

Evolution in biological radiations; insights from the Triassic archosaur radiation

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ABSTRACT

Adaptive radiations, or evolutionary diversifications, are the evolutionary divergence of a single lineage into many different adaptive forms. They play a critical role in the history of life as groups of organisms speciate and fill new ecological roles over geologically rapid time intervals. There is currently no agreed upon operational unit, timeframe, or amount of divergence for organisms to be considered to have undergone an adaptive radiation. Additionally, the paucity of both comparative and fossil studies has limited the utility of the adaptive radiation in framing macroevolutionary questions, such as, is ecological and morphological diversification simultaneous? An ideal fossil clade to test this question is the Archosauriformes (crocodylans, birds, and their closest relatives). Archosauriforms radiated following the end-Permian mass extinction and their lineage diversification through the Early to Late Triassic is well documented in the literature. Prior to the end-Permian mass extinction, these reptiles were both species poor and ecologically limited, but by the Late Triassic they dominated terrestrial ecosystems in both species abundance and ecological breadth. However, continued environmental instability following the end-Permian extinction has led to the hypothesis that ecological expansion of archosauriforms lagged behind the diversification of lineages.

The first chapter of my dissertation uses a Middle Triassic archosauriform tooth assemblage from Tanzania to reconstruct dietary specialization, estimated by morphological disparity of teeth. In addition to comparing tooth disparity of isolated and

in situ teeth, this also provides a lens for comparing the timing of dietary specialization and species diversification. I found the archosauriforms to be faunivorous with little morphological disparity amongst the teeth. The second chapter uses an Early Triassic reptile tooth assemblage from South Africa to reconstruct the dietary specialization of archosauriforms early in their radiation to compare the amount of morphological disparity and lineage diversity. I use methods from Chapter 1 and integrate 3D morphometrics to better capture shape. I described several tooth morphotypes including six new to the locality. The morphological and dietary differences were minimal, indicating a greater species diversity than ecological diversity. The third chapter is a description of a new pseudosuchian archosaur taxon from the Middle Triassic of Tanzania. As species descriptions form the basic data unit of macroevolutionary analyses, this assists future studies of the archosauriform radiation. I recover this new taxon as the oldest known aetosaur. This species provides insights into the evolution of an armored carapace in crocodylian-line archosaurs and shows morphology related to armor evolved prior to the evolution of an herbivorous diet.

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GENERAL AUDIENCE ABSTRACT

There is an incredible diversity of life on Earth, but this is a small fraction of the life that once existed on our planet. The fossil record provides us a window into the past to reconstruct the history of life on our planet. Two of the patterns we see in the fossil record are rapid drops in biodiversity called mass extinctions, and rapid increases in biodiversity called biological radiations. Both of these events are often related and mass extinctions are followed by biological radiations throughout earth history. A particularly interesting case is the end-Permian mass extinction, not only because it is the largest extinction event, but also because the subsequent radiation was delayed by continuing environmental instability. An ideal group of animals to study in this time period are the archosaurs, the group of reptiles including crocodylians, birds, and their extinct relatives. Archosaur reptiles went from very few species before the extinction, to dominate ecosystems for the next 200 million years. However, we do not know if the radiation of many archosaur species occurred at the same time as they filled new roles in their communities.

The first two chapters of my dissertation focus on using fossil teeth to reconstruct the diets of archosaurs at a single location. My first chapter describes teeth from the Middle Triassic (247-237 million years ago) of Tanzania. I measured the shapes of these teeth and used that to help assign them to diets. Doing this I found there were more species than types of diets indicating the radiation of species may have occurred

before specialization of life habits. In the second chapter where I describe a reptile tooth assemblage from the Early Triassic (252-247 million years ago) of South Africa. I added additional methods for measuring tooth shape, found several different types of teeth (likely different species) but mostly similar diets, indicating again a delay in life habit specialization. In my third chapter I name a new species of archosaur reptile from the Middle Triassic of Tanzania. This new species helps us to understand how heavily armored plant eaters evolved in early crocodylian relatives during the archosaur radiation.

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ATTRIBUTION

Chapter 1 was conceived by DKH with input from SJN and HE and published by DKH with input from listed co-authors. Chapter 2 was conceived by DKH and PJH, designed by DKH with input from PJH and SJN. Chapter 3 was conceived by DKH with input from SJN, and designed by DKH with input from listed co-authors. All figures were made by DKH and all chapters were written by DKH with advice from SJN and listed co-authors. Data were collected by DKH (and HE and PMB Chapter 1). All analyses were conducted by DKH with input from listed co-authors.

CHAPTER 1: Reconstructing the Archosaur Radiation using a Middle Triassic Archosauriform
Tooth Assemblage from Tanzania

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ABSTRACT

Following the Permo-Triassic mass extinction, Archosauriformes – the clade that includes crocodylians, birds, and their extinct relatives – rapidly diversified into numerous distinct lineages, became distributed globally, and, by the Late Triassic, filled a wide array of resource zones. Current scenarios of archosauriform evolution are ambiguous with respect to whether their taxonomic diversification in the Early–Middle Triassic coincided with the initial evolution of dietary specializations that were present by the Late Triassic, or if their ecological disparity arose sometime after lineage diversification. Late Triassic archosauriform dietary specialization is recorded by morphological divergence from the plesiomorphic archosauriform tooth condition (laterally-compressed crowns with serrated carinae and a generally triangular lateral profile). Unfortunately, the roots of this diversification are poorly documented, with few known Early–Middle Triassic tooth assemblages, limiting characterizations of morphological diversity during this critical, early period in archosaur evolution. Recent fieldwork (2007–2017) in the Middle Triassic Manda Beds of the Ruhuhu Basin, Tanzania, recovered a tooth assemblage that provides a window into this poorly sampled interval. To investigate the taxonomic composition of that collection, we built a dataset of continuous quantitative and discrete morphological characters based on *in situ* teeth of known taxonomic status (e.g., *Nundasuchus*, *Parringtonia*: N = 65) and a sample of isolated teeth (N = 31). Using crown heights from known taxa to predict tooth base ratio (= base length/base width), we created a quantitative morphospace for the tooth assemblage. The majority of isolated, unassigned teeth fall within a region of morphospace shared by several Manda taxa (e.g., *Nundasuchus*, *Parringtonia*); two isolated teeth fall exclusively within a ‘*Pallisteria*’ morphospace. A non-metric multidimensional scaling ordination (N = 67) of 11 binary characters reduced overlap between species. The majority of the

isolated teeth from the Manda assemblage fall within the *Nundasuchus* morphospace. This indicates these teeth are plesiomorphic for archosauriforms as *Nundasuchus* exhibits the predicted plesiomorphic condition of archosauriform teeth. Our model shows that even the conservative tooth morphologies of archosauriforms can be differentiated and assigned to species/genus level, rendering the model useful for identifying isolated teeth. The large overlap in tooth shape among the species present and their overall similarity indicates that dietary specialization lagged behind species diversification in archosauriforms from the Manda Beds, a pattern predicted by Simpson's 'adaptive zones' model. Although applied to a single geographic region, our methods offer a promising means to reconstruct ecological radiations and are readily transferable across a broad range of vertebrate taxa throughout Earth history.

1. INTRODUCTION

Adaptive radiations, or evolutionary diversifications, play a critical role in the history of life as clades speciate and fill new ecological roles over geologically rapid time intervals (Simpson, 1944; Schluter, 1996). Although there are examples of adaptive radiations that are not speciose (e.g. Darwin's finches), or adaptively disparate (e.g. crotaphytine and oplurine iguanids), such a framework is still useful for structuring macroevolutionary questions and explaining present (and past) biological diversity (Gavrilets and Losos, 2009). Adaptive radiations and the shifts in evolutionary rates associated with them are among the most studied aspects of evolutionary biology (e.g. Stanley, 1979; Losos and Miles, 1994, 2002; Gavrilets and Losos, 2009; Revell et al., 2018; Slater and Friscia, 2019). However, empirical uncertainties remain regarding many of the properties of adaptive radiations (Gavrilets and Losos, 2009; Slater and Friscia, 2019), with the relative timings of lineage diversification and ecological disparity during adaptive radiations being one such problem. Does lineage diversification come first, followed by specialization and evolution within an 'adaptive zone' (Simpson, 1944, 1953) or does ecological specialization drive lineage diversification simultaneously (Schluter, 1996)? In the former case species fill the same resource zones using similar, ancestral morphological structures (e.g. identical tooth morphologies), whereas in the latter each species would be expected to have a unique, derived morphology for its resource zone at the start of the radiation (for an empirical example, see Slater and Friscia, 2019). Determining which of these competing hypotheses operated in a particular case requires us to reconstruct an evolutionary radiation where a species-poor, adaptively constrained clade diversifies into a species-rich, adaptively disparate clade.

One such radiation occurred during the Triassic Period, following the Permo-Triassic mass extinction (PTME: Raup, 1979; Erwin, 1994; Chen and Benton, 2012; Benton and Newell, 2014) as archosauriforms recovered, rapidly diversified, and spread across Pangea to dominate terrestrial ecosystems for the next 150 million years (Nesbitt, 2011; Ezcurra and Butler, 2018). In addition to Archosauriformes being a speciose and disparate radiation, they also provide an opportunity to test adaptive radiations at a higher phylogenetic level. Lineage diversification of archosaurs was rapid after the PTME, and by the Middle Triassic many non-archosaurian archosauriform and crown archosaur clades had appeared (Ezcurra, 2016; Foth et al., 2016; Ezcurra and Butler, 2018). By the Late Triassic archosaurs filled a wide variety of ecological roles, from top predators to large herbivores, and were represented in terrestrial, freshwater, and even marine ecosystems (e.g. Li et al., 2006; Butler et al., 2019). If lineage diversification occurs first, followed by subsequent ecological disparity, we would expect Middle Triassic archosauriforms from across the tree to present a limited range of ecologies. The question that arises is how best to measure ecological disparity? Ecological disparity covers a variety of physiological, behavioral, and morphological traits but the nature of the fossil record limits its measure primarily to morphology. Previous work has used cranial morphology as a measure of disparity (e.g. Foth et al., 2016); however complete, or even partial, skulls are rare for Early–Middle Triassic archosauriforms. Therefore, an alternative morphological system to approximate ecological disparity is needed. In this study we use teeth as an indicator of ecological disparity because they have relatively high preservation potential (e.g. Turner-Walker, 2008) and offer a direct link to ecology through diet (Lucas, 1979; Dessem, 1985; Scallion and Shine, 1988; Sander, 1997; Linde, Palmer & Gómez-Zurita, 2004; Santana, Strait & Dumont, 2011; Zahradnick et al., 2014). We consider diet as the aspect of ecology of interest for both the

relative ease of inference from morphology alone and the use of diet in previous studies of evolutionary radiations (e.g. Slater and Friscia, 2019).

Although tooth assemblages are rare in Middle Triassic terrestrial settings, recent fieldwork (2007, 2008, 2012, 2015, 2017) in the Manda Beds of the Ruhuhu Basin, Tanzania (Sidor and Nesbitt, 2017), has revealed a rich assemblage of archosauriforms known from postcrania and partial crania, including teeth (e.g. Nesbitt et al., 2010; 2014; Smith et al., 2018). Specifically, these teeth come from the middle and upper Lifua Member bone accumulations (Smith et al., 2018), which are thought to be Anisian in age (Rubidge, 2005) but may be as young as early Carnian (Ottone et al., 2014; Marsicano et al., 2016; Wynd et al., 2018; Peacock et al., 2018). If the Anisian age is correct, then this is one of the oldest, diverse archosaur faunas known that is also represented by specimens from historical collections (e.g. Butler et al., 2009; 2017; Nesbitt et al., 2010; 2013; 2014; 2017; Barrett, Nesbitt & Peacock, 2015). Using a combination of information from these new and historical collections, we quantify tooth disparity in this earliest part of the archosaur radiation to generate a morphospace visualization. From this we can assign isolated teeth to specific taxon, visualize inter- and intraspecific variation as well as intra-individual variation, and use this variation as a window into the ecological disparity of the archosauriforms within the Lifua Member assemblage. To achieve these goals we use a combination of *in situ* teeth from jaw elements assignable to particular species (Figure 1), and isolated teeth attributable to Archosauriformes (Figure 2). Of particular interest is whether the isolated teeth fall within, or expand, the region of morphospace occupied by the described Manda Beds taxa.

Institutional Abbreviations – **NHMUK**, Natural History Museum, London, U.K.; **NMT**, National Museum of Tanzania, Dar es Salaam, Tanzania.

2. MATERIALS AND METHODS

The 31 isolated teeth included in this study were all collected from surface accumulations of vertebrate fossils during fieldwork in 2007, 2008, 2012, 2015, and 2017 from the Manda Beds of the Ruhuhu Basin by a multi-institutional team (Sidor and Nesbitt, 2017). All of the isolated teeth included in this study are currently housed at Virginia Tech Department of Geosciences and will be permanently repositied and managed in the National Museum of Tanzania. In addition to these isolated teeth (seven of which were referred to *Nundasuchus*: see Nesbitt et al., 2014), we also included teeth from within the tooth-bearing elements of five taxonomically distinct archosauriforms from the Manda Beds: *Nundasuchus* (NMT RB48), *Parringtonia* (NMT RB426), *Asilisaurus* (NMT RB837), ‘*Pallisteria*’ (NHMUK PV R36620), and one currently undescribed pseudosuchian that we refer to –by its specimen number (NMT RB187). We assign the isolated teeth to Archosauriformes on the basis of their serration morphology (Nesbitt, 2011) as well as their general ziphodont construction, including lateral compression (e.g. Godefroit and Cuny, 1997).

To quantify tooth shape, linear measurements (total crown height, base width, and fore-aft base length) and denticle counts were made following the protocol in Smith, Vann & Dodson (2005), although due to the smaller size of the teeth in our study, we used 1 mm denticle densities, rather than 5 mm densities. All statistical analyses were performed in R (v 3.1.2) and the RStudio console (v 1.1.383). All graphs of quantitative data were made using the R package “ggplot2” (Wickham, 2009). To capture tooth disparity (from log-transformed linear measurements) we used sum of variances with 95% predictive intervals following the methodology of Larson, Brown & Evans (2016). We chose to use sum of variances as our measure of disparity due to its prevalence in the literature and its robustness when working with

small sample sizes. Sample size varied from 2–14 teeth, however, sample size does not significantly affect the sum of variance analysis (Ciampaglio, Kemp, & McShea, 2001). In *Asilisaurus* the 14 teeth largely contributed base and width measurements because only three teeth were complete enough to measure crown height. We constructed a linear model in R predicting the variable of tooth base shape (ratio of mesiodistal length over labiolingual width) by the variables of total crown height and species-level assignment such that base shape = total crown height * species assignment. The effects of each species on predicting tooth base shape were elucidated using the R package “lsmeans” (Lenth, 2016) using a pairwise comparison in the model by taxon. We plotted the teeth of known taxonomic affinity using ggplot2 (Wickham, 2009) to produce a base morphospace into which we plotted results from the isolated teeth for comparison.

Simple quantitative measurements only capture the overall shape of the teeth, and all of the teeth in the study resemble the hypothetical ancestral archosauriform tooth (serrated, recurved, and laterally compressed: Nesbitt, 2011). In order to more fully capture and describe the subtle variation of these teeth, a method of capturing discrete variation is needed. Non-metric multidimensional scaling (NMDS) is an ordination method that visualizes variation that can incorporate discrete qualitative features. We created a set of 11 binary characters for scoring isolated and *in situ* teeth for NMDS (Table 1, Figure 3). All characters except one are new to this analysis (trait 6, dental caudae = shallow grooves extending from between two adjacent denticles present/absent is taken from Abler [1992]). None of the traits used in this study have been used in phylogenetic analyses of archosauriforms, in order to avoid circular reasoning when comparing our ecological signal to taxonomic and clade identity. The NMDS analysis was conducted in PAST (Hammer, Harper & Ryan, 2001) with a Bray-Curtis transformation. We ran

an additional NMDS analysis in PAST using average taxon and morphotype scores where traits were scored for each taxon with >50% agreement of *in situ* teeth. Traits for which <50% of the specimens in the taxon or morphotype were scored as unknown (“?”).

Isolated Tooth Descriptions

Morphotype A: These teeth (Figure 2A) are generally triangular in outline in lateral view and most are recurved (the point of the crown is distal to the distal-most extent of the crown base) although the remainder have crown tips that are level with the distal-most extent of the crown base. The labial and lingual sides of the crown lack ridges (i.e. no fluting), and the labial side of the crown exhibits greater convexity than the lingual side. The mesial denticle series terminates more apically along the crown margin than the distal series, which continues along the entire height of the crown though both start at the tip of the crown. The mesial denticle series is also offset from the mesial-distal long axis of the crown base, deflecting to the lingual side toward the crown base. The denticle densities range from 2–5 per mm. Denticle caudae (Abler, 1992), which are shallow grooves extending from between two adjacent denticles, are often present and directed parallel to the denticles. These denticle caudae are most easily viewed in mesial or distal view (Figure 3F).

In general, Morphotype A teeth strongly resemble both *in situ* and isolated teeth of *Nundasuchus* (Figure 1; Nesbitt et al., 2014). Particularly important features are the presence of denticle caudae, an unequal labial-lingual curvature, and the more apical termination of the mesial denticle series relative to the distal denticle series. Also like *Nundasuchus*, teeth of Morphotype A exhibit a mix of states in the changing curvature of the mesial crown edge in lateral view, with some teeth gradually changing angles and others exhibiting an abrupt shift in

angle. The *in situ* teeth of *Nundasuchus* can exhibit either state depending on the proximity of the mesial edge of the crown to the distal edge of the preceding tooth. Though this combination of traits is only found in *Nundasuchus* in the Manda Beds fauna, archosauriforms from the Middle and Upper Triassic elsewhere (e.g. de Oliveira and Pinheiro, 2017; Schoch et al., 2018).

Morphotype B: These teeth (Figure 2B) are triangular in shape in lateral view and are occasionally recurved, although in most the apical tip of the crown is approximately level with the distal-most end of the crown base. Morphotype B tooth crowns lack fluting and, in contrast to Morphotype A, the labial and lingual curvatures are equal. None of the teeth are bulbous (no labiolingual measurements are greater than crown base width). In the majority of Morphotype B teeth the mesial margin of the crown possesses a single point where the angle of the mesial carina changes abruptly. As in Morphotype A teeth, the mesial series of denticles in Morphotype B teeth terminates on the crown further apically than the distal series, which often terminates at the crown base. However, the mesial row of denticles is in line with the mesial-distal long axis of the crown base. The denticle densities range from 3–8 per mm. Denticle caudae are present on some of the teeth and are directed parallel to the denticles. Although these teeth bear a strong resemblance to Morphotype A, they can be differentiated by their equal labial and lingual curvatures. Morphotype B teeth are similar to some of the *in situ* and isolated *Nundasuchus* teeth (Figure 1,2; Nesbitt et al., 2014).

Morphotype C: This morphotype (Figure 2C) is represented by a single tooth in our assemblage, NMT RB831. The overall shape is tall, near conical, and recurved. The crown lacks fluting and the labial curvature is greater than the lingual curvature. Although its labial-lingual curvature is unequal, the mesial denticle series is positioned along the midline of the mesial-distal long axis. The orientation of the mesial edge of the tooth changes gradually, forming a long, continuous

curve. The tooth is not bulbous. Denticle densities range from 2–4 per mm, and no denticle caudae are present. There is no variation in either the shape or size of the denticles between the mesial and distal series or along the length of the crown. Unlike either Morphotypes A or B, the mesial series of denticles in Morphotype C ends at approximately the same level on the crown as the distal series, just above the crown base.

In general size and shape, as well as in many of its discrete features, the Morphotype C tooth is similar to the teeth of ‘*Pallisteria*’ based on our observations. The teeth of the latter taxon are large, conical, recurved, and possess unequal labial-lingual curvature. The denticle density is low (< 3 per mm) in the middle part of the tooth crown and denticles show little variation in shape or size. Unfortunately, none of the ‘*Pallisteria*’ teeth could be scored for Trait 7 (termination height of the mesial denticle series; Table 1) due to poor preservation of the denticles, which otherwise differentiates Morphotype C teeth from morphotypes A and B. If Morphotype C is similar to, or is, ‘*Pallisteria*’, then subsequent ‘*Pallisteria*’ tooth discoveries should be expected to have sub-equally extending mesial and distal denticle rows.

***In situ* Tooth Descriptions**

Nundasuchus: We included a total of 13 *Nundasuchus* teeth, six *in situ* and seven isolated, originally described in Nesbitt et al. (2014). The teeth range in height from 5.6 to 22 mm with denticle densities from 2–5 per mm. All the teeth are labio-lingually compressed and are serrated on both mesial and distal margins. Only one tooth possesses a recurved tip that extends past the distal-most end on the tooth base. Most teeth are smooth on the sides with a single exception exhibiting fluting. All of the teeth possess: unequal labial-lingual curvatures, a mesial row of denticles that terminates higher on the tooth crown than the distal row of denticles, and a mesial carina that is offset from the midline. Only two of the teeth possess dental caudae and one tooth

is bulbous. In some teeth the mesial and distal denticle rows differ in size and/or in shape. About half the teeth have a distinct point on the mesial margin where the angle of the edge changes abruptly. For the *in situ* teeth this seems to be related to how close the tooth is to the preceding socket, with the closer the distance being associated with an abrupt angle shift point.

Asilisaurus: We included 14 *in situ* teeth though only three of these included more than the very base of the tooth. These three ranged in height from 1.6 to 2.9 mm and had a denticle density of ~8 per mm. The teeth are closely packed, ankylosed to the sockets, and peg-like in shape (Nesbitt et al., 2010). All of the teeth have: smooth sides, equal labial-lingual curvature, and subeven mesial and distal row of denticles. None of the *Asilisaurus* teeth possess dental caudae and the mesial edge of the teeth changes angles gradually.

Parringtonia: Of the 14 teeth in the study, 12 were *in situ* and the other two larger, isolated teeth. The teeth range in size from 2.5–21.6 mm, though the tallest *in situ* tooth is 8.3 mm, and the denticle densities vary from 5–15 per mm. Most of the *Parringtonia* teeth lacked crown tips, though the two complete teeth are not recurved. All of the teeth are labio-lingually compressed and possess fluting and a mesial carina along the midline. The mesial and distal denticle series of all the teeth remain constant in both shape and size, though the mesial denticle series terminates higher on the crown than the distal series. In all the teeth the mesial edge angle changes gradually.

NMT RB187: All 13 teeth of the teeth included from NMT RB187 are *in situ*. The labio-lingually compressed teeth range from 5.3–13.4 mm tall with denticle densities of 8–14 per mm. All of the teeth are recurved, fluted, and lack dental caudae. The mesial edge of the teeth changes gradually and follows the mesial-distal long axis. In teeth with preserved crown tips the shape of

the denticles remains constant. Of all the taxa included here, NMT RB187 exhibits the greatest degree of recurvedness.

‘*Pallisteria*’: We included 11 *in situ* teeth from the left and right maxillae of ‘*Pallisteria*’. These teeth are the largest of all the taxa, ranging from 36.1–70.3 mm, and have the lowest density, from 2–3 per mm. All except one are recurved and all have smooth crowns and lack dental caudae. Most of the teeth have uneven labial-lingual curvature and a mesial edge that changes angles gradually. The mesial carina is offset from the mesiodistal long axis in most the teeth and the denticles remains constant in shape and size along the height of the crown.

3. RESULTS

For our linear model we predicted the tooth base shape (ratio of labiolingual base width to mesiodistal base length) using the total apicobasal crown height and the taxonomic affinity of the tooth ($\text{base} \sim \text{tch} + \text{taxon}$) with the `lm()` command in base R (Table 2). We found that tooth height was not a significant predictor of base shape ($p = 0.0933$). We used the R package “`lsmeans`” to further investigate the differences between the species’ tooth shape (Table 3). From this metric NMT RB187 has a significantly higher base shape ratio than all other taxa except *Parringtonia* ($p = 0.3788$).

The sum of variances analysis (Figure 4) included all known Manda Beds archosauriform taxa with associated dentition and two of the three morphotypes, as only a single tooth of Morphotype C is present in our assemblage. These variances provide a quantification of intraspecific variation in tooth size and shape, and allow for an equal interspecific comparison. Mean variances ranged from a low of 0.02 log units in ‘*Pallisteria*’, two large isolated teeth of *Parringtonia*, and Morphotype B, to a high of 0.145 log units in Morphotype A (Figure 4).

More useful for visualizing variation than the linear model and lsmeans contrasts are morphospace plots of the teeth from our generically determinate specimens, with the isolated, unidentified teeth added for comparison. There is much overlap in morphospace occupancy, particularly on the left side (shorter height) portion of the graph, although '*Pallisteria*' occupies its own section of morphospace in taller crown heights (Figure 5). Teeth towards the bottom of the morphospace (lower base ratio) are more rounded and cone-like, whereas those with higher base ratios are more laterally compressed. With size alone two of the Morphotype A teeth fall in '*Pallisteria*' morphospace and the Morphotype C tooth with *Nundasuchus* morphospace contrary to the discrete descriptive predictions. The relationship between base width and mesiodistal base length provides little more distinction of the taxa included, and the impact of crown size is still evident (Figure 6). In general the ratio of base mesiodistal length and labiolingual width follows a linear trend controlled by size.

A total of 21 isolated teeth and 46 *in situ* teeth of known affinity were complete enough to be scored for the NMDS analysis. Convex hulls are more differentiated than in the quantitative morphospace, with almost no overlap of *Nundasuchus* with either NMT RB187 or *Parringtonia* (Figure 7). Overlap of NMT RB187 and *Parringtonia* remains, but most of the isolated teeth fall exclusively within or adjacent to the zone of *Nundasuchus* and '*Pallisteria*' (Figure 7). The high degree of overlap between *Parringtonia* and NMT RB187 likely reflects their often-shared feature of having parallel ridges (fluting) along the labial and lingual sides of the tooth crown. The only other tooth in the study with fluting is a single example referred to *Nundasuchus*. The use of taxa and morphotype 'averages' in traits reveals similar groupings to the complete dataset, with average morphotype scores between those of known taxa (Figure 8).

4. DISCUSSION

We present the first quantitative description of a Middle Triassic archosauriform tooth assemblage, which reveals substantial conservation of tooth morphology at the beginning of the archosaur radiation. Intraspecific variation appears to be as great, if not greater, than interspecific variation. Morphotype A displays the greatest variance in tooth size in the sample, although *Nundasuchus* has a very similar sum of variance structure (Figure 4). Driving at least part of the pattern we see in our disparity analysis is whether more than a single individual of a given taxon is included in our study. For example, NMT RB187, ‘*Pallisteria*’, and *Parringtonia* all display low disparity, but our sample includes only elements from a single individual of each taxon, whereas the *Nundasuchus* sample includes *in situ* teeth from one lower jaw (the holotype specimen) and associated isolated teeth assigned to the holotype (Figure 4). Although two of the isolated teeth from our assemblage fall exclusively within the ‘*Pallisteria*’ quantitative morphospace, most of the isolated teeth fall within a zone of overlap between *Nundasuchus*, NMT RB187, and *Parringtonia* (Figure 5). Much of this quantitative variation reflects body size (Figure 6). *Nundasuchus* and ‘*Pallisteria*’ are much larger than the other taxa, which helps to differentiate their morphospace from that of smaller-bodied taxa. *Asilisaurus* is the smallest taxon in our sample, but there is postcranial evidence of a larger silesaurid in the Lifua assemblage (possibly a very large individual of *Asilisaurus*; Barrett, Nesbitt, & Peacock, 2015) that would be comparable in size to *Nundasuchus* and ‘*Pallisteria*’. Recovery of teeth from silesaurid individuals of this larger size might reduce some of the differentiation between them, *Nundasuchus*, and ‘*Pallisteria*’ though we would still expect silesaurid teeth to be smaller relative to the same body size.

The NMDS ordination improves the differentiation of taxa, with *Asilisaurus* and the large-bodied predator ‘*Pallisteria*’ more clearly separated from the still overlapping undescribed

pseudosuchian, and *Parringtonia* and *Nundasuchus* exhibiting wide variation in morphospace overall, bridging the space between all taxa, and overlapping a substantial part of ‘*Pallisteria*’ morphospace (Figure 7). These results identify two general areas of morphospace, one shared by the undescribed pseudosuchian and *Parringtonia* and the other by *Nundasuchus* and ‘*Pallisteria*’. The teeth of *Parringtonia* and the undescribed pseudosuchian share several features, notably presence of fluting, a mesial carina along the midline tooth axis, and a high denticle density (≥ 3 per mm). By contrast, *Nundasuchus* and ‘*Pallisteria*’ teeth lack fluting, possess an offset mesial carina, unequal labial/lingual curvature, and have a low denticle density (< 3 per mm). This result is further supported when the average or typical score of each taxon is used, with NMT RB187, *Asilisaurus*, and *Parringtonia* clustering together versus *Nundasuchus* and ‘*Pallisteria*’ on the other side of morphospace (Figure 8). Given that many of the isolated teeth resemble those of *Nundasuchus*, it is not surprising that most of the isolated teeth fall within the convex hull defined by *Nundasuchus* (Figure 7). We cannot, however, definitely assign these teeth to *Nundasuchus* due to the overlap in discrete characters among our included taxa.

Our results using both methods demonstrate that many of the isolated teeth resemble those from currently recognized taxa. However, several teeth fall outside of the morphospace defined by known taxa and could indicate either intraspecific variation (due to heterodonty or ontogeny) or could represent other, as yet unsampled, taxa. Our methodologies are flexible and the datasets can incorporate additional specimens as they are excavated, so these approaches could be applied to other tooth assemblages throughout the Triassic across a broad range of spatial, temporal, and taxonomic scales.

Ecological Differentiation. There are some hints of dietary separation between large- and small-bodied archosaurs based on minor changes in tooth morphology and consideration of body size. However, our results, which show high degrees of overlap in tooth morphology suggest that ecological differentiation, at least in diet, appears to lag behind lineage diversification, at least with respect to Manda archosauriforms. Four of the five recognized taxa included here possess ziphodont dentitions (=labiolingual narrow crown [labiolingual width < 60% of mesiodistal length], recurved, typically serrated carinae, and no constriction at the cervix *sensu* Hendrickx, Mateus & Araújo, 2015) indicative of a carnivorous diet. Only *Asilisaurus* differs in possessing a conodont dentition (=conical crowns with small denticles or no denticles, and typically fluted *sensu* Hendrickx, Mateus & Araújo, 2015). Conodonty is present in spinosaurids, many crocodylians, marine reptiles, and pterosaurs (Hendrickx, Mateus & Araújo, 2015) and has been linked to piscivory. Following this criterion *Asilisaurus* would be categorized as a potential piscivore. However, dietary reconstructions of *Silesaurus opolensis*, another silesaurid possessing similar dentition to *Asilisaurus*, have been herbivorous or omnivorous based upon dental microwear (Kubo and Kubo, 2014) or insectivorous based upon coprolites (Qvarnström et al., 2019). Thus, in the Manda Beds tooth assemblage there are two large-bodied carnivores (*Nundasuchus* and ‘*Pallisteria*’), two small-bodied carnivores (*Parringtonia* and an undescribed pseudosuchian), and one small-bodied, non-carnivore (*Asilisaurus*). The Middle Triassic Manda Beds may, therefore, be capturing the beginning of the ‘Explosive Phase’ of Simpson’s (1944) theoretical model as lineages split and begin to move towards new adaptive zones. Further tooth assemblages will need to be evaluated to see if this is a broader trend that holds across the Triassic archosaur radiation. We posit that the qualitative NMDS ordination method gives us the necessary lens for testing this hypothesis.

5. CONCLUSIONS

Simple quantitative measures of tooth shape were of limited use in characterizing the Middle Triassic Manda Beds archosauriform tooth assemblage because of the highly conserved morphology of many specimens. Instead, an ordination based on discrete characters provided a more effective means of differentiating the teeth of distinct taxa. Nevertheless, we found little evidence for significant ecological differentiation of tooth shape between the five taxa included in our study. Most isolated teeth ($n = 17/21$) fall within the spectrum of recognized taxon variation, and the remainder represent either unsampled taxa or unsampled intraspecific variation.

Our relatively simple metrics can be used to describe subtle differences in tooth morphology. These objective methods for grouping teeth provide a complimentary method for assigning teeth to dietary roles, a practice that typically relies on qualitative comparisons to the teeth of extant taxa of known diet (e.g. Fraser and Walkden, 1983; Sander, 1999; Barrett, 2000; Hungerbühler, 2000) or other fossil taxa (e.g. Dzik, 2003; Hendrickx, Mateus & Araújo, 2015; de Oliveira and Pinheiro, 2017). Furthermore, the methods applied herein provide an evaluation of ecological disparity that is separate from the features used in phylogenetic analyses, so that we can compare these two evolutionary phenomena independently. This method is readily transferable to tooth assemblages from other localities pertaining to any vertebrate clade. Our next step will be to apply this technique to richer Middle Triassic sites, as well as Late Triassic sites, to understand how morphological and ecological diversity changed during the early stages of the archosaur radiation.

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9. TABLES

	Description
1	Tooth apex, location, relative to the distal margin of the tooth base: tip mesial to or in the same vertical plane as the distal edge (0) or tip is located more distal than the distal edge (=recurved) (1)
2	Tooth lingual/labial, surfaces: texture is smooth (lack of crenulations, ridges, etc.) (0) or surface texture possess a series of parallel ridges from tooth apex to base (=fluted) (1)
3	Tooth labial/lingual, shape: crown curvature unequal (one side expanded relative to other) (0) or equal labial and lingual curvature (1)
4	Mesial tooth margin, shape: curvature angles change gradually (0) or angle changes abruptly at a single discrete point along mesial edge (1)
5	Tooth crown, size: labiolingual widths dorsal to the tooth crown base are all less than the crown base width (0) or a crown labiolingual width dorsal to the tooth crown base is greater than the crown base width (1)
6	Mesial/distal crown margins, surfaces: denticle caudae (= grooves on crown surface from between individual denticles) are absent (0) or present (1) (from Abler, 1992)
7	Mesial margin, length: mesial denticle row ends at a point sub-equal with distal denticle row (0) or mesial denticle row ends significantly further apically on crown than distal row (1). Can only be scored for teeth with both mesial and distal denticle series.
8	Mesial/distal margins, denticle density: number of mesial and distal denticles is < 3 per mm (0), or greater than or equal to 3 per mm (1). Measurements are taken near the middle of the carina.
9	Mesial margin, location: vertical axis of the mesial carina is in line the mesial-distal long axis (0) or laterally offset from the mesial distal long axis (1)
10	Mesial/distal margins, size: average size of mesial and distal denticles are the same (0) or the average size of the mesial and distal denticles is different (1)
11	Mesial/distal margins, shape: lateral profile shape of mesial and distal denticles remains constant (0) or denticles' lateral profile changes shape (e.g. rounded to square) (1)

TABLE 1: Summary of the discrete, binary traits used for scoring teeth in the NMDS analysis.

	Estimate	Standard Error	t-value	p-value
<i>Asilisaurus</i> (intercept)	1.1285	0.1011	11.156	<0.0001
Total Crown Height (mm)	0.0059	0.0035	1.714	0.0933
Undescribed	0.3718	0.1148	3.237	0.0022
<i>Nundasuchus</i>	0.0995	0.1247	0.798	0.4290
<i>'Pallisteria'</i>	-0.1249	0.2007	-0.622	0.5369
<i>Parringtonia</i>	0.2490	0.1127	2.210	0.0321

TABLE 2: Results of linear model (base ~ total crown height + taxon). All measures of significance are calculated in reference to the intercept, *Asilisaurus*. Therefore, while the undescribed pseudosuchian and *Parringtonia* can be differentiated in the model from *Asilisaurus*, the interrelationships are unknown.

Taxon	lsmeans	Standard Error	df	Lower CL	Upper CL
<i>Asilisaurus</i>	1.2354	0.1150	46	1.0039	1.4669
Undescribed	1.6071	0.0568	46	1.4929	1.7214
<i>Nundasuchus</i>	1.3348	0.0505	46	1.2332	1.4365
<i>'Pallisteria'</i>	1.1105	0.1225	46	0.8640	1.3570
<i>Parringtonia</i>	1.4844	0.0595	46	1.3645	1.6042

Contrast	Estimate	SE	df	t ratio	p-value
<i>Asilisaurus</i> – Undescribed	-0.3718	0.1148	46	-3.237	0.0181
<i>Asilisaurus</i> – <i>Nundasuchus</i>	-0.0995	0.1247	46	-0.798	0.9299
<i>Asilisaurus</i> – <i>'Pallisteria'</i>	0.1249	0.2007	46	0.622	0.9708
<i>Asilisaurus</i> – <i>Parringtonia</i>	-0.2490	0.1127	46	-2.210	0.1944
Undescribed – <i>Nundasuchus</i>	0.2723	0.0751	46	3.625	0.0062
Undescribed – <i>'Pallisteria'</i>	0.4967	0.1571	46	3.162	0.0222
Undescribed – <i>Parringtonia</i>	0.1228	0.0677	46	1.813	0.3788
<i>Nundasuchus</i> – <i>'Pallisteria'</i>	0.2244	0.1343	46	1.671	0.4614
<i>Nundasuchus</i> – <i>Parringtonia</i>	-0.1495	0.0770	46	-1.942	0.3107
<i>'Pallisteria'</i> – <i>Parringtonia</i>	-0.3739	0.1631	46	-2.292	0.1659

TABLE 3: Pairwise comparisons of taxa used in the linear model. The undescribed pseudosuchian is readily differentiable from most taxa, with the exception of *Parringtonia*. Confidence intervals were generated using a 95% confidence level.

10. FIGURES

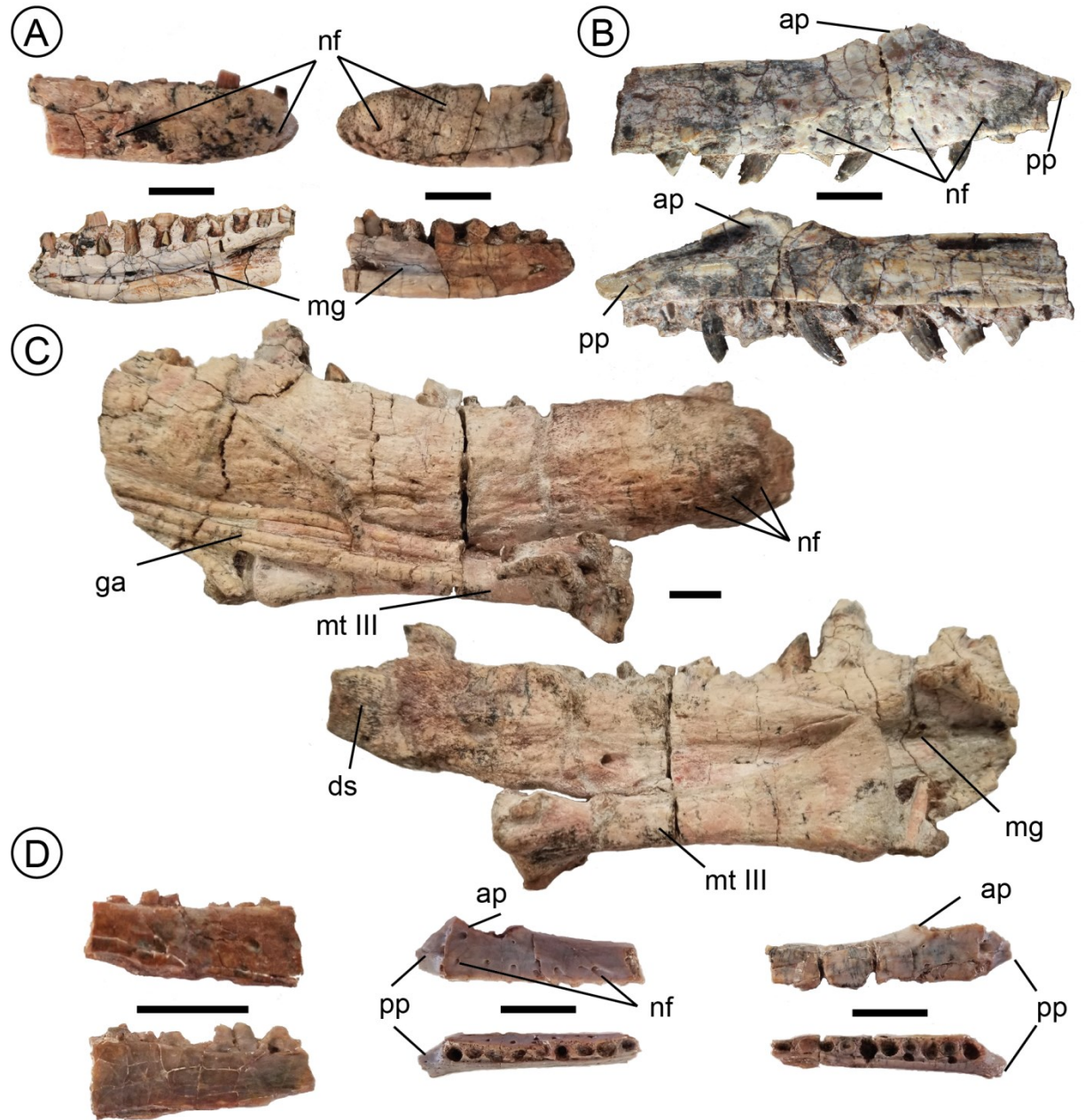


FIGURE 1: A sample of the *in situ* dental material used for baseline measurements in this study.

A – *Parringtonia* (NMT RB426) left dentary (left) in lateral (top) and medial (bottom) views and right dentary (right) in lateral and medial views. B – undescribed archosauriform taxon (NMT RB187) right maxilla in lateral and medial view. C – *Nundasuchus* (NMT RB48) holotype right

dentary in lateral and medial views. D – *Asilisaurus* (NMT RB 837) (from left to right) right dentary in lateral and medial views, left maxilla in lateral and occlusal views, and right maxilla in lateral and occlusal views. Abbreviations: ap, ascending process of the maxilla; ds, dentary symphysis; ga, gastralia; mg, Meckelian groove; mt III, metatarsal III; nf, nutrient foramen; pp, palatal process. All scale bars 1 cm.

(A)



(B)



(C)



(D)



FIGURE 2: Examples of isolated teeth from the Manda Beds tooth assemblage. A – Morphotype A specimens from left to right NMT RB807, NMT RB827, NMT RB809 in lateral and mesial views. B – Morphotype B, specimens from left to right, NMT RB810, NMT RB819, NMT RB811 in lateral and mesial views. C – sole representative of Morphotype C NMT RB831 in lateral and mesial views. D – isolated teeth of known taxa. Top – *Nundasuchus* NMT RB48. Bottom – *Parringtonia* NMT RB426 in lateral and mesial views. Scale bars A – 1 cm; B – 5 mm; C – 1 cm; D Top – 1 cm; D Bottom – 2 mm.

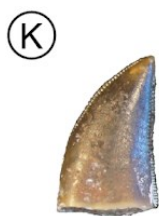
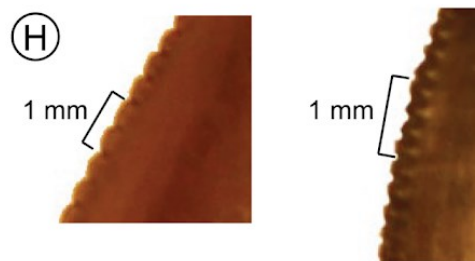
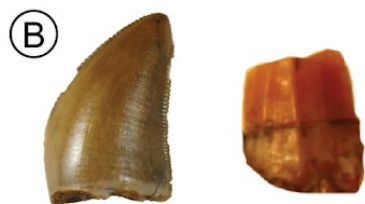
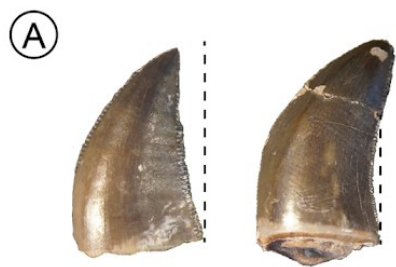


FIGURE 3: Visualization of discrete traits. In all traits score 0 on left and score 1 on right. A – Trait 1, degree of recurvature, NMT RB819 (left) and NMT RB827 (right). B – Trait 2, fluting, NMT RB809 (left) and NMT RB426 (right). C – Trait 3, labiolingual curvature, NMT RB811 (left) and NMT RB819 (right). D – Trait 4, mesial margin angle, NMT RB811 (left) and NMT RB827 (right). E – Trait 5, labiolingual bulge, NMT RB811 (left) and NMT RB48 (right). F – Trait 6, dental caudae, NMT RB809 (left) and NMT RB810 (right). G – Trait 7, mesial vs distal serration series length, NMT RB831 (left) and NMT RB810 (right). H – Trait 8, denticle density per mm, NMT RB809 (left) and NMT RB810 (right), black lines equal 1 mm. I – Trait 9, mesial margin alignment, NMT RB810 (left) and NMT RB809 (right). J – Trait 10, mesial vs distal denticle density, NMT RB810 (left) and NMT RB809 (right). K – Trait 11, denticle shape variation along crown, NMT RB810 (left) and NMT RB48 (right).

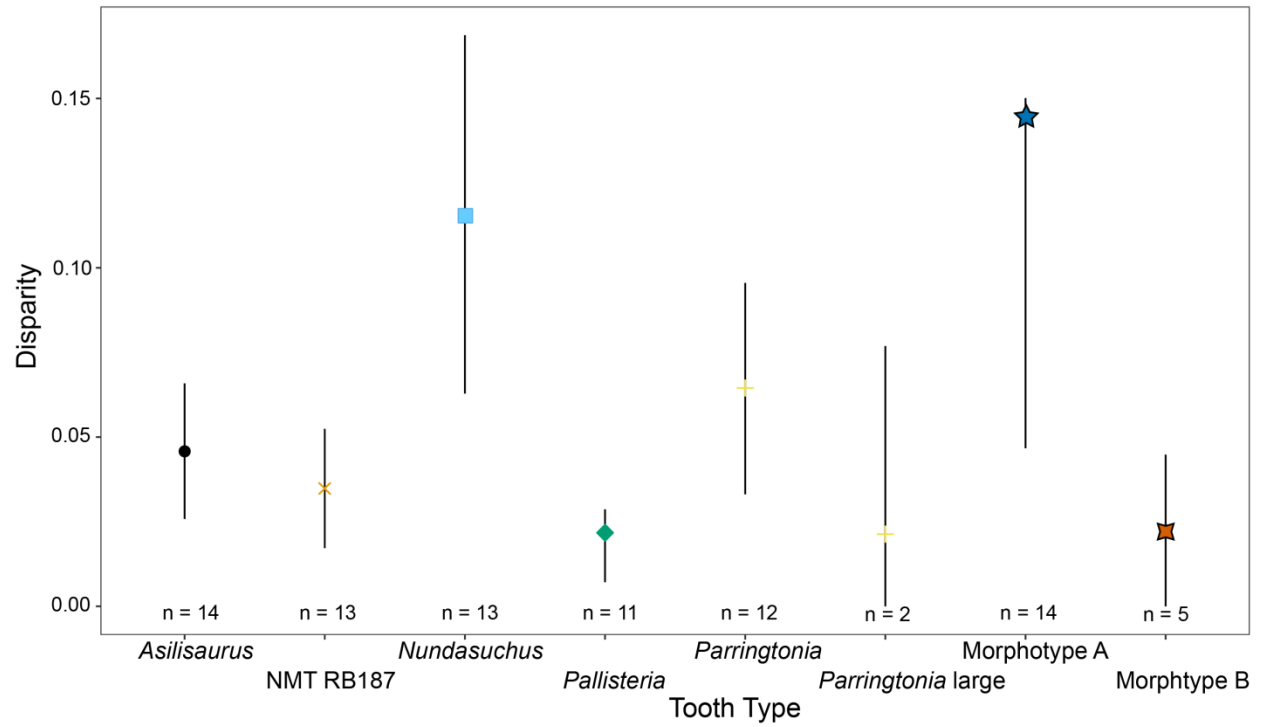


FIGURE 4: Disparity of teeth divided by taxon or morphotype. In the case of *Parringtonia* the two isolated teeth are an order of magnitude larger than the *in situ* teeth of this taxon, so this taxon was split. The sample sizes reflect the number of teeth with at least one of three measurements that was used to generate the predictive intervals.

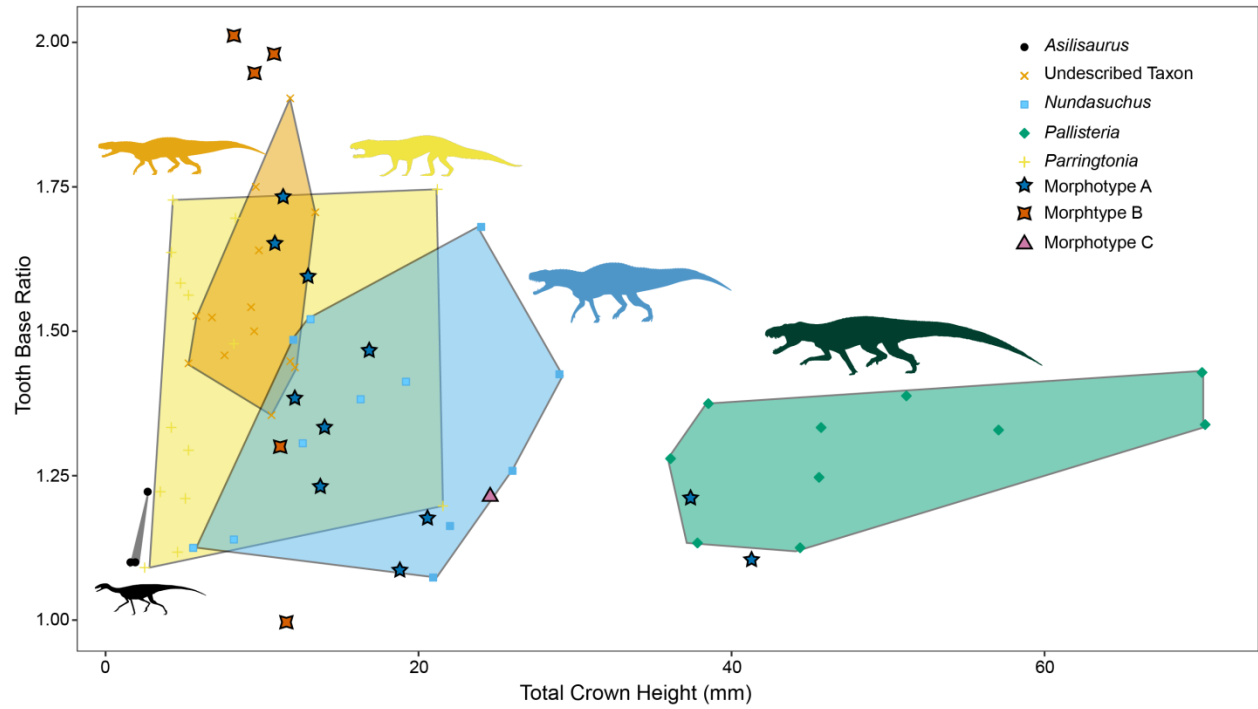


FIGURE 5: Relationship between height and base shape of teeth divided by taxon. The taxonomically unidentified teeth fall within a variety of the morphospaces generated by known taxa, rendering unambiguous referrals impossible. Some genera exhibit much greater variation in base shape ratio than others, potentially indicating a greater level of within-taxon variation.

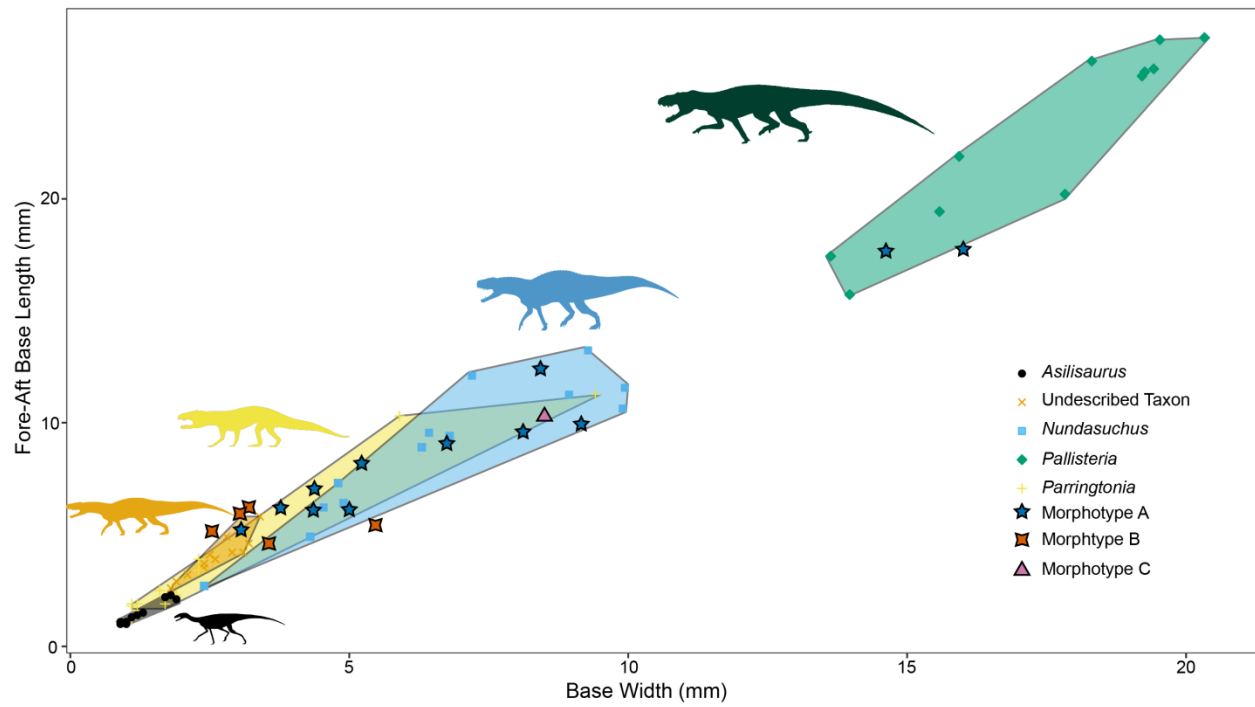


FIGURE 6: Relationship between base width and fore-aft base length divided by taxon. The overall ratio of base shape appears to be highly conserved with little deviation from the general trend. Differentiation between genera appears to be driven primarily by size.

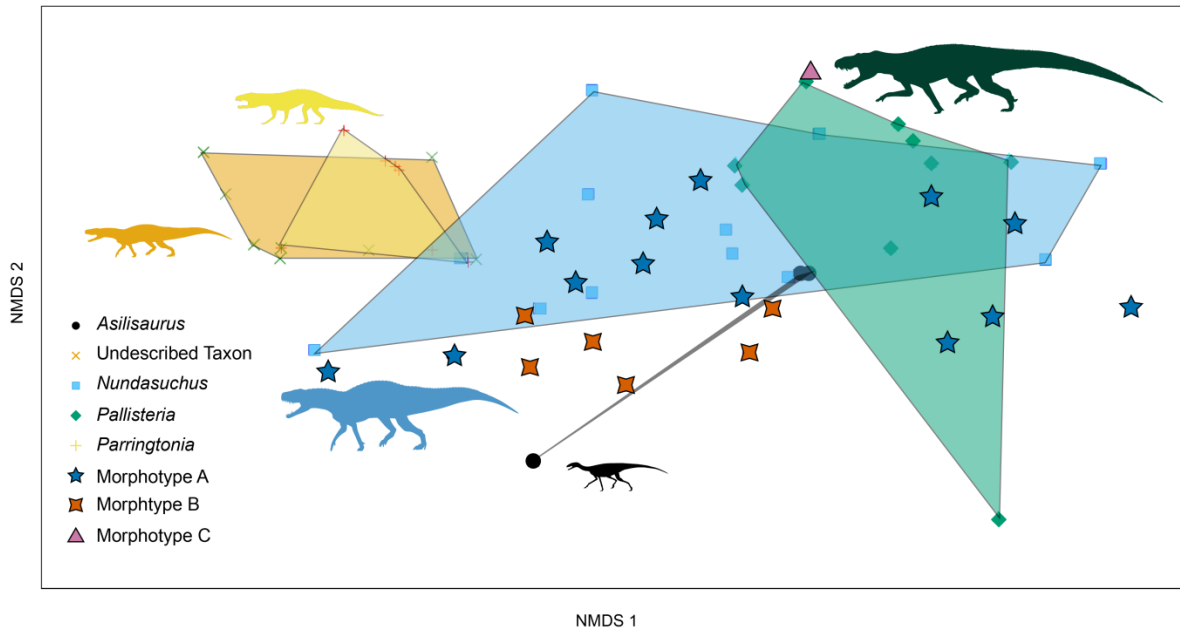


FIGURE 7: Ordination plot of first two major NMDS axes. Colored, transparent polygons represent the convex hulls of known taxa. Each point represents a separate tooth scoring. *Parringtonia* and NMT RB187 (undescribed taxon) share almost the same morphospace and there is substantial overlap between *Nundasuchus* and ‘*Pallisteria*’ also. Morphotype A appears to be more variable than Morphotype B, which is clustered closer together within a subsection of overall Morphotype A morphospace. The proximity of *Asilisaurus* to *Nundasuchus* and ‘*Pallisteria*’ is likely an artifact of incomplete scorings for *Asilisaurus* teeth.

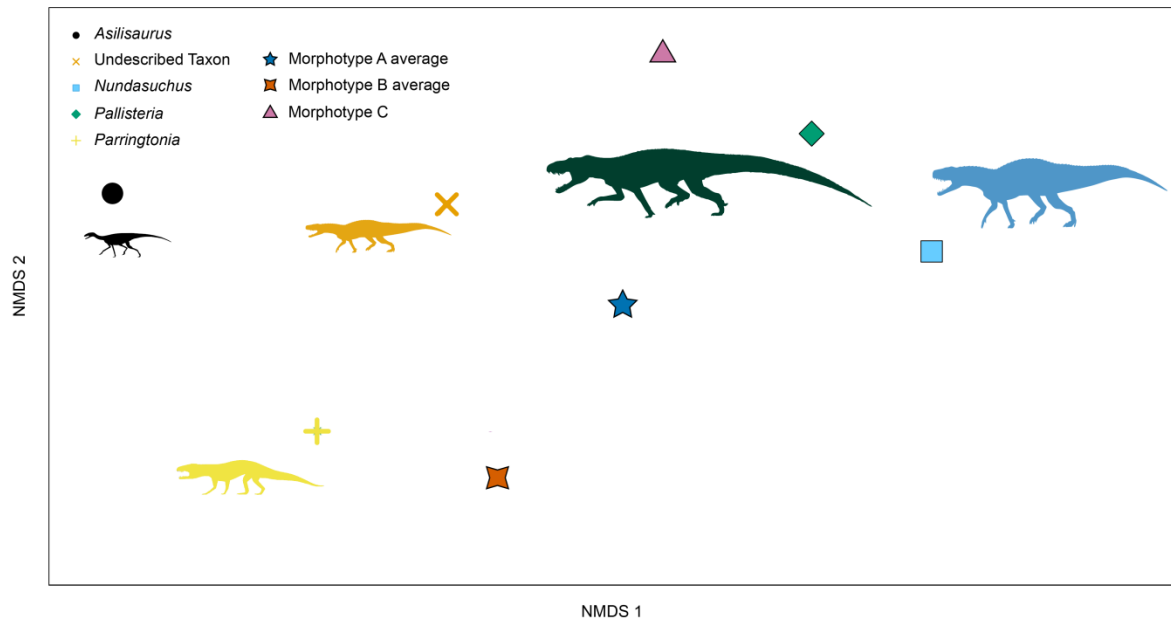


FIGURE 8: Ordination plot of first two primary NMDS axes. Taxa scoring represent “average” scores for each taxon. Only Morphotype C is represented by a single tooth. When using typical scores for taxa we find *Asilisaurus* is no longer near *Nundasuchus* and ‘*Pallisteria*’ morphospace, but on the far side of ordination space.

CHAPTER 2: Diverse reptile tooth assemblage from the Early Triassic Driefontein Locality of South Africa

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Abstract

Mass extinctions change the trajectory of evolution and restructure ecosystems. The largest mass extinction, the end-Permian, is a particularly interesting case due to the hypothesized delay in the recovery of global ecosystems, where total trophic level recovery is not thought to have occurred until 5-9 million years after the extinction event. Diapsids, especially archosauromorphs, play an important role in this recovery, filling niches left vacant by therapsids and anapsids. However, the nature of lineage and ecological diversification of diapsids is obscured by the limited number of continuous, well-dated stratigraphic sections crossing the Permian-Triassic boundary and continuing through the first half of the Triassic. The Karoo Basin of South Africa is one such record, and the late Early Triassic Driefontein locality fills an important sampling gap in the diapsid fossil record by sampling small member of the assemblage. We sampled a total of 78 isolated diapsid reptile teeth from a microvertebrate assemblage as well as 21 isolated temnospondyl teeth for comparison. From the sample, seven distinct tooth morphotypes of diapsids are recognized, six of which are not similar to previously described reptiles from the locality. We then used a combination of linear measurements, 3D geomorphometrics, and nMDS ordination to compare the morphotypes and make inferences about possible diets. Although the morphotypes are readily differentiated in nMDS, the overall morphological disparity is low, and we infer five of the seven morphotypes are faunivorous with the other two potentially omnivorous or piscivorous based on morphological similarities to dentitions of known diet. This work represents a survey of the otherwise unsampled diversity of diapsids in the Early Triassic. Although ecological specialization at Driefontein may be low, it likely records a diversity of diapsid taxa, specifically archosauromorph lineages.

1. INTRODUCTION

The end-Permian mass extinction was the largest in Earth history, resulting in the extinction of between 80-96% of marine species (Knoll et al., 1996; Jin et al., 2000; Chen and Benton, 2012; Stanley, 2016) and approximately 70% of terrestrial species (Benton and Twitchett, 2003; Chen and Benton, 2012). Accompanying these extinctions, entire ecosystems, like coral reefs (Chen and Benton, 2012) and forests (Shen et al., 2011; Benton and Newell, 2014; Zhang et al., 2016) were wiped out. One of the unique aspects of the end-Permian mass extinction is the apparent delayed recovery of both marine and terrestrial ecosystems following the extinction interval (Chen and Benton, 2012; Sun et al., 2012; Romano et al., 2013; Hochuli et al., 2016; Roopnarine et al., 2019; Viglietti et al., 2021). Global climate and ecosystems were destabilized following the end-Permian mass extinction and remained unstable throughout the Early Triassic, as evidenced by continued fluctuations in the carbon cycle, lack of coal deposition, and changes in river sedimentology (Xie et al., 2007; Sun et al., 2012; Romano et al., 2013; Hochuli et al., 2016; Dal Corso et al., 2022). Indeed, peak temperatures were not reached until almost 2 million years into the Triassic (Sun et al., 2012). This instability is associated with the “coral gap” in the marine record (e.g., Algeo et al., 2011) and the “coal gap” in the terrestrial record (e.g., Retallack et al., 2011), indicating contemporaneous loss of reef and coal-forest ecosystems. The thermal spikes in the Early Triassic are also associated with repeated extinctions in ammonoids, conodonts, bivalves, and algae, and are linked to a lack of equatorial marine vertebrates (Sun et al., 2012; Romano et al., 2013; Hochuli et al., 2016).

Marine ecosystems are not thought to have fully recovered until 5-9 million years after the end-Permian mass extinction, when the first top vertebrate predators and complete sets of marine trophic levels are again seen in the fossil record (Chen and Benton, 2012), though there

are exceptions from western North America (e.g., Brayard et al., 2017). Likewise, terrestrial vertebrate diversity does not return to pre-extinction levels until the Middle Triassic, and possibly even the Late Triassic (Benton and Newell, 2014; Hochuli et al., 2016; Hoffman et al., 2019). An exemplar clade for the Triassic terrestrial recovery is Archosauromorpha (taxa more closely related to crocodylians and birds than lepidosaurs) reptiles. These reptiles filled ecological niches left open by the extinction of therapsids and parareptiles, including large-bodied carnivorous and herbivorous roles (e.g., Romano et al., 2020). However, the timing and pattern of this recovery is still debated as phylogenetic hypotheses (e.g., Nesbitt et al., 2014; Ezcurra and Butler, 2018) and continued fossil discoveries (e.g., Gower and Sennikov, 1997; Butler et al., 2017 Nesbitt et al., 2014) place the origin of ecologically and anatomically disparate archosauromorph clades in the Early Triassic despite the delayed Triassic recovery, where “recovery” is complete, with a stable trophic system (Solé et al., 2002; Sahney and Benton, 2008). This disparity in lineage versus ecological diversification in archosauromorphs is complicated by limited radioisotopic dates in the Early to Middle Triassic and the limited number of basins that preserve terrestrial records of the end-Permian through Late Triassic recovery (see Romano et al., 2020). Reconstructing this pattern in archosauromorphs requires sampling throughout the entire Early and Middle Triassic.

The Karoo Basin in South Africa provides one of the best sampled terrestrial records from the Late Permian, the extinction interval, and much of the Triassic Period (e.g., Botha et al., 2020, Romano et al., 2020; Viglietti et al., 2021). This basin has been the subject for decades of paleontological fieldwork, providing a key window into the terrestrial biotic response and recovery from the end-Permian mass extinction (e.g., Roopnarine et al., 2019; Viglietti et al., 2021). The archosauromorph fossil record has been sampled from the Karoo Basin since the turn

of the 20th Century (e.g., Broom, 1906). Sampling within the Karoo Basin is not equal, though, and a crucial gap is in the late Early Triassic (= *Langbergia-Garjainia* Subzone, Hancox et al., 2020) inhibits reliable models of recovery (see Roopnarine et al., 2019). The late Early Triassic (Olenekian) Driefontein locality offers a glimpse into this gap, and we present the first community record of reptiles from the locality based largely on teeth. We used teeth as an alternative to skeletal remains because much of the skeletal material at the Driefontein locality is isolated and fragmentary (Hancox et al., 2020), and isolated teeth can provide both taxonomic and ecological information (Melstrom, 2017; Schoch et al., 2018; Hoffman et al., 2019; Melstrom and Irmis, 2019).

Locality

The Early Triassic (late Olenekian) aged Driefontein 11 locality of the Burgersdorp Formation in South Africa provides a rich source of vertebrate material from this poorly sampled, but key time interval. Three decades of collecting have revealed a diverse vertebrate assemblage at Driefontein, recording a lacustrine environment approximately 4 million years after the end-Permian mass extinction (Hancox et al., 1995; Shishkin et al., 1995; Hancox et al., 2020). This locality is the stratotype for the recently proposed *Langbergia-Garjainia* Subzone of the *Cynognathus* Assemblage Zone (see Hancox et al., 2020 for detailed lithostratigraphy). The age of the *Langbergia-Garjainia* Subzone is based on biostratigraphic correlation to the *Parotosuchus* Fauna of Russia (Hancox et al., 2020), which itself is correlated with Early Triassic (late Olenekian) ammonite-bearing rocks in Kazakhstan (Shishkin et al., 2000). This places the fossils at Driefontein within the 8-9 million year recovery interval proposed by past work (Chen and Benton, 2011; Smith et al., 2021), but after the *Lystrosaurus declivis* Assemblage Zone (Botha and Smith, 2020), which is thought to represent the “disaster” fauna of

the Early Triassic (Roopnarine et al., 2019; Viglietti et al., 2021). Currently, this assemblage is known to preserve freshwater non-tetrapod vertebrates including chondrichthyans (*Lissodus tumidoclavus*, *Polyacrodus* sp.), actinopterygians (*Saurichthys* sp.), and sarcopterygians (*Ptychoceratodus phillipsi*) in the form of fin spines, isolated teeth and jaw fragments (Bender and Hancox, 2004; Hancox et al., 2020). The known tetrapod record includes five species of temnospondyl amphibians (*Bathignathus poikilops*, *Kestrosaurus dreyeri*, *Kestrosaurus kitchingi*, *Parotosuchus haughtoni*, and *Trematosuchus sobeyi* [Hancox et al., 2020]), the therocephalian *Microgomphodon oligocynus* (Abdala et al., 2014), cynodonts (*Cynognathus crateronotus* and *Langbergia modisei* [Hancox et al., 2020]), isolated eucynodont teeth (Hancox et al., 2020), an indeterminate procolophonid (Hancox et al., 2020), the enigmatic diapsid reptile *Palacrodon browni* (Gow, 1999), and the erythrosuchid archosauriform *Garjainia madiba* (Gower et al., 2014). Despite the known vertebrate diversity at Driefontein, reptiles, particularly diapsids, are relatively rare, although phylogenetic hypotheses indicate early members of diapsid clades should have been present in the Early Triassic or earlier (Nesbitt, 2011; Butler et al., 2014; Ezcurra and Butler, 2018). This is in spite of abundant diapsid reptile material due to the manner of preservation in the Lower Burgersdorp Formation, where vertebrate elements tend to be isolated and not taxonomically informative at the genus or species level (Hancox et al., 2020).

2. MATERIALS AND METHODS

All isolated teeth were collected from outcrops on the farm Driefontein 11 in the Bethlehem District, Free State Province, South Africa by PJH (Fig. 1,2). Microvertebrate-rich sediment was collected from lag deposits at Driefontein 11. Sediment was then screened through sieves and picked under a light microscope. Teeth are currently on loan to the Virginia Tech Department of Geosciences and will be permanently repositied in the Evolutionary Studies Institute (University

of the Witwatersrand, Johannesburg, South Africa). In addition to measurements on isolated teeth from the locality, comparative measurements were taken from *in situ* teeth and alveoli of *Garjainia madiba* (NMQR 3051; BP/1/5525, 6232, 7138, 7153), which is known from the locality and other equivalent strata (Hancox et al., 2020). Approximately half the isolated reptile teeth can be assigned to Archosauriformes based on the presence of serrations (Nesbitt, 2011, character 168, states 1 & 2) and ziphodont morphology, including labial-lingual compression (Godefroit and Cuny, 1997). The remaining teeth may represent archosauromorphs, but can only be assigned to Reptilia due to the high degree of convergence among reptile teeth (e.g., Parker et al., 2005; Haridy et al., 2018; Melstrom and Irmis, 2019). We identified temnospondyl teeth by the presence of plicidentine and labyrinthine enamel, and the equally spaced, apico-basally straight grooves on the lateral surfaces.

A total of 78 reptile and 21 temnospondyl teeth were used in this study, although some analyses could only be performed on subsamples of the total sample. To quantify tooth morphology, linear measurements (total crown height, fore-aft basal length, basal width) to the nearest tenth mm and denticle densities (denticles per 1 mm) were taken using a digital caliper. These linear measurements were used to reconstruct the overall shape and size variation (Fig. 3,4) of the teeth as in Hoffman et al. (2019) using the package ‘ggplot2’ (Wickham, 2011) in the R environment (v. 4.1.1) with RStudio (v. 2021.9.1.372). We then controlled for size variation in the teeth by dividing total crown height by both fore-aft basal length (Fig. 5) and basal width by total crown height (Fig. 6). However, linear measurements are limited in their ability to capture the morphology of 3D structures. The past two decades have seen a surge in quantitative methods for quantifying tooth morphology, especially with regards to reptiles such as 2D/3D geometric morphometrics (e.g., Ciampaglio et al., 2005; Rajabizadeh et al., 2021), OPCR (e.g.,

Melstrom 2017; Melstrom and Wistort, 2021), and nMDS (Hoffman et al., 2019; see below).

Here we use 3D morphometrics to compare shape variation between tooth morphotypes using 3D semilandmarks and nMDS to ordinate features of tooth morphology.

For our 3D morphometrics, we generated 3D models of 92 individual teeth from μ CT scans made using a SkyScan 1172 located at Virginia Tech. All scans were conducted with the following settings: medium camera with 34.9 μ m pixel, rotation step of 0.9, frame averaging of five, random movement of 10, 360° rotation, an Al + Cu filter, and X-ray with 70 kV voltage, 142 μ A current, and 10 W power. The μ CT data were transformed into individual mesh models of each tooth using MeshLab (v. 2020.12, Cignoni et al., 2008). Mesh models were imported into the SlicerMorph module (Rolfe et al., 2021b) of the platform 3DSlicer (v. 4.11.0, Fedorov et al., 2012) and pseudolandmarks were placed using the PseudoLMGenerator extension (Rolfe et al., 2021a). We used the SlicerMorph extension ALPACA (Porto et al., 2021) to apply the same pseudolandmarks to all other meshes and following the recommendation of Porto et al. (2021), we used different template meshes from three different morphotypes to test for bias in template pseudolandmarks. A template mesh is necessary for creating the cloud of pseudolandmarks that are then placed on all other tooth meshes. We used Morphotype A (A382), D (A660), and E (A177) to test for any effect of template choice and these teeth were chosen because of their high level of completeness. Because there was no visual difference in results the A177 results were chosen arbitrarily. As all results were similar, we only present the results of one template using 321 pseudolandmarks (but see supplementary material). Due to current incompatibility between ALPACA in SlicerMorph and the R package ‘geomorph’ we used the R package ‘SlicerMorphR’ to convert the pseudolandmark data from SlicerMorph into a usable format (see supplementary). We then conducted PCA using ‘geomorph’ in the R environment (Fig. 7), and then a secondary

PCA on a modified set of teeth with outliers from the initial PCA removed (Fig. 8). This was used to produce thin-plate splines for visualization of PCs (Figs. 7-8).

As teeth are complex structures with features such as serrations, grooves, ridges, etc. that can have functional and phylogenetic implications, we use nMDS to capture qualitative features of teeth in a quantifiable and reproducible way. We created a set of 13 discrete characters, with 2-3 character states each, that capture morphology relevant to our sample of teeth. Nine are taken from Hoffman et al. (2019), one from Abler (1992), and the remaining three were created for this analysis (Table 1, Fig. 2). We used paleontological statistics (PAST, v. 2.17c, Hammer, et al., 2001) to run the nMDS analysis on 72 isolated reptile teeth using a Bray-Curtis transformation (Fig. 9). We ran an additional analysis with 21 temnospondyl ind. teeth included for additional comparisons (Fig. 10).

3. RESULTS

Morphotype A: The second most common tooth morphotype at the Driefontein locality (n = 18, Fig. 1A). They likely have thecodont implantation with deep roots, although they could also be ankylotheodont as the two are difficult to distinguish using isolated teeth. Within our sample, teeth varied in crown height from 2.4 to 18.9 mm, fore-aft basal length from 1.3 to 11 mm, and in basal width from 0.9 to 9.8 mm. These teeth are scalene triangular when viewed labio-lingually and are sometimes recurved (i.e., the tip of the tooth extends distally past the distal end of the crown base), but in the other cases the tip of the tooth is nearly even with the crown base. The crown surface lacks apico-basally oriented ridges and valleys (= fluting), and the labial surface is more convex, resulting in unequal labio-lingual curvature. In some Morphotype A specimens, the mesial edge of the tooth changes gradually but in others there exists a single point on the mesial edge that abruptly shifts angles. The fore-aft basal length of the crown is longer

than the labio-lingual width such that the tooth is slightly labio-lingually compressed.

Morphotype A teeth possess both mesial and distal serrated carinae. In some cases, the mesial carina is offset from the long axis of the tooth base. The distal series of denticles extends from the tip of the tooth to the crown base, but the mesial series only extends from the tooth tip partly down the crown. The denticles are often square shaped with others rounded and remain the same shape throughout the denticle series. The denticle density varies from 4 per mm in the largest teeth to 12 per mm in the smaller teeth, though the density varies along the carinae. Dental caudae (*sensu* Abler, 1992), shallow grooves between adjacent denticles, are present along the series and oriented perpendicular from the carina.

All known *Garjainia madiba* material bears this morphotype; however, we do not refer all morphotype A specimens to *Garjainia* because similar tooth morphology appears in archosauriforms from other localities, such as *Nundasuchus songeaensis* (Hoffman et al., 2019) and *Batrachotomus kupferzellensis* (Schoch et al., 2018).

Morphotype B: The third most common morphotype from our sample (n = 14, Fig. 1B). These teeth have a rounded hollow beneath the crown indicating an acrodont attachment. They range from 1.1 to 7.8 mm in total crown height, in fore-aft basal length from 0.7 to 3.2 mm, and in basal width from 0.9 to 3.8 mm. The tooth outline is isosceles triangular in labial/lingual view and is sometimes hooked, where the tooth tip is lingual to the lingual most edge of the crown base (= hooked), though in most the tooth tip is even with the distal end of the crown base. The labial and lingual surfaces of the teeth are covered apically-basally directed ridges and valleys (= fluting), and the labial curvature is convex whereas the lingual curvature is concave in mesial view. Unlike all the other reptile teeth of the Driefontein locality, morphotype B teeth have a longer basal width than fore-aft basal length (= bulbous). These teeth have both a mesial and

distal carina but lack any serrations on either carinae except for a single case (A845) which completely lacks a mesial carina. In most cases the mesial carina is along the fore-aft basal length axis, but there are two specimens where this is offset.

Morphotype C: This morphotype is the fourth most common in our sample ($n = 5$, Fig. 1C).

Two of these teeth are still attached to jaw fragments (A163 and A912), clearly showing thecodont implantation. These teeth range from 1.5 to 4.7 mm in total crown height, fore-aft basal length from 1 to 2.5 mm, and in basal width from 0.7 to 2.2 mm. Morphotype C teeth are scalene triangular in profile in labial/lingual view and are not recurved, although the distal margin is convex in lateral view. The labial and lingual surfaces are smooth and in all but one case the labial surface exhibits a greater degree of curvature. The fore-aft basal length is greater than the basal width, resulting in a slight labio-lingual compression. Both the mesial and distal edges have carinae, but only the distal carina possesses a denticle series. Most morphotype C teeth are too poorly preserved for accurate denticle density measurements, but in those that are well preserved, distal denticle densities vary from 9 to 12 denticles per mm. When denticles are preserved they remain a constant size and rounded shape along the denticle series. In some cases, dental caudae are present.

Morphotype D: The most common morphotype in our sample ($n = 32$, Fig. 1D). Most of the tooth crowns are broken above the root, but one example (A660) is preserved with a deep root that points to thecodont or ankylothecodont implantation. Teeth vary from 0.8 to 4.8 mm in total crown height, fore-aft basal length from 0.7 to 3.1 mm, and in basal width from 0.6 to 2.5 mm. These teeth are isosceles triangular in profile when viewed labial/lingual or distally and the tip of the tooth crown is within the area of the crown base (neither recurved nor hooked). The labial and lingual surfaces are smooth, and the labial margin is expanded relative to the lingual margin

in mesial or distal view. All teeth are bi-carinate and lack denticles. Unlike morphotype B, the other non-serrated, bi-carinate tooth morphotype, the fore-aft basal length is always greater than the basal width such that the tooth is slightly labio-lingually compressed. The mesial carina is most often along the long axis of the crown base.

Morphotype D teeth superficially resemble the temnospondyl teeth present at the Driefontein locality. In both cases the teeth are bi-carinate and lack serrations, are generally not recurved, and have a more pronounced labial surface. However, the temnospondyl teeth all possess deep grooves along the labial and lingual surfaces and plicidentine enamel (= labyrinthodont).

Morphotype E: The fifth most common morphotype in our sample (n = 5, Fig. 1E). As all the examples are mostly broken above the gumline, determining the implantation style is difficult, though G983 seems to show a transition from crown to root, suggesting thecodont or ankylotheodont implantation. Teeth range in size from 1.8 to 5.3 mm in total crown height, fore-aft basal length from 1 to 2.5 mm, and in basal width from 0.7 to 1.5 mm. In lateral view, these teeth are scalene triangular in profile and are recurved. The labial and lingual surfaces feature apically-basally oriented ridges, and the surfaces are approximately equal in their degree of curvature. As in most of the morphotypes, the fore-aft basal length is greater than the basal width, although in morphotype E the degree of labio-lingual compression is more extreme than other Driefontein morphotypes on average. All morphotype E teeth have a mesial and distal carina, though only the distal carina has denticles. The denticle series are poorly preserved in most specimens, but where reliable measurement can be taken denticle density is about 10 per mm. The denticles are rounded in lateral view and remain the same shape along the distal carina, although the size of the denticles change, with the largest near the crown base. The mesial carina always forms parallel to the long axis of the crown base.

Morphotype F: The least common morphotype in our sample ($n = 3$, Fig. 1F). Teeth are deeply rooted with thecodont or ankylothecodont implantation (E431). Teeth range in size from 0.9 to 3.2 mm in total crown height, fore-aft basal length from 0.7 to 1.7 mm, and in basal width from 0.5 to 1.1 mm. These teeth have a scalene triangular outline in lateral view and are recurved. The labial and lingual faces of the teeth are smooth, and both the labial and lingual faces have similar amounts of curvature. The fore-aft basal length is greater than that of the basal width such that teeth are laterally compressed. Morphotype F teeth have mesial and distal carinae but lack denticles on either. The mesial carina is along the midline of the long axis of the fore-aft basal length.

Morphotype G: The second least common morphotype in our sample ($n = 4$, Fig. 1G). All four teeth are broken above the crown base, making determining tooth attachment impossible in our sample. Teeth range in size from 8.3 to 11.2 mm in total crown height, fore-aft basal length from 3.5 to 4.9 mm, and in basal width from 2.4 to 3.3 mm. In labial view this morphotype is scalene triangular in outline and tends to be recurved. The labial and lingual surfaces of the teeth bear apically-basally oriented ridges and are equal in their labio-lingual curvatures. The fore-aft basal length is greater than that of the basal width such that morphotype G teeth are laterally compressed. These teeth have denticle bearing carinae on mesial and distal edges with the density of denticles varying from 5 to 8 per mm across the morphotype. Along the crown the denticles remain the same shape and size with square denticles. The mesial carina parallels the fore-aft basal length long axis.

Morphometric results

To visualize shape and size variation among the tooth morphotypes, we first used bivariate plots of linear measurements and included teeth from specimens of *Garjainia madiba* for

comparison. Within this sample, there is much overlap in morphospace occupancy, particularly on the left side of the plot (smaller sizes), with the taller *Garjainia madiba* teeth commonly on the right side of the plot (Figs. 3-4). Along the vertical component teeth with high values are more laterally compressed and those closer to a value of one have rounded bases (Fig. 3). Only Morphotype B falls below a base ratio value of one with bases wider than long (=bulbous). With crown height alone, three of the Morphotype A teeth fall within the *Garjainia madiba* space (Fig. 3), consistent with our descriptive predictions. When we break up the crown base ratio into its components, we see all morphotypes tend to follow a trend along the 1:1 line (Fig. 4). Again, the primary separation is based on tooth size with the larger *Garjainia* occupying the upper right quadrant of the plot. Because size appears to be the primary factor dividing morphotypes in the previous plots, we repeated these comparisons while controlling for size. When tooth base ratio is compared to total crown height divided by tooth base length, *Garjainia* is no longer separate from the isolated teeth morphotypes and most differentiation between morphotypes is along the vertical axis (Fig. 5). Comparing fore-aft base length divided by total crown height to base width divided by total crown height reduces variation from size, but likewise does not result in readily distinguishable morphospaces (Fig. 6). The exception is Morphotype B which consistently lies below the 1:1 line, indicative of a tooth base that is wider than long (=bulbous).

To more fully investigate tooth disparity we used 3D pseudolandmarks and visualized shape using a PCA plot (Fig. 7). The results presented in the main text use a Morphotype E tooth (A177) as the template, see supplementary materials for other 3D results using different template morphotypes. The first two principal components (PCs) represent approximately 50% of the total variation in the dataset (PC1 = 27.8% and PC2 = 21.5%) and are the axes we focus on for our results. PC1 seems to primarily capture the location of the tooth tip relative to the tooth base (=

recurvedness) with more recurved teeth negatively loaded and straight teeth positively loaded and lateral profile of the teeth with more spadelike teeth negatively loaded and more conical teeth positively loaded (Fig. 7). PC2 describes the labio-lingual width relative to mesio-distal length (=robustness), with more robust teeth positively loaded and more gracile teeth negatively loaded (Fig. 7). However, the majority of individual teeth cluster in the center of the plot with the morphotypes overlapping. We then excluded the teeth at the edge of the PCA plot as outliers (non-statistical determination) and repeated the same process. The first two PCs still represent almost 50% of the total variation (PC1 = 27.8% and PC2 = 19.3%). However, in this PCA plot, PC1 and PC2 seem to represent the opposite components of PC from the previous analysis. PC1 represents the lateral profile with more spadelike teeth positively loaded and more conical teeth negatively loaded (Fig. 8). PC2 then describes the recurvedness of teeth where more positively loaded values are strongly recurved, and negatively loaded values are again straighter (Fig. 8). Unlike the previous PCA (Fig. 7), in this morphospace plot the individual teeth are more separated (Fig. 8). However, there is still no obvious visual way to differentiate between morphotypes due to the high degree of overlap in data points.

The nMDS analyses resulted in clearer differentiation between the morphotypes and less overlap in convex hulls. In the reptile teeth only analysis, there is no overlap in tooth morphotypes at all (Fig. 9). The first major axis (nMDS 1) seems to be split by serrations and denticles, the two non-serrated morphotypes weighted negatively, with serrated morphotypes weighted positively. The second major axis (nMDS 2) continuum is less apparent but appears to be related to symmetry where the more positively weighted values corresponding to equal labio-lingual curvature and a midline mesial carina, and negatively weighted values corresponding to unequal labio-lingual curvature and an offset mesial carina. When the analysis is re-run with the

additional 21 temnospondyl teeth, some of the morphotypes overlap (Fig. 10). Specifically, the temnospondyl convex hull almost entirely overlaps Morphotype D's convex hull and there is minor overlap between Morphotype A and Morphotype C (Fig. 10).

4. DISCUSSION

We here present the first description of the abundant reptile tooth morphotypes present at the rich Early Triassic Driefontein 11 locality, which indicates a hitherto unknown diversity of diapsids. As in previous work on tooth disparity, there is substantial intra-morphotype variation, similar to that of the inter-morphotype variation (Hoffman et al., 2019). As expected, the large-bodied *Garjainia madiba* teeth dominated the larger size regions of morphospace as all known *G. madiba* material is from large individuals (Figs. 3,4). Morphotype A is the only isolated tooth morphotype that overlaps with *Garjainia madiba* in morphospace with size included (Figs. 3,4). Given the size range of Morphotype A, it is possible that it represents an ontogenetic sampling of *G. madiba*, which would indicate *G. madiba* maintained the same tooth morphology through growth. This offset from isolated tooth morphotypes was lost when we controlled for individual tooth size, and the *Garjainia madiba* teeth overlapped with several distinct morphotypes (Figs. 5,6). All the isolated teeth morphotypes overlap with one another, especially when size is controlled for, except for Morphotype B (Figs. 3-6). This is due to Morphotype B being the only set of teeth that have a tooth base width greater than the corresponding fore-aft basal length (=bulbous). Since the base ratio is ≤ 1 , Morphotype B falls below all other morphotypes in the study (Figs. 3-6).

Rather than capturing differences between the morphotypes, the PCA plots enable visualization of overall trends in shape difference among the entire sample of teeth. The first takeaway from the PCA plots is the conservation in overall tooth morphology among diapsids in

our sample. Despite using over 300 pseudolandmarks for the tooth meshes there was no clear separation between tooth morphotypes in the plots. This is unsurprising given that many of the differences between morphotypes, like serrations or carinae, are too small to be detected at computationally relevant pseudolandmark sampling. Instead, from the 3D geomorphometrics we were able to use the thin-plate splines (TPS) as a summary of tooth morphology variation across a spectrum, similar to the utility of TPS in other tooth assemblages (e.g., Grossnickle and Polly, 2013; Bazzi et al., 2018). This does a better job than the linear measurements of capturing shape and could be useful for determining features of interest in a tooth assemblage. For example, that recurvedness of teeth was a major variant, which also appeared to be an important axis of variation in the nMDS plots.

We recovered the tooth morphotypes in our study as distinct morphospace occupants using nMDS ordination unlike previous work (Hoffman et al., 2019). This is not true when we include the temnospondyl teeth, which have many similarities to Morphotype D teeth that were used for the discrete character scoring. Regardless, this provides us strong quantitative evidence that our tooth morphotypes are valid assignments and indicates nMDS is the preferred method for testing the validity of morphotype descriptions over arbitrary identifications of morphotype assignments.

When interpreting possible ecological differentiation between the tooth morphotypes, we use both tooth size and morphology. Five of the seven morphotypes are single pointed, labio-lingually compressed, and serrated to different degrees, all indicative of faunivory (Hendrickx et al., 2015; Schoch et al., 2018; Melstrom and Irmis, 2019). The variation among the faunivores is primarily due to size with teeth of *Garjainia madiba* and Morphotype A being orders of magnitude larger than the smaller morphotypes (Fig. 3,4). The other two morphotypes (B and D)

lack serrations, recurvedness, and other “hallmarks” of faunivorous diet, though they also lack the complexity associated with herbivory (Melstrom and Irmis, 2019). Therefore, it is difficult to assign these morphotypes to a trophic position, although the similarity to temnospondyl teeth could indicate a piscivorous diet (Fortuny et al., 2016). A single reptile tooth with coarse serrations that superficially resembles azendohsaurid teeth (e.g., Flynn et al., 2010) was found after the initial loan of material and could not be included in the analyses. However, its presence indicates that there were archosauromorphs, or another reptile, filling herbivorous roles during the late Early Triassic at Driefontein. Given the rarity of this type of tooth, this may represent a rarity in the paleocommunity. However, no other skeletal material from an azendohsaurid or other herbivorous reptile have been recovered from the Driefontein locality, making this the first observation of a new kind of reptile in the ecosystem.

Overall, the high overall similarity of the Driefontein teeth we examined agrees with previous work that the recovery of diverse ecosystems was delayed until the Middle Triassic or possibly even Late Triassic (e.g., Hoffman et al., 2019; Roopnarine et al., 2019). Despite phylogenetic evidence indicating that archosaur and other reptile clades are present in the Early Triassic (Butler et al., 2014; Ezcurra and Butler, 2018), the ecological expansion of these groups appears to lag behind. This may be indicative of the earlier phase of Simpson’s (1944) theoretical adaptive zone model, where lineages split prior to reaching new adaptive zones. As more microvertebrate tooth assemblages are described throughout the Triassic recovery from the end-Permian extinction, the picture of terrestrial ecosystem recovery will become clearer.

5. CONCLUSIONS

1. We present the first description of the abundant Driefontein Locality reptile tooth assemblage and a quantitative analysis of the tooth morphotypes.

2. Consistent with the hypothesis of a delayed recovery from the end-Permian mass extinction, the reptile teeth of the late Early Triassic Driefontein Locality seem to retain limited morphological disparity and inferred ecological breadth. This further supports the hypothesis of offset lineage splitting and ecological specialization in archosaurs during the Triassic.
3. Next steps for gauging reptile diversification and ecological specialization at the Driefontein Locality should focus on *in situ* teeth, that is teeth within jaws, to provide more certain taxonomic assignments, and provide estimates for individual variation in tooth morphology as well as test for heterodonty. The use of CT to visualize the morphology of replacement teeth can help in cases where erupted teeth are missing from sockets. Other methods of dietary interpretation for teeth should be used to confirmed ecological interpretations of morphotypes, like OPCR (e.g., Melstrom and Imris, 2019), microwear (e.g., Bestwick et al., 2020), and enamel microstructure (e.g., Whitney and Sidor, 2019; Hoffman et al. 2021).
4. The Driefontein Locality offers an important window into the terrestrial biotic recovery from the end-Permian mass extinction and our description of multiple tooth morphotypes shows there is a greater diversity of archosauromorphs and other diapsids than are currently known for the locality. Furthermore, microvertebrate tooth assemblages can be used both as a preliminary survey of bonebeds to gauge potential missing diversity and to make ecological inferences about ecosystem paleocommunities (e.g., Carrano et al., 2016; Schoch et al., 2018; Hoffman et al., 2019).

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7. TABLES

	Trait Description
1	Tooth apex, location, relative to the tooth base: tip within or above the edge of the tooth base (0), tip is located more distal than the distal edge (=recurved) (1), or lingual to the lingual most edge of the tooth base (2) (modified from Hoffman et al., 2019)
2	Tooth lingual/labial, surfaces: texture is smooth (lack of crenulations, ridges, etc.) (0) or surface texture possess a series of parallel ridges from tooth apex to base (=fluted) (1) (from Hoffman et al., 2019)
3	Tooth labial/lingual, shape: crown curvature unequal (one side expanded relative to other) (0) or equal labial and lingual curvature (1) (from Hoffman et al., 2019)
4	Mesial tooth margin, shape: curvature angles change gradually (0) or angle changes abruptly at a single discrete point along mesial edge (1) (from Hoffman et al., 2019)
5	Tooth crown, size: labiolingual widths dorsal to the tooth crown base are all less than the crown base width (0) or a crown labiolingual width dorsal to the tooth crown base is greater than the crown base width (1) (from Hoffman et al., 2019)
6	Mesial/distal crown margins, surfaces: denticle caudae (= grooves on crown surface from between individual denticles) are absent (0) or present (1) (from Abler, 1992)
7	Mesial/distal crown margins, surfaces: no serrations on either mesial or distal surface/carina (0) serrations on distal carina but no serrations on mesial surface (1), or serrations present on both mesial and distal carinae (2)
8	Mesial/distal margins, denticle density: number of mesial and distal denticles is < 6 per mm (0), or greater than or equal to 6 per mm (1). Measurements are taken near the middle of the carina. (modified from Hoffman et al., 2019)
9	Mesial margin, location: vertical axis of the mesial carina is in line the mesial-distal long axis (0) or laterally offset from the mesial distal long axis (1) (from Hoffman et al., 2019)
10	Mesial/distal margins, size: average size of mesial and distal denticles are the same (0) or the average size of the mesial and distal denticles is different (1) (from Hoffman et al., 2019)

11	Mesial/distal margins, shape: lateral profile shape of mesial and distal denticles remains constant (0) or denticles' lateral profile changes shape (e.g., rounded to square) (1) (from Hoffman et al., 2019)
12	Mesial margin, surface: the mesial surface of the tooth is smooth (0) or the mesial surface possesses a carina (1). Note this feature can still be scored (1) even if carina lacks serrations (Trait 7, State 0).
13	Mesial/distal margins, shape: lateral profile shape of mesial or distal denticles (if present) are square (0) or rounded (1)

Table 1: Summary of discrete, descriptive features of isolated teeth used in NMDS analysis.

8. FIGURES

A



B



C



D



E



F



G



FIGURE 1: Examples of isolated teeth from Driefontein locality divided by morphotypes.

(A) Morphotype A specimen in lateral and mesial views. (B) Morphotype B specimen in lateral and mesial views. (C) Morphotype C specimen in lateral and mesial views. (D) Morphotype D specimen in lateral and mesial views. (E) Morphotype E specimen in lateral and mesial views. (F) Morphotype F specimen in lateral and mesial views. (G) Morphotype G specimen in lateral and mesial views. All models made from CT data.

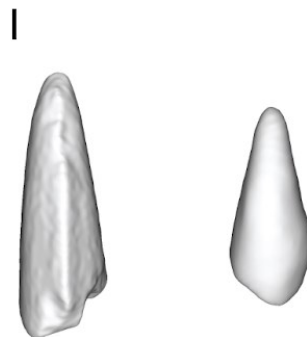
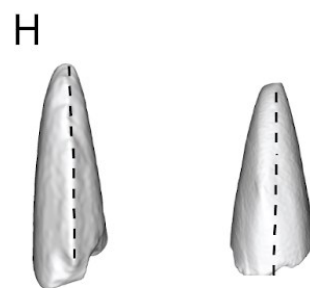
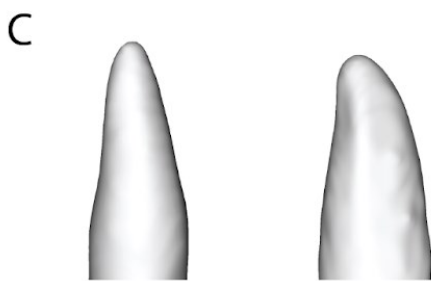
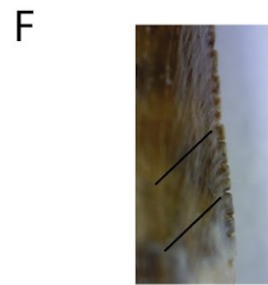
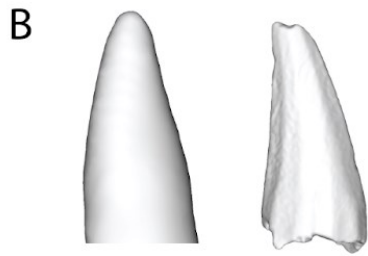
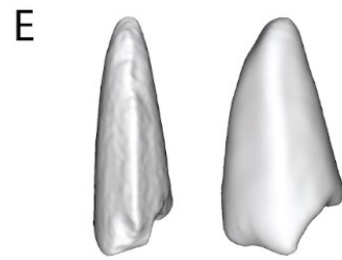
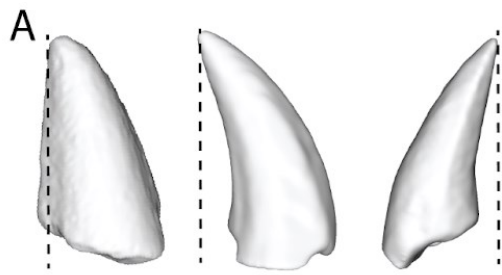


FIGURE 2: Visualization of traits used in discrete character analysis nMDS. Examples of teeth with different character states, see Table 1 for full descriptions of traits. (A) recurvedness point above base (left), recurved distally (center), recurved lingually (right), (B) fluting absent (left), present (right), (C) labio-lingual curvature even (left), unequal (right), (D) continuity of mesial edge continuous (left), abrupt shift (right), (E) bulbous – compressed (left), bulbous (right), (F) presence of dental caudae, (G) location of serrations – none (left), distal (center), mesial and distal (right), (H) position of mesial carina midline (left), offset (right), (I) presence of mesial carina present (left), absent (right). Traits 8, 10-12 not shown.

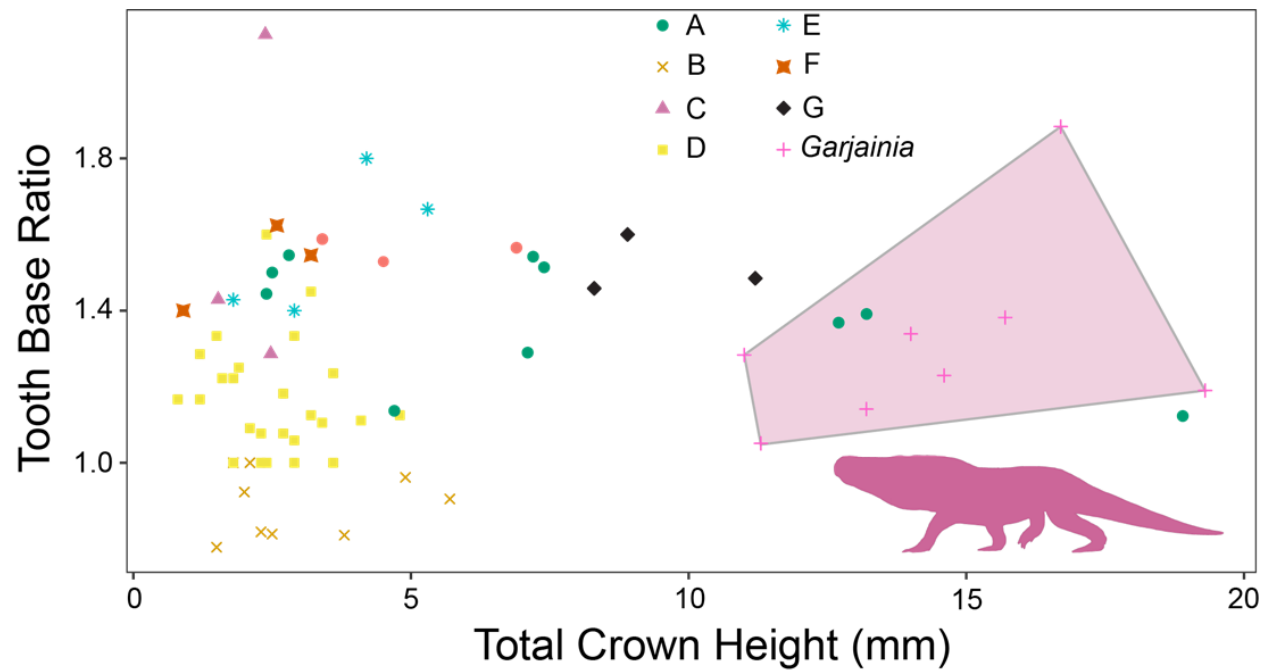


FIGURE 3: **Relationship between tooth height and tooth base ratio.** Teeth measurements divided and labeled by morphotype. All of the morphotypes have overlapping size and shape distributions. Transparent polygon represents the convex hull of *Garjainia madiba* tooth morphospace which is only shared by morphotype A teeth. Silhouette represents *Garjainia madiba*.

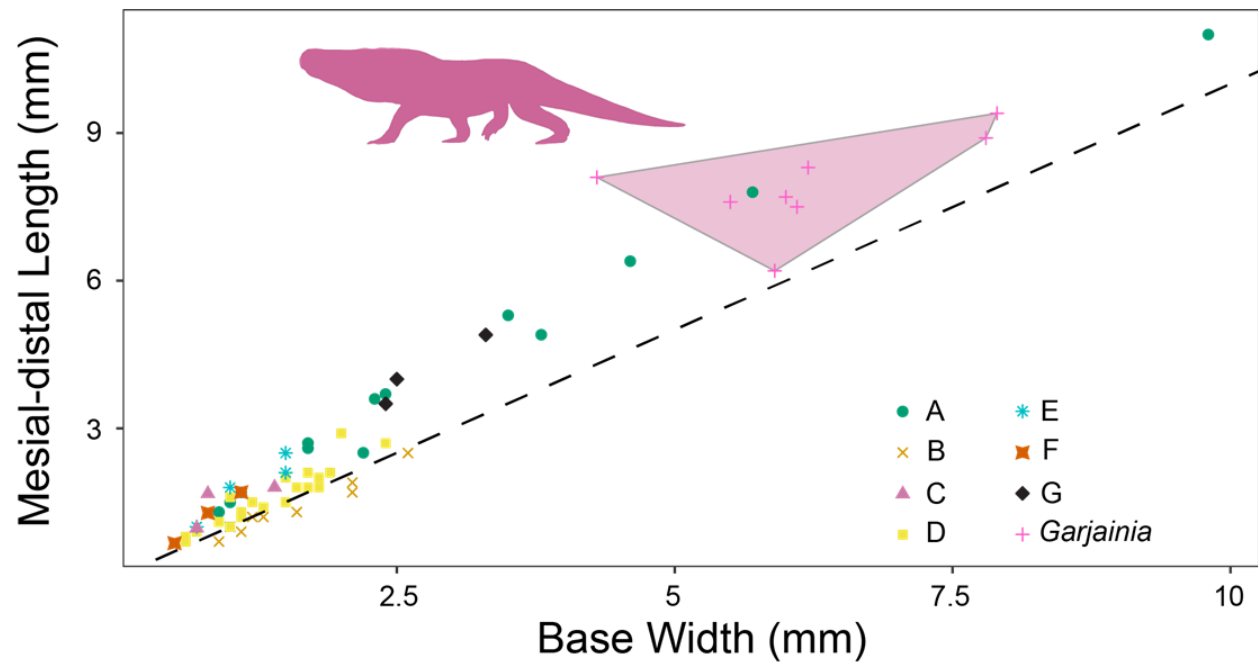


FIGURE 4: **Relationship between tooth base width and length.** Teeth measurements divided and labeled by morphotype. All of the morphotypes have overlapping size and shape distributions and only morphotype B lies below 1:1 line. Transparent polygon represents the convex hull of *Garjainia madiba* tooth morphospace which is only shared by morphotype A teeth. Silhouette represents *Garjainia madiba* and dashed black line represents 1:1 line or a perfectly circular tooth base.

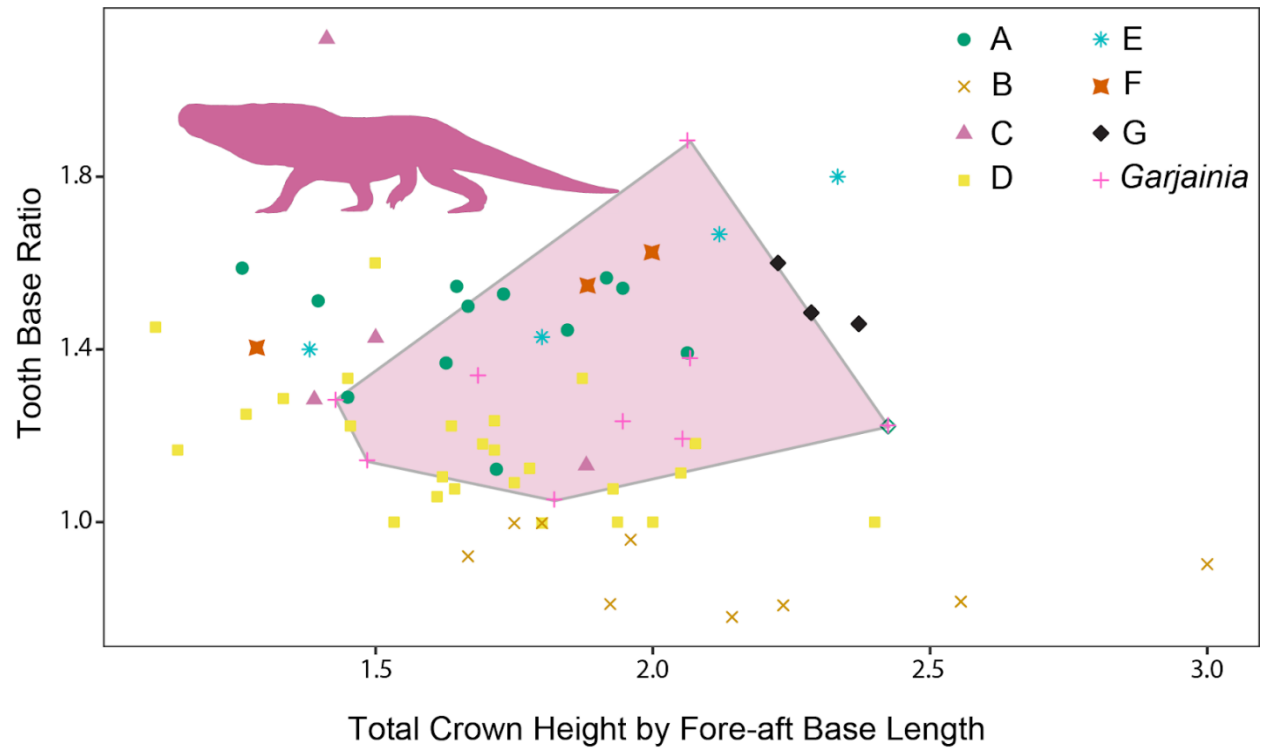


FIGURE 5: **Relationship between tooth height and tooth base ratio controlled for size.** Teeth measurements divided and labeled by morphotype. All of the morphotypes have overlapping morphospace with morphotype B being differentiated by a wider than long base (=bulbous). Transparent polygon represents the convex hull of *Garjainia madiba* tooth morphospace and the silhouette represents *Garjainia madiba*.

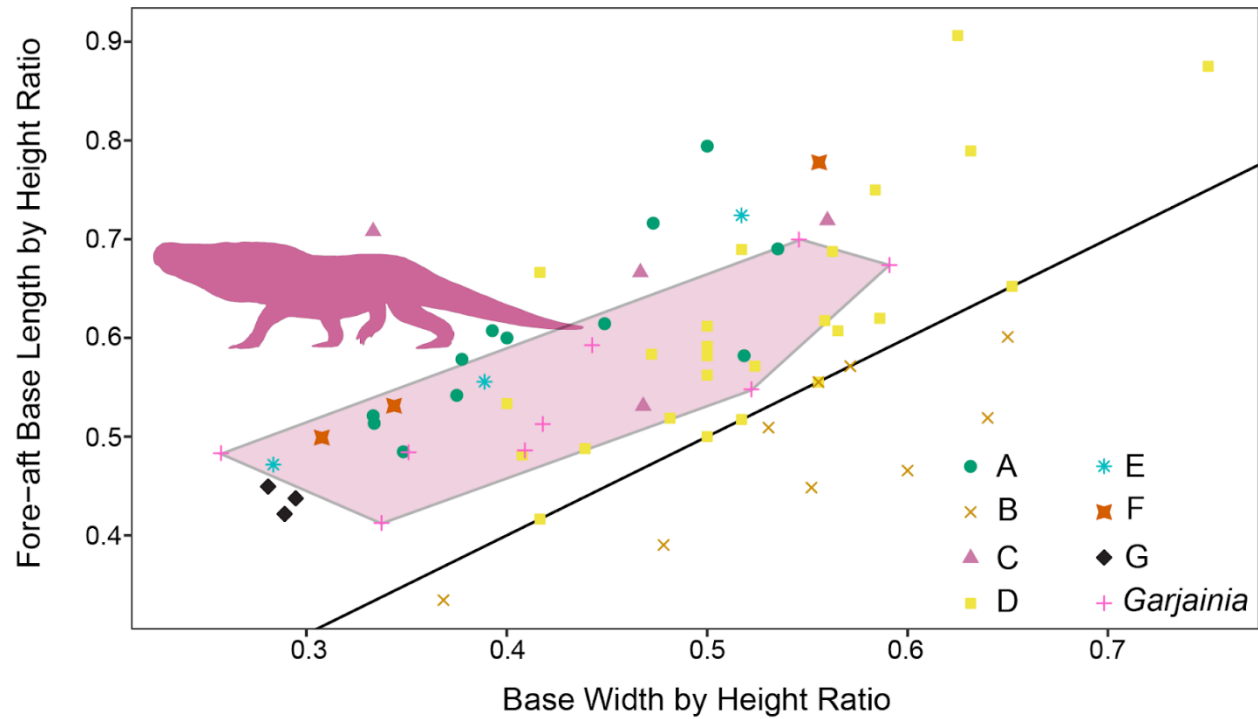


FIGURE 6: **Relationship between tooth base width and length controlled for size.** Teeth measurements divided and labeled by morphotype. Overlap between morphotypes is greater than without controlling for size. Transparent polygon represents the convex hull of *Garjainia madiba* tooth morphospace which is only shared by morphotype A teeth. Silhouette represents *Garjainia madiba* and black line represents 1:1 line or a perfectly circular tooth base.

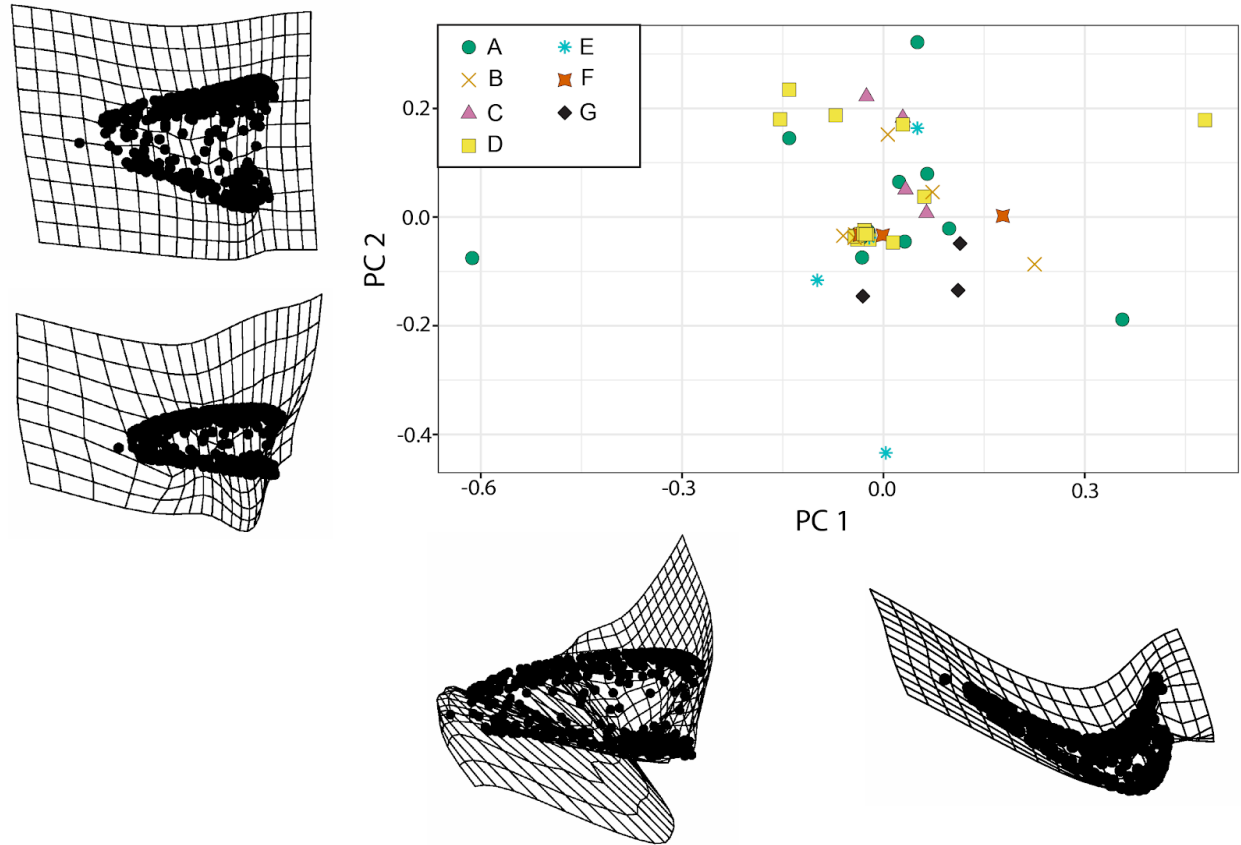


FIGURE 7: **PCA visualization with all complete reptile teeth.** Morphospace plotted on PC1 and PC2, each point represents a single tooth. Thin-plate splines for minimum (left) and maximum (right) PC values on the first major axis. Variation in this axis is dominated by recurvedness. Thin-plate splines for minimum (bottom) and maximum (top) PC values on the second major axis. Variation in this axis is dominated by labio-lingual compression.

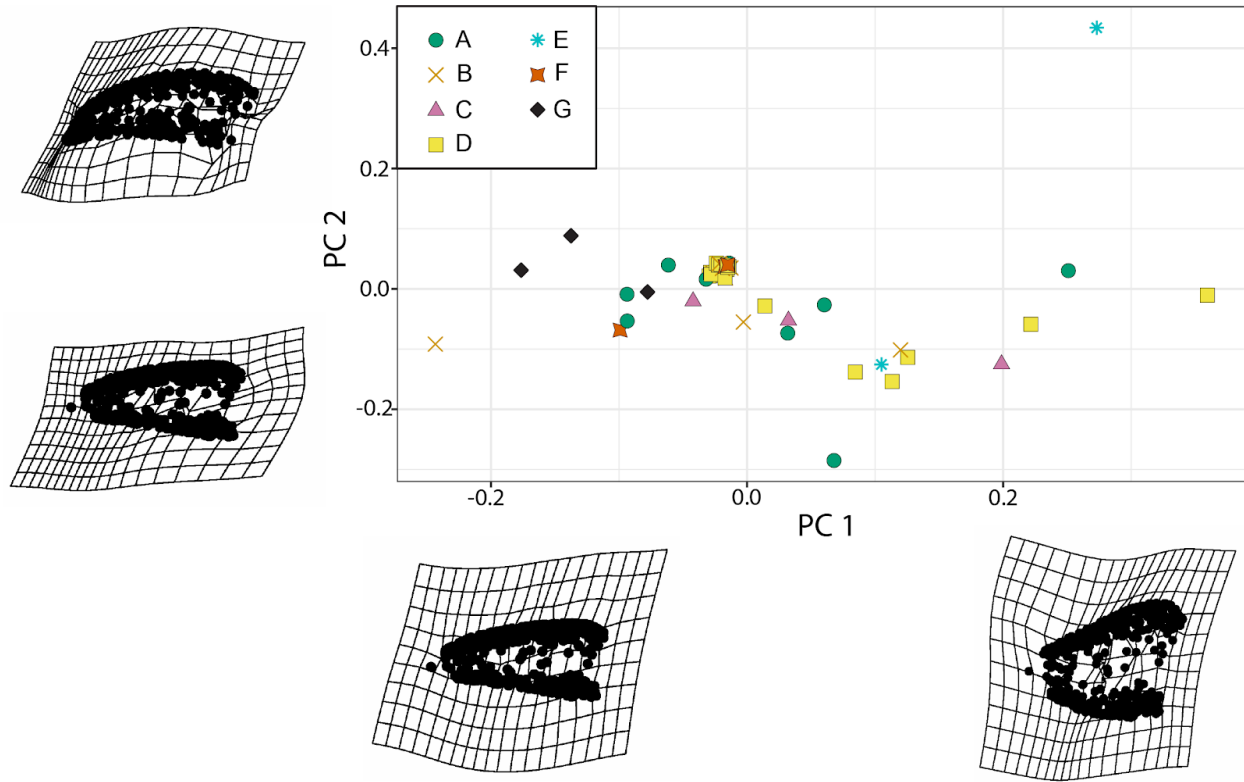


FIGURE 8: **PCA visualization with outliers removed.** Morphospace plotted on PC1 and PC2, each point represents a single tooth. Thin-plate splines for minimum (left) and maximum (right) PC values on the first major axis. Variation in this axis is dominated by lateral profile (spade-like versus conical). Thin-plate splines for minimum (bottom) and maximum (top) PC values on the second major axis. Variation in this axis is dominated by recurvedness.

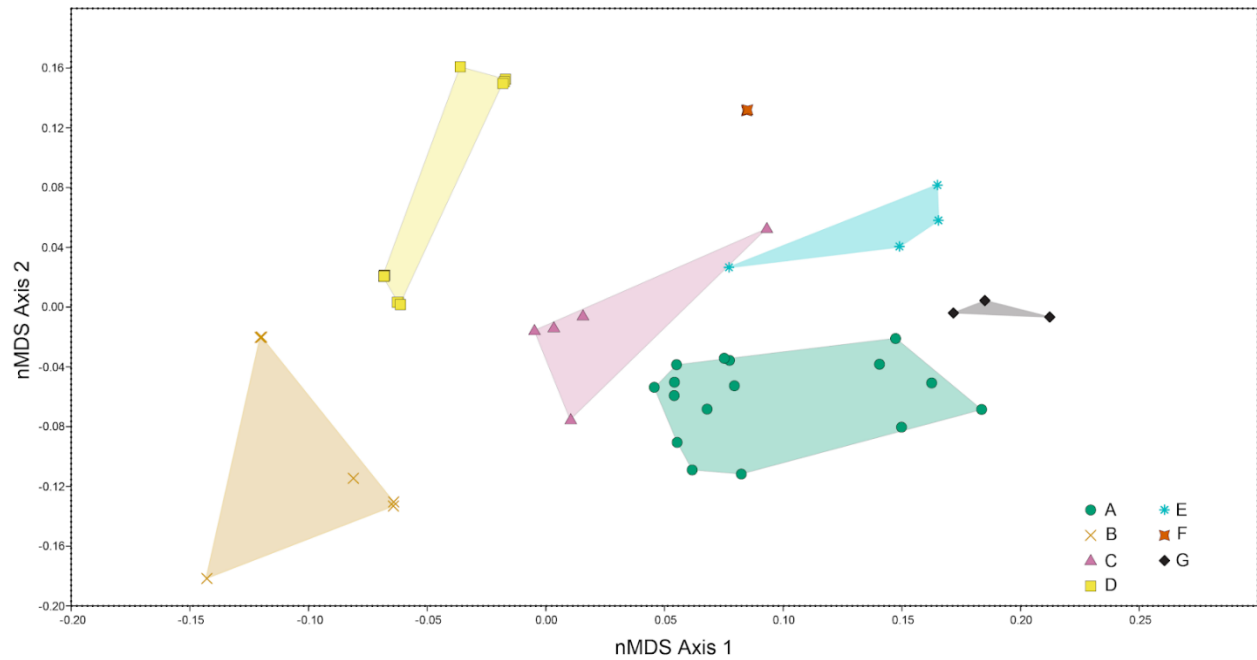


FIGURE 9: Ordination plot of first two major NMDS axes of reptile tooth morphospace.

Colored, transparent polygons are convex hulls of each reptile tooth morphotype, colors and symbols correspond to different morphotypes. None of the convex hulls overlap, indicating that the qualitative scoring for each tooth morphotype is quantitatively distinct. Axis one is mainly divided by serrations with non-serrated teeth having negatively weighted values and serrated teeth having positively weighted values.

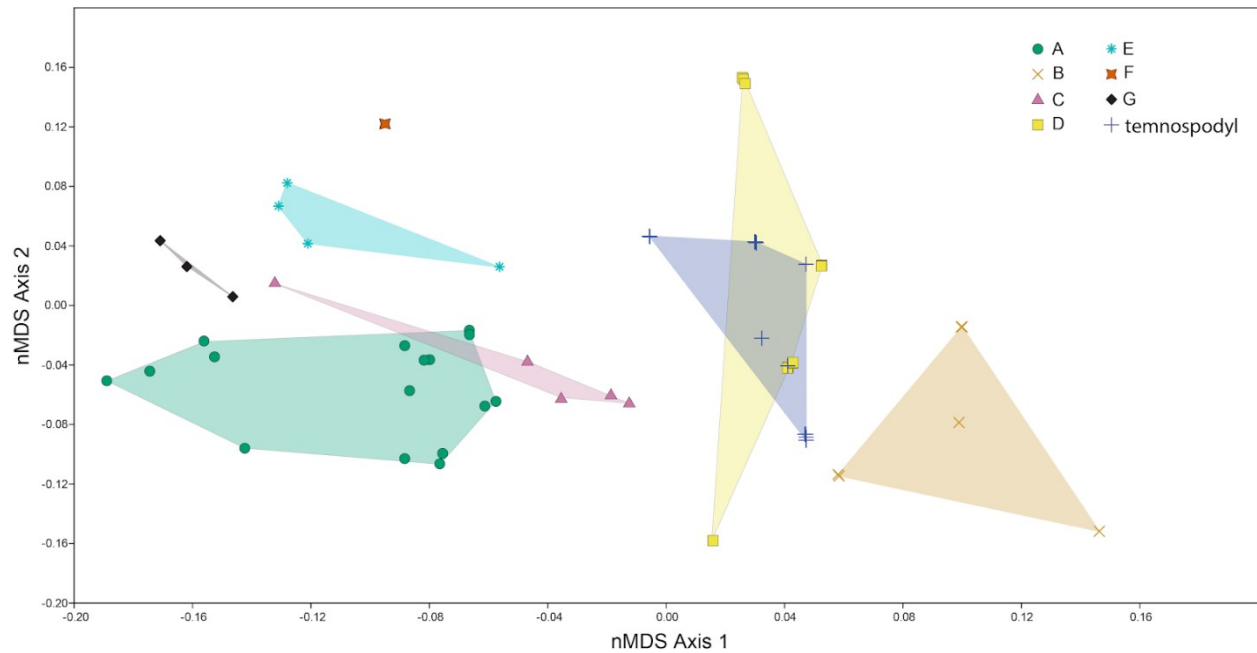


FIGURE 10: Ordination plot of first two major NMDS axes of reptile tooth morphospace and temnospondyls. Colored, transparent polygons are convex hulls of each reptile tooth morphotype and the temnospondyl morphotype, colors and symbols correspond to different morphotypes. There is some overlap in morphotypes A and C and between morphotype D and temnospondyl teeth. The first major axis is still split by serrations, though now positive weights are non-serrated and negative weights are serrated.

CHAPTER 3: Evolution of the suchian carapace: a new pseudosuchian archosaur from the Manda Beds (Middle Triassic: ?Anisian) of Tanzania

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ABSTRACT

Archosaurs (crocodylians, birds, and their extinct relatives) diversified and rose to ecological dominance following the end-Permian mass extinction (the largest of the Big Five mass extinctions in Earth history). In the Triassic, pseudosuchian archosaurs became speciose and exhibited disparate morphologies related to distinct ecologies. Although that radiation had started by the beginning of the Middle Triassic, as evidenced by the presence of well-nested pseudosuchians near the Early-Middle Triassic boundary, many distinct clades (e.g., aetosaurs, ornithosuchids) currently lack Middle Triassic representatives and have an entirely Late Triassic record. These gaps in their early evolutionary history result in a lack of transitional morphologies that, in turn, obscure relationships among early-diverging archosaurs. Poorly resolved phylogenies inhibit the study of macroevolutionary questions related to order of trait acquisition, convergence vs. homologous features, and ecological niche-breadth expansion.

Here we present a new species of suchian archosaur from the Lifua Member of the Manda Beds, Tanzania. One mostly complete skeleton is represented by well-preserved cranium, postcrania, and numerous osteoderms, and with two other referred individuals, represents about ~80% of the total skeletal anatomy of this taxon. We assign this taxon to Pseudosuchia based on its ‘crocodile-normal’ crurotarsal ankle joint. The maxillary and dentary dentition is recurved and laterally compressed with mesial and distal serrations. The skull shares character states with aetosaurs and erpetosuchids, such as the jugal contributing to the posterior margin of the antorbital fenestra between the two anterior articulation processes of the jugal, and the postorbital forming the majority of the postorbital bar. In addition to numerous paramedian osteoderms and likely lateral osteoderms, this taxon has abundant osteoderms covering the appendicular skeleton. Using broadly sampled phylogenetic analyses we recover this new taxon

as the earliest-diverging member of Aetosauria within a larger clade of Aetosauriformes. Resultant character optimizations indicate osteoderm, hindlimb, and cranial neurovascular trait shifts are important characters for reconstructing the relationships among these early members of Pseudosuchia. The new taxon sheds light on the evolution and expansion of carapaces and a transition from a longer-limbed suchian ancestor to a clearly quadrupedal, armored clade. The new taxon highlights the importance of sampling early lineages in rapidly diverging clades to reconstruct relationships and character evolution.

1. INTRODUCTION

The rapid speciation and global spread of archosauriforms during the Triassic Period has been linked to the faunal recovery following the end-Permian mass extinction (Romer, 1956; Benton, 1983, 2010; Brusatte et al., 2008, 2010b; Butler et al., 2011; Nesbitt, 2011; Sidor et al., 2013; Roopnarine et al., 2018). This pattern has been held up as an example of a biological radiation because of the rapid pace of speciation as well as the diversification of body forms (Benton, 1983, 2010; Brusatte et al., 2008, 2010a; Nesbitt, 2011). The archosauriform radiation has been constrained temporally by both discoveries of stem and crown archosaur fossils in the Early and Middle Triassic (e.g., Gower and Sennikov, 1997; Butler et al., 2011; 2017 Nesbitt et al., 2011; 2014), as well as refined phylogenetic hypotheses (e.g., Irmis et al., 2007; Nesbitt, 2011; Ezcurra, 2016). Based upon this increasing body of fossil evidence, the radiation of archosauriforms occurred in the Middle Triassic with many major groups of crown archosaurs originating no later than the Middle Triassic (e.g., paracrocodylomorphs, dinosauromorphs). Following this initial diversification, archosaurs have remained one of the most diverse and disparate group of vertebrates into the present.

Although time-calibrated phylogenetic hypotheses place the origination of most major Triassic archosaurian groups within the Early to Middle Triassic (e.g., Butler et al., 2011; Turner and Nesbitt, 2013; Ezcurra and Butler, 2018) and provide predictions for the timing of character acquisition, the limited number of specimens from this time hinders validation of these hypotheses. Crown group Archosauria diverged into the major lineages of Avemetatarsalia and Pseudosuchia during the latest Permian to earliest Triassic based on divergence time estimates (Ezcurra and Butler, 2018), but no crown group members have been recovered earlier than the latest Early Triassic. The oldest avemetatarsalians belong to Aphanosauria and date to the

Middle Triassic (Nesbitt et al., 2017b). Likewise, Pseudosuchia is constrained by the appearance of Ctenosauriscidae (Butler et al., 2011; Nesbitt et al., 2011) in the late Early Triassic (Olenekian stage), and the well-nested position of ctenosaurischids in current phylogenetic hypotheses implies that other clades, such as Aetosauria and Ornithosuchidae, must have diverged within the Early Triassic (Butler et al., 2017; Ezcurra and Butler, 2018). Yet in both cases, the earliest definitive members are Late Triassic in age (Nesbitt et al., 2014). If *Parringtonia gracilis* is closer to Aetosauria (Nesbitt et al., 2017c) than any other lineage, it would push the clade back to the Middle Triassic. Aetosaurs, like other archosaurian groups (e.g., phytosaurs, ornithosuchids), should have members in the Middle Triassic, but none are currently described.

Over the past two decades, extensive sampling of the ?late Anisian Lifua Member of the Manda Beds (Ruhuhu Basin, Tanzania) (Smith et al., 2018, Fig. 1A) has resulted in the discovery of numerous novel archosaurs (e.g. Barrett et al., 2015; Nesbitt et al., 2010; 2014; 2017b; Butler et al., 2018; 2022) and additional material of previously-known taxa (e.g. Nesbitt et al., 2017c), providing a glimpse into the Middle Triassic diversification predicted by phylogenies and now captured by the fossil record. About half of the Manda taxa are pseudosuchian-line archosaurs, which contributed either the majority (e.g., Brusatte et al., 2010b; Foth et al., 2016) or significant portion (Nesbitt et al., 2017a) of archosaur disparity and diversity during the Triassic. Here we describe a new species of pseudosuchian archosaur based on three partial skeletons, including cranial material, collected in the Manda Beds. This taxon shares features with aetosaurs, as well as other aetosauriforms like *Revueltosaurus callenderi*, adds to the diversity of the Manda Beds assemblage, demonstrates aetosaurs and other aetosauriforms independently shifted tooth shape from carnivorous to herbivorous-like, and informs the early morphological evolution of suchians.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, USA; **BGS GSM**, British Geological Survey, Geological Survey Museum, Keyworth, UK; **BP**, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; **CAPPA/UFSM**, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/ Universidade Federal de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil; **CM**, Carnegie Museum of Natural History; **CRILAR-Pv**, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica, Anillaco, Argentina; **GPIT**, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany; **GR**, Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico, USA; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MCN-PV**, Museu de Ciências Naturais – Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MMACR**, Museu Municipal Aristides Carlos Rodrigues, Candelária, Brazil; **MSM**, Mesa Southwest Museum, Mesa, Arizona, USA; **NHMUK** (formerly BMNH), Natural History Museum, London, UK; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **NMT**, National Museum of Tanzania, Dar es Salaam, Tanzania; **PEFO**, Petrified Forest National Park, Arizona, USA; **PVL**, Paleontología de Vertebrados, Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán Province, Argentina; **PVSJ**, Division of Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, Argentina; **SAM**, Iziko: South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **SNSB-BSPG**, Staatliche Naturwissenschaftliche Sammlungen Bayerns, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **TMM**, Vertebrate Paleontology Laboratory, Texas Natural Science Center, Austin, Texas, USA; **TTU**, Texas Tech University, Lubbock, Texas, USA; **UCMP**, University of California Berkeley

Museum of Paleontology, California, USA; **UFRGS-PV**, Paleovertebrate Collection of the Laboratório de Paleovertebrados of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **ULBRA-PVT**, Universidade Luterana do Brasil, Coleção de Paleovertebrados, Canoas, Rio Grande do Sul, Brazil; **UNC**, University of North Carolina, Chapel Hill, North Carolina, USA; **YPM**, Yale Peabody Museum, New Haven, Connecticut, USA; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

2. SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope 1869, *sensu* Gauthier and Padian, 1985

PSEUDOSUCHIA Zittel, 1887, *sensu* Gauthier and Padian, 1985

SUCHIA Krebs, 1974, *sensu* Nesbitt, 2011

AETOSAURIA Marsh, 1884 *sensu* Nesbitt, 2011

<Redacted for publication> gen. et sp. nov.

Etymology—<Redacted for publication>

Holotype—NMT RB187, partial skeleton including braincase and skull roof elements, vertebrae, pectoral girdle and forelimb elements, pelvic girdle and hind limb elements, and numerous osteoderms.

Type Locality—Field localities Z133 (holotype) Lifua Member of the Manda Beds (Middle Triassic: ?Anisian), Ruhuhu Basin, southwest Tanzania (Fig.1). Field collection has also recovered cynodonts (*Scalenodon angustifrons*, *Cricodon metabolus*, and *Aleodon brachyrhamphus*), dicynodonts (*Sangusaurus* and *Angonisaurus*), stereospondyl amphibians, archosauromorph *Stenaulorhynchus stockleyi*, pseudosuchians (*Nundasuchus songeaensis*, *Parringtonia gracilis*, *Mambawakale ruhuhu*, *Hypselorhachis mirabilis*, *Stagonosuchus nyassicus*), and avemetatarsalians (*Nyasasaurus parringtoni*, *Asilisaurus kongwe*) from

stratigraphically equivalent localities (Butler et al., 2009; Lautenschlager and Desojo, 2011; Nesbitt et al., 2010; 2014; Nesbitt and Butler 2013; Smith et al., 2018; Butler et al., 2022). Referred specimens—NMT RB679, partial skeleton including fragmentary skull (quadrate, postorbital), vertebrae, pectoral girdle (scapula) and forelimb elements (humerus, radii, ulnae, metacarpals, phalanges), hind limb elements (femur, tibia, astragalus), and paramedian, lateral, ventral(?), appendicular osteoderms (Fig. 2). Collected from locality Z145 Lifua Member of the Manda Beds (Middle Triassic: ?Anisian), Ruhuhu Basin, southwest Tanzania (Fig. 1). NHMUK R36616, partial but highly fragmented skeleton including isolated skull elements (parietal, dentary), vertebrae, hind limb elements (proximal end of femur, tibia), partial pelvic girdle (proximal end of pubis), and osteoderms (Fig. 3).

Diagnosis—Armored pseudosuchian diagnosed by the following unique combination of characters (*indicates autapomorphies): presence of an anteriorly opening foramen on the anterolateral maxillary surface; recurved, serrated teeth on the maxilla and dentary; presence of scattered teeth on palatal process of pterygoid; rounded longitudinal ridge on the lateral surface of the jugal; anterior caudal vertebrae bear a thin lamina that trends through the middle of the midline groove on the ventral centrum surface*; paired paramedian and lateral osteoderms with reticulated ornamentation; appendicular osteoderms present; distinct groove with associated foramen posterior to the groove on proximal end of radius*; pubis that is more than 70% the length of the femur; a straight, transverse groove present on the proximal surface of the femur; fourth trochanter of the femur with a sharp flange; and a diamond-shaped distal end of fibula with larger anterior point than posterior point*.

Differential diagnosis—There are several archosauriform taxa known from the Manda Beds, several of which have been described or redescribed recently. <Name Redacted> can be

differentiated from other Manda Beds archosauriforms by a number of features, though the following list is not comprehensive. <Name Redacted> differs from *Parringtonia gracilis* (NHMUK R8646) in having osteoderm ornamentation that is reticulated rather than randomly pitted, possessing osteoderms with an anterior bar, and a medial tuberosity of the femoral head that continues to the anterior surface rather than being restricted to the proximal surface. <Name Redacted> differs from *Nundasuchus songeaensis* (NMT RB48) in possessing diapophyses and parapophyses that are laterally extended in trunk vertebrae, proportionally more elongate caudal vertebrae, and a rounder and more anteriorly directed M. iliofibularis attachment on the fibula. <Name Redacted> differs from *Mandasuchus tanyauchen* (NHMUK R6792) in lacking a dorsolateral trochanter of the femur, possessing laterally expanded diapophyses and parapophyses of the trunk vertebrae, possessing caudal vertebrae with a spinal table, and a more pronounced anterior flexion of the fibula. <Name Redacted> differs from *Asperoris mnyama* (NHMUK R36615) in the presence of a antorbital fossa on the lateral surface of the maxilla, the presence of an anteriorly opening foramen on the lateral surface of the maxilla, and having a frontal that forms the majority of the dorsal border of the orbit. <Name Redacted> differs from *Stagonosuchus nyassicus* (GPIT/RE/3831) in lacking a hyposphene-hypantrum articulation and accessory neural spines on the caudal vertebrae, the presence of a rounded anterior corner of the antorbital fenestra in lateral view, and a distal end of the fibula that lacks a deep depression on the mediolateral side. <Name Redacted> differs from *Hypselorhachis mirabilis* (NHMUK R16586) in lacking highly elongated neural spines in the presacral vertebrae. <Name Redacted> differs from *Mambawakale ruhuhu* (NHMUK R36620) by the presence of an anteriorly opening foramen on the maxilla, presence of teeth on the pterygoid, and pterygoids that articulate along the midline of the skull. <Name Redacted> differs from *Nyasasaurus parringtoni* (NHMUK

R6856) by possessing a humerus with a more proximally restricted deltopectoral crest. *<Name Redacted>* differs from *Asilisaurus kongwe* (NMT RB9 and NMT RB159) by having dentition on the anterior end of the dentary, recurved, labiolingually compressed teeth, unfused scapulae and coracoids, a proximally restricted deltopectoral crest, and the lack of a prominent cnemial crest of the tibia.

Ontogenetic assessment—We find that sutures on all caudal vertebrae and the posterior-most trunk vertebrae from the holotype and referred specimens are closed using the neurocentral suturing descriptions of Brochu (1996) and following the recommendations of Griffin et al. (2021). However, the neurocentral sutures of the anterior trunk and all cervical vertebrae of the holotype are open *sensu* Brochu, 1996. We are confident that neurocentral suturing can be reliably used to determine that the holotype of *<Name Redacted>* is skeletally immature (see Griffin et al. 2021 for caveats) because we have representative vertebrae from the anterior to posterior portions of the axial skeleton. Because the neurocentral sutures of the posterior trunk and caudal vertebrae are closed we can say *<Name Redacted>* closed its sutures posterior-to-anterior, as in living crocodylians, phytosaurs, and aetosaurs (Brochu, 1996; Griffin et al. 2021). However, neurocentral suture closure cannot determine precise age, nor determine if an individual has finished growing. Histological analysis of the limb bones could provide additional insight into the specimens' ontogenetic stages, but was not undertaken for this description.

3. DESCRIPTION

Skull

Maxilla—The right maxilla is partially preserved in the holotype, NMT RB187 (Fig. 4A, B). The element is 66.5 mm long as preserved. The ventral margin is generally straight in lateral and medial view, though this margin is deflected slightly ventrally toward the contact

with the premaxilla. In ventral view, the bone is anteroposteriorly straight, aside from a slight medial expansion of the palatal process of the maxilla just posterior of the dorsal process.

A series of a dozen 1-2 mm, ventrally-opening nutrient foramina is present on the lateral face of the maxilla. The series trends dorsal and parallel to the alveolar margin with numerous additional smaller (<1 mm) nutrient foramina scattered dorsal to the primary series (Fig. 4A). The base of the dorsal process is positioned towards the anterior portion of the maxilla, dorsal to the second through sixth alveoli. Although largely incomplete, the base of the dorsal process is preserved in cross section, showing that it is a thin sheet of bone, narrowest anteriorly and broader posteriorly. The antorbital fossa emarginates the posterior edge of the dorsal process, but the shape of the dorsal process is unclear because it is broken (Fig. 4A). The anterior edge of the dorsal process becomes a sharp ridge that forms the dorsalmost portion of the premaxilla-maxilla articulation surface. A large, anteriorly-opening foramen is present on the lateral face of the maxilla, like that of many archosauriforms (e.g., *Euparkeria capensis*, SAM-PK 6047A; *Parringtonia gracilis*, NHMUK R3139; *Revueltosaurus callenderi*, PEFO 34274; *Mandasuchus tanyauchen*, NHMUK PV R6792).

On the medial surface of the maxilla, the palatal process extends anteromedially, dorsal to the first preserved alveolus, although it is incompletely preserved (Fig. 4B). A deep triangular fossa is present on the anteromedial margin of the dorsal process, resembling the condition in that of *Decuriasuchus quartacolonias* (MCN-PV10.004). The medial surface of the maxilla possesses ridges posteriorly that likely mark the articulation surface with the palatine. There is a thin ridge with a narrow anteroposteriorly oriented groove on the dorsomedial face that we interpret as the articulation with the jugal. A ledge extends anteroposteriorly, dorsal to the medial edge of the alveolar margin. Ventral to this ledge, unfused interdental plates are generally

triangular (Fig. 4B), like those of early diverging pseudosuchians (e.g., *Revueltosaurus callenderi*, PEFO 34561; *Mandasuchus tanyauchen*, NHMUK PV R6792) and differing from the fused interdental plates of rauisuchids (e.g., *Postosuchus kirkpatricki*, TTU 9000). There are 10 preserved alveoli in the maxilla, though there are likely more posteriorly (estimated 3-5 more based on density of alveoli and thinning of bone). Additionally, nine of the alveoli preserve part of a tooth and there four replacement teeth (second, fourth, sixth, and eighth alveoli) on the medial margin in varying states of growth. The teeth of *<Name Redacted>* are labiolingually compressed, recurved, and possess apicobasal ridges (=fluting). Both mesial and distal carina are serrated with denticle densities of 8–14 per mm and the teeth range in total crown height from 5.3 to 13.4 mm.

Nasal—The right nasal is incompletely preserved in NMT RB187, with both the anterior and posterior ends missing (Fig. 4E, F). The nasal is a mediolaterally slender element and is convex in anterior view. The nasal thins very slightly anteriorly from 10.7 to 9.8 mm wide. Towards the posterior end, the nasal is flat to convex as in the pseudosuchian archosaurs *Aetosaurus ferratus* (SMNS 5770), *Revueltosaurus callenderi* (PEFO 34561), *Riojasuchus tenuisiceps* (PVL 3827), *Effigia okeeffeae* (AMNH FR 30587), and *Protosuchus richardsoni* (AMNH FR 3024). The dorsolateral surface of the nasal is covered in small pits and anteroposteriorly oriented grooves, but it lacks the dorsolateral ridge found in *Postosuchus kirkpatricki* (TTU 9000) and *Batrachotomus kupferzellensis* (SMNS 52970). The nasal is 2.5 mm in dorsoventral thickness, so the thickness is a third of the mediolateral width. This ratio is like *Revueltosaurus callenderi* (PEFO 34561) and aetosaurs (e.g., *Aetosauroides scagliai*, UFSM 11505) and unlike the dorsoventrally thickened nasals of erpetosuchids (e.g., *Parringtonia gracilis*, NMT RB426). There is a small (~3 mm) ventrally projecting flange for the ascending

process of the maxilla on the anterolateral edge of the preserved nasal. With much of the nasal missing we cannot determine if there is nasal-prefrontal contact, a posterolateral process, or whether the nasal contributes to the dorsal margin of the antorbital fossa.

Frontal—The left and right frontals were found together with a clear midline suture. They are partially preserved in NMT RB187, missing the anterior and posterior portions as well as fragments from the left side (Fig. 4G, H). However, it is clear that the frontal is anteroposteriorly longer than wide, as in ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), *Revueltosaurus callenderi* (PEFO 34561), aetosaurs (e.g., *Aetosauroides scagliai*, PVL UFSM 11505), but differing from some loricatans (e.g., *Saurosuchus galilei*, PVSJ 32) with frontals that are equally long and wide. The dorsal surface is ornamented with large pits near the postfrontal suture and smaller pits scattered across the surface. The midline frontal suture is flat in the anterior two-thirds; the posterior one-third has a slight (~1mm) ridge similar to aetosaurs (e.g., *Aetosaurus ferratus* SMNS 5770) and loricatans (e.g., *Decuriasuchus quartacolonias* MCN-PV10.105a, d; MCN-PV10.004). The orbital margin of the frontal is smooth, unlike the rugose margin of poposauroids like *Effigia okeeffeae* (AMNH FR 30587) and *Arizonasaurus babbitti* (MSM 4590).

The ventral surface of the frontal is smooth, with curved ridges medial to the orbital margin. The midline region is recessed, except for a single, small (7 mm long) bulge near the posterior edge of the fused frontals (Fig. 4H). Because the frontals are incomplete anteriorly, it is unclear whether any structures related to the olfactory tract were present.

A striated surface is present on the right lateral side of the frontal that we interpret as the articulation surface for the prefrontal; none of the prefrontal is preserved in <Name Redacted>. This shows the prefrontal partially contributes to the dorsal margin of the orbit. The rest of the

dorsal margin of the orbit is formed by the postfrontal, which has an anteroposteriorly oriented suture with the frontals.

Postfrontal—The left and right postfrontals are partially preserved in NMT RB187 (Fig. 4E, F). Although the posterior portions are missing, the postfrontal is triangular in dorsal view. The postfrontals form the posterior dorsal margin of the orbit. The dorsal surface has several pits ranging from 0.6 to 1.2 mm wide. The ventral surface is smooth and forms the posterior continuation of the curved orbital fossa on the ventral surface of the frontals.

Pterygoid—The left and right pterygoids of NMT RB187 are incompletely preserved. The left pterygoid is missing portions of the palatal (= lateral) and quadrate (= posterior) processes (Fig. I, J) and the right pterygoid is missing the palatal (= lateral) and anterior processes, as well as part of the quadrate (= posterior) process. The pterygoid contacts the ectopterygoid ventrolaterally along the transverse process of the pterygoid and contacts the other pterygoid medially along the entire preserved length of the palatal process. We cannot interpret the states of the palatine or vomer contacts as the anterior portion of the pterygoid is missing. Neither can we fully interpret the quadrate or basisphenoid contacts as the quadrate process is almost entirely missing. However, the preserved portion of the quadrate process trends posterolaterally, as in early diverging pseudosuchians (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Erpetosuchus granti*, NHMUK R3139; *Neoaelosauroides engaeus*, PVL 5698; *Turfanosuchus dabaensis*, IVPP V3237). On the transverse process of the pterygoid, the articulation surface for the ectopterygoid is on the ventral surface of the pterygoid, as in non-archosaurian archosauriforms and pseudosuchian archosaurs (Serenó and Novas, 1994; Nesbitt, 2011). Along this articulation, the ectopterygoid forms the entire lateral edge of the transverse flange as in all archosauriforms (Nesbitt, 2011). The dorsal surface of the pterygoid is smooth, as is the ventral

surface of the transverse process. However, unlike the condition in most archosaurs, the ventral surface of the palatal process is covered in small teeth. Like the theropod dinosaurs *Eoraptor lunensis* (PVSJ 512) and *Eodromaeus murphi* (PVSJ 560), the early-diverging pseudosuchian *Nundasuchus songeaensis* (NMT RB48), the erpetosuchid *Parringtonia gracilis* (NMT RB426) and the gracilisuchid *Turfanosuchus dabaensis* (IVPP V3237) and many non-archosaurian archosauriforms (e.g., proterosuchids and proterochampsids), the pterygoid teeth of <Name Redacted> follow the palatal process along the medial half of the pterygoid. Therefore, <Name Redacted> adds a fifth case of the appearance of pterygoid teeth within crown Archosauria. The damaged palatal process makes determining the presence or absence of a palatine-ptyerygoid fenestra, a synapomorphy of Ornithosuchidae, impossible.

Jugal—The right jugal is mostly complete in NMT RB187, although the anteriormost parts of the articulation surfaces for the lacrimal and maxilla are not preserved, and chips of the posterior margin are missing (Fig. 4K, L). Overall, the jugal is 36 mm long anteroposteriorly and 21.2 mm tall dorsoventrally. The anterior part of the jugal is divided into two articulation surfaces, the anterodorsal articulation with the lacrimal and an anteroventral articulation with the maxilla. The jugal contributes to the posterior margin of the antorbital fenestra between these two articulation processes as in erpetosuchids (e.g., *Erpetosuchus granti*, NHMUK R3139; *Pagosvenator candelariensis*, MMACR PV 036-T), *Gracilisuchus stipanicicorum* (PVL 4597), *Parringtonia gracilis* (NMT RB426), and some aetosaurs (e.g., *Neoaetosauroides engaeus*, PVL 4363; *Desmotosuchus haplocerus*, TTU 9023). This contrasts with the exclusion of the jugal from the antorbital fenestra in crocodylomorphs (Clark et al., 2000), *Postosuchus kirkpatricki* (TTU 9000), *Revueltosaurus callenderi* (PEFO 34561), and some aetosaurs (e.g., *Aetosaurus ferratus*, SMNS 5770 S-16; *Longosuchus meadei*, TMM 31185-98). The antorbital fossa forms a

deep recess on the anterolateral margin of the jugal. The rim of the antorbital fossa forms a steep ridge, which overhangs the fossa in anterior view. A similar antorbital fossa on the jugal can be seen in *Riojasuchus tenuisiceps* (PVL 3827) and *Parringtonia gracilis* (NMT RB426), but not in *Revueltosaurus callenderi* (PEFO 34561) or aetosaurs (e.g., *Aetosauroides scagliai*, UFSM 11505; *Typothorax coccinarum*, PEFO 38001). The antorbital fossa is smooth, unlike the rest of the lateral surface of the jugal.

The lateral surface of the jugal has a longitudinal rounded ridge and is covered with numerous small (<1mm) foramina (Fig. 4K). This is the same state as in aetosaurs (e.g., *Aetosaurus ferratus*, SMNS 5770), *Revueltosaurus callenderi* (PEFO 34561), *Gracilisuchus stipanicorum*, (PVL 4597), early-diverging loricatans (e.g., *Saurosuchus galilei*, PVSJ 32), and crocodylomorphs (e.g., *Hesperosuchus 'agilis'* CM 29894). Ventrally, the jugal thins to a sharp edge; dorsally, the jugal forms the ventral border of the orbit.

The postorbital process of the jugal does not contribute to the postorbital bar; therefore, we interpret that the postorbital must have formed most, if not all, of the postorbital bar. The same arrangement is found in aetosaurs (e.g., *Aetosaurus ferratus*, SMNS 5770; *Desmotosuchus haplocerus*, TTU 9024) and shuvosaurids (e.g., *Effigia okeeffeae*, AMNH FR 30587; *Shuvosaurus inexpectatus*, TTU 9280), but differs from the condition in nearly all other archosauriforms (Nesbitt, 2011). Although the posterior process of the jugal is incompletely preserved in NMT RB187, the posterior edge of the process appears to end in a single point with articulation surfaces for the quadratojugal dorsal and ventral to this termination. <Name Redacted> shares this character state (Nesbitt 2011, character 71, state 2) with *Revueltosaurus callenderi* (PEFO 34561) and *Aetosaurus ferratus* (SMNS 5770 S-17).

The medial surface of the jugal is covered by a large (~50% total surface area) depression that corresponds to the pronounced longitudinal ridge on the lateral surface. Anterior to this depression, a single large (2.5 mm) oval foramen is present, which is directed anteroventrally-posterodorsally.

Quadrate—The right quadrate is preserved as a mostly complete, isolated element in NMT RB187, with only the anteromedial surface projection damaged (Fig. 5). The dorsal- and ventral-most portions of the right quadrate are preserved in NMT RB679 (Fig. 2D). Although not preserved in articulation, we interpret the quadrate as being near vertically oriented based upon the angle of the articular condyles and squamosal articulation. The quadrate is oriented vertically or posteroventrally in most archosauriforms (Nesbitt, 2011, character 8, state 0), but is oriented anteroventrally in aetosaurs (e.g., *Neoaetosauroides engaeus*, PVL 4363; *Paratypothorax andressorum*, SMNS 19003) and poposaurids (e.g., *Effigia okeeffeae*, AMNH FR 30587). The articular condyles are subrectangular in ventral view and are convex as in nearly all archosauriforms (Nesbitt, 2011). The articulation surface with the articular is divided into a relatively larger medial condyle directed ventrally and a relatively smaller lateral condyle oriented anteroventrally as in *Revueltosaurus callenderi* (PEFO 34561) but unlike the condition in aetosaurs (e.g., *Desmotosuchus haplocerus*, TTUP 9024) where the condyles are aligned in ventral view. The posterior surface of the quadrate body is smooth and concave with a large (~5mm) quadrate foramen on the boundary of the lateral articulation surface with the quadratojugal.

The quadrate head is fully preserved and includes the articulation surface with the squamosal on the mediodorsal surface. In dorsal view, the quadrate head is triangular with thin,

blade-like projections anteromedially toward the pterygoid articulation and anterolaterally toward the quadratojugal articulation. Though disarticulated, the squamosal articulation surface on the quadrate head demonstrates that the head would be partially exposed in lateral view as in *Arizonasaurus babbitti* (MSM 4590), *Revueltosaurus callenderi* (PEFO 34561), aetosaurs (e.g., *Aetosaurus ferratus*, SMNS 5770 S-16), and erpetosuchids (e.g., *Erpetosuchus granti*, NHMUK R3139).

Dentary—The anterior ~two-thirds of the right dentary of the holotype (NMT RB187) is preserved (Fig. 4C, D) as well as an edentulous section from NHMUK R36616. As preserved, the dentary of the holotype is 62.4 mm long anteroposteriorly and has a dorsoventral height of 12.1 mm. This anteroposteriorly elongate and dorsoventrally low dentary is typical of carnivorous archosauriforms (Nesbitt et al., 2014). The lateral surface is well-rounded along the anterior and ventral edges. Nutrient foramina cover the lateral face, ranging in size from 0.6 to 2.9 mm, and they become increasingly anteroposteriorly elongate towards the rear of the dentary. Some of these foramina form a series ventral and parallel to the tooth row, transitioning from circular to ovate posteriorly. The anterior end of the dentary is rounded in lateral view like that of *Parringtonia gracilis* (NMT RB426) and *Revueltosaurus callenderi* (PEFO 34561). This differs from the anterodorsally pointed dentary found in aetosaurs (e.g., *Aetosauroides scagliai*, UFSM 11505; *Typothorax coccinarum*, PEFO 38001).

Medially, the dentary surface is dominated by the Meckelian groove, which begins ventral to the third alveolus and expands posteriorly along the dentary (Fig. 4D), like the Meckelian groove of erpetosuchids (e.g., *Parringtonia gracilis*, NMT RB426), *Revueltosaurus callenderi* (PEFO 34561), and loricatans (e.g., *Decuriasuchus quartacolonias*, MCN-PV10.004;

Prestosuchus chiniquensis, UFRGS-PV-0629-T). Like the maxilla, the dentary possesses triangular, unfused interdental plates resting on a ledge on the medial surface between each alveolus. The symphysis is partially preserved and is ventral to the first two alveoli (Fig. 4D). It consists of a small region of rugosity and striations dorsally, and a flat, laterally-deflected surface ventrally.

A total of 14 alveoli are preserved, though another 1-3 may have been present posteriorly. Teeth are preserved in nine of these alveoli, three of which show signs of replacement teeth on the medial edge, directly replacing the tooth in the same alveolus. The dentition continues all the way to the anterior end of the dentary as in *Parringtonia gracilis* (NMT RB426) and *Revueltosaurus callenderi* (PEFO 34561). This differs from the edentulous anterior end of the dentary found in aetosaurs (e.g., *Aetosauroides scagliai*, UFSM 11505; *Typothorax coccinarum*, PEFO 38001). Although not as well preserved as the maxillary teeth, several character states are present: labiolingually compressed, recurved, apicobasal ridges (fluting) present, and a denticle density of 12 per mm.

Axial Skeleton

Elements of the cervical (including the atlantal intercentrum and axis), trunk, sacral, and caudal vertebral sections are all preserved in the holotype NMT RB187, and parts of the vertebral series also are preserved in NMT RB679 and NHMUK R36616. Because the vertebrae are disarticulated in all three individuals of *<Name Redacted>*, it is impossible to precisely seriate individual vertebrae and make full vertebral counts. Instead, we assign relative positions based on the position of the parapophyses and diapophyses: both below neurocentral suture = anterior cervical, diapophyses above neurocentral suture but parapophyses below = posterior cervical, both above neurocentral suture as separate articular surfaces = anterior trunk,

and both above neurocentral suture as single transverse process = posterior trunk vertebrae. Caudal vertebrae are ordered by overall centrum length decreasing posteriorly and size of neural spine decreasing posteriorly. These characters are based upon comparisons to *Riojasuchus tenuisiceps* (PVL 3827), *Revueltosaurus callenderi* (34561), and *Mandasuchus tanyauchen* (NHMUK R6792). Within these categories we assign a numbered order simply to improve repeatability of measurements and scoring, and we acknowledge that the numbers may not be the exact order of vertebrae. The region counts are consistent with typical archosaur vertebral columns (~8 cervical, ~15 trunk, 2 sacral, and 30-35 caudal vertebrae based upon *Euparkeria capensis* [Ewer, 1965] and *Alligator mississippiensis* [Higgins, 1923]). All preserved vertebrae are amphicoelous.

Atlas—The atlas is represented by the atlantal pleurocentrum and atlantal intercentrum in the holotype NMT RB187. The atlantal pleurocentrum is triangular in anterior and posterior views like *Revueltosaurus callenderi* (PEFO 34561) and unlike the rectangular pleurocentra of phytosaurs (e.g., PEFO 31219). The anterior articular surface is convex anteriorly with ridges along the left and right lateral and dorsal boundaries. The posterior articular surface is more strongly convex than the anterior surface, but lacks ridges at the margins. The dorsal articulation surface is concave and rectangular in dorsal view. Like *Revueltosaurus callenderi* (PEFO 34561), the atlantal pleurocentrum is twice as wide mediolaterally as it is long anteroposteriorly in dorsal view.

The atlantal intercentrum is rectangular in posterior view and semicircular in dorsal view. The posterior surface articulation with the axial pleurocentrum is smooth and convex posteriorly with a slight dorsoventral compression at the midline. The dorsal articulation surface with the atlantal pleurocentrum is concave dorsally. In anterior view, the atlantal intercentrum is

dorsoventrally constricted towards the midline with rounded lateral expansions. Overall, the morphology of the atlantal intercentrum is like that of *Revueltosaurus callenderi* (PEFO 34561) and aetosaurs (e.g., *Aetosauroides scagliai*, MCN-PV 2347).

Axis—The axis of NMT RB187 is well preserved, missing only small portions of the left prezygapophysis and right postzygapophysis as well as the central portion of the ventral midline ridge (Fig. 6A-G). The centrum of the axis is also preserved in NHMUK R36616 (Fig. 3I).

The axis centrum is 1.33 times longer than tall in lateral view and is laterally compressed in the center with a width half of that in the center as at anterior or posterior ends. In lateral view the anterior margin of the centrum is concave, and the posterior margin is flat. A single sharp ridge (< 1mm thick at the thinnest portions) is present on the midline of the ventral surface of the centrum, extending from the anterior to posterior edge. In ventral view, the anterior and posterior edges of the centrum are approximately the same width, though the posterior margin is anteroposteriorly thicker. The neurocentral suture (suture between centrum and neural arch) is clearly visible on left and right sides of the axis. There are no deep, rimmed pockets or fossae, commonly interpreted as evidence of pneumaticity on the axis, unlike the condition in some poposauroids (e.g., *Sillosuchus longicervix*, PVSJ 85) and dinosaurs (e.g., *Plateosaurus* SMNS F65). The anterior end of the centrum is divided into two surfaces by the odontoid process, similar to the condition in *Revueltosaurus callenderi* (PEFO 34561). The more dorsal surface is circular and concave with a rimmed margin. The more ventral surface forms a posteroventrally oriented flat surface that slopes towards the ventral midline ridge. The posterior end of the centrum is circular and concave with a raised margin. The parapophysis and diapophysis of the axis cannot be readily seen on the centrum, and, due to the high quality of preservation on the right lateral surface, this may represent a true absence. In NHMUK R36616 there are pits on the

lateral surface where the diapophysis would be in most archosauriform taxa. Diapophyses and parapophyses on the axis are present in ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), *Revueltosaurus callenderi* (PEFO 34561), aetosaurs (e.g., *Polesinesuchus aurelioi*, ULBRAPVT003), gracilisuchids (e.g., *Gracilisuchus stipanicorum*, PULR 08), and loricatans (e.g., *Mandasuchus tanyauchen*, NHMUK R6794). We consider this absence to be an autapomorphy of *<Name Redacted>* and may indicate a loss or reduction of the second cervical rib.

As in most archosauriforms, the neural spine of the axis is posterodorsally expanded (Nesbitt, 2011) with an angle of approximately 30° dorsal from horizontal, which contrasts with some ornithodirans (e.g., *Coelophysis bauri*, AMNH FR 7224) where the neural spine arcs dorsally such that the anterior and posterior ends are equal in height. In lateral view, the neural spine is triangular and extends beyond the anterior and posterior edges of the centrum; the anterior end is more extended than the posterior end. The posterior end of the neural spine is mediolaterally thickened relative to the rest of the spine such that the posterior edge of the neural spine forms a flattened surface. In posterior view, the neural spine possesses a deep fossa between the left and right postzygapophyses. The prezygapophyses are low on the neural spine, close to the neurocentral suture, and are oriented 45° dorsal from horizontal. The articular surfaces are not as well preserved on the prezygapophyses as on the postzygapophyses but they appear to be flat. The postzygapophyses extend posterior to the end of the centrum and neural spine. The articular surfaces of the postzygapophyses are sloped 15° dorsal from horizontal and are oval in ventral view. Laterally, the zygapophyses are connected by a thin lamina (continuous pre-/postzygapophyseal laminae *sensu* Wilson, 1999) as in *Revueltosaurus callenderi* (PEFO 34561). Dorsal to the postzygapophyses are weakly-developed (protruding 1-2 mm)

epipophyses, unlike the strongly-developed epipophyses of *Revueltosaurus callenderi* (PEFO 34561).

Postaxial Cervical Vertebrae—There are four cervical vertebrae preserved in NMT RB187 although one is heavily damaged (Fig. 6A, H-M). None of the postaxial cervical vertebrae preserve complete neural spines and the zygapophyses are poorly preserved in most.

The centra are anteroposteriorly longer than dorsoventrally tall along the cervical series, although not by a large margin (~1-3mm difference). In lateral view, the anterior and posterior ends of the centrum are flat, and the ventral margin is concave. The posterior end of the centrum is shifted ventrally relative to the anterior end. Like the axis, the center of the centrum is laterally compressed, making an hourglass shape in ventral view, though the degree of compression is less than in the axis. A single ventral midline ridge is present on the anterior cervical vertebrae. Both the diapophysis and parapophysis are located on the anterior end of the centrum. The diapophysis and parapophysis are well separated, as in most archosauriforms, with a shallow groove between them. In the anterior cervical vertebrae, the diapophysis and parapophysis are small protrusions without much lateral extent beyond the centrum. In the posterior cervical vertebrae, as they transition into trunk vertebrae, the parapophysis remains low, but the diapophysis is extended laterally upon a stalk. There are no laminae connecting the apophyses together nor present on the lateral face of the centrum. There is a spinoprezygapophyseal lamina connecting the posteromedial corner of the prezygapophyses to the anterolateral corner of the neural spine. Neurocentral sutures are clearly visible on all preserved cervical vertebrae. The anterior cervical vertebrae possess hypapophyses on both the anterior and posterior ventral surface of the centrum (Ce1 and Ce2, Fig. 4H-J). Unlike rauisuchids (e.g., *Postosuchus kirkpatricki*, TTU 9000, 9002), the middle cervical vertebrae do not possess anterior

hypapophyses. However, the middle cervical Ce3 (Fig. 6A) does possess paired projections on the ventral face of the posterior end of the centrum. We score *<Name Redacted>* as absent for this feature (Nesbitt, 2011, character 192, state 0) as vertebrae scored as present always have both anterior and posterior projections. The prezygapophyses are directed about 30° dorsal from horizontal in lateral view with a flat articulation surface that is rectangular in dorsal view. There is only a single partially preserved postzygapophysis on Ce4, which is directed approximately 35° dorsal from horizontal and is rectangular in ventral view. The dorsolateral margin of the postzygapophyses forms a ridge that extends anteroventrally and connects with the corresponding diapophysis. Posteriorly, the postzygapophyses are separated by a deep postspinal fossa, oval in outline, that is dorsoventrally taller than laterally wide.

Although a full cervical series is not preserved, there is a clear transition from anterior cervical vertebrae to anterior trunk vertebrae. Here we consider Ce4 (Fig. 4K-M) to be a posterior cervical because the position of the parapophysis low on the centrum, likely around the 8th to 11th vertebral position based on comparisons to *Revueltosaurus callenderi* (PEFO 34561) and *Alligator mississippiensis* (pers. obs.). The posterior cervical vertebra lacks a ventral midline ridge on the centrum, like the trunk vertebrae. The parapophyses of the posterior cervical vertebrae are undivided, and there is no hyposphene-hypantrum articulation on either the posterior cervical vertebrae or the anterior trunk vertebrae.

Trunk Vertebrae—A total of seven trunk vertebrae are preserved as isolated elements in the holotype NMT RB187, with an additional two preserved in a block with hindlimb and pelvic girdle material (Fig 6N-T). The centra tend to be completely preserved, and between the nine vertebrae representatives of all apophyses and the neural spine are preserved.

The anteriormost trunk vertebrae generally resemble the posteriormost cervical vertebrae with centra that are hourglass-shaped in ventral view and lack a midline ridge or hypapophyses-like processes. However, in all the anterior trunk vertebrae, the parapophyses are located far more dorsally than in the posterior cervical vertebrae, and in all cases they are positioned dorsal to the neurocentral suture on the neural arch based on comparisons to *Revueltosaurus callenderi* (PEFO 34561) and *Alligator mississippiensis* (pers. obs.). The anterior trunk centra are slightly longer than tall (ratio ~1.1) and the centra become equal in length/height posteriorly (Table 1). When viewed anteriorly or posteriorly, the centra articular facets are circular and become wider than tall posteriorly down the axial column. In lateral view, the anterior and posterior faces of the centra are vertical and the centra are anteroposteriorly concave without foramina or laminae. Like most other archosauriforms, there are shallow depressions on the lateral surfaces of the centra, just ventral to the neurocentral suture. The ventral and lateral surfaces of the centra grade smoothly into each other with no ridge separating the faces.

Parapophyses of the trunk vertebrae are positioned anterolaterally at the neurocentral suture (T1, Fig. 6O) and migrate dorsally towards the diapophyses until they are joined on the same laterally protruding process in the posteriormost trunk vertebrae (T9, Fig. 6R). The parapophyses are located anterior and ventral to the diapophyses and are laterally extended, though less so than the diapophyses. As there are no vertebrae from NMT RB187 with parapophyses between the anteroventral corner of the centrum (as seen in Ce4) and the anterior neurocentral suture position (as seen in T1). Therefore, we interpret there to be between three and five missing anterior trunk vertebrae in the holotype (e.g., Butler et al., 2017; Von Baczko et al., 2020), for a total of 22 presacral vertebrae. All preserved parapophyses are oval in cross section, with the long axis oriented dorsoventrally and projecting laterally from the neural arch

body. Posteriorly, the parapophyses become deflected posterodorsally as they migrate closer to the diapophyses, eventually forming a single lateral projection with two distinct faces like that of the transverse process in *Revueltosaurus callenderi* (PEFO 34561), although this lateral projection is less extensive in *<Name Redacted>*.

The diapophyses of the trunk vertebrae are consistently located at the anteroposterior center of the lateral part of the neural arch. In lateral cross section, the outline of the diapophyseal articulation surface is oval with the long axis oriented anteroventrally-posterodorsally, and shifting to anteriorly-posteriorly oriented in the more posterior trunk vertebrae. The diapophyses project lateral to the lateral surface of the centra, such that the width of the vertebrae at the diapophyses is twice that at the centra. This lateral extension is much greater than the co-occurring archosaurs *Nundasuchus songeaensis* (NMT RB 48) and *Mandasuchus tanyauchen* (NHMUK PV R6792) and in ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), and is more like that of the co-occurring *Parringtonia gracilis* (NHMUK R3139) and *Revueltosaurus callenderi* (PEFO 34561). In the posterior trunk vertebrae, the diapophyses and parapophyses protrude from the same process as in aetosaurs (e.g., *Polesinesuchus aurelioi*, ULBRAPVT003), *Revueltosaurus callenderi* (PEFO 34561), *Effigia okeeffeae* (AMNH FR 30587), and in dinosaurs (Nesbitt, 2011). In the anterior trunk vertebrae there is a clear centrodiapophyseal lamina emanating from the ventral side of the diapophysis, though it is less distinct in more posterior trunk vertebrae. This lamina forms the posterior border of a triangular, shallow, ventrally-opening centrodiapophyseal fossa, and the anterior border of a triangular, deep, posteriorly-opening postzygapophyseal-centrodiapophyseal fossa. In T3-4 the postzygapophyseal-centrodiapophyseal fossa is at its deepest of the preserved vertebrae and it becomes shallower in more posterior vertebrae. Neither the centrodiapophyseal fossa nor the

postzygapophyseal-centrodiapophyseal fossa possess foramina. However, the postzygapophyseal-centrodiapophyseal fossa in T3-4 does approach the dorsal fossa posterior to the spinoprezygapophyseal lamina, though they do not connect.

The neural canal openings are elliptical in outline in anterior and posterior view in the anterior trunk vertebrae, with the long axis directed dorsoventrally, whereas they are rectangular in outline in the same views in the posterior trunk vertebrae with the long axis directed mediolaterally. Open neurocentral sutures are clearly visible in anterior trunk vertebrae; posteriorly they transition through partially closed, to fully closed *sensu* Brochu, 1996. The prezygapophyses project anterodorsally in lateral view, beyond the anterior margin of the centra, and they are located anterodorsally to the diapophyses. The articular surfaces of the prezygapophyses are rectangular in outline in dorsal view. These articular surfaces are flat and are directed 30° dorsal from horizontal in anterior view. In all trunk vertebrae the prezygapophyses are separated by a 'V'-shaped gap visible in dorsal view that extends about two-thirds the length of the prezygapophyses to the neural spine. A robust spinoprezygapophyseal lamina extends from the posteromedial corner of the prezygapophysis and connects to the anterolateral corner of the neural spine. These left and right laminae frame a small (5mm) prespinal fossa and the ventral base of the neural spine. Posterior to the spinoprezygapophyseal laminae on the left and right are dorsally-opening fossae lateral to the neural spine and anterior of the postzygapophyses. In the anterior trunk vertebrae, there is also a thin but prominent prezygadiapophyseal lamina that extends from the ventrolateral point of the prezygapophysis along the anterior edge of the diapophysis projection. This lamina is not present in the more posterior trunk vertebrae.

The postzygapophyses project posteriorly and slightly dorsally in lateral view. In all trunk vertebrae, they extend past the posteriormost edge of the corresponding centrum. The postzygapophyseal articulation surfaces are flat and have a rectangular outline in ventral view. The postzygapophyses are angled 25° dorsal from horizontal in posterior view. The left and right postzygapophyses are separated by a small “V”-shaped gap visible in ventral view that extends along half the anterior-posterior length of the postzygapophyses. A postzygodiapophyseal lamina extends from the anteroventral corner of the postzygapophyses and forms the posterior boundary of the postzygapophyseal-centrodiapophyseal fossa. This lamina becomes relatively thicker in the posterior trunk vertebrae. The spinopostzygapophyseal laminae extends from the lateralmost point of the postzygapophysis to approximately halfway (in the anterior trunk vertebrae) to one-third (in the posterior trunk vertebrae) the height of the neural spine. The laminae define the lateral margins of a deep, slit-like postspinal fossa that is roughly half the dorsal-ventral height of the neural spine in posterior view.

The neural spines of the trunk vertebrae are rectangular in lateral view and are directed straight dorsally. The anterior and posterior borders near the base of the neural spine are bent posteriorly before becoming dorsoventrally straight such that the top of the neural spine is entirely dorsal to the centrum, rather than posteriorly offset like the postzygapophyses. The ventral portion of the neural spine is mediolaterally compressed, but becomes laterally expanded near the dorsalmost portion of the neural spine (= spine table). This surface is flat in lateral view and circular to oval in dorsal view. Similar expansions are present in the cervical and/or trunk vertebrae of other suchians such as ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), erpetosuchids (e.g., *Parringtonia gracilis*, NHMUK R3139), *Revueltosaurus callenderi* (PEFO 41387), aetosaurs (e.g., *Typothorax coccinarum*, TTU 9214), and loricatans (e.g., *Mandasuchus*

tanyauchen, NHMUK PV R6792). In dorsal view, the rounded expansion (=spine table) tapers posteriorly, most closely resembling that of *Revueltosaurus* and aetosaurs, rather than the rectangular spine table of ornithosuchids, erpetosuchids, and loricatans in homologous vertebrae. Both the anterior and posterior edges of the neural spine are excavated by midline grooves that extend for most of the length of the spine.

Sacral Vertebrae—The first primordial sacral vertebra is preserved in the holotype NMT RB187 (Fig. 5A-F). The vertebra is mostly complete but is slightly distorted and missing the neural spine. A fused first and second sacral vertebrae is preserved in NMT RB679. We determined the position based on the anterodorsal placement of the sacral rib on the centrum, a flange on the anterodorsal edge of the sacral rib, and the circular articular surface of the sacral rib. These features match closely with the first primordial sacral vertebrae of *Revueltosaurus callenderi* (PEFO 34561). The articular faces of the centrum are rounded, and although still amphicoelous, the posterior face is nearly flat. The anterior face of the centrum is wider and taller than the posterior face. In ventral view, the centrum is hourglass shaped and the surface is smooth with no midline ridge. The sacral rib joins with the centrum and neural arch at a facet in the anterodorsal portion of the element, occupying about half the length and height of the centrum, as well as the anteroventral portion of the neural arch.

The prezygapophyses project anterodorsally and extend just anterior to the anterior edge of the centrum. The articular surfaces are inclined 25° to 30° dorsal from horizontal in anterior view, with the angle becoming steeper dorsally. The prezygapophyses are separated by a ‘V’-shaped gap in dorsal view. In dorsal view, the articular faces of the prezygapophyses are rectangular and the surfaces themselves are concave, contributing to the changing angle of the surface. A thin spinoprezygapophyseal lamina connects the posterior edge of the

prezygapophysis to the anterior end of the neural spine. A small (1 cm tall), shallow prespinal fossa lies between the spinoprezygapophyseal laminae. A shallow, circular fossa lies posterior to the spinoprezygapophyseal lamina.

The postzygapophyses project posteriorly and extend just past the posterior edge of the centrum. The articular surfaces are declined 30° to 25° dorsal from horizontal in posterior view as the angle flattens ventrally. These surfaces are convex and rectangular in ventral view. The postzygapophyses are separated by a “V”-shaped gap in ventral view. A postzygodiapophyseal lamina forms the dorsal border of a shallow fossa on the posterior face of the neural arch and connects the postzygapophysis and sacral rib attachment. A tall, slit-like postspinal fossa between the left and right postzygapophyses appears to continue up the neural spine, but because the neural spine is lost it is unclear how far the feature extended.

The sacral ribs extend laterally with slight ventral and posterior components. A prominent, thin ridge of bone forms an anterior flange on the sacral ribs (broken on the right sacral rib) and sits dorsal to a shallow excavation on the anterior surface of the sacral ribs (Fig. 7A). In ventrolateral view, the rib articulation with the ilium is rounded and deflected medially. At the posterior end of the rib is a small, triangular expansion for the articulation with the anterior end of the second sacral rib. A ridge of bone extends from the sacral rib attachment at the neural arch to the posterolateral tip of the sacral rib on the posterodorsal surface of the rib.

Given the prominent anterior flange of the first primordial sacral vertebra it seems unlikely any trunk vertebrae were incorporated into the sacrum, though we cannot rule out the incorporation of caudal vertebrae. The small posterior articulation for the sacral rib following the first is inconsistent with the shape of archosaurs that possess an ‘inserted’ sacral vertebra (*sensu* Nesbitt 2011) between the first and second primordial vertebrae where the sacral ribs often fuse

to one another, and there is a fused sacral in NMT RB679, but again we cannot score this character with certainty. Additionally, some suchians, like *Revueltosaurus callenderi* (PEFO 34561 and PEFO 36876), may have been intraspecifically variable in whether the sacral vertebrae coossified. *<Name Redacted>* shows a similar pattern because the sacrum is not coossified in the holotype but it is fused in the referred specimen NMT RB679 (Fig. 2). This could also be the result of ontogenetic fusion of sacral vertebrae, which is common throughout reptiles (Griffin et al., 2021).

Caudal Vertebrae—At least seventeen caudal vertebrae are preserved in the holotype NMT RB187, and they provide examples of anterior and posterior forms (Fig. 5G-S). Preservation varies among the vertebrae: two of the anterior to middle caudal vertebrae (Ca4-5) preserve full neural spines, but only Ca5 preserves all constituent processes as well. In most posterior caudal vertebrae, the zygapophyses are broken, but they are preserved at least partially in four vertebrae such that their shape can be described.

The proportions of the caudal centra change along the axial column, elongating posteriorly. In the anterior most caudal vertebra (Ca1) the centrum is longer than tall (length to height ratio = 1.3); in the ~middle caudal vertebrae the centra become more elongate (length to height ratio = 1.7); in the posterior caudal vertebrae the centra are even more elongate (length to height ratio = 2.7). The anterior and posterior articular surfaces of the caudal centra are all concave (=amphicoelous) and oval (taller than wide), although they become more circular posteriorly from a height to width ratio of 1.2 to almost 1 at the posteriormost preserved vertebra. The anterior articular surfaces are the same height and width as the posterior articular surfaces on each centrum. Overall, the caudal vertebrae are relatively much more elongate (higher height to length ratio) than the caudal vertebrae of co-occurring suchians like *Nundasuchus songeaensis*

(NMT RB48), *Mandasuchus tanyauchen* (NHMUK PV R6792), and *Parringtonia gracilis* (NHMUK R3139); they are similar in proportion to *Revueltosaurus callenderi* (PEFO 34561).

In ventral view, the centra are hourglass shaped with a midline groove. In the anterior and middle caudal vertebrae, there is a thin lamina that trends through the middle of the midline groove on the ventral centrum surface, but this is not present in the posterior caudal centra with midline grooves. We consider this an autapomorphy of *<Name Redacted>*. At both the anterior and posterior ends of the centra, the midline groove ends in a ventrally expanded rim (Fig. 7S). The posterior end in all preserved caudal vertebrae bear chevron facets. These paired facets are “M”-shaped in ventral view and face posteroventrally. Ridges extend from the tips of the chevron facets to form the border of the midline groove, creating a distinct break from the lateral and ventral faces of the centra. In lateral view, the centrum surfaces are smooth and the ventral borders are concave because the anterior and posterior ends project ventral to the center of the centrum. The lateral surface of the posterior caudal centra possess an anteroposteriorly directed ridge of bone at the dorsal edge of the centra. In the posterior caudal vertebrae, this ridge forms the upper boundary of a shallow fossa on the lateral surfaces of the centra.

The neural canals are elliptical in both anterior and posterior view throughout the caudal series, and are wider than tall. The width of the canal increases relative to its length moving posteriorly in the caudal series. In the anterior and middle caudal vertebrae, the prezygapophyses project anterodorsally and slightly laterally, and they are angled 30° dorsal from horizontal in anterior view. The articulation surfaces are oval in dorsal view and slightly concave. The left and right prezygapophyses are separated by a deep, “V”-shaped notch in dorsal view and a shallow, circular prespinal fossa in anterior view. The anterior and middle caudal prezygapophyses bear both spinoprezygapophyseal and prezygodiapophyseal laminae. A circular fossa is located

posterior to each spinoprezygapophyseal lamina which is deep in the anterior caudal vertebrae and becomes shallower posteriorly. The prezygapophyses of the posterior caudal vertebrae project anterodorsally and are angled 75° dorsal from horizontal in anterior view. The articulation surfaces are oval and concave in dorsal view. The posterior caudal vertebrae do not possess a spinoprezygapophyseal lamina and the prezygodiapophyseal lamina is restricted to the anterior third of the vertebra (Fig. 7G).

The postzygapophyses are always located dorsally relative to the prezygapophyses in all caudal vertebrae. In the anterior and middle caudal vertebrae, the prezygapophyses project posterolaterally, angle 30° ventral from horizontal in anterior view, and are separated by a “V”-shaped notch in ventral view. The articulation surfaces are oval in ventral view and are flat. A spinopostzygapophyseal lamina extends from the dorsal surface of the postzygapophyses to the base of the neural spine. A circular postspinal fossa separates the postzygapophyses in posterior view in the anterior and middle caudal vertebrae. The postzygapophyses of the posterior caudal vertebrae project posteriorly, angle 70° ventral from horizontal in posterior view, and are joined onto a single process with a small notch between the distal ends. The articulation surfaces are oval and flat in lateral view. There are no laminae from the postzygapophyses of the posterior caudal vertebrae.

Transverse processes are present on the anterior and middle caudal vertebrae, which become smaller posteriorly with only small bumps remaining by Ca7 (Fig. 7G). The transverse process attachments are restricted to the neural arch, as in *Revueltosaurus*. In dorsal view, the transverse processes are triangular and are oval in cross section. The neural spines of the anterior and middle caudal vertebrae project dorsally and have straight anterior and posterior edges. Both the anterior and posterior edges bear a midline lamina that trends from the base of the neural

spine to approximately the midpoint. However, the anterior lamina does not possess the anterior laminar process found in some suchians (see Nesbitt, 2011). In anterior view, the neural spine thickens towards the dorsal end, but it does not form a lateral expansion (=spine table) like those present in the trunk vertebrae. As discussed by Butler et al. (2017) the phylogenetic signal of caudal expansions (=spine tables) is unclear. *Parringtonia gracilis* (NHMUK R3139), some aetosaurs (Parker, 2016b), and *Batrachotomus kupferzellensis* (Gower and Schoch, 2009) all possess caudal neural spines with expansions whereas *Revueltosaurus callenderi* (PEFO 34561), other aetosaurs (Parker, 2016a), and *Mandasuchus tanyauchen* (NHMUK PV R6792) lack expansions, although they still have a thickened dorsal end of the neural spine.

Osteoderms

The osteoderms of *<Name Redacted>* are represented by numerous isolated and some articulated (in the case of appendicular osteoderms) elements that would have covered the majority of the body in an armored carapace (Figs. 8-9). Although found in isolation, we can deduce that *<Name Redacted>* possessed the aetosaur-like arrangement of paramedian and lateral osteoderms based on the morphological similarities to both paramedian and lateral osteoderms of aetosaurs (see section below). This arrangement of paramedian and lateral osteoderm pairs is also found in the non-aetosaurian aetosauriforms *Revueltosaurus callendri* (PEFO 42442; Parker et al., 2021) and *Acaenasuchus geoffreyi* (UCMP 139574; Marsh et al., 2020), as well as erpetosuchids (e.g., *Erpetosuchidae* indet., BGS GSM Elgin A; Foffa et al., 2020). Because the osteoderms are often found associated with the skeleton, but not in articulation, precise identification of the position of osteoderms in the recommended carapacial region assignment (Parker, 2007; Desojo et al., 2013) is not possible. Ideally, we would use paramedians matched to the associated vertebral count (Parker, 2007; Desojo et al., 2013).

Instead, we assign osteoderms to regions based on shape, size, and articulation pattern compared to *Revueltosaurus callenderi* and aetosaurs (see Marsh et al., 2020).

Paramedian—All the paramedian osteoderms of <Name Redacted> are mediolaterally wider than anteroposteriorly long (W/L ratio of 1.27 to 1.39). The paramedian osteoderms have well-developed anterior bars (*sensu* Long and Ballew, 1985), an articular shelf along the anterior margin of osteoderms that is overlapped by the preceding osteoderm, which are unornamented (Fig. 8). The anterior bars of the paramedian osteoderms are smooth and featureless in *Revueltosaurus callenderi* (PEFO 34561) and aetosaurs (e.g., *Scutarx deltatylus*, PEFO 34045), but they are ornamented in *Acaenasuchus geoffreyi* (PEFO 40740), *Euscolosuchus olseni* (USNM 448587), and potentially *Tarjadia ruthae* (CRILAR-Pv 478, see Ezcurra et al., 2017 supplementary figure 7). The anterior bars of the paramedian osteoderms (Fig. 8A, C; 7A) also have anterior and anteromedial processes as in *Revueltosaurus callenderi* (PEFO 34561), *Acaenasuchus geoffreyi* (UCMP 139576), and non-desmotosuchin aetosaurs (e.g., *Scutarx deltatylus*, PEFO 34045). The paramedian osteoderms of <Name Redacted> are more similar to those of *Revueltosaurus callenderi* (PEFO 34561) and *Acaenasuchus geoffreyi* (PEFO 40000) in that osteoderm flexion (dividing the medial and lateral portions of the paramedian osteoderm) and the associated dorsal eminence are closer to the lateral edge than the medial edge. In aetosaurs (e.g., *Scutarx deltatylus*, PEFO 34045), the osteoderm flexion and dorsal eminence are closer to the medial edge (Parker, 2007; Marsh et al., 2020). Posterior to the anterior bars, the dorsal surface of the paramedian osteoderms of <Name Redacted> is ornamented with a series of reticulated grooves and pits, like the ornamentation found on the paramedian osteoderms of *Acaenasuchus geoffreyi* (PEFO 40740), *Euscolosuchus olseni* (USNM 448582), and aetosaurs (e.g., *Longosuchus meadei*, TMM 31185-84a; Parker et al., 2021,

character 422, state 1). This ornamentation appears to emanate from the osteoderm flexion and dorsal eminence also as in aetosaurs (e.g., *Longosuchus meadei*, TMM 31185-84a). The flexion of the paramedian osteoderms is at angles of between 30° and 45° ventral from horizontal.

The medial portion of the anterior border of the paramedian osteoderms is slightly concave because the anterior medial process and anterior process project further anteriorly than the space between them (Fig. 8). The lateral portion of the anterior border curves posterolaterally forming a rounded lateral border. This indicates that the lateral osteoderms likely under- or overlie the paramedian osteoderms when in articulation, rather than the vertical articulation between lateral and paramedian osteoderms found in *Acaenasuchus geoffreyi* (PEFO 40000). In anterior view, the paramedian osteoderms are medially flexed such that the medial edge and center of the osteoderms are dorsal relative to the lateral edge. The ventral surface of the paramedian osteoderms is smooth and unornamented although the anteroposterior center is slightly ventrally expanded such that the osteoderm thins anteriorly and posteriorly.

There is at least one paramedian osteoderm that we interpret as being from the caudal region (Fig. 9A-C) because it is longer than wide (W/L ratio of 0.82) with a stronger midline ridge that separates the medial and lateral portions of the osteoderm. This shape is very similar to the distal caudal paramedian osteoderms of *Revueltosaurus callenderi* (PEFO 34561). Like the more anterior paramedian osteoderms, the caudal paramedian possesses a dorsal eminence and osteoderm flexion (*sensu* Parker, 2016b). Unlike the precaudal paramedian osteoderms, the caudal paramedian osteoderm has a raised, anteroposteriorly-oriented ridge that trends from the dorsal eminence to the anterior process of the anterior bar coincident with the flexion (Fig. 9A). In dorsal view, the medial anterior margin is nearly straight, and the lateral anterior margin curves posteriorly. In anterior view, the caudal paramedian osteoderm is arched dorsally, like the

other paramedian osteoderms. The ventral surface of the caudal paramedian osteoderm is smooth and thins anteriorly and posteriorly from the anteroposterior middle.

Lateral—Only a single partial osteoderm (left lateral portion) is complete enough to be confidently identified as a lateral osteoderm (Fig. 9D, E). This element is a lateral osteoderm because of the large dorsal eminence (relative to the anteroposterior length of the osteoderm) and the shallower ornamentation than that of the paramedian osteoderms. It is unclear if *<Name Redacted>* has a single column of lateral osteoderms as in aetosaurs (Desojo et al., 2013) or a double column of lateral osteoderms as in *Acaenasuchus geoffreyi* (Marsh et al., 2020) because we do not find the osteoderms in articulation. The dorsal surface is ornamented with shallow pits and grooves, similar to the paramedian osteoderms, but they are only half the depth. The dorsal eminence is oblong, oriented anterolaterally-posteromedially, and doubles the dorsoventral depth of the osteoderm, compared to 25 to 50% in the paramedian osteoderms. The dorsal eminence does not form an elongate spine on the lateral osteoderm like in desmatosuchin aetosaurs (*sensu* Parker, 2016b, e.g., *Longosuchus meadei*, TMM 31185-84a), and are more similar to those of *Revueltosaurus callenderi* (PEFO 34561) in forming a small ridge. Although most of the osteoderm flexion is absent, a small portion is visible in posterior view that shows the angle of flexion is 60°, much greater than the angle of flexion in the paramedian osteoderms similar to what would be expected for a lateral osteoderm in an aetosaur (e.g., *Scutarx deltatylus*, PEFO 34045; Desojo et al., 2013). The lateral border is rounded such that it approximates a semicircle. The ventral surface is smooth with a slight rise in the anteroposterior middle.

Appendicular—Several appendicular elements bear osteoderms in association, most notably the articulated right radius and ulna, which together bear at least 21 small osteoderms. Small appendicular osteoderms are also found in aetosaurs (e.g., *Aetosauroides scagliai*, PVL

2052), erpetosuchids (e.g., *Tarjadia ruthae*, CRILAR-Pv 478), and phytosaurs (Stocker and Butler, 2013). The appendicular osteoderms are oval to diamond-shaped, ranging in size from < 6 to 16.8 mm in maximum width, but only ~1 mm in thickness. The ornamentation on the external surface of the appendicular osteoderms differs from that of the other osteoderms in being randomly pitted rather than anastomosing. Similar simple ornamentation in appendicular versus paramedian and lateral osteoderms is also seen in some aetosaurs (e.g., *Scutarx deltatylus*, PEFO 34616). There are two morphs of appendicular osteoderms: those that are flat with a few small random pits, and those with a central keel and small grooves, in addition to pits (Fig. 2H). In appendicular osteoderms with undamaged edges, the lateral surfaces are grooved (Fig. 9F).

Pectoral Girdle

Scapula—Both the scapulae are preserved in NMT RB187 (Fig. 10A-F), and a partial scapula is present in NMT RB679. The holotype right scapula is missing the anteriormost portion of the acromion process, and the holotype left scapula is missing the anterior portion of the acromion process and nearly the entire anterior edge of the scapular blade (Fig. 10A-F). The right scapula is 88.4 mm in length and is longer than the corresponding humeri, unlike the condition found in some crocodylomorphs (e.g., *Hesperosuchus agilis*, AMNH FR 6758) where the scapulae are less than 75% the humeral length, but like the condition in *Revueltosaurus callenderi* (PEFO 34561) or aetosaurs (e.g., *Longosuchus meadei*, TMM 31185-84). The scapulae are free from the coracoids, although coossification is known to be intraspecifically variable in other suchian taxa (e.g., *Revueltosaurus callenderi*; *Aetosaurus ferratus*) and the relationship of coossification of these elements with growth is not clearly defined in reptiles (Griffin et al. 2021). When the scapula and coracoid are in articulation, the concave surface of the glenoid is oriented posterolaterally, as is the ancestral state for archosauriforms (Nesbitt,

2011, character 227, state 0). The glenoid contribution of the scapula is approximately two-thirds that of the coracoid and is semicircular in outline in ventral view. Although in many early-diverging pseudosuchians the glenoid contribution of the scapula is less than that of the coracoid (e.g., *Riojasuchus tenuisiceps*, PVL 3828; *Parringtonia gracilis*, NMT RB426; *Revueltosaurus callenderi*, PEFO 34561; *Mandasuchus tanyauchen*, NHMUK PV R6792), <Name Redacted> more closely resembles the condition of *Parringtonia gracilis* (NHMUK R3139) and *Revueltosaurus callenderi* (PEFO 34561) in the scapular glenoid contribution being more than half of that of the coracoid. In the other taxa (e.g., *Riojasuchus tenuisiceps*, PVL 3828; *Mandasuchus tanyauchen*, NHMUK PV R6792) the scapular contribution is less than half that of the coracoid. The larger scapula contribution appears to be the result of the relative extensions of the supraglenoid rim and subglenoid lip (Ezcurra, 2016, character 399) but this character does not capture the variation in taxa with larger subglenoid lips and supraglenoid rims. The glenoid fossa of <Name Redacted> is framed by a well-developed supraglenoid rim on the scapula and an anteroposteriorly longer subglenoid lip of the coracoid. The articular surface of the scapula with the coracoid is weakly concave in proximal view, rugosely textured, comma-shaped in proximal view, and straight in lateral view. The thickest part of the articulation with the coracoid is oriented mediolaterally and is medially deflected. The articulation surface abuts the glenoid and then tapers anteriorly, like the shape of *Revueltosaurus callenderi* (PEFO 34561).

A low, teardrop-shaped tubercle is present distal to the glenoid on the posterolateral surface of the ventral end of the scapula (Fig. 10A, D), which likely corresponds to the origin of the M. triceps as suggested by Gower (2003) for archosauriforms. Plesiomorphically, archosauriforms possess a muscle scar in this location (Nesbitt, 2011), but a teardrop-shaped, knobby tubercle is present in ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827) and some

loricatans (e.g., *Batrachotomus kupferzellensis*, SMNS 80271; *Prestosuchus chiniquensis*, SNSB-BSPG XXV 12). <Name Redacted> exhibits an “intermediate” morphology wherein the tubercle is less robust (5.4 mm in proximodistal long axis, 1.1 mm extension laterally) than the corresponding supraglenoid rim, which is similar to the morphology of erpetosuchids (e.g., *Parringtonia gracilis*, NMT RB187), *Acaenasuchus geoffreyi* (PEFO 40720), and some aetosaurs (e.g., *Typothorax coccinarum*, UCMP 34255). Anteriorly, the ventral portion of the scapula thins towards the acromion process. Based upon what is preserved of the acromion process, the structure likely would have projected toward the lateral surface and would have been raised above the ventral edge of the scapula, as in crown archosaurs, but we score the feature as unknown (Nesbitt, 2011, character 220). Additionally, because the anterior margins of both scapulae are missing, it is unclear if there would be a notch between the scapula and coracoid, as is the ancestral condition for archosaurs (Nesbitt, 2011, character 221). Based upon the preserved portions of both elements, it appears <Name Redacted> retains the plesiomorphic trait of possessing a distinct notch (Nesbitt, 2011, character 220, state 0), rather than the derived condition in rauisuchids (e.g., *Postosuchus kirkpatricki*, TTU 9000) and crocodyliforms (e.g., *Protosuchus richardsoni*, AMNH FR 3024) in which there is an uninterrupted edge (Nesbitt, 2011, character 220, state 1), but we score the character as unknown here.

The scapular blade is mediolaterally compressed and forms approximately three-quarters of the total length of the scapula. The shaft of the scapula is teardrop-shaped in cross section with the expanded end formed by the posterior margin of the shaft and the tapered end formed by the anterior margin. Both the anterior and posterior margins of the scapular blade are concave in lateral view, and the lateral surface is convex in dorsal/distal view. In lateral view, the dorsal/distal edge of the scapular blade is dorsally convex. The narrowest portion of the scapular

blade is at mid-height and widens to the dorsal/distal end such that it is more than twice the anteroposterior length of the narrowest part of the scapula. This morphology is present throughout archosauriforms (e.g., *Garjainia madiba*, BP/1/7152; *Euparkeria capensis*, SAM-PK 5867; *Riojasuchus tenuisiceps*, PVL 3827; *Parringtonia gracilis*, NMT RB426; *Mandasuchus tanyauchen*, NHMUK PV R6793; *Hesperosuchus agilis*, CM 29894). The width of the distal end of the scapular blade is approximately half the height of the scapular blade, as in most archosauriforms (Nesbitt, 2011, character 218, state 0). The distal end of the scapula appears to be anteroposteriorly longer than the proximal end, however the proximal ends of the scapulae are broken in both the left and right specimens. The medial surface of the scapula is smooth and lacks the diagonal, anteroproximally-posterodistally oriented ridge found in some erythrosuchids (e.g., *Erythrosuchus africanus*, NHMUK PV R3592), and *Smilosuchus gregorii* (USNM 18313). The posterior edge of the scapular blade is rounded for the proximal most two-thirds but thins to a blade in the distal most third. The distal surface of the scapula is flat and is mediolaterally wider at the posterior end than the anterior end, such that the outline is triangular in distal view.

Coracoid—The right coracoid is completely preserved in NMT RB187 with only a small fragment of the anterior dorsal edge damaged; it remains in a block with a portion of the right ischium, the proximal end of the right calcaneum (the distal end of the calcaneum is still embedded in a matrix block), and the right metatarsal V (Fig. 10G-I). The coracoid is oval in lateral view with convexly rounded dorsal, anterior, and ventral edges. The ventral half of the glenoid is formed by the coracoid and the glenoid fossa is oriented posterolaterally. The subglenoid lip projects further laterally than the supraglenoid rim, and it forms the mediolaterally thickest part of the coracoid. The articulation surface for the scapula mirrors the corresponding surface of the scapula, with the mediolaterally widest portion on the posterior end and narrowing

anteriorly to form a comma-shape. Ventral to the subglenoid rim is a shallow fossa on the lateral face of the coracoid and a notch on the posterior margin of the coracoid that separate the subglenoid rim from the postglenoid process. Plesiomorphically, the coracoids of non-archosaurian archosauriforms are subcircular without a postglenoid notch (e.g., *Proterosuchus fergusi*, NMQR 1484; *Erythrosuchus africanus*, NHMUK PV R3592; *Euparkeria capensis*, SAM-PK-6049; and *Smilosuchus gregorii*, USNM 18313), but a postglenoid notch is found throughout pseudosuchian archosaurs (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Revueltosaurus callendri*, PEFO 34561; *Longosuchus meadei*, TMM 31185-84a; *Batrachotomus kupferzellensis*, SMNS 80271; *Effigia okeeffeae*, AMNH FR 30587; *Hesperosuchus agilis*, AMNH FR 6758). The postglenoid process is short, only extending 7 mm posterior to the posterior edge of the glenoid fossa when measured from the deepest portion of the notch posteriorly. A short postglenoid process is found across early diverging pseudosuchians (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Revueltosaurus callenderi*, PEFO 34561; *Longosuchus meadei*, TMM 31185-84a), but it becomes elongated in paracrocodylomorphs (e.g., *Effigia okeeffeae*, AMNH FR 30587; *Hesperosuchus agilis*, AMNH FR 6758; *Protosuchus richardsoni*, AMNH FR 3024; *Orthosuchus stormbergi*, SAM-PK-409).

The posteroventral edge of the coracoid is smooth, lacking the deep groove found in *Postosuchus kirkpatricki* (TTU 9000) and crocodylomorphs (e.g., *Hesperosuchus agilis*, AMNH FR 6758). The lateral surface of the posteroventral corner of the coracoid possesses an oblong lateral expansion (= biceps tubercle *sensu* Nesbitt, 2011) found in suchian archosaurs and some dinosauriforms (Langer et al., 2007; Nesbitt, 2011). There is an anteroventrally-opening coracoid foramen anterior to the glenoid and ventral to the articulation with the scapula; it opens posterodorsally on the medial surface. As in *Parringtonia gracilis* (NMT RB426) and

Revueltosaurus callenderi (PEFO 34561) the coracoid foramen is separated from the glenoid by a shallow, dorsoventrally-oriented fossa on the lateral face. The space between the coracoid foramen and glenoid lacks a distinct fossa in *Ornithosuchus tenuisiceps* (PVL 3827), *Aetosauroides scagliai* (PVL 2073), *Typothorax coccinarum* (UCMP 34255), *Effigia okeeffeae* (AMNH FR 30587), *Poposaurus gracilis* (YPM 57100), and *Postosuchus alisonae* (UNC 14475). The remainder of the lateral surface of the coracoid is smooth and slightly convex laterally. Although partially obscured, the medial surface of the coracoid is slightly concave, smooth, and featureless, except for the coracoid foramen.

Forelimb

The forelimb of *<Name Redacted>* is 0.66 the length of the hindlimb (= humerus + radius: femur + tibia). A forelimb-hindlimb ratio of more than 0.55 is common throughout early-diverging pseudosuchians, with the exception of shuvosaurids (Nesbitt, 2011).

Humerus—Both humeri are preserved in the holotype NMT RB187. The right humerus is complete, although the distal end has been anteroposteriorly crushed and a bone fragment is stuck to the anterior side of the proximal end (Fig. 11A-F). The left humerus is mostly complete but is missing the ulnar condyle and a portion of the medial humeral head, and the radial condyle is partially eroded (Fig. 11A-F). The right humerus is 93.5 mm long, approximately 0.65 the length of the right femur. A ratio of humeral length to femoral length of greater than or equal to 0.6 is found in all archosaurs except *Herrerasaurus ischigualastensis* (PVSJ 373), *Eoraptor lunensis* (PVSJ 512), and neotheropods (Langer and Benton, 2006; Nesbitt, 2011). The proximal and distal ends of the humeri are expanded relative to the midshaft such that the proximal end of the humerus is fan-shaped and four times the width of the midshaft. The proximal and distal heads are offset from one another such that the humerus is slightly

sigmoidal in medial view. The humeral head is restricted to the proximalmost surface and lacks the posteriorly-directed hooked expansion found in rauisuchids (e.g., *Postosuchus kirkpatricki*, TTU 9002) and crocodylomorphs (e.g., *Hesperosuchus agilis*, AMNH FR 6758; *Sphenosuchus acutus*, SAM-PK-3014). The head of the humerus can be divided into three structures in proximal view, lateral and medial tuberosities and the humeral head in the center, with the central humeral head being the largest of the three. A similar configuration can be seen in *Riojasuchus tenuisiceps* (PVL 3827), *Parringtonia gracilis* (NMT RB426), *Revueltosaurus callenderi* (PEFO 34561), *Acaenasuchus geoffreyi* (PEFO 40739), and aetosaurs (e.g., *Longosuchus meadei*, TMM 31185-84b). However, in both *Riojasuchus tenuisiceps* (PVL 3827) and *Parringtonia gracilis* (NMT RB426) the medial tuberosity is restricted to the proximal surface, whereas in *<Name Redacted>* and the other mentioned taxa this tuberosity continues onto the anterior surface. The medial corner is prominently deflected medially in anterior view, as in *Revueltosaurus callenderi* (PEFO 34561) and some aetosaurs (e.g., *Longosuchus meadei*, TMM 31185-84b), but unlike the condition in *Acaenasuchus geoffreyi* (PEFO 40739) and other aetosaurs (e.g., *Aetosauroides scagliai*, PVL 2073) where the medial corner is gently expanded. This prominent medial expansion results in an asymmetric proximal head of the humerus such that the medial margin of the humerus is arched. On the medial edge of the proximal end of the humerus is a thin, posteromedially-directed ridge of bone homologous with the internal tuberosity found in *Riojasuchus tenuisiceps* (PVL 3827). Laterally the humeral proximal articular surface is continuous with the deltopectoral crest as in most archosauriforms except dinosaurs, which have a gap separating the proximal end from the deltopectoral crest (e.g., *Tawa hallae*, GR 242). The apex of the deltopectoral crest is restricted to the proximal 30% of the length of the humerus, as in non-dinosaurian archosaurs (Langer and Benton, 2006; Nesbitt, 2011). A faint

supinator ridge is present on the lateral side of the posterior surface of the proximal end of the humerus, but <Name Redacted> lacks a distinct muscle scar for the M. triceps seen in some loricatans (e.g., *Mandasuchus tanyauchen*, NHMUK PV R6792; *Batrachotomus kupferzellensis*, SMNS 80276).

The cross-section of the humeral shaft is elliptical, with the long axis oriented mediolaterally. The distal end of the humerus is three times wider mediolaterally than the humeral shaft. The width of the distal end of the humerus (33 mm) is 0.35 the length of the humerus. A humeral distal width greater than 30% the humeral length is found in sauropodomorphs (Langer and Benton, 2006) as well as *Revueltosaurus callenderi* (PEFO 34561). The ent- and ectepicondyles are well-developed with a shallow fossa between them on the anterior surface. This anterior fossa is much shallower than that of *Revueltosaurus callenderi* (PEFO 34561), *Acaenasuchus geoffreyi* (PEFO 40739), and aetosaurs (e.g., *Desmotosuchus spurensis*, UCMP 32184), and is similar in proportion to that of *Parringtonia gracilis* (NMT RB426). The entepicondyle is more medially expanded than the ectepicondyle is laterally expanded, reflecting the arched medial margin formed by the distal end. In distal view, the ectepicondyle is posteriorly expanded such that it is 20% thicker than the entepicondyle, and it is separated from the entepicondyle by a shallow trochlear groove. An ectepicondylar groove is present on the lateral surface of the distal end of the humerus. However, the ectepicondylar flange does not fully enclose the groove to form an ectepicondylar foramen, as in some specimens of *Revueltosaurus callenderi* (PEFO 34269). This is unlike the condition in other specimens of *Revueltosaurus callenderi* (PEFO 34561) and most aetosaurs (e.g., *Longosuchus meadei*, TMM 31185-84a; *Desmotosuchus spurensis*, UCMP 32184) where the ectepicondylar flange fully encloses the groove to form a foramen.

Ulna—The left ulna is preserved in articulation with the left radius in the holotype NMT RB187, and a complete left ulna is preserved in NMT RB679. The left ulna is complete with some erosion to the proximal end, and it is partially covered by the left radius and several appendicular osteoderms (Fig. 11G-J). The ulna is slightly sigmoidal in medial view and is 84.2 mm long in total length in NMT RB187, approximately 90% the length of the humerus. The proximal end of the ulna is roughly triangular in proximal view and is mediolaterally expanded, with a prominent olecranon process. A mediolaterally-expanded proximal head is also found in *Revueltosaurus callenderi* (PEFO 34561) and aetosaurs (SMNS 5770). The articular surface for the humerus is partially eroded, but it is clearly concave and mediolaterally broad with a constricted anterior process (Fig. 11I-J). Although partially obscured by the radius, there is a distinct radial tuber on the dorsolateral surface of the ulna between the olecranon process and anterior process. The ulnar shaft is mediolaterally compressed such that the minimum shaft thickness is 2.9 times thinner than the proximal head of the ulna. The shaft bends anteriorly and is elliptical in cross-section. The distal end of the ulna expands mediolaterally from the midshaft and slightly anteriorly but, it lacks the “squared-off” morphology of loricatans (Nesbitt, 2011). There are two articular facets on the distal surface of the ulna, one posterolateral for the ulnare and one anteromedial for the intermedium (Fig. 11H).

Radius—Both the left and right radii are preserved in NMT RB187, the left in articulation with the left ulna and appendicular osteoderms and the right radius in isolation. A complete left radius is preserved in NMT RB679 (Fig. 11K, L). The right radius is completely preserved with some erosion of the distal end, and the left radius is mostly preserved although the proximal end has been eroded. The radius of NMT RB187 is 73.7 mm long, making it 78% the length of the humerus. A radial length less than 80% that of the humerus is also found in

ornithischians, sauropodomorphs, theropods (Langer and Benton, 2006; Nesbitt, 2011), and aetosauriforms (e.g., *Revueltosaurus callenderi*, PEFO 34561; see Parker et al., 2021). In proximal view, the radial head is greatly expanded such that it is four times as wide as the midshaft. The proximal surface of the radius is concave, as is typical in suchians (e.g., *Riojasuchus tenuisiceps*, PVL 3828; *Revueltosaurus callenderi*, PEFO 34561; *Batrachotomus kupferzellensis*, SMNS 80275). The anterolateral surface of the proximal end of the right radius possesses a distinct groove that is most visible in proximal view, along with a foramen just posterior to the groove (Fig. 11L). This feature appears to have been eroded off the left radius limiting comparisons, but the groove and associated foramen does not appear in other early pseudosuchians as far as we know and we treat it as an autapomorphy of *<Name Redacted>*. The radial midshaft is circular in cross-section and widens anteroposteriorly and mediolaterally towards the distal end. The distal end of the radius is oval in distal view with the long axis oriented mediolaterally. Because of wear, the articular surface of the distal end is unclear, but it appears to be mostly flat with a slight proximal deflection of the articular surface on the lateral edge. The posterior edge of the distal end of the radius bears a small depression, which we consider homologous to the longitudinal groove found in *Postosuchus kirkpatricki* (TTU-P 9002), *Hesperosuchus agilis* (AMNH FR 6758), *Revueltosaurus callenderi* (PEFO 34561), and some (e.g., *Aetosauroides scagliai*, PVL 2059), but not all, aetosaurs (e.g., *Stagonolepis olenkae*, Drózd, 2018).

Manus—A partial left manus is preserved in NMT RB187, represented by one complete metacarpal, two partial metacarpals (proximal ends), three complete phalanges, one partial phalanx (distal end), and one manual ungual all found associated, but isolated (Fig. 11M-Q). The proximal ends of the metacarpals overlap one another in dorsal view, as in most non-

archosaurian archosauriforms and pseudosuchians (Nesbitt, 2011). The metacarpals are mediolaterally longer than dorsoventrally tall, like *Revueltosaurus callenderi* (PEFO 34561), though not to the extreme found in some aetosaurs (e.g., *Stagonolepis olenkae*, ZPAL AbIII/3349/1). In proximal view, the lateral portion of the articulation surface is offset ventrally from the rest of the proximal surface. The dorsal surface of the proximal end of the metacarpals is flat, lacking the deep extensor pits found in some dinosaur taxa (Serenio et al., 1993; Langer and Benton, 2006; Nesbitt, 2011). In the complete metacarpal the mediolateral width of the midshaft is 40% that of the proximal end and 50% that of the distal end. The distal surface of the metacarpal is slightly convex, and there is a deep flexor pit on the dorsal surface of the distal end (Fig. M, N). As we are uncertain of the position of individual phalanges, there is little phylogenetic information to be gleaned from the manual phalanges. The manual phalanges that are preserved are proximodistally and dorsoventrally short, and mediolaterally expanded such that they are oval in cross-section (Fig. O-Q). The proximal surfaces are concave with a rim in proximal view, and the distal surfaces are convex in distal view with two distinct condyles separated by a proximodistally-oriented groove. There are medial and lateral pits on the distal ends of the phalanges, as well as prominent flexor pits. The singular manual ungual is arched anteroventrally and is mediolaterally compressed such that the distal end is a sharp point (Fig. O-Q). The medial and lateral surfaces of the manual ungual is covered in small pits and faint grooves. The proximal articulation surface is triangular and concave.

Pelvic Girdle

Pubis—Both pubes are preserved in the holotype NMT RB187, with the right pubis preserved (Fig. 12) in two pieces and missing portions of the pubic apron and the left pubis almost completely preserved with portions of the medial pubic apron broken. The left pubis

remains in a block that is still attached to other postcranial elements and is distorted (Fig. 13). The left pubis measures 111 mm from proximal to distal end. This is approximately 75% the femoral length, so *<Name Redacted>* can be considered as having an elongate (>70% femoral length) pubis relative to non-archosaurian archosauriforms (Nesbitt, 2011, characters 1 and 278). An elongate pubis is also found in ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), *Gracilisuchus stipanicorum* (PVL 4597), poposaurids (e.g., *Poposaurus gracilis*, YPM 57100), and crocodylomorphs (e.g., *Terrestriisuchus gracilis*, NHMUK R7562). A short (<70% femoral length) pubis is found in *Parringtonia gracilis* (NMT RB426), *Revueltosaurus callenderi* (PEFO 34561), and some aetosaurs (e.g., *Aetosaurus ferratus*, SMNS 5770). The proximal portion of the pubis is subtriangular in lateral view with a large obturator plate containing a single small obturator foramen, similar to the morphology found in *Riojasuchus tenuisiceps* (PVL 3827) and *Parringtonia gracilis* (NMT RB426) among other pseudosuchians.

The proximal portion of the pubis has two articular surfaces, an anterior one for the ilium and a more posteroventral one for the ischium. The articulation surface with the ilium is oval in proximal view, rugosely textured, and anteroposteriorly longer than mediolaterally wide. Posteroventral to this articulation surface is an anteroventrally-oriented groove that forms the anteroventral portion of the acetabulum. The acetabulum contribution of the pubis is restricted to the proximalmost surface, as in other early diverging pseudosuchians like ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), some aetosaurs (e.g., *Aetosaurus ferratus*, SMNS 5770), and loricatans (e.g., *Mandasuchus tanyauchen*, NHMUK PV R6792). This morphology differs from the acetabular contribution continuing onto the lateral surface as in rauisuchids (e.g., *Batrachotomus kupferzellensis*, SMNS 80270) and dinosaurs (e.g., *Herrerasaurus ischigualastensis*, PVSJ 373). The articular surface with the ischium is only preserved in the left

pubis and is a thin, long, plate-like surface that also forms the proximal and posterior boundaries of the obturator plate. The ventromedially-long, ventrally-directed puboischiadic contact is plesiomorphic for archosauriforms (Nesbitt, 2011), and this condition is retained in *<Name Redacted>*. The anterior edge of the proximal part of the pubis is flat with no prepubic process, like in most archosaurs (Nesbitt, 2011). The medial surface of the proximal portion of the pubis is smooth and forms a depression along the thin-plate like structure that contains the obturator foramen, similar to the morphology seen in *Riojasuchus tenuisiceps* (PVL 3827) and *Revueltosaurus callenderi* (PEFO 34561). The scar for the ambiens muscle can only be seen on the right pubis because it is covered by the left femur on the left pubis. The ambiens scar is oriented proximodistally, with a series of small, submillimeter-scale ridges and grooves just anterior to the pubic tubercle (Fig. 12C). The morphology of the ambiens scar resembles that of other early diverging pseudosuchians (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Gracilisuchus stipanicorum*, PVL 4597). In lateral view, the pubic tubercle forms a posteriorly curving ridge (Ezcurra, 2016, character 476, state 1) like that found in ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), *Nundasuchus songeaensis* (NMT RB48), and aetosaurs (e.g., *Aetosauroides scagliai*, PVL 2073). This differs from the plate-like pubic tubercle of non-archosauriform archosauromorphs (Ezcurra, 2016) and *Qianosuchus mixtus* (IVPP V14300), and the straight proximodistally-oriented ridge pubic tubercle of rauisuchids (e.g., *Batrachotomus kupferzellensis*, SMNS 80270) and dinosaurs (e.g., *Herrerasaurus ischigualastensis*, PVSJ 373).

Moving distally from the proximal end, the pubic shaft thins anteroposteriorly and expands medially such that the long axis is rotated 90° from the long axis of the proximal end. This medially-expanded, thin, rotated distal pubic shaft forms a broad pubic apron that would contact its counterpart along its distal half, based on the articulation surfaces found on the medial

edges of both pubic aprons. A similarly broad pubic apron is formed in early diverging pseudosuchians (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Revueltosaurus callenderi*, PEFO 34561; *Desmatosuchus spurensis*, MNA V9300) and differs from the mediolaterally compressed pubic aprons of paracrocodylomorphs (e.g., *Poposaurus gracilis*, PEFO 34865). This distal end of the pubis is approximately the same thickness as the mid-pubic apron, although there is a slight anterior expansion on the lateral corner of the distal pubis. Therefore, <Name Redacted> lacks the pubic boot found in some loricatans (e.g., *Postosuchus kirkpatricki*, UCMP 126747; *Effigia okeeffeae*, AMNH FR 30587) and dinosaurs (e.g., *Herrerasaurus ischigualastensis*, PVL 2566).

In anterior view the distal end of the pubis is rectangular with a flat distal edge and curved lateral and medial corners of the distal edge. A rectangular distal end of the pubis is also found in aetosaurs (e.g., *Typothorax coccinarum*, UCMP 34248), and is unlike the pointed distal edge found in gracilisuchids (e.g., *Turfanosuchus dabanensis*, IVPP V3237; *Gracilisuchus stipanicicorum*, PVL 4597) and the rounded distal edge found in ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3828). The combined widths of the left and right pubes result in a pubic apron that is 0.58 the length of the pubis (Ezcurra, 2016, character 478, state 0). This is a similar ratio as observed in gracilisuchids (e.g., *Turfanosuchus dabanensis*, IVPP V3237; *Gracilisuchus stipanicicorum*, PVL 4597) and ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3828), but it is unlike the proportionally much broader pubic apron of aetosaurs (e.g., *Aetosauroides scagliai*, PVL 2073; *Typothorax coccinarum*, UCMP 34248). The texture of the distal edge of the pubis in distal view is rugose.

Hind Limb

Femur—The right femur of NMT RB187 is completely preserved, and is 144 mm long and is 12.5 mm wide at its mediolateral narrowest midshaft (Fig. 14A-F). The femoral head is 37.7 mm long anteroposteriorly and 20.4 mm wide mediolaterally. The femur is sigmoidal in anterolateral view, with an offset of 45° between the long axes of the distal and proximal ends. This twisting is typical of *Euparkeria capensis* (SAM-PK 10548), early diverging dinosauromorphs (e.g., *Dromomeron gregorii*, TMM-31100-1306), and pseudosuchians (e.g., *Aetosaurus ferratus*, SMNS 5770 S-22, *Nundasuchus songeaensis*, NMT RB48). The epiphysal articular surfaces are covered in rugose bone where cartilage caps would have attached in life. The proximal articular surface bears a shallow groove oriented along the long axis of the head (Fig. 14E).

The proximal head of the femur has distinct anteromedial and posteromedial tubera with a shallow depression separating them on the medial surface. As in aetosaurs, *Revueltosaurus callenderi* (PEFO 34561), ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), and early avian-line archosaurs (e.g., *Dromomeron romeri*, GR 218), the posteromedial tuber is larger than the anteromedial tuber. The anterolateral tuber is present as a small projection that tapers to a small ridge along the dorsolateral surface. The femur lacks the dorsolateral trochanter found in dinosauriformes (Langer and Benton, 2006), the crocodyliforms *Terrestriusuchus* (NHMUK R7562) and *Kayentasuchus* (UCMP 131830), and the loricatan *Mandasuchus tanyauchen* (NHMUK PV R6792). The proximal head grades smoothly into the femoral shaft, as is plesiomorphic for archosauriforms (e.g., *Euparkeria capensis*, SAM-PK 5867).

The fourth trochanter is located just proximal to the mid-shaft of the femur and it forms a sharp ridge that rounds distally (Fig. 14B). The sides of the fourth trochanter are

symmetrical. The long axis of the trochanter follows the curvature of the femoral shaft such that it is deflected anteriorly towards the proximal end of the femur, as in the co-occurring pseudosuchian *Nundasuchus songeaensis* (NMT RB48). Two slight depressions are present adjacent to the fourth trochanter, one anteromedial to the trochanter that ends in a sharp ridge along the anterior edge of the femur, and another dorsoproximal to the trochanter. Above the dorsoproximal depression is a proximally-directed recess that is positioned similarly to the autapomorphic femoral foramen of *Mandasuchus tanyauchen* (NHMUK PV R6792), but the morphology of the recess clearly differs from the foramen found in *Mandasuchus*. Along the posteromedial margin of the femoral shaft is a sharp ridge that ends proximal to the distal head.

The distal end of the femur is well-preserved and more robust than the proximal head. The medial and lateral condyles are divided by shallow depressions on the anterior and posterior surfaces, but they are undivided along the distal articular surface (Fig. 14F). The medial condyle is slightly larger than the lateral condyle, and the medial condyle tapers to a point medially in distal view. The surface between the lateral condyle and crista tibiofibularis is smooth although the crista tibiofibularis is located slightly proximal to the lateral condyle, resulting in a slight offset. The crista tibiofibularis is much smaller than the medial condyle, as is plesiomorphic for archosauriforms (Nesbitt, 2011).

Tibia—The complete right tibia and the distal end of the left tibia (Fig. 14M-O) are preserved in the holotype of <Name Redacted> (NMT RB187). The right tibia is still partially embedded in a matrix block with other elements such that continued physical preparation is not possible. However, both the proximal and distal ends are visible as well as the medial side of the shaft. The tibia of <Name Redacted> is more robust than the fibula and is 113 mm in proximal-distal length. The proximal end of the tibia is oval in proximal view, with the long axis oriented

anteroposteriorly, and a rugose, convex to level surface as in most archosauriforms (Nesbitt, 2011). The anterior half of the lateral side of the tibial head is dominated by the lateral (=fibular) condyle. The lateral condyle is rounded in outline in proximal view and is concave and depressed ventrolaterally in lateral view. A rounded lateral condyle is found in nontheropod archosauriforms; theropods (e.g., *Coelophysis bauri*, AMNH FR 7246) possess a squared lateral condyle in proximal view. A depressed lateral condyle is found throughout pseudosuchian archosaurs (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Parringtonia gracilis*, NMT RB426; *Revueltosaurus callenderi*, PEFO 34273; *Batrachotomus kupferzellensis*, SMNS 52970; *Postosuchus kirkpatricki* TTU 9002; *Hesperosuchus agilis*, AMNH FR 6758). The depth of the lateral condylar depression is less than that of *Parringtonia gracilis* (NMT RB426) but greater than that of *Revueltosaurus callenderi* (PEFO 34273) and aetosaurs (Nesbitt, 2011). The medial condyle of the proximal end of the tibia is rounded, slightly depressed posteriorly, and occupies half the anteroposterior length of the tibial head in proximal view. *<Name Redacted>* retains the plesiomorphic archosauriform trait of having the lateral condyle positioned anterior to the medial condyle (Langer and Benton, 2006; Nesbitt, 2011). On the anterolateral surface of the tibial head is a short, proximodistally-oriented ridge, but the lateral margin of this sharp ridge is formed by a broken portion of the tibial head. Therefore, we cannot be certain if this represents the cnemial crest occasionally found in non-archosaurian archosauriforms and pseudosuchian archosaurs (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Mandasuchus tanyauchen*, NMHUK PV R6794) or if it is simply the result of deformation. Therefore, we scored the presence of a cnemial crest as unknown.

At about one-third down the length of the tibia from the proximal end is a shallow, small (~1 cm length) depression located on the posteromedial side of the shaft, which represents the

attachment site of *M. puboischiotibialis* (Gower, 2003). The tibial shaft is oval in cross section; at the midshaft the long axis is oriented roughly anteroposteriorly and at the distal end the long axis shifts to a mediolateral orientation. This change in tibial shaft orientation is typical of early pseudosuchians (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Parringtonia gracilis*, NMT RB426; *Revueltasaurus callenderi*, PEFO 34273; *Mandasuchus tanyauchen*, NMHUK PV R6794). The distal surface of the tibia is triangular in distal view and is formed by the articulation for the astragalus and the medial projection. In distal view the distal surface of the tibia is mediolaterally expanded relative to the anteroposterior length. The medial half of the distal surface is formed of rugose bone, whereas the proximally-shifted astragalar articulation surface is smooth. This ‘flexed’ arrangement, where the posteromedial portion is deflected distally and the posterolateral portion is deflected proximally, is common in early archosaurs (Nesbitt, 2011). As in pseudosuchians, there is a dorsoventrally-oriented groove on the posterior face of the distal tibia dividing the posteromedial and posterolateral portions (Nesbitt, 2011). The lateral margin of the distal end bears a smooth, flat articulation surface for the fibula, and the medial and anterior faces are rounded, unlike the condition in avemetatarsalians (e.g., *Dromomeron romeri*, GR 220).

Fibula—The left fibula of the holotype NMT RB187 is mostly complete, with portions of the attachment site for the *M. iliofibularis* missing and damage to the lateral and medial faces of the distal end (Fig. 14G-L). The fibula is a gracile element. As preserved, it is 111.5 mm long, with a proximal head length of 17.4 mm, a proximal width of 11.8 mm, a mid-shaft width of 7.3 mm, and a distal head length of 22.3 mm and width of 15.1 mm. The posterior portion of the proximal head is expanded posteriorly, as in most crown archosaurs (Nesbitt, 2011). Anteriorly the proximal head is rounded, as in non-archosaurian archosauriforms and

pseudosuchian archosaurs (Nesbitt, 2011). In proximal view the fibular head is round, and the articulation surface with the femur is flat and slightly medioventrally deflected. The fibular shaft is arched anteriorly on the proximal half of the shaft, like the fibulae of other early pseudosuchians (e.g., *Riojasuchus tenuisiceps*, PVL 3827 and *Aetosaurus ferratus*, SMNS 5770), though this flexure is more pronounced than in other Manda Beds taxa (e.g., *Mandasuchus tanyauchen*, NHMUK PV R6792 and *Nundasuchus songeaensis*, NMT RB48). Distal to the tibial articular surface on the medial side is a small muscle scar that forms a longitudinal ridge comparable to, but much smaller than, a muscle scar found in *Mandasuchus tanyauchen* (NHMUK PV R6794). Just proximal to the mid-length of the fibula is a robust, knob-shaped tubercle for the insertion of the M. iliofibularis (Fig. 14J). This tubercle is most pronounced anterolaterally and ridges extend distally from tubercle to the mid-length of the fibula and proximally to just below the proximal head. The morphology of the M. iliofibularis insertion resembles that of phytosaurs, ornithosuchids, and aetosaurs, though the location of the tubercle is more similar to that of ornithosuchids (e.g., *Riojasuchus tenuisiceps* PVL 3827).

In lateral view, the distal end of the fibula is asymmetrical, such that it angles anterodorsally, as is plesiomorphic for pseudosuchian archosaurs (Nesbitt, 2011). The fibula is diamond-shaped in distal view with more pointed anterior and posterior ends than the medial and lateral sides, like the distal end of the fibula of *Nundasuchus songeaensis* (NMT RB48) and *Dynamosuchus collisensis* (CAPPA/UFSM 0248). However, in *<Name Redacted>* the anterior point is larger than the posterior point, whereas the opposite is true in both *Nundasuchus* and *Dynamosuchus*. Although the medial side of the distal end of the fibula is damaged, it clearly lacks the banked articular facet present in rauisuchids (*Postosuchus kirkpatricki*, TTU 9002) and

crocodylomorphs (e.g., *Hesperosuchus 'agilis'*, AMNH FR 6758). The anterior edge is directed medially at its distal extent, whereas the posterior edge is directed laterally at its distal extent.

Tarsals—<Name Redacted> exhibits the ‘crocodile-normal’ (*sensu* Sereno, 1991) crurotarsal joint between the astragalus and calcaneum. As in other pseudosuchian archosaurs, the astragalus and calcaneum rotate relative to each other with a ‘peg and socket’ articulation between the two elements (Chatterjee, 1978; Cruickshank, 1979; Parrish, 1986; Sereno, 1991).

The left calcaneum of NMT RB187 is complete and well preserved (Fig. 15A-F), and a partial proximal portion of the right calcaneum is preserved in a block with the right coracoid (Fig. 10G). The description will therefore focus on the complete, isolated left calcaneum. Overall, the calcaneum is proximodistally compressed, resulting in greater mediolateral width than proximodistal height (ratio approximately 2:1). The fibular facet of the calcaneum is convex and hemicylindrical, like that in *Nundasuchus songeaensis* (NMT RB48) and *Polesinesuchus aurelioi* (ULBRAPVT003). The facet is approximately rectangular in proximal view, with little tapering in mediolateral width, and is directed anterodistally. The anterior end of the fibular facet gradually and smoothly transitions into the facet for the fourth tarsal at the anterior face of the calcaneum, as in other pseudosuchians (e.g., *Nundasuchus songeaensis*, NMT RB48; *Polesinesuchus aurelioi*, ULBRA-PVT003; *Gracilisuchus stipanicorum*, PVL 4597). Likewise, the articular surface for the astragalus also smoothly transitions into the fourth tarsal articular surface along the anterior margin of the calcaneum. Posteriorly, the articular facet for the astragalus is separated from the fibular facet by a deep groove that is directed anterodistally. Laterally, the articular surface with the astragalus is separated from the fibular facet by a laterally, and slightly proximally, directed concavity. A single large foramen is located in the center of this concavity, and a smaller foramen is proximally adjacent to this large foramen. The

articular surface itself is concave and complementary to the convex surface of the ‘peg’ of the astragalus (Fig. 15C). Therefore, the articulation for the ‘peg’ forms a distinct surface separated from the fibular facet as in aetosaurs (e.g., *Typothorax antiquum*, NMMNH P-36075; *Polesinesuchus aurelioi*, ULBRA-PVT003), and paracrocodylomorphs (e.g., *Effigia okeeffeae*, AMNH FR 30587; *Postosuchus kirkpatricki*, TTU 9002). This contrasts with the condition present in early avian-line archosaurs (e.g., *Dromomeron romeri*, GR 223; *Asilisaurus kongwe*, NMT RB159), phytosaurs (e.g., *Pseudopalatus buceros*, NMMNH P-34753; P-33930), *Euparkeria capensis* (CAMZM T.692), and *Nundasuchus songeaensis* (NMT RB48), in which the fibular facet and astragalus articulation surfaces are continuous.

The calcaneum tuber of <Name Redacted> is as broad mediolaterally as the rest of the calcaneum and it does not project far posteriorly, as in suchians (e.g., *Revueltosaurus callenderi*, PEFO 33793; *Nundasuchus songeaensis*, NMT RB48) but unlike the proportionally more elongated tubera of phytosaurs (e.g., *Pseudopalatus buceros*, NMMNH P-34753). Furthermore, the tuber of <Name Redacted> projects almost entirely posteriorly, with little lateral deviation. The maximal width of the posterior surface of the calcaneum tuber is roughly twice that of the fibular facet. The medial proximal edge of the calcaneum tuber is projected dorsally, as in aetosaurs (e.g., *Polesinesuchus*, ULBRA-PVT003) and *Gracilisuchus stipanicorum* (PVL 4597), and to a lesser extent in *Postosuchus kirkpatricki* (TTU 9002) and *Nundasuchus songeaensis* (NMT RB48). The tuber shaft of <Name Redacted> is oval in mediolateral cross-section, as is the posterior surface of the calcaneum tuber (Fig. 15E). The posterior surface is highly rugose, indicating that it was covered by a cartilage cap in life, as in *Nundasuchus songeaensis* (NMT RB48). <Name Redacted> lacks a dorsoventrally-oriented depression for the gastrocnemius tendon, as do *Nundasuchus songeaensis* (NMT RB48) and some early-branching

loricatan (e.g., *Mandasuchus tanyauchen*, NHMUK PV R36950). This morphology contrasts with some aetosaurs (e.g., *Polesinesuchus aurelioi*, ULBRA-PVT003), poposaurids (e.g., *Poposaurus gracilis*, YPM 57100), rauisuchids (e.g., *Postosuchus kirkpatricki*, TTU 9002), and crocodyliforms (e.g., *Protosuchus richardsoni*, AMNH FR 3024), which all exhibit the extant crocodylian trait of a dorsoventrally oriented channel. On the distal surface, the calcaneal tuber and the articulation surface of the fourth tarsal are separated by a distinct U-shaped fossa that opens distally, as in some aetosaurs (e.g., *Polesinesuchus aurelioi*, ULBRA-PVT003) and in loricatans (e.g., *Mandasuchus tanyauchen*, NHMUK PV R36950; *Postosuchus kirkpatricki*, TTU 9002; *Protosuchus richardsoni*, AMNH FR 3024).

The astragalus of <Name Redacted> (NMT RB679) is complete and well preserved (Fig. 15G-L), but is derived from a different individual than the calcaneum. The proximal surface bears two large articulation facets for the tibia and fibula. Medially, the tibial facet is approximately oval and inclines and narrows laterally toward the fibular facet. The tibial facet is slightly ‘flexed’ (sensu Sereno, 1991), so the surface is divided into two distinct basins by a convex structure. The posteromedial basin is more concave distally, whereas the anterolateral basin is concave anterodistally. This morphology matches that of other pseudosuchians and some avemetatarsalians (i.e., *Dromomeron romeri*, GR 223; *Marasuchus lilloensis*, PVL 3870, Nesbitt, 2011). The tibial facet is surrounded by broad, rounded edges. Posterolaterally, the tibial facet is separated from the fibular facet by a deep groove that contains a single, large foramen. This groove is continuous distally with the posterior groove of Sereno (1991).

The fibular facet of the astragalus approximates a diamond shape in outline with points at the anteroproximal, posteroproximal, anterior, and posterior corners. A large posterolaterally-directed process joins with the posterior groove, thereby elongating the facet. The facet surface is

concave with distinct ridges on the anterior and posterior margins. The distal margin of the fibular facet connects to the hemispherical, convex articular surface of the calcaneum when in articulation, though the calcaneum articulation surface of the astragalus is barely convex and nearly flat. Distally, the calcaneum facet narrows before joining the ‘peg’ of the astragalus. The ‘peg’ is strongly convex distally and approximately rectangular in distal outline. The ‘peg’ is well-separated from the rest of the body of the astragalus as in aetosaurs (e.g., *Polesinesuchus aurelioi*, ULBRA-PVT003), *Effigia okeeffeae* (AMNH FR 30587), and loricatans (e.g. *Mandasuchus tanyauchen*, NHMUK PV R36950; *Postosuchus kirkpatricki* TTU 9002; *Hesperosuchus ‘agilis’* YPM 41198), but is not well-separated from the body in phytosaurs (e.g. *Pseudopalatus buceros*, NMMNH P-34753) and early-diverging pseudosuchians (e.g. *Nundasuchus songeaensis*, NMT RB48). The anterior hollow of the astragalus is broad and concave with a single large foramen near the center of the depression. The outline of the anterior hollow is roughly diamond-shaped with the medial-most point elongated (Fig. 15L). This shape is similar to that of *Mandasuchus tanyauchen* (NHMUK PV R36950) and differs from the triangular outline of such taxa as *Nundasuchus songeaensis* (NMT RB48) and *Effigia okeeffeae* (AMNH FR 30587). The anterior hollow also divides the tibial facet and the astragalar ball that forms the majority of the lateral half of the anterior surface. The astragalar ball is similar in relative size to that of *Nundasuchus songeaensis* (NMT RB48), *Longosuchus meadei* (TMM 31185-97), and *Mandasuchus tanyauchen* (NHMUK PV R36950). The ball is not as well developed as that of either *Effigia okeeffeae* (AMNH FR 30587) or *Postosuchus kirkpatricki* (TTU 9002).

Of the distal tarsals, both the right distal tarsal 3 and 4 of <Name Redacted> are well-preserved in NMT RB187, although they were not found in articulation (Fig. 16). Distal tarsals 1

and 2 are either lost or were unossified, as in *Euparkeria*, proterochampsids, and members of Archosauria (Gauthier, 1984; Gower, 1996; Nesbitt, 2011). The transverse width of distal tarsal 3 is approximately half that of distal tarsal 4, such that the distal tarsal 3 is significantly narrower, as in the archosauriform *Erythrosuchus africanus* (BP/1/2096) and in pseudosuchian archosaurs (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Revueltosaurus callenderi*, PEFO 34561; *Effigia okeeffeae*, AMNH FR 30587). Distal tarsal 3 is rectangular in proximal view, mediolaterally compressed, and elongate along the dorsoventral axis, similar to that of *Riojasuchus tenuisiceps* (PVL 3827). Distal tarsal 4 articulates medially with distal tarsal 3, proximally with the calcaneum, anterolaterally with metatarsal V, and dorsolaterally with metatarsal IV. Both the articular surfaces for the calcaneum and distal tarsal 3 are concave, whereas the metatarsal articular surfaces are flat. The articulation surface for metatarsal V covers approximately two-thirds of the lateral surface, and a small ridge separates this articular facet from that of the articulation for metatarsal IV. On the dorsal edge of the articular facet for metatarsal IV are three ~1mm diameter foramina. The medial surface of distal tarsal 4 lacks any foramina, unlike the condition present in some suchian taxa such as *Effigia okeeffeae* (AMNH FR 30587), *Hesperosuchus 'agilis'* (YPM 41198), and *Poposaurus gracilis* (YPM 57100). On the posterior margin of the proximal surface is distinct expanded area, similar to that found in other pseudosuchian archosaurs such as *Riojasuchus tenuisiceps* (PVL 3827), *Revueltosaurus callenderi* (PEFO 34561), *Effigia okeeffeae* (AMNH FR 30587), and *Hesperosuchus agilis* (AMNH 6758).

Metatarsals—Disarticulated but associated metatarsals from the right and left pes are known from the holotype (Fig. 17A-J). From the right pes all metatarsals (I-V) are represented, though metatarsal II is only known from the proximal end, and from the left pes only metatarsal I

is represented. We identify the isolated metatarsal I's on the basis of the medial deflection of the proximal end in distal view; the isolated metatarsal IV because the distal end is "pinched" (= dorsoventrally compressed) on the lateral side and is the narrowest midshaft; the isolated metatarsal III on the basis of longest relative length and articulation with metatarsal IV; and the proximal end of metatarsal II based upon the articulation with metatarsals I and III, though without the distal end, we consider metatarsal II the most uncertain assignment. Metatarsals I-IV all: are expanded at the proximal and distal ends relative to the midshaft, have flat proximal surfaces that are oblong in proximal view, have convex distal surfaces that are rectangular with a distinct posterior gap in distal view, and possess deep extensor pits on their dorsal surfaces as in most archosauriforms (Nesbitt, 2011).

Overall, metatarsal III is the longest element in the series and metatarsal V is the shortest element. Unlike the other elements in the series, metatarsal V has a greatly expanded proximal end (= hooked *sensu* Nesbitt, 2011), and less developed distal end. However, like all non-crocodyliiform suchians, the distal articulation surface of metatarsal V can still accommodate a fully developed first phalanx (Nesbitt, 2011). The proximal ends of the metatarsals would have overlapped the adjacent metatarsal in dorsal view when articulated, as in other archosaurs (e.g., *Riojasuchus tenuisiceps*, PVL 3827; *Revueltosaurus callenderi*, PEFO 33807), such that metatarsal I anterodorsally overlaps metatarsal II, metatarsal II anterodorsally overlaps metatarsal III, and so on through metatarsal IV. We cannot accurately describe the articulation of metatarsal V with the other metatarsals as the medial surface is preserved attached to the coracoid. However, the large, proximal articulation with distal tarsal 4 is clearly evident. Because the proximal surface of metatarsal V is visible, we can see the absence of a concave gap

in the dorsal prominence, which is found in some loricatans (e.g., *Batrachotomus kupferzellensis*, SMNS 90018; *Postosuchus kirkpatricki*, TTU 9000).

Pedal digits—A minimum of four isolated but associated pedal digits were recovered from NMT RB187, of which two could be rearticulated (Fig. 17K-N). We determined a minimum of four pedal digits based upon the number of pedal unguals. Because the phalanges were disarticulated, determining a phalangeal formula is impossible, though the two digits that can be articulated have three and four elements (Fig. 17K-N). The longest phalanges are about a third the proximodistal length of the metatarsals, although direct comparison is impossible because we cannot match phalanges to their corresponding metatarsal with certainty. The non-ungual phalanges of <Name Redacted> are mediolaterally and dorsoventrally expanded at both the proximal and distal ends, with oval shafts that are wider mediolaterally than dorsoventrally tall and arched anteroventrally. The proximal articulation surfaces of the phalanges with either the metatarsals or proximal phalanx are concave in distal view. The distal articular surfaces of the phalanges with the following phalanx are convex in proximal view and are smaller mediolaterally and dorsoventrally than the proximal articular surfaces. The distal surface of the non-ungual phalanges is separated into two small elliptical condyles by a dorsoventral furrow that continues onto the ventral surface anteroposteriorly. The lateral surfaces of the distal end of the phalanges bear deep, circular lateral pits for the collateral ligaments. On the dorsal surface of the distal end of the phalanges is an extensor pit for the ginglymus joint, which is similar in depth to the lateral pits.

The pedal unguals of <Name Redacted> are curved anteroventally and triangular in cross section. The proximal articular surfaces with the previous phalanx are concave proximally. The ventral side of the unguals is flat, and the unguals are weakly mediolaterally compressed. A

weakly compressed pedal ungual that is triangular in cross-section is plesiomorphic for archosaurs (Nesbitt, 2011) and is retained in some early pseudosuchians (e.g., *Revueltosaurus callenderi*, PEFO 34561; *Aetosauroides scagliai*, PVL 2052). This is in contrast to the dorsoventrally compressed pedal unguals of poposaurids (e.g., *Poposaurus gracilis*, YPM 57100; *Effigia okeeffeae*, AMNH FR 30587) and the strongly mediolaterally compressed, dorsally-keeled pedal unguals of phytosaurs (e.g., *Machaeroprotopus* sp., UCMP 34239), ornithosuchids (e.g., *Riojasuchus tenuisiceps*, PVL 3827), and *Prestosuchus chiniquensis* (SNSB-BSPG XXV 11e). The lateral surfaces of the pedal unguals are covered in small pits and bear an anteroposteriorly-oriented groove.

4. PHYLOGENETIC RELATIONSHIPS

We scored <Name Redacted> for the morphological character-taxon matrix of Parker et al. (2021), the most recently published version of the Nesbitt (2011) matrix as modified by Butler et al. (2014), Nesbitt et al. (2017), and Marsh et al. (2020). We rescored character 219 for *Revueltosaurus callenderi*, *Riojasuchus tenuisiceps*, and *Ornithosuchus longidens*, and character 235 for *Riojasuchus tenuisiceps* and *Parringtonia gracilis* (Supplementary Material). Character scoring was completed using Mesquite v3.61 (Maddison and Maddison, 2018), and the final matrix includes 92 taxa and 444 characters (Supplementary Data). As in previous studies characters 32, 52, 75, 121, 137, 139, 156, 168, 188, 223, 247, 258, 269, 271, 291, 297, 328, 356, 399, and 413 were treated as ordered in this analysis, which we conducted in TNT v1.5 (Goloboff and Catalano, 2016; made available with the sponsorship of the Willi Hennig Society). Memory was set to 10,000 trees, and we conducted a heuristic search (= traditional search), increasing the number of replicates from 10 to 1,000, tree bisection reconnection swapping, keeping 10 trees per replicate, and selecting the “collapse trees after the search” option. We then

excluded suboptimal trees using the “best” function in the command line for a total of 119 MPTs of 1470 steps and combined the MPTs into a strict consensus tree. Much of the tree is unchanged relative to the studies we build upon (Nesbitt, 2011; Butler et al., 2014; Nesbitt et al., 2017c; Marsh et al., 2020; Parker et al., 2021): phytosaurs fall outside of Archosauria, ornithosuchids fall outside of Suchia, erpetosuchids form a clade with Aetosauriformes, and gracilisuchids form a clade with Paracrocodylomorpha (Fig. 18). The position of Ornithosuchidae as the earliest diverging branch of Pseudosuchia contrasts with the topology recovered by Ezcurra et al. (2017) and Müller et al. (2020), who recovered Ornithosuchidae as sister to Erpetosuchidae in a monophyletic clade with aetosaurs at the base of Suchia (see von Baczko et al. [2020] for additional discussion of ornithosuchid and erpetosuchid relationships within Pseudosuchia).

We recovered *<Name Redacted>* within Suchia as the earliest diverging taxon in Aetosauria (Fig. 18), within Aetosauriformes (*sensu* Parker et al., 2021). This relationship is weakly supported with minimal Bremer support (= 1) and low bootstrap stability (= 14 of 100 replications), and it is based on the following three synapomorphies: a maxilla anterodorsal margin at the base of the dorsal process that is concave (character 25, state 1), a knob-shaped, robust attachment site for the M. iliofibularis on the fibula (character 339, state 1), and the attachment site for the M. iliofibularis on the fibula located near the midpoint between the proximal and distal ends (character 340, state 1). Both of the fibular characters that unite *<Name Redacted>* with aetosaurs are also shared with Ornithosuchidae (although character 340 is not scored for *Ornithosuchus longidens*). The phylogenetic analysis recovered several topographically local autapomorphies for *<Name Redacted>*: the presence of an anteriorly opening foramen on the anterolateral maxillary surface (character 31, state 1), a rounded longitudinal ridge on the lateral surface of the jugal (character 75, state 2), the presence of teeth

on the palatal process of the pterygoid (character 175, state 1), a pubis that is more than 70% the length of the femur (character 278, state 1), a straight, transverse groove on the proximal surface of the femur (character 314, state 1), and a fourth trochanter of the femur with a sharp flange (character 316, state 1).

In order to test the effect of <Name Redacted> on the relationships of early diverging pseudosuchians, we scored it into the matrix of Ezcurra (2016) with changes from Ezcurra et al. (2017) and von Baczko et al. (2020). Following Ezcurra (2016) and subsequent analyses, we excluded the following taxa *a priori*: *Eorasaurus olsoni*, *Archosaurus rossicus*, *Vonhuenia fredericki*, *Chasmatosuchus rossicus*, *Chasmatosuchus magnus*, “*Chasmatosuchus*” *vjushkovi*, *Kalisuchus rewanensis*, *Shansisuchus kuyeheensis*, *Uralosaurus magnus*, and *Koilamasuchus gonzalezdiazi*. This resulted in a matrix with 108 active taxa and 676 characters. We repeated the same procedure as with the modified Parker et al. (2021) matrix and recovered 96 MPTs of 3357 steps. The immediate placement of <Name Redacted> is almost the same as in the previous analysis, although it is recovered in a polytomy with *Aetosauroides scagliai* and stagonolepid aetosaurs, rather than sister to *Aetosauroides scagliai* + stagonolepid aetosaurs (Fig. 19). Similar to the results of Ezcurra et al. (2017) and von Baczko et al. (2020), erpetosuchids are recovered as sister clade to ornithosuchids, and together form a larger monophyletic clade with Aetosauria, and Phytosauria is recovered within crown Archosauria (Fig. 19). This result reflects the current uncertainty over the placement of Ornithosuchidae within Pseudosuchia depending on whether the base matrix is that of Nesbitt (2011) or Ezcurra (2016), but resolving this discrepancy is beyond the scope of this paper.

5. DISCUSSION

The proximal tarsals are in the ‘crocodile-normal’ configuration, which indicates that *<Name Redacted>* is a pseudosuchian archosaur. *<Name Redacted>* also can be recognized as a suchian archosaur by the presence of a longitudinal ridge on the lateral surface of the jugal and a convex and a hemicylindrical articulation surface for the fibula on the calcaneum based upon our character optimizations for Suchia. *<Name Redacted>* is supported within Aetosauriformes by the postorbital bar being composed mostly by the postorbital, the presence of a shallow longitudinal groove on the posterior side of the distal end of the radius, and presacral osteoderms that are mediolaterally wider than anteroposteriorly long. Finally, *<Name Redacted>* is found within Aetosauria as described in the Phylogenetic Analysis section. *<Name Redacted>* is therefore a non-stagonolepid aetosaur, the most basal member of the Aetosauria, and the oldest currently known aetosaur. Because both the matrices of von Bazcko et al. (2020) and Parker et al. (2021) recover *<Name Redacted>* within Aetosauria we believe this is a robust result, but we prefer the Parker et al. (2021) matrix as it incorporates more characters and taxa within Aetosauriformes. This new taxon fills an important morphological and temporal gap in the evolution of aetosaurs and early suchians. As such *<Name Redacted>* serves as a test of the hypothesized order of morphological changes associated with the evolution of the highly specialized, heavily armored aetosaurian body plan.

For example, Parker et al. (2021) predicted intermediate changes to the anterior portion of the skull, more extensive carapace, and hypertrophied limbs in the transition from non-aetosaur aetosauriforms to aetosaurs. In *<Name Redacted>* we do not see many of the characteristic anterior skull features of aetosaurs, such as a “slipper-like” mandible and reduction of the anterior dentition. These two stagonolepid features are also absent in *Aetosauroides scagliai* (CAPPA/UFSM 11505), indicating carnivory as the plesiomorphic diet for Aetosauria

(Biacchi Brust et al., 2018). We do find an expanded carapace, as well as hindlimb features that may indicate a more robust musculature to support the weight of additional osteoderm coverage (characters 338, 339). Therefore, aetosaurs may have evolved their specialized carapace before modifying their skulls, providing further evidence for the independent evolution of herbivory in aetosaurs and *Revueltosaurus callenderi* (Marsh et al., 2020) and demonstrating the early importance of armor in the evolution of aetosaurs. Given the abundance of large carnivores (e.g., *Mambawakale ruhuhu*, *Nundasuchus songeaensis*) coeval with <Name Redacted>, the need for predator defense driving the evolution of armor could be a reasonable hypothesis.

The presence of teeth on the pterygoid in <Name Redacted> serves as an example of the complexity of tracing character evolution. The retention of pterygoid teeth in early dinosaurs (*Eoraptor lunesis* and *Eodromaeus murphi*) and early pseudosuchians (*Nundasuchus songeaensis*, <Name Redacted>, and *Turfanosuchus dabanensis*) indicates independent loss of teeth on the palate within crown archosaurs as discussed in Nesbitt et al. (2014). We show yet another set of losses must have occurred in aetosaurs and erpetosuchids, clades that have some members that lack pterygoid dentition. Such patterns of trait evolution can complicate phylogenetic reconstructions (Goloboff et al., 2018), making them important to identify.

Despite the mix of aetosaurian and early-diverging suchians traits present in <Name Redacted>, it retains the carnivorous diet plesiomorphic for archosauromorphs. The archosaur assemblage from the Manda Beds is dominated by carnivores as demonstrated by the archosaur tooth assemblage (Hoffman et al., 2019). This indicates that the phylogenetic diversity exceeded the ecological diversification of archosaurs at the Middle Triassic Manda Beds when diet is the aspect of ecology of interest. The evolution of the aetosaurian armored body plan in <Name

Redacted> does indicate that ecological diversification is a more complicate pattern to reconstruct and depends on the ecology of interest.

6. CONCLUSIONS

<*Name Redacted*> represents one of the most complete Middle Triassic archosaurs from southern Pangea and is part of a diverse archosauromorph assemblage. Although the Manda Beds are likely not as old as previously interpreted (Ottone et al., 2014; Peacock et al., 2018; Smith et al., 2018; Wynd et al., 2018), the Manda Beds still represent one of the earliest Triassic localities with diverse and disparate archosauromorphs following the end-Permian mass extinction. <*Name Redacted*> is a particularly important addition to this diversity not only because of its completeness, but for the morphological information it provides. A mixture of plesiomorphic archosauriform and derived morphologies present in paracrocodylomorphs are found in <*Name Redacted*>, demonstrating the complex trait evolution found in Triassic archosaur evolution. For example, <*Name Redacted*> retains pterygoid teeth, a feature found throughout non-archosaurian archosauriforms while also possessing highly specialized osteoderms and a crocodylian-like ankle. <*Name Redacted*> shows that the evolution of a heavily armored carapace occurred prior to the dietary specializations seen in Late Triassic aetosaurs and their closest relatives.

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8. TABLES

NMT RB187 Vertebra	Length (mm)	Anterior height (mm)	Posterior height (mm)	Anterior width (mm)	Posterior width (mm)
Axis	19.8	16.5	16.8	13.4	13.3
Cervical 1	20.5	20.4	18.9	15.1	14.5
Cervical 2	20.4	15.7	16.0	14.9	13.7
Cervical 3	18.5	16.7	16.6	16.0	16.1
Cervical 4	19.7	17.4	16.6	17.1	17.5
Trunk 1	20.6	18.3	18.1	16.9	17.8
Trunk 2	19.8	16.9	16.7	16.1	16.8
Trunk 3	19.9	16.9	17.1	17.2	16.6
Trunk 4	18.9	17.1	17.0	18.0	16.9
Trunk 5	20.6	19.4	19.6	18.7	20.6
Trunk 6	20.7	18.1	17.1	17.3	19.1
Trunk 7	20.2	20.1	20.3	21.7	22.6
Sacral 1	21.7	20.6	18.9	23.3	21.9
Caudal 1	21.6	NA	18.9	NA	15.0
Caudal 2	21.6	17.4	17.0	14.4	13.3
Caudal 3	20.9	14.8	14.6	14.1	13.6
Caudal 4	21.7	13.6	13.7	12.2	12.9
Caudal 5	21.2	13.2	13.5	12.4	11.4
Caudal 6	20.5	12.2	12.6	10.7	10.8
Caudal 7	20.1	11.7	11.7	10.1	10.8

Caudal 8	17.0	7.9	8.4	7.9	8.0
Caudal 9	16.1	8.0	7.6	7.3	7.3
Caudal 10	15.8	7.0	7.0	7.3	6.3
Caudal 11	16.7	7.6	7.8	7.3	7.1
Caudal 12	14.6	5.8	5.7	5.7	5.8
Caudal 13	15.4	6.4	6.4	6.2	6.1
Caudal 14	15.9	6.7	6.9	6.7	6.8
Caudal 15	15.1	6.0	6.2	5.6	6.1

TABLE 1: Measurements of holotypic vertebrae of *<Name Redacted>*.

9. FIGURES

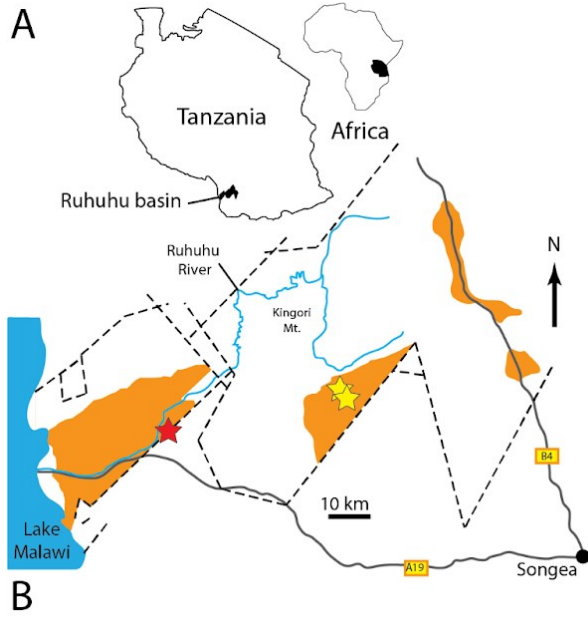


FIGURE 1: Field context of <Name Redacted>, gen. et sp. nov. **A**, Geographical map of field localities for holotype (NMT RB187, locality Z133) and paratypes (NMT RB679, locality Z133; NHMUK R36616). Map modified from Nesbitt et al., 2014. **B**, Field crew in 2015 excavating holotype locality, **C**, field jacket of holotype specimen after removal from horizon.

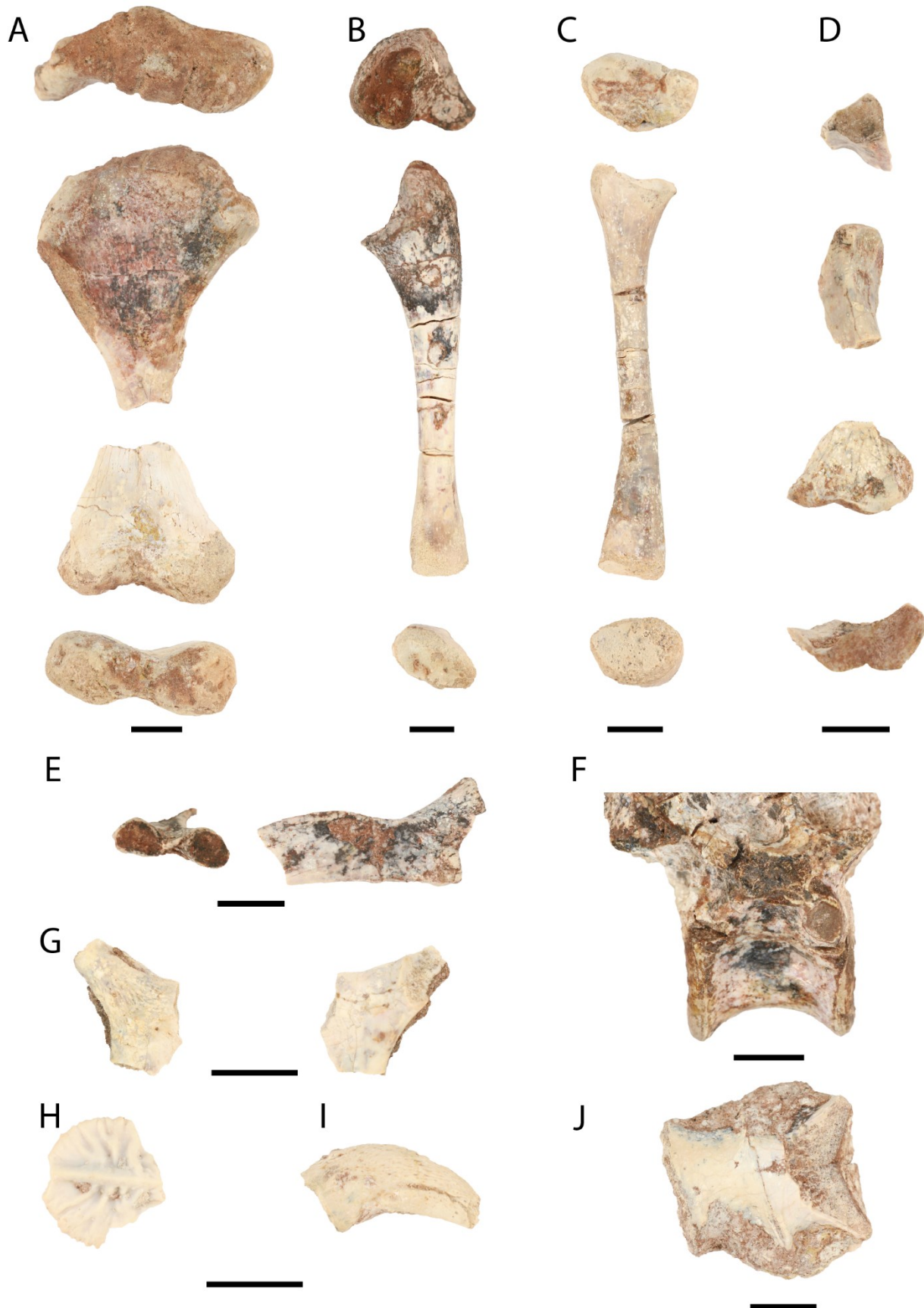


FIGURE 2: Selected elements from the referred specimen NMT RB679. **A**, right humerus in proximal, anterior, and distal views. **B**, left ulna in proximal, anterior, and distal views. **C**, left radius in proximal, anterior, and distal views. **D**, right quadrate in dorsal, anterior (missing central portion), and ventral views. **E**, trunk rib in proximal and dorsal views. **F**, posterior cervical or anterior trunk vertebra in right lateral view. **G**, postorbital in lateral and medial views. **H**, appendicular osteoderm in external view. **I**, ungual in lateral view. **J**, fused primordial sacral 1 and 2 in ventral view. Scale bars equal to 1 cm.

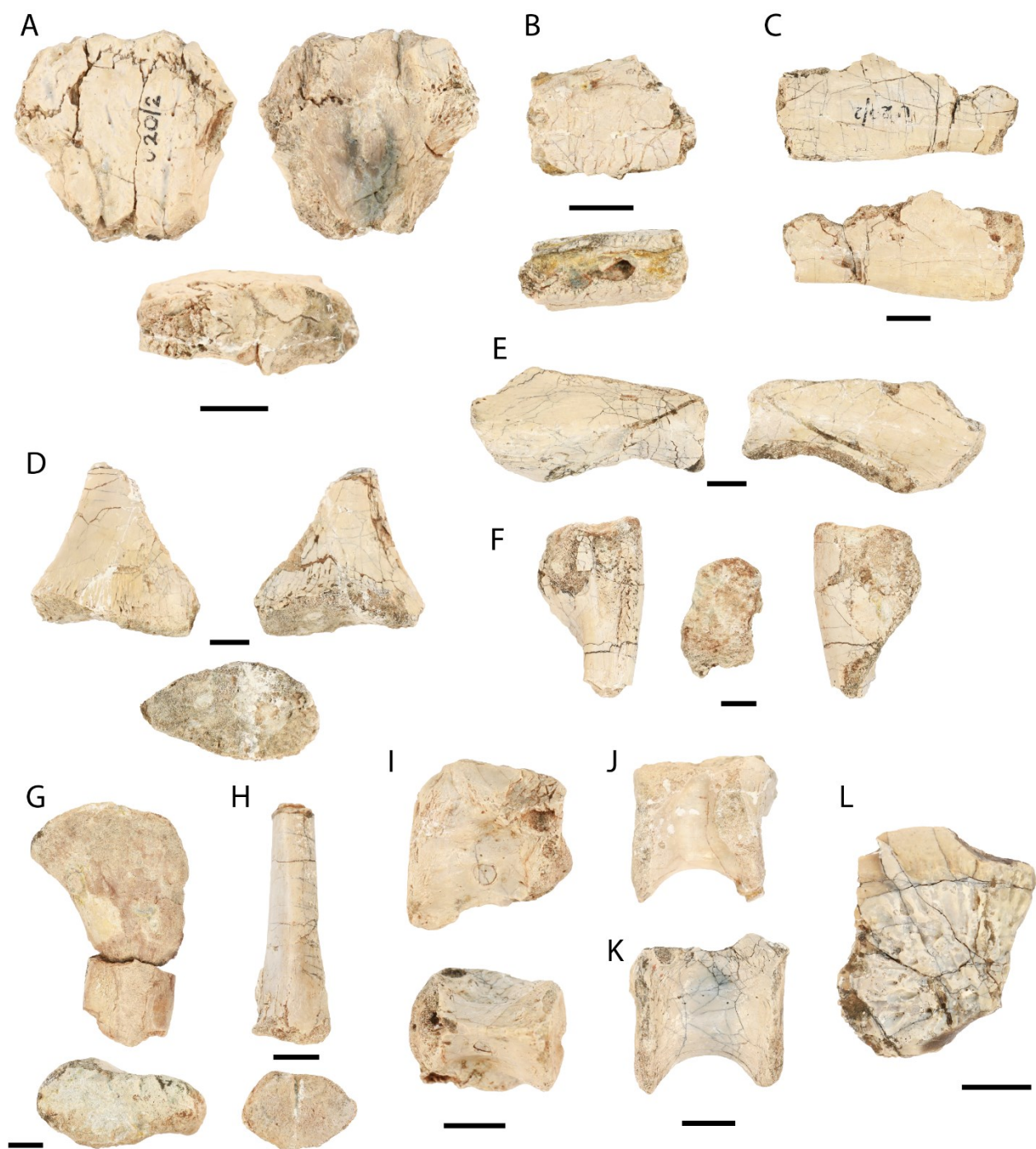


FIGURE 3: Selected elements from the referred specimen NHMUK R36616. **A**, parietal in dorsal, ventral, and left lateral views. **B**, partial left maxilla in lateral and occlusal views. **C**, partial left dentary in lateral and medial views. **D**, proximal portion of left(?) ischium in lateral, medial, and proximal views. **E**, postacetabular process of the right ilium in lateral and medial views. **F**,

proximal portion of pubis in lateral, proximal, and medial views. **G**, proximal portion of right femur in lateral and proximal views. **H**, distal portion of left fibula in anterior and distal views. **I**, axis in right lateral and ventral views. **J**, cervical vertebra in right lateral view. **K**, trunk vertebra in right lateral view. **L**, paramedian osteoderm in dorsal view. Scale bars equal to 1 cm.

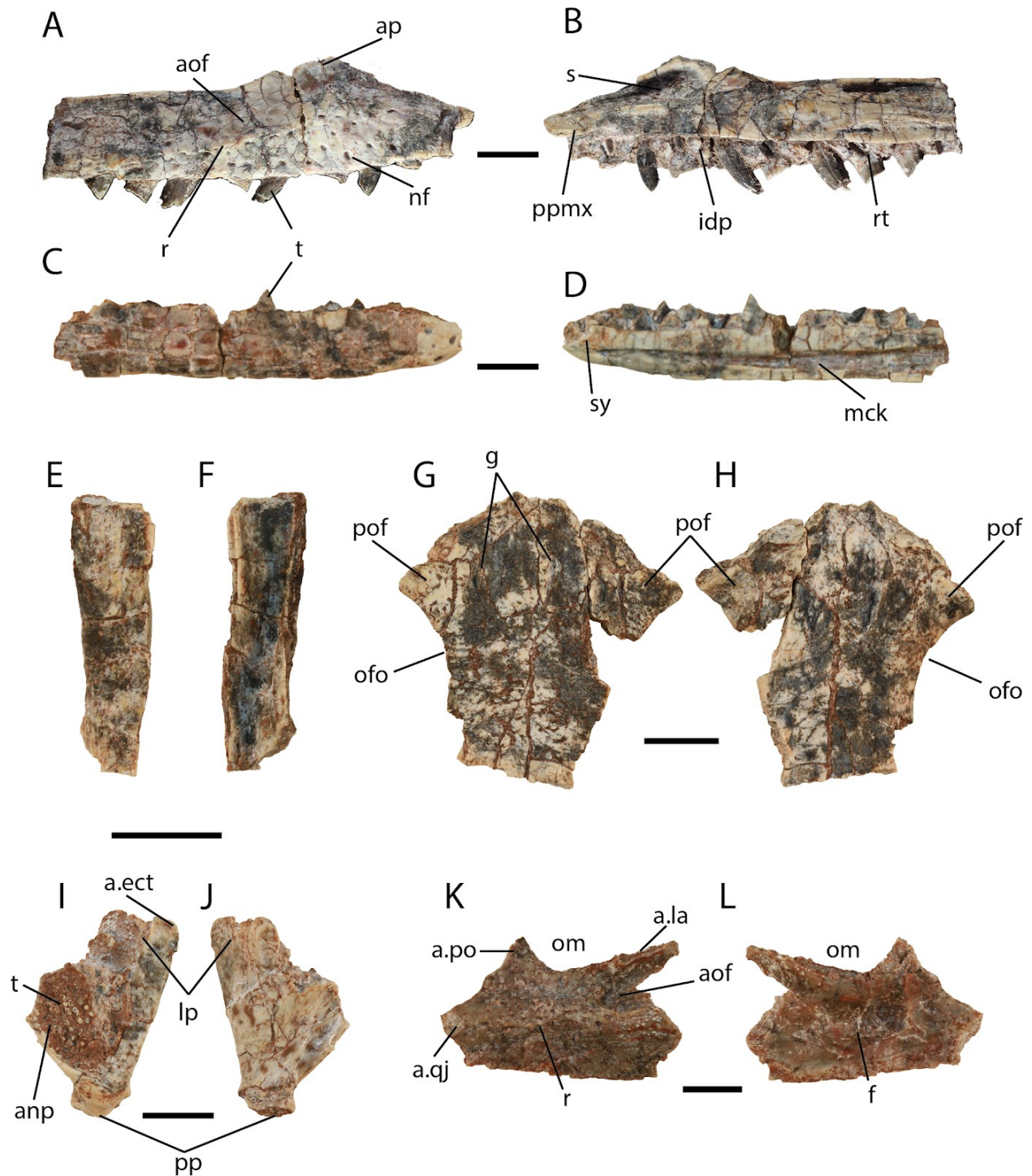


FIGURE 4: Skull elements from the holotype NMT RB187 of *<Name Redacted>*. Right maxilla in **A**, lateral, **B**, medial view. Right dentary in **C**, lateral, **D**, medial view. Right nasal in **E**, dorsal, **F**, ventral views. Articulated left and right frontals with partial left and right postfrontals

in **G**, dorsal, **H**, ventral views. Left pterygoid in **I**, ventral, **J**, dorsal views. Right jugal in **K**, lateral, **L**, medial view. Scale bars equal to 1 cm. **Abbreviations:** a., articulates with; anp, anterior process; aof, antorbital fossa; ap; ascending process; ect, ectopterygoid; f, fossa; g, groove; idp, interdental plate; la, lacrimal; lp, lateral process; mck, Meckelian groove; nf, nutrient foramen; ofo, orbital fossa; om, orbital margin; po, postorbital; pof, postfrontal; pp, posterior process; ppmx, palatal process of the maxilla; qj, quadratojugal; r, ridge; rt, replacement tooth; sy, symphysis; t, tooth.

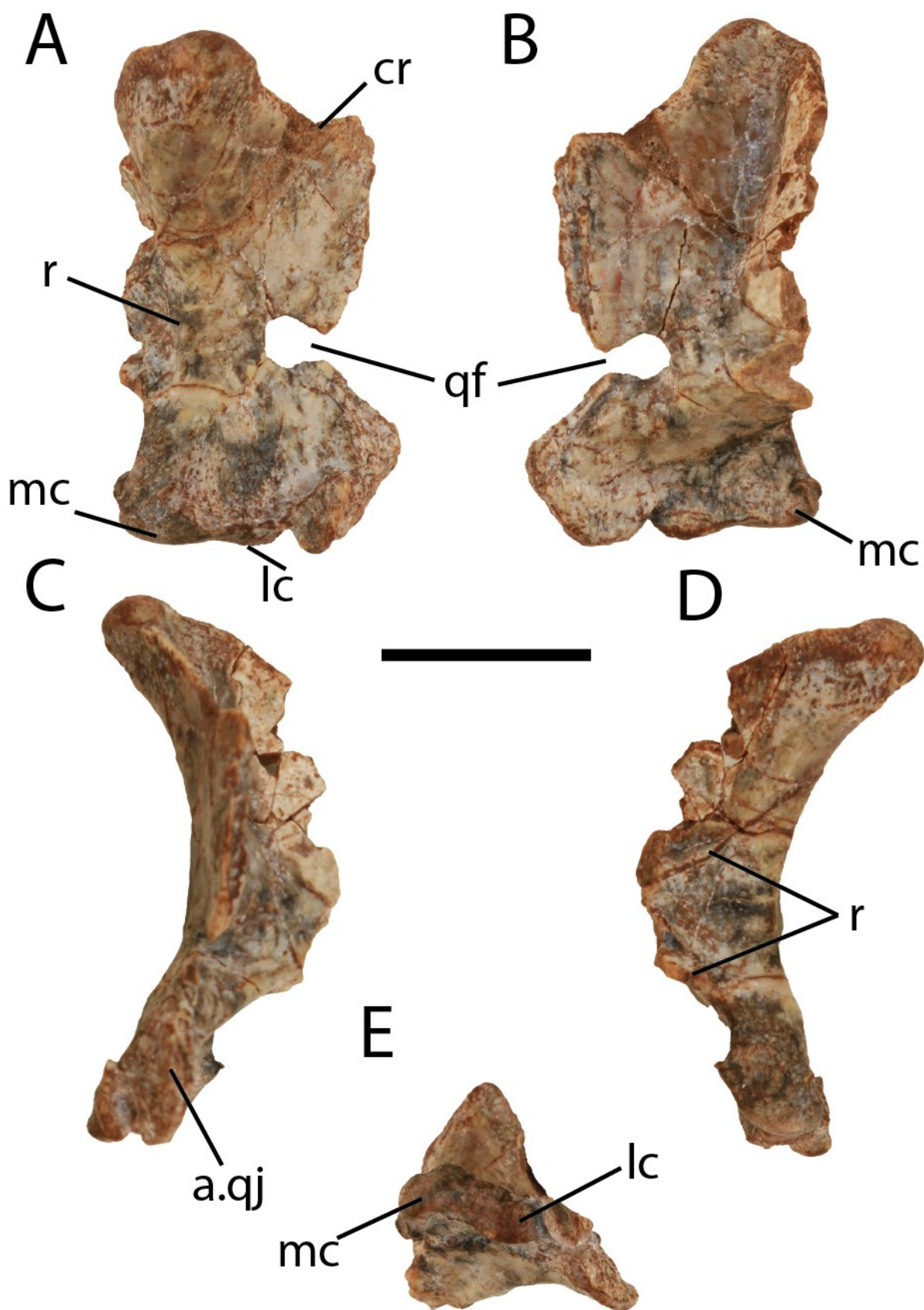


FIGURE 5: Right quadrate of <Name Redacted>, gen. et sp. nov. (NMT RB187). In **A**, posterior, **B**, anterior, **C**, lateral, **D**, medial, **E**, distal. Scale bar equal to 1 cm. **Abbreviations:** a., articulates with; cr, crest; lc, lateral condyle; mc, medial condyle; qf, quadrate foramen; qj, quadratojugal; r, ridge.

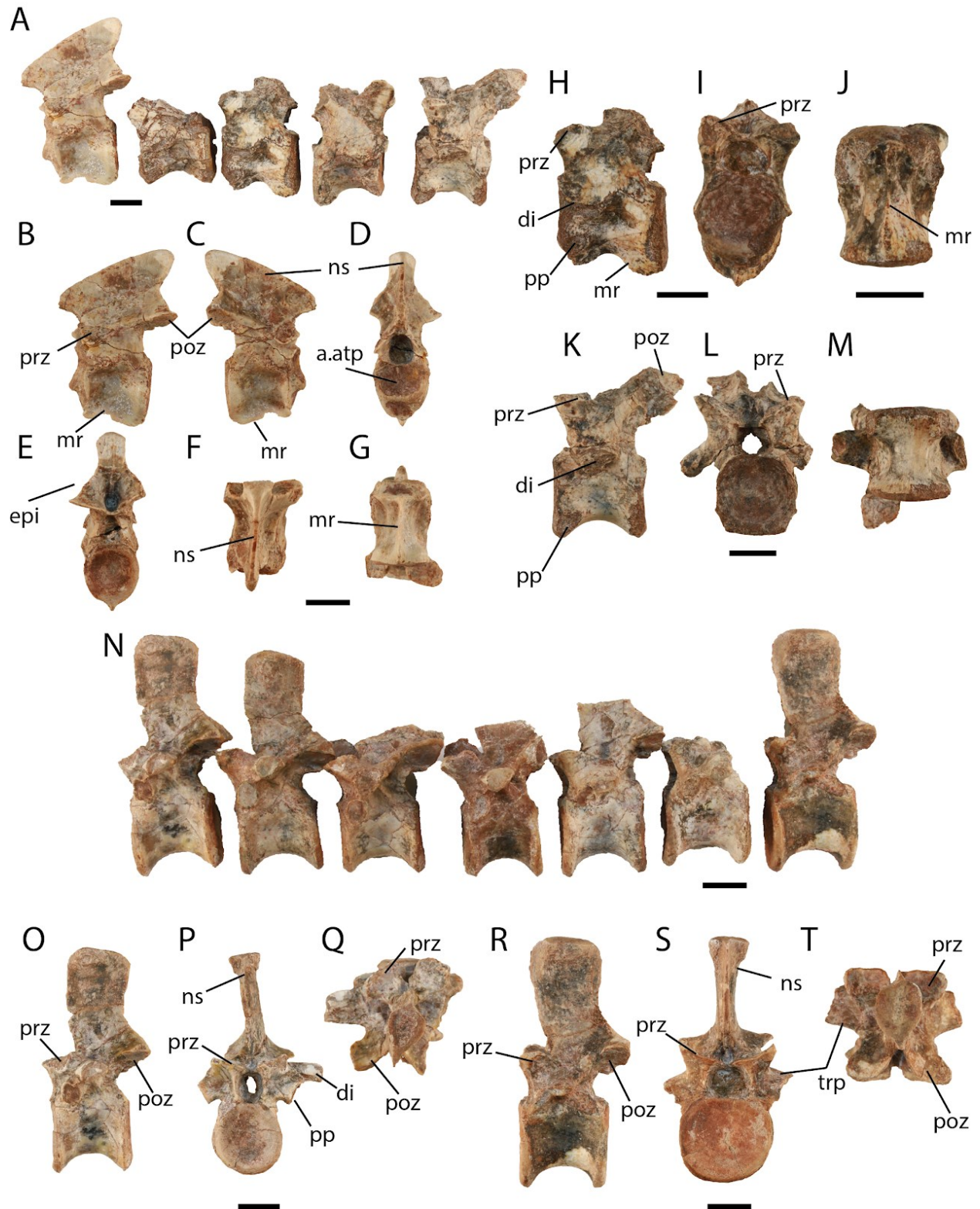


FIGURE 6: Presacral vertebrae from the holotype NMT RB187 of <Name Redacted>. Cervical series in **A**, left lateral view. Axis in **B**, left lateral, **C**, right lateral, **D**, anterior, **E**, posterior, **F**,

dorsal, **G**, ventral views. Anterior cervical vertebra in **H**, left lateral, **I**, anterior, **J**, ventral views. Posterior cervical vertebra in **K**, left lateral, **L**, anterior, **M**, ventral views. Trunk series in **N**, left lateral view. Anterior trunk vertebra in **O**, left lateral, **P**, anterior, **Q**, dorsal views. Posterior trunk vertebra in **R**, left lateral, **S**, anterior, **T**, dorsal views. Scale bars equal to 1 cm.

Abbreviations: a., articulates with; atp, atlantal pleurocentrum; di, diapophysis; epipophysis; mr, midline ridge; ns, neural spine; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis; trp, transverse process.

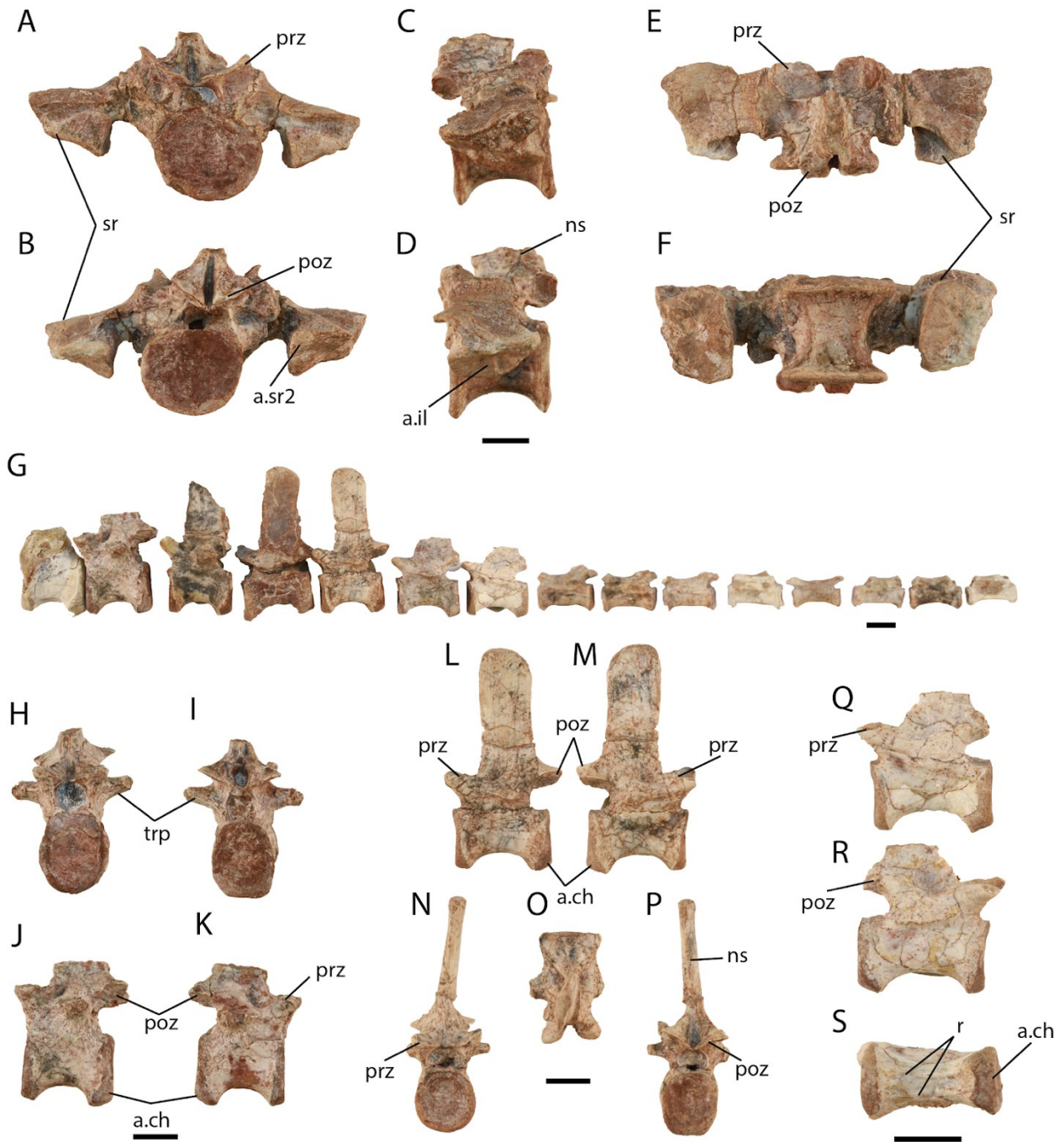


FIGURE 7: Sacral vertebra and caudal vertebrae from the holotype NMT RB187 of *<Name Redacted>*. First primordial sacral vertebra in **A**, anterior, **B**, posterior, **C**, right lateral, **D**, left lateral, **E**, dorsal, **F**, ventral views. Caudal series in **G**, left lateral view. Partial anterior caudal vertebra in **H**, anterior, **I**, posterior, **J**, left lateral, **K**, right lateral views. Anterior caudal vertebra

in **L**, left lateral, **M**, right lateral, **N**, anterior, **O**, dorsal, **P**, posterior views. Middle caudal vertebra in **Q**, left lateral, **R**, right lateral, **S**, ventral views. Scale bars equal to 1 cm.

Abbreviations: a., articulates with; ch, chevron; il, ilium; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; r, ridge; sr, sacral rib; sr2, second sacral rib; trp, transverse process.

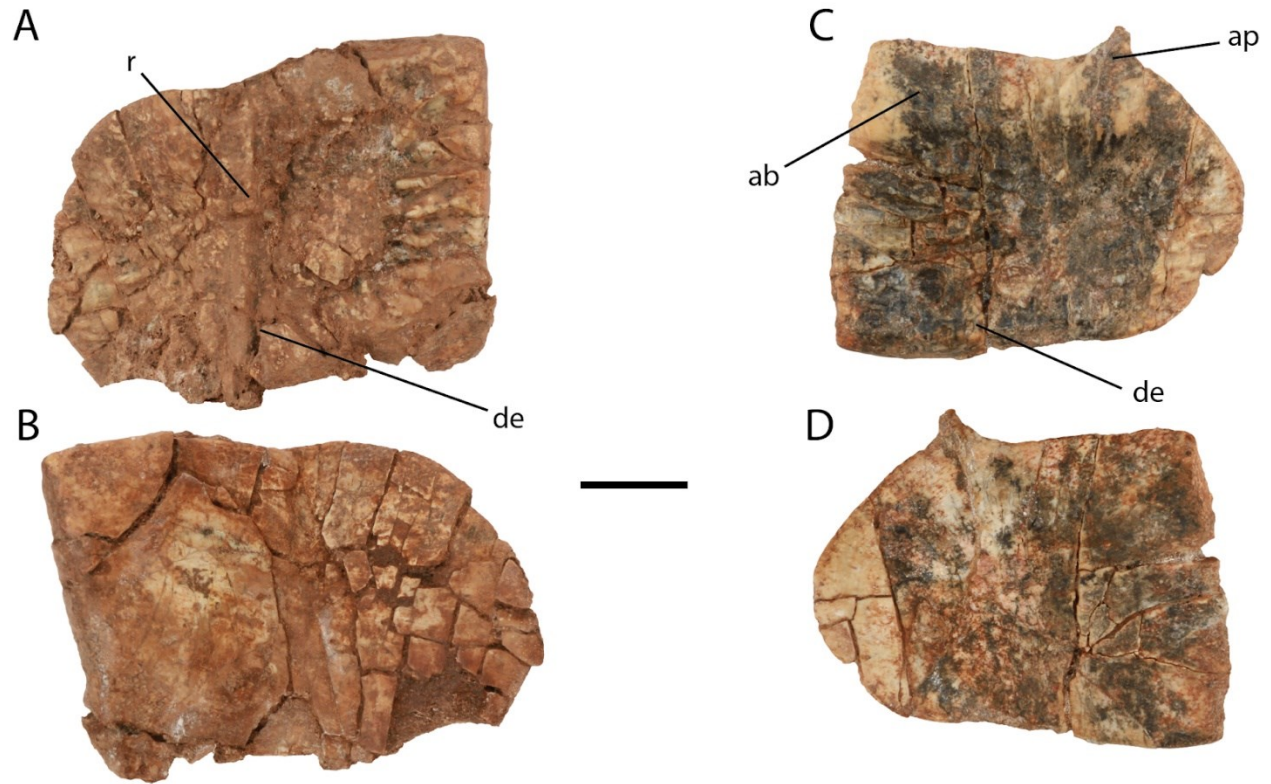


FIGURE 8: Presacral paramedian osteoderms (NMT RB187) of <Name Redacted>, gen. et sp. nov. Left paramedian osteoderm in **A**, dorsal, **B**, ventral views. Right paramedian osteoderm in **C**, dorsal, **D**, ventral views. Scale bars equal to 1 cm. **Abbreviations:** ab, anterior bar; ap, ascending process; de, dorsal eminence; r, ridge.

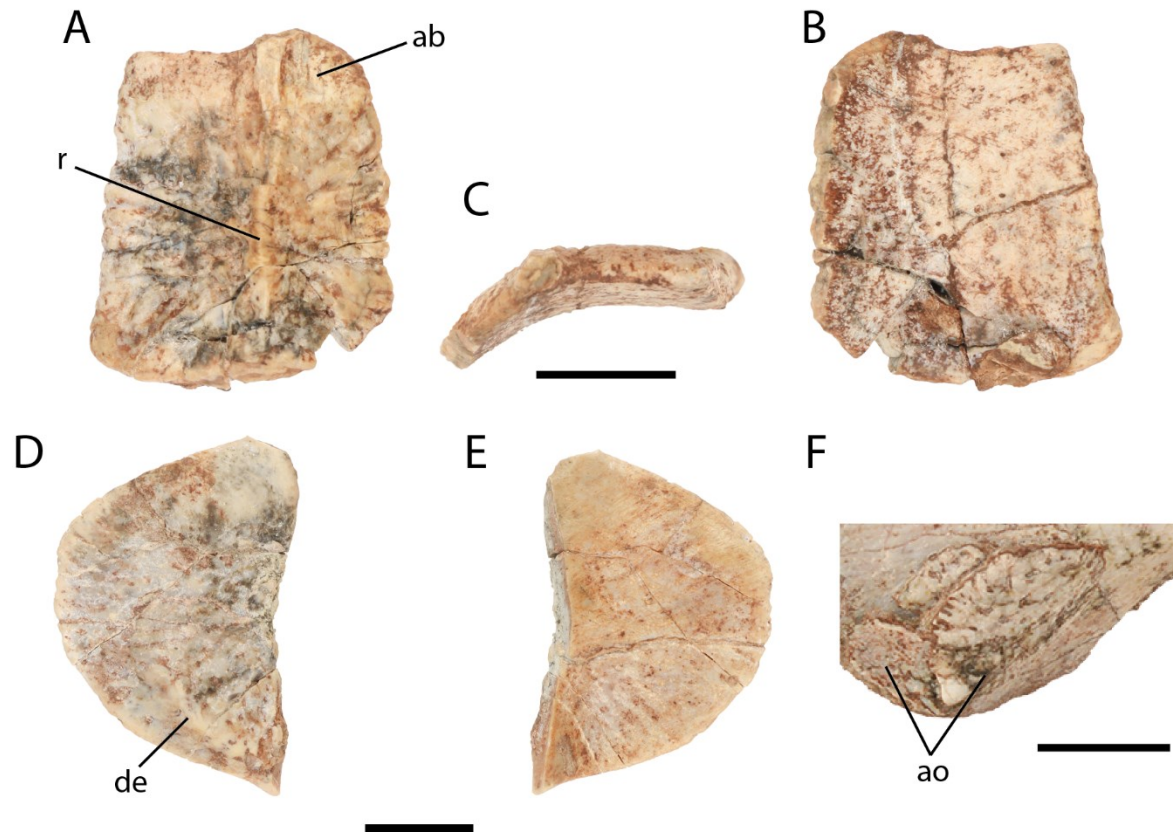


FIGURE 9: Additional osteoderms (NMT RB187) of *<Name Redacted>*, gen. et sp. nov. Left caudal paramedian osteoderm in **A**, dorsal, **B**, ventral, **C**, anterior views. Partial lateral osteoderm in **D**, dorsal, **E**, ventral views. **F**, appendicular osteoderms on left humerus in dorsal view. Scale bars equal to 1 cm. **Abbreviations:** ab, anterior bar; ao, appendicular osteoderm; de, dorsal eminence; r, ridge.

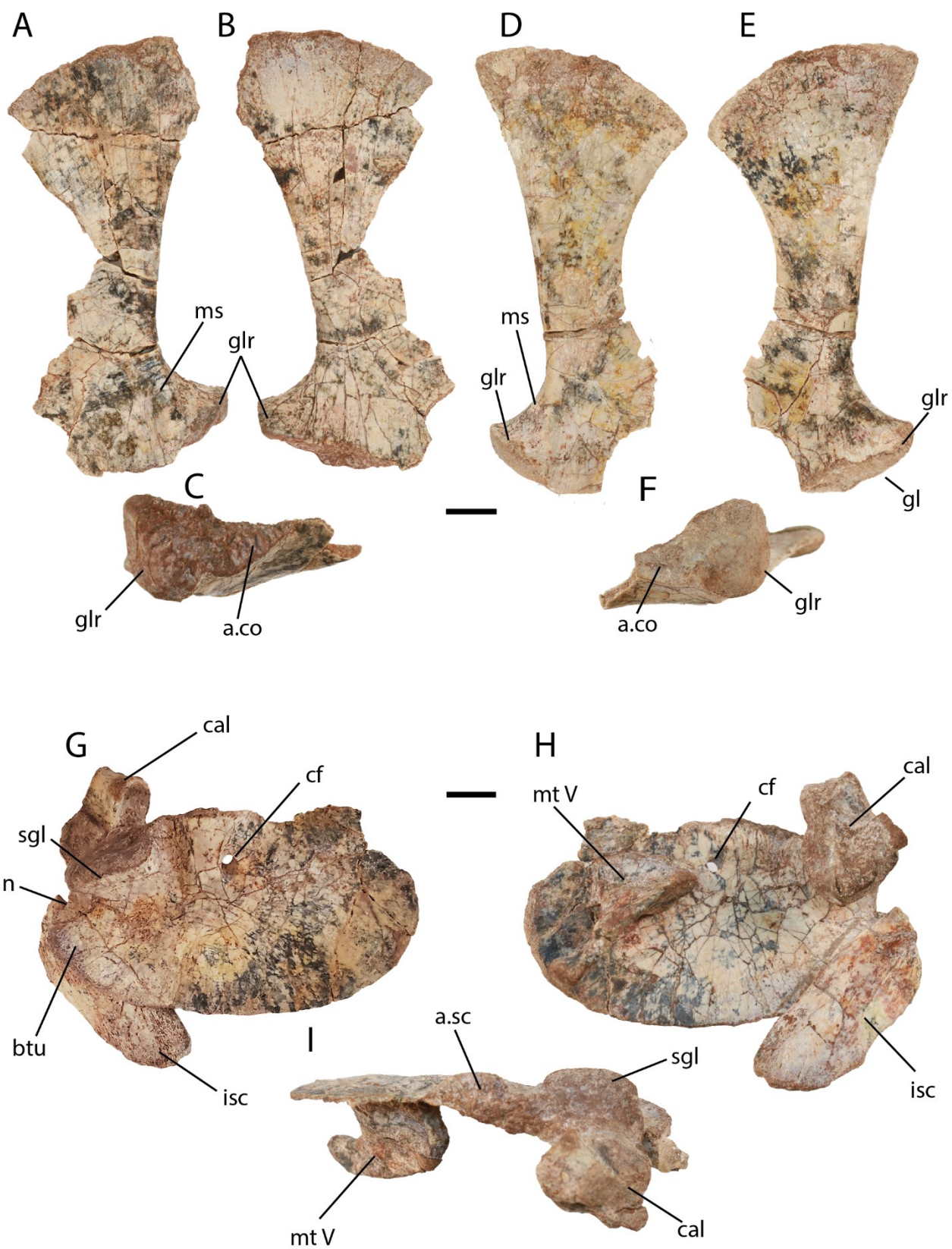


FIGURE 10: Pectoral girdle of <Name Redacted>, gen. et sp. nov. Left scapula (NMT RB187) in **A**, lateral, **B**, medial, **C**, proximal views. Right scapula (NMT RB187) in **D**, lateral, **E**, medial, **F**, proximal views. Right coracoid with partial ilium, calcaneum and metatarsal V (NMT RB187) in **G**, lateral, **H**, medial, **I**, proximal views. Scale bars equal to 1 cm. **Abbreviations:** a., articulates with; btu, biceps tubercle; cal, calcaneum; cf, coracoid foramen; co, coracoid; gl, glenoid; glr, supraglenoid rim; isc, ischium; ms, muscle scar; mt V, metatarsal V; n, notch; sc, scapula; sgl, subglenoid lip.

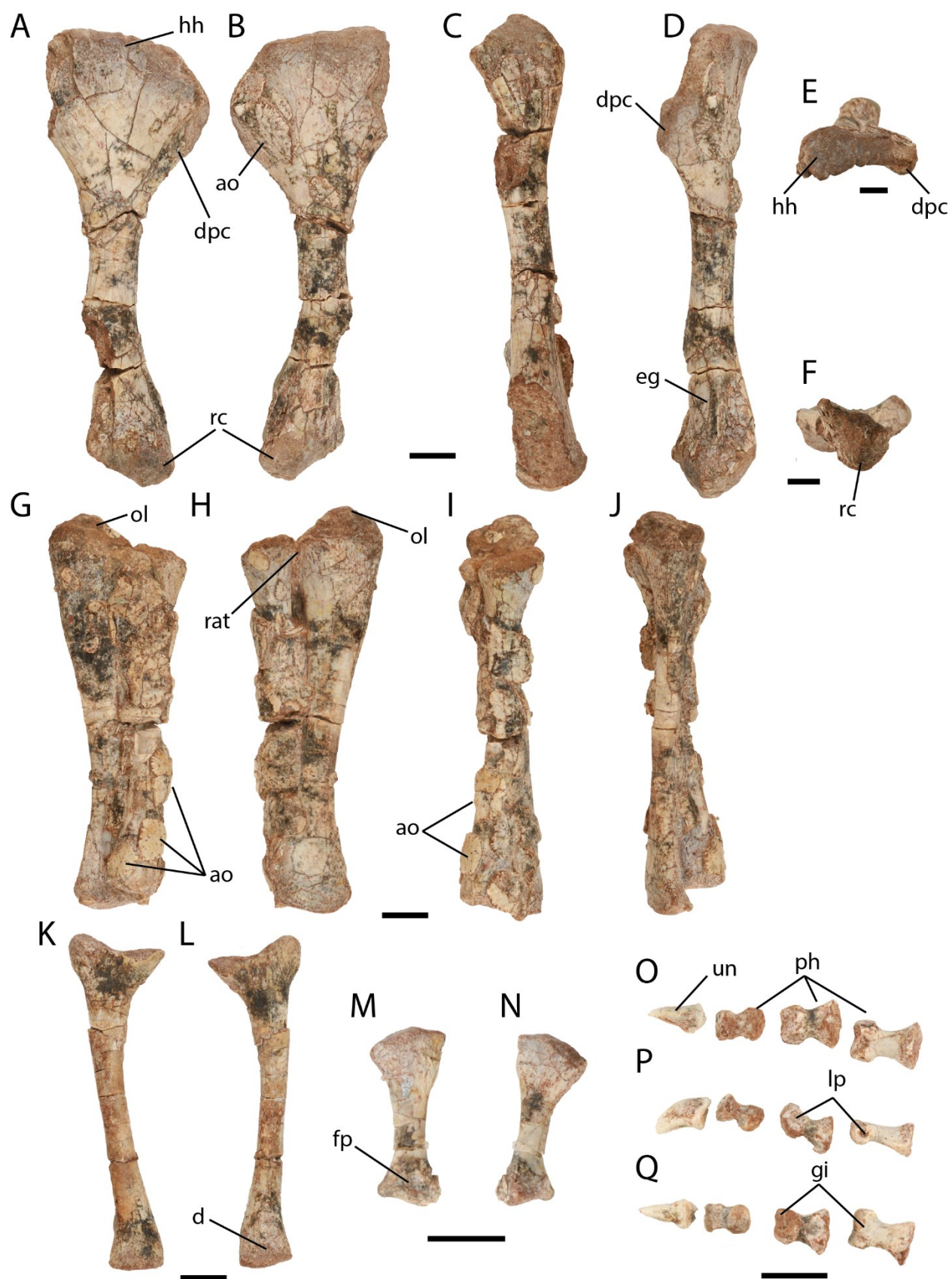


FIGURE 11: Forelimb bones of <Name Redacted>, gen. et sp. nov. Left humerus (NMT RB187) in **A**, anterior, **B**, posterior, **C**, medial, **D**, lateral, **E**, proximal, **F**, distal views. Left ulna and radius (NMT RB187) in **G**, anterior, **H**, posterior, **I**, lateral, **J**, medial. Right radius (NMT RB187) in **K**, anterior, **L**, posterior views. Metacarpal (NMT RB187) in **M**, dorsal, **N**, ventral views. Manual phalanges in **O**, dorsal, **P**, lateral, **Q**, ventral views. Scale bars equal to 1 cm.

Abbreviations: ao, appendicular osteoderm; d, depression; dpc, deltopectoral crest; eg, ectepicondylar groove; fp, flexor pits; gi, ginglymus; hh, humeral head; lp, lateral pits; ol, olecranon process; ph, phalanges; rat, radial tubercle; rc, radial condyle; un, ungual.

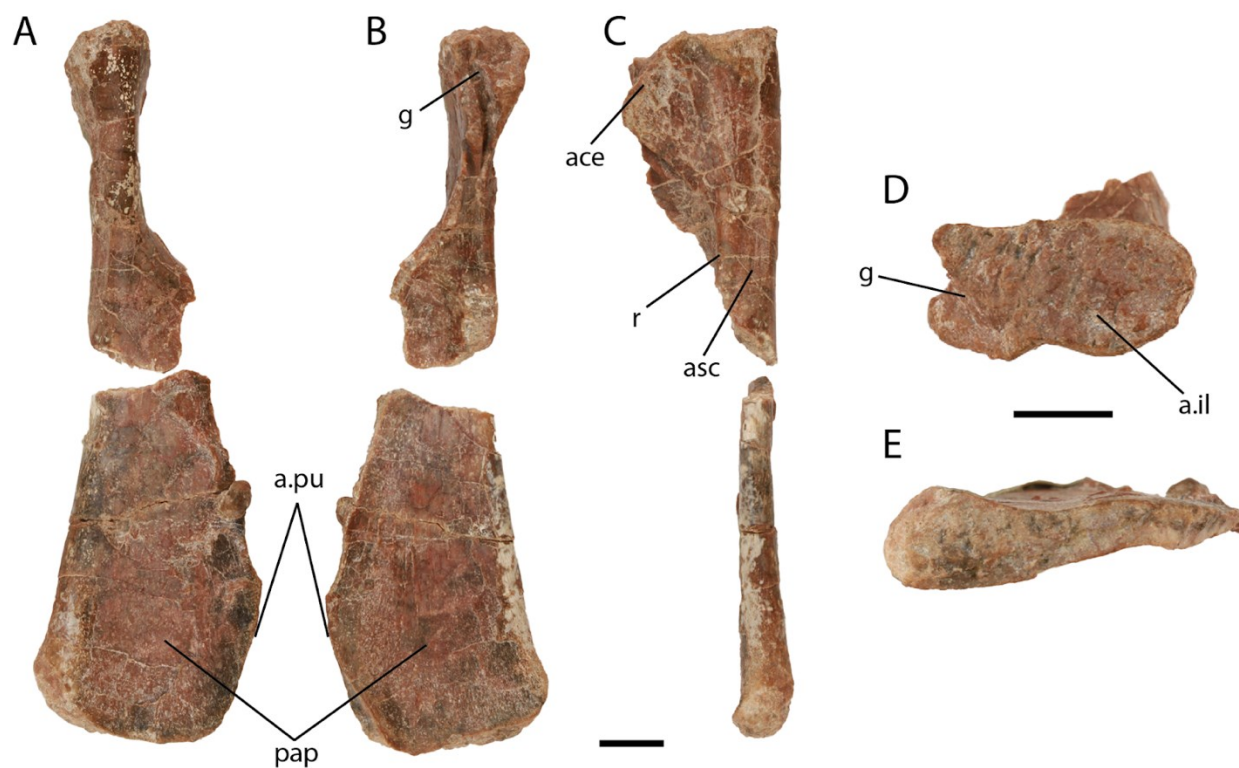


FIGURE 12: Right pubis of *<Name Redacted>*, gen. et sp. nov. (NMT RB187). In **A**, anterior, **B**, posterior, **C**, lateral, **D**, proximal, **E**, distal views. Scale bar equal to 1 cm. **Abbreviations:** a., articulates with; ace, acetabulum; asc, ambiens scar; g, groove; il, ilium; pap, pubic apron; pu, pubis; r, ridge.

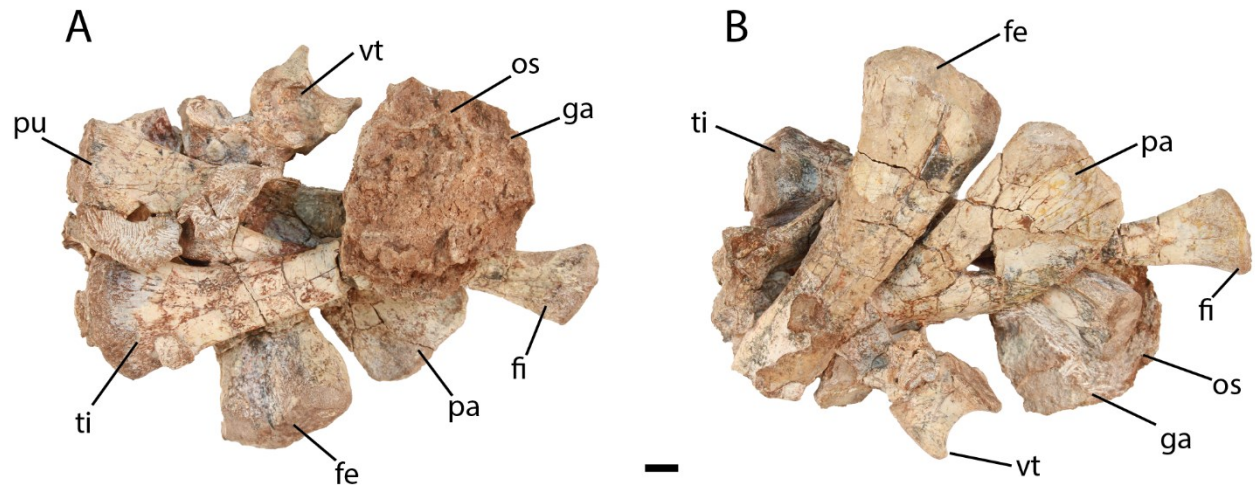


FIGURE 13: Block with vertebrae, gastralia, osteoderms, left pubis, and left hindlimb of *<Name Redacted>*, gen. et sp. nov. (NMT RB187) from **A**, top, **B**, bottom. Scale bar equal to 1 cm.

Abbreviations: fe, femur; fi, fibula; ga, gastralia; os, osteoderm; pa, pubic apron; pu, pubis; ti, tibia, vt, vertebra.

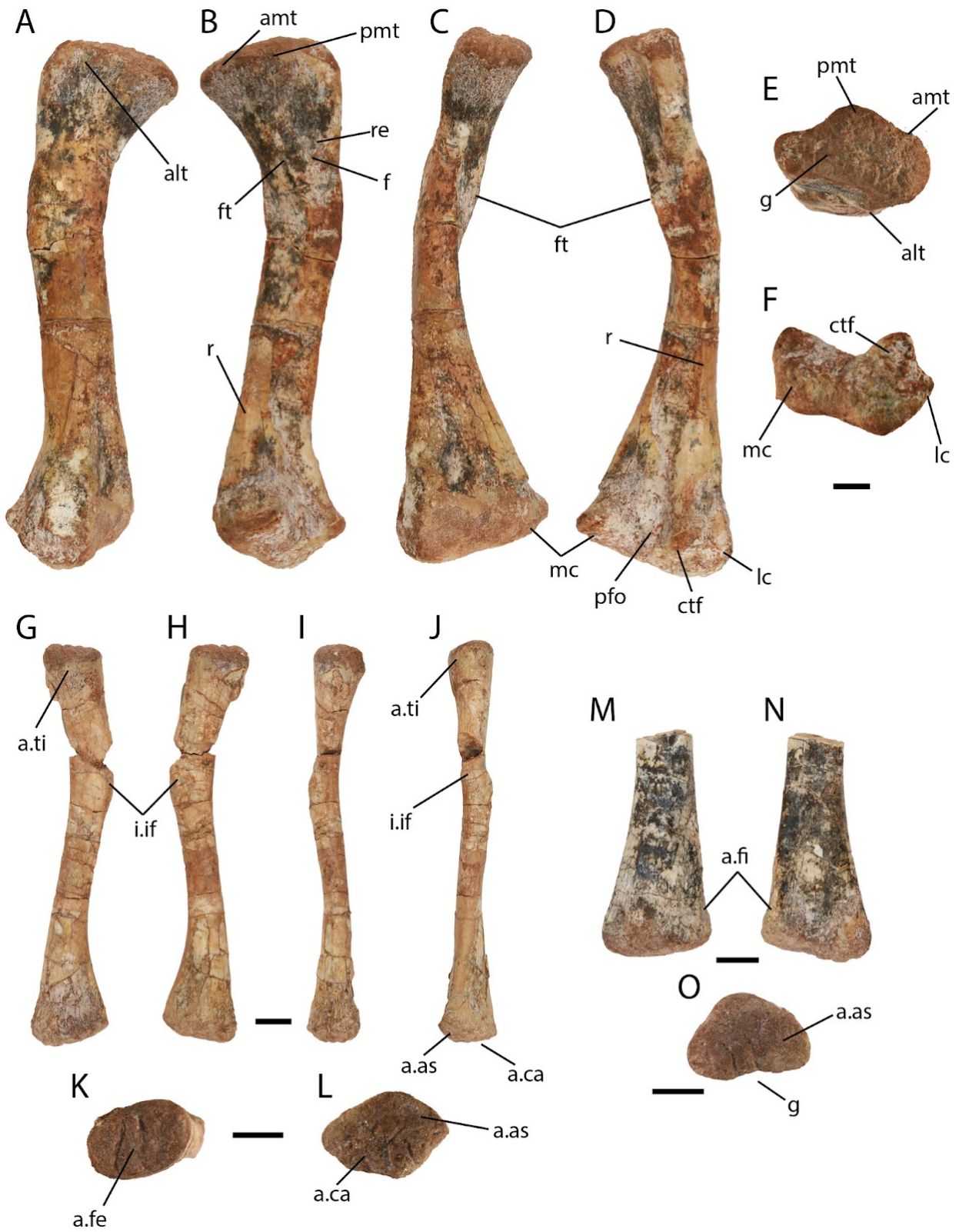


FIGURE 14: Hindlimb bones of <Name Redacted>, gen. et sp. nov. Right femur (NMT RB187)

in **A**, lateral, **B**, medial, **C**, anterior, **D**, posterior, **E**, proximal, **F**, distal views. Left fibula (NMT RB187) in **G**, lateral, **H**, medial, **I**, posterior, **J**, anterior, **K**, proximal, **L**, distal views. Distal end of left tibia (NMT RB187) in **M**, anterior, **N**, posterior, **O**, distal views. Scale bars equal to 1 cm.

Abbreviations: a., articulates with; alt, anterolateral tuber; amt, anteromedial tuber; as, astragalus; ca, calcaneum; ctf, crista tibiofibularis; f, foramen, fe, femur; fi, fibula; ft, fourth trochanter; g, groove; i.if, insertion for the M. iliofibularis; lc, lateral condyle; mc, medial condyle; pfo, popliteal fossa; pmt, posteromedial tuber; r, ridge, re, recess; ti, tibia.

FIGURE 15: Proximal tarsals of <Name Redacted>, gen. et sp. nov. Left calcaneum (NMT RB187) in **A**, proximal, **B**, distal, **C**, medial, **D**, lateral, **E**, posterior, **F**, anterior views. Left astragalus (NMT RB679) in **G**, proximal, **H**, distal, **I**, medial, **J**, lateral, **K**, posterior, **L**, anterior views. Arrows indicate anterior direction. Scale bars equal to 1 cm. **Abbreviations:** a., articulates with; ah, anterior hollow; as, astragalus; ca, calcaneum; cat, calcaneum tuber; fi, fibula; g, groove; mt, metatarsal; peg, peg of the astragalus that fits into the calcaneum; pg, posterior groove; t4, fourth tarsal; ti, tibia; tu, tuber.

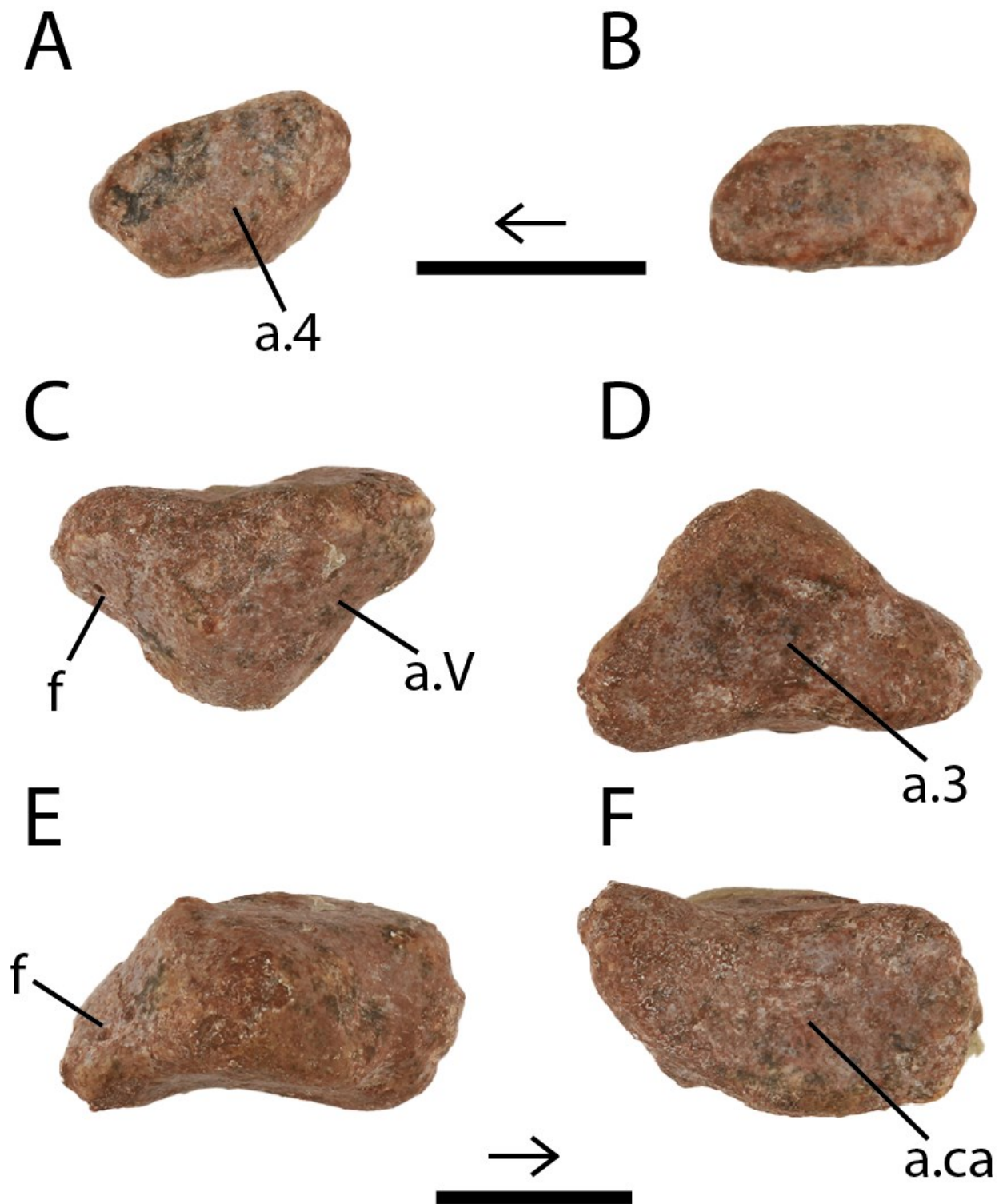


FIGURE 16: Distal tarsals (NMT RB187) of *<Name Redacted>*, gen. et sp. nov. Right tarsal 3 in **A**, lateral, **B**, ventral views. Right tarsal 4 in **C**, lateral, **D**, medial, **E**, posterior, **F**, proximal

views. Scale bars equal to 1 cm. Arrows indicate anterior direction. **Abbreviations:** a., articulates with; 3, distal tarsal 3; 4, distal tarsal 4; f, foramen; V, metatarsal V.

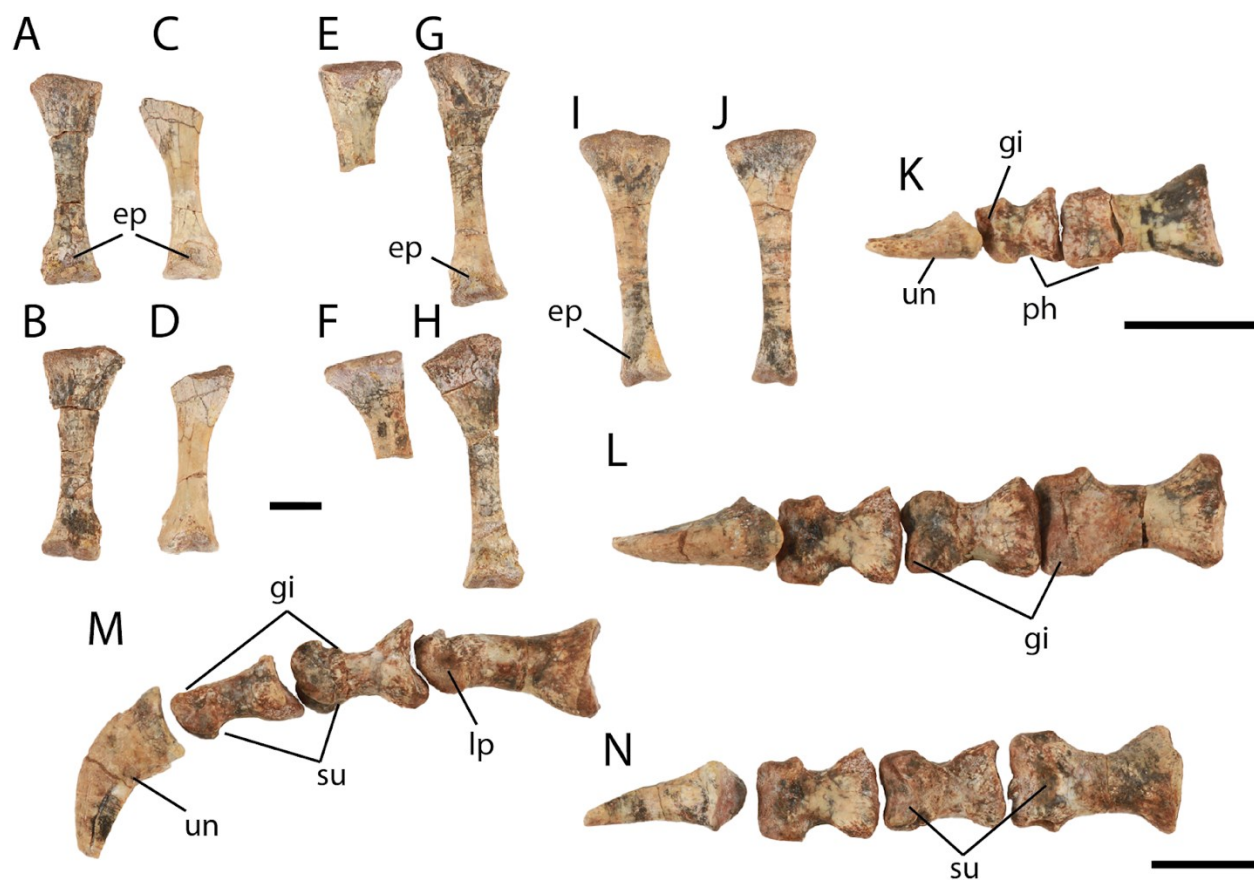


FIGURE 17: Pes of (NMT RB187) of *<Name Redacted>*, gen. et sp. nov. Right metatarsal I in **A**, anterior, **B**, posterior views. Left metatarsal I in **C**, anterior, **D**, posterior views. Right metatarsal II in **E**, anterior, **F**, posterior views. Right metatarsal III in **G**, anterior, **H**, posterior views. Right metatarsal IV in **I**, anterior, **J**, posterior views. Pedal phalange of uncertain position in **K**, dorsal view. Additional pedal phalange in **L**, dorsal, **M**, lateral, **N**, ventral views. Scale bars equal to 1 cm. **Abbreviations:** ep, extensor pits; gi, ginglymus; lp, lateral pits; ph, phalanx; su, sulcus; un, ungual.

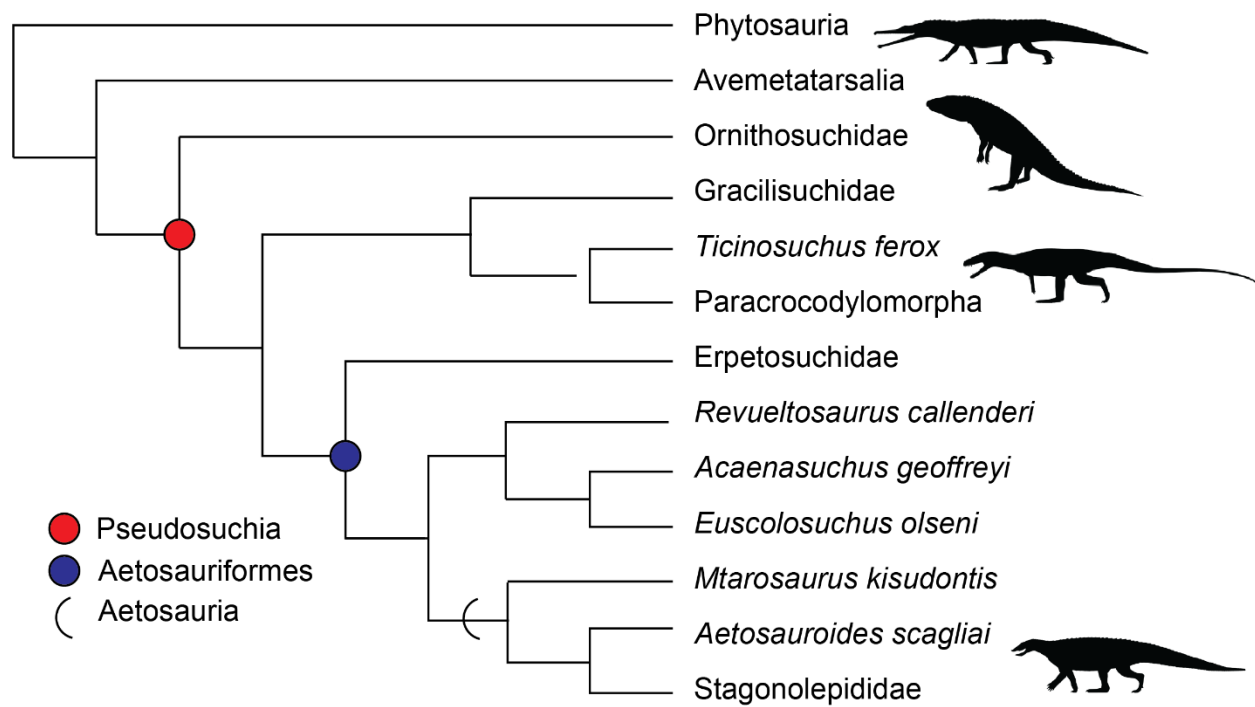


FIGURE 18: Phylogenetic position of <Name Redacted> within Pseudosuchia. Analysis run in TNT using the modified matrix of Parker et al., 2021. Silhouettes from PhyloPic.

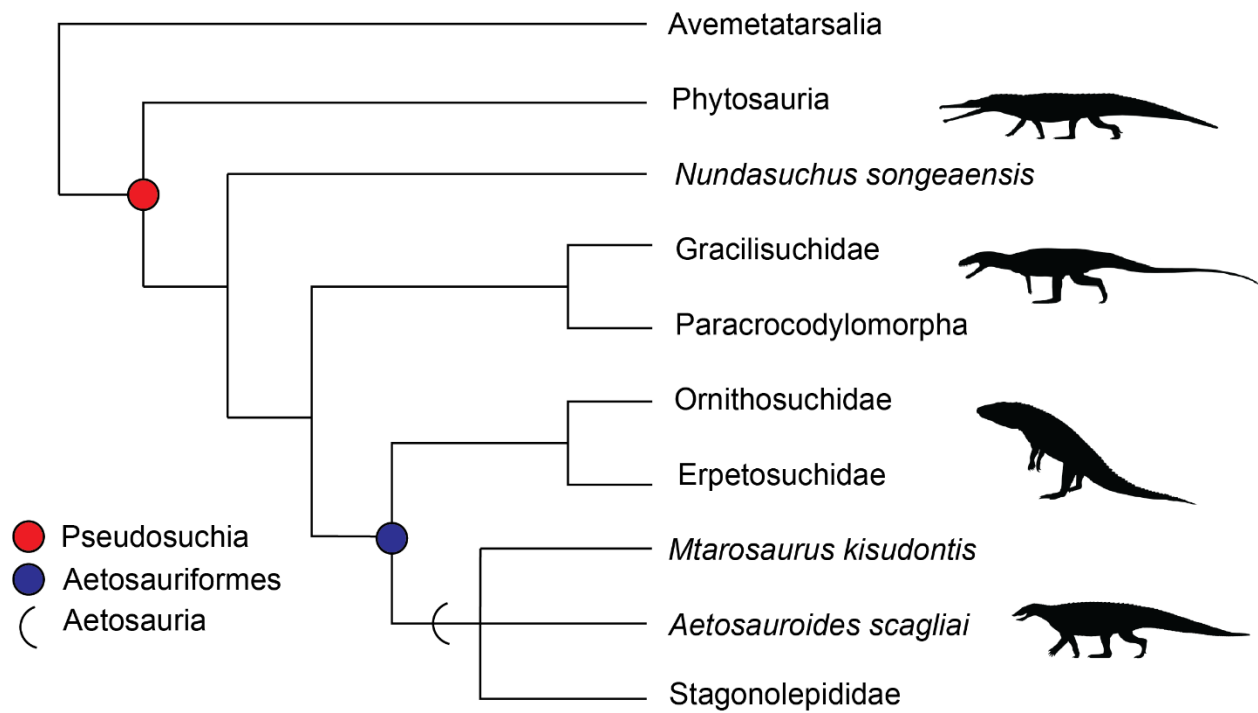


FIGURE 19: Phylogenetic position of <Name Redacted> within Archosauria. Analysis run in TNT using the modified matrix of Von Baczko et al., 2021. Silhouettes from PhyloPic.

DISSERTATION CONCLUSION:

Lineage diversification and ecological specialization are the two key processes of adaptive radiations. However, the relative timing of these two processes has been a matter of debate for decades, do they occur contemporaneously, and if not, in what order to they proceed? In order to investigate this question, I used the radiation of archosaur reptiles following the end-Permian mass extinction. Archosaurs make an ideal study system as the lineage diversification has been well constrained by fossils and phylogenetic hypotheses, and they evolved a wide range of ecologies by the Late Triassic. However, the pattern of ecological diversification through the Early and Middle Triassic has not been thoroughly investigated. I primarily used diet as the ecological aspect of interest in my dissertation projects. Diet was selected as it can reliably be reconstructed using teeth, including isolated teeth enabling me to include fragmentary material and sample smaller-sized individuals than are normally captured in Early and Middle Triassic vertebrate assemblages.

In my first chapter, I investigated dietary specialization using isolated and *in situ* archosaur teeth from the Middle Triassic Manda Beds of Tanzania. I used a combination of linear measurements and discrete character scoring to reconstruct the shape of teeth. I assigned diet with comparisons to teeth of known diet and body size. All teeth in the study belonged to faunivores indicating that even by the Middle Triassic, ecological diversification lagged behind lineage diversification. Additionally, I found the discrete character scoring method to be more effective than linear measurements in reconstructing tooth morphotypes.

For the second chapter, I investigated dietary specialization using primarily isolated and *in situ* reptile teeth from the Early Triassic Driefontein locality of South Africa. I expanded on the methods used in my first chapter to include 3D morphometrics in addition to linear

measurements and discrete characters. All morphotypes included in the study belong to faunivores, indicating little dietary specialization within ~3 million years of the end-Permian mass extinction. The presence of several new reptile tooth morphotypes indicates the reptile diversity at the Driefontein locality is greater than currently known. Additionally, the numerous, small teeth capture a size range not normally found in the Early Triassic of the Karoo Basin, providing an important window into the microvertebrate fauna of the Early Triassic. Despite using more advanced quantitative methods, the qualitative discrete scoring again proved to be the most reliable method for differentiating tooth morphotypes.

In my third chapter, I describe a new species of suchian reptile from the Middle Triassic Manda Beds of Tanzania. This new taxon is diagnosed by a unique combination of plesiomorphic and derived character states and recovered as the oldest and basal-most aetosaur in our phylogenetic analyses. This new species provides support to the hypothesis that aetosaurs and *Revueltosaurus callenderi* independently evolved herbivory and shows that the aetosaurian body plan evolved before cranial specialization for an herbivorous diet.

Together, my dissertation chapters indicate that the ecological diversification of archosaurs lagged behind their lineage diversification, at least through the lens of dietary specialization. These findings provide support the Simpsonian view of adaptive radiations where lineage diversification occurs prior to ecological specialization within adaptive zones (Simpson, 1944). Additionally, I find the discrete character scoring of teeth provides a reliable and repeatable metric for evaluating tooth shape. These methods are flexible and can be applied to tooth assemblages in other localities and time periods to reconstruct patterns of dietary specialization enabling a broader understanding of the pattern of adaptive radiations.