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REDESCRIPTION AND PHYLOGENETIC ANALYSIS OF THE MATERIALS ASSIGNED TO THE TAXON "CAPTORHINIKOS" CHOZAENSIS

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MATERIALS ASSIGNED TO THE TAXON

"*CAPTORHINIKOS*" *CHOZAENSIS*

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A Thesis

Presented to the

Faculty of

California State University,

San Bernardino

————————————————

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Biology

————————————————

by

Jason Paul Jung

March 2018

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Approved by:

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ABSTRACT

"Captorhinikos" chozaensis is a multiple-tooth-rowed captorhinid reptile from the Lower Permian Clear Fork Group, undivided formation. Upon re-examination of the materials associated with the species from both the Chicago Field Museum of Natural History, and the Smithsonian United States National Museum, I reaffirm their affinity and collective identity as a valid taxon. *"Captorhinikos" chozaensis* does not, however, belong with either of the two members of its genus, *C. valensis* or *"C." parvus*, instead occupying its own branch on the phylogenetic tree of the Captorhinidae. This conclusion is based in strong results from a combined phylogenetic parsimony analysis combined with an analytical apomorphy analysis. I then conclude the current designation *"Captorhinikos" chozaensis* to be a nomen ambiguum.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER ONE

INTRODUCTION

The Captorhinidae is a family of basal eureptiles ranging in age from the latest Carboniferous through the late Permian, (Müller and Reisz, 2006) and enjoyed a nearly global distribution by the middle Permian, with specimens from North America, Europe, Africa, and Asia (Modesto et al., 2007; Reisz et al., 2011). Members of the family ranged from faunivorous to herbivorous (Reisz et al., 2011). The family has been considered an important model organism for the study of basal eureptilian evolution owing to three factors: its generalized, conservative body morphology, its long and widely distributed record, and its important place as a component in first terrestrial paleoecological systems (Olson, 1952). Because the family possesses a post-cranium with little modification from earlier taxa, e.g. short stylopodia and zeugopodia, robust and dorsoventrall expanded ribs, spindle-shaped vetebral centra, and strongly anteriorly and posteriorly projecting zygophyses), the family has long thought to represent a good example of a conservative, little derived, terrestrial vertebrate. More recent interpretations of the family, however, suggest the Captorhinidae may not have been as morphologically conservative as was previously thought, but rather exhibited more derived and diverse morphologies (Sumida et al., 2010; Reisz et al., 2011).

Some members of the Captorhinidae represent amongst the earliest examples of terrestrial vertebrate herbivory (Hotton et al., 1997; Reisz and Sues, 2000). This has been suggested because a number of derived members of the family had multiple rows of maxillary and dentary teeth (between three and six rows), which would have facilitated oral processing of plant matter before ingestion and to increase the efficiency of digestion of nutrient-poor plant material (Hotton et al., 1997). More interestingly, multiple rows of teeth appear to have evolved at least twice, and possibly three times in the Captorhinidae (Dodick and Modesto, 1995). Classically, it was hypothesized the most derived species of the Captorhinidae were those with multiple rows of teeth. Early phylogenetic analyses grouped them into a sub-family called the Moradisaurinae (de Riqlès and Taquet, 1984). However, since the establishment of the Moradisaurinae, numerous phylogenetic analyses (Reisz et al., 2015; Modesto et al., 2014) have recovered multiple tooth rowed taxa in positions outside the Moradisaurinae. "*Captorhinikos*" *chozaensis* is one of those species, and although it possesses multiple tooth rows, recovered relationships based on the rest of its anatomy has recently and consistently placed it outside the Moradisaurinae, as the sister taxon to Labidosaurus + Moradisaurinae (Modesto et al., 2014; Reisz et al., 2011; Reisz et al., 2015).

Although *"Captorhinikos" chozaensis* has been included in the most recent studies of the members of the Captorhinidae, the character states used to score

it for phylogenetic analysis were restricted to the only available description before this study: Olson's (1954) original description of the genus. His description was a cursory examination of the species holotype accompanied by a simple line drawing of the holotypic mandibles, and an associated humerus, radius, and tibia (Olson, 1954). Since the publication of that description, several more species belonging to the Captorhinidae have been discovered and the use of computer-aided phylogenetic analysis has become both commonplace and standard practice. More comprehensive and detailed descriptions may now be made, allowing for a more confident hypothesis of phylogenetic relationships. Here *"Captorhinikos" chozaensis* is re-examined and described in detail to facilitate comparison with other members of the family and to provide updated character states for phylogenetic analysis.

Institutional Abbreviations

FMNH, Field Museum of Natural History, Chicago, Illinois; **USNM**, United States National Museum, Washington, D.C.

Anatomical Abbreivations

a, angular; **ar**, articular; **as**, astragalus; **beo**, basiexoccipital; **c**, coronoid; **ca**, calcaneum; **ce**, centrale; **cl**, clavicle; **d**, dentary; **ec**, ectopterygoid; **f**, frontal; **fe**, femur; **fm**, foramen magnum; **h**, humerus; **ic**, interclavicle; **ice**, intercentrum; **j,** jugal; **l**, lacrimal; **m**, maxilla; **mf**, Meckelian Foramen; **mt**, metatarsal; **n**, nasal; **o**, opisthotic; **pa**, palatine; **pbs**, parabasisphenoid; **pf**, postfrontal; **pm**,

premaxilla; **po**, postorbital; **pra**, prearticular; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **r**, rib; **ra**, radius; **s**, stapes; **sa**, surangular; **sc**, scapulocoracoid; **so**, supraoccipital; **sp**, spenial; **sq**, squamosal; **t**, tibia; **u**, ulna; **v**, vertebra.

CHAPTER TWO

MATERIALS AND METHODS

All of the specimens used in this study had been previously prepared.
Where additional preparation was required, pin vises were employed for removal
of matrix. Specimens were photographed with a Canon 5D digital SLR camera
and the images imported into Photoshop (Adobe Creative Suite 6) for
postprocessing (e.g. cropping, removal of background) and illustration.

Phylogenetic analysis was performed using a newly constructed data
matrix, drawing from several published sources (Reisz et al., 2015; Modesto et
al., 2014; Reisz et al., 2011; Sumida et al., 2010; Dodick and Modesto, 1995;
Berman and Reisz, 1986) and de novo observations. The newly reworked data
matrix is summarized in Appendix 2. The phylogenetic analysis was performed
with TNT (Goloboff et al., 2005). The TNT analysis was performed with
parsimony as the optimality criterion and a tree-bisection-reconnection search.
The strengths of the resulting clades were analysed with bootstrap analysis and
synapomorphy analysis. All characters in the phylogenetic analysis were
unordered and unweighted.

Stratigraphic Note

Historically the Lower Permian Clear Fork Group of north central Texas
was divided into three formations: the Arroyo, Vale, and Choza (Plummer and

Moore, 1921; Romer, 1973). However in a thorough geological restudy of the stratigraphy of Lower Permian strata in north central Texas, Hentz (1988 and 1989) concluded there was no compelling structural or stratigraphic evidence supporting such a division of the group. However, Plummer and Moore's (1921) system as adopted by Romer (1973) and others has persisted in the literature despite Hentz' compelling arguments. Hentz' (1988, 1989) recommendations are followed here, but the equivalents to the older scheme are included parenthetically to facilitate comparison to other studies and as a key to older locality data and records. Hook (1989) provided a useful tabular comparison of classic north-central Texas localities and his system is employed here.

CHAPTER THREE

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

CAPTORHINIDAE Case, 1911

CAPTORHINIKOS CHOZAENSIS Olson, 1954

Holotype

FMNH UR 97, right and left dentaries, a left maxillary fragment, and unknown bone fragment.

Referred Specimens

FMNH UR 98, vertebral fragments; FMNH UR 100, humerus, radius, a vertebral impression, and several bone fragments; FMNH UR 183, a partial skull; FMNH UR 857, partial skull and ventral post cranial elements; FMNH UR 859, a partial vertebral column and hind leg; USNM V21275, a partial skull, nine vertebrae, femur, tibia, and several postcranial fragments. Three specimens, FMNH UR 99 (bone fragments). FMNH UR 239 (bone fragments), and FMNH UR 858 (fragmentary postcranial elements) were not included in this study because their poor preservation rendered them uninformative. Locality and Horizon

FMNH UR 97, UR 98, UR 99, UR 100, UR 183, and UR 239 are all from the Clear Fork Group, undivided, "FA Site", Foard County, Texas, United States. FMNH UR 857, UR 858, UR 859, and USNM V21275 are all from the Hennessey formation, Cleaveland County, Oklahoma, United States.

CHAPTER FOUR

DESCRIPTION

Skull Roof

Of all the specimens used in this study, only FMNH UR 183 (Figs. 10-13), USNM V21275 (Fig. 3), and part of FMNH UR 97 (Figs. 6-9) retain useful anatomical information on the dermal skull roof. These specimens all suffer from some degree of incompleteness, damage, or moderate to severe deformation. FMNH UR 97 and UR 857 (Figure 5) appear to preserve bone fragments that may be from the skull roof, but their relationship to the skull roof as a whole cannot be confidently determined. All elements in the skull roof exhibit pitting or grooving, lending a sculptured appearance to its entirety. Of the dermal skull roof region, parts of the premaxilla, nasal, lacrimal, maxilla, prefrontal, frontal, jugal, postfrontal, postorbital, squamosal, quadratojugal, and quadrate are available for study, where as the parietals and postparietals are not visible in any of the specimens examined.
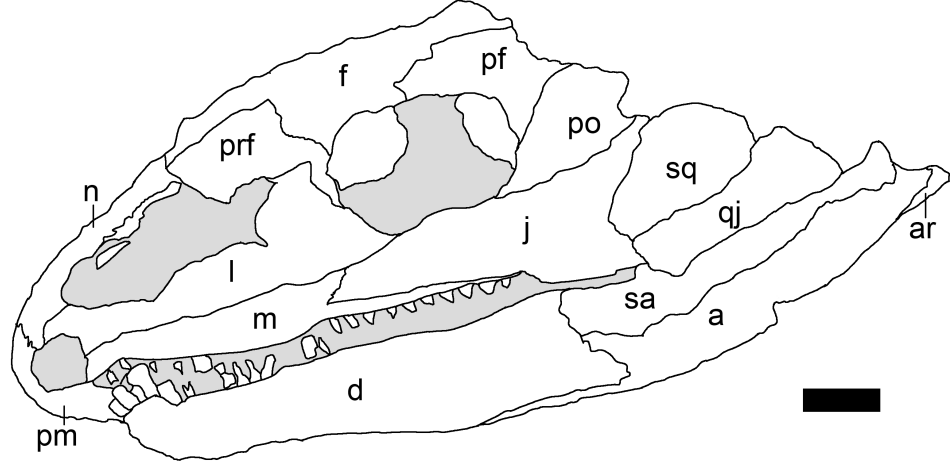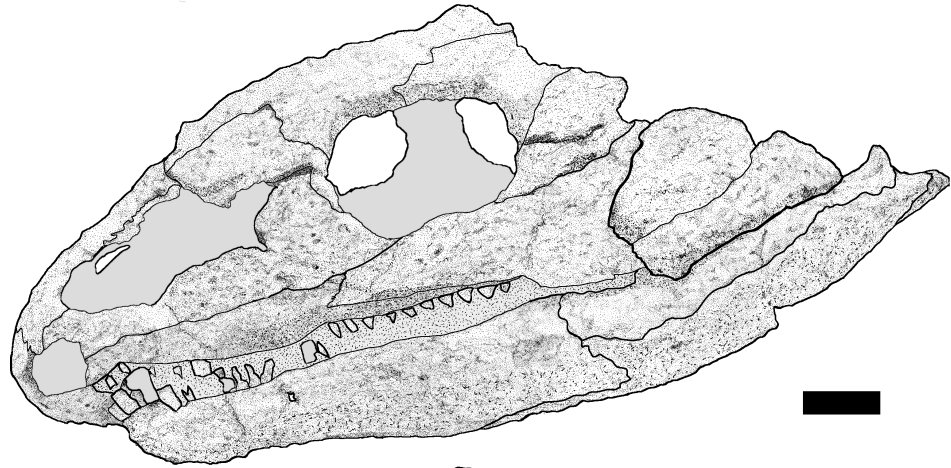
Figure 1. USNM V21275 Skull, Left Lateral View, Scale Bars = 1cm.
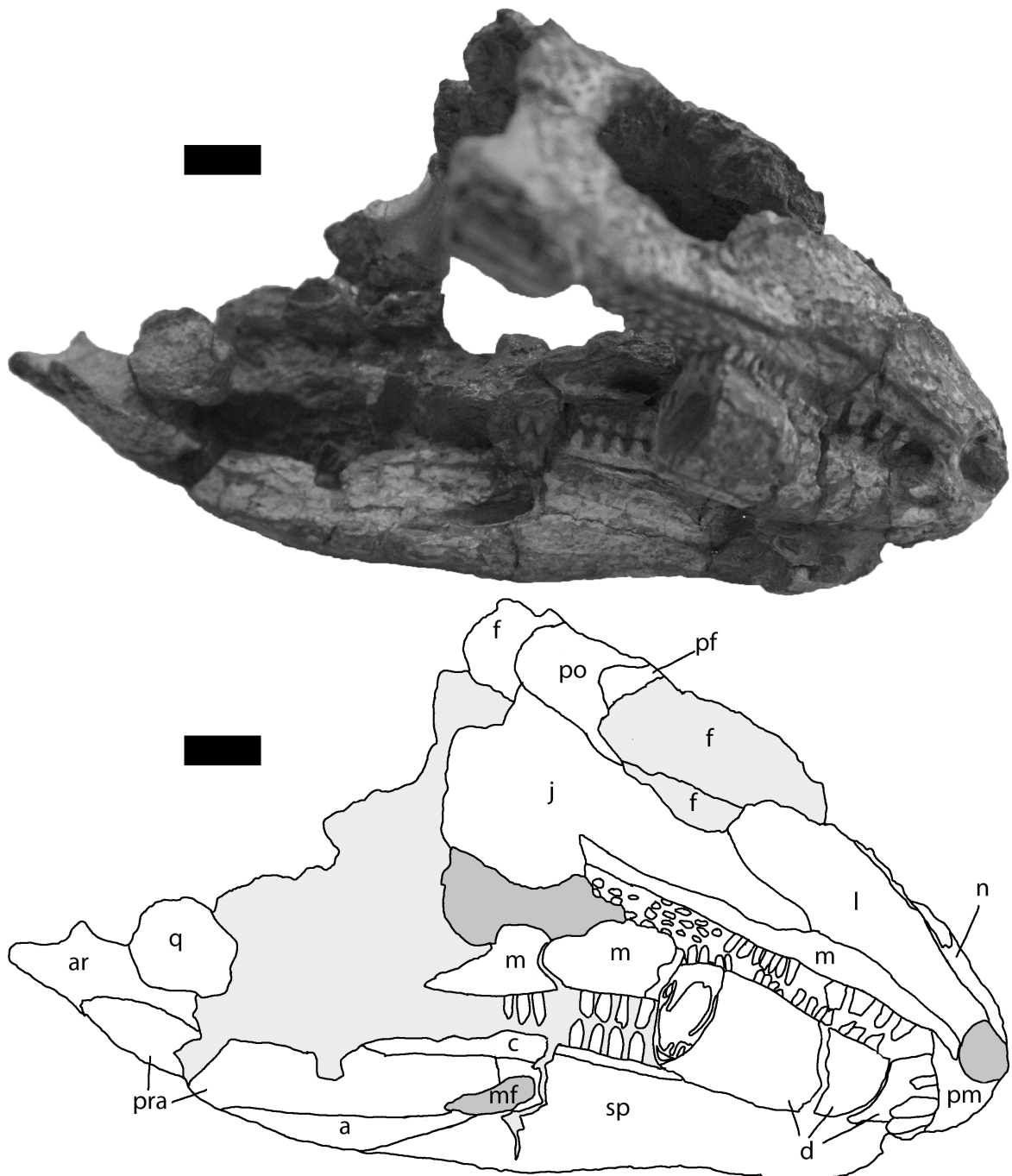
Figure 2. USNM V21275 Skull, Right Lateral View, Scale Bars = 1cm.

The premaxillae are present only in FMNH UR 183 (Figs. 10-13) and USNM V21275 (Figs. 1-4). The left and right premaxillae are sutured sagittally to

each other, with slight interdigitation of the bone junction. The element is the anterior-most in the cranium, and relatively flat anteriorly. The dorsal-most extent of the element comes to approximately fifty percent the dorsoventral height of the external naris. They abut on the dorsal aspect by the right and left nasal bones, which are sutured sagittally and which are fused to the premaxillae in a deeply interdigitated suture. The element recurves as it extends ventrally, posterodorsally meeting the maxilla in a narrow, posteriorly and dorsally extending process which is overlapped by an anteriorly and ventrally extending process of the maxilla. The angle of incidence of this suture is approximately 45° from horizontal, and the suture exhibits no interdigitation. Together the premaxillae are recurved, resulting in the recumbent angulation of the rostrum, giving the family and several of its members their names. Each premaxilla appears to hold three large, caniniform teeth. They are elongate, cyllindrical in the shaft, and conincal at the tips. The rostral-most tooth is the second largest of the three, the second the largest, and the lateral-most the smallest (Fig. 1). The teeth recurve, directly posteriorly at an angle of approximately 30° to the horizontal. No alary process is readily discernible in any of the specimens used in this study.
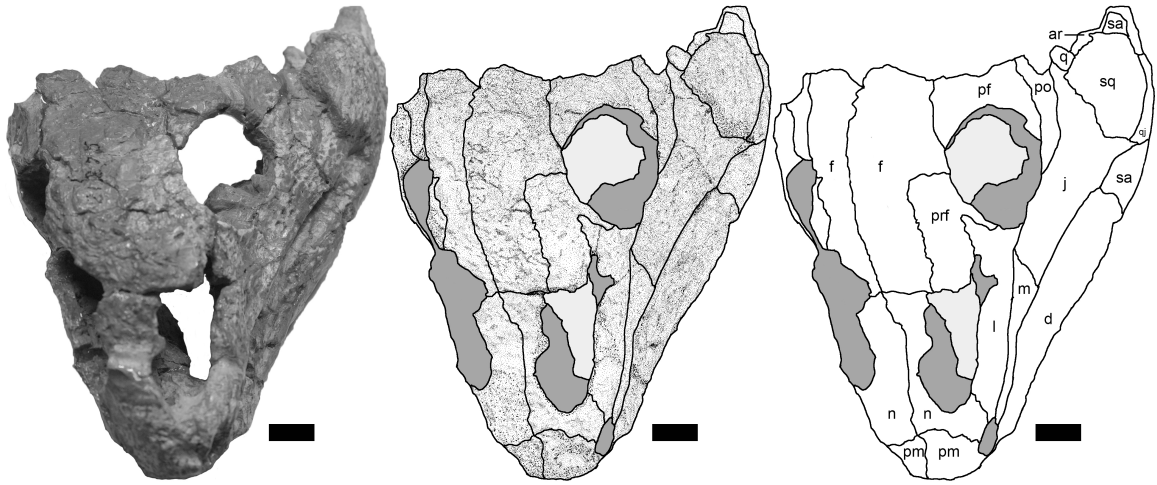
Figure 3. USNM V21275 Skull, Dorsal View, Scale Bars = 1cm.
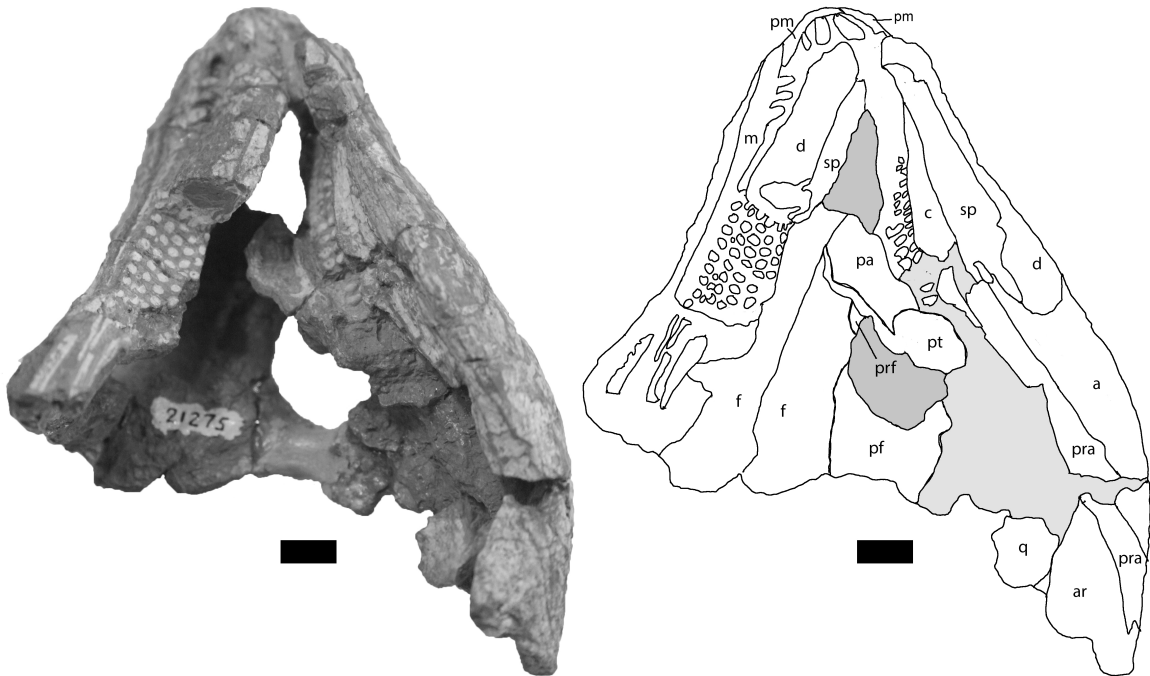
Figure 4. USNM V21275 Skull, Ventral View, Scale Bars = 1cm.

13

The nasals are only partially present on USNM V21275 (Figs. 1-3) and much more complete on FMNH UR 183 (Figs. 10-13). The element is relatively flat dorsoventrally and is overall roughly rectangular in shape. It sutures anteriorly with the premaxilla on its own side of the skull in a deeply interdigitated suture. Medially it abuts the opposite nasal bone in a relatively straight suture that extends posteriorly and is lightly interdigitated. Laterally the element abuts the lacrimal in a straight suture that lacks interdigitation. The nasolacrimal suture extends posteriorly, approximately twenty-five percent of the entire length of the skull. Posteriorly, the element is expected to abut the prefrontal, however this junction is present in neither specimen. More posteriorly, the elements suture to the frontal bones on either side in a moderately interdigitating suture.

Figure 5. FMNH UR857 Skull and Torso, Ventral View, Scale Bars = 1cm.

The lacrimals are present on both FMNH UR 183 (Figs. 10-13) and USNM V21275 (Figs. 1-3), however in FMNH UR 183, they are damaged and fragmentary, whereas in USNM V21275, the left lacrimal is partially missing and the right is mostly intact. Anteriorly the lacrimal forms the posterodorsal third of the posterior aspect of the external naris. The element abuts the nasal superiorly in a straight suture that exhibits no interdigitation. None of the specimens preserve the junction of the lacrimal with the prefrontals. Ventrally, the lacrimal abuts the maxilla in a straight, non-interdigitating suture until the lacrimal, maxilla, and jugal all meet. The suture with the jugal extends posteriorly as it curves up to the orbit. The suture exhibits slight interdigitation and terminates posteriorly at the anterior edge of the orbit. The lacrimal accounts for approximately fifteen to twenty percent of the anterior margin of the orbit.
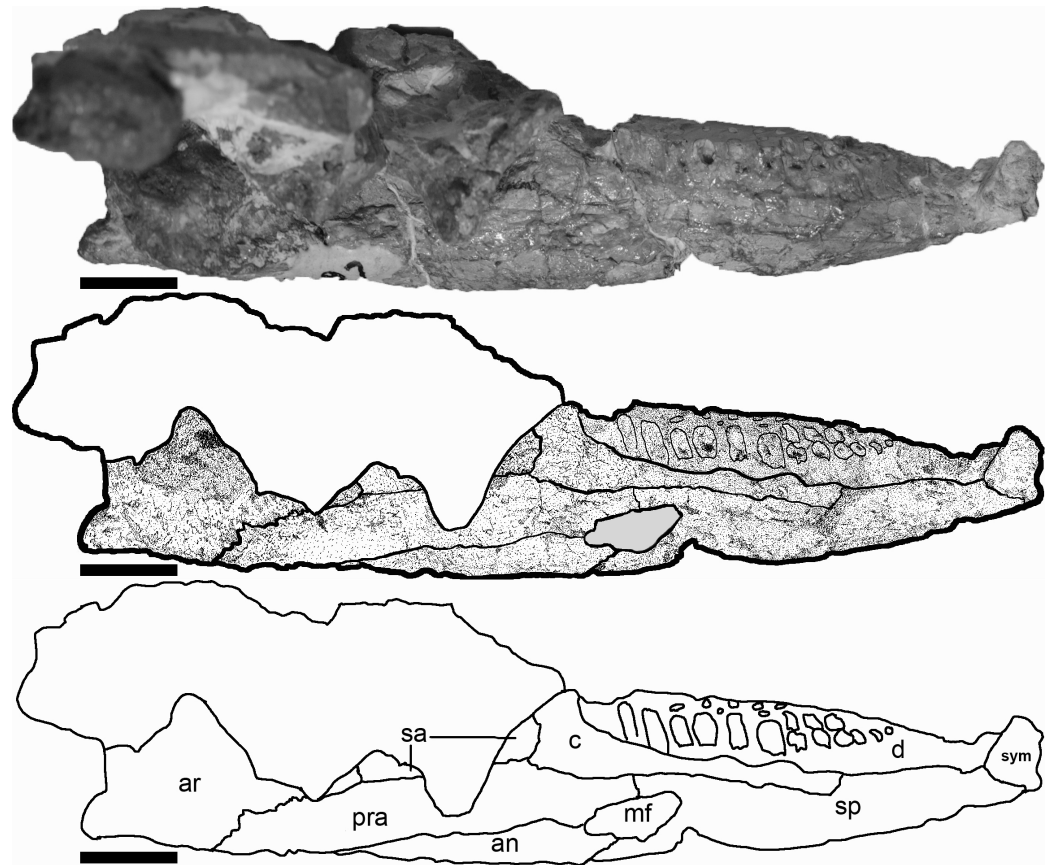
Figure 6. FMNH UR97, Left Lower Jaw, Lateral View, Scale Bars = 1cm.

The maxilla is preserved in FMNH UR 97 (Figs. 6-9), UR 183 (Figs. 10-13), UR 857 (Figure 5), and USNM V21275 (Figs. 1-4). In FMNH UR 97 and UR 857 the maxillae are fragmentary and badly damaged, however in FMNH UR 183 and USNM V21275, the state of preservation is much better and worthy of description. The maxilla is a long, thin, and flat element, trapezoidal in profile, flexing laterally at its posterior end. Anteriorly, the element abuts the premaxilla in a very short, angled, overlapping suture that exhibits no interdigitation. The anterior-most extent of the element forms a very small portion (approximately ten

16

percent) of the posterior margin of the external naris. Dorsally the element contacts the lacrimal in a straight, posteriorly ascending suture that exhibits no interdigitation and which continues until its junction with the jugal. Medially the element articulates with the palatine in a straight suture, exhibiting no interdigitation. The suture with the palatine runs the entire posterior half of the tooth-bearing region of the element. Posterior from the junction with the jugal, the maxilla abuts the jugal anteriorly at a sharp, descending angle which becomes somewhat more shallow approximately twenty-five percent of the way posteriorly and continuing through the last seventy-five percent of the element. The suture with the jugal is straight, angled ventrally and posteriorly, and exhibits no interdigitation. Posteriorly, the maxillae become increasingly narrow dorsoventrally until finally terminating against the jugal at approximately halfway through its anteroposterior extent, as well as approximately halfway through the anteroposterior length of the orbit.
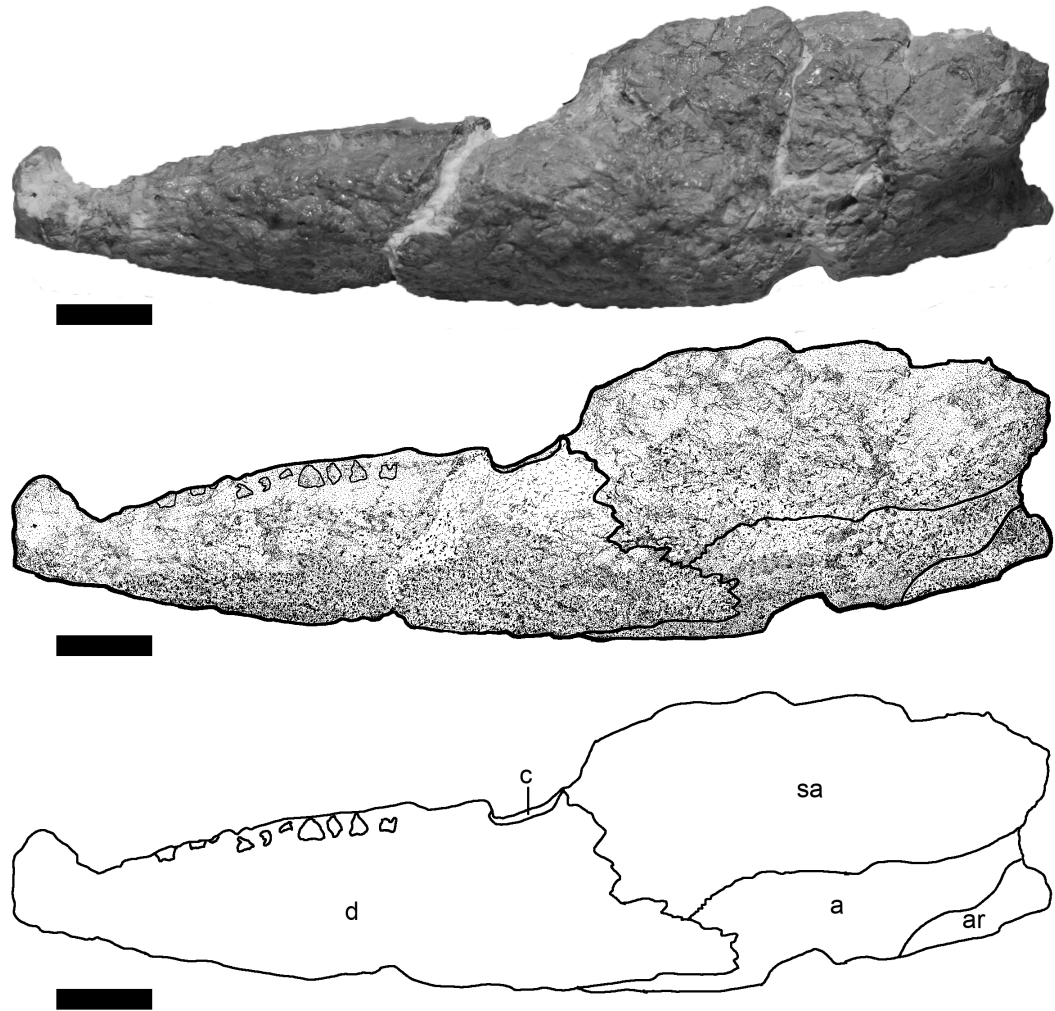
Figure 7. FMNH UR 97, Left Lower Jaw, Mesial View, Scale Bars = 1cm.

The maxillae bear two types of teeth: those found in the more anterior, single rowed (SR) region, and the more posterior, multiple rowed (MR) teeth. In all specimens with an exposed maxilla, the dental surface has been intentionally ground down to expose the apices of the underlying teeth. There appears to be five teeth in the SR region, and those surviving appear cylindrical at the base and conical at the apex. All of them exhibit heavy wear, however it cannot be

reasonably ruled out to be due to damage or poor preservation. Posteriorly the MR region of teeth extends to a point just anterior of the posterior margin of the orbit. The MR region of teeth is comprised of five rows of smaller teeth that also exhibit cylindrical bases with conical apices. In all specimens, the exposed MR region of teeth are incomplete due to the incompleteness of their maxillae. As preserved, the intact maxillae cannot be lifted off the adjacent dentaries without extensive and likely destructive preparation. FMNH UR 183 exhibits forty-one MR teeth in the accessible region and USNM V21275 exhibits thirty-four.

Figure 8. FMNH UR 97, Maxilla, Lower Jaw, and Bone Fragment, Dorsal View, Scale Bar = 1cm.

The prefrontal is only preserved in USNM V21275 (Figs. 1-4). The element is missing the anterior third to half, however the posterior portion of the element remains. Medially the element contacts the frontal; the portion of the element that abuts the nasal is not preserved. The suture between the prefrontal and the frontal is relatively straight laterally, exhibiting no interdigitation. The frontal suture extends toward the orbit as it runs laterally and which exhibits moderate interdigitation. The suture between these two elements terminates at the anterior aspect of the orbit, with an inferiorly extending wing of the element forming the anterior-most portion of the orbit, and approximately one tenth of the orbital border overall. Contact with the lacrimal is a single suture, however the anterior-most extent of which is not preserved. Posteriorly, this suture angles posterodorsally toward the orbit, turning sharply inferiorly just anterior to the anterior border of the orbit, creating a dorsally projecting embayment of the lacrimal juxtaposed against a more posterior, inferiorly extending embayment of the prefrontal. The suture exhibits no interdigitation but is not straight for any appreciable length.

Figure 9. FMNH UR 97, Bone Fragment, Lower Jaw, and Maxilla, Ventral View, Scale Bar = 1cm.

The frontal is preserved only in USNM V21275 (Figs. 1-4). The element is relatively flat and forms the dorsal-most extent of the cranium of what is visible and preserved. Anteriorly, the frontal is narrow and contacts the nasal in a short, relatively straight, moderately interdigitated suture. Sagittaly, the two frontals abut each other in a meandering suture that extends the entire anteroposterior length of the elements and which exhibits deep interdigitation. Posteriorly the frontal abuts the prefrontal in a posteriorly extending, relatively straight suture that exhibits no interdigitation, but which continues toward the orbit inferiorly and which exhibits moderate interdigitation. Approximately midway through the element, an embayment extends ventrolaterally to form part of the anterodorsal

21

orbit, accounting for approximately twenty-five percent of the orbit. The posterior

aspect of this embayment contacts the postfrontal, as a jagged suture that

extends posterodorsally with little interdigitation. The posterior terminus of this

suture is not preserved however as the posterior portion of the element is not

preserved in any specimen used in this study.

Figure 10. FMNH UR 183, Skull, Dorsal View, Scale Bar = 1cm.
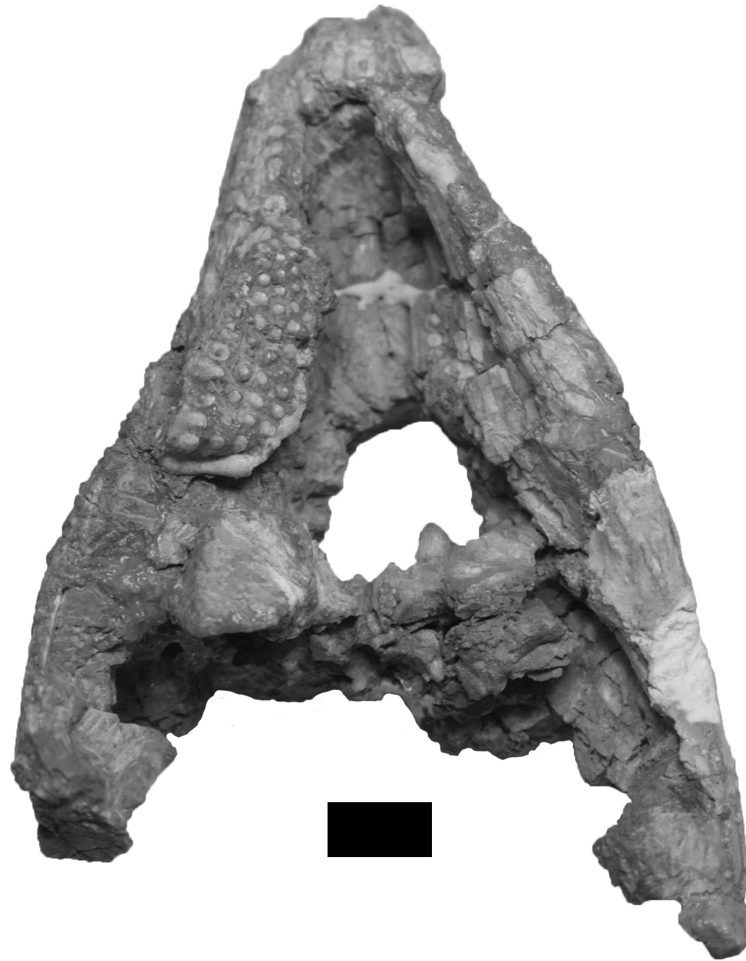
Figure 11. FMNH UR 183, Skull, Ventral View, Scale Bar = 1cm

The jugal is preserved in FMNH UR 183 (Figs. 10-13) and USNM V21275 (Figs. 1-3). None of the specimens' jugal is complete, and the alary process (if present), as well as the subtemporal process, are missing. The element is mostly flat, but exhibits slight curvature as the element extends posteriorly to

accommodate the widening of the skull to house the braincase. Additionally as it extends posteriorly, the element's dorsoventral length increases. Anteriorly the suture with the maxilla extends dorsoposteriorly at an angle approximately 30° from the horizontal. It is relatively straight and moderately interdigitated. Anterior to the orbit, the element abuts the lacrimal in a suture that curves gently dorsally toward the orbit, terminating there with no interdigitation. Approximately ten percent of the jugal extends anterior of the orbital margin. Posterior to the orbit, the jugal contacts the postorbital superiorly in a suture that curves dorsally as it extends posteriorly and is moderately interdigitated. On its posterior border the jugal abuts the squamosal superiorly and the quadratojugal inferiorly. The junction with the quadratojugal is seen clearly only in FMNH UR 183. Although present in USNM V21275, the surviving portion of the squamosal and the quadratojugal have been fractured, coming to overlie the posterior portion of the jugal where the elements would normally meet one another as well as overlying a portion of the surangular. The suture between the jugal and the quadratojugal is relatively straight, nearly perpendicular to the horizontal, and moderately interdigitated. The junction of the jugal with the squamosal is not preserved in any specimen available in this study.

Figure 12. FMNH UR 183 Skull, Left Lateral View, Scale Bar = 1cm.

Figure 13. FMNH UR 183 Skull, Right Lateral View, Scale Bar = 1cm.

Only the anterior portion of the postfrontal is preserved in USNM V21275 (Figs. 1-4), however the frontal suture dorsally and the postorbital suture ventrally are both preserved. The frontal suture is jagged, ascending posterodorsally as it extends and exhibits little interdigitation. More ventrally, the postorbital suture begins approximately halfway through the dorsoventral height of the orbit and ascends sharply posterodorsally as it extends posteriorly. The suture exhibits

little to no interdigitation. The posterior terminus of neither the suture with the postfrontal nor the postorbital have been preserved due to loss of the entire posterior portion of the bone.

The postorbital is preserved only in FMNH UR 183 (Figs. 10-13) and USNM V21275 (Figs. 1-3), however in FMNH UR 183, the portion of the element that survives is quite small. In USNM V21275 it appears part of the anterior half of the element has been preserved. Anteriorly the postorbital is acuminate, forming the posterodorsal border of the orbit, accounting for just under twenty-five percent of the entire orbital margin. Dorsally it abuts the postfrontal in a suture that angles posterodorsally sharply with little to no interdigitation. The posterior terminus of the suture between these two elements is not preserved in any specimen examined in this study. Inferiorly the postorbital abuts the jugal in a suture that curves dorsally as it extends posteriorly, with moderate interdigitation.

The squamosal is preserved only fragmentarily in FMNH UR 183 (Figs. 10-13), and only small portions of the element survive in FMNH UR 857 (Figure 5) and USNM V21275 (Figs. 1,3). The element abuts the quadratojugal inferiorly. Where present, the suture appears relatively straight with slight interdigitation. Its junctions with its neighbors anteriorly, dorsally, and posteriorly are not visible in the surviving fragments.

The quadratojugal is incompletely preserved in both FMNH UR 183 (Figs. 10-13) and USNM V21275 (Figs. 1,3), retaining the posterior portion of the element and its junction with the squamosal, whereas FMNH UR 183 retains the anterior portion of the element and its junction with the jugal. Anteriorly it abuts the jugal and is rectangular in shape. The suture with the jugal is relatively straight, perpendicular to the horizontal, and moderately interdigitated. More posteriorly the suture with the squamosal can be seen, and is relatively straight curving and ascending dorsally as the elements round the border between the lateral and posterior aspects of the cranium. Slight interdigitation is exhibited in the suture between the two elements.

The quadrate may only be seen in USNM V21275 (Figs. 2-4). Most of the element appears to be preserved, however most of its abutment with the pterygoid is missing. Anteriorly the element appears to contact the pterygoid in a suture that progresses posteriorly and medially, rounding the anterior face of the quadrate. The suture with a small fragment of the stapes remains (not illustrated) and is moderately interdigitated. Posteriorly and laterally, the quadratojugal suture is a relatively straight suture with moderate interdigitation, however dorsally the suture is incomplete due to loss of part of the quadratojugal. Of the small remaining section, the suture is relatively straight and exhibits slight interdigitation.

Palate

Of the specimens with information on the palate (FMNH UR 183 (Figs. 10-13), UR 857 (Fig. 5), and USNM V21275(Figs 2,4), the elements survive only fragmentally and with significant wear and damage. Of the palatal region, the palatine, pterygoid, and ectopterygoid are available for study, where as the vomer is not visible in any of the specimens examined.

The palatine is preserved only in USNM V21275 (Figure 4) however only partially. Anteriorly, the abutment with the vomer is lost (as is the vomer itself). A very small fragment of the pterygoid is preserved, joined to the palatine medially in a straight line with no interdigitation. Laterally the element abuts the maxilla in a very gently, laterally curving suture as it extends posteriorly. The suture exhibits no interdigitation. Posteriorly the element abuts the pterygoid in an embayment to the anterior. The suture is very smooth and exhibits no interdigitation. No suture appears to be present with the ectopterygoid, however it is unclear due to damage and wear if the junction of these two elements existed in vivo. The element appears to bear no denticles.

The pterygoid survives only fragmentarily in FMNH UR 183 (Figs. 10-13), UR 857 (Figure 5), and USNM V21275 (Figure 4). In all three specimens, neither the anterior border of the element nor the vomer are preserved. In the posterior region of the element, it abuts the palatine laterally in a straight, posteriorly

extending suture that exhibits no interdigitation. Its abutment to the palatine also occurs mediolaterally more posteriorly, as the pterygoid corners around the medioposterior-most extent of the palatine. As the palatine abuts the pterygoid posteriorly, it forms an embayment and the pterygoid extends anteriorly as the palatine extends posteriorly to either side of the embayment. This forms the anterior part of the transverse flange. The transverse flange appears to be a relatively flat, rounded plate of bone, roughly triangular in shape, and is denticulated posteromedially. The suture between the two elements as it extends mediolaterally is gently curving and smooth. Laterally near the posterior extent of the transverse flange the element abuts the ectopterygoid. The suture between the two bones is short, straight, and exhibits no interdigitation. The quadrate flange is preserved only in FMNH UR 857 and is a flat, thin flange of bone, extending doromedially in profile while extending ventrolaterally along its length. None of the pterygoid's articulations with other elements along the quadrate flanges is preserved.

The ectopterygoid is preserved only in FMNH UR 857 (Figure 5). The element appears smooth, elongate, and flat. Medially its articulation with the pterygoid is preserved, and appears as a short, straight suture exhibiting no interdigitation. Its lateral articulation with the jugal is not preserved. Because the palatine was not preserved in FMNH UR 857, no information on the articulation between the palatine and ectopterygoid is available.

Braincase and Occiput

The elements comprising the braincase and the occiput are preserved only in FMNH UR 857 (Figure 5). There is significant wear and damage to these elements, and as illustrated, the braincase itself has been broken free of the rest of the cranium and come to rest at a slightly unnatural angle to the other elements of the cranium. Of the braincase and occipital region, parts of the parabasisphenoid, stapes, basiexoccipital, opisthotic, and supraoccipital are available for study, where as the supratemporal and sphenethmoid are not visible in any specimens examined.

The shape of the foramen magnum can be observed in FMNH UR 857 (Figure 5), as a small, ovoid foramen formed by the basiexoccipital and the supraoccipital. It appears the foramen is complete, however its edges are worn, and the slightly off-center and asymmetrical shape of the foramen betrays the extent of preservational distortion and deformation present in this region of the cranium. The diameter of the foramen magnum measures approximately 5mm.

The parabasisphenoid is preserved in a single, damaged fragment. Anteriorly the element's articulation with the pterygoid is lost as is the cultriform process. The posterior region of the element survived, and laterally its articulation with the stapes is retained. More posteriorly the element articulates with the

basiexoccipital in a curving scarf joint that appears to extend slightly anteriorly as it curves. The suture exhibits no interdigitation. Just lateral to the articulation with the basiexoccipital, the parabasisphenoid articulates with the opisthotics. The suture between the elements is short, straight and exhibits moderate interdigitation.

The stapes is only fragmentally preserved in FMNH UR 857 (Figure 5). What remains is long, thin, slender, and roughly cylindrical. Its articulation with the parabasisphenoid is short, straight, and exhibits no interdigitation. As the element extends posterolaterally on the medial aspect and closer to the proximal end of the element, there is a small opisthotic process. The stapedial shaft is slightly waisted, increasing in diameter very gently through its distal end. The stapedial foramen is not discernible. Posteriorly, no articulation with the quadrate can be discerned.

The basiexoccipital is preserved only in FMNH UR 857 (Figure 5). It is flat, rounded and damaged from wear, and represents the dorsal-most extension of the braincase as well as the ventral margin of the foramen magnum, surrounding just under half of it as preserved in FMNH UR 857. It appears as a union of the basioccipital and exoccipital, with no discernible articulations between the two. The element is rounded anteriorly, abutting the parabasisphenoid in an arcing, semicircular suture which exhibits moderate interdigitation (Fig. 5). _The

opisthotics articulate on either side, in relatively smooth, curving sutures. Finally, posteriorly the element abuts the supraoccipital in a curving, smooth suture exhibiting no interdigitation.

The opisthotic is preserved bilaterally in FMNH UR 857 only (Figure 5). The left opisthotic appears to be much better preserved than its counterpart on the right, however in both cases the lateral ends of the elements are not preserved. Medially the element is robust, articulating with the braincase in a broad, flat head. Posteriorly and laterally, it decreases in width slightly just beyond its articulation with the supraoccipital. Anteriorly, the element abuts the parabasisphenoid, joined to it in a smooth, sigmoid suture. Medially and slightly posteriorly, it abuts the basiexoccipital in a rounded suture. From the end of the suture with the basiexoccipital and extending laterally is a short, rounded supraoccipital suture.

The supraoccipital is preserved only in FMNH UR 857 and is incomplete (Figure 5). The element is preserved ventrally and posteriorly, however the dorsal- and anterior-most portions of the element have been lost. The element abuts the basiexoccipital and opisthotic ventrally. Its suture with the basiexoccipital is short and curved, exhibiting no interdigitation. Along with the basiexoccipital, the supraoccipital forms the foramen magnum, with the basiexoccipital comprising just over half of the border of the foramen. More

laterally it abuts the opisthotic on its medial end. The suture is gently curving and wandering, however not very long. The suture exhibits no interdigitation. It appears the element extends posteriorly as it extends dorsally, however only two small flanges of bone are preserved, and the full posterior and dorsal extent is unknown.

Lower Jaw

The lower jaw elements are preserved in FMNH UR 97 (Figs. 6-9), UR 183 (Figs. 10-13), UR 857 (Figure 5), and USNM V21275 (Figs. 1-4). However, the preservation of the elements are extremely fragmentary in FMNH UR 857, and FMNH UR 183 shows moderate to severe damage on these elements. Of the lower jaw elements, the dentary, splenial, coronoid, prearticular, angular, surangular, and articular are available for study.

The dentary is best preserved in FMNH UR 97 (Figs. 6-9) and USNM V21275 (Figs. 1,2, and 4). The element is very badly damaged in both FMNH UR 183 (Figs. 10-13) and UR 857 (Figure 5), exhibiting severe fracturing and wear. However in FMNH UR 97 and USNM V21275, the element is well preserved. Mesially, it is short, increasing in dorsoventral measure as it extends posteriorly. Laterally, the dentary comprises the entire lateral half of the lower jaw, and anteroposteriorly, more than half of the jaw's length. At the anterior extent of the element, it abuts its counterpart from the other side on the midline. The suture is

smooth and straight, extending posteriorly between the two dentaries. The suture

exhibits moderate to deep interdigitation. Slightly more posteriorly from its suture

with the other dentary, the element abuts the splenial in a short suture that wraps

around the anterior aspect of the splenial. Ventrally the suture is smooth, and

curving, exhibiting little to no interdigitation. In all specimens this suture is either

inaccessible through its length or badly damaged, precluding the possibility of

further description. Medially it runs with the splenial along the majority of its

length ventrally, and dorsally through approximately one third its length. Dorsally,

the suture with the splenial is relatively straight, terminating at the anterior-most

projection of the coronoid. The suture exhibits no interdigitation. Ventrally, the

medial abutment with the splenial is also relatively straight through most of its

anteroposterior length, but begins to veer medially, narrowing the splenial at

approximately the anterior-most extent of the prearticular. Posteriorly the element

abuts the angular, in a smooth, curving suture that creates a posterior

embayment into the angular. The suture occurs at the thinnest extent of the

dentary, but the thickest point of the angular, creating a lap joint. The suture

curves throughout its extent, and exhibits moderate interdigitation. Medially,

posterior to the splenial suture, the dentary contacts the coronoid medially. The

suture between the two elements is relatively straight in USNM V21275, though

less regular in FMNH UR 97, likely due to preservational distortion and damage.

Laterally and posteriorly, the dentary abuts the surangular dorsally in a jagged,

deeply interdigitated suture. Slightly more posteriorly and ventrally, the dentary

contacts the angular in an arcing manner as described above, and laterally it is deeply embayed to receive the posterior extension of the dentary. The suture between the dentary and the angular is jagged posteriorly, however less so where the angular extends anteriorly under the dentary, and exhibits deep interdigitation through its length. The dorsal aspect of the element almost solely serves as a dental platform. Anteriorly, the first third of the element is occupied by large, single-rowed (SR) teeth. These teeth are best preserved in USNM V21275, but are severely damaged or missing in FMNH UR 97, UR 183, and UR 857. The SR teeth are approximately one and a half times the diameter of the multiple row region teeth, and twice the height. They are cylindrical at the base and bluntly pointed at the apex, resulting in a bullet-like appearance. There is no visible, gross wear that cannot be discounted as damage. The posterior two-thirds of the dentary serve as a platform for the multiple rows (MR) of teeth. They begin anteriorly at first as two rows, increasing to four rows after a few tooth positions. The teeth are small, cylindrical at the base and appear to be pointed at the apex. In FMNH UR 97, the only specimen with good access to the MR section of the dentary, the elements and apical-most extents of the teeth have been intentionally ground off, presumably in an attempt to reveal the number of tooth rows present. Posteriorly this specimen also exhibits damage and the posterior-most extent of the element is not present. The left dentary retains forty-five teeth in the MR section, and the right dentary thirty-three.

The splenial is fairly well preserved in FMNH UR 97 (Figs. 6-9) and USNM V21275 (Figs. 1,2, and 4). The element, along with the dentary, comprises the mesial aspect of the anterior half of the lower jaw. From anterior to posterior, it becomes slightly wider, terminating at the Meckelian foramen. Anteriorly, the dentary wraps around the splenial, and it abuts the dentary ventrally in a short, smooth, and curving suture. As mentioned above, the splenial-dentary suture is relatively straight, terminating at the anterior margin of the coronoid. The suture with the dentary terminates at the anterior-most extent of the coronoid, where a new suture with that element begins. The splenial smoothly abuts the cornoid for the rest of its length as it extends posteriorly on its dorsal aspect. The suture with the dentary is straight as it extends posteriorly until the anterior most extent of the Meckelian foramen where the suture curves dorsally, narrowing the splenial. Posteriorly, the splenial abuts the prearticular in a very short, straight suture. Posteriorly and more ventrally, after forming the anterior half of the Meckelian foramen, the splenial abuts the angular, in a relatively straight suture, angled approximately 30° from the horizontal.

The coronoid is preserved in FMNH UR 97 (Figs. 6-9) and USNM V21275 (Figs. 1,2, and 4). The element is elongated anteroposteriorly with a long, gracile anterior process. Posteriorly it widens following the posterior-most extent of the dentary and extends to its lateral surface. Anteriorly it contacts the splenial in a short suture that curves ventrally and proceeds posteriorly until the splenial

meets the prearticular. The suture continues along the dorsal aspect of the prearticular for approximately one third of its length, where the suture extends dorsally, along the anterior aspect of the surangular. The sutures with the splenial and prearticular are relatively straight, whereas the suture with the surangular is curved slightly anteriorly. Neither exhibit any interdigitation. The suture with the dentary is a relatively straight suture, curving dorsally to wrap around the posterior two-thirds of that element.

The elongate prearticular is preserved in FMNH UR 97 (Figs. 6-9) and USNM V21275 (Figs. 1,2, and 4). Beginning halfway through the Meckelian foramen and curving ventrally through its anteroposterior length, it terminates near the posterior end of the lower jaw. The element abuts the splenial anteriorly in a short, straight suture. Anteriorly it forms the posterior and dorsal two-thirds of the Meckelian foramen. At the posterior-most extent of the Meckelian foramen, the prearticular contacts the angular in a slightly jagged suture which angles ventrally as it extends posteriorly, terminating at the lowest extent of the lower jaw. Dorsally the prearticular abuts the coronoid anteriorly, the articular posteriorly, and the surangular in between. The sutures with the coronoid and the surangular are relatively straight, whereas the suture with the articular is relatively straight anteriorly, but becomes jagged as it progresses posteriorly and ventrally. Ventrally, the prearticular is overlapped for most of its length by the angular, which decreases in dorsoventral height as it extends posteriorly. This

provides a similar arrangement of the two elements as seen with the splenial and angular, with the more anterior of the element overlying the more posterior element in a broad lap joint. Posteriorly, the abutment with the articular is wide, extending almost the entire width of the articular, but the articulation extends only so far as the suture between the angular and the articular laterally. The posterior suture with the articular is also jagged.

The angular is preserved in FMNH UR 97 (Figs. 6-9) and USNM V21275 (Figs. 1,2, and 4). It is roughly wedge shaped, and the dorsal aspect of its most anterior extent forms the posteroventral corner of the Meckelian foramen. Anteriorly the lightly interdigitated articulation with the splenial angles anterolaterally approximately 30° from the horizontal. Anterolaterally, it contacts the dentary in an extensive, jagged suture, accepting the large posterior embayment into which the dentary extends. The suture with the dentary recurves upon itself to accommodate this embayment, and exhibits moderate interdigitation, and at its anterior-most extent, the angular overlies the dentary in a peninsular plate of bone that thins as it extends anteriorly. The suture along this region is smooth and exhibits little to no interdigitation. Dorsomedially, the angular contacts the prearticular in an angled suture extending from the dorsoventral midpoint of the Meckelian foramen to the ventral-most extent of the lower jaw. The suture exhibits no interdigitation. Laterally and dorsally the angular abuts the surangular in a gently meandering suture exhibiting little

interdigitation. The suture terminates at the posterior-most extent of the lower jaw as the angular thins between the surangular and articular. Posteriorly and laterally the angular abuts the articular. The moderately interdigitated suture follows a sigmoid path, terminating at the posterior-most extent of the angular.

The surangular is preserved in FMNH UR 97 (Figs. 6-9) and USNM V21275 (Figs. 1,2, and 4). The element is broad and maintains its width through most of its anteroposterior length. Anteriorly and medially it abuts the coronoid in a curving suture. Medially and ventrally it abuts the prearticular in a relatively straight suture which terminates at the anterior-most extent of the articular. Medially and posteriorly the element abuts the articular in a dorsoventrally traveling suture, exhibiting moderate interdigitation. Laterally and anteriorly, its contact with the dentary is a jagged, deeply interdigitated suture. The suture travels posteriorly and ventrally until the surangular, dentary, and angular all meet. Laterally and ventrally the element abuts the angular in a gently meandering suture that extends posteriorly to the posterior-most extent of the lower jaw.

The articular is preserved in FMNH UR 97 (Figs. 6-9) and USNM V21275 (Figs. 1,2, and 4). The majority of the anterior-most extent of the element is not visible in FMNH UR97 and the anterior portion of the element is missing in USNM V21275. Of what is observable, only a short portion of the ventral part of

the suture is visible, and exhibits moderate interdigitation. More ventrally and posteriorly, its moderately interdigitated contact with the prearticular angles posteroventrally. Ventrally this suture extends laterally to the point where the articular articulates with the angular, whereas laterally and ventrally the articular abuts the angular in a short, jagged suture. Posteriorly the articular terminates in a wide, flat retroarticular process that is wider mediolaterally than it is tall dorsoventrally.

The Meckelian foramen is preserved in FMNH UR 97 (Figs. 6-9), UR 857 (Figure 5), and USNM V21275 (Figs. 1,2, and 4). However, the elements surrounding the foramen are badly damaged in all specimens except USNM V21275. The foramen is formed by three different bones: the splenial, which encompasses just over half of the anterior border, the prearticular, and the angular. The prearticular forms the posterodorsal third of the foramen whereas the angular forms the posteroventral remainder of the border of the foramen. In all specimens the foramen is irregularly shaped, but is overall ovoid. In all specimens, the foramen's length accounts for less than ten percent of the overall length of the lower jaw.

Post Cranial Skeleton

The vertebrae in USNM V21275 (Figs. 14-16) are well preserved, however in FMNH UR 859 they are severely worn and damaged. The dorsal neural arches

are expanded laterally, increasingly so as the element extends posteriorly. The neural spines are well preserved, exhibiting no indication of fracture or wear, and vary randomly in height. More ventrally both anterior and posterior zygapophyses meet at an angle approximately 30° from the horizontal. The posterior zygapophyses face slightly ventrally, coming to the approximate anterposterior midpoint of the next centrum on its dorsal surface. Similarly, the anterior zygapophyses face dorsally in a complimentary manner, coming to meet the dorsal-most edge of the next vertebral centrum. The neural canal is markedly ovoid in shape, approximately two times wider laterally than it is ventrodorsally. Laterally, transverse processes are wide and knurled laterally, thinning as they progress medially but then re-expanding as they approach the neural arch. The centra of the vertebrae are, like the neural canal, ovoid and laterally wider than they are tall dorsoventrally. They exhibit deep, rounded fossae on their anterior and posterior faces. The centra are hourglass-shaped in sagittal section. Between the ventral-most extents of the central, small, wedge-shaped intercentra are present. The intercentral are wedge-shaped, though slightly flattened ventrally. It appears the elements were approximately one third the entire length of the centra in width.

Figure 14. USNM V21275 Vertebrae, Anterior View, Scale Bar = 1cm.

Figure 15. USNM V21275 Vertebrae, Dorsal View, Scale Bar = 1cm.

Figure 16. USNM V21275 Vertebrae, Left Lateral View, Scale Bar = 1cm.

The ribs are preserved in FMNH UR 857 (Figure 5) and UR 859, however the preservation in FMNH UR 859 is extremely poor with the elements exhibiting severe wear and damage. Those visible in FMNH UR 857 appear to all be dorsal ribs. None is completely intact, however the head of one of them is preserved, as well as the shafts of many others. The heads of the ribs appear dicephalous, with a broad, buttressing dorsal process forming the capitulum, and a smaller, more gracile ventral process forming the tuberculum. Ostensibly these would have articulated with the intercentrum and centrum respectively.

The clavicle is preserved in FMNH UR 857 (Figure 5). The element is a flat, broad plate of bone medially that comes to a very sharp, pointed protuberance at its lateral most extent. Medially and anteriorly the element meets its counterpart on the opposite side in a deeply interdigitating suture which extends approximately half of the elements' anteroposterior length, terminating at

the clavicle's abutment with the interclavicle. The suture with the interclavicle extends laterally and slightly posteriorly until a sharp, angled embayment gives way to a posteromedially reaching extension of the clavicle. Posteriorly, as soon as the embayment of the interclavicle recedes, an embayment of the clavicle is formed, accommodating a anterolateral extension of the interclavicle, giving the suture a bidirectionally toothed appearance. The suture angles sharply back posteromedially before coming to the edge of both elements and terminating. In the relatively straight part between the clavicle and interclavicle, the suture exhibits moderate interdigitation, but in the alternating, toothed region of the suture, little to no interdigitation is present. Laterally the clavicle would abut the scapulocoracoid, however the two elements are separated in FMNH UR 857. The suture appears sigmoidal, following the curves of the scapulocoracoid and exhibits no interdigitation on the border of either element.

No cleithrum was preserved in any of the specimens used in this study.

The scapulocoracoid is preserved in only one specimen used for this study, FMNH UR 857 (Figure 5). The element appears as a roughly sigmoidal plate in anteroposterior profile, thinning as it extends posteriorly. The element is approximately two times the width anteriorly as it is posteriorly. Unfortunately the glenoid fossa and other features are not accessible with the element in situ.

The interclavicle is preserved in FMNH UR 857 (Figure 5). The element is incomplete posteriorly and appears as an elongated, flat bone with an enlarged anterior end articulating with the clavicles. The articulation anteriorly and laterally with the scapulocoracoid is not preserved. Anteriorly the element is broad and slightly pointed, abutting the left and right clavicles. The suture between the interclavicle and clavicle extends slightly posteriorly and laterally, exhibiting moderate interdigitation, later alternating projections with embayments of the two elements creating a toothed suture. This portion of the suture exhibits no interdigitation.

Figure 17. USNM V21275 Humerus, Lateral View, Scale Bar = 1cm.
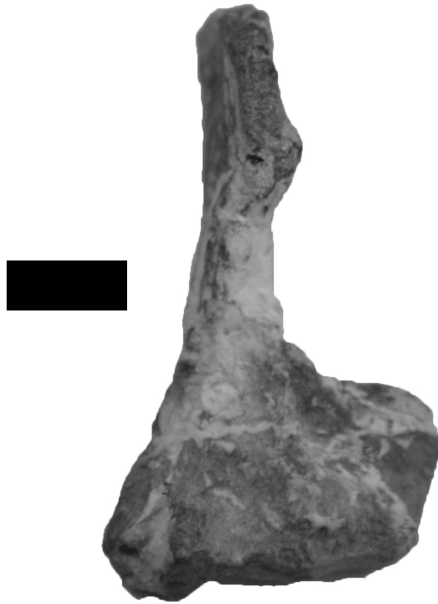
Figure 18. USNM V21275 Humerus, Ventral View, Scale Bar = 1cm.

The humerus is preserved in FMNH UR 100 (Figs. 17-18) and UR 857 (Fig. 5). The preservation in FMNH UR 100 is very good, and in FMNH UR 857 the humerus exhibits moderate damage. The element is robust and short, flattening at its proximal and distal ends. The head of the humerus is smaller (perhaps two-thirds size) than the distal terminus of the element, and the flat aspect of the head is rotated approximately 90° from the flat aspect of the distal end. Proximally, the head of the humerus is worn, making precise discernment of the articular surface difficult. However, distally the capitulum for radial articulation and trochlea for ulnar articulation are identifiable. Distally, the supinator process is present and is parallel to the shaft of the element. Similar to other captorhinids, the entepicondyles and ectepicondyles are well developed.

The radius is preserved in FMNH UR 100 (Fig. 19) and UR 857 (Fig. 5). In

FMNH UR 100, the element is fairly well preserved, however in FMNH UR 857 it

is badly damaged and only partially complete. The element appears as a long,

slender bone, slightly expanded proximally, forming a typical radial head. Distally,

the element expands again forming the articular surface for the radiale. At the

distal end of the element, a small notch is visible medially for articulation with the

intermedium.

Figure 19. FMNH UR 100 Radius, Anterior and Posterior Views, Scale Bar = 1cm.

The ulna is preserved only in FMNH UR 857 (Figure 5) and is very badly

damaged. Only the proximal two-thirds of the element is preserved, and is badly

worn. The olecranon of the ulna is wide and trapezoidal in shape, tapering off to

the diameter of the shaft distally.

A single left femur is preserved in USNM V21275 (Figure 20). The element is stout and robust, and appears slightly sigmoidal along its length, likely due to preservational distortion. Proximally there is some damage where a portion of the dorsal aspect of the head has been fractured and reattached. The intertrochanteric fossa is present as well as the fourth trochanter. Distally the intercondylar fossa is present, distinguishing the anterior and posterior condyles. Of the two condyles, the posterior is larger by approximately fifty percent. Overall, the articular surfaces for the pelvic girdle, tibia, and fibula are intact and fairly well preserved.

Figure 20. USNM V21275 Femur and Tibia, Scale Bar = 1cm.

The tibia is preserved in USNM V21275 (Figure 20). The element is robust, exhibiting a large proximal head, and slightly smaller distal end. The

lateral surface of the tibia is relatively straight and the curving medial surface follows the arches of the proximal and distal ends. The articular surfaces for the femur and astragalus are intact and fairly well preserved.
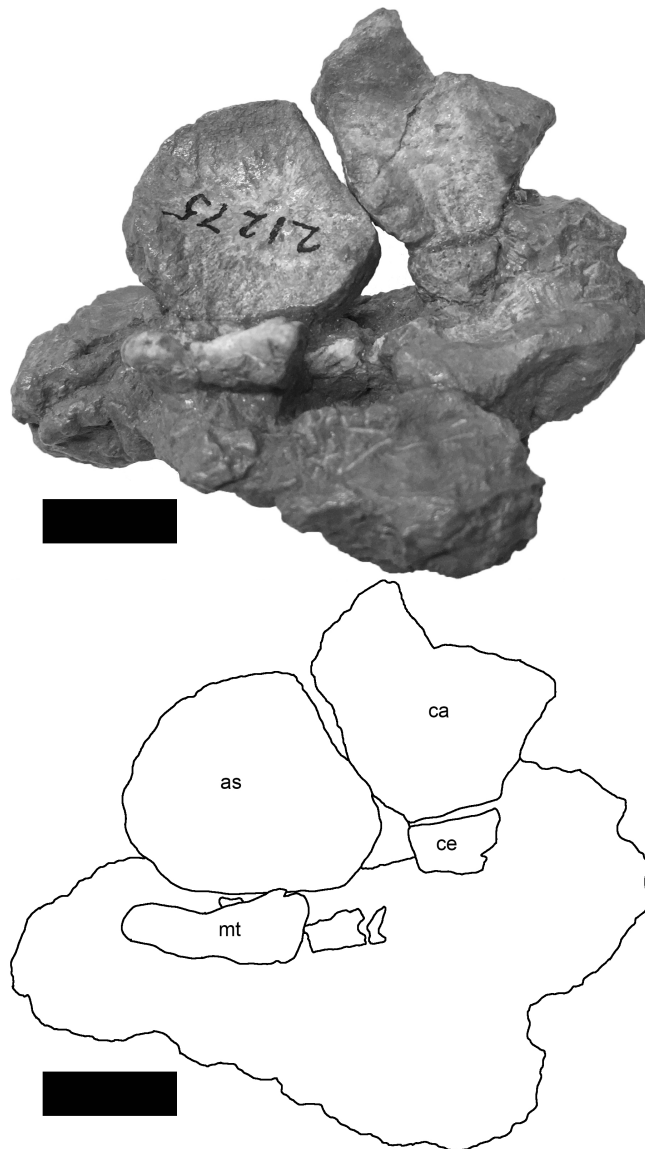
Figure 21. USNM V21275 Astragalus, Calcaneum, Metatarsal, and Centrale, Anterior View, Scale Bars = 1cm.

The astragalus is preserved in USNM V21275 (Figs. 21 and 22). The element is a flat, plate-like element with fairly smooth surfaces both anteriorly and posteriorly. The element is well preserved and the articular surfaces with the calcaneum and tibia are in good condition.
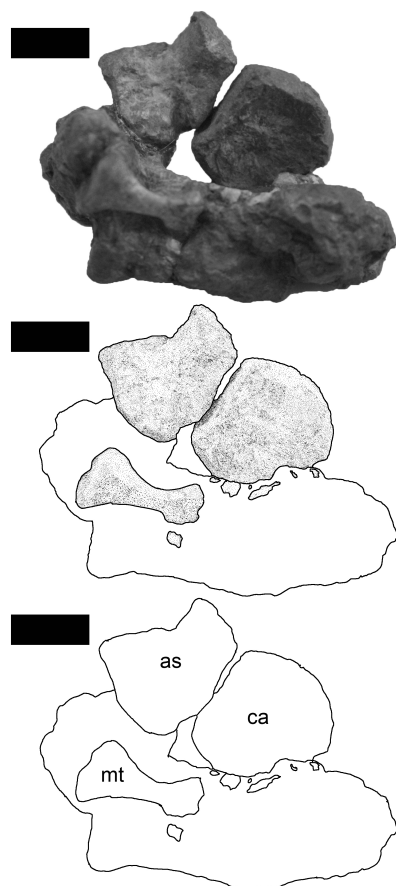
Figure 22. USNM V21275 Astragalus, Calcaneum, and Metatarsal, Posterior View, Scale Bar = 1cm.

The calcaneum is preserved in USNM V21275 (Figs. 21 and 22). The element is roughly flat and has an overall trapezoidal shape. As preserved, the

element retains the articular contacts with the fibula, astragalus, and centrale with fairly good preservation.

The centrale is preserved as a single example in USNM V21275 (Figs. 21). The element is trapezoidal in shape, and the line of its articular surface with the calacaneum has been preserved. It appears centrale IV is the one preserved, however lacking the other centralia or complete preparation from the matrix, that assertion cannot be confidently confirmed. Between the distal margins of the astragalus and calcaenum is a distinct, triangular notch, characteristic of the proximal margin of the large, pentagonal fourth distal tarsal typical of captorhinid reptiles. Distal to the astragalus, parts of two more worn elements that could be distal tarsals or fractured centralia are present, but are not preserved well enough for identification.

A number of more distal elements are preserved in USNM V21275 (Figs. 21 and 22). These include at least two metatarsals, each of which exhibit expanded proximal and distal ends, with a more slenderly waisted shaft. The elements have an overall stout, robust appearance. Specific identity of the metatarsals is not possible without full preparation and accounting for the other metatarsals which are not preserved.

CHAPTER FIVE

DISCUSSION AND PHYLOGENETIC ANALYSIS

"*Captorhinikos" chozaensis* was included in the most recent phylogenetic analysis of the Captorhinidae (Reisz et al., 2015). According to Modesto et al. (2014), the character states for *Captorhinikos choizaensis* and *C. valensis* were combined and used for the then previous study performed by Reisz et al. (2011). The study presented here includes a greater number and more complete specimens. Further, a number of characters and character states for "*Captorhinikos" chozaensis* used in Reisz et al. (2015) differ from my observations. Because of the previous suggestions of conflation of this data and in order to be as accurate as possible, the characters and character states for *"Captorhinikos" chozaensis* are not derived from the literature*,* and Modesto et al.'s (2014) description of *Captorhinikos valensis* which included no other taxa in the assessment of that genus and species. Further, each specimen assigned to "*Captorhinikos" chozaensis* was coded independently to confirm they sorted together as a valid taxon. Because all of the specimens were indistinguishable as separate species when using the same methods later used in this study, there is strong support for confirming their common identity and subsequent assignment to "*Captorhinikos*" *chozaensis.*

The phylogenetic analysis published by Resiz et al. (2015) designated a new captorhinid genus, *Opisthodontosaurus*, noting its remarkable similarly to

the microsaurian gynarthrid *Eurydus.* A preliminary examination of the latter

suggests inclusion of *Opisthodontosaurus* may be premature until *Eurydus* is

carefully restudied. However, that kind of comparison is outside the scope of this

analysis. Thus, I did not include it in this analysis.

Characters used in the phylogenetic analysis here are derived from

Sumida et al. (2010), Modesto et al. (2014), and new observations included from

this study. The characters were recombined into a renumbered character list

(Appendix 1 lists the source of each character's original interpretation, though a

number of them have been reworded or interpreted slightly differently here.

Seventy-nine characters (Appendix 1) were assessed for 21 taxa. Of the 79

characters in the matrix, 53 could be coded for *"Captorhinikos" chozaensis*, well

within the range for inclusion in such an analysis. The data matrix was compiled

in Microsoft Excel, exported into a plain text file, formatted, and imported into

TNT. There, a tree-bisection-reconnection search was performed with parsimony

as the optimality criterion. The characters were neither weighted nor ordered.

The parsimony analysis yielded twenty four most parsimonious trees. Of

these trees, the strict consensus tree was extracted and then used for bootstrap

support analysis. Average bootstrap support for the branches was 35.9, with a

Consistency Index (CI) of 0.53 and a Retention Index (RI) of 0.70. These metrics

yield a Rescaled Consistency Index (RC) of 0.37 (Figure 23). (Modesto et al.

(2014) obtained the following results: CI=0.64, RI=0.78, RCI=0.50, and Reisz et

al. (2015) the following: CI=0.35, RI=0.69, and RCI=0.24).
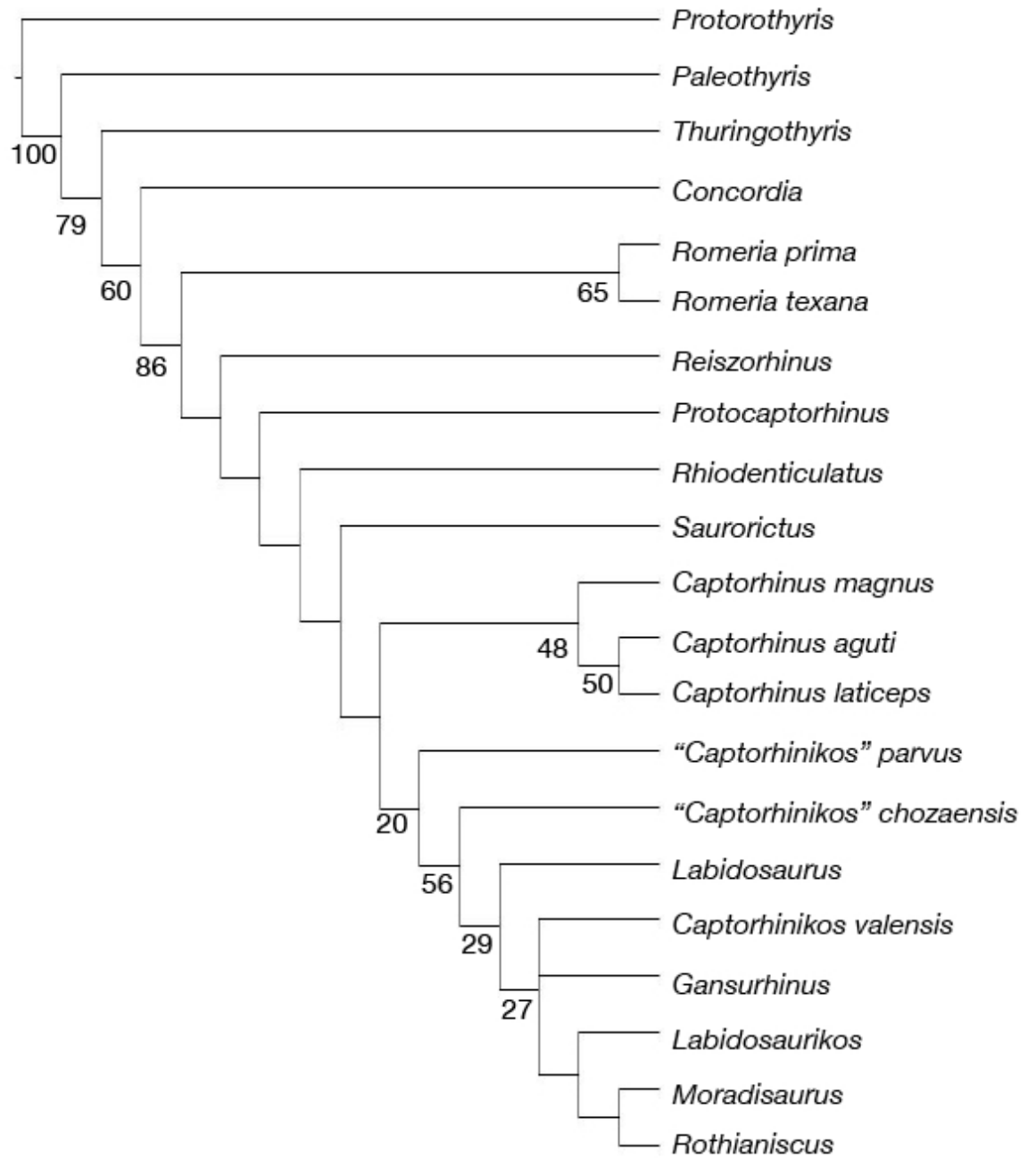
Figure 23. Phylogenetic Tree of the Captorhinidae, Bootstrap Values ≥50 and
Those Closely Related to *"Captorhinikos" chozaensis* are Given at the Branches.

The apomorphy analysis (Figure 24) yielded 4 or more synapomorphies supporting the nodes containing *Thuringothryis, Concordia, Romeria,* *"Captorhinikos" parvus*, *"Captorhinikos" chozaensis, Labidosaurus,* and *Moradisaurus/Rothianiscus*. The autopomorphy analysis yielded 4 or more characters supporting *Paleothyris, "Captorhinikos" parvus,* and *"Captorhinikos"* *chozaensis.*
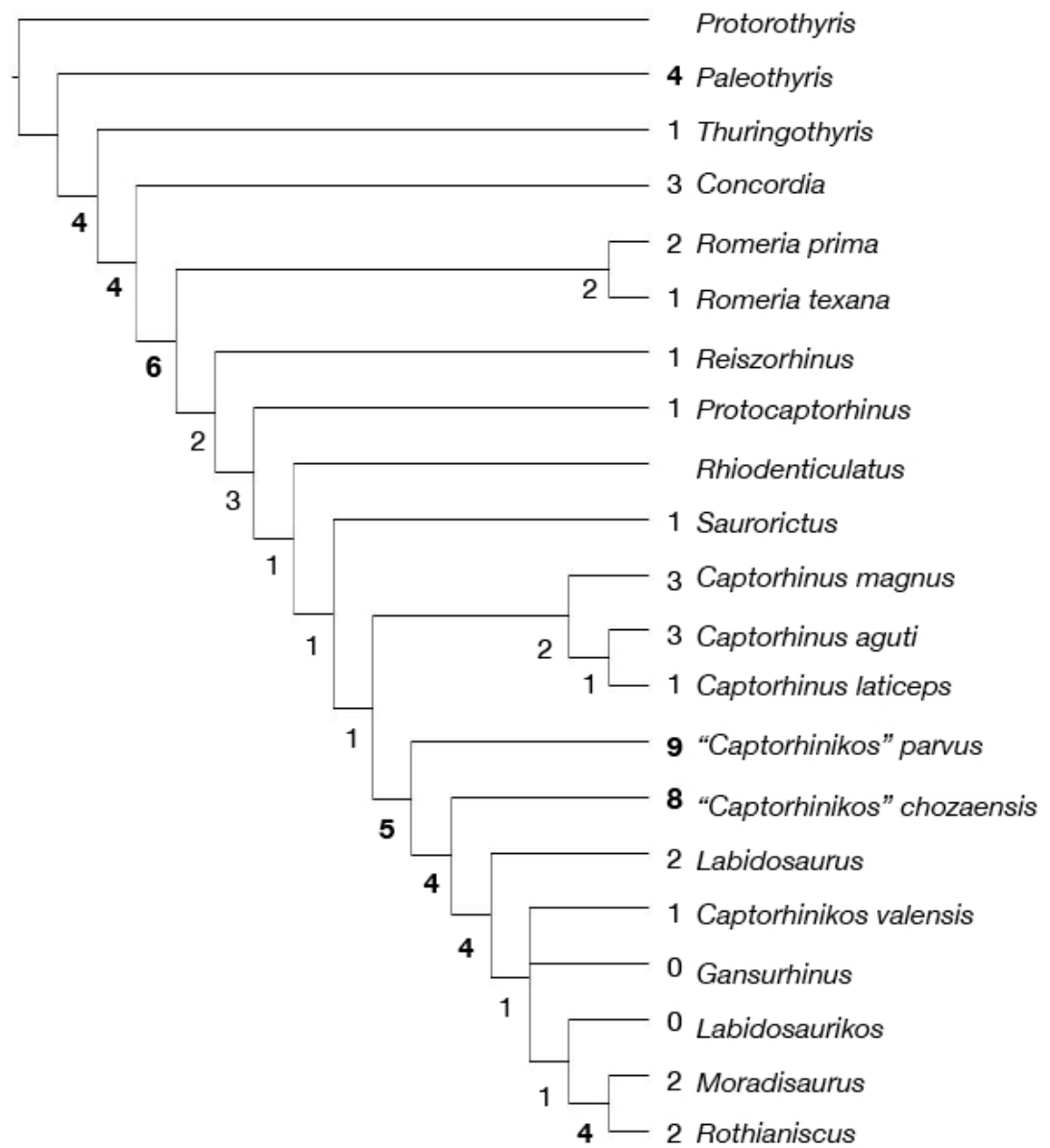
Figure 24. Phylogenetic Tree of the Captorhinidae with Apomorphy Analysis; Synapomorphic Character Count is Given at the Branches, Autapomorphic at the Nodes.

The phylogenetic analysis performed in this study recovered a hypothesis

of relationships between the members of the Captorhinidae not unlike those seen

in recent studies (Modest et al. 2014; Reisz et al. 2015). The positions of

Protorothyris, *Paleothyris*, *Thuringothyris*, and *Concordia* remain consistent between the three studies. This consistency is supported by similar, very high boostrap support values across all three studies. However the positions of *Romeria*, *Reiszorhinus*, *Protocaptorhinus*, and *Rhiodenticulatus* vary between the three. Modesto et al. (2014) and Reisz et al. (2015) both recovered a hypothesis of relationships placing *Rhiodenticulatus* in a position just basal to *Romeria* whereas my study places it immediately basal to *Saurorictus*. Similarly, my study found *Romeria* to be the sister taxon to *Resizorhinus*+all more derived taxa. The only other notable difference between the studies was the internal relations of the Moradisaurinae, wherein my study was unable to resolve a polytomy between *Captorhinikos valensis*, *Gansurhinus*, and the remaining members of the sub-family. my study also recovered *Moradisaurus* and *Rothianiscus* as the two most derived taxa in this study.

CHAPTER SIX

CONCLUSIONS

Early attempts (de Riqlès and Taquet, 1982; Gaffney and McKenna, 1979)

at resolving the phylogenetic relationships of captorhinid reptiles accorded

disproportionate significance to body and skull size and to tooth row number.

Captorhinids were presumed to have demonstrated strict orthogenetic change

from smaller to larger, and from single tooth rowed taxa to multiple tooth rowed

taxa in a strictly additive manner. Somewhat more recent studies (Sumida et al.,

2010; Modesto et al., 2014; Reisz et al., 2015) have shown this is not the case

with large size having developed in the family at least twice and multiple tooth

rows at least twice. my data here suggest these conclusions may well have been

too conservative, with large size and multiple tooth rows having developed

possibly as many as three times.

The synapomorphy analysis gives strong morphological support for the

placement of "*Captorhinikos*" *chozaensis* relative to its nearest taxonomic

neighbors. The last common ancestor of "*Captorhinikos" parvus* and more

derived taxa is distinguished by five synapomorphies: a long and narrow

prefrontal, fusion of the supratemporal with the postparietal, a mandibular ramus

size greater than 14% of overall jaw length, a deep coronoid process, and a

straight nasolacrimal suture (although this may be an ontogenetically labile

feature). These traits appear to be unrelated and it is hypothesized here none of

58

them constitutes a morphological suite with any of the others. The last common ancestor of "*Captorhinikos" chozaensis* and more derived taxa is distinguished by four synapomorphies: skull length of 5cm or more, snout length 25% or less of skull length, a sigmoidal mandibular ramus, and the presence of the lateral shelf below the coronoid process. These traits also appear to be unrelated to each other and it is again hypothesized here none of them constitutes a morphological suite with any of the others. Finally, the last common ancestor of *Labidosaurus* and the more derived taxa are distinguished by four synapormophies: a long anterior frontal process, a deep subtemporal process of the jugal, absence of maxillary caniniform teeth, and presence of a singular caniniform tooth on the dentary. These traits do not appear to constitute a morphological suite with each other.

Autapomorphy analysis further corroborates the findings of the synapomorphy analysis. The two closest neighbors of "*Captorhinikos"* *chozaensis* in either direction are "*Captorhinikos" parvus* and *Labidosaurus*. *"Captorhinikos" parvus* is distinguished morphologically by the absence of a premaxillary alary process, extensive contact between the vomer and pterygoid, absence of a suborbital foramen, a denticulate parasphenoid, short stapedial distal process, short coronoid anterior process, a straight maxilla, a posterior-most maxillary tooth positioned anterior to the posterior margin of the orbit, and a small first premaxillary tooth relative to the maxillary caniniforms. "*Captorhinikos"*

chozaensis is distinguished autapomorphically by the absence of an alary process, an anteriorly far-reaching jugal, a dorsally expanded, acuminate quadratojugal, a denticulated transverse flange of the pterygoid, a broadly expanded mandibular ramus, a retroarticular process that is broader than long, and a humeral supinator process parallel to the shaft. Finally, *Labidosaurus* is distinguished by a parietal that separates the postfrontal and postorbital bones, and chisel-shaped teeth.

The discrepancies between the studies have several explanations. First, the reassessment of "*Captorhinikos*" *chozaensis* shifted the nature of the taxon's phylogenetic signal. The previously published descriptions of the taxon gave it stronger affinity with traits seen in the Moradisaurinae as well as an artificial affinity with *Captorhinikos valensis* due to the conflation of the morphological data of the two species. The inclusion of the newly described "*Captorhinikos*" *parvus* also altered the topology of phylogenetic signal. The species exhibits morphological traits that give it affinity to the more basal clades of the Captorhinidae (e.g. small body size) on the one hand, but more derived clades as well (e.g. multiple rows of teeth). It is suggested here this explains the increased uncertainty near the middle of the tree, and the new, less confident placement of *Reiszorhinus, Rhiodenticulatus, Protocaptorhinus,* and *Romeria.* Ostensibly, the high degree of homoplasy present in *"Captorhinikos" parvus* has introduced increased morphological affinity between these species and those

found in the Moradisaurinae, additionally propagating this uncertainty in the more derived branches from this taxon. Modesto et al. (2014) and Reisz et al. (2015) used the branch-and-bound search algorithm for tree discovery, however with the addition of another taxon to the data matrix, the tree-bisection-reconnection search algorithm was chosen due to the theoretical twenty taxon limit of the branch-and-bound algorithm(Hendy and Penny, 1982). Although they produce similar results, the output from the search algorithms are not always identical. Both Modesto et al. (2014) and Reisz et al. (2015) used 75 characters in their data matrix. my matrix added a few characters, bringing the total to 79, and although this increase adds greater opportunity for higher resolution of a phylogenetic hypothesis of relations, it also adds the potential for greater uncertainty in the phylogenetic signal present in the taxa included. The unresolved polytomy recovered in my study is likely due to the limited cranial morphological information available on *Gansurhinus qingtoushanensis* and *Captorhinikos valensis* combined. Further, *Gansurhinus qingtoushanensis* had zero distinguishing autapomorphies in my analysis, which resulted in a high degree of uncertainty as to its true placement within the Moradisaurinae. Finally and most compellingly the Captorhinidae exhibit an unusually high degree of homoplasy. The complement of the Consistency Index is a measure of the homoplasy present in phylogenetic analysis, and in this case 1-0.53=0.47, or 47% homoplasy (Egan, 2006). However, the number of derived traits is robust

given the results of the apomorphy analysis (below), and the Retention Index (the amount of apparent synapomorphy), of 0.70 or 70% (Egan, 2006).

Morphologically, "*Captorhinikos*" *chozaensis* fits into what I would anticipate seeing between *Captorhinus* and *Labidosaurus* well. The former genus exhibits cranial and dental features that appear to pave the way evolutionarily for the changes seen later in both *"Captorhinikos" parvus* and *chozaensis*: the beginnings of multiple tooth rows, the progression or re-evolution of large body size in the family, and the maintenance of an otherwise conservative body morphology.

Functionally, *"Captorhinikos" chozaensis*' derived dental morphology fits what we would expect to see from an herbivorous, or possibly insectivorous animal. However, they are not the only case of a vertebrate evolving multiple tooth rows. In the Triassic, Rhynchosaurs evolved multiple tooth rows on both their maxillae and dentaries (Benton, 1984), for the oral processing of plant matter. Mosasaurs retain teeth on their pterygoid bones, to aid in the capture and ingestion of whole prey (Lingham-Soliar, 1991). Also in the Cretaceous, hadrosaurs evolved a derived, multiple tooth bank that aided in oral processing of plant matter (Hopson, 1980). These examples continue into extant species as well. Sphenodontids exhibit multiple tooth rows on the maxilla, also for aiding in herbivory (Jones et al., 2009). Ophidians have teeth on their palatines and

pterygoids for prey capture (Scanlon and Shine, 1988). Finally eublepharid geckoes replace their teeth laterally, with new teeth growing mesially to the tooth that will be replaced, giving them a quasi-multi tooth rowed dentition (Handrigan et al., 2010). Captorhinids are likely the first, but certainly not the last vertebrate to evolve multiple tooth rows. In each case, however, the tooth morphology itself is the determining factor for ecological role, not the possession of multiple rows itself.

I conclude by confirming the two most recent phylogenetic results of this family: "*Captorhinikos" chozaensis* is confidently assigned its own taxon just basal to *Labidosaurus*+Moradisaurinae. As the study performed by Modesto et al. (2014) reaffirmed that species' inclusion in the genus *Captorhinikos*, and the results of every subsequent phylogenetic analysis (Reisz et al., 2015) have excluded "*Captorhinikos" chozaensis* from that designation, a new generic name must be chosen and the species current assignment to "*Captorhinikos"* is designated a nomen ambiguum.

APPENDIX A

PHYLOGENETIC DATA MATRIX

Protorothyris   0000000000 0001000100 1000000000 0000000000 000000?000 0000000000 0000000000 111?011??

Paleothyris   0000000001 0?01000000 0000200100 0010000000 0000?00000 000000??0 0000000000 111101111

Thuringothyris   0000000010 0000011000 1000100000 0001000000 1?10?00000 0000000000 0000000000 11??01011

Concordia   0000110111 00001?0?00 1000100001 000??0000 1000?00000 0?0000???0 100000000? ?????????

Romeria prima   1011101000 0?01110100 00000?0?01 ?0?1?????0 1010000?00 1?0000???0 100000100? 0?0?1?0??

Romeria texana   101110??01 0?01110100 10001?0101 001100?000 10?0?00?0? 100000???0 100000100? ?????????

Protocaptorhinus   0011100100 0?00110?00 0010101101 010???1000 10?0??0001 1?0000???1 1000001001 0??1020??

Reiszorhinus   1011101010 0?00100000 1000101101 111????0?? ??????000? 1?010?11?0 100000100? ?????????

Rhiodenticulatus   0011101110 0100101001 10??1?1101 ?1??111000 101000?00? 1000001??? 0000001001 ?01?020??

Saurorictus   00?1111?00 0?00001000 00??0011?1 2?0??????? 1?????0??? ??0??????? 100000100? ?????????

Captorhinus aguti   0011111100 0200101001 1010101111 1201112100 1111000001 1000101002 1200221111 000002000

Captorhinus laticeps   001111?100 0200101001 1010101111 1201112100 1111000001 1000101002 1000011101 000002000

Captorhinus magnus   1011111?00 0?01101001 1?1010??0? ?????????? ????00???? ??00101??2 1000021101 00??120??

Labidosaurus   1111111001 1110101001 1110111111 1211111100 1112001111 1011111111 1001012001 000012001

Labidosaurikos   1111111001 1110101011 0111111211 1211111111 1112102111 1011110111 121153202? ?????????

Moradisaurus   101?101?1? ??1??????2 ???111??1? ?1?111111? 2112111101 ?111110111 1200532122 0???1?00?

Rothianiscus   011?10???? ???0????12 ???111???? ?1?111?112 211??????? ??111????1 1111432?22 00??0?0??

Gansurhinus   1?1?1????? ?????????? ?????????? ?????????? ?1???????? ?1???????? ?20143??02 00??2???

Captorhinikos valensis   1????????? ?????????? ?????????? ??????000 0????????? ?????????? ?201432?22 0????????

"Captorhinikos" parvus   0010001001 0100001000 01??101?01 2?01011000 010100???? 0001100?11 0010231101 0????????

Opisthodontosaurus   0???111??? ?201110?01 1???10???? ???0?02?00 11000????? 1?00011010 0100030101 ?1??1?1??

"Captorhinikos" chozaensis   111?11100? 0001000101 0?????????? ?????110?1 ??1??02?1? 10110111?2 1210431?1 00??010??

65

APPENDIX B

PHYLOGENETIC MORPHOLOGICAL CHARACTERS

Skull Shape

1   Skull Length: less than 5cm anteroposteriorly in mature specimens (0); greater than 5cm anteroposteriorly in mature specimens (1)

2   Snout width: broad, greater than or equal to 35% of skull length (0); large, l25% of skull length or less (1).

Dermal Skull Roof

3   Premaxilla: ventral margin straight (0); ventral margin flexed and aligned anteroventrally in lateral view (1).

4   Premaxilla: alary process absent (0); alary process present on posterodorsal process (1).

5   Maxilla: relatively straight (0); posterior end flexed laterally (1).

6   Maxilla: posterior-most tooth positioned at level of posterior margin of orbit (0); positioned more anteriorly (1).

7   Lacrimal: suture with jugal small (0); suture with jugal well developed (1).

8   Nasolacrimal suture: straight (0); interdigitating (1).

9   Antorbital/cheek region: mainly formed by lacrimal and prefrontal (0); mostly formed by lacrimal due to a strong dorsal expansion of the bone (1).

10   Prefontal: anterior process short and broad, approximately equal to the posterodorsal process in anteroposterior length (0); long and narrow, approximately two times the anteroposterior length of the posterodorsal process (1).

11   Frontal: anterior process short less than 55% total frontal sagittal length (0); long anterior process, approximately 60% total frontal sagittal length (1).

12   Jugal: alary process is absent (0); alary process is present, positioned no higher than the midpoint of the suborbital process of the jugal and is distinct from the orbital margin (1); alary process is present and positioned dorsally on the medial surface of the jugal, flush with the orbital margin (2).

13   Jugal: subtemporal process dorsoventrally low (equal to or less than 25% of skull height through orbital midpoint) (0); subtemporal process dorsoventrally deep (greater than or equal to 40% of skull height through orbital midpoint) (1).

14   Jugal: anterior extent reaches beyond anterior orbital margin (0); not (1).

15   Jugal: postorbital extent shorter than remaining anterior extent (0); equal or longer (1).

16   Quadratojugal: anteroposteriorly elongate, subrectangular in shape (0); relatively shorter, almost square in shape (1).

17   Quadratojugal: acuminate/convex upward (0); square-tipped anteriorly (1).

18   Quadratojugal: posteriorly straight or decreasing in height (0); expanded dorsally (1).

19   Quadratojugal: maximum height approximately equal to ⅓ the height of squamosal or less (0); nearly equal to ½ of squamosal height or greater (1)

20   Postorbital Cheek: Mostly straight/ little lateral convexity (0); convex/expanded laterally (1).

21   Parietal: does not strongly project between postfrontal and postorbital (0); distinct anterolateral process present that partially separates postfrontal and postorbital (1).

22   Supratemporal: separation from the postparietal (0); solid fusion with the postparietal (1).

23   Supratemporal: obliquely oriented into anteromedial direction, thereby lying within a facet of the parietal (0); positioned mediolaterally at the posterior edge of the parietal (1).

24   Supratemporal: small, slender element (0); large, contributing to skull table (1).

25   Parietal foramen: positioned at midpoint of interparietal suture (0); positioned anterior to midpoint of interparietal suture (1); posterior to midpointt of inter parietal suture (2).

26   Sculpturing: skull surface relatively smooth, with only small honeycombing pits or grooves (0); with pits and grooves with notably larger, randomly positioned pits on posterior skull table (1).

27   Postparietal: contacts mate fully along dorsal-ventral thickness (0); contacts mate dorsally only, postparietals separated slightly on ventral side by dorsal aspect of supraocciptal (1).

28   Postparietal: flat in parasagittal section (0); concave in parasagittal section (1).

29   Postparietal: majority of postparietal on occipital surface and unsculptured (0); majority of postparietal on dorsal skull surface and sculptured (1).

30   Postparietal: transversely short with tabular present (0); transversely elongate with tabular absent (1).

31   Supratemporal: no contact with postparietal (0); contact with postparietal (1); absent (2).

32   Occipital margin of skull table: embayed bilaterally (0); straight (1); single medial embayment (2).

33   Supratemporal horn: absent (0); present (1).

Palate

34   Vomer: denticulate (0); edentulous (1).

35   Vomer/pterygoid contact: extensive (greater than or equal to 50% median border of vomer) (0); short (less than or equal to 33% median border of vomer) (1).

36   Palatine: denticulate (0); edentulous (1).

37   Jugal/ectopterygoid: ectopterygoid present and alary process absent (0); ectopterygoid absent and alary process present, but no higher than the midpoint of the suborbital process of the jugal and distinct from the orbital margin (1); ectopterygoid absent and alary process present and positioned dorsally on the medial surface of the jugal, flush with orbital margin (2).

38   Pterygoid: transverse flange broad-based and distinctly angular in ventral view (0); narrow and tongue-like in ventral view (1).

39   Dentition on palatal ramus of pterygoid: present (0); greatly reduced or absent (1).

40   Pterygoid: transverse flange dentition consists of shagreen of denticles (0); at least one row of functional teeth (1); absent (2).

41   Suborbital foramen: absent (0); present (1); anteroposteriorly elongate (2).

Braincase and Occiput

42   Parasphenoid: deep ventral groove absent between cristae ventrolateralis (0); deep ventral groove between cristae ventrolateralis (1).

43   Parasphenoid: denticulate (0); edentulous (1)

44   Cultriform process: extends anteriorly (0); extends anterodorsally at an angle of approximately 15° to the horizontal plane (1); extends anterodorsally at an angle greater than 45° to basal plane (2).

45   Parasphenoid: posterolateral wing narrow, meets narrow head of stapes (0); wing broad, meets large head of stapes, in an elongate, nearly parasagittal suture (1).

46   Opisthotic: paroccipital process long, extending near to medial edge of squamosal (0); process short, extending only slightly beyond body of opisthotic (1).

47   Supraoccipital: in lateral view slopes anterodorsally (0); vertical (1); angled posterodorsally (2).

48   Supraoccipital, lateral ascending process: accounts for greater than or equal to 50% of height of supraoccipital (0); accounts for two thirds or more of height of supraoccipital (1).

49   Occipital condyle: at level of quadrate condyles in ventral view (0); immediately anterior to quadrate condyles in ventral view (1).

50   Paroccipital process: short (1/2 length or less of stapedial columella) (0); long and 'rod-like' (1/2 length or more of stapedial columella) (1).

51   Stapes: distal process short (0); elongate (1).

52   Exoccipital: lateral process on dorsal ramus absent (0); present (1).

Lower Jaw

53   Mandibular Ramus Shape: Ventrally relatively straight (0); Ventrally, sigmoidal shaped (1).

54   Mandibular Ramus Size: less than or equal to 8% of total jaw length (0); greater than or equal to 14% of total jaw length (1).

55   Posterior Mandibular Ramus: rectilinear (broadly expanded) (0); acuminate (pointed) (1).

56   Lateral Shelf: Absent below coronoid process (0); present below coronoid process (1).

57   Coronoid Anterior Process: short (0), long (1).

58   Meckelian Foramen small (less than 9% of lower jaw) (0); anteroposterior length greater than or equal to 14% of lower jaw (1).

59   Coronoid Process: slender and does not form wall of adductor fossa (0); deep and forms dorsal most third of lateral wall of adductor fossa (1).
60   Retroarticular Process: absent (0); present and slender (1); present and broader transversely than long (and short) (2).

Dentition
61   Premaxillary Dentition: first tooth relatively small relative to maxillary caniniform (0); subequal to maxillary caniniform (1); In taxa lacking maxillary caniniforms, state 1 applies when the 1st premaxillary tooth is the largest marginal tooth present.
62   Maxillary dentition: none (0); 40 or fewer (1); more than 40 (2).
63   Maxilla:double row of teeth extend far anteriorly on tooth row absent (0); present (1).
64   Maxillary caniniform teeth: present (0); absent (1).
65   Number of tooth rows in upper jaw: one (0); 2 (1); 3 (2); 4 (3); 5 (4); 6 or more (5).
66   Marginal Dentition: 'cheek' teeth recurved (0); chisel-shaped (1); bulbous and ogival (2); bulbous at base and conical above (3).
67   Dentary Teeth Isodont (0), caniniform region present anteriorly (1); caniniform tooth present mesially with caniniform region absent (2).
68   Dentary : first tooth oriented mainly vertically (0); first tooth leans strongly rostrally (1).
69   Dental tooth wear: absent (0); present, modest (1); present, saddle-shaped (2).

Postcrania
70   Dorsal neural arches: narrow (0); lateral expansion present (1); exaggerated lateral expansion with swelling present (2).
71   Neural spines of dorsal vertebrae: height or shape alternation present (0); absent (1).
72   Anterior dorsal centra: not strongly ventrolaterally constricted (0); strongly ventrolaterally constricted (1).
73   Sacral ribs: first sacral rib larger than second rib (0); both ribs of roughly equal size (1).
74   Ilium: iliac blade expanded dorsally (0); narrow dorsally (1).
75   Stylo- and zeugopodium: shaft massive and with proximal and distal heads significantly expanded, resulting in an overall stout impression (0); shaft slender and heads only moderately expanded (1).
76   Humerus: supinator process not parallel to shaft (0); parallel (1); supinator process absent (2).
77   Manus and pes: elements short and broad (0); long and slender (1).
78   Fourth metatarsal: less than ½ the length of tibia (0); more than ½ the length of tibia (1).

79   First metacarpal: more than ½ the length of 4th metacarpal (0); less than half the length of 4th metacarpal (1).

APPENDIX C

CHARACTERS FOR SYNAPOMORPHY AND AUTAPOMORPHY ANALYSIS

Synapomorphic Characters

Thuringothyris	14, 34, 41, 77
Concordia	5, 15, 30, 61
Romeria	3, 4, 7, 28, 51, 67
"Captorhinikos" parvus	8, 10, 22, 54, 59
"Captorhinikos" chozaensis	1, 2, 53, 56
Labidosaurus	11, 13, 64, 67
Moradisaurus/Rothianiscus	6, 20, 32, 41

Autapomorphic Characters

Paleothyris	10, 21, 28, 33
"Captorhinikos" parvus	4, 5, 6, 35, 41, 43, 51, 57, 61
"Captorhinikos" chozaensis	12, 14, 17, 18, 40, 55, 60, 76

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