Palaeoecology and taphonomy of the Early Permian cave system near Richards Spur, Oklahoma, and its parareptilian fauna

by

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A thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy
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Abstract

The Early Permian Richards Spur locality, located at the Dolese Brothers limestone quarry in Oklahoma, USA, is one of the most unique and important terrestrial tetrapod faunas of the Palaeozoic. As one of the few upland localities known from this period, it offers a view of the Early Permian that is distinct from those available at the more common and well-studied lowland deltaic/fluvial assemblages. The locality is represented by a vast cave system that possesses a highly fossiliferous infill. Well over 30 tetrapod taxa have been described from Richards Spur, many of which are endemic, making it the most taxonomically diverse terrestrial Palaeozoic locality currently known. However, aside from alpha taxonomy, there has been little to no work done looking at other aspects of the locality, such as taphonomy and palaeoecology. This thesis represents the first large scale study of the unique Richards Spur locality. I further add to the immense
tetrapod diversity of the site through the description of several new parareptiles, as well as new parareptile material, which also grants a much better understanding of the early evolution and diversification of the clade. Furthermore, I reconstruct the distinct preservational environment associated with the cave system at Richards Spur, as well as use taxonomic and relative abundance data to interpret details of the locality's paleoecology, allowing for better comparisons with other Early Permian localities to be made.
Time passed, slipping through the waist of the universe's great hourglass like the eroded soil of this continent slipping down her rivers to the seas.

-Gene Wolfe
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Writing a thesis is not a feat that I could have accomplished without the support and assistance of many, many people. It is, at its simplest, the culmination of all the research I have done over the course of my degree, but it was also shaped by the numerous relationships, both new and old, that I have been privileged to be a part of over the last six years. I hope I don't forget to mention anyone here, and if I do, know that it was not intentional.

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Chapter 1

General Introduction
1.1. Background

The Permian period (298.9 - 252.2 ma) represents a time in Earth's history when many of the characteristics that we associate with modern terrestrial ecosystems were just beginning to appear, and a time of great diversification for many tetrapod clades (Berman et al., 2000). Of particular importance was the usage of land plants as a food source by tetrapods; this resulted in drastic shifts of the trophic structure of terrestrial ecosystems, leading to the herbivore dominated tetrapod assemblages of the Late Permian and beyond (Sues and Reisz, 1998; Reisz and Sues, 2000). However, herbivorous tetrapods were relatively rare components of Early Permian terrestrial communities, as they had yet to acquire the success they achieved later in the Permian, and did not from a major component of terrestrial ecosystems. Thus, Early Permian terrestrial ecosystems were largely dominated by predatory taxa (Reisz and Sues, 2000). The Early Permian, therefore, offers a unique view into the initial stages of terrestrial tetrapod evolution, an important chapter in vertebrate evolution, one that is unfortunately often overlooked.

Much of our knowledge of Early Permian terrestrial assemblages comes from the numerous deltaic/fluvial lowland red bed localities found predominantly throughout Texas, Oklahoma, and New Mexico in the Southern USA (Case, 1907, 1915; Williston, 1917; Olson, 1967). There have been numerous studies that have concentrated on cataloguing and interpreting the tetrapod diversity of these localities (Case, 1915; Vaughn, 1962, 1966; Olson, 1970; Sander, 1989). However, Early Permian upland assemblages are much rarer, and our understanding of the palaeoecology and taphonomy of such localities is very poor (Eberth et al., 2000; Sullivan et al., 2000), resulting in a significant gap in our knowledge of the Early Permian. Thus, the study of upland localities and their integration with contemporaneous lowland localities will be essential in gaining a full picture of tetrapod evolution and diversification during the Early Permian.

Currently, there are three known upland assemblages that are Early Permian in age, the Bromacker locality in Germany (Eberth et al., 2000; Martens et al., 2005), the Bally Mountain locality in Oklahoma (Olson, 1967; Busbey, 1990), and the Richards Spur locality (Olson, 1967; Sullivan and Reisz, 1999; Sullivan et al., 2000), which is also found in Oklahoma.

Of these three known upland localities, the Richards Spur locality is of particular interest because of its richness and taxic diversity (Sullivan et al., 2000; MacDougall and Reisz, 2012). The Richards Spur locality (formerly known as the Fort Sill locality) is located at the Dolese
Brothers limestone quarry in Southwestern Oklahoma, USA, and is comprised of a network of fissures containing a highly fossiliferous Early Permian infill (Sullivan and Reisz, 1999; MacDougall and Reisz, 2012), from which all fossil material is obtained. Richards Spur is notable for several reasons, the first is that it is the most taxonomically diverse terrestrial tetrapod locality of the Palaeozoic, with more than 30 taxa described from the assemblage (MacDougall and Reisz, 2012). Described taxa include reptiles (Kissel et al., 2002), synapsids (Reisz, 2005), and various anamniotes (Bolt, 1969). The second notable feature of the locality is that many of the taxa are endemic (MacDougall and Reisz, 2012). Lastly, Richards Spur is notable because many of the larger synapsid taxa that are common at most Early Permian lowland assemblages (Sullivan et al., 2000) are not preserved within the fissures. Together these characteristics differentiate Richards Spur from contemporaneous lowland localities, solidifying it as a unique view into the Early Permian that is not available elsewhere.

Included among the Richards Spur locality’s tetrapods is the largest and most taxonomically diverse parareptilian fauna of the Early Permian (MacDougall et al., 2016; in press). Reptilia is composed of two clades, Eureptilia and Parareptilia, both of which first appear in the fossil record during the Late Carboniferous (Müller and Reisz, 2006; Modesto et al., 2015). Parareptilia is a clade that is historically rare during this period in time (Tsuji et al., 2010), but parareptilian taxa become prominent members of Middle and Late Permian terrestrial vertebrate communities, and gained a worldwide distribution (deBraga and Reisz, 1996). The diversity of parareptiles known to be present at Richards Spur is the result of much recent work (Reisz et al., 2002; Tsuji et al., 2010; MacDougall and Reisz, 2012, 2014; Reisz et al., 2014; MacDougall et al., 2016), and the locality now represents what is the best source of information on the Early Permian diversification and evolution of the clade.

The Richards Spur locality offers one of the best opportunities to study an Early Permian upland assemblage. Most of the studies on the Richards Spur tetrapods have largely been concerned with the description of new fossil taxa, with very little work being done on other aspects of the locality, like palaeoecology and taphonomy of the cave system that comprise the fissures. This thesis represents a more comprehensive approach to the study of the Richards Spur locality, filling several gaps in our current knowledge of the Early Permian world. Firstly, I describe several new parareptile taxa from Richards Spur, as well as new material of previously described taxa. This part of the thesis also includes histological studies of the dentition of several
parareptiles. The data gained from the study of the new parareptilian material facilitated the creation of an updated phylogenetic analysis of the clade, and a better understanding of parareptilian evolution during the Early Permian. Secondly, I reconstruct the processes that led to the preservation of the fossils within the cave system at Richards Spur in order to determine potential biases. This understanding of the taphonomy and preservational environment is crucial for interpreting the vast amount of fossil material that has been obtained from Richards Spur. Lastly, I perform the first analysis of relative abundance at Richards Spur, using the results of the analysis and our knowledge of taxonomic diversity at the locality to interpret details of the palaeoecology of the ancient ecosystem found there, as well as compare it with another Early Permian upland locality.

Overall, my thesis updates our knowledge of Early Permian parareptile diversity and evolution, areas that have been largely ignored in the past. More importantly, it substantially increases our understanding of the Richards Spur locality, illustrating its unique characteristics and its importance as a crucial, unique window into the Early Permian world.

1.2. Thesis design and overview

Chapters two through four concentrate on the parareptile component of the Early Permian Richards Spur locality and include descriptions of new taxa, histological analyses of parareptilian dentition, a new phylogenetic analysis of the clade, as well as discussions regarding the Early Permian evolution and diversification of the clade. Chapters five and six examine and discuss the taphonomy of the cave system at the locality, as well as the paleoecology of the assemblage using relative abundances of taxa. Chapter seven is a concluding chapter that uses the data from all of the previous chapters to summarize the importance of the Richards Spur locality in understanding terrestrial vertebrate evolution during the Early Permian.
1.2.1. Chapter two

Chapter two describes three new Early Permian parareptile taxa from the Richards Spur locality: the lanthanosuchoids *Feeserpeton oklahomensis* and *Colobomycter vaughni*, and the nycitphruretid *Abyssomedon williamsi*. Furthermore, two new specimens of the enigmatic *Colobomycter pholeter* are described, these new specimens are much more complete than any previously described material, and offer important new information regarding its cranial anatomy. The new species and new material grant us a better understanding of parareptilian anatomy, as well as a much better view of parareptile diversity at Richards Spur. *A. williamsi* represents the earliest and first nycitphruretid known from outside the Middle Permian of Russia. The two other new taxa increase to six the known diversity of lanthanosuchoids in this region of North America, suggesting a potential Early Permian radiation for the clade.

1.2.2. Chapter three

Chapter three is a histological investigation of folded dentine, known as plicidentine, within the parareptile *Colobomycter pholeter*, as well as in several of its Early Permian relatives (*Delorhynchus, Feeserpeton oklahomensis, Microleter mckinzieorum*, and *Bolosaurus*). Plicidentine is now known to be present in numerous amniote groups; however, it has not been thoroughly investigated within Parareptilia. The thin sections of the various parareptile teeth reveal a surprising diversity of plicidentine within Parareptilia. Taxa such as *Delorhynchus* and *M. mckinzieorum* exhibit a very loosely folded type of dentine, whereas the plicidentine in *C. pholeter* exhibits different levels of folded dentine depending on the region of the marginal dentition. Thus, the characteristic enlarged premaxillary tooth exhibits very tightly folded dentine, reminiscent of that observed in labyrinthodont anamniotes. The enlarged maxillary teeth also exhibit tightly folded dentine, but not to the degree observed in the enlarged premaxillary tooth, and the smaller marginal teeth show a loosely folded dentine similar to that of *Delorhynchus* and *M. mckinzieorum*. This level of variation in plicidentine along the marginal dentition is unique to *C. pholeter*. Lastly, the teeth of *Bolosaurus* do not exhibit any type of plicidentine. The utility of computed tomography (CT) scans in the identification of plicidentine was shown using *Colobomycter pholeter* and *Feeserpeton oklahomensis*, avoiding the need for
destructive sampling in rare and unique specimens. These results indicate that the functional purpose of plicidentine in parareptiles is likely to increase the surface area for tooth attachment tissues, and that parareptilian plicidentine is a problematic character for inclusion in phylogenetic analyses of the clade.

1.2.3. Chapter four

Chapter four includes a new phylogenetic analysis of Parareptilia, as well as a discussion of the early evolution and diversification of the clade, drawing data from the numerous new taxa that have been described from the locality in recent years. A new phylogenetic analysis was conducted, heavily modifying the characters of an existing matrix. Compound characters were broken up into their own distinct characters, several other characters were removed because they were uninformative, and several new characters were added. Lastly, new taxa were added to the analysis, especially those found at the Richards Spur locality. These taxa include the three new parareptiles described in chapter two. The results of this phylogenetic analysis produced a very well supported Parareptilia, as well as high support values for many of the clades within it. A stratigraphically calibrated phylogeny was also produced in order to illustrate that the age of the parareptiles known from Richards Spur pulls several parareptile clades well back into the Early Permian. The results of the analysis and the abundance of parareptile fossil material from Richards Spur allows for consideration of several aspects of parareptilian diversification and evolution. Specifically, the radiation of the clade during the Early Permian, and the diversity of parareptiles during the Early Permian are compared to that of contemporaneous eureptiles. Patterns of temporal fenestration within parareptiles are also discussed, historically a problematic characteristic for classifying early amniotes. The character is mapped out on the newly obtained cladogram, allowing me to demonstrate the extreme variability of this trait within Parareptilia.
1.2.4. Chapter five

Chapter five is a taphonomic study concentrating on the unique preservational environment of the Richards Spur locality. The upland nature of Richards Spur, combined with the extensive cave system found there suggests that it has a unique preservational environment, and may also have taphonomic biases that are different from those of Early Permian lowland deltaic/fluvial localities. Using palaeontological, geological, and geochemical data the unique preservational environment of the Richards Spur cave system is reconstructed. The results of this study indicate that there are likely two main modes through which tetrapod taxa become preserved at Richards Spur. The first of these modes involved tetrapods falling, or being washed into the caves largely whole, which would explain the preservation of articulated fossil material at the locality. The second preservational mode involved tetrapods decomposing on the surface, becoming disarticulated, and with their remains eventually being washed in to the caves and becoming preserved, which resulted in the abundant disarticulated fossil material that is found at Richards Spur. Either way, once animal remains entered into the caves, they would have been exposed to the flow of water within them, which would have worn and concentrated disarticulated or formerly articulated remains. Stable isotope analysis of various speleothems from the caves confirms details regarding the climate that was present in this region of Laurasia, as well as providing information regarding the variability of the environment within the cave system. Furthermore, new absolute ages for the locality were determined using speleothems from the caves, granting a better range for the time that the caves would have been active.

1.2.5. Chapter six

Chapter six is the first study of relative abundance at the Richards Spur locality, undertaken in order to quantify the immense diversity at the locality and to infer palaeoecological details of the assemblage, and its likely community structure. A large calcite clay block obtained from the caves at the locality was used for this analysis; the block contained numerous disarticulated fossil elements of various taxa. The block was chemically prepared to separate out the fossil material, which was then sorted, identified where possible, and counted. Relative abundances of all the taxa identified from the sample were measured using the minimum number of individuals (MNI)
metric. The results of this analysis show that the most abundant amniote is the eureptile *Captorhinus*, whereas the most abundant anamniote is the amphibamid temnospondyl *Doleserpeton*. Other taxa are less common, notably, other anamniotes, other eureptiles, parareptiles, and synapsids. The results are compared with relative abundance data that has been obtained from the Bromacker locality in Germany, another Early Permian upland locality.

1.2.6. Chapter seven

Chapter seven offers overall conclusions regarding the Richards Spur locality, drawn from the results of the prior chapters. Primarily, the importance of the unique upland nature of Richards Spur, and how incorporating it with the more typical deltaic/fluvial lowland localities of the Early Permian is essential for understanding the bigger picture that is the initial stages of terrestrial tetrapod evolution.

1.2.7. Contributions to co-authored chapters

Chapters two and four are composed of four papers published in the following journals: two papers in *The Journal of Vertebrate Paleontology*, and two papers in *The Zoological Journal of the Linnean Society*. Chapter three is published in the journal *PLoS One*, and chapter five is published in the journal *Palaeogeography, Palaeoclimatology, Palaeoecology*. I am the primary author on all of these publications and all of the coauthors are listed at the start of each chapter. In the near future I plan to submit material from chapter six as part of a lead-authored paper.
1.3. References


Vaughn, P. P. 1966. Comparison of the Early Permian Vertebrate Faunas of the Four Corners Region and North-Central Texas. Los Angeles County Museum of Natural History.

Chapter 2

New parareptile (Amniota: Reptilia) material from the Early Permian Richards Spur locality.

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2.1. Abstract

Parareptilia, the sister clade of Eureptilia, was a group of reptiles that first appears in the fossil record during the Late Carboniferous. By the Middle and Late Permian they had become prominent members of terrestrial ecosystems, as well as achieving a cosmopolitan distribution. However, our Early Permian knowledge of parareptiles has historically been much poorer, they were considered to be rare members of ecosystems and have low taxonomic diversity during this point in Earth's history. The Early Permian Richards Spur locality of Oklahoma has proven to be an incredible source of terrestrial tetrapod fossil material, and has been instrumental in increasing our understanding of Early Permian tetrapods. In recent years, six new parareptiles have been described from the locality, bringing the total of known parareptiles at the locality up to eight. These new parareptilian species have dramatically increased our knowledge of the clade during the Early Permian. Here we describe three of these six new parareptiles, *Feeserpeton oklahomensis*, *Abyssomedon williamsi*, and *Colobomycter vaughni*, as well as new material of the enigmatic *Colobomycter pholeter*. The abundance of parareptiles found in this region of Laurasia, suggests that this area was important for the diversification of the clade.

2.2. Introduction

The Dolese Brothers Limestone Quarry, located near the town of Richards Spur in southwestern Oklahoma, is known for preserving a large number of Early Permian terrestrial tetrapods within an extensive network of fissures (Olson, 1967; Sullivan and Reisz, 1999). It has yielded one of the most diverse and well preserved terrestrial Paleozoic tetrapod faunas in the world (Sullivan and Reisz, 1999; Sullivan et al., 2000; MacDougall and Reisz, 2012). Large numbers of well-preserved disarticulated and partly associated skeletal remains have been recovered from the clay and breccia infillings that make up the locality (Olson, 1967). This rich fauna of Early Permian tetrapods possesses an unusually large number of currently endemic taxa, ranging from temnospondyl (Bolt, 1969; Fröbisch and Reisz, 2008) and lepospondyl (Carroll and Gaskill, 1978) anamniotes, to various types of basal amniotes, such as varanopids (Reisz et al., 1997), captorhinids (May and Cifelli, 1998), and caseids (Reisz, 2005). The large number of terrestrial endemic taxa found at the locality has led to the suggestion that the locality preserves an upland
fauna, as it exhibits a distinct faunal composition from that of the common Early Permian lowland assemblages (Sullivan et al., 2000). Furthermore, all of the taxa known from Richards Spur are considered to be fully terrestrial, lending support to this hypothesis (Sullivan et al., 2000; MacDougall and Reisz, 2012).

Among the numerous endemic forms found at Richards Spur are several parareptiles (Modesto, 1999a; Reisz et al., 2002; Modesto et al., 2009a; Tsuji et al., 2010; Reisz et al., 2014). Parareptiles are a clade of amniotes, which were common elements in terrestrial vertebrate communities of the Middle and Late Permian, and one clade, the Procolophonoidea, survived the Permo-Triassic mass extinction event, before going extinct by the end of the Triassic (Modesto et al., 2001, 2003; Tsuji and Müller, 2009). However, little is known of parareptilian evolution and diversity during the Early Permian. The recently discovered parareptiles at Richards Spur are unexpected for an Early Permian locality, as they are quite rare in other similarly aged faunal assemblages (Berman et al., 2000; Tsuji et al., 2010), with the exception of the bolosaurid *Bolosaurus* (Cope, 1878). Previously described parareptiles from the Richards Spur Locality include *Colobomycter pholeter* Vaughn, 1958, *Delorhynchus priscus* Fox, 1962, *Bolosaurus grandis* Reisz et al., 2002, *Microleter mckinzieorum* Tsuji et al., 2010, and *Delorhynchus cifellii* Reisz et al., 2014.

Perhaps the most unusual parareptile to be described from the Richards Spur locality, and the Early Permian as a whole, is the lanthanosuchoid *Colobomycter pholeter* Vaughn, 1958. Although initially described as a synapsid (Vaughn, 1958), this species was later reassigned to Parareptilia (Modesto, 1999a). *Colobomycter* is very distinct from all other known parareptiles, and coeval tetrapods in general, largely due to its extremely conspicuous and unique marginal dentition. The single, very large anteriormost tooth of the premaxilla, and the paired enlarged teeth of the maxilla characterize the dentition of *Colobomycter*. These exaggerated teeth uniquely characterize *Colobomycter*, and it has been the subject of several studies since its discovery (Modesto, 1999a; Modesto and Reisz, 2008; MacDougall et al., 2014).

The number of parareptiles from the Richards Spur locality continues to grow with the addition of several new parareptiles. Here we describe three new species from the locality: the lanthanosuchoid *Feesperpeton oklahomensis*, the nyctiphruretid *Abyssomedon williamsi*, and a new species of the aforementioned unusual *Colobomycter*. Furthermore, we describe two new
specimens of *Colobomycter pholeter*, which are much more complete than any previously studied material, they reveal important new information about the skull of the taxon. These new species, and new material of previously known taxa, further contributes to our understanding of the anatomy and early evolution of Parareptilia, and tetrapods as a whole.

**Institutional Abbreviations**— BMRP, Burpee Museum of Natural History, Rockford Illinois, USA; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UWBM, University of Washington Burke Museum of Natural History and Culture, Seattle, Washington, USA.

### 2.3. Material and Methods

Permission was obtained from all relevant institutions (BMRP, OMNH, UWBM) to borrow and work on all of the specimens described and illustrated here. All specimens were loaned to R.R. Reisz at the University of Toronto Mississauga.

#### 2.3.1. *Feeserpeton oklahomensis*

The skull of *Feeserpeton oklahomensis* (OMNH 73541) was originally preserved in a nodule of clay-rich calcite collected at the Dolese Brothers quarry near Richards Spur, Oklahoma, USA. Preparation of the specimen was performed at the University of Toronto Mississauga, using airscribes and pin vices. The specimen was then photographed using a digital camera, the images (Fig. 2.1) were then imported into Adobe Illustrator CS5, and interpretive illustrations were drafted from the images (Fig. 2.2). Computed tomography (CT) data of the skull were collected at the University of Texas High Resolution X-ray Computed Tomography Facility. The CT dataset consists of 623 slices, taken at an inter-slice spacing of 0.04528 mm in transverse planes from the anterior-most end of the skull to the posterior-most end.
2.3.2. Abyssomedon williamsi

The specimen described and illustrated here (BMRP 2008.3.3a) was found preserved on a small slab of clay-rich calcite collected at the Dolese Brothers quarry near Richards Spur, Oklahoma, USA. The piece of calcite was collected by Scott Williams of the Burpee Museum of Natural History because of the presence of a partial skull of the parareptile Colobomycter, but preparation of the other side of the slab revealed the presence of the new parareptile described here. Preparation of the specimen was performed using airscribes and pin vices at the University of Toronto Mississauga. The specimen was photographed using a digital camera. Interpretive illustrations were made by using Adobe Illustrator CS5 to make outlines, and then detail was added using coquille.

2.3.3. Colobomycter vaughni

Two partial skulls of Colobomycter vaughni found in nodules of calcite are described here: BMRP 2008.3.3b and UWBM 96304. These two specimens were prepared using airscribes and pin vices, and photographed at the University of Toronto Mississauga. Comparisons and observations were made with three specimens assigned to Colobomycter pholeter: OMNH 73535, described previously by Modesto and Reisz (2008), and the two new specimens BMRP 2008.3.1 and BMRP 2008.3.10. All anatomical measurements were obtained using Mitutoyo digital calipers. Interpretive illustrations were made using Adobe Illustrator CS5 to create outlines, and then further detail was added using coquille.

2.3.4. New material of Colobomycter pholeter

Two new specimens of Colobomycter pholeter are described here: BMRP2008.3.1 and BMRP2008.3.10. Preparation was done using both airscribes and pin-vice at the university of Toronto Mississauga. Outlines of the interpretive illustrations were made using Adobe Illustrator CS5, with further details added using coquille. The photographs of BMRP2008.3.1 differ slightly from the drawings, in that the posterior end of the right mandibular ramus is only present in the
photographs. This is due to the posterior end of the right mandibular ramus having been lost, the drawings were based on this condition, and it was only recently that the missing end was found and reattached.

2.4. Systematic Palaeontology

2.4.1. *Feeserpeton oklahomensis*

AMNIOTA Haeckel, 1866

REPTILIA Laurenti, 1768

PARAREPTILIA Olson, 1947

PROCOLOPHONOMORPHA Romer, 1964

ANKYRAMORPHA deBraga and Reisz, 1996

LANTHANOSUCHOIDEA Efremov, 1946

*FEESERPETON OKLAHOMENSIS* gen. et sp. nov.

(Figs. 2.1, 2.2, 2.3)

**Diagnosis**—Parareptile characterized by its triangular skull, large postorbitals, but small squamosals, and the presence of large caniniform teeth on the maxilla and mandible, being at least twice as large as any of the other marginal teeth.

**Etymology**—Genus name honors Mr. Mike Feese, former manager of the Dolese Brother’s Limestone Quarry, and an avid collector. Species name refers to the state in which the locality of the specimen is found.

**Holotype**—OMNH 73541 nearly complete skull.
Locality and Horizon—Dolese Brothers Limestone Quarry, Richards Spur, Comanche County, Oklahoma, USA. The first absolute dating for an Early Permian locality indicates that the Dolese infills are 289 ± 0.68 Ma, or Mid-Sakmarian stage of the Early Permian (Woodhead et al. 2010).

2.4.2. Abyssomedon williamsi

AMNIOTA Haeckel, 1866

REPTILIA Laurenti, 1768

PARAREPTILIA Olson, 1947

NYCTIPHRURETIDAE (Lee, 1997) Efremov, 1938

ABYSSOMEDON WILLIAMSI gen. et sp. nov.

(Figs. 2.4, 2.5, 2.6, 2.7)

Diagnosis—Small parareptile exhibiting the following autapomorphic features: premaxilla with seven tooth positions, and an anterior depression of the maxilla with the anterolateral maxillary foramen being found on the raised edge of the depression. Differs from other parareptiles at Richards Spur in the presence of the slender L-shaped jugal.

Etymology—Genus name derives from abyssos for deep pit, referring to the caves in which the specimen was preserved and would have lived around, and medon for guardian. Species name honours Mr. Scott Williams, who collected the specimen.

Holotype—BMRP 2008.3.3a, semi-articulated partial skull with disarticulated postcranial elements.

Locality and Horizon—The Dolese Brothers Quarry, located near Richards Spur, Comanche County, Oklahoma, USA. Mid-Sakmarian stage (289 ± 068 Ma) of the Early Permian.
2.4.3. *Colobomycter vaughni*

AMNIOTA Haeckel, 1866

REPTILIA Laurenti, 1768

PARAREPTILIA Olson, 1947

PROCOLOPHONOMORPHA Romer, 1964

ANKYRAMORPHA deBraga and Reisz, 1996

LANTHANOSUCHOIDEA Efremov, 1946

*COLOBOMYCTER* Vaughn, 1958

**Diagnosis**—Reptile characterized by a premaxilla that possesses only two teeth, the anteriormost of which is greatly enlarged compared to the rest of the marginal dentition. Additional distinguishing characteristics are the paired enlarged teeth on the maxilla, which are larger than the rest of the maxillary dentition.

*COLOBOMYCTER VAUGHNI* sp. nov.

(Figs. 2.8, 2.9, 2.10)

**Diagnosis**—Distinguished from the type species in that the anterior lateral exposure of lacrimal at the junction of the maxilla, prefrontal and nasal is absent in lateral view; there are at least 17 tooth positions on the maxilla, versus the maximum of 14 documented for *Colobomycter pholeter*, and the enlarged teeth of the premaxilla and maxilla are not as robust as those found in *C. pholeter*. 
**Etymology**—Specific epithet honours Peter Vaughn for his contributions to the paleontology of late Paleozoic vertebrates.

**Holotype**—UWBM 96304, a partial skull with a few disarticulated cranial and postcranial elements (Figs. 2.8, 2.9).

**Referred Specimen**—BMRP 2008.3.3b, interior surface of a partial skull and two disarticulated vertebrae (Fig. 2.10).

**Locality and Horizon**—The Dolese Brothers Quarry, located near Richards Spur, Oklahoma, Comanche County, USA. Mid-Sakmarian stage (289 ± 068 Ma) of the Early Permian.

### 2.4.4. New material of *Colobomycter pholeter*

AMNIOTA Haeckel, 1866

REPTILIA Laurenti, 1768

PARAREPTILIA Olson, 1947

PROCOLOPHONOMORPHA Romer, 1964

ANKYRAMORPHA deBraga and Reisz, 1996

LANTHANOSUCHOIDEA Efremov, 1946

*COLOBOMYCTER PHOLETER* Vaughn, 1958

(Figs. 2.12, 2.13, 2.14, 2.15)

**Diagnosis**—Small parareptile characterized by premaxilla bearing 2 teeth, the anteriormost one being considerably enlarged; maxillary dentition that includes two enlarged teeth; splenial that does not contribute to mandibular symphysis.
**Referred Specimens**—BMRP 2008.3.1, near-complete skull (Figs. 2.12, 2.13); BMRP 2008.3.10, interior surface of a partial skull (Fig. 2.14); FMNH 272, holotype, portion of the skull roof; OMNH 73535, partial skull.

**Locality and Horizon**—The Dolese Brothers Quarry, located near Richards Spur, Oklahoma, Comanche County, USA. Mid-Sakmarian stage (289 ± 068 Ma) of the Early Permian.

### 2.5. Descriptions

#### 2.5.1. *Feeserpeton oklahomensis*

The skull of *Feeserpeton oklahomensis* is well preserved and largely undistorted, with most elements being present. The small size of the skull and large orbits do not necessarily indicate immaturity, more likely the skull is representative of a sub-adult; this is suggested by several observations. There is obvious tooth wear present on the palatal teeth, which indicates that they had seen extensive use, which would likely not be the case if the specimen were a juvenile. As for the large orbits, they may indicate that *F. oklahomensis* was nocturnal rather than suggesting juvenility, as large orbits are generally considered indicators of nocturnality in both extant and extinct animals (Schmitz and Motani, 2011). Lastly, although there are some unfused sutures associated with the braincase, the skull roof exhibits highly interdigitated sutures, as well as very robust sculpturing; these are characteristics that are not associated with immaturity in Paleozoic reptiles. These traits indicate a stage of development consistent with a fully mature individual, or at most a sub-adult.

#### 2.5.1.1. Skull roof

The premaxilla is for the most part not preserved, excluding a few uninformative fragments; none of the premaxillary dentition is preserved. The maxilla of *Feeserpeton oklahomensis* is an elongate element that in lateral aspect is tallest anteriorly, near the edge of the external naris. An anterolateral maxillary foramen is present close to the anterior edge of the maxilla.
maxilla shows that there are at least 14 tooth positions, with 13 alveoli being occupied by teeth. The teeth are clearly heterodont, being conical with a single pointed cusp. As the maxilla possesses a clearly defined caniniform region the canine teeth themselves are quite distinct, being twice as large as any of the other maxillary teeth. The canines appear to be the anteriormost teeth of the maxilla, on the right maxilla there are two preserved canines, and between them is an empty tooth position, which suggests that there may have been three canine positions on the maxilla.

The nasals are relatively well preserved, although they are weathered anteriorly. Taken together they reveal that the nasal is a rectangular element, which contacts the frontal and prefrontal posteriorly, and the lacrimal laterally.

The lacrimals, prominent elements of the snout, are weathered anteriorly, but relatively well preserved. The long, curved lacrimal extends from the orbit to the naris, as seen in other parareptiles, such as *Microleter mckinzieorum* (Tsuji et al., 2010). Ventrally the lacrimal articulates with the maxilla, and dorsally contacts the prefrontal and nasal. A small posteroventral flange of the lacrimal contacts the palatine. In lateral view it is broad posteriorly, but as it extends anteriorly it becomes narrow as it reaches the posterior border of the external naris. This makes it quite different from the triangular shaped lacrimal seen in *Acleistorhinus pteroticus* (deBraga and Reisz, 1996), and the condition seen in most Middle and Late Permian forms, where the lacrimal has been greatly reduced in length. The posterior, orbital surface of the lacrimal has a large foramen for the lacrimal duct.

The prefrontal is a quadrangular element that contributes to the anterodorsal portion of the orbit and extends anteriorly to the level of the posterior end of the nasals. The prefrontal of *Feeserpeton oklahomensis* does not preclude contact between the nasal and lacrimal, which is unlike the prefrontal of *Acleistorhinus pteroticus* (deBraga and Reisz, 1996). The prefrontal narrows ventrally to a thin flange that contacts the palatine.

The frontals are long rectangular elements, which together make up a large proportion of the skull roof. The anterolateral and posterolateral portions of the frontal are in contact with the medial edge of the prefrontal and postfrontal respectively, which results in only the middle part of the postorbital contributing to the anterior edge of the orbit. The middle portion of the frontal has an orbital process that is best described as a lateral lappet, which is also found in
Acleistorhinus pteroticus and procolophonids (deBraga and Reisz, 1996), the lateral lappet also makes up a portion of the dorsal orbital margin. Anteriorly the frontal contacts the nasal and posteriorly it contacts the parietal.

The postfrontal is a small triangular element that contributes to the posterodorsal edge of the orbit. Its small size is similar to that of the small postfrontals found in procolophonids (Reisz and Scott, 2002). It is broad posteriorly and tapers off anteriorly. It contacts posteriorly with the parietal and postorbital, and medially it meets the frontal.

The jugals are largely unpreserved; the only traces of them are in the form of impression, the sutures where they would have met with the maxillae, and a small mostly uninformative fragment of the right jugal that articulates with the postorbital. The impression that is present indicates that it is likely that the jugal was a slim element; this would make the temporal fenestra quite large, making up a considerable portion of the posterolateral skull.

The postorbital of Feeserpeton oklahomensis is a very large element with a significant contribution to the skull table lateral to the parietal, and a well-developed anteroventral process. It is therefore different from the small triradiate postorbital found in Microleter mckinzieorum (Tsuji et al., 2010). The anterior edge of the postorbital, together with the anteroventral process makes up the posterodorsal and posterior edges of the orbit. The large ventral process articulated with the jugal, and although there is little jugal preserved, it is clear that the postorbital sheathed the posteriormost end of the jugal. Although slightly damaged, the ventral process of the postorbital has a clearly recognizable edge for the lateral temporal fenestra. A small flange at the posterior of the postorbital articulates with the squamosal.

The squamosal, one of the bones that make up the temporal region of the skull, is a small flat element, considerably smaller than the squamosals found in Macroleter poezicus (Tsuji, 2006). It is smooth across its whole surface, and exhibits none of the sculpturing found on most of the other elements of the skull roof. The posterodorsal edge of the bone is overlapped by the supratemporal, obscuring a portion of its surface. Ventrally the squamosal contacts the quadratojugal, and together they form the posterior edge of the temporal fenestra.

The quadratojugal is an elongate triangular element, consisting of a fairly massive posterior end and a long, slender anterior process, which terminates at a fine point. This anterior process
extends as far anteriorly and contacts the posterior end of the maxilla. The tall posterior segment of the bone contacts with the squamosal dorsally and the quadrate ventrally.

The supratemporal makes up the posterolateral corner of the skull roof, as is the case in most parareptiles (Tsuji et al., 2010). It is sub-rectangular in outline and is rather small in size, most likely because of the large size of the postorbital extending far posteriorly. It closely resembles the supratemporal described in *Acleistorhinus pteroticus* (deBraga and Reisz, 1996).

The large paired parietals make up the majority of the skull roof. The parietal is a large rectangular element, separated from the surrounding bones by jagged sutures. The large pineal foramen is found along the midline of the two parietals, centered exactly in the middle of the parietals. It is a large circular opening sheltered within a shallow ovoid depression. Anteriorly the parietal contacts the frontal and postfrontal, laterally the postorbital and supratemporal, and posteriorly the postparietal.

The postparietal is a wide triangular bone, and unlike the postparietals found in most other parareptiles, including *'Owenetta' kitchingorum* (Reisz and Scott, 2002) and *Barasaurus besairei* (Meckert, 1995), the postparietal of *Feeserpeton oklahomensis* is a single unpaired median element. It is broad anteriorly, where it occupies one-half of the total parietal width, but is much narrower posteroventrally, resulting in a triangular outline that is three times as wide as it is long.

### 2.5.1.2. Palate

Whereas the left side of the palatal surface is covered by supportive matrix, the right side is mostly exposed and the various elements of the palate can be discerned. Matrix was left on the palate in various areas to support the impressive batteries of palatal teeth that are found on most of the palatal elements, many of these palatal teeth exhibit obvious wear.

The vomer is the anteriormost element of the palate, with a triangular outline, broad posteriorly and transversely narrow anteriorly. The presence of a battery of teeth is immediately obvious, arranged in several rows along the medial half of the ventral surface. The teeth found on the vomer vary in size, most of the teeth being relatively small, while two larger teeth are present anteriorly, and a few additional larger teeth along the posterolateral edge of the dental battery.
The rest of the vomer, about one-third of its ventral surface is smooth between the medial battery and the edge of the internal naris. The vomer contacts the palatine and pterygoid posteriorly.

The palatine is a lateral element of the palate, and much of its ventral surface is obscured by the matrix that supports the mandible. While not showing as many teeth as the vomer, there are two clearly exposed clusters of teeth supported by matrix, one positioned anteromedially and one posterolaterally. The posterolateral cluster of teeth consists of smaller teeth, while the anteromedial cluster exhibits much larger teeth. The palatine contacts with the vomer anteriorly, the pterygoid posteromedially, and presumably with the maxilla laterally. The dorsal exposure of the palate, visible in the orbit (Figs. 2.1A, D, and 2.2A, D) indicates that the palatal surface of this bone is much greater than the relatively small surface that is exposed in ventral view, and similar in size to other parareptiles.

The ectopterygoid is the smallest element of the palate, and much of its ventral surface is covered by matrix that supports the mandible. Overall, it has a concave ventral surface, and does not have any dentition on that surface, as is the case in all parareptiles (Laurin and Reisz, 1995). Although its posterior margin is obscured by matrix it is obvious that it would have contacted with the transverse flange of the pterygoid.

The largest element of the palate is the pterygoid, contacting the vomer anteriorly, the palatine and ectopterygoid laterally, and the quadrate posteriorly. It is roughly triangular in outline, possessing a flat anterior process, a large ventrally oriented transverse process, and a laterally flaring posterior process known as the quadrate ramus. The transverse flange of the pterygoid is dominated by a strong ridge that possesses a single row of teeth that run along its length. The teeth of the ridge are larger laterally, becoming smaller as the ridge curves posteromedially. Medially the transverse flange transitions smoothly into the quadrate ramus. Startlingly, the teeth on the transverse flange extend onto the quadrate ramus. The quadrate ramus is transversely quite broad, best exposed on the right pterygoid, with a strongly excavated ventrolateral surface. The anterior process of the pterygoid is broad, forming much of the palatal surface of the skull, and possessing several batteries of teeth along its length. The teeth are arranged in two clearly defined rows running anteriorly on the main body of the bone, and are continued on the vomer, one row bordering the interpterygoid vacuity and two additional anterolaterally directed rows, one extending to the palatine, and another extending between the palatine and ectopterygoid.
bones. As in other basal reptiles, these rows of teeth converge towards a medial emargination of the pterygoid located at the level of the transverse flange. This emargination forms part of the basicranial articulation.

The quadrate is a relatively large bone in *Feererpeton oklahomensis*, with a long anteromedial pterygoid process, and a tall dorsal process. The pterygoid process of the quadrate is long and thin and meets medially the quadrate ramus of the pterygoid. The body of the quadrate forms the broad saddle-shaped articulation with the articular bone of the mandible, and articulates posterolaterally with the quadratojugal. *F. oklahomensis* has a quadrate with a very well-developed dorsal process, exposed in occipital view. It is a relatively straight, vertical structure, indicating that there was no tympanic emargination in this parareptile. The lateral edge of the dorsal ramus of the quadrate has a well-developed groove for the attachment of the squamosal.

### 2.5.1.3. Mandible

Both mandibles of *Feererpeton oklahomensis* are preserved in articulation with the skull. Although well preserved, important anatomical features of the mandibles cannot be observed directly because of their tight attachment to the skull. For example, the majority of the mandibular teeth are not exposed because the skull roof covers them. However, CT imaging has revealed the anatomy of the mandibular dentition of *F. oklahomensis* (Fig. 2.3), facilitating their description.

The dentary is the longest mandibular element of *Feererpeton oklahomensis*; it extends from the symphysis anteriorly to well beyond the posterior border of the orbit. It contacts with the angular and surangular posteriorly and posteroventrally, and the splenial medially. Anteriorly the dentary forms the entirety of the mandibular symphysis; there is no contribution made by the splenials, a characteristic common of all parareptiles (Laurin and Reisz, 1995). In both lateral and medial views the teeth of the dentary are obscured. However, CT data indicate that the dentary possesses a single row of heterodont teeth, possessing the same conical single cusp structure as the maxillary teeth (Fig. 2.3). The first tooth in the series is quite small, but the second and third teeth in the series, much like on the maxilla, are significantly larger than the other teeth of the mandibular series.
The splenial is a long, roughly triangular bone that covers most of the lingual face of the mandibular ramus, opposite the dentary bone. The splenial does not contact its pair at the symphysis, and does not appear to contribute to the articular surface. It extends posteriorly from the symphysis and borders the dentary, covers medioventrally the angular and the prearticular. The splenial also has a slight lateral exposure when the mandible is observed in lateral view. The foramen intermandibularis caudalis (also known as the Meckelian foramen, e.g., Reisz and Scott, 2002) is found at the junction where the splenial meets both the angular and prearticular, as is seen in 'Owenetta' kitchingorum (Reisz and Scott, 2002).

The angular, along with the dentary forms the ventral edge of the mandible; it is slightly shorter than the dentary, but a significant fragment of the bone is covered by the surrounding elements, the splenial and the dentary. Thus, the narrow anterior portion of the element is pinched between the dentary externally and the splenial internally. Besides contributing to the ventral margin, the angular also continues onto the medial surface of the mandible, articulating dorsally with the prearticular. Posterior to the dentary, the angular articulates with the surangular dorsally, and the articular posteriorly.

The surangular, a significant element of the posterior portion of the mandible is exposed only in lateral view. It forms the dorsal margin of the mandible posterior to the dentary. Only a thin medial splint of the prearticular, a long slender bone is visible because it is largely restricted to the medial surface of the mandible. As in other parareptiles (Laurin and Reisz, 1995), it appears to extend posteriorly from its contact with the splenial and underlies the articular posteriorly.

The articular is a relatively small element at the posterior end of the mandible that forms the articular surface with the dentary. The detailed anatomy of articular surface cannot be determined because the mandibles are tightly attached to the skull. As in other parareptiles, most of the lateral surface of the bone is sheathed by the angular and surangular, leaving only a small portion of it visible laterally. Similarly, much of it is covered by the prearticular medially. The exposed posterior surface of the bone below the articulation with the quadrate is rounded, indicating that Feeserpeton oklahomensis lacks a retroarticular process, as in Acleistorhinus pteroticus (deBraga and Reisz, 1996).
2.5.1.4. Braincase

The braincase of *Feeserpeton oklahomensis* is visible in occipital and palatal views of the skull. The floor of the braincase is composed of the parasphenoid and basioccipital bones. The parasphenoid is a large triangular bone that makes up most of the floor of the braincase. Anteriorly, the parasphenoid has a well-developed cultriform process; posteriorly it fans out considerably, giving it a triangular outline, and forming the broader body of the bone. There are two regions of the parasphenoid that have preserved teeth, most obviously the rows of larger teeth on the pair of small curved ridges that extend between the cultriform process to the lateral edges of the body of the bone, curving over the basisphenoid tubera. The second set of teeth is small and extends along the ventral edge of the cultriform process. Only one of the two basisphenoid tubera is exposed, and is slightly separated from the pterygoid recess where it would have articulated in the living organism.

The basioccipital-exoccipital complex not only forms the posterior floor of the braincase, but also the occipital condyle and the ventral and lateral walls of the foramen magnum. It has separated from the parasphenoid, exposing its surface of articulation with that element. The exposed articular surface is a flat, roughly rectangular area that does not possess the slight sculpturing seen on the rest of the basioccipital. It is a compact element centrally where it forms the ovoid occipital condyle. Dorsally the exoccipital portion of the complex forms paired processes that contribute to the sides of the foramen magnum. The occipital condyle is a fairly large surface with a central depression. The contribution of the paired exoccipital and the median basioccipital to the occipital condyle cannot be determined because of the fusion of the elements.

The supraoccipital is a single, plate-like median element that is visible only in dorsal aspect; it is a flat butterfly shaped bone that extends from the posterior skull roof towards to the basioccipital-exoccipital complex. It has a pronounced mid-sagittal ridge, with the lateral wings of the bone having mostly smooth surfaces. Normally, it would articulate with the wings of the exoccipital and forms the dorsal margin of the foramen magnum. Laterally it is slightly separated from the opisthotics.

In *Feeserpeton oklahomensis* the opisthotic is a particularly large, predominantly triangular bone in occipital view, it extends far ventrolaterally to the exoccipital-basioccipital complex, and has a
narrow lateral process that extends dorsally. In all these features, it is surprisingly similar to the opisthotic of *Acleistorhinus pteroticus* (deBraga and Reisz, 1996). Anteriorly, the small suture joining the two elements is faint but discernable; the anteriormost element closest to the parasphenoid is the prootic, while the more posterior, much larger element is the opisthotic. The prootic is only visible in palatal view; it is a thin bone with a triangular outline. The stapes, a rarely preserved element of the skull, unknown in most Paleozoic parareptiles, is preserved in *F. oklahomensis*. It is a relatively massive element, in stark contrast to the small stapes found in Late Permian milleretid parareptiles (Gow, 1972). It has a broad proximal head, a well-developed dorsal process, and the remains of a broken stem.

### 2.5.2. *Abyssomedon williamsi*

The new nyctiphruretid specimen, although mostly disarticulated, and incomplete, exhibits several key elements of the skull and a few postcranial bones (Figs. 2.4, 2.5). The left side of the jaw and the majority of the preserved elements are disarticulated and spread across the surface of the block on which they are preserved. Several skull elements are preserved in orientations that reveal their interior surfaces. There are also numerous elements scattered across the slab that do not show enough information to be confidently identified.

Nyctiphruretidae is a very small clade of parareptiles that previously contained only two Russian taxa: *Nyctiphruretus acudens* Efremov, 1938 and *Nyctiphruretus optabilis* Bulanov, 2002. The two Russian nyctiphruretids are differentiated on the basis of slight differences in the morphology of the dentition, so for the purposes of the present study will be considered henceforth at the generic level, *Nyctiphruretus*.

#### 2.5.2.1. Skull roof

Both premaxillae are preserved, although isolated. They are exposed in lateral view with the right being complete, and the left slightly damaged (Fig. 2.6). The premaxilla is triradiate in structure, exhibiting the slender, posteriorly curving dorsal process that is characteristic of
parareptiles, a ventral tooth-bearing surface that would have articulated with the maxilla, and ventromedially a flat process that would have articulated with the vomer. Anteriorly, two small foramina can be seen just below the dorsal process. The tooth-bearing surface of the right premaxilla exhibits only four partially exposed teeth. However, the left premaxilla clearly shows the presence of six teeth, with a single empty tooth position in the middle of the tooth-bearing surface, suggesting that it would have possessed at least seven premaxillary teeth. The number of teeth found on the premaxilla is larger than in other parareptiles from Richards Spur, and parareptiles in general with the exception of the Gondwanan mesosaurs, which have very large premaxillae with numerous teeth (Modesto, 1999b, 2006), and the enigmatic *Lanthanosuchus watsoni* from Russia (deBraga and Reisz, 1996).

Only the left maxilla is exposed (Fig. 2.6), partially obscured by an overlying disarticulated quadrate; however, much of its lateral surface is still visible. The exposed lateral surface is largely smooth, not exhibiting the sculpturing seen on many of the other elements of the skull roof. This is the usual condition in most parareptiles (Modesto et al., 2009; Tsuji et al., 2010; MacDougall and Reisz, 2012) with notable exceptions, like *Lanthanosuchus watsoni* and *Acleistorhinus pteroticus* (deBraga and Reisz, 1996). The maxilla is tall anteriorly where it would have articulated with the premaxilla and nasal, it tapers off considerably towards its posterior end, where it is associated with, but not articulating with the jugal. Anterodorsally, it exhibits a large depression near where it would have articulated with the premaxilla and nasal. The anterior region of the maxilla also exhibits a series of foramina, the anterior-most of which is significantly larger than the others, as is the case in most parareptiles (Laurin and Reisz, 1995). In *Nyctiphruretus* the enlarged anterolateral maxillary foramen is found within the depression on the anterior part of the maxilla (Säilä, 2010). In *Abyssomedon williamsi* the foramen is found just prior to this depression, on the raised portion of the maxilla. The tooth bearing area of the maxilla is partially obscured, and only five maxillary teeth are visible.

The teeth of the premaxilla and maxilla are simple, and conical in outline, with a sharp distal tip. The well-exposed premaxillary teeth are slightly recurved. However, it is difficult to determine the curvature of the maxillary teeth because it was not possible to expose them in full lateral view. Neither the premaxillary nor maxillary teeth exhibit mesial and distal cutting edges, as is seen on some of the teeth of *Colobomycter pholeter* (Modesto and Reisz, 2008). There is a distinct lack of size related heterodonty among the maxillary and premaxillary teeth, a trait
shared by all nyctiphuretids (Säilä, 2010), and many other parareptiles (Reisz and Scott, 2002; Tsuji et al., 2010, 2012; MacDougall and Modesto, 2011; Reisz et al., 2014).

Only the left jugal is exposed (Fig. 2.6), it is in lateral view and in association but not articulated with the left maxilla. It is a curved, L-shaped element, similar to that seen in *Nyctiphuretus* (Säilä, 2010). Anteriorly, the element is gracile culminating in a point; this anterior region also exhibits the ventral facet where it would have articulated with the posterior process of the maxilla, forming the ventral margin of the orbit. As the jugal curves posterodorsally to where it would have articulated with the postorbital and quadratojugal it becomes slightly more robust. The curved shape of the jugal, absence of a posterior extension, and lack of articulating surface posteroventrally indicates that *Abyssomedon williamsi* would have possessed a lower temporal emargination, as is the case in other parareptiles, such as *Nyctiphuretus* (Säilä, 2010), *'Owenetta' kitchingorum* (Reisz and Scott, 2002), and *Microleter mckinzieorum* (Tsuji et al., 2010).

Only the right nasal is visible, however it is significantly damaged (Fig. 2.7), missing most of its anterior portion. What little remains of the right nasal indicates that it exhibits the same sculpturing pattern that is seen on most of the other elements of the skull roof, this sculpturing pattern is characterized by the presence of smooth raised regions of various shapes separated by small depressions running between them.

Both frontals are disarticulated and exposed in different views, with the left frontal being found in ventral view and the right in lateral view (Fig. 2.7). The left frontal is partially obscured by an overlying fragmentary element of unknown identity. The frontal exhibits a lateral process extending ventrally, from this process the smooth interior surface then curves medially to the opposite edge, where it would have articulated with the other frontal. The right frontal exhibits its lateral surface (the previously mentioned lateral process), the portion of the frontal that would have contributed to the dorsal margin of the orbit. It exhibits smooth facets on its anterior and posterior ends, which would be for articulating with the prefrontal and postfrontal respectively.

The lacrimals are exposed in the specimen (Fig. 2.7), with the left lacrimal being found in association with the left prefrontal and nasal, while the right is only found to articulate with the other prefrontal. The lacrimal is a roughly triangular element when viewed laterally that exhibits sculpturing similar to that observed on the nasal and other elements of the skull roof. Posterodorsally the lacrimal articulates tightly with the prefrontal, while anterodorsally it meets
the nasal along a wavy suture. Ventrally the lacrimal would have met with the maxilla, however, it cannot be determined if the suborbital ramus of the lacrimal would have met with the jugal posteriorly, although it most likely did as is the case in all parareptiles. Also, due to the disarticulation and damage to certain elements it cannot be determined if the lacrimal would have extended to the external naris, as it does in *Nyctiphruretus* (Säilä, 2010).

The right and left prefrontals are both exposed (Fig. 2.7), but in different orientations. The right prefrontal reveals an articulation with the nasal and lacrimal anteriorly, and its exposed exterior surface exhibits the same sculpturing seen on many of the other elements of the skull roof. Laterally, on the suture between the prefrontal and lacrimal are two foramina formed by a lateral contribution of the lacrimal and a medial contribution by the prefrontal, a thin process of the prefrontal separating them. The prefrontals would have formed the anterodorsal corner of the orbit, and the interior surface of this orbital contribution can clearly be seen on the inverted left prefrontal, as a smooth surface exhibiting only minute sculpturing.

Only the left postfrontal is exposed (Fig. 2.6), it is a triangular element that exhibits a sloped lateral surface that contributes to the posterolateral margin of the orbit. It is considerably broader than the postorbitals of *Nyctiphruretus*, which are small boomerang shaped elements (Säilä, 2010). In *Nyctiphruretus* there is a prominent crest found on the prefrontal, frontal, and postfrontal that borders the dorsal margin of the orbit (termed the orbitotemporal crest by Cisneros et al. (2004)). This crest is absent in *Abyssomedon williamsi*, as can be clearly observed on the left postfrontal and right prefrontal.

The left parietal (Fig. 2.6) is exposed in ventral view. The visible part is triangular in outline, being very broad posteriorly and narrowing anteriorly. The posterolateral portion of the parietal is dominated by a large depression, being deepest at its curved posterior edge, and then gradually becoming shallower until the medial and anterior portions of the parietal are reached, where the parietal is flat. The exposed ventral surface is largely smooth, exhibiting only a few faint ridges. The flat medial edge of the element exhibits half of the pineal foramen, which is displaced posteriorly. The medial edge would have articulated with its counterpart resulting in the complete pineal foramen.
2.5.2.2. Palate

Of the palatal elements, only a single vomer and ectopterygoid are exposed (Fig. 2.6). The vomer is exposed such that only its dorsal surface is visible, which is completely smooth, and devoid of any sculpturing. It is rectangular in shape overall, although rounded along its anterolateral edge where the alar flange extends from the body of the vomer. The medial edge of the element, where it would have articulated with the other vomer, curves slightly ventrally and then rises up dorsally to form the dorsal lamina. Anteriorly, the vomer diverges into two processes where it would have contacted the flat ventromedial process of the premaxilla. Posteriorly, it tapers off into two small processes that would have articulated with the palatine and pterygoid. The ectopterygoid is approximately rectangular in outline, and does not appear to possess any dentition, as is the case in most parareptiles. It also exhibits a small foramen positioned near the center of the element.

2.5.2.3. Mandible

The mandibular rami of the holotype are present and largely articulated, with the left mandibular ramus in lateral view and the right in ventral view. Both dentaries are preserved, but the right is not as informative due to its position in the matrix, with only a small amount of its ventral surface visible.

The left dentary is preserved in lateral view (Fig. 2.6), however, like its counterpart maxilla it is partially obscured by the disarticulated quadrate. The dentary is a long element that makes up the entire anterolateral portion of the mandibular ramus. Posteriorly, it articulates with the surangular dorsally and the angular ventrally. The tooth-bearing surface of the left dentary has six teeth exposed, although there are clearly empty tooth positions and the overlying quadrate obscures some of the tooth-bearing surface, indicating that the dentary would have held more teeth.

Both of the splenials are visible (Fig. 2.6), but only the right splenial is informative, as all that is exposed of the left splenial is a long, thin sliver near the ventral edge of the left dentary. The right splenial is exposed in medial view, and has been disarticulated from its usual position on the anteromedial portion of the mandibular ramus; it now overlies the ventral side of the
mandibular ramus. It is a long rectangular element that is slightly bowed laterally. The disarticulated nature of the right splenial, as well as the fact that its anterior end is damaged, makes it difficult to determine if it would have contributed to the mandibular symphysis, but the slenderness of the anterior portion of the element suggests that the splenials of *Abyssomedon williamsi* did not contribute to the symphysis, as is characteristic of all parareptiles (Laurin & Reisz, 1995).

The left angular is exposed in lateral view (Fig. 2.6); it is a long element (though not to the extent of the dentary) that is broad in the middle, tapering off anteriorly and posteriorly. The dorsal edge of the angular is curved for its entire length, the anterior portion of this edge articulates with the posterior end of the dentary, while the middle and posterior portions articulate with the surangular. The ventral surface of the element curves medially into the matrix where it presumably wraps around to the medial side of the mandibular ramus. The right angular is also present, exposed in ventral view, but does not offer any new information other than showing its articulation with the splenial anteriorly.

The left surangular (Fig. 2.6) is a broad crescent-shaped element, 2/3 the length of the angular. Anteriorly it tapers off to a point that is wedged between the dentary dorsally and the angular ventrally, posteriorly, it bifurcates into two small processes; this is also seen in *Microleter mckinzieorum* (Tsuji et al., 2010) where the articulation of the posterior of the surangular with the articular results in a foramen between them. Although the articular is not preserved in *Abyssomedon williamsi*, making it difficult to determine with confidence if it would have also possessed the foramen, but given the morphology of the surangular it likely did. The entirety of the dorsal edge articulates with the angular, while only the wedged anterodorsal portion articulates with the dentary. Along the anteroposterior midline of the surangular there are two small foramina, as is the case in *Nyctiphruretus* (Säilä, 2010).

Only the right prearticular is visible, found in association with the right angular. It is exposed in ventral view and offers little information.
2.5.2.4. Braincase

The elements of the braincase are largely absent from the holotype and only known specimen of *Abyssoomedon williamsi*, with only the parabasisphenoid and quadrate being exposed (Fig. 2.6). The parabasisphenoid is a long, triangular element that culminates anteriorly with the cultriform process, the longest and most slender portion of the element. The remainder of the element is made up of the actual body of the parabasisphenoid, which is narrow anteriorly and broadens posteriorly, giving it a triangular outline. At the point where the body of the parabasisphenoid meets the cultriform process there are two bulbous facets: the basipterygoid processes, one on each side of the element, which would have articulated with the pterygoids, forming the basal articulation of the braincase with the palate. The parabasisphenoid also possess a few very small teeth on the anterior portion of its body, in contrast to the edentulous parabasisphenoid of *Nyctiphruretus* (Säilä, 2010).

A single left quadrate is exposed in the specimen; it is disarticulated and found resting on top of the left maxilla with its posterior and lateral surfaces visible. It is composed of slightly concave dorsal and lateral extensions, and a convex ventromedial portion. Owing to its disarticulation the dorsal portion of the quadrate is exposed revealing sutural regions where it would have been sheathed by the squamosal. Ventrolaterally, the area where it would have articulated with the quadratojugal is visible. Opposite the region where it would have met the quadratojugal the pterygoid ramus extends medially.

2.5.2.5. Hyoid apparatus

The hyoid apparatus of *Abyssoomedon williamsi*, like many of the other elements, is found to be disarticulated and not in its proper place. Two of the three elements that make up the hyoid apparatus are preserved, the copula (or corpus hyoideum (Reisz and Scott, 2002)) and one of the two ceratohyals (Fig. 2.6). The medial element of the complex, the copula, possesses a bulky boomerang outline that terminates posteriorly in two processes on either side of the element, which would have articulated with the ceratohyals. The single preserved ceratohyal is an elongated, asymmetrical element that is flattened at its anterior end, while being much narrower...
posteriorly, as seen in some parareptiles such as *Owenetta kitchingorum* (Reisz & Scott, 2002) and *Sauropareion anoplus* (MacDougall et al., 2013).

### 2.5.2.6. Postcranial axial skeleton

The only elements of the axial skeleton that are exposed in *Abyssomedon williamsi* are several vertebrae and some disarticulated rib fragments, all of which are disarticulated. The vertebrae are partially exposed, and found in various orientations (Fig. 2.5). When taken together they grant an idea of the general vertebral morphology of this species. The centra are expanded and robust cylindrical structures, pinching off ventrally to form a small ridge on the ventral surface. The only obvious transverse process (Fig. 2.6) is gracile in structure, with its height being much greater than its anteroposterior width; it ends distally in a rounded tip. The exposed zygapophyses are flat processes that exhibit slightly different orientations depending on their position, with the anterior ones being tilted inward, and the posterior ones tilting outward. The rib fragments reveal little about the ribs other than their gracile structure.

### 2.5.2.6. Postcranial appendicular skeleton

Much like the axial skeleton, there is little of the appendicular skeleton preserved in this specimen. The clavicles are long, curved elements in lateral view. Although not articulating with any other elements, the clavicles exhibit prominent smooth facets on their proximal and distal ends, where each would have articulated with their respective scapula and cleithrum.

An elongate, slender element located near the two clavicles is tentatively identified here as a cleithrum (Fig. 2.7), usually a rarely preserved or absent element in most parareptiles. It is a flat, thin element, and if our identification is correct, it is significantly longer than the cleithra known from *Owenetta kitchingorum* (Reisz and Scott, 2002), *Mesosaurus tenuidens* (Modesto, 2010), *Emeroleter levis* (Tsuji et al., 2012), and *Sauropareion anoplus* (MacDougall et al., 2013). It exhibits a large, flat facet on its proximal end where it presumably articulated with one of the clavicles.
A single long bone, here tentatively identified as a humerus, is preserved together with the other elements that can be confidently assigned to *Abyssomedon williamsi* (Fig. 2.6). It is a long, gracile element, similar to the humeri seen in *Owenetta kitchingorum* (Reisz and Scott, 2002). Unfortunately, both the proximal and distal ends of this element are heavily damaged, making it impossible to be certain about its identity.

An isolated astragalus is also present (Fig. 2.6); it is a bulky, L-shaped element that is made up of two distinct parts, a broad rectangular base and a large articular surface extending dorsally, where the distal end of the tibia would have articulated. There are also several isolated phalanges spread across the surface of the slab. The exposed unguals are small, slightly recurved elements that terminate in a sharp point. The other non-terminal phalanges are small, gracile elements, being longer than they are wide.

### 2.5.3. *Colobomycter vaughni*

Together, the two specimens of *Colobomycter vaughni* described here reveal much of the anatomy of the skull, including posterior portions of the skull table, as well as the mandible. BMRP 2008.3.3b preserves part of the interior surface of the left side of the skull, as well as two vertebrae. While in UWBM 96304 the exterior surface of the left side of the skull is exposed rather than the interior, it also preserves a left mandible, disarticulated portions of the right side of the skull, and a few disarticulated postcranial elements.

#### 2.5.3.1. Skull roof

The premaxilla is only present in UWBM 96304; it is disarticulated and only partially preserved as it is missing the dorsal process that would form the anterodorsal margin of the naris. However, the tooth-bearing portion of the element is present and clearly exhibits the enlarged tooth that characterizes the genus (Fig. 2.8). This enlarged tooth exhibits fluting on its base, which is most likely the result of plicidentine in the tooth, a feature first observed in *Colobomycter pholeter* by MacDougall et al. (2014). The enlarged premaxillary tooth is also not as robust as its counterpart
in *C. pholeter*, with the base of the tooth being only about half as wide. In UWBM 96304 the enlarged premaxillary tooth has an anteroposterior base diameter of 1.84 mm, whereas a similarly sized individual of *C. pholeter* (BMRP 2008.3.1) possesses an enlarged premaxillary tooth that has an anteroposterior base diameter of 3.85 mm. The second, smaller tooth of the premaxilla cannot be observed due to the overlying left mandibular ramus.

The left maxilla is present in both specimens, but preserved in different aspects. A portion of the disarticulated right maxilla is also preserved in UWBM 96304. The left maxilla of UWBM 96304 is largely complete, missing only its posterior end (Fig. 2.8). It exhibits a tall anterodorsal process that meets the nasal dorsally in a long contact, separating the lacrimal from the narial opening, as is typical of the maxillae in *Colobomycter pholeter* and *Delorhynchus cifellii* (Modesto and Reisz, 2008; Reisz et al., 2014). Numerous superlabial foramina perforate the entire length of the maxilla; the much larger anterolateral maxillary foramen common to most parareptiles can be found on the anteriormost end of the element. The internal view of the maxilla available in BMRP 2008.3.3b (Fig. 2.10) reveals that a much smaller portion of the maxilla is visible medially, lacking the large dorsal process that is visible laterally, as it is covered by the nasal and lacrimal in this internal view. It also clearly shows the interior aspect of part of the lacrimal duct, as a long depression found anterodorsally on the maxilla.

The maxilla possesses at least 17 tooth positions in BMRP 2008.3.3b (Fig. 2.10), and the maxilla of UWBM 96304 has 13 (Fig. 2.8), but the posterior end of the latter maxilla is missing and it is clear that there would have been several more tooth positions. The presence of at least 17 tooth positions is important in that it is a distinct difference from the 14 tooth positions that are present on complete maxillae of *Colobomycter pholeter* (e.g. Laurin and Reisz, 1989). This difference in maxillary tooth number is not the result of these new specimens being different ontogenetic stages of *C. pholeter*, as there are specimens of *C. pholeter* (Laurin and Reisz, 1989; BMRP 2008.3.1) that are equivalent in size to the *Colobomycter vaughni* specimens. In both UWBM 96304 and BMRP 2008.3.1 the distance from the narial opening to the orbit is just over 9 mm. It is also worth noting that *Delorhynchus*, the sister taxon of *Colobomycter*, does not appear to exhibit changes in tooth number through ontogeny, as two specimens of different sizes both possess 24 teeth on their maxilla (OMNH 73515 and OMNH 73524 from Reisz et al., 2014). Another example from the fossil record is the Triassic reptile *Trilophosaurus*, which was remarked to have no changes in tooth number associated with growth (Demar and Bolt, 1981).
There are also examples of modern lizards that do not show any significant changes in tooth count throughout ontogeny (Dessem, 1985; Delgado et al., 2003). It is unlikely that this difference in tooth number represents sexual dimorphism within *C. pholeter*, as differing tooth counts is not a characteristic of sexual dimorphism in extant lizards (Carothers, 1984; Pinto et al., 2005). The only potential examples of sexual dimorphism in the dentition of fossil taxa is the presence of a tusk in one sex, such as in the dicynodont *Dictodon feliceps*, which have no other dentition aside from their tusks (Sullivan et al., 2003), making comparisons with this group not particularly useful.

Aside from the differences in tooth counts, the teeth are largely similar to those in *Colobomycter pholeter*, being conical in shape with a single cusp. As in the enlarged premaxillary tooth, the maxillary teeth show evidence of plicidentine; this is visible in the form of plications that are present on the bases of the enlarged teeth, as documented for *C. pholeter* (see MacDougall et al., 2014). However, as is the case with the enlarged premaxillary tooth, the enlarged maxillary teeth of *Colobomycter vaughni* are more gracile then those of *C. pholeter*, being similar in length but with a tooth-base diameter that is about 2/3 the size of those in similarly sized individuals of *C. pholeter* (BMRP 2008.3.1). In UWBM 96304 the enlarged maxillary teeth have an anteroposterior base diameter of 1.50 mm, in contrast a similarly sized individual of *C. pholeter* (BMRP 2008.3.1) exhibits enlarged maxillary teeth has an anteroposterior base diameter of 2.48 mm.

The left nasal of UWBM 96304 is preserved, but is missing some of its anterior end (Fig. 2.8). It is a roughly rectangular element that possesses a ventromedial curvature. The damaged anterior end in combination with the disarticulated and damaged premaxilla makes it impossible to determine what their contact would have looked like. Posteriorly it contacts the frontal along a jagged suture. BMRP 2008.3.3b reveals that the nasal forms an extensive overlapping contact with the lacrimal posteriorly, a sutural relationship that is not clear in the exterior view (Fig. 2.10).

The exterior of the left lacrimal is fully visible in UWBM 96304, as well as a portion of the disarticulated right lacrimal (Fig. 2.9). The exposed lateral surface of the lacrimal is a small, semicircular element that contributes to part of the anterior margin of the orbit and contacts the prefrontal dorsally and the anterodorsal process of the maxilla anteriorly. Interestingly, the
maxilla does not split the facial exposure of the lacrimal into two portions, as can be seen in *Colobomycter pholeter* and *Delorhynchus cifellii*. Originally, *C. pholeter* was described as having a lacrimal morphology similar to *Colobomycter vaughni*, in that laterally it is only exposed as a small lunate shape (Modesto and Reisz, 2008). However, reexamination of OMNH 73535 (Modesto and Reisz, 2008) reveals that the lacrimal of *C. pholeter* is in fact split into the lunate posterior portion and a smaller anterodorsal portion found wedged between the maxilla, prefrontal, and nasal (Fig. 2.11); this is also observed in BMRP 2008.3.1. The medial surface of the lacrimal of *C. vaughni* can be observed in BMRP 2008.3.3b (Fig. 2.10), and a narrow suborbital process of the lacrimal that cannot be seen clearly in UWBM 96304 is visible. Interestingly, *C. pholeter* also exhibits the presence of an anteroposterior ridge on the medial surface of the lacrimal (which continues onto the nasal) that is not present in *C. vaughni*, further displaying the difference in the lacrimal morphology of the two species.

The left jugal is slightly disarticulated but fully preserved in UWBM 96304 (Fig. 2.8), and the partial right jugal is found in articulation with the fragmentary right maxilla (Fig. 2.9). The jugal is a long, triangular element, being very narrow anteriorly and becoming much wider posteriorly. Due to the disarticulation of the left jugal, the long anterodorsal facet is visible where it articulated with the maxilla. The smooth dorsal surface of this element is its contribution to the posteroventral portion of the orbital margin.

The disarticulated left quadratojugal is preserved in UWBM 96304 (Fig. 2.8), where it is partially obscured dorsally by the left jugal, but most of its lateral surface is visible. It is a short element that possesses a slight convex ventral curvature for its entire length. It is shorter anteriorly where it would have articulated with the jugal, whereas posteriorly it becomes slightly taller and proceeds to curve medially. The overlying jugal obscures much of the dorsal edge of the quadratojugal, making its probable contributions to the lower temporal fenestra unobservable. Presumably, *Colobomycter vaughni* would have possessed a lower temporal fenestra much like that in *Colobomycter pholeter* (BMRP 2008.3.1); however, little can be said for certain about the fenestra because the temporal region of the skull is largely absent or obscured.

The left prefrontal of UWBM 96304 is partially damaged posteriorly, but most of its finer details can be made out (Fig. 2.8). It is a large element that contributes to a significant portion of the
orbital margin. The anterior portion of the prefrontal is found wedged between the nasal dorsally and the maxilla and the posterior portion of the lacrimal ventrally, as in *Colobomycter pholeter* (e.g., Modesto and Reisz, 2008). The anteriormost tip of the prefrontal contacts the anterior portion of the lacrimal, whereas the posterior end of the element meets with the anterolateral portion of the frontal. The interior view of the prefrontal in BMRP 2008.3.3b clearly shows its contribution to the orbital margin and reveals that it extends ventrally quite a bit farther than can be observed in UWBM 96304 (Fig. 2.10), as this ventral extension is obscured by matrix and the lacrimal in the lateral view of the latter specimen.

The left frontal of UWBM 96304 is a long, roughly rectangular element that meets the nasal and the prefrontal anteriorly and extends to meet the postfrontal posterolaterally (Fig. 2.8); it also would have contacted the disarticulated parietal posteriorly along a V-shaped suture. A portion of its lateral edge contributes to the top of the orbital margin.

The left postfrontal of UWBM 96304 is a small tri-radiate element, possessing an anterior, a posterior, and a ventral process (Fig. 2.8). The anterior and ventral processes form the posterodorsal corner of the orbit, articulating with the frontal and the postorbital, respectively. The posterior process extends back onto the temporal region of the skull and meets with the frontal dorsally and the postorbital ventrally.

The left postorbital present in UWBM 96304 is one of the larger elements of the skull roof, and makes up a large area of the temporal region (Fig. 2.8). The anterior edge of the element contributes to part of the posterior orbital margin. Posteriorly, the element is more rounded and the circular sculpturing present anteriorly on the bone is succeeded by smoother surface bearing anteroposteriorly-aligned grooves. The dorsal edge of the postorbital also curves slightly medially where it would have contacted the parietal.

In UWBM 96304, parts of the disarticulated parietals can be found posterior to the articulated portions of the skull (Fig. 2.9), allowing for some details regarding the element to be described. The parietal is a broad flat element, the posterior edge of which lacks sculpturing and curves slightly ventrally, where it would have met with the occiput. There is little else that can be determined from what is present.
The exterior surface of most of the elements of the skull roof exhibit a sculpturing pattern that is characterized by numerous circular depressions, giving many of the elements a pockmarked appearance. There are similar circular depressions present on the skull roof elements of *Colobomycter pholeter*, although they appear to be more numerous and oftentimes form honeycomb-like clusters (Modesto and Reisz, 2008).

2.5.3.2. Mandible

The left dentary of UWBM 96304 is exposed in lateral view (Fig. 2.8); it is a long element that is two-thirds the length of the entire mandible. As in the other elements of the mandible, the dentary lacks most of the sculpturing observed on the elements of the skull roof, being largely smooth with the occasional foramen. Twelve tooth positions are visible on the dentary, 11 of which are occupied; however, much of the tooth-bearing surface of the dentary is obscured by the maxilla, and it is apparent that there were several more tooth positions present. Most of the visible teeth are similar in shape and size to the smaller teeth of the maxilla, the exception being the anteriormost teeth, which are larger, though not to the degree of the enlarged teeth found on the premaxilla and maxilla of the upper jaw. Posteriorly, the dentary articulates with the angular and the surangular along a diagonal suture, and ventrally it gently curves into the matrix of the specimen where it would presumably meet with the unexposed splenial.

The angular is a long element, though not to the extent of the dentary, being about half the length of the mandible (Fig. 2.8). Dorsally it possesses a medially curving edge, which articulates with the surangular for two-thirds of its length, before ending with the suture with the dentary anteriorly. The anterior end of the element is quite narrow, but it broadens considerably moving posteriorly. Like the dentary, its ventral edge curves into the matrix, making any details of its medial extent unknown.

The surangular is roughly rectangular, and the shortest of the exposed mandibular elements (Fig. 2.8). It exhibits a slight dorsoventral curvature from its articulation with the angular to its dorsal end where it becomes obscured by the overlying quadratojugal. Its anterior end is found wedged between the dentary and the angular.
2.5.3.3. Hyoid apparatus

What appears to be a ceratohyal is found among the disarticulated material of UWBM 96304 (Fig. 2.9). It is a slender rod of bone that is too small to be a stylopodial element, and it is very similar to the ceratohyal of *Delorhynchus cifellii* as illustrated by Reisz et al. (2014); however, both of its ends are damaged, making it difficult to say with certainty if it is in fact a ceratohyal. No other elements of the hyoid can be observed in the specimens.

2.5.3.4. Postcranium

There are currently no vertebrae known from *Colobomycter pholeter*. Thus, we do not know what the vertebrae of the genus look like, and as the vertebrae present in the BMRP 2008.3.3b are not in articulation with the skull, it is not possible to be certain whether they belong to *Colobomycter vaughni*. However, the vertebrae found associated with the skull of BMRP 2008.3.3b are similar in structure to those found in its close relative *Delorhynchus cifellii* (Reisz et al., 2014: fig. 5) suggesting that they do belong to the specimen. They are therefore described here. The disarticulated nature of the vertebrae also makes it difficult to determine whether they are cervicals or dorsals, but because both vertebrae are found preserved near the skull of the specimen they may be representative of cervicals.

BMRP 2008.3.3b exhibits two disarticulated vertebrae (Fig. 2.10); although neither is exposed in their entirety, they reveal some details regarding their morphology. These vertebrae reveal the sizes and orientations of the zygapophyses: the small anterior zygapophyses project inwards and anteriorly, whereas the larger posterior zygapophyses project outwards and posteriorly. The neural spines of the vertebrae are short but robust. Laterally, the neural arches show the presence of a small pocket, as in the vertebrae of *D. cifelli* (Reisz et al., 2014). A small portion of an intercentrum is visible in BMRP 2008.3.3b, but little detail can be made out as the two preserved vertebrae obscure most of it. Other than these details, there is little else that can be observed from these vertebrae.
A partial scapula and clavicle are the only identifiable girdle elements that are found associated with the disarticulated postcranial material of UWBM 96304 (Fig. 2.9), and the two elements are reminiscent of the pectoral girdle preserved in *Delorhynchus cifellii* (Reisz et al., 2014:fig. 2). The fragmentary flat scapula is found articulating dorsally with the clavicle. What is preserved of the clavicle reveals a long, slightly curved element; the medial and lateral heads of the clavicle are expanded, in contrast to the narrower shaft.

Finally, there is a single phalanx that is found exposed among the various disarticulated material of UWBM 96304 (Fig. 2.9); its preservation near the skull would suggest it is likely a manual phalanx, but there is no way to confirm this. It has a rounded, bulbous anterior end that transitions into a narrower flattened shaft, it then expands again into the posterior end, which does not exhibit the roundness observed anteriorly.

### 2.5.4. New material of *Colobomycter pholeter*

Over the past few decades several partial skulls of *Colobomycter pholeter* have been described (Vaughn, 1958; Laurin and Reisz, 1989; Modesto, 1999a; Modesto and Reisz, 2008). BMRP2008.3.1 and BMRP2008.3.10, the newest specimens of *C. pholeter*, provide information that was previously unknown for several areas of the skull, especially regarding the palate and the mandible. Since much of the skull anatomy of *C. pholeter* has been previously described, only new information that has been obtained from the two new specimens will be described here.

#### 2.5.4.1. Skull roof

The skull roof of *Colobomycter pholeter* has been partially described in the literature (Vaughn, 1958; Modesto, 1999a; Modesto and Reisz, 2008), however, BMRP 2008.3.1 exhibits the most complete skull roof to date, and offers some new details regarding this region of the skull. Most of the elements of the skull roof exhibit the sculpturing pattern of shallow, round pits that has been previously described for *C. pholeter* (Laurin and Reisz, 1989). BMRP 2008.3.10 is only
exposed in medial view, thus the interior surfaces of many elements of the anterior skull roof are visible (Fig. 2.15).

In BMRP 2008.3.10 the medial surface of the nasal and the lacrimal show the presence of a long prominent anteroposterior shelf, just below the interior nasal lacrimal fossa (Fig. 2.15). Much of the medial surface of the skull roof was also visible in FMNH 272; however, Laurin and Reisz (1989) do not mention the presence of this shelf despite it being visible in their illustrations. The interior nasal lacrimal fossa that is anterior to the shelf is also quite deep, with the same fossa being much shallower in the new species of *Colobomycter* (MacDougall et al., 2016). The new species also lacks the aforementioned prominent ridge on the nasal and lacrimal, instead exhibiting a slight rise where the lacrimal duct is found (MacDougall et al., 2016). The posterior part of the lacrimal is a rounded element that contributes to the anterior margin of the orbit; it extends posteriorly to meet with the anterior end of the jugal. The anterior exposure of the lacrimal is much smaller than the posterior one and is found wedged between the maxilla, the prefrontal, and the nasal.

As discussed briefly in MacDougall et al. (2016), the maxilla of *Colobomycter pholeter* possesses a dorsal extension that covers part of the lacrimal in lateral view and divides it into an anterior and posterior portion (Fig. 2.14E). This double lateral exposure of the lacrimal was not described in prior studies (Vaughn, 1958; Modesto and Reisz, 2008) due to missing anatomical information or misinterpretations of the anterior skull roof anatomy (MacDougall et al., 2016).

The septomaxilla is exposed in BMRP 2008.3.1 as only a small portion found between the maxilla and the premaxilla (Figs. 2.13, 2.14), the rest being covered by overlying elements. However, the medial surface of the element is visible in its entirety in BMRP 2008.3.10 (Fig. 2.15). In medial view the septomaxilla has a dorsal process that extends slightly posteriorly to meet the maxilla. The ventral portion of the element extends posteriorly to also contact the maxilla. The posterodorsal and posteroventral extensions of the element plus a contribution of the maxilla result in the oval septomaxillary foramen.

The quadratojugal is an L-shaped element in lateral view that meets the jugal anteriorly and the squamosal posterodorsally, whereas posteriorly it curves medially to the occipital portion of the skull to make contact with the quadrate (Figs. 2.13, 2.14). The dorsal edge of the quadrate curves posterodorsally and forms the posterolateral margin of the lower temporal fenestra.
The postorbitals of *Colobomycter pholeter* are broad flat elements, much larger than those found in most other parareptiles, as they extend very far posteriorly, and along with the parietals, make up the posterior margin of the skull roof (Figs. 2.13, 2.14). The posterior edges of the element curve slightly ventrally, where it contacts with both the jugal and the squamosal. Anteriorly, the postorbital contributes to the posterior margin of the orbit, as well as contacting the postfrontal. The supratemporal is not preserved in either specimen, which is unfortunately the case for most specimens of *C. pholeter* that have been described. However, there is a groove in the parietal where the supratemporal would have fit. The indeterminate element that was described by Vaughn (1958) in the description of the holotype is likely a broken portion of the supratemporal.

The squamosal is one of the larger elements of the temporal region (Figs. 2.13, 2.14). It contacts the quadratojugal ventrally and the postorbital dorsally. The anteroventral edge of the squamosal is slightly curved and forms the posterodorsal margin of the lower temporal fenestra. Like the quadratojugal, the posterior end of the squamosal curves medially to wrap around to the occipital portion of the skull.

The postparietal is not a single median element as in some parareptiles (deBraga and Reisz, 1996; MacDougall and Reisz, 2012), but instead composed of two paired elements (Figs. 2.13, 2.14), as in parareptiles such as *Delorhynchus cifellii* (Reisz et al., 2014). Each postparietal is a small triangular element that exhibits a few small ridges running anteroposteriorly; the two postparietals meet each other medially along a faint straight suture. Anteriorly, each one contacts with the posteromedial edge of their respective parietal.

### 2.5.4.2. Palate

The palate of *Colobomycter pholeter* is a region of the skull that has never been fully preserved in any previous specimens; only a fragmentary vomer and palatine were described in OMNH 73535 (Modesto and Reisz, 2008). Fortunately, the left side of the palate is largely complete in BMRP 2008.3.1 (Figs. 2.13, 2.14), facilitating description of this area.

The vomer is the triangular anteriormost element of the palate; it is broader posteriorly but narrows anteriorly, becoming a narrow process that contacts the premaxilla. The lateral edge of
the vomer contributes to most of the medial margin of the choana. It exhibits the presence of several small, pointed vomerine teeth across its surface; the anteriormost vomerine tooth is much larger than the succeeding teeth. Posteriorly, the vomer makes contact with both the palatine and the pterygoid.

The palatine makes up a significant portion of the lateral side of the palate. It contacts the vomer anteriorly and forms the posterior border of the choana, whereas laterally it meets the pterygoid, and posteriorly it contacts the ectopterygoid. The dentition of the palatine is primarily found as a large cluster that continues onto the pterygoid.

The pterygoid is the largest element of the palate; roughly triangular in shape, it is composed of a broad anterior process, a laterally projecting transverse process, and a quadrate ramus that flares posterolaterally. The broad main body of the pterygoid extends anteriorly to meet the vomer and palatine, there are two large clusters of teeth present in this area, one located anterolaterally and the other found medially, which continues onto the palatine. There is also a small line of pterygoid teeth that runs along the posteromedial edge of the element. In addition to these main batteries there are a few other scattered teeth across the area. The transverse process rises ventrally from the pterygoid, extending ventrolaterally towards the side of the skull, a row of several large pterygoid teeth run along the highest part of the process, and there are numerous smaller teeth that cover the rest of the process. Medially, the transverse process curves laterally and transitions into the quadrate ramus. The quadrate ramus is a smooth process that curves posterolaterally and exhibits the presence of several small teeth; it is missing its posterior end where it would have contacted with the quadrate. The ectopterygoid is found wedged between the base of the transverse process and the lateral edge of the anterior extension. The ectopterygoid is the smallest element of the palate; it is roughly triangular in shape and lacks the dentition observed on the other elements of the palate.

The quadrate is partially obscured by its articulation with the left mandibular ramus, but some details of its morphology are still visible. In occipital view the quadrate possesses a narrow finger of bone that extends laterally, whereas medially it broadens into a small triangle. In medial view the smooth surface of the quadrate curves dorsally to where it would have met with quadrate ramus of the pterygoid. The quadrate fits snugly into the articulating facet of the articular.
2.5.4.3. Mandible

The mandible of *Colobomycter pholeter* has never been found preserved in any previous specimens. Fortunately BMRP 2008.3.1 preserves nearly the entire mandible in articulation with the rest of the skull (Figs. 2.13, 2.14). The medial surface of the mandibular ramus exhibits an adductor fossa that is one-third the length of the ramus.

The dentary is the longest element of the mandibular ramus, extending posteriorly from the very tip of the lower jaw for three-quarters the length of the mandibular ramus. It is dorsoventrally tall for most of its length, but tapers off dorsally at its posterior end. The dentary is the sole contributor to the mandibular symphysis, as it excludes the splenial. Posteriorly, the dentary meets with the angular and the surangular along a long ascending curved suture, and anteroventrally it contacts the anterior half of the splenial. Also of note is that the anterior end of the dentary exhibits a cluster of labial foramina. Although the maxillary teeth obscure the dentary teeth laterally, some of the dentary teeth can be seen in medial view. The dentary teeth that can be observed are very similar in size to the non-enlarged maxillary teeth; they exhibit a single cusp, terminate at a sharp point, and in total 18 teeth can be observed. A portion of the medial surface of the coronoid eminence can also be observed; it exhibits the presence of a small pad of teeth.

The splenial is a smooth element mostly restricted to the medial surface of the mandibular ramus, with the exception of a small portion that wraps around ventrally to the lateral side to meet the dentary and the angular. The medial part of the element extends anteriorly, narrowing considerably, but does not reach the symphysis, as is the case for many other parareptiles (Laurin and Reisz, 1995). Posteriorly, the splenial contacts both the prearticular and the angular; the small foramen intermandibularis caudalis is also found where these three elements intersect.

The angular is a smooth curved element that is broad posteriorly but tapers to a narrow band anteriorly. This narrow anterior end is found wedged between the dentary dorsally and the splenial ventrally. The posterior half of the angular wraps around to the medial side of the mandibular ramus, and then extends dorsally to meet the prearticular. This medial portion of the angular also exhibits a slight concavity, which results in the ventral edge of the bone being
narrower than the rest of the lateral edge of the mandibular ramus. The anteromedial portion of the angular is found between the prearticular and the splenial. Posterodorsally, the lateral surface of the angular contacts the surangular along a curved suture. The surangular is a slightly curved rectangular element that is shorter than the angular, being around two-thirds its length; it meets the posterior end of the dentary along a diagonal suture. Posteriorly, both the angular and the surangular contact the articular.

The articular is a small, broad element that is very short anteroposteriorly. The posterodorsal surface of the articular exhibits two distinct facets for articulation with the upper jaw. Anteriorly, most of its surface meets with the prearticular, with the exception of its lateral edge, which contacts the angular and the surangular. In contrast to the articular, the prearticular is a long element, similar in length to the angular, found on the medial side of the mandibular ramus. Its posterior end is expanded to meet with much of the broad articular, it immediately starts to narrow moving anteriorly, where it meets the splenial. Ventrally, it contacts the medial portion of the angular along a horizontal suture.

2.5.4.4. Braincase

The only element of the braincase that is preserved is the disarticulated and damaged parabasisphenoid of BMRP 2008.3.1 (Figs. 2.13, 2.14), as its anterior and posterior extremities are missing; only a few details regarding it can be determined. The body of the parabasisphenoid is triangular in outline, being broad posteriorly and narrow anteriorly, and the cultriform process that would have continued from the narrow anterior end is missing. The lateral edges of the element curve ventrally and show the presence of small teeth.

2.6. Discussion

The new parareptile material described here, in particular the three new species, contributes significantly to our knowledge of early Parareptilia. It also further increases the large terrestrial tetrapod diversity at the Richards Spur locality, which has been growing quite steadily over the
past few decades. We now have more than 30 tetrapod taxa reported to be present at the locality, many of which have been described in the past decade. Besides new taxa, like the three parareptiles described here, many taxa previously known to be present at this locality are much better known now than they were previously (Sullivan and Reisz, 1999; Evans et al., 2009; Reisz et al., 2009, 2014). This has resulted in a much better understanding of the composition of the Richards Spur fauna, although there is still much work that needs to be done, as many of the taxa found at the locality are represented by only a single specimen (e.g. Anderson et al., 2009), some are only known from cranial material (e.g. Reisz et al., 2011), and several others have never been thoroughly described (e.g. Carroll, 1968; Reisz, 1980; Modesto, 1996). Fortunately, there is an abundance of unstudied material that will likely further contribute to our knowledge of Richards Spur in the years to come.

The presence of *Feeserpeton oklahomensis*, *Colobomycter vaughni*, *Abyssomedon williamsi*, and new material of *Colobomycter pholeter* at Richards Spur is important, as these new specimens add to our limited knowledge of Early Permian parareptiles, in particular our understanding of the little studied clades Lanthanosochoidea and Nyctiphruretidae. Our knowledge of Lanthanosochoidea has been extremely limited until recently (Reisz et al., 2014), as for many years very little material represented the group. The lanthanosuchoids are not broadly distributed geographically, with all known members of the clade being restricted to Laurasia (deBraga and Reisz, 1996; Tsuji et al., 2010). The life histories of the known members of the clade are also poorly understood; *Lanthanosuchus watsoni* is likely aquatic or amphibious (Reisz, 1997), whereas *Acleistorhinus pteroticus* and the Richards Spur taxa are considered to be fully terrestrial (deBraga et al., 1996; MacDougall and Reisz, 2012), other than that little else is known. Similarly, prior to the discovery of *Abyssomedon williamsi* the clade Nyctiphruretidae was known from only two species of *Nyctiphruretus* (Efremov, 1938; Bulanov, 2002; Säilä, 2010), both of which are restricted to Russia. The new information gained from the North American *A. williamsi* provides more information regarding the distribution of this poorly known clade.

Currently, the parareptile taxa found at the Richards Spur locality currently consist of *Delorhynchus priscus*, represented by maxillary fragments (Modesto, 1999) *Bolosaurus grandis*, represented by dentary and maxillary fragments (Reisz et al., 2002), *Colobomycter pholeter*, represented by three fragmentary skulls (Modesto, 1999), as well as the two new skulls described
here, Microleter mckinzieorum, represented by a fragmentary skull (Tsuji et al., 2010), and several specimens of Delorhynchus cifellii (Reisz et al., 2014). Thus, with Feeserpeton oklahomensis, Abyssomedon williamsi, and Colobomycter vaughni we have eight parareptiles known from Richards Spur; this is in strong contrast to the known fauna of Early Permian parareptiles in North America. The species Bolosaurus striatus, although represented by fragmentary materials, is well known in Early Permian localities in Texas (Cope, 1878), and has also been found in New Mexico (Lucas et al., 2005). The only other known parareptile from North America is a single skull of Acleistorhinus pteroticus from the Grand Field locality in Oklahoma (Daly, 1969; deBraga and Reisz, 1996). Thus, the Richards Spur parareptile fauna provides a unique window into early parareptilian evolution and diversification, and permit a more detailed evaluation of the clade during the Early Permian. These aspects are discussed in more depth in chapter 4.

2.7. Conclusions

The Richards Spur locality exhibits an immense diversity of tetrapod taxa, with many new taxa being described on a regular basis, among these newly described taxa are several parareptiles. We described three new parareptiles: the lanthanosuchoids Feeserpeton oklahomensis and Colobomycter vaughni, and the nyctiphruretid Abyssomedon williamsi. New, more complete material of the lanthanosuchoid Colobomycter pholeter is also described. The three new parareptiles described from the locality further add to the impressive tetrapod diversity at Richards Spur. These new taxa, along with the new material of C. pholeter, are important for better understanding parareptilian diversity during the Early Permian. Furthermore, this new material has granted us a much better understanding of parareptilian anatomy, especially of poorly known clades like Lanthanosuchoida and Nyctiphruretidae.
2.8. Acknowledgments

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2.9. References


2.10. Figures and Figure Captions

*Figure 2.1. Ffeeserpeton oklahomensis*, OMNH 73541, holotype specimen. Photographs of skull in A, dorsal, B, palatal, C, occipital, and D, right lateral views.
Figure 2.2. *Feeserpeton oklahomensis*, OMNH 73541, holotype specimen. Outline drawings of skull in **A**, dorsal, **B**, palatal, **C**, occipital, and **D**, right lateral views. **Abbreviations:** an, angular; ar, articular; bo, basioccipital; d, dentary; ec, ectopterygoid; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pal, palatine; pf, postfrontal; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; prm; premaxilla; pro, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; sa, surangular; so, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; v, vomer.
Figure 2.3. *Feeserpeton oklahomensis*, OMNH 73541, holotype specimen. CT scans of the skull in right parasagittal view showing A, the enlarged tooth of the mandible, and B, some of the more posterior non-caniniform teeth of the mandible. **Abbreviations:** d, dentary; f, frontal; j, jugal; n, nasal; o, orbit; p, parietal; pt, pterygoid; sp, splenial. Arabic numerals indicate tooth positions of the dentary series. The 4th tooth of the dentary series is representative of an enlarged tooth ("caniniform").
Figure 2.4. *Abyssomedon williamsi*, BMRP 2008 33a, holotype specimen. Photograph of the slab that contains the specimen.
Figure 2.5 *Abyssomedon williamsi*, BMRP 2008 33a, holotype specimen. Line drawing of the specimen. The question marked element is likely either a humerus or femur. **Abbreviations:** an, angular; as, astragalus; cer, ceratohyal; cl, clavicle; cle, cleithrum; co, copula; d, dentary; ec, ectopterygoid; f, frontal; h, humerus; j, jugal; la, lacrimal; m, maxilla; n, nasal; p, parietal; pbs, parabasisphenoid; pf, postfrontal; ph, phalanx; pra, prearticular; prf, prefrontal; pm, premaxilla; q, quadrate; r, rib; s, splenial; sa, surangular; u, ungual; v, vomer; ve, vertebra.
Figure 2.6. Abyssomdeon williamsi, BMRP 2008 33a, holotype specimen. Interpretive drawing of the left side of the specimen. The question marked element is likely either a humerus or femur. **Abbreviations:** an, angular; as, astragalus; cer, ceratohyal; co, copula; d, dentary; ec, ectopterygoid; h, humerus; j, jugal; m, maxilla; n, nasal; p, parietal; pbs, parabasisphenoid; pf,
postfrontal; \textbf{ph}, phalanx; \textbf{pra}, prearticular; \textbf{pm}, premaxilla; \textbf{q}, quadrate; \textbf{r}, rib; \textbf{s}, splenial; \textbf{sa}, surangular; \textbf{u}, ungual; \textbf{v}, vomer; \textbf{ve}, vertebra.
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**Abbreviations:** a, angular; d, dentary; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; pf, postfrontal; po, postorbital; prf, prefrontal; prm, premaxilla; qj, quadratojugal; sa, surangular; v, vertebra.
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**Abbreviations:** a, angular; an, angular; art, articular; d, dentary; ec, ectopterygoid; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pbs, parabasisphenoid; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal; v, vomer.
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Chapter 3

Plicidentine in the Early Permian parareptile *Colobomycter pholeter*, and its phylogenetic and functional significance among coeval members of the clade.

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3.1 Abstract

Once thought to be an exclusively anamniote characteristic, plicidentine, a pattern of infolding of dentine, is now known to be found in various amniote clades, including Parareptilia. In the absence of detailed analyses of parareptilian dentition, most parareptiles were assumed to lack plicidentine due to the absence of external indicators, such as plications on the tooth base. The clear presence of this dentinal feature in the largest premaxillary and maxillary teeth of *Colobomycter pholeter*, led us to the present detailed study within the dentition of this unusual parareptile, and those of coeval members of this clade. Our study reveals that there is large variability in the degree of dentine infolding within *C. pholeter* dentition, as well as within those of closely related parareptiles. This variability ranges from a lack of plications, to very complex anamniote-like plicidentine. Utilizing computed tomography scans in conjunction with histological sections we also demonstrate the utility of computed tomography scans in conducting non-destructive sampling in the identification of plicidentine. Given the variability of plicidentine in this sample of parareptiles, we hypothesize that one function of parareptilian plicidentine is to increase the surface area for attachment tissues, and we suggest that the use of plicidentine as a character in phylogenetic analyses of parareptiles may be misleading.

3.2 Introduction

Parareptilia, the sister taxon to Eureptilia, was a clade of amniotes that lived during the Palaeozoic and Early Mesozoic Eras. Parareptiles were uncommon members of most Early Permian communities, but by the Middle and Late Permian, parareptiles had obtained a global distribution, becoming integral components of terrestrial tetrapod communities (Tsuji et al., 2010; MacDougall and Reisz, 2012). Although most were fairly small-bodied, parareptiles were strikingly diverse, ranging in form from small, superficially lizard-like predators to large armored herbivores. However, the Permo-Triassic extinction event resulted in a significant decline in the number of parareptilian lineages, with only one clade, the Procolophonoidea, surviving into the Mesozoic and eventually going extinct by the end of the Triassic (Modesto et al., 2001, 2003; Tsuji and Müller, 2009).
Despite morphological differences between the major groups of parareptiles, the exact phylogenetic positions of some remain contentious (Ivakhnenko, 1979; Lee, 1995; Bulanov, 2002; Tsuji, 2006; Müller and Tsuji, 2007; Säilä, 2010). The discrepancy in interpretations of their interrelationships illustrates the need for more phylogenetically informative characters. Recent studies have focused on parareptilian dentitions and tooth implantation (Cabreira and Cisneros, 2009; MacDougall and Modesto, 2011) and have highlighted the potential for differences in dental anatomy and attachment within several parareptilian groups to be informative in this regard. One of these features is the presence of plicidentine (Modesto and Reisz, 2008). Plicidentine is a structural term that refers to the infolding of the dentine around the pulp cavity (Maxwell et al., 2011; LeBlanc and Reisz, 2013), and its presence has historically been attributed to several anamniote groups, including labyrinthodont amphibians (Warren and Turner, 2005). Plicidentine was first described by Owen (1841) in the temnospondyl *Mastodonsaurus*, and was subsequently described in other anamniotes. The broad distribution of plicidentine (commonly referred to as “labyrinthine infoldings” sensu Owen (1841)) in amphibians, coupled with the absence of plicidentine in most derived groups of amniotes, has led many authors to suggest that plicidentine was lost early in the evolutionary history of Amniota (Laurin and Reisz, 1995; Hill, 2005). However, over the last century plicidentine has been documented in ichthyosaurs (Mazin, 1981), choristoderes (Edmund, 1969), mosasaurs (Schultze, 1970), varanoids (Kearney and Rieppel, 2006), snakes (Scanlon and Lee, 2002), captorhinids (de Ricqlès and Bolt, 1983), and of particular interest, in a single parareptile, *Colobomycter pholeter* (Modesto and Reisz, 2008).

*Colobomycter pholeter* is an Early Permian (289 ma) parareptile from the Richards Spur locality in Oklahoma, USA. This locality is unique in preserving multiple taxa of small parareptiles, in strong contrast to all other Early Permian localities, where parareptiles are either absent, or represented by the remains of single taxa. The Dolese Brothers Limestone Quarry near Richards Spur has yielded the remains of several cranial fragments of *C. pholeter*, a second, new species of this genus (MacDougall et al., 2016), at least two species of *Delorhynchus* (Fox, 1962; Reisz et al., 2014), the enigmatic *Feeserpeton oklahomensis*, as well as *Microleter mckinzieorum*, all basal parareptiles. In addition, the more derived parareptile taxon *Bolosaurus grandis*, is known from jaw fragments. This unprecedented diversity of coeval parareptiles provides the basis of the
current study, allowing us to compare in great detail the anatomy of the teeth of relatively closely related taxa.

Among early parareptiles, *C. pholeter* is readily distinguishable by the presence of two greatly enlarged maxillary and a single, enormous premaxillary tooth (Vaughn, 1958; Modesto and Reisz, 2008). In the case of the enlarged premaxillary tooth, it is much larger than any of the other teeth in the jaws, significantly surpassing even the size of the enlarged maxillary teeth. The unique dentition of *C. pholeter* is unlike any other found within the Palaeozoic, or even among reptiles. As previously mentioned, Modesto and Reisz (2008) were able to determine the presence of plicidentine within the maxillary teeth of *C. pholeter*. This determination was possible because externally the bases of the teeth possessed the well-developed plications characteristic of plicidentine. More importantly, many of the teeth were broken, revealing the presence of folded dentine. However, other than determining that plicidentine was present in *C. pholeter* they were able to say little else regarding the nature of the plicidentine, as histological analysis is required to determine the finer details of tooth tissues. The presence of plicidentine within *C. pholeter* combined with its unique and poorly studied dentition warranted a much more thorough examination of its teeth through histological examination.

Currently, histological examinations of parareptilian teeth have only been conducted on the procolophonid *Soturnia caliodon* (Cabreira and Cisneros, 2009), the mesosaur *Stereosternum tumidum* (Pretto et al., 2014), the procolophonid *Procolophon trigoniceps* (Sander, 1999), and an indeterminate pareiasaur (Sander, 1999). However, none of these studies was able to determine the nature and extent of the plicidentine in these animals. This is largely a result of the plane of section of the teeth that underwent histological analysis for the two former taxa, and an emphasis on studying enamel microstructure in the two latter taxa. The documentation of tooth tissues in longitudinal section makes the identification of plicidentine difficult, because the folds generally run parallel to the long axis of the tooth. In order for the infolding of the dentine (or lack thereof) to be clearly visible, and to document its interactions with the adjacent attachment tissues, it is necessary to take serial cross-sections of teeth as well as longitudinal sections through the tooth bearing elements.

Here we present the first comparative histological examination of plicidentine in Parareptilia through the examination of *Colobomycter pholeter* and several of its contemporaneous relatives.
We also demonstrate the potential use of X-ray micro-computed tomography (CT) scans for the study of different types of plicidentine, and hence avoidance of destructive methods. We also provide the first survey of the distribution of plicidentine in coeval parareptilian taxa, including Bolosauridae, three members of Lanthanosuchoida, and Microleter mckinzieorum, and assess the phylogenetic and functional significance of parareptilian plicidentine.

**Institutional Abbreviations**—OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; UWBM, University of Washington Burke Museum of Natural History and Culture, Seattle, Washington, USA.

### 3.3 Material and Methods

The data presented here was obtained from the study of five different parareptile taxa: *Colobomycter pholeter* Vaughn, 1958 (e.g., Modesto, 1999), *Bolosaurus striatus* Reisz et al. 2002, *Microleter mckinzieorum* Tsuji et al., 2010, *Feeserpeton oklahomensis* MacDougall and Reisz, 2012, and *Delorhynchus cifellii* Reisz et al., 2014. With the exception of *B. striatus*, these taxa are all found at the Richards Spur locality of Oklahoma, USA, and in the case of *B. striatus* its dentition is similar in shape and age to that of *Bolosaurus grandis*, making these comparisons valid. Of these taxa, only *C. pholeter, B. striatus, M. mckinzieorum*, and *Delorhynchus cifellii* were chosen for histological preparation. *F. oklahomensis* (which is currently known from only a single specimen) was studied using CT scans and the imaging software Avizo 7.

Permission was obtained from all of the applicable institutions (Sam Noble Museum of Natural History in Norman, Oklahoma; University of Washington Burke Museum in Seattle, Washington; Goldfuß Museum, Bonn, Germany; Royal Ontario Museum in Toronto, Canada) to borrow and work on the specimens that are presented herein. All specimens were loaned to R. R. Reisz with permission for preparation, and in the case of those that were thin-sectioned, histological analysis.
Material that was thin-sectioned included two dentary fragments of *Bolosaurus striatus* from the Lower Permian of Texas (StlPB-R 636, StlPB-R 637), as well as a partial maxilla (ROM 67372) and dentary (ROM 67373) of *Delorhynchus cifeii*, a partial maxilla (ROM 67375) of *Microleter mckinzieorum*, and a premaxilla (UWBM 95405) and partial maxilla (ROM 67374) of *Colobomycter pholeter* from the Lower Permian of Oklahoma. Specimens were embedded in Castolite AP polyester resin under vacuum, and then left to dry for a 24-hour period. The specimens were then cut using a Buehler Isomet 1000 wafer blade low-speed saw. Cut specimens were then mounted to glass or plexiglass slides using Scotch-Weld SF-100 cyanoacrylate. The mounted specimens were ground down to approximately 180 µm thick using a Hillquist grinding cup, and then further ground manually using progressively finer grits of silicon carbide powder; lastly specimens were polished using one-micron grit aluminum oxide powder. Photography of specimens was performed using a Nikon DS-Fi2 camera mounted to a Nikon AZ-100 microscope fitted with crossed-polarizing filters, as well as an oblique illumination slider. Image processing was performed using Nikon NIS-Elements (Basic Research) imaging software registered to R. R. Reisz of the University of Toronto Mississauga.

CT scanning of *Colobomycter pholeter* was performed at the University of Calgary, and the CT scanning of *Feesperpeton oklahomensis* was performed at the University of Texas High Resolution X-ray CT Facility. The CT data set for *C. pholeter* consists of 950 slices at a resolution of 1120 x 1120 pixels, and the data set for *F. oklahomensis* consists of 623 slices at a resolution of 1024 x 1024 pixels. The slices were then imported into and manipulated using the imaging software Avizo 7 registered to R. R. Reisz of the University of Toronto Mississauga.

### 3.4 Results

#### 3.4.1. *Colobomycter pholeter*

As previously indicated, *Colobomycter pholeter* is unique among parareptiles, and Palaeozoic reptiles in general, in that it possesses a pair of greatly enlarged maxillary teeth and a single, very large tooth on the premaxilla (Fig. 3.2A). The remaining teeth of the maxilla and the single other premaxillary tooth are small and homodont. Modesto and Reisz (2008) described plications on
the exterior of the enlarged premaxillary and maxillary teeth, and broken maxillary teeth revealed that the walls of the tooth bases were folded. The thin sections of the teeth of *C. pholeter* reveal the presence of extensive plicidentine in cross-section. In particular, the dentine at the base of the enlarged premaxillary tooth of *C. pholeter* is arranged into a series of tight folds that radiate towards the pulp cavity (Fig. 3.2B, C). The central component of each fold is composed solely of dentine, signifying that these dentine folds, termed lamellae (Kearney and Riepepl, 2006), are so highly infolded that no attachment tissues from the outside of the tooth base contribute to the fold. The presence of convoluted folding and lamellae is very reminiscent of the complex plicidentine seen in labyrinthodont amphibians (Warren and Davey, 1992). In *C. pholeter*, short, unbranched folds alternate with folds that are considerably longer and sinuous (Fig. 3.2B-E). The midsection of the enlarged premaxillary tooth reveals that the folds maintain their complexity well above the jaw line. They exhibit the same alternating pattern of short and long lamellae seen lower in the tooth, although the spaces between lamellae are now occupied by dentine. Several of the lamellae exhibit primary branching, something that is not observed at the base of the tooth. Dentine tubules extending from the primary folds converge and form dark dentine. A byproduct of the dark dentine is the formation of lighter petaloid dentine, similar to that observed in embolomeres and temnospondyls (Warren and Turner, 2005). Thin sections near the tip of the crown still exhibit plicidentine (Fig. 3.2F, G). The folds are simpler, consisting of very short lamellae and none of the complex folding seen in lower sections through the tooth. The alternation between shorter and longer folds is largely maintained. Dark dentine is still apparent, although it is not quite as concentrated as it is in the midsection of the tooth. Due to the presence of lamellae in the crown of the tooth, the enamel that surrounds the tooth crown never enters into any of the folds of the tooth. However, the folding results in the enamel being grooved slightly wherever the folds are occurring (Fig. 3.3).

Interestingly, the dentine in the enlarged maxillary teeth of *Colobomycter pholeter* shows a folding pattern that is quite distinct from that seen in the enlarged premaxillary tooth. Thin sections at the base of this tooth reveals that the dentine is highly folded, however, unlike in the enlarged premaxillary tooth it is much more irregular. Folds are still highly convoluted, but do not consist of lamellae, because the surrounding attachment tissues invade the centers of the folds (Fig. 3.4B, C). In the midsection of the tooth, the irregular folding seen lower in the tooth is entirely absent and the dentine forms a circular outline of the tooth (Fig. 3.4D, E).
The smaller teeth of *C. pholeter* do not show the complex infolding of the enlarged teeth, although they still clearly show the presence of infolding, albeit of a much simpler nature (Fig. 3.4B, C). This suggests that, much like in temnospondyl amniotes (Warren and Davey, 1992), the number and complexity of folds observed in the teeth of *C. pholeter* increases with tooth size.

CT scans of the teeth of another specimen of *Colobomycter pholeter* (OMNH 73535) revealed that it was possible to clearly view the infolding in the enlarged maxillary and premaxillary teeth (Fig. 3.5). However, aside from being able to see the gross morphology of the folds, finer details such as the structural differences between the plicidentine in the enlarged premaxillary tooth and the enlarged maxillary teeth could not be observed. It was also difficult to see the folds of the smaller teeth, due to their small size and the limits on the resolution of the CT scans. The CT scans also indicated that both the enlarged and smaller teeth of *C. pholeter* are very shallowly implanted in a low, saucer-shaped alveolus.

Three other parareptiles, all from the same locality as *Colobomycter pholeter*, and considered to be fairly closely related to the latter, have yielded sufficient materials to make detailed study of their dentition possible. As is the case with *C. pholeter*, these are all small predators, and show various levels of heterodonty.

### 3.4.2. Delorhynchus cifellii

The sister taxon of *Colobomycter pholeter*, *Delorhynchus* possesses a homodont dentition composed of simple conical teeth. The thin sections of the maxillary teeth in *Delorhynchus cifellii* reveal the presence of plicidentine (Fig. 3.6), but not with the same degree of complexity seen in the enlarged teeth of *C. pholeter*. It is much more reminiscent of the plicidentine that was observed in smaller homodont teeth of *C. pholeter*. Longitudinal sections through a maxilla of *D. cifellii* show that plicidentine is restricted to the bases of the teeth, well below the jaw line (Fig. 3.6B–D). The longitudinal sections also show that the dentine folds encircle several canals, which extend from the exterior of the tooth base to the pulp cavity. These canals are very similar to those observed by Cabreira and Cisneros (2009) in their longitudinal sections of the procolophonid *Soturnia caliodon*, and by Pretto et al. (2014) in the longitudinal sections of the mesosaur *Stereosternum tumidum*. This suggests that the teeth of these parareptiles would also
have exhibited loose folding of the dentine around these canals. In transverse sections, the
dentine consists of loose folds and therefore does not possess lamellae, or any sort of branching.
Deeper sections through individual teeth reveal the same systems of canals extending into the
pulp cavity (Fig. 3.6F). Overall, the plicidentine of the homodont dentition in *D. cifellii* is similar
to that seen in the small homodont teeth of *C. pholeter*.

**3.4.3. Microleter mckinzieorum**

Despite being outside of the clade Lanthanosuchoidea the thin sections of the simple homodont
maxillary teeth of *Microleter mckinzieorum* show the presence of plicidentine reminiscent of that
found in *Delorhynchus cifellii*, and the small homodont teeth of *Colobomycter pholeter* (Fig.
3.7). The teeth in *M. mckinzieorum* also show the presence of a canal system similar to that
observed in *D. cifellii*. The midsection of the teeth reveals that loose folding is still present,
although the canals are absent.

**3.4.4. Feeserpeton oklahomensis**

*Feeserpeton oklahomensis* exhibits a heterodont dentition consisting of simple conical teeth,
three enlarged teeth on the maxilla, and two on the dentary (Fig. 3.8A). *F. oklahomensis* was the
only parareptile that was not examined histologically, because it is currently only known from
the holotype (OMNH 73541). Since CT scans were shown to be useful in identifying plicidentine
in *Colobomycter pholeter*, this technique was also applied to the holotype of *F. oklahomensis*.
The CT scans revealed that the teeth of *F. oklahomensis* possess extensively folded dentine that
is found at the bases of the enlarged maxillary and dentary teeth (Fig. 3.8B, C), reminiscent of
the folding observed in *Delorhynchus cifellii* and *Microleter mckinzieorum*. Due to the resolution
of the CT scans it could not be determined if the folds of the enlarged teeth were lamellae as in
the enlarged premaxillary tooth of *C. pholeter*. The midsection of the teeth reveals that the
folding stops and unfolded dentine makes up the rest of the teeth. The CT scans did not have the
resolution to confidently identify plicidentine within the smaller teeth.
3.4.5. **Bolosaurus**

Another parareptile, *Bolosaurus grandis* is present in the Dolese Brothers Limestone Quarry, near Richards Spur, but this material is too rare for sectioning and destructive analysis. However, this species of bolosaurid has the same kind of tooth attachment as another species of *Bolosaurus* commonly found in many localities in North America, *B. striatus* (Fig. 3.9). The latter has slightly smaller dentition than *B. grandis*, and varies slightly in the pattern of the striations on the crown from those on *B. grandis*, but these differences are subtle, and are not expected to affect the presence or absence of plicidentine.

Bolosaurids are distinct from other parareptiles in having a highly specialized, heterodont dentition that was adapted to dental occlusion (Reisz et al., 2002; Reisz, 2006). *Bolosaurus striatus* exhibits the bulbous laterally expanded teeth common to all bolosaurids (Fig. 3.9). External plication of the tooth base, often a telltale sign of plicidentine (Schultze, 1970; Maxwell et al., 2011), is not present on the teeth of *B. striatus*. Cross-sections taken below the alveolar margin of the dentary show a distinct lack of folding of the dentine, a stark contrast to what was observed in *Colobomycter pholeter*. The cross-sections of the tooth bases of *B. striatus* are oval-shaped, with their long axes oriented diagonal to the anteroposterior axis of the dentary (Fig. 3.9B, C). The dentine tubules of each tooth base extend parallel to one another in a straight line from the external surface of the dentine wall to the pulp cavity, suggesting that there were no folds of the dentine as it developed in each tooth. Longitudinal sections through a dentary fragment of *B. striatus* show the distinct crowns of the teeth capped in thick layers of enamel. The size of the roots in comparison to the crowns shows that the teeth were deeply implanted into the jaw (Fig. 3.9D, E). The teeth were held in place by extensive amounts of attachment tissue, presumably alveolar bone, sensu LeBlanc and Reisz (2013). The bases of the teeth are open, and show no evidence of complex infoldings towards the base.
3.5 Discussion

3.5.1. Identification of plicidentine in CT scans

CT scanning has the potential to reveal dental variation in specimens that are not amenable to destructive sampling, and is thus a potentially useful technique for examining plicidentine in vertebrates. Prior to this study, only Kearney and Rieppel (2006) in their description of squamate plicidentine had used CT scans and compared them to histological samples. Here we present a comparison of CT scans of the dentition of Colobomycter pholeter with histological thin sections of its teeth in order to show the benefits and limitations of using CT scans for determining the fine structure of teeth, including the presence of plicidentine within teeth. C. pholeter is an ideal sample to evaluate the utility of this technique because of the fine-scale variation in the infolding patterns of its maxillary and premaxillary teeth. The thin sections of the teeth of C. pholeter clearly demonstrate the presence of complex plicidentine, and using CT scans with appropriate imaging software revealed the same folding pattern of the dentine (Fig. 3.5). This technique was then applied to material that could not be histologically sampled, specifically the holotype and only known specimen of Feeserpeton oklahomensis (Fig. 3.8).

The available evidence shows that this technique is useful for determining the gross morphology of the dentine within a tooth, but comparisons with histological thin sections indicate that the micro CT should be used with caution as it does have limitations. The CT scans of C. pholeter lacked the resolution required to identify plicidentine near the tip of the crown in the enlarged premaxillary tooth, whereas plicidentine was clearly visible in the histological thin sections of that area. Plicidentine within the smaller teeth was very difficult to see due to the size of the teeth and the resolution of the CT scans. This method does not make it possible to make out finer details of the dentine tubules, which highlight the folds in the histological thin sections. Despite these restrictions micro CT offers a method for determining whether or not plicidentine is present in a tooth, and can provide limited information about the complexity of the folds.
3.5.2. Functional significance of plicidentine within Parareptilia

There have been several hypotheses proposed for the functional significance of plicidentine. One of the oldest hypotheses is that it strengthens the tooth base without increasing the amount of mineralized tissue used (Besmer, 1947; Peyer, 1968). Some argue that plicidentine also increases the surface area for attachment tissues (Besmer, 1947; Scanlon and Lee, 2002). Scanlon and Lee (2002) have also suggested that it allows for slight flexibility of the tooth base to absorb shock during feeding. It is worth noting that the functional purpose of plicidentine could be the result of interplay between these hypotheses, as they are not necessarily mutually exclusive (Maxwell et al., 2011).

Given the diversity of infoldings in this small sample of parareptiles, it is difficult to attribute a single function to the presence of plicidentine in Parareptilia. However, it appears that parareptiles with deeply implanted teeth, such as *Bolosaurus striatus*, lack plicidentine, whereas parareptiles with shallowly implanted teeth can exhibit very complex plicidentine, especially in larger teeth. Longitudinal thin sections of the teeth of *B. striatus* show that the teeth are deeply implanted within the tooth bearing elements, and transverse thin sections of its teeth show that they lack plicidentine. By comparison, CT scans of *C. pholeter* show that the teeth are very shallowly implanted, merely resting on the tooth-bearing surface, and thin sections of these teeth show very complex plicidentine, particularly at the base. This suggests that the complex, tightly folded plicidentine observed in the teeth of *C. pholeter* is probably associated with an increase in the surface area for attachment to compensate for their shallow implantation, as is observed in some teleostean fish (Meunier et al., 2013, 2014), whereas in *B. striatus* plicidentine is not necessary due to the deep implantation of the teeth. In order for enlarged maxillary or premaxillary teeth, such as those in *C. pholeter*, to be supported without folded dentine, the skull would require extensive modification. For example, saber teeth in mammals are very deeply implanted with the root extending very far into the skull; this deep implantation requires numerous modifications to the architecture of the skull in order to accommodate them (Savage, 1977). Thus it seems that an increase in surface area to accommodate the enlarged dentitions in *C. pholeter* is a reasonable hypothesis.

It is very important to note that *Colobomycter pholeter* exhibits different types of folding depending on the tooth position, suggesting that the various shapes and sizes of teeth served
different functions, and may have had a significant impact on the degree of folding associated with the plicidentine. The enlarged premaxillary tooth, which possesses very tight folds for its entire length, probably served a different purpose than the paired large maxillary teeth that exhibit very convoluted plicidentine at their bases. However, there is currently little that can be said about the reason for this difference beyond the hypothesis that the enlarged teeth of *C. pholeter* played different roles than the small homodont teeth. Planned Finite Element Analyses of these teeth may help in resolving this interesting problem.

The most common type of plicidentine observed in our study was the loosely folded type seen in *Delorhynchus cifellii* and *Microleter mckinzieorum*. The loose folds are only found at the base of the teeth and are punctuated by radial canals. These canals are similar to what is observed in the teeth of the reptile *Captorhinus aguti* (de Ricqlès and Bolt, 1983), their function is presumably to allow the entry of blood vessels into the pulp cavity (Maxwell et al., 2011). The functions of the loose folds cannot be determined at this time, but may have had a role similar to that of the tight folds found in the enlarged teeth of *Colobomycter pholeter*, except on a smaller scale.

### 3.5.3. Phylogenetic utility of plicidentine within Parareptilia

Many previous phylogenetic analyses of Parareptilia have used a character that concerns the presence/absence of labyrinthodont infolding (i.e. plicidentine) in teeth (Laurin and Reisz, 1995; Tsuji et al., 2010; MacDougall and Reisz, 2012). This character has generally been coded as present for many of the anamniote outgroup taxa, and has been coded as absent for amniote taxa (Laurin and Reisz, 1995; Tsuji et al., 2010; MacDougall and Reisz, 2012). This character was initially coded in this manner largely due to the previous lack of knowledge regarding dentine folding within amniotes. Thus, many of the codings of older analyses were carried over to subsequent studies without reevaluation. The apparent lack of plicidentine in most anatomical studies of parareptiles is most likely the result of the fact that most of the folded portions of the tooth roots in parareptiles were found below the jawline in our analysis, with no obvious external plications being visible on the teeth. The only exception to this was the extensive grooves along the enlarged teeth of *Colobomycter pholeter* (Fig. 3.5). However, as there is now evidence supporting the presence of plicidentine within many other amniote taxa (Edmund, 1969;
This study, combined with the results of others (Cabreira and Cisneros, 2009; Pretto et al., 2014), indicates that there is a wide spectrum of dentine folding across parareptilian taxa (Fig. 3.1), making this character much more complex than a simple binary character: presence or absence of plicidentine. Perhaps most important is the discovery that plicidentine can vary significantly in adjacent teeth in the same taxon, as exemplified by Colobomycter pholeter. Related to the plicidentine variation in C. pholeter and the other parareptiles is that larger teeth exhibit more complex dentine folding patterns (as in labyrinthodont amniotes), which suggests that different types of plicidentine are more related to tooth size rather than phylogeny. Thus, it is recommend that for the time being, characters involving plicidentine should be removed from phylogenetic analyses of Parareptilia, at least until there is more complete data on the distribution of the feature within the clade. The variability of plicidentine within the teeth of a single taxon must also be examined prior to any future inclusion of plicidentine characters into parareptilian phylogenetic analyses.

3.6 Conclusions

Comparisons of several coeval parareptilian taxa reveal that plicidentine is much more common within Parareptilia than previously thought. Different members of the clade exhibits a wide array of dentine folding, ranging from a lack of folding entirely, as seen in Bolosaurus, to very complex folding that is reminiscent of the plicidentine observed in temnospondyl amphibians. We also describe for the first time variation in plicidentine within a single taxon; Colobomycter pholeter, which exhibits three different folding patterns depending on the tooth position and size. This variation also reinforces the likelihood that heterodonty in C. pholeter is associated with different functions for the different teeth. The presence of plicidentine in parareptiles also supports the hypothesis that one function of plicidentine is to increase the surface area for tissue attachment between dentine and the periodontium. However, this function can only be attributed to those teeth that are shallowly implanted and exhibit the most extensive infolding patterns.
towards the base of the tooth, where it interacts with the attachment tissues. Bolosaurids have deeply implanted teeth that do not exhibit plicidentine. It is likely that the relationship between the dentine and periodontium in bolosaurids may be related to the evolution of dental occlusion (Reisz, 2006). With the information gained from this study it is now apparent that the presence of plicidentine in parareptiles has a complicated evolutionary history. However, the large variability of plicidentine within the clade, its variability within a single taxon, and its apparent relation to tooth size diminishes the phylogenetic utility of plicidentine. Given the problematic nature of this feature of parareptilian dentitions, we suggest that it should not be used as a character within phylogenetic analyses of Parareptilia, at least until we gain a better understanding of the distribution and evolutionary history of this feature.

3.7 Acknowledgements

I would like to thank Bill May for providing material of *Colobomycter pholeter*, *Delorhynchus cifelli*, and *Microleter mckinzieorum*, Martin Sander for providing *Bolosaurus striatus* material, and Chris Sidor for providing thin sections of *Colobomycter pholeter*. I would also like to thank Diane Scott for the photographs of *Feeserpeton oklahomensis*. Further thanks goes to Erin Maxwell and Juan Cisneros for reviewing the manuscript in which this chapter was published. Support for this project came from a Natural Sciences and Engineering Research Council of Canada doctoral student scholarship (PGSD) to MJ MacDougall and a Natural Sciences and Engineering Research Council of Canada Discovery Grant to RR Reisz.

3.8 References

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3.9 Figures and Figure Captions

**Figure 3.1.** Cladogram showing the relationships of sampled parareptile taxa. Bolded taxa represent those sampled in this study. Taxa marked with an asterisk represent taxa that are known to exhibit plicidentine. The cladogram was modified from the MacDougall and Reisz (2012) and Reisz et al. (2014) analyses.
Figure 3.2. Cross-sectional views of the enlarged premaxillary tooth of *Colobomycter pholeter* (UWBM 95405). A: diagram indicating from what parts of the premaxilla the histological sections were taken. B: cross-section taken towards the base of the enlarged premaxillary tooth showing the complex infolding of the dentine and the presence of lamellae. C: interpretation of the cross-section in B. Light grey areas indicate dentine, while darker grey areas indicate alveolar
bone. The thick black lines represent the axes of the folds. D: cross-section taken midway up the enlarged premaxillary tooth showing the presence of dark dentine. E: interpretation of the cross-section in D. Light grey areas indicate dentine, while the thick black lines represent the axes of the folds. F: cross-section taken towards the tip of the enlarged maxillary tooth. G: interpretation of the cross-section of F. Light grey areas indicate dentine, while the thick black lines represent the axes of the folds. dd, dark dentine; dl, dentine lamellae; pc, pulp cavity; pm, premaxilla.
Figure 3.3. Microstructure in the crown of the enlarged premaxillary tooth of *Colobomycter pholeter* (UWBM 95405). A: Crown of the enlarged premaxillary tooth under polarized light. Note the presence of the globular zone of dentine, which tightly infolds to form lamellae. Also visible are dark dentine and the slight grooves formed in the dentine by the folding. B: same image as in A, but under cross-polarized light. Note the presence the thin enamel layer on the exterior of the tooth. dd, dark dentine; dg, dentine groove; dl, dentine lamellae; en, enamel; gzd, globular zone of the dentine.
Figure 3.4. Cross-sectional views of the maxillary teeth of *Colobomycter pholeter* (ROM 67374). A: diagram indicating from what parts of the maxilla the histological sections were taken. B: cross-section taken towards the base of the maxillary teeth showing the convoluted dentine infolding of one of the enlarged maxillary teeth, and the simpler infolding of the smaller maxillary teeth. C: interpretation of the cross-section in B. Light grey areas indicate dentine, while darker grey areas indicate alveolar bone. The thick black lines represent the axes of the folds. D: cross-section taken near the midpoint of the enlarged maxillary tooth and towards the tip of the smaller maxillary tooth showing a distinct lack of dentine infolding in both of the teeth. E: interpretation of the cross-section in D. Light grey areas indicate dentine, while the thick black lines represent the axes of the folds. de, dentine; m, maxilla; pc, pulp cavity.
Figure 3.5. Cross-sectional and longitudinal views of the maxillary and premaxillary dentition of *Colobomycter pholetter* (OMNH 73535) obtained via X-ray computed tomography (CT) scans. A: diagram indicating from what parts of maxilla and premaxilla the virtual sections were obtained. B: virtual long-section of the enlarged premaxillary tooth showing its shallow implantation within the premaxilla. C: virtual cross-section of the base of the enlarged premaxillary tooth, which clearly shows the tight infolding of the dentine and the lamellae. D: virtual long-section of the maxillary dentition, shows their shallow implantation within the maxilla regardless of size. E: virtual cross-section of the bases of the maxillary dentition showing
the complex dentine infolding of the enlarged maxillary teeth. The looser dentine infolding of the smaller maxillary teeth cannot be seen. de, dentine; dl, dentine lamellae; df, dentine fold; m, maxilla; pc, pulp cavity; pm, premaxilla.
Figure 3.6. Cross-sectional and longitudinal views of the teeth of *Delorhynchus cifellii*. A: diagram indicating from what parts of the maxilla and dentary the histological sections were taken. B: long-section of the maxilla (ROM 67372). C: close up view of one of the posterior maxillary teeth from B. Shows the presence of radial canals surrounded by dentine at the base of the tooth. D: close up view of one of the anterior maxillary teeth from B. Shows how far the dentine folds project into the pulp cavity E: cross-section of the dentary (ROM 67373). F: close
up view of some of the dentary teeth from E. Shows the loose dentine folding that is found at the base of the teeth. G: close up view of some of the dentary teeth from E. Shows that as you move towards the tip of the teeth the dentine loses its infolding. c, canal; d, dentary; de, dentine; m, maxilla; pc, pulp cavity.
Figure 3.7. Cross-sectional views of the maxillary teeth of *Microleter mckinzieorum* (ROM 67375). A: diagram indicating from what parts of the maxilla the histological sections were taken. B: cross-section of the maxilla. C: close up view of one of the maxillary teeth from B. Shows the presence of radial canals in the dentine. D: close up view of one of the maxillary teeth from B. Shows the loose dentine infolding that is found at the base of the teeth. c, canal; de, dentine; m, maxilla; pc, pulp cavity.
Figure 3.8. Cross-sectional views of the maxillary and dentary dentition of *Feererpeton oklahomensis* (OMNH 73541) obtained via X-ray computed tomography (CT) scans. A: skull of *F. oklahomensis* in right lateral view showing from where the virtual sections of the maxilla were taken. B: skull of *F. oklahomensis* in ventral view showing from where the virtual sections of the dentary were taken. C: virtual cross-section of the base of one of the enlarged maxillary teeth showing the presence of tight dentine infolding. D: virtual cross-section of the bases of the dentary teeth showing the presence of dentine infolding. d, dentary; de, dentine; df, dentine fold; m, maxilla; pc, pulp cavity.
Figure 3.9. Cross-sectional and longitudinal views of the dentary teeth of *Bolosaurus*. A: diagram indicating from what parts of the dentary the histological sections were taken. B: cross-section of a *Bolosaurus striatus* dentary fragment (StlPB-R 636), showing a complete lack of any dentine infolding. C: interpretation of the cross-section in B. Light grey areas indicate dentine, while darker grey areas indicate alveolar bone. D: long-section of a *B. striatus* dentary fragment (StlPB-R 637), showing the deep implantation of the associated teeth. E: interpretation of the long-section in D. Light grey areas indicate dentine, while darker grey areas indicate alveolar
bone. The white area on the crowns of some of the teeth indicates enamel. F: Occlusal view of the dentary of *Bolosaurus grandis* showing the deep sockets of the teeth. d, dentary; de, dentine; e, enamel; pc, pulp cavity.
Chapter 4
A new phylogenetic analysis of Parareptilia, with discussion on the early evolution and diversification of the clade

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4.1. Abstract

Parareptilian phylogeny has often been problematic, with numerous different studies producing various tree topologies over the years. Many of the problems in these studies came from a lack of information regarding certain parareptile clades, as well as the usage of problematic characters in their analyses. In order to rectify some of these problems we conducted a new and heavily updated phylogenetic analysis of parareptiles as part of this study; notably it includes the numerous new Richards Spur parareptile taxa that have been described over the last decade, as well as new taxa from elsewhere in the world. This updated phylogenetic analysis recovers strong support for many of the clades within Parareptilia. This new phylogeny facilitates discussion on several aspects of early parareptilian evolution and diversification. The presence of lateral temporal fenestration within the clade is discussed, contrary to earlier studies we now know that temporal fenestration is quite common in parareptiles, the current topology of Parareptilia indicates that there was considerable variability in the patterns of lateral temporal openings among the various members of the clade, suggesting that there may have been multiple, independent modifications to this region of the skull. Furthermore, with the new species that have been produced from Richards Spur in recent years, we now have a much better view regarding the diversity of parareptiles during the Early Permian, with their diversity coming close to matching that of contemporaneous Early Permian eureptiles. Richard Spur is also unique in that more than half of all known Early Permian parareptiles are found there, as well as in capturing representatives of all major lineages of terrestrial parareptiles present during the Early Permian. Together, the new information presented on these various aspects of parareptiles allows for a much better understanding of the clades evolution and diversification, as well as that of their eureptile relatives.

4.2. Introduction

Parareptilia has had a long and tumultuous history leading up to the modern version of the clade that we know today. Historically, the taxa now considered to be parareptiles were found scattered across Tetrapoda, largely due to their morphological variation (Tsuji and Müller, 2009), though many ended up being placed in what would later be considered a wastebasket group,
Cotylosauria (Cope, 1895; Tsuji and Müller, 2009). Eventually, Olson (1947) determined that Cotylosauria was an inadequate and problematic grouping of tetrapods, and the reptiles found within Cotylosauria were reorganized into the now familiar groups, Parareptilia and Eureptilia. However, most workers ignored this new split Reptilia for quite some time, they instead continued to use the older terminology (Tsuji and Müller, 2009). It was not until the advent of modern phylogenetic systematics that the groups Eureptilia and Parareptilia fell back into usage, as they were recovered in various studies as distinct clades within Reptilia (Reisz and Laurin, 1991; Laurin and Reisz, 1995; Lee, 1995; deBraga and Reisz, 1996). Today, using modern phylogenetic methodology Parareptilia is recognized as a well-supported formal clade (Müller and Tsuji, 2007; Tsuji and Müller, 2009).

The Dolese Brothers limestone quarry near Richards Spur, Oklahoma, USA, is well known for preserving a large number of Early Permian terrestrial tetrapods within an extensive system of caves. As shown in chapter 2, recent discoveries have shown that the assemblage includes a strikingly diverse parareptile component. Parareptiles are rare in other Early Permian localities, usually represented by a single taxon even in assemblages with otherwise rich taxic diversity (Daly, 1969; Berman et al., 2000; Reisz et al., 2002), or common elements in depauperate, unusual faunas (Modesto, 2010). Early Permian parareptiles currently known from other localities are the Laurasian taxa Acleistorhinus pteroicus (Daly, 1969; deBraga and Reisz, 1996), Eudibamus cursoris Berman et al., 2000, Bolosaurus striatus Cope, 1878, Belebey augustodunensis Falconnet, 2012, and the Gondwanan Mesosauridae (Mesosaurus tenuidens (Gervais, 1865; Modesto, 2006, 2010), Stereosternum tumidum (Cope, 1886; Modesto, 1999a), and Brazilosaurus sanpauloensis Shikama and Ozaki, 1966).

In contrast, there are currently eight described parareptiles known from the Richards Spur locality: Colobomycter pholeter (Vaughn, 1958; Modesto, 1999b), Delorhynchus priscus Fox, 1962, Bolosaurus grandis Reisz et al., 2002, Microleter mckinzieorum Tsuji et al., 2010, Feeserpeton oklahomensis MacDougall and Reisz, 2012, Delorhynchus cifellii MacDougall and Reisz, 2014, Abyssomedon williamsi MacDougall and Reisz, 2014 and Colobomycter vaughni MacDougall et al., 2016. This high taxic diversity makes Richards Spur a unique and important asset for studying the early diversification and evolution of Parareptilia during the Early Permian. The large number of new parareptile taxa described from the locality in recent years warrants an updated phylogenetic analysis of the clade.
Here, we present a new phylogenetic analysis of Parareptilia, one that is heavily modified in order to rectify problems with past analyses. This updated analysis allows for the early diversification and evolution of the clade to be discussed in the context of the extensive new information that is now available to us.

**Institutional Abbreviations**—BMRP, Burpee Museum of Natural History, Rockford Illinois, USA; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UWBM, University of Washington Burke Museum of Natural History and Culture, Seattle, Washington, USA.

### 4.3. Material and Methods

#### 4.3.1. Phylogenetic analysis - character modifications and additions

The phylogenetic analysis conducted for this study used a revised and heavily modified version of the data matrix used by MacDougall and Reisz (2012), which was the newest in a series of parareptile data matrices that were largely derived from a study of amniote phylogeny by Laurin and Reisz (1995). Many of the previously coded characters were found to be compound characters, several were deemed uninformative for the present study, and some character states were found to be incorrect, warranting the current major revision. The new data matrix consists of 36 taxa and 170 characters, and was constructed using Mesquite. Character codings can be found in Appendix S4.1, while the character list can be found in Appendix S4.2.

One of the main problems identified in prior versions of this matrix was the abundance of compound characters. Compound characters, as defined by Brazeau (2011), are multistate characters that require two or more conditional qualifiers to specify them. A prime example of this is character 17 from the MacDougall and Reisz (2012) analysis, the nature of the supratemporal in tetrapods. Originally this character had three character states: large (0), small (1), and absent (2). However, closer inspection of this character it reveals that it is in fact composed of two variables: size of the supratemporal and presence/absence of the
supratemporal. Brazeau (2011) recommends taking characters composed of multiple variables, and splitting them into other characters, one for each variable. It is worth noting that this issue can also be tackled through the use of ordered characters. In the case of character 17 from MacDougall and Reisz (2012), we decided to split it into two characters, one concerning the presence or absence of the supratemporal (character 26) and another concerning the size of the supratemporal if it is present (character 27). Had this character not been split then information about the presence condition would have been lost. Thus, splitting such characters allows maximization of information regarding the anatomy being evaluated. This type of character splitting was performed for all applicable multistate characters, which were characters 1, 3, 7, 11, 16, 17, 20, 29, 31, 38, 41, 49, 53, 58, 59, 60, 66, 70, 84, 86, 87, 102, 108, 112, and 122 of MacDougall and Reisz (2012). It should be noted that not all multistate characters were split, only those that contained multiple variables.

However, of the new characters resulting from the splitting some were found to be phylogenetically uninformative, as all taxa currently included in this study exhibited the same character state. This is a byproduct of the fact that some of the characters that were split exhibited a character state that was not actually found (or could not be found) in any of the taxa, or in some cases only a single taxon exhibited one of the states. These characters were removed, as they currently offer no useful information. These uninformative characters were derived from characters 3, 20, 31, and 86 of MacDougall and Reisz (2012). They are as follows:

1) If frontal lateral lappet is present, it is: large, occupies at least one-third of the dorsal margin of the orbit (0); narrow, less than one-third of dorsal margin (1).
2) Anterior lateral maxillary foramen: absent (0); present (1).
3) If quadratojugal-lateral temporal fenestra contribution is present: the quadratojugal contributes to its ventral border (1); the quadratojugal contributes to its ventral and posterior borders (2).
4) If a lateral shelf is present on the articular region, it is found on the: articular (0); surangular (1).

With the removal of these characters the number of new characters resulting from the splitting of compound characters was reduced to 46.
The splitting of multistate characters resulted in a large number of new characters, many of which were dependent on the presence or absence of a particular element or structure. Returning to the previous example of character 17 in the MacDougall and Reisz (2012) analysis, it is now split into two distinct characters: presence/absence of the supratemporal and size of the supratemporal. If a taxon exhibits a supratemporal then the size of the supratemporal can be simply coded accordingly. However, if a taxon is coded as lacking a supratemporal then the size character cannot logically be coded. Thus, this character needs to be coded as inapplicable in the data matrix, represented by '-' for the sake of clarity. It is important to stress that inapplicable character codings will still be treated as missing data by the phylogenetic algorithm, which can potentially result in spurious results (Strong and Lipscomb, 1999). To partially counter this problem, the phylogenetic software being used should be set to collapse branches with a minimum length of zero (Strong and Lipscomb, 1999).

There were also some characters of the MacDougall and Reisz (2012) matrix that were found to be uninformative with regards to determining homology. Character 23 (caniniform region: present (0); absent (1)) and character 24 (single caniniform maxillary tooth: absent (0); present (1)), were removed and replaced by two new characters that better describe the condition of enlarged teeth in early tetrapods. The justification behind the removal of character 23 and 24 has to do with the usage of the term "caniniform". Historically, the term "caniniform" has been used to describe teeth thought to be analogous to the mammalian canine in non-mammalian taxa. A canine is defined as being the large conical, pointed first tooth of the maxilla (Owen, 1840-1845); from this one would assume "caniniform" implies a tooth in a non-mammalian tetrapod with the same shape, size, and position as a canine. However, in the large majority of studies "caniniform" is simply used to describe an enlarged tooth near the anterior end of the maxilla or dentary (Modesto, 1999b; Cisneros et al., 2008; Modesto and Reisz, 2008; MacDougall and Reisz, 2012). This results in the likely scenario that the "caniniforms" of many taxa are not actually homologous to each other. In order to deal with this problem, we instead decided to look for size related heterodonty in the jaws, which takes into account any enlarged teeth of the anterior 2/3 of the tooth series. Thus, the original characters were replaced with two new characters that deal with the presence (0) or absence (1) of size related heterodonty on the anterior 2/3 of the maxilla and dentary, respectively. Only the anterior 2/3 of the maxilla and dentary were looked at for these new characters because in most early tetrapod taxa the
posterior-most teeth of these elements are often much smaller than the more anterior teeth. Also, character 75 was removed entirely from the matrix; this character was concerned with the presence or absence of labyrinthodont infolding in the teeth of the jaws. MacDougall et al. (2014) suggest that characters involving dentine infolding should be removed from phylogenetic analyses of Parareptilia due to its extreme variability among members of the clade, thus the character was removed from the analysis.

In addition, some of the characters from the MacDougall and Reisz (2012) analysis were found to be vague and difficult to interpret. In order to rectify this problem these characters were modified to be more concise, so as to facilitate repeatability. In most cases where this was an issue, the main problem was the usage of qualifier terms such as broad, slim, large, small, etc. without ever specifying what these terms actually mean with respect to the element or structure to which they are referring. Character 120 of MacDougall and Reisz (2012) exhibits this problem quite clearly. Originally the character was formulated as follows: Femoral shaft: short and broad (0); long and slender (1). Such coding raises various questions: what is broad? What is slender? Based on the available information this character can be interpreted in different ways by different individuals, which could potentially result in two people coding the same taxon in two different ways. To avoid this ambiguity the character was reworded so that one would know what exactly those qualifying terms mean. In this case, a short and broad femoral shaft is clarified in our study as being one that has an anteroposterior length that is equal or less than the mediolateral width of the distal head in ventral view.

Along with the splitting of compound characters and the modification of others, seven new characters were added to the matrix. The first new character involves the presence or absence of the ectopterygoid. The second character involves the suborbital ramus of the jugal and whether or not it is dorsoventrally expanded. The third character involves whether or not the jugal contributes to the temporal portion of the skull. The fourth character involves the number of maxillary tooth positions, whereas the fifth new character is concerned with the number of tooth positions on the premaxilla. The sixth character involves the presence or absence of a single large tooth on the anterior end of the vomer. Lastly, the seventh new character is concerned with whether or not the marginal dentition is bulbous (as in bolosaurid parareptiles).
4.3.2. Phylogenetic analysis - taxa modifications and additions

Along with the above modifications related to characters, there were also changes to the taxa used in the analysis. The original analysis included several super-generic taxa, resulting a large number of polymorphic character codings. In order to alleviate this problem all of the super-generic taxa were removed and replaced with genus level representatives. Limnoscelidae was replaced with Limnoscelis, Diadectidae was replaced by Orobas, Synapsida was replaced with Eothyris and Archaeovenator, Captorhinidae was replaced with Captorhinus and Rhiodenticulatus, Araeoscridia was replaced by Petrolacosaurus, Younginiformes was replaced with Youngina and Acerosodontosaurus, Mesosauridae was replaced with Mesosaurus, and Millerettidae was replaced with Milleretta. Several parareptiles were also added, including the three new taxa described in chapter 2. We also recognize that recent studies regarding Eunotosaurus africanus raise questions regarding its parareptilian affinities (e.g. Bever et al., 2016), as this is beyond the scope of the current study it has tentatively been left in the analysis.

Where possible new taxa and characters were coded using actual specimens, otherwise coding was performed using photographs and the literature (reconstructions were never used). Taxa coded from actual specimens include Archaeovenator, Captorhinus, Rhiodenticulatus, Petrolacosaurus, Milleretta, Microleter, Macroleter, Acleistorhinus, Feeserpeton, Abyssomedon, Erpetonyx, Bolosaurus, Colobomycter, and Delorhynchus. In the cases of Lanthanosuchus and Eudibamus casts of specimens were also used.

4.4. Results

The phylogenetic analysis was conducted by importing the new data matrix into PAUP 4.0a131 (Swofford, 2013), the outgroup was defined as being composed of Seymouria, Limnoscelis, Orobas, Eothyris, and Archaeovenator, thus the ingroup was composed of only reptiles. A heuristic search using parsimony as the optimality criterion was then performed, resulting in 26 most parsimonious trees, with each one having a tree length of 571. PAUP was then set to collapse branches if their minimum length was zero (in order to compensate for inapplicable
character codings (Strong and Lipscomb, 1999; Brazeau, 2011), which resulted in 6 most parsimonious trees. Strict consensus trees were then obtained for both of these scenarios, the two trees were found to be identical (Fig. 4.1). The support values obtained from a bootstrap analysis (1000 replicates) and a Bremer decay analysis are also recorded on the strict consensus tree.

4.4.1. *Feeserpeton oklahomensis*

The results of the phylogenetic analysis found that *Feeserpeton* is the most basal member of the lanthanosuchoids included in the analysis. *Feeserpeton* is the sister taxon of a clade that has within it two smaller clades, one consisting of *Acleistorhinus* and *Lanthanosuchus*, and another consisting of *Colobomycter* and *Delorhynchus* (Fig. 4.1). These results are consistent with previous phylogenetic analyses of Parareptilia as far as the sister-taxon relationship between *Acleistorhinus* and *Lanthanosuchus* (deBraga and Reisz, 1996; Tsuji, 2006; Müller and Tsuji, 2007; Tsuji et al., 2010). Unequivocal character states that support the position of *Feeserpeton* are as follows: the absence of a posterior extension of the jugal that contributes to the temporal region of skull (character 20), the absence of a tabular element (character 24), the presence of heterodont dentation on the maxilla (character 35), and the presence of 15 or less teeth on the maxillae (character 167).

4.4.2. *Abyssomedon williamsi*

The results of the phylogenetic analysis found that *Abyssomedon* is the sister taxon of *Nyctiphruretus* (Fig. 4.1), confirming it to be the first member of Nyctiphruretidae known from outside of Russia. The Nyctiphruretidae is unequivocally supported by the presence of paired surangular foramina (character 112), and the presence of a grooved tibio-astragular joint (character 160). The clade Nyctiphruretidae itself was found in our analysis to be the sister taxon of a clade containing the pareiasaurs, procolophonoids, and 'nycteroleters', this is of interest as the position of Nyctiphruretidae has been historically variable. This sister taxon relationship is unequivocally supported by a postparietal that is dorsally exposed (character 10), strong prefrontal-palatal contact (character 12), the lack of a postorbital contribution to the lateral
temporal opening (character 45), a posteriorly extended orbit (character 53), a Meckelian fossa that occupies less than 25% of the lower jaw length (character 109), and a broad, dorsally concave retroarticular process (character 116).

4.4.3. *Colobomycter*

The results of the phylogenetic analyses clearly confirm that *Colobomycter pholeter* and *Colobomycter vaughni* are sister taxa (Fig. 4.1), this relationship is supported unequivocally by the following character states: the absence of a tabular element (character 24), dermal sculpturing in the form of round pits (character 55), and three or less premaxillary teeth (character 168). The clade *Colobomycter* itself is recovered as being the sister taxon of *Delorhynchus* (Fig 4.1), as *Delorhynchus* was not included in phylogenetic analysis until more complete material became available (Reisz et al., 2014), this represents a new and interesting sister-taxon relationship. This clade is unequivocally supported by the presence of a single median postparietal (character 8), the presence of a small postparietal (character 9), and a broad, dorsally concave retroarticular process (character 116).

4.5. Discussion

4.5.1. Phylogenetic position of Nyctiphruretidae, Lanthanosuchoida, and other parareptiles

The phylogenetic position of the parareptilian clade Nyctiphruretidae is a contentious issue, with it being recovered in several different places depending on the analysis. Bulanov (2002) assigned the nyctiphruretids to the Procolophonidae, while other studies recovered nyctiphruretids as close relatives (Ivakhnenko, 1990; Tverdokhlebova and Ivakhnenko, 1994; MacDougall and Modesto, 2011). However, several phylogenetic analyses do not support this view (Lee, 1995; Tsuji, 2006; Müller and Tsuji, 2007) recognizing nyctiphruretids as non-procolophonoid parareptiles, either
recovering Nyctiphruretidae as being more closely related to the 'nycteroleters' (Lee, 1995), or pareiasaurs (Tsuji, 2006; Müller and Tsuji, 2007).

A recent study by Säilä (2010), using new cranial information from several specimens of *Nyctiphruretus* and updated phylogenetic analyses, also confirmed that the nyctiphruretids did not fall within Procolophonoidea. However, the possibility of Nyctiphruretidae being a sister taxon to the Procolophonoida was not rejected, along with the alternative topology of Nyctiphruretidae being the sister taxon to the pareiasaurs (Säilä, 2010). The results of this new analysis recover the nyctiphruretids as the sister to a clade containing procolophonoids, pareiasaurs, and 'nycteroleters' (Fig. 4.1). This is a relationship that is distinct from past analyses that have included the clade, but given the sparse information available for the clade and its varying positions in past studies, this is not unexpected. It remains to be seen if this new position of the clade will be maintained as more information regarding the clade and its close relatives is obtained.

Much like Nyctiphruretidae, the parareptilian clade Lanthanosuchoidea was little studied for quite some time. It originally consisted of very few taxa (deBraga and Reisz, 1996), but it has grown considerably in recent years, with several new taxa having been described (Table 4.1), two of which are described in chapter 2. However, despite the numerous additions to the clade the results of this new analysis indicate that the phylogenetic position of the clade has changed little from past studies (deBraga and Reisz, 1996; Reisz et al., 2014). The interrelationships of the taxa within the clade are consonant with those of other studies (MacDougall and Reisz, 2012; MacDougall et al. 2016).

Interestingly, the results of this analysis also show that *Microleter mckinzieorum* is found as a member of the clade Ankyramorpha, this is in contrast to the results of past phylogenetic analyses where it is found closer towards the base of Parareptilia (Tsuji et al., 2010; MacDougall and Reisz, 2012; Tsuji et al., 2012). The relationships of the remaining parareptiles are in agreement with the results of other recent phylogenetic analyses of Parareptilia (Tsuji et al., 2012; MacDougall and Reisz, 2012).

4.5.2. Parareptile diversity at the Richards Spur locality
The Richards Spur locality offers the best view of Early Permian parareptile diversity currently available. Of the 15 known species, eight of them are from Richards Spur (Vaughn, 1958; Fox, 1962; Reisz et al., 2002, 2014; Tsuji et al., 2010; MacDougall and Reisz, 2012; MacDougall and Reisz, 2014), which is more than half of all currently known Early Permian parareptiles. The presence of these parareptiles at Richards Spur also pulls back the ages of the parareptilian clades Nyctiphruretidae and Lanthanosuchoidea back into the Early Permian (Fig. 4.2). Furthermore, Richards Spur captures at least one member of all the major parareptile lineages present during the Early Permian, with the exception of the Gondwanan-restricted aquatic Mesosauridae (Table 4.1, Fig. 4.2). The high parareptile diversity at Richards Spur suggests that the locality was located in an important region for parareptile diversification during the Early Permian. This is exemplified by the Richards Spur lanthanosuchoids, of which there are five from the locality, as well as one from the nearby Grand Field locality (Daly, 1969). The members of this clade found at the locality represent a wide variety of small predatory forms with varying dentitions (MacDougall et al., 2016), ranging from the aforementioned unique dentition of *Colobomycter* to the more homodont dentition of *Delorhynchus* (Reisz et al., 2014). It is quite apparent that there was a large amount of experimentation among the Early Permian lanthanosuchoids with regards to dentition. It should be noted that eureptiles are also quite diverse at Richards Spur, with eight taxa being known from the locality (MacDougall et al., 2012; Reisz et al., 2015). Furthermore, six of these are currently only found at the locality, which suggests that it was similarly important for the diversification of early eureptiles.

It is also important to consider that the high parareptile diversity at Richards Spur may not be restricted to this locality. The unique preservational environment associated with the fissures found at Richards Spur (chapter 5) likely resulted in taphonomic biases that were much more conducive to the preservation of terrestrial vertebrates, hence the large number of parareptiles, eureptiles, and terrestrial anamniotes (MacDougall and Reisz, 2012) being present at the locality. In strong contrast, the more typical deltaic/fluvial localities of the Early Permian would not have been as likely to preserve the remains of small, fully terrestrial tetrapods, creating the differences we observe in the continental vertebrate fossil record.
4.5.3. Evolutionary patterns of lateral temporal fenestration and emargination in parareptiles

Although lateral temporal openings have long been used as a character in phylogenetic analyses, the formation and function of temporal openings in the skull of early amniotes is poorly understood. Two alternative hypotheses for the origin of these structures have been proposed, the first being that the formation of these openings lightened the skull and concentrated areas of ossification to increase resistance to the forces acting upon the skull that result from feeding (Carroll, 1982), while the second hypothesis is that jaw adductor muscle attachments in the temporal region may have been a contributing factor. It has been suggested that these muscles may have caused bone to thicken at their point of attachment (the boundaries of the fenestra), but as a consequence this resulted in reduced bone thickness in the surrounding areas due to less stress, eventually leading to the formation of fenestrae (Frazzetta, 1968). However, it is quite possible that the development of temporal openings is a complex phenomenon, caused by the interplay between several factors that cannot be readily tested. Parareptiles represent a fascinating case with regard to temporal fenestration.

Historically, reptiles with lateral temporal fenestrae were assigned to Synapsida and Diapsida (Osborn, 1903). Many of the taxa now classified as parareptiles were considered to be members of Anapsida (Williston, 1917). However, the presence of lateral temporal fenestrae is now known to be a common occurrence within Parareptilia (Cisneros et al., 2004; Modesto et al., 2009; Tsuji et al., 2010; MacDougall and Reisz, 2012), thus it is apparent that Anapsida is a name that does not reflect the anatomy of the clade (Tsuji, 2006; Müller and Tsuji, 2007). Parareptiles exhibit three significant anatomical patterns in the temporal region of the skull, the presence of lower temporal fenestrae, the presence of lower temporal emarginations, and the presence of a solid, unbroken temporal region. When present, the shape of the lateral temporal openings and the bones that form the borders of these openings are also quite variable within Parareptilia, with almost every parareptile clade exhibiting a different shape and arrangement of bounding elements (Fig. 4.3). This wide array of temporal openings suggests that there is extensive variability in this region of the skull within Parareptilia.
Parareptiles that exhibit temporal fenestration include the millerettids (Gow, 1972), the owenettid *Candelaria barbouri* (Cisneros et al., 2004), the 'nycteroletter' *Macroleter poezicus* (Tverdokhlebova and Ivakhnenko, 1984; Tsuji, 2006), the bolosaurids (Reisz et al., 2007), the procolophonid *Australothyris smithi* (Modesto et al., 2009), and all lanthanosuchoids (Daly, 1969; deBraga and Reisz, 1996; Modesto and Reisz, 2008; MacDougall and Reisz, 2012; Reisz et al., 2014). The procolophonid formerly known as *Procolophon laticeps* was also described as possessing temporal fenestration (Hamley and Thulborn, 1993). However, Cisneros (2008) determined this species to be a junior synonym of *Procolophon trigoniceps*, as the specimens described as *P. laticeps* did not differ morphologically from *P. trigoniceps* aside from the supposed temporal fenestration, which he considered to be an anomalous condition lacking any taxonomic significance. Since it was unlikely that the temporal fenestration seen in the specimen was caused by ontogenetic or individual variation, Cisneros suggested that the fenestration was the result of an embryological failure to close the sutures of the bones that made up the fenestrae.

It has also been suggested that the basal parareptile *Mesosaurus tenuidens* exhibits temporal fenestration (von Huene, 1941; Piñeiro et al., 2012). In the case of the specimens described by von Huene (1941), Modesto (2006) argued effectively that the supposed temporal fenestration was the result of misinterpretation of the jugal morphology of *M. tenuidens*. In the case of the Piñeiro et al. (2012) study, the proposed temporal fenestration is likely an artifact of the specimen’s poor preservation, as much better preserved specimens of *M. tenuidens* do not exhibit the supposed fenestration (Modesto, 2006). Thus, the lack of temporal fenestration in mesosaurs, the most basal parareptiles, suggests that a solid, unbroken temporal region is the primitive state for Parareptilia.

Aside from those parareptiles possessing temporal fenestration, there are also several that exhibit a lower temporal opening that is not bounded ventrally, termed a ventral temporal emargination. These parareptiles include *Eunotosaurus africanaus* (Keyser and Gow, 1981), owenettids (Reisz and Scott, 2002), *Nyciphruretus acudens* (Säälä, 2010), *Microleter mckinzieorum* (Tsuji et al., 2010), procolophonids (Cisneros, 2008) and now *Abyssomedon williamsi* (chapter 2). Interestingly, the owenettid *Candelaria barbouri* exhibits a lower temporal emargination along with what appears to be an upper temporal fenestra (Cisneros et al., 2004).
To further complicate the matter of temporal openings in parareptiles, the temporal fenestration in parareptiles does not just show variability between taxa; there is also evidence for possible ontogenetic variability in the temporal fenestra of some millerettids (Gow, 1972), as well as in Delorhynchus cifellii (Reisz et al., 2014). *Milleretta* exhibits a temporal fenestrae in juvenile individuals, bounded by the jugal, quadratojugal, postorbital, and squamosal, but throughout ontogeny the quadratojugal contribution to the fenestra is eventually lost, and the temporal fenestration is completely closed up by adulthood, as adult individuals of *Milleretta* have a solid temporal region with no fenestration (Gow, 1972). *D. cifellii* (Reisz et al., 2014) shows considerable changes in shape, although not complete loss, of the temporal fenestra throughout ontogeny, which could potentially be the result of ontogenetic variability.

For further support regarding the variability of reptilian temporal fenestration, one needs only look to diapsid reptiles, which exhibit a number of takes on the diapsid condition. The classic diapsid condition of an upper and lower temporal fenestra can be clearly seen in *Petrolacosaurus* (Reisz, 1981). Modifications on this type of fenestration include: the loss of the lower temporal fenestra as seen in *Araeoscelis* (Reisz et al., 1984), the loss of the lower temporal bar (resulting in a lower temporal emargination) as exhibited by squamates (Rieppel and Gronowski, 1981; Rieppel, 1993), and lastly an extreme modification seen in snakes and amphisbaenians where both the lower temporal bar and the upper temporal bar are lost resulting in a much more pronounced temporal emargination (Rieppel and Gronowski, 1981; Rieppel, 1993). The numerous types of temporal fenestration observed in diapsids leaves little question that the phenomenon of temporal fenestration within Reptilia is highly variable, making it no surprise that we see such significant variability of temporal fenestration within Parareptilia.

A solid temporal region and the absence of temporal fenestration or emargination is likely the primitive state for amniotes, as the sister taxon of Amniota, Diadectidae, does not exhibit temporal fenestration of any kind. This is further reinforced by the fact that the earliest and basalmost eureptiles (e.g. captorhinomorphs) and parareptiles (e.g. mesosaurs) do not exhibit temporal fenestration. Within Parareptilia, lateral temporal fenestration appears very early in the evolution of the clade (Fig. 4.3), being found in the basal taxa: Millerettidae, Bolosauridae, and Australothyris smithi. Even when characters involving temporal openings are removed from the phylogenetic analysis the positions of these basal taxa are maintained. This seems to indicate that lateral temporal fenestration is primitive for all parareptiles, exclusive of the Mesosauridae, as
has been suggested by Tsuji et al. (2010). Over the course of parareptilian evolution, the lower temporal bar is lost in some taxa resulting in a ventral temporal emargination (e.g. Microleter, procolophonoids, nyctiphruretids), and others redevelop an unfenestrated temporal region (e.g. pareiasaurs, all 'nycteroletes' with the exception of Macroleter).

Overall, it is clear that the evolution of temporal openings within Parareptilia was a complex affair with much experimentation, even more so than during the early stages of diapsid evolution. It can be concluded that using the presence/absence of temporal fenestration as a character for phylogenetic analyses will likely be problematic when performing large-scale analyses encompassing many early amniote clades. This is largely due to the widespread occurrence of temporal openings within early Amniota and the highly variable nature of temporal fenestration within Parareptilia, and Reptilia as a whole. Also, as stated by Modesto and Anderson (2004), it is clear Anapsida is a historical artifact and should not be used as a formal name. Likewise, with the abundance of parareptiles that exhibit temporal fenestration, when Synapsida and Diapsida are used, it should be clearly understood that these names reflect historically used terms to diagnose these groups, but these characteristics are no longer exclusive to them.

4.5.4. Patterns of Early Permian reptile diversity

The amniote clade Eureptilia first appears in the fossil record during the Late Carboniferous (Müller and Reisz, 2006), and by the Early Permian eureptiles are present in the form of four known lineages. The eureptilian lineages present during the Early Permian are Captorhinidae, Araeoscelidae, Protorothyrididae, and Neodiapsida. Captorhinids make up the bulk of the eureptiles present during the Early Permian with 15 described taxa, two of which are unnamed (Reisz, 1980; Modesto, 1996). Araeoscelids are represented in the fossil record by 4 Early Permian taxa. There are also two known Early Permian protorothyridids, as well as two known diapsids, one of which is unnamed (Carroll, 1968). Lastly, there is Thuringothyris from Germany, which is considered to be the sister taxon to Captorhinidae. Thus, there are currently 26 eureptiles that are known to have been present during the Early Permian (Table 4.1).

Being the sister taxon of Eureptilia, the clade Parareptilia also first appears in the fossil record during the Carboniferous, with only a single species being currently known from that period.
However, the diversity of the clade increases significantly by the end of the Palaeozoic (deBraga and Reisz, 1996) before being reduced to a single clade (Procolophonoidia) after the Permo-Triassic mass extinction event (Modesto et al., 2001). Currently, known parareptile lineages present during the Early Permian are Mesosauridae, Lanthanosochoidea, Nyctiphruretidae, and Bolosauridae. The lanthanosuchoids are the most diverse parareptilian clade of the Early Permian, with six species being known. There are also four known bolosaurids, three known mesosaurids, a single nyctiphruretid, and lastly there is the basal parareptile *Microleter mckinzieorum*, which does not currently group with any of the other parareptile clades (Tsuji et al., 2010; MacDougall and Reisz, 2014; this study). Thus, there are 15 parareptile species currently known to be Early Permian in age (Table 4.1).

Interestingly, whereas there are more eureptiles currently known from the Early Permian (26 species), parareptiles are not far behind in taxonomic diversity (15 species). Historically, parareptiles were not considered to be a particularly diverse clade during the Early Permian (Tsuji et al., 2010), and it was not until the Middle and Late Permian that they were considered to have become a diverse clade of reptiles (Tsuji and Müller, 2009; Tsuji et al., 2010). However, thanks to the numerous parareptiles that have been described from the Richards Spur locality in recent years we are now starting to see a more detailed picture of parareptilian diversity during the Early Permian. The similar taxonomic diversity of the two reptilian clades is reasonable given that the two are sister taxa originating in the Late Carboniferous (Modesto et al., 2015). The evolutionary history of the two clades up to the end of the Carboniferous and into the Early Permian is actually quite similar; both are largely composed of small-bodied forms, having not yet matched the large body sizes of contemporaneous synapsids. Furthermore, most reptiles are considered to have been carnivorous, though some species are considered to have adopted omnivory, such as the eureptiles *Captorhinus aguti* and possibly *Labidosaurus hamatus*, or herbivory, like the parareptile *Bolosaurus grandis* and the moradisaurine eureptiles (Reisz et al., 2002; Modesto et al., 2007, 2014), although plant eating members of these clades would not become widespread until the Middle and Late Permian (Reisz and Sues, 2000).

While current fossil evidence indicates that eureptiles were slightly more diverse than parareptiles during the Early Permian, it is interesting that there are four currently known lineages of eureptile present during the Early Permian (Captorhinidae, Araeoscelidae, Protorothyrididae, and Neodiapsida), and there are also four known lineages of parareptiles
(Mesosauridae, Lanthanosuchoida, Nyctiphruretidae, and Bolosauridae). Thus, despite parareptiles exhibiting lower species diversity than eureptiles, based on current fossil and cladistic evidence, the number of distinct lineages was equal in number to that of eureptiles.

4.6. Conclusions

This study presents the most up to date phylogenetic dataset for Parareptilia currently available; it includes characters that are more clearly defined in an attempt to facilitate repeatability in future work. The new phylogenetic analysis indicates the relationships of the three new Richards Spur parareptiles, confirming their positions within Parareptilia. With the new data regarding parareptilian interrelationships granted by this analysis several aspects regarding early reptilian evolution and diversification are discussed, notably the variation in lateral temporal fenestration within the clade. Lastly, eureptile diversity during the Early Permian is compared with that of parareptiles, thanks to the numerous new Richards Spur parareptiles, the Early Permian diversity of the clade comes close to matching that of contemporaneous eureptiles, contrary to what was historically thought.

4.7. Acknowledgments

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4.8. References


Hamley, T., and T. Thulborn. 1993. Temporal fenestration in the primitive Triassic reptile


### 4.9. Tables and Table Captions

**Table 4.1.** Reptile taxa of the Early Permian. Richards Spur taxa are indicated with an asterisk.

<table>
<thead>
<tr>
<th>Parareptilia</th>
<th>Eureptilia</th>
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<tbody>
<tr>
<td><strong>Lanthanosuchoida</strong></td>
<td><strong>Captorhinidae</strong></td>
</tr>
<tr>
<td><em>Colobomycter pholeter</em></td>
<td><em>Captorhinus aguti</em></td>
</tr>
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<td>(Vaughn, 1958)</td>
<td>(Cope, 1895)</td>
</tr>
<tr>
<td><em>Colobomycter vaughni</em></td>
<td><em>Captorhinus magnus</em></td>
</tr>
<tr>
<td>(MacDougall et al., 2016)</td>
<td>(Kissel et al., 2002)</td>
</tr>
<tr>
<td><em>Delorhynchus priscus</em></td>
<td><em>Captorhinus laticeps</em></td>
</tr>
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<td>(Fox, 1962)</td>
<td>(Williston, 1909)</td>
</tr>
<tr>
<td><em>Delorhynchus cifellii</em></td>
<td><em>Protocaptorhinus pricei</em></td>
</tr>
<tr>
<td>(Reisz et al., 2014)</td>
<td>(Clark and Carroll, 1973)</td>
</tr>
<tr>
<td><em>Feeserpeton oklahomensis</em></td>
<td><em>Labidosaurus hamatus</em></td>
</tr>
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<td>(MacDougall and Reisz, 2012)</td>
<td>(Cope, 1895)</td>
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<td><em>Acleistorhinus pteroticus</em></td>
<td><em>Labidosaurikos meachami</em></td>
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<td>(Daly, 1969)</td>
<td>(Stovall, 1950)</td>
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<td><strong>Bolosauridae</strong></td>
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<td><em>Bolosaurus striatus</em></td>
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<tr>
<td>(Cope, 1878)</td>
<td><em>Rhiodenticulatus heatoni</em></td>
</tr>
<tr>
<td></td>
<td>(Berman and Reisz, 1986)</td>
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<tr>
<td>Bolosaurus grandis*</td>
<td>Baeotherates fortilensis*</td>
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<tr>
<td>(Reisz et al., 2002)</td>
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<td>Eudibamus cursoris</td>
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<td>(Berman et al., 2000)</td>
<td>(Price, 1937)</td>
</tr>
<tr>
<td>Belebey augustodunensis</td>
<td>Romeria prima</td>
</tr>
<tr>
<td>(Falconnet, 2012)</td>
<td>(Clark and Carroll, 1973)</td>
</tr>
</tbody>
</table>

**Mesosauridae**

**Mesosaurus tenuidens**

(Gervais, 1865–66)

**Stereosternum tumidum**

(Cope, 1886)

**Brazilosaurus sanpauloensis**

(Shikama and Ozaki, 1966)

**Nyctiphruretidae**

**Abyssomedon williamsi***

(MacDougall and Reisz, 2014)
<table>
<thead>
<tr>
<th>Basal parareptile</th>
<th>Captorhinid sister taxon</th>
</tr>
</thead>
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<tr>
<td><em>Microleter mckinzieorum</em></td>
<td><em>Thuringothyris mahlendorffiae</em></td>
</tr>
<tr>
<td>(Tsuji et al., 2010)</td>
<td>(Boy and Martens, 1991)</td>
</tr>
</tbody>
</table>

**Araeosclidia**

*Araeoscelis*

(Williston, 1910)

*Zarcasaurus tanyderus*

(Brinkman et al., 1984)

*Aphelosaurus lutevensis*

(Gervais, 1858)

*Kadaliosaurus priscus*

(Credner, 1889)

**Protorothyrididae**

*Protorothyris archeri*

(Price, 1937)

*Protorothyris morani*

(Romer, 1952)
<table>
<thead>
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<th>Diapsida</th>
</tr>
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<tbody>
<tr>
<td><em>Orovenator mayorum</em></td>
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<tr>
<td>(Reisz et al., 2011)</td>
</tr>
<tr>
<td>Unnamed diapsid*</td>
</tr>
<tr>
<td>(Carroll, 1968)</td>
</tr>
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</table>
4.10. Figures and Figure Captions
**Figure 4.1.** Strict consensus tree obtained from the six most parsimonious trees produced by the phylogenetic analysis. Tree Length=571, Consistency Index (CI)=0.338, Rescaled CI=0.215, Retention Index=0.635. Nodes of clades of interest are labeled: **A**, Amniota; **B**, Reptilia; **C**, Parareptilia. Bootstrap support values are indicated above nodes, and Bremer Decay values are indicated below nodes. *Orobates* and *Limnoscelis* are collapsed into the terminal taxon Diadectomorpha, likewise *Eothyris* and *Archaeovenator* are collapsed into the terminal taxon Synapsida.
Figure 4.2. Time-calibrated phylogeny showing ages and relationships of various parareptiles. Solid bars indicate known ranges of taxa, while open bars indicate inferred ranges. Timescale is based on Cohen et al. (2013; updated). Parareptilian taxa that are present at Richards Spur are indicated with a star.
Figure 4.3. Cladogram showing the distribution of temporal fenestrae and emarginations across Parareptilia, as well as which elements contribute to the borders of these openings. Red elements represent jugals, yellow elements represent postfrontals, purple elements represent squamosals, light blue elements represent quadrates, green elements represent maxillae, and dark blue elements represent supratemporals.
4.11. Appendices

**Appendix S4.1.** Data matrix used for the phylogenetic analysis of Parareptilia.

*Seymouria*

| 0-0-000000 | 100000-000 | 00000000000 | 0000011000 | 00---0000 | 0001200000 | 0000100000 |
| 0000000000 | 01-0000--3 | 10000-0000 | -00100-000 | 0000000000- | 0000000000 | 0000000000 |
| 000-000010 | 00000000-- | -?0??001200 |

*Limnoscelis*

| 0-0-010101 | 0-0000-100 | 1110000000 | 100010-010 | 000---2000 | 0100-0011? | 0000000000 |
| 2000000000 | 00100000-00 | 001?0-0000 | -0?0?0100 | 0000000000- | 0000110010 | 01?000000 |
| 000-001000 | 100000010? | ?0??001100 |

*Orobates*

| 0-0-010101 | ?0?0??000 | 1010000000 | 10001-010 | 000---0011 | 0101010200 | 001?000010 |
| 0000000000 | ?0??0000-00 | 01110-0??? | ?0??0?001 | 001001000- | 0000110010 | 00??0000? |
| 00-001000 | 11000000-- | -01000000 |

*Eothyris*

| 0-10000001 | 0-0000-000 | 0010100000 | 0000011010 | 0010002001 | ?100-0021? | ?0???0??00 |
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*Archaeovenator*

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Captorhinus

0-11020001 1000010100 1021-01000 1000000101 000--0101 010120021? 0000100000 000001--10 0001000-02 000?110100 -000010000 00101--00- 0010010010 0100001000 0011300000 0000000110 0100002100

Rhiodenticulatus

0-11020001 1000010100 1021-01000 100000101 000--2101 0000-0021? 0000100010 000001--?0 0001000-02 000?110100 -00001000? 00??1--0?? 00?????0?? 0100001000 0011300??? 0000000110 0??????2000

Petrolacosaurus

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Youngina


Acerosodontosaurus

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Mesosaurus

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**Eunotosaurus**

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0010100??0  010?0001110 0100001000

**Milleretta**

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1000001010  01-1001000  0000111100 -0010-010  001000000- 0010011011  ??0001010
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**Australothyris**

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**Microleter**

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**Nyctiphruretus**

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**Eudibamus**

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-?1??01?20  0001??0-??  0??????01?  ?????011???  ???11--?11  00????0000?  00?11??01?
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Belebey

0-11010011 1110011000 1-2001-111 000011-100 0010111100 0110-0001? 10000?1121 - 010001000 0001000-?? 00????0??? ?0??011011 00111-011 1?????00?? ???????0?? ??10????? 00????1??? ??????0001

Macroleter


Bradysaurus

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Pareiasuchus


Scutosaurus

0-0-020110 10000??100 1110100111 1?0011-000 100---0000 1201111110 1111011010 1010101011 01-1010-11 0101110100 -101211111 001101?110 01?10000?1 12?1?1-111 1011201012 0110010110 111?200000

Procolophon

Owenetta


Barasaurus

1010020010 ??110??011 1111-00111 100011-010 0011111200 0210-00100 0000011011 - 0?1001110 01-1010-11 01??11?101 00??0????? 0000011011 0011011011 0010012010 01?0001??? 11??01100

B. mesensis

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B. bashkyricus

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Nycteroleter

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Emeroleter

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Lanthanosuchus

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Acleistorhinus

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Feeserpeton

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C. pholeter

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C. vaughni

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Delorhynchus

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Abyssomedon

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Erpetonyx

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Bolosaurus

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Appendix S4.2. List of characters used in the phylogenetic analysis of Parareptilia.

(1) Narial shelf: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #1)

(2) If narial shelf is present, it is: found on the nasal (0); found on the nasal and maxilla (1).
   (Modified from Laurin and Reisz, 1995 #1)

(3) Prefrontal-postfrontal contact in dorsal view: present (0); absent (1). (Modified from Laurin
   and Reisz, 1995 #2)

(4) If prefrontal-postfrontal contact is absent, the frontal contribution to the orbital margin in
dorsal view is: narrow (0); broad (1). (Modified from Laurin and Reisz, 1995 #2) When the
frontal contribution is narrow, the frontal occupies less than 1/3 of the dorsal orbital
margin.

(5) Frontal lateral lappet: absent (0); present (1). (Modified from deBraga and Reisz, 1996 #7)

(6) Pineal foramen position: in the middle of the body of the parietal (0); displaced posteriorly
   (1); displaced anteriorly (2). (Modified from deBraga and Rieppel, 1997 #49)

(7) Postparietal: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #4)

(8) If postparietal is present, it is: paired (0); median (1). (Modified from Laurin and Reisz, 1995
    #4)

(9) If postparietal is present, its size is: large (0); small (1). (Modified from Laurin and Reisz,
    1995 #4). Postparietal (either both paired elements together or a single median one) is large
    when it is at least the width of one of the parietals (at their widest point).

(10) If postparietal is present, it is positioned such that it is: dorsally exposed, integrated into
    skull table (0); occipital (1). (Laurin and Reisz, 1995 #5)

(11) Prefrontal-palatal contact: absent (0); present (1). (Modified from Laurin and Reisz 1995
    #6)

(12) If prefrontal-palatal contact is present, it is: narrow and acuminate (0); strong, with sutural
    base (1). (Modified from Laurin and Reisz, 1995 #6)
(13) Prefrontal medial flange: narrow (0); wide (1). (Modified from Laurin and Reisz 1995 #7)
When narrow, the mediolateral length of the prefrontal medial flange is equal to or less than 1/5 the height of the orbit.

(14) Bulbous medial process of prefrontal: absent (0); present (1). (Laurin and Reisz, 1995 #8)

(15) Lacrimal narial contact: present (0); absent (1). (Laurin and Reisz, 1995 #9)

(16) Foramen orbitonasale: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #10)

(17) If foramen orbitonasale is present, it is: represented by a medial indentation on the lacrimal and a dorsal indentation on the palatine (0); enclosed between prefrontal, lacrimal and palatine (1). (Modified from Laurin and Reisz, 1995 #10)

(18) Jugal anterior process: does not extend to anterior orbital rim (0); extends at least to level of anterior orbital rim (1). (Laurin and Reisz, 1995 #11)

(19) Suborbital ramus of jugal: dorsoventrally broad (0); slender or reduced with no dorsoventral extension (1). (MacDougall and Reisz, 2014) When the suborbital ramus of the jugal is slender, its dorsoventral height is less than that of the dorsoventral height of the suborbital portion of the maxilla.

(20) Posterior extension of jugal that contributes to temporal region of skull roof: present (0); absent (1). (MacDougall and Reisz, 2014)

(21) Postorbital posterior process shape in lateral view: slender, anteroposterior length is at least twice its dorsoventral width (0); increased width, length is less than twice its width (1). (Modified from deBraga and Reisz, 1996 #14)

(22) Postorbital-supratemporal contact: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #12)

(23) Posterolateral corner of skull roof; formed by tabular (0); formed mostly by supratemporal (1); formed by parietal and small supratemporal or parietal alone (2). (Laurin and Reisz, 1995 #15)
(24) Tabular: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #17)

(25) If tabular is present, it is: part of skull table (0); largely occipital (1). (Modified from Laurin and Reisz, 1995 #17)

(26) Supratemporal: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #18)

(27) If supratemporal is present, it is: large (0); small (1). (Modified from Laurin and Reisz, 1995 #18) When small the mediolateral width of the element is equal to or less than 1/10 of the midline skull length.

(28) Premaxillary dorsal process: broad, narial opening faces predominantly laterally (0); narrow, narial opening faces anteriorly (1). (deBraga and Reisz, 1996 #1)

(29) Anterodorsal process of the maxilla: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #19)

(30) Anterior lateral maxillary foramen: equal in size to other maxillary foramina (0); much larger than other foramina (1). (Modified from Laurin and Reisz, 1995 #20)

(31) Maxilla and quadratojugal: in contact (0); separated (1). (Laurin and Reisz, 1995 #22)

(32) Suture between jugal and maxilla: straight, jugal thins out smoothly towards anterior direction (0); ‘stepped’, anterior most tip of jugal very narrow but expands broadly posteriorly along with a dramatic thinning of the posterior process of the maxilla (1). (Müller and Tsuji, 2007 #133)

(33) Contact between maxilla and prefrontal: absent (0); present (1). (Müller and Tsuji, 2007 #136)

(34) Contribution of maxilla to external naris: maxilla is either excluded from naris or forms only its ventral/posterior edge (0); maxilla extends also to the posterodorsal margin of naris (1). (Müller and Tsuji, 2007 #137)

(35) Presence of size related heterodonty on the anterior 2/3 of the maxilla: present (0); absent (1). (MacDougall and Reisz, 2014). Size related heterodonty as used here refers to the
presence of significantly larger teeth on the anterior 2/3 of the maxilla. Significantly larger as used here refers to teeth that have a base width that is at least 50% larger than the other teeth.

(36) Presence of size related heterodonty on the anterior 2/3 of the dentary: present (0); absent (1). (MacDougall and Reisz, 2014) Size related heterodonty as used here refers to the presence of significantly larger teeth on the anterior 2/3 of the dentary. Significantly larger as used here refers to teeth that have a base width that is at least 50% larger than the other teeth.

(37) If size related heterodonty is present on the maxilla, it is represented by: one tooth (0); two or more teeth (1). (MacDougall and Reisz, 2014)

(38) Squamosal and post-temporal fenestra: separated (0); in contact (1). (Laurin and Reisz, 1995 #26)

(39) Quadratojugal shape: does not reach beyond the level of the ventral orbital margin (0); extends dorsally beyond the level of ventral orbital margin (1). (Modified from Laurin and Reisz, 1995 #28)

(40) Quadratojugal anterior extent: reaches posterior border of orbit (0); does not reach level of posterior border of orbit (1). (Modified from Laurin and Reisz, 1995 #23)

(41) Quadratojugal ornamentation: confluent with the cheek and not ornate in any manner (0); ornamented, dermal protuberances project from its surface (1). (deBraga and Rieppel, 1997 #43)

(42) Upper temporal fenestra: absent (0); present (1). The upper temporal fenestra is formed by contributions from the postorbital, the parietal, the squamosal. (Laurin and Reisz, 1995 #29)

(43) Lower lateral temporal opening (fenestra or emargination): absent (0); present (1). (Modified from Laurin and Reisz, 1995 #30)
(44) If a lower temporal opening is present, it is: bounded ventrally, forming a fenestra (0); unbounded ventrally, forming an emargination (1). (Modified from Laurin and Reisz, 1995 #30)

(45) Postorbital contribution to lateral temporal opening (fenestra or emargination): present (0); absent (1). (Modified from deBraga and Reisz, 1996 #20)

(46) Quadratojugal contribution to lateral temporal opening (fenestra or emargination): absent (0), present (1). (Modified from Laurin and Reisz, 1995 #16)

(47) Region of skull posterior to the orbit, anteroposterior length: equals anteroposterior extension of orbit (0); shorter than anteroposterior extension of orbit (1); longer than anteroposterior extension of orbit (2). (Modified from Laurin and Reisz, 1995 #32)

(48) Ventral margin of skull region posterior to orbit: expanded below ventral extent of maxilla (0); rectilinear (1); emarginated (2). (Modified from Laurin and Reisz, 1995 #33)

(49) Lateral surface of quadrate: covered by squamosal and quadratojugal (0); not covered (1). (Modified from Laurin and Reisz, 1995 #34)

(50) Quadrate anterior process: extends anteriorly for at least 50% the length of the quadrate ramus (0); extends anteriorly for less than 50% the length of the quadrate ramus (1). (Modified from Laurin and Reisz, 1995 #35)

(51) Quadrate condyle articular surfaces: strongly convex, anteroposteriorly longer than they are wide (0); nearly flat, anteroposteriorly shorter than they are wide (1). (Modified from Laurin and Reisz, 1995 #65)

(52) Jaw articulation position: posterior to occiput (0); even with occiput (1); anterior to occiput (2). (Laurin and Reisz, 1995 #36)

(53) Posterior extension of orbit: absent (0); present (1). (Laurin and Reisz, 1995 #37)

(54) Dermal sculpturing: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #38)
(55) If dermal sculpturing is present, it is in the form of: tuberosities (0); round pits (1); honeycomb pattern of ridges and pits (2). (Modified from Laurin and Reisz, 1995 #38)

(56) Sculpturing involving circumorbital bumps: no distinctive ornamentation (0); circumorbital tubercles (1). (Tsuji, 2006 #45)

(57) Dorsal dermal ossifications: absent (0); present (1). (Laurin and Reisz, 1995 #124)

(58) Posterior margin of skull roof: roughly straight (0); with a single, median embayment (1); embayed bilaterally (2). (Modesto, 1999b #125)

(59) Temporal notch: present (0); absent (1). (Müller and Tsuji, 2007 #134)

(60) Temporal depression associated with posterolateral excavation: restricted to the posterior half of the cheek (0); closely approaches the orbital margin (1). (Müller and Tsuji, 2007 #135)

(61) Interpterygoid vacuity anterior extent: reaches beyond posterior border of palatine (0); reaches level of palatine or less (1). (Reisz et al., 2007 #127)

(62) Anterior shape of interpterygoid vacuity: acuminate (0); rounded (1).

(63) Choana: parallel to maxilla; palatine forms its posterior edge only (0); curved posteromedially; palatine forms its posterior and part of its lateral edge (1). (Laurin and Reisz, 1995 #40)

(64) Alar flange of the vomer (thin anterolateral flange of vomer): absent (0); present (1). (Tsuji, 2006 #50)

(65) Arcuate flange of pterygoid: present (0); absent (1). (Laurin and Reisz, 1995 #42)

(66) Cranio-quadrate space: small, quadrate ramus of pterygoid and paraoccipital process of opisthotic converge posterolaterally (0); large, quadrate ramus of pterygoid and paraoccipital process of opisthotic are parallel to each other (1). (Laurin and Reisz, 1995 #43)
(67) Pterygoid anterior extent: reaches level of posterior end of choana (0); posterior to choana (1). (Laurin and Reisz, 1995 #44)

(68) Transverse flange of the pterygoid: large, approaches cheek, a noticeable lateral projection (0); small, does not approach cheek (1). (Modified from Lee, 1997 #19)

(69) Transverse flange of pterygoid orientation: directed posterolaterally or transversely (0); directed anterolaterally (1); directed anteriorly (2). (Modified from Laurin and Reisz, 1995 #45)

(70) Transverse flange of pterygoid dentition: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #46)

(71) If dentition is present on the transverse flange of the pterygoid, it is a: shagreen of very small teeth, no ventral ridge (0); single row of large teeth, no ventral ridge (1); single row of large teeth, with a shagreen of very small teeth, no ventral ridge (2). (Modified from Laurin and Reisz, 1995 #46)

(72) Quadrate flange of pterygoid dentition: absent (0); present (1).

(73) Quadrate ramus of pterygoid: merges smoothly into transverse flange without distinctive excavation (0); deep excavation on posterolateral surface (1). (deBraga and Reisz, 1996 #29)

(74) Quadrate ramus of pterygoid relation to transverse flange: not continuous with transverse flange (0); continuous with transverse flange, forming a ridge (1).

(75) Lateral pocket on the pterygoid found between quadrate ramus and transverse flange: absent (0); present (1).

(76) Ectopterygoid: present (0); absent (1). (MacDougall and Reisz, 2014)

(77) If ectopterygoid is present, ectopterygoid dentition is: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #48)
(78) If ectopterygoid is present, its relationship to transverse flange: distal to transverse flange, does not contribute to lateral portion of flange (0); makes contact with lateral portion of transverse flange (1). (Modified from deBraga and Reisz, 1996 #33)

(79) Suborbital opening on the palate: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #49) Refers to the suborbital foramen or fenestra.

(80) Basicranial articulation: kinetic/synovial (0); sutured and/or immobile (1). (Modified from Lee, 1997 #2)

(81) Length of basicranial articulation: restricted to anterolateral margin of the parasphenoid (0); extends over much of length of main body of parasphenoid (1). (deBraga and Reisz, 1996 #36)

(82) Parasphenoid pocket for cervical musculature (one or two): present (0); absent (1). (Laurin and Reisz, 1995 #50)

(83) If a parasphenoid pocket for cervical musculature is present it is represented by: a single median pocket (0); two pockets (1).

(84) Parasphenoid wings; present, parasphenoid broader posteriorly than long (0); absent, parasphenoid narrower posteriorly than long (1). (Modified from Laurin and Reisz, 1995 #51)

(85) Cultriform process: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #52)

(86) If cultriform process is present, it is: longer than the body of the parasphenoid (0); shorter than the body of the parasphenoid (1). (Modified from Laurin and Reisz, 1995 #52)

(87) Parasphenoid teeth: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #53)

(88) If parasphenoid teeth are present, they are found: in rows (0); as a shagreen (1). (Modified from Laurin and Reisz, 1995 #53)
(89) Supraoccipital: plate-like, with no sagittal crest (0); constricted at midline, forming sagittal crest (1); plate-like, with a sagittal crest (2). (Modified from deBraga and Rieppel, 1997 #56)

(90) Paroccipital process: vertically broad (0); anteroposteriorly expanded (1); narrow (2); tubular, composed of opisthotic (3). (Laurin and Reisz, 1995 #56)

(91) Paroccipital process orientation: directed primarily laterally (0); oriented obliquely, at an angle of at least 45 degrees from the horizontal plane of the skull (1). (deBraga and Reisz, 1996 #44)

(92) Sutural contact between paroccipital process and dermatocranium: absent (0); present (1). (Modified Laurin and Reisz, 1995 #57)

(93) Otic trough in ventral flange of opisthotic: absent (0); present (1). (Laurin and Reisz 1995 #58)

(94) Medial wall of inner ear (made of prootic): unossified (0); ossified with acoustic nerve foramina (1). (Laurin and Reisz, 1995 #59)

(95) Post-temporal fenestra: absent (0); present (1). (Modified from deBraga and Rieppel, 1997 #59)

(96) If post-temporal fenestra is present, it is: small, diameter less than the diameter of foramen magnum (0); large, diameter at least equal to foramen magnum (1). (Modified from deBraga and Rieppel, 1997 #59)

(97) Osseous contact between basioccipital and basisphenoid: present (0); absent (1). (Lee, 1993 #A3, scored as per Laurin and Reisz, 1995 #61)

(98) Occipital condyle shape: transversely broad (0); reniform to circular (1). (Laurin and Reisz, 1995 #62)

(99) Ventral exposure of basioccipital: contributes extensively to ventral surface of the braincase (0); restricted to condylar region (1). (deBraga and Reisz, 1996 #37)
(100) Ventral braincase tubera: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #63, and deBraga and Rieppel 1997 #65)

(101) If ventral braincase tubera are present, they are: restricted to basioccipital (0); very large and restricted to basisphenoid (1). (Modified from Laurin and Reisz, 1995 #63, and deBraga and Rieppel, 1997 #65)

(102) Lateral flange of exoccipital: absent (0); present (1). (Laurin and Reisz, 1995 #64)

(103) Stapes: robust, greatest depth exceeding one-third of total length (0); slender, length at least four times depth (1). (Modified from deBraga and Rieppel, 1997 #45)

(104) Stapedial dorsal process: ossified (0); unossified (1). (Laurin and Reisz, 1995 #67)

(105) Morphology of marginal dentition: single cusp (0); two to seven cusps (1); more than seven cusps (2). (Modified from Lee 1997, #59)

(106) Foramen intermandibularis: an anterior symphysial foramen (0); an anterior symphysial foramen and a posterior foramen (1). (Modified from Laurin and Reisz, 1995 #69)

(107) If there are two intermandibular foramina the posterior foramen is located: anterior to coronoid process (0); posterior to or at level of coronoid process (1). (Modified from Laurin and Reisz, 1995 #69)

(108) Meckelian fossa orientation: faces mediodorsally (0); faces dorsally (1). (Modified from Laurin and Reisz, 1995 #70)

(109) Meckelian fossa anteroposterior length: long, occupies at least 25% of lower jaw length (0); short, occupies less than 25% of lower jaw length (1). (Modified from Laurin and Reisz, 1995 #71)

(110) Surangular length: extends beyond coronoid eminence (0); does not extend beyond coronoid eminence (1). (Laurin and Reisz, 1995 #72)

(111) Accessory lateral shelf on surangular anterior to articular region: absent (0); present (1). (Laurin and Reisz, 1995 #73)
(112) Two laterally located foramina on the anteroposterior midline of the surangular: absent (0); present (1).

(113) Coronoid number: two or three (0); one (1). (Laurin and Reisz, 1995 #74)

(114) Prearticular extends: beyond the coronoid eminence (0); does not extend beyond coronoid eminence (1). (Modified from Laurin and Reisz, 1995 #75)

(115) Retroarticular process: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #76)

(116) If present, the retroarticular process is: small and narrow (0); transversely broad, dorsally concave (1). (Modified from Laurin and Reisz, 1995 #76)

(117) If present, the retroarticular process is composed of: articular body (0); three or more elements (articular, prearticular, angular and surangular) (1). (Modified from Laurin and Reisz, 1995 #77)

(118) Lateral shelf on articular region: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #78)

(119) Coronoid process: low (0), high (1). (Modified from Laurin and Reisz, 1995 #79)

(120) If coronoid process is high, it is: composed of coronoid only (0); composed of dentary and coronoid (1). (Modified from Laurin and Reisz, 1995 #79)

(121) Splenial: contributes to mandibular symphysis (0); excluded from mandibular symphysis (1). (Laurin and Reisz, 1995 #80)

(122) Presacral vertebral count: more than twenty (0); twenty or less (1). (Laurin and Reisz, 1995 #81)

(123) Axial centrum orientation: in plane of axial skeleton (0); sloping anterodorsally (1). (Laurin and Reisz, 1995 #82)

(124) Atlantal neural arch: possesses epipophysis (0); lacks epipophysis (1). (Lee 1995, scored as per Modesto, 1999b #126)
(125) Axial intercentrum: with rounded anteroventral edge (0); with strong anterior process (1). (Laurin and Reisz, 1995 #84)

(126) Atlantal pleurocentrum and axial intercentrum: separate elements (0); attached or fused (1). (Laurin and Reisz, 1995 #85)

(127) Trunk neural arches: swollen (0); narrow (1). (Modified from Laurin and Reisz, 1995 #86)

(128) Ventral surface of anterior pleurocentra: ventral surface of vertebral centra uniform (0); ventral surface of vertebral centra bearing an excavation on either side of the midline, coupled with a flattened median crest between them (1). (Modified from Laurin and Reisz, 1995 #87)

(129) Number of sacral vertebrae: one (0); two (1); three or more (2). (Laurin and Reisz, 1995 #88)

(130) Sacral rib distal overlap: broad with narrow gap between ribs (0); small or absent with wide gap between ribs (1). (Laurin and Reisz, 1995 #89)

(131) Transverse process or ribs: present only on a few anterior caudals (0); present on at least thirteen caudals (1). (Laurin and Reisz, 1995 #90)

(132) Anterior caudal rib size: elongate and extend posteriorly to the end of the next vertebra (0); curve posteriorly but do not extend to the end of the next vertebrae (1); straight, with no posterior curvature (2).

(133) Caudal hemal arches: wedged between centra (0); attached to anterior centrum (1). (Laurin and Reisz, 1995 #91)

(134) Interclavicle: diamond-shaped (0); T-shaped, with long, slender lateral processes (1). (Laurin and Reisz, 1995 #92)

(135) Interclavicle attachment for clavicle: ventral sutural area (0); anteriorly directed groove (1); tightly sutured into plastron (2). (Laurin and Reisz, 1995 #93)

(136) Cleithrum: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #94)
(137) If cleithrum is present, it: caps scapula anterodorsally (0); does not cap scapula at all (1).
   (Modified from Laurin and Reisz, 1995 #94)

(138) Scapula: broad and low (0); narrow and high (1). (Modified from Laurin and Reisz, 1995 #96) When low the height of the scapula is equal to or less than two and a half times its anteroposterior length.

(139) Supraglenoid foramen: present (0); absent (1). (Laurin and Reisz, 1995 #97)

(140) Glenoid: helical, composed of a single facet (0); bipartite, composed of two facets (1).
   (Modified from Laurin and Reisz, 1995 #98)

(141) Acromion: absent (0); present (1). (Laurin and Reisz, 1995 #99)

(142) Sternum: not mineralized (0); mineralized (1). (Laurin and Reisz, 1995 #100)

(143) Supinator process: strongly angled relative to shaft (0); parallel to shaft (1). (Modified from Laurin and Reisz, 1995 #101)

(144) If supinator process is parallel to shaft it is: separated from it by a groove (0); not separated from shaft (1). (Modified from Laurin and Reisz, 1995 #101)

(145) Ectepicondylar foramen: only groove present (0); groove and foramen present (1); only foramen present (2); both absent (3). (Laurin and Reisz, 1995 #102)

(146) Entepicondylar foramen: present (0); absent or not fully enclosed (1). (Laurin and Reisz, 1995 #103)

(147) Humerus: with robust heads and a short shaft (0); short and robust, without a distinct shaft (1); slender with long shaft (2). A short shaft is one that has a proximodistal length that is equal to or less than the mediolateral width of the heads. (Modified from Laurin and Reisz, 1995 #104)

(148) Olecranon process: present (0); absent (1). (Modified from Laurin and Reisz, 1995 #105)
(149) If present, the olecranon process is: large, with articular facet of ulna facing medially (0); small, with articular facet of ulna facing proximally (1). (Modified from Laurin and Reisz, 1995 #105)

(150) Manual phalangeal formula: 2 3 4 5 3 (0); 2 3 4 4 3 (1); 2 3 3 3 3 or less (2). (Laurin and Reisz 1995, #106)

(151) Dorsolateral shelf on iliac blade: absent (0); present (1). (Laurin and Reisz, 1995 #107)

(152) Iliac blade: low, with long posterodorsal process that extends beyond the posterior edge of the iliac body (0); dorsally expanded, distally flaring, the posterodorsal process does not extended beyond the posterior edge of the iliac body (1). (Laurin and Reisz, 1995 #108)

(153) Acetabular buttress: small, overhangs acetabulum only moderately (0); large, overhangs acetabulum strongly (1). (Laurin and Reisz, 1995 #109)

(154) Oblique ventral ridge of femur (adductor crest): present (0); absent (1). (Laurin and Reisz, 1995 #110)

(155) Femoral proximal articulation: anteroposteriorly long (0); round (1). (Laurin and Reisz, 1995 #111)

(156) Greater trochanter of femur: absent (0); present on posterior edge of femur (1). (Laurin and Reisz, 1995 #112)

(157) Femoral shaft: short and broad (0); long and slender (1). A short and broad femoral shaft is one that has a proximodistal length that is equal to or less than the mediolateral width of the distal head in ventral view (Laurin and Reisz, 1995 #113)

(158) Astragalus: absent (0); present (1). (Modified from Laurin and Reisz, 1995 #115)

(159) If astragalus is present, it: incorporates incompletely fused tibiale, intermedium, and perhaps centrale 4 (0); is without traces of compound origin (1). (Modified from Laurin and Reisz, 1995 #115)
(160) Tibio-astragal joint: flat (0); tibial ridge fits into astragalar groove (1). (Laurin and Reisz, 1995 #116)

(161) Astragalus and calcaneum: separate (0); sutured or fused (1). (Laurin and Reisz, 1995 #117)

(162) Medial pedal centrale: present (0); absent (1). (Laurin and Reisz, 1995 #118)

(163) Number of distal tarsals: five (0); four or less (1). (Laurin and Reisz, 1995 #119)

(164) Metapodials: not overlapping (0); overlapping (1). (Laurin and Reisz, 1995 #121). When metapodials are not overlapping the carpus or tarsus is short and broad. Likewise, when metapodials are overlapping the carpus or tarsus is long and slender.

(165) Pedal phalangeal formula: 2 3 4 5 4 (0); 2 3 4 4 3 (1); 2 3 3 4 3 or less (2). (Laurin and Reisz, 1995 #122)

(166) Ratio between length of metatarsal I to length of metatarsal IV: at least 0.5 (0); less than 0.5 (1). (Laurin and Reisz, 1995 #123)

(167) Number of maxillary tooth positions: 0-15 (0); 16-30 (1); more than 30 (2). (Modesto et al., 2015)

(168) Number of premaxillary tooth positions: 0-3 (0); 4-6 (1); more than 6 (2). (Modesto et al., 2015)

(169) Single large tooth on anteriormost end of vomer: absent (0); present (1). In some taxa there is a single larger tooth found on the anterior end of the vomer, rather than numerous small teeth. (MacDougall et al., 2016)

(170) Bulbous marginal teeth: absent (0); present (1). Teeth of the maxilla and dentary are considered to be bulbous when the largest teeth have maximum widths that are equal to or more than their maximum height. (MacDougall et al., 2016)
Chapter 5

The unique preservational environment of the Early Permian fossiliferous cave deposits of the Richards Spur locality.

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5.1 Abstract

The Richards Spur locality, Oklahoma, USA, represents an Early Permian infill in a series of Ordovician limestone and dolostone karst fissures. It exhibits the most diverse terrestrial Palaeozoic community currently known, with more than 40 distinct tetrapod taxa. Speleothems intimately associated with the site indicate that Richards Spur is a cave system, suggesting a preservational environment that is distinct from those of more typical Early Permian lowland deltaic/fluvial localities. Fossil material obtained from the caves is often found in disarticulation, although articulated material is not uncommon. This suggests that there were several factors that affected how animal remains became deposited within the caves. Many animals that died outside the caves were likely disarticulated on the surface and then washed in during rainfall events, resulting in mostly disarticulated remains. Alternatively, animals could be washed in before being disarticulated and some probably fell into the caves, resulting in less chance for their remains to become disarticulated. Supporting evidence for these preservational hypotheses comes in the form of wear caused by attritional processes. Disarticulated elements can exhibit high levels of wear, likely due to the water transport that would carry them into the caves from the surface, as well as reworking within the caves. The partially and completely articulated remains are normally unworn, presumably due to a lesser degree of transport and reworking. X-ray diffraction and stable isotope analysis of cave infill further supports the interpretations made from fossil material. The results of this study provide a much-improved understanding of the preservational environment at Richards Spur, and will be useful in integrating information from this unique upland locality with that from the more extensively studied lowland localities of the Early Permian.

5.2 Introduction

The Dolese Brothers limestone quarry in Oklahoma, USA, is home to the unique Early Permian (289–286 Ma) Richards Spur locality. The quarrying operation that has been ongoing at Richards Spur for over a century has exposed a series of fissures in the limestone of the quarry (Sullivan et al., 2000). The clay and mudstone that fills these fissures stands out from the surrounding limestone, making their shape and extent quite apparent (Sullivan et al., 2000), the clay being the
result of decalcified mudstone. All fossil material known from Richards Spur has been obtained from the infill of the fissures.

The abundant fossil material found in the fissures represents a fauna that is currently the most diverse known from a continental Palaeozoic locality (Sullivan et al., 2000; MacDougall and Reisz, 2012), being a source of numerous small- to medium-sized terrestrial tetrapods. More than 30 described taxa are known from the locality (Sullivan and Reisz, 1999; MacDougall and Reisz, 2012); when including as yet undescribed material, the number of taxa surpasses 40 (pers. obs., M.J.M. and R.R.R.). Taxa found at the locality include synapsids, reptiles, and various anamniotes (Table 1), many of which are currently endemic to Richards Spur (MacDougall and Reisz, 2012). The unique faunal composition of Richards Spur and the absence of aquatic taxa there has led to the suggestion that it represents an upland locality (Sullivan et al., 2000). This makes it one of only three Early Permian upland localities that are currently known, the others being the Bally Mountain locality, also located in the Slick Hills of Oklahoma (Olson, 1967; Busbey, 1990), and the Bromacker locality in Germany (Eberth et al., 2000).

During the Early Permian Richards Spur was situated in equatorial Southwestern Laurasia (Blakey, 2007). Based on climate information obtained from speleothems Richards Spur is suggested to have experienced monsoonal weather conditions, and thus strong seasonality, alternating between periods of aridity and periods of heavy rainfall (Tabor and Yapp, 2005; Woodhead et al., 2010). The Early Permian paleoclimate for the region around Richards Spur is consistent with conditions that have been proposed for lowland localities in the greater region of equatorial Southwestern Laurasia via analysis of paleosols (Tabor and Montañez, 2002; Tabor et al., 2008), as well as fossil plant material (DiMichele et al., 2006).

Despite the large body of work devoted to taxonomy at the Richards Spur locality (Table 1), there has been little integrative work done on the geological and taphonomic nature of the locality and its fossiliferous infills. Unfortunately, the ongoing commercial quarrying at the locality has prevented detailed in-situ study of the sedimentology, stratigraphy, and taphonomy of the site. For this reason the preservational environment of the locality has historically been poorly understood.

Here we discuss the Richards Spur cave system and the various taphonomic pathways through which tetrapod taxa became preserved, using both palaeontological and geological information.
X-ray Diffraction (XRD) and stable isotope analysis are two techniques that have proven to be useful in understanding the factors contributing to a diversity of taphonomic modes at a given site (Tabor and Montañez, 2004; Tabor et al., 2004; DiMichele et al., 2006). For this study XRD analysis has allowed for the unambiguous identification of what minerals make up the infill of the fissures, and stable isotope analysis was used to determine $\delta^{13}C$ and $\delta^{18}O$ of samples. Several samples from the caves were analyzed (Table 2); these were carefully chosen to represent the variability in fossil articulation and array of mineral types found at Richards Spur. These analyses were used to augment and revise interpretations of the preservational environment that were made from the fossil material. Furthermore, absolute dating of new speleothems from the locality, allows for a better estimate of how long the caves would have been active.

**Institutional Abbreviations**—OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA.

### 5.3 Material and Methods

#### 5.3.1. Preparation of material

Several specimens obtained from the Richards Spur locality were examined for the purposes of this study: OMNH 73361, 73511, 77667-77672 (Table 3). Most of the specimens referred to in this study occur on slabs that contain articulated or disarticulated skeletal elements of various Richards Spur taxa. Specimens were chosen to illustrate the variety of states that fossil material occurs in at Richards Spur, specifically to show varying levels of both articulation and wear. When necessary, the specimens were prepared mechanically using air scribes and pin vices.

#### 5.3.2. X-ray diffraction analysis of cave infill sedimentary rock

Five samples from the Richards Spur locality were analyzed at the Department of Earth Sciences at Southern Methodist University. These samples were chosen to represent the various types of
infill found at Richards Spur. These include (i) crystalline, strongly calcareous deposits that surrounded vertebrate bone elements, as well as a cubic sulfide mineral, (ii) chalky, strongly calcareous deposits with inclusions of finely crystalline, clastic-rich, rounded granule-to-pebble sized grains and vertebrate bone elements, and (iii) finely crystalline, rounded, clastic-rich granule-to-pebble grains that are slightly to moderately calcareous (Table 2). The type i sample is characteristic of speleothems and calcite nodules that are obtained from the cave system; this type of material tends to be uncommon. The type ii and type iii samples are characteristic of the clay infill that fossils and detrital minerals are found in; this type of material is very common and would have originated on the surface and washed into the caves over the time that they were open to the surface.

Care was taken to select bulk powders using a dremel tool equipped with a 30µm bit and mounted magnifying glass in order to sample areas enriched in calcareous cements and to avoid bone material and sulfides. The resulting powders were ground in a corundum mortar and pestle and sieved to collect only the <44µm equivalent spherical diameter (e.s.d.) grain/crystal size for subsequent analyses.

The <44µm (e.s.d.) fractions were mounted as dry powders in an aluminum metal sample holder and then examined using X-ray diffraction analysis (XRD) in order to determine the dominant minerals present within these samples. X-ray diffraction analyses of powder mounts involved scans between 2° and 70° 2Θ, with a scan speed of 2° 2Θ per minute. These XRD analyses were conducted with a Rigaku Ultima III X-ray diffractometer using Cu-Kα radiation and scan window of 0.04° 2Θ. Mineral identification follows the methods outlined by Moore and Reynolds (1997) and Brown and Brindley (1984).

### 5.3.3. Stable isotope analysis of cave infill sedimentary rock

Samples from the Richards Spur locality that contained only calcite-bearing calcareous cements, as determined through XRD analysis, were used for stable isotope analysis. For each sample, between 5 and 13 mg of bulk <44µm powders were used in the analyses. Samples were reacted overnight (~14 hours) at 25° C in-vacuo with 100% anhydrous phosphoric acid solution, and
reaction products were cryogenically purified in a high-vacuum glass extraction system. CO$_2$ yields were determined via mercury manometry, and $\delta^{13}$C and $\delta^{18}$O values of extracted CO$_2$ samples were measured at Southern Methodist University using a Finnigan MAT 253 isotope ratio mass spectrometer. Isotope ratios are reported in standard delta ($\delta$) notation: $\delta^{18}$O (or $\delta^{13}$C) = ($R_{\text{sample}}/R_{\text{standard}}$ – 1) *1000, where $R$ is the ratio of heavy-to-light stable isotope present in the sample or standard; delta values are reported relative to the PeeDee Belemnite standard (PDB; Craig, 1957) for carbon and oxygen isotope values. Repeat analyses of a Carrara marble working standard indicate reproducibility of 0.1‰ for $\delta^{13}$C values and 0.2‰ for $\delta^{18}$O values.

5.3.4. Absolute dating of speleothems

Two speleothems, considered to be stalactites due to their shape, were obtained from the cave infill of Richards Spur and were analyzed for this study. Much like the fossil material obtained from the locality, the nature of the quarrying operation makes it impossible to determine the exact portion of the cave from which they originated. The geochronology methods employed follow closely those published previously by Woodhead and colleagues (2010, 2012). Multiple aliquots, typically weighing ~50 mg, were removed from each speleothem sample using a dental drill. The pieces of calcite removed in this way were then placed into pre-cleaned disposable polyethylene cups and moved to a multiple-HEPA filtered clean room environment. Samples were briefly leached 2 times in very dilute (~0.01 M), three-times teflon distilled, HCl, with each cycle lasting around a minute, and then repeatedly washed in ultra-pure water before being dried in a HEPA filtered laminar flow hood. This step is critical for the elimination of Pb contaminants resulting from sample handling, which can easily dominate the Pb budget of the entire sample unless removed.

Individual samples were weighed into pre-cleaned teflon beakers and treated with sufficient 6N HCl to ensure complete dissolution. A mixed $^{233}$U-$^{205}$Pb tracer, calibrated against EarthTime (http://www.earth-time.org) reference solutions, was then weighed into the vials and each one sealed and refluxed on the hotplate for several hours to ensure complete sample-spike equilibration. Samples were then dried down and taken up in 0.6N HBr for Pb separation using
AG 1X-8 anion exchange resin. The eluate was subsequently processed through the same column, now filled with Eichrom TRU ion-specific resin, to separate U.

Isotope ratios were determined on a Nu Plasma MC-ICPMS using a DSN-100 desolvation unit and MicroMist glass nebuliser, operating in the range 50-100 µl/min uptake. Instrumental mass bias effects were monitored and corrected using NIST SRM 981 reference material in the case of Pb, and the sample’s internal $^{238}U/^{235}U$ ratio in the case of U. Instrument data files were processed initially using an in-house designed importer, operating within the Iolite environment (Paton et al., 2011) which considers all data and reference material analyses obtained throughout a particular analytical session and permits a variety of corrections for instrumental mass bias and drift. The resulting data, now corrected for instrumental effects, were then blank corrected and isotope-dilution calculations performed using the Schmitz and Schoene (2007) software.

Isochron regressions were calculated using ‘Isoplot Ex’ (Ludwig, 2001). Given the antiquity of the samples no corrections have been made for initial disequilibrium conditions in the U-series decay chain, which amount to only a few hundred thousand years in most cases.

5.4 Results

5.4.1. X-ray diffraction and stable isotope analyses

X-ray diffraction analysis shows that all five samples contain calcite in various amounts, as expected, given that sampling concentrated on calcareous elements. Sample DQ-2 (a Type i sample; Table 2) is nearly pure calcite, while samples DQ-3 and DQ-4 (both Type ii samples; Table 2) also contain noncalcareous components such as kaolinite, sulfides and quartz, and samples DQ-1 and DQ-5 (both Type iii samples) are similar to type ii samples except that they also contain smectite and do not include sulfide cements (Table 2).

CO$_2$ yields from H$_3$PO$_4$ dissolution of the Richards Spur samples provide estimates of the weight-percent calcite preserved within each of the sample powders analyzed in the $<44\mu$m fraction (Table 2). Based upon these criteria sample DQ-2 (a Type i sample) contains the greatest amount of calcite, 84%. Samples DQ-3 and DQ-4 (both Type ii samples; Table 2) contain
moderate amounts of calcite, 74% and 60% respectively, and samples DQ-1 and DQ-5 (Both Type iii samples) contain the least amount of calcite, 24% and 21% respectively. The CO₂ yields from acid-dissolution support the general observations made from hand specimens and x-ray diffraction; these results suggest different processes under which these samples formed and incorporated variable amounts of detrital sediments and calcareous versus non-calcareous components.

Stable carbon and oxygen isotope compositions of calcite among the samples are presented in Table 2. Stable oxygen isotope values exhibit relatively little variation, ranging from -4.2 to -5.5‰, similar to other cave-fill calcites in this region (Tabor and Yapp, 2005; Woodhead et al., 2010). In contrast, stable carbon isotope values of calcite among the same samples record a very large range, from +9.2 to -12.3‰; this exceeds the range of δ¹³C values observed in cogenetic speleothems (Woodhead et al., 2010) and aqueous cave-fill calcite-spar cements observed in previous studies of Permian cave-fill materials in the region, ~ -7 to -9‰ (Tabor and Yapp, 2005).

5.4.2. Radiogenic isotope analyses

The two new speleothem samples analyzed here provided U-Pb age estimates of 286.7±2.9 Ma, and 286.2±0.2 Ma (uncertainties quoted as 2 sigma). Multiple aliquots from both samples produced well-defined isochrons with MSWD (Mean Square Weighted Deviations) of 18 and 1.2 respectively.

5.5 Discussion

5.5.1. The cave system at Richards Spur

A century of quarrying at the Dolese Brothers quarry has revealed the presence of a network of fissures in the limestone found there. The Arbuckle limestone in which the fissures occur is Ordovician in age; after deposition, the limestone was uplifted and became subaerial during the
Pennsylvanian and Permian (Donovan et al., 1986, 1992). This uplift changed the angle of the bedding planes from their original horizontal orientation to one that is nearly vertical, a condition that facilitated water infiltration and dissolution along bedding planes. Dissolution of these Ordovician carbonates eventually developed a cave system. The fossiliferous infill that is found within portions of the cave remnants today, which contains vertebrate fossils of types characteristic of Lower Permian deposits, indicates that the cave system was connected with the surrounding Early Permian land surface. During the Cretaceous the Arbuckle limestone was submerged under the Western Interior Seaway and a sandy formation covered the limestone (Reeds, 1927). Following the retreat of the Seaway this formation was eroded away, exhuming the limestone and the fissures (Reeds, 1927) since at least Pleistocene time (Tabor and Yapp, 2005).

While the full extent and exact morphology of the fissures is unknown, it is now apparent that they are components of an extensive karst system. The main evidence for such a system is the layout of the fissures themselves (Fig. 2) and the occurrence of various karst structures within them, the most obvious of which are calcite speleothems (Donovan et al., 1992; Woodhead et al., 2010) – secondary cave carbonates such as stalactites, stalagmites, flowstone, and cave popcorn, all of which are found in the infill (Fig. 1). Recently, speleothems recovered from the fissures have been used to determine an age of 289.2±0.68 Ma for the locality, as well as assess its likely Permian paleoclimate (Woodhead et al., 2010). Two additional speleothems analyzed as part of this study produced very similar results. Together with the original age determination, these new radiometric ages provide an estimate of the timing of the formation of the Richards Spur fissure fills to around 289 to 286 Ma. These data further support the suggestion that Richards Spur is Artinskian in age, and give a potential time frame for how long the caves could have been active during the Early Permian. Using all currently available ages, the minimum and maximum possible duration of the period of active cave formation was 2.1 Ma and 6.1 Ma, respectively. Future analysis of more speleothems from Richards Spur may result in a wider range of dates, potentially extending both the minimum and maximum age estimates.

The presence of speleothems also indicates that the caves were hydrologically active. Thus, it can be inferred that water would have been an important component of the initial development and subsequent filling of the cave system during the Early Permian. Additional evidence for the presence of water in the caves is that many of the fossil specimens obtained from Richards Spur
are found encased within blocks of coarsely crystalline calcite (similar to the Type i sample; Table 2), which must have precipitated around submerged animal remains. Analyzed samples of this sort (Table 2) exhibit a large range of carbon isotope values, which suggests that they experienced a larger range of biochemical conditions and depositional/crystallization processes than has been presented in previous studies of speleothem cements at Richards Spur (Woodhead et al., 2012). This wide range of carbon isotope values could potentially be influenced by the hydrocarbons that are associated with the karst deposits at Richards Spur, something that is common throughout the Slick Hills of Oklahoma (Busbey 1990; Donovan et al., 1992). It is because of these hydrocarbons that the majority of the fossils at the locality are stained black. However, there is variation in the level of staining among the fossil materials, there are some fossil specimens, including limb bones and skulls that are only partly stained, and there are fossils not stained by hydrocarbons and are instead white or light brown. This indicates variability in the degree of hydrocarbon permeation depending on the part of the cave system, and this variability would most likely also affect the carbon isotope values.

The passages that make up the cave system are generally small, being about 40-60cm wide (R.R.R., pers. obs.), and run mostly parallel with the tilted bedding planes of the Ordovician carbonate strata observed in the quarry face. Numerous passages branch out and meet with other parts of the cave system, and occasional large passages occur (Fig. 2). Olson (1991) estimated that the fissures had a depth exceeding 30 meters; however, he does not indicate how this measurement was determined. Currently, we do not know exactly how deep the cave system extends into the limestone, as the caves have never been mapped after being exposed, and are constantly being destroyed by the quarrying operation. Likewise, for similar reasons the lateral extent of the cave system is not known. The exposed fissures are composed of Lower Permian infill which includes detrital clays and conglomerates in variable concentrations that are also usually highly fossiliferous (similar to the Type ii and Type iii samples; Table 2); the fossils and detrital minerals indicate that the caves would have been open to the surface during the Early Permian. Unfortunately, in most cases the infill of the caves is discarded during quarrying activities, which makes it impossible to know from exactly which parts of the caves fossil and mineral material is obtained. This results in difficulties determining the precise stratigraphic occurrence of fossils at the locality, as there is no stratigraphic control over the cave-infill
material. The active quarrying at the locality also makes more detailed sedimentological analysis of the caves difficult (Sullivan et al., 2000).

It appears that only the infill from the top 25 meters of the cave system contains fossils. While we do not know the full extent of the caves, the active quarrying operation has extended below 25 meters and apparently below the level of the fossil-producing infill, with no fossil material being discovered below this depth (Burkhalter and May, 2002). However, thanks to the wealth of fossil material that was obtained prior to exceeding the 25 meter limit, new Richards Spur taxa are still being discovered and described on a regular basis (Tsuij et al., 2010; Fröbisch and Reisz, 2012; MacDougall and Reisz, 2012, 2014; Anderson and Bolt, 2013; Reisz et al., 2014; MacDougall et al., 2016). It is also possible that new fossil material could be found in the future should the quarrying operation extend laterally to new parts of the quarry face.

5.5.2. Depositional environment at Richards Spur

It is unlikely that there was much vertebrate habitation deep within the caves. However, it is possible that some of the smaller animals would have lived in the entrances of the caves or at a shallow depth within them. There are a variety of small animals in modern systems, such as salamanders and arthropods, that live in the entrances of caves in order to hunt or avoid predation (Culver and Pipan, 2009). Most of the remains found at Richards Spur are likely those of animals that were originally living outside of the caves on the surface. We propose two likely interpretations regarding how animal remains became deposited in the caves at Richards Spur.

The first of these involves disarticulated material arriving in the caves via allochthonous transport processes, specifically deposition via meteoric water movement from surface runoff through parts of the cavern. Analysis of speleothems obtained from the caves revealed that the Early Permian climate of Richards Spur was likely to have been semi-arid, with periods of monsoonal activity (Woodhead et al., 2010), similar to the climate that is proposed to have been present in the surrounding lowlands of Southwestern Laurasia (Tabor and Montañez, 2002; DiMichele et al., 2006). $\delta^{18}O$ values obtained from calcite in the cave infill (Table 2) are quite similar to those previously reported from other calcite material in the region (Tabor and Yapp,
2005; Woodhead et al., 2010), which further supports similar Early Permian regional precipitation trends. Episodic heavy rainfall that would be common during these monsoonal periods would have been an important factor in transporting the remains of any animal that died on the surface near the caves into them through surface runoff processes. Further evidence for water transport of animal remains is provided by detritus that washed in from the surface and co-occurs with fossil material as Lower Permian sedimentary fill. This includes detrital carbonate and disseminated clay-sized detrital grains including minerals such as quartz, kaolinite and smectite (Table 2), within which much of the fossil material is preserved (Donovan et al., 1992); this is represented by the Type ii and Type iii samples discussed above (Table 2). Once washed in from the surface, these detrital minerals would have become mixed with the calcite clay and animal remains to form the infill that is present within the caves today.

Prior to abiotic transport, scavengers and predators would likely disarticulate deceased tetrapods, as this can occur within minutes of death in modern systems (Behrensmeyer, 1991). This assumes that Early Permian carnivores and scavengers present at Richards Spur were capable of the same swift disarticulation commonly carried out by modern animals. Once disarticulated, skeletal elements would be more susceptible to transport by overland flow of water into the cave system, as many entrances were likely natural low points on the surface and vertical conduits for flowing water. Most of the disarticulated and some of the partially articulated remains recovered from Richards Spur likely entered the cave system in this manner, as they are usually found preserved in soft, clay-rich calcareous cave fill that presumably washed in with them (Fig. 3A). Most commonly this fossiliferous cave-fill is collected at the quarry waste dumps, and then disaggregated with water or weak acetic acid. This makes it very difficult to tell if articulated material would have been deposited into the caves via this mode of deposition. However, articulated specimens such as strings of vertebrae are occasionally collected intact from the clay-rich sediments (Fig. 4B).

The second possible mode of fossil deposition involves whole animals entering the caves before disarticulation could occur. During periods of monsoonal rain animals that died on the surface could have been washed in before experiencing disarticulation by decay and predation (Fig. 3B). Alternatively, the caves at Richards Spur could have acted as animal pitfall traps, with the animals living around the cave system falling in on occasion (Fig. 3C), or in some cases being washed in alive. It is also worth noting that if some animals were living within the entrances of
the caves at a shallow depth, they too would occasionally fall or wander deeper into the caves and become trapped. Once in the caves the trapped animal would eventually die and then partially or completely decompose. In either case, whole animals that entered the fissures would have been more prone to being preserved in articulation, as there would have been little chance for the connective tissues that held the skeleton together to be scavenged or decomposed. Many of the more completely articulated fossil specimens from the locality are found entirely encased in calcite rather than soft clay (Fig. 4A). This suggests that at some point after death calcite would precipitate out of the water in the caves with crystalline growth surrounding the animal remains, eventually encasing them in the Lower Permian calcite cave-fill material. This would require subaqueous conditions, or at least continuously wet surfaces, that would have facilitated continuous and fairly rapid calcite crystal growth to surround the organisms before complete deterioration. The Type i sample in Table 2 represents this process, as articulated remains tends to be associated with the calcite nodules. Furthermore, in some cases two or more articulated individuals can co-occur, excellent examples being an articulated skeleton of *Delorhynchus cifelli* that has a partial foot of *Captorhinus* on its palate, and part of the skull of a varanopid overlying the anterior part of its own vertebral column (Reisz et al., 2014). On occasion disarticulated material can be found in calcite as well, though it is usually associated with articulated material (Fig. 4A).

The mineral pyrite is often found formed inside cavities and depressions on both articulated and disarticulated fossil material (Fig. 5). Pyrite is also found without any obvious link to the animal remains themselves, such as in association with speleothems. The pyrite formation is likely the result of early diagenesis involving reducing fluids passing through the system (Canfield and Raiswell, 1991).

The proposed taphonomic modes are not mutually exclusive; they would have been occurring simultaneously over the time that the caves were open to the surface. Much of the Richards Spur infill material we see is caused by the interplay of these modes of deposition. It is not uncommon to find disarticulated and articulated material of various animals occurring side by side.

Regardless of how animal remains came to reside in the caves it is important to note that there would also have been extensive reworking of deposited material within the cave system, especially disarticulated material. Once animal remains entered into the cave system they would
have been moved through the passages by meteoric water that flowed through the caverns at levels above the local-to-regional groundwater table. This would have caused the sorting and concentration of fossil elements, eventually redepositing them elsewhere in the cave system. The taphonomic concentration of fossil material is especially apparent when looking at disarticulated elements; detrital clay/mud-granule and pebble conglomerates with numerous bones are a regular occurrence, similar to the Type ii and Type iii samples (Table 2). Concentrations of disarticulated material from a single taxon are not uncommon at Richards Spur; examples of this being entire blocks composed of disarticulated elements from the amphibamid *Doloserpeton annectens*, with the occasional disarticulated elements of other small taxa (Fig. 4D). In the case of *D. annectens*, the small size of its elements would have facilitated their transport by water, moving them farther than other larger elements; this likely resulted in their tendency to accumulate together. Less common articulated specimens recovered from the locality are animals that fell into the caves or were washed into the cave before significant disarticulation could occur. Connective tissue would have helped to hold some of their skeletal elements together during the process of reworking, keeping them from fully disarticulating prior to being entombed in the caves.

### 5.5.3. Presence of wear on Richards Spur fossil material

Originally it was thought that any wear or breakage found on Richards Spur fossil material was the result of the quarrying operation rather than attritional processes (Sullivan et al., 2000). However, the discovery of new fossil material and investigation of older known material from the locality reveals that wear due to attritional processes played a much more significant role than was previously recognized. Wear has been observed on many different fossil elements from Richards Spur, and understanding the reasons for its presence is important for interpreting the preservational environment. The varying degrees of wear that can occur on Richards Spur material is demonstrated quite clearly by the reptile *Opisthodontosaurus carrolli*, as there are dentaries from several individuals (Fig. 6) that range from pristine elements that have little or no wear to those that are very heavily worn. The dentaries showing the least wear are complete elements that exhibit clearly defined foramina and sculpturing (Fig. 6A), while some dentaries are starting to show wear features but still retain structures such as foramina (Fig. 6B). Elements
that show heavy wear look considerably different, having lost finer details, with no obvious foramina or sculpturing apparent (Fig. 6C). Lastly, there are dentaries of *O. carrolli* that are so heavily worn that the only details that can be discerned are the remnants of the tooth sockets (Fig. 6D).

Variation in wear on skeletal elements is likely the result of several factors: how the animals entered into the caves, how long elements remained on the surface, the size of the elements, possible chemical processes, as well as how much they were moved around once in the cave system. The transport of elements via water, both on the surface and within the caves, and associated interactions with detrital grains during transport is likely the cause for most of the wear found on the bones obtained from the fissures. The type i and type ii samples (Table 2) provide evidence for this, as they exhibit the presence of various detrital minerals of various sizes. The elements of animals that died closer to the openings of the cave system or fell in to the caves would have had to travel less distance, reducing the amount of wear accumulated prior to entry into the system, and vice versa. Once in the caves, the sorting process that would be caused by the movement of meteoric water would have resulted in additional wear on transported elements. Together these processes likely account for the bulk of the wear found on many Richards Spur elements, and are consistent with the range of sediment sample types presented here (Table 2).

Aside from the wear visible on individual disarticulated elements, damage is apparent when looking at other material obtained from Richards Spur, in particular the clusters of detrital clay and mud-ball conglomerates that are associated with various disarticulated elements. Some of these clusters of bones exhibit breakage so extensive that details of elements are lost, leaving a conglomerate of featureless bone fragments (Fig. 4E). Thus, it is likely that in some cases the previously discussed processes were causing very intense damage. There are also clusters of bone that exhibit some wear, but for the most part elements are still identifiable (Fig. 4B, C).

Despite the abundant disarticulated material found at Richards Spur, it is apparent that there is also material that is articulated with little or no evidence of reworking (e.g. Polley and Reisz, 2011; MacDougall and Reisz, 2012, 2014). Wear due to attritional processes is most common on disarticulated elements and uncommon on more articulated specimens. This is likely the result of the previously discussed modes through which animal remains were introduced into the cave.
system. Animals that fell or were washed into the caves prior to being disarticulated would exhibit the least amount of wear because their skeletal elements were not initially exposed directly to the environment. In contrast, animals that died and became disarticulated outside of the caves and were then washed in would exhibit higher degrees of wear due to a combination of factors, like prolonged exposure and tumbling during water transport. Once in the caves, the water that would have transported the elements would also have caused deposited elements to be moved around within the confines of the cave system, resulting in further wear and damage. However, animals that were not initially disarticulated on the surface could have had much of their soft tissues still intact, making them less susceptible to disarticulation and displacement by the movement of water.

5.6 Conclusions

The Richards Spur locality provides a unique view of the Early Permian that is unavailable elsewhere, making it an extremely important asset in understanding the early stages of terrestrial vertebrate evolution. In order to integrate this locality with results from other Early Permian sites, a more thorough understanding of the taphonomy of the deposits has been required. The unique qualities of the locality are largely a result of its nature as an upland cave deposit and the distinct preservational environment associated with it. There are two distinct modes of preservation present at the locality. The first of these involves animals dying and becoming disarticulated on the surface and then being washed into the caves, resulting in the abundance of disarticulated material we find. The second mode of preservation involves partial or complete carcasses, or even live tetrapods, falling or being washed into the caves and becoming preserved, resulting in the articulated material found at the locality. Thus, the cave system found at Richards Spur can be interpreted as an unusual pitfall trap. Furthermore, many of the disarticulated elements exhibit varying levels of wear, indicating that transport and tumbling was an important taphonomic factor at the locality. This new understanding of the locality's preservational environment will affect how the immense taxonomic diversity found at Richards Spur is interpreted.
5.7 Acknowledgements

We would like to thank Diane Scott for the preparation of fossil material, the photographs found in the figures, and the drawings in figure 6. David Mazierski for the interpretive drawing of the caves in figure 2. Bill May and the OMNH for the loan of several specimens. We also thank Corwin Sullivan and another anonymous reviewer for their helpful reviews of the manuscript. This research was supported by a PGS-D scholarship from NSERC to MJM, and grants from NSERC Discovery and University of Toronto to RRR.

5.8 References


### 5.9 Tables and Table Captions

**Table 5.1.** Faunal list of described tetrapod taxa from the Lower Permian Richards Spur locality, Oklahoma, USA.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Reptilia</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Parareptilia</strong></td>
<td></td>
</tr>
<tr>
<td><em>Colobomycter pholeter</em> Vaughn, 1958</td>
<td></td>
</tr>
<tr>
<td><em>Delorhynchus priscus</em> Fox, 1962</td>
<td></td>
</tr>
<tr>
<td><em>Bolosaurus grandis</em> Reisz et al., 2002</td>
<td></td>
</tr>
<tr>
<td><em>Microleter mckinzieorum</em> Tsuji et al., 2010</td>
<td></td>
</tr>
<tr>
<td><em>Feeserpeton oklahomensis</em> MacDougall and Reisz, 2012</td>
<td></td>
</tr>
<tr>
<td><em>Delorhynchus cifellii</em> Reisz et al., 2014</td>
<td></td>
</tr>
<tr>
<td><em>Abyssomedon williamsi</em> MacDougall and Reisz, 2014</td>
<td></td>
</tr>
<tr>
<td><em>Colobomycter vaughni</em> MacDougall et al., 2016</td>
<td></td>
</tr>
<tr>
<td><strong>Captorhinomorpha</strong></td>
<td></td>
</tr>
<tr>
<td><em>Baeotherates fortsillensis</em> May and Cifelli, 1998</td>
<td></td>
</tr>
<tr>
<td><em>Captorhinus aguti</em> Cope, 1882</td>
<td></td>
</tr>
<tr>
<td><em>Captorhinus magnus</em> Kissel et al., 2002</td>
<td></td>
</tr>
<tr>
<td><em>Opisthodontosaurus carrolli</em> Reisz et al., 2015</td>
<td></td>
</tr>
<tr>
<td>Unnamed basal captorhinomorph (Reisz, 1980)</td>
<td></td>
</tr>
<tr>
<td>Unnamed basal captorhinid (Modesto, 1996)</td>
<td></td>
</tr>
</tbody>
</table>
Diapsida

Unnamed diapsid (Carroll, 1968)

*Orovenator mayorum* Reisz et al., 2011

Synapsida

Caseidae

*Oromycter dolesorum* Reisz, 2005

Varanopidae

*Mycterosaurus* sp. (Maddin et al., 2006)

*Varanops cf. V. brevirostris* Maddin et al., 2006

Sphenacodontidae

Unnamed sphenacodontid (Evans et al., 2009)

Anamniote tetrapods

Dissorophidae

*Doleserpeton annectens* Bolt, 1969

*Pasawioops mayi* Fröbisch and Reisz, 2008

*Cacops morrisi* Reisz et al., 2009

*Cacops woehri* Fröbisch and Reisz, 2012

*Tersomius dolesensis* Anderson and Bolt, 2013
Trematopidae

*Acheloma dunni* Polley and Reisz, 2011

Seymouriidae

*Seymouria* sp. (Sullivan and Reisz, 1999)

Aïstopoda

*Sillerpeton permianum* Lund, 1978

Diadectidae

Unnamed diadectid (Reisz and Sutherland, 2001)

Microsauria

*Euryodus dalyae* Carroll and Gaskill, 1978

*Cardiocephalus peabodyi* Carroll and Gaskill, 1978

*Llistrofus pricei* Carroll and Gaskill, 1978

*Bolterpeton carrolli* Anderson and Reisz, 2003

*Nannaroter mckinziei* Anderson et al., 2009
Table 5.2. Mineralogical and geochemical data from samples analyzed in this study.

<table>
<thead>
<tr>
<th>Sample</th>
<th>¹Type</th>
<th>²Mineralogy</th>
<th>³δ¹³C</th>
<th>³δ¹⁸O</th>
<th>Wt. % CaCO₃</th>
</tr>
</thead>
<tbody>
<tr>
<td>DQ1</td>
<td>iii</td>
<td>smectite, kaolinite, quartz, calcite</td>
<td>5.4</td>
<td>-4.2</td>
<td>24</td>
</tr>
<tr>
<td>DQ2</td>
<td>i</td>
<td>calcite</td>
<td>-7.8</td>
<td>-5.5</td>
<td>84</td>
</tr>
<tr>
<td>DQ3</td>
<td>ii</td>
<td>calcite, kaolinite, quartz</td>
<td>-7.1</td>
<td>-4.8</td>
<td>74</td>
</tr>
<tr>
<td>DQ4</td>
<td>ii</td>
<td>calcite, sulfides, quartz, kaolinite</td>
<td>-12.3</td>
<td>-3.8</td>
<td>60</td>
</tr>
<tr>
<td>DQ5</td>
<td>iii</td>
<td>smectite, kaolinite, quartz, calcite</td>
<td>9.2</td>
<td>-4.4</td>
<td>21</td>
</tr>
</tbody>
</table>

¹Types i, ii, iii are those described in the section “X-ray Diffraction Analysis of Cave Infill Sedimentary Rock” in this manuscript.

²Mineralogy is based upon macroscopic and magnified inspection of hand specimens as well X-ray diffraction of powders collected from the samples.

³δ¹³C and ³δ¹⁸O values are reported in per-mil units (‰) with respect to the standard V-PDB.
Table 5.3. Information regarding the fossil specimens that were examined in this study.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Taxon</th>
<th>Completeness</th>
<th>(^1\text{Size})</th>
<th>Figure</th>
</tr>
</thead>
<tbody>
<tr>
<td>OMHH 73361</td>
<td><em>Cardiocephalus</em></td>
<td>Articulated skull</td>
<td>28 mm</td>
<td>5</td>
</tr>
<tr>
<td>OMNH 73511</td>
<td><em>Cacops</em></td>
<td>Articulated skull and vertebral column, as well as various disarticulate elements</td>
<td>220 mm</td>
<td>4</td>
</tr>
<tr>
<td>OMNH 77667</td>
<td>Unknown reptile</td>
<td>Portion of an articulated vertebral column, as well as a few disarticulated postcranial elements</td>
<td>92 mm</td>
<td>4</td>
</tr>
<tr>
<td>OMNH 77668</td>
<td>Various animals</td>
<td>Numerous disarticulated cranial and postcranial elements</td>
<td>64 mm</td>
<td>4</td>
</tr>
<tr>
<td>OMNH 77669</td>
<td><em>Doloserpeton</em></td>
<td>Numerous disarticulated elements</td>
<td>55 mm</td>
<td>4</td>
</tr>
<tr>
<td>OMNH 77670</td>
<td>Unknown</td>
<td>Numerous heavily damaged bone fragments</td>
<td>65 mm</td>
<td>4</td>
</tr>
<tr>
<td>OMNH 77671</td>
<td><em>Captorhinus</em></td>
<td>Articulated skull and some disarticulated postcranial elements</td>
<td>110 mm</td>
<td>1</td>
</tr>
<tr>
<td>OMNH 77672</td>
<td>Various animals</td>
<td>Numerous disarticulated elements</td>
<td>85 mm</td>
<td>1</td>
</tr>
</tbody>
</table>

\(^1\text{Maximum length of calcite block in which specimens occur; or maximum length of specimen if specimen is not embedded in block.}\)
Figure 5.1. Examples of various speleothems obtained from the infill of the caves at the Richards Spur locality. A, speleothem that has grown through the skull of a captorhinid reptile.
(OMNH 77671). B, portion of a stalactite. C, cave popcorn, D, flowstone with associated fossil material (OMNH 77672).
Figure 5.2. The caves at the Richards Spur locality as they are found today. A, photograph of part of the quarry face at Richards Spur; B, interpretive drawing of the outlines of the cave remnants found in the quarry face.
**Figure 5.3.** Diagram showing proposed modes of deposition at the Richards Spur locality. **A,** depositional mode in which animals die outside the caves, become disarticulated due to predation and/or decomposition, and are then washed in; **B,** second depositional mode in which animals die outside the caves, and their corpses are washed in before major disarticulation can occur; **C,** part of the second depositional mode in which animals fall into the caves and become trapped, preventing major disarticulation.
Figure 5.4. Richards Spur fossil material showing varying degrees of articulation and wear.  
A, OMNH 73511, articulated skull and vertebral column of *Cacops*; B, OMNH 77667, portion of an articulated reptile vertebral column, exhibiting little wear; C, OMNH 77668, various disarticulated elements, most are identifiable and not heavily worn; D, OMNH 77669, high-density collection of worn disarticulated *Doleserpeton* skeletal elements; E, OMNH 77670, extremely high-density collection of bone fragments, heavy wear makes it impossible to identify any elements.
Figure 5.5. Example of the pyrite that is found on much of the fossil material obtained from the caves. A, pyrite found on the skull of the reptile Cardiocephalus (OMNH 73361); B, scanning electron microscope image of a pyrite crystal on a Captorhinus vertebrae.
Figure 5.6. Interpretive drawings showing different levels of wear on four dentaries of *Opisthodontosaurus carrolli*. A, dentary exhibiting very low levels of wear; B, dentary exhibiting intermediate levels of wear; C, dentary exhibiting heavy levels of wear; D, dentary exhibiting extreme levels of wear.
Chapter 6
Relative abundances of tetrapod taxa from the Early Permian Richards Spur locality, and their potential utility in palaeoecological reconstructions

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6.1. Abstract

Determining relative abundance of organisms in an ecosystem is crucial to understanding many aspects of community ecology, including predator prey interactions, potential trophic structures, and overall community structure. Similarly, looking at relative abundance in fossil assemblages is potentially useful for paleoecological interpretations, despite the inherent problems associated with preservational biases of the fossil record. While studies of relative abundance at fossil assemblages are not uncommon, there has been very little work of this kind done on continental Early Permian localities, during the initial stages of continental vertebrate evolution. Most studies of the Early Permian Richards Spur locality of Oklahoma have largely concentrated on describing new species and documenting the immense taxonomic diversity found there. Despite its richness, there has been no quantitative analytical work undertaken at Richards Spur. However, the distinct preservational environment associated with the caves system makes it uniquely suited for more quantitative studies of community ecology, due to the large amount of fossil material that is preserved there. In order to make improved inferences about the palaeoecology of the ancient ecosystem preserved at Richards Spur, a better understanding of aspects such as relative abundance of taxa is required. The study presented here analyzes the relative abundances of various tetrapods obtained from a large fossiliferous block that was retrieved from the caves at Richards Spur. This analysis has allowed for the first look at the relative abundances of tetrapods at the locality. Several tetrapod taxa were recovered from the block, notably numerous reptile and anamniote elements. Among reptile taxa Captorhinus was the most abundant taxon present in this sample, with the large majority of identifiable elements found belonging to it. The small amphibamid Doleserpeton was the most abundant anamniote, with its relative abundance almost matching that of Captorhinus. Interestingly, there were no identifiable synapsid elements recovered from the block. The results obtained from this sample appear to indicate that captorhinid reptiles and small amphibamids would have numerically dominated the locality, with larger tetrapod taxa being uncommon, similar to modern terrestrial ecosystems. Furthermore, based on this sample it seems that despite their taxonomic diversity at Richards Spur, parareptiles were rarer than eureptiles like Captorhinus. This new data also supports the hypothesis that the Richards Spur locality was distinct from contemporaneous lowland localities. The Richards Spur relative abundance data was also compared with similar
data obtained from the Early Permian Bromacker locality in Germany, highlighting the differences between the two upland assemblages.

6.2. Introduction

To gain a better understanding of both past and present ecosystems, in-depth knowledge of their constituent taxa is necessary (May, 1988). This knowledge includes details regarding the taxonomic diversity of a community, the abundances of individual taxa, as well as how the individual members of a community interact with one another (Vermeij and Herbert, 2004). Thus, it is no simple feat to make ecological inferences regarding an assemblage, especially with limited information.

Inferring palaeoecological details of a fossil assemblage is oftentimes fraught with difficulty, largely due to the incomplete nature of the fossil record and the large amounts of missing information regarding ancient ecosystems (Vermeij and Herbert, 2004). Furthermore, taphonomic biases at a locality can potentially obscure ecological information. Nonetheless, palaeontologists have increasingly recognized the importance and utility of studying the structure of fossil communities, using what fossil material is available (Vermeij and Herbert, 2004; Moore et al., 2007).

To obtain a real understanding of diversity within an ecosystem, it is necessary to look at the relative abundances of taxa, and not just at their presence or absence at a locality (May, 1988). It is clear that the nature of the fossil record, and the provenance of a particular assemblage needs to be kept in mind when measuring relative abundance (Vermeij and Herbert, 2004), but by combining overall taxonomic diversity data and relative abundance data with a good understanding of the taphonomy of a particular locality, it is possible to reconstruct some aspects of community structure (Behrensmeyer et al., 1979). Currently, there is very little in the way of studies that have looked at tetrapod relative abundance at Early Permian continental localities, the only major work done to date was that of Eberth et al. (2000), who discussed the relative abundances of taxa from the upland Bromacker locality of Germany. Historically, the majority of studies of relative abundance during the Permian concentrate on plant and invertebrate
communities during the Late Permian and End-Permian mass extinction event (Twitchett et al., 2001). Thus, there are considerable gaps in our knowledge regarding the diversity of Early Permian terrestrial tetrapod taxa. The Early Permian Richards Spur locality of Oklahoma, and the large amount of fossils found there, offers an opportunity to fill in some of these gaps.

The upland Richards Spur locality is distinct in many ways compared to its lowland equivalents (Sullivan and Reisz, 1999; Sullivan et al., 2000; MacDougall and Reisz, 2012), but the quality that is perhaps most useful for palaeoecological studies is the large amount of fossils that have been obtained from the caves at the locality. The large amount of fossil material, much of which is well preserved, is largely the result of the unique preservational environment associated with the cave system present at Richards Spur (chapter 5). With more than 30 taxa known from the locality (chapter 5, Table 5.1), and thousands of specimens, there is a large amount of material available to use for palaeoecological studies. Most notably, there are large calcite-clay blocks filled with disarticulated tetrapod material that have been occasionally retrieved from the caves at Richards Spur (Fig. 6.1). Although most of these blocks have been disarticulated and catalogued in various collections, some have been largely untouched and therefore not affected by sampling biases. Such blocks are very useful for palaeoecological analyses, and the sheer number of undisturbed elements in these blocks lend themselves to determining relative abundances of the numerous animals preserved within them.

However, even the rather ideal conditions of the Richards spur locality have problems that cannot be ignored. It is clear that the cave system found at Richards Spur represents a natural trap (Chapter 5), and there are likely taphonomic factors associated with it that will affect interpretations of relative abundance and potential structure of the tetrapod assemblage. For example, the disarticulated material from the aforementioned blocks of calcite clay would likely be exposed to some degree of transport and sorting, which will affect what elements would be preserved together. There are also numerous taxa from the locality that are only or largely known from skulls, thus we lack information regarding the postcrania of many taxa, making it difficult to confidently identify disarticulated all postcranial elements. These potential biases need to be taken into account when interpretations are made regarding the palaeoecology of the locality.

Here we present the first quantitative analysis of tetrapod relative abundance at the Richards Spur locality, in order to gain a better understanding of the large tetrapod diversity found at the
locality. Using this new data set, as well as combining what is known regarding the taxonomic diversity of the locality, we present new interpretations regarding the palaeoecology of the assemblage. The Richards Spur locality is also compared and contrasted with the Bromacker locality in Germany, as it is the only other well known upland Early Permian locality.

**Institutional Abbreviations**—OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA.

6.3. Material and Methods

6.3.1. Preparation of fossil material

The fossil material studied and analyzed here was prepared with the permission of the OMNH. All of the fossil specimens analyzed were obtained from a single large block of calcite rich clay that was collected from the Richards Spur locality. The fossil material was separated from the sediment in the block at the University of Toronto Mississauga by using a mixture of water and weak acetic acid. This mixture helped to break up and dissolve the soft calcite clay that surrounded the fossil material and other detritus, allowing for the disarticulated fossils to be separated and studied individually.

6.3.2. Analysis of relative abundance

After preparation of the block, the fossil material was sorted, identified where possible, and counted. Fossils were identified to the generic level when possible, but this was not always feasible due to our incomplete knowledge of many Richards Spur genera. Thus, fossil material was assigned to more inclusive taxonomic ranks when generic level identification was not possible. The main relative abundance metric used in this study was minimum number of individuals (MNI), however, number of identified specimens (NISP) was also determined for comparative purposes. Identified elements for each taxon were sorted into lefts and rights where applicable, and then the set of elements that was most numerous was used as the abundance
indicator for that taxon. The data set was compiled in Microsoft Excel and then imported into the statistical software program R to generate plots, which were then edited using Adobe Illustrator CS5. The full dataset of all identified elements can be found in appendix S6.1.

6.4. Results

The block produced 4250 elements that could be identified. The block largely consisted of reptile and anamniote remains, interestingly there were no elements in the block that could be confidently attributed to synapsids (Table 6.1), despite various synapsids being present at Richards Spur. Disarticulated vertebrae and ribs were by far the most common types of elements recovered from the block. However, they were largely ignored because they offer little useful information for calculating relative abundance. Except when they were the only type of element recovered for a taxon, as was the case for the aïstopod Listrofus. Among the identified reptilian material, remains of the captorhinid Captorhinus were exceedingly common, with large numbers of vertebrae, limb elements, and skull bones being present. Aside from Captorhinus, a few limb elements and vertebrae were determined to be parareptilian, but they could not be identified to the generic level. A few parasphenoids of a non-Captorhinus eureptile were also found. Much of the anamniote material obtained from the block belongs to the small amphibamid Doleserpeton, with numerous limb elements of the animal being found; microsaur material in the form of limbs, vertebrae, and jaw elements was also quite common. Fossil material of large anamniotes was also identified, notably an intercentrum of Acheloma, and various elements of Cacops. Several characteristic ribs of the aïstopod Listrofus were also found in the block. There were also various elements that clearly belonged to both small and large anamniotes but could not be confidently identified to a specific taxon; in most cases this was due to damage on the elements.

The results of the relative abundance analysis are summarized in figure 6.2 and table 6.1. The analysis revealed that the reptile Captorhinus was the most abundant tetrapod in the block (MNI=47), with its most abundant element being right articulars. The next most abundant animal was the anamniote Doleserpeton (MNI=36), with its most abundant element being right femora. Together these two taxa make up much of the abundance in the sample. For parareptiles no particular genera could be confidently identified, but several postcranial elements were clearly
present, with left humeri being the most abundant parareptilian element (MNI=8). Similarly, distinct microsaur genera could not be identified, but numerous microsaurian elements were found, the most abundant element being right radiuses (MNI=6). Other identified taxa had lower relative abundances (Fig 6.2). The results of the MNI analysis regarding which taxa were most abundant were confirmed using NISP methodology (Table 6.1), which resulted in a similar pattern of abundance.

6.5. Discussion

6.5.1. Palaeoecological interpretations of the Richards Spur locality using taxonomic diversity and relative abundance data

Taking what is currently known regarding the large taxonomic diversity at the Richards Spur locality and combining it with the relative abundance data presented here we can start to make several inferences regarding the palaeoecology of the locality.

Before any interpretations can be made, it is important to note that there are a few potential biases associated with the dataset that need to be taken into account. The first is that in this study only one large block from Richards Spur was sampled, the disarticulated material that was found throughout this block would have likely undergone some of the transport and sorting discussed in chapter 5. This could result in a slightly different distribution of elements than similar blocks from other parts of the cave. A second potential bias is that there is no stratigraphic control at the locality, due to the fossiliferous infill of the caves being left in waste piles after it is removed from the surrounding limestone. Thus, we do not know where exactly in the caves fossil material comes from, which means we do not know for certain if all of the taxa known from Richards Spur were living at the same time. Thus, is it possible that we are not seeing certain taxa in this sample due to changes in the faunal composition of the assemblage over time, a problem that is difficult to rectify given the nature of the Richards Spur locality. Future work will have to involve the study of other highly fossiliferous blocks from the locality, in order to determine if the patterns observed in this study are apparent throughout the locality.
It is quite obvious that the basal reptile *Captorhinus* is very common at Richards Spur (MNI=47), not only was it the most abundant tetrapod in the analyzed sample (Fig. 6.2), but a large majority of the identified elements belonged to the genus (Appendix S6.1). This is not unexpected, as it has been noted in several other studies that *Captorhinus* is one of the more common taxa found at Richards Spur (Fox and Bowman, 1966; Sullivan et al., 2000; Reisz et al., 2002), and captorhinids in general were very successful during the Permian (Sues and Reisz, 1998). The abundance of this reptile suggests that it was an important part of the ecosystem at Richards Spur, likely being one of the main predators at the assemblage. There was also another eureptile of unknown identity found in the block, though its abundance (MNI=4) was much lower than that of *Captorhinus*. Other eureptiles were likely not as prominent as *Captorhinus* at Richards Spur.

The sister taxon to Eureptilia, Parareptilia, is one of the more notable clades found at Richards Spur. As the locality exhibits a taxonomically diverse parareptilian component, with eight taxa being present (MacDougall et al., 2016), more than half of all known Early Permian parareptiles are found there. However, despite the clades taxonomic diversity at the locality, its determined relative abundance was low (MNI=8) in comparison to eureptiles like *Captorhinus*, suggesting that parareptiles were less common than eureptiles at Richards Spur (Fig. 6.2). All parareptiles known from Richard spur are small predatory forms (MacDougall et al., 2016; in press), which means that they likely would have been competing with the more common captorhinids for similar food sources. This competition may have contributed to the low abundance of parareptiles that was observed.

The most abundant anamniote from the locality was the small amphibamid *Doleserpeton* (Fig. 6.2), the relative abundance (MNI=36) coming in slightly below that of *Captorhinus*. *Doleserpeton* is one of the most commonly found tetrapods at the Richards Spur locality, with disarticulated remains of the taxon being often recovered from the caves (Bolt, 1969; Sigurdsen and Bolt, 2010), supporting the large relative abundance recorded from this block. *Doleserpeton* is one of the smallest tetrapods known from Richards Spur, being only a few centimeters long (Sigurdsen and Bolt, 2010). The small size of the taxon, combined with its high abundance at the locality would have likely made it a major prey source for many of the other taxa at Richards Spur. This conclusion is supported by the discovery of other, larger tetrapod specimens from the locality that show *Doleserpeton* remains in and around the jaws (pers. obs.).
Other anamniote taxa were not as abundant as *Doleserpeton* (Fig. 6.2), with microsaurs being the next most common anamniote (MNI=6). The larger anamniotes from Richards Spur had even lower abundances (Table 6.1), suggesting that the ecosystem at Richards Spur would have been dominated by smaller anamniotes.

Interestingly, there was no clearly identifiable synapsid material in the block (Fig. 6.2). Keeping in mind that there may be taphonomic biases at play, this still suggests that synapsids might be rare at Richards Spur, in contrast to the more common reptiles and anamniotes. There are currently only four described synapsids from Richards Spur, and of those four taxa there are few specimens known for each (Reisz, 2005; Maddin et al., 2006; Evans et al., 2009). This finding supports the idea that the group may have been a rare component of the ecosystem around Richards Spur, with most synapsids living in the Early Permian lowlands. Furthermore, the two known varanopids from the locality would have been some of the largest tetrapods there (Maddin et al., 2006; Evans et al., 2009). As larger predatory taxa, they would have likely preyed upon many of the other tetrapods at the locality, making them some of the top predators in the community found at Richards Spur.

With regards to synapsids, Richards Spur has long been notable for lacking many of the larger synapsid taxa that dominate many Early Permian lowland localities. The apparent absence of larger synapsid taxa is part of the reason Richards Spur is considered to be an upland locality (Sullivan et al., 2000; MacDougall and Reisz, 2012). With the more in-depth understanding of the preservational environment of Richards Spur presented in chapter 5, we can be quite confident that very large synapsid taxa are absent from the locality, as none of their readily identifiable, smaller isolated skeletal elements have been recovered from the large amount of disarticulated material that has been retrieved from the caves at Richards Spur. This suggests that only small to medium sized synapsid taxa would have been present at the locality (Reisz, 2005; Maddin et al., 2006; Evans et al., 2009), with their larger relatives dominating the Early Permian lowlands.

The high relative abundances for both *Captorhinus* and *Doleserpeton* support the hypothesis that smaller taxa would have been numerically dominant at Richards Spur, as is the case in modern terrestrial ecosystems (Elton, 1927; Woodward et al., 2005). The numerical dominance of smaller taxa is something that likely extends to Early Permian lowland localities, however it is
not typically observed with fossils of larger taxa being more common. This lack of smaller taxa is likely the result of taphonomic biases that are associated with deltaic/fluvial systems, which tend to obscure details regarding the true diversity of an ecosystem (Behrensmeyer et al., 1979).

6.5.2. Absences of Richards Spur taxa from the analyzed sample

As has been mentioned, there were several taxa absent from the sample that are known to be present at the Richards Spur locality, most notably synapsid taxa. The fossiliferous calcite block that was used for the analysis was originally found prior to the year 2000. Since then numerous other similar blocks have been obtained from different parts of the caves at Richards Spur. Unfortunately many of these blocks were broken down without any analyses of relative abundance being conducted, and the fossils that were within them are now accessioned at various institutions. However, many of these blocks contained taxa that were not found in the block analyzed for this study, suggesting that these differences in composition are the result of taphonomic biases.

While there were no synapsid taxa identifiable in the block used for this study, there are varanopid (Maddin et al., 2006), caseid (Reisz, 2005), and sphenacodontid (Evans et al., 2009) taxa known from the Richards Spur locality. Overall, synapsid material is relatively rare at the locality compared to some of the reptilian and anamniote taxa. Varanopids are known from a few braincases, vertebral material, and semi articulated limbs (Maddin et al., 2006; pers. obs.). Caseids are known from various disarticulated skull elements, vertebrae, and some phalanges (Reisz, 2005). Sphenacodontid material is even rarer, currently consisting of some teeth, a vertebra, and a neural spine (Evans et al., 2009; pers. obs.).

Aside from synapsids, there were other tetrapods that were absent from the sample. For example, the stem amniote Seymouria, a taxon currently known from various limb elements and vertebrae (Sullivan and Reisz, 1999) was not preserved in the sample. Some of the unidentified anamniote limb elements may belong to these taxa, although without more information it is difficult to assign them a specific taxon. The aëtopod Sillerpeton was absent as well, though this is not
surprising, as material of it is very rare, being known only from a string of vertebrae and one braincase (Lund, 1978; Anderson, 2002).

The absence of fossils of these various taxa in the studied block is most likely the result of the preservational environment associated with the cave system at Richards Spur (Chapter 5). While larger taxa such as synapsids were not found in the block analyzed here, other calcite blocks from the locality have been found containing such material; it is probable that fossil sorting is the result of what is being observed. As indicated in chapter 5, transport by water and sorting of elements would have been occurring within the caves at Richards Spur, thus the absence of large taxa within the block was likely the result of sorting by the flow of water within the caves. In the case of this particular block, larger taxa and elements would have been deposited in other parts of the cave, while smaller elements would travel farther within the caves before settling out.

6.5.3. Comparisons with the Bromacker locality of Germany

The Bromacker locality in Thuringia, Germany is the only other terrestrial Early Permian locality where any attempt at calculating relative abundances of taxa has been undertaken (Eberth et al., 2000). Despite being one of the few other upland localities known from the Early Permian, Bromacker is dramatically different from Richards Spur in two main regards. Firstly, the taxonomic diversity at Bromacker is much lower than that of Richard Spur, with only 13 tetrapod taxa being known from the locality (Berman et al., 2000a, 2000b, 2001, 2004, 2011, 2014; Eberth et al., 2000; Martens et al., 2005; Reisz, 2005; Müller et al., 2006; Anderson et al., 2008), although numerous plant fossils and ichnofossils are preserved (Haubold, 1998). Secondly, Bromacker exhibits a preservational environment that is very different from the limestone cave system at Richards Spur, as the palaeoenvironment of the locality is considered to represent a small internally drained basin, in which flooding was common (Eberth et al., 2000). However, Bromacker is similar to Richards Spur in that it lacks fully aquatic taxa, such as fish and certain anamniotes (Eberth et al., 2000; Martens et al., 2005).

For the purposes of their study Eberth et al. (2000) used all of the specimens that had been obtained during the prior 25 years to calculate relative abundance, an approach referred to as total number of identified specimens (NISP). Updated relative abundance data for the entire
Bromacker locality using NISP can be found in table 6.2. It is important to note that this methodology is different from what we have used to determine relative abundance at the Richards Spur locality. With disarticulated material included, there are at minimum tens of thousands of specimens known from Richards Spur spread across numerous institutions, which would make it an incredibly arduous task to calculate relative abundance of the entire locality in a similar manner to Eberth et al. (2000). We did however calculate NISP for the analyzed block for comparative purposes. Bromacker has a much lower taxonomic diversity then Richards Spur, and significantly less fossil material, making the approach used by Eberth et al. (2000) actually feasible. Despite the differences in methodology it is still worth comparing the relative abundances from these two localities, in order to identify potential palaeoecological differences between them.

Richards Spur has an obviously wider array of known taxa than the Bromacker locality. However, the differences in relative abundances further suggest very different Early Permian upland ecosystems. The most notable feature of Bromacker is the abundance of diadectids found there. Between the two known genera *Diadectes absitus* and *Orobates pabsti* (formerly known as *Diadectes* sp.) there are 11 distinct diadectid specimens reported from Bromacker, making diadectids the most common tetrapod taxon found at the locality (Eberth et al., 2000; Berman et al., 2004). In contrast, in the sample analyzed from Richards Spur it was determined that there was only a single individual of an unidentified diadectid present (Fig. 6.2). This leads to the obvious conclusion that diadectids were much rarer at Richards Spur than Bromacker, and this interpretation is also supported by the fact that only known diadectid specimens from Richard Spur were recovered from an unusual part of the quarry (Reisz and Sutherland, 2001). Permo-Carboniferous diadectids, such as those found at Richards Spur and Bromacker, are some of the earliest herbivores (Hotton et al., 1997; Reisz and Sutherland, 2001), and this may suggest these early herbivores played a bigger role in the ancient ecosystem of Bromacker than that of Richards Spur. This could perhaps be related to differences in the amount of plant material present at the localities, but unfortunately this is currently impossible to confirm due to the lack of plant fossils at Richards Spur.

The second most common anamniote from Bromacker is the seymouriid *Seymouria*, of which there are four known specimens (Berman et al., 2000a; Eberth et al., 2000). *Seymouria* is also present at Richards Spur (Sullivan and Reisz, 1999), though material is relatively rare, with
recently discovered partial skulls, a few articulated strings of vertebrae, and some limb bones being known (pers. obs.). Unfortunately, there were no identifiable seymouriid remains found in the block used for this study. There were several larger anamniote limb elements that could potentially have belonged to *Seymouria* (Fig. 6.2), but they were too damaged to make a confident attribution to a more exclusive taxon.

Regarding smaller anamniote taxa, the small amphibamid *Doleserpeton* is very abundant at Richard Spur, while microsaurs were not quite as abundant but were clearly a significant presence at this locality (Table 6.1). However, very few smaller taxa are known from Bromacker, all that is currently known are four dissorophoid taxa (Table 6.2), most of which are known from a single specimen, the exception being an unnamed dissorophoid known from two specimens. There is also one specimen of what might be a microsaur (Eberth et al., 2000). This suggests that smaller anamniotes may not have been abundant at Bromacker, but it could also be the result of Bromacker’s preservational environment not being conducive to the preservation of smaller taxa.

Moving on from the anamniotes of these two localities, we also see some interesting contrasts regarding the relative abundances of amniotes. There are currently no known captorhinid eureptiles known from Bromacker, which is a stark contrast to Richards Spur where they make up a large percentage of identified taxa (Fig. 6.2). Once again, this suggests that Bromacker represents a very different type of upland locality from Richards Spur. Eureptile presence at Bromacker consists solely of the basal reptile *Thuringothyris* (Müller et al., 2006), of which there are five known specimens, essentially matching the determined non-captorhinid eureptile abundance in the single sampled block from Richards Spur (MNI=4).

There is a single species of parareptile known from the Bromacker locality, the facultatively bipedal bolosaurid *Eudibamus cursoris*, which is known from one described specimen (Berman et al., 2000b), and partial skeleton of a second, undescribed specimen (pers. obs.). Based on our analysis, parareptiles were determined to be more abundant at Richards Spur (MNI=8). Parareptiles are also much more taxonomically diverse at Richards Spur (MacDougall et al., 2016), where there is also a bolosaurid (Reisz et al., 2002), a nyctiphruretid (MacDougall and Reisz, 2014), and several lanthanosuchoids (MacDougall et al., 2016), which appears to indicate taxic diversity at Bromacker is lower than at Richards Spur.
There are at least three distinct synapsids known from the Bromacker locality (Berman et al., 2000b, 2001, 2014; Eberth et al., 2000). However, as has been mentioned previously, there were no identifiable synapsid elements recovered from the Richards Spur block, despite there being synapsids known from the locality. Even with the lack of synapsid taxa in the analyzed sample, it is still worth discussing the similarities between synapsids known from both localities. Bromacker and Richards Spur exhibit similar synapsid faunas, which is in contrast to the very different anamniote and reptile components of the two localities. Of the three synapsids known from Bromacker there is a caseid (Berman et al., 2000), a varanopid (Berman et al., 2014), and a sphenacodontid (Berman et al., 2001). Similarly, there are only four synapsids described from Richards Spur; a single caseid (Reisz, 2005), two varanopids (Maddin et al., 2006), and a single sphenacodontid (Evans et al., 2009). Thus, the synapsid components of both localities are taxonomically similar, both currently consisting of caseid, sphenacodontid, and varanopid taxa. This suggests, that despite numerous differences between the two localities, they appear to have had very similar synapsid faunas.

6.6. Conclusions

Determining the relative abundances of taxa at locality is an important step in gaining a better understanding of the diversity and palaeoecology at a fossil assemblage. Using a large calcite block of disarticulated fossil material from the caves at the Richards Spur locality allowed for relative abundance at the locality to be sampled for the first time. While this sample was likely affected to some degree by taphonomic biases associated with Richards Spur’s unique preservational environment, the data obtained from it allowed for palaeoecological inferences to be made. The results of the analysis revealed that the captorhinid Captorhinus and the amphibamid Doleserpeton were by far the most common tetrapods in the sample, indicating their prominence in the ancient ecosystem captured at Richards Spur. The absence of certain taxa, notably synapsids, from the studied block was most likely the result of taphonomic sorting in the cave system of the locality. This new abundance data, combined with the current known taxonomic diversity of tetrapods at Richards Spur, allowed for detailed discussions of the palaeoecology of the locality, and supports the hypothesis that localities during the Early Permian would have been dominated by smaller taxa, as is the case in typical modern terrestrial
ecosystems. Furthermore, the relative abundances of Richards Spur taxa were compared with those from the contemporaneous upland locality of Bromacker, Germany, revealing that despite being the only known Early Permian upland localities, they appear to have had significantly different faunal communities.

6.7. Acknowledgments

We would like to thank the OMNH for the loan of the material used in this study, specifically the large calcite block that was sampled. We also thank Corwin Sullivan for performing the early work that eventually became this project, as well as for useful discourse on the subjects presented here. We further thank Tooba Meer for performing preliminary work that was later expanded upon. Support for this project came from a Natural Sciences and Engineering Research Council of Canada doctoral student scholarship (PGSD) to MJ MacDougall and a Natural Sciences and Engineering Research Council of Canada Discovery Grant to RR Reisz.

6.8. References


Fox, R. C., and M. C. Bowman. 1966. Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). The University of Kansas Paleontological Contributions. Vertebrata 11:1–79.


6.9. Tables and Table Captions

**Table 6.1.** Tetrapod taxa identified from the calcite block obtained from the cave system at the Richards Spur locality, as well as their relative abundances, measured using the metrics minimum number of individuals (MNI) and total number of identified specimens (NISP).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>MNI</th>
<th>NISP</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Captorhinus</em></td>
<td>47</td>
<td>2777</td>
</tr>
<tr>
<td><em>Cacops</em></td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>Large anamniote of unknown identity</td>
<td>4</td>
<td>13</td>
</tr>
<tr>
<td>Diadectidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Achseloma</em></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Microsaur</em></td>
<td>6</td>
<td>70</td>
</tr>
<tr>
<td>Small anamniote of unknown identity</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td><em>Listrofus</em></td>
<td>1</td>
<td>24</td>
</tr>
<tr>
<td><em>Doleserpeton</em></td>
<td>36</td>
<td>94</td>
</tr>
<tr>
<td>Parareptilia</td>
<td>8</td>
<td>37</td>
</tr>
<tr>
<td>Eureptilia (not <em>Captorhinus</em>)</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td><strong>Total number of distinct individuals</strong></td>
<td>111</td>
<td>3040</td>
</tr>
</tbody>
</table>
Table 6.2. Updated list of known tetrapod taxa from the Bromacker locality of Germany and their relative abundances. Relative abundances are based on total number of identified specimens (NISP) from the locality that have been published in the literature, as per Eberth et al. (2000).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>NISP</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Orobates</em> (diadectid)</td>
<td>4</td>
</tr>
<tr>
<td><em>Diadectes</em> (diadectid)</td>
<td>7</td>
</tr>
<tr>
<td><em>Seymouria</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Rotaryus</em> (dissorophoid)</td>
<td>1</td>
</tr>
<tr>
<td><em>Tambachia</em> (dissorophoid)</td>
<td>1</td>
</tr>
<tr>
<td><em>Georgenthalia</em> (dissorophoid)</td>
<td>1</td>
</tr>
<tr>
<td>Unnamed (dissorophoid)</td>
<td>2</td>
</tr>
<tr>
<td>Possible microsaur</td>
<td>1</td>
</tr>
<tr>
<td><em>Eudibamus</em> (parareptile)</td>
<td>1</td>
</tr>
<tr>
<td><em>Thuringothyris</em> (eureptile)</td>
<td>5</td>
</tr>
<tr>
<td><em>Tambacarnifex</em> (synapsid)</td>
<td>2</td>
</tr>
<tr>
<td><em>Dimetrodon</em> (synapsid)</td>
<td>1</td>
</tr>
<tr>
<td>Unnamed caseid (synapsid)</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total number of distinct individuals</strong></td>
<td><strong>31</strong></td>
</tr>
</tbody>
</table>
6.10. Figures and Figure Captions

Figure 6.1. Photograph of one of the large fossiliferous calcite blocks that are retrieved from the caves at the Richards Spur locality. A similar block was used for the analysis of relative abundance conducted in this study.
Figure 6.2. Bar graph indicating the percent relative abundances of all the tetrapod taxa identified from the large calcite block that was analyzed for this study. Based on the results of the minimum number of individuals (MNI) analysis.
6.11 Appendices

Appendix S6.1. The complete data set obtained from the large calcite block that was sampled and used in the analysis of relative abundance. It includes identified taxa and elements, total number of each element, total number of left and right elements when applicable, and the calculated MNI for each element. The sample size was 4250 identifiable elements.

<table>
<thead>
<tr>
<th>Element</th>
<th>Number</th>
<th>Rights</th>
<th>Lefts</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phalanges</td>
<td>638</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Unguals</td>
<td>42</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Captorhinus.postorbitals</td>
<td>17</td>
<td>13</td>
<td>4</td>
<td>13</td>
</tr>
<tr>
<td>C.postfrontals</td>
<td>10</td>
<td>1</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>C.prefrontals</td>
<td>5</td>
<td>1</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>C.jugals</td>
<td>25</td>
<td>12</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>C.maxillae</td>
<td>73</td>
<td>41</td>
<td>32</td>
<td>41</td>
</tr>
<tr>
<td>C.premaxillae</td>
<td>29</td>
<td>14</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>C.frontals</td>
<td>18</td>
<td>8</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>C.lacriminals</td>
<td>22</td>
<td>10</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>C.nasals</td>
<td>8</td>
<td>2</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>C.parietals</td>
<td>11</td>
<td>5</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>C.quadrates</td>
<td>25</td>
<td>11</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>C.quadratojugals</td>
<td>3</td>
<td>2</td>
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<td>2</td>
</tr>
<tr>
<td>C.squamosals</td>
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Chapter 7
Summary and conclusions
As a period in Earth's history when terrestrial vertebrate evolution was still in its initial stages, the Early Permian represents an important window into the humble beginnings of modern ecosystems (Sues and Reisz, 1998). Our current knowledge of Early Permian terrestrial tetrapods largely comes from the work that has been done on the lowland deltaic/fluvial localities that are found throughout southwestern USA (Case, 1915; Olson, 1967; Sander, 1989). The Early Permian Richards Spur locality in Oklahoma, USA, offers a unique opportunity to expand our knowledge of the Early Permian, as it offers a distinct view of this time period that is not available elsewhere (Sullivan et al., 2000; MacDougall and Reisz, 2012). Most studies of the Early Permian Richards Spur locality have largely concentrated on the anatomy, taxonomy, and taxic diversity of the constituent fauna, largely ignoring other aspects of the locality, such as taphonomy, palaeoecology, and community structure, resulting in a significant gap in our knowledge of the unique fossil assemblage found there. Richards Spur represents one of the two known upland localities of the Early Permian (Sullivan and Reisz, 1999; Sullivan et al., 2000), making a comprehensive study of its fauna and depositional environment critical to any study of the Early Permian terrestrial vertebrate community, and its evolution. An improved understanding of Richards Spur from paleontological, geological, and biological perspectives will undoubtedly lead to a better, more integrated view of terrestrial vertebrate evolution during the Early Permian.

Two main problems of the Early Permian are addressed in my thesis; the first is our poor understanding of the initial stages of parareptilian evolution. The second problem is the lack of knowledge regarding many aspects of the Richards Spur locality, the most productive upland locality of the Early Permian. Throughout this thesis I have added to our knowledge of the Richards Spur locality in order to better interpret its distinctive Early Permian faunal assemblage, and integrate it with some of the better studied terrestrial lowland localities of the Early Permian.

In chapters two through four I contributed to the taxonomic diversity of the Richards Spur locality, and have updated our knowledge of the taxonomy and evolution of the clade Parareptilia during the Early Permian. I described three new parareptiles from the locality: the lanthanosuchoids *Feeserpeton oklahomensis* and *Colobomycter vaughni*, and the nyctiphruretid *Abyssomedon williamsi*. New material of the enigmatic *Colobomycter pholeret* was also described. The information obtained from this new material resulted in an enhanced and updated phylogenetic analysis of Parareptilia, which facilitated discussions regarding the Early Permian
evolution and diversification of the clade. Furthermore, through histological examination of the teeth of several parareptiles, I showcased the variability of folded dentine within Parareptilia, indicating a likely functional usage for it within parareptiles, as well as how its usage as a phylogenetic character was problematic.

There has been very little non-taxonomic work done at the Richards Spur locality, including little or no taphonomic and palaeoecological studies, two research approaches and endeavors that are very important for understanding and interpreting the diversity found at any fossil assemblage. In chapter five I used palaeontological, geological, and geochemical data to reconstruct the preservational environment associated with the cave system that is present at Richards Spur, and determined what taphonomic modes produced the abundant fossil material present at the locality. The nature of the fossil material, combined with geochemical analysis, shows that there are likely two main modes through which fossil material became preserved at Richards Spur. The first suggests that the abundant disarticulated material present at the locality is the result of animals dying on the surface and being thoroughly disarticulated by predators and scavengers, before eventually being washed in by the monsoonal rains that would have been present in the region, as indicated by speleothems and isotope data. The second suggests that the more articulated material found at the locality is the result of animals falling, or being washed, into the caves before they could become disarticulated on the surface. Once animal remains entered into the caves they would have been subject to transport and sorting by water, especially disarticulated material. This new understanding of the preservational environment that is found at Richards Spur, gives us important context for interpreting the large taxonomic diversity of the locality.

Lastly, in order to start rectifying the lack of palaeoecological studies at Richards Spur, in chapter six I performed the first analysis of relative abundance at the locality. The abundance of fossil material at the locality makes it well suited for this type of study, especially the large fossiliferous blocks that are obtained from the caves. This analysis reveals that the reptile Captorhinus and the anamniote Doleserpeton represent the large majority of the tetrapod abundance in the analyzed sample. Other taxa are not quite as common, notably synapsid taxa, which is probably the result of size sorting of this particular sample by water within the cave system. Using this new relative abundance data and the known taxonomic diversity of the locality, several palaeoecological interpretations were made regarding the tetrapod fauna found
there. The analysis also provided evidence that smaller taxa were numerically dominant at Richards Spur, as in modern terrestrial ecosystems. This pattern are likely applicable to Early Permian lowland assemblages as well, but the preservational environment and taphonomic biases of these sites probably obscure this trend. The Richards Spur locality is also compared and contrasted with the Bromacker locality in Germany, one of the other upland localities of the Early Permian, underscoring just how different these two localities are.

Overall, my thesis showed that parareptiles were a taxonomically diverse component of the Richards Spur assemblage, having a much higher diversity during the Early Permian than previously known. Furthermore, my thesis illustrated the importance of the Richards Spur locality as a rich, taphonomically and palaeoecologically complex system that has yielded valuable new insights into the composition of this upland faunal assemblage. This updated view of Richards Spur allows us to better integrate this unique locality with the more common lowland localities of the Early Permian, enhancing our understanding of this period and the initial stages of terrestrial vertebrate evolution.

7.1. References


