy was not applied to this data set as many of the paleosols documented contain near-surface carbonate accumulations and bulk carbonate $>5\% \text{ wt}\%$ (Sheldon et al., 2002; Prochnow et al., 2006).

MAP (mean annual precipitation) estimates were calculated using the relationship between CALMAG and MAP reported by Nordt and Driese (2010):

$$\text{MAP (mm yr}^{-1}\text{)} = (22.69 \times \text{CALMAG}) - 435.8.$$  

MAP estimates calculated for this study from the CALMAG values range from 268 to 1486 mm yr$^{-1}$ with an average of 867 mm yr$^{-1}$. The average MAP estimate based on CALMAG values from the Early Cretaceous Twin Mountains Formation of north-central Texas (345 mm yr$^{-1}$) is significantly less than the Antlers Formation of southern Oklahoma (1119 mm yr$^{-1}$) and Woodbine Formation (1460 mm yr$^{-1}$) sites. The average MAP estimate from the north-central Texas Antlers Formation site (650 mm yr$^{-1}$) is higher than the Twin Mountains Formation estimates, but is also significantly less than the Oklahoma Antlers Formation and Woodbine Formation sites (Table 4.3).
Table 4.3. X-ray Fluorescence data and mean annual precipitation estimates

<table>
<thead>
<tr>
<th>Sample</th>
<th>Paleosol Type</th>
<th>$\text{Al}_2\text{O}_3$ (wt %)</th>
<th>MgO (wt %)</th>
<th>CALMAG</th>
<th>MAP mm/yr (±110mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AAS-2</td>
<td>gleyed Vertisol</td>
<td>15.08</td>
<td>0.35</td>
<td>82.9</td>
<td>1444.7</td>
</tr>
<tr>
<td>15CS717-21</td>
<td>gleyed Vertisol</td>
<td>16.99</td>
<td>0.35</td>
<td>83.1</td>
<td>1449.0</td>
</tr>
<tr>
<td>ABP</td>
<td>gleyed Vertisol</td>
<td>18.99</td>
<td>0.43</td>
<td>84.7</td>
<td>1486.1</td>
</tr>
<tr>
<td>RNT-6</td>
<td>calcic Vertisol</td>
<td>5.13</td>
<td>0.35</td>
<td>45.5</td>
<td>597.4</td>
</tr>
<tr>
<td>RNT-5</td>
<td>calcic Vertisol</td>
<td>5.51</td>
<td>0.35</td>
<td>50.2</td>
<td>702.8</td>
</tr>
<tr>
<td>JR-3</td>
<td>calcic Vertisol</td>
<td>6.50</td>
<td>0.35</td>
<td>31.9</td>
<td>288.2</td>
</tr>
<tr>
<td>JR-2-40</td>
<td>calcic Vertisol</td>
<td>6.96</td>
<td>0.35</td>
<td>38.8</td>
<td>443.7</td>
</tr>
<tr>
<td>PL-4</td>
<td>calcic Vertisol</td>
<td>10.99</td>
<td>0.35</td>
<td>31.0</td>
<td>268.0</td>
</tr>
<tr>
<td>PL-2</td>
<td>calcic Vertisol</td>
<td>11.29</td>
<td>0.35</td>
<td>32.8</td>
<td>309.2</td>
</tr>
<tr>
<td>PL-1</td>
<td>calcic Vertisol</td>
<td>11.44</td>
<td>0.35</td>
<td>37.5</td>
<td>415.6</td>
</tr>
<tr>
<td>Dean-2</td>
<td>calcic Vertisol</td>
<td>7.13</td>
<td>0.35</td>
<td>76.0</td>
<td>1289.0</td>
</tr>
<tr>
<td>Dean-1</td>
<td>calcic Vertisol</td>
<td>6.15</td>
<td>0.35</td>
<td>61.6</td>
<td>962.6</td>
</tr>
<tr>
<td>Cross-A2</td>
<td>calcic Vertisol</td>
<td>8.26</td>
<td>0.35</td>
<td>71.3</td>
<td>1181.5</td>
</tr>
<tr>
<td>Cross-A1</td>
<td>calcic Vertisol</td>
<td>10.11</td>
<td>0.35</td>
<td>72.5</td>
<td>1209.8</td>
</tr>
<tr>
<td>Cross C</td>
<td>calcic Vertisol</td>
<td>11.62</td>
<td>0.35</td>
<td>61.1</td>
<td>951.7</td>
</tr>
</tbody>
</table>

Note: MAP—mean annual precipitation; CALMAG—calcium and magnesium weathering index.
Figure 4.5. Graph displaying average paleoprecipitation for each locality based on CALMAG estimates in Table 4.3.

4.9 Calculation of oxygen and hydrogen fractionation factors for naturally occurring phyllosilicates

The samples analyzed in this study are mineralogic mixtures of 2:1 phyllosilicates and kaolinite; thus, unique phyllosilicate mixture-water hydrogen and oxygen fractionation factors were calculated for each sample (Table 4.4). This was accomplished by calculating the mole fraction of oxygen and hydrogen contributed from 2:1 phyllosilicates and kaolinite. Oxygen
Fractionation equations for the 2:1 phyllosilicate end members were calculated using the bond-model approach of Savin and Lee (1988) (Appendix 8). The oxygen and hydrogen stable isotope fractionation equations for kaolinite proposed by Sheppard and Gilg (1996) were employed for this study. Hydrogen stable isotope fractionation equations for the 2:1 phyllosilicate end members were calculated using the equation developed by Tabor and Montañez (2005). Using the derived oxygen isotope fractionation factors for the phyllosilicate mixtures and their respective crystallization temperatures, the oxygen isotope composition of the meteoric water from which the phyllosilicate crystallized was estimated using the following equation:

\[ \delta^{18}O_{\text{water}} = \left( 1000 + \delta^{18}O_{\text{mix}} - 1000\alpha_{\text{mix-water}} \right) / \alpha_{\text{mix-water}} \]

4.10 Calculation of phyllosilicate crystallization temperatures

Previous research of the isotopic composition of authigenic minerals in both modern soil-weathering systems (Girard et al., 2000; Yapp, 1987) and paleosols (Yapp, 1993) indicate that isotopic equilibrium with meteoric water, or near-equilibrium values, is approached by various minerals in soil. Assuming ancient hydroxylated minerals formed under isotopic equilibrium with meteoric water and retained their original isotopic compositions, numerous studies (Yapp 1987, 1993, 2000; Delgado and Reyes, 1996; Tabor and Montañez, 2005; Tabor, 2007; Rosenau and Tabor, 2013) proposed that hydroxylated minerals may provide an estimate of phyllosilicate crystallization temperature.

Studies by Savin and Lee (1988), Capuano (1992), and Delgado and Reyes (1996) proposed the following equation as a single-mineral geothermometer for smectite minerals precipitated in equilibrium with meteoric waters:
\[ 3.54 \times 10^6 T^{-2} = \delta^{18}O_{sm} - 0.125\delta D_{sm} + 8.95 \]

where \( \delta^{18}O_{sm} \) and \( \delta D_{sm} \) are measured smectite \( \delta^{18}O \) and \( \delta D \) values. However, given the mineralogical and chemical mixture present in the phyllosilicate samples generated from paleosol matrix in this study, a single phyllosilicate mineral geothermometer equation is not applicable for crystallization temperature estimates. To account for the mixture of 2:1 phyllosilicates and kaolinite of the phyllosilicate mixtures the following equation was proposed by Rosenau and Tabor (2013):

\[
1000\ln^D \alpha_{\text{mix-water}} - \delta D_{\text{mix}} = 8(1000\ln^{18} \alpha_{\text{mix-water}} - \delta^{18}O_{\text{mix}}) - 10
\]

where \( D \alpha_{\text{mix-water}} \) and \( ^{18} \alpha_{\text{mix-water}} \) are the unique calculated temperature-dependent hydrogen and oxygen isotope fractionation for the phyllosilicate samples, and \( \delta^{18}O_{\text{mix}} \) and \( \delta D_{\text{mix}} \) are the measured oxygen and hydrogen isotope values of the phyllosilicate samples (Table 4.4).
<table>
<thead>
<tr>
<th>Sample</th>
<th>Stage</th>
<th>Formation</th>
<th>δ¹⁸O&lt;br&gt;V-SMOW (±0.3%)</th>
<th>δD&lt;br&gt;V-SMOW (±4%)</th>
<th>Wt. % Kaolinite (±5%)</th>
<th>¹⁰¹⁰ln[^θHOT][¹⁸O]&lt;sub&gt;LOHOT&lt;/sub&gt;</th>
<th>¹⁰¹⁰ln[^θHOT][¹⁸O]&lt;sub&gt;HOT-LLOHOT&lt;/sub&gt;</th>
<th>¹⁰¹⁰ln[^θHOT][¹⁸O]&lt;sub&gt;LLOHOT-LVSMOW&lt;/sub&gt;</th>
<th>δ¹⁸O&lt;br&gt;V-SMOW&lt;br&gt;(VSMOW)</th>
<th>δ¹⁸O&lt;br&gt;SMOW&lt;br&gt;(VSMOW)</th>
<th>Surface Domain</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AAS2</td>
<td>Cenomanian</td>
<td>Woodbine</td>
<td>18.5</td>
<td>-67</td>
<td>71</td>
<td>2.85*10⁵</td>
<td>-16.89</td>
<td>2.78*10⁴</td>
<td>-8.82</td>
<td>26</td>
<td>-5.6</td>
</tr>
<tr>
<td>15CS717-21</td>
<td>Cenomanian</td>
<td>Woodbine</td>
<td>18.5</td>
<td>-64</td>
<td>69</td>
<td>2.87*10⁵</td>
<td>-16.06</td>
<td>2.79*10⁴</td>
<td>-8.76</td>
<td>27</td>
<td>-5.5</td>
</tr>
<tr>
<td>ABP</td>
<td>Cenomanian</td>
<td>Woodbine</td>
<td>18.6</td>
<td>-65</td>
<td>72</td>
<td>2.90*10⁵</td>
<td>-16.40</td>
<td>2.80*10⁴</td>
<td>-8.68</td>
<td>27</td>
<td>-5.5</td>
</tr>
<tr>
<td>RNT-6</td>
<td>Albian</td>
<td>Antlers</td>
<td>20.9</td>
<td>-52</td>
<td>1</td>
<td>2.83*10⁵</td>
<td>-15.85</td>
<td>2.83*10⁴</td>
<td>-15.61</td>
<td>31</td>
<td>-3.0</td>
</tr>
<tr>
<td>RNT-5</td>
<td>Albian</td>
<td>Antlers</td>
<td>20.1</td>
<td>-61</td>
<td>1</td>
<td>2.84*10⁵</td>
<td>-15.42</td>
<td>2.84*10⁴</td>
<td>-15.18</td>
<td>31</td>
<td>-4.1</td>
</tr>
<tr>
<td>JR-3</td>
<td>Aptian</td>
<td>Twin Mountains</td>
<td>21.7</td>
<td>-52</td>
<td>1</td>
<td>2.85*10⁵</td>
<td>-13.26</td>
<td>2.85*10⁴</td>
<td>-13.10</td>
<td>28</td>
<td>-3.4</td>
</tr>
<tr>
<td>JR-2-40</td>
<td>Aptian</td>
<td>Twin Mountains</td>
<td>21.6</td>
<td>-60</td>
<td>6</td>
<td>2.83*10⁵</td>
<td>-13.87</td>
<td>2.82*10⁴</td>
<td>-12.88</td>
<td>27</td>
<td>-5.1</td>
</tr>
<tr>
<td>PL-4</td>
<td>Aptian</td>
<td>Twin Mountains</td>
<td>21.0</td>
<td>-50</td>
<td>14</td>
<td>2.83*10⁵</td>
<td>-15.78</td>
<td>2.82*10⁴</td>
<td>-13.11</td>
<td>29</td>
<td>-3.0</td>
</tr>
<tr>
<td>PL-1</td>
<td>Aptian</td>
<td>Twin Mountains</td>
<td>20.1</td>
<td>-56</td>
<td>13</td>
<td>2.83*10⁵</td>
<td>-16.41</td>
<td>2.82*10⁴</td>
<td>-13.69</td>
<td>30</td>
<td>-3.8</td>
</tr>
<tr>
<td>Oklahoma</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dean-2</td>
<td>Albian</td>
<td>Antlers</td>
<td>19.4</td>
<td>-56</td>
<td>72</td>
<td>2.69*10⁵</td>
<td>-28.38</td>
<td>2.74*10⁴</td>
<td>-9.94</td>
<td>27</td>
<td>-4.2</td>
</tr>
<tr>
<td>Cross-A2</td>
<td>Albian</td>
<td>Antlers</td>
<td>19.1</td>
<td>-60</td>
<td>71</td>
<td>2.64*10⁵</td>
<td>-29.60</td>
<td>2.73*10⁴</td>
<td>-10.14</td>
<td>26</td>
<td>-4.5</td>
</tr>
</tbody>
</table>

Table 4.4. Measured phyllosilicate oxygen and hydrogen-isotope compositions, oxygen and hydrogen isotope fractionation equations, and calculated phyllosilicate crystallization temperatures.

* Calculated oxygen isotope fractionation equations between the <0.2μm phyllosilicate fraction and water. Fractionation equations were calculated using the bond-model data of Savin and Lee (1988) in conjunction with the calculated chemical composition end-member 2:1 phyllosilicates presented in Table.

b Calculated hydrogen isotope fractionation equations between the <0.2μm phyllosilicate fraction and water. Fractionation equations were calculated based on the molar fraction of Al, Mg, and Fe in the octahedral layer as proposed by Gilg and Sheppard (1995) and Tabor and Montañés (2005).

c Calculated oxygen isotope fractionation factors between mixed phyllosilicate mineralogies in the <0.2μm phyllosilicate fraction and water. Fractionation factors were calculated based on the molar fraction of Al, Mg, and Fe in the octahedral layer as proposed by Gilg and Sheppard (1996).

* Calculated hydrogen isotope fractionation factors between mixed phyllosilicate mineralogies in the <0.2μm phyllosilicate fraction and water. Fractionation factors were calculated based on the molar fraction of oxygen contributed from kaolinite and 2:1 phyllosilicates in each sample (Sheppard and Gilg, 1996).

e Calculated equilibrium crystallization temperatures for each phyllosilicate mixture.

f Calculated δ¹⁸O of meteoric water in equilibrium with the phyllosilicate mixture.
The measured $\delta$D and $\delta^{18}$O values of the $<$0.2µm phyllosilicate fraction in the Early to Late Cretaceous paleosols range from -50.1‰ to -67‰ and 18.5‰ to 21.7‰ respectively (Table 4.4). Assessing the magnitude of analytical uncertainty associated with the paleotemperature estimates is difficult given the uncertainty propagated from the temperature-dependent oxygen and hydrogen isotope fractionation factors between the phyllosilicate minerals and water. The uncertainty reported herein of $\pm$3°C for the paleotemperature estimates reflects the analytical uncertainty in measured phyllosilicate oxygen ($\pm$0.3‰) and hydrogen ($\pm$4‰) isotopic values.

Crystallization temperatures calculated from phyllosilicates preserved in Cretaceous paleosols in Texas and Oklahoma range from 26 ± 3°C to 31 ± 3°C (Table 4.4; Fig). This is significantly higher than modern mean annual surface air temperatures reported in the region (~16-17 °C). No statistically significant trends are recognized in the data suggesting temperature did not vary significantly across the Early to Late Cretaceous interval of this region. However, there appears to be slight cooling from the Twin Mountains Formation (Aptian) to middle Antlers Formation (Albian) from 30 ± 3°C to 26 ± 3°C. This is followed by a rise in temperature to 31 ± 3°C in the upper Antlers Formation (Albian) followed by cooling toward the Woodbine Formation (Cenomanian), which averages 27 ± 3°C. Previous studies have revealed mean annual soil temperatures are typically ~2°C warmer than the mean annual air temperature (Chang, 1958; Barron and Moore, 1994; Barron and Fawcett, 1995; Buol et al., 2003). Additionally, the relationship between timing of phyllosilicate crystallization and seasonally-biased temperature estimates is unknown (Passey et al., 2010; Quade et al., 2013). Thus, the temperatures estimated from the pedogenic phyllosilicates are best considered as maximum estimates or slight overestimates (~2°C) of mean annual surface air temperatures.
Figure 4.6. Calculated phyllosilicate crystallization temperatures compared to modern mean annual temperature of the study area.

4.11 Meteoric waters and phyllosilicate surface domain arrays

The two principal factors that affect the $\delta^{18}$O and $\delta$D values of naturally occurring phyllosilicates are the oxygen and hydrogen composition of the water from which the phyllosilicates precipitate and the temperature at which the phyllosilicates crystallize. Given this relationship, a global database of meteoric water $\delta^{18}$O and $\delta$D compositions and mean annual surface air temperatures, in conjunction with oxygen and hydrogen isotope fractionation factors
for a given mineral may be used to produce an array of isotope compositions that reflects possible mineral δ\(^{18}\)O and δD values expected at modern surface temperatures. Assuming the global meteoric water line (Craig, 1961) accurately represents the relationship between δ\(^{18}\)O and δD values of meteoric water throughout geologic time, Yapp (1993, 2000) applied this method to the IAEA global precipitation database (Rozanski et al., 1993) to define a modern surface domain (MSD) and warm earth surface domain (WESD) for the low-temperature mineral goethite. Savin and Hsieh (1998), Tabor and Montañez (2005), and Rosenau and Tabor (2013) demonstrated a similar relationship for phyllosilicates.

The MSD model employs waters from IAEA sites with a mean annual temperature >0°C as it is expected that liquid water is required for the crystallization of hydroxylated minerals. When applied to the IAEA database this condition results in 184 data points ranging from 0 to ~30°C (Rozanski et al., 1993; Yapp, 2000; Tabor and Montañez, 2005; Rosenau and Tabor, 2013). The WESD model reflects a temperature range from 0 to ~35°C with the assumption that the average δ\(^{18}\)O value of the oceans may have been ~1‰ more negative than modern oceans due to deglaciation (Savin, 1977). The modern GMWL (δD=8*δ\(^{18}\)O+10; Craig, 1961) is assumed in the calculation of both the MSD and WESD. Yapp (2000) concluded that the negative shift of oceanic δ\(^{18}\)O and δD values, which would accompany the melting of the ice sheets, would plot along a mixing line nearly parallel to the meteoric water line, thus the slight decrease of ~1‰ of oceanic δ\(^{18}\)O accompanying the melting of the ice sheets would have a minimal effect on the intercept of the GMWL (Yapp, 2000).

Previous studies have defined surface domain arrays for goethite and phyllosilicate minerals (Yapp 1993, 2000; Savin and Hsieh, 1998; Tabor and Montañez, 2005; Rosenau and Tabor, 2013). It is not necessary for phyllosilicate δ\(^{18}\)O and δD values to plot within their
respective MSD or WESD; however, this method provides a means to assess the likelihood that δ\textsuperscript{18}O and δD compositions of hydroxylated minerals preserve information regarding ancient climate (Yapp 1993, 2000; Savin and Hsieh, 1998; Tabor and Montañez, 2005; Rosenau and Tabor, 2013). Therefore, this approach is applied to phyllosilicate δ\textsuperscript{18}O and δD values collected from Cretaceous pedogenic phyllosilicates of Texas and Oklahoma to determine the preservation of information regarding paleotemperature of crystallization.

Calculation of the MSD and WESD for the 11 pedogenic phyllosilicate samples using their respective oxygen and hydrogen isotope fractionation factors reveals 9 of the phyllosilicate samples plot within or upon the limits of their respective MSD (Fig 4.7; Appendix 9). The remaining two samples collected from the Antlers Formation north Texas Hartman fossil locality plot within their respective WESD suggesting their phyllosilicate crystallization temperature occurred at slightly higher temperatures (>30°C) than those observed on modern Earth (Fig 4.7b; Appendix 9).
Figure 4.7. Calculated surface domain arrays. $\delta D$ vs. $\delta^{18}O$ plot showing hypothetical oxygen and hydrogen isotope composition of phyllosilicate sample 15CS717-21 and RNT-5 calculated using their respective hydrogen and oxygen fractionation equations (Table 4.4) in conjunction with mean annual $\delta^{18}O$, $\delta D$, and temperature information in the IAEA database (Rozanski et al., 1993). The limits of the Modern Surface Domain (MSD) and corresponding Warm Earth Surface Domain (WESD) are defined by solid polygons and dashed polygons, respectively. The solid
black square represents the measured $\delta^{18}$O and $\delta ^D$ values. (A) Plot of sample 15CS717-21 MSD and WESD with the measured phyllosilicate $\delta^{18}$O and $\delta^D$ values of sample 15CS717-21 whose isotopic composition plots within the MSD. (B) Plot of sample RNT-5 MSD and WESD with the measured phyllosilicate $\delta^{18}$O and $\delta^D$ values of sample RNT-5 whose isotopic composition plots within the WESD.

4.12 Assessment of diagenesis of phyllosilicate minerals

Verifying whether an ancient phyllosilicate mineral has preserved its original isotopic composition is challenging. Nevertheless, the following discussion presents evidence that the measured isotope values of the observed phyllosilicates and the estimated paleotemperatures reflect Early to Late Cretaceous pedogenic conditions. First, the minerals observed in each sample are consistent and indicative of pedogenesis. Second, the Cretaceous deposits of north-central Texas and southern Oklahoma have undergone a low-temperature diagenetic history. Third, the phyllosilicate samples analyzed plot within their respective MSD and WESD. Fourth, calculated phyllosilicate crystallization temperatures are significantly higher than modern temperatures recorded in the study area, consistent with previous research of Cretaceous climate.

4.13 Paleoclimate of Early-Late Cretaceous of north-central Texas and southern Oklahoma with possible implications

Data produced from analyses of pedogenic minerals spanning the Early to Late Cretaceous interval of north-central Texas and southern Oklahoma reveal two periods of significant increase in precipitation. The earlier occurs between the Twin Mountains Formation (Aptian), which averages ~345mm/yr, and the middle Antlers Formation (Albian), averaging ~1119mm/yr based on CALMAG estimates. The later occurs between the upper Antlers Formation (Albian), which averages 650 mm/yr, and the Woodbine Formation (Cenomanian), averaging 1460mm/yr based on CALMAG estimates. The periods of increased precipitation are
also supported with increased kaolinite content, formed during periods of increased weathering. Estimated δ¹⁸O values of soil water from which phyllosilicates crystalized display a negative shift during both periods of increased precipitation (Fig 4.8). The δ¹⁸O values of soil water display a negative shift of ~1.1‰ from an average value of -3.3 ± 0.2‰ in the Twin Mountains Formation (Aptian) to an average value of -4.4 ± 0.2‰ in the middle Antlers Formation (Albian). Additionally, the δ¹⁸O values of soil water display a negative shift of ~1.9‰ from an average value of -3.6 ± 0.2‰ in the upper Antlers Formation (Albian) to an average value of -5.5 ± 0.2‰ in the Woodbine Formation (Cenomanian). This negative shift in soil water δ¹⁸O values could be attributed to a decrease in soil temperature, a decrease in soil water evaporation, or a combination of both factors. The periods of increased precipitation indicate a decrease in phyllosilicate crystallization temperatures with an average value of 28.5 ± 3°C in the Twin Mountains Formation (Aptian) to an average value of 26.5 ± 3°C in the middle Antlers Formation (Albian) and an average value of 31 ± 3°C in the upper Antlers Formation (Albian) to an average value of 26.7 ± 3°C in the Woodbine Formation (Cenomanian).

Both periods of increased precipitation and slightly decreased temperature coincide with the presence of extensive shallow seas on the Western Interior of North America, the first corresponding to the transgression of the Glen Rose sea and the second to the completion of the Western Interior Seaway. This suggests a link between moisture availability, variability in temperature, and proximity to large bodies of ocean water. The results indicate that a substantial increase in precipitation between the Early and Late Cretaceous may have played a role in the significant shifts in faunal and floral composition during this time interval, in particular, the rise of dominance of angiosperms.
Figure 4.8. Calculated meteoric water values. Average calculated $\delta^{18}$O values of meteoric water in equilibrium with phyllosilicates from each time interval spanning the Early-Late Cretaceous boundary.

4.14 Comparison to regional paleoclimatic trends across the Early to Late Cretaceous boundary

The paleoclimatic evidence presented in this study suggests a semi-arid environment during the Early Cretaceous (Aptian) with a marked spike in precipitation in the earliest parts of the Albian followed by a decrease in precipitation. There is then a marked increase in
precipitation suggesting more humid environments present during the Cenomanian. Several previous studies of the Western Interior of North America indicate these changes in precipitation were widespread. Mack (1992) and Kirkland et al. (1999) described Lower Cretaceous paleosols from southwestern New Mexico and east-central Utah with calcic Bk horizons indicating semi-arid conditions and paleosols in the Upper Cretaceous that lack pedogenic carbonate suggesting more humid conditions. Mack (1992) noted an increase in kaolinite content in Upper Cretaceous paleosols from New Mexico that was interpreted to indicate increased weathering of the soil profiles that was likely related to higher amounts of meteoric precipitation.

Witzke et al. (1994) describe paleosols from the Dakota Formation in Iowa as being dominated by quartz and kaolinite suggesting high amounts of weathering of the soil. The soil morphology indicated seasonal variability (Witzke et al., 1994). Retallack and Dilcher (2012) studied paleosols in the Dakota Formation from cores recovered in Kansas. Using chemical weathering indices, samples collected from these cores produced paleoprecipitation estimates of ~1500 mm/yr, similar to the estimates produced in this study of the Cenomanian Woodbine Formation of Texas in this study (~1460 mm/yr). Further work conducted by Wolf and Upchurch (1987) using fossil plants collected from the Western Interior of North America including sites in Texas and Kansas suggested a warm, subhumid climate with rainfall estimates <1600 mm/yr and averaging around 1000 mm/yr during the Cenomanian. The similarity in rainfall estimates of this study in Texas and Oklahoma along with previous reports from the western United States of America suggests the humid climate of the Cenomanian was regionally extensive.

Several attempts have been made to model the Cretaceous climate of North America by applying parameters of modern climate to Cretaceous paleogeography. Models proposed by Parrish and Curtis (1982), Parrish et al. (1982), Parrish et al. (1984) suggest an arid climate in the
study region due to the Cordilleran mountain chain blocking moisture from the Pacific and an absence of circulation over the Western Interior Seaway. In contrast, models proposed by Barron and Washington (1982) and Barron et al. (1985) suggest high amounts of rainfall as a result of zonal circulation over the Western Interior Seaway. Likewise models proposed by Poulson et al. (2007) suggest an increase in precipitation at the Albian-Cenomanian boundary of North America. The data presented in this study suggests a compromise between these models with arid conditions existing in the Early Cretaceous, but increases in annual precipitation due to moisture provided by various transgressions onto the Texas craton.

Few quantitative studies of paleosols have been conducted across the Early to Late Cretaceous interval; however, Retallack (2009) provides quantitative estimates of paleoprecipitation and paleotemperature from paleosols found in the Cedar Mountain Formation and Dakota Formation in Utah. This produced a paleoprecipitation curve suggesting an increase in precipitation around the Albian/Aptian boundary before a sharp decrease followed by another dramatic increase in rainfall during the Cenomanian. Given the limited time constraints on the sites in this study it is impossible to exactly match these curves, but the overall pattern is remarkably consistent with results produced by this study including the quantitative rainfall estimates. Estimated paleotemperatures from Retallack (2009) range from 13-18°C, significantly lower than the estimates produced in this study. This difference could be due to difference in latitude between the two study areas and difference in methodology.

4.15 Conclusions

Mineralogical and isotopic analyses of pedogenic phyllosilicates collected from paleosols spanning the Early to Late Cretaceous interval of north-central Texas and southern Oklahoma produce paleoprecipitation and paleotemperature estimates revealing significant trends in
paleoclimate. XRD analyses of the <0.2µm phyllosilicate fraction of paleosols from 7 fossil localities indicate that the pedogenic minerals are various mixtures of illite, smectite, and kaolinite. Paleosols sampled form the middle Antlers Formation (Albian) and Woodbine Formation (Cenomanian) contain significantly higher amounts of kaolinite suggesting increased weathering of the soil profiles. This is supported by MAP estimates produced from XRF analyses of bulk sediment from paleosols at each locality, revealing a significant increase in precipitation between the Twin Mountains Formation (Aptian), averaging ~345mm/yr, to the middle Antlers Formation (Albian), averaging ~1119mm/yr, and between the upper Antlers Formation (Albian), averaging 650 mm/yr, to the Woodbine Formation (Cenomanian), averaging 1460mm/yr based on CALMAG estimates.

The chemical composition and mineralogical data from the <0.2µm phyllosilicate size fraction combined with previously published thermodynamic data were used to calculate unique oxygen and hydrogen isotope fractionation factors for each sample. Assuming the phyllosilicate samples formed in equilibrium with meteoric water, the calculated oxygen and hydrogen fraction factors combined with measured oxygen and hydrogen isotopic compositions indicate crystallization temperatures ranging from 26 ± 3°C to 31 ± 3°C. Although no statistically significant trend is observed, the results indicate slight cooling from the Twin Mountains Formation (Aptian) averaging 28.5 ± 3°C to an average value of 26.5 ± 3°C in the middle Antlers Formation (Albian) and cooling from the upper Antlers Formation (Albian) averaging 31 ± 3°C in to an average value of 26.7 ± 3°C in the Woodbine Formation (Cenomanian). The range of estimated temperature produced from this study are considered consistent with pedogenic minerals formed in a near surface, low-temperature Cretaceous weathering environment. The oxygen and hydrogen isotope compositions measured from the samples plot within their
respective calculated Modern Surface Domain array or Warm Earth Surface Domain array, suggesting the pedogenic phyllosilicates preserve an isotopic record consistent with Cretaceous Earth-surface conditions.

The calculated $\delta^{18}$O values of meteoric water from which the analyzed phyllosilicates crystallized ranges from -3.0‰ to -5.6‰. The $\delta^{18}$O values of meteoric water display a negative shift of ~1.1‰ from an average value of -3.3 ± 0.2‰ in the Twin Mountains Formation (Aptian) to an average value of -4.4 ± 0.2‰ in the middle Antlers Formation (Albian) and a negative shift of ~1.9‰ from an average value of -3.6 ± 0.2‰ in the upper Antlers Formation (Albian) to an average value of -5.5 ± 0.2‰ in the Woodbine Formation (Cenomanian). This trend in the $\delta^{18}$O values of meteoric water is consistent with cooling trends calculated during these intervals and correlates to times of significant increase in paleoprecipitation. These intervals also correlate with the presence of extensive shallow seas upon the Texas craton and significant changes in fauna and flora composition.
### Complete Femora

<table>
<thead>
<tr>
<th>SMU-SMP</th>
<th>Quarry Loc.</th>
<th>Element</th>
<th>Modifier</th>
<th>Length</th>
<th>prox. condylar width</th>
<th>dist. condylar width</th>
<th>min. circum.</th>
</tr>
</thead>
<tbody>
<tr>
<td>70445</td>
<td>BMQ</td>
<td>Femur</td>
<td>Rt.</td>
<td>51</td>
<td>10.1</td>
<td>10.4</td>
<td>23.9</td>
</tr>
<tr>
<td>70456</td>
<td>2BQ</td>
<td>Femur</td>
<td>Lt.</td>
<td>273</td>
<td>60</td>
<td>70</td>
<td></td>
</tr>
<tr>
<td>70456</td>
<td>2BQ</td>
<td>Femur</td>
<td>Right</td>
<td>273.7</td>
<td>62</td>
<td>73</td>
<td></td>
</tr>
<tr>
<td>71836</td>
<td>3BS2</td>
<td>Femur</td>
<td>Lt.</td>
<td>98.9</td>
<td>22</td>
<td>21.7</td>
<td>37.4</td>
</tr>
<tr>
<td>71840</td>
<td>3BS2</td>
<td>Femur</td>
<td>Rt.</td>
<td>107.5</td>
<td>23.4</td>
<td></td>
<td>38.5</td>
</tr>
<tr>
<td>71842</td>
<td>3BS2</td>
<td>Femur</td>
<td>Lt.</td>
<td>100</td>
<td>23.8</td>
<td>23.14</td>
<td>45.4</td>
</tr>
<tr>
<td>71843</td>
<td>3BS2</td>
<td>Femur</td>
<td>Lt.</td>
<td>99</td>
<td>21</td>
<td>24</td>
<td>45</td>
</tr>
<tr>
<td>73568</td>
<td>3BS2</td>
<td>Femur</td>
<td>Lt.</td>
<td>84.1</td>
<td>21</td>
<td>20.4</td>
<td>35.3</td>
</tr>
<tr>
<td>74085</td>
<td>2DU</td>
<td>Femur</td>
<td>Lt.</td>
<td>139</td>
<td></td>
<td></td>
<td>60.4</td>
</tr>
<tr>
<td>74093</td>
<td>2DU</td>
<td>Femur</td>
<td>Rt.</td>
<td>130.1</td>
<td>34.3</td>
<td>34.12</td>
<td>51</td>
</tr>
<tr>
<td>74094</td>
<td>2DU</td>
<td>Femur</td>
<td>Lt.</td>
<td>133.6</td>
<td>36.4</td>
<td>34</td>
<td>53</td>
</tr>
<tr>
<td>74536</td>
<td>3BS1</td>
<td>Femur</td>
<td>Rt.</td>
<td>99</td>
<td>21.85</td>
<td>25</td>
<td>41</td>
</tr>
<tr>
<td>74665</td>
<td>3BS1</td>
<td>Femur</td>
<td>Rt.</td>
<td>107.6</td>
<td>22.8</td>
<td>17.1</td>
<td>39</td>
</tr>
<tr>
<td>74665</td>
<td>3BS1</td>
<td>Femur</td>
<td>Lt.</td>
<td>105.7</td>
<td>22.5</td>
<td>19.8</td>
<td>39</td>
</tr>
<tr>
<td>#######</td>
<td>3BS</td>
<td>Femur</td>
<td>Lt.</td>
<td>93.4</td>
<td>19.7</td>
<td>19.5</td>
<td>37</td>
</tr>
<tr>
<td>#######</td>
<td>3BS</td>
<td>Femur</td>
<td>Rt.</td>
<td>100</td>
<td>22.7</td>
<td>25.7</td>
<td></td>
</tr>
<tr>
<td>#######</td>
<td>5-10-93-A</td>
<td>Femur</td>
<td>Rt.</td>
<td>315</td>
<td>72.4</td>
<td></td>
<td>114.5</td>
</tr>
<tr>
<td>#######</td>
<td>N-Quad</td>
<td>Femur</td>
<td>Lt.</td>
<td>107.5</td>
<td>25</td>
<td>26.1</td>
<td>42</td>
</tr>
<tr>
<td>#######</td>
<td>N-Quad</td>
<td>Femur</td>
<td>Rt.</td>
<td>125</td>
<td>27</td>
<td>31</td>
<td>52</td>
</tr>
</tbody>
</table>

*Measurements in (mm).*
<table>
<thead>
<tr>
<th>SMU-SMP</th>
<th>Quarry Loc.</th>
<th>Element</th>
<th>Modifier</th>
<th>prox. condylar width</th>
<th>dist. condylar width</th>
<th>min. circum.</th>
<th>Predicted Length Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>70447</td>
<td>BMQ</td>
<td>Femur</td>
<td>Lt. prox.</td>
<td>10.4</td>
<td></td>
<td></td>
<td>47.2</td>
</tr>
<tr>
<td>70448</td>
<td>BMQ</td>
<td>Femur</td>
<td>Rt. prox.</td>
<td>12</td>
<td></td>
<td></td>
<td>54.1</td>
</tr>
<tr>
<td>71465</td>
<td>1A38</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>24.1</td>
<td></td>
<td></td>
<td>104.4</td>
</tr>
<tr>
<td>71493</td>
<td>2AY</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>82.5</td>
<td></td>
<td></td>
<td>307.4</td>
</tr>
<tr>
<td>71628</td>
<td>3BS</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>23</td>
<td></td>
<td></td>
<td>100.6</td>
</tr>
<tr>
<td>71652</td>
<td>3AP</td>
<td>Femur</td>
<td>Rt. prox.</td>
<td>23</td>
<td></td>
<td></td>
<td>101.5</td>
</tr>
<tr>
<td>71839</td>
<td>3BS2</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>21</td>
<td></td>
<td></td>
<td>93.7</td>
</tr>
<tr>
<td>71841</td>
<td>3BS2</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>26.5</td>
<td>38</td>
<td></td>
<td>102.8</td>
</tr>
<tr>
<td>72316</td>
<td>3AS</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>76.5</td>
<td>104</td>
<td></td>
<td>282.1</td>
</tr>
<tr>
<td>72450</td>
<td>BMQ</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>14.1</td>
<td>27.1</td>
<td></td>
<td>66.0</td>
</tr>
<tr>
<td>72451</td>
<td>BMQ</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>15.7</td>
<td></td>
<td></td>
<td>75.2</td>
</tr>
<tr>
<td>72452</td>
<td>BMQ</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>14.6</td>
<td></td>
<td></td>
<td>71.4</td>
</tr>
<tr>
<td>72543</td>
<td>BMQ</td>
<td>Femur</td>
<td>Lt. prox.</td>
<td>12.6</td>
<td></td>
<td></td>
<td>64.5</td>
</tr>
<tr>
<td>72567</td>
<td>BMQ</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>17.1</td>
<td></td>
<td></td>
<td>80.1</td>
</tr>
<tr>
<td>72568</td>
<td>BMQ</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>16.6</td>
<td></td>
<td></td>
<td>78.4</td>
</tr>
<tr>
<td>72569</td>
<td>BMQ</td>
<td>Femur</td>
<td>Lt. prox.</td>
<td>16.7</td>
<td></td>
<td></td>
<td>74.4</td>
</tr>
<tr>
<td>72634</td>
<td>8-25-86A</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>85</td>
<td></td>
<td></td>
<td>316.1</td>
</tr>
<tr>
<td>73569</td>
<td>1B7</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>62</td>
<td></td>
<td></td>
<td>236.2</td>
</tr>
<tr>
<td>74097</td>
<td>2DU</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>35.8</td>
<td></td>
<td></td>
<td>145.1</td>
</tr>
<tr>
<td>75564</td>
<td>1B7</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>62</td>
<td></td>
<td></td>
<td>236.2</td>
</tr>
<tr>
<td>77617</td>
<td>2CN</td>
<td>Femur</td>
<td>Lt. prox.</td>
<td>52.5</td>
<td>83</td>
<td></td>
<td>223.7</td>
</tr>
<tr>
<td>77817</td>
<td>2CN</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>44.6</td>
<td>91</td>
<td></td>
<td>208.5</td>
</tr>
<tr>
<td>#######</td>
<td>1B7</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>68.5</td>
<td>98</td>
<td></td>
<td>259.8</td>
</tr>
<tr>
<td>#######</td>
<td>1B7</td>
<td>Femur</td>
<td>Lt. distal</td>
<td>63</td>
<td>110</td>
<td></td>
<td>267.0</td>
</tr>
<tr>
<td>#######</td>
<td>3BS</td>
<td>Femur</td>
<td>Lt. prox.</td>
<td>22.6</td>
<td></td>
<td></td>
<td>99.8</td>
</tr>
<tr>
<td>#######</td>
<td>3BS</td>
<td>Femur</td>
<td>Rt. distal</td>
<td>22.9</td>
<td></td>
<td></td>
<td>100.3</td>
</tr>
</tbody>
</table>

*Measurements in (mm).*
<table>
<thead>
<tr>
<th>Specimen</th>
<th>Site</th>
<th>Premaxillary tooth row length (mm)</th>
<th>Number of premaxillary teeth</th>
<th>Maxillary tooth row length (mm)</th>
<th>Number of maxillary teeth</th>
<th>Dentary tooth row length (mm)</th>
<th>Number of dentary teeth</th>
<th>Scapula length (mm)</th>
<th>Humerus length (mm)</th>
<th>Femur length (mm)</th>
<th>Tibia length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>70444</td>
<td>3BS</td>
<td>11</td>
<td>4</td>
<td>-</td>
<td>30 (rt)</td>
<td>8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>75380</td>
<td>3BS</td>
<td>11</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>74664</td>
<td>3BS</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>75 (lt)</td>
<td>75 (lt)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>71836</td>
<td>3BS</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>99 (lt)</td>
<td>100 (lt)</td>
</tr>
<tr>
<td>74749</td>
<td>3BS</td>
<td>-</td>
<td>-</td>
<td>38 (lt)</td>
<td>8</td>
<td>-</td>
<td>-</td>
<td>94 (rt)</td>
<td>95 (rt)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>74097</td>
<td>2DU</td>
<td>17</td>
<td>4</td>
<td>48 (lt)</td>
<td>9</td>
<td>52 (rt)</td>
<td>11</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>74093</td>
<td>3DU</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>130 (rt)</td>
<td>155 (rt)</td>
</tr>
<tr>
<td>75564</td>
<td>East</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>192 (rt)</td>
<td>175 (rt)</td>
<td>-</td>
<td>*236 (rt)</td>
<td>-</td>
</tr>
<tr>
<td>70635</td>
<td>1B7</td>
<td>-</td>
<td>-</td>
<td>50 (rt)</td>
<td>10</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>72516</td>
<td>SAS</td>
<td>25</td>
<td>4</td>
<td>60 (rt)</td>
<td>10</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>*282 (lt)</td>
<td>*314 (lt)</td>
</tr>
<tr>
<td>72834</td>
<td>S6A</td>
<td>-</td>
<td>-</td>
<td>87 (lt)</td>
<td>10</td>
<td>95 (rt)</td>
<td>*11</td>
<td>239 (rt)</td>
<td>221 (rt)</td>
<td>*316 (rt)</td>
<td>*352 (lt)</td>
</tr>
</tbody>
</table>

* Indicates estimated length based on linear regression.
APPENDIX 3

CHARACTER DESCRIPTIONS

1. Skull proportions: 0. Preorbital skull length more than 45 per cent of basal skull length; Preorbital length less than 40 per cent of basal skull length.

2. Skull length (rostral–quadrate): 0. 10 per cent or less of body length; 1. 13 per cent or more of body length (modified following Xu et al. 2006).


4. Rostral bone, anteriorly keeled and ventrally pointed: 0. Absent; 1. Present.

5. Rostral bone, ventrolateral processes: 0. Rudimentary; 1. Well-developed.

6. Premaxilla, edentulous anterior region: 0. Absent, first premaxillary tooth is positioned adjacent to the symphysis; 1. Present, first premaxillary tooth is inset the width of one or more crowns.

7. Premaxilla, posterolateral process, length: 0. Does not contact lacrimal; 1. Contacts the lacrimal, excludes maxilla–nasal contact.

8. Oral margin of the premaxilla: 0. Narial portion of the body of the premaxilla slopes steeply from the external naris to the oral margin; 1. Ventral premaxilla flares laterally to form a partial floor of the narial fossa.
9. Position of the ventral (oral) margin of the premaxilla: 0. Level with the maxillary tooth row;
   1. Deflected ventral to maxillary tooth row.


11. Premaxillary palate: 0. Strongly arched, forming a deep, concave palate; 1. Horizontal or
    only gently arched.

12. Overlap of the dorsal process of the premaxilla onto the nasal: 0. Present; 1. Absent.


14. Premaxilla–maxilla diastema: 0. Absent, maxillary teeth continue to anterior end of maxilla;
    1. Present, substantial diastema of at least one crowns length between maxillary and
    premaxillary teeth.

15. Form of diastema; 0. Flat; 1. Arched ‘subnarial gap’ between the premaxilla and maxilla.

16. Narial fossa surrounding external nares on lateral surface of premaxilla, position of ventral
    margin of fossa relative to the ventral margin of the premaxilla: 0. Closely approaches the
    ventral margin of the premaxilla; 1. Separated by a broad flat margin from the ventral
    margin of the premaxilla.

17. External nares, position of the ventral margin: 0. Below the ventral margin of the orbits; 1.
    Above the ventral margin of the orbits.

18. External naris size: 0. Small, entirely overlies the premaxilla; 1. Enlarged, extends posteriorly
    to overlie the maxilla.

20. Internal antorbital fenestra size: 0. Large, generally at least 15 per cent of the skull length; 1. Very much reduced, less than 10 per cent of skull length, or absent.


22. External antorbital fenestra, shape: 0. Triangular; 1. Oval or circular.

23. Additional opening(s) anteriorly within the antorbital fossa: 0. Absent; 1. Present.

24. Maxilla, prominent anterolateral boss articulates with the medial premaxilla: 0. Absent; 1. Present.


27. Eminence on the rim of the buccal emargination of the maxilla near the junction with the jugal: 0. Absent; 1. Present.

28. Slot in maxilla for lacrimal: 0. Absent; 1. Present.

29. Accessory ossification(s) in the orbit (palpebral/supraorbital): 0. Absent; 1. Present.

30. Palpebral/supraorbital: 0. Free, projects into orbit from contact with lacrimal/prefrontal; 1. Incorporated into orbital margin.


32. Palpebral/supraorbital, number: 0. One; 1. Two; 2. Three.

33. Free palpebral, length, relative to anteroposterior width of orbit: 0. Does not traverse entire width of orbit; 1. Traverses entire width of orbit.
34. Exclusion of the jugal from the posteroventral margin of the external antorbital fenestra by lacrimal–maxilla contact: 0. Absent; 1. Present.

35. Anterior ramus of jugal, proportions: 0. Deeper than wide, but not as deep as the posterior ramus of the jugal; 1. Wider than deep; 2. Deeper than the posterior ramus of the jugal.

36. Widening of the skull across the jugals, chord from frontal orbital margin to extremity of jugal is more than minimum interorbital width: 0. Absent; 1. Present, skull has a triangular shape in dorsal view.

37. Position of maximum widening of the skull: 0. Beneath the jugal–postorbital bar; 1. Posteriorly, beneath the infratemporal fenestra.

38. Jugal (or jugal–epijugal) ridge dividing the lateral surface of the jugal into two planes: 0. Absent; 1. Present.


41. Node-like ornamentation on jugal, mostly on, or ventral to, the jugal–postorbital bar: 0. Absent; 1. Present.

42. Jugal–postorbital bar, width broader than infratemporal fenestra: 0. Absent; 1. Present.


44. Jugal, form of postorbital process: 0. Not expanded dorsally; 1. Dorsal portion of postorbital process is expanded posteriorly.

45. Jugal–squamosal contact above infratemporal fenestra: 0. Absent; 1. Present.
46. Jugal posterior ramus, forked: 0. Absent; 1. Present.

47. Jugal, posterior ramus: 0. Forms anterior and ventral margin of infratemporal fenestra; 1.

Forms part of posterior margin, expands towards squamosal.


49. Postorbital, orbital margin: 0. Relatively smooth curve; 1. Prominent and distinct projection into orbit.


51. Postorbital–parietal contact: 0. Absent, or very narrow; 1. Broad.

52. Contact between dorsal process of quadratojugal and descending process of the squamosal: 0.

Present; 1. Absent.

53. Quadratojugal, shape: 0. L-shaped, with elongate anterior process; 1. Subrectangular with long axis vertical, short, deep anterior process.

54. Quadratojugal, ventral margin: 0. Approaches the mandibular condyle of the quadrate; 1.

Well-removed from the mandibular condyle of the quadrate.

55. Quadratojugal, orientation: 0. Faces laterally; 1. Faces posterolaterally.

56. Quadratojugal, transverse width: 0. Mediolaterally flattened; 1. Transversely expanded and triangular in coronal section.

57. Prominent oval fossa on pterygoid ramus of quadrate: 0. Absent; 1. Present.

58. Quadrate lateral ramus: 0. Present; 1. Absent.
59. Quadrate shaft: 0. Anteriorly convex in lateral view; 1. Reduced in anteroposterior width and straight in lateral view.

60. Paraquadratic foramen or notch, size: 0. Absent or small, opens between quadratojugal and quadrate; 1. Large.

61. Paraquadratic foramen, orientation: 0. Posterolateral aspect of quadrate shaft; 1. Lateral aspect of quadrate or quadratojugal.


63. Quadrate mandibular articulation: 0. Quadrate condyles subequal in size; 1. Medial condyle is larger than lateral condyle; 2. Lateral condyle is larger than medial.

64. Paired frontals: 0. Short and broad; 1. Narrow and elongate (more than twice as long as wide).

65. Supratemporal fenestrae: 0. Open; 1. Closed.

66. Supratemporal fenestrae, anteroposteriorly elongated: 0. Absent, fenestrae are subcircular to oval in shape 1. Present.


68. Parietosquamosal shelf: 0. Absent; 1. Present.

69. Parietosquamosal shelf, extended posteriorly as distinct frill: 0. Absent; 1. Present.
70. Composition of the posterior margin of the parietosquamosal shelf: 0. Parietal contributes only a small portion to the posterior margin; 1. Parietal makes up at least 50 per cent of the posterior margin.


73. Enlarged tubercle row on the posterior squamosal: 0. Absent; 1. Present.

74. Frontal and parietal dorsoventral thickness: 0. Thin; 1. Thick.

75. Paroccipital processes: 0. Extend laterally and are slightly expanded distally; 1. Distal end pendent and ventrally extending.

76. Paroccipital processes, proportions: 0. Short and deep (height $\geq 1/2$ length); 1. Elongate and narrow.

77. Posttemporal foramen/fossa, position: 0. Totally enclosed with the paroccipital process; 1. Forms a notch in the dorsal margin of the paroccipital process, enclosed dorsally by the squamosal.

78. Supraoccipital, contribution to dorsal margin of foramen magnum: 0. Forms entire dorsal margin of foramen magnum; 1. Exoccipital with medial process that restricts the contribution of the supraoccipital.

79. Basioccipital, contribution to the border of the foramen magnum: 0. Present; 1. Absent, excluded by exoccipitals.

80. Basisphenoid: 0. Longer than, or subequal in length to, basioccipital; 1. Shorter than basioccipital.


84. Premaxilla–vomeral contact: 0. Present; 1. Absent, excluded by midline contact between maxillae.

85. Dorsoventrally deep (deeper than 50% of snout depth) median palatal keel formed of the vomers, pterygoids and palatines: 0. Absent; 1. Present.

86. Pterygovomerine keel, length: 0. Less than 50% of palate length; 1. More than 50% of palate length.

87. Pterygoid–maxilla contact at posterior end of tooth row: 0. Absent; 1. Present.

88. Pterygoquadrate rami, posterior projection of ventral margin: 0. Weak; 1. Pronounced.

89. Cortical remodeling of surface of skull dermal bone: 0. Absent; 1. Present.

90. Predentary: 0. Absent; 1. Present.

91. Predentary size: 0. Short, posterior premaxillary teeth oppose anterior dentary teeth; 1. Roughly equal in length to the premaxilla, premaxillary teeth only oppose predentary.

92. Predentary, rostral end in dorsal view: 0. Rounded; 1. Pointed.

93. Predentary, oral margin: 0. Relatively smooth; 1. Denticulate.

94. Tip of predentary in lateral view: 0. Does not project above the main body of predentary; 1. Strongly upturned relative to main body of predentary.

96. Predentary, ventral process: 0. Present, well-developed; 31. Very reduced or absent.


98. Dentary tooth row (and edentulous anterior portion) in lateral view: 0. Straight; 1. Anterior end downturned.


100. Ventral flange on dentary: 0. Absent; 1. Present.

101. Coronoid process: 0. Absent or weak, posterodorsally oblique, depth of mandible at coronoid is less than 140% depth of mandible beneath tooth row; 1. Well-developed, distinctly elevated, depth of mandible at coronoid is more than 180% depth of mandible beneath tooth row.

102. Anterodorsal margin of coronoid process formed by posterodorsal process of dentary: 0. Absent; 1. Present.

103. Coronoid process, position: 0. Posterior to dentition; 1. Lateral to dentition.

104. External mandibular fenestra, situated on dentary-surangular-angular boundary: 0. Present; 1. Absent.


106. Ridge or process on lateral surface of surangular, anterior to jaw suture: 0. Absent; 1. Present, anteroposteriorly extended ridge; 2. Present, dorsally directed finger-like process.


109. Level of jaw joint: 0. Level with tooth row, or weakly depressed ventrally; 1. Strongly depressed ventrally, more than 40% of the height of the quadrate is below the level of the maxilla.

110. Mandibular osteoderm: 0. Absent; 1. Present.

111. Premaxillary teeth: 0. Present; 1. Absent, premaxilla edentulous.

112. Premaxillary teeth, number: 0. Six; 1. Five; 2. Four; 3. Three; 4. Two; 5. One. (ordered character)

113. Premaxillary teeth, crown expanded above root: 0. Crown is unexpanded mesiodistally above root, no distinction between root and crown is observable; 1. Crown is at least moderately expanded above root.

114. Premaxillary teeth increase in size posteriorly: 0. Absent, all premaxillary teeth subequal in size; 1. Present, posterior premaxillary teeth are significantly larger in size than anterior teeth.


116. Maxillary/dentary teeth, marginal ornamentations: 0. Fine serrations set at right angles to the margin of the tooth; 1. Coarse serrations (denticles) angle upwards at 45 degrees from the margin of the tooth.

117. Enamel on maxillary/dentary teeth: 0. Symmetrical; 1. Asymmetrical.
118. Apicobasally extending ridges on maxillary/dentary teeth: 0. Absent; 1. Present.

119. Apicobasally extending ridges on lingual/labial surfaces of maxillary/dentary crowns confluent with marginal denticles: 0. Absent; 1. Present.

120. Prominent primary ridge on labial side of maxillary teeth: 0. Absent; 1. Present.

121. Prominent primary ridge on lingual side of dentary teeth: 0. Absent; 1. Present.

122. Position of maxillary/dentary primary ridge: 0. Centre of the crown surface, giving the crown a relatively symmetrical shape in lingual/labial view; 1. Offset, giving crown asymmetrical appearance.

123. At least moderately developed labiolingual expansion of crown (‘cingulum’) on maxillary/dentary teeth: 0. Present; 1. Absent.

124. Heterodont dentary dentition: 0. No substantial heterodonty is present in dentary dentition; 1. Single, enlarged, caniform anterior dentary tooth, crown is not mesiodistally expanded above root; 2. Anterior dentary teeth are strongly recurved and caniform, but have crowns expanded mesiodistally above their roots and are not enlarged relative to other dentary teeth.

125. Peg-like tooth located anteriorly within dentary, lacks denticles, strongly reduced in size: 0. Absent; 1. Present.

126. Alveolar foramina (‘special foramina’) medial to maxillary/dentary tooth rows: 0. Present; 1. Absent.

127. Recurvatur in maxillary and dentary teeth: 0. Present; 1. Absent.

128. Overlap of adjacent crowns in maxillary and dentary teeth: 0. Absent; 1. Present.
129. Crown is mesiodistally expanded above root in cheek teeth: 0. Absent; 1. Present.


131. Close-packing and quicker replacement eliminates spaces between alveolar border and crowns of adjacent functional teeth: 0. Absent; 1. Present.

132. Fusion between the intercentrum of the atlas and the neural arches: 0. Absent; 1. Present.

133. Epipophyses on anterior (postaxial) cervicals: 0. Present; 1. Absent.

134. Cervicals 4-9, form of central surfaces: 0. Amphicoelous; 1. At least slightly opisthocoelous.

135. Cervical number: 0. Seven/eight; 1. Nine; 2. Ten or more. (ordered character).


137. Dorsals, number: 0. 12–13; 1. 15; 2. 16 or more. (ordered character)

138. Sacrals, number: 0. Two; 1. Three; 2. Four/five; 3. Six or more. (ordered character).

139. Sacrum, accessory articulation with pubis: 0. Absent; 1. Present.

140. Posterior sacral ribs are considerably longer than anterior sacral ribs: 0. Absent; 1. Present.

141. Anterior caudal vertebrae, length of transverse processes relative to neural spine height: 0. Subequal; 1. Longer than neural spine.
142. Proximal caudal neural spines: 0. Height the same or up to 50 per cent taller than the centrum; 1. More than 50 per cent taller than the centrum.

143. Elongate tail (59 or more caudals): 0. Absent; 1. Present.

144. Chevron shape: 0. Rod-shaped, often with slight distal expansion; 1. Strongly asymmetrically expanded distally, width greater than length in mid caudals.


146. Gastralia: 0. Present; 1. Absent.

147. Ossified clavicles: 0. Absent; 1. Present.


149. Proportions of humerus and scapula: 0. Scapula longer or subequal to the humerus; 1. Humerus substantially longer than the scapula.

150. Scapula blade, length relative to minimum width: 0. Relatively short and broad, length is 5-8 times minimum width; 1. Elongate and strap-like, length is at least 9 times the minimum width.

151. Scapula acromion shape: 0. Weakly developed or absent; 1. Well-developed spine-like.

152. Scapula, blade-shape: 0. Strongly expanded distally; 1. Weakly expanded, near parallel-sided.

153. Humeral length: 0. More than 60% of femoral length; 1. Less than 60% of femoral length.
154. Deltopectoral crest development: 0. Well-developed, projects anteriorly as a distinct flange;
   1. Rudimentary, is at most a thickening on the anterolateral margin of the humerus.

155. Humeral shaft form, in anterior or posterior view: 0. Relatively straight; 1. Strongly bowed
   laterally along length.

156. Longest manual phalanx as percentage of length of humerus: 0. Less than 10%; 1. More
   than 15%.


158. Metacarpals 1 and 5: 0. Substantially shorter in length than metacarpal 3; 1. Subequal in
   length to metacarpal 3.

159. Penultimate phalanx of the second and third fingers: 0. Shorter than first phalanx; 1. Longer
   than the first phalanx.

160. Manual digit 3, number of phalanges: 0. Four; 1. Three or fewer.

161. Manual digits 2–4: 0. First phalanx relatively short compared to second phalanx; 1. First
   phalanx more than twice the length of the second phalanx.

162. Extensor pits on the dorsal surface of the distal end of metacarpals and manual phalanges: 0.
   Absent or poorly developed; 1. Deep, well-developed.


164. Acetabulum: 0. At least a small perforation; 1. Completely closed.

165. Preacetabular process, shape / length: 0. Short, tab-shaped, distal end is posterior to pubic
   peduncle; 1. Elongate, strap-shaped, distal end is anterior to pubic peduncle.
166. Preacetabular process, length: 0. Less than 50% of the length of the ilium; 1. More than 50% of the length of the ilium.

167. Preacetabular process, lateral deflection: 0. 10–20 degrees from midline; 1. More than 30 degrees.

168. Dorsal margin of preacetabular process and dorsal margin of ilium above acetabulum: 0. Narrow, not transversely expanded; 1. Dorsal margin is transversely expanded to form a narrow shelf.

169. In dorsal view preacetabular process of the ilium expands mediolaterally towards its distal end: 0. Absent; 1. Present.

170. Dorsal margin of the ilium in lateral view: 0. Relatively straight or slightly convex; 1. Sinuous, postacetabular process is strongly upturned.

171. Subtriangular process extending medially from the dorsal margin of the iliac blade: 0. Absent; 1. Present.

172. Subtriangular process, form and position: 0. Short and tab-like, above acetabulum; 1. Elongate and flange-like, on postacetabular process.

173. Brevis shelf & fossa: 0. Fossa faces ventrolaterally and shelf is near vertical and visible in lateral view along entire length, creating a deep postacetabular portion; 1. Fossa faces ventrally and posterior of shelf portion cannot be seen in lateral view.

174. Length of the postacetabular process as a percentage of the total length of the ilium: 0. 20% or less; 1. 25-35%; 2. More than 35%. (ordered character).
175. Medioventral acetabular flange of ilium, partially closes the acetabulum: 0. Present; 1. Absent.

176. Supra-acetabular ‘crest’ or ‘flange’: 0. Present; 1. Absent.

177. Ischial peduncle of the ilium: 0. Projects ventrally; 1. Broadly swollen, projects ventrolaterally.

178. Pubic peduncle of ilium: 0. Large, elongate, robust; 1. Reduced in size, shorter in length than ischial peduncle.

179. Pubic peduncle of ischium, shape: 0. Transversely compressed; 1. Dorsoventrally compressed.


182. Ischial shaft: 0. Expands weakly, or is parallel-sided, distally; 1. Distally expanded into a distinct ‘foot’; 2. Tapers distally.

183. Groove on the dorsal margin of the ischium: 0. Absent; 1. Present.

184. Tab-shaped obturator process on ischium: 0. Absent; 1. Present.

185. Ischial symphysis, length: 0. Ischium forms a median symphysis with the opposing blade along at least 50% of its length; 1. Ischial symphysis present distally only.

186. Pubis, orientation: 0. Anteroventral; 1. Rotated posteroventrally to lie alongside the ischium (opisthopubic).

188. Shaft of pubis (postpubis), length: 0. Approximately equal in length to the ischium; 1. Reduced, extends for half or less the length of the ischium.

189. Reduction of postpubic shaft: 0. Postpubic shaft extends for around half the length of ischium; 1. Postpubic shaft is very short or absent.

190. Body of pubis, size: 0. Relatively large, makes substantial contribution to the margin of the acetabulum; 1. Reduced in size, rudimentary, nearly excluded from the acetabulum.

191. Body of the pubis, massive and dorsolaterally rotated so that obturator foramen is obscured in lateral view: 0. Absent; 1. Present.

192. Prepubic process: 0. Absent; 1. Present.


194. Prepubic process, length: 0. Stub-like and poorly developed, extends only a short distance anterior to the pubic peduncle of the ilium; 1. Elongated into distinct anterior process.

195. Prepubic process, extends beyond distal end of preacetabular process of ilium: 0. Absent; 1. Present.

196. Extent of pubic symphysis: 0. Elongate; 1. Restricted to distal end of pubic blade, or absent.

198. Femoral head: 0. Confluent with greater trochanter, fossa trochanteris is groove-like; 1. Fossa trochanteris is modified into distinct constriction separating head and greater trochanter.

199. ‘Anterior’ or ‘lesser’ trochanter, morphology: 0. Absent; 1. Trochanteric shelf ending in a small, pointed, spike; 2. Broadened, prominent, ‘wing’ or ‘blade’ shaped, sub-equal in anteroposterior width to greater trochanter; 3. Reduced anteroposterior width, closely appressed to the expanded greater trochanter.

200. Level of most proximal point of anterior trochanter relative to level of proximal femoral head: 0. Anterior trochanter is positioned distally on the shaft, and separated from ‘dorsolateral’ trochanter/greater trochanter by deep notch visible in medial view; 1. Anterior trochanter positioned proximally, approaches level of proximal surface of femoral head, closely appressed to ‘dorsolateral’/greater trochanter (no notch visible in medial view).

201. Fourth trochanter of femur, shape: 0. Low eminence, or absent; 1. Prominent ridge; 2. Pendent.

202. Fourth trochanter, position: 0. Located entirely on proximal half of femur; 1. Positioned at midlength, or distal to midlength.

203. Anterior (extensor) intercondylar groove on distal end of femur: 0. Absent; 1. Present.

204. Posterior (flexor) intercondylar groove of the femur: 0. Fully open; 1. Medial condyle inflated laterally, partially covers opening of flexor groove.
205. Lateral condyle of distal femur, position and size in ventral view: 0. Positioned relatively laterally, and slightly narrower in width than the medial condyle; 1. Strongly inset medially, reduced in width relative to medial condyle.

206. Distal tibia: 0. Subquadrate, posterolateral process is not substantially developed; 1. Elongate posterolateral process, backs fibula.

207. Fibular facet on the lateral margin of the proximal surface of the astragalus: 0. Large; 1. Reduced to small articulation.

208. Calcaneum, proximal surface: 0. Facet for tibia absent; 1. Well-developed facet for tibia present.

209. Medial distal tarsal: 0. Articulates distally with metatarsal 3 only; 1. Articulates distally with metatarsals 2 and 3.

210. Metatarsal arrangement: 0. Compact, closely appressed to one another along 50-70% of their length, spread distally; 1. Contact each other only at proximal ends, spread strongly outwards distally.

211. Digit 1: 0. Metatarsal 1 robust and well-developed, distal end of phalanx 1-1 projects beyond the distal end of metatarsal 2; 1. Metatarsal 1 reduced & proximally splint like, end of phalanx 1-1 does not extend beyond the end of metatarsal 2; 2. Metatarsal 1 reduced to a vestigal splint or absent, does not bear digits.

212. Pedal digit 4 phalangeal number: 0. Five; 1. Four or fewer.

213. Metatarsal 5, length: 0. More than 50 per cent of metatarsal 3; 1. Less than 25 per cent of metatarsal 3.
214. Metatarsal 5: 0. Bears digits; 1. Lacks digits.


216. Epaxial ossified tendons present along vertebral column: 0. Absent; 1. Present.

217. Ossified hypaxial tendons, present on caudal vertebrae: 0. Absent; 1. Present.


219. Parasagittal row of dermal osteoderms on the dorsum of the body: 0. Absent; 1. Present.

220. Lateral row of keeled dermal osteoderms on the dorsum of the body: 0. Absent; 1. Present.


222. Wear facets on teeth: 0. Absent or sporadically developed; 1. Systematic development of wear facets along the entire tooth row.

223. Head of humerus is separated from prominent medial tubercle on proximal surface by a groove: 0. Absent; 1. Present.

224. Pendent fourth trochanter, rod-like with subparallel anterior and posterior surfaces: 0. Absent; 1. Present.

225. Fibula, distal end is strongly reduced and splint-like: 0. Absent; 1. Present.

226. Astragalus and calcaneum are indistinguishably fused to one another: 0. Absent; 1. Present.
227. Maximum expansion of distal tibia relative to proximal: 0. Distal tibia is considerably less expanded than proximal; 1. Maximum expansion of distal tibia is subequal to that of proximal tibia.

New characters

C. 228. Position of pterygoid wing on the quadrate: 0. The pterygoid wing of the quadrate arises at the dorsal head of the quadrate; 1. Pterygoid wing of the quadrate arises below the dorsal head of the quadrate. (Scheetz 1999: ch. 8).

C. 229. Ventral extent of the jugal wing on the quadrate: 0. Ventral extent of the jugal wing of the quadrate positioned at or near the distal end of the quadrate; 1. Ventral extent of the jugal wing of the quadrate positioned above the distal end of the quadrate. (Scheetz 1999: ch. 9).

C. 230. Shape of maxillary tooth roots: 0. Maxillary tooth roots straight in anterior or posterior view; 1. Maxillary tooth roots curved in anterior or posterior view. (Scheetz 1999: ch. 33).

C. 231. Shape of dentary tooth roots: 0. Dentary tooth roots straight in anterior or posterior view; 1. Dentary tooth roots curved in anterior or posterior view. (Scheetz 1999: ch. 59).

C. 232. Height of sacral neural spines: 0. Sacral neural spines less than twice the height of the sacral centra; 1. Sacral neural spines between 2 and 2.5 times the height of the sacral
centra; 2. Sacral neural spines greater than 2.5 times the height of the sacral centra.  
(Scheetz 1999: ch 82).

APPENDIX 4

CHARACTER MATRIX

Taxon-by-character matrix with 55 taxa (54 from Baron et al. 2016 with the addition of the Proctor Lake taxon) and 233 characters (#1-227 from Baron et al. 2016; #228-232 from Scheetz 1999; and one new character, #233: presence of medial groove on buccal surface of premaxillary teeth). Numbers refer to character states listed in the character descriptions (Appendix 2).

(?) refers to a character that could not be scored due to incomplete preservation
(-) refers to a character not applicable to the taxon
(a) refers to polymorphic scoring of 0/1
(b) refers to polymorphic scoring of 1/2
(c) refers to polymorphic scoring of 0/1/2
(d) refers to polymorphic scoring of 0/2
(e) refers to polymorphic scoring of 2/3

_Euparkeria capensis_

000??0000 000?0000 000000000? 0?000?000 0000000000
000000000 00100000? 0000010000 00000?0000 00000?0000
000000000 02000000?0 0?10010000 0010001000 00000?1000
11000?00? ?0?1000000 0??2010000 00000000?0 00??0000?
000000000 000000?1? 000?000?? ?

_Marasuchus liloensis_

?0???????? ?????????? ?????????? ?????????? ??????????
?????????? ?????????? ??????????0 0?0???????? ??????????
?????????? ?????????? ?????????? ?010?0?000 00?0??????
?000????? ???0000?1 0??2000000 00000000?0 00??00010
Herrerasaurus
000??00000 0000?11010 010000000? ???000?000 0000010000
0000000000 001000000? 0000001000 000?0?0000 ????000000
0000000000 020000000? 0?10010000 0000201000 00000?000?1
1100011010 0110000000 0?01000000 10000000?0 00??00010
1000000000 0000000000 001?0001?? ???

Pisanosaurus mertii
?0???????? ?????????? ?????1???? ?????????? ?????????
?????????? ?????????? ?????????? ?????????? ???????000
?10?000000 ????1??0?0 0??0?1111 0??0?????? ?????????
?????????? ?????????? ?????????? ??????????0 ?????????
?????0?0?0 ??????0?00 01??000??? ???

Abrictosaurus consors
000??10011 ??011000?1 00??010010 0000?0???? ?????????
????0???? ?????????? ?????????? ??????????01 1000?10000
11000?00?0 030011?0?0 ??001?1111 0????????0 ??????????0
1000?10?? 01?0100000 0?11?100?? ?????????? ?????????0?2?
200??1???0 10110????00 01?11????? ???

BMNH A100
??0??1?0?? 1?01100??1 00?00100?? ?????0?0?? 00?00????
?????????? ?????000?? ?????0???? ??????????0? ???????0000
??????????0 030111?0?0 ??01111111 0????????? ?????????
?????????? ?????????? ?????????? ?????????? ?????????
?????????? ?????????? ?????????? ?????????? ????
Fruitadens haagarorum

Tianyulong

Heterodontosaurus tucki

Lycorhinus angustidens

Eocursor parvus
Lesothosaurus diagnosticus
000??10001 1000?000?1 0000010110 000000?000 0000010000
001000000 000000000? 0000000000 000?0001 0000001000
010001000 00101100?0 0?00001111 0000?01200 00?????00
10000000? 0000100000 0?01000000 0111110?0 0100010020
200011100 1?11010000 01000010?0 0??

Scutellosaurus lawleri
?00????0?1 1????00?? ????10??? ????10?000 00000100??
????0??0?? ??1100???? ? ??????? ??? ?????1? ?????????00
0????1?0?0 00?01100?0 0?0?001111 00?01012?? 0?1???????
1?000?00?? 0000100000 0??1?0??00 00000110?0 010??10020
20001???0 0???01??11 000000100? 0??

Laquintasaura
??????1???? ???????????1 000??0???? ?????1??000 000?????00
????????0?0 ?????100???? ?????0???? ????????? ?? ????????00
00??????0??0?0000 00?0101110 00?01111110 010??10020
20001111?? ?????0????? ?0?0?01??? ?0

Emausaurus ernstii
0?0??000? 1000?000?1 0000010010 100010?000 0000010000
001000?000 00?000000? 000?????00 ?0??????1? 0??????1100
010001000 01101100?0 0?00001111 0???????? ???????????
Scelidosaurus harrisonii
000??100?? 0?0?0????10 0100010011 ?2?010?000 0100010000
001000000 00100000?? 000000?001 001?10001? 0??????1100
0101010001 01101100?0 0?00001111 000002200 0000010?00
1000????? ???010100 0?00000000 00001110?0 1100010020
2100011100 0011110011 1100001??? ???

Stegosauria
000??10001 10a0?00001 0000010011 ?2?010?000 0000000000
0110001100 00100000?? 000a01001 00001?0001 0000001100
110000000 a?101100?0 0?00001111 0110c0c200 0100010?00
1100?0101 0000111100 0?00000000 02001110?0 a1010110??
01000111?1 121111a0011 000?001??? ??0

Ankylosauria
000??10001 1000?00001 1?00010011 ?2??10?000 0110000000
0?1?100100 00101?10?? 100000?001 0000110011 0000?11100
0101000001 0?101100?0 0?00001111 011000?b00 0000010100
?1000?0101 0001111100 0?00000010 0d001111a1 11000110??
01000111?1 2111110011 1a0?0?1??? ??0

Agilisaurus louderbacki
000??10001 1000?00011 000?010?10 111000?000 0000000000
0?10001000 00100000?? 000010?000 00??0?0001 0?00001000
1101000000 01101100?0 0?02001111 001101200 0000010?10
10100????? ???0100000 0?01000100 00110110?0 0101010020
2000011100 1011010000 0100001??? ??a0
**Hexinlusaurus multidens**

?00??0??? ????0???011 000??10?10 000100?000 0000000000
0?1000?000 00?00000?? 00001????? ?????????0? ???????1000
110????000 ????110100 0?0?001111 0010101200 0000010?10
1000000000 0000100000 0?11010100 00011110?0 0111110020
200011110 1011010000 0000001??? ??0

**Othnieliosaurus consors**

??????????? ?????????? ?????????? ?????????? ???????????
??????????? ?????????? ?????????? ?????????? ???????????00
???????0?0 ????1110?0 0?0????1?1? 0??0?013?0 00?0110100
1000????? ???0100000 0?11111100 00011110?0 0111110131
200011110 101101?000 0?00001??0 000

**Wannanosaurus yansiensis**

??????????? ?????????? ?????????11 ????0?000 101000000?
??????????? ?????00100 1101?????? ?????????0? ???????000
1001000000 ????11?0?? 0?0????1111 0???0????? ???????????
??111????? ????1?111? ?????1????? ?????????? ???????0???
?00??1???? ???????????? ?0001?0??? ??0

**Goyocephale lattimorei**

??0???001? ??01100001 ????10?11 ?1??00?000 1?10??????
1???????? ???0000100 111110???? ?1?1??0?0? ???????000
1?010?0100 031111?aa0 0?01???111? 00???1?2?? ?????????2??
??111????? ???0101110 101211???? ?????????? ??????????
?????1??1? ???011100 010???????? ??0

**Homalocephale calathocercos**
Pachycephalosauridae
000??10011 1001a00001 1??010011 ?1??00?000 111000000?
111000000 00001?1100 111110?a00 11010?a10? ?????0000
1001000100 03aa11?aa0 0?0b?0a111 0????1?3?1 1??0????201
1011????? ???0101110 112111111 00001????? ??????0131
10?0????? ??????11100 01001?1??? ??0

Micropachycephalosaurus hongtuy
?????????? ?????????? ?????????? ?????????? ???????????
????????00? ??2?????? ?????????? ?????????? ???????????
?????????? ?????11?0?? ??0??111? 0????????? ???0??????
?????????? ???01?000? ?????1?1?? ?????????? ???????0131
?0?0?????? ?????????? ?0?????? ??0

Stenopelix valdensis
?????????? ?????????? ?????????? ?????????? ???????????
?????????? ?????????? ?????????? ?????????? ???????????
?????????? ?????????? ?????????? ????????3?0 0??0??????
?1???????? ???0100110 0?11110102 00001111?0 0121?10131
?????1???0 0011010000 0???001??? ??0

Chaoyangosaurus youngi
1?1001?00? 0?000110?1 ????011??? ?????210000 1????000??
??1000?000 002??????? ??????????0? ?0??0?0?01 1101?01000
Yinlong downsi
111011?001 0??0?00011 010??10?10 0000210100 1000000000
011000?000 0020010101 0110100?00 112??0001 0100101000
1100101100 031011?0?0 ??00?1111 0????????? ?????????
 ??????? ??00100110 0?1?110?? ??????11100 0121010?21
20??????? ??????0???00 0???????0? ??0

Albalophosaurus yamaguchiorum
????????? ????????? 00????0?10 10?????0?0 0?????????
????????0?? ???0?????? ???00???? ??????02????0? ?????????
110????0?0 ?????11111 110????111? 0????????? ?????????
 ????????? ????????? ????????? ????????? ?????????
 ????????? ????????? ????????? ????????? ?1??????? ??0

Psittacosauridae
1110011001 000??11001 ???0011010 100?210100 0000010000
011000000 002000101 0000a0000 00010?1001 1a00001001
111aa0000 1??11111 100001111 001a00310 0?0001110a
100000000 0000100000 0??211a100 0000111110 0121010a31
2010011100 0011010000 0100001??? ??0

Liaoceratops yanzigouensis
0?11111001 000?100011 000?0110?? ???0211100 0101100001
011000010 002001011 00001?010 001?0?0001 1001001001
1111001100 031011111 1100001111 0????????? ?????????
 ????????? ????????? ????????? ????????? ?????????
Archaeoceratops oshimai
0111110001 0001000001 000?010010 1000211110 1101100001
0?1011?010 0020010111 000001?01? ?01?0???01 1101101000
1111011100 031011??1 1?00001111 1????10311 0??0??????
????????? ???0100000 0?12111110? 0000111110 012101?131
????11110 0011010000 01??0?10? ??0

Unnamed taxon Coronosauria L
011111000? 0001010001 0100010010 1000211110 0101100001
0110110010 0020010111 000001?010 00b10?1001 11011010?0
1111011100 a41011111 1100001111 1?102?03?0 0?0011101
1000000000 1000100001 0?12111100 0000111110 0100010131
2010011110 0011a10000 0100001?? ?0

Orodromeus makelai
000??10001 1?10?00011 0101010010 000000?001 0000000010
0110000000 00010000?? 0000100000 000?????01 0??0?0100
1101100000 01101100?0 0?00001111 0010101310 00?0?10100
10?0000000 0000100000 0?12111100 00011110?0 0111110131
2010a11110 001101?000 010001?100 000

Zephyrosaurus schaffi
??0??1?011 10?10000?1 0??1010?10 100?00?001 00000?0?10
0??0??100? ??01000000 001????0?0 ??????????
?????????? 0110111?10 0?00?01111 0???????? ??????????
?????????? ????????? ????????? ????????? ?????????
?????????? ????????? ????????? ????????? ?????????

159
Hayagriva
0?0??10001 ?011011011 0010010010 0101000000 0001010010
0110000001 11010000?? 0000100000 000?001001 110?101000
1101100000 0110110110 0?00001111 0010101310 00?0?10100
10000?00?? ?0?0100000 0?12110000 0001?110?0 0111110131
2000011?10 00??010000 0000001??? ??0

Changchunsaurus parvus
000??1?001 1?110000?1 0???010?10 ?0??00?001 10??100??
?11000000? ??0????0?? 000?????000 ?0000?0001 1101101010
1111100000 01101101a0 0?00001111 00101?1??? ???????1?0
10?0?????? ???0?????? ??1?1?1??? ??????????? ?????????1
??????1?1?0 1???01?000 010000???? ??0

Jeholosaurus shangyuanensis
0?0??11001 1010?00011 000??10?10 000100?000 1000010000
0110000001 11010000?? 0000100?00 ?001???001 1100001000
1101000000 001011?110 0?00001111 00001??300 00?0?1??10
01000?????? ???0100000 0?11101100 00110110?? 01???10131
2000011110 10??01?000 0??000100? ?0

Hypsilo phodon foxii
000??10011 1011000011 0010010010 000100?000 0000000000
0110000001 11010000?? 0001000000 00100?0001 1100001000
1101100010 01101111a0 1000001111 0010101310 0000110100
1000000000 0000100000 0?12111100 00011110?0 0111110131
2000011110 0011011000 0100001000 100

Proctor Taxon
000--10011 1011000001 0000010010 0111000000 0000000000
<table>
<thead>
<tr>
<th>Species</th>
<th>Binary Code</th>
<th>Hexadecimal Code</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thescelosaurus neglectus</td>
<td>0110000001</td>
<td>1101000000</td>
<td>000??10011 10110000?1 0101010010 010100000 00000000010</td>
</tr>
<tr>
<td>Parksosaurus warreni</td>
<td>00????0???</td>
<td>??10??0010</td>
<td>0?10??10010 0?1000000 0001?00000</td>
</tr>
<tr>
<td>Gasparinisaura cincosaltensis</td>
<td>00?????????</td>
<td>??10??????1</td>
<td>010??10010 001000000 000000000</td>
</tr>
<tr>
<td>Talenkauen santacrucensis</td>
<td>?00??101??</td>
<td>1?010000?1</td>
<td>0???010000 0000000000 000000000000</td>
</tr>
</tbody>
</table>

161
Rhabdodontidae
000??10010 100??000001 01000100?? ???100?000 0000001100
0111000000 0?2000000?? 0000101000 ?01?????01 1000101010
111??0000 ??111111 1010001111 0?11?0?3?0 01?0?10??0
00?00?????? ???0100100 0??1110110 10001????? ???????1131
2111?111?? ???111?00 01000010?? 110

Tenontosaurus tilleti
000??11110 100??00101 0100110010 000100?000 0000000100
0111000001 11000000?? 0000101100 001?0?0001 1010001010
1111120000 1???111110 1010001111 0001202310 0110010100
0000000001 1000100001 0?11111100 0101111100 0101111131
2111111110 001101100 0100001??1 110

Tenontosaurus dossi
000--11111 100100101 0100010010 0001000000 0000000100
0110000001 110000000? 0000101100 ?0?00?0?01 1010001010
1111?20000 0???111110 1010001111 0?0120?3?0 0110?10100
10000000?? ?000100001 0-11111100 01011110-0 0101110131
2111111110? 0011011000 0100001?11 110

Dryosauridae
000??11110 110??00101 0100110110 001000?000 0000001000
0111000001 1?000000?? 0000101100 00100?0001 1010101000
1111000000 1???211101 1010001111 0?11101310 0100010100
0000?????? ???0100001 0?11111110 11011110?0 0101110131
2011111110 201010000 01000011?1 110

162
Ankylopellexia

000??11110 100??00101 0100110010 000000?000 0000001000
011100000a 1000000?? 0000101100 00200?0001 1010101010
1111100010 1???211101 1010001111 1011b02e?0 0100010b00
a000000001 100010000a 0?11111110 1101111100 01011111e1
2111111100 0011010200 0100001?? ??0
APPENDIX 5

CHARACTER CHANGES MADE TO *TENONTOSAURUS DOSSI*

Table lists changes made to the scoring of *Tenontosaurus dossi* in the original character matrix Baron et al. 2016.

<table>
<thead>
<tr>
<th>Character</th>
<th>Original Score</th>
<th>Updated Score</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>?</td>
<td>-</td>
<td>not applicable</td>
</tr>
<tr>
<td>5</td>
<td>?</td>
<td>-</td>
<td>not applicable</td>
</tr>
<tr>
<td>6</td>
<td>?</td>
<td>1</td>
<td>(Winkler et al. 1997 Fig 2,3)</td>
</tr>
<tr>
<td>25</td>
<td>1</td>
<td>0</td>
<td>(Winkler et al. 1997 Fig 2,3,4)</td>
</tr>
<tr>
<td>37</td>
<td>?</td>
<td>0</td>
<td>Personal observation</td>
</tr>
<tr>
<td>54</td>
<td>1</td>
<td>0</td>
<td>(Winkler et al. 1997 Fig 3,4)</td>
</tr>
<tr>
<td>69</td>
<td>?</td>
<td>-</td>
<td>not applicable</td>
</tr>
<tr>
<td>70</td>
<td>?</td>
<td>-</td>
<td>not applicable</td>
</tr>
<tr>
<td>80</td>
<td>?</td>
<td>0</td>
<td>(Winkler et al. 1997 Fig 7,9)</td>
</tr>
<tr>
<td>84</td>
<td>?</td>
<td>0</td>
<td>(Winkler et al. 1997 Fig 2,3,4)</td>
</tr>
<tr>
<td>104</td>
<td>?</td>
<td>1</td>
<td>Personal observation</td>
</tr>
<tr>
<td>106</td>
<td>?</td>
<td>2</td>
<td>Personal observation</td>
</tr>
<tr>
<td>151</td>
<td>0</td>
<td>1</td>
<td>Personal observation</td>
</tr>
<tr>
<td>172</td>
<td>?</td>
<td>-</td>
<td>not applicable</td>
</tr>
<tr>
<td>189</td>
<td>?</td>
<td>-</td>
<td>not applicable</td>
</tr>
<tr>
<td>197</td>
<td>?</td>
<td>0</td>
<td>(Winkler et al. 1997 Fig 18)</td>
</tr>
</tbody>
</table>
APPENDIX 7

Relative abundance of clay minerals present in each sample based on X-ray Diffraction analyses.

Mineral abundance was determined using the area of the background-subtracted intensities of the 001 peak for glycerol-solvated samples (17-20 Å for smectite, 9.9-10.1 Å for illite, 7.1-7.2 Å for kaolinite)

<table>
<thead>
<tr>
<th>Locality</th>
<th>Kaolinite %</th>
<th>Illite %</th>
<th>Smectite %</th>
</tr>
</thead>
<tbody>
<tr>
<td>PL-4</td>
<td>14</td>
<td>86</td>
<td>0</td>
</tr>
<tr>
<td>PL-3</td>
<td>11</td>
<td>89</td>
<td>0</td>
</tr>
<tr>
<td>PL-2</td>
<td>8</td>
<td>92</td>
<td>0</td>
</tr>
<tr>
<td>PL-1</td>
<td>13</td>
<td>87</td>
<td>0</td>
</tr>
<tr>
<td>JR-2-0</td>
<td>7</td>
<td>42</td>
<td>51</td>
</tr>
<tr>
<td>JR-2-30</td>
<td>0</td>
<td>54</td>
<td>46</td>
</tr>
<tr>
<td>JR-2-40</td>
<td>6</td>
<td>36</td>
<td>58</td>
</tr>
<tr>
<td>JR-2-50</td>
<td>0</td>
<td>46</td>
<td>54</td>
</tr>
<tr>
<td>JR-3</td>
<td>0</td>
<td>60</td>
<td>40</td>
</tr>
<tr>
<td>JR-4</td>
<td>0</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>Cross A-1</td>
<td>73</td>
<td>27</td>
<td>0</td>
</tr>
<tr>
<td>Cross A-2</td>
<td>71</td>
<td>29</td>
<td>0</td>
</tr>
<tr>
<td>Cross-C2</td>
<td>31</td>
<td>25</td>
<td>44</td>
</tr>
<tr>
<td>Dean-1</td>
<td>51</td>
<td>49</td>
<td>0</td>
</tr>
<tr>
<td>Dean-2</td>
<td>72</td>
<td>28</td>
<td>0</td>
</tr>
<tr>
<td>RNT-5</td>
<td>0</td>
<td>19</td>
<td>81</td>
</tr>
<tr>
<td>RNT-6</td>
<td>0</td>
<td>23</td>
<td>77</td>
</tr>
<tr>
<td>15CS717-21</td>
<td>69</td>
<td>31</td>
<td>0</td>
</tr>
<tr>
<td>AAS-2</td>
<td>75</td>
<td>35</td>
<td>0</td>
</tr>
<tr>
<td>ABP</td>
<td>72</td>
<td>6</td>
<td>22</td>
</tr>
</tbody>
</table>
Woodbine Formation Oxygen Bond Model Equations

15CS717-21: $1000\ln a = 2.8659 \times 10^6/T^2 - 8.2285$

AAS-2: $1000\ln a = 2.8507 \times 10^6/T^2 - 8.1788$

ABP: $1000\ln a = 2.9014 \times 10^6/T^2 - 8.3443$
RNT-5: \(1000\ln a = 2.8397 \times 10^6/T^2 - 6.641\)

RNT-6: \(1000\ln a = 2.833 \times 10^6/T^2 - 6.8963\)

Cross-A2: \(1000\ln a = 2.6429 \times 10^6/T^2 - 8.1021\)

Dean-2: \(1000\ln a = 2.6886 \times 10^6/T^2 - 7.7575\)
Twin Mountains Formation Oxygen Bond Model Equations

JR-2-40: $1000\ln a = 2.8313 \times 10^6/T^2 - 6.8311$
JR-3: $1000\ln a = 2.853x \times 10^6/T^2 - 6.5275$
PL-1: $1000\ln a = 2.828 \times 10^6/T^2 - 7.0173$
PL-4: $1000\ln a = 2.8315 \times 10^6/T^2 - 7.1469$
APPENDIX 9

AAS-2

\[ \delta D (\text{‰ V-SMOW}) \]
\[ \delta^{18}O (\text{‰ V-SMOW}) \]

- AAS-2 MSD
- AAS-2 WESD
- Measured AAS-2


Goloboff, P.A. and S.A. Catalano. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics. 32.3: 221-238.


