The early evolution of diapsid reptiles and the origin of Sauria

A Dissertation Presented

by

Adam Carl Pritchard

to

the Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Anatomical Sciences

Stony Brook University

August 2015

Stony Brook University

The Graduate School

Adam Carl Pritchard

We, the dissertation committee for the above candidate for the
Doctor of Philosophy degree, hereby recommend
acceptance of this dissertation

Alan H. Turner—Dissertation Advisor

Associate Professor, Department of Anatomical Sciences

Nathan J. Kley—Chairperson of Defense

Associate Professor, Department of Anatomical Sciences

Erik R. Seiffert

Associate Professor, Department of Anatomical Sciences

Jack Conrad

Assistant Professor, Department of Anatomy

New York College of Osteopathic Medicine

This dissertation is accepted by the Graduate School

Charles Taber

Dean of the Graduate School

Abstract of the Dissertation

The early evolution of diapsid reptiles and the origin of Sauria

By

Adam Carl Pritchard

Doctor of Philosophy

In

Anatomical Sciences

Stony Brook University

2015

All living reptiles belong to the crown clade Sauria, a subgroup of the ancient amniote clade Diapsida. Modern divergence estimates suggest an origin for Sauria in the Permian Period, just prior to the Permo-Triassic Extinction, which wiped out an estimated 95% of species. Although the Permian record of Diapsida is quite small, the subsequent Triassic record is substantial, with a huge array of body sizes and bauplans evident very early in the period. However, phylogenetic hypotheses for these early-diverging taxa are wildly inconsistent, such that our understanding of the origin and early radiation of the crown reptile clade during the Permian and Triassic is very poorly understood. For this dissertation, I present new insights into this important diversification event using novel phylogenetic data matrices. I employ this phylogenetic context to interpret a small reptile fauna from a Triassic fossil site in New Mexico, to resolve a problematic fossil lineage through description of the first three-dimensional material from the group and analysis of those fossils, and to examine the broad-scale patterns of taxonomic and morphological diversification before and after the PTE.

I first employ this analysis to examine well-preserved fossils of early-diverging diapsid groups from the Upper Triassic Hayden Quarry (Chinle Formation) of New Mexico, a site that preserves some of the best fossil materials of small vertebrates in North America. The phylogenetic hypothesis allows the small reptile fauna to be analyzed in an apomorphy-based framework. One set of fossils belongs to Tanystropheidae, a clade of long-necked archosaur-line reptiles. These represent the first strong evidence for the group from western North America. The second set of fossils includes forelimb material from *Drepanosaurus unguicaudatus*, a small drepanosauromorph diapsid, previously known from Italy, with a highly modified forelimb. The three-dimensional fossils allow a conclusive determination of the homologies of the forelimb bones in *Drepanosaurus*, and the phylogenetic context illustrates a series of trait acquisitions in Drepanosauromorpha.

I address long-standing questions about the affinities of Drepanosauromorpha among Triassic diapsid lineages through description the first three-dimensionally preserved skull from the group, also from the Upper Triassic of New Mexico. The material shows many morphological similarities to archaic, Permian diapsids in contrast to other early saurians, suggesting that drepanosauromorphs are outside of the crown clade Sauria. I describe the new skull in detail, with extensive comparisons to other Permo-Triassic reptiles.

Finally, I present a novel data matrix of 303 morphological characters and present detailed results of this phylogenetic analysis. Although the phylogeny is well-resolved, there is substantial instability within the early-diverging saurian lineages, suggesting that small changes in character and taxon sampling can produce conflicting topologies. The results do suggest that much of the early diversification of Sauria occurred within the Permian, indicating many gaps in the diapsid fossil record. The optimizations of characters suggest that the ancestor of most archosaur-line reptiles was a long-necked and small-headed taxon. These studies illustrate a substantial complexity in the early diversification of Diapsida during the Permian Period. They also show that many of these early-diverging lineages radiated widely, attaining a substantial degree of morphological diversity during the Triassic Period.

Table of Contents

List of Figures

List of Table

Acknowledgments

I cannot express enough gratitude for the help and guidance I have received throughout my life from a large number of people. Honestly, as I like placing things in a narrative context, I think it's best I approach this chronologically.

I first thank my close family for their constant support and guidance throughout my life. My mother and father, Nancy and Carl Pritchard, have never wavered in their support for my dreams, and I would never have arrived here without them. I thank them for the Saturday trips to the Smithsonian that continually fired my imagination. I also thank my grandmother and grandfather, Carol and James Adams and my Aunt Kristi for their love and support.

I received a great deal of intellectual and emotional support from my teachers in both grade school and college. Special thanks go to Teresa Wilson of Governor Thomas Johnson High School and my undergraduate advisor Dr. Wilbur Long. Mrs. Wilson invested substantial time in here more academically inclined students and their well-being. Dr. Long proved a kindred spirit in my interest in biology, and strongly supported my decision to pursue paleontology.

I thank all of my close friends from McDaniel College for their love in support in the past several years, especially Jennifer Sandler, Alex Vazzano, and Tommy Dembeck. However, I must especially thank Eric Lemmon and Ashleigh Pritchard (then Smith) in particular, who galvanized my decision to pursue graduate school. I would not have made that choice without them.

The colleagues I have had at Stony Brook University have fired my intellectual interests and continue to provide a powerful support network. Gina Sorrentino, Sara Burch, Jacob McCartney, Joseph Sertich, Simone Hoffmann, Nathan Thompson, Nick Holowka, Stephanie Maiolino, Phil Nicodemo, Jennifer Nestler, Kate Corbin, and Bonnie Sumner have all helped support this project. My greatest thanks must go to Matthew Borths, my partner in Past Time.

The professors and post-docs at Stony Brook continue to contribute to my intellectual development as a researcher and an academic. Michael D'Emic, Sergio Alemejica, Ashley Hammond, Susan Larson, Brigitte Demes, William Jungers, Jack Stern, and Randall Susman have all improved the quality of my work. Special thanks goes to Paul Gignac, who not only helped with my research but also invested in me the importance of narrative in communicating science. I also thank the members of my committee (Nathan Kley, Erik Seiffert, and Jack Conrad) for their criticism and guidance in the course of this project.

David Krause has been one of the best bosses a research assistant could have. He invested in me the importance of order in dealing with fossil collections and greatly improved the quality of my reasoning and writing during our collaboration. I must also thank Sarah Werning, who has been a great friend and a strong support during my final years here. I thank her for both her paleontological insights and emotional support. I also thank Joe Groenke for balancing my chaos with order and his assistance with preparation. On a logistical side, I thank Chris Johnson and Linda Benson for their help in keeping invoices, insurance, payrolls, and all the other bureaucratic sundries that I cannot fully fathom in line.

I received a great deal of training and assistance with fieldwork at the Hayden Quarry site in northern New Mexico. I thank Randall Irmis, Sterling Nesbitt, and Nathan Smith, who have invited me to work on the Triassic fossil material they have excavated there over the past ten years. I also thank all who have helped excavate at the site in the past several years and who have also taught me a great deal, including Michele Stocker, Jenn Olori, Katie Criswell, Elizabeth Ferrer, Ashley Poust, Zachary Morris, Adam Marsh, Keegan Melstrom, Caitlin Colleary, Chris Griffin, Tylor Birthisel, Robert Katz, Charles Beightol, Connie Rasmussen, Carrie Levitt-Bussian, and Brian Switek.

The travel component of this dissertation required extramural funding. I am very grateful to the following private foundations for their contributions: Sigma Xi, the Evolving Earth Foundation, the Geological Society of America, and the Doris and Samuel Welles Fund. I also thank the National Science Foundation for the award of a Doctoral Dissertation Improvement Grant.

This research would not have been possible without the museum and technical staff at museum facilities worldwide. I thank Alex Downs (Ruth Hall Museum of Palaeontology), Carl Mehling (American Museum of Natural History), Dan Brinkman and Chris Norris (Yale Peabody Museum of Natural History), Chris Sagebiel (Texas Memorial Museum), Jessica Cundiff (Museum of Comparative Zoology), Alton Dooley (Virginia Museum of Natural History), Michael Brett-Surman (National Museum of Natural History), Spencer Lucas and Thomas Williamson (New Mexico Museum of Natural History), David Gillette (Museum of Northern Arizona), Bill Parker (Petrified Forest National Park), Lorna Steel and Sandra

Chapman (Natural History Museum of the UK), Ronan Allan (Museum National d'Histoire Naturelle), Andrea Tintori and Christina Lombardo (Università degli Studi di Milano), Cristiano Dal-Sasso (Museo Civico di Storia Naturali), Anna Paganoni (Museo Civico di Storia Naturali Enrico Caffi), Giuseppe Muscio and Luca Simonetto (Museo Friulano di Storia Naturali), Liu Jun (Institute of Paleontology and Paleoanthropology), Da-Yong Jiang (Geological Museum of Peking University), Andrea Sennikov (Paleontological Institute of the Russian Academy of Sciences), Heinz Furrer (Paleontological Institute and Museum of the University of Zürich), Rainer Schoch and Erin Maxwell (Staaliches Museum für Naturkunde Stuttgart), Magdalena Borsuk-Bialynicka (Paleobiology Institute of the Polish Academy of Sciences), Bernhard Zipfel (Evolutionary Studies Institute, University of Witwatersrand), Roger Smith and Zaituna Erasmus (Iziko Museum), and Elize Butler (National Museum, Bloemfontein) for providing me access to fossil collections that provided insights for this project. I also thank James Thostenson (formerly of the American Museum, now at Duke University) for assistance with μCT scanning material for chapters three, four, and five of this dissertation. I also thank Bhart-Anjan Bhullar and Jacques Gauthier, who have invited me to advance this work for the next stage of my career at Yale University.

My deepest thanks go to my advisor Alan Turner for his guidance in the past six years. I appreciate his kindness, understanding, and inclination *not* to, as he says, "blow smoke up my ass." He warned me from the beginning that this was a path laced with self-loathing and uncertainty, and he has never wavered from supporting me since I elected to follow this path. He and his colleagues have welcomed me into the fold with the Ghost Ranch project and have kindly introduced me to the vertebrate paleontology community.

Finally, I thank my wife, Ashleigh Pritchard for her love and support. Nearly eight years ago, she pushed me to pursue this career path, and she has stood by me ever since. And, she made the table of contents!

Chapter 1

Introduction and Overview

Diapsida is an ancient clade of amniotes, today represented by Archosauria (birds and crocodylians), Lepidosauria (lizards, snakes, tuatara), and Testudines (turtles). Taken together, these taxa represent nearly 20,000 extant species and a greater proportion of modern terrestrial vertebrate diversity than extant mammals and lissamphibians. The enormous range of morphospace occupied by extant diapsids pales in comparison to the diversity of the group during the Mesozoic Era. However, the origins of all three major diapsid clades remain very poorly understood.

Although Diapsida as a whole originated deep in the Paleozoic (Reisz, 1977; Müller, 2004), current molecular and fossil evidence suggests that the common ancestor of Archosauria and Lepidosauria (united in the crown clade Sauria) originated during the latter half of the Permian Period (Sennikov, 1988; Ezcurra et al., 2014). Recent molecular estimates suggest a split just over 270 million years ago (Shedlock and Edwards, 2009), not long before the first appearance by Sauria in the fossil record (Ezcurra et al., 2014). During the Permian, diapsid reptiles are extremely uncommon and members of Sauria are very rare. However, their earliest diversification coincides with the Permo-Triassic Extinction (PTE), the largest known mass extinction in the fossil record with a loss of >90% of known species (Knoll et al., 2007; Shen and Bowring, 2015), although the impact on vertebrates is poorly understood (Irmis and Whiteside, 2012; Benton et al., 2013). In the wake of that event in the Triassic Period, the known diapsid record becomes substantially more diverse and commonplace. Understanding the Permo-Triassic diversification of Diapsida is therefore important for understanding both the origin of all modern reptile groups and impact of the PTE on the taxonomic and morphological diversity of vertebrates.

Classical systematic studies of reptile origins offer only a vague sense of relationships between the major lineages and their ancestry (e.g., Baur, 1887; Watson, 1957; Reig, 1970). The advent of cladistics allowed a repeatable mechanism for generating hypotheses of relationships between the earliest saurian lineages. Perhaps most remarkable is the enormous diversity of bauplans present within these early saurian and near-saurian lineages, including gliders, climbers, specialized herbivores, hypercarnivores, swimmers, and generalists (e.g., Sues and Fraser, 2013). However, no consistent hypothesis has been offered for the relationships among these (e.g., Gauthier, 1984; Benton, 1985; Dilkes, 1998; Müller, 2004; Pritchard et al., 2015). In the absence of such a hypothesis, there is no robust framework for understanding the Permo-Triassic diapsid diversification. Some critical questions include:

1) **What is the distribution of morphological features among early diapsid lineages?** A framework for understanding that distribution is essential for interpreting not only new skeletons, but also fragmentary specimens. Recent faunal analyses based on fragmentary fossils employ an apomorphy-based approach to identifications (e.g., Nesbitt and Stocker, 2008; Bell et al., 2010), and the absence of this framework prevents study of faunas containing members of these Permo-Triassic lineages. This distribution is also critical to understanding the ancestral morphology from which all living reptiles emerged some time in the Permian Period.
2) **How did the diverse bauplans of Permo-Triassic diapsids arise?** Although a great deal of diversity is recognized among early saurian taxa, the morphological transitions upon which those bauplans were derived cannot be understood outside of a phylogenetic context. This sort of understanding requires species-level sampling to interpret the possible timing of such transitions and the diversity within these lineages?
3) **Where do certain highly problematic taxa fall within the Permo-Triassic diapsid diversification?** There is robust consensus regarding the position of some taxa on the stems of Archosauria and Lepidosauria and on the stem of Sauria itself. However, some taxa have yet to be "pinned" to even this basic level within the phylogeny. Such taxa include the climbing drepanosauromorphs, which are known from extremely poorly preserved fossils. Integrating better materials of such a taxon into a robust phylogenetic framework should help create a stronger picture of early diapsid phylogeny.
4) **How does the diversification of Permo-Triassic diapsids and early saurians relate to the PTE?** Most of the incredible diversity of these early diapsids is known from the Triassic Period; only two saurian reptiles are known with certainty from the Permian Period. However, many past hypotheses for early Sauria suggest that many of the diverse lineages have ghost lineages stretching into the Permian Period (e.g., Dilkes, 1998; Nesbitt et al., in press), such that they survived the extinction event. Reducing the uncertainty in this portion of reptile phylogeny is critical to understanding how diapsid diversification, from both a taxonomic and morphological perspective, relates to the environmental tumult of the PTE.

For this dissertation, I have developed a novel phylogenetic data matrix focused on Diapsida known from the Permo-Triassic interval. Characters and taxon-selection has been informed by past cladistic studies (see chapter 6), but I have expanded the degree of species-level sampling from all of the major lineages considered to belong to the early saurian radiation. In nearly all cases, I have studied material from these taxa firsthand to code the original morphological characters and develop new ones. For each of the primary chapters of this dissertation, I seek to describe the morphology of a number of new fossils relevant to the Permo-Triassic diapsid diversification and examine them using a phylogenetic framework as discussed above.

Chapter 2—In this chapter, I describe the morphology of a collection of small vertebrae and limb elements from the Hayden Quarry site in the Chinle Formation of New Mexico (~212 my). My phylogenetic analysis resolves this material as the first strong evidence of Tanystropheidae, a group of very long-necked, lizard like archosauromorphs, from western North America. The material shares many traits with similar fossils from the Upper Triassic of eastern North America, which suggests a previously unrecognized diversification event on the continent.

Chapter 3—I describe new limb material from *Drepanosaurus unguicaudatus*, a small, chameleon-like reptile with an extremely bizarre forelimb construction, also discovered at the Hayden Quarry site. This taxon exhibits an enormously expanded second manual ungual, proximal carpals that are longer than its zeugopodial bones, and non-paralleling radial and ulnar shafts. I examine the patterns of forelimb change in drepanosauromorphs, examining all described specimens, which suggest that this extreme condition derived first from a slight elongation of the carpals and a reduction in manual phalangeal count.

Chapter 4—I examine a new drepanosauromorph skull from the *Coelophysis* Quarry site in New Mexico (~205 my), which is the first such skull known to be preserved in three dimensions. The fragility of the specimen made mechanical preparation impossible, such that I digitally prepared all preserved skull elements using μCT scan data. The new data from the skull strongly suggests that drepanosauromorphs, although they appear in the fossil record late in the Triassic, are distantly related to crown reptiles. They preserve many plesiomorphic cranial features that suggest that their lineage diverged deep in the Permian Period.

Chapter 5—I describe each skull element from the specimen analyzed in chapter 4 in detail. These are compared to a wide range of Permo-Triassic reptile taxa. I employ the morphological insights from this skull to re-assess the morphology of several distorted drepanosauromorph specimens from the Upper Triassic of Europe.

Chapter 6—I present a detailed discussion and description of my phylogenetic data matrix, with detailed descriptions of the fossil material and characters employed. I describe all resultant clades, their relative supports, and comparisons with past phylogenetic hypotheses. I address the implications of this phylogeny on understanding diapsid diversification in a stratigraphic and morphological context.

Chapter 7—This chapter briefly summarizes results from all preceding chapters and suggests future avenues for strengthening our understanding of PT diapsid evolution.

LITERATURE CITED

Baur G. (1887) On the phylogenetic arrangement of the Sauropsida. J Morphology 1:93-104.

Bell CJ, Gauthier JA, Bever GS. (2010) Covert biases, circularity, and apomorphies: a critical look at the American Quaternary herpetofaunal stability hypothesis. Quat Int 217:30–36.

Benton MJ. (1985) Classification and phylogeny of the diapsid reptiles. Zool J Linn Soc 84:97–164.

Benton MJ, Zhang Q, Hu S, Chen Z-Q, Wen W, Liu J, Huang J, Zhou C, Xie T, Tong J, Choo B. (2013) Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. Earth-Sci Rev 125:199–243.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Proc Roy Soc B 353:501–541.

Ezcurra MD, Scheyer TM, Butler RJ. (2014) The origin and early evolution of Sauria: the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS One 9:e89165.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, University of California Berkeley.

Irmis RB, Whiteside JH. (2012) Delayed recovery of non-marine tetrapods after the end-Permian mass extinction tracks global carbon cycle. Proc Roy Soc B 279:1310–1318.

Knoll AH, Bamback RK, Payne JL, Pruss S, Fischer WW. (2007) Paleophysiology and end-Permian mass extinction. Earth * Planet Sci Lett 256:295–313.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Nesbitt SJ, Stocker MR. (2008) The vertebrate assemblage of the Late Triassic Canjilon Quarry (northern New Mexico, USA) and the importance of apomorphy-based assemblage comparisons. J Vert Paleo 28:1063–1072.

Nesbitt SJ, Flynn JJ, Pritchard AC, Parrish JM, Ranivoharimanana L, Wyss A. (in press) Postcranial anatomy and relationships of *Azendohsaurus madagaskarensis*. Bull Am Mus Nat Hist.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2015). Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. Journal of Vertebrate Paleontology 35: e911186.

Reig O. (1967) Archosaurian reptiles: a new hypothesis on their origins. Science 157:565–568.

Reisz RR. (1977) *Petrolacosaurus*, the oldest known diapsid reptile. Science 196:1091–1093.

Sennikov AG. (1988) The role of the oldest thecodonts in vertebrate assemblages of eastern Europe. Paleo Journal 1988:74–82.

Shedlock AM, Edwards SV. (2009) Amniotes (Amniota). The Timetree of Life. SB Hedges, S Kumar (eds.) (Oxford University Press, Oxford), pp. 375–379.

Shen S-Z, Bowring SA. (2015) The end-Permian mass extinction: a still-unexplained catastrophe. Nat Sci Rev 2014:492–495.

Watson DMS. (1957) On *Millerosaurus* and the early history of the sauropsid reptiles. Phil Trans Roy Soc B 240:325–400.

Chapter 2

Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae

ABSTRACT—We report on tanystropheids from the Late Triassic (middle Norian) Hayden Quarry of northern New Mexico (Chinle Formation, Hayden Quarry). These elements, consisting of isolated vertebrae and appendicular bones, represent the first unambiguously identified tanystropheid from western North America and likely the latest occurrence of the group, post-dating *Tanytrachelos* in the Eastern United States. A new phylogenetic analysis of early saurians identifies synapomorphies of tanystropheid subclades, which are recognized in the recovered vertebrae and a calcaneum. The femora are consistent with referral to Tanystropheidae. However, there is no clear association between the remains so we refrain from erecting a new taxon. The analysis also indicates that the Hayden Quarry tanystropheid fossils belong to a newly recognized clade including the Late Triassic taxa *Langobardisaurus* and *Tanytrachelos*. As most tanystropheid specimens are two-dimensionally crushed skeletons, the Hayden Quarry tanystropheid fossils provide valuable insights into the three-dimensional osteology of derived tanystropheids. The most striking feature of the Hayden vertebrae is a rugose, flattened expansion of the neural spines in the dorsal, sacral, and caudal regions, probably linked to a ligamentous bracing system. These fossils and others from Late Triassic sites in the American West suggest that tanystropheids underwent a previously unrecognized radiation in North America just prior to their extinction.

INTRODUCTION

The fossil record of Triassic reptiles in western North America is extensive, with excellent skeletons known from a number of lineages including *Trilophosaurus*, *Doswellia*, phytosaurs, dinosauromorphs, and suchian archosaurs (Gregory, 1945; Long and Murry, 1995; Heckert et al., 2012). This record is strongly biased in favor of large animals (> 5–10 kg), with the most noted exception being numerous mid-sized skeletons from the *Coelophysis* Quarry of Ghost Ranch in New Mexico (Schwartz and Gillette, 1994; Harris and Downs, 2002; Nesbitt et al., 2009a) and other isolated finds (e.g., Berman and Reisz, 1992; Fraser et al., 2005).

Small reptile fossils are found in many western North American sites, but these are often limited to isolated elements, rendering taxonomic identifications difficult (e.g., Murry, 1987, 1989; Kaye and Padian, 1994; Heckert, 2004; Irmis, 2005; Renesto et al., 2009). Reanalyses of isolated remains employing apomorphy-based criteria, revealed a wider range of small reptiles, including drepanosaurs (Renesto et al., 2009; Martz et al., 2013) and dinosauromorphs (Nesbitt and Chatterjee, 2008; Nesbitt and Stocker, 2008; Nesbitt et al., 2009b).

New data on small reptiles come from localities with higher preservation potential for small elements, including the Hayden Quarry (HQ) in the upper Chinle Formation of northern New Mexico. Located near the *Coelophysis*, Canjilon, and Snyder quarries (Downs, 2005; Irmis et al., 2007), the HQ has yielded over 15,000 vertebrate fossils, including small reptiles (Irmis et al., 2007; Nesbitt et al., 2009b; Pritchard et al., 2012).

Here we report new small-bodied archosauromorph reptile material from HQ consisting of isolated vertebrae, femora, and a calcaneum. The vertebrae and calcaneum possess numerous apomorphies of the long-necked archosauromorph group Tanystropheidae. The femora, though lacking clear tanystropheid apomorphies, are likely referable to the clade based on a combination of features. The three-dimensional preservation of these fossils provides valuable insights on the morphology of tanystropheids.

Institutional Abbreviations—AMNH FARB, American Museum of Natural History, New York, New York, U.S.A.; **BP**, Bernard Price Institute for Paleontological Research, Johannesburg, South Africa; **GMPKU**, Geological Museum of Peking University, Beijing, China; **GR**, Ruth Hall Museum of Paleontology, Ghost Ranch, Abiquiu, New Mexico, U.S.A.; **MCSN**, Museo Civico di Storia Naturale, Milano, Italy; **MCSNB**, Museo Civico di Scienze Naturale Enrico Caffi, Bergamo, Italy; **MFSN**, Museo Friulano di Storia Naturale, Udine, Italy; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona; **NHMUK R**, Natural History Museum of the United Kingdom, London, U.K.; **NMQR**, National Museum, Bloemfontein, South Africa; **TMM**, Texas Memorial Museum, Austin, Teas, U.S.A.; **VMNH**, Virginia Museum of Natural History, Martinsville, Virginia, U.S.A.; **YPM**, **YPM PU**, Princeton University Collections, Yale Peabody Museum of Natural History, New Haven, Connecticut, U.S.A..

MATERIALS AND METHODS

Geological Context

The Petrified Forest Member of the upper Chinle Formation, as it outcrops in the Chama Basin of northern New Mexico (Fig. 1), is characterized locally by an abundance of paleochannels and associated levee deposits (Dubiel, 1989; Irmis et al., 2007). These outcrops consist of variegated mudstones, siltstones, and sandstones that frequently preserve fossil vertebrates and include three major localities: the Canjilon; Snyder; and Hayden quarries (Irmis et al., 2007). The HQ preserves a diverse assemblage of dinosauromorphs, pseudosuchians, and small-bodied diapsids (Irmis et al., 2007; Nesbitt et al., 2009b; Pritchard et al., 2012). The HQ consists of three closely associated paleochannels spaced over 12 meters of section near the base of the Petrified Forest Member (Irmis et al., 2007, 2011). In stratigraphic order, these sites are referred to as H4, H2, and H3 (the numbering of the channels follows the order of discovery, not stratigraphy). Radioisotopic work yielded a detrital zircon CA-TIMS $^{238}U/^{206}Pb$ age of 211.9 +/- 0.7 Ma from the bone-bearing level of the H2 paleochannel, which is a maximum age constraint for this level and strata above it (i.e., H3; Irmis et al., 2011). This indicates a middle Norian age for the locality, which is consistent with data from palynomorph and vertebrate biostratigraphy (Irmis et al., 2011). Vertebrae assignable to Tanystropheidae and the femora assignable to Archosauromorpha occur in all three HQ paleochannels. The tanystropheid calcaneum is from H4. For details on fossil preparation, see Appendix 1S (Supplementary Data).

Notes on Specimen Referrals—None of the material is unambiguously associated, and thus cannot be definitively assigned to a single individual. We refrain from establishing a new taxon, considering the possibility that these elements could belong to more than one closely related species. Apomorphies were derived from the phylogenetic analysis, and clade diagnoses are discussed below. Although synapomorphies of Tanystropheidae and included subclades are recognized, we identify no autapomorphies or a unique combination of characters that would allow erection of a new species. The calcaneum exhibits newly recognized apomorphies of *Tanytrachelos ahynis* although the HQ specimen is substantially larger in size than known specimens attributed to the species. Pending the recognition of these calcaneal apomorphies in a higher taxon, the calcaneum is referred to *Tanyt. ahynis*.

Three-dimensional morphological data on *Tanyt. ahynis* has largely been derived from AMNH FARB 7206, a partial tanystropheid skeleton from the Lockatong Formation of New Jersey. Olsen (1979) noted similarities between this specimen and *Tanyt. ahynis*, but he did not make a conclusive referral. The tanystropheid material exhibits a combination of characters only known in *Tanyt. ahynis* (e.g., unicuspid teeth, procoelous vertebrae, elongate caudal transverse processes) and one autapomorphy known in *Tanyt. ahynis* (robust cervical ribs, proximodistally broader than anteroposteriorly long). Pending a thorough taxonomic revision of tanystropheids from eastern North America, we consider AMNH FARB 7206 referable to *Tanyt. ahynis*.

Notes on comparisons—Unless otherwise noted, references to other reptile taxa are based on the following: *Czatkowiella harae* (see Borsuk-Bialynicka and Evans, 2009); *Langobardisaurus pandolfii* (MCSNB 2883); *Macrocnemus bassanii* (MCSN V 457); *Mesosuchus browni* (see Dilkes, 1998); *Petrolacosaurus kansensis* (see Reisz, 1981); *Prolacerta broomi* (BPI 2675); *Proterosuchus fergusi* (NMQR 1484); *Protorosaurus speneri* (see Gottmann-Quesada and Sander, 2009); *Tanyt. ahynis* (see Olsen, 1979); and *Trilophosaurus buettneri* (TMM 31025-140). Information derived from other sources or specimens are noted separately. Comparisons for *Tanystropheus longobardicus* are largely based on MCSN BES SC 1018, an exquisitely preserved skeleton from Monte San Giorgio, Italy. The specimen was described as a juvenile *Tanys. longobardicus* (see Nosotti, 2007) and is comparable to small *Tanys.* specimens described as juveniles by Wild (1973). However, there are some questions as to whether these small specimens actually represent juveniles of *Tanys. longobardicus* or a separate species (Fraser et al., 2004). We accept the synonymy of *Langobardisaurus pandolfii* and *L. tonelloi* as suggested by Saller et al. (2013).

SYSTEMATIC PALEONTOLOGY

DIAPSIDA
SAURIA
ARCHOSAUROMORPHA
TANYSTROPHEIDAE Gervais, 1859
(Figs. 2, 4–7)

Referred Specimens—GR nos. 266–269, partial cervical vertebrae; GR nos. 273–279, partial dorsal vertebrae; GR nos. 308, 309, partial second sacral vertebrae; GR nos. 280–284, 310, 357, 358, partial anterior caudal vertebrae; GR nos. 285–298, 311, partial mid/posterior caudal vertebrae.

Locality—H2, H3, and H4 paleochannels, Hayden Quarry, Petrified Forest Member of the Chinle Formation, Rio Arriba County, New Mexico, U.S.A.

Age and Distribution—Approximately 212 Ma, middle Norian Stage of the Late Triassic (Irmis et al., 2011; see Geologic Context for more detail).

Cervical Vertebrae—All HQ cervical vertebrae assigned to Tanystropheidae share diagnostic features (Fig. 2): the centra are elongate (~5 times anteroposteriorly longer than dorsoventrally tall) with a planar ventral surface and ventromedian keel, the cotyles and condyles are dorsoventrally compressed with a dorsally concave crescent shape in anterior and posterior views, the posterior condyle is strongly convex, the cervical neural spine is dorsoventrally short with an anterior process that overhangs the prezygapophyses, there is a midline cleft in the dorsum of the neural spine, and the postzygapophyses exhibit short epipophyses (pointed processes that project posterodorsally beyond the postzygapophyses).

The low, elongate neural arch is only complete in one cervical vertebra (GR 269). The neural spine is dorsoventrally short and extends nearly the whole length of the neural arch (Fig. 2A). It is anteriorly notched, a consequence of a slender anterodorsal process that extends anterior to the cotyle. The entire dorsal margin of the spine is marked by a deep groove (Fig. 2B, D). Posteriorly, the neural spine terminates anterior to the postzygapophyses.

Laterally, a prominent interzygapophyseal lamina extends posteroventrally for one-quarter the length of the vertebra before curving anterodorsally to reach the postzygapophysis. In lateral view the postzygapophyses are elevated dorsally above the level of the prezygapophyses (Fig. 2A). Posteriorly, each postzygapophyseal facet is canted about 45° above horizontal. Pointed epipophyses are present, although they barely extend posteriorly beyond the postzygapophyses. A thin flange of bone connects the postzygapophyses immediately anterior to the facets (Fig. 2E). There is no postzygapophyseal trough, which is a webbing joining the postzygapophyses dorsal to the neural canal in certain *Tanystropheus* species (Rieppel, 2001).

The pedicles are transversely narrow, projecting dorsally from the dorsolateral surface of the centrum. The pedicle terminates well anterior to the condyle. In anterior view, the neural canal forms a transversely broad oval. Each prezygapophysis is canted 45° from horizontal. An elliptical pit is situated between both the pre- and postzygapophyses, just dorsal to the neural canal, presumably for attachment of the interspinous ligament (Fig. 2D–E).

The centrum is dorsoventrally compressed, anteroposteriorly elongate, and transversely waisted near its anteroposterior midpoints (Fig. 2C). The diapophyseal and parapophyseal articulations are quite small (~2 mm) relative to the pedicles, and both surfaces are nearly confluent with the ventrolateral cotylar border. Sharp ridges extend posteriorly from both the diapophysis and the parapophysis (Fig. 2A), extending posteriorly less than one-quarter the length of the centrum.

The ventral surface of the centrum is flat in a transverse plane (Fig. 2C). Postparapophyseal ridges define the anterolateral margins of the ventral surface. The transversely slender, midline keel arcs dorsally near the anteroposterior midpoint of the vertebra. The keels range from prominent and sharp crests (GR 267) to extremely subtle ridges (e.g., GR 266 and GR 269), although it is unclear if individual, serial, or taxonomic variation explains this variation. Centra are not beveled ventrally, suggesting the absence of intercentra.

Comparisons—Several features of the HQ cervical vertebrae suggest archosauromorph affinities. The dichocephalous, ventrally positioned cervical rib facets are shared with archosauromorphs (e.g., *Protoro. speneri*; *Czatkowiella harae*; and *Prolacerta broomi*). This feature seems to correlate with the elongate cervical ribs that parallel the cervical column. Anteroventrally positioned rib facets and cervical vertebrae with a high length/height ratio also occur in the long-necked diapsid *Araeoscelis* (MCZ 4380). The keel on the ventral surface of the centrum is widespread among diapsid reptiles (Gow, 1975; Evans, 1981; Gower, 2003).

The short epipophyses in the HQ cervical vertebrae and several other early archosauromorphs are similar to those in *Tanytrachelos* (AMNH FARB 7206), *Prol. broomi*, and *Mesosuchus browni*. Stronger cervical epipophyses projecting well posterior to the postzygapophyseal facets are evident in *Malerisaurus langstoni* (TMM 31099-11), *Tanystropheus longobardicus* (see Wild, 1973), and *Trilophosaurus buettneri*.

The HQ cervical vertebrae share an anterodorsal process on the neural spine with *Langobardisaurus pandolfii*, *Mac. bassanii* (MCSN BES SC 111), *Tanys. conspicuus* (see Wild, 1973), and *Tanys. longobardicus*. The flattened ventral surface of the centrum is more difficult to assess, due to crushed specimens; however, the feature is evident in *Tanys. longobardicus* (see Dalla Vecchia, 2005) and *Tanyt. ahynis* (AMNH FARB 7206, VMNH 120042).

A small subset of long-necked, early archosauromorphs share additional features with the HQ cervical vertebrae. Strongly convex, procoelous centra are present in *L. pandolfii* (MCSNB 4860, MFSN 1921), and *Tanyt. ahynis* (AMNH FARB 7206, Fig. 3). Procoely with a weak posterior convexity occurs in *Tr. buettneri*. Both *Tanyt. ahynis* and *L. pandolfii* exhibit compressed cervical centra as in the HQ vertebrae.

Dorsal Vertebrae—All HQ dorsal vertebrae attributed to Tanystropheidae share a suite of diagnostic features (Fig. 4): procoely with an expansive ball-like posterior condyle, a laterally rounded interzygapophyseal ridge, and an elliptical, deeply grooved neural spine expansion.

The neural arches are tall and robust with transversely broad pedicles. The prezygapophyses are inclined at a 45° angle. A thick, laterally rounded interzygapophyseal ridge extends posteroventrally from the prezygapophysis (Fig. 4A, B). This ridge is interrupted by the diapophyseal or compound synapophyseal facet as it passes posteroventrally for one-quarter the length of the vertebra before curving posterodorsally towards the postzygapophyses. A substantial, buttress-like spinopostzygapophyseal lamina connects the dorsum of the postzygapophysis to the posterolateral margin of the neural spine.

The base of the neural spine is transversely broad. Moving dorsally it expands anteroposteriorly and transversely to form an anteroposteriorly elongate, elliptical spinous expansion (Fig. 4C, D). The transverse width of the spinous expansions is variable, but any correlation with vertebral position requires additional articulated remains. The dorsum of the spinous expansion is marked by irregular transversely oriented ridges that border deep troughs. The ridges anastomose sporadically, but remain consistently oriented transversely. The ridges are tall enough that the dorsum of the neural spine appears rugose in lateral view.

The subcircular cotyle is concave with an anteroventral inclination. The similarly shaped condyle is correspondingly convex with a posterodorsal inclination. There is no ventral beveling of the intervertebral articulations that might suggest the presence of intercentra in the dorsal column. Neither the diapophyses nor the parapophyses are confluent with the cotyle (Fig. 4C).

Variability in the morphology of the rib is interpreted as serial variation within the dorsal column. Certain HQ specimens exhibit both a diapophysis and a parapophysis, with the larger diapophysis positioned dorsal to the parapophysis (GR 274, GR 279). The diapophysis is situated just posterior to the prezygapophysis within the interzygapophyseal ridge, whereas the parapophysis is positioned on a shorter stalk at the dorsolateral margin of the cotyle. Other specimens exhibit a single costal facet (e.g., GR 277) that is roughly circular with a slight ventral extension. These morphologies indicates that the former are anterior trunk vertebrae, as most reptiles with dichocephalous trunk rib facets exhibit a greater inter-facet distance anteriorly with increasing confluence of the facets further posteriorly (e.g., Gregory, 1945; Hughes, 1963). Certain archosauromorphs (e.g., *Proterosuchus*), however, exhibit conjoined facets further anteriorly within the column than in other archosauriforms (e.g., erythrosuchids; Hughes, 1963). HQ dorsal vertebrae with preserved costal facets exhibit a lamina (or laminae) that extend(s) from the dorsoventral midpoint of the cotyle to the synapophysis (GR 277, GR 278).

The ventral surface of the centrum is rounded in all the dorsal vertebrae. A ventral keel is not evident (Fig. 4A, B). Anterior trunk vertebrae are transversely waisted near the anteroposterior midpoint of the centrum, whereas posterior trunk vertebrae exhibit less waisting.

Comparisons—Various features suggest tanystropheid affinities for the dorsal vertebrae. The shape and proportions of the centra and neural spines are more consistent with Triassic archosauromorphs, which tend to exhibit substantially higher centrum height/length ratios (Peyer, 1937; Gregory, 1945) than do lepidosauromorphs (e.g., Hoffstetter and Gasc, 1969; Evans, 1981) and early diapsids (e.g., Currie, 1981).

As a massive spinous expansion is the most salient feature of the HQ dorsal vertebrae and is widespread in Archosauromorpha, the diversity and phylogenetic distribution of expansions of neural spine tips will be discussed further (see DISCUSSION). The spinous expansions in the HQ specimens are most similar to those of a probable juvenile specimen of *Tanys. longobardicus* (MCSN BES SC 265), which exhibits similar shape and dorsal texturing. Spinous expansions with transverse crests are also present in *Tanytrachelos*. (VMNH 120019, YPM PU 8600). The dorsal vertebrae of *Gwyneddosaurus* (identified as anterior cervical vertebrae by von Huene, 1948), which is likely referable to *Tanyt. ahynis* (hypothesized by Olsen, 1979) were described by Bock (1945:2) as having a "boat-like outline with a straight dorsal margin," similar to the HQ vertebrae. Two specimens of *L. pandolfii* and the Austrian *Langobardisaurus* are preserved belly-up (Saller et al., 2013) and the column in MFSN 1921 is crushed, obscuring neural spines in the taxon

Sacral Vertebrae—Two second sacral vertebrae are recognized from HQ (GR 308, GR 309). GR 308 resembles second sacral vertebrae in many reptiles (Hoffstetter and Gasc, 1969; see below), exhibiting the anterolateral orientation of the single preserved rib and a facet on the anterior surface of that rib (Fig. 5). GR 309 is referred based on a similar centrum shape.

The neural arch is highly distinctive. The prezygapophyses are close set, sitting at the anterodorsal corner of the vertebral foramen. There is a distinct interspinous fossa medial to the zygapophyses. In anterior view, the interspinous fossa is trapezoidal with a tapered dorsal margin. The postzygapophyses are separated by a small interspinous fossa, much like the prezygapophyses (GR 309) (Fig. 5A). Spinopostzygapophyseal laminae extend from the posterior margins of the postzygapophyses to the posterior surface of the neural spine (Fig. 5B).

The neural spine is extremely slender at its base anteriorly, widening slightly posteriorly (Fig. 5C). At its dorsal tip, the neural spine expands transversely to approximately three times its basal width, forming a transverse expansion of the neural spine tip as in the dorsal vertebrae. The anterodorsal and posterior margins of the spine are eroded. The dorsolateral margins of the neural spine tip bear dorsoventral striations, suggesting a rugose dorsum for the neural spine.

In anterior view, the dorsal and ventral margins of both anterior and posterior articular surfaces are horizontal, whereas the lateral margins are strongly convex. The neural canal is rectangular, being transversely broader than tall (Fig. 5A). The sacral ribs are large with dorsoventrally tall bases subequal in height to the cotyle. In anterior view, the ventral margin of the rib is at the midpoint of the cotyle, whereas the dorsal margin sits at the midpoint of the neural canal (Fig. 5A, C).

Ventrally, the centrum is marked by a stout keel that tapers at its anteroposterior midpoint (Fig. 5D). The anterior and posterior portions of the keel are roughly half as broad transversely as the cotyle and condyle. The middle portion of the keel is tapered to roughly one-third that width. The keel is laterally marked by anteroposteriorly oriented striations.

The sacral ribs expand laterally, increasing in dorsoventral height (Fig. 5A, C). The dorsal margin is horizontal and the ventral margin angles strongly ventrolaterally in anterior view. The lateral articular facets for the ilium are eroded. A distinct facet marks the anterodorsal margin of the lateral tip of the rib, presumably for articulation with the first sacral rib. Posterodorsally, the sacral rib has a slender, posteriorly projecting lamina, which is eroded in the only specimen preserving a sacral rib (GR 308) (Fig. 5C). A subtler lamina extends from the dorsomedial margin of the sacral rib to the anteroposterior midpoint of the larger posterodorsal lamina. An additional lamina extends from near the anteroposterior midpoint of the posterodorsal lamina to reach the lateral margin of the postzygapophysis.

Comparisons—The single sacral vertebra preserving a sacral rib (GR 308) exhibits features that suggest it belongs to the same taxon or a similar taxon to the HQ tanystropheid; a procoelous centrum with a ball-like condyle and an elliptical spinous expansion at the neural spine apex. The elongated rib with a stout articular facet laterally supports its identification as a sacral, and the strong anterolateral inclination of the rib compares favorably with the condition in the second sacral vertebrae of many early archosauromorphs (e.g., Gregory, 1945; Nosotti, 2007). GR 309 is a vertebra missing its neural spine, prezygapophyses, and the posterior half of the centrum. Large broken surfaces dorsolateral to the cotyle suggest the bases of sacral ribs, and the proportions of the vertebra compare well with GR 308.

The distinct sacral ribs resemble the second sacral ribs of *Sphenodon* in being anteroposteriorly short and dorsoventrally tall distally (Hoffstetter and Gasc, 1969). The second sacral vertebrae in *Tanys. longobardicus* (MCSN BES SC 265) and *Tr. buettneri* have sacral ribs that expand dorsoventrally at their distal ends and exhibit a thin flange posterodorsally. There is a posterior accessory process on the second sacral rib in *Me. browni*, all tanystropheids except *Tanyt. ahynis*, *Prol. broomi*, and certain lepidosaurs (e.g., *Agama*; Hoffstetter and Gasc, 1969; and *Clevosaurus hudsoni*; Fraser, 1988). The dorsoventral expansion of the rib laterally is substantial, similar to that in *Mac. bassanii* (MCSN BES SC 111), *Tanys. longobardicus* (MCSN BES SC 265; Wild, 1973) and *Tr. buettneri*. Some other archosauromorphs exhibit ribs that are dorsoventrally tall medially (e.g., rhynchosaurs; Benton, 1990; *Erythrosuchus*; Gower, 2003).

The presence of a ventral keel on the sacral centra is shared with *Mac. bassanii*, *Tanys. longobardicus* (MCSN BES SC 265), *Tr. buettneri*, and certain lepidosaurs (e.g., Hoffstetter and Gasc, 1969). Among archosauromorphs, only *Tanystropheus* (MCSN BES SC 265; Wild, 1973) clearly possesses a dorsal expansion of the sacral neural spine. The morphology of the sacral spines is unclear in *Tanytrachelos ahynis* and *Langobardisaurus pandolfii*.

Caudal Vertebrae—The caudal vertebrae from HQ attributed to Tanystropheidae have a hemispherical posterior condyle and small chevron articulations. Two distinct vertebral morphologies are recognized, which we interpret to represent serial variation.

In the anterior caudal vertebrae, the neural arches are highly distinct. Anteroposteriorly elongate transverse processes arise from the neural arch near the base of the pedicles (Fig. 6A–C). Each process is dorsoventrally flattened and anteroposteriorly long, ranging between one-half and one-third the length of the centrum. No anterior caudal vertebrae preserve a complete transverse process, so there is no indication of their transverse width or distal shape.

The prezygapophyses project anterolaterally, in line with the angling of the cotyle and pedicle margin. A thin plate of bone extends between the facets. A thickened interzygapophyseal lamina sits between pre- and postzygapophyses. The postzygapophyses greatly overhang the vertebral condyle, and are closely appressed (Fig. 6C). The facets are angled ventrolaterally. An ovoid interspinous ligament pit sits dorsal to the neural canal both anteriorly and posteriorly. A spinous expansion occurs in the anterior caudal region. It is elliptical, transversely more slender than in the dorsal region, and marked by thicker margins (Fig. 6A). In certain specimens (e.g., GR 357), the expansion of the spine is strongly canted anteroventrally.

Specimens interpreted as anterior caudal vertebrae have a distinct angling of the primary articular surfaces (Fig. 6) similar to the condition in the trunk region. The anterior cotyle faces anteroventrally, with the dorsal margin exceeding the plane of the ventral margin (Fig. 6A). The posterior condyle is correspondingly angled. Cotyles and condyles are subcircular and similar in size. The cotyle exhibits a very thin margin. Bilateral articulations for the chevron bones are positioned at the ventrolateral margins of the spherical condyles. Each of the roughly circular chevron articular surfaces is oriented posteroventrally. Anteroposteriorly short, thick paramedian ridges extend anteriorly from each facet.

The vertebra undergoes a substantial tapering at its anteroposterior midpoint, resulting in an hourglass shape in ventral view (Fig. 6B). The vertebra possesses a sharp keel that does not intersect with the paramedian ridges that extend anteriorly from the chevron facets. The tapering of the centrum results in strongly recessed lateral surfaces. The anterior and posterior margins of the pedicles are inclined anterodorsally, paralleling the inclination of the cotyles and condyles. A thickened lamina extends anterodorsally from the condyle to the transverse process.

In the specimens interpreted as posterior caudal vertebrae, the neural arches exhibit only tiny transverse processes. The interzygapophyseal ridge is weak and medially placed (Fig. 7A). The postzygapophyses are closely appressed, and slender spinopostzygapophyseal laminae extend directly ventrally from the ventrolateral margins of the neural spine (Fig. 7B). Ovoid interspinous ligament pits sit dorsal to the neural canal.

The neural spine is elongate, extending the entire length of the neural arch. It is transversely narrow throughout much of its dorsoventral height, before broadening dorsally into a spinous expansion (Fig. 7E). In certain vertebrae, the spines are tall, nearly the height of the rest of the vertebra (GR 294). In others, the spines are significantly shorter, forming less than one-third of the height of the vertebra (e.g., GR 285, GR 295) (Fig. 7C). It is likely that the spines were proportionally taller anteriorly within the caudal vertebral column, decreasing in height posteriorly as is evident in *Tanystropheus* (MCSN BES SC 265).

The spinous expansion in posterior caudal vertebrae is proportionally longer and narrower than in dorsal and anterior caudal regions. The spine is expanded anteroposteriorly relative to its base, overhanging the postzygapophyses posteriorly. There is variation in the dimensions of these expansions, with narrower tables occurring farther posteriorly in the column, but limited material makes further comparisons difficult. The outer margin of the spine tip is marked by tiny, inwardly facing striations. Internally, the spinous expansion exhibits thick, anastomosing ridges; there is no consistent transverse orientation of the ridges as observed in dorsal vertebrae.

In posterior caudal vertebrae, the centra are proportionally longer than in the anterior caudal vertebrae (Fig. 7A, C). The centra have parallel lateral margins, with no sign of transverse tapering. The ventromedian keel is absent, but bilateral ridges extend the length of the ventral surface of the centrum (Fig. 7D). These ridges appear to represent expansions of the laminae that originate at the chevron facets in anterior caudal vertebrae. Posterior caudal vertebrae exhibit cotyles and condyles that are oriented perpendicular to the long-axis of the centrum (Fig. 7A).

Comparisons—The anterior caudal vertebrae from the HQ tanystropheids are more incomplete than those from other regions in the vertebral column. Anteroposteriorly elongate bases for caudal transverse processes are similar to many early archosauromorphs (e.g., *Prol. broomi*; *Tanys. longobardicus*). The neural spines of the mid- and posterior caudal vertebrae exhibit expanded neural spine tips similar to those in several archosauromorph taxa including *Tanys. longobardicus* (MCSN BES SC 265) and *Tanyt. ahynis* (YPM PU 23082). The caudal neural spines of *L. pandolfii* are distinct in shape (MFSN 1921), with posterodorsally inclined anterior margins and an absence of spine tables.

The chevron facets in the HQ caudal vertebrae are small and distinctly offset from one another, a feature in *L. pandolfii* and *Tanys. longobardicus* (MCSN BES SC 265). This trait is correlated with loss of the intercentral portion of the chevron, leaving two strongly offset ‘pedicles’ that articulate to a caudal vertebra (Hoffstetter and Gasc, 1969; Merck, 1997). The paramedian ventral ridges resemble the condition in *L. pandolfii* and *Tanys. longobardicus*.

ARCHOSAUROMORPHA

(Figs. 8, 9)

Referred Specimens— GR nos. 299–305, 312, femora.

Age and Distribution—Approximately 212 Ma, middle Norian Stage of the Late Triassic (Irmis et al., 2011; see Geologic Context for more detail).

Femora—Femora from HQ exhibit a suite of features suggesting an affinity with the vertebral material described above (Fig. 8). The size (5.3–8.0 cm in length; fig. 9) and morphology of the HQ femora do not preclude referral to the same tanystropheid taxon (or taxa) evinced by the vertebral elements. Employing strict apomorphy-based rules for referral (e.g., Bell et al., 2004; Nesbitt and Stocker, 2008), we refer the HQ femora discussed here to Archosauromorpha. A single possible apomorphy is shared with derived tanystropheids (straight proximal femoral shaft with limited sigmoid curvature). Examined in a preaxial or postaxial perspective, the femur is almost straight. It tapers strongly distally from its broad proximal head (Figs. 8A, B; 9). In mediolateral profile, the femoral shaft downturns ventrally just proximal to the distal condyles.

The proximal end of the bone is weakly ossified, resembling squamate femora with the proximal epiphysis removed (Haines, 1969). The proximal surface is concave with a distinct, dorsoventral groove extending dorsoventrally. The bone surrounding the proximal groove is unfinished, distinct from the smooth, cortical bone of the femoral shaft (Fig. 8F). The groove is broader in small specimens, suggesting that the unfinished bone ossified more as size increased.

Two primary crests project from the femoral shaft near the proximal end. The thicker crest, interpreted as the internal trochanter (as in lepidosaurs per Hutchinson, 2001; Russell and Bauer, 2008; and early archosauromorphs per Gower, 2003; Gregory, 1945), extends along the medial (preaxial) aspect of the femur and reaches the proximal end (Fig. 8A, D, F). It tapers distally along its length before becoming indistinct from the femoral shaft. It remains distinct for approximately one-third the length of the shaft in small individuals (e.g., GR 299) and nearly one-half the length of the shaft in larger individuals (e.g., GR 301).

A thin crest along the lateral (postaxial) margin of the femur corresponds to the posterior trochanter (sensu Romer, 1956) (Fig. 8A, D, F). The two trochanters border a small but distinct intertrochanteric fossa on the ventral aspect of the femur (Fig. 8A, D). Well-defined striations within the fossa represent an attachment site for an extensive m. puboischiofemoralis externus

(Snyder, 1954; Romer, 1956) proximally and m. iliofemoralis further distally (Snyder, 1954; Hutchinson, 2001). Two small foramina pierce the proximal end of the fossa.

The posterior trochanter exhibits substantial variation. In GR 299 and GR 304 the crest is broad proximally, although it remains only half as wide as the internal trochanter. In GR 301 and GR 305 this crest is extremely narrow, appearing distinctly ‘pinched’ proximally. In all specimens the crest is substantially shorter than the internal trochanter, extending only one-quarter the proximal length of the femoral shaft.

Proximally, the medial (preaxial) surface of the bone is weakly rounded. This surface exhibits long proximodistally-oriented striations (Fig. 8B). There is a subtle but distinct oblique muscle scar one-fifth of the way down the femoral shaft, which may correspond to an insertion of m. puboischiofemoralis internus (Snyder, 1954; Romer, 1956; Hutchinson, 2001).

The lateral (postaxial) surface of the proximal end of the femur forms a flat surface bordered ventrally by the posterior trochanter and dorsally by a sharp angle that demarcates the proximolateral and proximodorsal faces of the femur (Fig. 8A, C). Like the internal and posterior trochanters, this proximolateral ridge arises from the unfinished femoral head and extends distally. The ridge is short, extending less than one-sixth the length of the femur. A crescentic muscle scar characterized by a zone of unfinished and weakly rugose bone interrupts the ridge distally. The scar, and likely the ridge, corresponds to the attachment of m. ischiotrochantericus in early reptiles and saurians (Snyder, 1954; Romer, 1956; Hutchinson, 2001).

The femur tapers substantially along its length. The cross-section of the bone becomes roughly circular near the point where the bone curves ventrally. After turning ventrodistally the femur broadens proximal to the distal condyles (Fig. 8E). A subtle raised margin on the posteromedial margin of the femoral shaft may represent an adductor ridge. The distal end of the femur is marked by two distinct tibial condyles and a fibular condyle. A well-developed mediolateral (preaxial-postaxial) expansion divides the condyles from the femoral shaft. A dorsoventral expansion of the condyles themselves projects them beyond the ventral limit of the femoral shaft. The condyles appear more coarsely textured than the shaft. The two large condyles, which articulate to the tibia, include a medial (preaxial) and lateral (postaxial) condyle. The well-defined lateral crest is a small fibular condyle. This terminology, “medial tibial condyle”, “lateral tibial condyle”, and “fibular condyle”, conforms most closely to terminology used in squamates and is closest to the plesiomorphic condition for saurian reptiles (e.g., Fraser, 1988; Conrad, 2006). The lateral tibial condyle is homologous to the crista tibiofibularis in archosaurs, based on the identical position of the latter relative to the fibular and lateral condyles (compare with distal femora illustrated in Figure 7 of Nesbitt, 2011).

The lateral tibial condyle is largest, expanding beyond the axis of the femoral shaft, and projects considerably farther distally than the medial tibial condyle (Fig. 8D). A small fibular condyle sits on the dorsolateral surface of the lateral tibial condyle (Fig. 8E). The fibular condyle projects beyond the lateral border of the lateral tibial condyle; it is thus shelf-like with a flat ventral surface that forms a right angle (when viewed in distal aspect) with the lateral tibial condyle. A shallow triangular fossa is formed between the proximoventral edge of the fibular condyle and a low ridge extending proximally from the proximal tip of the lateral tibial condyle. The distal portion of the medial tibial condyle is smoothly rounded in distal view.

Comparisons—Many characters of the HQ femora suggest affinities with early archosauromorphs. Weakly ossified proximal articular heads roughly continuous with the femoral shaft are present in early archosauromorphs (e.g., *Prolacerta*, *Trilophosaurus*). Other diapsid reptiles exhibit femora with prominently convex and rounded proximal femora, including araeoscelids (Reisz, 1981; Reisz et al., 1984), kuehneosaurids (*Kuehneosaurus latus*, AMNH FARB 7776), and drepanosaurids (*Vallesaurus cenensis*, MCSNB 4751).

The transition from the plesiomorphic ‘ventral ridge system’ (Romer, 1956) of proximal trochanters, including an internal trochanter and a posterior trochanter (e.g., *Erythrosuchus africanus*, NHMUK R 3592; *Tr. buettneri*), to the archosaur condition of a large ‘fourth trochanter’ and extensive greater trochanter (e.g., *Alligator*; Hutchinson, 2001; dinosaurs; Nesbitt et al., 2009b) occurred within Archosauriformes (Hutchinson, 2001; Nesbitt, 2011).

The HQ femora possess an internal trochanter but lack a fourth trochanter suggesting that they pertain to a taxon outside of Archosauriformes. The internal trochanter is well developed, projecting from the ventral margin of the weakly ossified proximal end of the femur. This condition is present in early archosauromorphs, including tanystropheids (e.g., *Mac. bassanii* and *Tanys. longobardicus*). An internal trochanter that does not reach the proximal surface of the femur is evident in rhynchosaurs (e.g., Benton, 1990), *Prote. fergusi* (see Cruickshank, 1972), and, per Gower (2003), *E. africanus* (NHMUK R 3592).

The curvature of the femoral shaft is subtly sigmoidal, but less pronounced than the curvature in most tanystropheids (e.g., *Mac. bassanii*, *Tanys. longobardicus*) and *Tr. buettneri*

(TMM 31025-67). It is similar, but not as straightened as in the curiously straight femoral shafts observed in *L. pandolfii* (MCSNB 4860, MFSN 1921) and *Tanyt. ahynis* (VMNH 120049).

The smooth distal roundness of the medial tibial condyle in the HQ femora is unlike most early archosauriforms, which possess a medially tapering distal end to the medial tibial condyle (Nesbitt, 2011). The articular surfaces of the medial and lateral tibial condyles are continuous on the distal articular surface as in most early archosauriforms (Nesbitt, 2011). The ventral projection of the two condyles frames a shallow popliteal fossa posteriorly. This shallow fossa is unlike the groove that separates the medial and lateral tibial condyles in many archosaurs, such as *Protosuchus* (Nesbitt, 2011).

The accentuation of the fibular condyle is shared with other archosauromorphs (*Prol. broomi* and *Tr. buettneri*), and squamates (e.g., Conrad, 2006). The fibular condyle in most non-archosauriform archosauromorphs is thickened, covering much of the lateral surface of the lateral condyle (e.g., *Tr. buettneri*, TMM 31025-787; *Mal. langstoni*, TMM 31099-11), contrasting with the small and dorsally recessed condyle in the HQ femora. Similarly developed fibular condyles are evident in *Kuehneosaurus* (AMNH FARB 7776). Wild (1973) figured large femora referred to *Tanys. conspicuus* that exhibit a fibular condyle more similar to that in *Tri. buettneri* and *Prote. fergusi* than to the HQ femora.

ARCHOSAUROMORPHA

TANYSTROPHEIDAE Gervais, 1859

TANYTRACHELOS Olsen, 1979

TANYTRACHELOS AHYNIS Olsen, 1979

(Fig. 10)

Referred Specimens— GR 306, isolated calcaneum.

Age and Distribution—Approximately 212 Ma, middle Norian Stage of the Late Triassic (Irmis et al., 2011; see Geologic Context for more detail).

Calcaneum—A left calcaneum (Fig. 10) is consistent with belonging to a non-archosauriform archosauromorph, although it exhibits apomorphic conditions previously unreported in Triassic reptiles. In light of the semi-sprawling gait of early archosauromorphs, the description that follows uses the terms medial and lateral to describe the faces of the bone that are directed medially and laterally in a stationary, sprawling position. Preaxial and postaxial are used to describe the faces of the bone that are directed anteriorly and posteriorly in a stationary, sprawling position. Lateral curling of the calcaneal tuber and the extreme breadth of the distal tarsal facet in the specimen are only otherwise known in *Tanytrachelos ahynis*.

The calcaneum is roughly quadrangular in lateral view and wider in a preaxial-postaxial plane than it is proximodistally (Fig. 10D). The bone terminates postaxially in a well-defined, thickened tuber. The tuber is bipartite with proximal and distal components divided by a constriction. The distal component curves laterally (Fig. 10A, B, D).

The proximal surface of the calcaneum is marked by a roughened articular surface (Fig. 10A). A tiny extension of cortical bone divides the fibular articular surface from the tuber. The astragalar articular surface extends proximodistally interrupted by a poorly defined groove near the proximodistal midpoint of the surface (Fig. 10E). This groove may serve the ‘perforating’ vasculature, but there is no perforating foramen. The astragalar contact surface dorsal to the groove is subtly convex, whereas the surface ventral to the groove is subtly concave. Distally, the astragalar articular surface is continuous with the articulation for distal tarsals (Fig. 10B). This distally facing surface is twice the width of the rest of the calcaneum (Fig. 10E). In distal view the bone is quadrangular, with a distinct non-articular surface on the distal face of the calcaneum separating the distal tarsal articulation from the distalmost margin of the calcaneal tuber.

In medial view, the bone is morphologically complex. The expanded facet for the distal elements has a prominent buttress proximal to it on the medial surface (Fig. 10C). The postaxial surface of the buttress bears a distinct fossa. The bone surface surrounding the buttress is smooth, cortical bone. Laterally, the surface of the calcaneum is nearly featureless. The lateral twisting of the calcaneal tuber and the marginal articular surfaces frame a distinct fossa on the lateral surface.

Comparisons—We refer the isolated calcaneum to *Tanyt. ahynis*, based on a number of features. A disarticulated calcaneum is present in a specimen of *Tanytrachelos* from the Lockatong Formation (AMNH FARB 7206; Fig. 11). This element is preserved in oblique view and embedded in matrix. The element has several features identical to the HQ specimen (e.g., distal facet on strongly expanded mediolaterally, distal curling of calcaneal tuber, and a longer calcaneal tuber than other tanystropheids.

Some authors have argued for the absence of calcaneal tubera in tanystropheids (e.g., Rieppel, 1989; Nosotti, 2007). Rieppel (1989) suggested that this might be attributable to an aquatic habitus. However, the only apparent anatomical distinction between this structure and the calcaneal tubera accepted by most authors in *Tr. buettneri* and *Prol. broomi* (Dilkes, 1998; Rieppel, 1989) is a slightly greater postaxial (lateral) projection of the 'wing' of the calcaneum. *Tanys. longobardicus*, *Tr. buettneri*, *Prol. broomi*, and rhynchosaurs all exhibit a distinct thickening of the postaxial margin of the calcaneum (evident in MCSN BES 265; TMM 31025-258; BP/1 2676; Carroll, 1976) homologous with the substantial tuber in derived archosauriforms (Nesbitt, 2011). Considering the subtle distinctions in morphology among these early-diverging archosauromorphs, we consider the calcaneal tuber to consist of two primary features: (1) a distinct postaxial 'winging' of the bone; and (2) a prominent postaxial thickening of the bone. *Tanystropheus* fulfills one of these criteria, suggesting that it does have one of the primary characteristics of a calcaneal tuber. Thus, instead of characterizing the calcaneal tuber as a feature that is either present or absent, we employ two separate characters to describe the calcaneal tuber. AMNH FARB 7206 and the HQ calcaneum differ from *Tanystropheus* in the postaxial expansion of the element, as in most early archosauromorphs.

The absence of space between dorsal and ventral astragalar articular facets on GR 306 is of interest. In other early archosauromorphs, there is a distinct cleft for a perforating artery between these facets, and the dorsal facet is angled proximo-postaxially relative to the ventral facet (e.g., *Noteosuchus*; Carroll, 1976; *Trilophosaurus*, AMNH FARB 30836; *Proterosuchus*, MCZ 4301). Certain specimens of *Tanystropheus* exhibit a noticeably small, pinched perforating foramen and relatively coplanar dorsal and ventral astragalar facets on the calcaneum, although the astragalar facet is not completely exposed in any observed specimens (e.g., MCSN V 3730). Wild (1973) and Nosotti (2007) argue for the presence of a perforating foramen in *Tanystropheus*, whereas Rieppel et al. (2010) consider the foramen absent in *Tanystropheus* cf. *Tanys. longobardicus*. No perforating foramen is present in *Langobardisaurus* (MCSNB 2883, MCSNB 4870, MFSN 1921, MFSN 26829) and *Tanytrachelos* (VMNH 120015; YPM 8600), although this may be a consequence of small size, or a preservational artifact. Although heavily eroded, the calcaneum of AMNH FARB 7206 does not have a perforating foramen. A larger perforating foramen is noted in *Mac. bassanii* (Peyer, 1937; Rieppel, 1989) and *Amotosaurus* (Fraser and Rieppel, 2006). Expansion of the facet for distal elements in the medial-lateral plane is evident in *Proterosuchus* (MCZ 4301; Carroll, 1976) and *Tr. buettneri*, but the expansion is not as great as in *Tanyt. ahynis* (AMNH FARB 7206) and the HQ calcaneum (GR 306). A gap between the distal tarsal articulation and the tuber in GR 306, as in *Noteosuchus colletti* (Carroll, 1976), *Prote. fergusi, Tr. buettneri*, and archosauriforms more derived than phytosaurs (Nesbitt, 2011). Certain archosauriforms (e.g., *Erythrosuchus, Euparkeria*, proterochampsids) exhibit continuity between the distal articular surface and the ventral margin of the tuber (Nesbitt, 2011).

PHYLOGENETIC ANALYSIS

Taxon Sampling

We developed a new phylogenetic dataset for basal saurian reptiles and used this to examine the phylogenetic affinities of HQ fossils described herein. The new character matrix consists of 200 characters and 24 ingroup taxa. Ingroup taxa include two early diapsid taxa (*Orovenator mayorum* and *Youngina capensis*), three lepidosauromorphs (*Gephyrosaurus bridensis*, *Shinisaurus crocodilurus*, and *Uromastyx* sp.), and eighteen archosauromorphs. *Petrolacosaurus* was designated as the outgroup, as many analyses (e.g., Reisz et al., 2011) recover araeoscelidians (including *Pe. kansensis*) as the most plesiomorphic diapsids. Reference specimens and literature consulted for information on the ingroup taxa are presented in Appendix 2S. Individual character attributions and ordering are addressed in Appendix 3S. The dataset is available on MorphoBank (O'Leary and Kaufman, 2007), and is presented in Table 2.1.

Tree Search Strategy

This phylogenetic analysis incorporated a hypothetical taxon including all of the elements of the HQ tanystropheid (hereafter HQT). Experimental runs including individual elements as single operational taxonomic units (OTUs) (e.g., one cervical vertebra, one calcaneum) always placed those elements within a tanystropheid subclade including *Langobardisaurus pandolfii* and *Tanytrachelos ahynis*, supporting the decision to concatenate the OTUs. Exclusion of any HQ materials from the analysis yielded no topological changes. Incorporating a taxon based on the isolated cervical vertebra resulted in a polytomy of that taxon with *Tanytrachelos* and *Langobardisaurus*. The same result occurred when an isolated dorsal or an isolated femur was incorporated. The similarity in neural spine and centrum morphology between the dorsal, sacral, and caudal vertebrae strongly suggests that these belong to a single taxon or a clade of similar taxa. The HQ calcaneum nests as the sister to *Tanytrachelos ahynis*.

All phylogenetic analyses were performed using the Tree Analysis using New Technology software package (TNT) v. 1.1 (Goloboff et al., 2008a, 2008b). Heuristic searches were employed, performing 10,000 replicates of Wagner trees (using random addition sequences), followed by tree bisection and reconnection (TBR) holding 10 trees per TBR replicate. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (i.e., rule 1 of Coddington and Scharff, 1994). Recent morphological phylogenetic analyses employed similar methods (e.g., Nesbitt et al., 2013). Consistency index (CI) and retention index (RI) values were recovered using the STATS.RUN script supplied with TNT. The CI for individual characters was calculated using the STATSALL.RUN script.

General Results

This analysis recovered a single most parsimonious tree (MPT) of 441 steps (CI = 0.472, RI = 0.644), found in 10,000 out of all 10,000 replicates (Fig. 12).

Prolacerta is recovered as the sister taxon to Archosauriformes, as in Dilkes (1998) and modifications thereof (e.g., Sues, 2003; Modesto and Sues, 2004). *Protorosaurus* is resolved as the basalmost archosauromorph, similar to the modified Dilkes (1998) analysis by Borsuk-Bialynicka and Evans (2009) and Gottmann-Quesada and Sander (2009). The clade including *Teraterpeton* and *Trilophosaurus* is the sister taxon to *Prolacerta* + Archosauriformes, and Tanystropheidae is the next taxon outside of the *Trilophosaurus* + (*Prolacerta* + Archosauriformes) node, although deeper nodes are poorly supported as *Prolacerta* + Archosauriformes, Rhynchosauria, Tanystropheidae, and the *Teraterpeton* + *Trilophosaurus* collapse into a polytomy with a single additional step.

TANYSTROPHEIDAE: TREE TOPOLOGY AND CLADE SUPPORT

Our analysis incorporated a range of fossil taxa that have traditionally been allied with *Tanystropheus* and *Macrocnemus*. For this study, we employ a branch-based definition of Tanystropheidae as all taxa more closely related to *Tanystropheus longobardicus* than to

Sphenodon punctatus, *Protorosaurus speneri*, *Rhynchosaurus articeps*, *Trilophosaurus buettneri*, *Azendohsaurus madagaskarensis*, *Prolacerta broomi*, and *Passer domesticus*. Character supports are discussed, and characters with a CI of 0.5 or more are marked with an asterisk.

Macrocnemus + all other Tanystropheidae [Bremer = 4, GC (frequency difference) = 88]

Unambiguous Synapomorphies—*Lacrimal fails to reach ventral margin of nasal ([character]12.[state]1); *anterodorsal process on cervical neural spines (115.1); dorsal tip of neural spines expanded into flattened platform (125.1); absence of dorsal intercentra (128.1); *posterior process of second sacral rib distally pointed (132.1); posterolateral angling of anterior caudal transverse processes (134.1); *strong posterodorsal curvature of scapular blade (145.1); loss of humeral entepicondylar crest (154.0); prominent posterior process on ischium (176.1); absence of distal tarsal two (194.1); absence of pointed outer process of metatarsal five (196.0).

Discussion—Illustrations of selected apomorphies are shown in Figure 13. Many past analyses have suggested a derived protorosaur grouping including *Tanystropheus*, *Macrocnemus*, and similar taxa (e.g., *Langobardisaurus*, *Cosesaurus*), and *Macrocnemus* is normally recovered as the earliest-diverging taxon within the group (Evans, 1987, 1988; Benton and Allen, 1997; Jalil, 1997; Merck, 1997; Dilkes, 1998; Rieppel et al., 2003). Müller (2004) recovered a non-monophyletic Tanystropheidae, finding *Tanystropheus* and *Macrocnemus* as successive sister taxa to a *Prolacerta* + (*Trilophosaurus* + Rhynchosauria + Archosauriformes) clade.

Macrocnemus (Bremer = 2, GC = 65)

Unambiguous Synapomorphies—Frontoparietal contact forms anteriorly curved ‘U’-shape (16.1); posterolateral processes of parietal oriented strongly posterolaterally (21.1); teeth recurved, with posteriorly concave distal margin (91.1).

Discussion—*Macrocnemus bassanii* and *Mac. fuyuanensis* are recovered as sister taxa.

Unnamed Clade (*Amotosaurus* + *Tanystropheus*) + (*Langobardisaurus* + *Tanytrachelos*) (Bremer = 2, GC = 83)

Unambiguous Synapomorphies—Presence of pineal foramen (22.0); one field of teeth on anterior process of pterygoid (49.0); *ventrally planar surface of cervical centra (109.1);

*fusion of ribs to transverse processes in posterior trunk region (124.1); *dorsal neural spine expansion textured with transverse striations (127.1); absence of first distal tarsal (193.1); *short and blocky metatarsal five, lacking preaxial concavity (198.1); *proximal phalanx of fifth pedal digit elongate (199.1).

Discussion—Illustrations of selected synapomorphies are shown in Figure 14.

Unnamed Clade *Amotosaurus* + *Tanystropheus* (Bremer = 1, GC = 72)

Unambiguous Synapomorphies—*Cervical neural spine low at its anteroposterior midpoint, confluent with dorsal surface of neural canal (118.1).

Discussion—This character describes a morphology widespread in species attributed to *Tanystropheus* (e.g., Wild, 1973; Jurcsák, 1975; Rieppel, 2001), and it appears to correlate well with extreme elongation in cervical vertebrae. In contrast, a greater dorsoventral height of the cervical neural spines is apparent in *Tanystropheus* (=*Protanystropheus*) *antiquus* (Wild, 1980a; Sennikov, 2011). Our analysis resolves the taxon as the sister to *Tanystropheus longobardicus*, which could support the inclusion of *Amotosaurus rotfeldensis* within *Tanystropheus*; the *Amotosaurus* material was long considered referable to *Tanystropheus antiquus* (Ortlam, 1967; Wild, 1980a, 1980b). Fraser and Rieppel (2006) described the material as *Amotosaurus rotfeldensis*, distinguishing it from other species of *Tanystropheus*, including *Tanys. antiquus*. Indeed, the referral of *Tanys. antiquus* to the genus *Tanystropheus* has also been questioned (Fraser and Rieppel, 2006), and Sennikov (2011) suggested the genus name *Protanystropheus*.

Unnamed Clade *Langobardisaurus* + (*Tanytrachelos* + HQT) (Bremer = 3, GC = 94)

Unambiguous Synapomorphies—Procoelous vertebrae, with convex posterior condyle (102.2); *cervical centrum dorsoventrally compressed (107.1); *cervical neural spines exhibit midline cleft (117.1); iliac blade with strongly projecting anterior process (170.1); *femoral shaft straight, with slight posteroventral downturn at condyles (177.1).

Discussion—Illustrations of selected apomorphies are shown in Figure 15.

A novel result of our analysis is the recovery of a clade of tanystropheids including *La. pandolfii, Tanyt. ahynis*, and the HQT. This relationship has not been found in any previous analysis, which often recover *Tanys. longobardicus* and *Tanyt. ahynis* as sister taxa (e.g., Benton and

Allen, 1997; Evans, 1988; Jalil, 1997; the ordered analysis of Merck, 1997; Rieppel, et al., 2008). The HQT OTU is the sister taxon to *Tanyt. ahynis*.

Our analysis differs from many past studies in character sampling and scoring. Character 107 describes the distinctive, dorsoventrally flattened morphology of the cervical centra in the HQ material and *Tanyt. ahynis* (an isolated cervical in AMNH FARB 7206). It appears present in *L. pandolfii* (MCSNB 2883); the posterior condyle of the second preserved cervical may exhibit the compressed morphology, and there is a strong change in relative height of the intervertebral articulations from mid-cervical to anterior dorsal vertebrae. A projecting anterior process of the ilium is apparent in *Tanyt. ahynis* (AMNH FARB 7206. The outline of the ilium in *L. pandolfii* (MFSN 1921) appears virtually identical.

A number of characters have been considered to unite *Tanystropheus* and *Tanytrachelos*. Evans (1988), Benton and Allen (1997), Jalil (1997), and Merck (1997) all considered both taxa to have twelve cervical vertebrae (character E26 of Evans, 1988; character 18 of Benton and Allen, 1997; character 56 of Jalil, 1997; character 285 of Merck, 1997), although recent estimates suggest that both taxa had thirteen cervical vertebrae (Rieppel et al., 2010). Incomplete preservation of the neck in certain specimens (MCSNB 2883) and poor preservation of the neck in others (MCSNB 4860, MFSN 1921; Saller et al., 2013) precludes an accurate count, although Saller et al. (2013) estimate a count of eight.

Benton and Allen (1997), Jalil (1997), and Merck (1997) grouped *Tanystropheus* and *Tanytrachelos* based in part on the perceived absence of an intermedium (character 29 of Benton and Allen, 1997; character 47 of Jalil, 1997; character 426 of Merck, 1997), a contention supported by past descriptions of *Tanystropheus* (Kuhn-Schnyder, 1959; Wild, 1973; Nosotti, 2007). The well-preserved, articulated hand in a specimen of *Tanys. longobardicus* (MCSN BES SC 1018) strongly suggests that the preaxial carpal was misidentified. Its articulation with the ulnare and framing of a perforating foramen suggests that it is actually an intermedium. This identity is also supported by the known ossification sequence for early diapsid carpals, in which the radiale is one of the last carpals to ossify (Caldwell, 1994).

Merck (1997) also considered four phalanges in the fourth manual digit as synapomorphic for these two taxa (character 421 of Merck, 1997). The fourth manual digit in *Tanystropheus* and *Tanytrachelos* possess four phalanges, in contrast to the recovered ancestral condition of five phalanges in diapsids and in *Macrocnemus* and *Langobardisaurus* (Wild, 1973;

Olson, 1979; Nosotti, 2007). In our analysis, this feature is ambiguous in its distribution within Tanystropheidae.

Among sampled tanystropheids, the absence of the pedal centrale is shared by *Amotosaurus*, *Tanystropheus*, and *Tanytrachelos* (character E20 of Evans, 1988; character 42 of Benton and Allen, 1997; character 53 of Jalil, 1997; character 472 of Merck, 1997; character 112 of Dilkes, 1998). The optimization of this character is ambiguous in our analysis. The centrale is either lost or fused independently in the *Amotosaurus* + *Tanystropheus* clade and *Tanytrachelos*, or lost/fused in the clade of (*Amotosaurus* + *Tanystropheus*) + (*Tanytrachelos* + *Langobardisaurus*) with a reacquisition in *Langobardisaurus*.

The presence of postcloacal (heterotopic) bones has been posited as a synapomorphy of the clade *Tanystropheus* + *Tanytrachelos* by Benton (1985:character G2), Evans (1988:character E29), Benton and Allen (1997:character 48) and Jalil (1997:character 60). This character is problematic as these ossifications are reported in only half of known specimens of *Tanytrachelos*, which has been used to suggest it as a sexual dimorphic feature (Casey et al., 2007). The feature is recognized in certain specimens of *Tanystropheus* (e.g., Rieppel et al., 2010), and past analyses have considered the structures present in only *Tanystropheus* and *Tanytrachelos*. However, the sample size of specimens for other tanystropheid taxa is often very small (n = 4 for *L. pandolfii*). Assuming synonymy of the two *Langobardisaurus* species, only four skeletons are known with the sacral region preserved. Assuming a 50% probability of finding a specimen belonging to either sex, a sample size of five intact specimens is required to have a greater than 95% confidence of having found members of both sexes. As such, most taxa (including *Langobardisaurus* and *Amotosaurus*) are scored as '?' for this character in our analysis.

Unnamed Clade *Tanytrachelos* + HQT (Bremer = 2, GC = 95)

Unambiguous Synapomorphies—Second sacral vertebra not distally bifid (131.0); *distal portion of calcaneal tuber curls externally (190.1)

Discussion—This relationship and the statistics offered in support of it pertain only to the second analysis, which incorporated a theoretical OTU combining the HQ tanystropheid materials. The recognition of a calcaneum among the disarticulated *Tanytrachelos ahynis* elements of AMNH FARB 7206 expands the number of shared characters between it and the HQ materials. Informative calcaneal characters in *Tanytrachelos* and the HQ calcaneum are illustrated in Figure 16.

DISCUSSION

Phylogenetic Position of the Hayden Quarry Material—The morphologies evident in the HQ archosauromorph materials are most parsimoniously explained if the materials belong to a taxon (or closely related taxa) of derived tanystropheid most closely related to *Tanytrachelos ahynis*, within a newly reported subclade of exclusively Late Triassic tanystropheids including *Tanytrachelos* and *Langobardisaurus*. The overall similarity between *Tanytrachelos* and *Langobardisaurus*, which represent the latest-known tanystropheid taxa, is accentuated by the smaller body size and the proportionally large head size in known specimens.

Three-dimensional preservation of the HQ materials allowed for the development of new characters and the re-interpretation of crushed tanystropheid fossils. The recognition of the flattened cervical centra and the *Tanytrachelos* calcaneum apomorphies was invaluable in reconstructing the relationships in the taxon. Although the HQT cannot be currently formally recognized as a new taxon, the individual characters derived from this study inform the morphologies and relationships in badly crushed specimens.

Tanystropheid Occurrences in Western North America—Most past authors have only tentatively referred material from the Chinle Formation to Tanystropheidae or *Tanytrachelos* sp. Murry and Jacobs (1980) considered *Tanytrachelos* definitively present in the Chinle Formation based on “small procoelous vertebrae and plowshare-shaped cervical ribs.” Kaye and Padian (1994) tentatively agreed, and one biogeographic analysis noted the presence of Tanystropheidae in the formation (Shubin and Sues, 1991). Our apomorphy-based referral of the HQ material to Tanystropheidae represents the first well-supported evidence of that clade in western North America and has implications for understanding archosauromorph diversity and biogeography in the Late Triassic. The recognition of the HQ tanystropheid material allows identification of additional fossils from penecontemporaneous sites.

A partial cervical rib from the *Placerias* Quarry (MNA V3627) was referred to *Tanytrachelos* sp. based on an apomorphically plowshare-like shape (Kaye and Padian, 1994:fig. 9.76A–B), which is autapomorphic for *Tanytrachelos ahynis* (Olsen, 1979). Murry and Jacobs

(1980) noted similar ribs to be present at the Downs Quarry. Vertebrae from the *Placerias* Quarry (Arizona, Kaye and Padian, 1994; Renesto et al., 2009:fig. 2R–V), Mesa Montosa (New Mexico, Zeigler et al., 2005:fig. 4A), Colorado City (Texas, Heckert et al., 2004), Post Quarry (Texas, Atanassov, 2001; Martz et al., 2013), and unnamed localities in west Texas (Case, 1932) all exhibit some combination of procoely, spinous expansions, wide-spaced chevrons, and compressed cervical centra. The stratigraphy of occurrences in the Chinle Formation is shown in Figure 17, with dates derived from Irmis et al. (2011) and Zeigler et al. (2008). These occurrences indicate that the group was widespread in North America in the Late Triassic throughout much of the Norian.

Paleobiogeography of Tanystropheidae—The earliest fossil taxa referred to Tanystropheidae are the Early Triassic *Amotosaurus rotfeldensis* from the 'Buntsandstein' of Germany (Fraser and Rieppel, 2005) and *Augustaburiania* from the Olenekian of Russia (Sennikov, 2011), both representing occurrences of the clade in non-marine sediments.

Middle Triassic tanystropheids are significantly more widespread, diverse, and better known. *Macrocnemus bassanii* is known from the Anisian-aged Besano and Monte San Giorgio localities in alpine Europe (Peyer, 1937) and *Mac. fuyuanensis* is known from the Ladinian-aged Zhuganpo Member of the Falang Formation in southeastern China (Li et al., 2007; Jiang et al., 2011). Additional long-necked archosauromorphs (*Dinocephalosaurus orientalis*; *Fuyuansaurus acutirostris*) from the Middle Triassic of China may also be tanystropheids (Rieppel et al., 2008; Fraser et al., 2013). *Protanystropheus antiquus* is known from the Middle Triassic (Anisian) Gogolin Formation of Poland and sites in Eastern Europe (for a review of localities see Fraser and Rieppel 2006). *Tanystropheus longobardicus* occurs in the Middle Triassic (Anisian–Ladinian) of Monte San Giorgio, Switzerland (Wild, 1973; Nosotti, 2007), assorted localities in eastern Italy (Dalla Vecchia, 2007), and Yunnan, China (Rieppel et al., 2010). Additional occurrences of *Tanystropheus* are known from the Middle Triassic (Anisian) of Kupferzell, Germany (*Tanys. conspicuus*; see Wild, 1973), Makhtesh Ramon, Israel (*T. haasi*; see Rieppel, 2001), and Bihor, Romania (*Tanys. biharicus*; see Jurcsák, 1975). A *Tanystropheus*-like vertebra is recognized from the Middle Triassic Jihl Formation of Saudi Arabia (Vickers-Rich et al., 1999). Although a large number of excellent Middle Triassic tanystropheid fossils come from marine deposits (e.g., Wild, 1973; Rieppel et al., 1999; Nosotti, 2007), certain taxa occur in deposits with weaker marine influences (Wild, 1980c). Wild (1973) speculated that in *Tanys.*

longobardicus at least, there might be an ontogenetic shift in environmental preferences with juveniles living in a terrestrial environment and adults subsequently moving to a marine habitat.

Material referred to ‘prolacertiforms’ from the Bromsgrove Sandstone Formation of England may be the westernmost-known tanystropheids from the Middle Triassic (Anisian) based on cervical vertebrae with tanystropheid-like anterior processes and dorsal vertebrae bearing spinous expansions (Benton and Walker, 1996). Other members of the Bromsgrove fauna (terrestrial pseudosuchians, rhynchosaurs) suggest a greater terrestrial influence than in other Middle Triassic tanystropheid-bearing localities. As yet, no tanystropheids have been reported from Middle Triassic-aged marine deposits in western North America, and material referred to ‘prolacertiforms’ from the non-marine fluvial Moenkopi Formation of Arizona is too fragmentary for adequate comparisons (Schoch et al., 2010). However, the terrestrial vertebrate record of the Early and Middle Triassic in North America is poorly sampled.

The only certain tanystropheid specimens from Late Triassic Europe include *Langobardisaurus pandolfii* from the Calcare di Zorzino Formation (Renestso, 1994), the Dolomia di Forni Formation (Muscio, 1996), and the Seefeld Formation of Austria (Saller et al., 2013). A third species referred to *Langobardisaurus*, *L. rossii*, may represent a lepidosauromorph (as argued by Renesto and Dalla Vecchia, 2007). All *Langobardisaurus* specimens are from middle Norian deposits (Dalla Vecchia, 2006, 2008; Renesto, 2006; Saller et al., 2013). A partial series of elongate cervical vertebrae described as *Tanystropheus fossai* by Wild (1980b) from the late Norian Argillite di Riva Solto locality in northern Italy may represent the latest-known record of a tanystropheid, although Renesto (2006) questioned the referral and no tanystropheid apomorphies are apparent from published descriptions. Renesto (2006) argued that the Calcare di Zorzino Formation was formed in anoxic freshwater lakes on offshore islands (reiterated in Berra et al., 2010 and Sues and Fraser, 2010). A similar depositional environment was suggested for the Seefeld Formation of Austria, from which another *Langobardisaurus* specimen was described (Saller et al., 2013).

Tanystropheids from eastern North America are known from the Newark Supergroup. The earliest record of tanystropheids in North America may be a partial cervical vertebra referred to a ‘protorosaur’ from a purportedly Middle Triassic site in the Fundy Basin of Nova Scotia, although the age of this deposit is as-yet unresolved (Sues and Fraser, 2010). *Tanytrachelos ahynis* has been reported from the Norian-aged Lockatong Formation of New Jersey (Olsen, 1979; Sues and Fraser, 2010). Others are known from Lockatong sites in Pennsylvania; vertebrae comparable to *Tanytrachelos* and the HQ vertebrae form part of the holotype of *Gwyneddosaurus* (Bock, 1945; Huene, 1948). Some material described by Cope (1866) as the pterosaur '*Pterodactylus*' *longispinus* and later renamed *Rhabdopelix longispinus* from Triassic deposits near Gwynedd, Pennsylvania (Cope, 1870) likely pertains to a *Tanytrachelos*-like taxon. Although the Cope material is lost, descriptions and published figures of procoelous and compressed vertebrae suggest similarity to *Tanytrachelos* (Cope, 1870:fig. 46).

The Solite Quarry (Cow Branch Formation, Dan River Basin) of southern Virginia has produced hundreds of partial and complete skeletons of *Tanytrachelos* (Olsen, 1979; Sues and Fraser, 2010). The Solite Quarry, positioned in the upper part of the Cow Branch Formation, and the Lockatong Formation are early Norian in age (~226–220 Ma; see Olsen et al., 2011 and Whiteside et al., 2011). The HQ material thus represents a later occurrence of tanystropheids in North America. The recovery of the HQ tanystropheid material as the sister taxon to *Tanytrachelos ahynis* hints at a diversification of small tanystropheids on the North American continent during the Triassic. Depending on the age of *Langobardisaurus* material (described as middle Norian), the western fossils may represent the very last known tanystropheids (depending on the affinities of the possible Rhaetian *Tanystropheus fossai*). That these last occurrences occur in terrestrial, seasonally dry environments far removed from the marine deposits tanystropheids are best known from is a testament to the diversity of the group and our poor understanding of early saurian evolution.

Recent work suggests that climatic zonation across low-latitude Pangea may have resulted in faunal provincialism in the Late Triassic. Whiteside et al. (2011) document that in the Late Triassic of eastern North America, equatorial Pangea (± 5° of the equator) was hot and humid, whereas above 5° latitude, conditions became more arid. As Pangea drifted northward during the Late Triassic, eastern North America traveled through these climate zones (Kent and Tauxe, 2005; Whiteside et al., 2011). Some herbivorous reptiles in the Newark Supergroup appear to track these climate zones, with traversodont cynodonts occurring within 5° of the equator, and procolophonid parareptiles found above 5° (Whiteside et al., 2011). Most of Chinle and Dockum deposition occurred above 5°N (Kent and Irving, 2010), so it appears that certain other reptile taxa occupied both of these climatic zones in North America, including *Postosuchus* (Peyer et al., 2008) and *Revueltosaurus* (Parker et al., 2005; Heckert et al., 2012) The recognition of tanystropheids across North America suggests that *Tanytrachelos*-like animals were able to occupy a range of climatic conditions.

Although tanystropheid material from HQ is limited, we can make inferences about body size. Dorsal vertebrae with complete centra are 14–15 mm in length, roughly twice the length of the dorsal vertebrae reported for *Tanytrachelos* by Olsen (1979), suggesting an animal with a snout-vent length of 30 cm, presuming proportions similar to *Tanytrachelos*. This size is intermediate between the *Tanytrachelos* and *Langobardisaurus,* similar to lengths reported for *Macrocnemus* (~35–86 cm total body length based on Peyer, 1937), and substantially smaller than large individuals of *Tanystropheus* (> 5 m total body length based on Wild, 1973). The absence of cranial material precludes evaluation of the ecology of the HQT, as tanystropheids exhibited a wide range of feeding apparatuses (Renesto and Dalla Vecchia, 2000).

Distribution and Functional Morphology of the Neural Spine Expansion in Saurians—The three-dimensional preservation in the HQ vertebrae vastly expands our knowledge of tanystropheid morphology. Although widely known to have broad neural spine tips, three-dimensional tanystropheid fossils are limited. Wild (1973) and Dalla Vecchia (2005) described three-dimensional dorsal vertebrae referred to *Tanystropheus*, although none exhibit the degree of expansion in the HQ fossils. This suggests a greater degree of morphological diversity in the axial anatomy of the group than previously known.

Presacral neural spines in some lepidosaur lineages exhibit transverse expansions with irregular texturing. In *Sphenodon* and certain squamates (e.g., snakes, chameleons) a cartilaginous epiphysis attaches to the dorsum of the bony neural spine (Hoffstetter and Gasc, 1969; Winchester and Bellairs, 1977). This is most apparent in large snakes, such as *Python* and *Eunectes*. This structure is associated with a cartilaginous epiphysis characteristic of lepidosaurs (Hoffstetter and Gasc, 1969), although it does not fuse in snakes, leaving a rugose bony base (Winchester and Bellairs, 1977). The neural spine tip also serves for the attachment of the supraspinous ligament in archosaurs (e.g., Frey, 1988; Tsuihiji, 2004) and squamates (e.g., Surahya, 1989). Although certain portions of the transversospinalis musculature attach to the dorsalmost portion of the neural spine in extant saurians (e.g., Gasc, 1981; Frey, 1988; Tsuihiji, 2005), no musculature is directly associated with the median tip of the neural spine. Crocodylians exhibit an additional complex of cingulate ligaments for the anchoring of osteoderms to vertebrae (Frey, 1988; Schwarz-Wings et al., 2009).

Among extinct reptile taxa, choristoderes exhibit distinct dorsal platforms on their dorsal neural spines, marked by roughened texturing (e.g., Evans, 1991). However the dorsal neural spine tips in the putative choristodere *Pachystropheus rhaeticus* are convex with anteromedially-oriented striations (visible in NHMUK R 6857), as opposed to the concave expansions with transversely oriented striations noted in tanystropheids.

Expansion of the dorsal surfaces in neural spines is common among early archosauromorphs, including *Czatkowiella harae*, proterosuchids (Cruickshank, 1972; Thulborn, 1979), *Euparkeria* (Ewer, 1965), phytosaurs (McGregor, 1906), aetosaurs (Walker, 1961; Long and Murry, 1995; Parker, 2008), early loricatans (Gower and Schoch, 2009), and early dinosaurs Novas, 1994; Nesbitt, 2011). Multiple gains and losses of this feature are suggested by current phylogenetic hypotheses for saurians (e.g., Sereno, 1991; Sereno and Arcucci, 1994; Nesbitt, 2011). In many of these cases, the expansions likely functioned as support for cingulate ligaments (e.g., Frey, 1988; Schwarz-Wings et al., 2009).

The expanded neural spine tip is ubiquitous among tanystropheids. The dorsal vertebrae in observed specimens of *Macrocnemus bassanii* possess spinous expansions that are smoothly textured. Extensive expansion and dorsal striations on the spinous expansions appear in the unnamed clade (*Tanystropheus* + *Amotosaurus*) + (*Langobardisaurus* + (*Tanytrachelos* + HQT)). The spine tables in *Tanys. longobardicus* are proportionally narrower with more densely set striations than in the HQT. Probable caudal spinous expansions are apparent in one *Tanys. longobardicus* specimen (MCSN BES SC 1018). *Tanytrachelos* specimens exhibit spinous expansions in the dorsal, sacral, and caudal regions (e.g., YPM PU 23082). Tschanz (1985) speculated on the influence of the anterior dorsal epaxial musculature on the stabilization of the elongate neck in *Tanystropheus*, suggesting that the anterior dorsal neural arches had inadequate muscle attachment sites to allow for elevation of the neck. Further analysis of this problem requires study of three-dimensional fossils to reconstruct ligamentous and muscular attachments, making the HQ vertebrae integral in resolving this problem.

There is no evidence of osteoderms in Tanystropheidae, suggesting that cingulate ligaments do not explain the expanded neural spines. Considering the morphology of the neural spines and associated structures in Lepidosauria and Archosauria, the expanded spine tips may have served an expanded supraspinous ligament or an extensive attachment of the bone to the dermis. Such an expanded ligament system would work to prevent the trunk from falling into flexion, a possible consequence of the extreme elongation of the neck. The neural spines in some sauropods are expanded to accommodate a similarly strong bracing system for extension in the vertebral column (Schwarz and Frey, 2005; Schwarz et al., 2007). The reason for the gracile neural spines in the cervical vertebrae is unclear, although the ligaments in the neck of saurians are distinct from those in the trunk region (e.g., Seidel, 1978; Tsuihiji, 2004, 2005).

CONCLUSIONS

The material described herein confirms the presence of derived tanystropheid archosauromorphs in the Late Triassic of western North America and thus represents an expansion of their known geographic range in the Triassic. Depending on the ages of the *Langobardisaurus* localities in Western Europe, these fossils could represent the geologically latest tanystropheids in the fossil record. The three-dimensional preservation and quality of these fossils makes them a critical contribution to the morphology of Tanystropheidae, informing both phylogenetic analysis and functional morphology. Available appendicular elements, especially the unique morphologies of the calcaneum, highlight the similarities between the HQ tanystropheid and *Tanytrachelos ahynis*. Even the preliminary results reported here suggest that the number of occurrences of tanystropheids outside of HQ in North America will expand greatly. In light of this newfound diversity and biogeographic range, the contribution of tanystropheids to Triassic ecosystems deserves further consideration.

ACKNOWLEDGMENTS

The material described herein was discovered by numerous volunteers and students over the past six years, and was expertly prepared by Stony Brook University preparator V. Heisey. We thank the Ghost Ranch Conference Center for the continued support of our fieldwork at Hayden Quarry. We thank numerous museum curators and staff for their assistance: A. Bhart-Bhullar, F. Jenkins, and J. Cundiff (MCZ); M. Brett-Surman (USNM); C. Dal-Sasso (MCSN); A. Downs (GR); C. Mehling (AMNH); L. Murray and J. C. Sagebiel (TMM); G. Muscio and L. Simonetto (MFSN); C. Norris and D. Brinkman (YPM); A. Dooley and N. Fraser (VMNH); A. Paganoni (MCSNB); D.-Y. Jiang (GMPKU), and L. Steel (NHMUK). We thank P. Nicodemo for assistance regarding soft tissue morphology in snakes, S. Hoffman for assistance with translation, S. Burch for assistance with figure development, and J. Nestler for assistance with photography. Comments and discussion from JVP editor S. Modesto and Reviewers S. Renesto, D. Dilkes, and N. Fraser greatly improved this manuscript. This work was funded by the Research Foundation of New York and a Sigma Xi Grant in aid of Research.

LITERATURE CITED

Atanassov MN. (2001). Two new archosauromorphs from the Late Triassic of Texas. J Vert Paleo 21(3 Supplement):30A.

Bell CJ, Head JJ, Mead JI. (2004) Synopsis of the herpetofauna from Porcupine Cave. *Biodiversity Response to Climate Change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado*, ed. AD Barnosky (University of California Press, Berkeley, California) pp. 117–126

Benton MJ. (1990) The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. Phil Trans Roy Soc B 328:213–306.

Benton MJ, Allen JL. (1997) *Boreopricea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles. Palaeo 40:931–953.

Benton MJ, Walker AD. (1996) *Rhombopholis*, a prolacertiform reptile from the Middle Triassic of England. Palaeo 39:763–789.

Berman DS, Reisz RR. (1992) *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. J Paleontology 66:1001–1009.

Berra F, Jadoul F, Anelli A. (2010) Environmental control on the end of the Dolomia Principale/Hauptdolomit depositional system in the central Alps: coupling sea-level and climate changes. Palaeogeo, Palaeoclimat, Palaeoeco 290:138–150.

Bock W. (1945) A new small reptile from the Triassic of Pennsylvania. Notulae Naturae Acad Nat Sci Philadelphia 154:1–8.

Borsuk-Bialynicka M, Evans SE. (2009b) A long-necked archosauromorph from the Early Triassic of Poland. Palaeontologia Polonica 65:203–234.

Caldwell MW. (1994) Developmental constraints and limb evolution in Perian and extant lepidosauromorph diapsids. J Vert Paleo 14:459–471.

Carroll RL. (1976) *Noteosuchus*—the oldest known rhynchosaur. Annals S Afr Mus 72:37–57.

Case EC. (1932) On the caudal region of *Coelophysis* sp. and on some new or little known forms from the Upper Triassic of western Texas. Cont Mus Paleo, U MI 4:81–91.

Casey MM, Fraser NC, Kowalewski M. (2007) Quantitative taphonomy of a Triassic reptile *Tanytrachelos ahynis* from the Cow Branch Formation, Dan River Basin, Solite Quarry, Virginia. Palaios 22:598–611.

Coddington J, Scharff N. (1994) Problems with zero-length branches. Cladistics 10:415–423.

Conrad JL. (2006) Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). J Morph 267:769–775.

Cope ED. (1866) Meeting Report from October 23rd. Proc Acad Nat Sci Philadelphia 180:290.

Cope ED. (1870) Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. Trans Amer Phil Soc 14:1–252.

Cruickshank ARI. (1972) The proterosuchian thecodonts. *Studies in Vertebrate Evolution: Essays Presented to F. R. Parrington*, eds TS Kemp, KA Joysey. (Olive and Boyd, Edinburgh, U.K), pp. 89–119.

Currie PJ. (1981) The vertebrae of *Youngina* (Reptilia: Eosuchia). Can J Earth Sci 18:815–818.

Dalla Vecchia FM. (2005) Resti di *Tanystropheus*, saurotterigie e "rauisuchi" (Reptilia) nel Triassico Medio della Val Aupa (Moggio Udinese, Udine). Gortania 27:25–48.

Dalla Vecchia FM. (2006) The tetrapod fossil record from the Norian–Rhaetian of Friuli (northeastern Italy). Bull NM Mus Nat Hist Sci 37:432–444.

Dalla Vecchia FM. (2008) Vertebrati fossili del Friuli. Pub Mus Friulano Storia Naturale 50:1–303.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Phil Trans Roy Soc B 353:501–541.

Downs A. (2005) The Hayden Quarry, a new Upper Triassic fossil locality at Ghost Ranch, New Mexico. NM Geo Soc Guidebook 56:339–340.

Dubiel RF. (1989) Depositional environments of the Upper Triassic Chinle Formation in the eastern San Juan Basin and vicinity, New Mexico. U.S. Geo Survey Bull 1808-B:1–22.

Evans SE. (1981) The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. Zool J Linn Soc 73:81–116.

Evans SE. (1987) The phylogeny of Prolacertiformes. *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Drumheller, Alberta, Short Papers*, eds. PJ Currie and E Koppelhus. Tyrrell Museum of Paleontology, Occasional Papers 3:117–126.

Evans SE. (1988) The early history and relationships of the Diapsida. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 221–260.

Evans SE. (1991) The postcranial skeleton of the choristodere *Cteniogenys* (Reptilia: Diapsida) from the Middle Jurassic of England. Geobios 24:187–199.

Ewer RF. (1965) The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil Trans Roy Soc B 248:379–435.

Fraser NC. (1988) The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). Phil Trans Roy Soc B 321:125–178.

Fraser NC, Rieppel O. 2006. A new protorosaur (Diapsida) from the Upper Buntsandstein of the Black Forest, Germany. J Vert Paleo 26:866–871.

Fraser NC, Irmis RB, Elliott DK. (2005) A procolophonid (Parareptilia) from the Owl Rock Member, Chinle Formation of Utah, U.S.A. Palaeo Elect 8:1–7.

Fraser NC, Nosotti S, Rieppel O. (2004) A re-evaluation of two species of *Tanystropheus* (Diapsida, Protorosauria) from Monte San Giorgio, southern Alps. J Vert Paleo 24(Supplement):60.

Fraser NC, Rieppel O, Chun L. (2013) A long-snouted protorosaur from the Middle Triassic of southeastern China. J Vert Paleo 33:1120–1126.

Frey E. (1988).Anatomie des Körperstammes von *Alligator mississippiensis* Daudin. Stuttgarter Beiträge zur Naturkunde: Serie A (Biologie) 424:1–60.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph. D. dissertation, University of California, Berkeley, California, 564 pp.

Gervais, P. 1859. Zoologie et Paléontologie Française. Bertrand, Paris, 544 pp.

Goloboff PA, Farris JS, Nixon KC. (2008a). TNT: tree analysis using new technology, vers. 1.1. Willi Hennig Society. Available at http://www.zmuc.dk/public/phylogeny/tnt. Accessed February, 2, 2013.

Goloboff PA, Farris JS, Nixon KC. (2008b). TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Gottmann-Quesada A, Sander PM. (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. Palaeontographica Abteilung A 287:123–220.

Gow CE. (1975) The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeontologia Africana 18:89–131.

Gower DJ. (2003) Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. Annal S Afr Mus 110:1–88.

Gower DJ, Schoch RR. (2009) Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. J Vert Paleo 29:103–122.

Gregory JT. (1945). Osteology and relationships of *Trilophosaurus*. University of Texas Publication 4401:273–359.

Haines RW. (1969). Epiphyses and bony sesamoids. *Biology of the Reptilia, Volume 1: Morphology*, ed. C. Gans. (Academic Press, London and New York), pp. 81–15

Harris JD, Downs A. (2002) A drepanosaurid pectoral girdle from the Ghost Ranch (Whitaker) Coelophysis Quarry (Chinle Group, Rock Point Formation, Rhaetian), New Mexico. J Vert Paleo 22:70–75.

Heckert AB. (2004) Late Triassic microvertebrates from the Upper Triassic Chinle Group (Otischalkian–Adamanian, Carnian), southwestern U.S.A. Bull NM Mus Nat Hist Sci 27:1–170.

Heckert AB, Lucas SG, Spielmann JA. (2012) A new species of the enigmatic archosauromorph *Doswellia* from the Upper Triassic Bluewater Creek Formation, New Mexico, U.S.A. Palaeo 55:1333–1348.

Hoffstetter R., Gasc J-P. (1969) Vertebrae and ribs of modern reptiles. *Biology of the Reptilia, Volume 1: Morphology*, ed. C. Gans. (Academic Press, London and New York), pp. 209–301.

Huene F von. (1948) Notes on *Gwyneddosaurus*. Amer J Sci 246:208–213.

Hughes B. (1963) The earliest archosaurian reptiles. S Afr J Sci 59:221–241.

Hutchinson JR. (2001). The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). Zool J Linn Soc 131:169–197.

Irmis R B. 2005. The vertebrate fauna of the Upper Triassic Chinle Formation in northern Arizona. *Guidebook of the Triassic Formations of the Colorado Plateau*, eds. SJ Nesbitt, WG Parker, RB Irmis. Mesa Southwest Museum 9:63–88.

Irmis RB, Mundil R, Martz JW, Parker WG. (2011). High-resolution U-Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. Earth Planet Sci Letters 309:258–267.

Irmis RB, Nesbitt SJ, Padian K, Smith ND, Turner AH, Woody D, Downs A. (2007). A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317:358–361.

Jacobs L, Murry PA. (1980) The vertebrate community of the Triassic Chinle Formation near St. Johns, Arizona. *Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert*, ed. LL Jacobs. (Museum of Northern Arizona Press: Flagstaff), pp. 55–71.

Jalil N-E. (1997) A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. J Vert Paleo 17:506–525.

Jiang D-Y, Rieppel O, Fraser NC, Motani R, Hao W-H, Tintori A, Sun Y-L, Sun Z-Y. (2011) New information on the protorosaurian reptile *Macrocnemus fuyuanensis* Li et al., 2007, from the Middle/Upper Triassic of Yunnan, China. J Vert Paleo 31:1230–1237.

Jurcsák T. (1975). *Tanystropheus biharicus* n. sp. (Reptilia, Squamata) o noua specie pentru fauna Triasica Romaniei. Nymphaea 3:45–52.

Kaye FT, Padian K. (1994) Microvertebrates from the *Placerias* Quarry: a window on Late Triassic vertebrate diversity in the American Southwest. *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, eds. NC Fraser, H-D Sues. (Cambridge University Press, Cambridge, U.K.), pp. 171–196.

Kent DV, Tauxe L. (2005) Corrected Late Triassic latitudes for continents adjacent to the North Atlantic. Science 307:240–244.

Kuhn-Schnyder VE. (1959) Hand und Fuss von *Tanystropheus longobardicus* (Bassani). Eclogae Geologicae Helvetiae 52:921–941.

Li C, Zhao L, Wang L. (2007) A new species of *Macrocnemus* (Reptilia: Protorosauria) from the Middle Triassic of southwestern China and its palaeogeographical implication5. Sci in China D 50:1601–1605.

Long RA, Murry PA. (1995) Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. NM Mus Nat Hist Bull 4:1–254.

Martz JW, Mueller B, Nesbitt SJ, Stocker MR, Parker WG, Atanassov M, Fraser NC, Weinbaum J, Lehane J. (2013) A taxonomic and biostratigraphic re-evaluation of the Post Quarry vertebrate assemblage from the Cooper Canyon Formation (Dockum Group, Upper Triassic) of southern Garza County, western Texas. Earth Env Sci Trans Roy Soc Edin 103:339–364.

McGregor JH. (1906) The Phytosauria, with especial reference to *Mystriosuchus* and *Rhytidodon*. Mem Amer Mus Nat Hist 9:87–100.

Merck JA. (1997) A phylogenetic analysis of the euryapsid reptiles. Ph.D. thesis, University of Texas at Austin.

Modesto SP, Sues H-D. (2004) The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. Zool J Linn Soc 140:335–351.

Müller. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Murry PA. (1987) New reptiles from the Upper Triassic Chinle Formation of Arizona. J Vert Paleo 61:773–786.

Murry PA. (1989) Microvertebrate fossils from the Petrified Forest and Owl Rock members (Chinle Formation) in Petrified Forest National Park and vicinity, Arizona. *Dawn of the Age of Dinosaurs in the American Southwest*, eds. SG Lucas and AP Hunt. (New Mexico Museum of Natural History, Albuquerque), pp. 249–277.

Muscio, G. 1996. Preliminary note on a specimen of Prolacertiformes (Reptilia) from the Norian (Late Triassic) of Preone (Udine, north-eastern Italy). Gortania 18:33–40.

Muscio G. (1996) Preliminary note on a specimen of prolacertiform (Reptilia) from the Norian (Late Triassic) of Preone (Udine, north-eastern Italy). Gortiana 18:33–40.

Nesbitt SJ, Chatterjee S. (2008) Late Triassic dinosauriforms from the Post Quarry and surrounding areas, west Texas, U.S.A. Neues Jahr für Geol und Paläo Abh 249:143–156.

Nesbitt SJ, Stocker MR (2008) The vertebrate assemblage of the Late Triassic Canjilon Quarry (northern New Mexico, USA), and the importance of apomorphy-based assemblage comparisons. J Vert Paleo 28:1063–1072.

Nesbitt SJ, Butler RJ, Gower DJ. (2013). A new archosauriform (Reptilia: Diapsida) from the Manda Beds (Middle Triassic) of southwestern Tanzania. PLoS One 8:e72753. doi:10.1371/journal.pone.0072753.

Nesbitt SJ, Stocker MR, Small BJ, Downs A. (2009a). The osteology and relationships of *Vancleavea campi* (Reptilia: Archosauriformes). Zool J Linn Soc 157:814–864.

Nesbitt SJ, Irmis RB, Parker WG, Smith ND, Turner AH, Rowe T. (2009b). Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. J Vert Paleo 29:498–516.

Nosotti S. (2007). *Tanystropheus longobardicus* (Reptilia, Protorosauria): re-interpretations of the anatomy based on new specimens from the Middle Triassic of Besano (Lombardy, northern Italy). Mem. Mus Civ Storia Nat Milano 35:1–88.

O'Leary MA, Kaufman SG. (2007). Morphobank 2.5: web application for morphological phylogenetics and taxonomy. http://morphobank.org.

Olsen PE. (1979). A new aquatic eosuchian from the Newark Supergroup (Late Triassic–Early

Jurassic) of North Carolina and Virginia. Postilla 176:1–14.

Olsen PE. (1990). Tectonic, climatic, and biotic modulation of lacustrine ecosystems—examples from Newark Supergroup of eastern North America. *Lacustrine Basin Exploration: Case Studies and modern Analogs*, ed. BJ Katz. AAPG Memoir 50:209–224.

Olsen PE, Kent DV, Whiteside JH. (2011). Implications of the Newark Supergroup-based astrochronology and geomagnetic polarity time scale (Newark-APTS) for the tempo and mode of the early diversification of the Dinosauria. Earth Env Sci Trans Roy Soc Edin 101:201–229.

Ortlam D. (1967). Fossile Böden als Leithoriztone für die Gliederung des Höheren Butsandsteins im nördlichen Schwarzwald und südlichen Odenwald. Geol Jahrbuch 84:485–590.

Parker WG. (2008) Description of new material of the aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*. PaleoBios 28:1–40.

Parker WG, Irmis RB, Nesbitt SJ , Martz JW, Browne LS. (2005). The Late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs. Proc Roy Soc B 272:963–969.

Peyer B. (1937) Die Triasfauna der Tessiner Kalkalpen XII. *Macrocnemus bassanii* Nopcsa. Schweizerische Paläo Abh 59:1–140.

Peyer K, Carter JG, Sues H-D, Novak SE, Olsen PE. (2008). A new suchian archosaur from the Upper Triassic of North Carolina. J Vert Paleo 28:363–381.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2012). A new drepanosaurid from the Late Triassic of New Mexico: insights into the forelimb evolution and biogeography of drepanosaurs. J Vert Paleo 32(3, Supplement):158–159.

Ramezani J, Hoke GD, Fastovsky DE, Bowring SA, Therrien S, Dworkin SI, Atchley SC, and LC Nordt. (2011) High-precision U-Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): temporal constraints on the early evolution of dinosaurs. Geo Soc Amer Bull 123:2142–2159.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Special Publication of the Museum of Natural History, University of Kansas 7:1–74.

Reisz RR, Berman DS, Scott D. (1984) The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. J Vert Paleo 4:57–67.

Reisz RR, Modesto SP, and Scott MD. (2011) A new Early Permian reptile and its significance in early diapsid evolution. Proc Roy Soc B 278:3731–3737.

Renesto S. (1994) A new prolacertiform reptile from the Late Triassic of northern Italy. Riv Ital Paleo Strat 100:285–306.

Renesto S. (2006) A reappraisal of the diversity and biogeographic significance of the Norian (Late Triassic) reptiles from the Calcare di Zorzino. NM Mus Nat Hist Bull 37:445–456.

Renesto S, Dalla Vecchia FM. (2000) The unusual dentition and feeding habits of the prolacertiform reptile *Langobardisaurus* (Late Triassic, northern Italy). J Vert Paleo 20:622–627.

Renesto S, Dalla Vecchia FM. (2007) A revision of *Langobardisaurus rossii* Bizzarini and Muscio, 1995 from the Late Triassic of Friuli, Italy. Riv Ital Paleo Strat 113:191–201.

Renesto S, Spielmann JA, Lucas SG. (2009). The oldest record of drepanosaurids (Reptilia, Diapsida) from the Late Triassic (Adamanian Placerias Quarry, Arizona, USA) and the stratigraphic range of the Drepanosauridae. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 252:315–325.

Rieppel O. (1989) The hind limb of *Macrocnemus bassanii* (Nopcsa) (Reptilia, Diapsida): development and functional anatomy. J Vert Paleo 9:373–387.

Rieppel O. (2001) A new species of *Tanystropheus* (Reptilia: Protorosauria) from the Middle Triassic Makhtesh, Ramon, Israel. N Jahr fur Geo Paleo Abh 221:271–287.

Rieppel O, Fraser NC, Nosotti S. (2003) The monophyly of Protorosauria (Reptilia, Archosauromorpha): a preliminary analysis. Atti della Soc ital di sci nat del mus civ di storia nat di Milano 144:359–382.

Rieppel O, Mazin J-M, Tchernov E. 1999. Sauropterygia from the Middle Triassic of Makhtesh Ramon, Negev, Israel. Fieldiana Geology 40:1–85.

Rieppel O, Jiang D-Y, Fraser NC, Hao W-H, Motani R, Sun Y-L, Sun Z-Y. 2010. *Tanystropheus* cf. *T. longobardicus* from the early Late Triassic of Guizhou Province, southern China. J Vert Paleo 30:1082–1089.

Romer AS. (1956) *Osteology of the Reptiles*. (University of Chicago Press, Chicago), 772 pp.

Russell AP, Bauer AM. (2008) The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. *Biology of the Reptilia, Volume 21: The Skull and Appendicular Locomotor Apparatus of Lepidosauria*, eds. C Gans, AS Gaunt, K Adler. (Academic Press, London and New York), pp. 1–466.

Saller F, Renesto S, Dalla Vecchia FM. (2013). First record of *Langobardisaurus* (Diapsida, Protorosauria) from the Norian (Late Triassic) of Austria, and a revision of the genus. N Jahrb fur Geo Paleo Abh 268:83–95.

Schwartz HL, Gillette DD. (1994) Geology and taphonomy of the Coelophysis Quarry, Upper Triassic Chinle Formation, Ghost Ranch, New Mexico. J Paleo 68:1118–1130.

Schwarz D, Meyer CA, Frey E. (2005) New frontiers in reconstructing sauropods. Abstracts of the 3rd Swiss Geosciences Meetings:59–60.

Schwarz D, Frey E, Meyer CA. (2007) Pneumaticity and soft tissue reconstruction in the neck of diplodocid and dicraeosaurid sauropods. Acta Paleo Pol 52:167–188.

Schwarz-Wings D, Frey E, Martin T. (2009) Reconstruction of the bracing system of the trunk and tail in hyposaurine dyrosaurids (Crocodylomorpha; Mesoeucrocodylia). J Vert Paleo 29:453–472.

Schoch RR, Nesbitt SJ, Müller J, Lucas SG, Boy JA. (2010) The reptile assemblage from the Moenkopi Formation (Middle Triassic) of New Mexico. N Jahr fur Geo Paleo Abh 255:345–369.

Seidel MR. (1978) The somatic musculature of the cervical and occipital regions of *Alligator mississippiensis*. Ph.D. dissertation, City University of New York, New York, New York, 327 pp.

Sennikov AG. (2011) New tanystropheids (Reptilia: Archosauromorpha) from the Triassic of Europe. Paleont J 45:90–104.

Sereno PC. (1991) Basal archosaurs: phylogenetic relationships and functional implications. Soc Vert Paleo Mem 2:1–53.

Sereno PC, Arcucci AB. (1994) Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. J Vert Paleo 14:53–73.

Shubin NH, Sues H-D. (1991) Biogeography of early Mesozoic continental tetrapods: patterns and implications. Paleobio 17:214–230.

Snyder RC. (1954) The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. Amer J Anat 95:1–45.

Spielmann JA, Lucas SG, Rinehart LF, Heckert AB. 2008. The Late Triassic archosauromorph *Trilophosaurus*. Bull NM Mus Nat Hist Sci 43:1–177.

Sues H-D. (2003) An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. Can J Earth Sci 40:635–649.

Sues HD, Fraser NC. (2010) *Triassic Life on Land*. (Columbia University Press, New York), 236 pp.

Surahya S. (1989) *Atlas Komodo: studi anatomi dan kedudukannya dalam sistematik hewan*. (Gadjah Mada University Press, Gadjah Mada, India), 419 pp.

Thulbor RA. (1979) A proterosuchian thecodont from the Rewan Formation of Queensland. Mem Queens Mus 19:331–355.

Tschanz K. (1985) *Tanystropheus*—an unusual reptilian construction. Konstruktionsprin Lebender und Austgestorbener Reptilien. Konz Sonderforschungsbereich 230:169–178.

Tsuihiji T. (2004) The ligament system in the neck of *Rhea americana* and its implications for the bifurcated neural spines in sauropod dinosaurs. J Vert Paleo 24:165–172.

Tsuihiji T. (2005). Homologies of the transversospinalis muscles in the presacral region of Sauria (crown Diapsida). J Morph 263:151–178.

Vickers-Rich P, Rich TH, Rieppel O, Thulborn RA, McClure HA. (1999). A Middle Triassic vertebrate fauna from the Jihl Formation, Saudi Arabia. N Jahr fur Geo Paleo Abh 213:201–232.

Walker AD. (1961) Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. Phil Trans Roy Soc B 244:103–204.

Whiteside JH, Grogan DS, Olsen PE, Kent DV. (2011) Climatically driven biogeographic provinces of Late Triassic tropical Pangea. Proc Nat Acad Sci 108:8972–8977.

Wild R. (1973) Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergenbisse). Abhandlungen der Schweizerischen Paläontologischen Gesellschaft 95:1–162.

Wild R. (1980a) *Tanystropheus* (Reptilia: Squamata) and its importance for stratigraphy. Mém Soc Géo France 139:201–206.

Wild R. (1980b) Die Triasfauna der Tessiner Kalkalpen. XXIV. Neue funde von Tanystropheus (Reptilia, Squamata). Abh Schweiz Paläo Gesellschaft 102:1–44.

Wild, R. (1980c). The fossil deposits of Kupferzell, southwest Germany. Mesozoic Vertebrate Life 1:15–18.

Winchester L, Bellairs AA. (1977). Aspects of vertebral development in lizards and snakes. J Zool Soc London 181:495–525.

Zeigler KE, Lucas SG, Morgan VL. (2005). Vertebrate fauna of the upper Triassic Mesa Montosa Member (Petrified Forest Formation, Chinle Group), Chama Basin, northern New Mexico. NM Geol Soc Guidebook 56:335–

SUPPLEMENTARY DATA

SUPPLEMENTARY APPENDIX 1. Preparatory Notes.

Specimens were collected and consolidated in the field using Vinac™ (Air Products & Chemicals, Inc.), a polyvinyl acetate, or Butvar® B-76 (Solutia Company), a terpolymer of vinyl butyral, vinyl alcohol, and vinyl acetate monomers. Initial preparation was conducted by the authors, with final laboratory preparation by Virginia Heisey at Stony Brook University. At Stony Brook, the specimens were first bulk-consolidated with an acrylic colloidal dispersion in water sold as Primal/Rhoplex WS-24 by Conservation Resources, UK. This was allowed to dry completely and then followed by bulk consolidation with cyclododecane (supplied by Kremer Pigmente), a cyclic alkane hydrocarbon that sublimates at room temperature. During matrix removal Butvar® B-76 was used to adhere detached fragments. Consolidation of the bone was accomplished with Paleobond™ PB002 Penetrant Stabilizer (ethyl cyanoacrylate).

SUPPLEMENTARY APPENDIX 2. Taxon list for phylogenetic analyses.

Bibliographic references and institutional accession numbers of specimens that were scored based on firsthand examination.

Batrachotomus kupferzellensis–Gower, 1999, 2002; Gower et al., 2003.
Erythrosuchus africanus–NHMUK R 3592; Gower, 2003.
Euparkeria capensis–Ewer, 1965.
Gephyrosaurus bridensis–Evans, 1980, 1981.
Langobardisaurus pandolfii–MCSNB 2883, 4860; MFSN, 1921; Saller et al., 2013.
Macrocnemus bassanii–MCSN BES SC 111, V 457; Peyer, 1937.
Macrocnemus fuyuanensis–GMPKU-P-3001, Li et al., 2007; Jiang et al., 2011.
Mesosuchus browni–Dilkes, 1998.
Orovenator mayorum–Reisz et al., 2011.
Petrolacosaurus kansensis–Reisz, 1981.
Prolacerta broomi–BP/1/2675, 2676, 5375; Modesto and Sues, 2004.
Proterosuchus fergusi–NMQR 1484; Hughes, 1963; Cruickshank, 1972; Welman, 1998.
Protorosaurus speneri–USNM 442453, YPM 2437; Gottmann-Quesada and Sander, 2009.

Rhynchosaurus articeps–NHMUK R 1235, 1236; Benton, 1990.
Shinisaurus crocodilurus–Bever et al., 2005; Conrad, 2004, 2006.
Tanystropheus longobardicus–MCSN BES SC 61, SC 265, BES SC 1018, V 3663, V 3730; Wild, 1973; Nosotti, 2007.
Tanytrachelos ahynis–AMNH FARB 7206; YPM 7482, 8600; VMNH nos. 2826, 3423, 120015, 120016, 120019, 120042, 120043, 120046, 120047, 120048, 120049; Olsen, 1979.
Teyumbaita sulcognathus–Montefeltro et al., 2010, 2013.
Teraterpeton hrynewichorum–Sues, 2003.
Trilophosaurus buettneri–Hundreds of specimens from TMM, largely TMM 31025-140.
Trilophosaurus jacobsi–Spielmann et al., 2008.
Uromastyx sp.–complete skeleton in Stony Brook University comparative anatomy collection; El-Toubi, 1949.
Youngina capensis–BP/1/375, BP/1/2871; Gow; 1975; Currie, 1981; Gardner et al., 2010.

SUPPLEMENTARY APPENDIX 3. Characters employed in phylogenetic analyses.

Parentheses indicate datasets that included a variant of the character described. Most characters have been modified to accommodate this dataset and to improve descriptive informativeness. Further details on the correspondences between the current characters and those from past datasets can be found in each character's individual 'citations' listing on MorphoBank. Ordered characters are noted.

Note that 201 characters are present in this list, in contrast to the 200 presented in the phylogenetic analysis in the paper. The 201st character is an experimental "classical calcaneal tuber" character, intended to test the effects of splitting the morphology of the calcaneal tuber into two, separate characters. A run of this phylogenetic analysis incorporating this classical character and excluding the novel calcaneal tuber characters (189 and 190) produced no changes in the topology.

[1] Premaxilla, lateral surface: surface is smoothly sculptured (0); premaxilla is marked by anteroventral striations (1).

NOVEL character. This describes the tooth-like external sculpturing evident in all known cranial material of *Langobardisaurus*. Although initially regarded as having procumbent premaxillary and anterior dentary teeth (Renesto, 1994; Muscio, 1996), restudy suggests that the anterior 'teeth' are external striations on the surface of the bone (Saller et al., 2013). We incorporated this character to test the sister-group relationship of the initial *L. pandolfii* (MCSNB 2883, 4860) specimens with those attributed to *L. tonelloi* (MFSN 1921).

[2] Premaxilla, orientation of ventral margin: horizontal, roughly inline with maxillary ventral margin (0); slight downturn, such that the margin trends anteroventrally (1).

Derived from similarly informative characters in Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[3] Premaxilla, anterodorsal process (=nasal process): present, separating the nares (0); absent or reduced, creating a confluent external naris (1).

Derived from similarly informative characters in Gauthier et al. (1988b), Benton and Allen (1997), DeBraga and Rieppel (1997), Dilkes (1998), and Müller (2004).

[4] Premaxilla, posterodorsal process (= maxillary process, = subnarial process): (0) contributes a small ventral margin for the naris; (1) elongate, fitting across the anterior face of the maxilla.

Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Müller (2004), and Nesbitt (2011). Taxa scored as '0' for this character are scored as inapplicable ('-') for characters 5 and 6.

[5] Premaxilla, posterodorsal process (= maxillary process, = subnarial process): absent, such that premaxilla contributes a small ventral margin for the naris (0); posterodorsal process present, framing the posteroventral margin of the naris. (1).

Derived from similarly informative characters in DeBraga and Rieppel (1997), Dilkes (1998), and Nesbitt (2011). ORDERED.

[6] Premaxilla, posterodorsal process/maxilla contact: contact is a simple, straight margin (0); knob on the posterior margin of the posterodorsal process of the premaxilla fits into notch in the anterior surface of the maxilla. (1).

Derived from similarly informative characters in Dilkes (1998).

[7] Maxilla, orientation of ventral margin: ventral margin of maxilla is horizontal (0); ventral margin of maxilla is convex. (1).

Derived from similarly informative characters in Gauthier et al. (1988b) and Dilkes (1998).

[8] Maxilla, posterolateral surface: directly adjacent to alveolar margin (0); lateral process of maxilla present, creating distinct space between maxillary alveoli and posterolateral surface of the maxilla (1).

NOVEL character to describe the substantial space between the lateral surface of the cheek and the posteriormost portion of the upper tooth row in *Teraterpeton* (see Sues, 2003) and *Trilophosaurus* (see Gregory, 1945).

[9] Nasal, orientation of contact with prefrontal: oriented parasagitally (0); oriented anterolaterally (1).

Derived from similarly informative characters in Gauthier (1984), Jalil (1997), and Merck (1997).

[10] Prefrontal, contact with contralateral prefrontal: no contact, due to fronto-nasal contact (0); prefrontals approach medially, constricting fronto-nasal contact (1).

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[11] Lacrimal, facial contribution: forms a portion of lateral surface of the face, reaching anteriorly to the external naris (0); forms a portion of the lateral surface of the face, but does not reach naris (1); limited to orbital margin (2).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Müller (2004), and Conrad (2008). ORDERED.

[12] Lacrimal, anterior extension: lacrimal extends dorsally to reach the ventral margin of the nasal externally (0); lacrimal fails to reach nasal (1).

Derived from similarly informative characters in Gauthier et al. (1988), Benton and Allen (1997), Jalil (1997), Dilkes (1998), and Müller (2004).

[13] Antorbital fenestra: absent (0); present (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Dilkes (1998), and Nesbitt (2011).

[14] Frontals, degree of fusion: frontals unfused to one another (suture patent) (0); frontals fused in the midline (1).

Derived from similarly informative characters in Benton (1985), Gauthier (1988a), Rieppel (1994), Merck (1997), and Conrad (2008).

[15] Frontals, shape: frontal maintains transverse width throughout its anteroposterior length (0); frontals expand transversely posteriorly (1).

Derived from similarly informative characters in Gauthier et al. (1988a) and Conrad (2008).

[16] Frontal, shape of contact with parietal in dorsal view: roughly transverse in orientation (0); frontal exhibits posterolateral processes, forming anteriorly curved U-shaped contact (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[17] Frontal and postfrontal, surface texture: dorsal surface relatively smooth (0), dorsal surface exhibits distinct pitting. (1).

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[18] Postfrontal, medial contact with frontal and parietal: postfrontal forms broad contact with midline skull elements, without bifurcation (0); postfrontal bifid, fitting broadly across both parietal and frontal (1).

Derived from similarly informative characters in Gauthier et al. (1988a) and Hutchinson et al. (2012).

[19] Parietals, degree of fusion: parietals unfused to one another (patent suture) (0); parietals fused in the midline (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), Merck (1997), Müller (2004), and Nesbitt (2011).

[20] Parietal, sagittal cresting: parietal skull table flattened (0); dorsal exposure of parietal forms a raised margin, elevated above lateral excavation for jaw adductor musculature (1); thin, blade-like sagittal crest (2).

Derived from similarly informative characters in Gauthier et al. (1988), DeBraga and Rieppel (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011). ORDERED.

[21] Parietal, orientation of post-temporal process: roughly transverse (0); strong posterolateral angling (1).

Derived from similarly informative characters in Merck (1997) and Nesbitt (2011).

[22] Pineal foramen: present (0); absent (1).

Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988b), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Merck (1997,), and Nesbitt (2011). Taxa scored as '1' for this character are scored as inapplicable ('-') for character 23.

[23] Pineal foramen, position: entirely surrounded by parietals (0); situated within the frontoparietal suture (1).

Derived from similarly informative characters in Gauthier (1984), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[24] Postparietals: absent (0); present (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Müller (2004), and Nesbitt (2011). Taxa scored as '0' for this character are scored as inapplicable ('-') for character 25.

[25] Postparietals, degree of fusion: unfused to one another (0); fused as a midline interparietal (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b), DeBraga and Rieppel (1997), and Merck (1997).

[26] Postorbital, presence of medial process: medial process absent, with contributions of the frontal, parietal or postfrontal forming the posterodorsal orbital margin (0); present, postorbital contributing to posterodorsal orbital margin (1).

Derived from similarly informative characters in DeBraga and Rieppel (1997), Dilkes (1998), and Müller (2004).

[27] Postorbital, location of medial process: situated deep to postfrontal (0); dorsally excludes postfrontal from supratemporal fenestra margin. (1).

Derived from similarly informative characters in Benton (1985), DeBraga and Rieppel (1997), Merck (1997), Dilkes (1998), and Müller (2004).

[28] Postorbital, length of posterior process: contributes to less than one-half the length of the supratemporal bar (0); contributes to more than one-half the length of the supratemporal bar. (1).

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[29] Infratemporal fenestrae, conformation: present, distinct opening framed by squamosal, postorbital and jugal (0); postorbital, jugal, and squamosal fit against one another as a 'lateral temporal plate' present, with squamosal extending anteriorly to slot into a notch on the jugal (1).

Derived from similarly informative characters in Gauthier et al. (1988a), Merck (1997), and Müller (2004).

[30] Jugal, ornamentation of lateral surface: unornamented (0), distinct anteroposteriorly running shelf present (1).

Derived from similarly informative characters in Benton (1985), Jalil (1997), Merck (1997), and Müller (2004).

[31] Jugal, ascending process relative to supratemporal bar: process terminates ventral to bar (0); process intersects between postorbital and squamosal within bar (1).

Derived from similarly informative characters in Merck (1997).

[32] Jugal, posterior process: absent (0); present, but failing to contact the quadratojugal posteriorly (1); present, contacting the quadratojugal posteriorly (2).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), Benton and Allen (1997) DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011). ORDERED.

[33] Squamosal, descending process: present (0); absent (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Dilkes (1998), and Müller (2004). Taxa scored as '1' for this character are scored as inapplicable ('-') for character 34.

[34] Squamosal, size of descending process: forms massive flange that covers the quadrate entirely in lateral view (0), anteroposteriorly slender (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), and Merck (1997).

[35] Squamosal, posterior process: no posterior process (0); posterior process, extending beyond quadrate contact (1).

Derived from similarly informative characters in Merck (1997).

[36] Supratemporals: absent (0); present (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Merck (1997), Müller (2004), and Nesbitt (2011).

[37] Tabulars: (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), and Müller (2004).

[38] Quadratojugal: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Müller (2004), and Conrad (2008). Taxa scored as '1' for this character are scored as inapplicable ('-') for characters 39 and 40.

[39] Quadratojugal, anterior process: prominent anterior process for jugal articulation (0); no anterior process (1).

Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[40] Quadratojugal, anterior process: paralleling dorsal and ventral borders (0); anteriorly tapering anterior process (1).

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b), Merck (1997), and Müller (2004).

[41] Quadrate, posterior margin: straight, vertical posterior margin (0); concave, excavated posterior margin (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), and Müller (2004).

[42] Quadrate foramen/quadratojugal foramen, position: foramen positioned b/t quadrate and quadratojugal (0); foramen positioned within the quadrate (1).

Derived from similarly informative characters in Hutchinson et al (2012).

[43] Quadrate, tympanic crest: quadrate has no lateral expansion (0); flattened tympanic crest projects from lateral surface of quadrate (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), and Müller (2004).

[44] Palatal teeth: present (0); absent (1).

Any taxon scored as '1' for character 43 is scored as inapplicable ('-') for characters 45, 47, 48, 49, 50, and 51. This results in a single-step transition from present to absent, and vice versa, for palatal teeth. Benton (1985) employed a similar character.

[45] Vomerine teeth: (0) present, (1) absent.

Derived from similarly informative characters in Rieppel (1994), Merck (1997), Dilkes (1998), and Müller (2004).

[46] Vomer, contact with maxilla: vomer only contacts premaxilla (0), vomer-premaxilla contact expands onto maxilla (1).

Derived from similarly informative characters in Rieppel (1994), Merck (1997), Dilkes (1998), and Müller (2004).

[47] Palatine teeth: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier et al. (1988b, 1988a), Dilkes (1998), and Müller (2004).

[48] Pterygoid, anterior process dentition: (0) absent, (1) present.

Derived from similarly informative characters in Benton (1985), Merck (1997), Müller (2004) and Nesbitt (2011). Taxa scored as '0' for this character are scored as inapplicable ('-') for character 49.

[49] Pterygoid, anterior process dentition: one field (0); two fields (1); three fields (2).

Derived from similarly informative characters in Benton (1985), and Dilkes (1998).

[50] Pterygoid, transverse process dentition: (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b, 1988a), Rieppel (1994), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[51] Pterygoid, morphology of tooth row on transverse process: multiple rows on transverse process (0); one row on transverse process (1).

Derived from similarly informative characters in Benton (1985) and Müller (2004).

[52] Pterygoid, contact with contralateral pterygoid: pterygoids separated from one another in midline (0); pterygoids have small midline contact anteriorly (1); pterygoids meet broadly in the midline (2).

Derived from similarly informative characters in Benton (1985), Merck (1997), Dilkes (1998), and Müller (2004). ORDERED.

[53] Pterygoid, transverse process: lateral orientation in ventral view (0); anterolateral orientation in ventral view (1).

Derived from similarly informative characters in DeBraga and Rieppel (1997) and Müller (2004).

[54] Pterygoid, interpterygoid vacuity: pterygoids meet to form anteriorly tapering space (0); pterygoids meet to form anteriorly curved space (1).

Derived from similarly informative characters in DeBraga and Rieppel (1997) and Müller (2004).

[55] Supraoccipital, posterior surface: smooth posterior surface, (0); distinct dorsoventrally running crest in the midline (1).

Derived from similarly informative characters in DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[56] Supraoccipital: consists of a flattened posterior lamina (0), pillar-like (1).

Derived from similarly informative characters in Dilkes (1998).

[57] Opisthotic, ventral ramus: ventral ramus is a slender process (0); ventral ramus has distinct club-shaped expansion ventrally (1).

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[58] Opisthotic, paroccipital process: ends freely (0); contacts the suspensorium (1).

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988a), Jalil (1997), Dilkes (1998), and Müller (2004).

[59] Exoccipital, morphology of dorsal surface: exoccipital columnar throughout dorsoventral height, forming transversely narrow dorsal contact with more dorsal occipital elements (0); dorsal portion of exoccipital exhibits dorsomedially inclined process that forms transversely broad contact with more dorsal occipital elements (1).

NOVEL character.

[60] Exoccipital, contralateral contact dorsal to foramen magnum: exoccipitals do not meet dorsal to foramen magnum, such that supraoccipital contributes to foramen magnum (0); exoccipitals meet dorsal to foramen magnum, preventing supraoccipital contribution (1).

Derived from similarly informative characters in Rieppel (1994), Müller (2004), and Nesbitt (2011).

[61] Exoccipital, contralateral contact on floor of foramen magnum: absent, basioccipital contributes to floor of foramen magnum (0); present, excluding basioccipital from floor of the foramen magnum (1).

Derived from similarly informative characters in DeBraga and Rieppel (1997), Merck (1997), and Nesbitt (2011).

[62] Exoccipitals, fusion with opisthotic: absent (0); present (1).

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b, 1988a), Merck (1997), Hutchinson et al. (2012).

[63] Opisthotic, paroccipital process morphology: (0) unflattened and tapered, (1) anteroposteriorly-flattened distally.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b, 1988a), DeBraga and Rieppel (1997), and Merck (1997).

[64] Basioccipital, basal tubera: (0) poorly developed, failing to extend ventral to occipital condyle or absent, (1) present, extending ventral to level of occipital condyle.

Derived from similarly informative characters in DeBraga and Rieppel (1997) and Müller (2004).

[65] Parabasisphenoid, dentition on cultriform process: (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Dilkes (1998), and Müller (2004).

[66] Parabasisphenoid, parasphenoid crests: absent such that there is no ventral floor for the vidian canal (0); present as prominent ventrolateral extensions of the caudoventral processes, framing the ventromedial floor of the vidian canal (1).

As recognized in Merck (1997) for certain diapsids (e.g., *Youngina*, *Prolacerta*), the parasphenoid is developed into ventrolateral crests that form a ventromedial floor for the vidian canals. In several archosauromorph taxa (e.g., *Trilophosaurus*, rhynchosaurs), such crests are absent such that the foramina for the internal carotid arteries are not posteriorly preceded by crests.

[67] Parabasisphenoid, passage for internal carotid arteries: (0) within lateral wall of braincase, (1) within ventral surface of the parabasisphenoid.

Derived from similarly informative characters in Benton (1985), Merck (1997), Dilkes (1998), and Nesbitt (2011).

[68] Parabasisphenoid, conformation of ventral surface: (0) roughly planar, (1) distinct depression posterior to carotid canals (parabasisphenoid recess sensu Nesbitt, 2011).

Derived from similarly informative characters in Nesbitt (2011).

[69] Parabasisphenoid, length of cultriform process: (0) extremely elongate, reaching level of nares; (1) short, failing to reach level of nares.

Derived from similarly informative characters in DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[70] Parabasisphenoid, basipterygoid process orientation in transverse plane: (0) anterolateral, (1) lateral.

Derived from similarly informative characters in Dilkes (1998) and Müller (2004).

[71] Parabasisphenoid, location of abducens foramina: (0) within the dorsum sella; (1) track across dorsal surface of dorsum sella, or within prootic.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988a), Merck (1997), Dilkes (1998), and Nesbitt (2011).

[72] Laterosphenoid: (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b), Dilkes (1998), and Nesbitt (2011).

[73] Prootic, crista prootica: (0) present, (1) absent.

Derived from similarly informative characters in Jalil (1997), Merck (1997), and Dilkes (1998).

[74] Prootic, anterior inferior process: process present, sitting anterior to trigeminal foramen (0); absent, trigeminal foramen unframed anteriorly (1).

Derived from similarly informative characters in Jalil (1997) and Dilkes (1998).

[75] Prootic, paroccipital contribution: (0) does not contribute to anterior surface of paroccipital process, (1) contributes laterally tapering lamina to the anterior surface of the prootic.

Derived from similarly informative characters in Merck (1997) and Nesbitt (2011).

[76] Stapes, dorsal process: (0) absent, (1) present.

Derived from similarly informative characters in Benton (1985), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[77] Stapes, foramen for stapedial artery: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Jalil (1997), and Merck (1997).

[78] Dentary, divergence at symphyseal region of mandible: dentaries do not diverge (0); dentaries diverge into prominent anterolateral processes (1).

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[79] Coronoid process: (0) absent, (1) present.

Derived from similarly informative characters in Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), Müller (2004), and Nesbitt (2011).

[80] Surangular, lateral surface, foramen positioned near surangular-dentary contact: absent (0); present (1).

Derived from similarly informative characters in Modesto and Sues (2004).

[81] Surangular, lateral surface, foramen positioned directly anterolateral to glenoid fossa: absent (0); present (1).

Derived from similarly informative characters in Modesto and Sues (2004) and Nesbitt (2011).

[82] Angular, exposure on lateral mandibular surface: (0) broadly exposed, (1) limited to posteroventral sliver by dentary and surangular.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), and Müller (2004).

[83] Angular, exposure on lateral mandibular surface: (0) terminates anterior to the glenoid, (1) extends to the glenoid.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988a), and Merck (1997).

[84] External mandibular fenestra (EMF): (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b), Dilkes (1998), and Nesbitt (2011).

[85] Splenial, contribution to mandibular symphysis: (0) splenials contribute to symphysis; (1) splenials fail to contribute.

Derived from similarly informative characters in Benton (1985), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[86] Retroarticular process: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), and Dilkes (1998). Taxa scored as '1' for this character are scored as inapplicable ('-') for character 87.

[87] Retroarticular process, composition: (0) articular only, (1) fused articular-prearticular.

Derived from similarly informative characters in Benton (1985), Jalil (1997), Merck (1997), and Dilkes (1998).

[88] Marginal dentition on anteriormost portions of premaxilla and dentary: (0) present, (1) absent.

Derived from similarly informative characters in Benton (1985), DeBraga and Rieppel (1997), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[89] Marginal dentition, enlarged caniniform teeth in maxilla: (0) present, (1) absent, maxillary teeth subequal in size.

Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[90] Marginal dentition: non-serrated (0), serrated (1).

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b), Dilkes (1998), and Nesbitt (2011).

[91] Marginal dentition, shape of posterior margin of tooth: (0) convex or straight, (1) concave.

This represents an anatomical description of the recurved dentition in many archosauromorphs (e.g., *Macrocnemus*, *Prolacerta*, Archosauriformes) as characterized in Gauthier (1984), Benton (1985), Jalil (1997), Merck (1997), Dilkes (1998), and Nesbitt (2011).

[92] Marginal dentition, arrangement: (0) single row of marginal teeth, (1) multiple zahnreihen in maxilla and dentary.

Derived from similarly informative characters in Benton (1985) and Dilkes (1998).

[93] Marginal dentition, morphology of crown base: tooth crown forms a single, pointed crown (0); tooth crown forms a flattened platform with pointed cusps (1); tooth crown has three, mesiodistally arranged cusps (2).

This character represents an expansion on the dental morphology characters in Merck (1997) and Dilkes (1998); state (1) represents the assumption that the labiolingually broad tooth form apparent in *Teraterpeton* and *Trilophosaurus* is homologous.

[94] Marginal dentition, implantation: (0) teeth situated in shallow dental groove (pleurodonty + thecodonty), (1) teeth on dorsal surface of tooth-bearing bones (acrodonty).

This and subsequent dental implantation characters represent novel subdivisions of certain past characters that describe tooth implantation in simpler terms (e.g., acrodonty, thecodonty, subthecodonty). Past characters describing the rooting of teeth appear in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), and Conrad (2008). Taxa scored as '1' are scored as inapplicable ('-') for characters 95, 96, and 97.

[95] Marginal dentition, lingual surface: (0) teeth walled by minimal lingual wall (subthecodonty), (1) no lingual wall.

Past characters describing the rooting of teeth appear in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), and Conrad (2008).

[96] Marginal dentition, lingual surface: (0) teeth walled by minimal lingual wall only, (1) interdental plates are present.

Interdental plates contribute to the 'true' thecodont condition evident in many archosauriforms; forming the mesial, distal, and lingual walls of the alveoli. Triangular interdental plates are apparent in the maxillae of *Tanystropheus langobardicus* specimens (MCSN BES SC 265, 1018), suggesting that thecodonty is not restricted to derived archosauriforms. Past characters describing the rooting of teeth appear in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), and Conrad (2008).

[97] Marginal dentition, rooting: (0) tooth crowns are not attached to dentigerous bones when fully erupted (1) teeth ankylosed to tooth-bearing elements when fully erupted.

Characters in Gauthier (1984), Benton (1985), DeBraga and Rieppel (1997), Merck (1997), and Nesbitt (2011) address the superficial attachment of rooted teeth to the tooth-bearing element (e.g., ankylothecodonty).

[98] Marginal dentition, tooth shape at crown base: (0) circular, (1) labiolingually compressed, (2) labiolingually wider than mesiodistally long.

Gauthier (1984), Benton (1985), Jalil (1997), and Merck (1997) all employ characters to describe the degree of labiolingual compression in marginal teeth. This formulation represents the first to describe labiolingual tooth breadth across diapsids, including the compression in archosauriforms and extreme breadth in *Trilophosaurus*.

[99] Palatal dentition, morphology: small, button-like teeth (0); small, conical teeth (1).

Derived from similarly informative characters in Merck (1997).

[100] Marginal dentition, procumbency: (0) anteriormost marginal teeth have similar apicobasal orientation to posterior teeth, (1) anteriormost teeth are procumbent.

Derived from similarly informative characters in Rieppel (1994), Merck (1997), and Müller (2004).

[101] Presacral vertebrae, shape of anterior articular surface: planar (0), concave (1).

Derived from similarly informative characters in Rieppel (1994), DeBraga and Rieppel (1997), and Müller (2004).

[102] Presacral vertebrae, shape of posterior articular surface: planar (0); concave (1), convex (2).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), and Müller (2004). Taxa scored as either '0' or '1' for character 103 are scored as inapplicable ('-') for character 103.

[103] Presacral vertebrae, development of posterior articular surface convexity: moderate (0), hemispherical (1).

NOVEL character. This addresses the sampled diversity in posterior vertebral condyles. In certain archosauromorphs (e.g., *Trilophosaurus*), there is only a slight, centralized posterior expansion of the posterior articular surface of the vertebra (state 0). In the sampled squamates and certain derived tanystropheids, the entire posterior articular surface is hemispherical (state 1).

[104] Anterior cervical ribs, shaft shape: tapering rapidly, roughly triangular in lateral view (0); ribs taper gradually, elongate and splint-like in lateral view. (1).

Derived from similarly informative characters in Jalil (1997), Merck (1997), and Dilkes (1998).

[105] Cervical ribs, anterior process: (0) absent, (1) present.

Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), and Müller (2004).

[106] Cervical vertebrae, intercentra: (0) present, (1) absent.

Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), Dilkes (1998), and Nesbitt (2011).

[107] Anterior post-axial cervical vertebrae, shape of anterior articular surface: subcircular, roughly equivalent in dorsoventral height and transverse width (0); compressed, with a greater transverse width than dorsoventral height (1).

NOVEL character. This describes the newly recognized morphology of the cervical centra in *Langobardisaurus*, *Tanytrachelos*, and the Hayden Quarry remains.

[108] Cervical vertebrae, ventral keel: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier et al. (1988b), Rieppel (1994), and DeBraga and Rieppel (1997).

[109] Anterior post-axial cervical vertebrae, shape of ventral surface excluding keel: ventrally rounded (0); ventral face flattened (1).

NOVEL character. The ventral surfaces of cervical centra in *Tanystropheus*, *Tanytrachelos*, and the Ghost Ranch remains exhibit a flattened ventral surface in coronal section. No other taxa sampled exhibit this feature.

[110] Cervical vertebrae, number of costal facets: (0) one, (1) two.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Jalil (1997), Merck (1997), Dilkes (1998), and Müller (2004). Taxa scored as ‘0’ for this character are scored as inapplicable (‘-‘) for characters 111 and 112.

[111] Anterior post-axial cervical vertebrae, position of diapophysis (or dorsal margin of synapophyses): at or near dorsoventral level of pedicles (0); further ventrally, near the dorsoventral midpoint of the centrum. (1).

This character and subsequent characters describing the articulations between ribs and vertebrae are couched in terms of costal facets, in contrast to past formulations describing the morphologies of individual ribs [e.g., Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Jalil (1997), Merck (1997), Müller (2004)]. We herein employ a formulation directly addressing the anatomy of the vertebrae, as that requires one less level of inference about the rib anatomy of the Hayden Quarry tanystropheid.

[112] Anterior post-axial cervical vertebrae, relative location of costal facets: facets distinctly offset from one another (0); facets very closely appressed to one another with little or no finished bone separation. (1).

NOVEL character. We employ this character to describe the extremely close-set costal facets in tanystropheid cervical vertebrae.

[113] Anterior post-axial cervical vertebrae, shape of neural spine base: elongate, subequal in length to the neural arch (0); short, spine restricted to posterior half of neural arch (1).

Derived from similarly informative characters in Benton and Allen (1997) and Jalil (1997).

[114] Anterior post-axial cervical vertebrae, neural spine shape in cross-section: transversely narrow (0), elliptical or circular (1).

Derived from similarly informative characters in Merck (1997).

[115] Cervical vertebra, shape of anterior margin of neural spine: (0) linear, (1) anterodorsal process present forming an anterior notch.

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[116] Anterior post-axial cervical vertebrae, anterior margin of neural spine, direction of inclination: inclined posterodorsally (0); inclined anterodorsally (1).

NOVEL character. Archosauromorphs (excluding rhynchosaurs) are characterized by cervical neural spines with a long axis oriented anterodorsally, in contrast to the condition in other reptiles. Nesbitt (2011) uses a similar character to describe the anterodorsal inclination of the posterior cervical neural spines in certain poposauroids.

[117] Anterior post-axial cervical vertebrae, transverse width of dorsal tip of neural spine: transversely slender (0); expanded transversely with a midline cleft (1).

This character describes the morphology evident in the cervical neural spines of certain ‘prolacertiforms’, including *Langobardisaurus* (MCSNB 2883), the Hayden Quarry tanystropheid cervical vertebrae, and *Rhombopholis* (Benton and Walker, 1996). Benton and

Allen (1997) and Dilkes (1998) employed a similar character, describing this morphology as a tabling of the cervical neural spines.

[118] Cervical vertebrae, relative location of dorsal margin of mid-cervical neural spines: (0) spines are equivalent in height and length to other cervical neural spines; (1) spines are dorsoventrally depressed at their anteroposterior midpoints, leaving them little more than midline dorsal ridges.

NOVEL character. This character describes the dorsoventrally low midpoint of the cervical neural spine in *Tanystropheus* and *Amotosaurus*. Despite a similar degree of cervical elongation to *Amotosaurus*, the neural spines in *Langobardisaurus* and the Hayden Quarry cervical vertebrae remain similar in dorsoventral height throughout their anteroposterior lengths.

[119] Cervical vertebrae, dorsal surface of postzygapophyses: (0) smooth and rounded, (1) posteriorly pointed projections (epipophyses) present.

Derived from similarly informative characters in Nesbitt (2011).

[120] Anterior dorsal vertebrae, position of parapophysis (or ventral margin of dorsal synapophysis): positioned partially on lateral margin of centrum (0); positioned entirely on neural spine (1).

Derived from similarly informative characters in Merck (1997).

[121] Posterior dorsal vertebra, position of parapophysis (or ventral margin of dorsal synapophysis) in trunk vertebrae: positioned partially on lateral margin of centrum (0); positioned entirely on neural arch. (1).

Derived from similarly informative characters in Merck (1997).

[122] Anterior dorsal vertebrae, number of pectoral costal facets: one (holocephaly) (0); two (dichocephaly) (1); three (tricephaly) (2).

Benton (1985), Jalil (1997), Merck (1997), Dilkes (1998), and Müller (2004) employ characters to describe holocephaly and dichocephaly in the dorsal column. A third state is added here to describe the three-headed 'pectoral' vertebrae in early archosauriforms (e.g., *Erythrosuchus*, *Proterosuchus*).

[123] Posterior dorsal vertebrae, costal facets: single rib facet (0); inverse-L rib facet (suggesting partial confluence of diapophysis and parapophysis) (1); double rib facet (2).

Benton (1985), Jalil (1997), Merck (1997), Dilkes (1998), and Müller (2004) employ characters to describe holocephaly and dichocephaly in the dorsal column. State (1) is novel, differentiating the complex shape of the facets in certain archosauromorphs (e.g., *Trilophosaurus*) from rounded facets evident in certain saurians (e.g., lepidosaurs).

[124] Posterior dorsal vertebra, ribs and vertebrae: unfused (0); fused (1).

Derived from similarly informative characters in Benton and Allen (1997), Jalil (1997), Merck (1997), and Dilkes (1998).

[125] Dorsal vertebrae, neural spine, dorsal portion: similar width as the more distal portion of the neural spine (0); expanded transversely into a flattened tip (= spine table) (1).

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b), Merck (1997), Dilkes (1998), and Nesbitt (2011). Taxa scored as ‘0’ for this character are scored as inapplicable (‘-‘) for characters 126 and 127.

[126] Dorsal vertebrae, breadth of neural spine expansion: little lateral expansion relative to the neural spine base (0); transversely broad, much wider than neural spine base. (1).

NOVEL character. This character differentiates between the subtle transverse expansion in certain archosauriforms (e.g., *Euparkeria*) and the extensive transverse broadening in tanystropheids.

[127] Dorsal vertebrae, texturing on dorsum of neural spine expansion: marked by irregular rugosities (0); marked by transverse striations (1).

In his character describing the dorsal surface of the neural spine table, Nesbitt (2011) had three states: one to describe absence of tables, one to describe flat-topped tables, and one to describe domed tables. This renders the presence of tables non-homologous. Our coding here instead suggests that the presence of a table is homologous.

[128] Dorsal vertebrae, intercentra: present (0); absent (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), and Nesbitt (2011).

[129] Dorsal vertebra, height of neural spines: (0) tall, greater in dorsoventral height than anteroposterior length (1) long and low, lesser in dorsoventral height than anteroposterior length.

Derived from similarly informative characters in Benton (1985) and Dilkes (1998).

[130] Dorsal vertebrae, accessory zygosphene-zygantrum articulations: (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Müller (2004), and Conrad (2008).

[131] Second sacral rib, shape: (0) rib is a single unit, (1) rib bifurcates distally into anterior and posterior processes.

Derived from similarly informative characters in Gauthier et al. (1988a), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011). Taxa scored as ‘0’ for this character are scored as inapplicable (‘-‘) for character 132.

[132] Second sacral rib, morphology of posterior process: (0) terminally blunted, (1) sharp distally.

Dilkes (1998) incorporates three states in his character describing the bifurcation of the second sacral rib: one for an unbifurcated rib, one for a bifid rib with a blunted distal end, and one for a bifid rib with a tapered distal end. This characterization thus does not recognize the homology of the bifurcated morphology. Our characterization assumes homology between sampled bifurcated second sacral ribs.

[133] Caudal vertebrae, shape of transverse processes: (0) processes curve posterolaterally, (1) processes straight.

Derived from similarly informative characters in DeBraga and Rieppel (1997), Merck (1997), and Dilkes (1998).

[134] Caudal vertebrae, orientation of transverse processes: (0) base of process perpendicular to the long axis of the vertebra, (1) processes angled posterolaterally from base.

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[135] Caudal vertebrae, autotomic septa within the centrum: (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b, 1988a), and Merck (1997).

[136] Chevron, shape of hemal spine: (0) tapers along its anteroposterior length tapers along its anteroposterior length (0); maintains breadth along its length (1); broadens distally, forming inverted T shape (2); broadens distally, forming subcircular expansion (3).

Derived from similarly informative characters in Dilkes (1998).

[137] Gastralia, ossification: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988a), DeBraga and Rieppel (1997), Merck (1997), Dilkes (1998), and Müller (2004). Taxa scored as ‘1’ for this character are scored as (‘-‘) for character 138.

[138] Gastralia, pairs of lateral gastralia: (0) two, (1) one.

Derived from similarly informative characters in Merck (1997).

[139] Epiphyses of limb elements, secondary ossification centers: (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a) and Merck (1997).

[140] Cleithrum: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), and Müller (2004).

[141] Clavicle, portion articulated with the interclavicle, shape: broader than distal portion of clavicle (0), similar in narrowness to the distal portion of the clavicle. (1).

Derived from similarly informative characters in Merck (1997), Dilkes (1998), and Müller (2004).

[142] Interclavicle, shape: transversely robust, forming broad diamond anteriorly (0); transversely gracile anteriorly, forming anchor-like shape anteriorly. (1).

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. 1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), Dilkes (1998), and Müller (2004).

[143] Interclavicle, shape of anterior surface anteromedial to clavicular articulations: (0) smooth margin, (1) prominent notch in margin.

Derived from similarly informative characters in Merck (1997), Dilkes (1998), and Müller (2004).

[144] Interclavicle, shape of caudal stem: slender, tapering (0); marked expansion (1).

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[145] Scapula, scapular blade, orientation of the long axis: (0) blade oriented directly dorsally, (1) curves posterodorsally.

Derived from similarly informative characters in Benton and Allen (1997).

[146] Scapula, morphology just distal to the glenoid fossa, lateral side: (0) prominent tubercle developed, (1) slight depression or smooth bone present,

Derived from similarly informative characters in Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), and Merck (1997).

[147] Coracoid, number of ossifications: (0) two, (1) one.

Derived from similarly informative characters in Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[148] Coracoid, infraglenoid morphology: (0) no development of coracoid posteroventral to glenoid (1) prominent post-glenoid process on coracoid, terminating in thickened margin.

Derived from similarly informative characters in Benton (1985) and Nesbitt (2011).

[149] Sternum, ossification of sternal plates: (0) absent, (1) present.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[150] Humerus, ectepicondyle, presence of radial nerve groove: absent (0), present (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), Benton and Allen (1997), Jalil (1997), and Dilkes (1998).

[151] Humerus, ectepicondyle, morphology of radial nerve groove: groove has no roof (0); groove roofed, forming ectepicondylar foramen (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), Benton and Allen (1997), Jalil (1997), and Dilkes (1998).

[152] Humerus, ectepicondyle morphology: prominent preaxial crest (0); no crest (1).

Derived from similarly informative characters in DeBraga and Rieppel (1997) and Merck (1997).

[153] Humerus, entepicondyle morphology: entepicondylar foramen absent (0); entepicondylar foramen present (1).

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), and Dilkes (1998).

[154] Humerus, entepicondyle morphology: smooth margin between shaft and post-axial condyle (0); prominent entepicondylar crest present (1).
Derived form similarly informative characters in DeBraga and Rieppel (1997) and Müller (2004). Taxa coded as ‘0’ for this character are coded as ‘-‘ for character 155.

[155] Humerus, entepicondylar crest morphology: crest exhibits a curved proximal margin (0); crest exhibits a prominently angled proximal margin (1).
Derived from similarly informative characters in DeBraga and Rieppel (1997) and Müller (2004).

[156] Humerus, distal condyle morphology: (0) distinct trochlear and capitular articulations; (1) low, double condyle.
Derived from similarly informative characters in DeBraga and Rieppel (1997) and Müller (2004).

[157] Ulna, ossified olecranon process: (0) present, (1) absent.
Derived from similarly informative characters in Benton (1985), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

[158] Medial centrale of hand: (0) absent, (1) present.
Derived from similarly informative characters in Gauthier (1984), Benton and Allen (1997), Jalil (1997), and Dilkes (1998).

[159] Distal carpal five: (0) absent, (1) present.
Derived from similarly informative characters in Merck (1997) and Nesbitt (2011).

[160] Intermedium: (0) present, (1) absent.
Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988a), Benton and Allen (1997), Jalil (1997), and Merck (1997). Taxa scored as ‘1’ are scored as ‘-‘ for 161.

[161] Ulnare and intermedium, perforating foramen between elements: (0) present, (1) absent.
Derived from similarly informative characters in Benton (1985), DeBraga and Rieppel (1997), and Merck (1997).

[162] Manual digit four, phalangeal formula: (0) five phalanges, (1) four phalanges.
Merck (1997) character 414 similarly describes the phalangeal count of manual digit four, but with additional states to describe hyperphalangy in certain marine reptiles.

[163] Puboischiadic plate, fenestration: (0) no fenestrae, (1) thyroid fenestra within plate.
Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988a), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), and Müller (2004).

[164] Ilium, long axis of orientation for iliac blade: horizontal orientation (0); posterodorsal orientation (1).

Derived from similarly informative characters in Gauthier et al. (1988b, 1988a).

[165] Ilium, anteroventral process extending from anterior margin of pubic peduncle: absent (0); present, process draping across anterior surface of pubis (1).

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b, 1988a), and Merck (1997).

[166] Ilium, supra-acetabular crest: crest absent, posterodorsal margin of acetabulum similar in development of anterodorsal margin (0); prominent anterodorsal bony lamina frames the anterodorsal margin of the acetabulum. (1).

Derived from similarly informative characters in Gauthier et al. (1988b).

[167] Ilium, shape of supra-acetabular margin: dorsalmost margin of acetabulum is unsculptured (0); prominent, bulbous rugosity superior to acetabulum. (1).

NOVEL character. A stout expansion of the supraacetabular crest at the dorsalmost point on the ilium appears in multiple archosauromorphs (e.g., *Tanystropheus*, *Proterosuchus*).

[168] Ilium, acetabulum shape: irregular, marked by posterodorsal invasion by finished bone (0); roughly circular, no posterodorsal invasion (1).

Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), Dilkes (1998), and Müller (2004).

[169] Ilium, anterior margin of iliac blade, anterior process or tuber: absent, smooth anterior margin (0); process or tuber present (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), DeBraga and Rieppel (1997), Dilkes (1998), and Müller (2004).

[170] Ilium, anterior process/tuber of ilium: (0) anterior process/tuber small, with anterodorsal margin of ilium curving smoothly into dorsal margin of iliac blade; (1) large and anteriorly projecting tuber, with dorsal margin of tuber nearly continuous with dorsal margin of iliac blade.

NOVEL character. This character serves to describe the distinctions in shape of the anterior margin of the ilium in certain archosauromorphs. The ilium in certain taxa (e.g., *Mesosuchus*, *Tanystropheus*, *Trilophosaurus*) exhibits a small anterior tubercle that interrupts an anterodorsally curved border to the iliac blade (state 0). Other taxa (e.g., derived rhynchosaurs, *Tanytrachelos*, *Erythrosuchus*) exhibit a substantial anterior projection of the tubercle, such that there is no anterodorsal curvature.

[171] Ilium, development of posterior process: (0) weakly developed, failing to extend well posterior of acetabulum; (1) strongly developed, extending well posterior to the acetabulum.

Derived from similarly informative characters in Gauthier (1984), Dilkes (1998), and Müller (2004).

[172] Ilium, morphology of dorsal blade margin: (0) smoothly textured dorsal border, (1) distinct dorsoventral striations running from acetabulum to dorsal margin of iliac blade.

NOVEL character.

[173] Pubis, morphology of symphysis: (0) pubic apron present, with distinct anteroventral downturn of the symphyseal region, (1) pubic apron absent, symphyseal region only in coronal plane.

Derived from similarly informative characters in Dilkes (1998).

[174] Pubis, pubic tubercle: absent (0); present (1).

Derived from similarly informative characters in DeBraga and Rieppel (1997) and Müller (2004). This character describes the thickening of the ventrolateral surface of the pubis. Such a thickening is evident in early diapsids [e.g., *Araeoscelis* (Vaughn, 1955), *Petrolacosaurus* (Reisz, 1981)], lepidosaurs [e.g., *Clevosaurus* (Fraser, 1988), *Gephyrosaurus* (Evans, 1981)], and archosauromorphs [e.g., archosauriforms (Nesbitt, 2011), rhynchosaurs (Benton, 1983, 1990)]. The homologizing of the craniolateral expansion of the pubic surface in archosauromorphs with elongate pubic symphyses with the pubic tubercle in other reptiles is in contrast to Hutchinson (2001).

[175] Pubis, lateral surface, development of a lateral tubercle (sensu Vaughn, 1955): (0) present, (1) absent.

NOVEL character. This describes the accessory tubercle present on the lateral surface of the pubis in the most primitive diapsids (Vaughn, 1955; Reisz, 1981). This structure may be homologous with the smaller, crest-like ambiens process in early archosauromorphs.

[176] Ischium, shape of posterior margin: linear posterior margin (0), posterior process extends from posterodorsal ischiadic margin (spina ischii sensu El-Toubi, 1949) (1).

Derived from similarly informative characters in Merck (1997).

[177] Femur, profile in pre-axial view: (0) femoral shaft exhibits sigmoidal curvature, (1) femoral shaft linear with slight ventrodistal curvature.

Gauthier et al. (1988b) and Benton and Allen (1997) employ a similar character to describe straightness in the femoral shafts of certain reptile taxa. Our character describes the complete lack of a proximodorsal incline of the proximal end of the femur in certain derived tanystropheids (e.g., *Tanytrachelos*, *Langobardisaurus*).

[178] Femur, morphology of proximal end of head; (0) well-ossified convex head, hemispherical; (1) concave surface with groove.

Ezcurra (2006) and Nesbitt (2011) employed a similar character to differentiate proximally grooved proximal femora (e.g., *Erythrosuchus*) from the smooth and rounded heads in other lineages (e.g., crocodylomorphs). Here, it differentiates the flattened and grooved proximal femora in archosauromorphs (e.g., *Protorosaurus*, *Prolacerta*, early archosauriforms) from the prominent and rounded heads in lepidosaurs and early diapsids (e.g., *Petrolacosaurus*, *Coelurosauravus*). The grooved proximal femora of certain basal lineages (e.g., tanystropheids, *Trilophosaurus*, *Proterosuchus*) very closely resembles lepidosaur femora from which the proximal epiphysis is removed.

[179] Femur, development of internal trochanter crest: (0) trochanteric crest does not reach femoral head; (1) trochanteric crest reaches far proximally, continuous with the femoral head.

Derived from similarly informative characters in Gauthier et al. (1988b).

[180] Femur, size of distal condyles (medial and lateral), comparison: about equal in size (0); unequal, lateral condyle larger than the medial condyle. (1).

Derived from similarly informative characters in Benton (1985), Rieppel (1994), DeBraga and Rieppel (1997), Dilkes (1998), and Müller (2004).

[181] Femur, expansion of distal condyles relative to femoral shaft: (0) distinct expansion beyond the circumference of the femoral shaft, (1) limited expansion beyond the circumference of the femoral shaft.

Derived from similarly informative characters in Gauthier et al. (1988b) and Nesbitt (2011).

[182] Femur, shape of medial tibial condyle in distal view: (0) medial surface is rounded and mound-like, (1) medial surface is triangular and sharply pointed.

NOVEL character. This describes the prominent ventral pointedness of the pre-axial portion of tibial condyle in certain archosauromorphs (e.g., *Trilophosaurus*, *Prolacerta*, *Proterosuchus*).

[183] Femur, crista tibiofibularis, shape of ventral surface: (0) flattened and planar, (1) rounded and mound-like.

NOVEL character. This character describes the massive and bulbous cristae tibiofibularis in certain archosauromorphs (e.g., *Trilophosaurus*, *Prolacerta*, *Proterosuchus*), in contrast to the smaller and ventrally flattened cristae in sampled lepidosaurs and the Hayden Quarry femora.

[184] Pedal centrale: (0) absent as distinct ossification, fused to astragalus; (1) present as distinct ossification.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Benton and Allen (1997), DeBraga and Rieppel (1997), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[185] Astragalus-calcaneum, extent of co-ossification: (0) present as distinct ossifications (1) co-ossified.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[186] Astragalus-calcaneum, perforating foramen at contact: (0) distinct foramen situated between astragalus and calcaneum, (1) no foramen evident between astragalus and calcaneum.

Derived from similarly informative characters in Gauthier (1984), Benton and Allen (1997), Merck (1997).

[187] Calcaneum, distal facet: (0) distal facet is little broader than is the proximal facet, (1) distal facet is markedly expanded, more than twice the breadth of the proximal facet.

NOVEL character. State (1) describes the marked expansion of the distal tarsal facet in the calcanei of *Tanytrachelos ahynis* and the Hayden Quarry tanystropheid. From a pre-axial view (i.e. looking at the astragalar contact surface of the calcaneum), the bone is narrow proximally. At its proximodistal midpoint, the pre-axial portion of the calcaneum broadens to more than twice its proximal breadth, making the distal facet substantially wider.

[188] Calcaneum, development of lateral margin (0) calcaneum terminating in unthickened margin, (1) roughened tuberosity present laterally.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al (1988b), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[189] Calcaneum, expansion of lateral margin (0) calcaneum has little postaxial expansion; (1) lateral wing of calcaneum is twice as broad or broader than the distal calcaneal facet.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al (1988b), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[190] Calcaneum, lateral projection (0) ventrolateral margin of calcaneum projection coplanar with dorsolateral margin of projection, (1) ventrolateral margin of calcaneum 'curls' externally.

NOVEL character. State (1) describes the curious condition of the calcaneal tuber in *Tanytrachelos* and the Hayden Quarry calcaneum, in which the ventral margin of the postaxial 'wing' of the calcaneum curls away from the midline. Thus, the ventral and postaxial margin of the bone would arc away from the animal, presuming the hindlimb was held in a sprawling position.

[191] Distal tarsal four, morphology of proximal contact: (0) smooth contact surface for proximal tarsals, (1) prominent process for contact with proximal tarsals.

Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988a), DeBraga and Rieppel (1997), Merck (1997), Dilkes (1998), and Müller (2004).

[192] Pedal centrale, contact with tibia: (0) absent, (1) present.

Derived from similarly informative characters in Merck (1997) and Dilkes (1998).

[193] First distal tarsal: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

[194] Second distal tarsal: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Benton and Allen (1997), Dilkes (1998), and Nesbitt (2011).

[195] Fifth distal tarsal: (0) present, (1) absent.

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), and Müller (2004).

[196] Metatarsal five, shape of proximal postaxial margin: smooth, curved margin (0); prominent, pointed process (outer process sensu Robinson, 1975) (1).

NOVEL character, describing a prominent proximal prong on the postaxial margin of the fifth metatarsal in certain archosauromorphs, including *Trilophosaurus* (TMM 31025-140).

[197] Metatarsal five, angling of primary shaft with proximal tarsal articulation: metatarsal is straight, with proximal tarsal articulation forming straight line with primary shaft (0); metatarsal is hooked, with proximal tarsal articulation forming right angle with primary shaft (1).

Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b, 1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011). Taxa scored as '0' for this character are scored as inapplicable ('-') for character 198.

[198] Metatarsal five, concavity along preaxial margin: (0) prominent concavity present, (1) concavity absent, creating blocky metatarsal five.

Derived from similarly informative characters in Benton (1985), Benton and Allen (1997), and Merck (1997).

[199] Pedal digits, morphology of digit five: (0) proximal phalanx shorter than proximal phalanx of digit four; (1) proximal phalanx elongate, longer than all other proximal phalanges.

Derived from similarly informative characters in Benton (1985), Benton and Allen (1997), Jalil (1997), Merck (1997), and Dilkes (1998).

[200] Heterotopic ossifications: (0) absent in a minimum of 5 individuals, (1) present.

This character is modified from those employed by Benton (1985), Benton and Allen (1997), Jalil (1997), Merck (1997), and Dilkes (1998). In many taxa studied herein, a limited number of fossil individuals are known; in those taxa with heterotopic ossifications, they are anticipated to exist in male individuals. Presuming a 1:1 male-female ratio, taxa are only scored as (0) if five or more individuals are known not to exhibit heterotopic ossifications. Therefore there is a p (all 5 individuals are of one sex) = $0.5^5 = 0.03125$. Requiring five individuals thus allows greater than 95% confidence that a sexually heterogeneous sample of individuals exists.

[201] Classical calcaneal tuber character: (0) tuber absent, (1) tuber present.

EXCLUDED FROM FIGURED/DISCUSSED PHYLOGENETIC ANALYSIS. This character represents the standard calcaneal tuber character employed in past phylogenetic analyses. This character is divided into two separate features in the final analysis, characters 189 and 190.

SUPPLEMENTARY LITERATURE CITED

Benton MJ. (1985) Classification and phylogeny of the diapsid reptiles. Zool J Linn Soc 84:97–164.

Benton MJ. (1990) The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. Phil Trans Roy Soc B 328:213–306.

Benton MJ, Allen JL. (1997) *Boreopricea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles. Palaeo 40:931–953.

Bever GS, Bell CJ, Maisano JA. (2005) The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). Paleo Elect 8:1–36.

Conrad JL. (2004) Skull, mandible, and hyoid of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). Zool J Linn Soc 141:399–434.

Conrad JL. (2006) Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). J Morph 267:759–775.

Conrad JL. (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bull Am Mus Nat Hist 310:1–182.

Cruickshank ARI. (1972) The proterosuchian thecodonts. *Studies in Vertebrate Evolution: Essays Presented to F. R. Parrington*, eds TS Kemp, KA Joysey. (Olive and Boyd, Edinburgh, U.K), pp. 89–119.

Currie PJ. (1981) The vertebrae of *Youngina* (Reptilia: Eosuchia). Can J Earth Sci 18:815–818.

DeBraga M, Rieppel O. (1997) Reptile phylogeny and the interrelationships of turtles. Zool J Linn Soc 120:281–354.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Phil Trans Roy Soc B 353:501–541.

El-Toubi MR. (1949) The post-cranial osteology of the lizard Uromastyx aegyptia (Forskal). J Morph 84:281–292.

Evans SE. (1980) The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool J Linn Soc 70:203–264.

Evans SE. (1981) The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. Zool J Linn Soc 73:81–116.

Ewer RF. (1965) The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil Trans Roy Soc B 248:379–435.

Gardner NM, Holliday CM, O'Keefe FR. (2010) The braincase of *Youngina capensis* (Reptilia, Diapsida): new insights from high-resolution CT scanning of the holotype. Palaeo Elect 13:1–16.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph. D. Dissertation, University of California, Berkeley, California, 564 pp.

Gauthier JA, Estes R, de Queiroz K. (1988a) A phylogenetic analysis of Lepidosauromorpha. The Phylogenetic Relationships of the Lizard Families, eds R. Estes in R. Estes (Stanford University Press, Palo Alto, California); pp. 15–98

Gauthier JA, Kluge AG, Rowe T. (1988b) Amniote phylogeny and the importance of fossils. Cladistics 4:105–209.

Gottmann-Quesada A, Sander PM. (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. Palaeont Abt A 287:123–220.

Gow CE. (1975) The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeont Afr 18:89–131.

Gower DJ. (1999) Cranial osteology of a new rauisuchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. Stuttgarter Beitrage zur Naturkunde B 280:1–9.

Gower DJ. (2002) Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. Zool J Linn Soc 136:49–76.

Gower DJ. (2003) Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. Ann S Afr Mus110:1–84.

Gower DJ, Schoch RR. (2009) Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. J Vert Paleo 29:103–122.

Hughes B. (1963) The earliest archosaurian reptiles. S Afr J Sci 59:221–241.

Hutchinson JR. (2001) The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). Zool J Linn Soc 131:123–168.

Hutchinson MN, Skinner A, Lee MSY. (2012) *Tikiguania* and the antiquity of squamate reptiles (lizards and snakes). Bio Lett 8:665–669.

Jalil N-E. (1997) A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. J Vert Paleo 17:506–525.

Jiang D-Y, Rieppel O, Fraser NC, Motani R, Hao W-H, Tintori A, Sun Y-L, Sun Z-Y. (2011) New information on the protorosaurian reptile *Macrocnemus fuyuanensis* Li et al., 2007, from the Middle/Upper Triassic of Yunnan, China. J Vert Paleo 31:1230–1237.

Li, C., Zhao L. J., Wang L. T. 2007. A new species of *Macrocnemus* (Reptilia: Protorosauria) from the Middle Triassic of southwestern China and its palaeogeographical implication. Science in China Series D, Earth Sciences 50:1601–1605.

Merck JW. (1997). A phylogenetic analysis of euryapsid reptiles. Ph.D. dissertation, University of Texas at Austin, Austin, Texas, 785 pp.

Modesto SP, Sues H-D. (2004) The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. Zool J Linn Soc 140:335–351.

Montefeltro FC, Langer MC, Schultz CL. (2010) Cranial anatomy of a new genus of hyperodapedontine rhynchosaur (Diapsida, Archosauromorpha) from the Upper Triassic of southern Brazil. Earth Env Sci Trans Roy Soc Edin 101:27–52.

Montefeltro FCJ, Bittencourt JS, Langer MC, Schultz CL. (2013) Postcranial anatomy of the hyperodapedontine rhynchosaur *Teyumbaita sulcognathus* (Azevedo and Schultz, 1987) from the Late Triassic of southern Brazil. J Vert Paleo 33:67–84.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Muscio G. (1996) Preliminary note on a specimen of Prolacertiformes (Reptilia) from the Norian (Late Triassic) of Preone (Udine, north-eastern Italy). Gortania 18:3–40.

Nesbitt SJ (2011) The early evolution of archosaurs: relationships and the origin of major clades. Bull American Mus Nat History 352:1–292.

Nosotti S. (2007) *Tanystropheus longobardicus* (Reptilia, Protorosauria): re-interpretations of the anatomy based on new specimens from the Middle Triassic of Besano (Lombardy, northern Italy). Mem Soc Ital Sci Natu Mus Civ Storia Nat Milano 35:1–88.

Olsen PE. (1979) A new aquatic eosuchian from the Newark Supergroup (Late Triassic–Early Jurassic) of North Carolina and Virginia. Postilla 176:1–14.

Peyer B. (1937) Die Triasfauna der Tessiner Kalkalpen XII. *Macrocnemus bassanii* Nopcsa. Schweizerische Paläo Abh 59:1–140.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Special Publication of the Museum of Natural History, University of Kansas 7:1–74.

Reisz, R. R., S. P. Modesto, and D. M. Scott. 2011. A new Early Permian reptile and its significance in early diapsid evolution. Proceedings of the Royal Society, B 278:3731–3737.

Renesto S. (1994) A new prolacertiform reptile from the Late Triassic of northern Italy. Riv Ital Paleo Strat 100:285–306.

Robinson PL. (1975) The functions of the hooked fifth metatarsal in lepidosaurian reptiles. Colloque International C.N.R.S. 218:461–483.

Romer AS. (1956) *Osteology of the Reptiles*. (University of Chicago Press, Chicago), 772 pp.

Saller F, Renesto S, Dalla Vecchia FM. (2013). First record of *Langobardisaurus* (Diapsida, Protorosauria) from the Norian (Late Triassic) of Austria, and a revision of the genus. N Jahrb fur Geo Paleo Abh 268:83–95.

Spielmann JA, Lucas SG, Rinehart LF, Heckert AB. (2008) The Late Triassic archosauromorph *Trilophosaurus*. Bull NM Mus Nat Hist Sci 43:1–177.

Sues H-D. (2003) An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. Can J Earth Sci 40:635–649.

Welman J. (1998) The taxonomy of the South African proterosuchids. J Vert Paleo18:340–347.

Wild R. (1973) Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus langobardicus* (Bassani) (Neue Ergenbisse). Abhandlungen der Schweizerischen Paläontologischen Gesellschaft 95:1–162.

TABLE 2.1 Phylogenetic data matrix employed to assess the affinities of the Hayden Quarry tanystropheid material.

Petrolacosaurus kansasensis
0000--000000000100000001011000020101100000000000101010000000000010110000?0???1000
0000011-0000000000000011-00000010?1000000000100--0000-00010?000100011?01001100011
00?0100000-0-110000010?-100000000000-0-0?0

***Uromastyx* sp.**
0000--00102-01100?101010-0??00101-0001--1111-0-----01-11010-0101010010001100101101?
01010100001---0-002100000000-1000000000000--1110-1011011111000110110011100110101
110?11-1011110000100011000001-111110000

Trilophosaurus buettneri
00011001102-0000000201-0-100101-001000??1011-0-----10?01111011?10011111000101 01?1
010000110001000?12--12011100011100010010111 10--0000-10021?011101001101010110 0100
00000111101101100110011100011001001 1100?1

Trilophosaurus jacobsi
0?0???01002-000?00010???01??101?001??0?????????0?????????????????????????????01????0
???1100010??12?-????????????????0????????????????????????????????10?011????????0??????
??????????0????????????????????

Prolacerta broomi
00011000101000001000 10{0,1}00-11000010011001-10100001111100{0,1}0111100110111111
000001001100010001010000 1110011-111000110000100000?000--00010110???11010011001
0100-11????000010100100110011001110001100100 11100?1

Teraterpeton hrynewichorum
00010001101?000000001??0?0-0101?001000??1010?0010?????10?100010?0???11?00????00?1
000?0011000100?102-11-?1101010?0001001????0???100??????0??111?00???????????????????
?????????????????????????????????????

Protorosaurus speneri
0000--000010000000 1101-?011000010011001-1010??????????10??00010?????????????001?0
00?0001000000?00?010-1110??1110000000???000--0000-?0010??1?110001?010101010 10000
000?????1?111?011????10000000000 1?10000

Proterosuchus fergusi
010110000010101000 0111-101110002001 1001-1010000111100-101111111101111111000??00
11001?00011100001110010-11001011000000000??2?0110?0010100100?110110110010101011?
????000111?1110110010001110001100100 11100?1

Youngina capensis

0000--00001000010100000101010002000100010000000111110000010000010100100011010 0
0????0?0001010000000000010-??00?000-01010000??000--000101001???111000?10110111?0001
??0110?010-0?111?01?0???10000?000000-0-0?0

Gephyrosaurus bridensis
0000--00002-01000110100001000001000000001-1010000110-100????0000?10100?000?????01?0
??0?0101000001-000010-00?0?000-00000?000?000--?111011110??111000010?11011????????
1110011-10111?000000?01100?01????110??0

Mesosuchus browni
00112?00111-000010{0,1}11000-11100010011001-1010010110-20?101100001101101110 00??
?00?01100000100100??100010-?1101011?110000110?000--00010110100?111100?1?0??10101
10000?100??1001111100110000100011001001110 0?1

Rhynchosaurus articeps
01112010111-0000101101-0-111010200110000101 1-?-----20?????????1100101110 0????11??0
?00001100100??10--10-??00?0100110100011?000--?000-100100?1111101100101010110?0000
00?0111111111001?-0??1000??0010010100?1

Langobardisaurus pandolfii
100???00????0???????????????00???0?????0??
?11000200?00?01211111?1111001?101????1???1?011110?00011110????010100-11??0?010??
11111??1111110??0100?1?001??10111?0

Langobardisaurus tonelloi
1011?00???1?000??????????????00??01?????1??????????????????????????????0?????01????0?
0?1100020??00?012111???????001??0?????1?????0??1103000?????????010100-11?00?0100??
?111?111?11100?0100???0?1111011 1?0

***Langobardisaurus pandolfii* concatenation**
1001?00???1?000??????????????00??01?????1??????????????????????????????0?????01????0?
0?01000200?00?01211111?1111001?101????1?????011110300011110????010100-11?00?0100
?11111?111111100?0100?1?001111011 1?1

Tanystropheus longobardicus
00011000?0110000000001001??11000011-?10???1?10000100-1001???00?1010??011?00???100?
?0?010001000{0,2}001001011-111001111001?01101?11111100111101000111101111010100-
11000011001111011111011000000001000-111011110

Tanytrachelos ahynis
0001?000?01?00000000?01??110?001?-??????1?1000?100-100???????0???????????????????0?
0?0?01000000?0000121111101??10011?01???11?110?0-100?000?????1?11010100-11????110
0?1111111111111100??0001??1??11?01111?

Hayden Quarry Sacral

???
??0-???
?????????????????????????

Hayden Quarry Tanystropheid
???
????????????121??1101111001110101?1?111?000-??0???0????????????????????????????????
????1110000?00?111???????????

Hayden Quarry Femur
???
???
1110000??????????????????

Hayden Quarry Dorsal
???
????????????121????????????????01?1?111?00???
???????????????????????????

Hayden Quarry Cervical
???
????????????121??11111110011101???
????????????????????????????

Hayden Quarry Caudal
???
????????????121???????????????????????????????0???????????????????????????????????????
??????????????????????????

Hayden Quarry Calcaneum
???
???
????????001111???????????

Macrocnemus bassanii
00011000101100010001111???1100001001?0???1?100?0110-?????????????0???11?0?????00??0
?010?01010000000001011-1110?01110011000-???01?0100111101000111101111010100-11?00?0
10011110111?1101100?010000?001011010010

Macrocnemus fuyuanensis
0001100010110001001111-??110000100100???1?10???1??????????????????????????????00??0
10?0?0101000??00?011-1110??1110011?00001001??10011110?000111??111??10??0-1000??0
1001011010111101101001000?00010110100?0

Amotosaurus rotfeldensis

?0????0?????0??????????????0001???????????01?01????????????????????????????????????
?0100000????1001-1110??11100???11??????????011??0?????????1?11???????????????100???1
01?1??0???????000???0?-101???1??

Erythrosuchus africanus
0001111000101010000111-11110000200110000100??0?????100001?111111001 0?111001??00
11001100011100001 01-010-0?00001101000000012100--0000-1001000111100?1001010101 1??
???00011111110110010000100??1000???1??00?0

Shinisaurus crocodilurus
0000--00101-011001101000---000001-01011-1110101100-01-1001000111010011000010 10111
10010101010001-000012100001000-1000000000000--1100-1011111111000110010011100110
101100010-10111000010000110 10?1?001010000

Orovenator mayorum
0000--00?00000010000?00??11?00-1????1???0?00??01211?0???????????1?00???0???1?01??0?
00??01010000000010-???00000???000?0??????????0????0?????????????????????????????????
??????????????????????????????????

Euparkeria capensis
0001100000101001000 1?1-11111000200100000 1010?00110?100??1?1?11110?11?11100?0100
11011?0001110000101001 0-010000100?00?000??1??1100000-??0?0??11??00??0???1?0-11???
??000??11111??1?01?011100001100-1111100?1

Batrachotomus kupferzellensis
0001011010101000000111-0-11000020010000 01011-0-----1001011101011?001?1010?1??00?1
00100001110000101-011-011000110{0,1}0010011121010 01000-??0100011???001001010 0010
?????0001011111101100??01??001011?0-???110??1

Teyumbaita sulcognathus
?1112010111-0000001201-0-1010102011?00001011-1-----201110110001 10????1?000???10011
00-001100100??10--11-??10001001?0000101?0?0--100????0?0?01????0010?10100-1?????????
????????????1010??10??????1?????????

FIG 2-1. The Hayden Quarry locality from the Late Triassic of New Mexico (modified from Irmis et al., 2011).


HQ
Abiquiu
Gallup
Santa Fe
Albuquerque
NEW MEXICO
100 km

FIG 2-2. Photographs of cervical vertebra (GR 269) in **A**, left lateral; **B**, dorsal; **C**, ventral; **D**, anterior; and **E**, posterior views. **Abbreviations**: **dia**, diapophysis; **epi**, epipophysis; **ns**, neural spine; **par**, parapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis; **vk**, ventromedian keel.

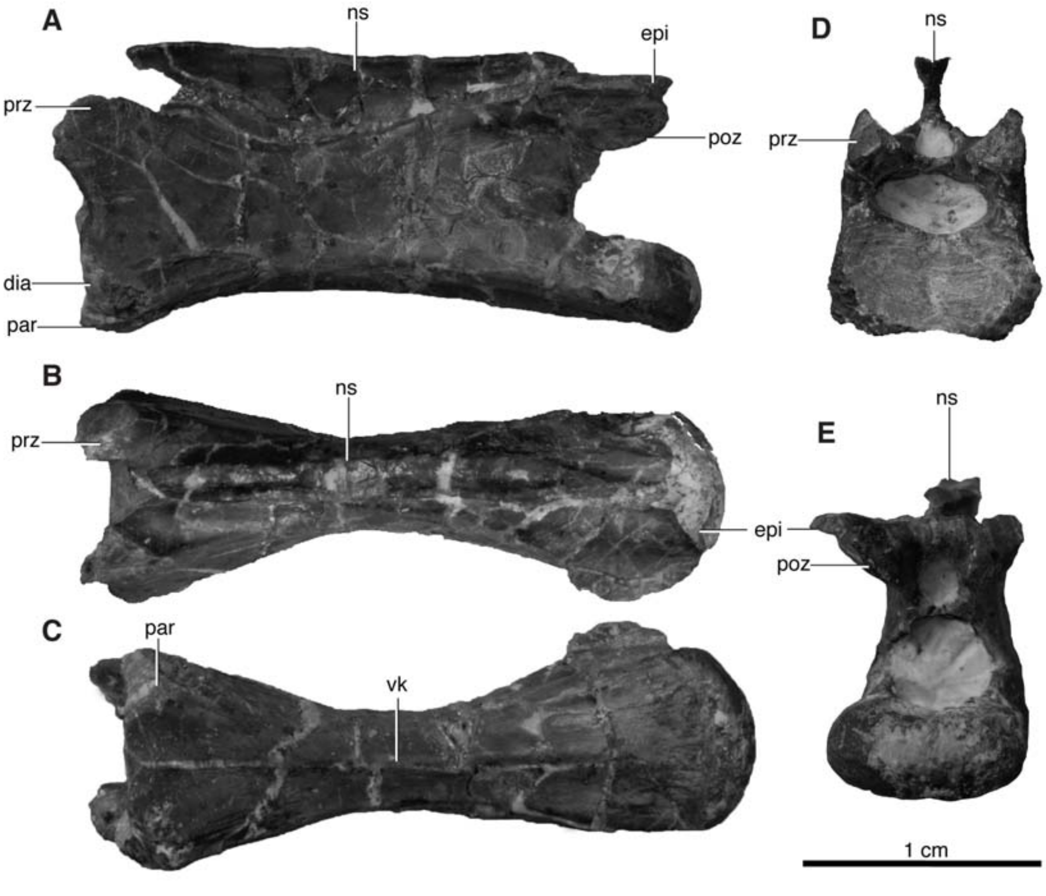

A
ns
epi
prz
poz
dia
par
B
ns
prz
epi
C
par
vk
D
ns
prz
E
ns
epi
poz
1 cm

FIG 2-3. Photograph of a cervical vertebra of *Tanytrachelos ahynis* (AMNH FARB 7206) in oblique right lateral view.

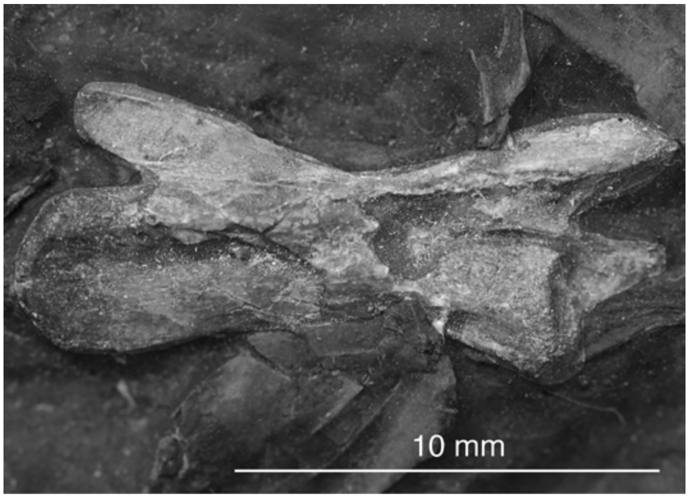

10 mm

FIG 2-4. Photograph of dorsal vertebra (GR 275) in **A**, right lateral view; dorsal vertebra (GR 294) in **B**, left lateral view; a cartoon reconstruction of a mid-posterior dorsal vertebra (scale based on GR 294) in **C**, left lateral view; and the neural spine of GR 275 in **D**, dorsal view. Upper scale bar corresponds to images A, B, and C. Lower scale bar corresponds to image D. **Abbreviations**: **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis; **syn**, synapophysis (compound diapophysis-parapophysis).

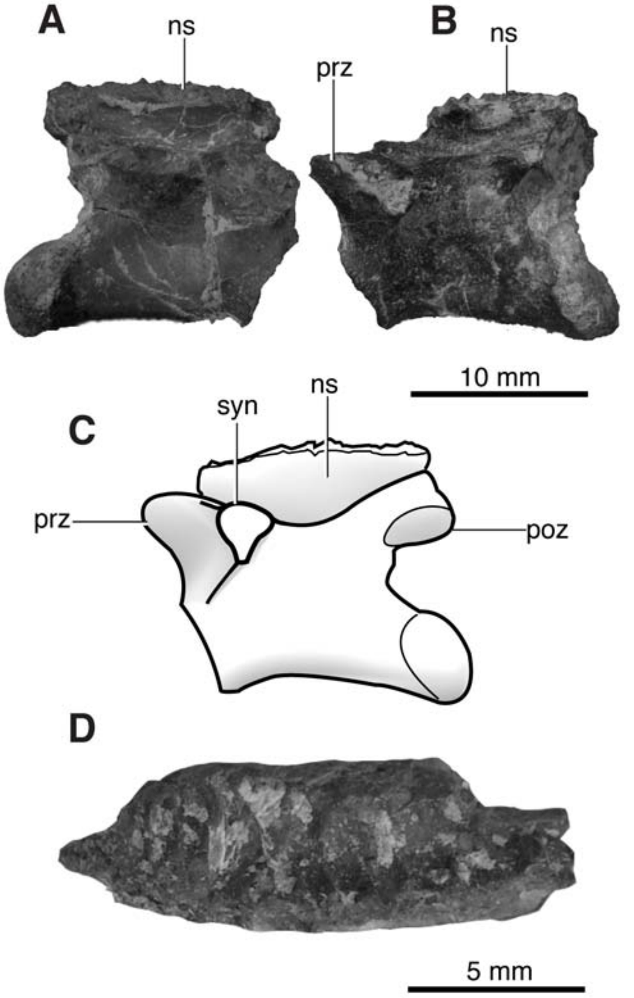

A
ns
prz
B
ns
10 mm
syn
ns
C
prz
poz
D
5 mm

FIG 2-5. Photograph of second sacral vertebra (GR 308) in **A**, anterior; **B**, right lateral; **C**, posterior; and **D**, ventral views. **Abbreviations**: **ns**, neural spine; **poz**, postzygapophysis; **nst**, neural spine tip; **s1**, probable articular surface for sacral rib 1; **sr**, sacral rib; **vk**, ventromedian keel.

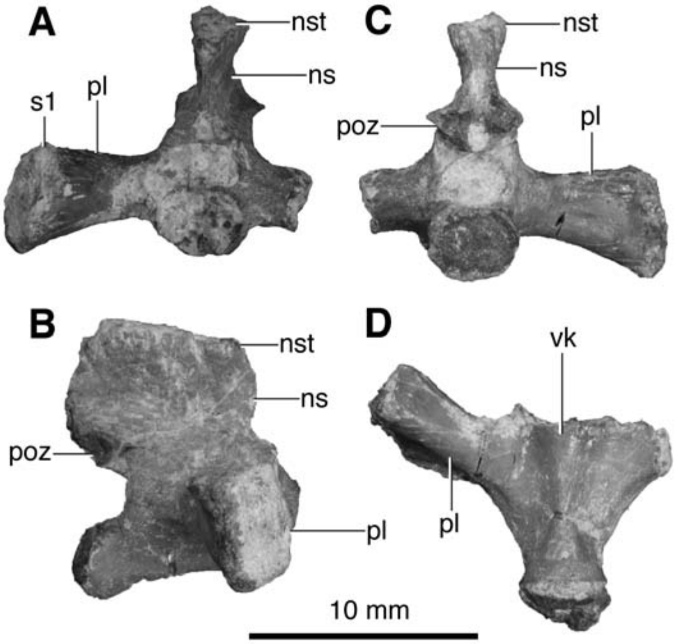

A
nst
ns
s1
pl
C
nst
ns
poz
pl
B
nst
ns
poz
pl
D
vk
pl
10 mm

FIG 2-6. Photograph of tanystropheid partial anterior caudal vertebrae (GR 357) in **A**, right lateral view; GR 281 in **B**, ventral; and **C**, posterior views. **Abbreviations**: **ca**, chevron articulations; **ns**, neural spine; **poz**, postzygapophysis; **tp**, transverse process (broken); **vk**, ventromedian keel.

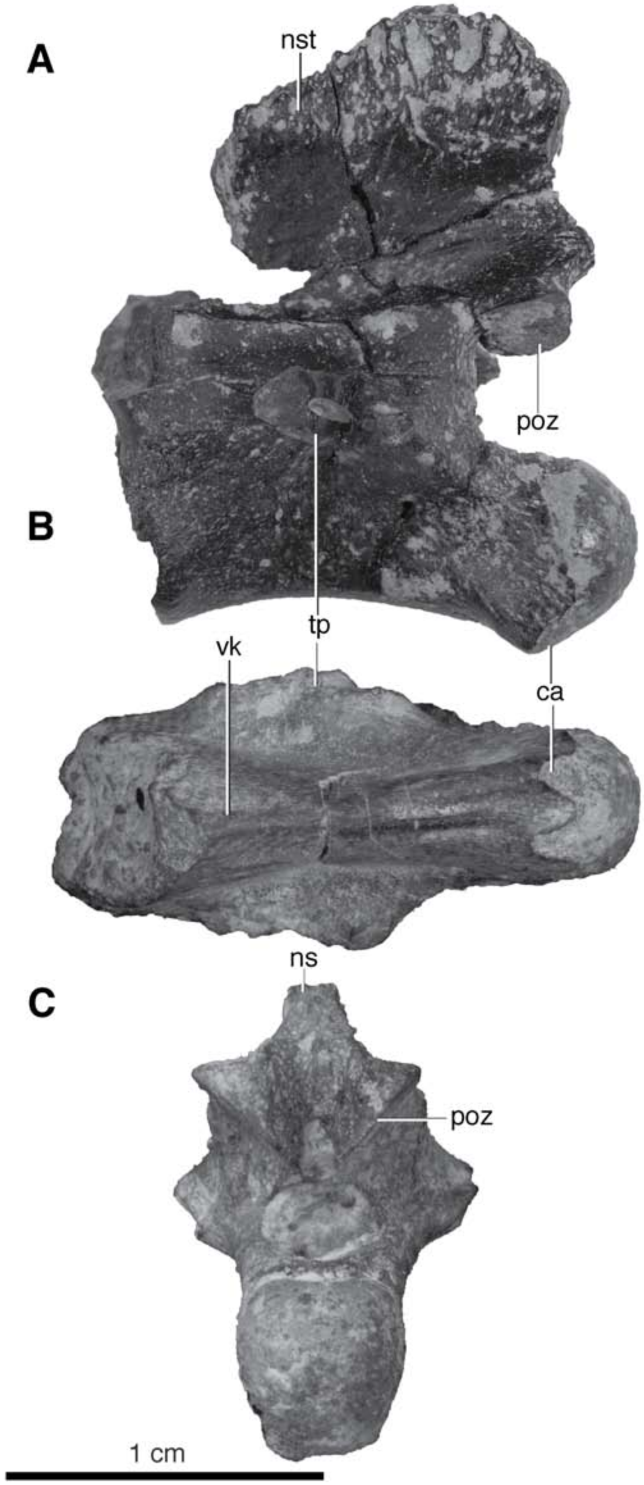

A
nst
poz
B
tp
vk
ca
C
ns
poz
1 cm

FIG 2-7. Photograph of a mid/posterior caudal vertebra (GR 294) in **A**, right lateral and **B**, posterior views. Photograph of a mid/posterior caudal vertebra (GR 285) in **C**, right lateral and **D**, ventral views. Photograph of mid/posterior caudal vertebral neural spine (GR 294) in **E**, dorsal view. Upper scale bar corresponds to images A–D. Lower scale bar corresponds to image E. **Abbreviations**: **ca**, chevron articulations; **poz**, postzygapophysis; **nst**, neural spine tip; **sr**, subcentral ridge.

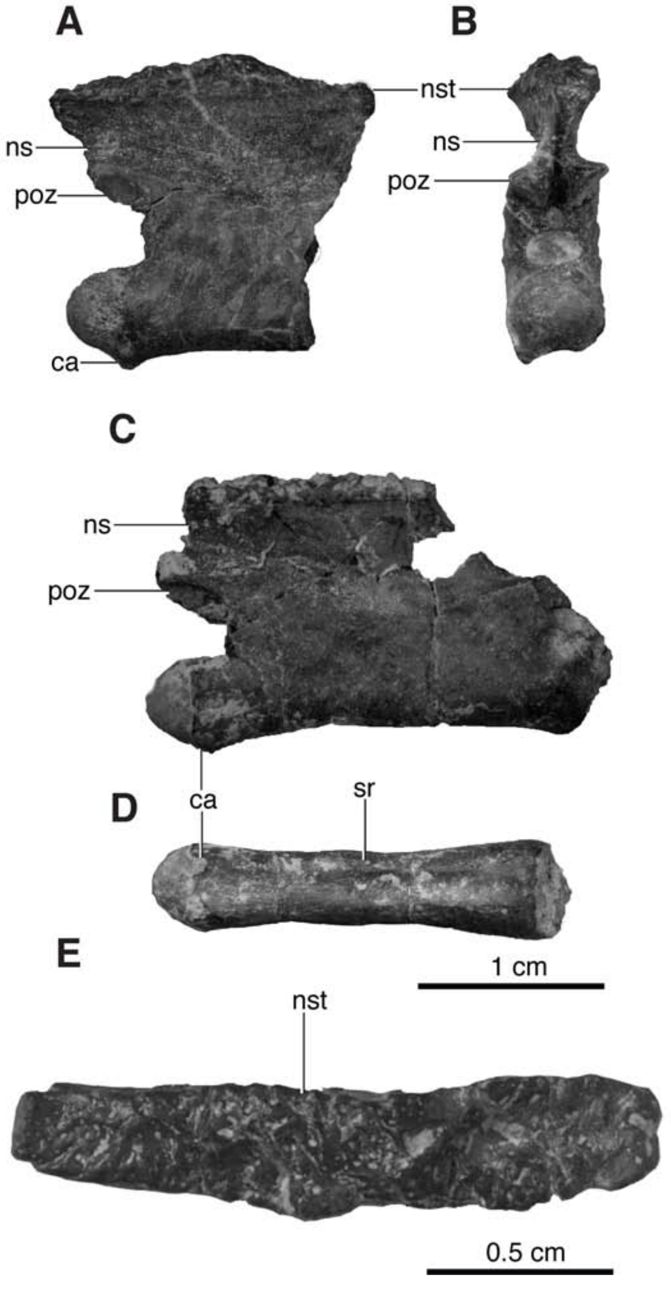

A
B
nst
ns
poz
ca
nst
ns
poz
C
ns
poz
ca
D
ca
sr
E
1 cm
nst
0.5 cm

FIG 2-8. Photograph of a left archosauromorph femur (GR 304) in **A**, pre-axial; **B**, postaxial; **C**, dorsal; **D**, and ventral views; and a right archosauromorph femur (GR 301), mirrored for ease of comparison, in **E**, proximal and **F**, distal views. **Abbreviations**: **ad**, adductor ridge; **fc**, fibular condyle; **it**, internal trochanter; **itr**, probable insertion of m. ischiotrochantericus; **ltc**, lateral tibial condyle; **mtc**, medial tibial condyle; **pifi**, probable insertion of m. puboischiofemoralis internus (damaged); **pt**, posterior trochanter; **tf**, intertrochanteric fossa.

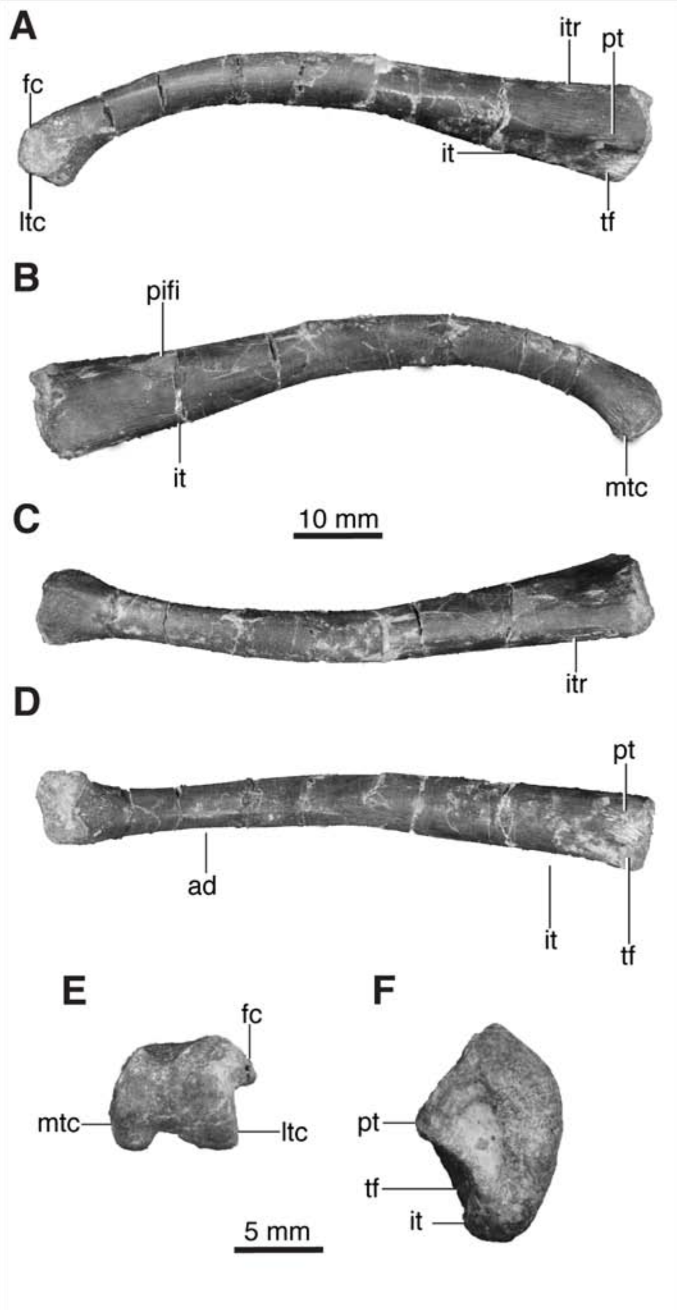

A
itr
pt
fc
it
ltc
tf
B
pifi
it
mtc
C
10 mm
itr
D
pt
ad
it
tf
E
fc
mtc
ltc
5 mm
F
pt
tf
it

FIG 2-9. Photograph of archosauromorph femora, showing the size range of Hayden Quarry elements in postaxial view. **A**, GR 301; **B**, GR 304; and **C**, GR 305. B has been mirrored for ease of comparison.

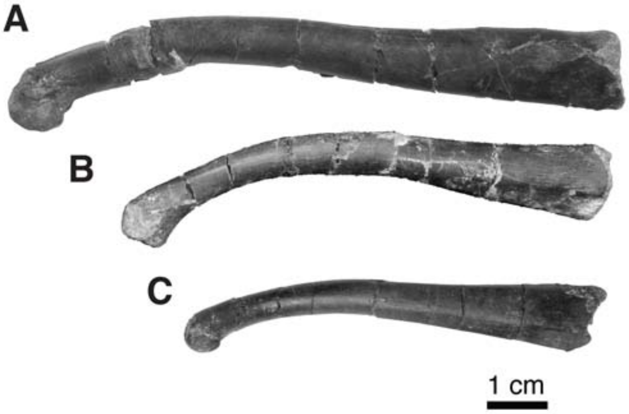

A
B
C
1 cm

FIG 2-10. Photograph of a left archosauromorph calcaneum (GR 306) in **A**, proximal; **B**, distal; **C**, medial; **D**, lateral; and **E**, preaxial views. **Abbreviations**: **af**, contacts for astragalus; **ct**, calcaneal tuber; **dtf**, distal tarsal facet; **ff**, fibular facet; **perf**, calcaneal contribution to perforating foramen.

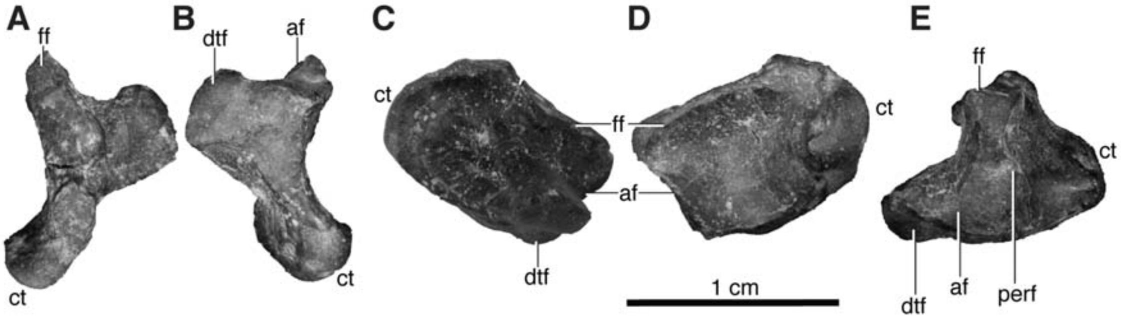

A
ff
ct
B
dtf
af
ct
C
ct
ff
af
dtf
D
ct
1 cm
E
ff
ct
dtf
af
perf

FIG 2-11. Photograph of a left calcaneum of *Tanytrachelos ahynis* (AMNH FARB 7206) in oblique view (preaxial and slightly lateral views). **Abbreviations**: **af**, contact surface for astragalus; **ct**, calcaneal tuber; **ff**, fibular facet.

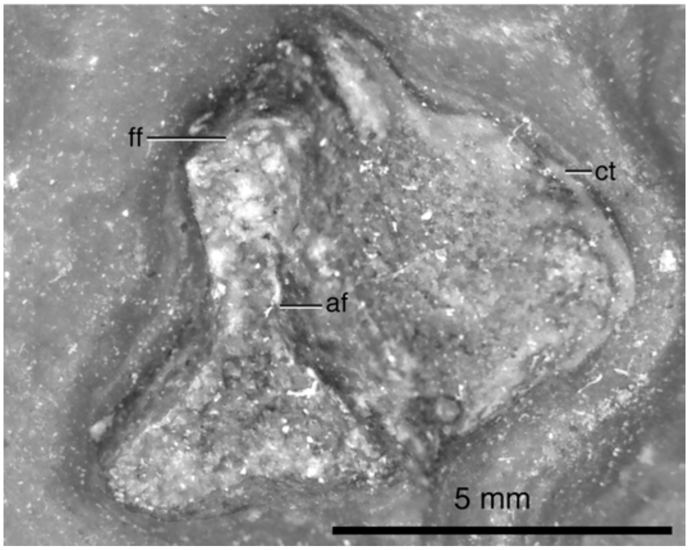

ff
ct
af
5 mm

FIG 2-12. Results of our phylogenetic analyses of early archosauromorph interrelationships, incorporating all Ghost Ranch tanystropheid material as one OTU. **Abbreviations**: **A**, Archosauromorpha; **L**, Lepidosauromorpha.

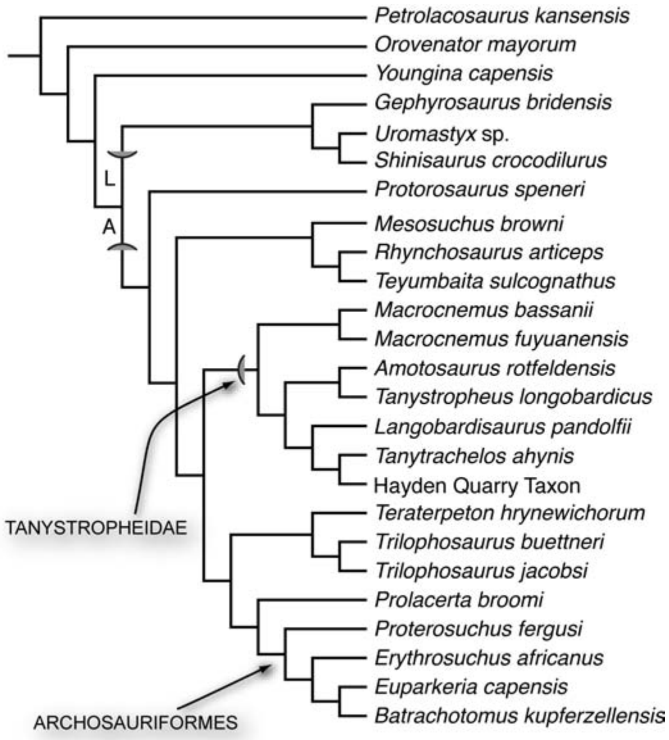

Petrolacosaurus kansensis
Orovenator mayorum
Youngina capensis
Gephyrosaurus bridensis
Uromastyx sp.
Shinisaurus crocodilurus
L
Protorosaurus speneri
A
Mesosuchus browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
Macrocnemus bassanii
Macrocnemus fuyuanensis
Amotosaurus rotfeldensis
Tanystropheus longobardicus
Langobardisaurus pandolfii
Tanytrachelos ahynis
Hayden Quarry Taxon
TANYSTROPHEIDAE
Teraterpeton hrynewichorum
Trilophosaurus buettneri
Trilophosaurus jacobsi
Prolacerta broomi
Proterosuchus fergusi
Erythrosuchus africanus
Euparkeria capensis
Batrachotomus kupferzellensis
ARCHOSAURIFORMES

FIG 2-13. Selected postcranial synapomorphies of the clade Tanystropheidae. **A**, cervical vertebrae of *Trilophosaurus buettneri* (TMM 31025-140) in right lateral view; **B**, a Hayden Quarry tanystropheid (GR 269) in right lateral view; **C**, left ischium of *Trilophosaurus buettneri* (TMM 31025-78) in lateral view; and **D**, left ischium of *Macrocnemus bassanii* (MCSN V 457) in lateral view.

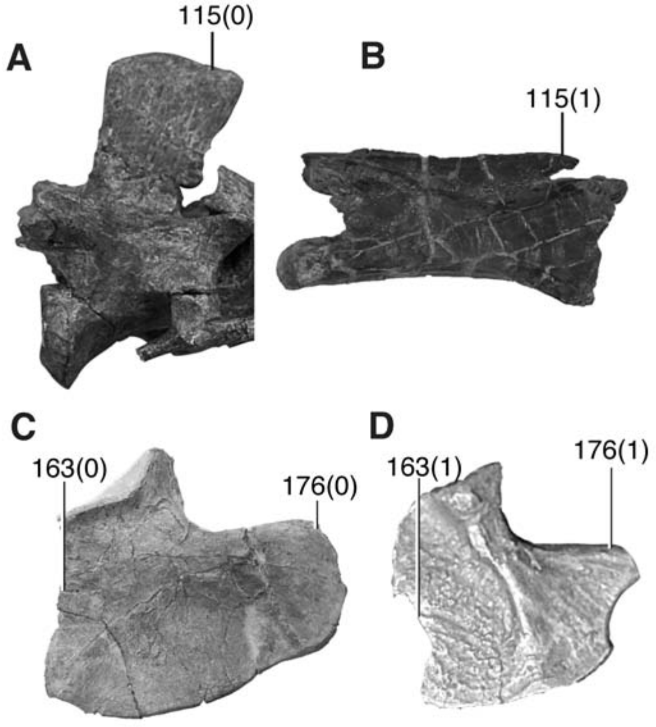

115(0)
A
B
115(1)
C
163(0)
176(0)
D
163(1)
176(1)

FIG 2-14. Selected postcranial synapomorphies of the clade of (*Tanystropheus* + *Amotosaurus*) + (*Tanytrachelos* + *Langobardisaurus*). **A**, cervical vertebra of *Trilophosaurus buettneri* (TMM 31025-140) in posterior view; **B**, cervical vertebra of a Hayden Quarry tanystropheid (GR 269) in posterior view; **C**, posterior trunk region of *Macrocnemus bassanii* (MCSN BES SC 111); **D**, posterior dorsal vertebrae and ribs of *Langobardisaurus pandolfii* (MFSN 1921); **E**, pes of *Prolacerta broomi* (AMNH FARB 9502) in dorsal view; and **F**, pes of *Tanystropheus longobardicus* (MCSN BES SC 1018) in plantar view.

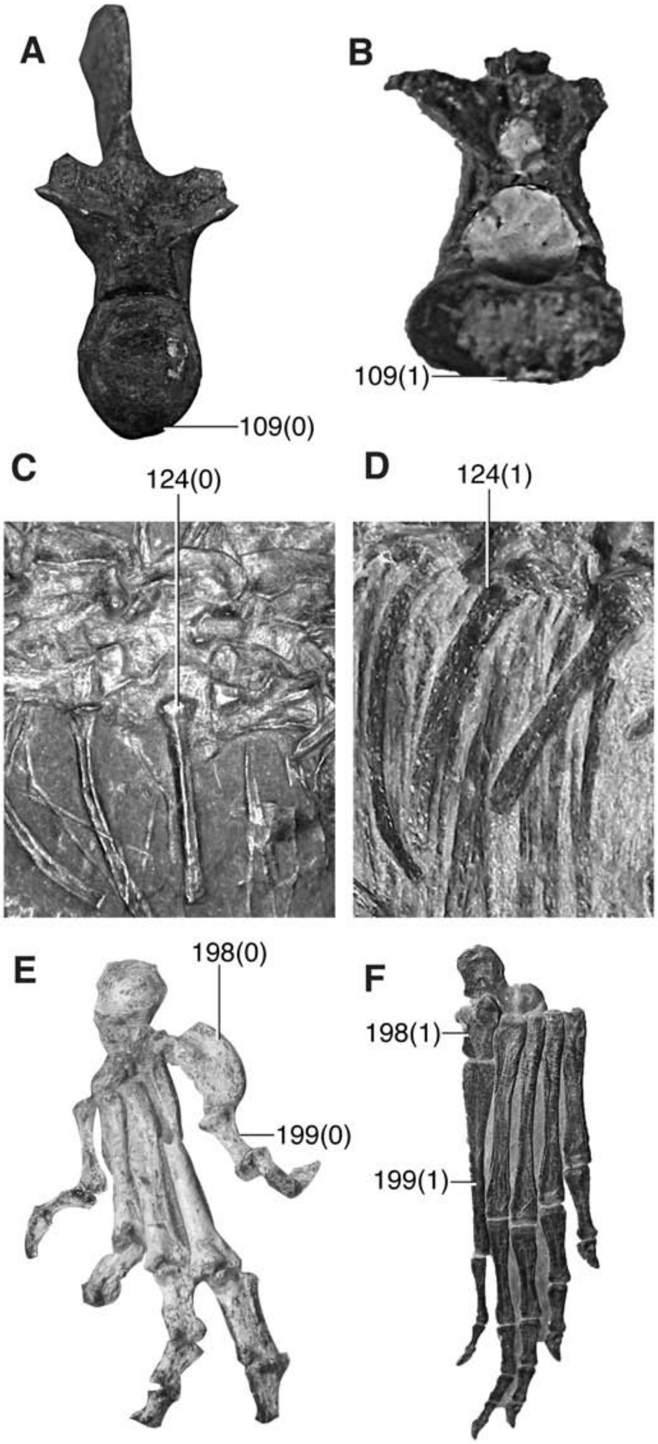

A
B
109(1)
109(0)
C
124(0)
D
124(1)
E
198(0)
199(0)
F
198(1)
199(1)

FIG 2-15. Selected postcranial synapomorphies of the clade of *Tanytrachelos* + *Langobardisaurus*. **A**, dorsal vertebra of a juvenile *Tanystropheus longobardicus* (MCSN BES SC 1018) in right lateral view; **B**, dorsal vertebra of a Hayden Quarry tanystropheid (GR 273) in right lateral view; **C**, cervical vertebra of *Tanystropheus longobardicus* (modified from Dalla Vecchia, 2005) in anterior view; **D**, cervical vertebra of a Hayden Quarry tanystropheid (GR 269) in anterior view; **E**, cartoon of right ilium of *Macrocnemus bassanii* (based on MCSN V 457 and Peyer, 1937) in lateral view; and **F**, right ilium of *Tanytrachelos ahynis* (AMNH FARB 7206) in lateral view.

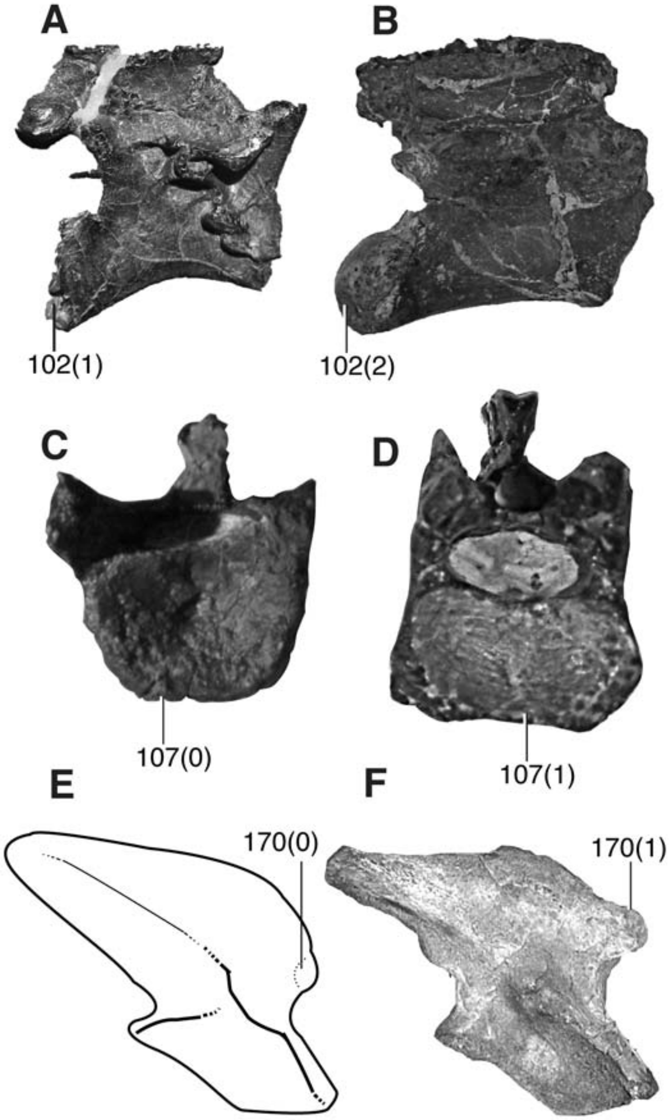

A
B
102(1)
102(2)
C
D
107(0)
107(1)
E
F
170(0)
170(1)

FIG 2-16. Selected calcaneal characters. Left calcaneum of *Trilophosaurus buettneri* (AMNH FARB 30836) in **A**, external and **C**, preaxial views and left calcaneum of the Hayden Quarry tanystropheid (GR 306) in **B**, external and **D**, preaxial views.

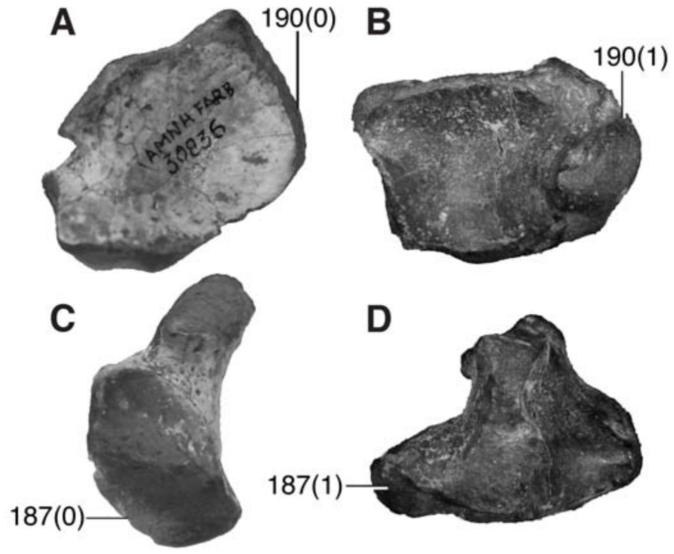
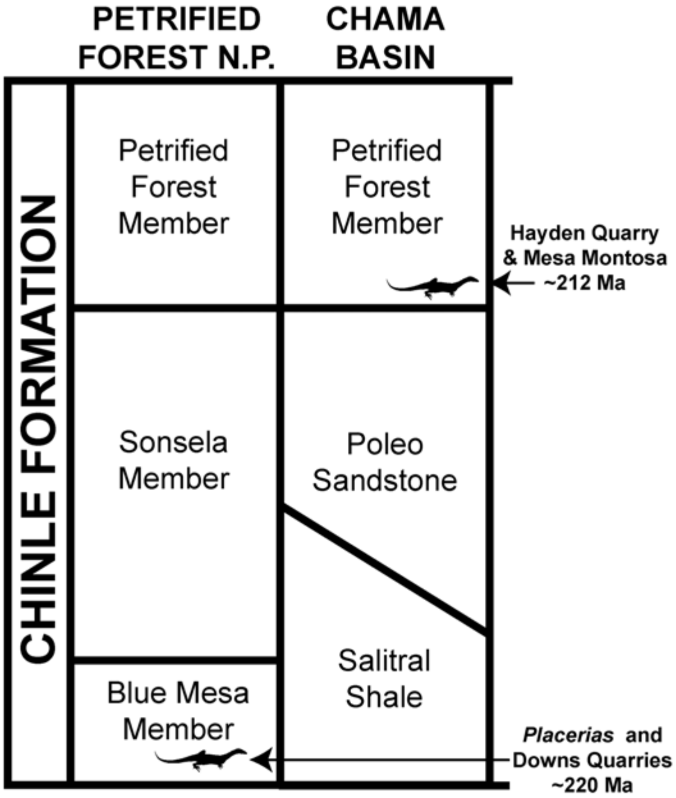

A
190(0)
AMNH FARB 30836
B
190(1)
C
187(0)
D
187(1)

FIG 2-17. Stratigraphy of tanystropheid occurrences from the Late Triassic Chinle Formation. Stratigraphic scheme is modified from Irmis et al. (2011). Note that this does not represent all members of the Chinle Formation in either eastern Arizona or the Chama Basin.


PETRIFIED FOREST N.P.
CHAMA BASIN
CHINLE FORMATION
Petrified Forest Member
Petrified Forest Member
Hayden Quarry & Mesa Montosa ~212 Ma
Sonsela Member
Poleo Sandstone
Salitral Shale
Blue Mesa Member
Placerias and Downs Quarries ~220 Ma

Chapter 3

Extreme modification of the forelimb in a Triassic reptile

ABSTRACT—Despite the diversity in the function of the tetrapod forelimb, some elements of its construction remain remarkably consistent across nearly all Tetrapoda. This includes the construction of the zeugopodium, in which the radius and ulna form proximodistally elongate shafts that parallel one another to meet a series of short carpals. One fossil diapsid taxon, *Drepanosaurus unguicaudatus*, has been presented as a divergence from this pattern, although the crushed quality of the only known specimen has made study difficult. Here, we present well-preserved new material of *D. unguicaudatus* from the Upper Triassic Hayden Quarry (Petrified Forest Member, Chinle Formation) of New Mexico that clarifies the homologies of the forelimb bones. The taxon exhibits a flattened, crescent-shaped ulna with a long axis roughly perpendicular to that of the radius. The former element meets two carpals, the intermedium and ulnare, which are proximodistally longer than the radius. Integration of the material into a phylogenetic analysis of Drepanosauromorpha suggests that the carpal elongation preceded the changes in forelimb bone shape.

INTRODUCTION

The tetrapod forelimb is remarkably adaptive, with an incredible capacity to be reinvented for distinct functions. Since its initial development in early tetrapodomorph fishes (Coates, 1996; Shubin et al., 2006), the forelimb has been modified for flight (Sereno and Chenggang, 1992; Padian and Rayner, 1993; Simmons et al., 2008), aquatic paddling (Fordyce and Barnes, 1994; Motani, 1999; Caldwell, 2002), digging (Hopkins and Davis, 2009), specialized grasping (Sustaita et al., 2013), and extreme reduction (Burch and Carrano, 2012). Despite this diversity of function, the forelimb bones retain certain characteristic features and relationships in nearly all tetrapods. Among these relationships is that of the radius, ulna, and proximal carpal series—the radius and ulna exhibit proximodistally elongate, paralleling shafts of subequal length that distally contact a series of proximodistally shorter carpal bones.

The Triassic reptile *Drepanosaurus unguicaudatus* represents a substantial deviation from this pattern (Pinna, 1980; Renesto et al., 1994a). A member of Drepanosauromorpha, a clade of small-bodied (>1 meter) diapsid reptiles known exclusively from the Late Triassic of Euramerica (Renesto et al., 2010), *D. unguicaudatus* is known from a single nearly complete but badly crushed, postcranial skeleton from the Upper Triassic Zorzino Limestone of Italy. The taxon is characterized by extreme asymmetry in the size of its manual unguals, such that the second ungual is the largest forelimb bone. The most striking characteristic of the limb is the construction of the zeugopodium and carpal series. The shapes of the constituent bones are unlike those of any other known tetrapod (Fig. 1), and the crushing of the specimen heavily obscures their homologies. A number of hypotheses have been offered for their identities (Supplemental S1), all suggesting a substantial modification of the ancestral tetrapod condition. In the absence of a robust hypothesis for the homologies of the forelimb bones in *Drepanosaurus*, exactly what that modification is and any interpretation of its evolutionary origin and functional morphology remain out of reach.

We describe a series of three-dimensionally preserved drepanosaurid forelimbs and isolated forelimb elements from the Upper Triassic Chinle Formation of New Mexico. These share a number of autapomorphies with the holotype of *Drepanosaurus unguicaudatus*, allowing referral to the taxon. Taken together, these discoveries represent the complete humerus, zeugopodium, proximal carpus, and several partial digits. With these we develop a model of homology in the extreme forelimb condition of *Drepanosaurus*, indicating that the forelimb construction indeed differs from that in all other tetrapods. In *Drepanosaurus,* the long axis of the ulna is perpendicular to that of the radius. A pair of elongate proximal carpal elements, the intermedium and ulnare link the distal end of the ulna to the remainder of the carpus. Broad-scale comparisons with other tetrapod taxa illustrate convergence with a number of extant mammalian taxa, although no modern animal approaches the extremes in forelimb development as *Drepanosaurus*.

MATERIALS AND METHODS

Systematic Paleontology

Diapsida Osborn, 1903; Simiosauria Senter, 2004; Drepanosauromorpha Renesto et al., 2010; Drepanosauridae Carroll, 1988; *Drepanosaurus* Pinna, 1980; *Drepanosaurus unguicaudatus* Pinna, 1980

Referred Specimens

Two partial articulated forelimbs (H3-037-080527, H4-570-110830) and several dozen isolated bones representing the entire forelimb and much of the manus (Supplemental S4).

Horizon and Locality

All specimens described here come from the Hayden Quarry (HQ), a series of outcrops in the Petrified Forest Member of the Chinle Formation in the Chama Basin of northern New Mexico. Described drepanosaur materials come from all three of the paleochannels that make up the quarry (in stratigraphic order: H4, H2, H3). Radioisotopic records indicate an age of 211.9 ± 0.7 Ma, a middle Norian Age (Irmis et al., 2011). This is roughly equivalent in age to the Italian deposit that has produced the highest diversity of drepanosauromorph taxa, the Zorzino Limestone (Renesto, 2006).

Justification for Referral

The partially articulated, associated forelimbs recovered from the HQ exhibit an identical arrangement of identically shaped bones to the *Drepanosaurus unguicaudatus* forelimb. Unfortunately, extreme differences in preservational quality between the heavily crushed holotype and the three-dimensional, fragmentary HQ material preclude some of the detailed comparisons that would allow autapomorphies to be identified to distinguish between the Italian and North American material. Until such autapomorphies can be identified, we tentatively refer the new HQ fossils to *Drepanosaurus unguicaudatus* on the basis of the autapomorphic forelimbs features. A list of all referred materials can be found in Table 1.

Description

Drepanosaurid limb elements are among the most abundant small tetrapod fossils recovered from the Hayden Quarry. The robust second manual unguals and the metacarpals to which they articulate are the most common. The remaining forelimb elements have distinctively thin cortical bone, internally supported by slender trabeculae (Fig. 2A). This has resulted in crushing deformation of nearly all represented bones, although some retain their original shape due to infilling of matrix. Only two limbs have been recovered in partial articulation, which provide the basis for the associations drawn here. Prior to preparation, one specimen (H3-037-080527) was μCT scanned to allow 3D visualization and rearticulation of all elements.

A single fragment of a pectoral girdle is preserved with one articulated forelimb (H3-037-08), suggesting a glenoid oriented laterally. The same condition occurs in a drepanosaurid pectoral girdle from the Upper Triassic *Coelophysis* Quarry (described by Harris and Downs, 2002). This contrasts with the posterolateral orientation ancestral for diapsids and most drepanosaurs (Renesto et al., 1994b; Colbert and Olsen, 2001).

Although thin-walled, the humerus is exceptionally robust and short with a transversely narrow humeral head. The deltopectoral crest is elongate and extends for more than half the total length of the bone, but does not project far from the shaft. Near the proximal margins of the ect- and entepicondyles, the entire distal end of the bone curves in an anterior direction. The ect- and entepicondyles are broader and more wing-like than in any known drepanosauromorph (Renesto et al., 1994b; Renesto and Binelli, 2006) except the holotype of *D. unguicaudatus*, indicating extensive development of digital flexors and extensors. The radial condyle is massive and ovoid, sitting almost entirely on the flexor aspect of the humerus. In contrast the ulnar condyle is extremely small, sitting on the distal aspect of the bone.

The radius is a relatively simple and hourglass-shaped bone, with a dorsoventrally broad and elliptical cross-section at midshaft. The proximal and distal ends are substantially expanded. The proximal articular surface is tall and ovoid, fitting snugly over the radial condyle. There is a prominent, tab-like expansion of the articular surface that fits into a corresponding notch in the ulna. This tight articulation would allow little to no pronation or supination. The distal articulation of the radius forms a half-circle, flattened on the flexor aspect. The surface is rimmed by a thin margin on all sides except the flexor surface. There is a deep concavity in the center of the distal articular surface.

The ulna of *Drepanosaurus* exhibits a broad, paper-thin, crescent-shaped “shaft” between the proximal humeral articulation and the distal carpal articulation. Deep bowing of the ulnar shaft occurs in a number of diapsids (e.g., Feduccia, 1999; Rogers, 2003), and flattened shafts occur in early tetrapods (e.g., Coates, 1996; Jarvik, 1996), but no other tetrapods approach this unique shape. Proximally, the ulna has deep cotyles for the humeral condyles, with the surfaces for the radial and ulnar condyles divided by a thin ridge. The articular surface for what is traditionally the radial condyle of other tetrapods is substantially wider than that for the traditional ulnar condyle, coincident with the relative elaboration of these condyles in the humerus. On the anterior surface of the ulna, just distal to the humeral condylar surface, there is a triangular concavity that would have accommodated the radial "tab." The distal articular surface of the ulna is strongly convex and ovoid.

A single large carpal articulates with the distal end of the radius. Based on this contact, we consider this element homologous to the radiale of other tetrapods, although its proximodistal elongation and apparently complex articulation with distal carpal elements suggest that the *Drepanosaurus* radiale may incorporate other preaxial carpal bones.

The radiale comprises a proximodistally tapering cone-shaped segment proximally. At its distal tip, this cone expands abruptly into a broad, flattened tab-shaped structure. The proximal articular surface is strongly convex and semicircular, indicating a tight fit with the distal radius. The dorsal surface of the conical portion of the radiale is subtly convex along its length, whereas the palmar surface exhibits a deep pit. The post-axial surface forms a thin margin along the length of the conical portion, whereas the preaxial surface is marked by an oblong, bipartite contact surface distally. The post-axial margin of the distal tab is an irregular, flattened contact surface.

A pair of proximal carpals, the intermedium and ulnare, articulate with the distal condyle of the ulna. Both are proximodistally elongate, slender, and longer than the radius. Although these carpals are moderately elongate in one other drepanosaurid (*Megalancosaurus preonensis*), the relative length in *Drepanosaurus* is unique. The intermedium is elliptical in cross-section and expanded at both ends. The proximal articular surface is roughly subcircular, broader than the oval-shaped distal ulnar convexity. The shaft of the intermedium is heavily curved, arcing laterally along its length. The distal end of the bone is fused to a three-lobed distal carpal element. The central lobe of this carpal is large, angled laterally, and supported the base of the expanded second digit. The ulnare is laterally compressed and parallels the intermedium along its length. The proximal end contacts the ulna and intermedium at a small facet. Distally, the ulnare possesses a small, elliptical facet that formed the joint for the second metacarpal.

We identify a number of transversely broad, flattened metapodials as second metacarpals. An elliptical proximal articular concavity, fitting over the primary convexity of the distal carpals, is framed by two proximally projecting tubera. The distal articular surface is ginglymoid, forming a hinge joint with the second manual ungual. The ungual itself is extremely large and hooked, transversely compressed, and tall. The proximal surface of the bone forms a tapering isosceles triangle, with the deep cotylar articular surface for the second metacarpal at the base.

The surface dorsal to the articular cotyles served a broad extensor attachment. The ventral surface of the claw has a deep, distally tapering concavity that is framed by two elongate, tapering tubera. This concavity terminates just proximal to the primary curvature of the claw, marked by a large, hemispherical flexor tubercle. The proximal margin of this tubercle exhibits two deep pits, likely for the *m. flexor digitorum longus*.

Phylogenetic Analysis

We tested the phylogenetic position of the HQ drepanosaurid material using a novel phylogenetic dataset. Our study incorporated characters from past analyses of early diapsid and drepanosauromorph affinities (e.g., Dilkes, 1998; Müller, 2004; Senter, 2004; Renesto et al., 2010; Pritchard et al., 2015; Nesbitt et al., in press). We sampled all known drepanosauromorph taxa (see Supplemental 5), and four non-drepanosauromorph diapsids known from complete forelimbs. *Petrolacosaurus*, the oldest-known diapsid reptile (Pennsylvanian, Kansas), served as the outgroup (as in Dilkes, 1998; Pritchard et al., 2015). Analysis parameters can be found in Supplement 5d. The study produced a single most-parsimonious tree (length = 63 steps, CI = 0.937, RI = 0.952) (Fig. 3). The data matrix is presented in Table 2.

The topology of drepanosauromorph genera is congruent with Renesto et al. (2010). In all iterations of this analysis (see Supplemental S5), the HQ *Drepanosaurus* is recovered as the sister taxon of *Drepanosaurus unguicaudatus*. In an analysis incorporating drepanosaurids known from complete forelimbs, this relationship is supported by a number of synapomorphies: an enlargement of manual ungual II (39.1), a crescent-shaped ulna (40.1), a flattened proximal tab of the radius (41.1), the lateral positioning of the glenoid fossa (51.1), the distal curvature of the humerus (54.1), and the massive, elongate epicondyles (56.1).

The results of this phylogenetic analysis strongly support a sister group relationship between *Drepanosaurus unguicaudatus* and the Hayden Quarry *Drepanosaurus*. The model for the forelimb homologies described above also illustrates a pattern of trait acquisition preceding the extreme condition in *Drepanosaurus* (Fig. 4). *Hypuronector limnaios* and *Vallesaurus cenensis*, the first and second most basal divergences within Drepanosauria, exhibit comparatively normal diapsid forelimb condition, with zeugopodial elements being equal in length and multiple phalanges forming each digit. In *Megalancosaurus preonensis*, recovered in the analysis as the sister taxon of *Drepanosaurus*, the phalangeal count in the manus of

Megalancosaurus is reduced considerably (2 phalanges in the digits I–III and 3 in digits IV and V). Most strikingly, the ulnar shaft in *Megalancosaurus* is substantially shorter than that of the radius, with consequent elongation of the ulnare and intermedium. The intermediate position of *Megalancosaurus* strongly suggests that reductions to interphalangeal mobility and an increase in proximal carpal length preceded the enlargement of the unguals and changes to ulnar shape. It must be noted that, despite the clear pattern of forelimb trait acquisition, some of the functional "stages" of forelimb evolution co-occur in time and space in the Norian of both Italy and North America (Renesto, 2006; Berman and Reisz, 1992), akin to the pattern noted in dinosauromorph assemblages in Late Triassic North America (Irmis et al., 2007). This implies that the forelimb variation in drepanosaurids played a part in niche partitioning within the group.

DISCUSSION

Homology

Character optimizations in the analysis illustrate a series of anatomical transitions in the drepanosauromorph forelimb involving changes in shape and proportions of the ancestral tetrapod carpal series (e.g., Romer, 1956; Reisz, 1981; Coates, 1996). Among the hypotheses of homology for the *Drepanosaurus* forelimb (see Supplement 1), ours is consistent with the digital axes proposed by Shubin and Alberch (1986). This evidence supports a modification of the *Drepanosaurus* zeugopodium and carpus that involved a unique series of changes to the shapes and proportions rather than the development of neomorphs or fusions between elements.

Current studies of amniote forelimb development suggest that major changes in the ulna and carpal series of *Drepanosaurus* must have occurred very early in development. In modern archosaurs (e.g., Rieppel, 1993a; Maxwell and Larsson, 2009), lepidosaurs (e.g., Rieppel, 1994; Maisano, 2002), and turtles (e.g., Sheil, 2003; Sheil and Portik, 2008), the basic shapes of the zeugopodial and carpal elements are laid down in cartilage extremely early in development. Most subsequent modifications to the elements involve fusions of adjacent chondrifications and ossifications; indeed the highly modified carpal arrangement of chameleons is present from the initial chondrification of the carpus (Rieppel, 1993b).

Although bowing of the ulnar shaft occurs in a number of tetrapod taxa (Supplemental S3), none show the bizarre shape of the *Drepanosaurus* ulna. The most deeply bowed ulna known among modern tetrapods occurs in humans exhibiting "radial club hand," a condition linked to hypoplasia or aplasia of the radial digits and radius. These developmental failures can co-occur with a strong bowing of the ulna, which manifests a deep posterior convexity (Buck-Gramcko, 2004). Ulnar development in *Drepanosaurus* was not linked to a failure of the radius and radial digits to form, but the presence of this anomaly in a modern tetrapod shows that the genetic and developmental mechanisms required for an extensive bowing of the ulna still exists.

Functional Morphology

Although the forearm morphology of *Drepanosaurus* has no modern analogue, other facets of its forelimb anatomy suggest functional analogues. An arboreal habitus has been posited for drepanosaurids based on a suite of anatomical traits (e.g., girdle shape, opposable digits, prehensile and clawed tails as in Renesto, [1994a]). The novel morphology we describe is congruent with this hypothesis. The lateral orientation of the glenoid fossa indicates that the humerus was held out laterally in neutral position, rather than posterolaterally as in most early diapsids (e.g., Romer, 1956). The naturally flexed posture of the forelimb indicates that the hands would be positioned under the anterior trunk region, a posture appropriate for branch-clinging. This would also allow extensive protraction and retraction, analogous to the motion in chameleons (Peterson, 1984). In addition to these morphological traits, the phylogenetic position of *Drepanosaurus* among other taxa with traits correlated with arboreality (Renesto, 1994b; Renesto and Binelli, 2006; Renesto et al., 2010), indicates that the taxon derived from arboreal ancestors.

Renesto (1994a) favorably compared the hypertrophy of the second manual ungual and short, unsegmented second digit to extant scratch-digging mammals (e.g., Taylor, 1978; Hildebrand and Goslow, 2001). Similar manual modifications occur in certain fossil mammals with scratch digging adaptations throughout the skeleton (e.g., Rose and Emry, 1983; Xu et al., 2011; Luo et al., 2015). Our new data support comparisons of *Drepanosaurus* to *Cyclopes didactylus* (see Renesto, 1994a), the modern silky anteater (AMNH M 139220; Taylor, 1985; Hayssen et al., 2012). The broad, wing-like epicondyles would support powerful forearm and digital extensors and flexors. The broad, posterior ulnar surface suggests a prominent attachment for *m. triceps brachii* and an extremely powerful extensor mechanism for the forearm. The expansion of the medial surface of the ulna, and the hypertrophy of the proximal carpal series is likely associated with expansion in the digital flexor and extensor musculature as well. The large proximal tuberosities framing the proximal articulation of the second metacarpal likely served the digital extensor tendons. The distal articulation between the penultimate and ungual segments exhibits a tight fit that would allow extensive flexion and extension, but no lateral excursion.

The mobility of this digit corresponds extremely well to that in anteaters. The recognition of a single non-ungual segment in the second digit of *Drepanosaurus* is functionally similar to the immobilized interphalangeal joint in anteaters (Taylor 1978, 1985). The well-defined, tight-fitting articulation between the second metacarpal and second ungual would limit motion at the joint to flexion and extension, similar to a majority of scratch-digging mammals (Taylor, 1978; Hildebrand and Goslow, 2001). The tall, narrow, and elongate unguals are similar to those in modern climbing, clinging squamates (Zani, 2000; Tulli et al., 2009).

Rather surprisingly, the Hayden Quarry *Drepanosaurus* and the Italian *D. unguicaudatus* occupied highly distinct environments at roughly the same time in the middle Norian, the Hayden Quarry preserving a semiarid, riverine environment and the Zorzino Limestone preserving a nearshore environment, although wood is present in abundance at both sites. The arboreal hypothesis of *Drepanosaurus* is congruent with trees being a significant environmental requirement for the taxon, although it is remarkable that this extremely specialized taxon subsisted in such otherwise different environments.

The ecological niche occupied by modern Vermilingua involves the exploitation of social insect colonies (Taylor, 1978), and the comparable morphology in *Drepanosaurus* suggests the possibility of similar exploitation. Trace fossils of insect burrows in fossil wood from the Chinle Formation are known, and some workers argue that some of these represent early bee nests (e.g., Hasiotis, 1997; Hasiotis et al., 1998). However, others (e.g., Grimaldi, 1999; Engel, 2001; Lucas et al., 2010) argue that the borings were instead made by beetles or non-insects, such that the co-occurrence of *Drepanosaurus* with social insects is equivocal. Nevertheless, the ichnofossil record suggests that the wooded plants of the Chinle Formation did play host to invertebrate communities that could have served as possible food sources.

The extreme specialization of the limb in *Drepanosaurus* did not prevent it from persisting in a particularly wide range of environments. The versatility of *Drepanosaurus* is particularly remarkable in that, between its existence in the Late Triassic and the appearance of scratch-digging, climbing mammals in the Cenozoic (Rovereto, 1914; Hirschfield, 1976), no other vertebrate is known to have explored this remarkable ecomorphology.

ACKNOWLEDGMENTS

The material described herein was discovered by numerous volunteers and students over the past six years, and was expertly prepared by Stony Brook University preparator V. Heisey. We thank the Ghost Ranch Conference Center for the continued support of our fieldwork at Hayden Quarry. We thank numerous museum curators and staff for their assistance: C. Mehling (AMNH), A. Downs (GR), A. Tintori (MCSNB), G. Muscio and L. Simonetto (MFSN), R. Allain (MNHN), A. Tintori (MPUM), R. Schoch (SMNS), and M. Brett-Surman (USNM). We thank J. Thostenson for assistance with scanning at AMNH. This project work was funded by NSF Award 1349650 And the Evolving Earth Foundation.

LITERATURE CITED

Berman DS, Reisz RR. (1992) *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. J Paleo 66:1001–1009.

Buck-Gramcko D. (2004) Congenital disorders: radial and ulnar club hand. *Hand Surgery*, eds RA Berger, APC Weiss (Lippincott Williams & Williams), pp. 1453–1464.

Burch SH, Carrano MT. (2012) An articulated pectoral girdle and forelimb of the abelisaurid theropod *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar. J Vert Paleo 32:1–16.

Caldwell MW. (2002) From fins to limbs to fins: limb evolution in fossil marine reptiles. Amer J Med Gen 112:236–249.

Carroll RL (1988). *Vertebrate Paleontology and Evolution*. WH Freeman.

Coates MI. (1996) The Devonian tetrapod *Acanthostega gunnari*
Jarvik: postcranial anatomy, tetrapod interrelationships, and patterns of skeletal evolution. Trans Roy Soc Edinburgh 87:363–421.

Colbert EH, Olsen PE. (2001) A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). Amer Mus Nov 3334:1–24.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Proc Roy Soc B 353:501–541.

Engel MS. (2001) A monograph of the Baltic amber bees and the evolution of the Apoidea (Hymenoptera). Bull Am Mus Nat Hist 259:1–192.

Feduccia A. (1999). *The Origin and Evolution of Birds*. Yale University Press.

Fordyce RE, Barnes LG. (1994). The evolutionary history of whales and dolphins. Ann Rev Earth Planet Sci 22:419–455.

Grimaldi D. (1999) The co-radiations of pollinating insects and angiosperms in the Cretaceous. Annals MS Bot Garden 86:373–406.

Harris JD, Downs A. (2002) A drepanosaurid pectoral girdle from the Ghost Ranch (Whitaker) *Coelophysis* Quarry (Chinle Group, Rock Point Formation, Rhaetian), New Mexico. J Vert Paleo 22:70–75.

Hasiotis ST. (1997) Abuzz before flowers…. Plateau, J Mus N AZ 1:20–27.

Hasiotis ST, Dubeil RF, Kay PT, Demko TM, Kowalska K, McDaniel D. (1998) *National Park Service Paleontological Research. Technical Report NPS/NRGRD/GRDTR-90/01*, eds Santucci VL, McClelland L, pp. 116–121.

Hayssen V, Miranda F, Pasch B. (2012) *Cyclopes didactylus* (Pilosa: Cyclopeidae). Mammalian Species 44:51–48.

Hildebrand M, Goslow GE. (2001). *Analysis of Vertebrate Structure, Fifth Edition*. John Wiley & Sons.

Hirschfield S. (1976) A new fossil anteater (Edentata, Mammalia) from the Miocene of Columbia, S.A. and evolution of the Vermilingua. J Paleo 50:419–432.

Hopkins SSB, Davis EB. (2009). Quantitative morphological proxies for fossoriality in small mammals. J Mammal 90:1449–1460.

Irmis RB, Mudil R, Martz JW, Parker WG. (2011). High-resolution U-Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. Earth & Planet Sic Lett 309:258–267.

Irmis RB, Nesbitt SJ, Padian K, Smith ND, Turner AH, Woody D, Downs A. (2007) A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317:358–361.

Jarvik E. (1996) The Devonian tetrapod *Ichthyostega*. Fossils & Strata 40:1–213.

Lucas SG, Minter NJ, Hunt AP. (2010) Re-evaluation of alleged bees' nests from the Upper Triassic of Arizona. Palaeogeo, Palaeoclimat, Palaeoeco 286:194–201.

Luo Z-X, Meng Q-J, Ji Q, Liu D, Zhang Y-G, Neander AI. (2015) Evolutionary development in basal mammaliaforms as revealed by a docodontan. Science 347:760–764.

Maisano JA. (2002) Postnatal skeletal ontogeny in five xantusiids (Squamata: Scleroglossa). J Morph 254:1–38.

Maxwell EE, Larsson HCE. (2009) Comparative ossification sequence and skeletal development of the postcranium of palaeognathous birds (Aves: Palaeognathae). Zool J Linn Soc 157:169–196.

Motani R. (1999) On the evolution and homology of ichthyosaur forefins . J Vert Paleo 19:28–41.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Nesbitt SJ, Flynn JJ, Pritchard AC, Parrish JM, Ranivoharimanana L, Wyss AR. (in press) Postcranial osteology of *Azendohsaurus madagaskarensis* (?Middle to Upper Triassic, Isalo Group of Madagascar) and its systematic position among stem archosaurs. Bull Amer Mus Nat Hist.

Osborn HF. (1903) On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. Science 17:275, 276.

Padian K, Rayner JMV. (1993) The wings of pterosaurs. Amer J Science 293A:91-166.

Peterson JA. (1984) The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. J Zool London 202:1–42.

Pinna G. (1980) *Drepanosaurus unguicaudatus*, nuovo genere e nuova specie di lepidosauro del Trias alpino. Atti della Soc ital di sci nat del mus civ di storia nat di Milano 121:181–192.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2015). Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. J Vert Paleo 35.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Spec Pubs Mus Nat Hist, U KS 7:1–74.

Renesto S. (1994a) The shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the upper Triassic (Norian) of northern Italy. Zool J Linn Soc 111:247–264.

Renesto S. (1994b) *Megalancosaurus*, an arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. J Vert Paleo 14:38–52.

Renesto S, Binelli G. (2006) *Vallesaurus cenensis* Wild, 1991, a drepanosaur (Reptilia, Diapsida) from the Late Triassic of northern Italy. Riv Ital di Paleo e Strat 112:77–94.

Renesto S, Spielmann JA, Lucas SG, and Spagnoli GT. (2010) The taxonomy and paleobiology of the Late Triassic (Carnian–Norian: Adamanian–Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha). Bull NM Mus Nat Hist Sci 46:1–81.

Rieppel O (1993a) Studies on skeleton formation in reptiles. V. Patterns of ossification in the skeleton of *Alligator mississippiensis* Daudin (Reptilia, Crocodylia). Zool J Linn Soc 109:301–325.

Rieppel O (1993b) Studies on skeleton formation in reptiles. II. *Chamaeleo hoehnelii* (Squamata: Chamaeleoninae), with comments on the homology of carpal and tarsal bones. Herpetologica 49:66-78.

Rieppel O. (1994) Studies on skeleton formation in reptiles. Patterns of formation in the skeleton of *Lacerta agilis exigua* Eichwald (Reptilia, Squamata). J Herpeto 28:145–153.

Rogers JV. (2003) *Pachycheilosuchus trinquei*, a new procoelous crocodyliform from the Lower Cretaceous (Albian) Glen Rose Formation of Texas. J Vert Paleo 23:128–145.

Romer AS. (1956). *Osteology of the Reptiles*. University of Chicago Press.

Rose KD, Emry RJ. (1983) Extraordinary fossorial adaptations in the Oligocene palaeanodonts *Epoicotherium* and *Xenocranium* (Mammalia). J Morph 175:33–56.

Rovereto C. (1914) Los Estratos Araucanos y sus Fósiles. Anal Mus Nacio Hist Nat Buenos Aires 25:1–250.

Senter P. (2004) Phylogeny of Drepanosauridae (Reptilia: Diapsida). J Sys Palaeo 2:257–268.

Sereno PC, Chenggang R. (1992). Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. Science 255:845–848.

Shubin NH, Alberch P. (1985) A morphogenetic approach to the organization of the tetrapod limb. *Evolutionary Biology, Vol. 20*, eds MK Hecht, B Wallace, GT Prance (Springer US), pp. 319–387.

Sheil CA. (2003) Osteology and skeletal development of *Apalone spinifera* (Reptilia: Testudines: Trionychidae). J Morph 256:42–78.

Sheil CA, Portik D. (2008) Formation and ossification of limb elements in *Trachemys scripta* and a discussion of autopodial elements in turtles. Zool Sci 25:622–641.

Shubin NH, Daeschler EB, and Jenkins FA. (2006) The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. Nature 440:764–771.

Simmons NB, Seymour KL, Habersetzer J, Gunnell GF. (2008). Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451:818–821.

Susaita D, Pouydebat E, Manzano A, Abdala V, Hertel F, Herrel A. (2011). Getting a grip on tetrapod grasping: form, function, and evolution. Biol Rev 88:380–405.

Taylor BK. (1978) The anatomy of the forelimb in the anteater (*Tamandua*) and its functional implications. J Morph 157:347–368.

Taylor BK. (1985) Functional anatomy of the forelimb in Vermilinguas (anteaters). *The Evolution and Ecology or Armadillos, Sloths, and Vermilinguas*, eds GG Montgomery (Smithsonian Institution Press), pp. 163–171.

Tulli MJ, Cruz FB, Herrel A, Vanhooydonck B, Abdala V. (2009) The interplay between claw morphology and microhabitat use in neotropical iguanian lizards. Zoology 112:379–392.

X Xu, et al. (2011) A monodactyl nonavian dinosaur and the complex evolution of the alvarezsauroid hand. Proc Nat Acad Sci 108:2338–2342.

Zani PA. (2000) The comparative evolution of lizard claw and toe morphology and clinging performance. J Evo Bio 13:316–325.

SUPPLEMENTARY DATA

SUPPLEMENTARY APPENDIX 1. Past hypotheses for the homologies of the *Drepanosaurus* forelimb.

Pinna (1980) described the *Drepanosaurus unguicaudatus* holotype and presented the first hypothesis for the homologies of its forelimb bones (Fig. 3-5). Pinna hypothesized that both the left and right forelimbs were disarticulated in an identical way. The clavicle and interclavicle were considered to be massive and robust, whereas they remain unidentified in any of the subsequent hypotheses. Pinna (1984, 1986) reiterated this hypothesis.

Renesto (1994a) was the first to suggest that the forelimb in the *Drepanosaurus* holotype was still in articulation. He argued that the elements identified by Pinna as the clavicle and interclavicle were actually the articulated scapulocoracoid. The centrally placed elements identified as the scapula and coracoid by Pinna were reidentified as bones of the forearm. The hourglass-shaped bone described as the scapula by Pinna was reidentified as a radius by Renesto (1994a). However, the massive and crescent-shaped bone identified as the coracoid by Pinna proved more difficult.

Renesto (1994a) provided two hypotheses for the crescent-shaped bone. First, he suggested that it might represent “an enormous process of the radius” (Renesto, 1994a: 254). Under this hypothesis, the slender complex of bones positioned distal to the crescent-shaped element are identified as a single ulna. However, he questioned why both the left and right ulnae would be displaced from the humerus in the same way. He postulated that the relative hypertrophy of the radius might have “displaced the ulnae from their articulation with the humerus” (Renesto, 1994a: 254). He noted that this hypothesis would preclude the possibility of pronation and supination of the forelimb.

Renesto’s second hypothesis identified the crescent-shaped bone as a bizarrely shaped ulna (Fig. 6). Based on that identification, he suggested that there were two bones distal to the crescent. These he suggested as the “?ulnare and ?intermedium” (Renesto, 1994a: 255). He considered this hypothesis problematic, noting that the radioulnar contact in the *Drepanosaurus* holotype resembled a suture. This would also preclude pronation and supination, although in a very different way from the homologies suggested in Renesto’s first hypothesis. Senter (2004) followed this hypothesis in developing characters for his phylogenetic analysis of drepanosaurs and other diapsids.

Renesto et al. (2010) reviewed the record of drepanosauromorphs. He redescribed the forelimb of the *Drepanosaurus* holotype, offering two hypotheses for the forelimb bone homologies (Fig. 3-6). The first hypothesis was identical to the second hypothesis offered by Renesto (1994a), with the crescent-shaped bone identified as an expanded ulna. The second hypothesis of Renesto et al. (2010) suggested that the crescent-shaped bone was “an accessory ossification, which is possibly the more feasible option” (Renesto et al., 2010: 4). Under this hypothesis, the accessory ossification would meet an elongate, slender ulna distally.

SUPPLEMENTARY APPENDIX 2. Museum abbreviations used in comparative description/phylogenetic analysis.

AMNH–American Museum of Natural History (New York, NY)
BP–Bernard Price Institute (Witwatersrand, South Africa)
CMNH–Carnegie Museum of Natural History (Pittsburgh, PA)
GMPKU–Geological Museum of Peking University (Beijing, China)
GR–Ruth Hall Museum of Paleontology (Abiquiu, NM)
IVPP–Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China)
MCSN–Museo Civico di Storia Naturali Milano (Milano, Italy)
MCSNB–Museo Civico di Scienze Naturali Enrico Caffi (Bergamo, Italy)
MCZ–Museum of Comparative Zoology (Cambridge, MA, USA)
MFSN–Museo Friulano di Storia Naturale (Udine, Italy)
MNHN–Muséum National d’Histoire Naturelle (Paris, France)
MPUM–Museo di Paleontologia Università di Milano (Milano, Italy)
PIMUZ–Paleontological Institut und Museum (Zürich, Switzerland)

PIN–Paleontological Institute (Moscow, Russia)
SMNS–Staaliches Museum für Naturkunde Stuttgart (Stuttgart, Germany)
TMM–Texas Memorial Museum (Austin, TX, USA)
UA–Université d'Antananarivo (Antananarivo, Madagascar)
USNM–United States National Museum of Natural History (Washington, DC, USA)
WMsN–Westfäliches Museum für Naturkunde, Münster (Münster, Germany)

SUPPLEMENTARY APPENDIX 3. Comparative anatomical description of *Drepanosaurus unguicaudatus* forelimb elements.

For the elements of the forelimb, we employ two distinct descriptive terminologies. The elements of the arm and forearm are described based on a traditional anterior-posterior, lateral-medial axes. For the components of the manus we employ a distinct framework, using dorsal and palmar and pre-axial and postaxial to describe the radial and ulnar sides of the manus. All specimens of *Drepanosaurus unguicaudatus* identified from the Hayden Quarry are listed in Table 1. A three-dimensional model of the semi-articulated forelimb specimen that is the focus of this description is offered in Fig. 3-7.

Scapulacoracoid

A single fragment of the pectoral girdle is preserved with the collection of forelimb elements that make up H3-037-080527 (Fig. 3-8). It consists of the entire articular portion of the girdle and the dorsal and ventral ridges that frame the glenoid fossa. The dorsal margin is broader and better developed than the ventral margin, although both manifest as prominent "lips" that frame the glenoid fossa. The articular surface framed by these lips is made up of unfinished bone. It is elongate, suggesting that a great deal of motion in the anteroposterior plane framed by the glenoid margins was possible.

Comparisons

The identification of this fragment as the glenoid fossa is due in large part to comparison with the complete, three-dimensional drepanosaurid pectoral girdle from the *Coelophysis* Quarry (GR 1113). This remarkable specimen, described by Harris and Downs (2002), exhibits a strongly verticalized coracoid and a glenoid fossa that is positioned far ventrally relative to the base of the scapular blade. This unique combination of features is most comparable to the *Drepanosaurus unguicaudatus* holotype (MCSNB 5728). The position of the glenoid fossa in GR 1113 strongly suggests that the articular surface faced laterally, allowing for a great deal of anterior and posterior motion of the humeral head. The preserved portion of the girdle from H3-037-080527 is nearly identical, except for its size, suggesting a similar range of motion. Additional drepanosaurid pectoral girdle material with a similarly distally placed glenoid fossa have been discovered in the Upper Triassic Post Quarry (Cooper Canyon Formation, Dockum Group) of west Texas. These were briefly described by Martz et al. (2013).

The pectoral girdle of *Drepanosaurus unguicaudatus*, as represented by the Hayden Quarry material, and that of the *Coelophysis* Quarry drepanosaurid differ strongly from those of most Permo-Triassic diapsids (e.g., *Araeoscelis* spp., MCZ 2043; *Trilophosaurus buettneri*, TMM 31025-140) and most drepanosauromorphs (e.g., *Hypuronector limnaios*, AMNH FARB 1721; *Megalancosaurus preonensis*, MPUM 6008), in which the glenoid is oriented posterolaterally. The postural changes suggested by this shift include a lateral direction of the humerus in anatomical position and the restriction of forelimb motions to a fore-aft plane. Although it is initially tempting to associate this change with the extreme forelimb adaptations in *Drepanosaurus unguicaudatus*, it must be noted that the *Coelophysis* Quarry drepanosaurid exhibits a combination of a laterally oriented glenoid and a plesiomorphic ulna (see below).

Humerus

The proximal humerus is represented by two specimens: a badly crushed specimen that preserves nearly the full length of the humerus (H4-570-110830) and a well-preserved specimen that appears to maintain its original dimensions due to matrix infilling (H4-175-10). Descriptive terminology will follow Russell and Bauer (2008).

The proximal surface of the humerus is heavily weathered in H4-570-110830 (Fig. 3-9). The surface proximal to the deltopectoral crest is the most damaged, obscuring the morphology of the lateral tuberosity and the lateral margin of the humeral head. Medially, the preserved portion of the humeral head is roughly egg-shaped with its long-axis oriented in a flexor-extensor plane. The medial tuberosity is broader in a transverse plane and canted strongly distally.

The flexor surface of the proximal humerus is marked by a substantial depression (likely the bicipital fossa), framed dorsally by the lateral tuberosity and the humeral head and medially by the medial tuberosity. A slender medial ridge runs from the ventral margin of the bicipital fossa down to roughly the midshaft. The ridge is taller proximally, shallowing substantially along its length. Comparison with extant taxa suggests the ridge separated the attachments of *m. brachialis* (on the flexor surface) and *m. triceps medialis* (on the medial surface).

The deltopectoral (DP) crest is proximodistally elongate, but is shallow when viewed in lateral view. The proximalmost portion of the crest is weathered away, although the weathered surface suggests it reached to the level of the lateral tuberosity. The crest shallows abruptly just proximal to the midshaft, although it does not reach as far distally as the medial ridge.

The lateral surface of the humerus is angled strongly relative to the anterior surface, at roughly a ninety-degree angle. This surface is marked posteriorly by another strong ridge, which runs distally from the extensor surface of the weathered lateral tuberosity. The ridge runs just distal to the midshaft. Comparison with extant taxa suggests that the lateral surface framed by the DP crest and the extensor ridge may represent an expanded attachment site for *m. deltoideus clavicularis*.

The posterior surface of the proximal end of the humerus is marked by a substantial depression, framed proximolaterally by the lateral tuberosity and proximomedially by the extensor surface of the humeral head. Comparison with extant taxa suggests this depression served as an attachment site for *m. deltoideus scapularis*, although the absence of a distinctive scar for *m. latissimus dorsi* suggests it may have inserted in this area as well.

The proximal, medial margin of the extensor surface is marked by slight scarring, which may represent the attachment of *mm. scapularis*. The scar is framed by the humeral head proximolaterally and the medial tuberosity proximomedially.

Further distally, there is a medially concave ridge that marks the medial margin of the extensor surface of the humerus. The ridge is relatively shallow proximally, growing slightly taller further distally.

The extremely thin-walled bone that comprises the humeral shaft results in severe crushing as seen in H3-037-080527 (a complete distal end of a humerus) and H4-570-110830 (a badly crushed, partial humerus). The well-preserved proximal end of the humerus in H4-570-110830 retains its original shape. Distal to the deltopectoral crest, the humerus is roughly a semicircle in cross-section, with its rounded surface facing towards the flexor surface of the bone.

The shaft of the humerus exhibits a distinct transverse expansion just distal to midshaft (H4-570-110830). Although no humerus is complete, this expansion almost certainly represents the proximalmost margins of the ect- and entepicondyles. The entepicondyle originates slightly further proximally than does the ectepicondyle. The ectepicondyle is smoothly curved throughout its length. In lateral view the bone is strongly angled relative to the primary axis of the humeral shaft, appearing to “curl” towards the flexor surface of the bone. The margin of the ectepicondyle is thickened relative to the remainder of the humerus, such that is uncrushed relative to the rest of the bone in the complete distal humerus (H3-037-080527). However, damage makes reconstruction of extensor and flexor muscle attachments tentative.

An ectepicondylar foramen is present in the HQ drepanosaurid humeri. Its origin is visible as a subcircular opening on the extensor surface of the humerus, arising near the proximal margin of the ectepicondyle. The distal opening is apparent on the flexor surface of the humerus, very near the distal margin of the ectepicondyle and almost directly adjacent to the large radial condyle.

The entepicondyle is only preserved in one specimen (H3-037-080527) (Fig. 3-10). It grades out from the medial surface of the humeral shaft slightly further proximally than does the ectepicondyle. In this specimen, the outermost margin of the entepicondyle appears broken away, such that only a straight, roughened margin is preserved. It is unclear whether or not there was an entepicondylar foramen. The preserved margin of the entepicondyle does suggest that it was not thickened in the way similar to that of the ectepicondyle.

Of the distal condyles, the radial condyle is by far the larger of the two. Viewed from a flexor aspect, it is egg-shaped with its long-axis oriented proximodistally. The proximal margin is angled slightly medially relative to its distal margin. The condyle is almost entirely situated on the flexor aspect of the humerus, with only a small portion of the distal end situated on the distal margin of the humerus (seen in H2-383-10).

The ulnar condyle is not well preserved in H3-057-080527, but it is preserved in a nearly complete, but badly crushed specimen (H4-570-11). As with the radial condyle, the ulnar condyle is egg-shaped, but is situated almost entirely on the distal end of the humerus, with a slight exposure when the humerus is viewed in an extensor aspect. The ulnar condyle is roughly half the length and breadth of the radial condyle. The two condyles are separated by a small gap of finished bone.

Comparisons

The overall proportions of the HQ *Drepanosaurus* humerus suggest a shorter, squatter element than in *Hypuronector* (AMNH FARB 7759), *Vallesaurus* (MCSNB 4751), and *Megalancosaurus* (MPUM 6008, MFSN 1769). In these proportions it closely resembles the condition in the *Drepanosaurus unguicaudatus* holotype (MCSNB 5728). The exceptionally wide and flaring epicondyles also closely resemble *Drepanosaurus*, in contrast to the subtle epicondyles preserved in an uncrushed specimen of *Megalancosaurus* (MPUM 6008). The massive size of the radial condyle is also evident in *Drepanosaurus*.

The extremely robust, stocky build of the *Drepanosaurus* humerus differs greatly from any other Triassic diapsid. Even taxa with comparatively robust, broad humeri (e.g., *Azendohsaurus madagaskarensis*, *"Chasmatosaurus" yuani*) do not achieve a similar breadth. However, the extremely thin cortical bone compares better with Pterosauria (de Ricqlès et al., 2000) and *Kuehneosaurus* (AMNH FARB 7784).

The extreme development of the deltopectoral crest is distinct from any known Permo-Triassic diapsid. The length of the crest is proportionally greater than in robust saurians, such as *Azendohsaurus madagaskarensis* (UA 7-13-99-577) and *"Chasmatosaurus" yuani* (IVPP V4067) The extreme breadth of the crest in lateral view is unprecedented. This broad surface would likely serve the *m. deltoideus clavicularis* (Dilkes, 2000; Burch, 2014).

The extensor surface of the proximal humerus is overall similar to those of other Permo-Triassic diapsids. The extensive depression on the lateral margin of the posterior surface is more pronounced than in any other early diapsid. The location of this depression is comparable to the attachment of *m. deltoideus scapularis* in other early saurians. There is a shallow groove that runs distally from this depression, framed laterally by the expanded lateral surface of the bone. This likely served the *m. latissimus dorsi*. A shallow groove for the attachment of this muscle occurs in certain early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, UA 7-13-99-577) and dinosauromorphs (e.g., Burch, 2014). This contrasts with the ossified ridge that occurs in *Kuehneosaurus* (AMNH FARB 7784) and an Early Triassic Russian humerus referred to the tanystropheid *Augustaburiania vatagini* (PIN 1043/771).

The extensor surface of the humerus, medial to the posterior expansion of the humeral head is subtly depressed. This accommodates the *mm. scapulohumeralis* in modern reptiles. Distal to this site, there is a smoothly curved margin between the posterior and medial surfaces of the humerus. This margin appears comparable to other known Permo-Triassic reptiles. Both of these surfaces accommodate the *m. triceps medialis brachii medialis* in modern reptiles.

Broad ect- and entepicondyles, as occur in the HQ *Drepanosaurus*, are common among early diapsids (e.g., *Araeoscelis*, MCZ 2043) and lepidosaurs (e.g., *Sphenodon punctatum* [see Carroll, 1985]; *Shinisaurus crocodilurus* [see Conrad, 2006]). In both cases, these frame the passages of ect- and entepicondylar foramina. In most Permo-Triassic taxa that possess the former opening, the ectepicondylar foramen passes near the external margin of the ectepicondyle (e.g., *Araeoscelis*, MCZ 2043; *Kuehneosaurus*, AMNH FARB 7784). This stands in contrast to the passage in the HQ *Drepanosaurus*, which appears to travel deep within the ectepicondyle.

The externally rounded margin of the ectepicondyle in the HQ *Drepanosaurus* resembles early diapsids (e.g., *Araeoscelis*, MCZ 2043) and some lepidosaurs (e.g., *Uromastyx*, Stony Brook anatomical collections; *Shinisaurus crocodilurus*, Conrad, 2006). In *Kuehneosaurus*, the ectepicondyle is triangular and pointed laterally. This contrasts with early archosauromorphs (e.g., *Trilophosaurus buettneri*, TMM 31025-140; *Prolacerta broomi*, BP/1 2675), in which the ectepicondyle is weakly developed, leaving a groove for the radial nerve. The modest curvature and deflection of the crest to the extensor aspect of the humerus in *Drepanosaurus* does not compare to other known diapsids (e.g., Romer, 1956; Lécuru, 1969), including the drepanosaurid *Megalancosaurus* (MPUM 6008).

The development of a broad entepicondyle is comparable to most Permo-Triassic diapsids (*Araeoscelis*, MCZ 2043; *“Chasmatosaurus” yuani*, IVPP V4067; *Trilophosaurus buettneri*, TMM 31025-140), although the breadth of that in the Hayden *Drepanosaurus* cannot be assessed with certainty. The extremely thin nature of the structure differs from the epicondyles that are roughly equivalent to the remainder of the distal humerus in breadth (e.g., *Araeoscelis*, MCZ 2043). That the entepicondyle does not extend distal to the level of the humeral condyles differs from the humeri of *Sphenodon* (Carroll, 1985) and Weigeltisauridae (e.g., *Coelurosauravus elivensis*, MNHN MAP 317; *Rautiania* sp., PIN 5130/54).

The extensive ossification and smooth texturing of the distal humeral condyles resemble the condition in Permian non-diapsid reptiles (e.g., *Captorhinus aguti*, Fox and Bowman, 1966), early diapsids (e.g., *Araeoscelis*, MCZ 2043), and the condylar epiphyses of modern lepidosaurs (e.g., Lécuru, 1969). This contrasts with the roughened, and less well-defined condyles in many early saurians (e.g., *Spinosuchus caseanus*, NMMNH-P; *Azendohsaurus madagaskarensis*, UA 7-13-99-577) and low double condyle in many archosauriforms (e.g., *Batrachotomus kupferzellensis*, SMNS 80276; *Chanaresuchus bonapartei*, MCZ 4035).

Radius

The radius is a complex bone, elliptical in cross-section at mid-diaphysis and expanded at bone ends. Multiple partial radii are preserved from the Hayden Quarry, although only two are complete (H4-570-110830 and H3-037-080527). The latter is depicted in Figure 3-11.

The proximal surface of the radius is deeply concave and egg shaped, with a tapered, pointed ventral margin. In proximal view, the surface appears subtly concave laterally and flattened medially. There is a dorsoventrally deep, tab-like process that extends proximoventrally from the ventral margin of the proximal articulation. The process is marked by articular bone proximally, where it appears to have fitted into a corresponding notch on the ulna. The articular bone extends onto the dorsal surface of the tab-like process, where it appears to have met the radial condyle.

The shaft of the radius is proximodorsally marked by a ridge of bone that runs proximodistally. The ridge begins slightly distal to the rim of the proximal radial articular surface. On the best-preserved proximal radius (H4-38-130813), a small fossa marks the surface of the bone just proximal to the ridge. This may represent a compound attachment site for *m. biceps brachii* and *m. brachialis* as in modern saurians (e.g., Meers, 2003, lizards, Russell and Bauer, 2008). The distal terminus of the ridge is unclear due to crushing in the complete radii. The humerus at midshaft was elliptical in cross-section, with its long-axis oriented in a dorsoventral plane.

The distal end of the radius exhibits a number of strong proximodistally running ridges that divide it into distinct planes: a dorsolateral face, a ventrolateral face, and a medial face. The broad medial face is roughly flat in distal view, although it is interrupted by a thick, proximodistally running ridge. The dorsolateral face is convex in distal view, with a thick rugosity at its dorsal apex. The ventrolateral face is also convex and broader than the dorsolateral face. The dorsal margin of the ventrolateral face is also marked by a thickened tuberosity.

The medial face of the distal radius is marked by a distinct proximodistal ridge that separates two, planar surfaces that broaden distally. The dorsalmost of these surfaces likely serves the *m. flexor carpi ulnaris*, whereas the ventralmost serves the *m. pronator teres*. On the lateral face of the radius, the bone is distinctly separated into a dorsal and ventral faces. The dorsal face likely served the *m. brachioradialis* (*m. supinator longus* per Holmes, 1977). The ventral surface likely served the *m. extensor carpi radialis*. A thin margin on the ventral surface of the distal end of the radius may have served the *m. pronator quadratus*.

The distal articular surface of the radius is deeply concave, with a deeper central depression positioned at the medial margin of the bone. The dorsolateral and ventrolateral faces of the distal articular surface are marked by a tall rim of bone, whereas the medial articular face exhibits no bordering rim.

Comparisons

The deep, elliptical concavity of the proximal surface of the radius differs from the shallow concavities (e.g., *Azendohsaurus madagaskarensis*, UA 7-16-99-607) or flattened surfaces (e.g., *Boreopricea funerea*, PIN 3078/1) that typify early archosauromorphs. Similar shallow concavities occur in more basal reptiles (e.g., *Captorhinus aguti*, Holmes, 1977). The proximal tab in *Drepanosaurus* appears homologous to a proximal flexure of the proximal articular surface of the radius in certain early archosauromorphs (e.g., *Trilophosaurus buettneri*, TMM 31025-140; *Azendohsaurus madagaskarensis*, UA 7-16-99-607). A similar extension may occur in the drepanosaurid *Megalancosaurus* (MPUM 6008).

The flattened extensor surface of the proximal radius appears distinct from the convex surfaces in early reptiles (e.g., *Captorhinus aguti*) and early saurians (e.g., *Azendohsaurus madagaskarensis*, UA 7-16-99-607; *Trilophosaurus buettneri*, TMM 31025-140). The subtle concavity on the flexor surface that sits at the junction between the primary humeral articulation and the proximal tab seems equivalent to the concavity that fits against the extensor surface of the ulna in early reptiles (e.g., *Captorhinus aguti*; *Trilophosaurus buettneri*, TMM 31025-140).

The position of the *m. biceps brachii* towards the extensor aspect of the bone in *Drepanosaurus* appears quite distinct from the position of the attachment closer to its flexor aspect in *Sphenodon* (Miner, 1925) and early reptiles (*Captorhinus aguti*, Holmes, 1977) and the central position in the early dinosaur *Tawa hallae* (Burch, 2014). The lack of curvature along the length of the radius in *Drepanosaurus* is shared with other drepanosaurs (e.g., *Megalancosaurus preonensis*, MPUM 6008, 8437; *Vallesaurus cenensis*, MCSNB 4751) and some early eureptiles (e.g., *Captorhinus aguti*, Holmes, 1977; *Petrolacosaurus kansensis*, Reisz, 1981). This contrasts with the strong, sigmoid curvature of the radius prevalent in some Permian diapsids (e.g., *Thadeosaurus colcanapi*, MNHN MAP 360; *Youngina capensis*, Gow, 1975) and early archosauromorphs (e.g., *Protorosaurus speneri*, Gottmann-Quesada and Sander, 2009; *Trilophosaurus buettneri*, TMM 31025-140).

The multiple, angled surfaces that mark the distal end of the radius correspond well with that of *Captorhinus aguti* (Fox and Bowman, 1966; Holmes, 1977) and differ from the elliptical distal humeri in early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, UA 7-16-99-607). The complex, groove distal articular surface of the radius in *Drepanosaurus* appears distinct from other Permo-Triassic reptiles. The radius exhibits a largely flat articular surface for the radiale in *Captorhinus aguti* (Holmes, 1977) or bearing a subtle, medial concavity in early archosauromorphs (e.g., *Trilophosaurus buettneri*, TMM 31025-140; *Azendohsaurus madagaskarensis*, UA 8-29-97-153).

Ulna

The ulna is a bizarre bone, crescent shaped in both lateral and medial view (Fig. 3-12). The bone is represented by three partial specimens. One preserves only the proximal cotylar contacts for the humerus (H4-570-110830). The remaining two specimens include a nearly complete ulna, associated with the partially articulated forelimb (H3-037-080527) and an isolated, nearly complete specimen. The bizarre shape of this bone demands definition of the visual axes for its description. The proximal surface refers to the articular cotyles for the humerus views in the long axis of the humerus. Distal refers to the condylar surface contacted by the intermedium and ulnare, viewed from the long-axis of the intermedium. Lateral and medial are employed in the same manner as the other descriptive components.

In proximal view, the ulna exhibits two deep cotylar surfaces for the reception of the humeral condyles. Both are more elongate in the anterior-posterior plane than in a transverse plane. The facet for the radial condyle is far broader transversely is the contact for the ulnar condyle, which corresponds well with the size of the distal humeral condyles. These two cotylar surfaces are divided by a very prominent intercotylar ridge.

The anterior surface of the ulna is marked by a triangular concavity for reception of the radial tab-like process that is oriented in a roughly proximodistal plane. This contact surface is framed by lateral and medial ridges. The lateral ridge is sharp, thin, and extends distally from the site of the intercotylar ridge of the proximal surface of the ulna. The medial ridge is not as sharp, exhibiting a rounded edge. Both ridges converge distally to form the tip of the triangular concavity. The convergence is marked by a rounded tuberosity, which is flattened in the transverse plane. A thin lamina of bone links the distal tip of this triangular concavity to the proximalmost margin of the distal condyle. The distal condyle itself is oval-shaped, with a subtle tapering at its ventral margin.

The extensor surface of the ulna is eroded away in all known specimens from the Hayden Quarry. Based on the proportions of the complete ulnae in the *Drepanosaurus unguicaudatus* holotype, a substantial portion of the posterior side of the bone is missing. The crescentic ulnar "shaft" is deeply flattened throughout its length, less than one millimeter in length in the preserved specimens. It is unclear whether the bone would have tapered further towards its extensor aspect. The least-crushed ulnar specimen (H3-076-090605) shows that the "shaft" is composed of two, deeply flattened sheets of cortical bone that lay atop one another, framing a thin and flattened internal cavity. This specimen suggests that the shaft may have been subtly sigmoidal along its length.

Although overall flattened, the lateral surface of the bone is thickened at its proximal end, just below the radial cotylar surface, resulting in the surface being subtly convex at this level. Distally, there is a ridge that runs from the side of the distal condyle towards the extensor surface. The bone surface proximal to this ridge is smooth and finished, whereas the surface distal to the ridge is thickened and subtly roughened. This roughened surface tapers towards the posterior margin of the ulna.

Comparisons

The proximal articular surface of the ulna and the olecranon process are extremely variable in development among Permo-Triassic diapsids. In araeoscelids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Araeoscelis* spp., Vaughn, 1955) and captorhinomorphs (*Captorhinus aguti*, Holmes, 1977) the sigmoid notch for the humeral condyles is well ossified and there is a stout, non-articular olecranon process extending beyond the notch. Among large Triassic archosauromorphs, the notch is well ossified in *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (UA 7-16-99-607), and *"Chasmatosaurus" yuani* (IVPP V4067), although there is no apparent projection of the bone beyond the notch. This condition is comparable to the proximal ulnar epiphyses in modern squamates (e.g., *Varanus exanthematicus*, Landsmeer, 1983; *Iguana iguana*, Russell and Bauer, 2008). Finally, there are a range of other Permo-Triassic taxa, in which the proximal surface of the ulna is poorly ossified. This condition can involve a slight proximal inclination of the proximal ulnar surface (e.g., *Thadeosaurus colcanapi*, MNHN MAP 360; *Sarmatosuchus otschevi*, PIN 2865/68) or a nearly planar articular surface (e.g., *Tanystropheus longobardicus*, GMPKU P-1527; *Boreopricea funerea*, PIN 3078/1).

Drepanosaurs exhibit a wide range of proximal ulnar anatomies. Although the ulnae in *Hypuronector* are heavily crushed (AMNH FARB 7759) they are roughly in articulation with the humerus, and the shape suggests a prominent proximal extension. By contrast, *Vallesaurus cenensis* (MCSNB 4751) exhibits only a very subtle proximal inclination. However, it should be noted that the bones in the only known forelimbs of *Vallesaurus* appear poorly ossified. In *Megalancosaurus preonensis*, the ulna is well ossified proximally, exhibiting a prominent sigmoid notch and olecranon process that "cups" the distal humeral condyles (MPUM 6008). The latter condition resembles the cupping of the condyles in the ulna of *Drepanosaurus*.

A septated proximal articular surface of the ulna, as in *Drepanosaurus*, is shared with virtually all tetrapods exhibiting a well-ossified sigmoid notch. A clear separation for the receptions of the ulnar and radial condyles is evident in *Varanus* (Landsmeer, 1983), *Trilophosaurus buettneri* (TMM 31025-140), and *Captorhinus aguti* (Holmes, 1977). However, the septation is by way of a subtly convex ridge rather than the sharp, prominent crest in *Drepanosaurus*. *Drepanosaurus* does appear to be autapomorphic, with regards to the extreme development of the articular surface for the humeral radial condyle on the ulna.

Although a broad contact between the proximal part of the ulna and the proximal part of the radius is present in nearly all diapsid forelimbs, the extremely deep, prominent groove on the ulna of *Drepanosaurus* for reception of the proximal tab of the radius may be unique. The single exception may be *Megalancosaurus preonensis*; although all known specimens are heavily compressed, MPUM 6008 may exhibit a prominent depression on the ulna distal to the sigmoid notch against which the radius is appressed. In most diapsids, the proximolateral surface of the ulna is convex alongside the articular surface for the radial condyle.

There are very few tetrapods that exhibit an ulnar shaft at all comparable to that in *Drepanosaurus*. Bowing of the ulnar shaft occurs in a number of archosaurs, including the crocodylomorphs *Isisfordia duncani* (Salisbury et al., 2006), *Pachycheilosuchus trinquei* (Rogers, 2003), and *Susisuchus anatoceps* (Salisbury et al., 2003). A number of bird clades have also developed strongly bowed ulna throughout their evolutionary histories (Feduccia, 1999).

The prominent ridge on the lateral surface of the ulna, demarcating two probable muscle attachments, appears more strongly divided than in most Permo-Triassic diapsids (e.g., *Captorhinus aguti*, Holmes, 1977; *Azendohsaurus madagaskarensis*, UA 7-16-99-607; *"Chasmatosaurus" yuani*, IVPP V4067). In some other taxa the lateral surface of the distal end of the ulna exhibits no such division (e.g., *Trilophosaurus buettneri*, TMM 31025-140). By contrast, the medial surface of the ulna in nearly all diapsids forms a broad, flattened surface, as in *Drepanosaurus*.

The distal convexity is broader in a transverse plane than the convex distal ulnar surfaces in most Permo-Triassic reptiles (e.g., *Captorhinus aguti*, Holmes, 1977; *Trilophosaurus buettneri*, TMM 31025-140; *Tawa hallae*, Burch, 2014). Transversely broader, near-hemispherical distal ulnar articulations occur in some modern lepidosaurs (e.g., *Varanus*, Landsmeer, 1983; *Iguana iguana*, Russell and Bauer, 2008).

A note on the *Coelophysis* Quarry drepanosaurid

The matrix block that contains the specimen described by Harris and Downs (2002) preserves a small, nearly complete ulna alongside the pectoral girdle. This element has not been described previously. The bone is elongate and slender, with a prominent proximal expansion for the olecranon process and sigmoid notch and a more moderate distal expansion for the distal condyle.

The proximal surface exhibits a prominent, well-defined articular surface for the distal humeral condyles. Matrix obscures the center of the sigmoid notch, thus that it is unclear whether or not there was a strong ridge septating the space for the ulnar and radial condyles. Proximal to the sigmoid notch is a clear, non-articular olecranon process. That the sigmoid notch is separated from the olecranon is rare among saurian reptiles (e.g., *Azendohsaurus madagaskarensis*, UA 7-16-99-607; *"Chasmatosaurus" yuani*, IVPP 4067) and is a feature better known in more plesiomorphic reptile ulnae (e.g., *Captorhinus aguti*, Holmes, 1977; *Araeoscelis*, MCZ 1262).

The shaft of the element is elongate and slender, similar in robusticity to those of *Megalancosaurus preonensis* (MPUM 6008, 8437). The surface of the shaft is roughened, obscuring the morphology and positions of muscle attachment sites. Distally, the shaft expands into a prominent articular condyle. This closely resembles the distal condyle in the Hayden *Drepanosaurus unguicaudatus* material in its egg-like shape and ventral tapering (H3-076-090605).

Radiale

A large proximal carpal element is preserved in association with the radius in H3-037-080507 and H4-570-110830. The element is only complete in H4-570-110830 (see Fig. 3-13); in H3-037-080507, the element is incomplete and broken into three pieces. It consists of a cone-shaped proximal portion and a tab-like distal process. The proximal portion of an additional specimen is also preserved (H3-037-080527).

The proximal articular surface of the radiale corresponds perfectly to that of the radius. The surface is strongly convex along its post-axial margin, with that convexity fitting firmly into the notch in the distal articular surface of the radius. A dorsally convex rim of flattened articular bone frames the dorsal margin of the convexity, approximating the position of the raised distal rim on the radius. In the specimen preserving only the proximal articulation (H3-037-040, there is a small, accessory facet that sits at the post-axial margin of the bone, facing slightly distally. It is likely this contacted the distal carpal complex (see below).

The preaxial surface of the proximal cone of the radiale is largely made up of smooth, cortical bone. There is a large, quadrangular articular facet at the ventrodistal margin of the cone, a portion of which extends onto the edge of the preaxial surface. The proximal margin of the quadrangular surface is connected to the proximal articular surface of the radiale by a thin bony lamina.

The postaxial surface of the proximal cone is also made up largely of smooth, cortical bone. However, there is a depressed concavity near the dorsal margin of the cone. As several cracks can be seen running in and around this depression, it is possible that the bone is "caved in" here, rather than this being a real anatomical structure. Ventrodistally, the postaxial side also has a small exposure of the quadrangular facet.

The cone of the radiale tapers distodorsally before expanding into a broad distal process that is roughly semicircular in preaxial or postaxial view. The postaxial margin exhibits a broad, flattened facet surface that likely contacted the large distal carpal block. This sutural surface appears continuous with the postaxial facet surface on the distal margin of the conical portion of the radiale. Pre-axially, the distal process is flattened and tapered along its length.

Comparisons

Radialia in Permo-Triassic reptiles are comparatively simple bones. The element undergoes substantial ontogenetic changes during growth, transitioning from a small, irregular ossification to a more complex element with multiple articulations with other carpal elements (Caldwell, 1994). They are often proximodistally short elements that are compressed in a dorsal/palmar plane, including *Captorhinus aguti* (Holmes, 1977), *Thadeosaurus colcanapi*, and *Hovasaurus boulei* (Caldwell, 1994). *Azendohsaurus madagaskarensis* exhibits a complex radiale, with a tapered proximal articulation and a broadened distal articulation that meets the first and second distal carpals (UA 7-16-99-607). Ossified radialia are not universally present in early saurian reptiles; no radiale is known in large, adult individuals of *Trilophosaurus* (Nesbitt et al., in press) or *Tanystropheus longobardicus* (GMPKU P-1527, PIMUZ T/2817).

That the bone in *Drepanosaurus* is substantially proximodistally longer than any other Permo-Triassic reptile may suggest that it is a fusion of a radiale with additional, more distally positioned carpals. The radiale distally articulates with a medial centrale in many early reptiles, including *Captorhinus aguti, Thadeosaurus colcanapi* (Caldwell, 1994), and *Protorosaurus speneri* (Gottmann-Quesada and Sander, 2009). By contrast the medial centrale can be smaller and positioned more centrally within the hand in *Azendohsaurus madagaskarensis* (UA 7-16-99-607). That the element exhibits a complex medial facet, apparently for multiple additional surfaces, supports the hypothesis of a fusion of the ancestral radiale with additional distal bones.

Intermedium

The intermedium is extremely elongate proximodistally, substantially longer than the radius in H3-037-080527. It is roughly elliptical in cross-section at mid-diaphysis and expanded at both ends. Partial intermedia are common in the Hayden Quarry, quite often fused to a fused distal carpal block (see below). The compound intermedium-ulnare fro H3-037-080527 is imaged in Fig. 3-14.

The proximal surface of the intermedium is marked by a deep concavity. This concavity is roughly circular, subtly broader in a preaxial-postaxial plane than it is in a dorsal-plantar view. At the post-axial margin of the proximal concavity, there is a small secondary concavity for contact with the ulnare.

In dorsal view, the intermedium is overall flattened. The shaft of the bone appears straight and columnar in the partially articulated specimen #1 (H3-057-080527). Based on additional specimens (H3-237-070526. H4-712-100626), the shaft actually curves dorsally along its length. Proximally, the dorsal surface is marked by a prominent ridge that runs obliquely in a distal-preaxial direction. This divides the proximal portion of the dorsal surface of the intermedium into two surfaces. The postaxial of these is continuous with the dorsal margin of the facet for the ulnare. The preaxial surface is continuous with the dorsal margin of the large concavity for the ulna. The ridge grows shallower distally, such that these two surfaces are nearly indistinguishable at the midshaft of the intermedium. The preaxial concavity exhibits a smaller, secondary ridge that runs proximodistally for less than one-eighth the length of the bone.

Further distally, the dorsal surface of the intermedium is overall featureless. There may be a subtle convexity just proximal to the contact for the distal carpal block. The postaxial margin of the distal end of the intermedium exhibits a prominent, forked structure, which exhibits proximal and distal tines. The proximal tine angles subtly proximally and is twice as long as the distal tine, which angles distally.

The plantar surface of the intermedium is subtly convex at its proximal end. Further distally, a thick, rounded ridge that divides the bone into sharply offset preaxial and postaxial surfaces. The postaxial surface becomes so strongly angled distally that it is barely visible in plantar view. The ridge is still present at the distalmost end of the intermedium.

In a number of specimens, the intermedium is indistinguishably fused to the fused complex of distal carpals. In those specimens where the bone surface between the two elements is exposed, there is no margin evident where the two would have met originally. This fusion is evident in all specimens, regardless of relative size, suggesting the following:

i) The distal carpals and intermedium fused to one another early in ontogeny.

ii) Our sample of elements includes a number of taxa of different body sizes, all of which exhibit this fusion.

The latter scenario seems unlikely, considering the identical morphologies evident in all of these intermedium-distal carpal complexes.

Comparisons

The extreme elongation of the intermedium into a shaft-like bone is not unprecedented among tetrapods. A number of araeoscelid diapsid reptiles exhibit proximodistally elongated intermedia (e.g., *Araeoscelis* spp., Vaughn, 1955; *Petrolacosaurus kansensis*, Reisz, 1981). Particularly elongated proximal carpal elements occur in Crocodylomorpha (e.g., *Dibothrosuchus* IVPP V7907; *Simosuchus clarki*, Sertich and Groenke, 2010; *Alligator mississippiensis*, Romer, 1956), although the postaxial elements are reduced to an ulnare. However, although some fossil crocodylomorphs expanded these proximal elements such that they are proximodistally subequal in length to the zeugopodial bones (Irmis and Nesbitt, 2012), the radial and ulnar carpals elongate in parallel. This stands in stark contrast to the segmental asymmetries in drepanosaurs, incipient in *Megalancosaurus* and advanced in *Drepanosaurus*.

Despite extensive modifications to the shape of the intermedium in *Drepanosaurus*, the proximal part of the bone exhibits points of homology comparable to non-saurian diapsids and early saurians. The bone exhibits a prominent facet for the ulnare on its proximal-postaxial surface, positioned just distal to the ulnar articulation, similar to that seen in stem-saurians (e.g., *Hovasaurus boulei*, Caldwell, 1994) and early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, UA 7-16-99-607; *Protorosaurus speneri*, Gottmann-Quesada and Sander, 2009; *Tanystropheus longobardicus*, MCSN BES SC 1018). The slender, midshaft portion of the bone is also comparable to most Permo-Triassic diapsids (e.g., *Thadeosaurus colcanapi*, MNHN MAP 360; *Azendohsaurus madagaskarensis*, UA 7-16-99-607), in which the intermedium is tapered at its proximodistal midpoint to allow passage of a perforating artery of the manus (Romer, 1956).

The comparison of the distal intermedium in *Drepanosaurus* with those of other diapsids is highly problematic. The complex post-axial forked structure, which appears to have distally articulated with the ulnare, is unlike the intermedium in any other diapsid, including the closely related *Megalancosaurus preonensis* (MPUM 8437). In most taxa, the intermedium distally makes a broad contact with the medial centrale (e.g., *Captorhinus aguti*, Holmes, 1977; *Azendohsaurus madagaskarensis*, UA 7-16-99-607). The flattened palmar surface of the distal end of the intermedium may have served the *m. extensor digitorum communis brevis* as in tetrapods (e.g., Holmes, 1977). A fusion between the intermedium and more distal elements is not recognized in other Permo-Triassic tetrapods (e.g., Miner, 1925; Romer, 1956).

Ulnare

The ulnare is substantially different in shape from the paralleling intermedium. The bone is flattened in a palmar-dorsal plane, although it expands into a semicircular cross-section at its distal fourth. The contact surfaces of the bone for the intermedium proximally and the distal carpal complex distally strongly supports identification as the ulnare, considering the homologous contact surfaces in other Permo-Triassic tetrapods. This description is based on a single, complete specimen, a part of H3-037-080527) that exhibits a large degree of distortion (Fig. 3-14).

Proximally the ulnare exhibits a small, broad convexity, which articulates with the proximal, post-axially facing contact for the intermedium. Immediately distal to this articular surface, the bone becomes heavily flattened. It curves distally, such that it parallels the shaft of the intermedium. In H3-037-080527, the shaft of the ulnare arcs dorsally along its length. This curvature corresponds well to the undistorted intermedia in the sample (H3-237-070526), suggesting that both bones curved along their lengths.

At the proximodistal level of the contact between the intermedium and the distal carpal complex, the ulnare develops a semicircular cross-section. The bone is convex dorsally and flattened on its palmar aspect. The dorsal surface exhibits a small ridge that sits just proximal to the distal articular surface. The ridge runs preaxially. The ventral surface of the bone is poorly preserved, made up of small, glued bone fragments. This portion of the ulnare curves subtly in a preaxial direction, such that its distal articular surface would meet the distal carpal complex just distal to the intermedium.

The distal articular facet of the ulnare is semicircular, convex dorsally and flattened on its palmar face. The surface itself is subtly convex, with a tiny, centrally placed dome. The surface is formed of unfinished bone, contrasting with the finished bone that encircles the remainder of the distal ulnare. Based on the available material, it is unclear how the distal ulnare contacted the distal carpal complex.

Comparisons

The relative equal length of the elongate ulnare and intermedium is comparable to the condition in *Megalancosaurus preonensis* (MPUM 8347) and early diapsids (e.g., *Araeoscelis* spp., Vaughn, 1955; *Petrolacosaurus kansensis*, Reisz, 1981), although as with the intermedium, the hyper-elongation of the ulnare in *Drepanosaurus* is not comparable to any other known tetrapod.

The contact surfaces for the other carpals are comparable to those in most Permo-Triassic amniotes (e.g., *Captorhinus aguti*, Holmes, 1977; *Azendohsaurus madagaskarensis*, UA 7-16-99-607). The proximal facet surfaces on the ulnare are proportionally larger in other Permo-Triassic reptiles than in *Drepanosaurus*; most taxa exhibit an intermedium and ulnare that equally contribute to the contact for the distal ulna. Such proportions appear to be retained in the sister taxon to *Drepanosaurus unguicaudatus*, *Megalancosaurus preonensis* (MFSN 1729; MPUM 8437).

In Permo-Triassic diapsids, the distal end of the ulnare meets the portion of the carpal series just distal to the intermedium. In a large majority of early reptiles, this bone distally forms a broad contact with the fourth distal carpal (e.g., *Azendohsaurus madagaskarensis*, UA 7-16-99-607; *Tanystropheus longobardicus*, MCSN BES SC 1018) and a smaller preaxial contact for the medial centrale (*Azendohsaurus madagaskarensis*, UA 7-16-99-607; *Trilophosaurus buettneri*, Nesbitt et al., in press).

Distal Carpal

A complex distal carpal (or complex of distal carpals) (DC) is fused to the distal end of the intermedium (Fig. 3-14). The element superficially appears similar to a boxing glove, with the central concavity on the dorsal surface. These are among the most common drepanosaurid elements recovered in the Hayden Quarry, which could be attributed to the density of the bone relative to other drepanosaurid limb elements.

In dorsal view, the DC exhibits two primary expansions. One is very large and wider in a pre-axial-postaxial plane than in a proximodistal plane. This expansion exhibits a broad, egg-shaped, unfinished surface. This expanded contact surface also angles dorsally. The dorsal angling of the larger expansion produces a subtly concavity on the dorsal surface of the DC, which exhibits small, proximodistally oriented grooves. A second expansion is oriented preaxially and is subtly convex. This convexity, results in the expansion being only partially visible in dorsal view. These expansions are separated by only a thin margin of finished bone.

In ventral view, the entire DC appears convex. There are three primary expansions visible in this view. The largest of these is the ventral surface of the expanded surface visible in dorsal view. The other expansions are smaller, one sitting on the preaxial margin of the DC and the other sitting on its postaxial margin. The preaxial expansion forms a subtly convex tuber, whereas the postaxial expansion exhibits a convex dorsal surface and a flattened palmar surface. Both of these expansions are linked by a subtly convex ridge on the palmar surface.

Comparisons

A broad comparison of the relationships between the intermedium and more distal carpal series in a broad sample of Permo-Triassic reptiles suggests that the medial centrale is almost always positioned directly distal to the intermedium, indicating that the DC in *Drepanosaurus* likely incorporates this element. This suggestion is congruent with the observation that the ulnare makes contact with the medial centrale in a range of early reptile taxa.

It is likely that the second distal carpal contributed to the largest of the primary convexities in *Drepanosaurus*. Permo-Triassic diapsids tend to vary between five distal carpals (occurring in non-saurian reptiles, e.g., *Hovasaurus boulei*, *Claudiosaurus germaini*, Caldwell, 1994 and putative early lepidosaurs, e.g., *Saurosternon bainii*, NHMUK R 1234) and four distal carpals (the fifth distal carpal is absent in most early saurian reptiles, e.g., *Protorosaurus speneri*, Gottmann-Quesada and Sander, 2009; *Macrocnemus fuyuanensis*, GMPKU-P-3001). In these taxa, each distal carpal sits directly proximal to the corresponding metacarpal, such that the second distal carpal is almost certainly the origin of the primary convexity.

It is as-yet unclear whether the smaller convexities on the DC in *Drepanosaurus* correspond to any of the other ancestral distal carpals in diapsids. Confirmation of this homology will rely on the future discovery of articulated manual materials, to determine whether the other manual digits articulate with any of the convexities.

Metacarpal II

A number of exceptionally broad and flat manual elements are herein referred to as second metacarpals based on comparison with *Drepanosaurus unguicaudatus*. The elements in that taxon are exposed in postaxial view, with the left metacarpal II being the best preserved. The Hayden elements shared a number of features with *D. unguicaudatus*, including exceptionally deep ligament pits on the distal condyles, a strong postaxial ridge running across the distal half of the element, and a prominent depression of the dorsal surface just proximal to the condyles.

The second metacarpal in the Hayden drepanosaurid is roughly quadrangular in dorsal and ventral views and dorsoventrally flattened in preaxial and postaxial views (Fig. 3-15). There are 12 complete and partial metacarpals preserved in the Hayden collections that differ only in size.

The proximal surface is marked by a dorsoventrally flattened, ovoid concavity framed both preaxially and postaxially by prominent tuberosities. The preaxial tuberosity is substantially larger than the postaxial, projecting far proximally relative to the central concavity. The angles ventrally at its preaxialmost margin, hanging well ventral of the central concavity. It also exhibits a small accessory tuberosity on its preaxial surface.

The central concavity is ovoid in shape. The dorsal margin of the surface is convex, whereas the ventral margin is roughly horizontal. The ventral margin also extends further proximally than the dorsal margin, such that the concavity is visible in dorsal view. The smaller, postaxial tuberosity forms a dorsoventrally tall oval in proximal view. It extends slightly proximal relative to the central concavity.

The ventral surface of the second metacarpal is concave along its length, framed by the ventrally expanded preaxial and postaxial surface of the bone. Just proximal to the distal condyles, there is an additional, deeper concavity.

The preaxial and postaxial surfaces are similar in morphology, although the preaxial surface extends further proximally due to the expanded tuberosity. A thin ridge extends anteriorly from the tuberosities. This ridge expands dorsoventrally into slightly taller, flat plates that extend to the level of the distal condyles. The equivalent preaxial plate is visible on the holotype metacarpal II on *Drepanosaurus unguicaudatus*.

Comparisons

Metacarpals among Permo-Triassic reptiles are typically proximodistally elongate, roughly elliptical in cross-section and expanded at both ends. These differ substantially from the flattened element found in *Drepanosaurus*.

The proximal articular surface of the metacarpals in most early reptiles is relatively planar or subtly convex (e.g., *Azendohsaurus madagaskarensis*, UA 7-16-99-607; *Prolacerta broomi*, BP/1 2676). It is unclear if the pre- and postaxial tuberosities that frame the proximal concavity of metacarpal II in *Drepanosaurus* are equivalent to the processes that allow the overlap of the proximal metacarpals in a number of early reptiles (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Trilophosaurus buettneri*, TMM 31025-140). This contrasts with a number of non-diapsid tetrapods (e.g., *Eryops megacephalus*, Miner, 1925; *Captorhinus aguti*, Holmes, 1977), in which the metacarpals exhibit no such overlap.

Although the relative cross-sections of early reptile metacarpals vary, no taxa exhibit the strong dorsal convexity, the corresponding ventral concavity, and the overall flattened morphology of the metacarpal in *Drepanosaurus*. In general, taxa with proportionally shorter metacarpals exhibit flatter and broader dorsal and ventral surfaces relative to the rounded shape present in taxa with elongate metacarpals (compare *Trilophosaurus buettneri*, TMM 31025-140 to *Azendohsaurus madagaskarensis*, UA 7-16-99-607).

The broad, planar surfaces on the preaxial and postaxial edges of the *Drepanosaurus* metacarpal appear distinct from any Permo-Triassic diapsids. The condition is similar to the fused metacarpophalanx in a number of mammal taxa, including the extinct palaeanodont *Xenocranium* (Rose and Emry, 1983). These share with the *Drepanosaurus* metacarpal both the broad, planar surfaces externally and a prominent dorsal pit, just proximal to the distal condyles. Despite these similarities, we refrain from considering the element in *Drepanosaurus* a fusion of multiple manual elements until supporting developmental data can be found.

Extremely well-defined, ginglymoid distal articular surfaces are rare in the metapodials and phalanges of Permo-Triassic diapsids. Such articulations are apparent in a number of drepanosaurs, including *Hypuronector* (AMNH FARB 7759) and *Megalancosaurus* (MPUM 6008). The distal articular surfaces of the phalanges in a number of early saurians are also somewhat divided into lateral and medial condyles, although these are distinct from the equivalent surfaces in the *Drepanosaurus* metacarpal in that they angle towards the center of the phalanx dorsally (e.g., *Trilophosaurus buettneri*, TMM 31025-140; *"Chasmatosaurus" yuani*, IVPP V4067). The articulations between these archosauromorph phalanges and elements further distally are not as well defined as in the second digit of *Drepanosaurus*.

Manual ungual II

Among the most common fossils referable to drepanosaurs found from the Hayden Quarry are enormous manual unguals. Only two gigantic unguals have been found in articulation with second metacarpals, suggesting that some of these giant elements represent the second manual ungual. This observation is consistent with the gigantic size of the second ungual in the type specimen of *Drepanosaurus unguicaudatus*. However, there are two distinct morphologies represented by the giant unguals from the Hayden Quarry, one substantially shorter (Fig. 3-16 and Fig. 3-17) than the other (Fig. 3-18). We refer to these as Morphotype I and Morphotype II respectively. The presence of two distinct morphologies suggests two possibilities:

i. The two ungual morphotypes represent distinct drepanosaurid taxa or two morphs of a single drepanosaurid taxon.

ii. The two ungual morphotypes belong to different manual digits of a single drepanosaurid taxon.

Although often reconstructed as bearing a single large manual ungual, the manus in *Drepanosaurus unguicaudatus* is heavily obscured in the type and only known specimen. The morphology of the first manual digit is almost entirely unknown; all that is visible is a tiny portion of the proximal end of the first manual ungual and the post-axial surface of the distal end of the digital element to which the ungual articulated (either a proximal phalanx or a metacarpal).

For this description, we will address common features of the two ungual morphotypes. We will specify the distinctions between the two where they occur.

The very large manual unguals are extremely tall and flattened in a pre-axial-postaxial plane. Throughout their lengths, the cross-section of the unguals form a strongly tapered, isosceles triangle Both morphotypes exhibit a strong curvature, although this differs in degree. One morphotype exhibits a stronger and more abrupt curve, tapering to a slender, pointed apex. The second is straighter throughout much of its length, curving and tapering to a pointed apex only at its distal end.

The articulation for the more proximal digital element is positioned at the flexor aspect of the proximal end of the ungual. The articular surface is deeply concave and divided into two well-defined cotyles, which are separated by a thin ridge. Each cotyle angles slightly preaxially towards its dorsal margin.

Dorsal to the proximal articulation, the ungual is marked by a dorsally tapered extensor surface. This region is framed by a thin bony margin that is weathered in all but a few specimens (e.g., H2-275-06). The margin is more pronounced on the preaxial side of the claw. At a point two-thirds the dorsoventral height of the extensor surface, there is a small, subcircular depression.

The flexor surface of the ungual exhibits a deep, distally tapering pit framed preaxially and postaxially by two prominent ridges. The preaxial ridge is proximodistally shorter, capped by small dome of unfinished bone. The postaxial ridge is more elongate, approximately twice as elongate as the preaxial ridge. It is capped by a thick margin of unfinished bone. The depression on the flexor surface is proportionally more elongate in the claws of Morphotype II.

Just distal to the tip of the flexor depression there is a prominent flexor tubercle, roughly hemispherical in shape. In palmar view, the tubercle tapers very slightly towards its distal aspect. The proximal aspect of the tuber in both morphotypes is marked by two prominent pits, positioned at its preaxial and postaxial margins. The proximal surface of the tuber also exhibits a midline groove, which runs proximodistally to the proximodistal midpoint of the tuber.

The ungual tapers along its length, most prominently distal to the flexor tubercle. The strong curvature of the element extends ventral to the flexor tubercle before tapering to a blunt point. The lateral surfaces of all of the claws are flattened. A groove for a keratinous sheath is only apparent in the least distorted specimens (e.g., H2-275-06). It is extremely shallow, such that even slight transverse compression obscures its presence.

Comparisons

Ungual morphology is well known in a number of early saurian taxa, although there is little context for their morphology in other Permo-Triassic diapsid groups. Available specimens of non-saurians preserve the manus in a way in which it is currently uninterpretable (e.g., as an impression or deeply embedded bone in the Permian diapsids from the Sackamena Formation of Madagascar (Piveteau, 1926). The unguals of *Araeoscelis* and *Petrolacosaurus* have only been superficially described (Vaughn, 1955; Reisz, 1981; Reisz et al., 1984).

The manual unguals of early archosauromorphs are particularly well understood. Most are similar to those of *Drepanosaurus* in being dorsoventrally taller than transversely wide and strongly recurved (e.g., *Protorosaurus speneri*, SMNS cast of WMsN P 47361; *Trilophosaurus buettneri*, TMM 31025-140). Certain other early saurians exhibit substantially longer, slenderer manual unguals (e.g., *““Chasmatosaurus””* *yuani*, IVPP 4067; *Boreopricea funerea*, PIN 3078/1) The proximal articular surfaces of these early saurian claws are very distinct from *Drepanosaurus*; although the terminal phalanges in some early archosauromorphs (e.g., *Trilophosaurus buettneri*) are well separated into distinct condyles, the articular surface of the ungual is poorly defined, separated only by a weak, dorsoventrally running ridge. The articular surface occupies nearly the entire proximal surface of the bone, distinct from the ventrally placed articular surface for the second metacarpal in *Drepanosaurus*.

The proximoventral surface of the claw in early archosauromorphs is often marked by a substantial flexor tubercle that extends ventral to the ventral margin of the articular surface (e.g., *Trilophosaurus buettneri*, TMM 31025-140; "*"Chasmatosaurus"*" *yuani*, IVPP 2720) in contrast to the distally placed tubercle in *Drepanosaurus*. The primary shaft of the saurian claws are transversely narrow throughout their dorsoventral heights, in contrast to the strong dorsal tapering in *Drepanosaurus*. All of the aforementioned saurian claws exhibit distinct keratin sheath grooves on both the lateral and medial surfaces, in contrast to the planar surfaces in the drepanosaurs.

The unguals of *Drepanosaurus* and *Megalancosaurus* have informed past hypotheses regarding the ecomorphology of drepanosauromorphs (Renesto, 1994a, 1994b; Renesto et al., 2010). The extreme asymmetry in ungual size in *Drepanosaurus* and the high aspect ratio of the enlarged claws have been favorably compared to a number of modern scratch-digging mammal taxa (see Discussion). The recognition of three-dimensionally preserved drepanosaurid unguals allows us to further contextualize these past comparisons.

Renesto (1994a:256), while speculating on the possibility of scratch-digging in *Drepanosaurus*, notes that the second ungual "is deep, but rather thin and probably could not have been used for loosening soil or other hard materials without damage." Nevertheless, he later deems the modern silky anteater, *Cyclopes*, the best extant analogue for the ecomorphology of *Drepanosaurus*, in light of the similar combination of ungual asymmetry, body size, and arboreal adaptations. The new fossil material demonstrates that the unguals were substantially more robust than is apparent in the *Drepanosaurus* holotype. The dorsal tapering of these claws, combined with the extensive development of flexor and extensor attachments supports a manual morphology similar to that of *Cyclopes*.

Metacarpals and/or phalanges

Both H3-037-080527 and H4-570-110830 preserve a small fragment of a distal metapodial. These exhibit a poorly defined, dorsally convex and ventrally concave unfinished articular surface distally. One side of this distal articular surface, the bones exhibit a proximodistally elongate groove, which could represent a ligament pit. The opposite side of these distal structures are marked by a thick, dorsally positioned ridge. It is unclear if these are equivalent to any of the manual elements in the *Drepanosaurus unguicaudatus* holotype, as the metacarpals are particularly poorly preserved.

Three small ginglymoid articular condyles are preserved with H4-570-110830. These are substantially smaller and narrower than the distal articular surfaces of the second metacarpals. These share with the second metacarpals the presence of a deep ligament pit alongside the primary articular surface. These compare quite favorably with the preserved proximal phalanges of the third through fifth manual digits in the *Drepanosaurus* holotype, strongly suggesting that the Hayden Quarry *Drepanosaurus* exhibited comparable small manual digits.

Manual ungual (Not second)

Additional manual unguals that are similar in morphology to those described above have been discovered in the quarry. These exhibit a number of morphological similarities to the enlarged second manual unguals, including a well-defined proximal articulation, a prominent flexor surface that is framed by two ridges, a ball-like flexor tubercle marked by an anteroposteriorly running groove, and a dorsally tapering extensor surface. However, these unguals are never as large or tall as the second unguals. We consider it likely that these do represent a part of the same taxon, as the less robust claws have been recognized in association with the second manual unguals.

The smaller unguals are relatively shorter in dorsoventral height than are the second unguals. These are still distinctly tapered dorsally, curving along their lengths. Although the distal tip is weathered away in all unguals of this morphotype, the tip clearly extended ventral to the level of the proximal articular surface. The extensor surfaces of these unguals are proportionally shorter than those of the second unguals, although the details of this surface are obscured by weathering.

Additional Elements

The most complete forelimb specimens described herein (H3-037-080527 and H4-570-110830) preserve a number of small bone fragments that cannot be homologized with any specific tetrapod forelimb elements. We describe a number of these below, with preliminary hypotheses as to their identities.

Metacarpals?

A pair of small, tapering elements is preserved with the H3-037-080527 specimen, preserving a broad elliptical depression that connects to a rapidly tapering shaft. In both specimens the shafts are broken. The margins of the depression are deeper on one side relative to the other. In this way, these bones resemble the large second metacarpals prevalent at the site.

The distal end of a probable metacarpal is also preserved with the H3-037-080527 materials. This specimen is transversely narrow, with only the apparent distal end preserved. The distal end is marked by a broad, flattened articular surface that extends ventrally onto the ventral face of the bone. The distal articular face itself is pointed dorsally and strongly angles to one side. A small extension of the articular face also extends onto either the lateral or medial side of the element. On the side opposite this small extension, there is a prominent ligament pit.

Manual phalanx?

Among the elements recovered in H4-570-110830 are two very small elements found in close association. The first includes a tapering shaft that exhibits a broad, bipartite articular surface on one end. This surface is not strongly concave and exhibits a poorly defined margin. The bone tapers rapidly from that point and curves below the level of the articular surface before expanding slightly. The second element includes a poorly preserved ginglymoid condyle, with a prominent groove separating two sharply defined hemicondyles. It is likely that these two fragments belong to a single bone.

A second element includes what appears to be the distal end of a dorsoventrally compressed phalanx. The element appears to exhibit a distal terminus with two widely separated condyles, not unlike the distal ends of the second metacarpal. There is evidence on one side of a deep ligament pit, similar to that in the second metacarpals as well.

SUPPLEMENTARY APPENDIX 4. Taxon list for phylogenetic analyses.

Bibliographic references and institutional accession numbers of specimens that were scored based on firsthand examination.

Petrolacosaurus kansensis–Reisz, 1981.
Thadeosaurus colcanapi–MNHN MAP 360; Carroll, 1981; Caldwell, 1994.
Hovasaurus boulei–MNHN MAP 336; Currie, 1981; Caldwell, 1994.
Protorosaurus speneri–USNM 442453; SMNS cast of WMsN P 47361; Gottmann-Quesada and Sander, 2009.
Azendohsaurus madagaskarensis–Hundreds of specimens accessioned with Université d'Antannanarivo. Forelimb codings primarily based on UA 7-16-99-607.
Shinisaurus crocodilurus–Conrad 2004, 2006.
Sphenodon punctatum–Günther, 1867; Howes and Swinnerton, 1901; Hoffstetter and Gasc, 1969; Rénous-Lécuru, 1973; Carroll, 1985, Evans 2008.
Hypuronector limnaios–AMNH FARB 1721, 7759; Colbert and Olsen, 2001.
Vallesarus cenensis–MCSNB 4751; Renesto and Binelli, 2006.
Dolabrosaurus aquatilis–CMNH 28589; Berman and Reisz, 1992.
Megalancosaurus preonensis–MFSN 1721; MPUM 6008, 8437; Renesto, 1994b; Renesto et al., 2010.
Drepanosaurus unguicaudatus–MCSNB 5728; Renesto, 1994a.
GR 1113–Includes all drepanosaurid material preserved on a small block of matrix from the *Coelophysis* Quarry. Initially described by Harris and Downs, 2002.

SUPPLEMENTARY APPENDIX 5. A note on drepanosauromorph taxonomy and taxon choice.

Of the taxa referred to the drepanosaurid clade in the scientific literature, we chose to exclude only the putative drepanosauromorph *Kyrgyzsaurus bukhanchenkoi* from the Middle Triassic Madygen Formation of Kyrgyzstan (Alifanov and Kurochkin, 2011). The characters offered for the drepanosaurid affinities of the taxon include "large nares and orbits, low position of the quadrates, the absence of gradual transition between vertebrae of the cervical and thoracic regions, arches clavicles, subtriangular section of thoracic ribs, and cranial inclination of the dorsal end of the scapulae" (Alifanov and Kurochkin, 2011:p. 645). The cranial characters offered are extremely homoplastic among early diapsids and subject to a great deal of ontogenetic change. The purported abrupt transition between the cervical and dorsal regions of the vertebral series is difficult to discern, although the anterior dorsal neural spines may exhibit some degree of craniocaudal expansion similar to the condition in *Vallesaurus cenensis* (based on Plate 10 of Alifanov and Kurochkin, 2011). If the clavicles in *Kyrgyzsaurus* do indeed exhibit midline facets for one another, this would represent a character shared with GR 1113 from the Upper Triassic of western North America. However, this character is difficult to discern in Plate 10 of Alifanov and Kurochkin (2011). The "anterior inclination" of the scapula bears little resemblance to the anterior curvature of the slender blade in drepanosauromorphs more derived than *Vallesaurus*. The morphological argument for the drepanosauromorph affinities of *Kyrgyzsaurus* is thus insufficient, and the available description and images do not allow detailed recoding of the specimen. Pending restudy of the specimen or further description, we refrain from including *Kyrgyzsaurus* in this analysis.

Renesto et al. (2010) named two new species of drepanosauromorph, *Megalancosaurus endennae* and *Vallesaurus zorzinensis*. *M. preonensis* and *M. endennae* were considered to differ only in hindlimb anatomy. Renesto et al. (2010) argued that *M. preonensis* exhibited a narrow interosseus space between its tibia and fibula and a narrow first metatarsal similar in morphology to the remaining metatarsals, whereas *M. endennae* exhibited a distinctly bowed fibula and a first metatarsal at a right angle to the other digits with a complex, opposable hallux.

The establishment of this new species is problematic. The holotype specimen of *Megalancosaurus preonensis* (MFSN 1769) does not preserve any portion of the hindlimb, such that it does not preserve the characters presented as distinguishing *M. endennae* and *M. preonensis*. If a specific distinction does exist between *M. endennae* and *M. preonensis*, such that specimens must preserve a hindlimb to distinguish between them, that would render the holotype specimen of the genus non-diagnostic. However, we do not accept the characters offered to diagnose between these two species of *Megalancosaurus*, so the question of establishing a neotype for *M. preonensis* is academic.

The only specimen referred to *M. preonensis* to preserve the foot and hindlimb, MPUM 8437, is heavily crushed in the region of the zeugopodium, with the tibiae and fibulae overlying one another such that the interosseus space is obscured. It is extremely difficult to assess whether or not MPUM 8437 exhibited a bowed fibula as in the specimens referred to *M. endennae* considering the condition of the hindlimb. This leaves the construction of the first pedal digit as the distinguishing character between the two *Megalancosaurus* species.

Although this distinction is very real, one drepanosauromorph taxon appears to exhibit dimorphism in the construction of the first manual digit. A collection of nearly complete drepanosaurid skeletons from a single site in the Upper Triassic?/Lower Jurassic? Nugget Sandstone of Utah preserves multiple individuals that only differ in the morphology of the pes. Some individuals exhibit an opposable first digit, whereas others do not, which suggests that conspecific drepanosaurs can exhibit distinct pedal morphologies (Chure et al., 2013). This discovery supports the hypothesis that only one species of *Megalancosaurus* and *Vallesaurus* are represented from the Zorzino Limestone.

SUPPLEMENTARY APPENDIX 6. Character list for phylogenetic analysis

This matrix is a modification of Pritchard et al. (2015) and its subsequent expansion for Nesbitt et al. (in press). Characters describing the ingroup relationships of drepanosaurids have been integrated (see below). References to characters from Renesto et al. (2010) refer specifically to the novel character set developed to assess the ingroup relationships of Drepanosauromorpha, the results of which are presented on pages 55 through 59 of that text.

1) Premaxilla, posterodorsal process (=maxillary process, = subnarial process): absent, such that premaxilla contributes a small ventral margin for the naris (0); posterodorsal process present, framing the posteroventral margin of the naris. (1).
    - Character 4 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Müller (2004), and Nesbitt (2011).

2) Lacrimal, facial contribution: forms a portion of lateral surface of the face, reaching anteriorly to the external naris (0); forms a portion of the lateral surface of the face, but does not reach naris (1); limited to orbital margin (2).
    - Character 11 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Müller (2004), and Conrad (2008). ORDERED.

3) Parietal, dorsal surface: parietal skull table flattened (0); dorsal exposure of parietal forms a raised margin, elevated above lateral excavation for jaw adductor musculature (1); thin, blade-like sagittal crest (2).
    - Character 20 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier et al. (1988b), DeBraga and Rieppel (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011). ORDERED.

4) Jugal, posterior process: absent (0); present, but failing to contact the quadratojugal posteriorly (1); present, contacting the quadratojugal posteriorly. (2).
    - Character 32 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a, 1988b), Rieppel (1994), Benton and Allen (1997) DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011). ORDERED.

5) Squamosal, size of descending process: forms massive flange that covers the quadrate entirely in lateral view (0); anteroposteriorly slender (1).
    - Character 34 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), and Merck (1997).

6) Quadrate, shape of posterior margin: straight, vertical posterior margin (0); concave, excavated posterior margin (1).
    - Character 43 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), and Müller (2004).

7) Anterior cervical ribs, shaft shape: tapering rapidly, roughly triangular in lateral view (0); ribs taper gradually, elongate and splint-like in lateral view. (1).
    - Character 104 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Jalil (1997), Merck (1997), and Dilkes (1998).

8) Cervical ribs, anterior process: absent (0); present (1).
    - Character 105 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), and Müller (2004).

9) Cervical vertebrae, intercentra: present (0); absent (1).
    - Character 106 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), Dilkes (1998), and Nesbitt (2011).

10) Cervical vertebra, dorsal surface of postzygapophyses: smooth and rounded (0); posteriorly pointed projections (epipophyses) present. (1).
    - Character 119 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Nesbitt (2011).

11) Sternum, ossification of sternal plates: present (0), absent.
    - Character 149 in Pritchard et al. (2015) and Nesbitt et al. (in press).
    - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

12) Coracoid, number of ossifications: two (0); one (1).
    - Character 147 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

13) Humerus, ectepicondyle, morphology of radial nerve groove: groove has no roof (0); groove roofed, forming ectepicondylar foramen (1).
    - Character 151 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a, 1988b), Rieppel (1994), Benton and Allen (1997), Jalil (1997), and Dilkes (1998).

14) Humerus, distal condyle morphology: distinct trochlear and capitular articulations (0); low, double condyle (1).
    - Character 156 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in DeBraga and Rieppel (1997) and Müller (2004).

15) Ulna, ossified olecranon process: present (0); absent (1).
    - Character 157 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Benton (1985), DeBraga and Rieppel (1997), Merck (1997), and Müller (2004).

16) Medial centrale of hand: absent (0); present (1).
    - Character 158 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier (1984), Benton and Allen (1997), Jalil (1997), and Dilkes (1998).

17) Distal carpal five: absent (0); present (1).
    - Character 159 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Merck (1997) and Nesbitt (2011).

18) Manual intermedium: present (0); absent (1).
    - Character 160 in Pritchard et al., 2015 and Nesbitt et al., in press.
    - Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b), Benton and Allen (1997), Jalil (1997), and Merck (1997).

19) Puboischiadic plate, fenestration: no fenestra (0); thyroid fenestra within plate (1).
   - Character 163 in Pritchard et al., 2015 and Nesbitt et al., in press.
   - Derived from similarly informative characters in Benton (1985), Gauthier et al. (1988b), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), and Müller (2004).

20) Ilium, long axis of orientation for iliac blade in lateral view: horizontal orientation (0); posterodorsal orientation (1); anterodorsal orientation (2).
   - Character 164 in Pritchard et al., 2015 and Nesbitt et al., in press.
   - Derived from similarly informative characters in Gauthier et al. (1988b, 1988a).

21) Ilium, anterior margin of iliac blade, anterior process or tuber: absent, smooth anterior margin (0); process or tuber present (1).
   - Character 169 in Pritchard et al., 2015 and Nesbitt et al., in press.
   - Derived from similarly informative characters in Gauthier (1984), Benton (1985), DeBraga and Rieppel (1997), Dilkes (1998), and Müller (2004).
   -

22) Femur, morphology of proximal end of head: well-ossified convex head, hemispherical (0); concave surface with groove (1).
   - Character 178 in Pritchard et al., 2015 and Nesbitt et al., in press.
   - Pritchard et al. (2015) distinguishes between this character and similar characters in datasets concerning Archosauriformes. In this dataset, the prominently ossified femoral head describes the smoothly textured convexities in many early reptiles, such as captorhinomorphs (Fox and Bowman, 1966; Sumida, 1989), araeoscelids (Vaughn, 1955; Reisz, 1981), weigeltisaurids (MNHN MAP 325), and drepanosaurs (AMNH FARB 7759, MCSNB 4751) are characterized as state 0. In archosauriform datasets (e.g., Ezcurra, 2006; Nesbitt, 2011), a similar character describes the unfinished-but-convex proximal femoral surfaces in many early archosaur groups (e.g., pseudosuchians).

23) Femur, size of distal condyles (medial and lateral), comparison: about equal in size (0); unequal, lateral condyle larger than the medial condyle. (1).
   - Character 180 in Pritchard et al., 2015 and Nesbitt et al., in press.
   - Derived from similarly informative characters in Benton (1985), Rieppel (1994), DeBraga and Rieppel (1997), Dilkes (1998), and Müller (2004).

24) Calcaneum, expansion of lateral margin: calcaneum has little postaxial expansion (0); lateral wing of calcaneum is twice as broad or broader than the distal calcaneal facet. (1).
   - Character 189 in Pritchard et al., 2015 and Nesbitt et al., in press.
   - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al (1988a), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

25) First distal tarsal: present (0); absent (1).
   - Character 193 in Pritchard et al., 2015 and Nesbitt et al., in press.

- Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), Benton and Allen (1997), DeBraga and Rieppel (1997), Jalil (1997), Dilkes (1998), Müller (2004), and Nesbitt (2011).

26) Second distal tarsal: present (0); absent (1).
  - Character 194 in Pritchard et al., 2015 and Nesbitt et al., in press.
  - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988b), Benton and Allen (1997), Dilkes (1998), and Nesbitt (2011).

27) Fifth distal tarsal: present (0); absent (1).
  - Character 195 in Pritchard et al., 2015 and Nesbitt et al., in press.
  - Derived from similarly informative characters in Gauthier (1984), Benton (1985), Gauthier et al. (1988a), Rieppel (1994), DeBraga and Rieppel (1997), Jalil (1997), Merck (1997), and Müller (2004).

28) Metatarsal five, shape of proximal postaxial margin: smooth, curved margin (0); prominent, pointed process (outer process sensu Robinson, 1975) (1).
  - Character 196 in Pritchard et al., 2015 and Nesbitt et al., in press.

29) Gastralia: abundant, with individual gastral elements nearly contacting (0); small in number (= well separated) or unossified (1).
  - Character 238 in Nesbitt et al., in press.
  - Derived from similarly informative characters in Gauthier (1984), Gauthier et al. (1988b), DeBraga and Rieppel (1997), Merck (1997), Dilkes (1998), Müller (2004), and Pritchard et al. (2015).

30) Cervical vertebrae, hypapophysis: absent, ventral surface of centrum unexpanded posteroventrally (0); posteroventral surface of centrum exhibits massive, posteroventrally projecting crest (1).
  - Derived from character 4 in Renesto et al., (2010).

31) Terminal caudal vertebra(e): similar in morphology to other posterior caudals (0); modified into claw-like element (1).
  - Derived from character 37 in Senter (2004) and character 40 in Renesto et al., (2010).

32) Anterior chevrons, hemal spine morphology element forms single spine (0); element bifurcates ventrally (1).
  - Derived from character 41 in Senter (2004) and character 37 in Renesto et al., (2010). Taxa coded as “0” for character 32 are coded as inapplicable (“-“) for character 33.

33) Anteriormost chevrons, hemal spine morphology: bifid spines remain separate ventrally (0); bifid spines recontact ventrally, forming foramen (1).
  - Derived from character 41 in Senter (2004) and character 37 in Renesto et al., (2010).

34) Posterior chevrons, proximal articulation: articulate intervertebrally (0); contact anteroventral margin of centrum (1).

- Derived from character 39 in Renesto et al. (2010).

35) Chevrons, proximal articular morphology: chevrons remain separate from centra (0); chevrons fuse to centra (1).
    - NOVEL character. Describes the fusion of the chevrons and caudal centra throughout the tail in all known drepanosaurs. Well preserved examples of this condition include the holotypes of *Vallesaurus cenensis* (MCSNB 4751), *Dolabrosaurus aquatilis* (CMNH 28589), and *Drepanosaurus unguicaudatus* (MCSNB 5728).

36) Chevrons, hemal spine length: similar in length or shorter than caudal neural spines (0); substantially longer than caudal neural spines (1).
    - Derived from character 40 in Senter (2004) and character 38 in Renesto et al. (2010).

37) 37. Caudal vertebrae, anterior neural spines: spines unexpanded dorsally (0); spines exhibit slender anterior/posterior projections, forming T-shape (1).
    - Derived from character 36 in Senter (2004) and character 33 in Renesto et al. (2010).

38) Anterior dorsal vertebrae, pedicel height: substantially shorter than respective centra (0); taller than respective centra (1).
    - NOVEL character, describing the substantial height of the vertebral pedicels in *Vallesaurus* and drepanosauromorphs more derived than it. By contrast, the pedicels of the anterior dorsal vertebrae in *Hypuronector* (AMNH FARB 1721) and other diapsids in this analysis are shorter than their respective centra.

39) Anterior dorsal vertebrae, neural spine expansion: spines similar in morphology to posterior dorsal neural spines (0); spines dorsally broader anteroposteriorly than spine base (1); third dorsal spine anteroposteriorly expanded into hatchet shape (2). ORDERED.
    - Derived from character 31 in Senter (2004) and character 9 in Renesto et al. (2010). We have modified this character to accommodate and intermediate condition, in which the anterior dorsal neural spines exhibit a slight anteroposterior expansion at their dorsal tips, rather than the extreme expansion that produces the "pseudonotarium" condition of multiple fused neural spines (Renesto et al., 2010).

40) Second manual ungual: similar in morphology to other manual unguals (0); substantially taller and more massive than other manual unguals (1).
    - Derived from character 21 in Renesto et al. (2010). Describes the extreme asymmetries in ungual size in specimens of *Drepanosaurus unguicaudatus*. We employ this character to homologize the enormous second ungual in MCSNB 5728 and those in the Hayden Quarry sample.

41) Ulna, shape: similar to radius, with elongate shaft (0); flattened in pre-axial-post-axial plane, forming enormous crescent (1).
    - Derived from character 18 in Renesto et al. (2010). Describes the bizarre shape of the ulna in *Drepanosaurus unguicaudatus*. Note below that we do not employ a character to describe the extreme elongation of the ulnare and intermedium, as such

42) Radius, proximal tab: absent (0); prominent tab for articulation with ulna present (1).

- NOVEL character. Describes the postaxial proximal expansion of the proximal radial articular surface in *Drepanosaurus*. Although a number of Permo-Triassic diapsids exhibit an inflexion of the proximal radial surface (e.g., *Trilophosaurus buettneri*, TMM 31025-140; *Azendohsaurus madagaskarensis*, UA 7-16-99-607), no other taxon has developed the interlocking tab-slot mechanism seen in *Drepanosaurus*.

43) Scapula, curvature of long-axis of blade: blade directed dorsally (0); blade curves anterodorsally (1).
    - Derived from character 44 in Senter (2004).

44) Mid dorsal ribs, fusion to respective centra: fusion absent (0); fusion present (1).
    - Derived from character 11 in Renesto et al. (2010).

45) 45. Femur, morphology of internal trochanter: elongate, slender crest (0); rounded tuberosity (1).
    - NOVEL character.

46) Proximal tarsals, morphology of perforating foramen: broad, marked by finished bone on astragalus and calcaneum (0); pinched, marked by extremely constricted space between astragalus and calcaneum (1).
    - NOVEL character.

47) Calcaneum, lateral projection, ventral margin: margin is convex and continuous with the lateral margin of the projection (0); margin is concave, sharply angled relative to lateral margin of the projection (1).
    - NOVEL character. Describes the characteristic ventral concavity of the lateral expansion of the calcaneum in drepanosaurids.

48) Ilium, bone between acetabulum and iliac blade: bone broadens smoothly into blade (0); bone exhibits anteroposterior constriction between blade and acetabulum (1).
    - NOVEL character. Describes the prominent anteroposterior constriction of the iliac blade dorsal to the acetabulum in *Drepanosaurus*.

49) Chevrons, hemal spine curvature: spines roughly straight (0); spines convex anteriorly (1).
    - Derived from character 141 of Dilkes (1998).

50) Cervical ribs: present (0); absent (1).
    - Derived from character 5 of Renesto et al. (2010).

51) Pedal digit three (III), number of phalanges: four (0); three (1).
    - Derived from character 28 of Renesto et al. (2010).

52) Post-axial cervical vertebra, morphology of intervertebral articulations (for amphicoelous taxa): circular/elliptical articulations appressed to one another (traditional amphicoely) (0); saddle-shaped articulations (heterocoely) (1).
    - NOVEL character. Describes the complex, saddle-shaped intervertebral articulations within the cervical region of drepanosauromorphs (e.g., Renesto and Fraser, 2003).

53) Vertebrae, notochordal canal: present (0); absent (1).
    - Derived from similarly informative characters in Gauthier (1984, lepidosaur dataset), Gauthier et al. (1988a), Laurin (1991), Merck (1997), Dilkes (1998), and Müller (2004).

54) Humerus, distalmost end: (0) collinear with proximal shaft; (1) primary axis curves anteriorly relative to primary humeral shaft.
    - NOVEL character. Describes the moderate angling of the humeral shaft in the Italian *Drepanosaurus* holotype and the Hayden Quarry humeri.

55) Scapula & coracoid, position of glenoid fossa: at or near base of scapular blade (0); located far ventral of base of scapular blade (1).
    - NOVEL character. Describes the distance between the base of the primary scapular blade and the glenoid fossa in *Drepanosaurus unguicaudatus* and GR 1113. This character was not noted by Renesto et al. (2010), in which GR 1113 was referred to *Drepanosaurus* sp.

56) Humerus, epicondyles, proximal origination: positioned distal to midshaft (0); positioned at/near midshaft (1).
    - NOVEL character. We employ this character to describe the substantial differences in shape and robusticity between the humeri in early-diverging drepanosauromorphs and *Drepanosaurus unguicaudatus*. The proximal humeral specimen from the Hayden Quarry (H4-175-10) suggests similarly robust epicondyles with a similar proximal origination to the holotype of *Drepanosaurus unguicaudatus*.
    -

57) Supraneural ossification, bone growth positioned anterodorsal to anterior dorsal neural spines: absent (0); present (1).
    - NOVEL character. It has been recognized that several drepanosauromorphs (*Vallesaurus cenensis*, *Megalancosaurus preonensis*, *Drepanosaurus unguicaudatus*) exhibit a prominent ossification anterodorsal to the neural spines of dorsal vertebrae 2 and 3. The homology and three-dimensional osteology of this structure remains poorly understood. As its identification is difficult in disarticulated skeletons, this character is coded only for taxa in which a well-preserved, articulated anterior trunk region is known.

58) Scapulacoracoid, glenoid fossa, construction: oriented posterolaterally, ventral margin extends posterior of dorsal margin (0); oriented laterally, ventral margin positioned directly underneath to dorsal margin (1).
    - NOVEL character. Harris and Downs (2002) and Renesto et al. (2010) noted that the long axis of the coracoid in GR 1113 and *Drepanosaurus unguicaudatus* is verticalized, relative to the plesiomorphic, horizontalized coracoid in *Hypuronector*, *Vallesaurus*, and *Megalancosaurus*. In the former two taxa, this appears to result in the glenoid fossa becoming similarly verticalized, with a prominent dorsal margin completely overhanging the ventral margin. We employ this morphological feature to describe this character, as the fragmentary pectoral material available from the Hayden *Drepanosaurus* includes a verticalized glenoid fossa.

59) Scapula, blade, dorsoventral height-anteroposterior length (at base of blade) ratio: >.4 (0) .4–.25 (1) .25–0 (2). ORDERED.
   - Derived from similarly informative characters of Dilkes (1998), and Renesto et al. (2010). We employ multiple ratio categories to describe the difference between the slender scapula of *Hypuronector* and the relatively longer scapulae in *Vallesaurus*, *Megalancosaurus*, and *Drepanosaurus*.

SUPPLEMENTARY APPENDIX 7. Parameters of phylogenetic analyses.

All analyses are run in TNT v. 1.1 (Goloboff et al., 2008), employing the "Traditional Search" options including 10,000 replicates of Wagner trees (using random addition sequences), followed by tree bisection and reconnection (TBR) holding 10 trees for replicate. The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. We employed Coddington and Scharff (1994) Rule 1 for collapsing zero-length branches. We employed the STATS.RUN TNT script to obtain the Consistency Index and Retention Index for all trees. Taxa included all named drepanosauromorph taxa, the pectoral girdle and ulna that make up GR 1113 (Harris and Downs, 2002), two "younginiform" diapsids known from complete pectoral girdles and forelimbs, and two early archosauromorphs known from complete pectoral girdles and forelimbs. The first analysis included all coded taxa (Fig 3-19). The limited and non-overlapping nature of the drepanosaurs GR 1113 and *Dolabrosaurus aquatilis* contribute to a lack of resolution within derived Drepanosauridae.

The analysis was re-run in PAUP* 4.0 (Swofford, 2003) using the "Heuristic Search" option, employing the same numerical values in the TNT analysis. To assess the wildcard nature of taxa in the analysis, we constructed an Adams Consensus and assessed the topological differences between this and the most-parsimonious trees (MPTs). *Dolabrosaurus aquatilis* was collapsed to the bottom of a clade including *Megalancosaurus* + (GR 1113 + (*Drepanosaurus unguicaudatus* + HQ *Drepanosaurus*)).

In light of these results, we excluded *Dolabrosaurus aquatilis* from the second analysis of this phylogeny. This produced a topology in which *Megalancosaurus* and GR 1113 form successive sister taxa to *Drepanosaurus unguicaudatus* (Fig. 3-20). The absence of character data regarding the manual anatomy of the *Coelophysis* Quarry drepanosaurid produces ambiguity with regards to the optimization of manual character data.

A third analysis removed GR 1113 to develop greater resolution for the transitions in forelimb anatomy within derived drepanosauromorphs; all other taxa in the analysis are known from complete or nearly complete forelimbs (Fig. 3-21). We present the unambiguous synapomorphies (recovered by the TNT analysis) common to all most parsimonious trees resultant from this analysis below:

SUPPLEMENTARY APPENDIX 8. Unambiguous character transformations

(*Hovasaurus* + *Thadeosaurus*) + (*Azendohsaurus* + *Protorosaurus*)
23 (0->1), 44 (0->1).

Hovasaurus + *Thadeosaurus*
12 (0–>1), 28 (0->1).

Hovasaurus boulei
15 (0->1), 51 (0->1).

Azendohsaurus + *Protorosaurus*
5 (0->1), 7 (0->1), 8 (0->1), 17 (0->1), 20 (0->1), 53 (0->1).

Azendohsaurus madagaskarensis
1 (0->1), 10 (0->1), 15 (0->1), 47 (0->1).

Protorosaurus speneri
6 (0->1), 14 (0->1), 22 (0->1).

Hypuronector + (*Vallesaurus* + (*Megalancosaurus* +
(*Drepanosaurus unguicaudatus* + Hayden *Drepanosaurus*)))
19 (0->1), 20 (0->1), 35 (0->1), 36 (0->1), 50 (0->1), 52 (0->1), 59 (0->1).

Vallesaurus + (*Megalancosaurus* + (*Drepanosaurus unguicaudatus* + Hayden *Drepanosaurus*))

38 (0->1), 43 (0->1), 49 (0->1), 57 (0->1), 59 (1->2)

Vallesaurus cenensis

15 (0->1)?

Megalancosaurus + (*Drepanosaurus unguicadatus* + Hayden *Drepanosaurus*)

31 (0->1), 32 (0->1), 34 (0->1), 37 (0->1), 39 (1->2), 51 (0->1)

Drepanosaurus unguicaudatus + Hayden *Drepanosaurus*

40 (0->1), 41 (0->1), 42 (0->1), 54 (0->1), 56 (0->1), 58 (0->1)

LITERATURE CITED

Alifanov VR, Kurochkin EN. (2011). *Kyrgyzsaurus bukhanchenkoi*, gen. et sp. nov., a new reptile from the Triassic of southwestern Kyrgyzstan. Paleont J 45:639–647.

Benton MJ. (1985). Classification and phylogeny of the diapsid reptiles. Zool J Linn Soc 84:97–164.

Benton MJ, Allen JA. (1997). *Boreopricea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles. Palaeo 40:931–953.

Berman DS, Reisz RR. (1992) *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. J Paleo 66:1001–1009.

Burch SH (2014) Complete forelimb myology of the basal theropod dinosaur *Tawa hallae* based on a novel robust muscle reconstruction method. J Anat 225:271–297.

Caldwell MW. (1994) Developmental constraints and limb evolution in Perian and extant lepidosauromorph diapsids. J Vert Paleo 14:459–471.

Carroll RL. (1981). Plesiosaur ancestors from the Upper Permian of Madagsacar. Phil Trans Roy Soc B 293:315–383.

Carroll RL. (1985) A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Palaeont Abt A 189:1–28.

Chure DJ, Britt B, Engelmann G, Andrus A, Scheez R. (2013). Drepanosaurs in the desert: multiple skeletons of a new drepanosaurid from the eolian Nugget Sandstone (?Late

Triassic–Early Jurassic), Saints and Sinners Quarry, Utah: morphology, relationships, and biostratigraphic implications. Abstracts of the Soc Vert Paleo Annual Meeting, Los Angeles. J Vert Paleo 43:106A.

Coddington J, Scharff N. (1994) Problems with zero-length branches. Cladistics 10:415–423.

Conrad JL. (2006) Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). J Morph 267:769–775.

Conrad JL. (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology. Bull Amer Mus Nat Hist 310:1–182.

Currie PJ. (1981) *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeo Afr 24:99–168.

DeBraga M, Rieppel O. (1997) Reptile phylogeny and the interrelationships of turtles. Zool J Linn Soc 120:281–354.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Proc Roy Soc B 353:501–541.

Dilkes DW (2000) Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Trans Roy Soc Edin Earth Sci 90:87–125.

Evans SE. (2008) The skull of lizards and tuatara. *Biology of the Reptilia vol. 20, Morphology H: The Skull of Lepidosauria*, ed C Gans. (Society for the Study of Amphibians and Reptiles), pp.

Ezcurra MD. (2006) A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. Geodiversitas 28:649–684.

Fox RC, Bowman MC. (1966) Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). U KS, Paleo Cont 11:1–79.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. Dissertation, University of California Berkeley, 564 pp.

Gauthier JA, Kluge AG, Rowe T. (1988a) The early evolution of the Amniota. *The Phylogeny and Classification of the Tetrapods, Volume 1*, ed MJ Benton (Clarendon Press), pp. 103–155

Gauthier JA, Estes R, de Queiroz K. (1988b) A phylogenetic analysis of Lepidosauromorpha. *Phylogenetic Relationships of the Lizard Families,* eds R Estes and G Pregill (Stanford University Press), pp. 15–98.

Günther A. (1867) Contribution to the anatomy of *Hatteria* (Rhynchocephalus, Owen). Phil Trans Roy Soc London 157:595–629.

Goloboff PA, Farris JS, Nixon KC. (2008) TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Gottmann-Quesada A, Sander PM. (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. Palaeont Abt A 287:123–220.

Gow CE. (1975) The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeontologia Africana 18:89–131.

Harris JD and Downs A. (2002) A drepanosaurid pectoral girdle form the Ghost Ranch (Whitaker) *Coelophysis* Quarry (Chinle Group, Rock Point Formation, Rhaetian), New Mexico. J Vert Paleo 22:70–75.

Hayssen C, Miranda F, Pasch B. (2012) *Cyclopes didactylus* (Pilosa: Cyclopeidae). Mammalian Species 44:51–58.

Hoffstetter R, Gasc J-P. (1969) *Biology of the Reptilia vol. 1, Morphology A*, ed C Gans. (Academic Press), pp. 209–301.

Holmes R. (1977) The osteology and musculature of the pectoral limb of small captorhinids. J Morph 152:101–140.

Howes GB, Swinnerton HH. (1901) On the development of the skeleton of the tuatara, *Sphenodon punctatus*; with remarks on the egg, on the hatching, and on the hatched young. Trans Zool Soc London 16:1–85.

Irmis RB, Nesbitt SJ. (2012) The evolution of early crocodylomorph disparity and locomotor styles: new evidence from the latest Triassic of New Mexico. Abstracts of the Society of Vertebrate Paleontology Annual Meeting, Raleigh. J Vert Paleo 42:115A.

Jalil N-E. (1997) A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. J Vert Paleo 17:506–525.

Landsmeer JMF. (1983) The mechanism of forearm rotation in *Varanus exanthematicus*. J Morph 175:119–130.

Laurin M. (1991) The Lower Permian eosuchian from Texas and a review of diapsid phylogeny. Zool J Linn Soc 101:59–95.

Lécuru S. (1969) Étude morphologique de l'humérus des lacertiliens. Annales Sci Nat, Zool Paris 12:515–558.

Luo Z-X, Meng Q-J, Ji Q, Liu D, Zhang Y-G, Neander AI. (2015) Evolutionary development in basal mammaliaforms as revealed by a docodontan. Science 347:760–764.

Martz JW, et al. (2013) A taxonomic and biostratigraphic re-evaluation of the Post Quarry vertebrate assemblage from the Cooper Canyon Formation (Dockum Group, Upper Triassic) of southern Garza County, western Texas. Earth Env Sci Trans Roy Soc Edin 103:339–364.

Meers MB. (2003) Crocodylian forelimb musculature and its relevance to Archosauria. Anat Rec 274A:891–916.

Merck JW. (1997) A phylogenetic analysis of euryapsid reptiles. Ph.D Dissertation, University of Texas at Austin. 785 pp.

Miner RW. (1925) The pectoral limb of *Eryops* and other primitive tetrapods. Bulletin of the American Museum of Natural History 51:145–312.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Nesbitt SJ. (2011) The early evolution of archosaurs: relationships and the origin of major clades. Bull Amer Mus Nat Hist 352:1–292.

Nesbitt SJ, Flynn JJ, Pritchard AC, Parrish JM, Ranivoharimanana L, Wyss AR. (in press) Postcranial osteology of *Azendohsaurus madagaskarensis* (?Middle to Upper Triassic, Isalo Group of Madagascar) and its systematic position among stem archosaurs. Bull Amer Mus Nat Hist.

Pinna G. (1980) *Drepanosaurus unguicaudatus*, nuovo genere e nuova specie di lepidosauro del Trias alpino. Atti della Soc ital di sci nat del mus civ di storia nat di Milano 121:181–192.

Pinna G. (1984) Osteologia di *Drepanosaurus unguicaudatus*, lepidosauro triassico del sottordine Lacertilia. Mem della Soc ital. di sci nat e del Mus civ di storia nat di Milano 24:7–28.

Pinna G. (1986) On *Drepanosaurus unguicaudatus*, an Upper Triassic lepidosaurian from the Italian Alps. J Paleo 60:1127–1132.

Piveteau J. (1926). Paléontologie de Madasgascar XIII—amphibiens et reptiles Permiens. Annales Paléo 15:55–178.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Spec Pubs Mus Nat Hist, U KS 7:1–74.

Reisz RR, Berman DS, Scott D. (1984) The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. J Vert Paleo 4:57–67.

Renesto S. (1994a) The shouleder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the upper Triassic (Norian) of northern Italy. Zool J Linn Soc 111:247–264.

Renesto S. (1994b) *Megalancosaurus*, an arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. J Vert Paleo 14:38–52.

Renesto S, Spielmann JA, Lucas SG, and Spagnoli GT. (2010) The taxonomy and paleobiology of the Late Triassic (Carnian–Norian: Adamanian–Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha). Bull NM Mus Nat Hist Sci 46:1–81.

Rénous-Lécuru S. (1973) Morophologie comparée du carpe chez des Lepidosauriens actuels (Rhynchocéphales, Lacertiliens, Amphisbéniens). Gegenbaurs morphologisches Jahrbuch 119:727–766.

Rieppel O. (1994) Osteology of *Simosaurus gaillardoti* and the relationships of stem-group Sauropterygia. Fieldiana 28:1–81.

de Ricqlès A, Padian KA, Horner JR, Francillon-Viellot H. (2000) Paleohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications. Zool J Linn Soc 129:349–385.

Robinson PL. (1975) The functions of the hooked fifth metatarsal in lepidosaurian reptiles. Colloque International CNRS 218:461–483.

Rogers JV. (2003) *Pachycheilosuchus trinquei*, a new procoelous crocodyliform from the Lower Cretaceous (Albian) Glen Rose Formation of Texas. J Vert Paleo 23:128–145.

Romer AS. (1956). *Osteology of the Reptiles*. University of Chicago Press.

Rose KD, Emry RJ. (1983) Extraoridinary fossorial adaptations in the Oligocene palaeanodonts *Epoicotherium* and *Xenocranium* (Mammalia). J Morph 175:33–56.

Russell AP, Bauer AM. (2008) The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. *Biology of the Reptilia v. 21: The Skull and Appendicular Locomotor Apparatus of Lepidosauria*, eds C Gans, AS Gaunt, K Adler (Academic Press), pp. 1–466.

Salisbury SW, Frey E, Martill DM, Buchy M-C. (2003) A new crocodilian from the Lower Cretaceous Crato Formation of north-eastern Brazil. Palaeont Abt A 270:3–47.

Salisbury SW, Molnar RE, Frey E, Willis PMA. (2006) The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. Proc Roy Soc B 273:2439–2448.

Senter PJ. (2004) Phylogeny of Drepanosauridae (Reptilia: Diapsida). J Sys Palaeo 2:257–268.

Sertich JJW, and Groenke JR. (2010). The postcranial appendicular skeleton of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar, eds DW Krause, NJ Kley. Soc Vert Paleo Mem 30:177–236.

Swofford DI. (2003) PAUP*. Phylogenetic analysis using parsimony (* and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Sumida SS. (1989) The appendicular skeleton of the Early Permian genus *Labidosaurus* (Reptilia, Captorhinomorpha, Captorhinidae) and the hind limb musculature of captorhinid reptiles. J Vert Paleo 9:295–313

Taylor BK. (1978) The anatomy of the forelimb in the anteater (*Tamandua*) and its functional implications. J Morph 157:347–368.

Taylor BK. (1985) Functional anatomy of the forelimb in Vermilinguas (anteaters). *The Evolution and Ecology or Armadillos, Sloths, and Vermilinguas*, eds GG Montgomery (Smithsonian Institution Press), pp. 163–171.

Vaughn PP. (1955) The Permian reptile *Araeoscelis* restudied. Bull Mus Comp Zool 113:305–467.

TABLE 1. All specimens identified as *Drepanosaurus unguicaudatus* from the Hayden Quarry site. All specimens listed are field numbers of specimens accessioned with the Ruth Hall Museum of Paleontology.

Specimen #	**Identification**
H2-246-09	distal carpal complex
H2-289-11	distal carpal complex
H2-35-10	distal carpal complex
H2S-93-13	distal carpal complex
H3-165-07	distal carpal complex
H3-286-06	distal carpal complex
H3-356-06	distal carpal complex
H3-85-14	distal carpal complex
H4-596-11	distal carpal complex
H2S-73-13	distal carpal complexes (2), proximal radius
H3-092-07	drepanosaurid ICB, proximal radius, partial MC II, fragments
H2-367-10	humerus, distal
H2-383-10	humerus, distal
H3-103-07	humerus, distal condyles
H4-175-10	humerus, proximal
H2-196-09	intermedium fused to distal carpal complex
H2-299-11	intermedium fused to distal carpal complex
H2-534-09	intermedium fused to distal carpal complex
H3-273-07	intermedium fused to distal carpal complex
H4-405-11	intermedium fused to distal carpal complex
H4-712-10	intermedium fused to distal carpal complex; intermedium, distal, fused to distal carpal complex; distal carpal complexes (3), caudal vertebrae (3),

	partial dorsal vertebra, fragment
H2-10-10	intermedium, distal, fused to distal carpal complex
H2-204-07	intermedium, distal, fused to distal carpal complex
H3-15-08	intermedium, distal, fused to distal carpal complex
H3-38-07	intermedium, distal, fused to distal carpal complex
H3-700-06	intermedium, distal, fused to distal carpal complex
H4-1375-09	intermedium, distal, fused to distal carpal complex
H2-70-09	intermedium, distal, fused to distal carpal complex
H3JT-6-12	intermedium, fragmentary
H4-78-12	intermedium, proximal
H2-89-10	manual ungual (small)
H4-17-13	manual ungual (small)
H2-141-13	manual ungual II
H2-275-06	manual ungual II
H3-117-14	manual ungual II
H3-140-08	manual ungual II
H3-209-13	manual ungual II
H3-54-08	manual ungual II
H4-1130-09	manual ungual II
H3-110-07	manual ungual II
H3-130-10	manual ungual II
H3-26-10	manual ungual II
H3-645-06	manual ungual II
H4-160-10	manual ungual II
H4-49-06	manual ungual II
H4-53-10	manual ungual II
H3-81-07	manual ungual II
H3-760-07	manual ungual II
H3-316-07	manual ungual II, ungual (small)
H3-203-14	manual unguals (2)
H4-645-10	manual unguals (2)

H2-093-09	metacarpal II
H2-273-10	metacarpal II
H3-135-09	metacarpal II
H3-142-08	metacarpal II
H3-178-14	metacarpal II
H4-283-12	metacarpal II
H2-100-09	metacarpal II
H2-100-09	metacarpal II
H2-66-14	metacarpal II
H2-98-14	metacarpal II, distal
H2-149-07	metacarpal II, partial
H2-435-14	metacarpal II, partial
H3-34-07	metacarpal II, partial
H2S-102-13	metacarpal II, proximal
H4-35-10	metacarpal II, proximal
H4-390-11	radius
H2-257-10	radius
H3-76-09	ulna
H2-291-14	ungual, partial
H3-379-07	ungual, partial
H4-64-08	ungual, partial
H2-264-11	ungual, proximal articulation
H4-570-11	- Badly crushed left humerus with partially preserved head and ulnar condyle - Left humeral fragment with radial condyle - Left radius - Proximal articulation of left ulna, preserving two cotylar surfaces. - Left radiale. - Proximal portion of left second metacarpal. - Second manual ungual articulated to distal end of

	second metacarpal.
	- Complete phalanx? in two pieces.
	- 3 distal phalangeal fragments, preserving 3 ginglymoid articular fragments.
	- Distal end of flattened metacarpal?
	- Dorsal vertebra with fused ribs.
	- Over a dozen unidentifiable bone fragments.
H3-037-08	- Glenoid fossa of right scapulacoracoid
	- Distal end of right humerus.
	- Right radius.
	- Right ulna.
	- Proximal articular surface of right radiale.
	- Post-axial articular surface of right radiale.
	- Right intermedium, ulnare, and distal carpal articulated.
	- Proximal portion of right second metacarpal.
	- Right second manual ungual articulated with distal end of second metacarpal.
	- Distal end of small, flattened metacarpal?
	- 2 proximal metacarpals.
	- Caudal centrum fragment.
	- Small bone fragments.

TABLE 3.2 Phylogenetic data matrix employed to assess affinities of Hayden Quarry drepanosauromorph materials and forelimb character evolution.

Petrolacosaurus kansasensis
0020000000001001001-01000000?0?0-00000000001010000000000000

Azendohsaurus madagaskarensis
1111011110000010000?000010111000-000000000000010000?01000?00

Protorosaurus speneri
11111111000000?0000?100000110000-00000000000000000001000000

Hovasaurus boulei
???1000000111011001-0?0010[1,0]000?0-00000000?0?00000?0100000000

Thadeosaurus colcanapi
????0?0000111001001-000010?000?0-0000000000000000?000?00000?

Dolabrosaurus aquatilis
?????????0????????????001100?????1111??0????101?1????0??????

GR 113
??????????1???0??????????????????????????0?1?????????????1??12

Drepanosaurus unguicaudatus
?????????0???00?012-0?001000-?11011111211111?0111?11??111112

Hayden Quarry Drepanosaur
???????????1?????????????????1??????????111??????????101?1?1?

Hypuronector limnaios
?????????0???????12-0???????1?00-01100??0?0?1??0001?10?0?001

Megalancosaurus preonensis
10000???00???00?012???0010001111111111120001?1?1010111?000102

Vallesaurus cenensis
1?0?????00????1?01??010?0??01100-0110110001?0??01?10?000?102

FIG 3-1. Right forelimb of the holotype of *Drepanosaurus unguicaudatus* (MCSNB 5728) in A) photograph and B) cartoon. Interpretations of homologies of forelimb bones based on the current study. Scale bar is equal to 2 centimeters.

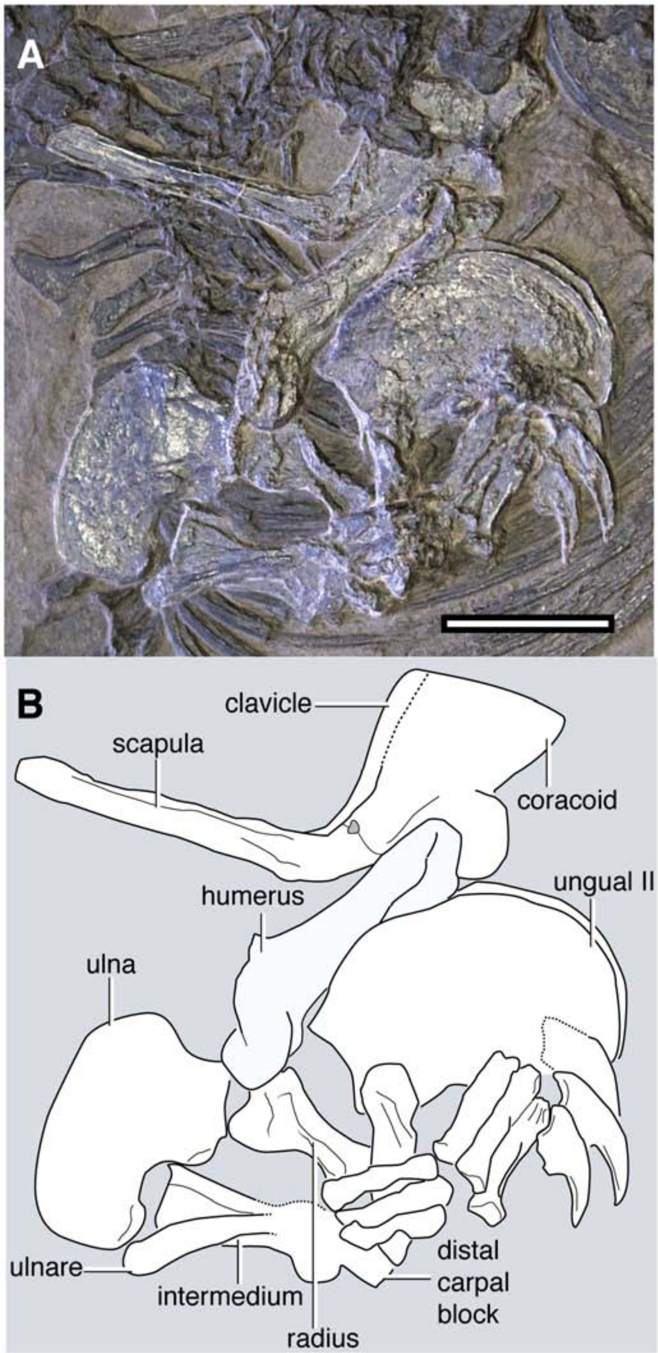

A
B
clavicle
scapula
coracoid
humerus
ungual II
ulna
ulnare
intermedium
radius
distal
carpal
block

FIG 3-2. Reconstruction of the forelimb of *Drepanosaurus unguicaudatus* based on the Hayden Quarry forelimb elements. **A**, proximal right humerus (H4-175-10) in anterior view, **B**, distal right humerus (H3-037-08) in anterior view, **C**, left radius and radiale (H4-570-11) articulated (image reversed) in lateral view, **D**, left second manual ungual (H2-315-07) in post-axial view, **E**, right ulna (H3-037-08) in lateral view, **F**, right intermedium, fused distal carpal complex, and ulnare (H3-037-08) in dorsal view, **G**, right second metacarpal (H4-185-08) in dorsal view. Scale bars equal to 5 millimeters.

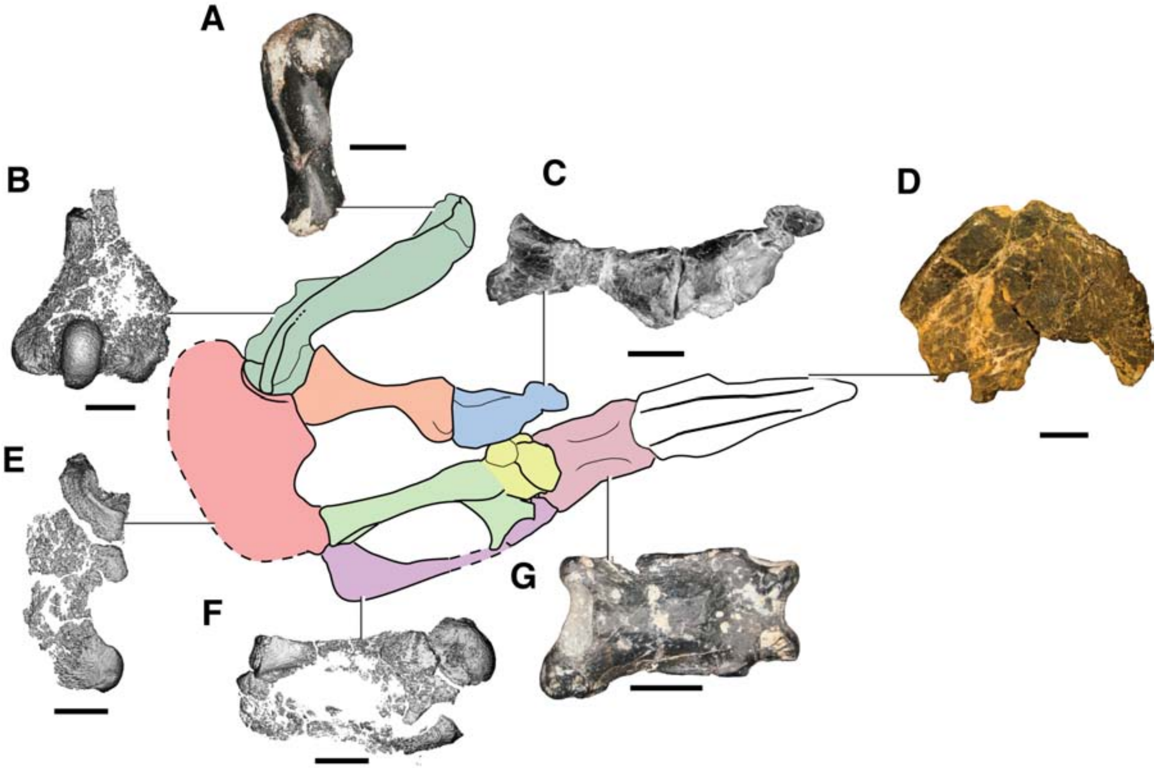

A
B
C
D
E
F
G

FIG 3-3. Results of phylogenetic analysis of diapsid affinities to resolve the interrelationships of drepanosauromorphs. Tree length = 67 steps, CI = 0.881, RI = 0.902.

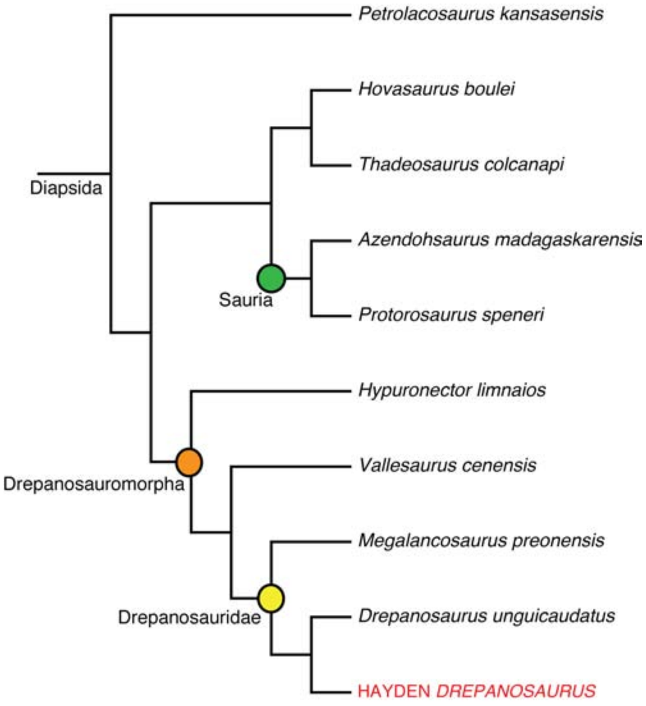

Petrolacosaurus kansasensis
Hovasaurus boulei
Thadeosaurus colcanapi
Diapsida
Azendohsaurus madagaskarensis
Sauria
Protorosaurus speneri
Hypuronector limnaios
Drepanosauromorpha
Vallesaurus cenensis
Megalancosaurus preonensis
Drepanosauridae
Drepanosaurus unguicaudatus
HAYDEN DREPANOSAURUS

FIG 3-4. Simplified phylogenetic tree of drepanosauromorph interrelationships, illustrating major character transformations in the pectoral girdle and forelimb. Cartoon reconstructions are as follows: *Thadeosaurus colcanapi* (pectoral girdle and forelimb based on MNHN MAP 360), *Hypuronector limnaios* (pectoral girdle and forelimb based on AMNH FARB 7759) *Vallesaurus cenensis* (pectoral girdle and forelimb based on MCSNB 4751 and Renesto and Binelli, 2006), *Megalancosaurus preonensis* (pectoral girdle and forelimb based on MFSN 1769, MPUM 6008), and *Drepanosaurus unguicaudatus* (pectoral girdle based on GR 1113, forelimb based on MCSNB 5728, GR specimens).

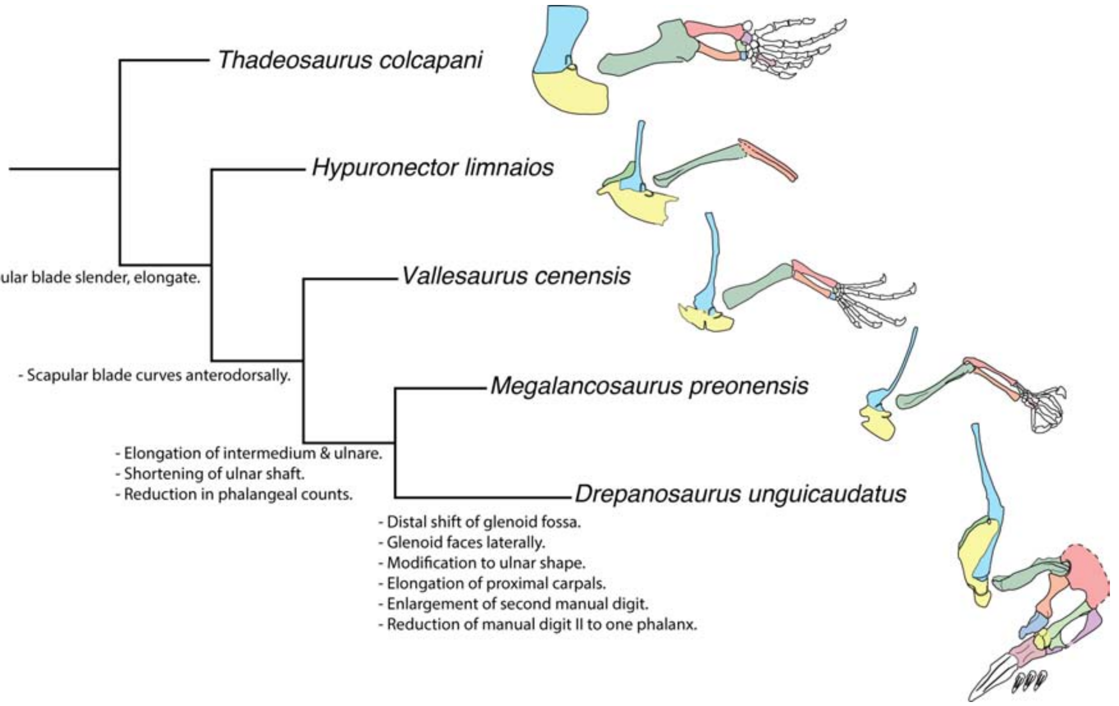

Thadeosaurus colcapani
Hypuronector limnaios
- Scapular blade slender, elongate.
Vallesaurus cenensis
- Scapular blade curves anterodorsally.
Megalancosaurus preonensis
- Elongation of intermedium & ulnare.
- Shortening of ulnar shaft.
- Reduction in phalangeal counts.
Drepanosaurus unguicaudatus
- Distal shift of glenoid fossa.
- Glenoid faces laterally.
- Modification to ulnar shape.
- Elongation of proximal carpals.
- Enlargement of second manual digit.
- Reduction of manual digit II to one phalanx.

FIG 3-5. Cartoon illustration of the right forelimb of the holotype specimen of *Drepanosaurus unguicaudatus* (MCSNB 5728) with homology assessment of Pinna (1980, 1984, 1986).

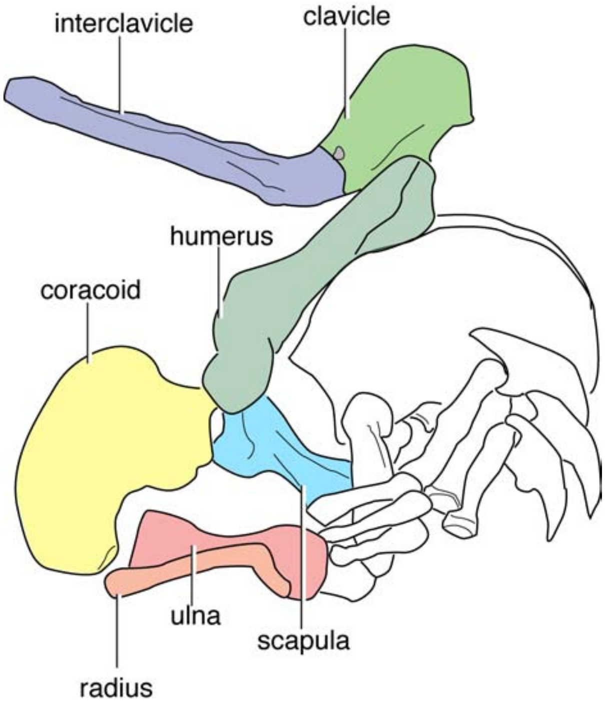

interclavicle
clavicle
humerus
coracoid
ulna
scapula
radius

FIG 3-6. Cartoon illustration of the right forelimb of the holotype specimen of Drepanosaurus unguicaudatus (MCSNB 5728) with homology assessments of Renesto (1994a) and Renesto et al. (2010).

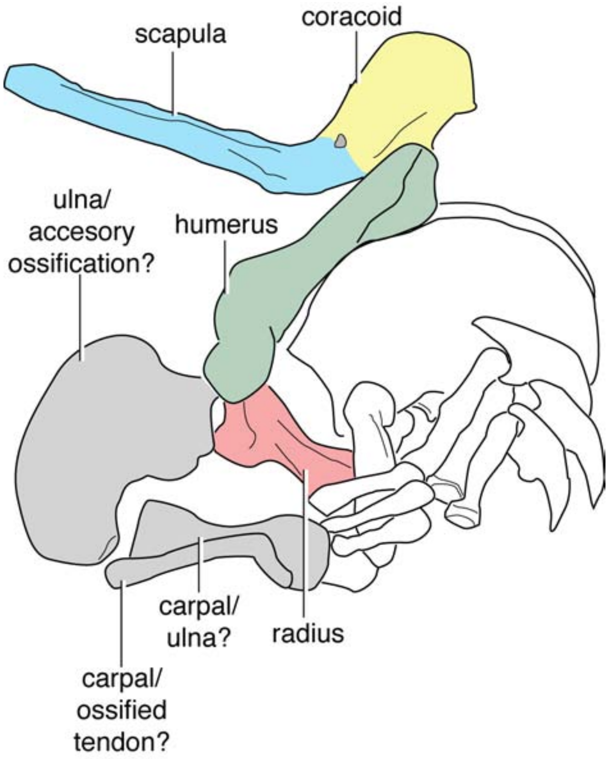

scapula
coracoid
ulna/
accesory
ossification?
humerus
carpal/
ulna?
radius
carpal/
ossified
tendon?

FIG 3-7. 3D reconstruction of the in situ partially articulated forelimb referred to *Drepanosaurus unguicaudatus* from the Hayden Quarry (H3-053-08), as rendered in GLC Player 2.3.0, in **A**, oblique anterior and **B**, oblique posterior views).

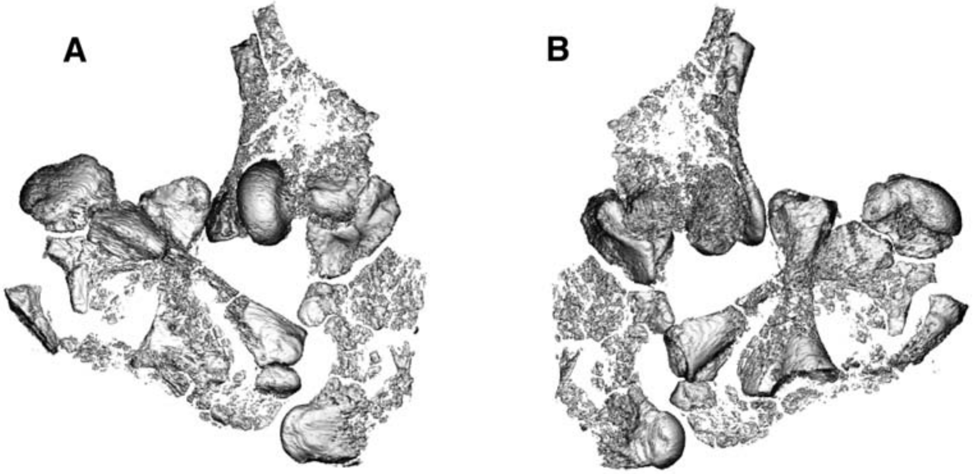

A
B

FIG 3-8. Fragment of glenoid fossa of right scapulocoracoid referred to *Drepanosaurus unguicaudatus* (H3-053-08) in **A**, posterior and **B**, anterolateral views. **C**, Focus on the glenoid region of a complete drepanosaurid pectoral girdle from the *Coelophysis* Quarry of New Mexico (GR 1113) in anterolateral view. Abbreviations: **cl**, clavicle; **dl**, dorsal lip of glenoid; **ga**, gap between scapula, coracoid, and clavicle; **vl**, ventral lip of glenoid.

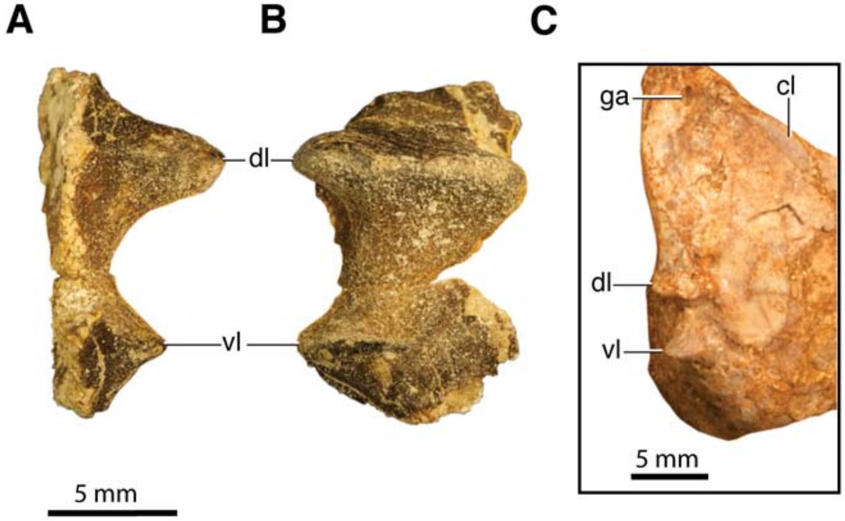
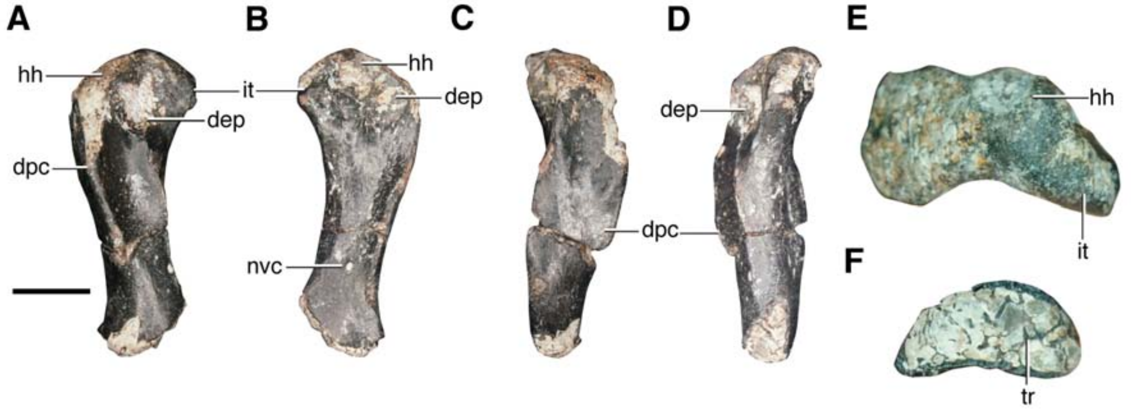

A
B
C
dl
vl
5 mm
ga
cl
dl
vl
5 mm

FIG 3-9. Proximal portion of right humerus referred to *Drepanosaurus unguicaudatus* from the Hayden Quarry (H4-175-10) in **A**, anterior, **B**, posterior, **C**, lateral, **D**, medial, **E**, proximal, and **F**, distal views. Abbreviations: **dep**, depression; **dpc**, deltopectoral crest; **hh**, humeral head; **it**, internal tuberosity; **nvc**, neurovascular canal; **tr**, trabeculae. Scale bar equals 5 millimeters.



A
B
C
D
E
F
hh
it
dep
dpc
hh
dep
nvc
dep
dpc
hh
it
tr

FIG 3-10. Distal portion of right humerus referred to *Drepanosaurus unguicaudatus* (H3-053-08) in **A**, anterior, **B**, posterior, **C**, lateral, and **D**, distal views. Abbreciations: **ect**, ectepicondyle; **ectf**, ectepicondylar foramen; **ent**, entepicondyle; **rc**, radial condyle, **uc**, ulnar condyle. Scale bar equals five millimeters.

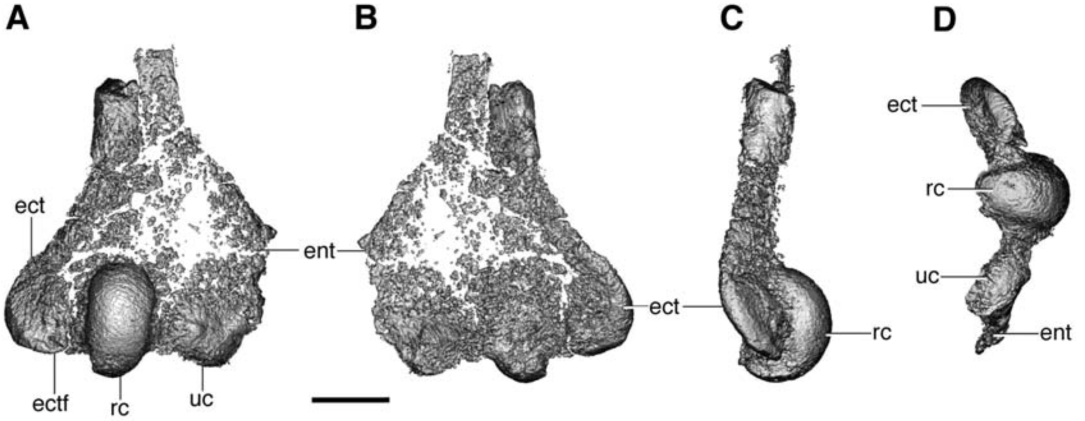

A
B
C
D
ect
ent
ectf
rc
uc
ent
ect
rc
ect
rc
uc
ent

FIG 3-11. Right radius referred to *Drepanosaurus unguicaudatus* (H3-053-08) in **A**, medial, **B**, lateral, **C**, posterior, **D**, anterior, **E**, proximal, and **F**, distal views.

Abbreviations: **br**, broken surface; **hc**, contact surface for humerus; **pt**, proximal tab; **rec**, contact surface for radiale. Scale bar equals five millimeters.

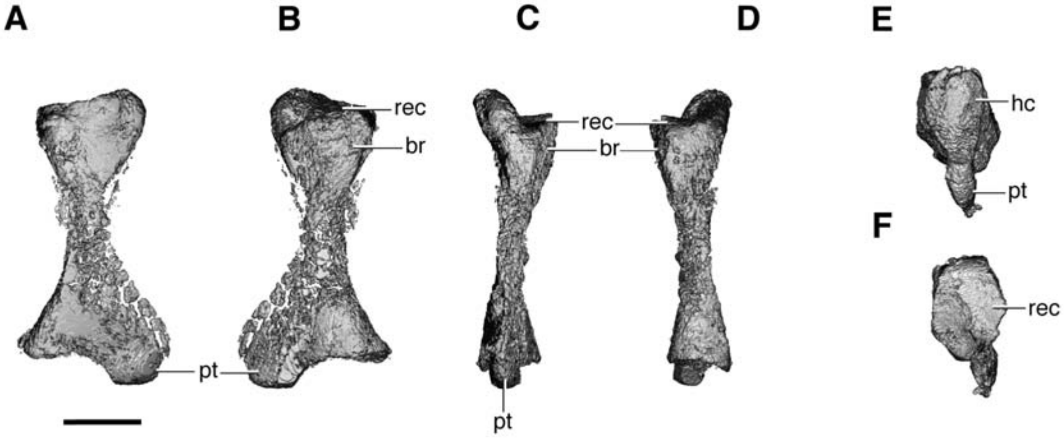

A
B
C
D
E
F
rec
br
pt
rec
br
pt
hc
pt
rec

FIG 3-12. Right ulna referred to *Drepanosaurus unguicaudatus* (H3-053-08) in **A**, lateral, **B**, medial, **C**, anterodistal, **D**, posterior, and **E**, proximal views. Abbreviations: **bb?**, tuber possibly for attachment of m. *biceps brachii* tendon; **dc**, distal ulnar condyle; **icr**, intercotylar ridge; **rcf**, facet for radial condyle; **rf**, facet for radius; **ucf**, facet for ulnar condyle. Scale bar equals five millimeters.

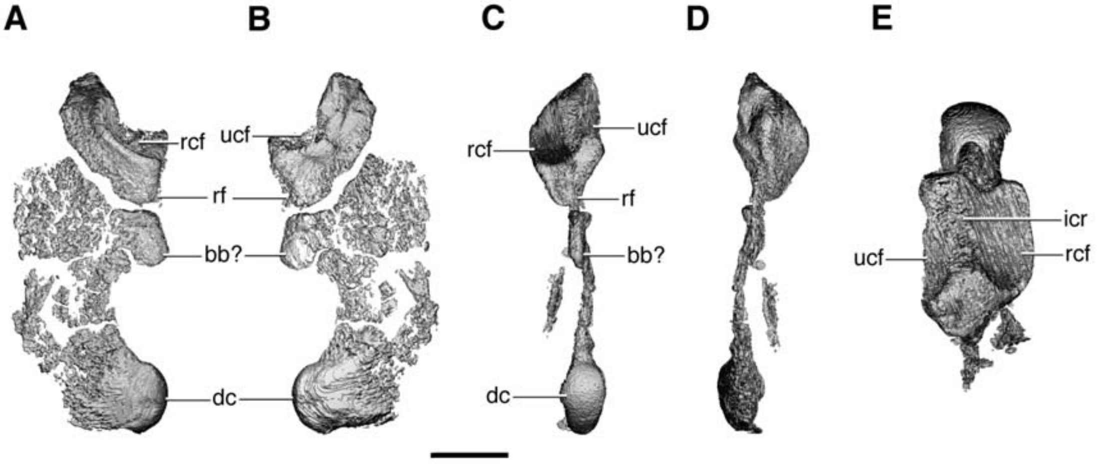

A
B
C
D
E
rcf
ucf
rf
bb?
dc
ucf
rf
bb?
dc
rcf
ucf
rf
bb?
dc
icr
ucf
rcf

FIG 3-13. Left radiale referred to *Drepanosaurus unguicaudatus* (H4-570-10) in **A**, dorsal, **B**, palmar, **C**, post-axial, **D**, preaxial, and **E**, proximal views. Abbreviations: **dt**, distal tab; **pof**, post-axial facet; **prc**, proximal contact for radius. Scale bar equals five millimeters

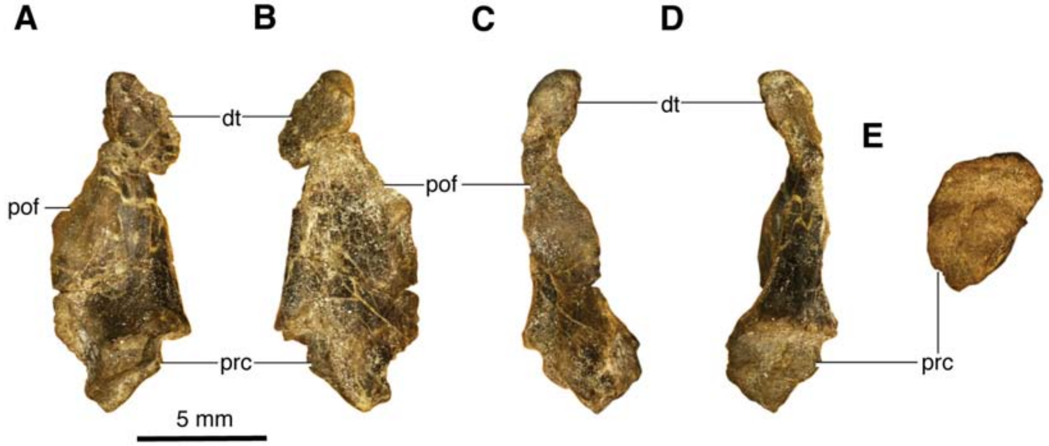

A
B
C
D
E
dt
dt
pof
pof
prc
prc
5 mm

FIG 3-14. Right intermedium, ulnare, and fused distal carpal complex referred to *Drepanosaurus unguicaudatus* (H3-053-08) in **A**, dorsal, **B**, palmar, and **C**, pre-axial views. Right intermedium of H3-053-08 in isolation in **D**, post-axial, and **E**, proximal views. Abbreviations: **duf**, distal facet of ulnare; **idp**, distal prong of intermedium for contact with distal ulnare; **pco**, primary convexity; **pif**, proximal facet of intermedium for contact with ulna; **poc**, post-axial convexity; **prc**, pre-axial convexity; **puf**, proximal facet of ulnare for contact with ulna; **uf**, proximal facet of intermedium for ulnare contact. Scale bar equals five millimeters.

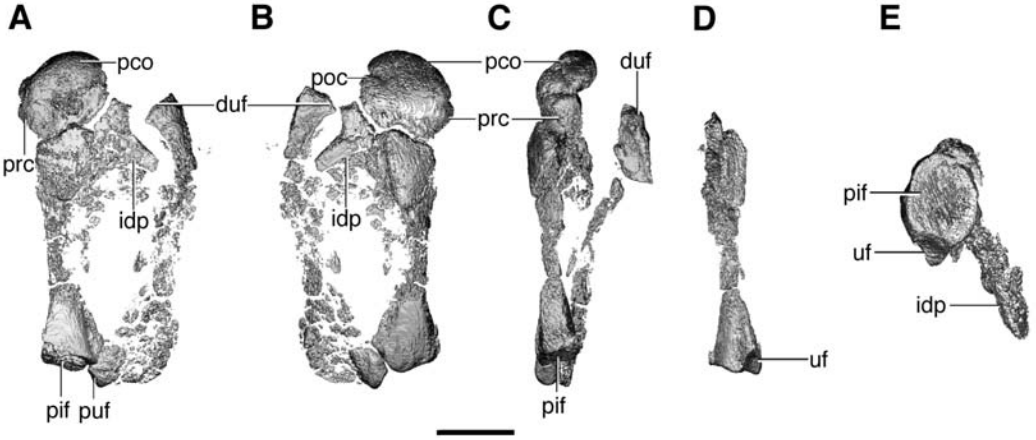

A
B
C
D
E
pco
prc
duf
idp
pif
puf
poc
pco
duf
prc
idp
pco
prc
duf
pif
uf
pif
uf
idp

FIG 3-15. Right second metacarpal referred to *Drepanosaurus unguicaudatus* (H4-185-08) in **A**, dorsal, **B**, palmar, **C**, preaxial, **D**, post-axial, **E**, distal, and **F**, proximal views. Abbreviations: **dco**, distal condyles; **ddp**, dorsal depression; **lp**, ligament pit; **pco**, proximal articular cotyle, likely for distal carpal complex; **pdp**, palmar depression; **pot**, post-axial tuberosity; **prt**, preaxial tuberosity.

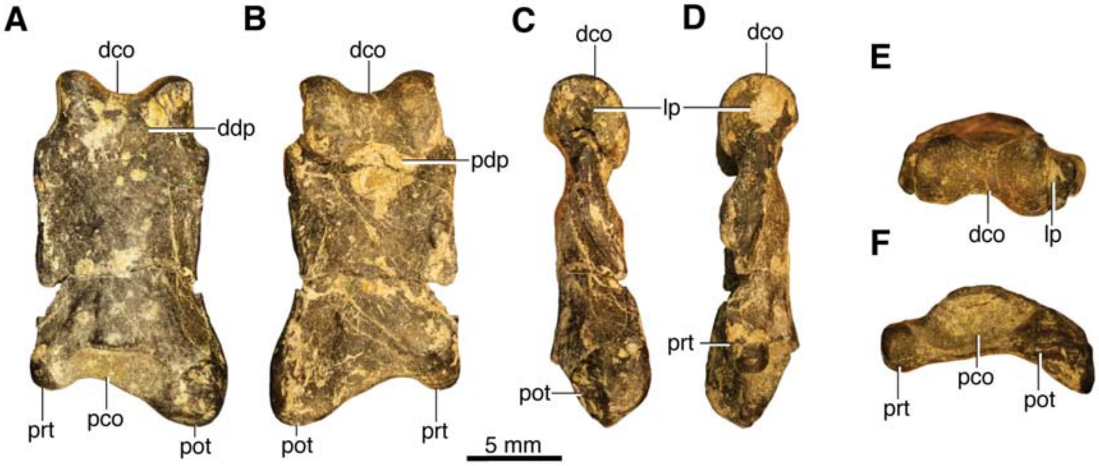

A
dco
ddp
prt
pco
pot
B
dco
pdp
pot
prt
C
dco
lp
pot
D
dco
prt
E
dco
lp
F
prt
pco
pot
5 mm

FIG 3-16. Right second manual ungual referred to *Drepanosaurus unguicaudatus* (H3-316-10) in **A**, post-axial, **B**, dorsal, **C**, preaxial, and **D**, palmar views. Abbreviations: **flx**, flexor tubercle; **pco**, proximal articular cotyles; **pit**, pit for flexor tendon; **pot**, postaxial tuberosity; **prt**, preaxial tuberosity.

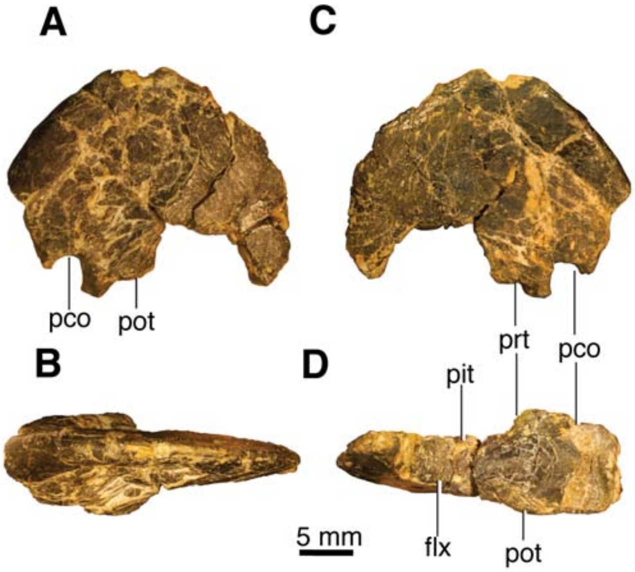

A
C
pco
pot
prt
pco
B
D
pit
5 mm
flx
pot

FIG 3-17. Left second manual ungual referred to *Drepanosaurus unguicaudatus* (H2-275-06) in **A**, preaxial and **B**, proximal views. Abbreviations: **ep**, extensor tendon pit; **ks**, groove for keratin sheath; **pad**, palmar depression; **pco**, proximal articular cotyles; **pot**, postaxial tuberosity.

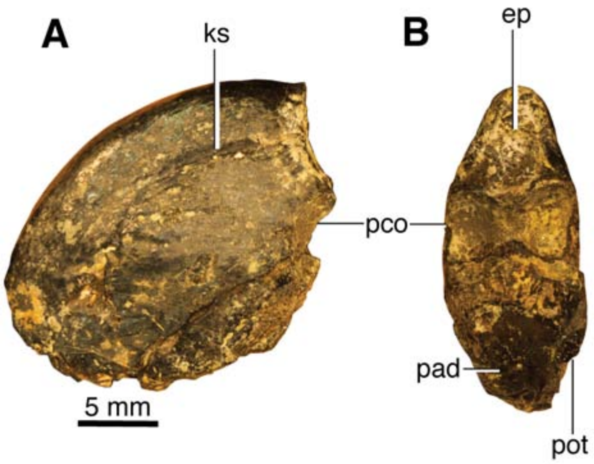

A
ks
B
ep
pco
pad
pot
5 mm

FIG 3-18. Left second? manual ungual referred to *Drepanosaurus unguicaudatus* (H3-117-14) in **A**, preaxial, **B**, dorsal, **C**, post-axial, and **D**, palmar views. Abbreviations: **flx**, flexor tubercle; **pad**, palmar depression; **pco**, proximal articular cotyles; **pot**, postaxial tuberosity; **prt**, preaxial tuberosity.

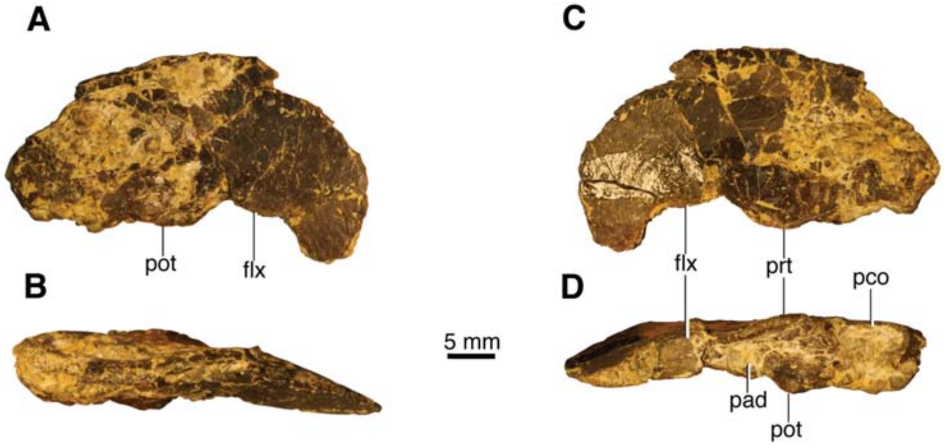
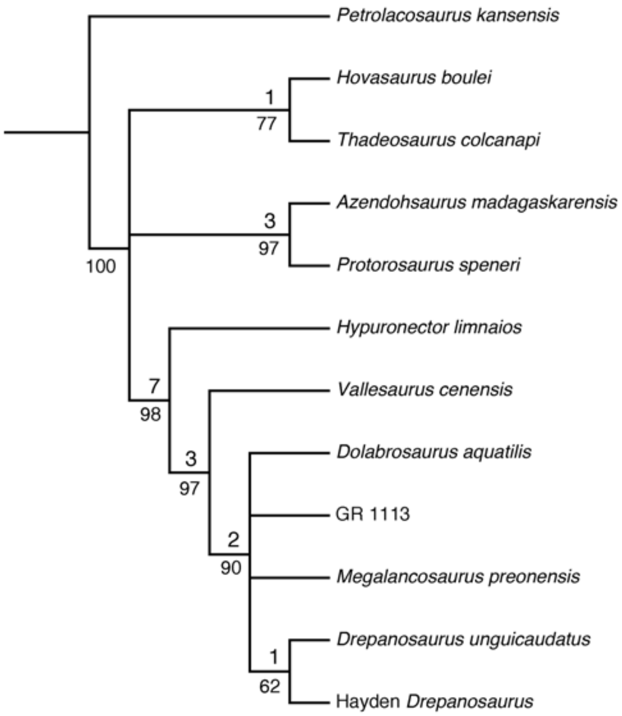
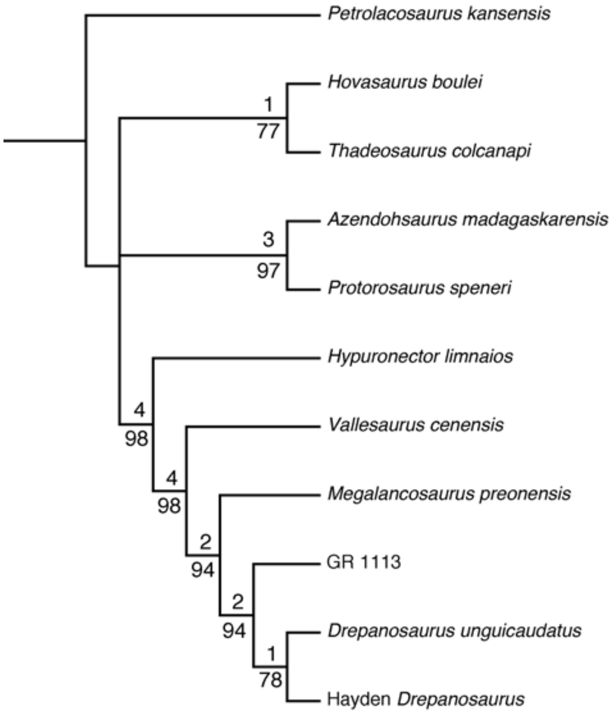

A
C
pot
flx
flx
prt
pco
B
D
5 mm
pad
pot

FIG 3-19. Results of phylogenetic analysis incorporating all drepanosaurid taxa and the *Coelophysis* Quarry drepanosaurid (GR 1113) as separate OTUs.



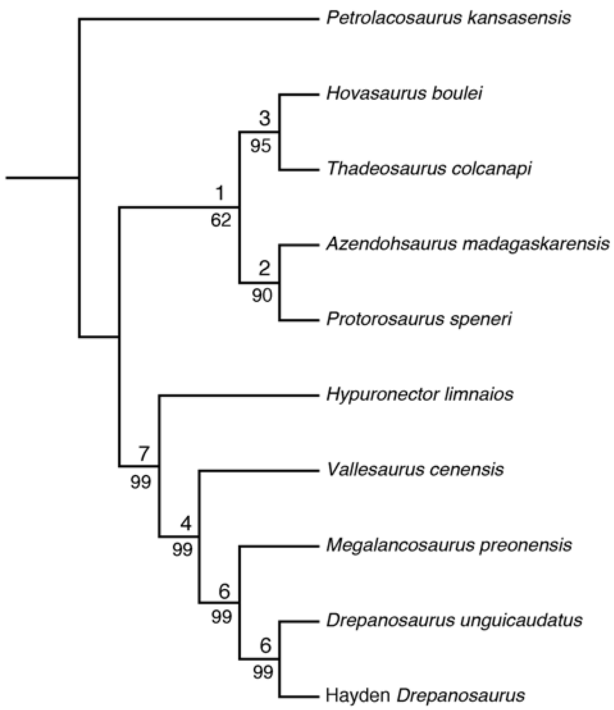
LENGTH = 69, 6 MPTs Best score hit
10000/10000.
CI = 0.855
RI = 0.878

FIG 3-20. Results of phylogenetic analysis excluding *Dolabrosaurus aquatilis*.



LENGTH = 68, 2 MPTs Best score hit
10000/10000.
CI = 0.868
RI = 0.890

FIG 3-21. Results of phylogenetic analysis excluding *Dolabrosaurus aquatilis* and the *Coelophysis* Quarry drepanosaurid.



LENGTH = 67, Best score hit
10000/10000.
CI = 0.881
RI = 0.902

Chapter 4

The skull of Drepanosauridae (Diapsida, Reptilia) and the post-Permian radiation of diapsid reptiles

ABSTRACT— Drepanosauromorphs are an exclusively Triassic clade of small-bodied, chameleon-like diapsid reptiles known from Europe and North America. Nearly all of the articulated skeletal material for the group is badly crushed, especially with regards to the skull. Without a robust understanding of the osteology, no one has offered a phylogenetic understanding of the group's affinities. Analyses have recovered drepanosauromorphs as deeply-nested archosauromorphs, a close sister taxon of Sauria, and as a sister taxon of the gliding Weigeltisauridae. Herein, I describe the first three-dimensional skull of a new genus and species of drepanosauromorph based on a specimen from the Upper Triassic Coelophysis Quarry of New Mexico. Due to the fragility of the specimen, the specimen was μCT-scanned and each skull element was digitally prepared from the matrix. This allows the first reconstruction of a drepanosaurid skull and a substantial expansion of the morphological characters known from the group. The new taxon exhibits a toothless rostrum, frontated orbits, and a massive endocranium. The bracing mechanism for the quadrate, the braincase, and the massive stapes are all more similar to archaic diapsid reptiles than contemporaneous Triassic taxa. A phylogenetic analysis incorporating a wide range of Permo-Triassic reptiles and all previously suggested sister taxa of Drepanosauromorpha indicates that the group represents an early-diverging diapsid clade that survived the Permo-Triassic Extinction (PTE) and radiated within the Triassic Period. The phylogeny suggests that the PTE did not cause the extinction of many diapsid reptile groups, and that our understanding of the extinction's impact on terrestrial amniote diversity is incomplete.

INTRODUCTION

Drepanosaurus are a clade of small-bodied diapsid reptiles known exclusively from the Late Triassic of North America and Europe. The group is characterized by elongate, dorsoventrally tall tails; narrow, slender scapular blades; and broad, barrel-shaped trunks. Derived members of the group exhibit bizarre synapomorphies, including a claw-like ossification at the tip of the tail; a fused complex of neural spines in the anterior dorsal region; and opposability of some manual digits. This suite of characters has led to the suggestion that drepanosaurs were the first arboreal specialists among diapsid reptiles. Despite an invasion of ecomorphospace shared with a number of modern taxa (e.g., chameleons, anteaters), the relationship of drepanosaurs to other diapsids is very poorly understood.

Contrasting hypotheses were offered for the first named drepanosaur taxa (Fig. 1); Pinna (1980, 1984, 1986) considered the headless material of the eponymous *Drepanosaurus unguicaudatus* to be a stem-lepidosaur, a position followed by Berman and Reisz (1992), although all of these authors perceived a mixture of primitive and derived diapsid characters in the specimens. By contrast, the skull and fragmentary postcrania of *Megalancosaurus preonensis* was initially considered to be a "thecodont" (i.e., Triassic archosauriform) (Calzavara et al., 1980; Carroll, 1988), and Evans (1988) suggested a position near "prolacertiforms," an arrangement of generally long-necked early archosauromorphs.

Later cladistic analyses of Permo-Triassic diapsid relationships have not resolved this question. Dilkes (1998) was the first to recover drepanosaurs nested within a clade of long-necked archosauromorphs, as the sister taxon of *Tanystropheus* (Fig. 1A). This analysis has been modified by subsequent authors (e.g., Sues, 2003; Gottmann-Quesada and Sander, 2009), all of who recover drepanosaurs deeply nested within Archosauromorpha. The most recent taxonomic revision of the group supported the archosauromorph position (Renesto et al., 2010). By contrast, other analyses have recovered drepanosaurs in various positions outside of Sauria altogether, placing them as the sister taxon to either the gliding Weigeltisauridae (Merck, 2003; Senter, 2004, depicted in Fig. 1B) or Kuehneosauridae (Müller, 2004, depicted in Fig. 1C). A later iteration of the Müller analysis (Bickelmann et al., 2009) noted that drepanosaurs acted as a wildcard taxon following the addition of new taxa. This phylogenetic instability relates to the meager amount of character data coded for drepanosaurs in most analyses, owing to the crushing distortion in nearly all drepanosaur skeletons (e.g., Renesto et al., 2010).

The absence of a coherent hypothesis for the relationships of this group has implications for interpreting the extreme ecomorphology of the group and the Permo-Triassic radiation of diapsid reptiles. The Dilkes hypothesis suggests that drepanosaurs are deeply nested among crown reptiles within the early archosauromorph radiation, specifically within a clade of long-necked, small-headed "protorosaurs." By contrast, the hypotheses of Merck, Senter, and Müller suggest that drepanosaurs are not crown reptiles, but instead are closely related to archaic Paleozoic lineages. These lineages are typically smaller in size, and both hypotheses suggest that the sister taxon of drepanosaurs were extreme gliding specialists. Resolving the ancestry of drepanosaurs provides important context for the diversification of small diapsids in the Permo-Triassic.

MATERIALS AND METHODS

Systematic Palaeontology

Diapsida Osborn, 1903
Simiosauria Senter, 2004
Drepanosauromorpha Renesto et al., 2010
Drepanosauridae Carroll, 1988

Drepanosauridae, n. gen., n. sp.

Holotype

American Museum of Natural History Fossil Amphibians, Reptiles, Birds Collection (AMNH FARB) 30834 (Fig. 2A), partial skull and articulated cervical series. Associated caudal series and partially articulated hindlimb and pes.

Type Locality and Horizon

Coelophysis Quarry ("siltstone member", Chinle Formation). Recovered during preparation of the holotype block of the shuvosaurid pseudosuchian *Effigia okeefae* by SJN (Nesbitt and Norell, 2006).

Diagnosis

A drepanosaurid diapsid differing from *Hypuronector limnaios*, *Megalancosaurus preonensis*, and *Vallesaurus cenensis* (the only drepanosaurs with skull material) in the complete absence of teeth, a dorsoventrally taller retroarticular process with a triangular shape in laterally view, and cervical neural spines with subequal anteroposterior lengths and transverse widths. Differs from *Drepanosaurus unguicaudatus* in the absence of a prominent groove on the ventral surface of the coracoid.

Note on Description

This specimen was initially recognized by SJN during preparation of the holotype skeleton of *Effigia okeefae*. The specimen was recognized as a drepanosaurid based on the saddle-shaped articular surfaces on the cervical vertebrae. Exposed portions of the skull include the right squamosal, postorbital, postfrontal, parietal, and fragments of the frontal and maxilla. The left frontal, parietal, postorbital, postfrontal, and squamosal are exposed, as is a portion of the rostrum in medial view. However, mechanical preparation of the skull elements proved untenable due to the extremely thin skull elements (<1 mm thickness). As such, this description is based almost entirely on 3D reconstructions of CT data (procedures detailed in supplement). A composite model is presented in Fig. 2B.

Description

The skull and partial skeleton in AMNH FARB 30834 is exposed to a limited degree. A badly broken portion of the rostrum, the dorsal surface of the skull table (Fig. 3), and a series of cervical vertebrae are exposed. The exposed cervical centra exhibit distinct, saddle-shaped articular surfaces, which allowed identification of the specimen as a drepanosauromorph (Renesto and Fraser, 2003).

Nearly the entire dorsal surface of the rostrum is absent, and the dorsal surfaces of the left maxilla and premaxilla are badly cracked. An elongate, concave surface on the anterodorsal surface of the maxilla suggests a massive external naris as in *Megalancosaurus* and *Vallesaurus* (Renesto et al., 2010). Small fragments posterodorsal to the left maxilla may belong to the lacrimal and prefrontal. The premaxillae appear to be fused in the midline. Neither the maxilla nor the premaxilla possess teeth, instead they have elongate, transversely narrow occlusal margins.

The left jugal is a slender C-shaped element completely lacking a posterior process. The T-shaped postorbital lacks a medial process, as the massive postfrontal intersects between that bone and the frontal and parietal. The appressed postfrontal and frontal contribute a transversely broad flattened orbital lamina that produces a heavily frontated orbit. The frontals exhibit a transversely wide contribution to the endocranium, in sharp contrast to the narrow contribution in most early diapsids. This portion of the bone is also domed well above the orbital margin.

The parietals exhibit a prominent doming in the region of their endocranial contributions. Posteriorly, the parietals have prominent posteroventral inclines that fit into prominent concavities in the dorsal surface of the supraoccipital. The squamosal is an exceptionally tall element that occupies the dorsoventral height of the postorbital region. The bone has plate-like lateral and posterior laminae that brace the quadrate in both views. I do not identify a quadratojugal among the remains, although the quadrate exhibits a facet for that element.

The quadrate lacks a lateral expansion for support of a tympanum and a prominent posterior concavity, comparable to archaic reptiles (Heaton, 1979) and early diapsids (Reisz, 1981) and contrasting with early saurians (Gow, 1975). It is unclear how the quadrate condyles were oriented relative to the rest of the skull. The palate is edentulous and made up of slender, plate-like bones. The pterygoids exhibit an elongate quadrate ramus and little expansion into transverse processes. The palatines have a prominent, L-shaped articulation with the anteromedial surface of the maxilla. It is unclear whether or not vomers were present, as neither the palatines nor pterygoids exhibit clear articular surfaces anteriorly. The epipterygoids are small and slender, with a small anteromedial lamina contributing to the basicranial articulations.

The braincase in Drepanosauridae n. gen., n. sp. is highly apomorphic and extremely transversely wide. The basioccipital and exoccipitals are indistinguishably fused and exhibit very little ventral expansion into basal tubera. The parabasisphenoid is somewhat verticalized (per Gower and Sennikov, 1996), and the basipterygoid processes are ventrolaterally inclined. The parabasisphenoid contributes to the extreme transverse breadth of the braincase through massive, dorsolaterally inclined processes for contact with the prootics. It is difficult to distinguish sutures between the prootic, opisthotic, and supraoccipital. The supraoccipital is prominently concave dorsally, allowing articulation of the posteroventral expansions of the parietals. The prootics are dorsoventrally tall and anteroposteriorly narrow. The paroccipital processes are drawn into long, tapering splints. These elements, along with the parabasisphenoid form a large, elliptical foramen ovale, which received the massive stapes. The stapes has no dorsal process nor a stapedial foramen.

The mandible is nearly complete, but badly eroded on the right side. As with the premaxillae, the dentaries appear fused in the midline. There is no trace of teeth on ether side.

The anterior portion is drawn into a broad, dorsoventrally flattened concavity resembling an avian beak. This tapers into transversely narrow, dorsally tapered occlusal margins that sit ventromedial to the upper jaws. It is difficult to identify the individual postdentary elements, but the surangular and articular appear to be fused. The retroarticular process is dorsoventrally tall and posterodorsally tapered.

Phylogenetic Analysis

This new specimen dramatically increases our knowledge of the three-dimensional osteology of the drepanosauromorph skull, previously represented by badly crushed specimens of *Megalancosaurus* and *Vallesaurus*, and provides a unique opportunity to reassess the phylogenetic position of the group. To do so, we employed a modification of the analysis of Pritchard et al. (2015), increasing the number of characters from 200 to 310. Taxon sampling of non-saurian diapsids was increased, all named drepanosauromorphs were included, and several representatives of all hypothetical drepanosaur sister taxa were included. The parameters of the analysis may be found in the electronic supplement. The matrix is listed in Table 4.1.

This analysis recovers Drepanosauromorpha, Weigeltisauridae, and Sauria in a polytomy (Fig. 4). The near-Sauria position of Drepanosauromorpha corroborates the hypothesis of Merck. In contrast to Senter, the clade including Permian "younginiform" diapsids is recovered outside to the clade including Weigeltisauridae, Drepanosauromorpha, and Sauria. In contrast to several recent analyses (e.g., Gauthier et al., 1988; Müller, 2004), Kuehneosauridae is recovered as the earliest divergence within Archosauromorpha as suggested by Evans (1988).

Alternative phylogenetic placements of Drepanosauromorpha were tested; recovery of the group within Archosauromorpha as the sister taxon to either *Tanystropheus* or *Protorosaurus* increased tree length by 19 and 16 steps respectively. In this analysis Kuehneosauridae was recovered as the earliest-diverging lineage within Archosauromorpha (see appendix), but alternative positions as the sister taxon to drepanosauromorphs among archaic diapsids only increased tree length by five steps. Placing drepanosauromorphs as the sister taxon to Weigeltisauridae in a monophyletic Avicephalia requires the addition of only a single additional step.

DISCUSSION

The Permo-Triassic Extinction and Diapsid Diversity

The recovery of drepanosaurs as nested far outside of Sauria has implications for understanding the dynamics of diapsid evolution at the time of the Permo-Triassic Extinction (PTE). Nearly all of the major diapsid lineages to radiate during the Triassic Period belong to the reptilian crown clade Sauria. However, drepanosauromorphs represent a substantial diversity of small-bodied reptile species during the Late Triassic. This analysis suggests the breadth of terrestrial diapsid diversity during the Triassic included at least one clade from far outside of crown reptiles, indicating that the recovery and radiation of terrestrial reptiles following the PTE was substantially more heterogeneous than previously recognized.

A strict reading of this phylogeny with regards to the stratigraphic occurrence of the included taxa requires a ghost lineage of drepanosauromorphs stretching from their first occurrence in the Norian (~220 my, Renesto et al., 2009) to the first occurrence of Weigeltisauridae and Sauria in the Late Permian (~252 my). Although the specific ingroup relationships of Drepanosauromorpha with other Permo-Triassic diapsid clades remain unresolved, all of the most-parsimonious trees require a similarly long ghost lineage.

Although the Late Permian diapsid record is quite meager, it is highly diverse, including non-saurian "younginiform" grade reptiles, the aquatic *Claudiosaurus germaini*, gliding weigeltisaurids, the early archosauromorphs *Aenigmastropheus parringtoni* and *Protorosaurus speneri*, and the archosauriform *Archosaurus rossicus* (Carroll, 1981; Currie, 1982; Evans and Haubold, 1987; Ezcurra et al., 2014). These taxa are spread widely across the diapsid phylogenetic tree, and the tree space they encompass demands that many additional lineages known only from Triassic records existed in the Permian (e.g., Gauthier, 1984; Dilkes, 1998; Müller, 2004).

The terrestrial Triassic fossil record of diapsids includes mostly saurian lineages, although a number of non-saurian taxa did survive the extinction (*Hovasaurus boulei*, Ketchum and Barrett, 2004; probable weigeltisaurids, Brinkman, 1988). The high diversity of drepanosauromorphs suggests that not only did some of these plesiomorphic taxa survive the extinction; at least one radiated extensively in the fifty million years following the PTE. The results of this analysis illustrate not only that the taxonomic diversity of diapsids was high prior to the PTE, but also that very few of the known lineages died out at the Permo-Triassic Boundary. This result stands in curious contrast to studies examining extinction events examining turnover at the species level (Smith and Ward, 2001; Irmis and Whiteside, 2012), illustrating that our understanding of terrestrial vertebrate diversity during this crisis remains incomplete.

The Osteology of Drepanosauromorpha

The cranial anatomy of drepanosaurs has been exceptionally poorly understood since the discovery of the first materials of the group, and recent reconstructions stem from two badly distorted specimens. This reconstruction of Drepanosauridae n. gen., n. sp. dramatically improves our understanding of the major features of the drepanosaur skull. Among the plesiomorphies recognized in the anatomy, the retention of many ancient characters associated with the absence of impedence-matched hearing is striking. The quadrate in most early saurians is embayed posteriorly and there is often a lateral crest for support of the tympanum (e.g., Carroll, 1975; Modesto and Sues, 2004; Borsuk-Bialynicka and Evans, 2009; Evans, 2009). The stapes is also quite slender in early saurians and also *Youngina capensis*, in contrast to the massive bone in Drepanosauridae n. gen., n. sp. Although these might be seen as adaptations to a fossorial habitus, in which impedence-matching would be unneeded, modern fossorial saurians retain an embayed quadrate and a slender stapedial stem in sharp contrast to Drepanosauridae n. gen., n. sp. (e.g., Gasc, 1968; Kearney et al., 2005; Rieppel and Maisano, 2007). Additionally, the prominent posterior lamina of the squamosal bracing the quadrate is a primitive character shared with araeoscelidians (Vaughn, 1955; Reisz, 1981) and weigeltisaurids (Bulanov and Sennikov, 2010).

The complete absence of teeth in Drepanosauridae n. gen., n. sp. is an extremely rare condition in Permo-Triassic diapsids, although the anterior tip of the jaw is toothless in *Hypuronector limnaios* and the teeth in *Megalancosaurus preonensis* are extremely small. It has thus far only been recognized in a small number of poposauroid archosaurs (e.g., Zhang, 1975; Nesbitt and Norell, 2006) and derived Testudines (e.g., Gaffney, 1990). The broad, flattened tip of the jaw and the apparently fused dentaries are very similar to many edentulous dinosaurs (e.g., oviraptorosaurs, Osmólska et al., 2004; Holliday and Nesbitt, 2013) that exhibited a rhamphotheca. This may suggest similar adaptations to dealing with strains during feeding to those in coelurosaurs (Lautenschlager et al., 2013). Edentulism is also a feature shared between Drepanosauridae n. gen., n. sp. and modern anteaters (Vaughan et al., 2000), a group long considered an ecomorphological analogue to *Drepanosaurus unguicaudatus* (Renesto, 1994).

Perhaps the most striking apomorphy in Drepanosauridae n. gen., n. sp. is the inflated endocranium. Renesto and Dalla Vecchia (2005) first recognized such an inflation of the endocranium in the type specimen of *Megalancosaurus preonensis*. In most Permo-Triassic diapsids, two primary depressions are visible on the ventral surfaces of the conjoined frontoparietal complex. The anterior depression tapers anteriorly, and may represent the cerebrum based on comparisons with shape and position in modern archosaurs (Hopson, 1979). The posterior depression probably represents some component of the cerebellum. If correct, our interpretation suggests an endocast of similar shape to derived maniraptorans and pterosaurs (e.g., Eddinger, 1927; Hopson, 1979; Witmer et al., 2003; Alonso et al., 2004; Balanoff et al., 2013).

LITERATURE CITED

Alonso PD, Milner AC, Ketcham RA, Cookson MJ, Rowe TB. 2004. The avian nature of the brain and inner ear of *Archaeopteryx*. Nature 430:666–669.

Balanoff AM, Bever GS, Rowe TB, Norell MA. (2013) Evolutionary origins of the avian brain. Nature 501:93–96.

Berman DS, Reisz RR. (1992) *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. J Paleo 66:1001–1009.

Bickelmann C, Müller J, Reisz RR. (2009) The enigmatic diapsid *Acerosodontosaurus piveteaui* (Reptilia: Neodiapsida) from the Permian of Madagascar and the paraphyly of “younginiform” reptiles. Can J Earth Sci 46:651–661.

Borsuk-Bialynicka M, Evans SE. (2009) A long-necked archosauromorph from the Early Triassic of Poland. Palaeo Pol 65:203–234.

Brinkman D. (1988) A weigeltisaurid reptile from the Lower Triassic of British Columbia. Palaeontology 31:951–955.

Bulanov VV, Sennikov AG. (2010) New data on the morphology of Permian gliding weigeltisaurid reptiles of eastern Europe. Paleo J 44:682–694.

Calzavara M, Muscio G, Wild R. (1980) *Megalancosaurus preonensis* n. g., n. sp., a new reptile from the Norian of Friuli, Italy. Gortiana 2:49–64.

Carroll RL. (1975) Permo-Triassic “lizards” from the Karroo. Palaeont Afr 18:71–87.

Carrol RL. (1981) Plesiosaur ancestors from the Upper Permian of Madagascar. Phil Trans Roy Soc London B 293:315–383.

Carroll RL. (1988) *Vertebrate Paleontology and Evolution*. WH Freeman.

Currie PJ. (1982) The osteology and relationships of *Tangasaurus mennelli* Haughton. Annals of S Afr Mus 86:247–265.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Proc Roy Soc B 353:501–541.

Eddinger T. (1927) Das gehirn der Pterosaurier. Zeitschrift für Anatomie und Entwicklungsgeschichte 83:105–112.

Evans SE. (1988) The early history and relationships of the Diapsida. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 221–260.

Evans SE. (2009) An early kuehneosaurids reptile from the Early Triassic of Poland. Palaeo Pol 65:145–178.

Evans SE and Haubold H. (1987) A review of the Upper Permian genera *Coelurosauravus, Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). Zool J Linn Soc 90:275–303.

Ezcurra MD, Scheyer TM, Butler RJ. (2014). The origin and early evolution of Sauria: the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS One 9:e89165.

Gaffney ES. (1990) The comparative osteology of the Triassic turtle *Proganochelys*. Bull American Mus Nat History 194:1–263.

Gasc J-P. (1968) Contribution à l’ostéologie et à la myologie de *Dibamus novaeguineae* Gray (Sauria, Reptila) discussion systematique. Ann. Sci Naturelles, Zool 12:127–150.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. thesis, University of California at Berkeley.

Gottmann-Quesada A, Sander PM. (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. Palaeont Ab A 287:123–220.

Gow CE. (1975) The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeont Afr 18:89–131.

Gower DJ, Sennikov AG. (1996) Morphology and phylogenetic informativeness of early archosaur braincases. Palaeo 39:883–906.

Heaton MJ. (1979) Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian Oklahoma and Texas. Bull OK Geo Soc 127:1–84.

Holliday CM, Nesbitt SJ. (2013) Morphology and diversity of the mandibular symphysis of archosauriforms. Geol Soc London, Special Pub 379:555–571.

Hopson JA. (1979) Paleoneurology. *Biology of the Reptilia, Vol 9*, ed C Gans (Academic Press, London), pp. 39–146.

Irmis RB, Whiteside JH. (2012) Delayed recovery of non-marine tetrapods after the end-Permian mass extinction tracks global carbon cycle. Proc Roy Soc B 279:1310–1318.

Kearney M, Maisano JA, Rowe T. (2005) Cranial anatomy of the extinct amphisbaenian *Rhineura hatcheri* (Squamata, Amphisbaenia) based on high-resolution X-ray computed tomography. J Morph 264:1–33.

Ketchum HF, Barrett PM. (2004) New reptile material from the Lower Triassic of Madagascar: implications for the Permian-Triassic extinction event. Can J Earth Sci 41:1–8.

Lautenschlager S, Witmer LM, P Altangerel, EJ Rayfield. (2013) Edentulism, beaks and biomechanical innovations in the evolution of theropod dinosaurs. Proc Nat Acad Sci 110:20657–20662.

Modesto SP, Sues H-D. (2004) The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. Zool J Linn Soc 140:335–351.

Merck J. (2003). An arboreal radiation of non-saurian diapsids. Abstracts of the Society of Vertebrate Paleontology Annual Meeting, St. Paul. J Vert Paleo 33:78A.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Nesbitt SJ, Norell MA. (2006) Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda) Proc Roy Soc B 273:1045–1048.

Osborn HF. (1903) On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. Science 17:275, 276.

Pinna G. (1980) *Drepanosaurus unguicaudatus*, nuovo genere e nuova specie di lepidosauro del Trias alpino. Atti della Soc ital di sci nat del mus civ di storia nat di Milano 121:181–192.

Pinna G. (1984) Osteologia di *Drepanosaurus unguicaudatus*, lepidosauro triassico del sottordine Lacertilia. Mem della Soc ital. di sci nat e del Mus civ di storia nat di Milano 24:7–28.

Pinna G. (1986) On *Drepanosaurus unguicaudatus*, an Upper Triassic lepidosaurian from the Italian Alps. J Paleo 60:1127–1132.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2015). Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. J Vert Paleo 35: e911186.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Spec Pubs Mus Nat Hist, U KS 7:1–74.

Renesto S. (1994) The shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the upper Triassic (Norian) of northern Italy. Zool J Linn Soc 111:247–264.

Renesto S, Fraser NC. (2003) Drepanosaurid (Reptilia: Diapsida) remains from a Late Triassic fissure infilling at Cromhall Quarry (Avon, Great Britain). J Vert Paleo 23:703–705.

Renesto S, Spielmann JA, Lucas SG. (2009) The oldest record of drepanosaurids (Reptilia, Diapsida) from the Late Triassic (Adamanian *Placerias* Quarry, Arizona, USA) and the stratigraphic range of the Drepanosauridae. N Jahr Geol Paläont Abh 252:315–325.

Renesto S, Spielmann JA, Lucas SG, and Spagnoli GT. (2010) The taxonomy and paleobiology of the Late Triassic (Carnian–Norian: Adamanian–Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha). Bull NM Mus Nat Hist Sci 46:1–81.

Rieppel O, Maisano JA. (2007) The skull of the rare Malaysian snake *Anomochilus leonardi* Smith, based on high-resolution X-ray computed tomography. Zool J Linn Soc 671–685.

Senter PJ. (2004) Phylogeny of Drepanosauridae (Reptilia: Diapsida). J Sys Palaeo 2:257–268.

Smith RMH, Ward PD. (2001) Pattern of vertebrate extinction across an event bed at the Permian-Triassic boundary in the Karoo Basin of South Africa. Geology 29:1147–1150.

Sues H-D. (2003) An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. Can J Earth Sci 40:635–649.

Vaughn PP. (1955) The Permian reptile *Araeoscelis* restudied. Bull Mus Comp Zool 113:305–467.

Vaughan TA, Ryan JM, Czaplewski NJ. (2000) *Mammalogy, 4th Edition*. (Saunders College Publishing, Fort Worth).

Witmer LM, Chatterjee S, Franzosa J, Rowe T. (2003) Neuroanatomy of flying reptiles and implications for flight, posture and behavior. Nature 425:950–953.

Zhang F-K. (1975) A new thecodont *Lotosaurus*, from the Middle Triassic of Hunan. Vert Pal 144–147.

SUPPLEMENTARY DATA

SUPPLEMENTARY APPENDIX 1. CT Reconstruction Methodology

The AMNH FARB 30834 block was scanned at the Duke University Shared Materials and Instruments facility in Durham, North Carolina. Scanning was supervised by CT tech James Thostenson. The final scan that I employed for the reconstruction was scanned at a resolution of 0.0448 millimeters for a total of 1,998 slices (190 kV, 78 mA).

The scan shows that many of the individual bones are invested with highly radio-opaque materials that appear brightest relative to air. The CT scan was reconstructed using the Avizo 7.1 software package. I initially reconstructed these regions employing a mixture of the “Magic Wand” and “Paintbrush” tools in Avizo. For the latter tool, I employed the “Limited Range” option to highlight only these strongly distinct regions.

However, much of the cortical bone surrounding these radio-opaque regions appears as a subtler halo that is only weakly differentiated from the surrounding matrix. For some elements (e.g., left frontal, parietals) this was simple, due to the sharp distinctions between the texture of the matrix and the bone. However, the reconstruction of other elements was more difficult due to the subtler distinction between the bony material and the matrix (e.g., anterior processes of the pterygoids).

SUPPLEMENTARY APPENDIX 2. Museum abbreviations used in taxon list for phylogenetic analysis.

AMNH FARB–American Museum of Natural History, Fossil Amphibian, Reptiles and Birds (New York, NY, USA)

BP–Evolutionary Studies Institute (formerly Bernard Price Institute; Johannesburg, South Africa)
CMNH–Carnegie Museum of Natural History (Pittsburgh, PA, USA)
FMNH–Field Museum of Natural History (Chicago, IL, USA)
GMPKU–Geological Museum of Peking University (Beijing, China)
GR–Ruth Hall Museum of Paleontology at Ghost Ranch (Abiquiu, NM, USA)
IVPP–Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China)
MCSN–Museo Civico di Storia Naturali (Milano, Italy)
MCSNB–Museo Civico di Storia Naturali Enrico Caffi (Bergamo, Italy)
MFSN–Museo Friulano di Scienze Naturali (Udine, Italy)
MNHN–Muséum National d'Histoire Naturelle (Paris, France)
MPUM–Museo di Paleontologia Univeristà degli Studi di Milano (Milano, Italy)
NHMUK–Natural History Museum of the United Kingdom (London, United Kingdom)
NMK–Naturkundmuseum im Ottoneum (Kassel, Germany)
NMMNHS–New Mexico Museum of Natural History and Science (Albuquerque, NM, USA)
NMQR–National Museum (Bloemfontein, South Africa)
PIMUZ–Paleontological Institute and Museum, University of Zürich (Zürich, Switzerland)
PIN–Paleontological Institute (Moscow, Russia)
SAM–Iziko Museum of South Africa (Cape Town, South Africa)
SMNS–Staaliches Museum fur Naturkunde Stuttgart (Stuttgart, Germany).
SSGW–Sektion Geologie, Ernst-Moritz-Arndt Universistät (Greifswald, Germany)
TMM–Texas Memorial Museum (Austin, TX, USA)
UA–Université d'Antannanarivo (Antannanarivo, Madagascar)
UCMP–University of California Museum of Paleontology (Berkeley, CA, USA)
UMMP–University of Michigan Museum of Paleontology (Ann Arbor, MI, USA)
USNM–United States National Museum (Washington, DC, USA)
VMNH–Virginia Museum of Natural History (Martinsville, VA, USA)
WMsN–Westfäliches Museum für Naturkunde (Münster, Germany)
YPM–Yale Peabody Museum (New Haven, CT, USA)

SUPPLEMENTARY APPENDIX 3. Taxon list for phylogenetic analysis.

Although nearly all Operational Taxonomic Units (OTUs) employed in this analysis were also incorporated into the analyses of Pritchard et al. (2015) and Nesbitt et al. (in press), codings for many taxa have been modified due to study or restudy of assigned fossil materials.

Petrolacosaurus kansensis (OUTGROUP)–Reisz, 1981.
Thadeosaurus colcanapi– MNHN MAP 360; Carroll, 1981; Caldwell, 1994.
Hovasaurus boulei–MNHN MAP 336; Currie, 1981; Caldwell, 1994.
Youngina capensis–AMNH FARB 5561; BP/1 375, 2871, 3859; SAM K7578; (possibly) SAM K7710; Goodrich, 1942; Gow, 1975; Evans, 1986; Gardner et al., 2010.
Hypuronector limnaios–AMNH FARB 1721, 7759; Colbert and Olsen, 2001.
Vallesaurus cenensis–MCSNB 4751; Renesto and Binelli, 2006.
Dolabrosaurus aquatilis–CMNH 28589; Berman and Reisz, 1992.

Megalancosaurus preonensis–MFSN 1721; MPUM 6008, 8437; Renesto, 1994a; Renesto et al., 2010.

Drepanosaurus unguicaudatus–MCSNB 5728; Renesto, 1994b.

Drepanosauridae n. gen., n. sp.–AMNH FARB 30834.

Rautiania spp.–Many isolated specimens from the Upper Permian Orenberg region of Russia studied at PIN; Bulanov and Sennikov, 2006, 2010.

Coelurosauravus elivensis–MNHN IP 1908-5-2, IP 1908-11-21, IP 1908-11-22; Evans, 1982; Evans and Haubold, 1987.

Coelurosauravus jaekeli–SMNS 59349 (cast of SSWG 113/7); Evans and Haubold, 1987.

Shinisaurus crocodilurus–Conrad 2004, 2006; Bever et al., 2005.

Kuehneosaurus spp.–Many isolated specimens from the Upper Triassic Emborough Quarry on hand at the AMNH and NHMUK; Robinson, 1962, 1967a; Evans, 1981, 2009.

Icarosaurus siefkeri–AMNH FARB 2101; Colbert, 1966, 1970.

Protorosaurus speneri–USNM 442453 (cast of NMK 180); SMNS (cast of WMsN P 47361); Gottmann Quesada and Sander, 2009.

Macrocnemus fuyuanensis–GMPKU-P3001; Li et al., 2007; Jiang et al., 2011.

Macrocnemus bassanii–Peyer, 1937; MCSN BES SC 111, V 457; PIMUZ T/2472, T/2477 T/4355, T/4822.

Amotosaurus rotfeldensis–SMNS 50691, 50830, 54783, 54784, 54810, 90549, 90600, 90601; Fraser and Rieppel, 2006.

Tanystropheus longobardicus–MCSN BES SC 265, 1018; PIMUZ T/1277, T/1377 (destroyed, illustrations on hand at PIMUZ), T/2484, T/2790, T/2817, T/2819.

Tanytrachelos ahynis– AMNH FARB 7206; YPM 7482, 8600; VMNH nos. 2826, 3423, 120015, 120016, 120019, 120042, 120043, 120046, 120047, 120048, 120049; Olsen, 1979.

Mesosuchus browni–SAM-PK-K5882, 6046, 6536, 7416, Dilkes, 1998.

Rhynchosaurus articeps–NHMUK R1235, R1236; Benton, 1990

Teyumbaita sulcognathus–Montefeltro et al., 2010, 2013.

Teraterpeton hrynewichorum–Sues, 2003.

Trilophosaurus buettneri–Several dozen partial skeletons accessioned at the Texas Memorial Museum (TMM); Gregory, 1945; Parks, 1969.

Trilophosaurus jacobsi– NMMNHS collection of specimens from the Kahle *Trilophosaurus* Quarry.

Spinosuchus caseanus– NMMNHS collection of specimens from the Kahle *Trilophosaurus* Quarry; UMMP 7507.

Pamelaria dolichotrachela–Sen, 2003.

Azendohsaurus laaroussii–

Azendohsaurus madagaskarensis–Dozens of specimens accessioned with Université d'Antananarivo; Flynn et al., 2010.

Prolacerta broomi–BP/1 471, 2675, 2676, 4504, 5066, 5375, 5880, UCMP 37151; Gow, 1975; Evans, 1986; Modesto and Sues, 2004.

Proterosuchus fergusi–BP/1 3393, 4601; NMQR 880, 1484; SAM PK-K10603; Cruickshank, 1972; Klembara and Welman, 2009; Ezcurra and Butler, 2015.

"Chasmatosaurus" *yuani*–IVPP field number 90002, V2720, V4067; Young, 1936, 1963.

Erythrosuchus africanus–NHMUK R3592, NMQR 3675; Gower, 1996, 1997, 2003.

Euparkeria capensis–Ewer, 1965; Gower and Weber, 1998.

Batrachotomus kupferzellensis–Nesbitt et al. (in press).

Coelophysis bauri–Colbert, 1989; Nesbitt et al. (in press).
Plateosaurus engelhardti–Prieto-Márquez and Norell, 2011; Nesbitt et al. (in press).

SUPPLEMENTARY APPENDIX 4. Character list for phylogenetic analysis.

This matrix is an expansion of Pritchard et al. (2015) and the subsequent study of Nesbitt et al. (in press). Additional characters have been incorporated from a wide range of studies. Characters modified from the Nesbitt et al. (in press) study are indicated in bold. Derivations of characters 1–200 may be found in Pritchard et al. (2015), and derivations of characters 201–245 may be found in Nesbitt et al. (in press), unless otherwise noted.

1) Premaxilla, external sculpturing: 0. surface is smoothly sculptured, 1. premaxilla is marked by anteroventral striations.

2) Premaxilla, orientation of ventral margin: 0. horizontal, roughly inline with maxillary ventral margin; 1. slight downturn, such that the margin trends anteroventrally; 2. extensive downturn, premaxilla extends to ventral margin of dentary. ORDERED
   - Note that this character was modified from a two-state character for Pritchard et al. (2015) to accommodate state 2 for Nesbitt et al. (in press).

3) Premaxilla, anterodorsal process (=nasal process): 0. present, separating the nares, 1. absent or reduced.

4) Premaxilla, posterodorsal process (=maxillary process, = subnarial process): 0. absent, such that premaxilla contributes a small ventral margin for the naris; 1. posterodorsal process present, framing the posteroventral margin of the naris.

5) Premaxilla, length of posterodorsal process (=maxillary process, = subnarial process): short, failing to exclude maxilla from narial margin; 1. long, excluding maxilla from narial margin; 2. extremely long, reaching the anteriormost part of the prefrontal. ORDERED.

6) Premaxilla, posterodorsal process/maxilla contact: 0. contact is a simple, straight margin; knob on the posterior margin of the posterodorsal process of the premaxilla fits into notch in the anterior surface of the maxilla.

7) Maxilla, orientation of ventral margin: 0. ventral margin of maxilla is horizontal, 1. ventral margin of maxilla is convex.

8) Maxilla, posterolateral surface: 0. directly adjacent to alveolar margin, 1. lateral process of maxilla present, creating distinct space between maxillary alveoli and posterolateral surface of the maxilla.

9) Nasal, orientation of contact with prefrontal: 0. oriented parasagitally, 1. oriented anterolaterally.

10) Prefrontal, contact with contralateral prefrontal: 0. no contact, due to fronto-nasal contact; 1. prefrontals approach medially, constricting fronto-nasal contact.

11) Lacrimal, facial contribution: 0. forms a portion of lateral surface of the face, reaching anteriorly to the external naris; 1. forms a portion of the lateral surface of the face, but does not reach naris; 2. limited to orbital margin.

12) Lacrimal, anterior extension: 0. lacrimal extends dorsally to reach the ventral margin of the nasal externally; lacrimal fails to reach nasal.

13) Antorbital fenestra: 0. absent, 1. present.

14) Frontals, degree of fusion: 0. frontals unfused to one another (suture patent), 1. frontals fused in the midline.

15) Frontals, shape: 0. retain similar transverse width through AP length, 1. frontals gradually expand transversely, 2. frontals expand abruptly at posterior margin of orbits.
  - The iteration of this character in Pritchard et al. (2015) and Nesbitt et al. (in press) included only two states to describe the relative transverse expansion of the frontals. I introduce a third state here to distinguish between the gradual expansion of the frontals posteriorly in squamates (e.g., Conrad, 2008) and the abrupt expansion in early archosauriforms (e.g., *Proterosuchus fergusi*, BP/1 4016)

16) Frontal, shape of contact with parietal in dorsal view: 0. roughly transverse in orientation, 1. frontal exhibits posterolateral processes, forming anteriorly curved U-shaped contact.

17) Frontal and postfrontal, surface texture: 0. dorsal surface relatively smooth, 1. dorsal surface exhibits distinct pitting.

18) Postorbital, medial contact with parietal: 0. present, 1. absent with postfrontal intersecting between the two.
  - Character 18 in Pritchard et al. (2015) and Nesbitt et al. (in press) described the relative anteroposterior breadth of the postfrontal contact with the elements of the skull table. However, in light of the vagueness of the states in the original character, I sought to instead describe a discrete consequence of the anteroposterior breadth of the postfrontals in non-saurians.

19) Parietals, degree of fusion: 0. parietals unfused to one another (patent suture), 1. parietals fused at the midline.

20) Parietal, dorsal surface: 0. parietal skull table flattened; 1. dorsal exposure of parietal forms a raised margin, elevated above lateral excavation for jaw adductor musculature; 2. thin, blade-like sagittal crest. ORDERED.

21) Parietal, orientation of post-temporal process: 0. roughly transverse, 1. strong posterolateral angling.

22) Pineal foramen: 0. present, 1. absent.

23) Pineal foramen, position: 0. entirely surrounded by parietals, 1. situated within the frontoparietal suture.

24) Postparietals: 0. absent, 1. present.

25) Postparietals, degree of fusion: 0. unfused to one another, 1. fused as a midline interparietal.

26) Postorbital, presence of medial process: 0. medial process absent, with contributions of the frontal, parietal or postfrontal forming the posterodorsal orbital margin; 1. present, postorbital contributing to posterodorsal orbital margin.

27) Postorbital, posterior process, length: 0. process contributes to superior margin of supratemporal fenestra, but does not reach the posterior aspect of that opening; 1. process contributes to the entire length of the supratemporal fenestra, reaching the posterior aspect of that opening.

- This character initially described the relative contribution of the posterior process of the postorbital to the supratemporal bar. However, reviewing the included taxa suggests that the initial states (>50% contribution, <50% contribution) were not particularly informative when most taxa exhibit a condition near the intersection of the two states. As such, I have modified the character to describe taxa with extremely elongate postorbital bars (e.g., *Youngina capensis*, BP/1 3859),

28) Postfrontal: 0. present, 1. absent.

- This character was not included in Pritchard et al. (2015) or Nesbitt et al. (in press). Its inclusion alters the numbering for a small portion of the remainder of the dataset.

29) Postfrontal: 0. anteroposteriorly short with a transversely oriented posterior margin, 1. posterior margin posteromedially inclined.

- This character represents a modification of character 27 from Pritchard et al. (2015), in which it described the distinction between the broad postfrontal articulation in “younginiform” diapsids and the comparatively narrow articulation in most saurians. However, reconsideration of the condition in a number of early saurians with broad postfrontals (e.g., *Mesosuchus browni*, SAM-PK-K6536; *Macrocnemus bassanii*, PIMUZ T/4822) suggests that the relative breadth of the articulation is not dramatically different in early saurian lineages. The major distinction occurs in the postfrontal-postorbital articulation (described in character 27 in this analysis).

30) Infratemporal fenestrae, conformation: 0. present, distinct opening framed by squamosal, postorbital and jugal; 1. postorbital, jugal, and squamosal fit against one another as a "lateral temporal plate."

- This character was present in Pritchard et al. (2015) and Nesbitt et al. (in press) as character 29.

31) Jugal, ornamentation of lateral surface: 0. unornamented 1. distinct anteroposteriorly trending shelf present.
  - This character was present in Pritchard et al. (2015) and Nesbitt et al. (in press) as character 30.

32) Jugal, dorsal process, squamosal contact: 0. absent, 1. present.
  - This character initially described contacts that involved the extreme dorsal extension of the ascending process to enter the supratemporal bar. However, some of the current taxonomic sample (e.g., *Sphenodon punctatum*) exhibit jugal-squamosal contacts that do not involve intersection into the postorbital-squamosal contact. Therefore, I have modified the included states.
  - The original iteration of this character was present in Pritchard et al. (2015) and Nesbitt et al. (in press) as character 31.

33) Jugal, posterior process: 0. absent; 1. present, but failing to contact the quadratojugal posteriorly 2. present, contacting the quadratojugal posteriorly.
  - This character was present in Pritchard et al. (2015) and Nesbitt et al. (in press) as character 32.

34) Squamosal, posterior lamina: 0. posterior lamina present, covering much of posterior aspect of quadrate, 1. posterior lamina absent, posterior aspect of quadrate exposed in occipital view.
  - I have substantially modified characters 33 and 34 of Pritchard et al. (2015) and Nesbitt et al. (in press), which initially described the presence and absence of the descending/lateral lamina of the squamosal and the relative development of that lamina. Study of the construction of the bracing of the quadrate in a wider range of taxa suggests some important modification. I modify this character from Laurin and Reisz (1995:27) and DeBraga and Rieppel (1997:37) to describe the extensive, posterior exposure of the squamosal evident in Drepanosauridae n. gen., n. sp. and other archaic diapsids.

35) Squamosal, lateral-descending lamina: 0. anteroposteriorly broad, covering much of quadrate in lateral view, 1. anteroposteriorly narrow, 2. absent. ORDERED.
  - I modified this character, which initially only described the relative size of the lateral exposure of the squamosal. However, our continued study of the squamosal bracing mechanism in Neodiapsida suggests that taxa lacking this process lost it as a result of a progressive reduction of the lateral lamina (described by Robinson, 1967b). As such, I integrate the absence of the lamina into this character. This removes the original iteration of character 35 from Pritchard et al. (2015) and Nesbitt et al. (in press).

36) Supratemporals: 0. absent, 1. present.

37) Tabulars: 0. absent, 1. present.

38) Quadratojugal: 0. present, 1. absent.
  - Note that I have removed the original Character 41 of Pritchard et al. (2015), which described the position of the quadrate foramen. In our analysis, this character is inextricably linked to the presence and absence of the quadratojugal, as the foramen is

only positioned within the quadrate when the quadratojugal is absent (as noted in Gauthier, 1984; Gauthier et al., 1988), resulting in an overprinting of this morphology. Merck (1997) employed a similar character to describe the position of the quadrate foramen within that bone in certain sauropterygians, but the morphology he described is not found in any taxa included in this study.

39) **Quadratojugal, anterior process: 0. present, 1. absent.**
  - I integrate this character to describe the anterior process of the quadratojugal in many early diapsids and archosauriforms. However, its presence is not perfectly correlated with the complete lower temporal bar in these reptiles, as is the case in *Proterosuchus* (see Ezcurra and Butler, 2015; IVPP V4067; BP/1 4016).

40) Quadratojugal, anterior process, shape: 0. paralleling dorsal and ventral borders, 1. tapering anteriorly.
  - Note that this character was present as Character 39 in Pritchard et al. (2015) and Nesbitt et al. (in press).

41) Quadratojugal, dorsal process, extent: 0. tall process, 1. weakly developed or absent.
  - Note that this character was present as Character 40 in Pritchard et al. (2015) and Nesbitt et al. (in press).

42) Quadrate, posterior surface, shape: 0. straight, vertical posterior margin; 1. anteriorly concave posterior surface.
  - Note that this character was present as Character 41 in Pritchard et al. (2015) and Nesbitt et al. (in press).

43) Quadrate, lateral flange (=tympanic crest): 0. absent, 1. present.

44) Palatal teeth: 0. present, 1. absent.

45) Vomer, palatal teeth: 0. present, 1. absent.

46) Vomer, contact with maxilla: 0. absent, vomer only contacts premaxilla; 1. present, vomer-premaxilla contact expands onto maxilla.

47) Palatine, palatal teeth: 0. present, 1. absent.

48) Pterygoid, anterior process, medial row of palatal teeth: 0. present, 1. absent.

49) Pterygoid, anterior process, lateral row of palatal teeth: 0. present, 1. absent.

50) Pterygoid, transverse process, dentition: 0. present, 1. absent.

51) Pterygoid, transverse process, number of tooth rows: 0. multiple rows, 1. one row.

52) Pterygoid, transverse process, orientation of long axis in ventral view: 0. lateral, 1. anterolateral.

53) Pterygoid, midline contact with contralateral pterygoid: 0. absent; 1. present, small contact anteriorly; 2. present, broad contact throughout length. ORDERED.

54) Pterygoid, shape of interpterygoid vacuity: 0. pterygoids meet to form anteriorly tapering space pterygoids meet to form anteriorly curved space.

55) Supraoccipital, texture of posterior surface: 0. smooth, 1. distinct dorsoventrally running crest in the midline.

56) Supraoccipital, shape: 0. consists of a flattened posterior lamina, 1. pillar-like.

57) Opisthotic, shape of ventral ramus: 0. slender process; 1. distinct, club-shaped expansion ventrally.

58) Opisthotic, paroccipital process contact with squamosal: 0. absent, ends freely; 1. present.

59) Exoccipital, dorsal contact with occipital elements: exoccipital columnar throughout dorsoventral height, forming transversely narrow dorsal contact with more dorsal occipital elements; 1. dorsal portion of exoccipital exhibits dorsomedially inclined process that forms transversely broad contact with more dorsal occipital elements.

60) Exoccipital, contralateral contact dorsal to foramen magnum: 0. absent, supraoccipital contributes to foramen magnum; 1. present, excluding supraoccipital from foramen magnum.

61) Exoccipital, contralateral contact on floor of foramen magnum: 0. absent, basioccipital contributes to floor of foramen magnum; 1. present, excluding basioccipital from floor of the foramen magnum.

62) Exoccipitals, fusion with opisthotic: 0. absent, 1. present.

63) Opisthotic, paroccipital process morphology: 0. unflattened and tapered; 1. anteroposteriorly flattened distally.

64) Basioccipital, basal tubera: 0. poorly developed, not extending well ventral of occipital condyle; 1. well developed, extending ventral to level of occipital condyle.

65) Parabasisphenoid, dentition on cultriform process: 0. absent, 1. prese

66) Parabasisphenoid, parasphenoid crests: 0. absent such that there is no ventral floor for the vidian canal; 1. present as prominent ventrolateral extensions of the caudoventral processes, framing the ventromedial floor of the vidian canal.

67) Parabasisphenoid, passage for internal carotid arteries: 0. within lateral wall of braincase, 1. within ventral surface of the parabasisphenoid.

68) Parabasisphenoid, conformation of ventral surface: 0. roughly planar, 1. distinct depression at the suture between the basioccipital and the parabasisphenoid, 2. distinct depression within the parabasisphenoid.

- In Pritchard et al. (2015), the original version of this character only described a depression within the ventral surface of the parabasisphenoid. The Nesbitt et al. (in press) version of the character subdivides the states to describe the position of the depression.

69) Parabasisphenoid, cultriform process: 0. extremely elongate, reaching to the level of the internal nares; 1. shorter, failing to reach internal nares.

70) Parabasisphenoid, basipterygoid process orientation in transverse plane: 0. anterolateral, 1. lateral.

71) Parabasisphenoid, location of abducens foramina: 0. pass through dorsum sella 1. track across dorsal surface of dorsum sella.

72) Laterosphenoid ossification: 0. absent, 1. present.

73) Prootic, crista prootica: 0. present, 1. absent.

74) Prootic, anterior inferior process: 0. process present, sitting anterior to trigeminal foramen; 1. absent, trigeminal foramen unframed anteriorly.

75) Prootic, paroccipital contribution: 0. does not contribute to anterior surface of paroccipital process; 1. contributes laterally tapering lamina to the anterior surface of the prootic.

76) Stapes, dorsal process: 0. absent, 1. present.

77) Stapes, foramen for stapedial artery: 0. present, 1. absent.

78) Dentary, anterior portion, symphyseal region of mandible: 0. dentaries do not diverge; 1. tips of dentaries diverge from one another.

- I modify the definition of this character to exclude discussion of the splenial contribution to the symphysis, as in Dilkes (1998).

79) Coronoid process: 0. absent, 1. present.

80) Surangular, lateral surface, foramen positioned near surangular-dentary contact: 1. absent, 1. present.

81) Surangular, lateral surface, foramen positioned directly anterolateral to glenoid fossa: 0. absent, 1. present.

82) Angular, exposure on lateral mandibular surface: 0. broadly exposed, 1. limited to posteroventral sliver by dentary and surangular.

83) Angular, exposure on lateral mandibular surface: 0. terminates anterior to the glenoid extends to the glenoid, 1. terminates anterior to the glenoid extends to the glenoid.

84) External mandibular fenestra: 0. absent, 1. present.

85) Splenial, contribution to mandibular symphysis: 0. splenials contribute to symphysis, 1. splenials fail to contribute.

86) Retroarticular process: 0. present, 1. absent.

87) Retroarticular process, composition: 0. articular only, 1. fused articular and prearticular.

88) Marginal dentition on anteriormost portions of premaxilla and dentary: 0. present, 1. absent.

89) Marginal dentition, enlarged caniniform teeth in maxilla: 0. present, 1. absent, maxillary teeth subequal in size.

90) Marginal dentition, serrations: 0. teeth are not serrated, 1. serrated.

91) Marginal dentition, shape of the posterior margin of tooth crown: 0. convex or straight; 1. concave, teeth are recurved.

92) Marginal dentition, arrangement: 0. single row of marginal teeth, 1. multiple zahnreihen in maxilla.

93) Marginal dentition, morphology of crown base: 0. single, pointed crown; 1. flattened platform with pointed cusps; 2. crown exhibits three mesiodistally arranged cusps.

94) Marginal dentition, implantation: teeth situated in shallow groove (pleurodonty + thecodonty)' 'teeth on dorsal surface of tooth-bearing bones (acrodonty).

95) Marginal dentition, lingual surface: 0. teeth walled by minimal lingual wall; 1. no lingual wall (=pleurodonty).

96) Marginal dentition, lingual surface: 0. teeth walled by minimal lingual wall only, 1. interdental plates are present.

97) Marginal dentition, rooting: 0. tooth crowns are not attached to dentigerous bones, 1. teeth ankylosed to bones of attachment.

98) Marginal dentition, tooth shape at crown base: 0. circular, 1. labiolingually compressed, 2. labiolingually wider than mesiodistally long.

99) Palatal dentition, morphology: 0. small, button-like teeth; 1. small, conical teeth.

100) Marginal dentition, procumbency: 0. anteriormost marginal teeth have similar apicobasal orientation to posterior teeth, 1. 0. anteriormost teeth are procumbent.

101) Presacral vertebrae, shape of anterior articular surface: 0. planar, 1. concave.

102) Presacral vertebrae, shape of posterior articular surface: 0. planar, 1. concave, 2. convex.

103) Presacral vertebrae, development of posterior articular surface convexity: 0. moderate, 1. ball-like.

104) Anterior cervical ribs, shaft shape: 0. tapering rapidly, roughly triangular in lateral view; 1. ribs taper gradually, elongate and splint-like in lateral view.

105) Cervical ribs, anterior process: 0. absent, 1. present.

106) Intercentra in the cervical column: 0. present, 1. absent.

107) Anterior post-axial cervical vertebrae, shape of anterior articular surface: 0. subcircular, roughly equivalent in dorsoventral height and transverse width; 1. compressed, with a greater transverse width than dorsoventral height.

108) Cervical vertebrae, ventral keel: 0. present, 1. absent.

109) Anterior post-axial cervical vertebrae, shape of ventral surface excluding keel: 0. ventrally rounded, 1. ventral face flattened.

110) Cervical vertebrae, number of costal facets: 0. one, 1. two.

111) Anterior post-axial cervical vertebrae, position of diapophysis (or dorsal margin of synapophyses): 0. at or near dorsoventral level of pedicles; 1. further ventrally, near the dorsoventral midpoint of the centrum.

112) Anterior post-axial cervical vertebrae, relative location of costal facets: 0. facets distinctly offset from one another; 1. facets very closely appressed to one another with little or no finished bone separation.

113) Anterior post-axial cervical vertebrae, shape of neural spine base: 0. elongate, subequal in length to the neural arch; 1. short, spine restricted to posterior half of neural arch.

114) Anterior post-axial cervical vertebrae, neural spine shape in cross-section: 0. transversely narrow, 1. elliptical or circular.

115) Cervical vertebra, shape of anterior margin of neural spine: 0. linear, 1. anterodorsal process present forming an anterior notch.

116) Anterior post-axial cervical vertebrae, anterior margin of neural spine, inclination of long axis: 0. inclined posterodorsally; 1. inclined anterodorsally.

117) Anterior post-axial cervical vertebrae, transverse width of dorsal tip of neural spine: 0. transversely slender; 1. expanded transversely with a midline cleft.

118) Cervical vertebrae, relative location of dorsal margin of mid-cervical neural spines: 0. spines are equivalent in height and length to other cervical neural spines; 1. spines are dorsoventrally depressed at their anteroposterior midpoints, leaving them little more than midline dorsal ridges.

119) Cervical vertebrae, dorsal surface of postzygapophyses: 0. smooth and rounded, 1. posteriorly pointed projections (epipophyses) present.

120) Anterior dorsal vertebrae, position of parapophysis (or ventral margin of dorsal synapophysis): 0. positioned partially on lateral margin of centrum; 1. positioned entirely on neural spine.

121) Posterior dorsal vertebra, position of parapophysis (or ventral margin of dorsal synapophysis) in trunk vertebrae: 0 .positioned partially on lateral margin of centrum; 1. positioned entirely on neural arch.

122) Anterior dorsal vertebrae, number of pectoral costal facets: 0. one (holocephaly); 1. two (dichocephaly); 2. three (tricephaly).

123) Posterior dorsal vertebrae, costal facets: 0. single rib facet; 1. inverse-L rib facet (suggesting partial confluence of diapophysis and parapophysis); 2. double rib facet.

124) Posterior dorsal vertebra, ribs and vertebrae: 0. unfused; 1. fused.

125) Dorsal vertebrae, neural spine, dorsal portion: 0. similar width as the more distal portion of the neural spine; 1. expanded transversely into a flattened tip (= spine table).

126) Dorsal vertebrae, breadth of neural spine expansion: 0. little lateral expansion relative to the neural spine base; 1. transversely broad, much wider than neural spine base..

127) Dorsal vertebrae, texturing on dorsum of neural spine expansion: 0. marked by irregular rugosities; 1. marked by transverse striations.

128) Dorsal vertebrae, intercentra: 0. present; 1. absent.

129) Dorsal vertebra, height of neural spines: 0. tall, greater in dorsoventral height than anteroposterior length 1. long and low, lesser in dorsoventral height than anteroposterior length.

130) Dorsal vertebrae, accessory zygosphene-zygantrum articulations: 0. absent, 1. present.

131) Second sacral rib, shape: 0. rib is a single unit, 1. rib bifurcates distally into anterior and posterior processes.

132) Second sacral rib, morphology of posterior process: 0. terminally blunted, 1. sharp distally.

133) Caudal vertebrae, shape of transverse processes: 0. processes curve posterolaterally, 1. processes straight.

134) Caudal vertebrae, orientation of transverse processes: 0. base of process perpendicular to the long axis of the vertebra, 1. processes angled posterolaterally from base.

135) Caudal vertebrae, autotomic septa within the centrum: 0. absent, 1. present.

136) Chevron, shape of hemal spine: 0. tapers along its anteroposterior length tapers along its anteroposterior length 0.; maintains breadth along its length 1.; broadens distally, forming inverted T shape 2.; broadens distally, forming subcircular expansion .

137) Gastralia: 0. abundant, with individual gastral elements nearly contacting, 1. small in number (= well separated) or unossified.
   - The original Pritchard et al. (2015) character simply described the presence or absence of ossified gastralia. In light of the tentative coding of “absence” in certain specimens (e.g., those with poorly articulated or fragmentary trunk regions), Nesbitt et al. (in press) restructured the character. I place that character here in place of the original Pritchard et al. (2015) character 137.

138) Gastralia, pairs of lateral gastralia: 0. two, 1. one.

139) Epiphyses of limb elements, secondary ossification centers: 0. absent, 1. present.

140) Cleithrum: 0. present, 1. absent.

141) Clavicle, portion articulated with the interclavicle, shape: 0. broader than distal portion of clavicle, 1. similar in narrowness to the distal portion of the clavicle.

142) Interclavicle, shape: 0. transversely robust, forming broad diamond anteriorly; 1. transversely gracile anteriorly, forming anchor-like shape anteriorly.

143) Interclavicle, shape of anterior surface anteromedial to clavicular articulations: 0. smooth margin, 1. prominent notch in margin.

144) Interclavicle, shape of caudal stem: 0. slender, tapering; 1. marked expansion.

145) Scapula, scapular blade, orientation of the long axis: 0. blade oriented directly dorsally, 1. curves posterodorsally, 2. curves anterodorsally.
   - This character required a new state to describe the scapula in drepanosaurids. In these taxa, the entire blade curves anterodorsally. This state was derived from Based on character 44 of Senter (2004). Employed as character 43 of Pritchard et al. (in prep).

146) Scapula, morphology just distal to the glenoid fossa, lateral side: 0. prominent tubercle developed, 1. slight depression or smooth bone present,

147) Coracoid, number of ossifications: 0. two, 1. one.

148) Coracoid, infraglenoid morphology: 0. no development of coracoid posteroventral to glenoid 1. prominent post-glenoid process on coracoid, terminating in thickened margin.

149) Sternum, ossification of sternal plates: 0. absent, 1. present.

150) Humerus, ectepicondyle, presence of radial nerve groove: 0. absent, 1. present.

151) Humerus, ectepicondyle, morphology of radial nerve groove: 0. groove has no roof; 1. groove roofed, forming ectepicondylar foramen.

152) Humerus, ectepicondyle morphology: 0. prominent preaxial crest; 1. no crest.

153) Humerus, entepicondyle morphology: 0. entepicondylar foramen absent; 1. entepicondylar foramen present.

154) Humerus, entepicondyle morphology: 0. smooth margin between shaft and post-axial condyle; 1. prominent entepicondylar crest present.

155) Humerus, entepicondylar crest morphology: 0. crest exhibits a curved proximal margin; 1. crest exhibits a prominently angled proximal margin.

156) Humerus, distal condyle morphology: 0. distinct trochlear and capitular articulations; 1. low, double condyle.

157) Ulna, ossified olecranon process: 0. present, 1. absent.

158) Medial centrale of hand: 0. absent, 1. present.

159) Distal carpal five: 0. absent, 1. present.

160) Intermedium: 0. present, 1. absent.

161) Ulnare and intermedium, perforating foramen between elements: 0. present, 1. absent.

162) Manual digit four, phalangeal formula: 0. five phalanges, 1. four phalanges.

163) Puboischiadic plate, fenestration: 0. no fenestrae, 1. thyroid fenestra within plate.

164) Ilium, long axis of orientation for iliac blade: 0. horizontal orientation; 1. posterodorsal orientation.

165) Ilium, anteroventral process extending from anterior margin of pubic peduncle: 0. absent; 1. present, process draping across anterior surface of pubis.

166) Ilium, supra-acetabular crest: 0. crest absent, posterodorsal margin of acetabulum similar in development of anterodorsal margin; 1. prominent anterodorsal bony lamina frames the anterodorsal margin of the acetabulum.

167) Ilium, shape of supra-acetabular margin: 0. dorsalmost margin of acetabulum is unsculptured; 1. prominent, bulbous rugosity superior to acetabulum.

168) Ilium, acetabulum shape: 0. irregular, marked by posterodorsal invasion by finished bone; 1. roughly circular, no posterodorsal invasion.

169) Ilium, anterior margin of iliac blade, anterior process or tuber: 0. absent, smooth anterior margin; 1. process or tuber present.

170) Ilium, anterior process/tuber of ilium: 0. anterior process/tuber small, with anterodorsal margin of ilium curving smoothly into dorsal margin of iliac blade; 1. large and anteriorly projecting tuber, with dorsal margin of tuber nearly continuous with dorsal margin of iliac blade.

171) Ilium, development of posterior process: 0. weakly developed, failing to extend well posterior of acetabulum; 1. strongly developed, extending well posterior to the acetabulum.

172) Ilium, morphology of dorsal blade margin: 0. smoothly textured dorsal border, 1. distinct dorsoventral striations running from acetabulum to dorsal margin of iliac blade.

173) Pubis, morphology of symphysis: 0. pubic apron present, with distinct anteroventral downturn of the symphyseal region, 1. pubic apron absent, symphyseal region only in coronal plane.

174) Pubis, pubic tubercle: absent 0.; present 1. absent.

175) Pubis, lateral surface, development of a lateral tubercle (sensu Vaughn, 1955): 0. present, 1. absent.

176) Ischium, shape of posterior margin: 0. linear posterior margin, 1. posterior process extends from posterodorsal ischiadic margin (spina ischii sensu El-Toubi, 1949).

177) Femur, profile in pre-axial view: 0. femoral shaft exhibits sigmoidal curvature, 1. femoral shaft linear with slight ventrodistal curvature.

178) Femur, morphology of proximal end of head; 0. well-ossified convex head, hemispherical; 1. concave surface with groove.

179) Femur, development of internal trochanter crest: 0. trochanteric crest does not reach femoral head; 1. trochanteric crest reaches far proximally, continuous with the femoral head.

180) Femur, size of distal condyles (medial and lateral), comparison: 0. about equal in size; 1. unequal, lateral condyle larger than the medial condyle.

181) Femur, expansion of distal condyles relative to femoral shaft: 0. distinct expansion beyond the circumference of the femoral shaft, 1. limited expansion beyond the circumference of the femoral shaft.

182) Femur, shape of medial tibial condyle in distal view: 0. medial surface is rounded and mound-like, 1. medial surface is triangular and sharply pointed.

183) Femur, crista tibiofibularis, shape of ventral surface: 0. flattened and planar, 1. rounded and mound-like.

184) Pedal centrale: 0. absent as distinct ossification, fused to astragalus; 1. present as distinct ossification.

185) Astragalus-calcaneum, extent of co-ossification: 0. present as distinct ossifications 1. co-ossified.

186) Astragalus-calcaneum, perforating foramen at contact: 0. distinct foramen situated between astragalus and calcaneum, 1. no foramen evident between astragalus and calcaneum.

187) Calcaneum, distal facet: 0. distal facet is little broader than is the proximal facet, 1. distal facet is markedly expanded, more than twice the breadth of the proximal facet.

188) Calcaneum, development of lateral margin 0. calcaneum terminating in unthickened margin, 1. roughened tuberosity present laterally.

189) Calcaneum, expansion of lateral margin 0. calcaneum has little postaxial expansion; 1. lateral wing of calcaneum is twice as broad or broader than the distal calcaneal facet.

190) Calcaneum, lateral projection 0. ventrolateral margin of calcaneum projection coplanar with dorsolateral margin of projection, 1. ventrolateral margin of calcaneum 'curls' externally.

191) Distal tarsal four, morphology of proximal contact: 0. smooth contact surface for proximal tarsals, 1. prominent process for contact with proximal tarsals.

192) Pedal centrale, contact with tibia: 0. absent, 1. present.

193) First distal tarsal: 0. present, 1. absent.

194) Second distal tarsal: 0. present, 1. absent.

195) Fifth distal tarsal: 0. present, 1. absent.

196) Metatarsal five, shape of proximal postaxial margin: 0. smooth, curved margin; 1. prominent, pointed process (outer process sensu Robinson, 1975).

197) Metatarsal five, angling of primary shaft with proximal tarsal articulation: 0. metatarsal is straight, with proximal tarsal articulation forming straight line with primary shaft; 1. metatarsal is hooked, with proximal tarsal articulation forming right angle with primary shaft.

198) Metatarsal five, concavity along preaxial margin: 0. prominent concavity present, 1. concavity absent, creating blocky metatarsal five.

199) Pedal digits, morphology of digit five: 0. proximal phalanx shorter than proximal phalanx of digit four; 1. proximal phalanx elongate, longer than all other proximal phalanges.

200) Heterotopic ossifications: 0. absent in a minimum of 5 individuals, 1. present.

201) Maxilla, medial surface dorsal to tooth row: 0. smooth, 1. prominent anteroposteriorly oriented ridge present.

202) Maxilla, dorsal portion, shape: 0. simply tapers to point dorsally; 1. the dorsal apex of the maxilla is a separate, distinct process that has a posteriorly concave margin.

203) Maxilla, anterolateral surface, large anteriorly opening foramen: 0. present, positioned just anterodorsal to primary row of neurovascular foramina; 1. absent.

204) Maxilla, anteromedial surface, palatal process: 0. absent; 1. present but fails to reach the midline; 2. present and touches its antimere at the midline. ORDERED.

205) Jugal, anterior process: 0. slender and tapering; 1. broad and expanded anteriorly.

206) Ectopterygoid, articulation with the pterygoid: 0. contacts part of the lateral edge of the pterygoid; 1. contacts the entire lateral edge of the pterygoid.

207) Quadrate, proximal portion, posterior side: 0. continuous with the shaft; 1. expanded and hooked.

208) Parabasisphenoid, orientation: 0. horizontal, 1. more vertical.

209) Parabasisphenoid, semilunar depression on the lateral surface of the basal tubera: 0. present; 1. absent.

210) Dentary, posteroventral portion: 0. just meets the angular; 1. laterally overlaps the anteroventral portion of the angular.

211) Dentition, crown height of the upper dentition compared with lower dentition: 0. similar tooth crown height; 1. the upper dentition is shorter relative to the taller lower dentition.

212) Antorbital fossa: 0. restricted to the lacrimal; 1. restricted to the lacrimal and dorsal process of the maxilla; 2. present on the lacrimal, dorsal process of the maxilla and the dorsal margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra). ORDERED.

213) Anterior cervical vertebrae (presacral vertebrae 3-5), postzygapophyses: 0. separated posteriorly; 1. connected through a horizontal lamina (=transpostzygapophyseal lamina) with a notch at the midline.

214) Cervical centra 3-5, length versus height: 0. length greater than height; 1. subequal.

215) Dorsal vertebrae, diapophysis, position: 0. anterior portion of the neural arch/centrum; 1. anteroposterior middle of the neural arch/centrum.

216) Sacral ribs, anteroposterior length of the first primordial sacral rib versus the second primordial sacral rib, dorsal view: 0. primordial sacral rib one is longer anteroposteriorly than primordial sacral rib two; 1. primordial sacral rib two is about the same length or longer anteroposteriorly than primordial sacral rib one.

217) Anterior caudal vertebrae, neural spines: 0. inclined posteriorly; 1. vertical.

218) Caudal vertebrae, length of the anterior caudal vertebrae (caudal vertebrae 1-10) relative to posterior caudal vertebrae (25+): 0. nearly the same length; 1. posterior caudal vertebrae much longer.

219) Scapula, entire anterior margin: 0. straight/convex or partially concave; 1. markedly concave.

220) Scapular blade, blade, anteroposterior length/dorsoventral height (at base of blade) ratio: 0. >0.4, 1. 0.4–0.25, 2. 0.25<.

- Modified from the original character in Nesbitt et al. (in press). The states have been further atomized to describe the extreme slenderness that occurs in derived drepanosauromorphs, as in character 59 of Pritchard et al. (in prep.)

221) Humerus, distal end, transverse width: 0. less than 2.5 times the minimum width of the shaft; 1. equal or more than 2.5 times the minimum width of the shaft.

222) Manual ungual, length: 0. about the same length or shorter than the last phalanx of the same digit; 1. distinctly longer than the last phalanx of the same digit.

223) Ilium, ventral margin of the acetabulum: 0. convex; 1. concave.

224) Ilium, iliac blade, maximum length: 0. less 3 times its maximum height; 1. more than 3 times its maximum height.

225) Ischium length: 0. about the same length or shorter than the dorsal margin of iliac blade; 1. markedly longer than the dorsal margin of iliac blade.

226) Femur, ridge of attachment of the M. caudifemoralis: 0. bladelike with a distinct asymmetric apex located medially; 1. low and without a distinct medial asymmetrical apex (= fourth trochanter).

227) Femur, anterior trochanter (M. iliofemoralis cranialis insertion): 0. absent; 1. present.

228) Astragalus, tibial and fibular articulations: 0. separated by a gap (or notch of Gower, 1996); 1. continuous.

229) Calcaneum, calcaneal tuber, shaft proportions at the midshaft of the tuber: 0. taller than broad; 1. about the same or broader than tall.

230) Calcaneum, articular surfaces for fibula and distal tarsal IV: 0. separated by a nonarticular surface; 1. continuous.

231) Calcaneum, calcaneal tuber, orientation relative to the transverse plane: 0. lateral, less the 20 degrees posteriorly; 1. deflected between 21-49 degrees posterolaterally; 2. between 50-90 degrees posteriorly.

232) Metatarsal IV: 0. longer than metatarsal III; 1. about the same length or shorter than metatarsal III.

233) Pes, unguals, ventral tubercle: 0. absent or small; 1. well developed and extended ventral to the articular portion of the ungual.

234) Distal pedal phalanges, distal articular portion: 0. lateral and medial sides parallel or near parallel; 1. lateral and medial sides converging anteriorly.

235) Pes, penultimate phalanx (last phalanx before the ungual): 0. shorter than the more proximal phalanx; 1. significantly longer than the more proximal phalanx.

236) Osteoderms: 0. absent; 1. present.

237) Prefrontal, orbital margin, lateral surface: 0. smooth or slight grooves present; 1. rugose sculpturing present.

238) Astragalus, margin between tibial and fibular facets: 0. margin grades smoothly into anterior hollow; 1. prominent ridge separates margin from anterior hollow.

- Note that Nesbitt et al. (in press) character 238 originally described the condition of the gastralia. That character has been shifted earlier within the character list to replace a character from Pritchard et al. (2015). This character was originally character 239 of Nesbitt et al. (in press).

239) Dentary, anterior portion in lateral view: 0. in the same horizontal plane as the middle portion of the dentary; 1. anteroventrally deflected.

- I have elected to remove the original Character 239 from Nesbitt et al. (in press), which described the anterior process of the chevrons evident in *Trilophosaurus*. A state in Character 136 addresses this morphology. Character 239 in this analysis is therefore equivalent to character 241 in Nesbitt et al. (in press).

240) Quadrate, posterior margin, distal half, lateral view: 0. concave, 1. convex.

- This is equivalent to Character 242 of Nesbitt et al. (in press).

241) Atlas, centrum: 0. separate from axial intercentrum; 1. fused to axial intercentrum.

- This is equivalent to Character 243 of Nesbitt et al. (in press).

242) Axis, neural spine, shape: 0. dorsal margin inclined anteroventrally; 1. dorsal margin inclined anterodorsally.

- This is equivalent to Character 244 of Nesbitt et al. (in press).

243) Presacral vertebrae, 5th vertebra to the sacrum, neural arch, posterior edge: spinopostzygapophyseal laminae absent 0.; spinopostzygapophyseal laminae present 1..

- This is equivalent to Character 245 of Nesbitt et al. (in press).

244) Dentary, lateral exposure, posterior extent: 0. posteriormost extent of dentary on dorsal margin of mandible; 1. posteriormost extent of dentary positioned ventral to surangular.

- This is equivalent to Character 246 of Nesbitt et al. (in press).

245) Premaxilla, medial surface, palatal process: 0. absent; 1. present.

- This is equivalent to Character 247 of Nesbitt et al. (in press).

246) Cervical vertebrae, hypapophysis: 0. absent, ventral surface of centrum unexpanded posteroventrally; 1. posteroventral surface of centrum exhibits massive, posteroventrally projecting crest.
  - Based primarily on character 4 of Renesto et al. (2010). Employed as Character 30 of Pritchard et al. (in prep).

247) Terminal caudal vertebra(e): 0. similar in morphology to other posterior caudal vertebrae; 1. modified into claw-like element.
  - Based primarily on character 37 of Senter (2004) and character 40 of Renesto et al. (2010). Employed as Character 31 of Pritchard et al. (in prep).

248) Anterior chevrons, hemal spine morphology: 0. element forms single spine; 1. element bifurcates ventrally.
  - Based primarily on character 41 of Senter (2004) and character 37 of Renesto et al. (2010). Employed as Character 32 of Pritchard et al. (in prep).

249) Anteriormost chevrons, hemal spine morphology: 0. bifid spines remain separate ventrally; 1. bifid spines recontact ventrally, forming foramen.
  - Based primarily on character 41 of Senter (2004) and character 37 of Renesto et al. (2010). Employed as Character 33 of Pritchard et al. (in prep).

250) Posterior chevrons, proximal articulation: 0. articulate intervertebrally; 1. contact anteroventral margin of centrum.
  - Based primarily on character 39 of Renesto et al. (2010). Employed as Character 34 of Pritchard et al. (in prep).

251) Posterior chevrons, proximal articulation: 0. articulate intervertebrally; 1. contact anteroventral margin of centrum.
  - Co-opted from Character 35 of Pritchard et al. (in prep.)

252) Chevrons, hemal spine length: 0. similar in length or shorter than caudal neural spines; 1. substantially longer than caudal neural spines.
  - Based primarily on character 40 in Senter (2004) and character 38 in Renesto et al. (2010). Employed as character 36 of Pritchard et al. (in prep).

253) Caudal vertebrae, anterior neural spines: 0. spines unexpanded dorsally; 1. spines exhibit slender anterior/posterior projections, forming T-shape.
  - Based primarily on character 36 in Senter (2004) and character 33 of Renesto et al. (2010). Employed as character 37 of Pritchard et al. (in prep).

254) Anterior dorsal vertebrae, pedicel height: 0. substantially shorter than respective centra; 1. taller than respective centra.
  - Based on character 38 of Pritchard et al. (in prep).

255) Anterior dorsal vertebrae, neural spine expansion: 0. spines similar in morphology to posterior dorsal neural spines; 1. spines dorsally broader anteroposteriorly than spine base; 2. third dorsal spine anteroposteriorly expanded into hatchet shape. ORDERED.

- Based primarily on character 31 in Senter (2004) and character 9 in Renesto et al. (2010). Employed as character 39 of Pritchard et al. (in prep).

256) Second manual ungual: 0. similar in morphology to other manual unguals; 1. substantially taller and more massive than other manual unguals.

- Based primarily on character 40 of Renesto et al. (2010). Employed as character 40 of Pritchard et al. (in prep).

257) Ulna, shape: 0. similar to radius, with elongate shaft; 1. flattened in pre-axial-post-axial plane, forming enormous crescent.

- Based on character 18 of Renesto et al. (2010). Employed as character 41 of Pritchard et al. (in prep).

258) Radius, proximal tab: 0. absent; 1. prominent tab for articulation with ulna present.

- Based on character 42 of Pritchard et al. (in prep).

259) Mid dorsal ribs, fusion to respective centra: 0. fusion absent; 1. fusion present.

- Based on character 11 of Renesto et al. (2010). Employed as character 44 of Pritchard et al. (in prep).

260) Femur, morphology of internal trochanter: 0. elongate, slender crest; 1. rounded tuberosity.

- Employed as Character 45 of Pritchard et al. (in prep). I employ this character to describe a notable modification of the internal trochanter I recognize in *Coelurosauravus elivensis* and drepanosauromorphs for which the morphology of the femur is evident (e.g., *Hypuronector limnaios*, AMNH FARB 1721). In these taxa, the ventral exposure of the internal trochanter manifests as a rounded tuberosity, in contrast to the flattened and slender crest in most early diapsids (e.g., *Youngina capensis*, BP/1 3859; *Prolacerta broomi*, BP/1 2676).

261) Proximal tarsals, morphology of perforating foramen: 0. broad, marked by finished bone on astragalus and calcaneum; 1. pinched, marked by extremely constricted space between astragalus and calcaneum.

- Employed as Character 46 of Pritchard et al. (in prep). This character represents an addition to the morphology of early Diapsida and Archosauromorpha. Small, pinched gaps in the astragalus and calcaneum occur in *Petrolacosaurus kansensis* (Reisz, 1981) and *Araeoscelis gracilis* (Vaughn, 1955) and also certain Tanystropheidae (e.g., MCSN V 3730).

262) Calcaneum, lateral projection, ventral margin: 0. margin is convex and continuous with the lateral margin of the projection; 1. margin is concave, sharply angled relative to lateral margin of the projection.

- Employed as Character 47 of Pritchard et al. (in prep).

263) Ilium, bone between acetabulum and iliac blade: 0. bone broadens smoothly into blade; 1. bone exhibits anteroposterior constriction between blade and acetabulum.

- Employed as Character 48 of Pritchard et al. (in prep).

264) Chevrons, hemal spine curvature: 0. spines roughly straight; 1. spines concave anteriorly.

- Based on character 181 of Dilkes (1998). Employed as Character 49 of Pritchard et al. (in prep).

265) Cervical ribs: 0. present; 1. absent.

- Based on character 5 of Renesto et al. (2010). Employed as Character 50 of Pritchard et al. (in prep). Cervical ribs are not apparent as distinct elements in any known drepanosauromorph specimen.

266) Pedal digit three (III), number of phalanges: 0. four, 1. three.

- Based on character 28 of Renesto et al. (2010). Employed as character 51 of Pritchard et al. (in prep).

267) Post-axial cervical vertebra, morphology of intervertebral articulations (for amphicoelous taxa): 0. circular/elliptical articulations appressed to one another (traditional amphicoely); 1. saddle-shaped articulations (heterocoely).

- Based on character 52 of Pritchard et al. (in prep).

268) Vertebrae, notochordal canal: 0. present; 1. absent.

- Employed as character 53 of Pritchard et al. (in prep). Derivation offered in that text.

269) Dorsal ribs, orientation: 0. ribs curve to frame trunk; 1. ribs splay laterally, forming patagium.

- NOVEL character. This character describes the straight-shafted, mobile ribs in some Permo-Triassic taxa (e.g., *Icarosaurus siefkeri*, AMNH FARB 2101) in contrast to the typically curved ribs in nearly all reptiles (e.g., *Drepanosaurus unguicaudatus*, MCSNB 5728; *Tanystropheus longobardicus*, MCSN BES SC 1018). Although the construction of the patagium is fundamentally different in Weigeltisauridae (see below), I code *Coelurosauravus elivensis* and *C. jaekeli* as lacking laterally directed ribs (e.g., Evans, 1982).

270) Posterior cranial table, ornamentation: 0. absent, 1. prominent horns on squamosal and quadratojugal.

- NOVEL character. Most early diapsids exhibit squamosals that are smoothly sculptured dorsally (e.g., *Prolacerta broomi*, BP/1 2675; *Trilophosaurus buettneri*, TMM 31025-140) or modestly rugose (e.g., *Mesosuchus browni*, SAM-PK-K6536). In contrast, weigeltisaurids have pointed horns arranged on the lateral surface of the squamosal and quadratojugal (Evans, 1982; Bulanov and Sennikov, 2010).

271) Ulnare and intermedium, elongation: 0. elements longer proximodistally than in pre-axial-post-axial plane; 1. elements short, equivalent in proximodistal and pre-axial-post-axial length.

- NOVEL character. In *Petrolacosaurus kansensis* (Reisz, 1981) and *Araeoscelis gracilis* (Vaughn, 1955) and a number of drepanosauromorphs (e.g., *Megalancosaurus preonensis*, MFSN 1769; *Drepanosaurus unguicaudatus*, MCSNB 5728), the intermedium and ulnare are proximodistally more elongate than they are in a pre-axial/post-axial plane. These elements of the carpus are proportionally proximodistally shorter in most neodiapsids (e.g., *Youngina capensis*, BP/1 3859; *Thadeosaurus colcanapi*, MNHN MAP 360) and early saurians (e.g., *Boreopricea funerea*, PIN 3708/1; *Trilophosaurus buettneri*, TMM 31025-140; Nesbitt et al., in press).

272) Metatarsal I, proximal articular surface, proportions: 0. proximal breadth is similar in axial plane relative to other metatarsals, 1. broader in pre-axial-post-axial breadth than other metatarsals.

- NOVEL character. This character describes the substantial breadth of the first metatarsal in known drepanosauromorph feet (e.g., *Dolabrosaurus aquatilis*, CMNH 28589; *Drepanosaurus unguicaudatus*, MCSNB 5728). By contrast, the first metatarsal is similar in its proximal narrowness to the other metatarsals in most neodiapsids (e.g., *Mesosuchus browni*, SAM PK-K7416; *Prolacerta broomi*, AMNH FARB 9502).

273) Metatarsal I, shaft, proximodistal length relative to proximodistal length of metatarsal IV: 0. >.42, 1. .42>.32, 2. <.32. ORDERED.

- Modified from Ezcurra et al. (2014) character 216, which was derived from Dilkes (1998), Müller (2004), and Modesto and Sues (2004), to accommodate the unique metatarsal proportions in Rhynchosauria.

274) Maxilla, tooth-bearing surface: 0. ungrooved, 1. single anteroposteriorly running groove within occlusal surface, 2. double anteroposteriorly running groove. ORDERED.

- Modified from Dilkes (1998) character 62.

275) Basioccipital, occipital condyle, posterior surface: 0. exhibits broad, elliptical notochordal depression that occupies much of posterior surface of condyle; 1. exhibits narrow, “pinprick” notochordal pit within posterior surface of condyle; 2. surface is smoothly convex, notochordal pit absent. ORDERED.

- Modified from LIST. We have modified this character to accommodate the broad spectrum of notochordal pits exhibited by Permo-Triassic diapsids. This character assumes that the reduction in the size of the pit is a continuous spectrum of morphologies.

276) Parabasisphenoid, cultriform process, dentition: 0. teeth run anteroposteriorly on process teeth, 1. clustered at base of process.

- NOVEL character. We employ this character to describe the distinction between the rows of parasphenoid teeth present in early reptiles (e.g., *Captorhinus aguti*, Heaton, 1979; *Petrolacosaurus kansensis*, Reisz, 1981) and the small cluster of teeth on the parasphenoid in kuehneosaurids (e.g., Colbert, 1970).

277) Humerus, internal tuberosity: 0. continuous with humeral shaft 1. prominent projection, offset from humeral shaft.

- NOVEL character. This describes a morphology we perceive in kuehneosaurids specimens, including *Icarosaurus* and humeri referred to *Kuehneosaurus* from Emborough Quarry. The internal tuberosity in these taxa is placed on a narrow pedicel relative to the other projections, in contrast to the more subtle offset in other early archosauromorphs (e.g., *Tanystropheus longobardicus*, PIMUZ T/1277; *Trilophosaurus buettneri*, TMM 31025-140).

278) Third manual digit, phalangeal formula: 0. multiple phalanges, 1. single, non-ungual phalanx.

- NOVEL character. In a number of derived drepanosauromorph taxa (e.g., *Megalancosaurus preonensis*, MFSN 1769; *Drepanosaurus unguicaudatus*, MCSNB 5728), the manual phalangeal count has been reduced to a single, non-ungual phalanx. It is unclear if this is accomplished through fusion of phalanges or the loss of those segments.

279) Glenoid fossa of pectoral girdle, position relative to scapular blade: 0. fossa positioned near base of scapular blade; 1. fossa shifted ventrally, nearer to ventral margin of primary body of coracoid.

- Equivalent to character 55 in Pritchard et al. (in prep.)

280) Humerus, ectepicondyle morphology: 0. squared off pre-axially; 1. pointed, triangular pre-axially.

- NOVEL character. In kuehneosaurids (e.g., *Kuehneosaurus latus*, AMNH FARB 7786; *Icarosaurus siefkeri*, AMNH FARB 2101), the ectepicondyle is drawn into a prominent, preaxially pointed, triangular projection. This contrasts with the subtle, rounded ectepicondyles in squamates (e.g., Conrad, 2006) and rhynchocephalians (e.g., Cocude-Michel, 1963).

281) Articular, retroarticular process, shape in lateral view: 0. shallow, dorsal margin positioned posteroventral to quadrate articulation; 1. deep, dorsal margin at dorsoventral level equivalent to quadrate articulation.

- NOVEL. The retroarticular process is a character of Neodiapsida (Benton, 1985), but its shape differs widely among diapsid groups. In early neodiapsids (e.g., *Youngina capensis*, AMNH FARB 5561; *Rautiania* spp., PIN 5130/47), the process is typically anteroposteriorly short and low, positioned well ventrally relative to the glenoid fossa. In early archosauromorph taxa (e.g. *Protorosaurus speneri*, USNM 442453; *Trilophosaurus buettneri*, TMM 31025-140), the process tends to be substantially dorsoventrally taller with a dorsal margin positioned near the level of the glenoid fossa.

282) Humerus, distalmost end: 0. collinear with proximal shaft, 1. primary axis of shaft curves towards flexor surface at distal end.

- Derived from Pritchard et al. (in prep) character 54.

283) Humerus, entepicondyle: 0. terminates proximal to the distal margin of the ulnar condyle, 1. extends distally relative to ulnar condyle.

- NOVEL. In most diapsid groups with a well-developed entepicondylar crest that projects outward from the humeral shaft, the ventral margin of that epicondyle is positioned proximally relative to the ulnar condyle (e.g., *Protorosaurus speneri*, SMNS cast of WMsN P47361; *Trilophosaurus buettneri*, TMM 31025-140). By contrast, the entepicondyle in Weigeltisauridae (e.g., *Coelurosauravus elivensis*, MNHN PI 1908-5-2; *Rautiania* sp., PIN 5130/54) extends further distally than the distal end of the ulnar condyle. A similar extension occurs in some rhynchocephalians (e.g., Carroll, 1985).

284) Ilium, iliac blade, post-acetabular portion: 0. relatively planar or lightly sculptured; 1. marked by posterodorsally running ridge, extending from posterior margin of supraacetabular margin.

- NOVEL. In most Permo-Triassic diapsid taxa, the lateral surface of the posterior process of the ilium is smoothly sculptured (e.g., *Youngina capensis*, BP/1 3859; *Trilophosaurus buettneri*, TMM 31025-). In most Tanystropheidae, the post-acetabular portion of the ilium exhibits a prominent, posterodorsally inclined ridge that runs the length of the blade (e.g., *Macrocnemus bassanii*, MCSN V457; *Tanytrachelos ahynis*, AMNH FARB 7206).

285) Humerus, epicondyles, proximal origination: 0. positioned distal to midshaft, 1. positioned at/near midshaft.

- Derived from Pritchard et al. (in prep) character 56.

286) Palatine, anterior transverse expansion: 0. absent, producing anteriorly curved suborbital fenestrae; 1. present, producing anteriorly tapered suborbital fenestrae.

- Derived from similarly informative characters in Gauthier et al. (1988). In most character sets (e.g., Benton, 1985; Evans, 1988), this character also makes reference to the enlarged palatine teeth that seem to co-occur with this transverse expansion of the bone.

287) Supraneural ossification, bone growth positioned anterodorsal to anterior dorsal neural spines: 0. absent, 1. present.

- Derived from Pritchard et al. (in prep) character 57.

288) Scapulacoracoid, glenoid fossa, construction: 0. oriented posterolaterally, ventral margin extends posterior of dorsal margin; 1. oriented laterally, ventral margin positioned directly underneath to dorsal margin.

- Derived from Pritchard et al. (in prep) character 58.

289) Accessory patagial ossification: 0. absent, 1. present, articulated to distal tips of ribs in dorsal region.

- NOVEL character. The patagium of Weigeltisauridae differs from those in Kuehneosauridae and modern *Draco* (e.g., Colbert, 1970) in that it is not completely supported by elongated, straightened dorsal ribs. Instead, the dorsal ribs meet a series of elongate, slender bony elements that formed the patagium (Evans, 1982; Frey et al., 1997). Evans (1982) described these bones as proximal and distal ribs, whereas Frey et al. (1997) considered them neomorphic dermal bones. We elect to simply describe the morphology of the elements rather than make a firm statement on their homology.

290) Quadrate, pterygoid ramus: 0. ventral margin of posterior base of ramus in line with quadrate condylar surface, 1. posterior base of ramus elevated dorsally relative to quadrate condylar surface.

- NOVEL character. In araeoscelids (e.g., Reisz, 1981), *Captorhinus* (e.g., Heaton, 1979), Drepanosauridae n. gen., n. sp., and *Rautiania* sp. (PIN 5130/33), the pterygoid ramus of the quadrate is dorsoventrally tall with a ventral margin on the same level as the quadrate condyles. By contrast, *Youngina capensis* (e.g., AMNH FARB 5561) and most early saurians (e.g., *Protorosaurus speneri*, USNM 442453; *Boreopricea funerea*, PIN 3708/1), the ventral margin of the quadrate ramus is elevated dorsally above the condylar portion.

291) Parietal, posterolateral processes: 0. slender and tapering, 1. anteroposteriorly flattened, such that parietal contributes prominently to occipital face of skull.

- NOVEL(?) character. The posterolateral process of the parietal is a narrow, dorsoventrally slender structure in most early diapsids (e.g., *Youngina capensis*, AMNH FARB 5561; *Rautiania* spp.,). This is a feature also found in Drepanosauridae n. gen., n. sp. and early lepidosauromorphs (e.g., *Gephyrosaurus bridensis*, Evans, 1980). By contrast, early archosauromorphs exhibit anteroposteriorly flattened processes that are easily visible in posterior view (e.g., *Prolacerta broomi*, BP/1 2675; *Azendohsaurus madagaskarensis*, UA 70-20-99-653). This feature is further accentuated in some early archosauriforms (e.g., *Erythrosuchus africanus*, Gower, 2003).

292) Stapes, robusticity: 0. robust, with thick shaft 1. slender, with rod-like shaft.

- Derived from similarly informative characters in Gauthier (1984) Benton (1985), Laurin (1991), Müller (2004), and Reisz et al. (2010).

293) Surangular, dorsolateral surface: 0. smooth, 1. marked by distinct shelf.

- Derived from similarly informative characters in deBraga and Rieppel (1997), Müller (2004), and Ezcurra et al. (2014).

294) Premaxilla, fusion to contralateral premaxilla: 0. unfused, 1. fused at maturity.

- Derived from similarly informative characters in Gauthier (1984), Benton (1985), Estes et al. (1988), Gauthier et al. (1988), and Conrad (2008). Most early iterations of this character (e.g., Gauthier, 1984; Estes et al., 1988) include a qualifier that the premaxillae become fused early in embryonic development. We follow Conrad (2008) in excluding this qualifier, as such detailed ontogenetic data is unavailable for most taxa in our dataset.

SUPPLEMENTARY APPENDIX 7. Parameters of phylogenetic analyses.

All of the phylogenetic analyses run as part of this study were performed using TNT v. 1.1 (Goloboff et al., 2008). We performed a heuristic search with 10,000 replicates of Wagner trees (using random addition sequences) followed tree-bisection and reconnection (TBR) branch swapping, holding 10 trees per replicate. The best trees obtained from this were subjected to a final round of TBR branch swapping. Zero-length branches were collapsed under rule one of Coddington and Scharff (1994).

For Bremer support values, we used the Bremer.run script available with TNT. We employed Jackknife resampling in TNT, using 10,000 replications with a 20% character removal probability. CI and RI were calculated using the STATS.run script available with TNT. Alternative topologies were constructed the tree editor window in Mesquite 3.02 (Maddison and Maddison, 2015). These were imported in TNT, where we enforced the topological constraints described below.

SUPPLEMENTARY APPENDIX 8. Results of phylogenetic analyses.

For the iteration of this analysis presented in the primary text (strict consensus illustrated in figure 4), we included all operational taxonomic units (OTUs). This analysis produced three most-parsimonious trees (MPTs) with a tree-length of 843 steps recovered in 9,788 times out of the 10,000 replicates. The consistency index (CI) was 0.375 and the retention index (RI) was 0.622.

In the strict consensus tree, the drepanosauromorph clade is recovered in a polytomy with Weigeltisauridae and Sauria. A clade including “younginiform” diapsids is recovered as the sister taxon to this clade. The topology of Sauria is overall similar to that recovered by Nesbitt et al. (in press), although *Protorosaurus* is recovered in a polytomy with Tanystropheidae and a clade including Rhynchosauria, Allokotosauria, and Archosauriformes. Kuehneosauridae is recovered as the earliest divergence in Archosauromorpha. These values are presented on the strict consensus in Figure 5. This topology is also displayed in Figure 6, with node numbers added rather than support metrics.

We employed a number of constraint analyses to explore past hypotheses for the relationships of Drepanosauromorpha:

Forcing a sister relationship with Weigeltisauridae produced three MPTs and required 844 steps (CI = 0.374, RI = 0.621), one additional step relative to the unconstrained tree (strict consensus presented in Fig. 7). In the resultant consensus tree, the monophyletic Avicephalia clade forms the sister taxon of Sauria. Kuehneosauridae is the sister taxon to all other Archosauromorpha. In contrasts to Pritchard et al. (2015) and Nesbitt et al. (in press), there is no resolution among the major early archosauromorph lineages.

Forcing a sister relationship with Kuehneosauridae produced two MPTS that required 849 steps (CI = 0.372, RI = 0.617), six additional steps relative to the unconstrained tree (strict consensus presented in Fig. 8). In the resultant consensus tree, the topology of Archosauromorpha closely resembles that in Nesbitt et al. (in press). *Protorosaurus* is once again the sister taxon of all other Archosauromorpha. Kuehneosauridae is pulled out of Sauria into a monophyletic Avicephalia; Weigeltisauridae is the sister taxon to Drepanosauromorpha + Kuehneosauridae.

Forcing a sister relationship with *Protorosaurus* produced six MPTs that required 860 steps (CI = 0.367, RI = 0.609), 17 additional steps relative to the unconstrained tree (strict consensus presented in Fig. 9). The *Protorosaurus* + Drepanosauromorpha clade is the sister taxon to all other Archosauromorpha (Kuehneosauridae included). The clade of Weigeltisauridae + Lepidosauria is the sister group to Archosauromorpha. In contrast to Pritchard et al. (2015) and Nesbitt et al. (in press), there is no resolution among the major early archosauromorph lineages.

Forcing a sister relationship with Tanystropheidae produced four MPTs that required 862 steps (CI = 0.367, RI = 0.608), 19 additional steps relative to the unconstrained tree (strict consensus presented in Fig. 10). The topology of archosauromorphs more derived than Tanystropheidae is consistent with the strict consensus. *Protorosaurus* is the sister taxon to the Drepanosauromorpha + Tanystropheidae clade. In this topology, Weigeltisauridae shifted within Sauria, forming the earliest divergence from Archosauromorpha. Outside of Sauria, *Youngina* and a clade of *Hovasaurus* + *Thadeosaurus* form successive sister taxa to Sauria.

LITERATURE CITED

Benton MJ. (1985) Classification and phylogeny of the diapsid reptiles. Zool J Linn Soc 84:97–164.

Benton MJ. (1990) The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. Phil Trans Roy Soc B 328:213–306.

Berman DS, Reisz RR. (1992) *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. J Paleontology 66:1001–1009.

Bulanov VV, Sennikov AG. (2006) The first gliding reptiles form the Upper Permian of Russia. Paleontological Journal 40:S567–S570.

Bulanov VV, Sennikov AG. (2010) New data on the morphology of Permian gliding weigeltisaurid reptiles of eastern Europe. Paleontological Journal 44:682–694.

Caldwell MW. (1994) Developmental constraints and limb evolution in Permian and extant lepidosauromorph diapsids. J Vert Paleo 14:459–471.

Carroll RL. (1981) Plesiosaur ancestors from the Upper Permian of Madagascar. Phil Trans Roy Soc London B 293:315–383.

Carroll RL. (1985) A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Palaeont Abt A 189:1–28.

Cocude-Michel M. (1963) Les rhynchocéphales et les sauriens des Calcaires Lithographiques (Jurassique supérieur) D'Europe Occidentale. Ph.D. thesis, Université de Nancy.

Coddington J, Scharff N. (1994) Problems with zero-length branches. Cladistics 10:415–423.

Colbert EH. (1966) A gliding reptile from the Triassic of New Jersey. Am Mus Nov 2246:1–23.

Colbert EH. (1970) The Triassic gliding reptile *Icarosaurus*. Bull American Mus Nat History 143:85–142.

Colbert EH. (1989) The Triassic dinosaur *Coelophysis*. Bulletin of the Museum of Northern Arizona 57:1–160.

Colbert EH and Olsen PJ. (2001) A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). Am Mus Novitates 3334:1–24.

Conrad JL. (2004) Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). Zool J Linn Soc 141:399–434.

Conrad JL. (2006) Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). J Morph 267:769–775.

Conrad JL. (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology Bull Am Mus Nat History 310:1–182.

Cruickshank ARI. (1972) The proterosuchian thecodonts. *Studies in Vertebrate Evolution: Essays presented to F. R. Parrington*, eds KA Joysey, TS Kemp. (Winchester Press, New York).

Currie PJ. (1981) *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeontologia Africana 24:99–168.

DeBraga M, Rieppel O. (1997) Reptile phylogeny and the interrelationships of turtles. Zool J Linn Soc 120:281–354.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Proc Roy Soc B 353:501–541.

Estes R, deQueiroz K, Gauthier JA. (1988) Phylogenetic relationships within Squamata. Eds R Estes and G Pregill (Stanford University Press, Palo Alto), pp. 119–281.

Evans SE. (1980) The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool J Linn Soc 70:203–264.

Evans SE. (1981) The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. Zool J Linn Soc 73:81–116.

Evans SE. (1982). The gliding reptiles of the Upper Permian. Zool J Linn Soc 76:97–123.

Evans SE. (1986) The braincase of *Prolacerta broomi* (Reptilia: Triassic). N Jarh fur Geo Paleo 173:181–200.

Evans SE. (1987) The braincase of *Youngina capensis* (Reptilia: Diapsida; Permian). N Jahrb fur Geo Paleo Monats 193–203.

Evans SE. (1988) The early history and relationships of the Diapsida. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 221–260.

Evans SE. (2009) An early kuehneosaurids reptile from the Early Triassic of Poland. Palaeontologia Polonica 65:145–178.

Evans SE and Haubold H. (1987) A review of the Upper Permian genera *Coelurosauravus, Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). Zool J Linn Soc 90:275–303.

Ewer RF. (1965) The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil Trans Roy Soc B 248:379–435.

Ezcurra MD, Butler RI. (2015) Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early archosauriform radiation. Palaeontology 58:141–170.

Ezcurra MD, Scheyer TM, Butler RJ. (2014) The origin and early evolution of Sauria: the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS One 9:e89165.

Fraser NC, Rieppel O. (2006) A new protorosaur (Diapsida) from the upper Bundsandstein of the Black Forest, Germany. J Vert Paleo 26:866–871.

Gardner NM, Holliday CM, O'Keefe FR. (2010) The braincase of *Youngina capensis* (Reptilia, Diapsida): new insights from high-resolution CT scanning of the holotype. Palaeontologia Electronica 13: 16 pp.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, University of California Berkeley.

Gauthier JA, Estes R, de Queiroz K. (1988) A phylogenetic analysis of Lepidosauromorpha. *Phylogenetic Relationships of the Lizard Families*, eds R Estes, G Pregill (Stanford University Press, Stanford), pp. 15–98.

Goloboff PA, Farris JS, Nixon KC. (2008) TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Goodrich ES. (1942) The hind foot of *Youngina* and fifth metatarsal in Reptilia. J Anat 76:308–312.

Gottmann-Quesada A, Sander PM. (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. Palaeontographica Abteilung A 287:123–220.

Gow CE. (1975) The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeontologia Africana 18:89–131.

Gower DJ. (1996) The tarsus of erythrosuchid archosaurs, and implications for early diapsid phylogeny. Zool J Linn Soc 116:347–375.

Gower DJ. (1997) The braincase of the early archosaurian reptile *Erythrosuchus africanus*. J Zool Soc London 242:557–576.

Gower DJ. (2003) Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. Annal S Afr Mus 110:1–88.

Gower DJ, Weber E. (1998) The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. Biol Rev 73:367–411.

Gregory JT. (1945) Osteology and relationships of *Trilophosaurus*. University of Texas Publication 4401:273–359.

Klembara J, Welman J. (2009) The anatomy of the palatoquadrate in the Lower Triassic *Proterosuchus fergusi* (Reptilia, Archosauromorpha) and its morphological transformation within the archosauriform clade. Acta Zool 90:275–284.

Jiang D-Y, Rieppel O, Fraser NC, Motani R, Hao W-C, Tintori A, Sun Y-L, Sun Z-Y. (2011) New information on the protorosaurian reptile *Macrocnemus fuyuanensis* Li et al., 2007, from the Middle/Upper Triassic of Yunnan, China. J Vert Paleo 31:1230–1237.

Laurin M, Reisz RR. (1995) A reevaluaton of early amniote phylogeny. Zool J Linn Soc 113:165–223.

Li C, Zhao L, Wang L. (2007) A new species of *Macrocnemus* (Reptilia: Protorosauria) from the Middle Triassic of southwestern China and its palaeogeographical implication5. Sci in China D 50:1601–1605.

Maddison WP, Maddison DR. (2015) Mesquite: a modular system for evolutionary analysis. Version 3.02. http://mesquiteproject.org

Merck JA. (1997) A phylogenetic analysis of the euryapsid reptiles. Ph.D. thesis, University of Texas at Austin.

Modesto SP, Sues H-D. (2004) The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. Zool J Linn Soc 140:335–351.

Montefeltro FC, Langer MC, Schultz CL. (2010) Cranial anatomy of a new genus of hyperodapedontine rhynchosaur (Diapsida, Archosauromorpha) from the Upper Triassic of Brazil. Earth Env Sci Trans Roy Soc Edin 101:27–52.

Montefeltro FC, Bittencourt JS, Langer MC, Schultz CL. (2013) Postcranial anatomy of the hyperodapedontine rhynchosaur *Teyumbaita sulcognathus* (Azevedo and Schultz, 1987) from the Late Triassic of southern Brazil. J Vert Paleo 33:67–84.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Nesbitt SJ (2011) The early evolution of archosaurs: relationships and the origin of major clades. Bull American Mus Nat History 352:1–292.

Nesbitt SJ, Flynn JJ, Pritchard AC, Parrish JM, Ranivoharimanana L, Wyss A. (in press) Postcranial anatomy and relationships of *Azendohsaurus madagaskarensis*. Bull Am Mus Nat Hist.

Olsen PE. (1979) A new aquatic eosuchian from the Newark Supergroup (Late Triassic–Early Jurassic) of North Carolina and Virginia. Postilla 176:1–14.

Parks P. (1969) Cranial anatomy and mastication of the Triassic reptile *Trilophosaurus*. M.S. Thesis, University of Texas at Austin

Prendini L. (2001). Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. Sys Bio 50:290–300.

Prieto-Márquez A, Norell MA. (2011) Redescription of a nearly complete skull of *Plateosaurus* (Dinosauria: Sauropodomorpha) from the Late Triassic of Trossingen (Germany). Am Mus Novitates 3727:1–58.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2015). Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. Journal of Vertebrate Paleontology 35: e911186.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Special Publication of the Museum of Natural History, University of Kansas 7:1–74.

Renesto S. (1994a) *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. J Vert Paleo 14:38–52.

Renesto S. (1994b) The shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the upper Triassic (Norian) of northern Italy. Zool J Linn Soc 111:247–264.

Renesto S and Dalla Vecchia FM. (2005) The skull and lower jaw of the holotype of *Megalancosaurus preonensis* (Diapsida, Drepanosauridae) from the Upper Triassic of Italy. Riv Ital Paleo Stat 111:247–257.

Renesto S and Binelli G. (2006) *Vallesaurus cenensis* Wild, 1991, a drepanosaurid (Reptilia, Diapsida) from the Late Triassic of northern Italy. Riv Ital Paleo Stat 112:77–94

Robinson PGL. (1962) Gliding lizards from the upper Keuper of Great Britain. Proc Geol Soc London 1601:137–146.

Robinson PGL. (1967a) Triassic vertebrates from lowland and upland. Sci & Cult 33:169–173.

Robinson PGL. (1967b) The evolution of the Lacertilia. Problèms actuels de paléontologie (evolution des vertébrés). Colloques Internationaux du Centre National de la Récherche Scientifique 163:395–407.

Robinson PGL. (1975) The functions of the hooked fifth metatarsal in lepidosaurian reptiles. Colloque international C.N.R.S. 218:461–483.

Sen K. (2003) *Pamelaria dolichotrachela*, a new prolacertid reptile from the Middle Triassic of India. J Asia Earth Sci 21:663–681.

Senter PJ. (2004) Phylogeny of Drepanosauridae (Reptilia: Diapsida). Journal of Systematic Palaeontology 2:257–268.

Sues H-D. (2003) An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. Canadian Journal Earth Sci 40:635–649.

Vaughn PP. (1955) The Permian reptile *Araeoscelis* restudied. Bull Mus Comp Zool 113:305–467.

Young CC. (1936) On a new *Chasmatosaurus* from Sinkiang. Bull Geol Soc China 15:291–311.

Young CC. (1963) Additional remains of *Chasmatosaurus yuani* Young from Sinkiang, China. Vertebrate PalAsiatica 7:215–222.

TABLE 4.1 Phylogenetic data matrix employed to analyze the phylogenetic position of Drepanosauromorpha and the *Coelophysis* Quarry drepanosauromorph.

Petrolacosaurus kansasensis
0000--00000000010000000101000000200110011000000111010000000000010111000?0???1000
0001011-00000000000011-00000010?100000000100--0000-0001?000100010?010011000110
0?0100000-0-110000010?-100000000000-0-0?00100000?00-000010000000000-0-000000?00-0
10000?0-000000000000100000000?[0,1]0000000-000000000000?00

Uromastyx sp.
0000--00102-01100?101010-0???001021001---111-0-----01-11010-0101010010001100101101 0
01010100001---0-002100000000-1000000000000--1110-1011-11110001100100111001101011
10?11-10111100001000110000 1-1111100000100?00?0?-010010?00?000?0-0-00000010000000
0100-00000000000-000001002-00?0010000000000010101?

Azendohsaurus madagaskarensis
00111000001000000000010010-10010001110001?0010000110-?001?1?10111101-210111010100
1100011-00100000110001 1-1110001100001001001110--1100-1103-0111110011010101001 10
0000001111?1101100000001100 00?1101001010001100001 1001-0000001110[1,0]00000000110
011111100000000-0000000000000100001002-000?01-1000000?00011100?

Azendohsaurus laaroussii
00111-00??0????????
01100000110?0???
??????????????????????????11?0??????1-????????????????????????1?1????00????????????????
???????0????????????????????????0?

Trilophosaurus buettneri
00011001102-0000000201-0-1001101-[0,1]1000???111-0-----10?01111011?100111110001010 1
?10100001100010 0?12--120111000111000100101101 0--0000-1002?01110100110101011001 00
0000011110110110011011110001100100111 00?00100011000-10101110000000000000 1110110
11100010?0-00000?0000000000001001-000?01-10000000010111000

Trilophosaurus jacobsi
0?0???01002-000?000101??0100?101?11??0??0?1??????????????????????????????????01??0?0
0??11000100?12?-110???0001110001?01???????????0-??0????????0?11?10101100??00?00010
1101?1?100110111?0001100?????????0010-0???00-10?0?1?0?000000000?1110??01?1?1?00??
??0?000?0?0000??001?0??000?01-?000?00?010??????

Pamelaria dolichotrachela
??1???00?0??0???00?0?????10000001?1??01???100?011?????????00???1???2?????????01??0?
0100011000000101011-???00011000010010011?0--??00-??0??0?????0010?10101000????0000

1?1101????0011001110001 1??????010??????0?10?00-00000?001000000000???001????000000
?0-?0000000000000000?001-000?01-1000000?0001???0?

Spinosuchus caseanus
???
????????????110???00011100??001001100--?00??
?????????????????????????????????????101?0?????????????????0???????1??0???????????????
????????????0?01????????0??0??????

Prolacerta broomi
0001100010100001000 10[0,1]00-1000000111 1001-0110000111 1100[0,1]0111 1001101110110
0010100110101000101000011 10011-1110001100001000 00?100--000101[1,0]01??1001001100
10100-11????000010100100110011001110001100100 11100?0000000000-0001100000000000
000???00?101000110?0-000000??000000001002-0?0001-100000?000011 1001

Teraterpeton hrynewichorum
0001000110 1?000000001??0?1001101?01000???110?0000?????10?100010?0???11?00????00?
1000?0011000100?10?-11-?1101010?0001001????0???100????????111?00??????????????????
????????????????????????????????????01?0010?00-??0???1?1?????????????01??10?????0????
???000??0?????0???0???0??01??????0?0?10?1??0?

Protorosaurus speneri
0000--0000100000001101-??100000011 11001-0110???1??????10??000?0?????????????? 001?0
10?0001000000000?010-1110??1110001000001000--0000-?001??1?110001101010100?100000
00?????1?111101100??100000000001?1000?0100?0??00-?0001000000000000000000000000?
0?000-000000000000000001001?000001-100??00000011?000

Proterosuchus fergusi
0201100000101020000111-1011000002011 00[1,0]-0110000 1?1100-1011101111011111 12000?
?0011011?0001110000111 0010-1100101100000000??2?1110000101001 0?1001101100101010?
1?????000111?1111110010001110001100100 11100?01000100000-00010?00?000000000?0000
?0101000110?0-000000?0?00000000?001-??0?01-1000000?00011?10?

“Chasmatosaurus” yuani
0201100000101020000111-1?1100000201100 1-0110?0??????0??????????1?????????????00??0
11?0001110000?1100?1-????101??????00?0???010000?0-1001?0100?101110101 11100??00?00
010?1?111110011001110?011001??10100?0100010???0-?001100110000000001 1?000?101???1
10?0-0000000000?00000100??00??01-1000?00000011??0?

Youngina capensis
0000--000010000101000000101101000201 1100100000000111 1100000100?[0,1]0101100010110
0000??0?0?0001010000010 0010-??001000-0100000000000--000101001??111000?111101110?
0110001101010-1?111001100??1000000000000 10-0??0100000?00-00001?100000000-0000?010
?00-??0010?0-0000000000??000001000-000000-00000000000101001

Gephyrosaurus bridensis

0000--00002-01000110100001?010001110001-1110000110-100????0000?10110?000?????01?0
??0?0101000001-100010-00?0?000-00000?000?000--?11101111??111000010?11011?????????1
110011-10111?000010?01100?01????110??00000000?10-0111??01?000000-0-?1?????000100?
00?0-00??0??0?00-?0000??00-??0?00?1000100?00?10?01?

Mesosuchus browni
00112?00111-000010[0,1]11000-10010001111001-0110010110-20?1011100011011011000?0
100?011000001001000?100010-?1101011?000100110?000--0001011010?101100?110??101011
0000?100??1001111100110000100011001001100?00000000000-0001001000000000000000000
10000000000?0-00000000000?00000?00?-?00001-1000000?000111002

Rhynchosaurus articeps
02112010111-0000101101-0-1001010211100000111-?-----20?????????11001011100????11??0
?00001100100??10--10-??00?010011010001 1?000--?000-10010?1111101100101010110?00000
0?011111111001?-0??1000??00100101 00??0000100?00-0101001000000000000000000000??0
000?0-0000??00?00?00000?01?-000001-?00000?0000?1?002

Teyumbaita sulcognathus
02112010111-0000001201-0-1101010211?00000111-1-----201110110001 10????1?000???10011
00-001100100??10--11-??10001001?0000101?0?0--100????0??01????0110?10100-1??????????
???????????1010??10???????1?????????0000100?00-011???11????000???????00?00000?000???
????00???000????0??22-0?0?01-0?0?00??00??1?00?

Langobardisaurus pandolfii
1011?00???1?000?????????????0?000?11???1??1??????????????????????????????0?????01????0?
0?01000200?00?0121111 1?1111001?101????1?????01111030011110????010100-11?00?0100?
11111?111111101?0100?1?0011110111???1?0?1???0-?00000?000000?0???1??0000000??0??00
000000??00000?00000?00??0000?1-?00??0?0??0???000

Tanystropheus longobardicus
00111000001100000011001??1100000121100 1?0110000100-1001???0001010??001?00?1?100
??01010001000[0,2]001001011-111001111001?01101111011000-1101001111011110101 00-1
10000110011110111 11[1,0]01101000000 1000-11101111011 00010?00-10[1,0]100000000000?0
-1?000000100100 00?0-00000000000 1000000001?000001-100100?000001?000

Tanytrachelos ahynis
0011?000?01?00000000?01??1??0?0012???????11000???0-100???????0???????????????????0?
0?0?01000000?000012111110 1??10011?01????11?110?0-100?00?????1?11010100-11????1100
?11111111111110 1??0001??1??11?0111100?00?????0-?0001000?0000?00001??00?0?0??1???0
???00?000?0?00100?00?00??0000?1-?001?0?0000?????0

Macrocnemus bassanii
0011100010110001000111???1001000111?001?01100?0110-?????????????0??001?0?????01?1
01010?010100000?01011-1110?01110011000-???01?01001111010011110111101 0100-11?00?0
10011110111?1101101?010000?0010110100?00?00?00?00-?00?10000010000???0?000000000
1?000??????????????0??????0?????0001-1001?0?000011?000

Amotosaurus rotfeldensis
00?1??00??1?0????????????????000[1,0]?1??????1?01?0110-?0???????????0??201???????00??
??0???0100000???01001-11100?1110011?010?1?0???10011?10????????1?11010?????0????010
0???101?1?1001101??000???0?-101?111?01100?00?00-?0000000?010000?000???0?0?10?1?0?
0??????000?0000000?00?00??000001?10???0?00001?????

Erythrosuchus africanus
0001111000101020000111-111100000201100000010??0?????100001?111110010?112001??00
110111000111000010l-010-0?00001101000000012100--0000-100100111100?1001010101l???
??0001111111011001000010O??1000???1??00?011111010101010l?011?0100000000???01?10
0?00110?0-000?00?0000?00000??02-0?0?01-10?000??00011?100

Shinisaurus crocodilurus
0000--00101-01100?101000---??000021101?--110101000-01-1001000111010011000010101 11
100101010100001-000012100001000-1000000000000--1100-1011111110001100100111001101
01100010-1011100001000011010?1?001010000?1?0100100-000?001010000?0-0-10001010001
0000100-00100000000-000001002-0000-10000000?0000001010

Euparkeria capensis
0001110000101021000l?1-11110100021100000001l0?00110?100??1?1?11110?11?11210?0100
11011?0001110000101001l-010000100?00?000??2??1100000-??0??11??00??0???1?0-11????
?0001?11111??1?01-011100001100-1111100001011101010101011000001110110110001 00-00
??01?0???????00?0000?00?00?002-000001-1000?0?0000?1?100

Batrachotomus kupferzellensis
000101101010100000011l-0-100000020100000011 1-0---0-10010111010 11?001?1020?1??00?1
001000011100001 01-011-011000110[0,1]00110111210100 1000-??010011???0010010100010?
????0001011111011001-01?1001011?0-???110??0112110111020101 1?00?01110?1121?0?1?0-
00?10110?0-000000?000--00000??02-0?0?01-100000??01011?00?

Coelophysis bauri
0101-10000101000000111-0-101-0102110000001111?10-0-100100?1001110?0111?21?10100?
?0011000111000010l-011-111000111000100111110 0--1100-1001?01----011000-1000100011-
0001011110011000-01110[0,1]10---0-11100--00112010111020001?1001111111-1-1000001-00
010??0??????????????????????????0001-?00000?0010????0?

Plateosaurus engelhardti
0001-10000101000000111-0-101-0102110000001111?10-0-?00100?1001110001110[1,2]10101
00?100110001100000100-011-111000110000100111110 0--1100-1001?01?---011000-10001000
11-0001011110011?00-01110010---0-11100--0011201011102000100011111111-1-1000011-00
000110??????????????????????2???0001-100000?001011??0?

Macrocnemus fuyuanensis
0011100010110001001111-??1000000111000???110???11??????????????????????????????0???0
10?0?0101000???0?011-1110??1110011?00001001??10011110?00111??111??101?0-1000??01

0010110101111011010010000000101101000??01?0?0??00-?000?00000000?00000??0000000?1
?0?0???????????????0??????0?????0001-100??0?0000???000

Hovasaurus boulei
??????00?????00101??1001?1101000?1111????000???111110010??00?00001?0?1????????????
???0???0000??????11-000000???0000?00?01000??000??1?0???0110101111111111011100001
0?010-1?1110000?1??10000100000[1,0]10?00???????0?????00?10000000000001??00?00??00
???0?0-00000000?000000001000-0001000?000?000000?00??0

Thadeosaurus colcanapi
?????????????00??????????1???0???????????0?0??0110-?0????????0010110?1???????????010?
???????????????11-00?0?0?????????0000000??0000-10001?1?1?0011111111110011000010???
0-1?111000101??100??100000?10?00???????0?????100100000000?00?01??00?00?-?????0?0-0
0000000000000000010?0?00000?0?00??0000?0?????1

Coelurosauravus elivensis
??????00??2?00010?00100??0?00?00000?001?100??????????????????????0??0?1??????????????
????100000???0??11-0011?0?0?0000?00?0??00--110????02??00??00????11001000110??0?????
111?111?000?1??10???0??100000-??00?00?00???-?00??000????0?0-??????0?0??-?????0?0-000
?00?0001?0?001100??000?000001???0???1?0?00?

Coelurosauravus jaekeli
0000--00??2-0000?000100??1000000?0??0?????0?
0?000000??????0?????1????????????00??0?0???11?????02?????????????1?011?00110?0????????
??????00?01??10???????0000000??0??0?????0-?01??0?00?????0??????0000?0??????0?0-00???
?00?0????0?1100??00000??001???0???1?0?00?

***Rautiania* spp.**
0000--00????00????0?100??????0???00??01-100?????????????????????????????????00?1010?
0001000001-10?0???????????????????????????????0-????????????????1101100?????0?????????
?????????????????????????????0?0??0???0????0???00?????????????????0-????0?????????0??
???????1??0??00?????001???0????00?00?

Dolabrosaurus aquatilis
???
????????????11-????????????????????110??000-??01??????????????????????????????????????
????????00??100?10000-0???????????????111?????????00?01??????0??????????1111??0??1?0
1?10??1????0???0???????????0?????0

***Coelophysis* Quarry Drepanosaur**
??????00????0001010001-0-1001000000?0????001-?-----00-000000000000?010?011?0100????
0?0?1?????????????11-??1?0??????0100?????????????????1??????????????????????????????
?????????????????????????????00??0?001???00??????????????????????0-?????1????11????
?????????0???0???1?10?1???01??12?0?001?

Drepanosaurus unguicaudatus

??
???????????????????????????????0?001???10?0-??01-??????2?1????0???00??0?-1200010-?011
10000????100??10?000000-0???????????????11100?00?0??00?01??10?-0????????11011111211
1?101110?01????111??0?100?111120?????0

Hypuronector limnaios
???0???
1?00000?????-11-???????????????????01???100??1101-?11???0111??????????????120???0-001
111000???????????????????????????????????0??100???00?????????0?1?0???????00-01100??0?
11??000???????01?10????0?0?0010??????

Icarosaurus siefkeri
??????001010000100011?????000000021?0????1100?01?????0????????0111?210???????00???
?0???010000???000011-??10??1000001?000?1?1???1000-100???1????1?1?0110?0??1?????100
?????1?1??0?0?01????????????????????0100?00?00-?111??0000000?????????00??0010?0?0???
????00?000?????10??0211?0?011?00???00?00?1??0?

Kuehneosaurus sp.
0011100010100001000111-??1?00000021??1???110??01111?0????110?0011112?110?????0?1
1100?0001000001-100011-???000100000010000111?10??000-100????1???0?11?1100100??????
1001010-10????1000100?0???????????0???0??00?00????1111??00?0000?????????01??00?01?1
0???????01???00??0?10??0211?0?0111000000?00011?00?

Megalancosaurus preonensis
000???00??1?00110?00?1-??1???00000???????0???????????????????????????????????00??0?0?
0?0100?0???0??011-??1?0????000100000??10??100???01????????2?11???????00??0??120???0
??????00??????1001?1???00000?00?0??0?????0-?0??100?0?0???00?01??10?100????0?1111111
1120001??1010001????1111??0000?001020?0???0

Vallesaurus cenensis
0000--00??1?00??0?0?????????000000???00????0?
0?0100000?????01????1?0??--??????000??00??10?????01-?1????2?11????????11?0001?0?????
??1???0001???10???0??1???00-0?????0?????0-?1??1010000???????1??10?1?0??????100-01101
100001??010011???0010?0??0???0?1020????00

FIG. 4-1. Simplified cartoons of past phylogenetic hypotheses for the interrelationships of Neodiapsida. A) Derived from strict consensus of analysis with ordering of multistate characters from Dilkes (1998:Fig. 24c), B) Derived from strict consensus of analysis from Senter (2004:Fig 1), C) Derived from strict consensus of analysis from Müller (2004:Fig. 1). Outlines drawn from illustrations by Knob Tamura taken from Wikimedia.org

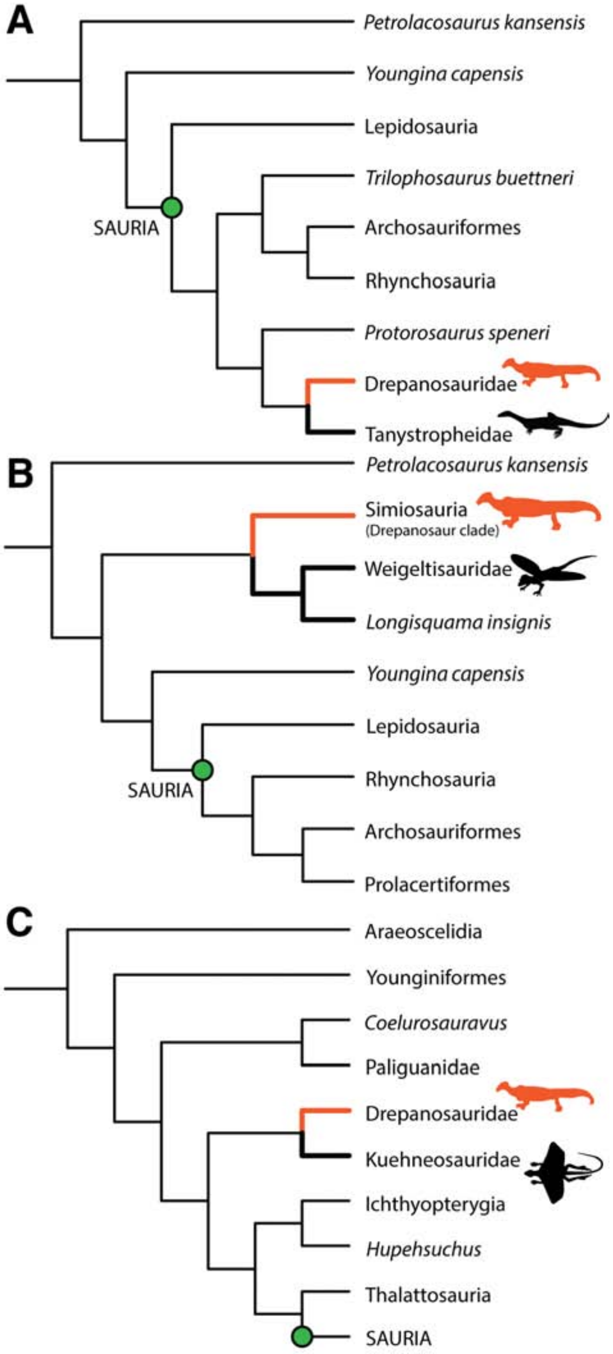

A
Petrolacosaurus kansensis
Youngina capensis
Lepidosauria
Trilophosaurus buettneri
SAURIA
Archosauriformes
Rhynchosauria
Protorosaurus speneri
Drepanosauridae
Tanystropheidae
B
Petrolacosaurus kansensis
Simiosauria
(Drepanosaur clade)
Weigeltisauridae
Longisquama insignis
Youngina capensis
Lepidosauria
SAURIA
Rhynchosauria
Archosauriformes
Prolacertiformes
C
Araeoscelidia
Younginiformes
Coelurosauravus
Paliguanidae
Drepanosauridae
Kuehneosauridae
Ichthyopterygia
Hupehsuchus
Thalattosauria
SAURIA

FIG. 4-2. A) Photograph of AMNH FARB 30834 in dorsal view. Skull elements exposed on the block have been outlined and shaded due to the poor contrast between the color of the matrix and the color of the bones. B) Three-dimensional model of the cranium and mandible of AMNH FARB 30834 in dorsal view, reconstructed using Avizo 7.1. Reconstruction parameters may be found in the electronic supplement.

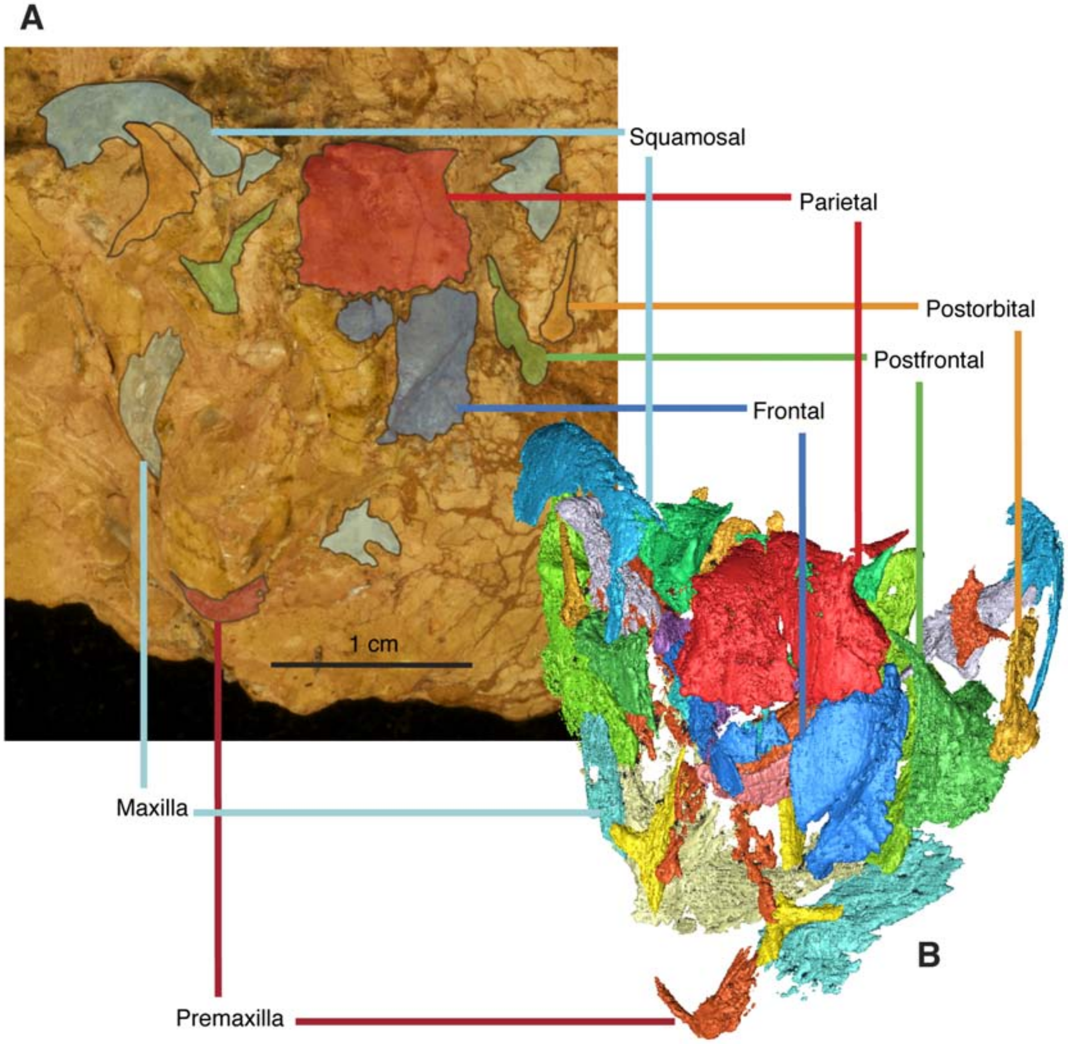

A
Squamosal
Parietal
Postorbital
Postfrontal
Frontal
1 cm
Maxilla
B
Premaxilla

FIG. 4-3. Cartoon illustration of the skull of Drepanosauridae n. gen., n. sp. in A) left lateral and B) dorsal views. Dashed outlines indicate possible outlines of the skull based on broken surfaces of AMNH FARB 30834 and comparisons with *Vallesaurus cenensis* (MCSNB 4751) and *Megalancosaurus preonensis* (MFSN 1769). Cartoon illustration of the braincase of Drepanosauridae n. gen., n. sp. in C) posterior, B) right lateral, and D) anterior views. Abbreviations: **be**, basioccipital-exoccipital; **de**, dentary; **fr**, frontal; **pa**, parietal; **pbs**, parabasisphenoid; **pd**, postdentary complex; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pr**, prootic; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal.

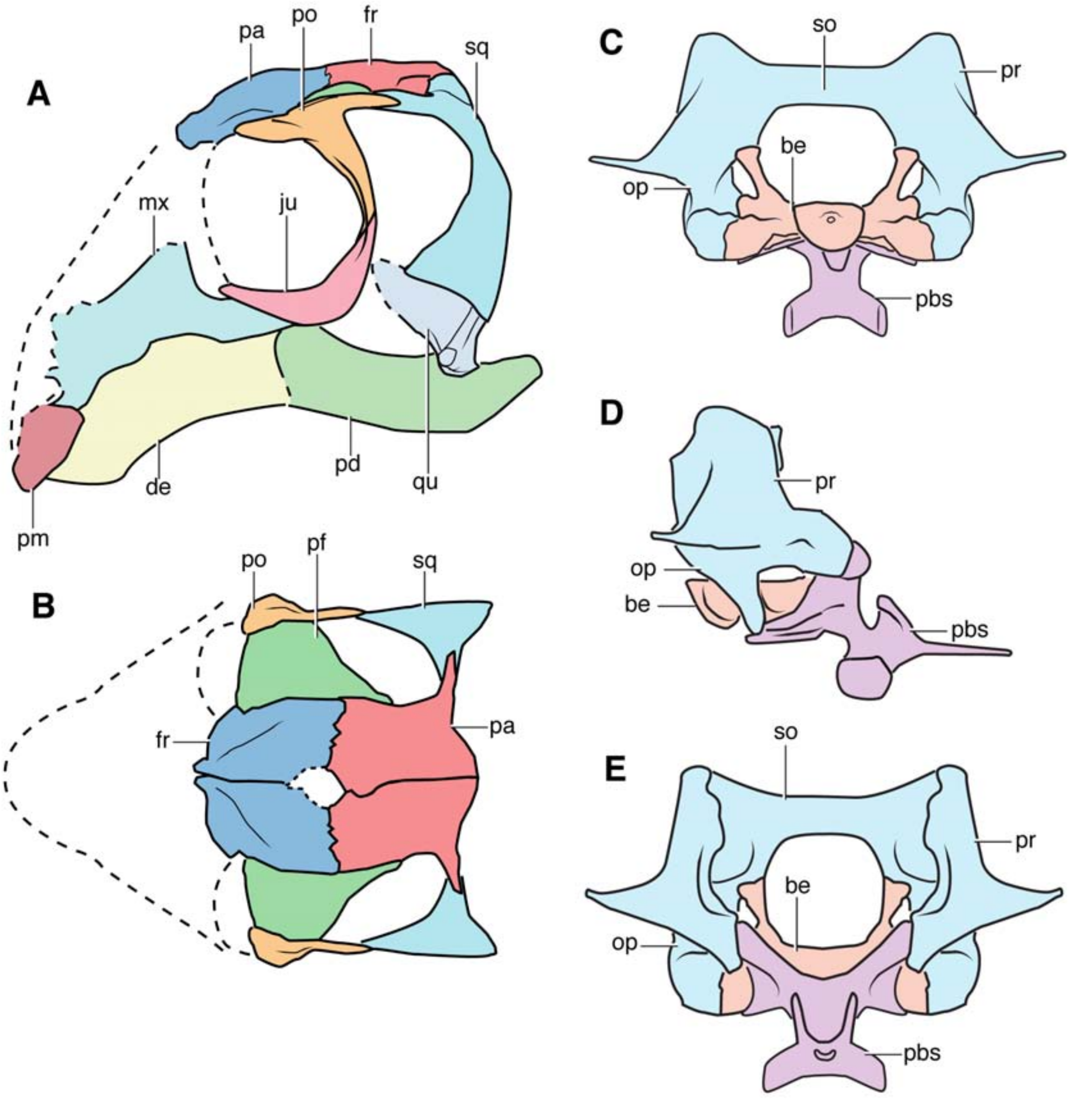

A
pa
po
fr
sq
mx
ju
pm
de
pd
qu
B
po
pf
sq
fr
pa
C
so
pr
be
op
pbs
D
pr
op
be
pbs
E
so
pr
be
op
pbs

FIG. 4-4. Stratigraphically calibrated strict consensus phylogeny of Neodiapsida recovered in this analysis. Ellipses indicate the likely stratigraphic range known in an included taxon. Solid lines indicate ghost lineages that are required by this topology. Dashed lines indicate possible ghost lineages whose presence is equivocal due to polytomies. Red line indicates the Permian-Triassic boundary.

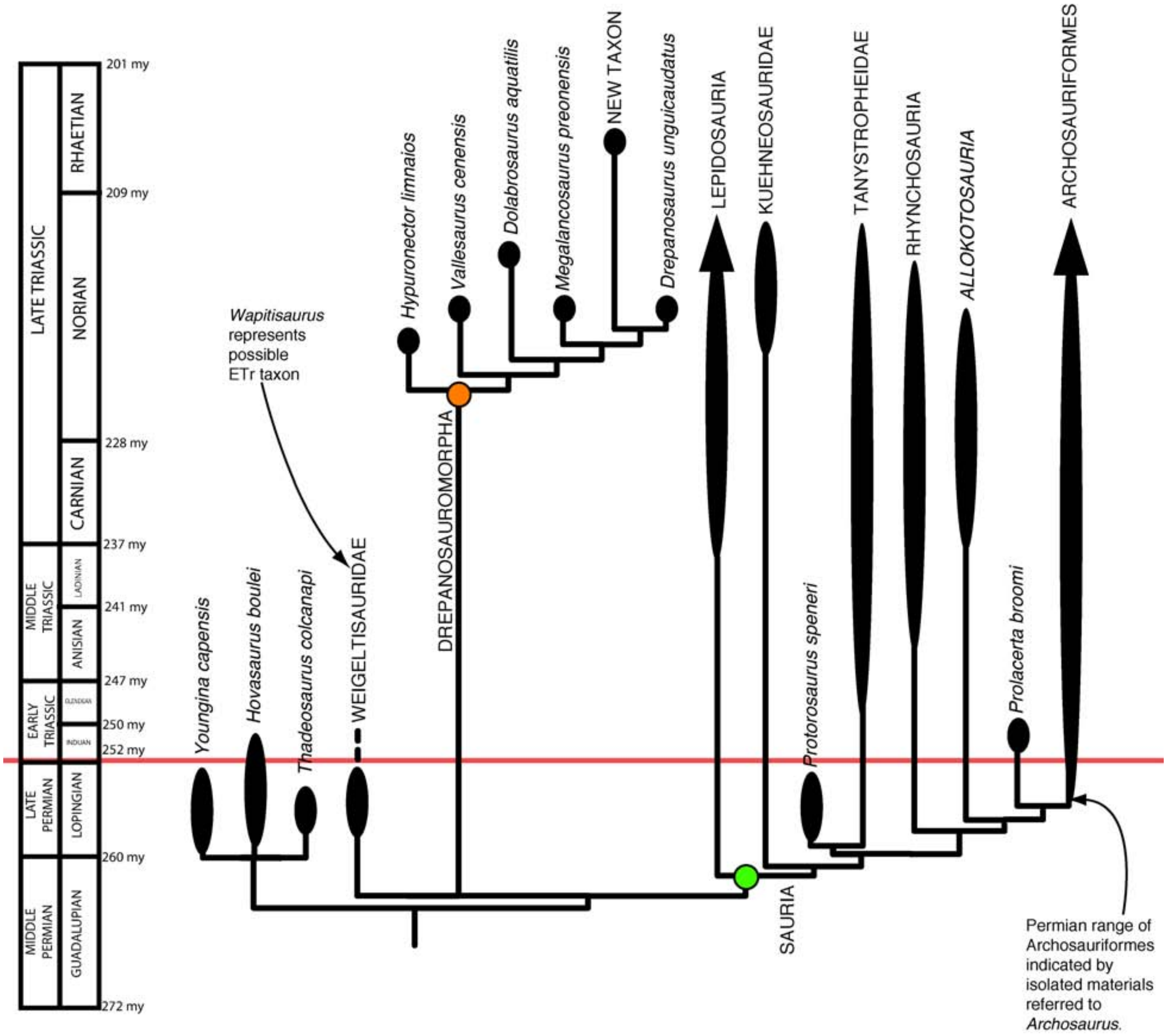

MIDDLE PERMIAN
GUADALUPIAN
LATE PERMIAN
LOPINGIAN
EARLY TRIASSIC
INDUAN
OLENEKIAN
MIDDLE TRIASSIC
ANISIAN
LADINIAN
LATE TRIASSIC
CARNIAN
NORIAN
RHAETIAN
272 my
260 my
252 my
250 my
247 my
241 my
237 my
228 my
209 my
201 my
Youngina capensis
Hovasaurus boulei
Thadeosaurus colcanapi
WEIGELTISAURIDAE
Wapitisaurus represents possible ETr taxon
DREPANOSAUROMORPHA
Hypuronector limnaios
Vallesaurus cenensis
Dolabrosaurus aquatilis
Megalancosaurus preonensis
NEW TAXON
Drepanosaurus unguicaudatus
LEPIDOSAURIA
KUEHNEOSAURIDAE
SAURIA
Protorosaurus speneri
TANYSTROPHEIDAE
RHYNCHOSAURIA
ALLOKOTOSAURIA
Prolacerta broomi
ARCHOSAURIFORMES
Permian range of Archosauriformes indicated by isolated materials referred to Archosaurus.

FIG. 4-5. Strict consensus of the primary phylogenetic analysis in this study. The number above the node indicates the frequency difference value recovered from the Jackknife analysis. The number below the node represents the Bremer support value.

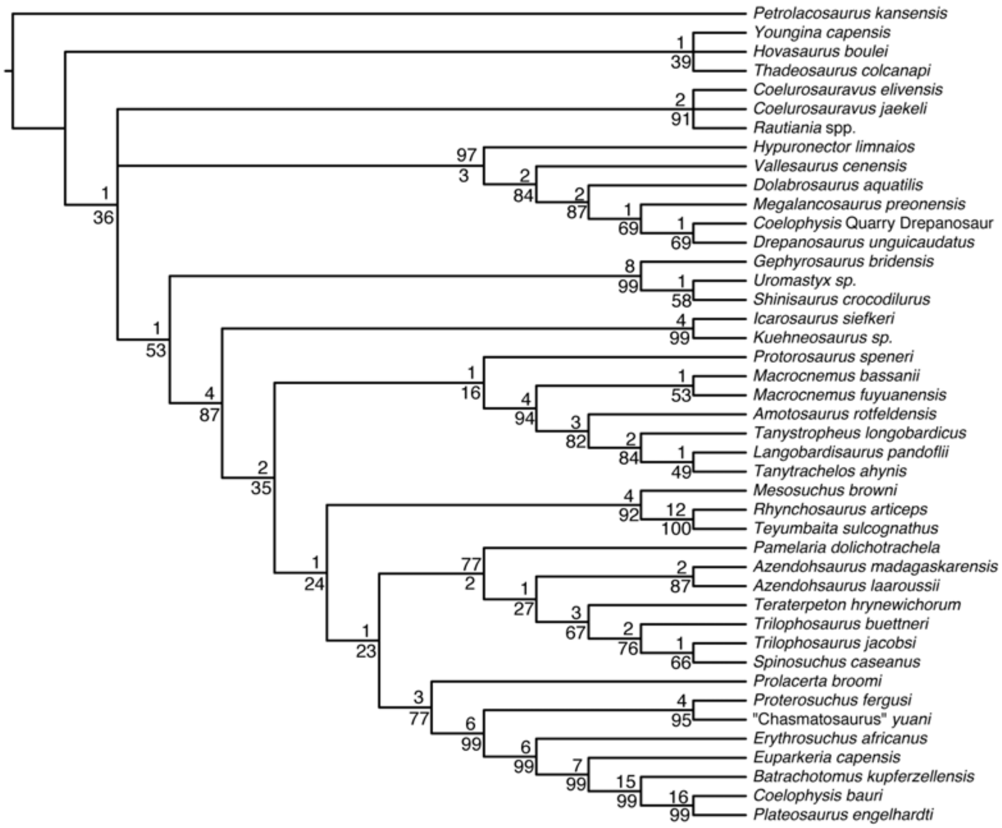

Petrolacosaurus kansensis
Youngina capensis
Hovasaurus boulei
Thadeosaurus colcanapi
Coelurosauravus elivensis
Coelurosauravus jaekeli
Rautiania spp.
Hypuronector limnaios
Vallesaurus cenensis
Dolabrosaurus aquatilis
Megalancosaurus preonensis
Coelophysis Quarry Drepanosaur
Drepanosaurus unguicaudatus
Gephyrosaurus bridensis
Uromastyx sp.
Shinisaurus crocodilurus
Icarosaurus siefkeri
Kuehneosaurus sp.
Protorosaurus speneri
Macrocnemus bassanii
Macrocnemus fuyuanensis
Amotosaurus rotfeldensis
Tanystropheus longobardicus
Langobardisaurus pandoflii
Tanytrachelos ahynis
Mesosuchus browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
Pamelaria dolichotrachela
Azendohsaurus madagaskarensis
Azendohsaurus laaroussii
Teraterpeton hrynewichorum
Trilophosaurus buettneri
Trilophosaurus jacobsi
Spinosuchus caseanus
Prolacerta broomi
Proterosuchus fergusi
"Chasmatosaurus" yuani
Erythrosuchus africanus
Euparkeria capensis
Batrachotomus kupferzellensis
Coelophysis bauri
Plateosaurus engelhardti
1
39
2
91
97
3
2
84
2
87
1
69
1
69
1
36
8
99
1
58
1
53
4
99
4
87
1
16
1
53
4
94
3
82
2
84
1
49
2
35
4
92
12
100
1
24
77
2
2
87
1
27
3
67
2
76
1
66
1
23
3
77
4
95
6
99
6
99
7
99
15
99
16
99

FIG. 4-6. Strict consensus of the primary phylogenetic analysis in this study. The numbers associated with each node represent node numbers assigned by TNT 1.1.

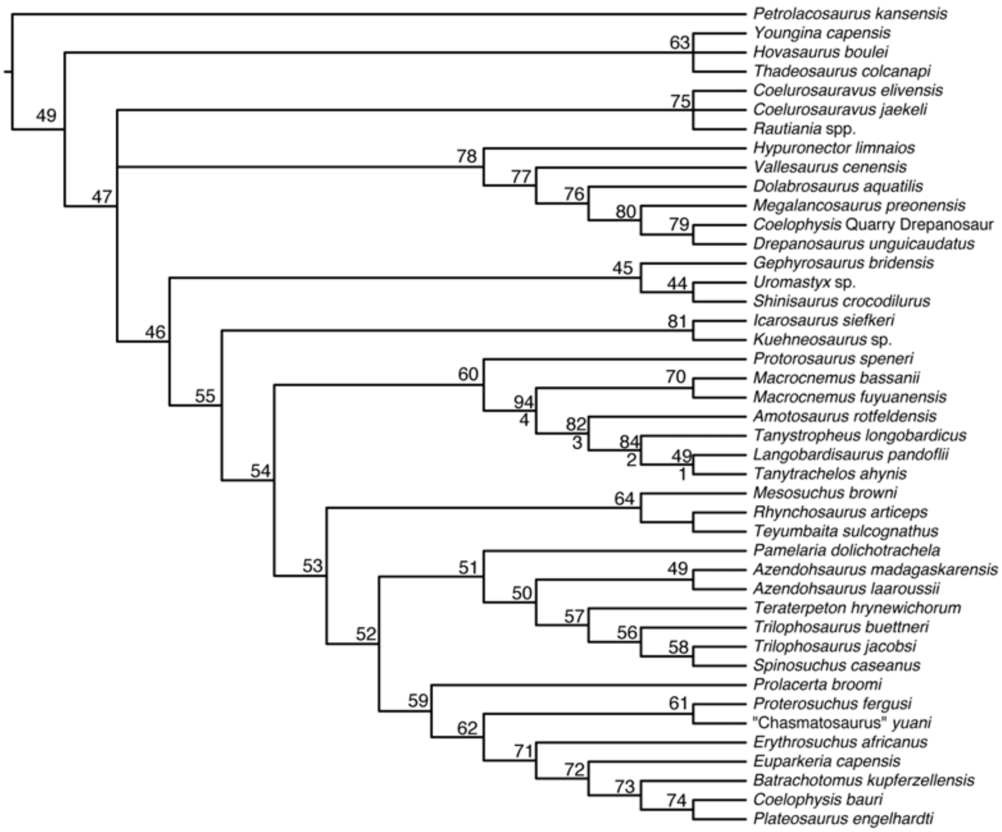

Petrolacosaurus kansensis
63
Youngina capensis
Hovasaurus boulei
Thadeosaurus colcanapi
49
75
Coelurosauravus elivensis
Coelurosauravus jaekeli
Rautiania spp.
78
Hypuronector limnaios
77
Vallesaurus cenensis
47
76
Dolabrosaurus aquatilis
80
Megalancosaurus preonensis
79
Coelophysis Quarry Drepanosaur
Drepanosaurus unguicaudatus
45
Gephyrosaurus bridensis
44
Uromastyx sp.
Shinisaurus crocodilurus
81
Icarosaurus siefkeri
46
Kuehneosaurus sp.
Protorosaurus speneri
60
70
Macrocnemus bassanii
55
Macrocnemus fuyuanensis
94
4
82
Amotosaurus rotfeldensis
3
84
Tanystropheus longobardicus
2
49
Langobardisaurus pandoflii
1
Tanytrachelos ahynis
54
64
Mesosuchus browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
Pamelaria dolichotrachela
51
49
Azendohsaurus madagaskarensis
53
Azendohsaurus laaroussii
50
Teraterpeton hrynewichorum
57
56
Trilophosaurus buettneri
52
58
Trilophosaurus jacobsi
Spinosuchus caseanus
Prolacerta broomi
59
61
Proterosuchus fergusi
"Chasmatosaurus" yuani
62
71
Erythrosuchus africanus
72
Euparkeria capensis
73
Batrachotomus kupferzellensis
74
Coelophysis bauri
Plateosaurus engelhardti

FIG. 4-7. Strict consensus phylogeny from an analysis enforcing a sister group relationship between Drepanosauromorpha and Weigeltisauridae.

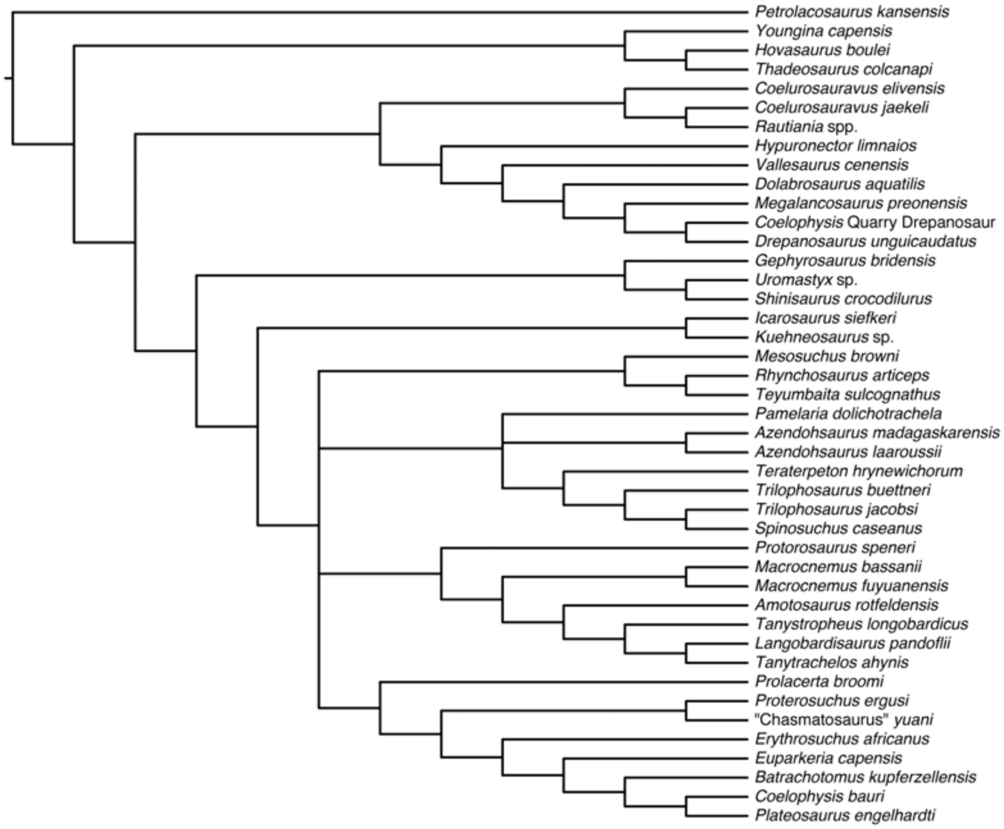

Petrolacosaurus kansensis
Youngina capensis
Hovasaurus boulei
Thadeosaurus colcanapi
Coelurosauravus elivensis
Coelurosauravus jaekeli
Rautiania spp.
Hypuronector limnaios
Vallesaurus cenensis
Dolabrosaurus aquatilis
Megalancosaurus preonensis
Coelophysis Quarry Drepanosaur
Drepanosaurus unguicaudatus
Gephyrosaurus bridensis
Uromastyx sp.
Shinisaurus crocodilurus
Icarosaurus siefkeri
Kuehneosaurus sp.
Mesosuchus browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
Pamelaria dolichotrachela
Azendohsaurus madagaskarensis
Azendohsaurus laaroussii
Teraterpeton hrynewichorum
Trilophosaurus buettneri
Trilophosaurus jacobsi
Spinosuchus caseanus
Protorosaurus speneri
Macrocnemus bassanii
Macrocnemus fuyuanensis
Amotosaurus rotfeldensis
Tanystropheus longobardicus
Langobardisaurus pandoflii
Tanytrachelos ahynis
Prolacerta broomi
Proterosuchus ergusi
"Chasmatosaurus" yuani
Erythrosuchus africanus
Euparkeria capensis
Batrachotomus kupferzellensis
Coelophysis bauri
Plateosaurus engelhardti

FIG. 4-8. Strict consensus phylogeny from an analysis enforcing a sister group relationship between Drepanosauromorpha and Kuehneosauridae.

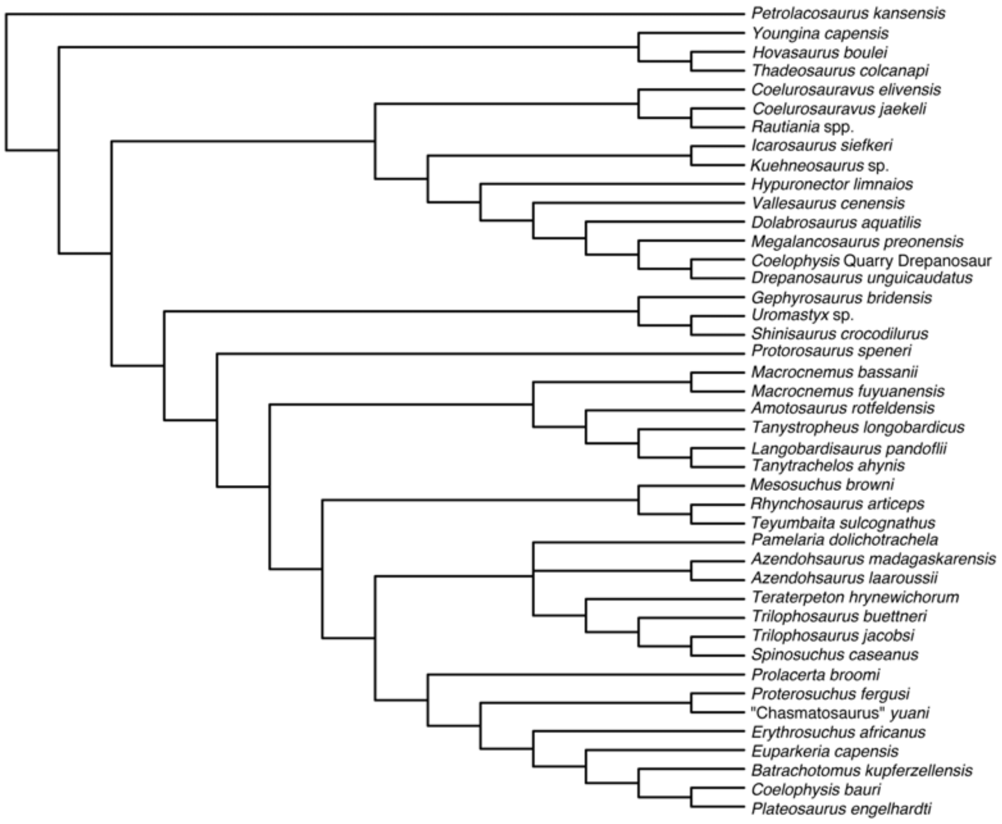

Petrolacosaurus kansensis
Youngina capensis
Hovasaurus boulei
Thadeosaurus colcanapi
Coelurosauravus elivensis
Coelurosauravus jaekeli
Rautiania spp.
Icarosaurus siefkeri
Kuehneosaurus sp.
Hypuronector limnaios
Vallesaurus cenensis
Dolabrosaurus aquatilis
Megalancosaurus preonensis
Coelophysis Quarry Drepanosaur
Drepanosaurus unguicaudatus
Gephyrosaurus bridensis
Uromastyx sp.
Shinisaurus crocodilurus
Protorosaurus speneri
Macrocnemus bassanii
Macrocnemus fuyuanensis
Amotosaurus rotfeldensis
Tanystropheus longobardicus
Langobardisaurus pandoflii
Tanytrachelos ahynis
Mesosuchus browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
Pamelaria dolichotrachela
Azendohsaurus madagaskarensis
Azendohsaurus laaroussii
Teraterpeton hrynewichorum
Trilophosaurus buettneri
Trilophosaurus jacobsi
Spinosuchus caseanus
Prolacerta broomi
Proterosuchus fergusi
"Chasmatosaurus" *yuani*
Erythrosuchus africanus
Euparkeria capensis
Batrachotomus kupferzellensis
Coelophysis bauri
Plateosaurus engelhardti

FIG. 4-9. Strict consensus phylogeny from an analysis enforcing a sister group relationship between Drepanosauromorpha and *Protorosaurus speneri*.

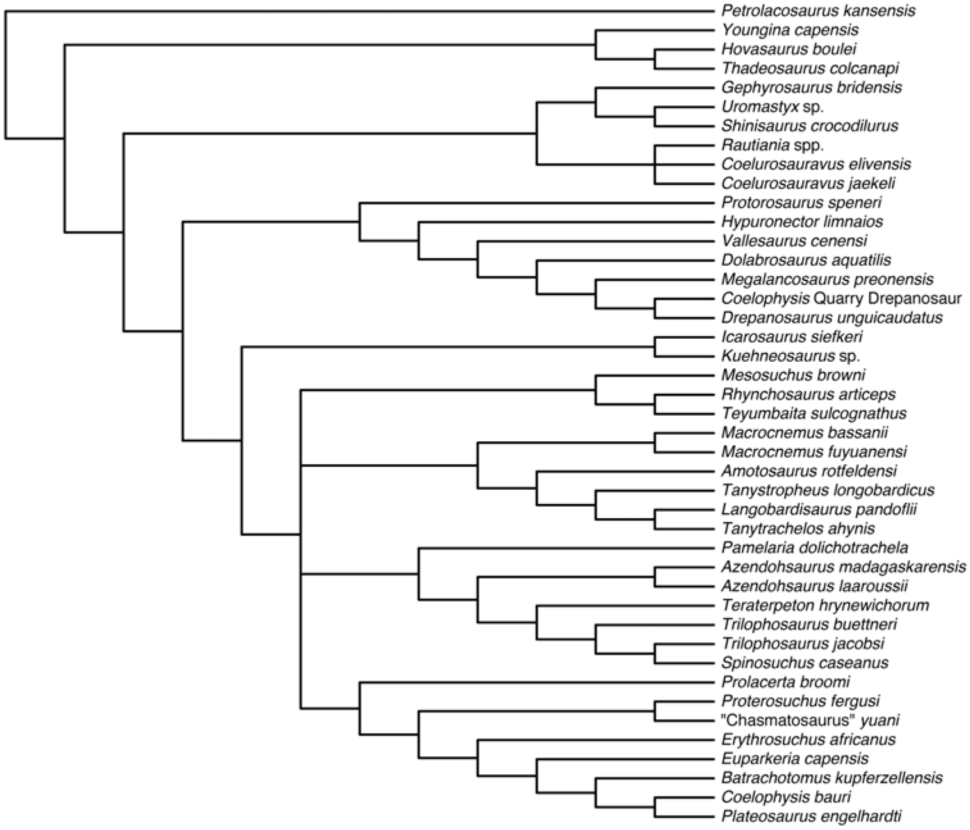
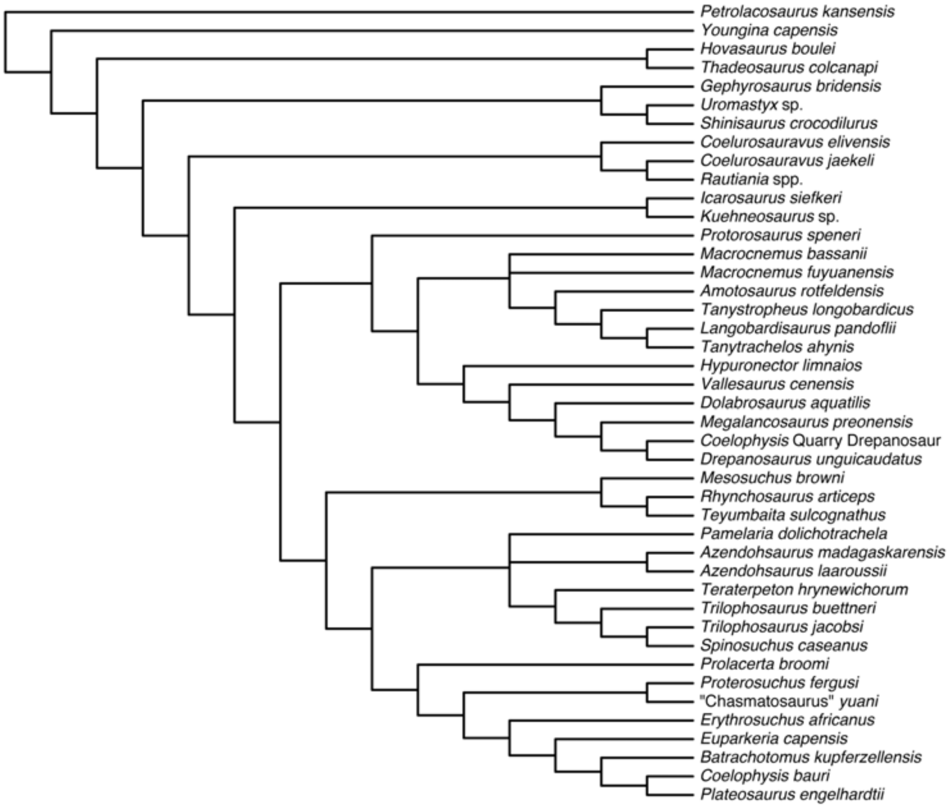

Petrolacosaurus kansensis
Youngina capensis
Hovasaurus boulei
Thadeosaurus colcanapi
Gephyrosaurus bridensis
Uromastyx sp.
Shinisaurus crocodilurus
Rautiania spp.
Coelurosauravus elivensis
Coelurosauravus jaekeli
Protorosaurus speneri
Hypuronector limnaios
Vallesaurus cenensi
Dolabrosaurus aquatilis
Megalancosaurus preonensis
Coelophysis Quarry Drepanosaur
Drepanosaurus unguicaudatus
Icarosaurus siefkeri
Kuehneosaurus sp.
Mesosuchus browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
Macrocnemus bassanii
Macrocnemus fuyuanensi
Amotosaurus rotfeldensi
Tanystropheus longobardicus
Langobardisaurus pandoflii
Tanytrachelos ahynis
Pamelaria dolichotrachela
Azendohsaurus madagaskarensis
Azendohsaurus laaroussii
Teraterpeton hrynewichorum
Trilophosaurus buettneri
Trilophosaurus jacobsi
Spinosuchus caseanus
Prolacerta broomi
Proterosuchus fergusi
"Chasmatosaurus" *yuani*
Erythrosuchus africanus
Euparkeria capensis
Batrachotomus kupferzellensis
Coelophysis bauri
Plateosaurus engelhardti

FIG. 4-10. Strict consensus phylogeny from an analysis enforcing a sister group relationship between Drepanosauromorpha and Tanystropheidae.


Petrolacosaurus kansensis
Youngina capensis
Hovasaurus boulei
Thadeosaurus colcanapi
Gephyrosaurus bridensis
Uromastyx sp.
Shinisaurus crocodilurus
Coelurosauravus elivensis
Coelurosauravus jaekeli
Rautiania spp.
Icarosaurus siefkeri
Kuehneosaurus sp.
Protorosaurus speneri
Macrocnemus bassanii
Macrocnemus fuyuanensis
Amotosaurus rotfeldensis
Tanystropheus longobardicus
Langobardisaurus pandoflii
Tanytrachelos ahynis
Hypuronector limnaios
Vallesaurus cenensis
Dolabrosaurus aquatilis
Megalancosaurus preonensis
Coelophysis Quarry Drepanosaur
Drepanosaurus unguicaudatus
Mesosuchus browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
Pamelaria dolichotrachela
Azendohsaurus madagaskarensis
Azendohsaurus laaroussii
Teraterpeton hrynewichorum
Trilophosaurus buettneri
Trilophosaurus jacobsi
Spinosuchus caseanus
Prolacerta broomi
Proterosuchus fergusi
"Chasmatosaurus" yuani
Erythrosuchus africanus
Euparkeria capensis
Batrachotomus kupferzellensis
Coelophysis bauri
Plateosaurus engelhardtii

Chapter 5

Cranial and mandibular osteology of Drepanosauridae (Diapsida, Reptilia)

ABSTRACT— Drepanosauromorphs are a poorly understood radiation of Triassic diapsid reptiles, known large from badly crushed skeletons from northern Italy. As a consequence, their osteology is extremely poorly understood, especially the cranial and mandibular skeletons, such that great ambiguity exists as to the anatomy of the skull. Herein, I describe the cranial osteology of Drepanosauridae n. gen., n. sp. from the Upper Triassic *Coelophysis* Quarry of New Mexico ("upper siltstone member," Chinle Formation). The specimen is preserved in three dimensions, although only a small portion of the skull roof has been exposed due to the friability of the specimen. The specimen is unique among Triassic reptiles in that it combines extremely plesiomorphic diapsid features (e.g., an *Araeoscelis*-like suspensorium, massive stapes) with highly apomorphic conditions (e.g., edentulousness, a massive and inflated endocranium, large and frontated orbits). Comparison with past reconstructions of drepanosauromorph skulls show similarities in the elongate, tapered rostrum and inflated endocranium. However, the reconstruction of the suspensorium in other taxa is extremely different, suggesting either high diversity in cranial anatomy or inaccurate interpretation of materials.

INTRODUCTION

Drepanosauromorpha is a clade of small-bodied diapsid reptiles known exclusively from Upper Triassic deposits on the Euramerica continent. Available skeletal material for the group is often articulated and nearly complete (e.g., the holotypes of *Drepanosaurus unguicaudatus*, MCSNB 5728, and *Vallesaurus cenensis*, MCSNB 4751), but badly crushed and distorted. As a consequence, little is known about the three dimensional osteology of the taxon, obscuring our understanding of the phylogenetic affinities and functional morphology of the group.

The skull is the most poorly understood aspect of drepanosauromorph anatomy. Only three specimens are known with articulated cranial materials and four from the mandibular materials respectively. The most complete skulls for the group belong to the holotype specimens of *Megalancosaurus preonensis* (MFSN 1769) and *Vallesaurus cenensis* (MCSNB 4751) respectively. A partial skull roof is preserved with another specimen of *Megalancosaurus preonensis* (MPUM 8437) and two isolated mandibles have been referred to *Hypuronector limnaios* (Colbert and Olsen, 2001).

The specimens of the *Megalancosaurus* skull have been the most three-dimensionally preserved skull material available. The holotype (MFSN 1769) is preserved as part and counterpart on two matrix slabs. The plane of the section cut through the midline of the skull, such the medial surfaces of the lateral skull elements are preserved on both slabs. Interpretations of these poorly preserved specimens have been offered by Calzavara et al. (1980), Renesto (1994a), and Renesto and Dalla Vecchia (2005). The first two attempts suggested the presence of an antorbital fenestra and a postorbital region similar to that of other diapsids (e.g., *Youngina capensis*). However, a specimen of the skull roof in *Megalancosaurus* (MPUM 8437) described by Renesto and Dalla Vecchia (2005) and reinterpretation of the holotype, suggested that the posterior portion of the skull was strongly convex and that the endocranial region was inflated. However, major details of the dermatocranial sutures and the anatomy of the palate and braincase remain unknown with the available specimens.

Three-dimensional specimens of drepanosauromorph vertebrae and appendicular elements have been described from Upper Triassic fissure fills in Europe (e.g., Renesto and Fraser, 2003; Fraser and Renesto, 2005) and from sites in western North America (e.g., Harris and Downs, 2002; Renesto et al., 2009, 2010), suggesting the possibility for three-dimensionally preserved skulls. Herein, I describe just such a specimen from the *Coelophysis* Quarry of New Mexico. The skull is three-dimensionally preserved, but extremely fragile. As such, the description centers around a three-dimensional reconstruction of the skull based on CT scan data. This study presents an enormous amount of new comparative data on the construction of the drepanosauromorph cranium and mandible.

MATERIALS AND METHODS

The specimen was discovered and prepared away from the matrix surrounding the holotype of the shuvosaurid archosaur *Effigia okeefae* by SJ Nesbitt. Nesbitt exposed the skull roof, right suspensorium, and a small portion of the rostrum. He found that mechanical preparation posed a danger to the specimen due to the extreme friability of the individual skull elements. As such, nearly all of the description below is based on three-dimensional models constructed using CT scan data of AMNH FARB 30834. The specimen was scanned at the Shared Materials and Instruments Facilities at Duke University with assistance from J. Thostenson. The final scan had a resolution of 0.0448 millimeters for a total of 1,998 slices (190 kV, 78 mA).

The individual skull elements preserved within AMNH FARB 30834 present as variably radiopaque structures within the matrix, which appear invested with radiopaque minerals. There is a substantial variation in the contrast values between certain elements. Figure 1A illustrates elements of the braincase that exhibit high contrast relative to the surrounding matrix. Figure 1B illustrates the parietal bone, which is clearly visible on the surface of the fossil, but appears only vaguely offset in contrast from the surrounding matrix. Each element was individually segmented using the "Segmentation Editor" tool in Avizo 7.1.1. Initial reconstruction a mixture of the "Magic Wand" and "Paintbrush" tools. For the latter tool, I employed the "Limited Range" option to highlight only these distinct regions. I note in the description to follow where I encountered ambiguity regarding the boundaries of individual bones.

To construct the three-dimensional models used to illustrate the cranial elements, I employed the "Grow Volume" option in Avizo 7.1.1 for an initial smoothing of the segmented cranial elements. I then used the "Generate Surface" option (Smoothing extent=5) to produce the individual models. Each model was imaged in the cardinal directions in the GLC Player v. 2.3.0.

DESCRIPTION

Premaxilla

A portion of the premaxilla is preserved (Fig. 2), in partial articulation with the left maxilla. The small fragment is difficult to interpret, and the dorsal margin of the bone is heavily chipped and broken. The ventral margin of the bone remains embedded in the matrix and is well preserved.

We identify the embedded portion of the premaxilla as the ventral margin due to the transversely narrow, blade-like surface (Fig. 2A). This corresponds well to the transversely slender distal (occlusal?) margin of the maxilla (see below). In dorsal view, the premaxillary fragment appears "J"-shaped, with an elongate portion preserving the distal margin and a smaller, medially directed element (Fig. 2B). We reconstruct this small portion as a part of the right premaxilla. There is no clear separation between these bones in the CT scans, suggesting that the premaxilla may be a fused, compound bone (Fig. 2C).

Posteriorly, the left portion of the premaxilla preserves a forked structure that appears to have met the anterior margin of the maxilla (Fig. 2A). This fork exhibits dorsal and ventral prongs. The body of the premaxilla is roughly triangular in a transverse section, with a prominent, laterally positioned ridge. Ventrally, the bone exhibits the ventrally convex, transversely narrow distal surface that corresponds well with the maxilla (Fig. 2D).

The medial surface of the left half of the premaxilla is complex. The dorsal half is transversely thicker than the ventral half, which exhibits a prominent medial depression. This depression produces the transversely narrow distal surface of the premaxilla.

Comparisons

The premaxilla of Drepanosauridae n. gen., n. sp. differs from nearly all other Permo-Triassic diapsids in the complete absence of teeth. Both of the drepanosauromorphs known from complete rostra (*Megalancosaurus preonensis*, MFSN 1769; *Vallesaurus cenensis*, MCSNB 4751) exhibit teeth in their premaxillae. *V. cenensis* exhibits small, subtriangular teeth, substantially smaller than those in the maxilla. The premaxillary teeth of *M. preonensis* are proportionally smaller, but similar in shape. Premaxillary teeth are otherwise absent only in *Teraterpeton hrynewichorum* (Sues, 2003), *Trilophosaurus buettneri* (TMM 31025-207), and shuvosaurids (e.g., *Effigia okeefae*, Nesbitt and Norell, 2006).

The absence of a posterodorsal process of the premaxilla excluding the maxilla from the external naris differentiates between Drepanosauridae n. gen., n. sp. and nearly all archosauromorphs (Dilkes, 1998; Nesbitt, 2011), kuehneosaurids (Robinson, 1962), and *Clevosaurus* (Robinson, 1973; Fraser, 1988). This contrasts with most non-saurian reptiles (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, BP/1 2871; Gow, 1975) and modern squamates (e.g., Jollie, 1960; Conrad, 2004). The contact between the premaxilla and maxilla in Drepanosauridae n. gen., n. sp. most closely resembles the condition in other drepanosauromorphs (*Megalancosaurus preonensis*, *Vallesaurus cenensis*) in which the posterior portion of the premaxilla overlies a small shelf on the maxilla.

Maxilla

Maxillae are represented on both the right and left sides in AMNH FARB 30834. The right maxilla is damaged; it lacks a complete anterior process, such that the anteroventral margin for the external naris and the premaxilla contacts are not preserved. Based on comparison with the left element, a large portion of the anterolateral surface of the right bone and the posterior process for contact of the jugal are both absent on the right maxilla. The left maxilla is much more complete (Fig. S3), although the anterodorsal surface appears badly cracked.

The maxillae in Drepanosauridae, n. gen., n. sp. are anteroposteriorly elongate and dorsoventrally low (Fig. 3A, 3B). There is a small, anteroventral shelf preserved on the anterior tip of the left maxilla, which appears to have accommodated the posterior process of the premaxilla. The anterodorsal portion of the left maxilla is heavily cracked and broken, such that its contribution to the external naris is unclear. However, posterior to this cracked margin, the dorsum of the maxilla is smoothly textured for much of its length back to the posterior third of the bone. This smooth margin is preserved on the partial right maxilla as well. We consider this margin to represent an extremely elongate maxillary contribution to the external naris. Posterodorsal to the narial margin of the left maxilla, there is an irregular margin that may represent an anteroposteriorly short contact surface for the nasal.

The alveolar margin of the maxilla lacks any evidence of teeth or alveoli (Fig 3D). The ventral margin is not straight, but subtly sigmoid and prominently convex at its anteroposterior midpoint (Fig. 3A, 3B).

At a point two-thirds the anteroposterior length of the bone, posterior to the level of the nasal contact of the maxilla, the bone tapers abruptly to a dorsoventrally short and tapering process (Fig. 3A, 3B). The ventral margin of this portion of the maxilla is prominently angled relative to the long-axis of the blade-like, distal margin.

The medial surface of the maxilla is overall featureless, except for a raised ridge at its anterior end (Fig. 3B). In medial view, the ridge is subtly arced, curving posterodorsally. The ridge on the left side is still in articulation with the left palatine. On the right side, the palatine is positioned anterodorsal to the anteriormost preserved portion of the right maxilla.

Comparisons

Although the anterior portion of the rostrum is edentulous in a small number of Triassic reptiles, complete edentulousness is far less common. Thus far, shuvosaurids (Chatterjee, 1993; Nesbitt and Norell, 2006) and derived turtles (e.g., Gaffney, 1990) are the only known Triassic reptiles to completely lack teeth. The maxillary teeth in drepanosauromorphs exhibit substantial variability. In *Vallesaurus cenensis* (MCSNB 4751), there are fewer than a dozen large and triangular maxillary teeth. In *Megalancosaurus preonensis* (MFSN 1769), there are a larger number of maxillary teeth, similar in shape to those in *Vallesaurus*; however, the teeth in *Megalancosaurus* are proportionally much smaller than those in *Vallesaurus*.

The ascending process of the maxilla in Drepanosauridae n. gen., n. sp. closely resembles the condition in *Vallesaurus cenensis* and *Megalancosaurus preonensis*, in which nearly the entire anterodorsal margin of the maxilla forms the contribution to the external naris. Among early saurian taxa, *Teraterpeton hrynewichorum* exhibits a similarly elongate narial margin (Sues, 2003).

Nasals, Lacrimal and Prefrontal

There are no elements that we confidently identify as belonging to the nasal bones. This is unsurprising, as the anterior portion of the frontals and the anteromedial portion of the premaxillae (and everything in between) are not preserved. On the left side of the skull, there are no complete bones dorsal to the posterior process of the maxilla, where one would expect to find the facial contributions of both the lacrimal and the prefrontal. There are some small bone fragments in this space, which may represent fragments of the facial laminae of both of these ossifications.

Jugal

Only the left jugal has been identified (Fig. S4). It is displaced medially relative to the other lateral skull elements, appressed to the lateral surface of the left pterygoid. In lateral view, the bone is rotated ninety degrees in a clockwise direction in a parasagittal plane. Our identification is based on comparisons with the two other drepanosauromorph specimens that preserve jugals (*Megalancosaurus preonensis*, MFSN 1769; *Vallesaurus cenensis*, MCSNB 4751); in these two taxa, the jugal is a smoothly curved posteroventrally, with no trace of a posterior process. The shape and proximity to the maxilla and postorbital lends support to our interpretation of the bone as a jugal. The bone is crescent-shaped in lateral view with a tapering anterior process and a tapering dorsal process.

The anterior process is subtly squared off at its anterior tip, which is slightly displaced laterally from the remainder of the bone (Fig. 4A). If this process were appressed to the dorsum of the posterior process of the maxilla, the dorsal process would have a subtle posterior inclination to its long axis. The long axes of the two processes form a right angle to one another. The bone is cracked posteroventrally, and no trace of a posterior process is preserved.

The dorsal process tapers to a more slender point than the anterior process (Fig 4A, 4B). No postorbital facet is apparent, although comparison with other amniotes suggest it contacted the posterior surface of the ventral process of the postorbital to complete the postorbital bar. The lateral surface of the dorsal process exhibits a subtle ridge that runs ventrally to the level of the anterior process.

The details of the medial surface of the jugal cannot be ascertained based on our reconstruction (Fig. 4B). The bone appears to be relatively smooth, although a slight ridge may be present at the ventral base of the dorsal process. There is no clear facet for the ectopterygoid.

Comparisons

The construction of the jugal has long been considered critical to understanding diapsid evolution, due to its contribution to the osseous lower temporal bar (e.g., Broom, 1925; Parrington, 1935; Robinson, 1967a). However, its role in understanding the interrelationships of fossil taxa has varied through time, especially now that incomplete lower temporal bars are recognized in a broad sample of Permo-Triassic reptile taxa (e.g., Müller, 2003; Modest and Reisz, 2003). The absence of a posterior process of the jugal in Drepanosauridae n. gen., n. sp. supports drepanosauromorphs as another diapsid lineage that lacked a complete bar.

The jugal in Drepanosauridae n. gen., n. sp. compares well with the exposed jugals in both *Vallesaurus cenensis* and *Megalancosaurus preonensis*. Since its initial description (Renesto and Binelli, 2006), the holotype of *Vallesaurus* (MCSNB 4751) has been considered to have a crescent-shaped jugal with no trace of a posterior process (Renesto et al., 2010). Such a shape is virtually identical to that in Drepanosauridae n. gen., n. sp.

The jugal of the holotype of *Megalancosaurus preonensis* (MFSN 1769) is more difficult to interpret. Calzavara et al. (1980:53) described the jugal as “triradiate,” with a distinct process forming the ventral margin of the lower temporal bar. Renesto (1994a) tentatively restored the skull as exhibiting a complete lower temporal bar. Renesto et al. (2010:11) described the jugal as bearing a “small, caudally-projecting process,” and they illustrated the skull with a complete lower temporal bar. Our study of the holotype of *Megalancosaurus* is equivocal with regards to a posterior process of the jugal. However, we do not think that such a process would be long enough to form a complete lower temporal bar. Thus, it appears that all drepanosauromorphs that preserve skulls lack a complete lower temporal bar.

Incomplete lower temporal bars with short jugal posterior processes occur in a number of non-saurian diapsids, including *Orovenator mayorum* (Reisz et al., 2011), *Claudiosaurus germaini* (Carroll, 1981), and *Lanthanolania ivakhnenkoi* (Modesto and Reisz, 2003). This is also noted in purported lepidosauromorphs (e.g., *Kuehneosaurus latus* and *Icarosaurus siefkeri*, see Colbert, 1970), and many early archosauromorphs (e.g., *Mesosuchus browni*, SAM-PK-K6536; *Prolacerta broomi*, e.g., BP/1 5375; *Protorosaurus speneri*, USNM 44253; *Tanystropheus longobardicus*, MCSN BES SC 1018). As in Drepanosauridae n. gen., n. sp., nearly all Permo-Triassic reptiles exhibit a dorsoventrally narrow, tapering anterior process of the jugal. Only derived archosauriforms (e.g., *Erythrosuchus africanus*, Gower, 2003) exhibit dorsoventrally broad, robust anterior processes.

Postorbital

The postorbital of Drepanosauridae n. gen., n. sp. exhibits three primary processes: an anterior process, a posterior process, and a ventral process. All three processes are complete and well preserved on the left side (Fig. 5). The right postorbital is missing the anterior process, apparently broken post-mortem (Fig. 6). The left postorbital remains in anatomical position. The right postorbital is rotated anteroventrally from its original position.

The complete anterior process on the left postorbital is transversely broad and dorsoventrally flat (Fig. 5C, 5D). In dorsal view, the process is rounded, convex laterally, and flat ventrally. The shape of the medial surface and its close association with the anterolateral margin of the postfrontal suggests that the anterior process was in full medial contact with the anterior portion of the postfrontal throughout its length. The overall flattened shape of the process forms a continuous, broad overhang with the anterior portion of the postfrontal, indicating a broad, overhanging shelf over the eye (Fig. 5A). The anterior process tapers transversely at its posterior terminus before meeting the ventral process and the posterior process.

The posterior process of the postorbital is roughly equivalent in length to the anterior process (Fig 5A, 5B). It is transversely slender throughout its anteroposterior length. It becomes dorsoventrally shallower throughout its anteroposterior length, tapering into a sharply pointed end. The dorsolateral margin of the process exhibits an anteroposteriorly running groove. Although neither postorbital remains in its original anatomical position relative to the other dermatocranial elements, the contacts between the anterior process, ventral process, and postfrontal indicate that the posterior process formed the anteromedial margin of the anteriorly tapered supratemporal fenestra.

The ventral process of the postorbital tapers distally (Fig. 5A, 5B). It is subtly concave anteriorly and subtly convex posteriorly. The process is transversely broader anteriorly than it is posteriorly. The shape of the ventral process parallels that of the ventrolateral portion of the postfrontal, and the similar, anteriorly flattened shape of both elements suggests that these together formed a continuous posterior orbital margin.

The articulation of the jugal with the postorbital is unclear, as that element is absent on the right side and heavily displaced on the left. It appears likely that the ventral process of the postorbital fitted across the dorsal process of the jugal as in most diapsid reptiles. In the reconstruction of the articulated skull, the relative positions of the jugal and postorbital are derived from the relative depth of the skull suggested by the dorsoventral height of the squamosal and the relationships between these elements in *Megalancosaurus* and *Vallesaurus*.

Comparisons

The construction of the postorbital in most Permo-Triassic diapsids is variable. The presence of an anterior process in Drepanosauridae n. gen., n. sp. is comparatively rare, as nearly all early diapsids have a homologous process that is inclined medially or anteromedially, situated posterior to the postfrontal. In most early taxa (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Protorosaurus speneri*, USNM 442453; and *Prolacerta broomi*, UCMP 37151), this medial process that is exposed on the dorsum of the skull. This condition also occurs in the drepanosauromorph *Vallesaurus cenensis*, which preserves a complete postorbital on the left side in MCSNB 4751. The process frames the anterior margin of the supratemporal fenestra and makes a medial contact with the lateral surface of the parietal. In certain other early diapsids and archosauromorphs, the postfrontal is anteroposteriorly broader, resulting in the medial process of the postorbital having a small, slender exposure on the dorsum of the skull (e.g., *Macrocnemus bassanii*, PIMUZ T/4822; *Macrocnemus fuyuanensis*, GMPKU P3001) or being entirely position deep to the postfrontal (e.g., *Trilophosaurus buettneri*, TMM 31025-140). Other taxa exhibit a complete separation of this process from the parietal (e.g., *Youngina capensis*, BP/1 3859), and the condition in Drepanosauridae n. gen., n. sp. appears to be an exaggerated development of this condition.

The ventral process of the postorbital is broadly similar to other diapsid reptiles. The only major distinction occurs in *Teraterpeton hrynewichorum* (Sues, 2003) and *Trilophosaurus* species (Spielmann et al., 2008), in which the ventral process is short and broadly in contact with both the jugal and squamosal, such that there is no infratemporal fenestra.

The posterior process of the postorbital in Drepanosauridae n. gen., n. sp. is also broadly similar to other Permo-Triassic diapsids. The slender, posteriorly pointed process is distinct from the posteriorly rounded condition in *Petrolacosaurus* (Reisz, 1981) and reconstructed in *Claudiosaurus germaini* (Carroll, 1981). A short and pointed process occurs in nearly all early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, UA 7-20-99-653; *Tanystropheus longobardicus*, MCSN BES SC 1018). Proportionally elongate posterior processes of the postorbital occur in a number of "younginiform" neodiapsids (e.g., *Acerosodontosaurus piveteaui*, Bickelmann et al., 2009; *Hovasaurus boulei*, Currie, 1981; *Youngina capensis*, BP/1 3859), in which the posterior process extends past the posterior margin of the infratemporal fenestra over the dorsal surface of the squamosal.

Postfrontal

The postfrontal in Drepanosauridae n. gen., n. sp. is a massive, triradiate bone. It consists of anterior, ventral, and posteromedial processes. The bone is completely intact on the left side (Fig. S7), but damaged on the right. The anterior process of the right postfrontal is largely missing (Fig. S8). The posteromedial process is preserved, but portions of the ventral margin of the bone are missing in several places.

The anterior process as preserved on the left element is enormous (Fig. 7A, 7B). The process is transversely broad throughout its anteroposterior length and dorsoventrally flattened. In lateral view, the bone is concave anteroventrally (Fig. 7C). It forms a prominent dorsomedial roof for the posterior portion of the orbit, which we construct as continuous with the anterior process of the postorbital. The medial aspect of the anterior process is dorsoventrally taller than the orbital roofing component, and forms a contact surface for the posterolateral portion of the frontal (Fig. 7D; Fig. 8D). The facet for contact with the frontal increases in dorsoventral depth posteriorly to the junction point between the anterior, ventral, and posteromedial processes.

The posteromedial process is transversely slender and dorsoventrally deep. In dorsal view, the bone curves posteromedially along its length (Fig. 7A; Fig. 8A, 8B). In lateral view, the process is convex dorsally along its length and flattened ventrally (Fig. 7C). The posterior tip of the posteromedial process arcs subtly ventrally (Fig. 7F; Fig. 8D). The entire medial surface of the bone consists of a facet for the posterolateral processes of the frontal and the anterolateral margin of the parietal (Fig. 7B). The lateral surface of the posteromedial process appears smoothly textured, forming the anteromedial margin of the supratemporal fenestra (Fig. 7A).

The ventral process is anteroposteriorly flattened, deeply concave anteroventrally, and convex posterodorsally in lateral view (Fig. 7C; Fig. 8C). The concave anterior surface is smoothly continuous with the orbital contribution of the anterior process. The posterolateral margin of the ventral process is marked by a prominent ridge that arcs ventrolaterally from the dorsomedial base of the process. This ridge continues along the length of the ventral process (Fig. 7B). In posterior view, the process appears dorsoventrally tall and plate-like. At its ventrolateral terminus, the process exhibits a laterally convex margin.

Comparisons

The postfrontal in Drepanosauridae n. gen., n. sp. is proportionally the largest known from any Permo-Triassic diapsid, especially with regards to the development of the massive dorsal roofing component of the orbit. In most early diapsid taxa (e.g., *Lanthanolania ivakhnenkoi*, Modesto and Reisz, 2003; *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, BP/1 2871) that portion of the postfrontal anterior to the posterior margin of the orbit is transversely very narrow. It fits against a depression in the frontal for a short span of that bone's anteroposterior length. In some early archosauromorphs (e.g., *Boreopricea funerea*, PIN 3708/1; *Macrocnemus bassanii*, PIMUZ A III/208; *Prolacerta broomi*, e.g., BP/1 471; *Protorosaurus speneri*, USNM 442453) the anterior portion of the postfrontal is transversely broader, giving the whole anterior half of the element a shape akin to a right triangle.

Although a postfrontal has not been described from the holotype of *Vallesaurus cenensis* previously (Renesto and Binelli, 2006; Renesto et al., 2010), we note that there is a transversely broad triangle of bone in contact with the lateral margin of the left frontal and the anterior margin of the medial process of the left postorbital. This appears similar to the postfrontals in early archosauromorphs. There is no indication of the transversely broad orbital roofing structure evident in Drepanosauridae n. gen., n. sp. The preservational quality of the holotype of *Megalancosaurus preonensis* (MFSN 1769), cracked into a part and counterpart through the transverse center of the sagittal plane, makes recognition of such a structure unclear.

The anterior process is transversely narrower in certain early archosauriforms (e.g., *Proterosuchus fergusi*, BP/1 3393; material referred to *Osmolskina czatkowicensis*, ZPAL RV/547, Borsuk-Bialynicka and Evans, 2009a), although this may be a consequence of the transverse expansion of the posterior portion of the frontals in these taxa. In juvenile individuals of *Tanystropheus longobardicus* (e.g., MCSN BES SC 1018), the frontals contribute a substantial dorsolateral shelf to the orbit, similar in shape to that formed by the postfrontal in Drepanosauridae n. gen., n. sp. However the structure in *Tanystropheus* (as reconstructed by Nosotti, 2007) frames the orbit dorsally, in contrast to the dorsomedial lamina in Drepanosauridae n. gen., n. sp.

Considering the apparent strong tapering of the rostrum anterior to the orbit, the massive expansion of the posterior orbital margin would have the effect of frontating the entire orbital cavity. Our reconstruction thus suggests that Drepanosauridae n. gen., n. sp. had eyes that faced more strongly anteriorly than any other known Permo-Triassic reptiles. It is possible that drepanosauromorphs were the first diapsids to develop binocular vision.

The dorsoventrally tall, anteroposteriorly elongate posterior process of the postfrontal in Drepanosauridae n. gen., n. sp. is distinct from most Permo-Triassic diapsids. In *Petrolacosaurus kansensis* (Reisz, 1981) and many early archosauromorphs (e.g., *Protorosaurus speneri*, USNM 442453; *Prolacerta broomi*; BP/1 5375), there is no posterior process at all. This is congruent with the presence of a dorsally exposed medial process of the postorbital in these taxa. Modest posterior expansion of the postfrontal occurs in other early diapsids (e.g., *Araeoscelis gracilis*; Vaughn, 1955) and archosauromorphs (e.g., *Macrocnemus bassanii*; PIMUZ T/4822), with these taxa tending to exhibit an anteroposteriorly restricted dorsal exposure of the medial process of the postorbital. In other such taxa, the broadened postfrontal entirely excludes the medial process of the postorbital from dorsal view (e.g., *Azendohsaurus madagaskarensis*, UA 70-20-99-653; *Trilophosaurus buettneri*; TMM 31025-140).

There is no extensive development of a ventral process in any other known Permo-Triassic diapsid. The existence of this process in Drepanosauridae n. gen., n. sp. may well be the product of the transverse expansion of the entire postorbital region and the broad contact with the ventral process of the postorbital.

Frontal

The frontals in Drepanosauridae n. gen., n. sp. are transversely broad and domed dorsally (Fig. 9). The frontal bone can be divided into a posteromedial, endocranial portion and an anteromedial orbital margin. The left frontal appears to be complete, whereas the right frontal is missing most of the endocranial portion.

The orbital portion of the frontal manifests as a dorsolaterally angled flange (Fig. 9C, 9E), with a lateral margin that is straight in dorsal view (Fig. 9A). At its posterior end, the orbital margin exhibits a lateral facet for the anterior portion of the postfrontal. This facet surface extends further posteriorly than the endocranial contribution as a posterolateral process. This posterolateral process fits into a corresponding notch on the postfrontal contact of the parietal. The orbital contribution is separated from the endocranial contribution by a dorsoventrally thickened ridge throughout its anteroposterior length. The ridge is oriented anteromedially (Fig. 9B).

The endocranial contribution of the frontal is domed dorsally above the margin of the orbital contribution (Fig. 9). This doming is the result of inflation of the endocranial volume, rather than a thickening of the bone in this region. The bone in this region is substantially thinner than any other portion of the frontal (>1 mm in thickness). The transversely broad endocranial contribution is transversely wide posteriorly (Fig. 9A, 9B), although it tapers sharply throughout its anteroposterior length. In dorsal view, this manifests as an egg shape.

At the anterior tip of the frontal, the endocranial contribution terminates as the anteromedially running ridge approaches the midline. The anterior tip of the endocranial contribution is not preserved on either side. It is unclear whether any portion of the prefrontal contact surface is preserved.

Comparisons

The frontal in Drepanosauridae n. gen., n. sp. is unique among Permo-Triassic in the massive inflation of the endocranial contribution. In nearly all other Permo-Triassic taxa, the dorsal surface of both the orbital and endocranial contributions of the frontal is continuous and flat throughout the transverse width of the bone (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, BP/1 3859; *Macrocnemus bassanii*, PIMUZ T/4822; *Proterosuchus fergusi*, SAM PK-K10603).

Frontals have been described in dorsal and lateral views for specimens of *Megalancosaurus preonensis* (dorsal view in MPUM 8437, lateral/medial views in MFSN 1769). In MPUM 8437, the frontals were described from two, transversely slender, flattened bony plates that sit anterior and deep to the appressed parietals. Renesto (2000) argued that this suggested that the frontals were transversely very slender anteriorly, broadening posteriorly at the frontoparietal contact in *Megalancosaurus*. Renesto and Dalla Vecchia (2005) described a similar shape for the laterally exposed frontals in the holotype of *Megalancosaurus preonensis*. Thus, the anteriorly tapering frontals in *Megalancosaurus* are distinct from the transversely wide condition in Drepanosauridae n. gen., n. sp.

The complete skull in the holotype of *Vallesaurus cenensis* (MCSNB 4751; Renesto and Binelli, 2006) is more difficult to interpret. We concur with Renesto and Binelli (2006) that both frontals are crushed and partially wedged underneath the nasals anteriorly. As reconstructed by Renesto and Binelli (2006), the frontals are similar in shape to those in *Megalancosaurus*, transversely narrow at their anterior tips and expanded posteriorly at the frontoparietal contact. If these reconstructions of *Vallesaurus* and *Megalancosaurus* are accurate, it indicates that Drepanosauridae n. gen., n. sp. is the only drepanosauromorph known to exhibit a transversely wide frontal and prominent orbital rim.

The most comparable condition among diapsid reptiles occurs in derived coelurosaurian theropods. A doming of the endocranial contribution dorsally above the orbital margin is evident in ornithomimosaurs (e.g., Osmólska et al., 1972; Kobayashi and Barsbold, 2005), oviraptorosaurs (e.g., Balanoff et al., 2009; Balanoff and Norell, 2013), *Archaeopteryx lithographica* (Alonso et al., 2004), and modern avians (e.g., Baumel et al., 1993). The presence of an inflated endocranial contribution of the frontal in these dinosaurs does not necessarily co-occur with a broad, everted orbital “lip” as in Drepanosauridae n. gen., n. sp. Within even a specific subgroup of Theropoda, such as Oviraptorosauria, such a lip can be present (e.g., *Incisivosaurus gauthieri*, Balanoff et al., 2009) or absent (e.g., *Khaan mckennai*, Balanoff and Norell, 2013).

The presence of a prominent posterolateral process of the frontal that fits into a corresponding notch on the anterolateral corner of the parietal is widespread among diapsid reptiles. Such processes are usually exposed on the skull roof, forming an anteriorly convex, U-shaped frontoparietal contact. These occur in primitive diapsids (e.g., *Hovasaurus boulei*, Currie, 1981; *Youngina capensis*, BP/1 3859) and a number of early archosauromorphs (e.g., *Macrocnemus basanii*, PIMUZ T/4822; *Prolacerta broomi*, UCMP 37151). By contrast, other early diapsid taxa exhibit a transversely straight frontoparietal contact (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Protorosaurus speneri*, USNM 442543; *Tanystropheus longobardicus*, PIMUZ T/2819). Such a contact also occurs in early archosauriform taxa that tend to exhibit an interdigitating frontoparietal suture (e.g., *Proterosuchus fergusi*, BP/1 3393; *Erythrosuchus africanus*, NHMUK R 3592).

Comparison with the endocrania from a broad sample of diapsid reptiles suggest that some inferences can be made about the brain of Drepanosauridae n. gen., n. sp. There are no paired impressions suggestive of the olfactory at the anterior tip of the preserved frontal, as in extant reptiles (Hopson, 1979). Such impressions occur in nearly all Permo-Triassic diapsids in which the ventral surfaces of the frontals are exposed [e.g., *Archosaurus rossicus* (PIN 1100/84); *Tanystropheus longobardicus* (PIMUZ T/2787)]. This is best typified by the exceptionally preserved Early Triassic diapsid fossils from the Czatkowice sites in Poland [*Osmolskina czatkowicensis* (ZPAL RV/405), *Pamelina polonica* (ZPAL RV/381), *Sophineta cracoviensis* (ZPAL RV/445)].

In most Permo-Triassic diapsids, the depressions for the olfactory bulbs sit anterior to dorsoventrally shallower and transversely narrower olfactory tracts (Hopson, 1979). These are laterally bounded by the cristae cranii frontalis, which are medially convex in ventral view. This condition is also easily seen in the frontals from the Czatkowice diapsids, but is widespread among diapsid reptiles. The anteromedial inclination of this ridge in Drepanosauridae n. gen., n. sp. appears unique among Permo-Triassic taxa. The substantial contribution to the bounds of the cerebrum and optic lobes in Drepanosauridae n. gen., n. sp. is continuous with the anteriormost of two cavities formed by the parietal (per Hopson, 1979).

Parietal

Both parietals are well preserved in Drepanosauridae n. gen., n. sp. Each consists of a dorsal lamina, a ventral lamina, and a posterolateral process. The left parietal is slightly damaged, with the base of the posterolateral process being broken and a small portion of the posterior surface of the dorsal lamina having been damaged (Fig. 10). The posterolateral process of the right parietal, although complete, appears to be deformed, such that it is ventrally directed under the rest of the bone (Fig. 11).

The dorsal lamina forms a posteriorly tapering plate (Fig. 10A, 11A). It is subtly convex and transversely broadest at its anterior margin, where it meets the frontal. On the right parietal, an interdigitating sutural surface for the frontal can be seen (Fig. 11A). The medial margin is weakly interdigitating where it contacts the contralateral parietal (Fig. 10A, Fig 11A). The dorsal lamina of the parietal is concave along its posterolateral margin, where the bone contributes to the supratemporal fenestra. Within the supratemporal fenestra, the surface of the dorsal lamina grades smoothly into the ventral lamina (Fig. 10D, 11D).

Posterior to the supratemporal fenestra, the dorsal lamina grows transversely broader towards the base of the posterolateral process (Fig. 10A, 11A). Further posteriorly, the dorsal lamina tapers dramatically to a posteriorly convex terminus. This posteriormost tapered section arcs subtly ventrally, such that the blunted tip of the dorsal lamina is exposed on the occipital face of the skull (Fig. 10E, 11E). This posteroventral inclination is more pronounced on the right side of the skull, which may be a consequence of the crushing distortion to the right side of the skull. The dorsal laminae of the parietals remain in midline contact throughout their anteroposterior lengths. The occipital facing posterior tips of the dorsa laminae fit into a corresponding concavity on the dorsal surface of the supraoccipital.

The ventral lamina is a dorsoventrally short bony flange that runs the anteroposterior length of the parietal contribution to the supratemporal fenestra (Fig. 10D, 11D). The reconstructed ventral laminae on both the right and left parietals are jagged at their ventral margins, suggesting that both may be substantially weathered. However, both appear to become dorsoventrally shorter at their posterior margins. There is a prominent anterior notch on both the right and left parietals for the reception of the posterolateral processes of the frontals.

The ventral surface of the parietal exhibits two prominent concavities, separated from one another by a transversely running ridge (Fig. 10B, 11B). The anterior of these two concavities appears to be continuous with the primary depression on the ventral surface of the frontal. The posterior depression actually produces a more prominent doming of the parietal bone than the anterior depression (Fig. 10C, 11C). The cavity itself extends to the posterior terminus of the ventrally deflected portion of the dorsal lamina.

The posterolateral process of the parietal is a dorsoventrally narrow, distally tapering strut (Fig. 10E, 11E). Damage to both the right and left processes makes determination of the natural orientation difficult to assess, although the relative height of the squamosal suggests that there was only a slight ventral inclination to the process. The reconstructions of the processes do not allow determination of the position or construction of the facet for the supratemporal and/or squamosal.

Comparisons

The anteriorly expanded, posteriorly tapering shape of the dorsal lamina of Drepanosauridae n. gen., n. sp. is rare among Permo-Triassic diapsids. Parietals in *Vallesaurus cenensis* and *Megalancosaurus preonensis* are similar in shape. To address this anatomical similarity, we must first present a revised reconstruction of the skull table in *Megalancosaurus preonensis*, specifically MPUM 8437 (Fig. 12).

In the initial description of the specimen, Renesto (2000) described three skull elements visible in dorsal view on MPUM 8437 (Renesto, 2000: fig. 4). Anteriorly, two transversely narrow portions of the frontal were visible. The broader, posterior portions of the frontals were argued to be positioned deep to the anterior portions of the parietals. The parietals were considered to be posteriorly in contact with a transversely wide supraoccipital, which exhibited short, slender paroccipital processes (Fig. 12A). This reconstruction was represented in Renesto and Dalla Vecchia (2005).

We argue that the transversely running suture between the parietal and supraoccipital described by Renesto (2000) is actually a crack, dividing the parietal into anterior and posterior parts at near the midpoint of the supratemporal fenestra (Fig. 12B). This reconstruction suggests that the “paroccipital processes” of Renesto (2000) are actually the posterolateral processes of the parietal, such that *Megalancosaurus preonensis* exhibits a parietal shape very similar to that of Drepanosauridae n. gen., n. sp. The crack within the parietal of *Megalancosaurus* may correspond to the position of the transverse ridge on the ventral surface of the parietal in

Drepanosauridae n. gen., n. sp. This updated reconstruction is similar to illustrations presented in Renesto et al. (2010: fig. 10E).

If our reconstruction of the skull in *Megalancosaurus preonensis* is correct, the shape of the dorsal lamina of the parietal in that taxon and Drepanosauridae n. gen., n. sp. is nearly identical. The concavity for the supratemporal fenestra is rather shallow, and there is no strong demarcation between the dorsal lamina and the ventral lamina. The anterior breadth of the parietal and shallow concavity for the supratemporal fenestra are also present in the holotype skull of *Vallesaurus cenensis* (MCSNB 4751).

The ventral ramus of the parietal in Drepanosauridae n. gen., n. sp. appears to be homologous to prominent anterolaterally positioned notches visible on the dorsum of the parietal in both *Megalancosaurus preonensis* and *Vallesaurus cenensis*. It is unclear if this notching would naturally have been visible in dorsal view in these taxa. Alternatively, the postmortem compression of these specimens may have flattened parietals that were naturally more three-dimensionally preserved. Either way, the notched construction of the parietal is common to all known drepanosauromorphs. The distribution of the notching in the parietal in other Permo-Triassic diapsid groups was described above in the discussion of the distribution of the posterolateral processes of the frontal; these two features occur concomitantly in these early diapsid taxa.

The ventral lamina of the parietal, extending into the supratemporal fenestra, is weakly differentiated from the dorsal lamina in some early diapsids (e.g., *Petrolacosaurus kansensis*; unnamed Fort Sill diapsid, Carroll, 1968; *Youngina capensis*, AMNH FARB 5561). This contrasts with the well-defined margins noted in early saurian groups (e.g., *Macrocnemus bassanii*, PIMUZ T/4822; *Prolacerta broomi*, BP/1 5375; *Proterosuchus fergusi*, BP/1 3393). In a number of early saurian lineages, these margins approach the midline (e.g., *Protorosaurus speneri*, USNM 442543) or converge on the midline to form a prominent sagittal crest (e.g., *Trilophosaurus buettneri*, TMM 31025-140; Hyperodapedontinae, Montefeltro et al., 2010).

The posterolateral processes of the parietal in Drepanosauridae n. gen., n. sp. appear transversely shorter proportionally than those of *Megalancosaurus preonensis*, suggesting a transversely wider supratemporal fenestra in the former. The crushed condition of the processes in the one specimen of *Megalancosaurus* to preserve a parietal (MPUM 8437) makes determination of their relative robusticity difficult to assess. However, it seems clear that the processes were not posteriorly flattened as in most archosauromorphs (e.g., *Prolacerta broomi*, BP/1 2675; *Trilophosaurus buettneri*, TMM 31025-140).

Squamosal

The squamosal is large and posteriorly convex in Drepanosauridae n. gen., n. sp. In addition to a massive, flattened lamina that broadly overlies the quadrate laterally and posteriorly, the squamosal exhibits an elongate, slender anterior process and a stout dorsomedial process. The prominent lamina may be divided into two distinct structures: a lateral lamina that broadly covers the quadrate in lateral view, and a posterior lamina that covers the occipital face of the quadrate.

The left anterior process is broken in multiple places, and its long axis now faces ventrally. The dorsomedial process appears to be partially preserved (Fig. 13). The right squamosal appears to preserve all of these processes in anatomical position (Fig. 14). There is some weathering at the ventral base of the lateral lamina, and the lateral base of the dorsomedial process is broken off. The reconstructed left squamosal is more heavily damaged. A flattened fragment of bone is positioned anterior to the preserved portion of the left lateral lamina; this may represent a displaced fragment from the broken part of the lamina.

The lateral and posterior laminae are dorsoventrally tall structures (Fig. 13A, 13D; 14A, 14D). In lateral view, the lamina exhibits a prominent anterior concavity that forms the posterior border of the infratemporal fenestra. The two laminae form a prominent trough anteriorly (Fig. 14C). At its ventral base, the lateral lamina is anteroposteriorly longer than the posterior lamina is transversely broad. The bone of the laminae is exceptionally thin (>1 mm) throughout the entirety of the structure.

In the reconstruction of the right squamosal, there is a posterodorsally pointed thickening on the anteroventral margin of the lateral lamina at the posteroventral corner of the supratemporal fenestra (Fig. 14A). This may be an artifact of the reconstruction of the CT scans, but it may also represent a small fragment of the quadratojugal (see below). We tentatively regard this structure as a portion of the primary lamina, as an identification as the quadratojugal would suggest a construction unlike any described diapsid taxon.

At its dorsal margin, the lateral lamina becomes anteroposteriorly shorter. At the posterodorsal corner of the supratemporal fenestra, the lateral and posterior laminae grade smoothly into the two remaining processes of the squamosal. The dorsolateral portion of the lateral lamina gives way to an anteroposteriorly elongate anterior process (Fig. 13A, 14A).

The anterior process is dorsoventrally slender throughout its anteroposterior length. The left anterior process preserves a small medial expansion at its posterodorsal corner (Fig. 13A), which is not evident in the right squamosal (Fig. 14A). There appears to be a subtle, anteroposteriorly running groove in the anterior half of the process. We interpret this as the facet for the posterior process of the postorbital. The left anterior process of the squamosal appears to taper to a point, whereas the right anterior process ends more bluntly.

The dorsomedial process is best seen on the right squamosal, where it appears as a dorsally pointed triangular structure in lateral view (Fig. 13A, 14A). The process is transversely narrow and tapers dorsally. Its base is broken in the right squamosal, such that its natural orientation cannot be discerned. There is a small groove on the posterior surface of the process, which may have received the supratemporal or the parietal.

Comparisons

The broad, posteriorly convex shape of the primary lamina of the squamosal in Drepanosauridae n. gen., n. sp. exhibits many similarities to non-diapsid eureptiles (e.g., Captorhinomorpha, Fox and Bowman, 1966; Heaton, 1979), the earliest-diverging diapsids (e.g., *Araeoscelis gracilis*, Vaughn, 1955; *Petrolacosaurus kansensis*, Reisz, 1981), and weigeltisaurids (e.g., *Rautiania* sp., PIN 5130/41). The shape of the squamosal has the effect of covering the quadrate in both lateral and posterior views. The posteriorly convex shape and dorsoventral height of the squamosal in Drepanosauridae n. gen., n. sp. is also shared with *Claudiosaurus germaini* (Carroll, 1981). However, the relationship of the quadrate to the squamosal is more difficult to assess in that taxon.

Most non-saurian diapsids from the Permian (e.g., *Hovasaurus boulei*, Currie, 1981; *Youngina capensis,* SAM K7578) do not exhibit a posterior exposure of the primary lamina. Instead, it consists of an anteroposteriorly broad sheet of bone that covers the quadrate in lateral view. Among early archosauromorphs, this ventral ramus is typically even slenderer anteroposteriorly and shorter dorsoventrally than in the "younginiform" diapsids (e.g., *Gephyrosaurus bridensis*, Evans, 1980; *Macrocnemus bassanii*, PIMUZ T/4822; *Mesosuchus browni*, SAM K6536; *Protorosaurus speneri*, USNM 442543). Other early saurian taxa do not exhibit any prominent ventral ramus of the squamosal (e.g., *Icarosaurus siefkeri*, AMNH FARB 2101; *Tanystropheus longobardicus*, PIMUZ T/2819).

A slender anterior process of the squamosal is relatively common among Permo-Triassic diapsids. The process is similarly transversely flattened and embayed laterally for reception of the posterior process of the postorbital in *Proterosuchus fergusi* (SAM-PK-10603) and *Azendohsaurus madagaskarensis* (UA 70-20-99-653). By contrast, the anterior process of the squamosal exhibits a complex, expansion that ventrally underlies the posterior process of the postorbital in *Youngina capensis* (BP/1 3859).

Supratemporal, Tabular, & Quadratojugal

We do not unequivocally identify any portion of the supratemporal, tabular, or quadratojugal in AMNH FARB 30834. A small, triangular thickening on the reconstructed right squamosal may represent a portion of the right quadratojugal, but this is unclear.

PALATE

Both the right and left palatines and right and left pterygoids are preserved in AMNH FARB 30834 (Fig. 15). Curiously there are no indications of palatal teeth on any of the preserved bones (Fig. 15B). This does not appear to be the result of weathering or low scan resolution; all elements exhibit distinctly smoothened palatal surfaces. Our reconstruction of the palate in Drepanosauridae n. gen., n. sp. is among the more tentative endeavors of this project. Although both palatines and the left pterygoid appear well defined in our 3D reconstruction, the poor quality of other portions of the pterygoid are evidence of the limited information available from this portion of the skull. That we do not recognize vomers, ectopterygoid, or contact surfaces for either in the preserved palate in AMNH FARB 30834 gives us pause. Ectopterygoids are indeed lost in certain amniote taxa including captorhinids and mesosaurs (e.g., Laurin and Reisz, 1995). Among diapsids, they are only known to be absent in modern Testudines (e.g., Gregory, 1946; Romer, 1956). However, our reconstruction of the drepanosaurid palate is quite distinct from any known amniote, and as such we recommend caution in its use.

Vomer

We have not recognized any portion of the vomers in AMNH FARB 30834. We hypothesize that they are absent, as there are no articular processes on the premaxillae, maxillae, palatines, or pterygoids for contact with the vomers. These are present broadly among diapsid reptile groups (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, BP/1 2871; *Mesosuchus browni*, SAM K6536; *Azendohsaurus madagaskarensis*, Flynn et al., 2010).

Palatine

Both the right and left palatines appear to be complete on both the right and left sides in AMNH FARB 30834, and both remain in articulation with the anterior ramus of the pterygoid. The palatine in Drepanosauridae n. gen., n. sp. consists of a dorsoventrally thin palatal lamina and a robust, L-shaped maxillary process. The right palatine is well preserved (Fig. 16). The palatal lamina of the left palatine is displaced from the maxillary process and is rotated out of articulation with the left pterygoid (Fig. 15B).

The maxillary process of the palatine is an anteroposteriorly elongate and shaped like a backwards "L" in lateral view (Fig. 16A). The ventral portion of the "L" is anteroposteriorly elongate, whereas the dorsal portion of the "L" is dorsoventrally shorter. The entire process articulates with a correspondingly shaped facet on the medial surface of the maxilla. The maxillary process tapers posteromedially towards its junction with the palatal lamina. It exhibits a prominent depression that sits at the junction of the dorsal and ventral portions of the "L"-shaped facet (Fig. 16A). Further medially, the maxillary process exhibits a transversely narrow, rounded facet on its dorsomedial surface. This facet is overlain by a small, rounded process at the anterior tip of the pterygoid (Fig. 16B).

At the posteroventral corner of the maxillary process, the palatine grades into the dorsoventrally flattened palatal lamina (Fig. 16D). This structure extends posteriorly, fitted against the anterolateral surface of the anterior process of the pterygoid. The shape of the left palatal lamina is roughly rectangular with a slight posterior tapering. The reconstruction of the palatal lamina of the right palatine exhibits a jagged posterior margin (Fig. 16D), but it is unclear whether this is the natural shape, or if this is the result of excess radiopaque artifacts.

Comparisons

The palatine in Drepanosauridae n. gen., n. sp. appears distinctly simpler than those of most Permo-Triassic diapsids. The maxillary process in taxa such as *Prolacerta broomi* (BP/1 2675) and *Azendohsaurus madagaskarensis* (FMNH PR 2751) is similarly narrow and roughly L-shaped. In most diapsids, there is a vertical column of bone sitting dorsal to the maxillary process (e.g., Oelrich, 1956; Iordansky, 1973). In numerous early diapsids (e.g., *Czatkowiella harae*, ZPAL RV/997) and modern lepidosaurs (e.g., *Ctenosaura pectinata*; Oelrich, 1956; *Gephyrosaurus bridensis*, Evans, 1980) there is an anterolaterally running canal within the strut. In modern squamates this accommodates the palatine branch of the facial nerve (cranial nerve VII) and a branch of the infranasal artery (per Oelrich, 1956). No such bony canal is apparent in Drepanosauridae n. gen., n. sp., although it is possible that the foramen is not apparent at the level of resolution of the reconstruction.

Most Permo-Triassic taxa also exhibit an anteroposteriorly elongate, dorsoventrally flattened process of the palatine that extends far forward relative to the maxillary process. This process makes contact with the vomer anteromedially. It is possible that this process is simply broken on both the right and left palatines in AMNH FARB 30834, but this would require that both elements be broken at the exact same points and that the broken margin appears smoothly textured in both. This raises the intriguing possibility that there is no contact between the vomer and palatine in Drepanosauridae n. gen., n. sp.

Pterygoid

Both pterygoids in Drepanosauridae n. gen., n. sp. are present and entirely encased in matrix. These were difficult to reconstruct, as the "ghost" of the cortical bone in the pterygoid is not apparent. Only the small portions of radiopaque material invested into the pterygoid are really apparent, and as such our description of these fossils are based on the shape outlines produced (Fig. 15). Each element possesses a posterolaterally directed quadrate ramus and an anterior ramus. The epipterygoid is positioned overtop of the lateral margin of the pterygoid, at the junction of the two rami.

The quadrate rami on the left and right pterygoids are complete on both the right and left sides, although it is dorsoventrally crushed on the right side. In dorsolateral view, the quadrate ramus is roughly rectangular, more elongate anteroposteriorly than tall dorsoventrally. Along its anteroposterior length the bone twists 3such that the posterior, laterally facing surface of the ramus faces dorsolaterally at its anterior extent. The quadrate ramus is smoothly continuous anteriorly with the anterior ramus. There is an embayment on the anterolateral surface of the anterior ramus, which accommodated the palatal process of the palatine.

There is an anterodorsally running ridge on the ventromedial surface of the quadrate ramus. The ridge runs from the posterodorsal corner of the quadrate ramus to the anterodorsal corner of that ramus. The ridge is well preserved on the left pterygoid, showing a prominent thickening at its anterior tip. We cannot identify much of the ramus on the reconstruction of the right pterygoid. At the anterodorsal tip of the quadrate ramus there is a subtle depression very near to the junction of the anterior and quadrate rami. Based on its position very near to the epipterygoid, we identify this as the basipterygoid articulation.

The anterior process of the pterygoid is among the more poorly reconstructed elements in Drepanosauridae n. gen., n. sp. On both sides in AMNH FARB 30834, the process is only apparent as bony flakes anterior to the quadrate ramus. The best-preserved portion of the bone is the anterior tip, which has a subcircular, dorsoventrally compressed terminus. The anterior process is in contact with the lateral margin of the palatal process of the palatine along its length. The rounded tip of the process fits over the dorsomedial corner of the maxillary process of the palatine.

Comparisons

The relatively short anteroposterior length of the anterior ramus relative to that of the quadrate ramus in Drepanosauridae n. gen., n. sp. is comparatively uncommon in Permo-Triassic diapsids. In most early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, UA 7-16-99-619; *Prolacerta broomi*, BP/1 5066), the anterior ramus is substantially longer than the quadrate ramus, which could relate to the relative elongation of the rostrum throughout Archosauromorpha. In Triassic lepidosauromorphs (e.g., *Clevosaurus hudsoni*, Fraser, 1988; *Gephyrosaurus bridensis*, Evans, 1980) and Permian non-saurian diapsids (e.g., *Youngina capensis*, BP/1 375; *Araeoscelis gracilis*, Vaughn, 1955; *Petrolacosaurus kansensis*, Reisz, 1981) the difference in relative length between the two processes tends to be lesser than in early archosauromorphs.

The broad, posterodorsally directed quadrate ramus of the pterygoid in Drepanosauridae n. gen., n. sp. is similar to that in *Petrolacosaurus kansensis* (Reisz, 1981) some early saurians (e.g., *Mesosuchus browni*, SAM-PK-6536). The anterodorsally directed ridge on the medial surface is similar to that in early archosauromorphs, such as *Azendohsaurus madagaskarensis* (UA 7-16-99-619) and *Prolacerta broomi* (UCMP 37151). In those archosauromorphs, the medial ridge of the ramus arcs dorsally at its anteriormost point—a feature not present in Drepanosauridae n. gen., n. sp. In a number of early diapsid taxa, the ventral surface of the pterygoid ramus is transversely broad. This condition occurs in early diapsids (*Petrolacosaurus kansensis*, Reisz, 1981, *Youngina capensis*, BP/1 375), archosauromorphs (*Prolacerta broomi*, UCMP 37151; "Chasmatosaurus" *yuani*, IVPP V4067), and lepidosauromorphs (*Clevosaurus hudsoni*, Fraser, 1988).

An anterior tapering of the anterior process of the pterygoid is evident in a broad range of reptiles (e.g., *Captorhinus aguti*, Heaton, 1979; *Petrolacosaurus kansensis*, Reisz, 1981; *Sphenodon punctatum*, Evans, 2009). However, this process usually terminates with some sort of anterior facet for contact with the vomer. The process is entirely dedicated to contact with the palatine in Drepanosauridae n. gen., n. sp., lacking any anterior extension for contact with vomers. This condition is currently unique to Drepanosauridae n. gen., n. sp.

Ectopterygoid

We have not recognized any portion of the ectopterygoids in AMNH FARB 30834.

SPLANCHNOCRANIUM

Quadrate

The quadrate of Drepanosauridae n. gen., n. sp. exhibits a distinct condylar portion for the jaw articulation, an anteromedially oriented pterygoid lamina, and a tall, dorsoventrally oriented dorsal lamina. The reconstructions of the left and right quadrate differ in the extent of the dorsal lamina. The left quadrate is reconstructed with a much taller dorsal lamina than the right (Fig. 17). This may be preservational, related to the more extensive disarticulation of the right quadrate and the consequent loss of part of the lamina (Fig. 18). Alternatively, we may have erroneously included a portion of the squamosal in our reconstruction of the left dorsal lamina, although we cannot identify any clear breaks or sutures that would indicate such a contact.

The orientation of the quadrate relative to the other cranial elements is difficult to reconstruct, based on the available evidence, as neither the left nor right quadrates remain in their natural anatomical position. Comparisons with the other known drepanosauromorph skulls (e.g., *Megalancosaurus preonensis*, MFSN 1769; *Vallesaurus cenensis*, MCSNB 4751) suggest that other drepanosauromorph quadrates were held with the long axis oriented anteroventrally (e.g., Senter, 2004; Renesto and Dalla Vecchia, 2005). The reconstruction of the lower jaws and squamosal suggest that a strong anteroventral inclination is unlikely for Drepanosauridae n. gen., n. sp. We tentatively reconstruct a slight inclination in this work.

The condylar portion of the quadrate is not separated into medial and lateral hemicondyles (Fig. 17C, 18E). Its surface is distinct from the remainder of the quadrate, defined by substantially smoother bone texture. In ventral view, the condyle is roughly triangular with rounded margins on all sides and an anterolaterally oriented long axis. The anterior and posterior surfaces of the quadrate condyle are proportionally longer than the medial surface in the left quadrate, whereas the surfaces are subequal in length on the right side. This may be the result of deformation on one or both sides. Anteromedially, the condyle bears a small, triangular process that points anteromedially in line with the ventral margin of the pterygoid ramus.

The smooth condylar surface of the quadrate has small expansions onto the anterior and posterior faces of the bone (Fig. 17B, 18A, 18B). The posterior expansion is overall medially placed, narrower than the ventral condylar surface. There is a small, subcircular facet surface on the lateral face of the quadrate, dorsolateral to the condylar margin (Fig. 17A, 18C). This may represent part of the articular surface for the quadratojugal, although no portion of that element has been definitively recognized.

The dorsal ramus of the quadrate consists of a dorsoventrally tall, thickened column of bone. In posterior view, ramus tapers dorsally to a narrow point (Fig. 17B, 18B). It is flattened posteriorly, without any prominent concavity. The anteromedial margin of the dorsal ramus is continuous with the anteromedially inclined pterygoid ramus of the quadrate. The left quadrate, at the junction of the quadrate and dorsal rami, exhibits a dorsoventrally tall, transversely narrow process (Fig. 17). The dorsal ramus of the right quadrate appears transversely narrower than does the left, just as the right quadrate condylar surface is transversely narrower than the left (Fig. 18). These shape distinctions suggest some degree of distortion in the shape of one or both quadrates.

The pterygoid ramus of the quadrate is extremely slender and poorly reconstructed on both sides. Each is visible mostly as spicules of radiopaque material in the CT slices. Although the general shape of each ramus can be seen, but we cannot yet accurately reconstruct the anteroposterior dimensions of the ramus. Substantially more of the anteroposterior length of the right pterygoid ramus is preserved than is the left. The ramus consists of a transversely flattened bony sheet that arcs anteromedially from the dorsal ramus and the quadrate condyle (Fig. 17B, 18D). The dorsoventral height of the ramus extends from the level of the quadrate condyle to the dorsoventral midpoint of the dorsal ramus. The ventral margin of the pterygoid ramus is strongly inclined anterodorsally. The medial surface of the pterygoid ramus appears to be flattened, whereas there is a prominent, anterodorsally running ridge on the lateral surface of the bone that parallels the ventral margin of the pterygoid ramus

Comparisons

The absence of distinct hemicondyles in Drepanosauridae n. gen., n. sp. is relatively uncommon among Permo-Triassic diapsids. In archaic diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Rautiania* sp., PIN 5130/33; *Youngina capensis*, AMNH FARB 5561) and most early saurians (e.g., *Boreopricea funerea*, 3708/2; *Prolacerta broomi*, UCMP 37151), the condylar surface is separated into two convex hemicondyles. In all of these taxa, the medial hemicondyle is broader anteroposteriorly, much as the medial surface of the condyle is broader in Drepanosauridae n. gen., n. sp. Among early archosauromorphs, weakly defined condylar surfaces occur in *Azendohsaurus madagaskarensis* (FMNH PR 2751) and *Trilophosaurus buettneri* (TMM 31025-140).

The shape of the dorsal ramus of the quadrate in Drepanosauridae n. gen., n. sp. shares many features with the quadrates in archaic diapsids and early reptiles. The transversely narrow dorsal ramus closely resembles the condition in *Captorhinus aguti* (Fox and Bowman, 1966; Heaton, 1979) and *Petrolacosaurus kansensis* (Reisz, 1981). In these two taxa, much of the dorsal ramus is occupied by a broad facet for the squamosal, which also seems to be the case in Drepanosauridae n. gen., n. sp. based on the dimensions of the quadrate and squamosal. This stands in contrast to the laterally expanded crest that develops in early saurian reptiles (e.g., *Paliguana whitei*, Carroll, 1975 *Prolacerta broomi*, BP/1 5375 *Proterosuchus fergusi*, BP/1

3393). This is homologous to the tympanic crest in lepidosaurs (e.g., Robinson, 1973; Evans 1980, 2008).

The dorsal rami of the quadrates in early saurians nearly always exhibit a prominent, posterior concavity in lateral view. This is evident throughout early Archosauromorpha (e.g., *Prolacerta broomi*, BP/1 471; *Mesosuchus browni*, SAM K6536; *Proterosuchus fergusi*; BP/1 3393) and early Lepidosauromorpha (e.g., *Paliguana whitei*, Carroll, 1975; *Clevosaurus hudsoni*, Fraser, 1988; *Gephyrosaurus bridensis*, Evans, 1980). This stands in contrast to the posteriorly verticalized quadrates in early reptiles (e.g., *Captorhinus aguti*, Fox and Bowman, 1966) and early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Claudiosaurus germaini*, Carroll, 1981). Although *Youngina capensis* is traditionally reconstructed with a verticalized dorsal ramus of the quadrate (e.g., Gow, 1975; Carroll, 1981), we note that several specimens exhibit a posteriorly inclined condylar region that produces a subtly concave posterior margin (AMNH FARB 5561, BP/1 2871). This may represent an intermediate condition between basal diapsids and early saurians.

The dorsal tapering of the dorsal ramus of the quadrate in Drepanosauridae n. gen., n. sp. is comparable to the condition in many early reptiles (e.g., *Captorhinus laticeps*, Heaton, 1979) and early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Rautiania* sp., PIN 5130/33; *Claudiosaurus germaini*, Carroll, 1981). By contrast, early saurian reptiles tend to exhibit a broad, dorsal convexity made up of unfinished bone. Such a structure is evident in a number of early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2751; *Boreopricea funerea*, PIN 3708/2 *Prolacerta broomi*, BP/1 5375; *Proterosuchus fergusi*, BP/1 3393) and putative early lepidosauromorphs (e.g., *Kuehneosaurus latus*, Evans, 2009).

A pterygoid ramus of the quadrate with a ventral margin roughly continuous with the condylar portion as in Drepanosauridae n. gen., n. sp. is found in captorhinomorphs (e.g., *Captorhinus laticeps*, Heaton, 1979; *Labidosaurus hamatus*, Modesto et al., 2007) and early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981). The ventral margin of the pterygoid ramus is elevated slightly above the condylar margin in *Youngina capensis* (AMNH FARB 5561). In early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2751; *Boreopricea funerea*, PIN 3708/2; *Protorosaurus speneri*, USNM 442543), and lepidosauromorphs (e.g., *Clevosaurus hudsoni*, Robinson, 1973; Fraser, 1988), the pterygoid ramus is relatively higher. We do not recognize a similar ridge on the medial surface of the ramus in other Permo-Triassic diapsids.

Epipterygoid

The epipterygoid in Drepanosauridae n. gen., n. sp. is a simple bone with a broad basal plate and a tall, slender dorsal stem. Both the left and right bones remain in articulation with their respective pterygoids (Fig. 15A). The right basal plate is complete (Fig. 19), whereas the posterior margin of the left plate is broken off and missing (Fig. 20). The dorsal stems are both broken along their lengths, with the dorsal portions disarticulated.

In lateral view, the basal plate of the epipterygoid is roughly rectangular with its long axis running anteroposteriorly (Fig. 19A). In articulation, the plate fits across the dorsolateral margin of the quadrate ramus of the pterygoid posterior to the junction of the quadrate and anterior rami. The base of the dorsal stem of the epipterygoid sits at the anteroposterior midpoint of the plate. Anterior to the base of the stem, the basal plate forms a small anteromedial lamina that extends dorsal to the dorsal margin of the quadrate ramus of the pterygoid (Fig. 19A, 20A).

The dorsal stem of the epipterygoid has a broad ventral base that grades smoothly from the anteroposterior midpoint of the basal plate. The stem tapers rapidly as it extends slightly anterodorsally (Fig. 19). This triangular base is slightly convex laterally. It exhibits a subtle, dorsally tapering concavity medially (Fig. 19B). It tapers to a thin splint that then extends further dorsally. The stem likely extended for nearly the full remaining dorsoventral height of the skull, but this is unclear due to the breakage of both stems in AMNH FARB 30834 (Fig. 19, 20). The relative orientation of the stem is also unclear; the right stem definitely exhibits an anterodorsal inclination (Fig 19), whereas the left stem appears to arc posterodorsally (Fig 20). This could well be the result of the overall crushing of the skull. At the dorsal tip of each dorsal stem, the bone expands slightly into a bulbous structure.

Comparisons

The transversely flattened, sheet-like basal plate of the epipterygoid in Drepanosauridae n. gen., n. sp. resembles the condition in a broad sample of Triassic archosauromorphs (e.g., *Mesosuchus browni*, SAM K6536; *Plateosaurus engelhardti*, Prieto-Marquez and Norell, 2011; *Proterosuchus alexanderi*, NMQR 1484) and *Youngina capensis* (Gow, 1975). Indeed, the description of the basal plate of the millerettid *Milleretta rubidgei* by Gow (1972), which he also considered applicable to *Youngina* (Gow, 1975), could easily be applied to Drepanosauridae n. gen., n. sp.: in each case the transversely narrow basal plate exhibits a small, medially directed expansion that contributes to the dorsum of the basipterygoid articulation.

The transversely narrow base in Drepanosauridae gen. nov., sp. nov. contrasts with the transversely and anteroposteriorly wider basal plates described for captorhinomorphs (Heaton, 1979) and a number of early synapsids (e.g., *Suminia getmanovi*, Rybczynski, 2000; *Dimetrodon limbatus*, *Lycaenops angusticeps*, Amson and Laurin, 2011). It is also far more substantial than the condition in modern squamates, in which the epipterygoid is reduced to a narrow column throughout its entire dorsoventral height such that there is no basal plate (Gauthier et al., 2012).

The narrow, tapering dorsal stem of the epipterygoid in Drepanosauridae n. gen., n. sp. is similar to captorhinomorphs (e.g., Heaton, 1979), early archosauromorphs (e.g., *Erythrosuchus africanus*, Klembara and Welman, 2009; *Mesosuchus browni*, SAM K6536; *Proterosuchus alexanderi*, NMQR 1484), and modern squamates (e.g., Jollie, 1960; Gauthier et al., 2012). This contrasts with the anteroposteriorly broad dorsal stem of the epipterygoid in *Sphenodon punctatum* (e.g., Evans, 2008; Gauthier et al., 2012). Intriguingly, the dorsal stems in early rhynchocephalians (e.g., *Diphydontosaurus avonis*, Whiteside, 1986; *Gephyrosaurus bridensis*, Evans, 1980) are extremely narrow and slender, more akin to the other conditions described.

Stapes

Both the stapedes of Drepanosauridae n. gen., n. sp. are preserved intact. The left stapes is displaced, shifted laterally such that it is anterior to the quadrate, but it appears to be relatively undistorted (Fig. 21). The right stapes is preserved in articulation, although it appears to have been heavily dorsoventrally crushed (Fig. 22). These bones are extremely massive and quite large relative to the other cranial elements; each is substantially more massive than the ipsilateral paroccipital process. The stapes is a simple bone, comprised of a broad footplate and a slenderer stapedial shaft.

Based on the articulated footplate of the left stapes, the footplate appears to have filled the entire foramen ovale framed by the opisthotic, prootic, and parabasisphenoid. The plate itself is roughly quadrangular (Fig. 21C, 21E, 22C, 22E). Its anterodorsal and posterodorsal margins extend further medially than its anteroventral and anteromedial margins (Fig. 21B, 22B). The posteroventral corner of the plate has a rounded margin and is equivalent in position to the ventral tip of the ventral ramus of the opisthotic. The margins of the plate continuous with the ventral ramus of the opisthotic and the dorsal margin of the foramen ovale are straight. The anterodorsal margin that parallels the inferior margin of the anterior inferior process of the prootic is rugose and subtly rounded. Finally, the anteroventral margin sits against the ventrolateral crest of the parabasisphenoid. The central portion of the footplate is subtly concave.

The stapedial shaft does not have a dorsal process or a stapedial foramen (Fig. 21A, 22A). It is possible that this reconstruction did not successfully recognize the presence of a genuine foramen in the radiopaque materials and bone halos that contributed to the model. However, the margins of the right stapes are well defined in the CT scan (Fig. 22), and the reconstruction of that element suggests that the stapedial shaft was smooth on all of its faces.

The base of the shaft originates from the lateral aspect of the footplate, opposite the anteroventral face of the plate. The shaft is compressed in a roughly dorsoventral plane and broadened in an anteroposterior plane. The dorsal and ventral faces of the shaft are smooth and flat (Fig. 21A, 21B). The posteroventral face of the shaft is subtly convex along its length. The anteroventral face exhibits a slender, transverse ridge that runs the length of the shaft (Fig. 22D).

The stapedial shaft turns posteroventrally very near to its lateral terminus (Fig. 21A, 22A). The tip is dorsoventrally flattened and squared off laterally. Dorsally, this tip exhibits a small convexity; on the reconstruction of the right stapes, this manifests as a small bump.

Comparisons

The robusticity and size of the stapes in Drepanosauridae n. gen., n. sp. is contrary to the condition of the stapes in nearly all other Triassic diapsid reptiles. In size and shape, it shares more in common with the stapes of primitive eureptiles (e.g., *Captorhinus aguti*, Price, 1935 and Fox and Bowman, 1966) and early diapsids (e.g., *Araeoscelis gracilis*, Vaughn, 1955; *Petrolacosaurus kansensis*, Reisz, 1981; *Orovenator mayorum*, Reisz, 2011). However, all of these taxa exhibit a distinct dorsal process of the stapes, which articulated with the undersurface of the prootic and opisthotic near the base of the paroccipital process (Price, 1935; Vaughn, 1955). In this regard, Drepanosauridae n. gen., n. sp. more closely resembles the condition in *Youngina capensis* (Gardner et al., 2010) and early saurian reptiles (e.g., *Azendohsaurus* *madagaskarensis*, UA 7-20-99-653; *Prolacerta broomi*, Gow, 1975), in which a dorsal process is absent.

Foramina for the stapedial artery are common in early reptiles and diapsids. In *Captorhinus aguti* (Fox and Bowman, 1966) and *Araeoscelis gracilis* (Vaughn, 1955) the foramen is large and positioned within the ventral portion of the stapedial shaft. A likely homologous foramen can also be found in diapsids and some saurian reptiles. In *Youngina capensis*, a large foramen pierces the slender stapedial shaft near its transverse midpoint (Gardner et al., 2010). Stapedial foramina are have never been reported in Archosauromorpha, but they are known in some modern lepidosaurs. Gauthier et al. (2012) recovered perforate stapes as apomorphic to Dibamidae and a number of gekkotan clades.

The combination of a massive stapedial shaft and the absence of a stapedial foramen in Drepanosauridae n. gen., n. sp. is unique among known diapsid reptiles. However, some analyses regard the stapedial artery as re-evolving multiple times within Lepidosauria. Indeed in different groups of modern lepidosaurs, the stapedial artery may pass “in front” or “behind” an imperforate stapes (Greer, 1965:591), suggesting that the shaft can develop relative to the vasculature in substantially different ways.

CHONDROCRANIUM

It is important to note that the prootic, opisthotic, and supraoccipital are not suturally distinct from one another externally in the available scans. Intriguingly, there are a series of facets present on the medial aspect that suggest the borders of the bones. It is possible that the reconstruction failed to recognize sutures that are apparent in the specimen, or that the lateral portions of these braincase elements fused completely. External fusion of the braincase elements occurs in *Araeoscelis gracilis* (Vaughn, 1955) and *Captorhinus aguti* (Price, 1935).

Basioccipital/Exoccipital

The basioccipital and exoccipitals form a single, compound element in Drepanosauridae n. gen., n. sp. The element is complete in AMNH FARB 30834 (Fig. 23). The right side of the bone is slightly dorsoventrally shorter than the left, which is congruent with the overall pattern of crushing of the skull. The bone itself consists of a midline occipital condyle, a broad and midline plate that contributed to the endocranium, two laterally directed articular processes that met the opisthotics, and the posterodorsally directed exoccipital struts.

The occipital condyle forms a broad, posteriorly convex semicircle in posterior view (Fig. 23C); the dorsal margin of the condyle is flattened. There is a prominent midline depression in the posterior surface of the condyle, the notochordal pit. The pit is deepest at its transverse center. The condyle is set apart from the endocranial plate by a stout neck, transversely as broad as the condyle itself. The condyle is dorsoventrally deeper than the neck that supports it (Fig. 23E, 23F). The smoothened bone that forms the articular surface of the condyle extends slightly onto the ventral surface of the condyle (Fig. 23A).

The occipital condyle appears to have been formed solely by the basioccipital. In contrast to reptile taxa in which the exoccipitals contribute to the dorsolateral portions of the condyle (see below), the struts of the exoccipitals are positioned well laterally relative to the lateral margins of the condyle itself (Fig. 23C). In this reconstruction, there is a prominent gap in the bone, ventromedial to the base of the exoccipital strut (Fig. 23A). Such a gap is present on both the right and left sides of the reconstructed element. This may represent a ventral hypoglossal foramen.

On the right exoccipital, I reconstruct a slit-like gap near the ventral base of the strut (Fig. 23B). A similarly shaped depression is reconstructed on the left exoccipital. We interpret these as a dorsal foramen for the hypoglossal nerve. The strut of the exoccipital remains at roughly the same transverse width throughout its dorsoventral height, although it tapers anteroposteriorly just dorsal to its base (Fig. 23C, 23D). The exoccipital struts angle posterodorsally from their base (Fig. 23E, 23F). These extend posterior to the posterior margin of the occipital condyle. The dorsal tip of the exoccipital broadens into a transversely and anteroposteriorly wider platform. This we interpret as a facet surface for the supraoccipital.

The central plate of the exoccipital-basioccipital is transversely broader than the occipital condyle. It is roughly pentagonal in dorsal view (Fig. 23B). Just posterior to the anterior margin of the basioccipital, we reconstruct a sizeable gap in the bone, equivalent in anteroposterior length to the occipital condyle. The gap is separated in the midline by a slender bony strut. It is unclear if this gap is a natural feature or the result of damage to the bone.

The anterior margin of the central plate is formed by two, anterolaterally facing facet surfaces (Fig. 23D). These are smoothly textured and dorsoventrally short. These would have met the posterior surface of the parabasisphenoid. In the midline there is a small, transversely narrow gap between the two facets. In anterior view, these facets angle ventromedially towards the midline gap.

Lateral to both the occipital condyle and the central plate, the basioccipital is expanded into complex facets for the opisthotic (23D, 23E). Directly ventrolateral to the base of the exoccipital strut, there is a laterally facing, elliptical facet for the opisthotic. This facet continues ventrolaterally as an anteroposteriorly flattened lamina. This lamina is positioned laterally relative to the dorsal facet for the opisthotic.

The posterior surface of the opisthotic facet portion of the basioccipital forms a transversely narrow, ventromedially rounded surface (Fig. 23C). The anterior surface of this portion of the basioccipital is concave, forming a laterally concave cup. It forms the posteroventral corner of the foramen ovale. Anteriorly, the portion of the basioccipital that contributes to this surface exhibits a small, anteriorly facing contact surface. This surface may relate to a small, smooth surface on the posterior surface of the parabasisphenoid just lateral to the transversely wide primary facets between the basioccipital and parabasisphenoid (see below).

Comparisons

The deep, transversely broad notochordal depression on the occipital condyle of Drepanosauridae n. gen., n. sp. is present throughout archaic reptile lineages, including Captorhinomorpha (e.g., Price, 1935; Heaton, 1979) and protorothyridids (e.g., Clark and Carroll, 1973). Similar depressions occur among nearly all non-saurian diapsids (e.g., *Araeoscelis gracilis*, Vaughn, 1955; *Hovasaurus boulei*, Currie, 1981; *Youngina capensis*, Gardner et al., 2010) and early lepidosauromorphs (e.g., *Gephyrosaurus bridensis*, Evans, 1980) This contrasts with the hemispherical, domed condyles typical in early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2765; *Prolacerta broomi*, UCMP 37151), although these occasionally exhibit small notochordal pits (e.g., *Proterosuchus fergusi*, Ezcurra and Butler, 2015; *Trilophosaurus buettneri*, TMM 31025-244).

Fusion of the exoccipitals and basioccipitals into a compound element is common in early reptiles. This is present in captorhinomorphs (e.g., *Captorhinus aguti*, Price, 1935) and in early diapsids (e.g., *Youngina capensis*, Gardner et al., 2010). Among araeoscelids, Vaughn (1955) reported poorly defined sutures between the two elements in *Araeoscelis gracilis*. Among

Mesozoic taxa, fused basioccipital-exoccipital complexes occur in *Kuehneosaurus latus* (NHMUK R6059) and many early lepidosaurs (e.g., *Diphydontosaurus avonis*, Whiteside, 1986; *Gephyrosaurus bridensis*, Evans, 1980). This feature is polymorphic in *Prolacerta broomi* (unfused in UCMP 37151; fused in BP/1 2675).

The construction of the ventral surface of the basioccipital in Drepanosauridae n. gen., n. sp. more closely resembles the condition in archaic reptiles and archaic diapsids. The presence of prominent ridges (basal tubera) on the posterolateral surfaces, abutting the opisthotic contact, resembles the condition in *Captorhinus aguti* (Price, 1935) and *Araeoscelis gracilis* (Vaughn, 1955). The tubera are also weakly extended ventrally in *Hovasaurus boulei* (Currie, 1981). Basal tubera are more elongate dorsoventrally, developed well ventral to the occipital condyle, in *Youngina capensis* (Gardner et al., 2010). Equivalent tubera are quite well developed ventrally in most archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, UA 70-20-99-653; *Prolacerta broomi*, BP/1 2675).

Parabasisphenoid

We cannot identify a distinction between the chondrocranial basisphenoid and the dermatocranial parasphenoid ossifications, suggesting that the two are fused into a single element, as is common in Diapsida (e.g., Gardner et al., 2010). As such, we describe the compound element collectively with the chondrocranial elements.

The parabasisphenoid is complete in AMNH FARB 30834, although some components are poorly preserved (Fig. 24). The bone itself consists of a prominent endocranial region, two wing-like alar processes (sensu Oelrich, 1956) with distal articulations for the prootics, a midline cultriform process, two basipterygoid processes, a ventromedian process, and two posteriorly positioned ventrolateral processes. Although the endocranial contribution and the articular surfaces for the prootic are well defined in the reconstruction, the basipterygoid processes, the base of the cultriform process, and the ventrolateral processes are poorly defined. The bone appears to be preserved in nearly its original articulation with the basioccipital.

The primary endocranial portion of the parabasisphenoid is transversely wide and dorsoventrally deep (Fig. 24A), forming an elliptical contribution to the endocranial cavity. It is framed laterally by the prootic processes. The posterior surface of the endocranial contribution is formed by two, ventromedially inclined articular facets (Fig. 24F), which would have met the basioccipital posteriorly. These are separated by a transversely narrow median gap. Anteroventrally the broad central portion of the parabasisphenoid forms a ventrally tapering surface that grades into the laterally directed basipterygoid processes and the anteriorly directed cultriform process. We do not recognize any foramina in the anterior surface of the endocranial contribution for the abducens nerves, nor are any foramina for the carotid arteries visible.

The ventrolateral processes are reconstructed as small, dorsoventrally flattened processes that project posteroventrally from the primary articulation of the parabasisphenoid for the basioccipital (Fig. 24C, 24D). The shape of the right process cannot be determined, whereas the left process appears to be posteriorly rounded in dorsal view. The anterior bases of each process appear to be broken on both sides (Fig. 24A, 24B). The processes reach to nearly the posterior surface of the braincase, underlying the basioccipital tubera.

The ventromedian process originates anteriorly from the underside of the endocranial contribution, just posterior to the level of the endocranial portion's anteriormost margin (Fig. 24B). The process consists of a thick, ventrally tapered projection, which projects posteriorly, presumably underlying the ventral surface of the basioccipital. Near the level of the posterior margins of the ventrolateral processes of the parabasisphenoid, the ventromedian process turns sharply ventrally and tapers rapidly to a point (Fig. 24C, 24D).

At the lateral margin of the endocranial contribution, the bone is drawn into robust, anteroposteriorly thick alar processes that angle dorsolaterally (Fig. 24E, 24F). Laterally, each process forms a facet for the anterior inferior processes of the prootic. The facets are concave, anteroposteriorly longer than they are dorsoventrally tall, and exhibit prominent anterior and posterior borders. Posteroventrally, the alar process exhibits a dorsoventrally flat, posteroventrally oriented projection that contributes to the foramen ovale.

The cultriform process and basipterygoid processes are positioned distinctly anteroventrally relative to the endocranial contribution (Fig. 24C, 24D). The dorsum sellae is a tall bony shelf that is dorsally capped by a sharply defined crista sellaris that runs between the prootic articulations. The hypapophyseal fossa is poorly defined, such that major structures (e.g., carotid foramina, retractor crests) cannot be identified (Fig. 24E). Anterior to the poorly reconstructed hypapophyseal fossa, the parabasisphenoid exhibits two small, posterodorsally directed pre-cultriform processes. Each process is flattened posteriorly and convex anteriorly.

The cultriform process exhibits a posterior origin just anterior to the small, posterodorsal processes (Fig. 24C). The process is broken in several places in AMNH FARB 30834, but its full length appears to be preserved. Posteriorly the cultriform is deeply concave dorsally and roughly "U"-shaped in cross-section (Fig. 24A). This concavity becomes shallower further anteriorly, developing a linear, dorsally flat cross-section. There is a poorly reconstructed, transversely narrow lamina that extends posteroventrally from the base of the cultriform process.

The basipterygoid processes are oriented strongly laterally and subtly posteriorly (Fig. 24C, 24E). In AMNH FARB 30834, the right process is positioned very close to the lateral margin of the endocranial contribution whereas the left process is drawn out far further laterally. The ventral margins of the processes are linked by an anteroposteriorly narrow transverse lamina. The cross section of the basipterygoid process is roughly quadrangular. The articular facet is oriented laterally, rounded anteriorly, and concave posteriorly.

Comparisons

The overall orientation of the parabasisphenoid, with the hypapophyseal fossa, cultriform process, and basipterygoid processes positioned well ventral to the endocranial contribution and ventrolateral processes, in Drepanosauridae n. gen., n. sp. is shared with a number of advanced archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2765; *Trilophosaurus buettneri*, TMM 31025-443). In most early reptiles (e.g., *Captorhinus aguti*, Price, 1935; *Petrolacosaurus kansensis*, Reisz, 1981) and many neodiapsid taxa (e.g., *Youngina capensis*, Gardner et al., 2010; *Prolacerta broomi*, Evans, 1986; *Proterosuchus fergusi*, Gow, 1975). A horizontally oriented parabasisphenoid is also common among lepidosaurs (e.g., Jollie, 1960; Evans, 2008). Thus far, Drepanosauridae n. gen., n. sp. is the only non-saurian diapsid known to exhibit a verticalized parabasisphenoid.

The relative breadth of the anterior portion of the endocranial contribution of the parabasisphenoid and the consequent broad separation of the prootic processes in Drepanosauridae n. gen., n. sp. appears unprecedented among Permo-Triassic reptiles. In captorhinomorphs (e.g., *Captorhinus aguti*, Price, 1935), early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, Gardner et al., 2010), early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2765; *Czatkowiella harae*, Borsuk-Bialynicka and Evans, 2009b), and lepidosauromorphs (e.g., Evans, 2008).

Another curious development is that of the parallel, posterodorsally oriented processes anterior to the hypapophyseal fossa in Drepanosauridae n. gen., n. sp. In nearly all Permo-Triassic reptiles, there are no such processes evident, the bone grading into the lateral portion of the cultriform process (e.g., *Captorhinus aguti*, Price, 1935; *Youngina capensis*, Gardner et al., 2010; *Czatkowiella harae*, ZPAL RV/117). In *Azendohsaurus madagaskarensis* (FMNH PR 2675), there is a vertical process extending dorsally anterior to the hypapophyseal fossa that could be homologous with the condition in Drepanosauridae n. gen., n. sp.

The orientation of the basipterygoid processes, with a strong ventral component to their angulation, is common among Permo-Triassic reptiles with verticalized parabasisphenoid. The processes are similarly angled in *Azendohsaurus madagaskarensis* (FMNH PR 2765), *Erythrosuchus africanus* (Gower, 1997), and *Arizonasaurus babbitti* (Gower and Nesbitt, 2005), although the facets remain facing anterolaterally in these taxa rather than strongly laterally as in Drepanosauridae n. gen., n. sp. In taxa with horizontalized parabasisphenoids, the basipterygoid processes tend to exhibit a lateral inclination, albeit with facets still facing anterolaterally. Examples of this include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (Gardner et al., 2010), modern lepidosaurs (e.g., Evans, 2008), *Prolacerta broomi* (BP/1 2675; UCMP 37151).

Supraoccipital

The supraoccipital in Drepanosauridae n. gen., n. sp. is a transversely broad element. It consists of an anteroposteriorly narrow posterior lamina and broader lateral complexes that contribute to the semicircular canals and the subarcuate fossa (Fig. 25A). The bone is broken at its right lateral end, the posterior lamina having been separated from the lateral complex on the right side (Fig. 26). The lamina remains attached to the left lateral complex (Fig. 25).

The posterior lamina is anteroposteriorly very narrow (Fig. 25D). It exhibits a very prominent ventral concavity, a contribution to the transversely broad foramen magnum. The supraoccipital also exhibits a distinct dorsal concavity, which corresponds well to the posteroventral expansions of the parietals. Ventrolaterally, along the lateral margin of the foramen magnum, the bone exhibits a ventrally facing, somewhat triangular facet for the dorsal tip of the exoccipital.

The supraoccipital becomes anteroposteriorly thicker at the level of the exoccipital facet as it expands into the lateral complex (Fig. 25). There is an additional, anteroventrally inclined facet positioned just anterolateral to the exoccipital contact. There is a distinct, dorsally tapering depression in the medial surface of the bone, positioned between these two facets.

Further laterally, it becomes difficult to distinguish the supraoccipital from the opisthotic and prootic due to the apparent lack of sutures. On the left side, there is a strong, dorsoventrally running crack that may indicate the position of the prootic-supraoccipital contact (Fig. 25A, 25B). On the right side, there is a subtle gap in a similar position that could indicate the same contact site (Fig. 26A). Further ventrally, lateral to the exoccipital contact, there is another prominent crack on the left side. On this side, the supraoccipital appears to be pressed ventrally onto the dorsal surface of the opisthotic. There is no similar gap on the right side. At its lateralmost extent, the bone contributes an anterior concavity to the posterior portion of the subarcuate fossa (Fig. 26B).

Comparisons

The supraoccipital in Drepanosauridae n. gen., n. sp. is unique among Permo-Triassic reptiles in exhibiting a strongly concave dorsal margin to its posterior surface. This margin is subtly concave in *Petrolacosaurus kansensis* (Reisz, 1981) and *Araeoscelis gracilis* (Vaughn, 1955) and roughly horizontal in *Youngina capensis* (Gardner et al., 2010) and many early archosauromorphs (e.g., *Prolacerta broomi*, Evans, 1986; *Trilophosaurus buettneri*, TMM 31025-443). However, the dorsum of the supraoccipital is strongly pointed anterodorsally in *Captorhinus aguti* (Price, 1935), *Protorothyris archeri* (Clark and Carroll, 1973), other early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2765; *Proterosuchus fergusi*, NMQR 1484), and some squamates (e.g., *Ctenosaura pectinata*, Oelrich, 1956; *Iguana iguana*, Evans et al., 2008). In some modern taxa (e.g., *Sphenodon punctatum*), a similar pointed process is present as in cartilage (Evans, 2008).

In contrast to the flattened, smooth texture of the supraoccipital in Drepanosauridae n. gen., n. sp., most Permo-Triassic reptiles exhibit a distinct, dorsoventrally running crest on the posterior surface of the supraoccipital. Such a feature is present in captorhinomorphs (e.g., *Captorhinus aguti*, Price, 1935), certain parareptiles (e.g., *Macroleter poezicus*, Tsuji, 2006; *Procolophon trigoniceps*, Carroll and Lindsay, 1985), *Hovasaurus boulei* (Currie, 1981), archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2765; *Tanystropheus longobardicus*, PIMUZ T2484), and lepidosauromorphs (e.g., Evans, 2008). One of the few taxa to exhibit a smoothly textured supraoccipital is *Youngina capensis* (Gardner et al., 2010), although some early archosauriforms (e.g., *Erythrosuchus africanus*) exhibit a narrow, largely uncrested supraoccipital (Gower, 1997).

The prominent contribution of the supraoccipital to the dorsal margin of the foramen magnum is common among Permo-Triassic reptiles. Broad exposures of the supraoccipital are common in early reptiles (e.g., *Captorhinus aguti*, Price, 1935), early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, Gardner et al., 2010), lepidosaurs (e.g., Oelrich, 1956; Evans, 2008), and some rhynchosaurs (e.g., *Mesosuchus browni*, Dilkes, 1998; *Bentonyx sidensis*, Hone and Benton, 2008). Early archosauromorphs typically exhibit a transversely narrow exposure of the supraoccipital within the foramen magnum, owing to convergence of the exoccipitals towards the midline (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2765; *Trilophosaurus buettneri*, TMM 31025-244) or complete exclusion of the supraoccipital (e.g., erythrosuchids and early archosaurs, Gower and Sennikov, 1996). *Prolacerta broomi* may be polymorphic for this character (Evans, 1986).

The contribution of the supraoccipital to the subarcuate fossa in Drepanosauridae n. gen., n. sp. is interesting among reptiles for its posterior position within the endocranium. In certain taxa, the anterodorsal inclination of the supraoccipital results in its contribution to the subarcuate fossa being positioned far anteriorly within the endocranium (e.g., *Captorhinus aguti*, Price, 1935; lepidosaurs, Oelrich, 1956). In some early archosauromorphs, the supraoccipital contribution to this cavity is relatively small (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2765; *Czatkowiella harae*, ZPAL RV/450).

Opisthotic

The opisthotic is relatively complete on both the right (Fig. 26D) and left side (Fig. 27). The element consists of a laterally positioned paroccipital process, a ventral ramus, and a complex endocranial contribution. On the right side, the element remains completely associated with the supraoccipital and prootic (Fig. 26), whereas the right opisthotic is broken away from the prootic and supraoccipital (Fig. 27). Additionally, the dorsal surface of the endocranial contribution is cracked away from the remainder of the bone. The right paroccipital process appears to be missing its lateral tip (Fig. 26D), whereas the left process appears complete (Fig. 27A, 27B).

The ventral ramus of the opisthotic is a transversely broad, anteroposteriorly flattened structure (Fig. 27A). The ramus exhibits a dorsomedially positioned facet, which met a corresponding facet on the basioccipital. Ventral to this contact, the entire medial margin of the bone fits against the lateral edge of the basioccipital tuber. The ramus is concave posteriorly, corresponding in shape to the posterior surface of the basioccipital tuber.

Dorsal to the ventral ramus, the opisthotic exhibits a medial embayment (Fig. 26D). This cavity forms the lateral aspect of the metotic foramen, the medial margin of which is formed by the exoccipital strut. Anterior to the foramen, there is a prominent cavity within the opisthotic that appears to be continuous with the horizontal and posterior semicircular canals, suggesting that it is the posterior ampullary recess (Fig. 26B). This cavity appears dorsoventrally quite tall on the complete right bone. On both the right and left elements, there are prominent gaps in the reconstruction, suggesting either that the bone was incompletely ossification of the medial aspect of the ear cavity.

Dorsolateral to the posterior ampullary recess and the ventral ramus, the bone of the opisthotic is drawn into a transversely elongate, tapering paroccipital process. The left process tapers to a narrow, blunted tip (Fig. 26D). We consider the right process broken as it appears transversely much shorter than the left and the degree of tapering is less substantial. Anteriorly, the paroccipital process is continuous with a prominent, lateral convexity that runs into the prootic (Fig. 26A), which houses the horizontal semicircular canal.

Internally, the opisthotic appears to contribute to two prominent ridges that frame the anterior and anterodorsal borders of the posterior ampullary recess (Fig. 26B). The anterodorsal border exhibits a dorsally concave surface that contributed to the subarcuate fossa. The posterodorsal margin of this ridge exhibits a distinct facet for the supraoccipital. The ventral surface of this margin provided a roof for a portion of the vestibule.

Comparisons

The construction of both the bony separation between the metotic fissure and the foramen ovale in Drepanosauridae n. gen., n. sp. is complex relative to the condition in Sauria. In *Captorhinus aguti* (e.g., Price, 1935) and *Araeoscelis gracilis* (Vaughn, 1955), the opisthotic is ventral drawn into an anteroposteriorly narrow plate that forms a prominent portion of the ventrolateral surface of the occiput. This contrasts with the condition in *Youngina capensis* (Gardner et al., 2010), in which the ventral ramus is dorsoventrally elongate, but exhibits no plate-like posterior surface. In many early archosauromorphs, the ventral ramus of the opisthotic is a slender strut that terminates ventrally in a curved, expanded contact surface for the basioccipital and parabasisphenoid (e.g., *Macrocnemus bassanii*, sexy PIMUZ specimen; *Mesosuchus browni*, Dilkes, 1998; *Prolacerta broomi*, BP/1 2675). Excluding the prominent ventral expansion, this construction is similar to extant *Sphenodon punctatum* (e.g., Gower and Weber, 1998).

Tapered paroccipital processes, as in Drepanosauridae n. gen., n. sp., are unprecedented among Permo-Triassic reptiles. The paroccipital processes do taper in captorhinomorphs (e.g., Price, 1935), *Youngina capensis* (Gardner et al., 2010), and some early archosauromorphs (e.g., *Tanystropheus longobardicus*, PIMUZ T/2819; *Trilophosaurus buettneri*, TMM 31025-140). However, the degree of tapering in Drepanosauridae n. gen., n. sp. is unprecedented. In contrast, other early archosauromorphs exhibit anteroposteriorly flattened processes that expand distally (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2675; *Proterosuchus fergusi*, NMQR 880); rhynchosaurs, Dilkes, 1998).

The distal end of the paroccipital process in Drepanosauridae n. gen., n. sp. does not exhibit any clear contact with the suspensorium. The contact of this process with the elements of the skull table are extremely variable in early diapsids and saurians. In *Youngina capensis*, the process braces the dorsum of the quadrate (Evans, 1987; Gardner et al., 2010), which contrasts with other tangasaurid “younginiforms” (Evans, 1987). In a number of early archosauromorph groups, the process makes a contact with the skull table at the lateral end of the supratemporal fenestra. Such cases include *Protorosaurus speneri* (Gottmann-Quesada and Sander, 2009), *Trilophosaurus buettneri* (Parks, 1969), and *Proterosuchus alexanderi* (NMQR 1484). Such contacts are also reported in *Kuehneosaurus* (Robinson, 1962), and a cartilaginous structure is reported fitting between the cephalic condyle of the quadrate, distal end of the squamosal, and paroccipital process in *Sphenodon* (Evans, 2008).

Prootic

The prootic in Drepanosauridae n. gen., n. sp. is anterodorsally tall. It exhibits a prominent endocranial contribution and a smaller, anteroventrally positioned anterior inferior process. The anterior inferior process is broken away from the endocranial contribution in the left prootic (Fig. 28), whereas the right element appears to be largely undistorted (Fig. 26).

The endocranial contribution of the prootic is very large and dorsoventrally tall. It forms much of the lateral surface of the braincase (Fig. 26A, 26B). It is anteriorly and dorsally convex, framed by a thickening that suggests the position of the anterior semicircular canal. Unfortunately, the canal itself is very difficult to see in the CT slices. On the left side, the entire endocranial contribution is displaced onto the top of the opisthotic, obscuring the height of the bone. Anterodorsally, the prootic exhibits a transversely stout, medially oriented projection (Fig. 26B. 26C). The projection on the right side is dorsoventrally tall and anteroposteriorly flattened, whereas the projection of the left prootic appears dorsoventrally shorter.

Medially, the endocranial contribution of the prootic forms a large contribution to the anterior portion of the subarcuate fossa (Fig. 26B). The prootic also exhibits a dorsoventrally flattened lamina that frames the ventral portion of the fossa. There is a line of breakage at the along the posterolateral margin of this lamina on the right side, which may represent the position of the prootic-opisthotic contact. Although more heavily distorted, a similar breakage is evident on the left side.

The anterior inferior process of the prootic projects from the anteroventral margin of the endocranial contribution of the prootic. The process is convex along its lateral surface (Fig. 26C, 28). The dorsal and ventral margins are weakly defined in the reconstruction of the right and left sides. The right process appears dorsoventrally taller than the left, although this is likely due to distortion on one or both sides.

Medially, the dorsum of anterior inferior process is continuous with the ventral margin of the subarcuate fossa (Fig. 28B). It is deeply concave along its anteroposterior length. The posterior portion of this concavity is deepest, which likely represents the position of the anterior ampullary recess, as this equivalent in position to the anteriormost portions of the anterior and horizontal semicircular canals. We cannot identify a foramen for the facial nerve on either the right or left side. The anterior inferior process terminates in in a medially oriented, spool-shaped facet for the parabasisphenoid (Fig. 26B, 28B). There is not an additional, anterodorsally directed process of the prootic to frame the anterior margin of the notch for the trigeminal nerve.

Comparisons

The prootic in Drepanosauridae n. gen., n. sp. is greater in proportional height than any other Permo-Triassic diapsid. The apparent verticalized nature of the prootic-supraoccipital contact differs from the typical anterodorsally inclined contact in *Captorhinus aguti* (Price, 1935), *Youngina capensis* (Gardner et al., 2010), and many early archosauromorphs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2675; *Czatkowiella harae*, Borsuk-Bialynicka and Evans, 2009b; *Hyperodapedon sanjuanensis*, MCZ 5646).

The smooth lateral margin of the prootic in Drepanosauridae n. gen., n. sp. is shared with *Captorhinus aguti* (Price, 1935), *Youngina capensis* (Evans, 1986; Gardner et al., 2010), and *Azendohsaurus madagaskarensis* (FMNH PR 2765). By contrast, a slender crest, the crista prootica, arcs anteroventrally along the lateral surface of the bone in many squamates (e.g., Oelrich, 1956; Conrad, 2006; Gauthier et al., 2012), *Trilophosaurus buettneri* (TMM 31025-244) and many archosauriforms (e.g., *Proterosuchus fergusi*, BP/1 3393; *Euparkeria capensis*, Gower and Weber, 1998). In these taxa, the crest overhangs the outlet of the facial nerve.

There is no process framing the anterior margin of the notch for the trigeminal nerve in Drepanosauridae n. gen., n. sp. In this way, the taxon resembles *Youngina capensis* (Gardner et al., 2010) and *Trilophosaurus buettneri* (TMM 31025-244). Most early archosauromorphs exhibit a prominent, anterodorsally inclined process that frames the anterior margin of the notch (e.g., *Mesosuchus browni*, SAM-PK-K6536; *Proterosuchus fergusi*, BP/1 3393).

MANDIBLE

The mandibles are nearly complete and partially articulated in AMNH FARB 30834 (Fig. 29). They have been substantially distorted due to dorsoventral crushing to the left side of the specimen. The ventral aspects of the dentaries are poorly reconstructed, made up of scattered, radiopaque fragments. Distinctions between the constituent bones of the mandibles are difficult to assess, although we identify a distinct separation between the dentaries and postdentary bone complexes.

The left dentary appears to be complete, although its ventromedial aspect is poorly reconstructed (Fig. 29B). The dorsolateral margin of the right dentary is heavily weathered. The broken margin of the bone is exposed on the right side of the block. The ventromedial portion of the right dentary is also poorly reconstructed.

There is a prominent, anteroposteriorly running break near the sagittal plane of the skull (Fig. 29). Although this could be interpreted as a symphysis, there is substantially more bone to the right side of the break. Also, the bone just to the right of the break exhibits a prominent, anteroposteriorly running dorsal depression. We consider it more likely that this depressed region represents the midline contact between two dentaries. As there is no clear separation between the left and right hemimandibles at this point, we consider it likely that the bones are fused or at least strong sutured to one another. Anteroventrally at this point, the bone exhibits a V-shaped cross-section in anterior view.

There is no evidence of teeth in either jaw (Fig. 29A). The complete dorsolateral margin of the left dentary forms an elongate, transversely narrow margin that runs the length of the bone. The equivalent region on the right side is eroded and broken. Ventromedial to this occlusal margin, the bone broadens transversely and dorsoventrally into a broad, dorsally facing surface beak. The bone exhibits a prominent, medially facing margin medial to this dorsal surface. We see only a subtle indentation on this surface indicative of a Meckelian groove. The presence or absence of a splenial is equivocal.

The postdentary portion of the mandible is divided into a dorsal and ventral portion by an anteroposteriorly running gap in the lateral surface of the bone (Fig. 29B). The ventral portion may be an angular, although its morphology is poorly reconstructed. On the right side of the jaw, this ventral portion is situated directly ventral to the dorsal portion (Fig. 30). The left ventral portion is displaced medially relative to the dorsal portion, apparently due to the distortion of the jaw.

The dorsal portion of the postdentary region is clearly made up of a fused articular and surangular. On the right side, this dorsal portion appears to be complete and relatively undistorted (Fig. 30). On the left side, the postdentary complex is broken through the anteroposterior middle of the contact surface for the quadrate, such that the posterior part of the adductor fossa and retroarticular process are displaced. The apparent surangular portion of the postdentary region is transversely narrow (Fig. 30C). It is concave medially and subtly concave lateral. In lateral view, the surangular exhibits a dorsoventral expansion at its anterior tip (Fig. 30A). This likely represents a coronoid eminence, which is strongly convex dorsally.

Medially, the postdentary complex shows a concave adductor fossa anterior to the articular (Fig. 30B, 30D). Although dorsoventrally deep, the fossa is transversely narrow. We did not identify a discrete prearticular. It is unclear if it was fused to the compound articular-surangular, or if it was simply absent. Regardless, the ventromedial border to the adductor fossa is quite shallow such that the cavity is open medially (Fig. 30B).

Posteriorly, the surangular portion gives way to a dorsally concave, transversely broad fossa for the quadrate, expanded both laterally and medially beyond the margins of the surangular (Fig. 30A 30B). There is no septation of the articular fossa, equivalent to the undifferentiated quadrate condyle (Fig. 30C). The fossa tapers transversely further posteriorly.

The retroarticular process is a transversely compressed blade of bone that extends posteriorly from the posteromedial margin of the articular fossa (Fig. 30A, 30B). The fossa remains transversely narrow to its posterior tip, where it expands transversely at its terminus. The process exhibits a straight, posterodorsally oriented dorsal margin and a posteroventrally concave ventral margin. The bone is subtly convex laterally and subtly concave medially.

Comparisons

Edentulous mandibles typically follow the same character distribution as edentulousness in upper jaw elements. The anterior half of the dentary in *Hypuronector limnaios*, the only skull bones known for the taxon, is also edentulous (AMNH FARB 2080). The posterior half in that taxon bears stout, conical teeth that resemble those in *Vallesaurus cenensis* (MCSNB 4751). *Hypuronector* further differs from Drepanosauridae n. gen., n. sp. in the absence of a fusion between the left and right dentaries.

Fused, edentulous mandibles occur in a number of later Mesozoic diapsid groups, most notably Coelurosauria. Derived oviraptorosaurs (e.g., Balanoff and Norell, 2012) and a number of avialan groups (e.g., Zhou and Zhang, 2002). Among dinosauromorphs, edentulous mandibles occur in a number of groups considered to be herbivorous. Indeed, edentulousness has been shown to correlate with evidence of herbivory in such taxa (Zanno and Makovicky, 2010). However, the fusion of the mandibles was not found to have a similar statistical relationship.

Without clear sutural relationships evident in the mandibular elements, it is difficult to assess features that Drepanosauridae n. gen., n. sp. with other reptiles. However, it definitely appears that the surangular extended anteriorly to nearly the occlusal margin of the dentary. This contrasts with the condition in rhynchocephalians, in which the dentary exhibits a posterior extension that extends laterally over the surangular.

The presence of a gap in the lateral surface of the mandible ventral to the surangular is equivocal in Drepanosauridae n. gen., n. sp. However, a similarly positioned external mandibular fenestra has been described for *Megalancosaurus preonensis* (e.g., Renesto and Dalla Vecchia, 2005; Renesto et al., 2010). We concur that such a fenestra occurs in MFSN 1769 and MPUM 8437. It is unclear whether the dentary contributes to the boundaries of this opening. Similar fenestrae occur throughout Archosauriformes (e.g., "Chasmatosaurus" *yuani*, IVPP V4067; *Erythrosuchus africanus*, Gower, 2003; *Plateosaurus engelhardti*, Prieto-Marquez and Norell, 2011).

The tall and tapering retroarticular process in Drepanosauridae n. gen., n. sp. is much more prominent than in other known drepanosauromorphs. The mandibles in *Hypuronector limnaios* (Colbert and Olson, 2001; AMNH FARB 2080), *Vallesaurus cenensis* (MCSNB 4751), and *Megalancosaurus* (MFSN 1769, MPUM 8437) exhibit dorsoventrally short retroarticular processes that are positioned well below the dentigerous margins. Similarly short, low processes occur in captorhinomorphs (Heaton, 1979), *Youngina capensis* (e.g., AMNH FARB 5561), weigeltisaurids (*Coelurosauravus jaekeli*, SMNS 53343; *Rautiania* spp., PIN 5130/35, 5130/49). No real retroarticular process occurs in *Petrolacosaurus kansensis* (Reisz, 1981). The tall, tapering retroarticular process of Drepanosauridae n. gen., n. sp. most closely resembles the condition in many early archosauromorphs (e.g., *Macrocnemus bassanii*, PIMUZ T/2472; *Protorosaurus speneri*, USNM 442453, SMNS 53343; *Trilophosaurus buettneri*, TMM 31025-140).

DISCUSSION

The reconstruction of AMNH FARB 30834 allows corroboration of some of the observations made by Renesto and Dalla Vecchia (2005) regarding the skull of *Megalancosaurus preonensis*. Drepanosauridae n. gen., n. sp. has a distinctly inflated frontoparietal region, closely mirroring the inflated posterodorsal portion of the skull in the latter taxon (MFSN 1769). As illustrated by Renesto and Dalla Vecchia (2005: fig. 5) for *Megalancosaurus* and by Renesto and Binelli (2006: fig. 2) for *Vallesaurus*, there is no evidence of a lower temporal bar in AMNH

FARB 30834. Although an incomplete bar was long considered a feature exclusive to lizards and their close relatives (e.g., Parrington, 1935; Robinson, 1962), incomplete lower temporal bars are now recognized widely in early saurian and non-saurian diapsids (e.g., Modesto and Reisz, 2003; Müller, 2003). Unfortunately, the available data from AMNH FARB 30834 are equivocal as to the presence of a mandibular fenestra as illustrated for *Megalancosaurus preonensis* (Renesto and Dalla Vecchia, 2005).

The reconstruction of the postorbital portion of the skull of Drepanosauridae n. gen., n. sp. is strikingly different from those of other drepanosauromorphs. Renesto and Dalla Vecchia (2005) and Renesto and Binelli (2006) both suggested that the squamosal was extremely slender in *Megalancosaurus* and *Vallesaurus*, only bracing a small portion of the quadrate. My own studies of the postorbital regions of these animals are equivocal regarding the sutural relationships of skull elements. The strong posterior convexity of the posteriormost skull elements in these taxa does suggest that a construction similar to Drepanosauridae n. gen., n. sp. was present, but this cannot be determined based on the available Italian materials. If *Megalancosaurus* and *Vallesaurus* did indeed have narrow, gracile squamosals, it would suggest a quadrate bracing mechanism very much unlike that in Drepanosauridae n. gen., n. sp. and a far greater diversity of suspensorium anatomy than is known in any other Triassic diapsid clade.

The critical comparative data offered by the braincase and palatal anatomy of Drepanosauridae n. gen., n. sp. illustrates the stronger similarities of the group with archaic Permian diapsids relative to known Triassic diapsids. Indeed, the isolated, three-dimensional postcranial elements known (e.g., Fraser and Renesto, 2005) also illustrate features similar to non-saurian diapsids, such as notochordal vertebral centra. These discoveries illustrate the importance of a wide range of preservational qualities for specimens when addressing the osteology of a poorly understood group.

CONCLUSIONS

This manuscript presents the first complete osteology of a drepanosauromorph skull, substantially expanding our knowledge of the anatomy of this enigmatic group. The material preserves a range of plesiomorphic traits relative to other Triassic reptiles, especially with regards to the suspensorium and the braincase. However, other characters are autapomorphic relative to other known Triassic diapsids (e.g., frontated orbits, massive endocranium). The reconstruction differs from some past reports of crushed and distorted drepanosauromorph skulls from Upper Triassic Europe, but it remains to be seen if these differences are the result of the poor material of the latter or a high degree of skull diversity in the clade.

LITERATURE CITED

Alonso PD, Milner AC, Ketchum RA, Cookson MJ, Rowe TB. 2004. The avian nature of the brain and inner ear of *Archaeopteryx*. Nature 430:666–669.

Balanoff AM, Norell MA. (2012) Osteology of *Khaan mckennai* (Oviraptorosauria: Theropoda). Bull Am Mus Nat Hist 372:1–77.

Balanoff AM, Xing X, Kobayashi Y, Matsufune Y, Norell MA. (2009) Cranial osteology of the theropod dinosaur *Incisivosaurus gauthieri* (Theropoda: Oviraptorosauria). American Mus Nov 3651:1–35.

Balanoff AM, Bever GS, Rowe TB, Norell MA. (2013) Evolutionary origins of the avian brain. Nature 501:93–96.

Benton MJ. (1985) Classification and phylogeny of the diapsid reptiles. Zool J Linn Soc 84:97–164.

Benton MJ. (1990) The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. Phil Trans Roy Soc B 328:213–306.

Berman DS, Reisz RR. (1992) *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. J Paleontology 66:1001–1009.

Bickelmann C, Müller J, Reisz RR. (2009) The enigmatic diapsid *Acerosodontosaurus piveteaui* (Reptilia: Neodiapsida) from the Permian of Madagascar and the paraphyly of “younginiform” reptiles. Canadian Journal 46:651–661.

Borsuk-Bialynicka M, Evans SE. (2009a) Cranial and mandibular osteology of the Early Triassic archosauriform *Osmolskina czatkowicensis* from Poland. Paleontologia Polonica 65:235–281.

Borsuk-Bialynicka M, Evans SE. (2009b) A long-necked archosauromorph from the Early Triassic of Poland. Palaeontologia Polonica 65:203–234.

Broom R. (1924) On the origin of lizards. Proc Zool Soc London 1925:1–16.

Bulanov VV, Sennikov AG. (2006) The first gliding reptiles form the Upper Permian of Russia. Paleontological Journal 40:S567–S570.

Bulanov VV, Sennikov AG. (2010) New data on the morphology of Permian gliding weigeltisaurid reptiles of eastern Europe. Paleontological Journal 44:682–694.

Caldwell MW. (1994) Developmental constraints and limb evolution in Permian and extant lepidosauromorph diapsids. J Vert Paleo 14:459–471.

Carroll RL. (1981) Plesiosaur ancestors from the Upper Permian of Madagascar. Phil Trans Roy Soc London B 293:315–383.

Carroll RL. (1985) A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Palaeont Abt A 189:1–28.

Chatterjee S. (1993) *Shuvosaurids*, a new theropod. National Geographic Research & Exploration 9:274–285.

Clark J, Carroll RL. (1973) Romeri reptiles from the Lower Permian. Bull Mus Comp Zool 144:353–407.

Cocude-Michel M. (1963) Les rhynchocéphales et les sauriens des Calcaires Lithographiques (Jurassique supérieur) D'Europe Occidentale. Ph.D. thesis, Université de Nancy.

Colbert EH. (1966) A gliding reptile from the Triassic of New Jersey. Am Mus Nov 2246:1–23.

Colbert EH. (1970) The Triassic gliding reptile *Icarosaurus*. Bull American Mus Nat History 143:85–142.

Colbert EH. (1989) The Triassic dinosaur *Coelophysis*. Bulletin of the Museum of Northern Arizona 57:1–160.

Colbert EH and Olsen PJ. (2001) A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). Am Mus Novitates 3334:1–24.

Conrad JL. (2004) Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). Zool J Linn Soc 141:399–434.

Conrad JL. (2006) Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). J Morph 267:769–775.

Conrad JL. (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology Bull Am Mus Nat History 310:1–182.

Cruickshank ARI. (1972) The proterosuchian thecodonts. *Studies in Vertebrate Evolution: Essays presented to F. R. Parrington*, eds KA Joysey, TS Kemp. (Winchester Press, New York).

Currie PJ. (1981) *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeontologia Africana 24:99–168.

Currie PJ. (1982) The osteology and relationships of *Tangasaurus mennelli* Haughton. Annals of South African Museum 86:247–265.

Currie PJ, Carroll RL. (1984) Ontogenetic changes in the eosuchian reptile *Thadeosaurus*. J Vert Paleo 4:68–84.

DeBraga M, Rieppel O. (1997) Reptile phylogeny and the interrelationships of turtles. Zool J Linn Soc 120:281–354.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Proc Roy Soc B 353:501–541.

Estes R, deQueiroz K, Gauthier JA. (1988) Phylogenetic relationships within Squamata. Eds R Estes and G Pregill (Stanford University Press, Palo Alto), pp. 119–281.

Evans SE. (1980) The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool J Linn Soc 70:203–264.

Evans SE. (1986) The braincase of *Prolacerta broomi* (Reptilia: Triassic). N Jarh fur Geo Paleo 173:181–200.

Evans SE. (1987) The braincase of *Youngina capensis* (Reptilia: Diapsida; Permian). N Jahrb fur Geo Paleo Monats 193–203.

Evans SE. (1988) The early history and relationships of the Diapsida. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 221–260.

Evans SE. (2008) The skull of lizards and tuatara. *Biology of the Reptilia Volume 20*, ed C Gans (Society for the Study of Amphibians and Reptiles), pp. 1–347.

Evans SE. (2009) An early kuehneosaurids reptile from the Early Triassic of Poland. Palaeontologia Polonica 65:145–178.

Evans SE. (1982). The gliding reptiles of the Upper Permian. Zool J Linn Soc 76:97–123.

Evans SE and Haubold H. (1987) A review of the Upper Permian genera *Coelurosauravus, Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). Zool J Linn Soc 90:275–303.

Ewer RF. (1965) The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil Trans Roy Soc B 248:379–435.

Ezcurra MD, Butler RI. (2015) Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early archosauriform radiation. Palaeontology 58:141–170.

Ezcurra MD, Scheyer TM, Butler RJ. (2014) The origin and early evolution of Sauria: the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS One 9:e89165.

Fox RC, Bowman MC. (1966) Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). University of Kansas Paleo Contributions 11:1–79.

Fraser NC. (1988). The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). Phil Trans Roy Soc London B 321:125–178.

Fraser NC, Olsen PE, Dooley AC, Ryan TR. (2007) A new gliding tetrapod (Diapsida: ?Archosauromorpha) from the Upper Triassic (Carnian) of Virginia. J Vert Paleo 27:261–265.

Gaffney ES. (1990) The comparative osteology of the Triassic turtle *Proganochelys*. Bull American Mus Nat History 194:1–263.

Gardner NM, Holliday CM, O'Keefe FR. (2010) The braincase of *Youngina capensis* (Reptilia, Diapsida): new insights from high-resolution CT scanning of the holotype. Palaeontologia Electronica 13: 16 pp.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, University of California Berkeley.

Gauthier JA, Estes R, de Queiroz K. (1988) A phylogenetic analysis of Lepidosauromorpha. *Phylogenetic Relationships of the Lizard Families*, eds R Estes, G Pregill (Stanford University Press, Stanford), pp. 15–98.

Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB. (2012) Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bull Peabody Mus Nat History 53:3–308.

Goloboff PA, Farris JS, Nixon KC. (2008) TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Gottmann-Quesada A, Sander PM. (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. Palaeontographica Abteilung A 287:123–220.

Gow CE. (1972) The osteology and relationships of the Millerettidae (Reptilia: Cotylosauria). J Zool Soc London 167:219–264.

Gow CE. (1975) The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeontologia Africana 18:89–131.

Gower DJ. (1997) The braincase of the early archosaurian reptile *Erythrosuchus africanus*. J Zool Soc London 242:557–576.

Gower DJ. (2003) Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. Annal S Afr Mus 110:1–88.

Gower DJ, Sennikov AG. (1996) Morphology and phylogenetic informativeness of early archosaur braincases. Palaeontology 39:883–906.

Gower DJ, Weber E. (1998) The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. Biol Rev 73:367–411.

Gower DJ, Nesbitt SJ. (2008) The braincase of *Arizonasaurus babbitti*—further evidence for the non-monophyly of 'rauisuchian' archosaurs. J Vert Palo 26:79–87.

Greer AE. (1976) On the occurrence of a stapedial foramen in living non-gekkonid lepidosaurs. Copeia 1976:591, 592.

Gregory JT. (1945) Osteology and relationships of *Trilophosaurus*. University of Texas Publication 4401:273–359.

Gregory WK. (1946) Pareiasaurs versus placodonts as near ancestors to the turtles. Bull Am Mus Nat Hist 86:275–326.

Heaton MJ. (1979) Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian Oklahoma and Texas. Bulletin of the Oklahoma Geological Society 127:1–84.

Hopson JA. (1979) Paleoneurology. *Biology of the Reptilia, Vol 9*, ed C Gans (Academic Press, London), pp. 39–146.

Iordansky NN. (1973) The skull of the Crocodylia. *Biology of the Reptilia Vol 4*, eds C Gans (Academic Press, London), pp. 201–262.

Jollie MT. (1960) The head skeleton of the lizard. Acta Zoologica 1960:1–64.

Klembara J, Welman J. (2009) The anatomy of the palatoquadrate in the Lower Triassic *Proterosuchus fergusi* (Reptilia, Archosauromorpha) and its morphological transformation within the archosauriform clade. Acta Zool 90:275–284.

Jiang D-Y, Rieppel O, Fraser NC, Motani R, Hao W-C, Tintori A, Sun Y-L, Sun Z-Y. (2011) New information on the protorosaurian reptile *Macrocnemus fuyuanensis* Li et al., 2007, from the Middle/Upper Triassic of Yunnan, China. J Vert Paleo 31:1230–1237.

Laurin M, Reisz RR. (1995) A reevaluaton of early amniote phylogeny. Zool J Linn Soc 113:165–223.

Li C, Zhao L, Wang L. (2007) A new species of *Macrocnemus* (Reptilia: Protorosauria) from the Middle Triassic of southwestern China and its palaeogeographical implication5. Sci in China D 50:1601–1605.

Maddison WP, Maddison DR. (2015) Mesquite: a modular system for evolutionary analysis. Version 3.02. http://mesquiteproject.org

Merck JA. (1997) A phylogenetic analysis of the euryapsid reptiles. Ph.D. thesis, University of Texas at Austin.

Modesto SP, Reisz RR. (2003) An enigmatic new diapsid reptile from the Upper Permian of eastern Europe. J Vert Paleo 22:851–855.

Modesto SP, Sues H-D. (2004) The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. Zool J Linn Soc 140:335–351.

Montefeltro FC, Langer MC, Schultz CL. (2010) Cranial anatomy of a new genus of hyperodapedontine rhynchosaur (Diapsida, Archosauromorpha) from the Upper Triassic of Brazil. Earth Env Sci Trans Roy Soc Edin 101:27–52.

Montefeltro FC, Bittencourt JS, Langer MC, Schultz CL. (2013) Postcranial anatomy of the hyperodapedontine rhynchosaur *Teyumbaita sulcognathus* (Azevedo and Schultz, 1987) from the Late Triassic of southern Brazil. J Vert Paleo 33:67–84.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Nesbitt SJ (2011) The early evolution of archosaurs: relationships and the origin of major clades. Bull American Mus Nat History 352:1–292.

Nesbitt SJ, Norell MA. (2006) Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda) Proc Roy Soc B 273:1045–1048.

Nesbitt SJ, Flynn JJ, Pritchard AC, Parrish JM, Ranivoharimanana L, Wyss A. (in press) Postcranial anatomy and relationships of *Azendohsaurus madagaskarensis*. Bull Am Mus Nat Hist.

Nosotti S. (2007) *Tanystropheus longobardicus* (Reptilia, Protorosauria): re-interpretations of the anatomy based on new specimens from the Middle Triassic of Besano (Lombardy, northern Italy). Mem Soc Ital Sci Natu Mus Civ Storia Nat Milano 35:1–88.

Oelrich TM. (1956) The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Misc Pub Mus Zool, U of Mich 94:1–122.

Olsen PE. (1979) A new aquatic eosuchian from the Newark Supergroup (Late Triassic–Early Jurassic) of North Carolina and Virginia. Postilla 176:1–14.

Osborn HF. (1903) On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. Science 17:275, 276.

Osmólska H, Roniewicz E, Barsbold R. (1972) A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. Paleontologia Polonica 27:103–143.

Osmólska H, Currie PJ, Barsbold R. (2004) Oviraptorosauria. *Dinosauria, 2nd Edition,* eds D Weishampel, P Dodson, H Osmólska (University of California Press, Berkeley), pp. 165–183.

Parks P. (1969) Cranial anatomy and mastication of the Triassic reptile *Trilophosaurus*. M.S. Thesis, University of Texas at Austin

Parrington FR. (1935) On *Prolacerta broomi*, gen. et sp. n., and the origin of lizards. Annales and Magazine of Natural History 16:197–205.

Pinna G. (1980) *Drepanosaurus unguicaudatus*, nuovo genere e nuova specie di lepidosauro del Trias alpino. Atti della Soc ital di sci nat del mus civ di storia nat di Milano 121:181–192.

Pinna G. (1984) Osteologia di *Drepanosaurus unguicaudatus*, lepidosauro triassico del sottordine Lacertilia. Mem della Soc ital. di sci nat e del Mus civ di storia nat di Milano 24:7–28.

Pinna G. (1986) On *Drepanosaurus unguicaudatus*, an Upper Triassic lepidosaurian from the Italian Alps. J Paleo 60:1127–1132.

Price LI. (1935) Notes on the brain case of *Captorhinus*. Proc Boston Soc Nat History 40:377–386.

Prieto-Márquez A, Norell MA. (2011) Redescription of a nearly complete skull of *Plateosaurus* (Dinosauria: Sauropodomorpha) from the Late Triassic of Trossingen (Germany). Am Mus Novitates 3727:1–58.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2015). Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. Journal of Vertebrate Paleontology 35: e911186.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Special Publication of the Museum of Natural History, University of Kansas 7:1–74.

Reisz RR, Modesto SP, Scott DM. (2011) A new Early Permian reptile and its significance in early diapsid evolution. Proc Roy Soc B 278:3731–3737.

Renesto S. (1994a) *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. J Vert Paleo 14:38–52.

Renesto S. (1994b) The shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the upper Triassic (Norian) of northern Italy. Zool J Linn Soc 111:247–264.

Renesto S. (2000) Bird-like head on a chameleon body: new specimens of the enigmatic diapsid reptile *Megalancosaurus* from the Late Triassic of northern Italy. Riv Ital Paleo Stat 106:157–180.

Renesto S and Dalla Vecchia FM. (2005) The skull and lower jaw of the holotype of *Megalancosaurus preonensis* (Diapsida, Drepanosauridae) from the Upper Triassic of Italy. Riv Ital Paleo Stat 111:247–257.

Renesto S and Binelli G. (2006) *Vallesaurus cenensis* Wild, 1991, a drepanosaurid (Reptilia, Diapsida) from the Late Triassic of northern Italy. Riv Ital Paleo Stat 112:77–94.

Renesto S, Spielmann JA, Lucas SG, and Spagnoli GT. (2010) The taxonomy and paleobiology of the Late Triassic (Carnian–Norian: Adamanian–Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha). Bull NM Mus Nat Hist Sci 46:1–81.

Robinson PGL. (1962) Gliding lizards from the upper Keuper of Great Britain. Proc Geol Soc London 1601:137–146.

Robinson PGL. (1967a) Triassic vertebrates from lowland and upland. Sci & Cult 33:169–173.

Robinson PGL. (1967b) The evolution of the Lacertilia. Problèms actuels de paléontologie (evolution des vertébrés). Colloques Internationaux du Centre National de la Recherche Scientifique 163:395–407.

Robinson PGL. (1973) A problematic reptile from the British Upper Trias. J Geol Soc London 129:457–479.

Romer AS. (1956) *Osteology of the Reptiles*. (University of Chicago Press, Chicago), 772 pp.

Fraser NC, Rieppel O. (2006) A new protorosaur (Diapsida) from the upper Bundsandstein of the Black Forest, Germany. J Vert Paleo 26:866–871.

Rybczynski N. (2000) Cranial anatomy and phylogenetic position of *Suminia getmanovi*, a basal anomodont (Amniota: Therapsida) from the Late Permian of eastern Europe. Zool J Linn Soc 130:329–373.

Coddington J, Scharff N. (1994) Problems with zero-length branches. Cladistics 10:415–423.

Sen K. (2003) *Pamelaria dolichotrachela*, a new prolacertid reptile from the Middle Triassic of India. J Asia Earth Sci 21:663–681.

Senter PJ. (2004) Phylogeny of Drepanosauridae (Reptilia: Diapsida). Journal of Systematic Palaeontology 2:257–268.

Sues H-D. (2003) An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. Canadian Journal Earth Sci 40:635–649.

Tsuji LA. (2006) Cranial anatomy and phylogenetic affinities of the Permian parareptiles *Macroleter poezicus*. J Vert Paleo 26:849–865.

Vaughn PP. (1955) The Permian reptile *Araeoscelis* restudied. Bull Mus Comp Zool 113:305–467.

Ward PD, Botha J, Buick R, de Kock MO, Erwin DH, Garrison GH, Kirschvink JL, Smith R. (2005) Abrupt and gradual extinction among Late Permian land vertebrates in the Karoo basin, South Africa. Science 307:709–714.

Whiteside DI. (1986) The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et sp. nov. and the modernizing of a living fossil. Phil Trans Roy Soc London 312:379–403.

Witmer LM, Chatterjee S, Franzosa J, Rowe T. (2003) Neuroanatomy of flying reptiles and implications for flight, posture and behavior. Nature 425:950–953.

Young CC. (1936) On a new *Chasmatosaurus* from Sinkiang. Bull Geol Soc China 15:291–311.

Young CC. (1963) Additional remains of *Chasmatosaurus yuani* Young from Sinkiang, China. Vertebrate PalAsiatica 7:215–222.

Zanno L, Makovicky PJ. (2010) Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. Proc Nat Acad Sci 108:232–237.

Zhang F-K. (1975) A new thecodont *Lotosaurus*, from the Middle Triassic of Hunan. Vertebrata PalAsiatica 5:144–147.

Zhou Z, Zhang F. (2002) A long-tailed, seed-eating bird from the Early Cretaceous of China. Nature 418:405–409.

SUPPLEMENTAL APPENDIX 1. Anatomical Abbreviations

aar–anterior ampullary recess
add–adductor fossa
ala–parabasisphenoid, alar process.
ang–angular
asc–anterior semicircular canal
bpt–parabasisphenoid, basipterygoid process
bpta–basipterygoid articulation
brm–broken margin
bt–basioccipital basal tubera
cdbo–opisthotic, dorsal contact for basioccipital
cvbo–opisthotic, ventral contact for basioccipital
cdop–basioccipital, dorsal contact for opisthotic
ceo–supraoccipital, contact for exoccipital

cfpa–frontal, contact for parietal
cfpo–frontal, contact for postfrontal
clt–parabasisphenoid, cultriform process
cmpa–maxilla, contact for palatine
copo–opisthotic, contact for prootic
cor–coronoid eminence.
cpp–parietal, contact for contralateral parietal
cse–parabasisphenoid, crista sellaris
csop–supraoccipital, contact for opisthotic
cvop–basioccipital, ventral contact for opisthotic
cfo–contribution to foramen ovale
cpbs–contact surface for parabasisphenoid
cpf–parietal, contact for frontal
cpff–postfrontal, contact for frontal
cpfp–postfrontal, contact for parietal
cpfpo–postfrontal, contact for postorbital
cppf–parietal, contact for postfrontal
deer–dentary, edentulous region
dep–depression
dse–parabasisphenoid, dorsum sellae
end–endocranial contribution
eo–exoccipital
epaml–anteromedial lamina
epds–epipterygoid, dorsal stem
epmc–epipterygoid, medial concavity
fo–foramen ovale
fpl–frontal, posterolateral process
gcnV–gap for trigeminal nerve (cranial nerve V)
gl–glenoid fossa
hsc–horizontal semicircular canal
ja–jugal, anterior process
mef–metotic fissure
mpp–maxilla, posterior process
nar–contribution to external naris.
np–notochordal pit
occ–occlusal margin
ol–postfrontal, orbital lamina
om–orbital margin
paap–palatine, anteriormost pterygoid articulation
pama–palatine, maxillary articulation
pamp–palatine, maxillary process
papl–palatine, palatal lamina
par–posterior ampullary recess
pbp–parabasisphenoid, contact for prootic
pbs–parabasisphenoid
pc–parietal, crack along margin of ventral transverse ridge

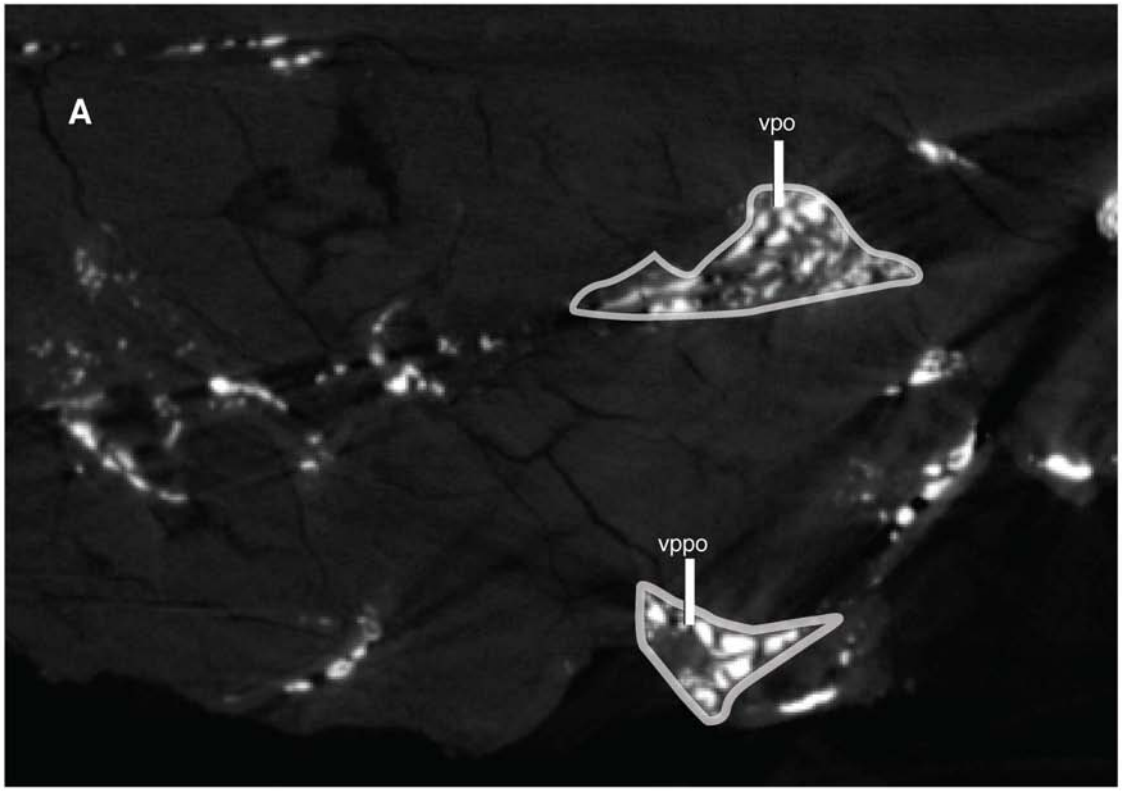
pcp–parabasisphenoid, pre-cultriform process
pdl–parietal, dorsal lamina
peop–posterior exposure of opisthotic
pfap–postfrontal, anterior process
pfpm–postfrontal, posteromedial process
pfstf–postfrontal, contribution to supratemporal fenestra
pfvp–postfrontal, ventral process
pl–parietal
pnf–parietal, notch for posterolateral process of frontal
poap–postorbital, anterior process
pop–paroccipital process
popp–postorbital, posterior process
povp–postorbital, ventral process
ppl–parietal, posterolateral process
prcm–premaxilla, contact for maxilla.
prmf–premaxilla, site of midline fusion.
pstf–parietal, contribution to supratemporal fenestra
pta–articulation for pterygoid
ptaf–pterygoid, anterior facet for palatine
ptar–pterygoid, anterior ramus
ptqr–pterygoid, quadrate ramus
pvl–parietal, ventral lamina
qcs–quadrate, condylar surface
qdr–quadrate, dorsal ramus
qjc–quadrate, quadratojugal contact
qmr–quadrate, medial ridge
qpr–quadrate, pterygoid ramus
ret–retroarticular process
rppo–rostral process of prootic
saf–subarcuate fossa
so–supraoccipital
soem–supraoccipital, dorsal embayment for parietals
sqap–squamosal, anterior process
sqdl–squamosal, descending lamina
sqdm–squamosal, dorsomedial process
sqpl–squamosal, posterior lamina
sqpo–squamosal, postorbital facet
stfp–stapes, stapedial footplate
stsd–stapes, expansion of the distal shaft
sym–fused symphyseal region of dentary
th–thickening (position of quadratojugal?)
vlc–parabasisphenoid, ventrolateral crest
vmp–parabasisphenoid, ventromedian process
vpo–visible portion of occipital condyle of basioccipital
vpp–visible portion of parietal
vppo–visible portion of prootic

vtr–parietal, ventral transverse ridge

SUPPLEMENTAL APPENDIX 2. Institutional Abbreviations.

AMNH FARB–American Museum of Natural History, Fossil Amphibian, Reptiles and Birds (New York, NY, USA)
BP–Evolutionary Studies Institute (formerly Bernard Price Institute; Johannesburg, South Africa)
CMNH–Carnegie Museum of Natural History (Pittsburgh, PA, USA)
FMNH–Field Museum of Natural History (Chicago, IL, USA)
GMPKU–Geological Museum of Peking University (Beijing, China)
IVPP–Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China)
MCSN–Museo Civico di Storia Naturali (Milano, Italy)
MCSNB–Museo Civico di Storia Naturali Enrico Caffi (Bergamo, Italy)
MCZ–Museum of Comparative Zoology (Cambridge, MA, USA)
MFSN–Museo Friulano di Scienze Naturali (Udine, Italy)
MNHN–Muséum National d'Histoire Naturelle (Paris, France)
MPUM–Museo di Paleontologia Università degli Studi di Milano (Milano, Italy)
NHMUK–Natural History Museum of the United Kingdom (London, United Kingdom)
NMK–Naturkundmuseum im Ottoneum (Kassel, Germany)
NMMNHS–New Mexico Museum of Natural History and Science (Albuquerque, NM, USA)
NMQR–National Museum (Bloemfontein, South Africa)
PIMUZ–Paleontological Institute and Museum, University of Zürich (Zürich, Switzerland)
PIN–Paleontological Institute (Moscow, Russia)
SAM–Iziko Museum of South Africa (Cape Town, South Africa)
SMNS–Staaliches Museum fur Naturkunde Stuttgart (Stuttgart, Germany).
SSGW–Sektion Geologie, Ernst-Moritz-Arndt Universistät (Greifswald, Germany)
TMM–Texas Memorial Museum (Austin, TX, USA)
UA–Université d'Antananarivo (Antananarivo, Madagascar)
UCMP–University of California Museum of Paleontology (Berkeley, CA, USA)
UMMP–University of Michigan Museum of Paleontology (Ann Arbor, MI, USA)
USNM–United States National Museum (Washington, DC, USA)
VMNH–Virginia Museum of Natural History (Martinsville, VA, USA)
WMsN–Westfäliches Museum für Naturkunde (Münster, Germany)
YPM–Yale Peabody Museum (New Haven, CT, USA)
ZPAL–Institute of Paleobiology (Warsaw, Poland)

FIG. 5-1. Illustration of contrasts visible in the μCT scan of AMNH FARB 30834. **A**, illustrates high contrast values evident for some bones of the skull, which appear as bright white against the dark gray value of the matrix. **B**, shows the low contrast the characterizes certain other bones, in which small flecks of bright and radiopaque materials are surrounded by a subtle light gray halo against the dark gray matrix.


A
vpo
vppo

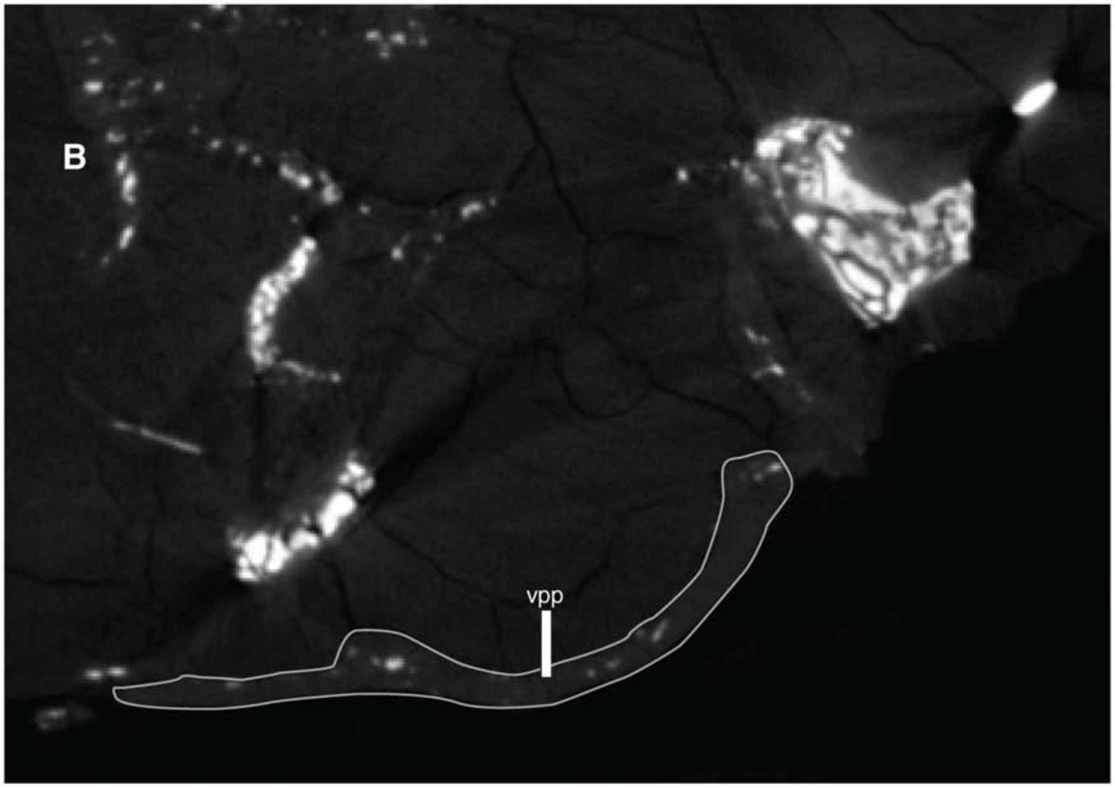

B
vpp

FIG. 5-2. Three-dimensional reconstruction of partial fused? premaxillary complex of Drepanosauridae n. gen., n. sp. in **A**, left lateral, **B**, dorsal, **C**, anterior, and **D**, ventral views.

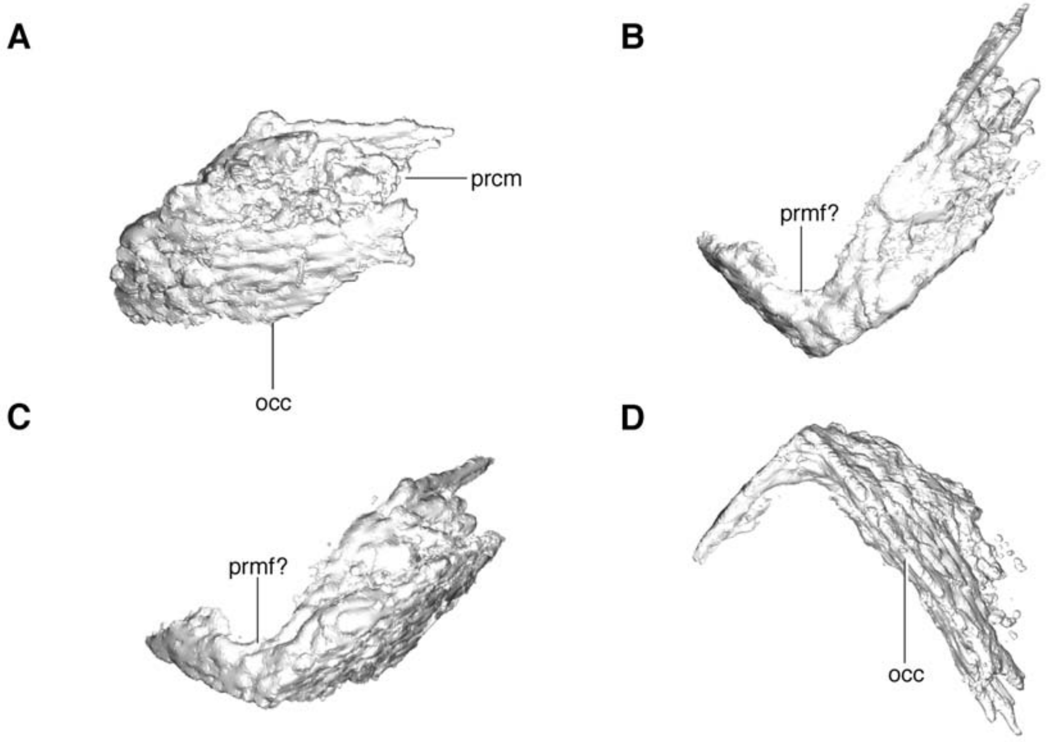

A
prcm
occ
B
prmf?
C
prmf?
D
occ

FIG. 5-2. Three-dimensional reconstruction of partial fused? premaxillary complex of Drepanosauridae n. gen., n. sp. in **A**, left lateral, **B**, dorsal, **C**, anterior, and **D**, ventral views.

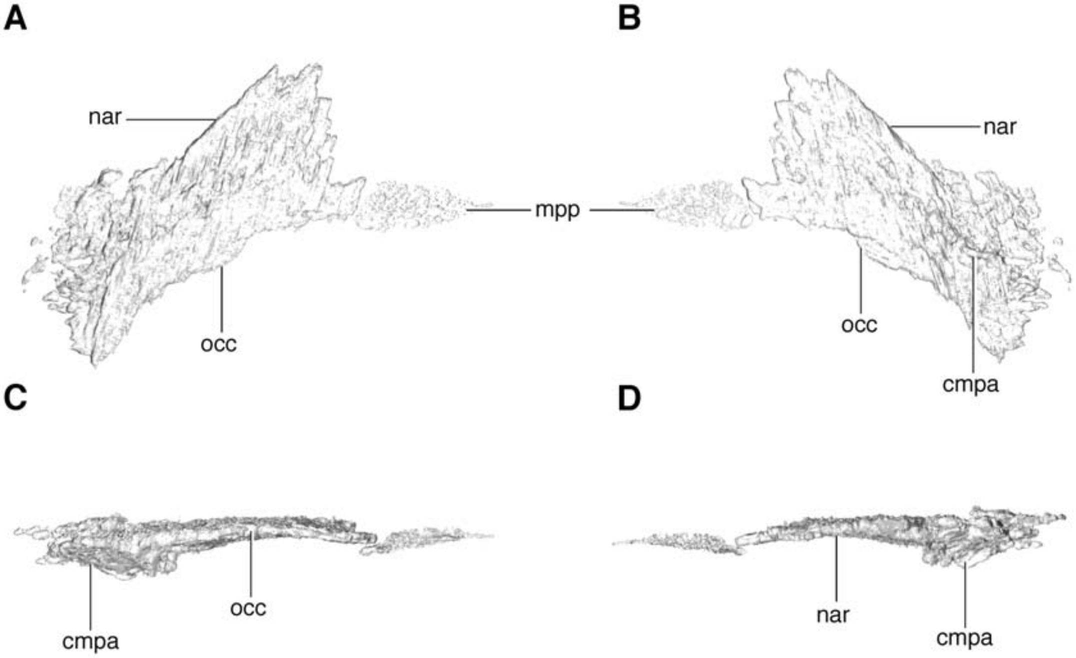

A
B
nar
nar
mpp
occ
occ
cmpa
C
D
cmpa
occ
nar
cmpa

FIG. 5-4. Three-dimensional reconstruction of left jugal of Drepanosauridae n. gen., n. sp. in **A**, lateral and **B**, medial views.

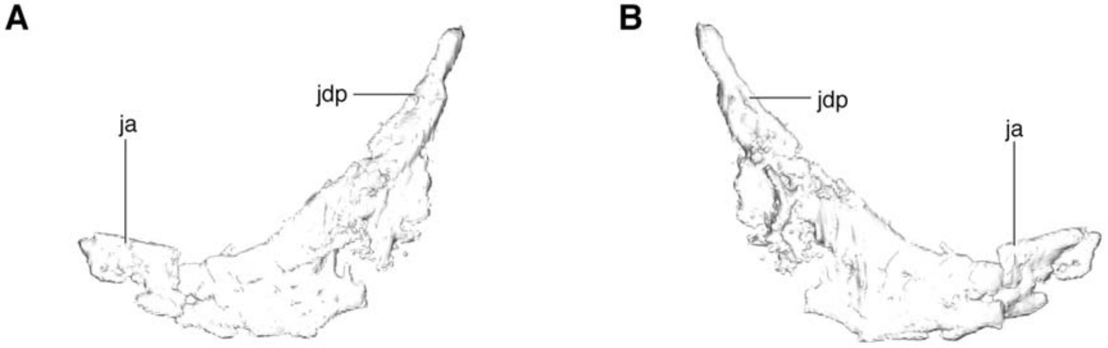

A
jdp
ja
B
jdp
ja

FIG. 5-5. Three-dimensional reconstruction of left postorbital of Drepanosauridae n. gen., n. sp. in **A**, lateral, **B**, medial, **C**, dorsal, and **D**, ventral views.

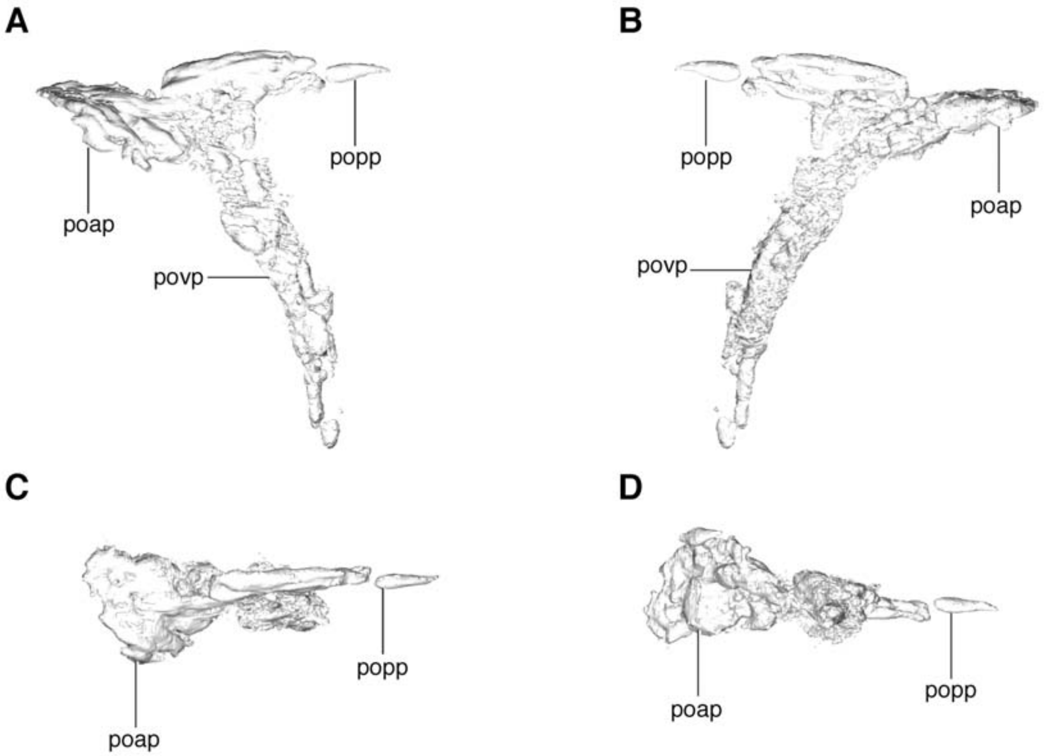

A
popp
poap
povp
B
popp
poap
povp
C
popp
poap
D
poap
popp

FIG. 5-6. Three-dimensional reconstruction of right postorbital of Drepanosauridae n. gen., n. sp. in **A**, lateral, **B**, medial, **C**, anterior, and **D**, posterior views.

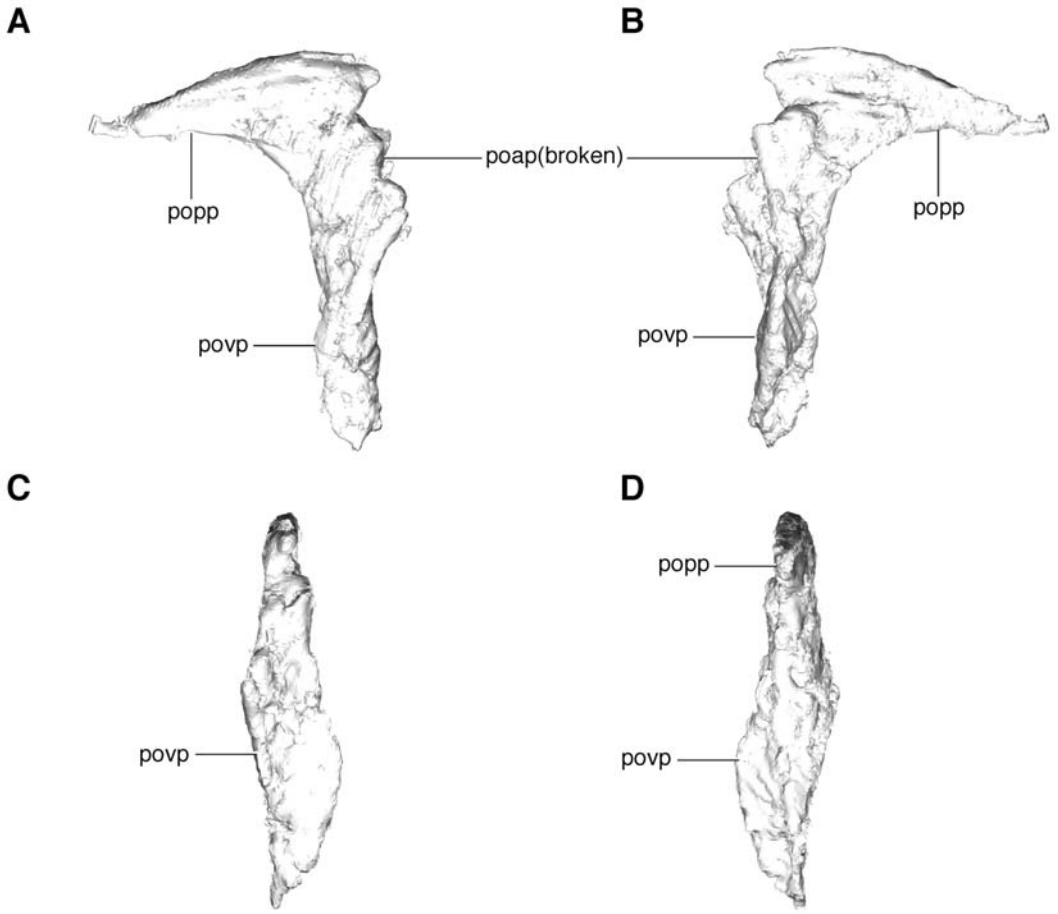

A
B
poap(broken)
popp
popp
povp
povp
C
D
popp
povp
povp

FIG. 5-7. Three-dimensional reconstruction of left postfrontal of Drepanosauridae n. gen., n. sp. in **A**, ventral, **B**, dorsal, **C**, lateral, **D**, medial, **E**, anterior, and **F**, posterior views.

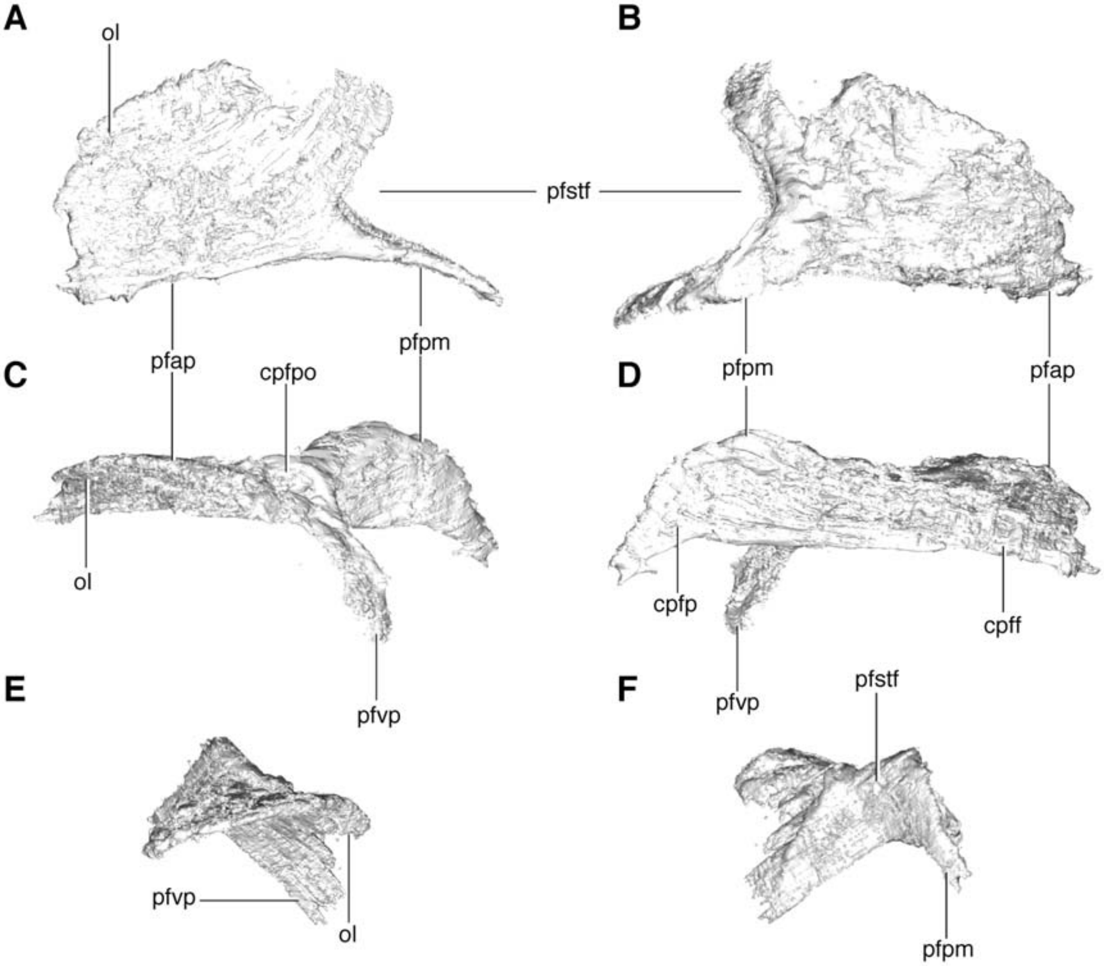

A
ol
B
pfstf
pfap
pfpm
C
cpfpo
D
pfpm
pfap
ol
cpfp
cpff
pfvp
E
F
pfvp
pfstf
pfvp
ol
pfpm

FIG. 5-8. Three-dimensional reconstruction of right postfrontal of Drepanosauridae n. gen., n. sp. in **A**, dorsal, **B**, ventral, **C**, lateral, and **D**, medial views.

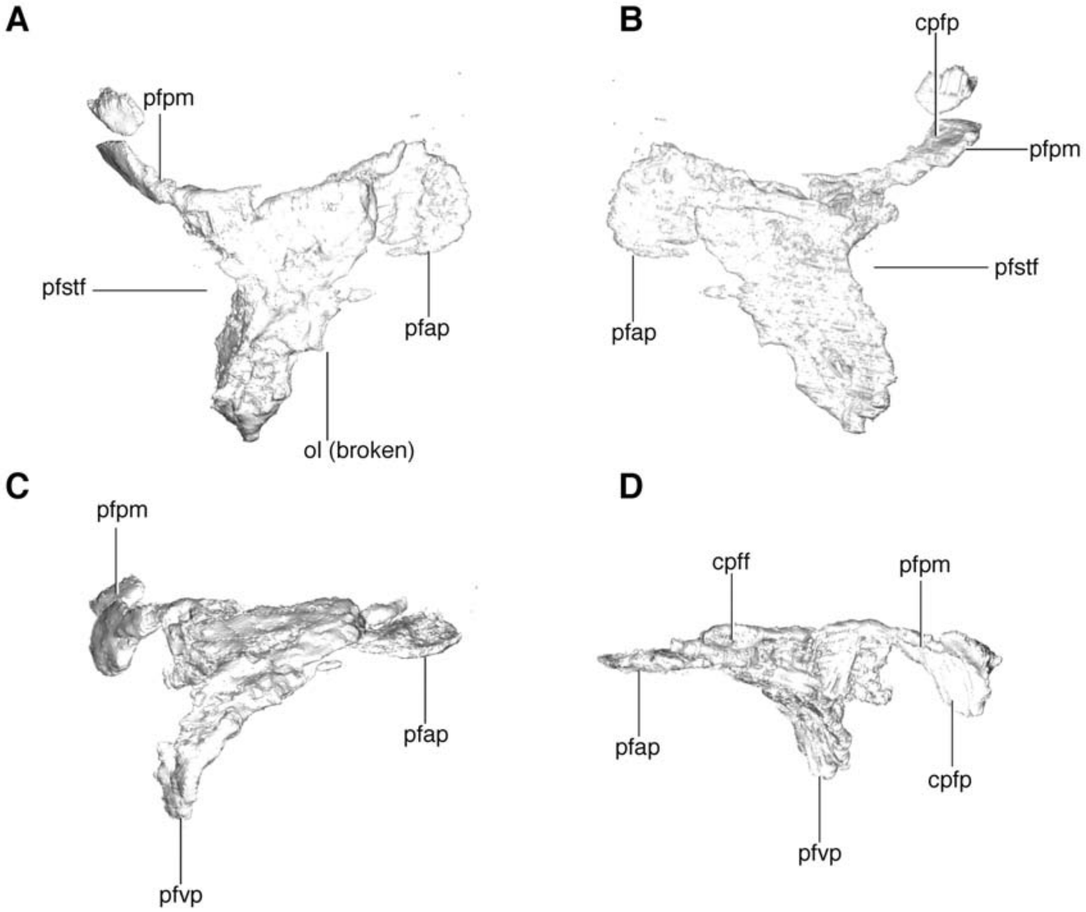

A
pfpm
pfstf
pfap
ol (broken)
B
cpfp
pfpm
pfstf
pfap
C
pfpm
pfap
pfvp
D
cpff
pfpm
pfap
cpfp
pfvp

FIG. 5-9. Three-dimensional reconstruction of left frontal of Drepanosauridae n. gen., n. sp. in **A**, dorsal, **B**, ventral, **C**, lateral, **D**, medial, **E**, anterior, and **F**, posterior views.

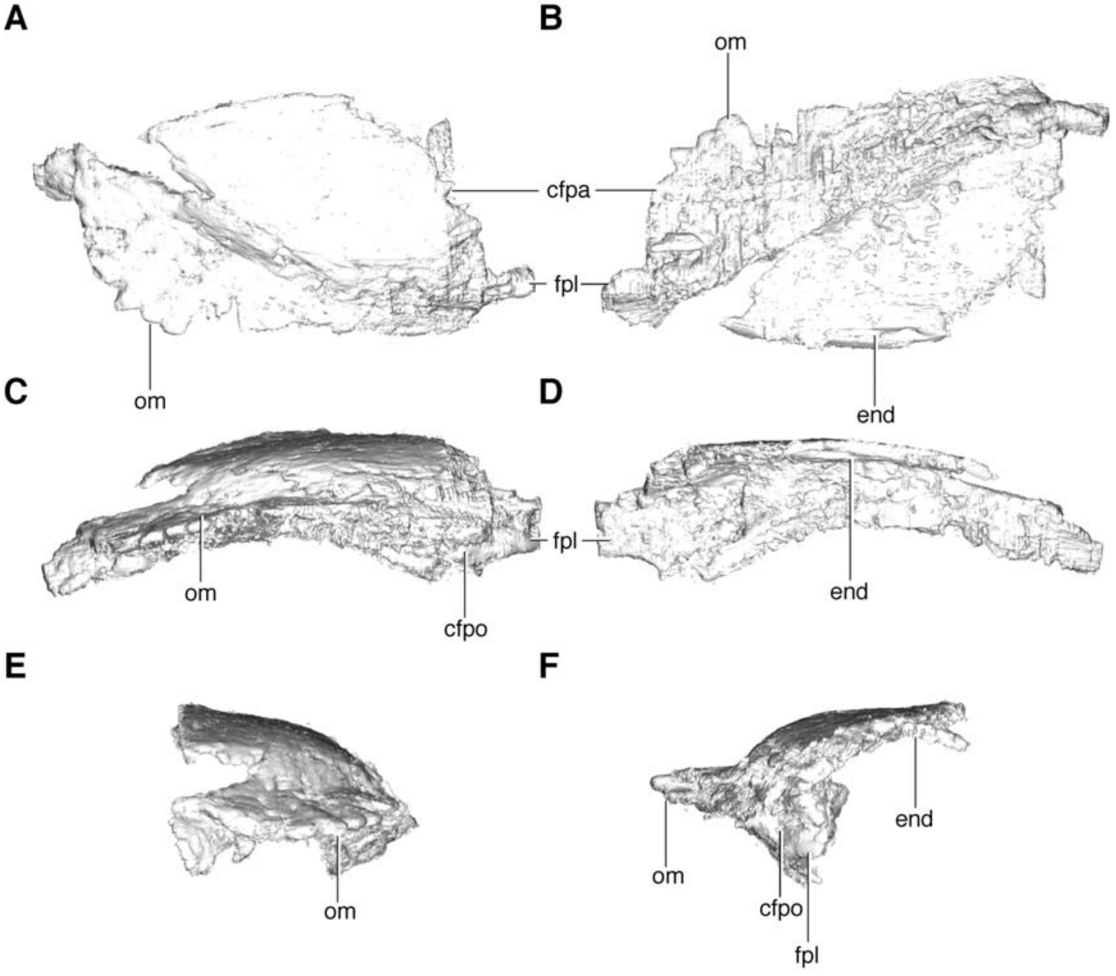

A
B
om
cfpa
fpl
om
C
D
end
fpl
om
cfpo
end
E
F
end
om
om
cfpo
fpl

FIG. 5-10. Three-dimensional reconstruction of left parietal of Drepanosauridae n. gen., n. sp. in **A**, dorsal, **B**, ventral, **C**, medial, **D**, lateral, **E**, posterior, and **F**, anterior views.

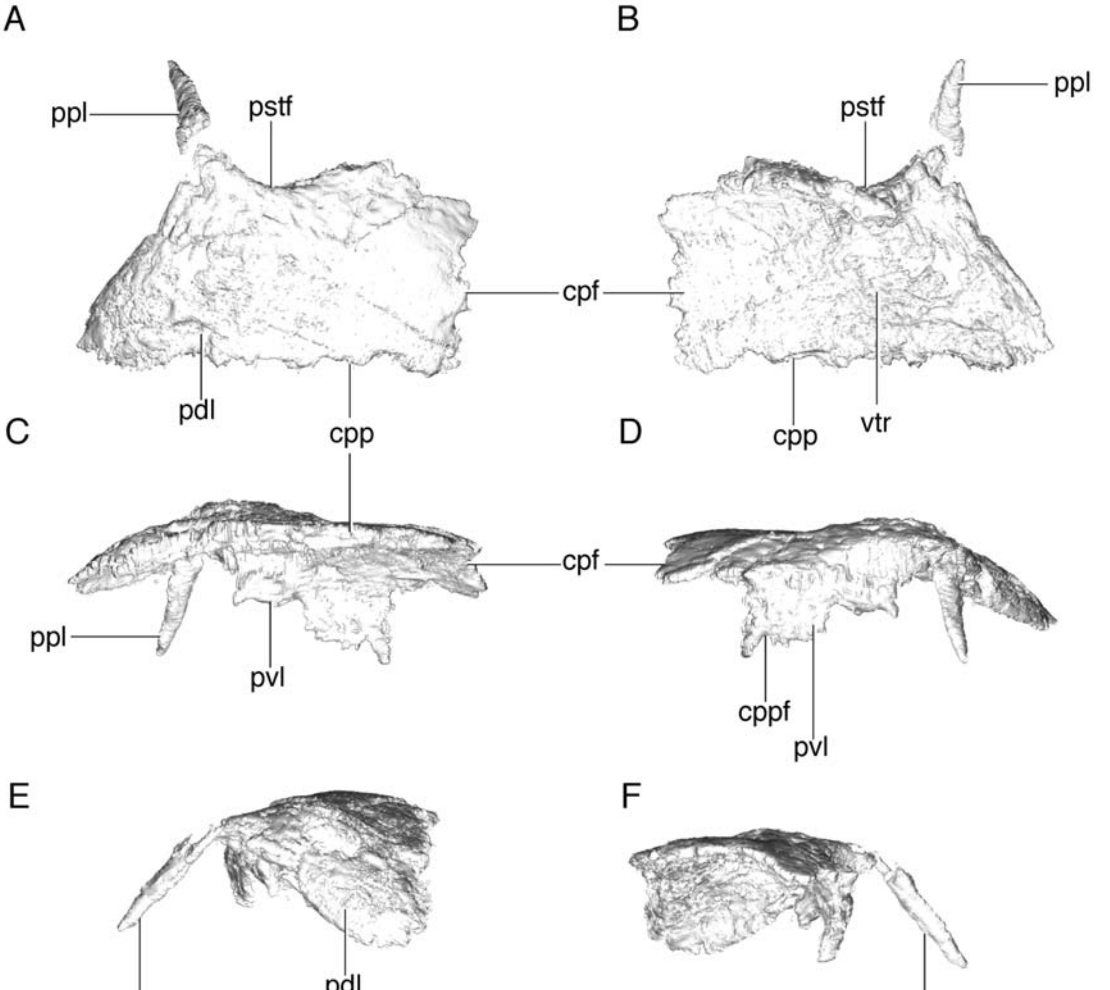

A
B
ppl
pstf
pstf
ppl
cpf
cpf
pdl
cpp
cpp
vtr
C
D
cpp
cpf
cpf
ppl
pvl
cppf
pvl
E
F
ppl
pdl
ppl

FIG. 5-11. Three-dimensional reconstruction of right parietal of Drepanosauridae n. gen., n. sp. in **A**, dorsal, **B**, ventral, **C**, medial, **D**, lateral, **E**, posterior, and **F**, anterior views.

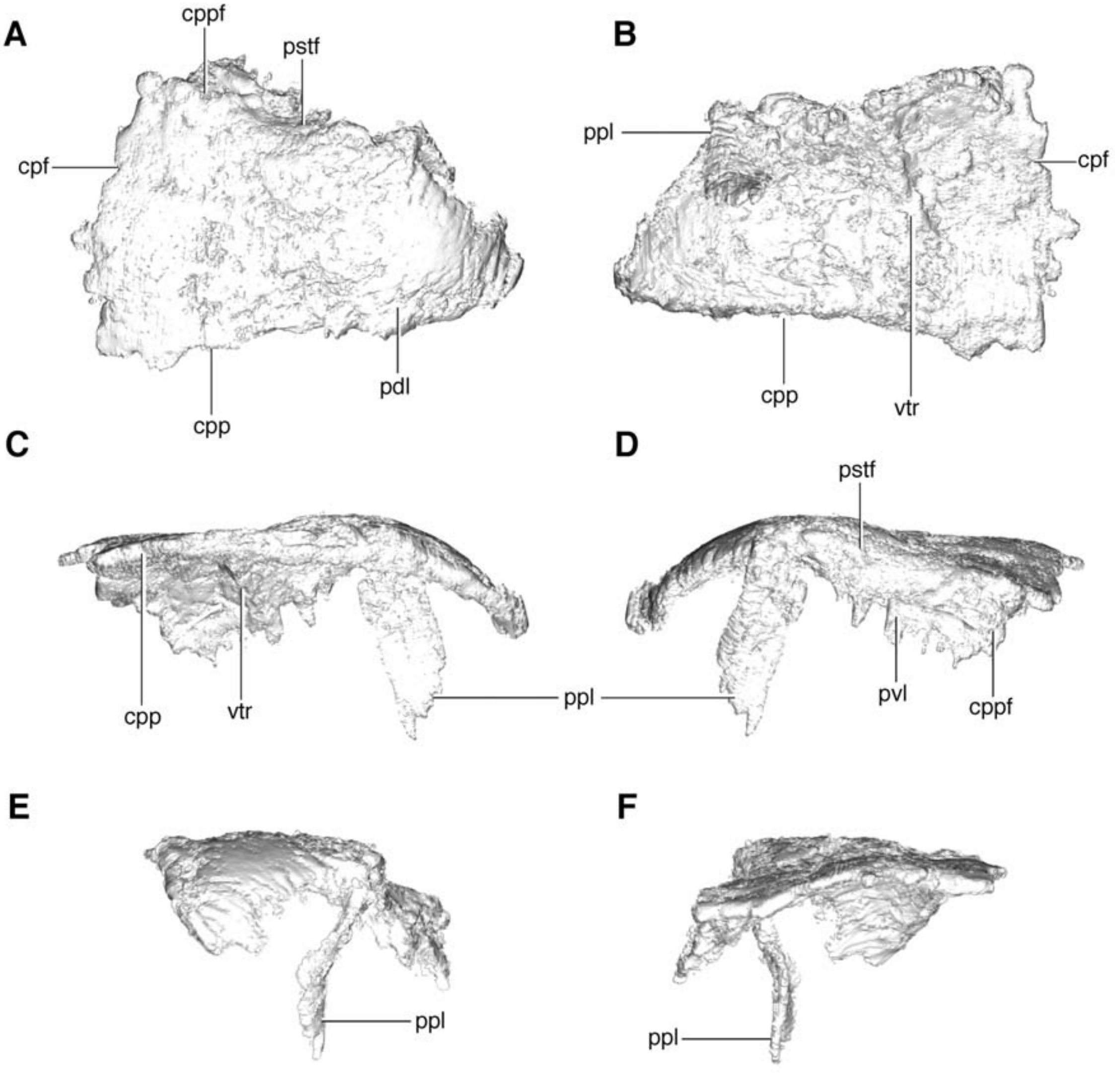

A
cppf
pstf
cpf
cpp
pdl
B
ppl
cpf
cpp
vtr
C
cpp
vtr
ppl
D
pstf
pvl
cppf
E
ppl
F
ppl

FIG. 5-12. Skull roof of *Megalancosaurus preonensis* (MPUM 8437) in dorsal view with descriptive outlines of elements **A**, as reconstructed by Renesto (2000) and **B**, my own interpretation. The latter reconstruction seems congruent with the illustrations of the skull of *Megalancosaurus* offered by Renesto and Dalla Vecchia (2005).

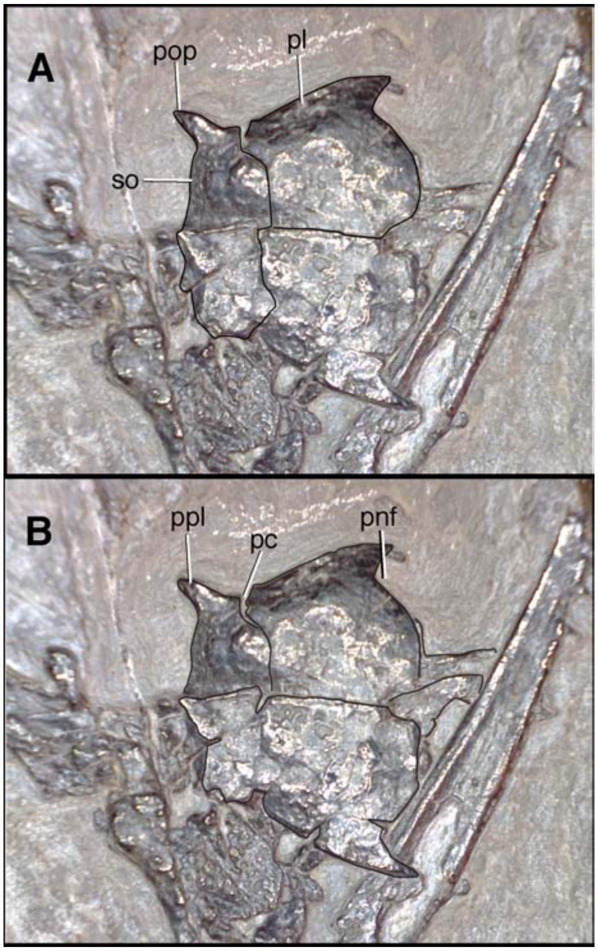

A
pop
pl
so
B
ppl
pc
pnf

FIG. 5-13. Three-dimensional reconstruction of left squamosal of Drepanosauridae n. gen., n. sp. in **A**, lateral, **B**, medial, **C**, posterior, and **D**, anterior views.

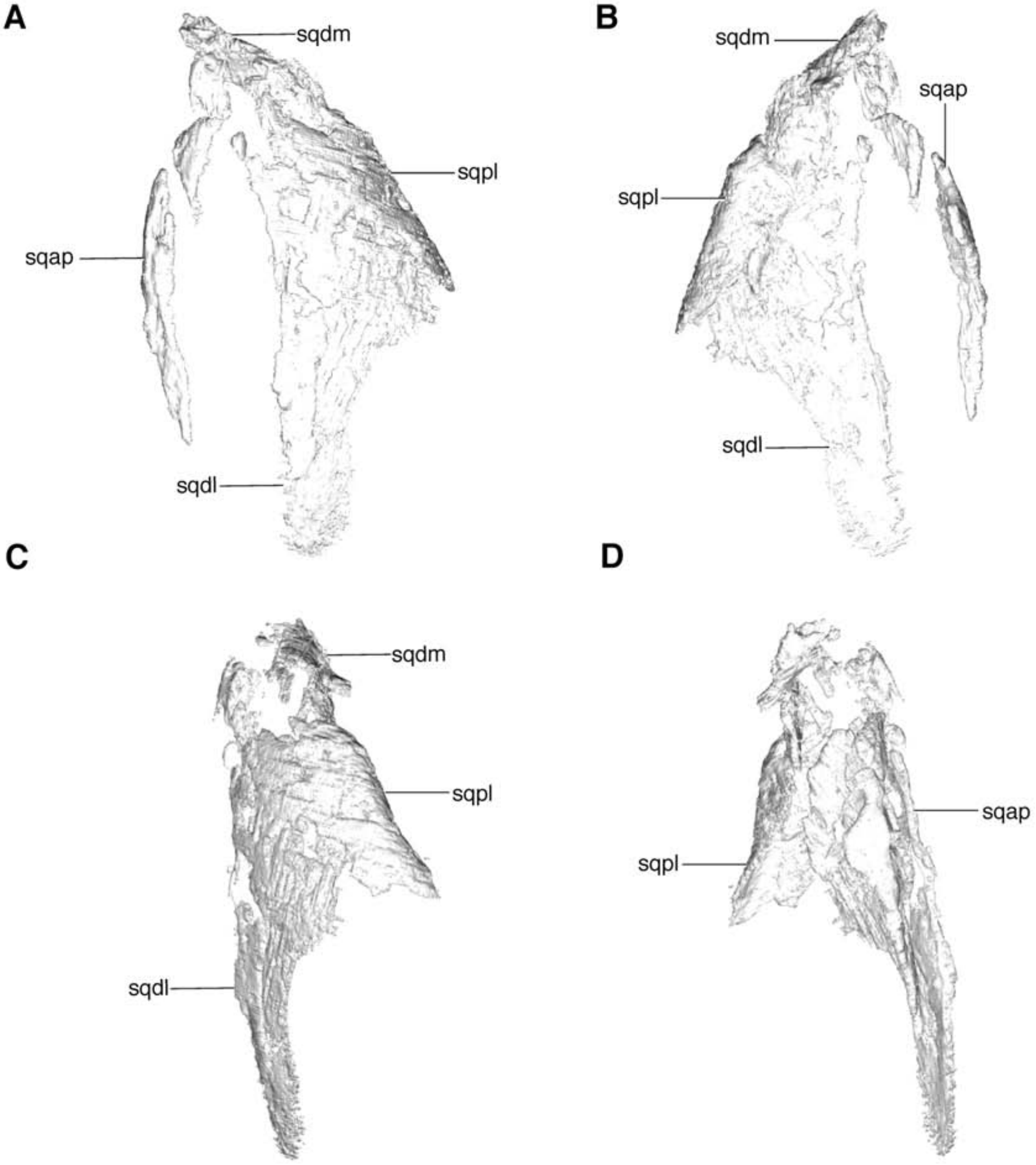

A
sqdm
sqpl
sqap
sqdl
B
sqdm
sqap
sqpl
sqdl
C
sqdm
sqpl
sqdl
D
sqap
sqpl

FIG. 5-14. Three-dimensional reconstruction of right squamosal of Drepanosauridae n. gen., n. sp. in **A**, lateral, **B**, medial, **C**, anterior, and **D**, posterior views.

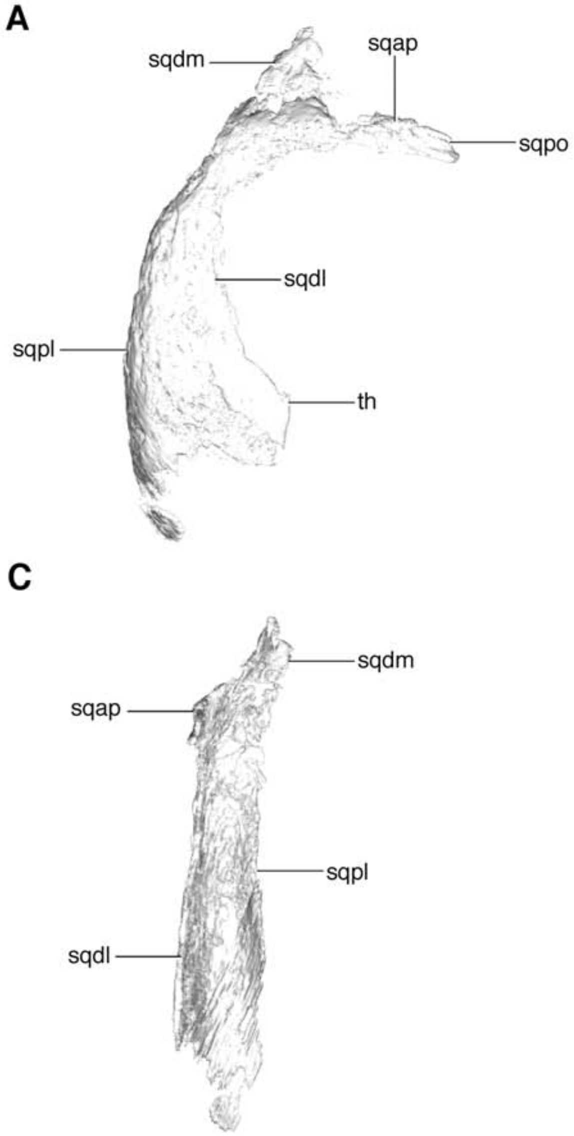

A
sqdm
sqap
sqpo
sqdl
sqpl
th
B
sqap
sqdm
sqpl
sqdl
th
C
sqdm
sqap
sqpl
sqdl
D
sqdm
sqpl

FIG. 5-15. Three-dimensional reconstruction of the palate in **A**, dorsal and **B**, ventral views.

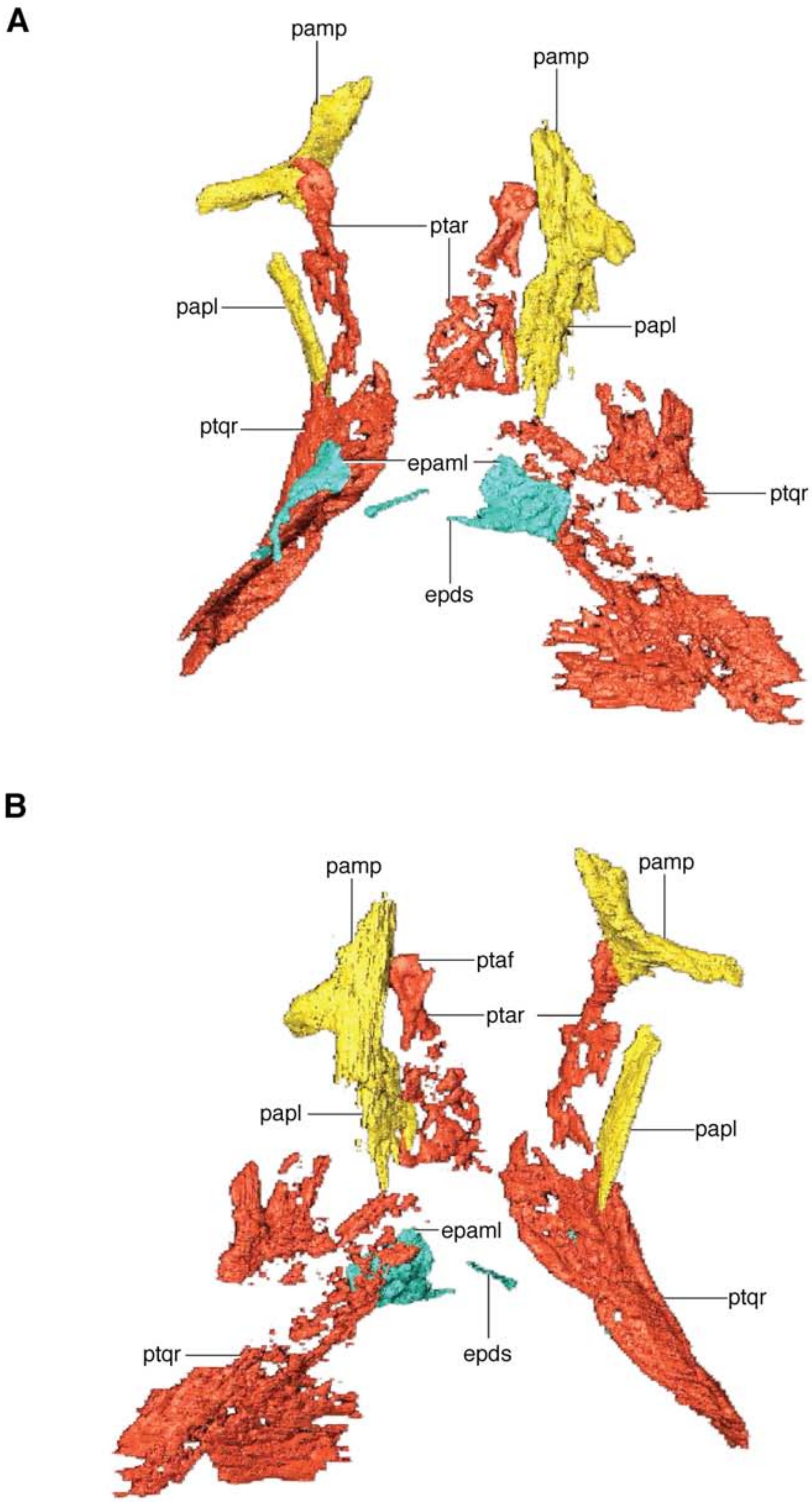

A
pamp
pamp
ptar
ptar
papl
papl
ptqr
epaml
ptqr
epds
B
pamp
pamp
ptaf
ptar
ptar
papl
papl
epaml
epds
ptqr
ptqr

FIG. 5-16. Three-dimensional reconstruction of right palatine of Drepanosauridae n. gen., n. sp. in **A**, lateral, **B**, medial, **C**, ventral, **D**, dorsal, and **E**, anterior views.

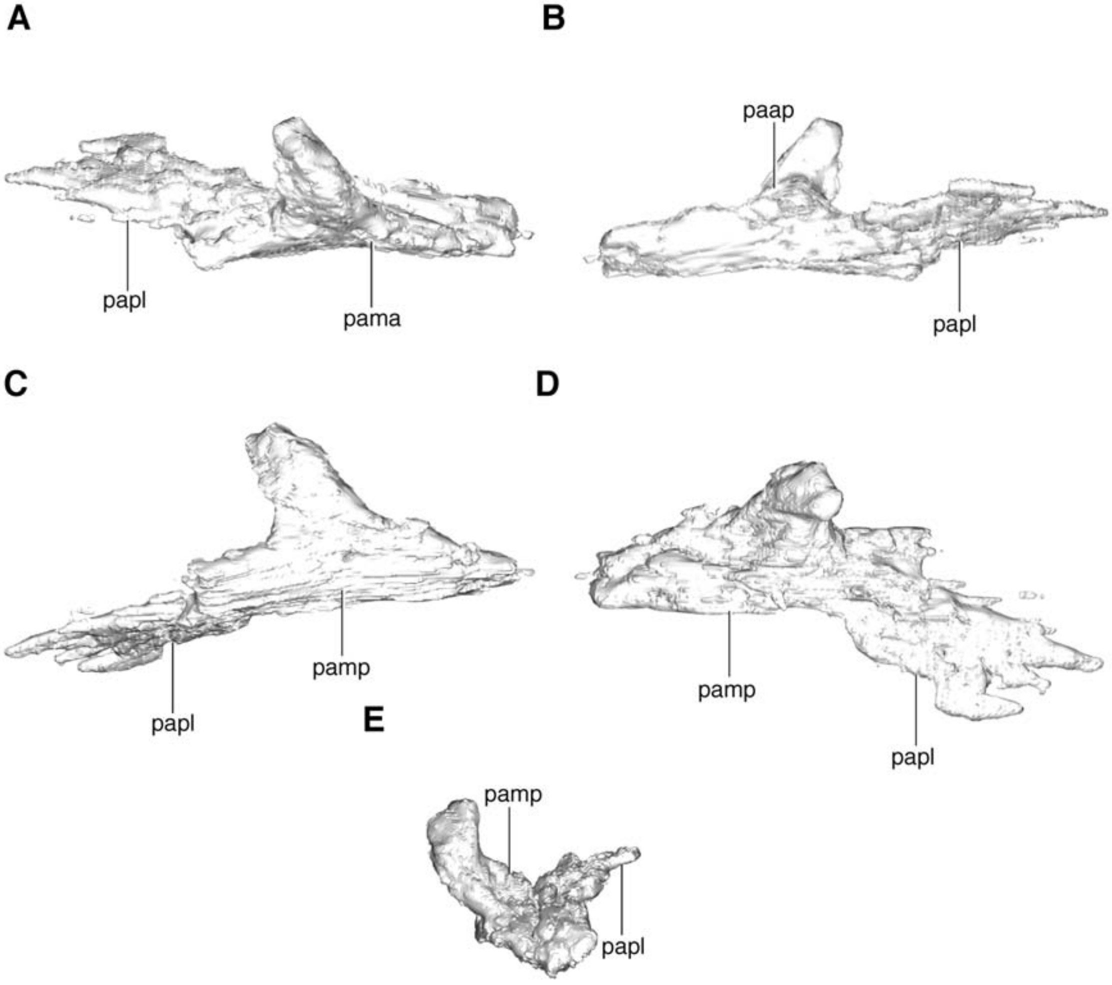

A
B
papl
pama
paap
papl
C
D
papl
pamp
pamp
papl
E
pamp
papl

FIG. 5-17. Three-dimensional reconstruction of left quadrate of Drepanosauridae n. gen., n. sp. in **A**, anterior, **B**, posterior, and **C**, ventral views.

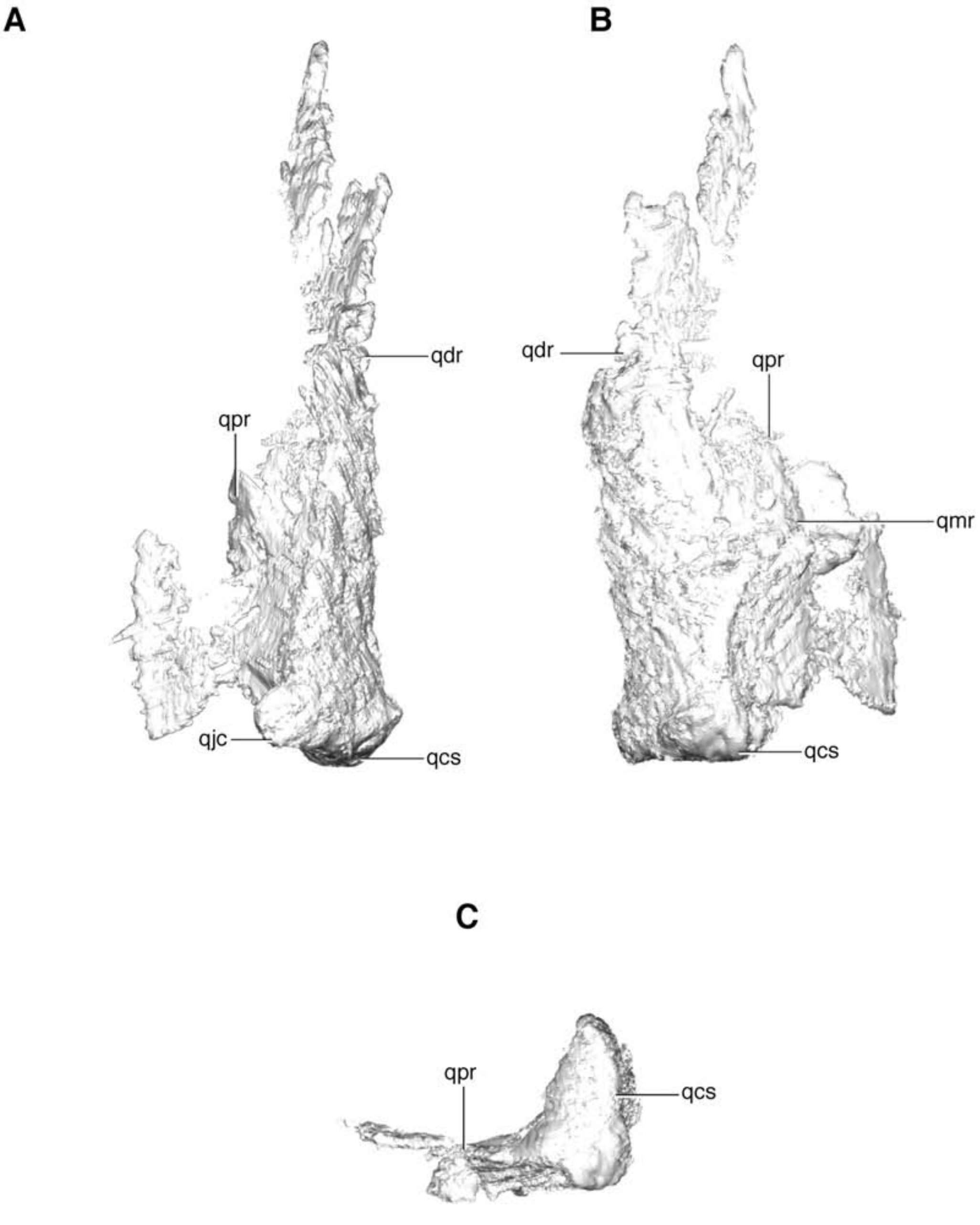

A
B
qdr
qpr
qjc
qcs
qdr
qpr
qmr
qcs
C
qpr
qcs

FIG. 5-18. Three-dimensional reconstruction of right quadrate of Drepanosauridae n. gen., n. sp. in **A**, anterior, **B**, posterior, **C**, lateral, **D**, medial, and **E**, ventral views.

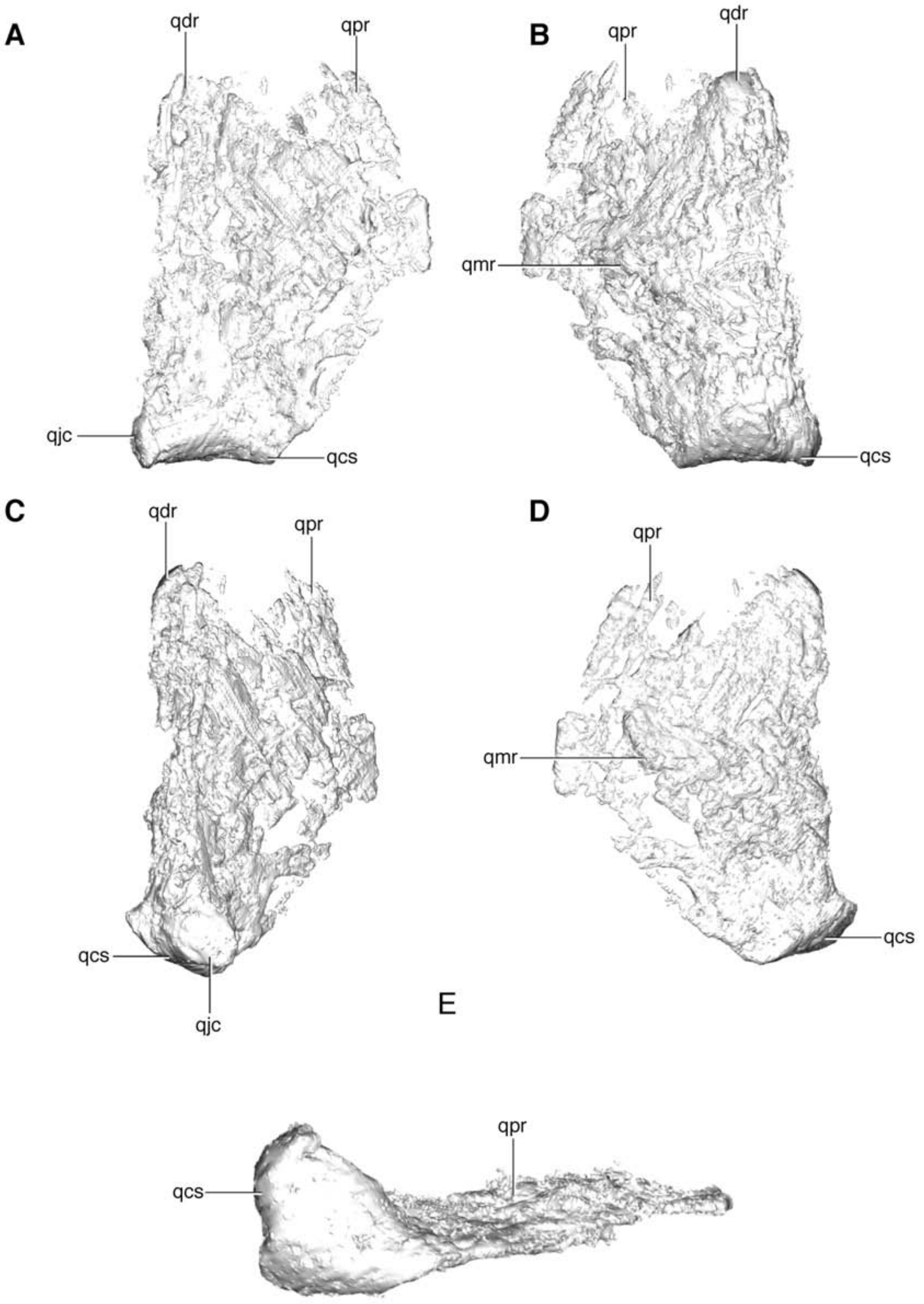

A
qdr
qpr
qjc
qcs
B
qpr
qdr
qmr
qcs
C
qdr
qpr
qcs
qjc
D
qpr
qmr
qcs
E
qpr
qcs

FIG. 5-19. Three-dimensional reconstruction of right epipterygoid of Drepanosauridae n. gen., n. sp. in **A**, lateral and **B**, medial views.

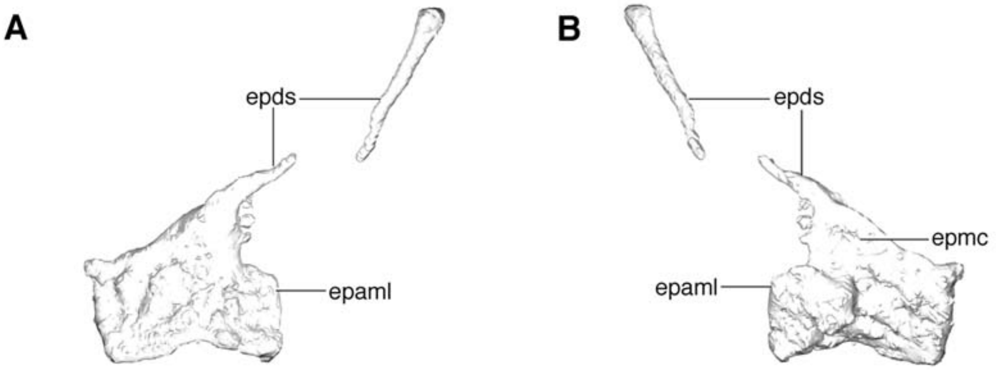

A
epds
epaml
B
epds
epmc
epaml

FIG. 5-20. Three-dimensional reconstruction of left epipterygoid of Drepanosauridae n. gen., n. sp. in **A**, lateral and **B**, medial views.

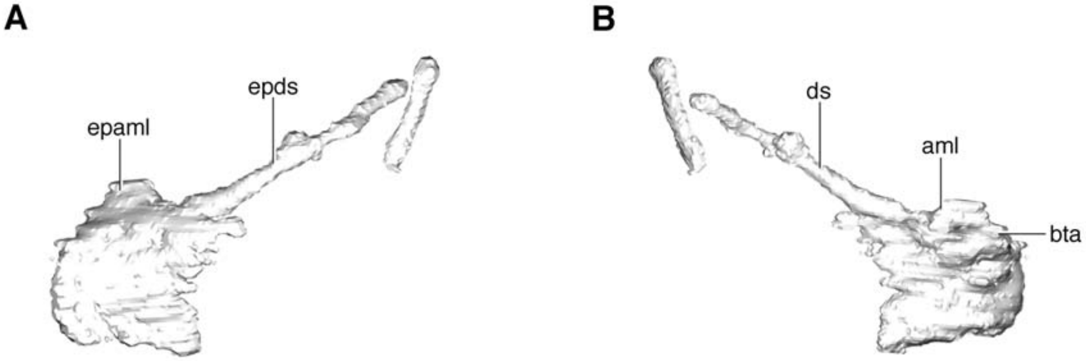

A
epaml
epds
B
ds
aml
bta

FIG. 5-21. Three-dimensional reconstruction of left stapes of Drepanosauridae n. gen., n. sp. in **A**, dorsal, **B**, ventral, **C**, posterior, **D**, anterior, **E**, proximal, and **F**, distal views.

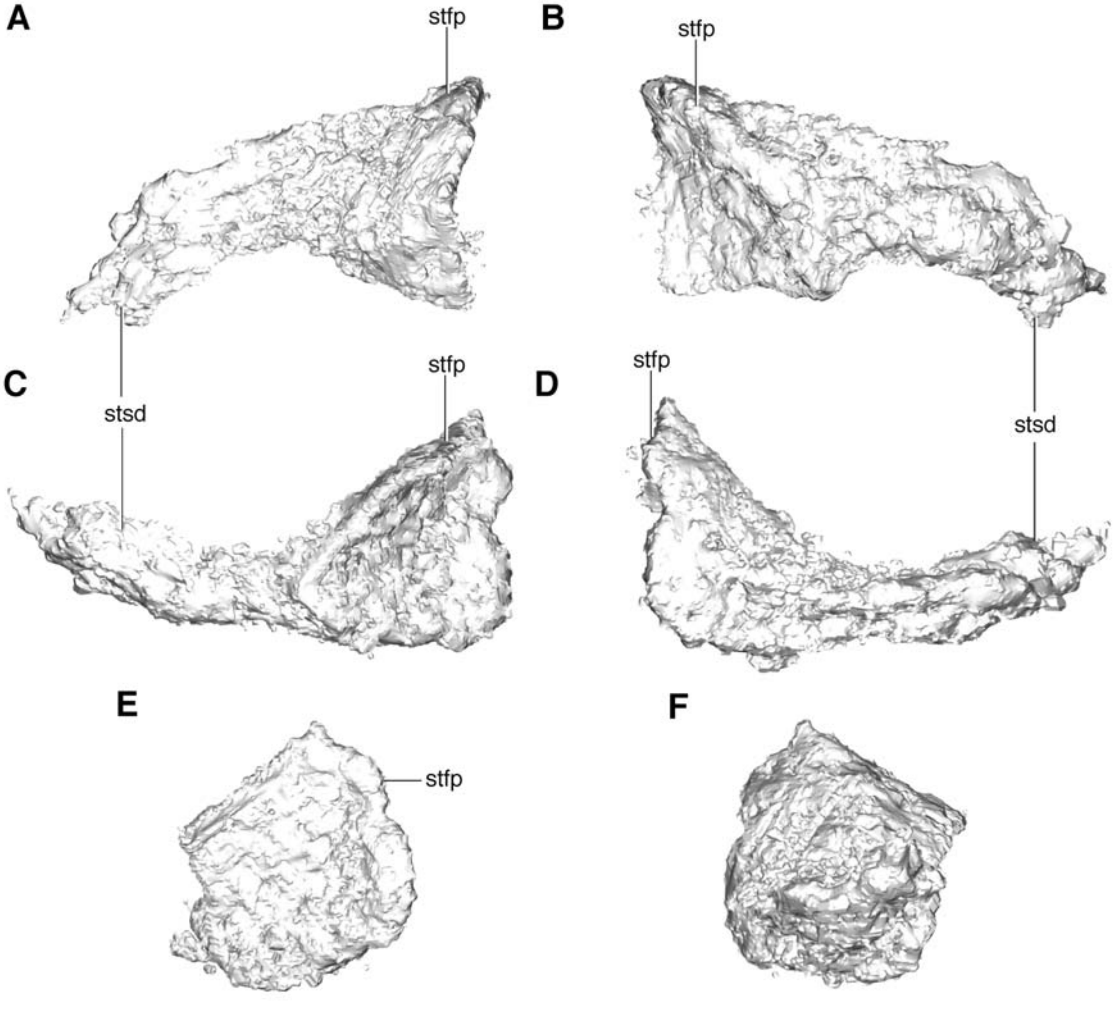

A
stfp
B
stfp
C
stsd
stfp
D
stfp
stsd
E
stfp
F

FIG. 5-22. Three-dimensional reconstruction of right stapes of Drepanosauridae n. gen., n. sp. in **A**, dorsal, **B**, ventral, **C**, anterior, and **D**, posterior views.

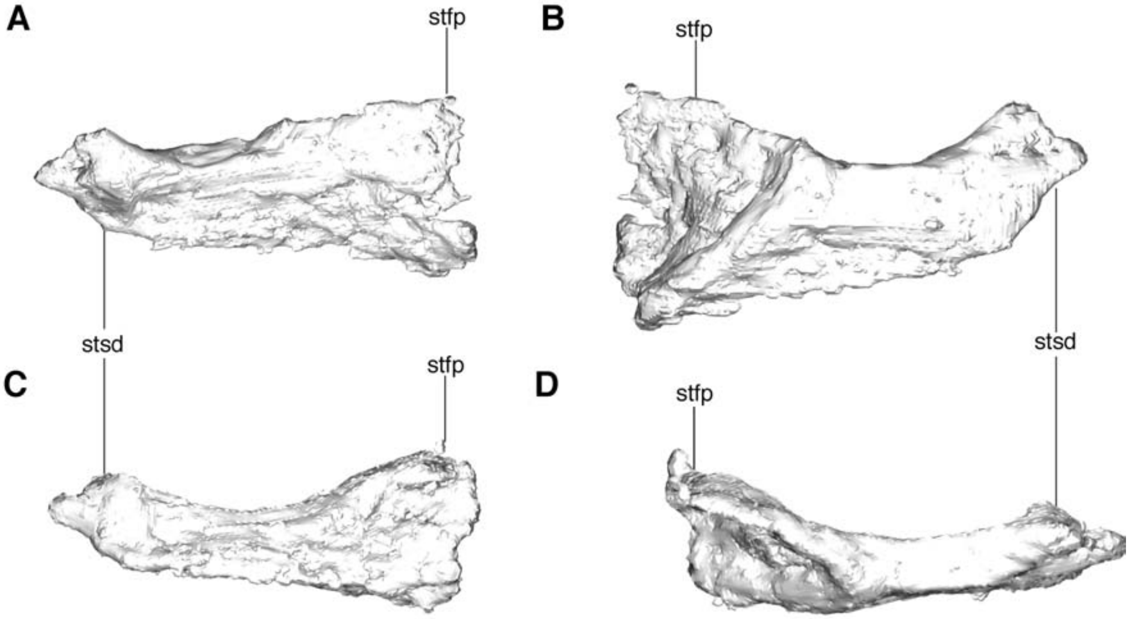

A
stfp
B
stfp
stsd
stsd
C
stfp
D
stfp

FIG. 5-23. Three-dimensional reconstruction of compound basioccipital-exoccipital of Drepanosauridae n. gen., n. sp. in **A**, ventral, **B**, dorsal, **C**, posterior, **D**, anterior, **E**, left lateral, and **F**, right lateral views.

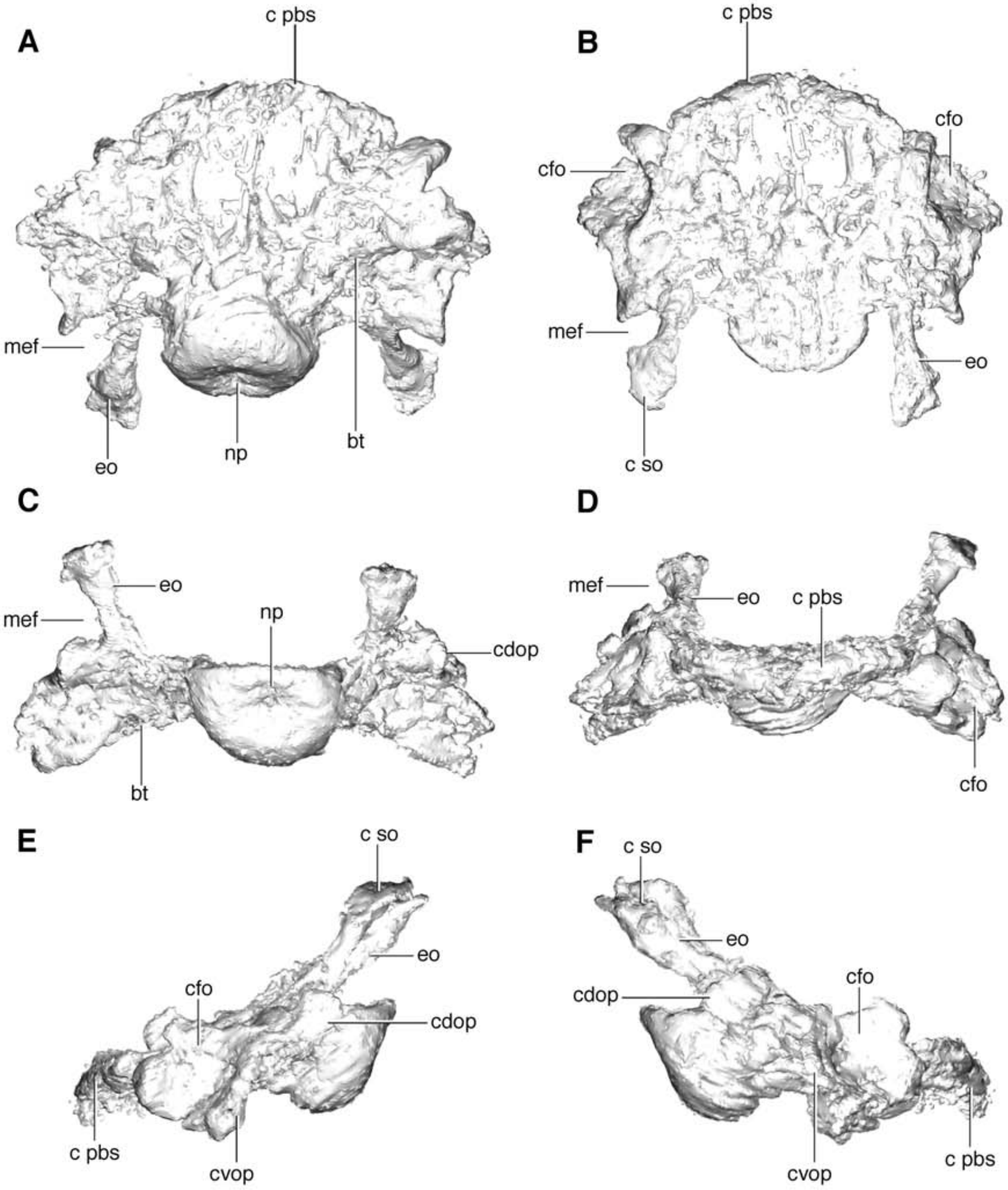

A
c pbs
mef
eo
np
bt
B
c pbs
cfo
cfo
mef
eo
c so
C
eo
mef
np
cdop
bt
D
mef
eo
c pbs
cfo
E
c so
eo
cfo
cdop
c pbs
cvop
F
c so
eo
cdop
cfo
cvop
c pbs

FIG. 5-24. Three-dimensional reconstruction of parabasisphenoid of Drepanosauridae n. gen., n. sp. in **A**, dorsal, **B**, ventral, **C**, right lateral, **D**, left lateral, **E**, anterior, and **F**, posterior views.

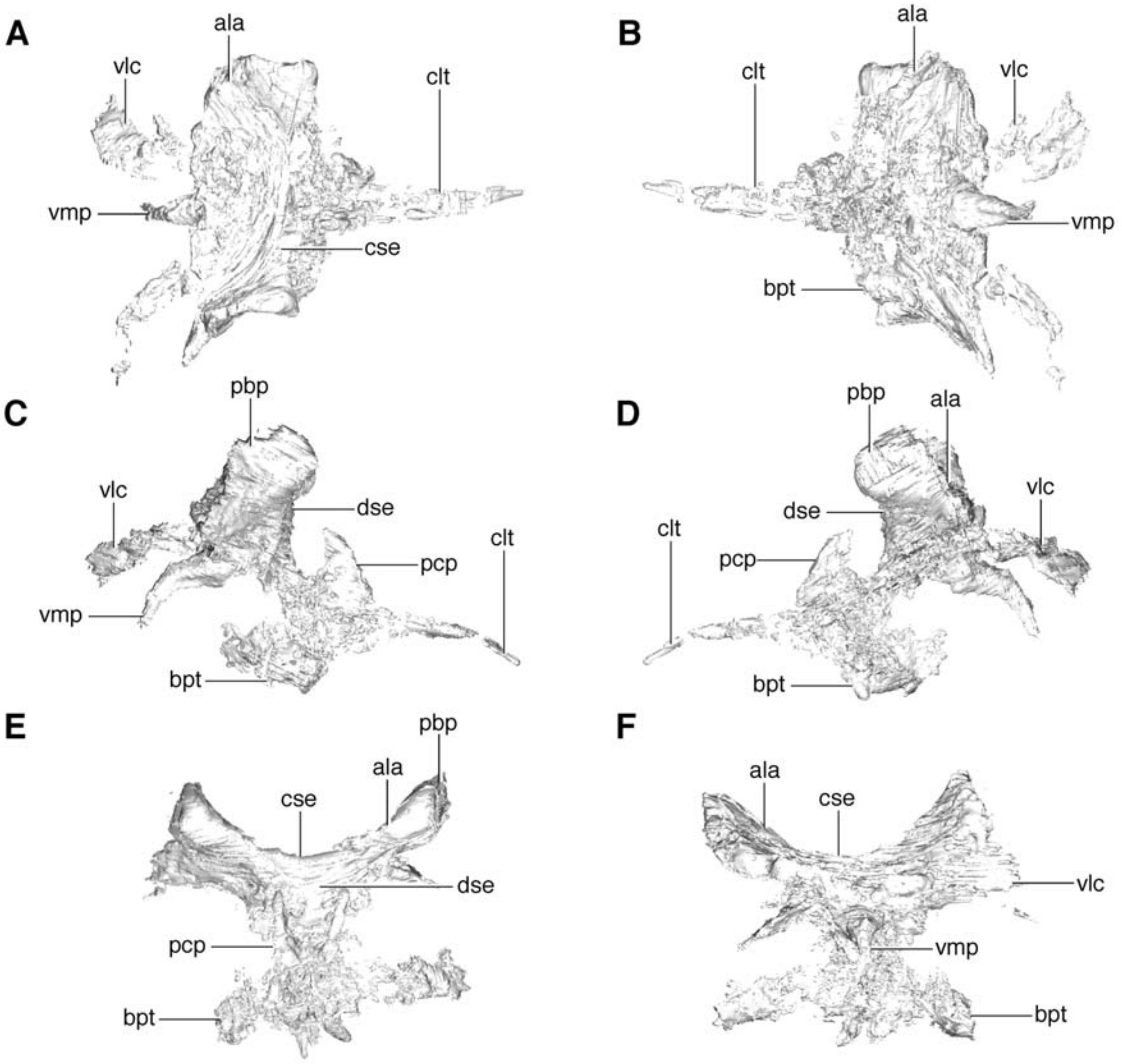

A
ala
vlc
clt
vmp
cse
B
ala
clt
vlc
vmp
bpt
C
pbp
vlc
dse
pcp
clt
vmp
bpt
D
pbp
ala
dse
vlc
clt
pcp
bpt
E
pbp
ala
cse
dse
pcp
bpt
F
ala
cse
vlc
vmp
bpt

FIG. 5-25. Three-dimensional reconstruction of fragment of braincase including most of supraoccipital in **A**, posterior, **B**, anterior, **C**, medial, and **D**, ventral views.

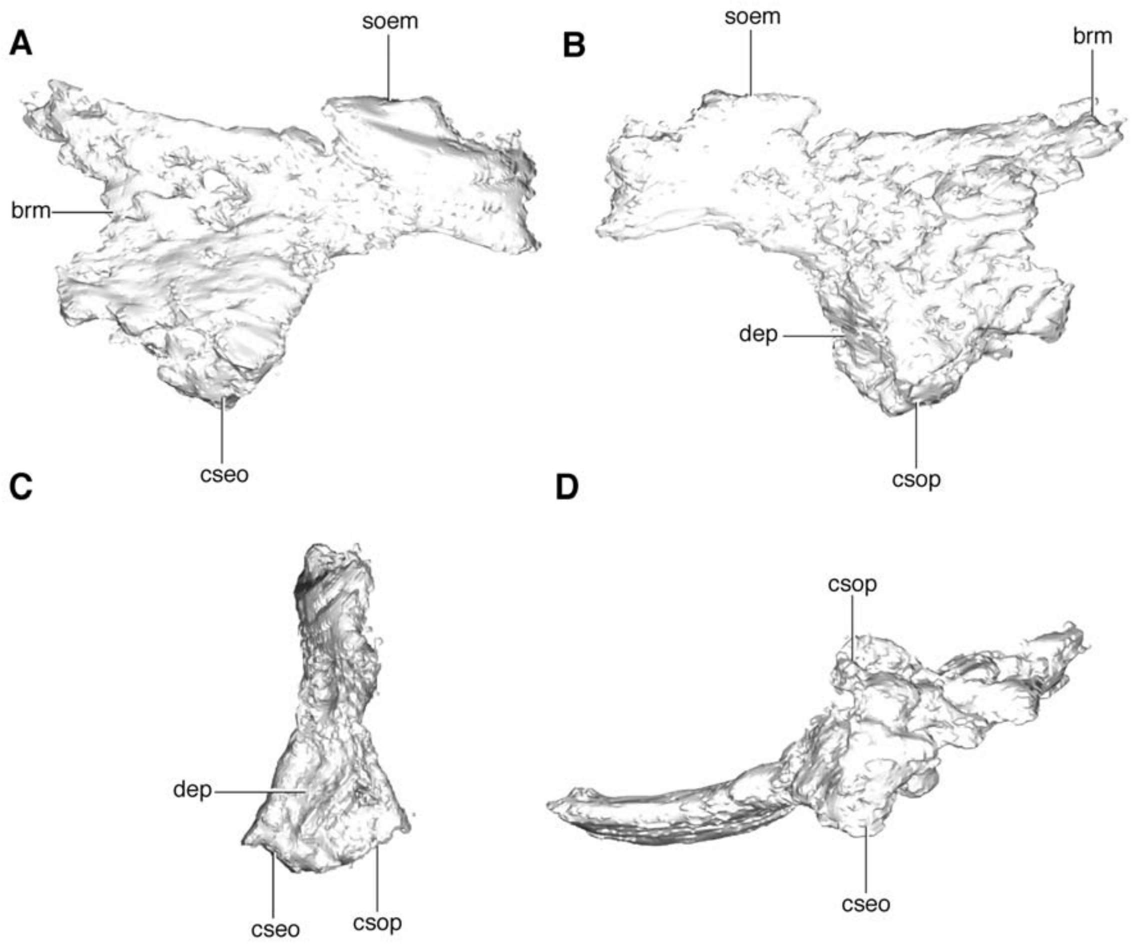

A
soem
brm
cseo
B
soem
brm
dep
csop
C
dep
cseo
csop
D
csop
cseo

FIG. 5-26. Three-dimensional reconstruction of right half of braincase, incorporating prootic, opisthotic, and partial supraoccipital in **A**, lateral, **B**, medial, **C**, anterior, and **D**, posterior views.

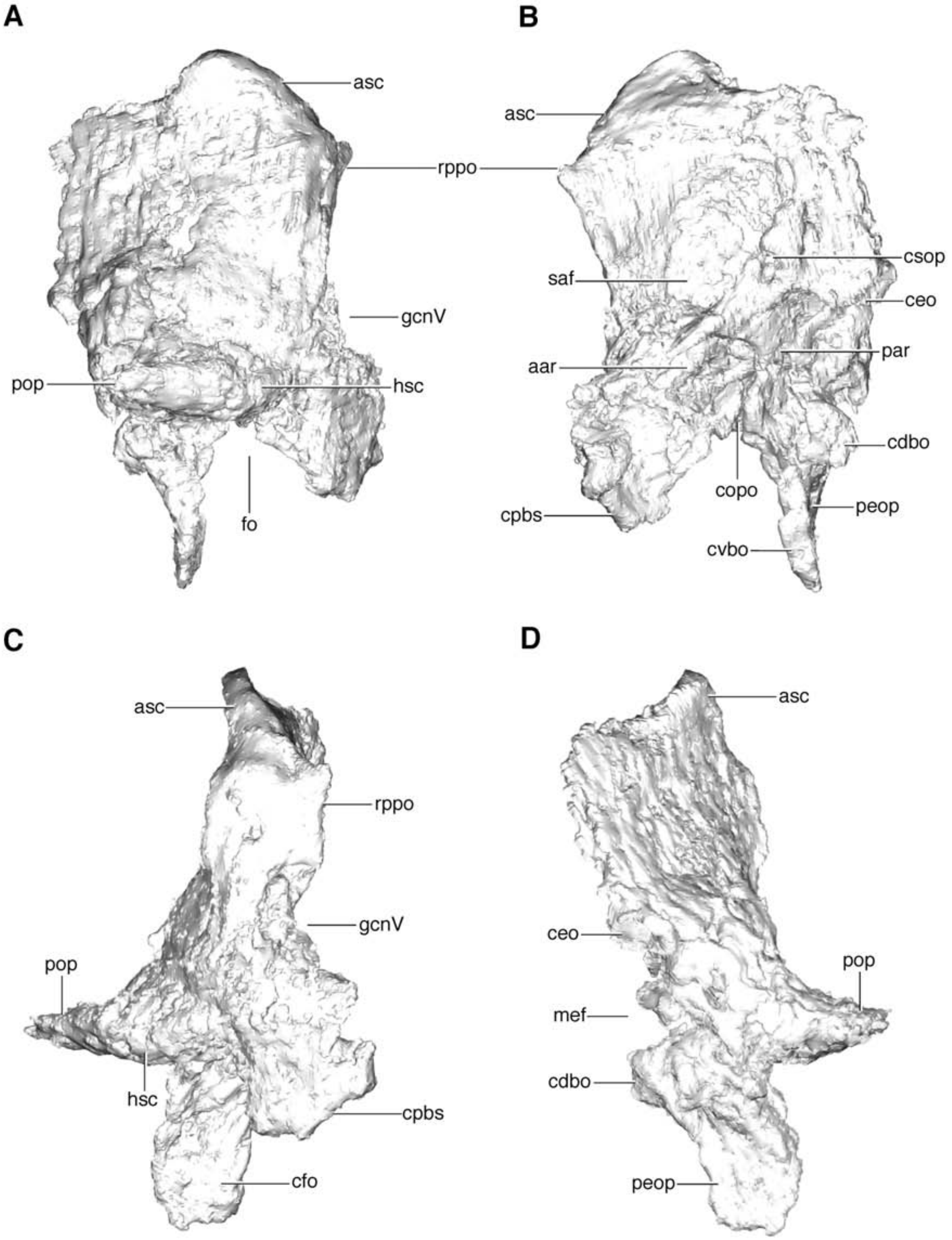

A
asc
rppo
gcnV
pop
hsc
fo
B
asc
csop
saf
ceo
par
aar
cdbo
copo
cpbs
peop
cvbo
C
asc
rppo
gcnV
pop
hsc
cpbs
cfo
D
asc
ceo
pop
mef
cdbo
peop

FIG. 5-27. Three-dimensional reconstruction of partial left opisthotic of Drepanosauridae n. gen., n. sp. in **A**, posterior, **B**, anterior, **C**, lateral, **D**, medial, and **E**, dorsal views.

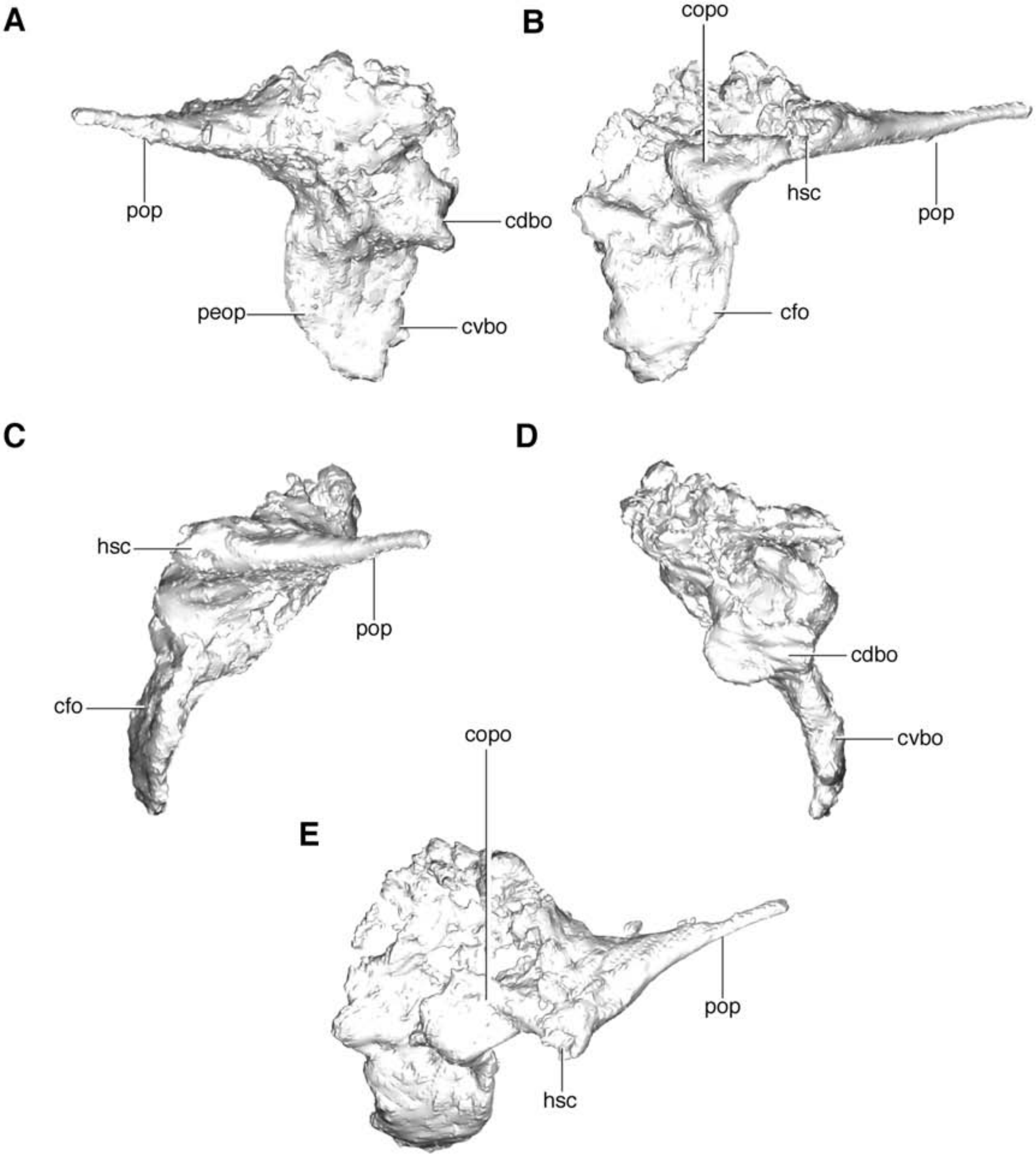

A
pop
cdbo
peop
cvbo
B
copo
hsc
pop
cfo
C
hsc
pop
cfo
D
cdbo
cvbo
E
copo
pop
hsc

FIG. 5-28. Three-dimensional reconstruction of partial anterior process of left prootic of Drepanosauridae n. gen., n. sp. in **A**, lateral and **B**, medial views.

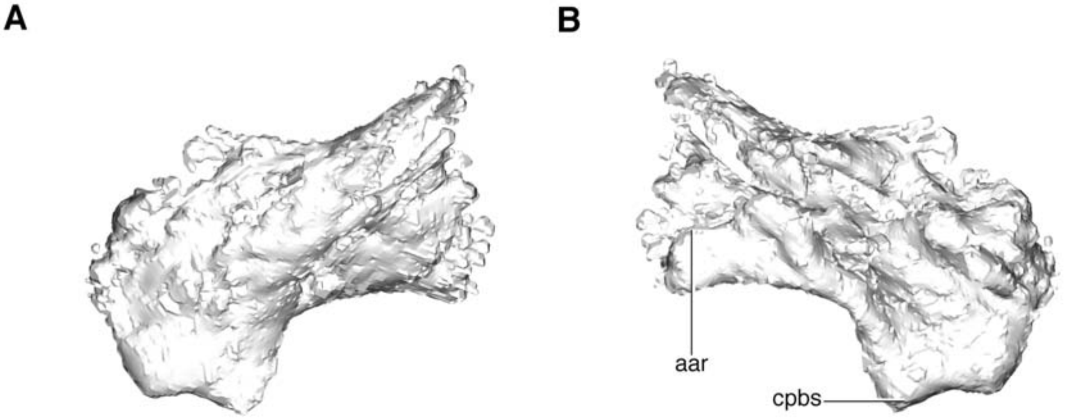

A
B
aar
cpbs

FIG. 5-29. Three-dimensional reconstruction of articulated mandibles of Drepanosauridae n. gen., n. sp. in **A**, dorsal and **B**, ventral views.

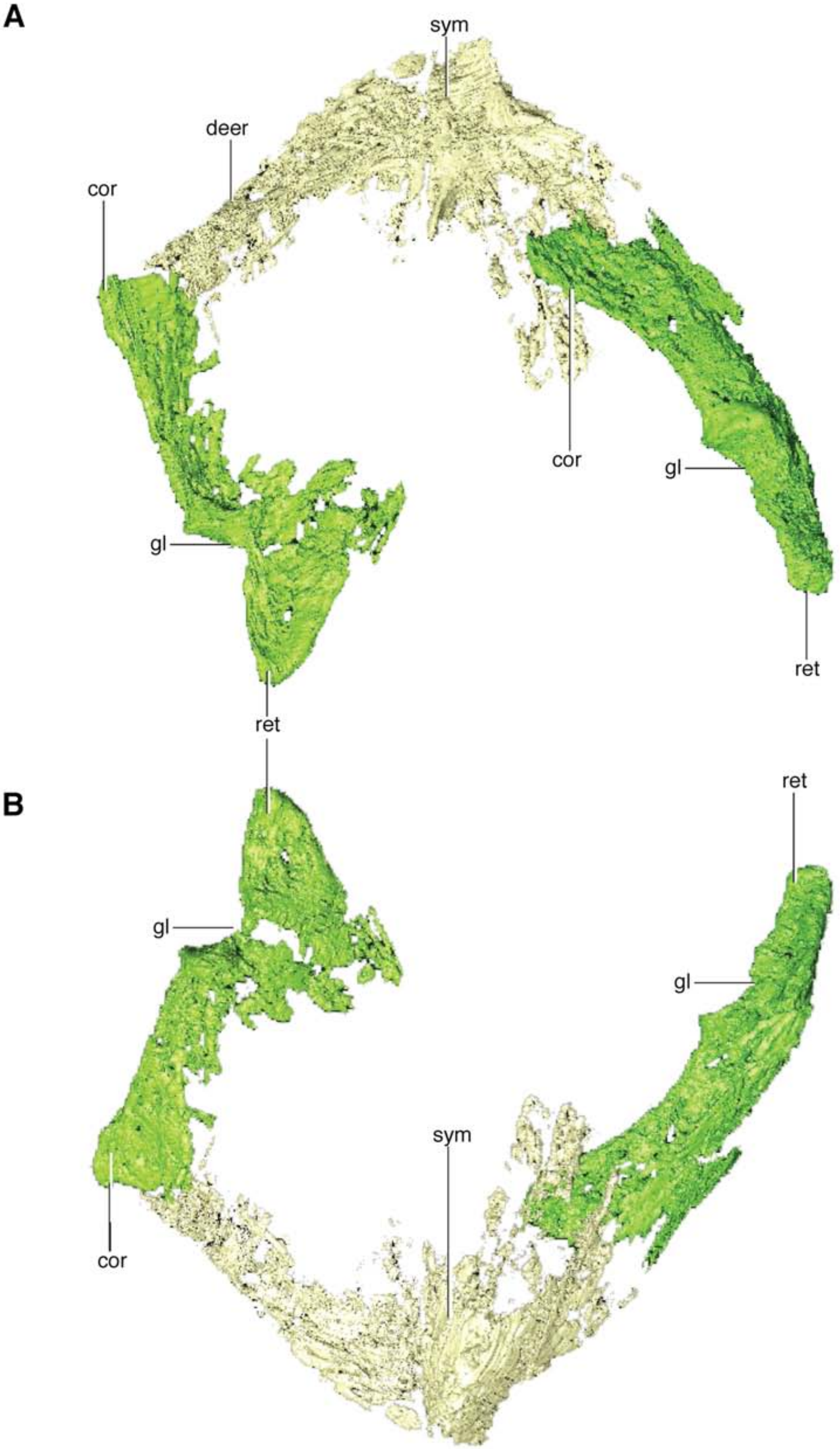
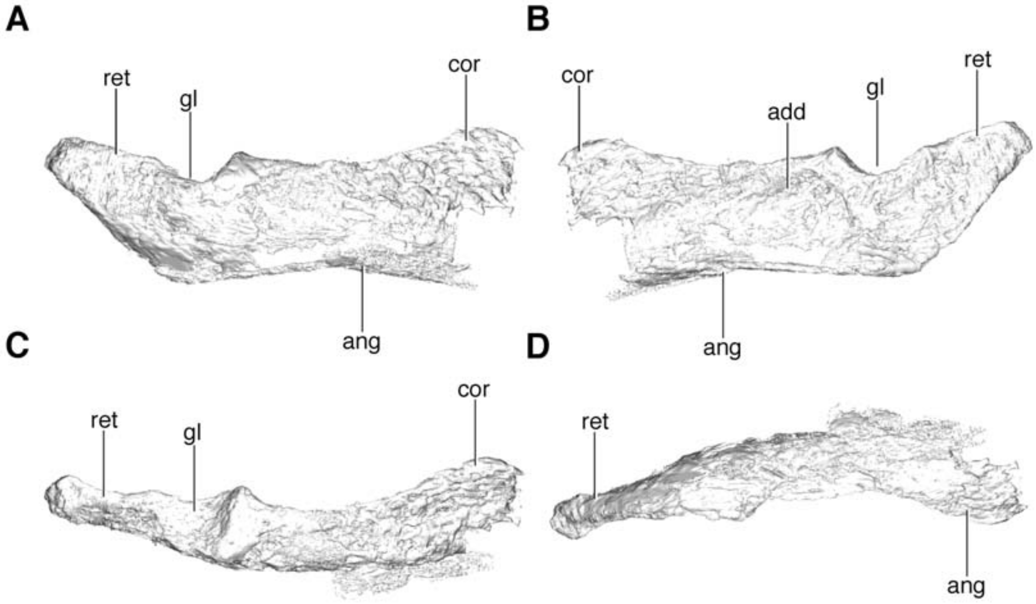

A
sym
deer
cor
cor
gl
gl
ret
ret
B
ret
ret
gl
gl
sym
cor

FIG. 5-30. Three-dimensional reconstruction of right postdentary complex in **A**, lateral, **B**, medial, **C**, dorsal, and **D**, ventral views.


A
ret
gl
cor
ang
B
cor
add
gl
ret
ang
C
ret
gl
cor
D
ret
ang

Chapter 6

The phylogeny of Permo-Triassic Diapsida and the early radiation of saurian reptiles

INTRODUCTION

The origin of modern reptiles has long been of interest to biologists, as has the nature of their initial diversification. Throughout the nineteenth and early twentieth centuries, numerous authors proposed various classifications and evolutionary scenarios for the interrelationships and origins of the major terrestrial reptile lineages (e.g., Cope, 1885; Baur, 1887; Osborn, 1903a; Goodrich, 1916; Romer, 1933, 1967; von Huene, 1956). These classifications typically attempted to link fossil taxa to one or another of the major extant lineages, through study of what were considered key anatomical innovations (e.g., the hooked fifth metatarsal in Goodrich, 1916).

An important subgroup in this discussion was Protorosauria (a name initially used by Huxley, 1871), a group described by Seeley (1887) for *Protorosaurus speneri*, a long-necked reptile from the Upper Permian of Germany. In describing the material of *Protorosaurus*, Seeley noted that the animal "had no predominant affinity with any existing order of animals" and that "[t]he animal is therefore of an ancient stock, and may have been derived from the group from which Ornithosaurs [a classical term for pterosaurs] were developed," (Seeley, 1887:213).

In subsequent pre-cladistic classifications, Protorosauria were generally considered a highly specialized offshoot of Permian reptiles (e.g., Osborn, 1903b; Goodrich, 1916; Williston, 1917) or completely ignored in broader discussions of reptile origins (e.g., Williston, 1904). The group was broadly considered to exhibit a single, upper temporal fenestra, as was noted in the purported close relative *Araeoscelis gracilis* (von Huene, 1926; Romer, 1947).

New taxa played an important part in framing the discussion of the origins of modern groups. Broom (1914) described a partial skull and skeleton of *Youngina capensis* from the Upper Permian of the Karoo Basin of South Africa as the first member of Eosuchia, a novel subgroup of "thecodont" reptiles (thecodont being an classical term for ancestral archosaur-line reptiles). Parrington (1935) later described a skull from the Lower Triassic of the Karoo as *Prolacerta broomi*. The animal, which exhibits an incomplete lower temporal opening, a long neck, and a small, lightly built skull, was considered an intermediate between Eosuchia and Squamata. Around this time, some authors began to note similarities between *Protorosaurus speneri* and some long-necked forms from the Middle Triassic of central Europe: *Tanystropheus* spp. (e.g., von Huene, 1931, 1944) and *Macrocnemus bassanii* (e.g., Peyer, 1937).

Camp (1945) described a new specimen of *Prolacerta broomi* and synthesized the current understanding of *Protorosaurus* and *Tanystropheus*-like taxa. He assigned *Prolacerta* to a subgroup of Protorosauria, the Prolacertiformes, and hypothesized that both Rhynchocephalia and Squamata derived from this clade ancestrally. Romer (1947) questioned the linkage of *Protorosaurus* to the ancestry of any modern taxa, suggesting instead that Protorosauria was an evolutionary dead end. He later considered the relationships of *Protorosaurus* extremely problematic (Romer, 1967).

Prior to the advent of cladistic studies of early Diapsida, most authors followed closely to Camp's hypothesis. Rhynchocephalia and Squamata were thought to originate from an "eosuchian" ancestor akin to *Prolacerta* (e.g., Robinson, 1967a; Carroll, 1969; Wild, 1973). However, Gow (1975) reviewed the complete osteology of both *Youngina capensis* and *Prolacerta broomi* and came to an altogether different conclusion. He concluded that the postcranial skeleton of *Prolacerta* shared far more in common with that of *Proterosuchus*, a lowermost Triassic taxon long considered a stem-archosaur (e.g., Broom, 1903; Brink, 1955). He also concluded that *Macrocnemus* and *Tanystropheus* were part of this stem-archosaur grouping. This hypothesis became a subject of controversy, with other workers maintaining the squamate relationships of *Prolacerta* and kin (e.g., Wild, 1980a).

CLADISTIC HYPOTHESES FOR DIAPSIDA

Following the advent of cladistic analysis (Hennig 1965), systematic hypotheses of reptile interrelationships became focused on synapomorphies in the early 1980's. Gauthier (1984) presented the first cladistic analysis of diapsid interrelationships in his dissertation (Fig. 1A). He presented strong character evidence to link a number of archaic reptile groups (Choristodera, Rhynchosauria, Trilophosauria, Protorosauria) to the archosaur stem, bearing out Gow's (1975) hypothesis that "protorosaurs" were not connected to the origin of lizards. By contrast, the stem to Lepidosauria included Younginiformes (*Youngina* and several taxa held to be allies by Carroll, 1981 and Currie, 1981a) and Kuehneosauridae (e.g., Robinson, 1967a). His analysis incorporated all of these groups as supraspecific taxa, incorporating data from a wide range of fossil species and chronological intervals.

Benton (1985) constructed an independent cladistic study of Diapsida (Fig. 1B) that came to many of the same conclusions of Gauthier (1984). This study also examined the in-group relationships of a number of the clades within both Lepidosauromorpha and Archosauromorpha, which Gauthier (1984) examined as supraspecific groups. His study offered the term Neodiapsida for the grouping of “all diapsids except *Petrolacosaurus kansensis* and a few other groups…” (Benton, 1985:112).

Evans (1988) presented a third cladistic hypothesis for the interrelationships of Permo-Triassic diapsids (an expansion of her 1987 analysis of prolacertiform interrelationships), integrating a larger number of taxa from that interval than either previous study (Fig. 1C). Her results presented a broadly similar hypothesis for the inclusiveness of Archosauromorpha and Lepidosauromorpha to Gauthier (1984) and Benton (1985). A major distinction was the ambiguity of the position of Kuehneosauridae, long held to be the sister taxon of Lepidosauria (e.g., Robinson, 1967; Gauthier, 1984), which resolved as equally plausible as an early archosauromorph lineage.

Laurin (1991) reassessed the affinities of early diapsid lineages using primarily genus-level taxa in an attempt to assess the affinities of a new taxon from the Early Permian of Oklahoma, *Apsisaurus witteri* (Fig. 2A). Although the taxon itself has more recently been recovered as a varanopid synapsid, the general conclusions of Laurin’s study have been broadly accepted. In his study, Younginiformes (based on *Youngina capensis* and *Acerosodontosaurus piveteaui*) were recovered as the sister taxon of Sauria rather than members of Lepidosauromorpha. *Coelurosauravus* and *Apsisaurus* were recovered as the successive sister taxa of the Younginiformes+Sauria clade.

Rieppel (1994) included a broad sample of early saurians in an analysis focused on early Sauropterygia (Fig. 2B). His results correspond well to the results in Laurin (1991), with Younginiformes falling outside of Sauria. Kuehneosauridae, Rhynchocephalia, and Squamata are recovered in a polytomy, and that clade fell as the sister taxon to a Testudines + Sauropterygia clade. He found virtually no resolution within Archosauromorpha, which contained Archosauriformes, Rhynchosauria, *Trilophosaurus*, Prolacertiformes, and Choristodera. A nearly identical topology for Sauria was recovered in the expanded analysis of DeBraga and Rieppel (1997), which sampled broadly from other analyses of non-diapsid reptiles (e.g., Laurin and Reisz, 1995).

Merck (1997) undertook a massive species-level study of Diapsida, focused on the interrelationships of “euryapsid” taxa, primarily marine reptiles. However, his conclusions on the relationships within Sauria bear repeating (Fig. 2C). The taxa he recovered within Archosauromorpha were comparable to those noted by Gauthier (1984), although he also found a clade containing the major marine reptile groups (Ichthyopterygia, Sauropterygia) and Drepanosauridae as the earliest divergence within Archosauromorpha. As in Laurin (1991), *Youngina* and its kin were recovered outside of Sauria.

In the mid-1990s, two analyses were produced focused specifically on long-necked “protorosaur” archosauromorphs. Benton and Allen (1997) constructed their study as part of a redescription of the Early Triassic Russian archosauromorph *Boreopricea funerea*. Their sample of outgroups included *Youngina*, Rhynchosauria, and *Trilophosaurus*, the latter two of which were described as “two non-prolacertiform archosauromorphs” (Benton and Allen, 1997:947). Their sample included a large number of fragmentary fossils, produced very little resolution. Jalil (1997) produced a similar study as part of his description of the Early Triassic reptile *Jesairosaurus lehmani*. His sample of saurians was broader, including *Proterosuchus* and Lepidosauria. He recovered a monophyletic Prolacertiformes.

Dilkes (1998) presented the first attempt to robustly address the interrelationships of early Archosauromorpha with a genus-level study (Fig. 2D). His results differed strikingly from past hypotheses in finding the taxon including *Protorosaurus*, *Tanystropheus*, and *Prolacerta* to be polyphyletic. *Prolacerta* was resolved as the sister taxon of Archosauriformes, while a clade including *Protorosaurus*, Drepanosauridae, and Tanystropheidae was found as the earliest divergence within Archosauromorpha. However, the ingroup relationships of Archosauromorpha were noted to be quite plastic when considering only slightly less parsimonious topologies. A modification of the Dilkes (1998) study by Gottmann-Quesada and Sander (2009) broke the long-necked clade into three separate lineages: *Protorosaurus speneri*, Tanystropheidae, and *Prolacerta broomi*.

Rieppel et al. (2003) examined various combinations of the matrices of Benton and Allen (1997), Jalil (1997), and Dilkes (1998). The combined results supported the *Prolacerta* + Archosauriformes conclusion of Dilkes (1998). Their results also supported a non-monophyletic protorosaur clade.

Müller (2004) offered a preliminary study of diapsid interrelationships on a large scale, with a study that incorporated many supraspecific and genus-level taxa to assess the impact of taxon selection on diapsid phylogeny (Fig. 3A). Incorporating a broad sample of characters from deBraga and Rieppel (1997) and Dilkes (1998), his phylogeny was again broadly congruent with past analyses with regards to the inclusiveness of Archosauromorpha. As in Dilkes (1998), he found the clade including all of the long-necked, small-headed archosauromorphs to be polyphyletic. Both Kuehneosauridae and Drepanosauridae were recovered as a clade outside of Sauria, as was Younginiformes. A modification of this analysis by Borsuk-Bialynicka and Evans (2009) further broke up the long-necked archosauromorphs into as many as four separate lineages.

Senter (2004) constructed an important analysis, incorporating a number of supraspecific diapsid taxa (Fig. 3B). This analysis was a test of statements by Feduccia and others regarding the possible affinities between drepanosaurs and Aves to the exclusion of Theropoda. Senter tested the hypothesis cladistically, recovering drepanosaurs, the gliding Weigeltisauridae, and *Longisquama* in a clade outside of Younginiformes + Sauria. This result corresponds well to an unpublished hypothesis described briefly by Merck (2003). This basal position for drepanosaurs, a taxon often considered within Archosauromorpha, compares well to the result in chapter 4 of this dissertation.

Ezcurra et al. (2014) presented a recent phylogeny of early Sauria by modifying the analysis of Reisz et al. (2010), which focused on early amniotes. Their topology followed that of Dilkes (1998) closely with regards to Archosauromorpha (Fig. 3C).

Pritchard et al. (2015) presented a large, species-level phylogeny of early saurian interrelationships (Fig. 3D). As in Gottmann-Quesada and Sander (2009), they resolved multiple lineages from the long-necked archosauromorph group: *Protorosaurus speneri* as the earliest divergence, a Tanystropheidae clade, and *Prolacerta broomi* as the sister taxon of Archosauromorpha. A modification of this study by Nesbitt et al. (in press), found yet another purported member of the long-necked group (*Pamelaria dolichotrachela*) to be a close relative of *Azendohsaurus* and *Trilophosaurus*. An additional modification by Pritchard and Nesbitt (in prep.) found that drepanosaurids, typically included within the long-necked clade (Renesto et al., 2010; Dilkes, 1998), were substantially removed from Sauria. It is this analysis that forms the basis of the following analysis.

JUSTIFICATION OF FURTHER ANALYSIS

POOR SAMPLING

A general consensus is emerging for the membership of early Archosauromorpha and Lepidosauromorpha, as has been seen in the past three decades of systematic analyses. A number of long-necked and small-headed reptiles typically referred to as Prolacertiformes and Protorosauria (e.g., *Prolacerta broomi*, *Macrocnemus bassanii*), *Trilophosaurus*, and Rhynchosauria have universally been found within Archosauromorpha. However, substantial ambiguity exists as to the positions of some other taxa (e.g., Drepanosauromorpha, Kuehneosauridae), and indeed many studies have not included these problematic groups. Also, no large-scale analysis has included many of the purported taxa within Protorosauria and Prolacertiformes. Considering the likely polyphyly of these groups, incorporation of many of their constituent taxa is important.

SUPRASPECIFIC TAXA

Nearly all of the aforementioned studies of diapsid phylogeny employ supraspecific taxa for many, if not all of their OTUs (criticized in Prendini, 2001). Such OTUs automatically assume the monophyly of included members. These also eliminate any sense of character polarities within the groups, such that basal members of the clade no longer inform the character states at the basal nodes. As such, a broad-scale analysis following in the footsteps of Ezcurra et al. (2014) and Pritchard et al. (2015) in employing only species-level taxa is important for fully assessing available character data in species of early Sauria.

INCONGRUITY

Although the inclusiveness of Archosauromorpha has achieved some consensus (but see above), the relationships of the taxa within Archosauromorpha have never been consistently resolved in analyses of the group. Virtually none of the studies discussed above concur on the relative positions of the early archosauromorph lineages, and many studies have shown that small changes in taxon sampling can cause major changes to the topology of early saurian reptiles (e.g., Müller, 2004). These incongruities can have major impacts on any hypotheses on the initial diversification of Sauria.

STRATIGRAPHY

The Permian fossil record preserves a very small number of saurian reptiles (recently reviewed by Ezcurra et al., 2014), and only two taxa have been accepted for some time. These include the long-necked, small-headed taxon *Protorosaurus speneri* from the Upper Permian of Western Europe (Evans and King, 1993; Gottmann Quesada and Sander, 2009) and the proterosuchid *Archosaurus rossicus* from the Upper Permian of Russia (Tatarinov 1961; Sennikov, 1988). Although the taxonomic diversity of Sauria in the Permian is thus extremely low, the phylogenetic implications of this diversity are striking.

A great deal of character data support the referral of *Archosaurus rossicus* to Archosauriformes, whereas *Protorosaurus speneri* exhibits a large number of plesiomorphic traits that suggest a more basal position within Archosauromorpha. As a result, the divergences of taxa in the tree space "between" these two taxa on a phylogeny is significant for understanding the timing of the initial taxonomic divergences of the major early archosauromorph clades. For example, the study of Dilkes (1998) suggests that the clades Drepanosauridae + Tanystropheidae, *Trilophosaurus*, Rhynchosauria, *Prolacerta*, Proterosuchidae, and *Erythrosuchus* + Archosauria were all present during the Late Permian and survivors of the Permo-Triassic Extinction. A more well resolved phylogenetic hypothesis for early Sauria is critical to understanding not only the number of lineages present during the Permian, but also the amount of morphological diversity present in those lineages prior to the Triassic Period.

CHARACTER EVOLUTION

The early-diverging lineages within Sauria have long been noted for their extreme morphological diversity (e.g., Sues and Fraser, 2013), and possible relationships between these lineages could suggest different patterns of trait acquisition among these groups. For example, Nesbitt et al. (in press) recovered a monophyletic group including *Trilophosaurus* and *Azendohsaurus*: Allokotosauria. Both of these taxa exhibit very distinctive adaptations for herbivory (crushing and occluding teeth in *Trilophosaurus*, leaf-shaped and cropping teeth in

Azendohsaurus), but the relationship between these two was used to suggest a possible single acquisition of herbivory in the common ancestry of Allokotosauria.

The resolution of early Sauria may also be beneficial to resolving the distribution of states at the base of Archosauromorpha as well. Borsuk-Bialynicka and Evans (2009) noted that the long-necked archosauromorphs, which had previously been regarded as a single, monophyletic entity, seemed to occupy disparate positions within Sauria. As a possible consequence, they noted the following:

> If this hypothesis of the relationship [the widespread distribution of "protorosaurs" within Archosauromorpha] is correct, then the similarities found between the cervical vertebrae and ribs of *Protorosaurus (sensu stricto*) and traditional "prolacertiforms" probably represent the retention of primitive character states, possibly synapomorphy for Archosauromorpha or…for a more inclusive group. The challenge of the future will be to resolve the phylogenetic relationships of the other, more fragmentary, taxa previously classified as prolacertiform. (Borsuk-Bialynicka and Evans, 2009:231).

Thus, not only would resolution to the phylogenetic relationships of early saurians provide context for the ancestral morphologies of archosauromorphs and lepidosauromorphs. That context would also allow for character-based assessments of the affinities of fragmentary fossil taxa. This reason was the initial purpose of the first iteration of the phylogenetic dataset described within (Pritchard et al., 2015). For these reasons, I chose to undertake this phylogenetic analysis.

MATERIALS & METHODS

This dataset was constructed using all past phylogenetic analyses of Sauria as an initial framework, using modified and concatenated versions of the characters employed. Taxon sampling attempted to integrate all of the major terrestrial taxa referred to Sauria from the Permian and Triassic. I undertook first-hand study of nearly all saurians included in this study, allowing coding of new and insufficiently described fossil taxa.

Although many early saurian taxa are known from fragmentary material, a small number are known from large samples of complete to partial skeletons. These include bonebeds of *Trilophosaurus buettneri* (from locality TMM 31025), *Trilophosaurus jacobsi* (from the Kahle Quarry of New Mexico), and *Azendohsaurus madagaskarensis* (from the Isalo Group of Madagascar) (Gregory, 1945; Spielmann, 2008; Nesbitt et al., in press). Many individuals of wide-ranging ontogenetic stages are known for *Tanytrachelos ahynis* (Olsen, 1979; Casey et al., 2007), *Tanystropheus longobardicus* (Wild, 1973; Nosotti, 2007), and *Macrocnemus bassanii* (Peyer, 1937; Rieppel, 1989). Study of these taxa allowed context for character variation within early saurians and across multiple ontogenetic stages. I have noted where these studies have influenced character construction within the individual character descriptions.

Terminal Taxa

Brief descriptions of each taxon in this study is presented below. Abbreviations for the institutions discussed are presented in Appendix 1.

Acerosodontosaurus piveteaui Currie, 1980

Holotype specimen: MNHN 1908-32-57, part and counterpart slabs preserving partial skull, forelimbs, dorsal region, sacrum, and right hindlimb.

Literature Consulted: Currie (1980), Bickelmann et al. (2009).

Localities: Lower Sakamena Formation, Madagascar (Late Permian) (Currie, 1980).

Notes: Bickelmann et al. (2009) included *Acerosodontosaurus piveteaui* in a modification of the Müller (2004) phylogenetic analysis. The taxon was found to nest as the sister taxon of *Hovasaurus boulei*, but they did not recover a monophyletic Younginiformes.

Amotosaurus rotfeldensis Fraser and Rieppel, 2006

Holotype specimen: SMNS 50830, partial, largely disarticulated skeleton with cervical series, scapulocoracoid, pelvis, and partial skull.

Material studied: SMNS 50691, partial skull and anterior portion of skeleton; 53783, multiple associated skeletons; 54784, two skulls, one with associated neck; 54810, dissociated skeleton; 90600, sacrum and partial tail; 90601, articulated maxilla and jugal.

Literature Consulted: Fraser and Rieppel (2006).

Localities: Kössig Quarry, Rotfelden, Germany ("upper Buntsandstein," ?Middle Triassic) (Fraser and Rieppel, 2006).

Notes: *Amotosaurus rotfeldensis* was named by Rieppel and Fraser (2006) for small skeletons of a long-necked early archosauromorph initially described by Wild (1980b) as belonging to juveniles of the much larger *Tanystropheus antiquus*, a taxon based on isolated vertebral material from Middle Triassic sits in eastern Europe (von Huene, 1905). However, the Fraser and Rieppel (2006) rejected this hypothesis, as the purported juveniles exhibited well-ossified tarsals in addition to other anatomical differences. Sennikov (2011) concurred with this distinction, coining the generic name *Protanystropheus* for the original material. Pritchard et al. (2015) recovered a sister relationship between *Tanystropheus longobardicus* and *A. rotfeldensis*, but this was based on incorrect and incomplete codings of the latter (see character 117).

Azendohsaurus laaroussii Dutuit, 1972

Holotype specimen: MNHN MTD XVI 1, mandibular fragment.

Material studied: Collections of maxillae and dentaries on hand at MNHN. A single premaxilla (MNHN ALM 365-16) has been identified (Nesbitt et al., in press).

Literature Consulted: Gauffre, 1993.

Localities: Argana Formation, Morocco (?Carnian) (Gauffre, 1993).

Notes: *Azendohsaurus laaroussii* was initially presented as a very early ornithischian dinosaur (Dutuit, 1972). Multiple authors (Thulborn 1973, 1974; Bonaparte, 1976) challenged this referral, suggesting that the taxon was a "prosauropod" dinosaur. Dutuit (1981) accepted this referral. Gauffre (1993) reviewed the material attributed to *A. laaroussii* and supported its referral to a very early sauropodomorph dinosaur.

Jalil and Knoll (2002) briefly noted postcranial material associated with *A. laaroussii*, which did not exhibit dinosaurian synapomorphies. These have not yet been fully described in the literature, nor have they contributed to the codings of the taxon. However, that the remains do not suggest dinosaurian affinities is congruent with the material of *A. madagaskarensis*.

***Azendohsaurus madagaskarensis* Flynn et al., 2010**

Holotype specimen: UA 7-20-99-653, nearly complete skull and associated vertebral material.

Material studied: Dozens of specimens accessioned with FMNH and UA.

Literature Consulted: Flynn et al. (2010); Nesbitt et al. (in press).

Localities: M-28 locality, Isalo Group, Madagascar (?Middle to Late Triassic) (Nesbitt et al., in press).

Notes: The discovery of *Azendohsaurus madagaskarensis* was originally reported by Flynn et al. (1999) as two distinct early sauropodomorph dinosaur taxa. Flynn et al. (2010) reported on the cranial anatomy, suggesting that all of the material belonged to a single taxon of early archosauromorph with dentition convergent on early dinosaur dentition. The postcranium of the taxon was described in Nesbitt et al. (in press).

Batrachotomus kupferzellensis **Gower, 1999**

Holotype specimen: SMNS 52970, partial skull and postcranium from a single individual.

Material studied: Specimens at SMNS

Literature Consulted: Gower (1999), Gower (2002), Gower and Schoch (2009).

Localities: Upper Lettenkeuper (Ladinian, Middle Triassic) (Gower, 1999).

Notes: *Batrachotomus kupferzellensis* represents one of the most completely understood, well-described pseudosuchian archosaurs based on exquisitely preserved remains from Germany. It thus serves as the exemplar taxon for Pseudosuchia in this study. The literature cited above was the source of the initial codings for Pritchard et al. (2015), augmented by codings by SJ Nesbitt for Nesbitt et al. (in press).

Boreopricea funerea **Tatarinov, 1978**

Holotype specimen: PIN 3708/1, partial skull and nearly complete postcranium.

Material studied: Holotype and PIN 3708/2, additional partial skull.

Literature Consulted: Tatarinov (1978), Benton and Allen (1997)

Localities: Charkabozh Formation, Kolguyev Island, Russia (Lower Triassic, Induan) (PBDB, Benton and Allen, 1997).

Notes: *Boreopricea funerea* was described from a nearly complete skeleton and two partial skulls by Tatarinov (1978). These were discovered during drill-coring at a depth of over 1,000 meters. The holotype skull is unfortunately no longer intact, due to an attempt at acid preparation, although a cast of the skull remains (noted by Benton and Allen, 1997). The postcranial skeleton of PIN 3708/1 is glued to an index card, where outlines have been drawn to indicate the presence of lost bones.

"*Chasmatosaurus*" *yuani* Young, 1936

Holotype specimen: IVPP V/36315 (field number 90002, as noted by Ezcurra and Butler, 2014), partial skull and postcranial skeleton

Material studied: Cast of holotype skull and IVPP V/4067, nearly complete skeleton embedded in matrix block.

Literature: Young (1936), Young (1963).

Localities: Jiucaiyan Formation, Shoukou Fukangshien, Xinjiang, China (Young, 1936; PBDB).

Notes: Young (1936) described a partial skeleton of this taxon, which was immediately compared favorably to *Chasmatosaurus vanhoepeni* (now *Proterosuchus fergusi* per Ezcurra and Butler, 2015) from the Lower Triassic Karoo Basin of South Africa. IVPP V/4067 likely represents the single most complete skeleton of a proterosuchid yet described, with complete forelimbs and hindlimbs (contra NMQR 1484, the most complete specimen of Karoo *Proterosuchus*). Taxonomic revisions of South African Proterosuchidae have rendered the genus *Chasmatosaurus* invalid (Welman, 1998; Ezcurra and Butler, 2015), but none of these have addressed the taxonomy of non-African proterosuchids. I retain the original name here, pending taxonomic revision by MD Ezcurra.

Clevosaurus hudsoni Swinton, 1939

Holotype specimen: NHMUK R5939, partial skull.

Literature Consulted: Fraser, 1988.

Localities: Multiple sites near Cromhall Quarry, United Kingdom (Rhaetian? per Whiteside and Marshall, 2008).

Notes: After its initial description (Swinton, 1939) as an archaic sphenodontid, Robinson (1973) reported in detail on the cranial osteology of *Clevosaurus*, noting its incomplete lower temporal opening and well-developed tympanic crest and contrasting these features with modern *Sphenodon*. She considered this a consequence of parallel evolution with a lineage include *Prolacerta*, Kuehneosauridae, and lizards. Fraser (1988) described a large quantity of additional material from the taxon, noting the presence of several articulated specimens. Since that time, a large number of additional *Clevosaurus* records have been reported in North America (Sues et al., 1994), South America (Bonaparte and Sues, 2006), Africa (Sues and Reisz, 1995), and Asia (Jones, 2006). I employ *Clevosaurus hudsoni*, as this taxon has been described in the greatest detail.

Coelophysis bauri Cope, 1887 (sensu Colbert, 1989)

Holotype specimen: AMNH FARB 7224, complete skeleton missing tip of tail.

Material studied: Codings by Nesbitt (2011) and Nesbitt et al. (in press); Colbert, 1989.

Localities: Chinle Formation, upper "Siltstone" Member, "*Coelophysis*" Quarry, New Mexico (?Norian–?Rhaetian) (Colbert, 1989; Nesbitt, 2011).

Notes: *Coelophysis bauri* is presented as one of two exemplar taxa for avian-line archosaurs (the other being *Plateosaurus engelhardti*, integrated as part of the expansion of the Pritchard et al. (2015) for Nesbitt et al. (in press). *Coelophysis* is represented by several hundred skeletons known from the eponymous *Coelophysis* Quarry at Ghost Ranch (Abiquiu, New Mexico).

***Coelurosauravus elivensis* Piveteau, 1926**

Holotype specimen: MNHN IP 1908-11-21a, skull and postcranial skeleton preserved as impression.

Material studied: MNHN IP 1908-5-2, partial postcranial skeleton preserved as impression; MNHN IP 1908-11-22a, skull and postcranium preserved as impression.

Literature Consulted: Evans (1982), Evans and Haubold (1987).

Localities: Sakamena Formation, Madagascar (Upper Permian) (Evans and Haubold, 1987; Wescott and Diggens, 1998).

Notes: Evans (1982) referred material described by Carroll (1978) as *Daedalosaurus* to *Coelurosauravus elivensis*.

***Coelurosauravus jaekeli* Weigelt, 1930 (sensu Evans and Haubold, 1987)**

Holotype specimen: SSWG 113/7, partial skull, forelimbs, partial hindlimbs, and dorsal region.

Material studied: SMNS 53349 (cast of Holotype).

Literature Consulted: Evans (1982), Evans and Haubold (1987), Schaumberg et al. (2007).

Localities: Kupferschiefer of Eisleben, Germany (Upper Permian) (Evans and Haubold, 1987; Schaumberg et al., 2007)

Notes: Weigelt (1930) originally coined the name *Palaeochameleo jaekeli* for this small reptile from the Upper Permian of Germany. Kuhn (1939) noted that this generic name was preoccupied (a Cenozoic lizard from France), and proposed the generic name *Weigeltisaurus* for the taxon. Evans and Haubold (1987) proposed the placement of *W. jaekeli* in the same genus as the Malagasy gliding taxon *Coelurosauravus elivensis*. I follow this synonymy here.

Diphydontosaurus avonis Whiteside, 1986

Holotype specimen: BU 23760, right dentary.

Material studied: (possibly) MCSNB 4862, complete and crushed skeleton exposed in ventral view.

Literature Consulted: Whiteside, 1986; Renesto, 1995.

Localities: Tytherington Quarry, United Kingdom (?Rhaetian) (Whiteside, 1986; Whiteside and Marshall, 2008); (possibly) Calcare di Zorzino, Italy (Norian) (Renesto, 1995, 2006).3

Notes: Whiteside (1986) named and described the cranial morphology of *Diphydontosaurus avonis*, which she considered to be a plesiomorphic rhynchocephalians. Although the material described was largely disarticulated, she noted that much of one block from the quarry "contained a minimum of 40 individuals of this lepidosaur which constituted over 90% of the fauna in the block" (Whiteside, 1986:381.) The postcranial anatomy of the taxon has not yet been described in the literature, although substantial material does exist (Whiteside, 1986). A partial articulated skeleton has been figured in the literature (Halstead and Nicoll, 1971).

To augment these codings, I incorporate information from a complete, badly crushed specimen of a sphenodontid from the Calcare di Zorzino of Italy. Renesto (1995) tentatively referred this specimen to the genus *Diphydontosaurus*, although he considered referral to *Planocephalosaurus* plausible as well. This specimen represents the most complete skeleton described for a Triassic lepidosaur, thus the morphology it preserves is uniquely valuable. To allow the specimen to inform the morphology of early lepidosaurs, I include information from MCSNB 4862 in codings for *Diphydontosaurus avonis*. I caution that a conclusive determination of the affinities of this skeleton will require a revision of Triassic Rhynchocephalia.

Dolabrosaurus aquatilis **Berman and Reisz, 1992**

Holotype specimen: CMNH 28589, largely disarticulated postcranial skeleton preserved in several blocks.

Material studied: Holotype.

Literature Consulted: Berman and Reisz (1992); Renesto et al. (2010).

Localities: Locality near Abiquiu Reservoir in New Mexico (Norian) (Berman and Reisz, 1992).

Notes: Berman and Reisz (1992) described *Dolabrosaurus* on the basis of an incomplete, but well-preserved skeleton from Chinle Formation outcrops near the Abiquiu Reservoir in New Mexico. Dilkes (1998) incorporated the taxon into his definition of Drepanosauridae, which I follow here.

Drepanosauridae n. gen., n. sp. Pritchard and Nesbitt (in prep.)

Holotype specimen: AMNH FARB 30834, nearly complete skull and partial postcranium embedded in matrix.

Localities: Chinle Formation, upper "Siltstone" Member, "*Coelophysis*" Quarry, New Mexico (?Norian–?Rhaetian) (Colbert, 1989; Nesbitt, 2011).

Notes: This is the taxon described in Chapter 3 of this dissertation. It will be referred to in-text as "the *Coelophysis* Quarry drepanosaurid." It represents the best-preserved cranial material from a drepanosauromorph currently known, and is therefore included in this analysis to contextualize the cranial anatomy of the group.

Drepanosaurus unguicaudatus **Pinna, 1980**

Holotype specimen: MCSNB 5728, nearly complete postcranial skeleton lacking skull and anteriormost cervical vertebrae.

Material studied: Holotype.

Literature Consulted: Renesto, 1994a; Renesto et al., 2010.

Localities: Calcare di Zorzino, Italy (Norian) (Renesto, 2006).

Notes: *Drepanosaurus unguicaudatus* has long been known from a single specimen from the Upper Triassic of Italy (Pinna, 1980, 1984, 1986). In chapter 2 of this dissertation, I refer a substantial amount of forelimb material from the Upper Triassic Hayden Quarry of New Mexico (see Irmis et al., 2007; Pritchard, 2015) to *Drepanosaurus unguicaudatus*. Pending review of this referral, this coding is based on the holotype.

Erythrosuchus africanus **Broom, 1905**

Holotype specimen: SAM 905, incomplete postcranial skeleton.

Material studied: NHMUK R3592, incomplete partial skeleton; NMQR 3765, nearly complete postcranial skeleton and partial skull.

Literature consulted: Gower (1996, 2003).

Localities: Sites in *Cynognathus* Assemblage Zone, Beaufort Group, South Africa (Gower, 2003).

Notes: *Erythrosuchus* is known from a large number of partial skeletons and isolated elements (e.g., AMNH FARB 5595). It represents one of the largest early archosauriforms known from the Triassic, substantially larger than known Early Triassic archosauriforms (e.g., *Proterosuchus* spp.). *Erythrosuchus* has been a part of nearly all cladistic studies of stem archosaur relationships (e.g., Gauthier, 1984; Benton, 1985; Dilkes, 1998). *Erythrosuchus* and its kin (Erythrosuchidae, see Parrish, 1992) have consistently been recovered as the first divergence within Archosauriformes following Proterosuchidae (e.g., Parrish, 1992; Dilkes, 1998; Nesbitt, 2011). However, *Erythrosuchus* is problematic in that its limb elements exhibit an apparently apomorphic reduction in the articular surfaces of its limbs (e.g., NHMUK R3592). The integration of a more plesiomorphic erythrosuchid taxon into the analysis would be beneficial in future iterations.

Euparkeria capensis Broom, 1913

Holotype specimen: SAM K5867, skull and partial postcranium.

Literature Consulted: Ewer, 1965; Nesbitt, 2011.

Localities: Multiple sites in the *Cynognathus* Assemblage Zone, Karoo Basin, South Africa (Ewer, 1965).

Notes: *Euparkeria* has long been recognized as a taxon near to the ancestry of Archosauria (Broom, 1913; Watson, 1957). Cladistic studies have recovered the animal as nested within Archosauria (Gauthier, 1984), as the sister taxon of Archosauria (Benton and Clark, 1988), as the sister taxon of the clade Proterochampsidae+Archosauria (Brusatte et al., 2010; Ezcurra et al., 2010), and as the sister taxon of Archosauria+Phytosauria (Nesbitt, 2011). A number of Triassic archosauromorphs have been suggested as close relatives of *Euparkeria* within a monophyletic Euparkeriidae (reviewed by Sookias and Butler, 2013). Codings of characters 1–247 from this taxon have been reviewed by SJ Nesbitt for Nesbitt et al. (in press).

***Gephyrosaurus bridensis* Evans, 1980**

Holotype specimen: UCL T.1503, right dentary

Literature Consulted: Evans (1980, 1981a, 1981b, 1985), Conrad (2008).

Localities: Type material from Pontalun Quarry, Glamorgan, United Kingdom (Hettagian or Sinemurian) (Evans, 1980).

Notes: *Gephyrosaurus bridensis* was named by Evans (1980) for a series of disarticulated cranial and postcranial elements from fissure fills on St. Bride's Island in Wales. Evans (1980) argued that nearly all of the St. Bride's fissures contained only a single reptile taxon, a fact supported by the consistency in cranial sculpturing in dermal ossifications and a consistent body size. I follow Gauthier et al. (1988a), Dilkes (1998), Conrad (2008), and Gauthier et al. (2012) in coding *G. bridensis* based on these disarticulated material.

***Hovasaurus boulei* Piveteau, 1926**

Holotype specimen: MNHN 1908-21-2 and MNHN 1908-21-7, part and counterpart slabs of headless skeleton.

Material studied: Holotype; MNHN 349, headless skeleton.

Literature Consulted: Currie (1981a), Caldwell (1994).

Localities: Lower Sakamena Formation, Madagascar (Upper Permian) (Currie, 1981a).

Notes: A substantial number *Hovasaurus boulei* specimens are known from the Sakamena Formation of Madagascar, providing excellent context to the ontogeny of the taxon. Currie (1981a, 1982) argued that *Hovasaurus* was the sister taxon of *Tangasaurus mennelli* in Tangasaurinae. Caldwell (1994) reviewed the pattern of acquisition of major features of the appendicular skeleton. These observations are noted in a number of character descriptions noted below.

Howesia browni **Broom, 1905b**

Holotype specimen: SAM K5884, partial disarticulated skull.

Material studied: SAM K5885, partial skull and anteriormost cervical region; SAM K5886, partial postcranium, around the pelvic girdle.

Literature consulted: Dilkes (1995).

Localities: Near Aliwal North, *Cynognathus* Assemblage Zone (Middle Triassic) (Dilkes, 1995).

Notes: *Howesia browni* was initially described by Broom (1905), but the osteology of the taxon was only fully described by Dilkes (1995). It has generally been considered the second earliest-diverging rhynchosaur after *Mesosuchus browni* (Dilkes, 1995, 1998; Montefeltro et al. 2010).

Hypuronector limnaios **Colbert and Olsen, 2001**

Holotype specimen: AMNH FARB 7759, nearly complete postcranial skeleton.

Material studied: Holotype, AMNH FARB 1721, articulated anterior trunk region with complete scapulocoracoid; AMNH FARB 2080, complete mandible and partial caudal vertebrae.

Literature Consulted: Colbert and Olsen, 2001.

Localities: Multiple sites from the Lockatong Formation of New Jersey (Ewing Creek and Nursery Members per Colbert and Olsen, 2001). Early Norian (Olsen et al., 1996).

Notes: Before its eventual description by Colbert and Olsen (2001), *Hypuronector limnaios* was referred to in the literature as the "'deep-tailed swimmer'" (e.g., Olsen, 1980:40). Although noted at the time to be of uncertain affinities, Olsen (1980) noted similarities with then-undescribed material from the Upper Triassic of Italy, which are now recognized as drepanosaurids. Additional material of *Hypuronector limnaios* accessioned at YPM are mentioned by Colbert and Olsen (2001), but these could not be found in the collections.

Icarosaurus siefkeri **Colbert, 1966**

Holotype specimen: AMNH FARB 2101, complete skull and partial postcranial skeleton lacking most of hindlimbs and tail.

Material studied: Holotype.

Literature Consulted: Colbert, 1966, 1970.

Localities: Granton Quarry, Lockatong Formation, New Jersey (early Norian) (Olsen et al., 2011).

Notes: The holotype of *Icarosaurus siefkeri* is the single most complete kuehneosaurids specimen yet-reported. Robinson (1962, 1967a, 1967b) noted that the *Icarosaurus* material were useful in her reports on the *Kuehneosaurus* material from the United Kingdom.

***Kuehneosaurus latus* Robinson, 1962**

Holotype specimen: NHMUK R 8172, partial articulated skeleton

Material studied: Collections of isolated elements at AMNH and NHMUK.

Literature Consulted: Robinson (1962, 1967a, 1967b).

Localities: Emborough Quarry, Keuper Beds, United Kingdom (Rhaetian? based on vertebrate biostratigraphy per Whiteside and Marshall, 2008).

Notes: *Kuehneosaurus latus* was first described as the type species of the genus *Kuehneosaurus* by Robinson (1962) who detailed the cranial and vertebral anatomy of the taxon, accompanied by detailed reconstructions of the skull. In the same publication, she named an additional species, *Kuehneosaurus latissimus*, from the stratigraphically equivalent (per Robinson, 1967b) Batescombe Quarry. Robinson (1962) and (1967b) noted only vertebral distinctions between these taxa, and Robinson (1967b) coined a new genus, *Kuehneosuchus* for that species. Robinson (1962) noted that a monographic study of the taxon was underway, but this was not published in her lifetime; Stein et al. (2008) made reference to an unpublished manuscript by Robinson dating from 1979, more fully describing Kuehneosauridae.

I employ *Kuehneosaurus latus* as the representative of European kuehneosaurids for two reasons: 1) it is the type species of the taxon; 2) substantial material of Emborough *Kuehneosaurus* were available at the American Museum of Natural History. However, a thorough revision of the European kuehneosaurids material is essential for understanding the taxonomy and osteology of the group.

Langobardisaurus pandolfii **Renesto, 1994b**

Holotype specimen: MCSNB 2883, distorted skull and postcranial skeleton lacking forelimb elements and tip of tail.

Material studied: Holotype; MCSNB 4860, complete but badly distorted juvenile skeleton; MFSN 1921, complete and crushed skull and postcranium; MFSN 26829, partial hindlimb and left foot.

Literature Consulted: Renesto, 1994b; Saller et al., 2013.

Localities: Calcare di Zorzino, Italy (Norian) (Renesto, 2006), Dolomia di Forni, Italy (Norian) (Renesto, 2006), Seefeld Formation, Austria (Norian) (Saller et al., 2013).

Notes: *Langobardisaurus pandolfii* was initially described on the basis of two nearly complete skeletons from the Calcare di Zorzino of Italy (Renesto, 1994). Soon after, Muscio (1996) described an additional skeleton from the Dolomia di Forni of Italy as a possible distinct species, *L.* ?*tonelloi*, based on perceived phalangeal and dental differences. Renesto (2006) noted that he did not recognize any significant differences between the species. Saller et al. (2013) described an additional specimen from the Norian of Austria and also argued for the synonymy of *L. tonelloi* and *L. pandolfii*. Pritchard et al. (2015) tested the sister relationship of the two species when coded as individual OTUs, and recovered a sister group relationship between them. This result and my own study of the Italian material lead me to accept the synonymy of the species.

Macrocnemus bassanii Nopcsa 1930

Holotype specimen: MCSN 14624, poorly preserved skeleton preserved as part and counterpart impressions. Destroyed in World War II.

Material studied: Cast of holotype (PIMUZ T/4823); MCSN BES SC 111, complete skeleton of young juvenile in left lateral view; MCSN V 457, disarticulated skull and partial postcranium of large adult; PIMUZ T/2472, crushed skull and partial postcranium; PIMUZ T/2477, complete, three dimensionally preserved skull, partial trunk and caudal region, hindlimb; PIMUZ T/4355, crushed skull and nearly complete articulated skeleton; PIMUZ T/4822, complete skull and postcranium lacking forelimbs and pectoral girdle.

Literature Consulted: Peyer (1937), Rieppel (1989).

Localities: Besano Formation, Italy; Meride Formation, Italy (Ladinian/Anisian).

Notes: Although numerous specimens of *Macrocnemus bassanii* are known from the same localities as *Tanystropheus longobardicus*, the available ontogenetic series of the former is less not as substantial as the latter. The smallest specimen known in detail (MCSN BES SC 111), described by Renesto and Avanzini (2002). The data from these specimens provides a limited sense of ontogenetic change in the taxon. The differences in cranial morphology noted from small to large *M. bassanii* are not nearly as significant as those noted between the smallest and largest *Tanystropheus longobardicus*.

Macrocnemus fuyuanensis Li et al., 2007

Holotype specimen: IVPP V15007, nearly complete skeleton.

Material studied: GMPKU P3001, nearly complete skull and skeleton lacking tail.

Literature Consulted: Li et al. (2007), Jiang et al. (2011).

Localities: Zhuganpo Member, Falang Formation, China (Ladinian) (Li et al., 2007).

Notes: Li et al. (2007) distinguished between *Macrocnemus bassanii* and *M. fuyuanensis* based largely on proportional differences in the limb skeleton and the dorsal vertebral count. Jiang et al. (2011) concurred with this diagnosis, and I accept the distinction between the two species here.

***Megalancosaurus preonensis* Calzavarra et al., 1980**

Holotype specimen: MFSN 1769, complete skull and anterior portion of postcranial skeleton, preserved as part and counterpart.

Material studied: Holotype; MFSN 1801, complete tail; MFSN 18443, complete tail; MPUM 6008, headless postcranial skeleton preserved anterior to the pelvis; MPUM 8437, skull roof and nearly complete postcranial skeleton missing tip of the tail.

Literature Consulted: Renesto et al., 2010.

Localities: Holotype from Dolomia di Forni, Italy (Norian); all other studied specimens from Calcare di Zorzino, Italy (Norian).

Notes: *Megalancosaurus* was first described as a bizarre thecodont reptile by Calzavarra et al. (1980). For some time the taxon was referred to the monotypic family Megalancosauridae (Renesto, 1994c), although some morphological similarities between it and *Drepanosaurus unguicaudatus* were noted (Renesto, 1994a, 1994c). Merck (1997) and Dilkes (1998) recovered *Megalancosaurus* and *Drepanosaurus* in a well-supported clade, and the two have been regarded as close relatives since that time. Renesto et al. (2010) named an additional species of

Megalancosaurus (*M. endennae*), which I do not regard as distinct from the type species (see chapter 3 of this dissertation).

Mesosuchus browni Watson, 1912

Holotype specimen: SAM K5882, partial skull, partial presacral and anterior caudal columns, partial pectoral girdle and fore and hindlimbs.

Material studied: SAM K6046, maxilla, articulated presacral, sacral, and anterior caudal columns, partial forelimbs, pelvic girdles, right hindlimb; SAM K6536, complete skull, cervical vertebrae, dorsal vertebrae, partial pectoral girdles, distal humerus, gastralia; SAM K7416, nearly complete trunk, hindlimbs, and anterior caudal region.

Literature Consulted: Dilkes, 1998.

Localities: Single, exhausted locality near Aliwal North, equivalent to the original *Euparkeria* locality, middle portion of *Cynognathus* Assemblage Zone

Notes: Watson (1912) presented the taxon as a close relative of what he perceived as early archosaurs (e.g., *Proterosuchus*, *Erythrosuchus*). Dilkes (1998) reviewed the phylogenetic hypotheses for the taxon, highlighting the emerging consensus that the animal was an early member of Rhynchosauria.

Pamelaria dolichotrachela Sen, 2003

Holotype specimen: ISIR 316, nearly complete and associated skeleton.

Literature Consulted: Sen (2003).

Localities: Yerrapalli Formation, Andhra Pradesh, India (Middle Triassic) (Sen, 2003).

Notes: Sen (2003) presented a preliminary description of *Pamelaria dolichotrachela*, addressing nearly all elements of the skeleton. In the description, Sen (2003) presented a systematic hypothesis, based on the framework of Benton (1985), that the animal was closely related to *Prolacerta* within a monophyletic clade of long-necked archosauromorphs. Gottmann-Quesada and Sander (2009) included the taxon in their analysis, recovering it as the sister taxon of a clade of *Prolacerta*+Archosauriformes. Nesbitt et al. (in press) in a modification of the Pritchard et al. (2015) analysis recovered *Pamelaria* within a clade including *Azendohsaurus*, *Trilophosaurus*, and *Teraterpeton*.

***Petrolacosaurus kansensis* Lane, 1945**

Holotype specimen: KUVP 1424, right hindlimb of adult individual.

Literature consulted: Reisz, 1981.

Localities: Stanton Formation, Garnett Quarry, Kansas; Late Carboniferous (Reisz et al., 1982)

Notes: *Petrolacosaurus kansensis* has long been recognized as the oldest-known and most plesiomorphic diapsid reptile (e.g., Reisz, 1977, 1981; Dilkes, 1998). It predates the next unequivocal diapsid by over ten million years (Reisz et al., 2011), and has long been recognized as lacking characteristic features of later diapsids (e.g., Benton, 1985; Evans, 1988). Following the footsteps of Dilkes (1998), I employ *Petrolacosaurus kansensis* as the outgroup of this study based on its extremely early stratigraphic position and plesiomorphic morphology.

***Plateosaurus engelhardti* Meyer, 1837**

Holotype specimen: SMNS 13200, nearly complete skull and skeleton. Considered the "unofficial holotype" by Yates (2003:332), due to the poor quality of assigned syntypes. Presented as proposed neotype by Galton (2012).

Literature consulted: Codings by Nesbitt (2011) and Nesbitt et al. (in press); Prieto-Marquez and Norell (2011).

Localities: Löwenstein Formation, *Plateosaurus* Quarry, Germany (middle Norian).

Notes: *Plateosaurus engelhardti* is one of two exemplar taxa of avian-line archosaur, the other being *Coelophysis* bauri. As with *Coelophysis*, *Plateosaurus* is represented by many partial skeletons studied by SJ Nesbitt for codings in Nesbitt (2011) and Nesbitt et al. (in press).

Prolacerta broomi Parrington, 1935

Holotype specimen: UMCZ 2003.40, partial skull.

Material studied: AMNH FARB 9502, partial skeleton with pes; AMNH FARB 9520, complete but crushed skull; BP/1 471, partial skull (former holotype of *Pricea longiceps*, Broom and Robinson, 1948); BP/1 2675 (disarticulated, acid-prepared skull and postcranium to anterior trunk region); BP/1 2676 (partial postcranial skeleton); BP/1 4504, partial skull and anterior cervical vertebrae; BP/1 5066, partial skull; BP/1 5375, partial skull lacking tip of snout; BP/1 5880, skull and anterior cervical vertebrae; NMQR 3763, two partially articulated skeletons with skulls; SAM K10802, nearly complete and partially articulated skeleton; UCMP 37151, skull and anterior cervical series.

Literature consulted: Parrington (1935), Gow (1975), Colbert (1987), Modesto and Sues (2004).

Localities: Sites in *Lystrosaurus* Assemblage Zone, Beaufort Group, South Africa (Induan) (Gow, 1975); Fremouw Formation, Antarctica (Early Triassic, Induan) (Colbert, 1987; Smith et al., 2011).

Notes: *Prolacerta broomi* was long regarded as a critical fossil taxon for interpreting the early history of lizards (e.g., Parrington, 1935; Camp, 1945; Robinson, 1967a), although recent studies have left it as one of the best-understood early archosauromorph species. Gow (1975) and Modesto and Sues (2004) reviewed the records of the taxon from the Karoo Basin of South Africa and concluded that the material studied belonged to a single species.

Colbert (1987) described a number of partial skeletons from the Fremouw Formation of Antarctica as belonging to *Prolacerta broomi*. Although he noted some anatomical distinctions between this and the South African material, he maintained the species referral. As in Pritchard et al. (2015), I follow this taxonomic referral in this analysis. The purported prolacertid *Kadimakara australiensis* Bartholomai, 1979 from the Early Triassic of Australia may also be a specimen of *Prolacerta broomi* (Evans and Jones, 2009).

In addition to the anatomical distinctions noted between the Antarctic and South African *Prolacerta* material by Colbert (1987), I note a degree of morphological diversity within the South African *Prolacerta* material as well. As has been recognized previously (Gow, 1975; Modesto and Sues, 2004), some specimens referred to *Prolacerta* exhibit a pineal opening in contrast to the holotype (Parrington, 1935). I also note a number of distinctions in the cervical vertebral morphology of a number of *Prolacerta broomi* specimens from the Karoo (discussed in character descriptions below). For the moment, I retain the single-species taxonomy proposed previously, but taxonomic revision of all *Prolacerta broomi* is necessary.

South African *Proterosuchus* (type: *Proterosuchus fergusi* Broom, 1903)

Holotype specimen: SAM K591, partial skull and postcranium.

Material studied referred to *Proterosuchus alexanderi*: Holotype (NMQR 1484, skull and nearly complete postcranial skeleton lacking most forelimb material).

Material studied referred to *Proterosuchus fergusi*: Holotype; BP/1 3393, complete skull, cervical vertebrae; BP/1 4016, skull and articulated cervical series; SAM K10802, nearly complete skull.

Material studied referred to *Proterosuchus goweri*: Holotype (NMQR 880, partial cranium lacking braincase).

Literature Consulted: Cruickshank, 1972; Welman, 1998; Ezcurra and Butler, 2014.

Localities: Sites in *Lystrosaurus* Assemblage Zone, Beaufort Group, South Africa (Induan) (Ezcurra and Butler, 2014).

Notes: Since the initial description of *Proterosuchus fergusi* (Broom, 1903), dozens of similar skulls and partial skeletons have been described from throughout South Africa (e.g., Haughton, 1924; Broom, 1932; Broili and Schroeder, 1934; Brink, 1955; Welman and Fleming, 1993; Welman, 1998), resulting in a large number of named species from this small region. In his review of the material, Cruickshank (1972:90–91) accepted the validity of *Proterosuchus fergusi*, although he noted that "[i]t is unlikely that any other specimen will ever be assigned to *P. fergusi* in the future," unsurprising due to the highly incomplete material. The remainder of his description focused on *Proterosuchus vanhoepeni*, to which he synonymized the remaining South African proterosuchid taxa.

Welman and Fleming (1993) and Welman (1998) further addressed the synonymy of the South African proterosuchids, with Welman (1998) further providing evidence of synonymy with the type specimen of *Proterosuchus fergusi*. Ezcurra and Butler (2015) came to an altogether different conclusion, providing novel anatomical data that at least three species of *Proterosuchus* were present in the *Lystrosaurus* Assemblage Zone of South Africa: *P. alexanderi*, *P. fergusi*, *P. goweri*. As MD Ezcurra and colleagues are currently performing further phylogenetic revision of Proterosuchidae and related forms, I refrain from incorporating this novel taxonomic hypothesis for *Proterosuchus*. I retain the South African *Proterosuchus* as a single OTU for this analysis.

Protorosaurus speneri Meyer, 1832

Lectotype specimen: NHMW 1934I4, almost complete skeleton.

Material studied: SMNS (cast of WMsN P 47361, complete skull and skeleton); SMNS (cast of privately owned Simon-Bartholomäus specimen); SMNS (cast of privately owned specimen numbered PSM 7 in Gottmann-Quesada and Sander, 2009); USNM 44 (cast of NMK S 180), complete skull, cervical series, and

Literature Consulted: Evans and King, 1993; Gottmann-Quesada and Sander (2009).

Localities: Kupferschiefer Formation, Germany (Upper Permian) (Gottmann-Quesada and Sander, 2009); Marl Slate, United Kingdom (Upper Permian) (Evans and King, 1993).

Notes: The first specimen of *Protorosaurus speneri* is among the oldest specimens of a fossil reptile described in the scientific literature, being first referenced in 1710 (Gottmann-Quesada and Sander, 2009). Since that time, over a dozen partial skeletons have been discovered from the Upper Permian Kupferschiefer Formation of Germany (Gottmann-Quesada and Sander, 2009). Two specimens have been described from Upper Permian deposits of Great Britain as well (Evans and King, 1993).

The history of understanding the relationships of *Protorosaurus* has been complex (detailed in the introduction). Although early cladistic studies tended to consider the taxon a close relative of *Prolacerta* and Tanystropheidae (e.g., Gauthier, 1984; Laurin, 1991; Dilkes, 1998), more recent analyses consider *Protorosaurus* to be part of the earliest divergence of Archosauromorpha (Borsuk-Bialynicka and Evans, 2009; Gottmann-Quesada and Sander, 2009).

Rautiania Bulanov and Sennikov, 2006 (type: *Rautiania alexandri* Bulanov and Sennikov, 2006)

Holotype specimen: PIN 5130/1, right parietal.

Material studied referred to *Rautiania alexandri*: Holotype; PIN 5130/4, left maxilla.

Material studied referred to *Rautiania minichi*: Holotype (PIN 5130/2, right parietal); PIN 5130/3, left maxilla.

Material studied not referable to either species: Several dozen specimens accessioned in PIN 5130.

Literature Consulted: Bulanov and Sennikov (2006, 2010).

Localities: Kul'chumovo-A locality, Orenberg Region, Russia (Upper Permian) (Bulanov and Sennikov, 2006).

Notes: Bulanov and Sennikov (2006) briefly reported on disarticulated material that they attributed to a new taxon closely related to *Coelurosauravus*. They presented two distinct species from a single locality, which they distinguished based on cranial ornamentation and dentition. They later (2010) reported on a large quantity of additional cranial and postcranial material of weigeltisaurids from the same locality. These were largely described as *Rautiania* sp., as none of the material exhibited characters diagnostic of either species.

The material of *Rautiania* is quite similar to equivalent skeletal elements in *Coelurosauravus elivensis* and *C. jaekeli*, supporting the referrals of Bulanov and Sennikov (2010). These are also very well preserved and three-dimensional, making them valuable for understanding the osteology of Weigeltisauridae. Thus I present a concatenated OTU for *Rautiania* in this analysis, combining the material from Kul'chumovo-A. However, to assess the ingroup relationships of Weigeltisauridae, it would be necessary to find apomorphies to link the isolated Kul'chumovo fossils to individual species of *Rautiania*.

Rhynchosaurus articeps Owen, 1842

Lectotype specimen: SHRBM G132/1982, nearly complete skull and mandible.

Material studied: NHMUK R1236, orbital and rostral portion of skull; R1237, dorsoventrally compressed skull; NHMUK R1238, partial, articulated skeleton preserved in ventral view.

Literature Consulted: Benton (1990).

Localities: Grinshill quarries, United Kingdom (Anisian) (Benton, 1990; Benton and Spencer, 2012).

Notes: *Rhynchosaurus articeps* is the type species of the *Rhynchosaurus* and thus the entire clade Rhynchosauria (Benton, 1990).

Shinisaurus crocodilurus Ahl, 1929

Extant species.

Literature Consulted: Conrad, 2004, 2006; Bever et al., 2005.

Localities: Southeastern China and adjacent Viet Nam (Nguyen et al., 2015).

Notes: The small anguimorph lizard *Shinisaurus crocodilurus* has been described in great detail in the past two decades, with extensive detail on its osteology and the ontogeny of skeletal elements. As most morphology-based phylogenetic studies have recovered two primary divisions within Squamata (e.g., Iguanomorpha and Scincogekkonomorpha per Conrad, 2008), I elect to include one modern representative of each group. *Shinisaurus crocodilurus* represents Scincogekkonomorpha. However, recent molecular phylogenies have produced starkly contrasting topologies for Squamata (e.g., Wiens et al., 2012), in which Iguania and

Anguimorpha are closely related. Future iterations of this study will benefit from the addition of other modern squamates, especially the gekkonomorphs that molecular studies resolve as an early divergence within the clade.

***Sphenodon punctatus* Gray, 1842**

Extant species.

Material studied: UCMP 123732, skeleton.

Literature Consulted: Carroll (1985); Evans (2008); Russell and Bauer (2008).

Localities: (modern) Offshore islands around New Zealand (Australasian Reptile & Amphibian Specialist Group, 1996).

Notes: *Sphenodon punctatus* is one of only two extant species of Rhynchocephalia. Long regarded as a morphologically conservative taxon, retaining many plesiomorphic morphologies of Diapsida (e.g., Romer, 1956). However, discovery of fossil relatives dating to the Triassic (e.g., Robinson, 1973; Whiteside, 1986) suggesting that the group was far more varied in its early history, and that many perceived plesiomorphies in *Sphenodon* were in fact secondarily evolved.

***Spinosuchus caseanus* von Huene, 1932**

Holotype specimen: UMMP 7507, partial presacral vertebral column.

Material studied: (see *Trilophosaurus jacobsi* section below).

Literature Consulted: Case (1927); Spielmann et al. (2009).

Localities: Unnamed site in Crosby County, Dockum Group, Texas (Norian?) (Spielmann et al., 2009).

Notes: See the section on *Trilophosaurus jacobsi* below. The *Spinosuchus caseanus* OTU is based on firsthand study by SJ Nesbitt for Nesbitt et al. (in press).

Tanystropheus longobardicus **(originally *Tribelesodon longobardicus* Bassani 1886)**

Holotype specimen: MCSN unnumbered, partial skull and disarticulated postcranium preserved as part and counterpart slabs (destroyed in WWII).

Neotype specimen: PIMUZ T/2791, nearly complete and very small skeleton.

Material studied: GMPKU P1527, extremely large, three-dimensional postcranial skeleton; MCSN BES SC 265, nearly complete, compressed skeleton; MCSN BES SC 1018, nearly complete, compressed juvenile skeleton with complete skull; PIMUZ T/2819, complete skull preserved in dorsal view, braincase, and cervical column.

Literature Consulted: Peyer (1931), Wild (1973), Nosotti (2007).

Localities: Besano Formation, Italy (Ladinian/Anisian) (Bassani, 1886); Monte San Giorgio, Switzerland (Anisian/Ladinian) (Wild, 1973); Zhuganpo Member, Falang Formation, China (Ladinian?) (Rieppel et al., 2010).

Notes: Although not the type species for the genus *Tanystropheus* (*T. conspicuus* Meyer, 1855), *T. longobardicus* is the best-known with many partial and complete skeletons. Bassani (1886) originally reported the type material as an early pterosaur, *Tribelesodon longobardicus*, although its close affinity with *T. conspicuus* was soon noted (Peyer, 1931). Although these specimens are typically heavily compressed, they represent a broad sample of ontogenetic states ranging from small juveniles under one meter in length to extremely large adults likely six times that length. Insights from the ontogenetic series of *Tanystropheus* for character construction are referenced in individual character descriptions.

Tanytrachelos ahynis **Olsen, 1979**

Holotype specimen: YPM VP 7496, nearly complete skeleton missing pedes and tail tip.

Material studied: Holotype; AMNH FARB 7206, well-preserved, disarticulated skeleton; VMNH 2826, partial skull and vertebral column; 3423 badly crushed skull and anterior axial skeleton; 120015, nearly complete skull and skeleton preserved anterior to mid-caudal region; 120016, complete skeleton; 120019, neck, forelimbs, and dorsal region; 120042, neck and partial forelimbs; 120043, skull and dorsal vertebral column; 120046, pectoral girdle elements; 120047, hindlimb and partial caudal skeleton; 120048, posterior dorsal region, sacrum, hindlimbs, and anterior caudal skeleton; 120049, forelimbs, dorsal region, hindlimbs, and anterior caudal region; YPM 7482, complete skull and partial skeleton; 8600, partial forelimb, vertebral column, hindlimb.

Note that all specimens from the Virginia Museum of Natural History are heavily distorted and preserved as part and counterpart slabs.

Literature Consulted: Olsen, 1979.

Localities: Solite Quarry, Cow Branch Formation, Virginia (Norian) (Fraser et al., 1996; PBDB); Lockatong Formation, New Jersey (Norian) (Olsen et al., 2011).

Notes: A relatively small tanystropheid, *Tanytrachelos* may be known from more complete skeletons than any other Triassic reptiles (Casey et al., 2007; collections at VMNH and YPM), most from the Solite Quarry of Virginia. Olsen (1979) described two morphotypes of the species, differing based on the presence of paired heterotopic bones posterior to the pelvis. As in Wild

(1973), Olsen (1979) speculated that these elements were sexually dimorphic. Casey (2005) noted the presence of heterotopics in ~40% of individuals.

Teraterpeton hrynewichorum Sues, 2003

Holotype specimen: NSM 999FG041, incomplete skull and partial postcranial skeleton preserving fragmentary limbs and vertebral column anterior to pelvis.

Literature Consulted: Sues, 2003.

Localities: Wolfville Formation, Newark Supergroup, Nova Scotia (Carnian) (Sues, 2003; Sues and Olsen, 2015).

Notes: *Teraterpeton hrynewichorum* is a highly apomorphic archosauromorph with an elongate, beaked rostrum; distinctive cusped teeth; an enormous external naris; and a closed infratemporal fenestra. Sues (2003) named a monotypic family, Teraterpetidae , for the taxon. It has been included in relatively few phylogenetic studies (Sues, 2003; Pritchard et al., 2015), all of which resolve the taxon as the sister group to *Trilophosaurus*.

Teyumbaita sulcognathus Azevedo and Schultz, 1987

Holotype specimen: UFRGS-PV-0232T, complete skull, partial cervical, dorsal, and caudal vertebral columns, pectoral girdles, left humerus, right femur, right tibia, phalanges (Montefeltro et al., 2010).

Literature Consulted: Montefeltro et al. (2010, 2013).

Localities: Linha Fação and Faixa Nova sites near Santa Maria, Brazil (Norian?) (Montefeltro et al., 2010).

Notes: *Teyumbaita sulcognathus* was originally named as a species of *Scaphonyx* (Azevedo and Schultz, 1987). Montefeltro et al. (2010) argued that the taxon instead warranted its own genus and extensively described its cranial and mandibular osteology. Montefeltro et al. (2013) described the postcranial osteology of the taxon. These works represent the most recent detailed descriptions of the osteology of a derived, hyperodapedontine rhynchosaur. I thus selected this taxon as a representative Late Triassic rhynchosaur.

***Thadeosaurus colcanapi* Carroll, 1981**

Holotype specimen: MNHN PM 1908-11-13a and MNHN PM 1908-1119a, part and counterpart slabs of a headless, but nearly complete postcranial skeleton, lacking the distal right forelimb and right hindlimb.

Material studied: Holotype.

Literature Consulted: Carroll, 1981; Currie and Carroll, 1984; Caldwell, 1994.

Localities: Lower Sakamena Formation, Madagascar (Late Permian) (Carroll, 1981).

Notes: Piveteau (1926) referred a small number of early reptile specimens from Permian Madagascar to the Late Permian taxon *Datheosaurus*, which was later recognized as an early synapsid (Currie, 1979). Carroll (1981) reviewed these specimens and referred them to a new genus and species of diapsid, *Thadeosaurus colcanapi*, which he considered to be close to the South African *Youngina capensis*. Currie and Carroll (1984) described additional specimens of *Thadeosaurus*, including the first partial skull of the taxon. Caldwell (1994) incorporated a growth series of *Thadeosaurus* into his broader study on ontogeny in Permian diapsids. The insights from this study have implications for character construction discussed below.

Trilophosaurus buettneri Case 1928a

Holotype specimen: UMMP 2339, extremely small right dentary.

Material studied: NMMNH and TMM collections.

Literature Consulted: Gregory (1945), Parks (1969), Spielmann et al. (2008), Nesbitt et al. (in press).

Localities: Multiple sites in the Dockum Group of Texas, Late Triassic (Spielmann et al., 2008; Irmis et al., 2013) and the Chinle Formation of Arizona, Late Triassic (Spielmann et al., 2008).

Notes: *Trilophosaurus buettneri* is known from a number of sites throughout the Upper Triassic of Texas, although the best material come from a single site in the Otischalkian faunachron (Late Triassic) of the Dockum Group of Texas (Spielmann et al., 2007). These material provided the basis for the monograph of Gregory (1945). Spielmann et al. (2008) reviewed known records of *T. buettneri*, noting the presence of fragmentary material from the Upper Triassic of Arizona as well.

Trilophosaurus jacobsi Murry, 1987

Holotype specimen: MNA V3192, fragmentary jaw with several preserved teeth (identified variably as a right mandible by Murry, 1987 and a possible left maxilla by Heckert et al., 2006).

Material studied: NMMNH collections.

Literature Consulted: Murry, 1987; Heckert et al., 2006; Spielmann et al., 2008

Localities: Holotype from the *Placerias* Quarry, Chinle Formation (Norian) (Irmis et al., 2013); Kahle Quarry material from Upper Triassic Dockum Group of west Texas (Heckert et al., 2006; Spielmann et al., 2008).

Notes: *Trilophosaurus jacobsi* was defined by Murry (1987) on the basis of a jaw fragment with teeth that distinguished it from *T. buettneri*. Sues and Olsen (1993) rejected the referral of *T. jacobsi* to *Trilophosaurus*, hypothesizing that it belonged to a procolophonian instead. They offered the generic name *Chinleogomphius* for the taxon. Heckert et al. (2006) reviewed the taxonomy of *Trilophosaurus* and presented new cranial material of *T. jacobsi*, which supported Murry's initial referral to *Trilophosaurus*. This and other extensive skeletal material referred to *T. jacobsi* were discovered at the Kahle Quarry (Dockum Group)

It has recently been suggested that *Trilophosaurus* is a very close relative of *Spinosuchus caseanus* (Spielmann et al., 2009; Nesbitt et al., in press). *Spinosuchus caseanus* was named by von Huene (1932), based on a series of tall-spined vertebrae described by Case (1927) as belonging to *Coelophysis*. Long and Murry (1995) speculated that the taxon belonged to Neodiapsida, but refrained from a more specific referral. Spielmann et al. (2009) presented the hypothesis that *Spinosuchus* and *Trilophosaurus* were close relatives, noting that vertebral material of *Spinosuchus* had been found at the Kahle Quarry. However, I note that little distinguishes the vertebrae referred to *T. jacobsi* and those referred to *S. caseanus* from the Kahle Quarry, to the point where I consider it likely that the Kahle material belong to a single taxon. The Kahle "*Spinosuchus*" vertebrae have been used in the coding of *Trilophosaurus jacobsi* in this analysis, but I refrain from synonymizing all *Spinosuchus* material with *T. jacobsi* pending further study.

***Uromastyx aegyptia* Forskal, 1775**

Extant species.

Literature Consulted: El-Toubi, 1949; Conrad, 2008; Gauthier et al., 2012.

Localities: Northeastern Africa, Arabian Peninsula, Iran.

Notes: As most morphology-based phylogenetic studies have recovered two primary divisions within Squamata (e.g., Iguanomorpha and Scincogekkonomorpha per Conrad, 2008), I elect to include one modern representative of each group. *Uromastyx aegyptia* is selected to represent Iguanomorpha.

Vallesaurus cenensis **Renesto and Binelli, 2006**

Holotype specimen: MCSNB 4751, complete but crushed skeleton

Material studied: Holotype.

Literature Consulted: Renesto and Binelli, 2006; Renesto et al., 2010.

Localities: Calcare di Zorzino, Italy (Norian) (Renesto, 2006)

Notes: The binomial *Vallesaurus cenensis* was first referenced by Wild (1991) without any description of the specimen. Although a full description of the specimen was not published until Renesto and Binelli (2006), the specimen was figured and referenced by Renesto (2000) and integrated into a phylogenetic study of Drepanosauridae (Senter, 2004).

Renesto et al. (2010) described an additional species of *Vallesaurus*, *V. zorzinensis*, which was differentiated from the type species based on a distinct anatomy of the first pedal digit. However, as noted in the third chapter of this dissertation, undescribed drepanosaurid material from Utah suggest that the pedal morphology of individual drepanosauromorph species might exhibit dimorphism (Chure et al., 2013). Pending further study, I accept only a single species of *Vallesaurus*.

Youngina capensis **Broom 1914**

Holotype specimen: AMNH FARB 5561 (complete skull and partial postcranial skeleton, preserving trunk, sacral, and anterior caudal vertebrae.

Material studied: Holotype, BP/1 570 (skull), BP/1 2781 (skull), BP/1 3859 (partial skull and nearly complete, disarticulated skeleton), SAM K7578; SAM K7710 (6 partial juvenile skeletons).

Literature studied: Broom (1914), Goodrich (1942), Gow (1975), Carroll (1981), Currie (1981b), Smith and Evans (1992), Gardner et al. (2010).

Localities: Sites in *Dicynodon* Assemblage Zone, Beaufort Group, South Africa; latest Late Permian (Rubidge et al., 1995). SAM K7710, a series of juvenile skeletons referred to *Youngina capensis* come from a site in the *Tropidostoma* Assemblage Zone, several million years older than all other occurrences.

Notes: *Youngina capensis* is the best-known Late Permian diapsid taxon, with many skulls and partial skeletons referred to it. The high quality of preservation from these material has allowed extremely detailed study of the endocranium (Evans, 1987; Gardner et al., 2010) and postcranium (Gow, 1975) in a way untenable with other Late Permian diapsid reptiles (see *Acerosodontosaurus piveteaui*, *Hovasaurus boulei*, *Thadeosaurus colcanapi*).

SAM K7710, a group of very small diapsid reptile skeletons referred to *Youngina capensis*, was first described by Smith and Evans (1992). These are substantially smaller than other described *Youngina* specimens, and they occur stratigraphically earlier than all other specimens. As these skeletons are the most complete postcrania referred to *Youngina capensis*, they provide critical insight into the osteology of the animal. However, a number of anatomical traits in these specimens appear to differ from later *Youngina* postcrania (based mostly on BP/1 5389), including a thyroid fenestra and a much more robust femur in the latter. For the moment, I follow the taxonomic hypothesis of Smith and Evans (1992) that these skeletons belong to *Y. capensis*, but these differences should make taxonomic reassessment of the material a priority. I note in the text where these skeletons have contributed to the character codings for the *Y. capensis* OTU.

Character Sampling

This analysis represents an expansion of a character matrix first developed by Pritchard et al. (2015), incorporating 24 diapsid species and 200 morphological characters. That matrix was expanded for Nesbitt et al. (in press), which expanded the dataset to thirty taxa and 247 morphological characters. For this analysis, I have added substantially to the sampling of non-saurian diapsids (derived from chapters 3 and 4 of this dissertation) and additional characters, resulting in a dataset of 51 diapsid taxa and 303 morphological characters. Below, I list the morphological characters analyzed for this study, and briefly address past usages and justification:

Character Sampling

This analysis represents an expansion of a character matrix first developed by Pritchard et al. (2015), incorporating 24 diapsid species and 200 morphological characters. That matrix was expanded for Nesbitt et al. (in press), which expanded the dataset to thirty taxa and 247 morphological characters. For this analysis, I have added substantially to the sampling of non-saurian diapsids (derived from chapters 3 and 4 of this dissertation) and additional characters, resulting in a dataset of 51 diapsid taxa and 303 morphological characters. Below, I list the morphological characters analyzed for this study, and briefly address past usages and justification:

CHARACTER 1: Premaxilla, external sculpturing: (0) smooth, (1) anteroventrally running striations.

Examples of past usage: Pritchard et al. (2015:1)

Justification/Ontology: The lateral exposure of the premaxilla in nearly all Permo-Triassic reptiles is smoothly sculptured (e.g., *Prolacerta broomi*, UCMP 37151; *Youngina capensis*, BP/1 2871), marked only by neuromuscular foramina. By contrast, the premaxillae in *Langobardisaurus pandolfii* exhibit deep, anteroventrally running ridges along their anteroposterior lengths (e.g., MCSNB 4860; MFSN 1921).

The two named species of this taxon (*Langobardisaurus pandolfii* from the Zorzino Limestone and *Langobardisaurus tonelloi* from the Dolomia di Friuli) were initially considered to exhibit strongly procumbent, pointed teeth in the premaxilla (Renesto, 1994a; Renesto and Dalla Vecchia, 2000). However, Saller et al. (2013) argued that there was no enamel apparent on these projections in MCSNB 4860 nor in MFSN 1921. They hypothesized that these structures may have supported a rhamphotheca in life.

Saller et al. (2013) also presented the hypothesis that *Langobardisaurus pandolfii* and *L. tonelloi* were conspecific based on the limited anatomical justification for separating the two. This analysis provides a test of at least a sister relationship of these materials by including three separate coding schemes for *Langobardisaurus* (one of the *L. pandolfii* material, one of the *L. tonelloi* holotype, and a concatenated version). An initial test of this hypothesis in Pritchard et al. (2015) found a sister relationship between the species, with this character supporting that node.

CHARACTER 2: Premaxilla, orientation of ventral, dentigerous margin: (0) in-line with dentigerous margin of maxilla; (1) downturned relative to ventral margin of maxilla, but less steeply angled than ventral margin of posterodorsal process of premaxilla; (2) downturned more steeply than ventral margin of posterodorsal margin of premaxilla. ORDERED.

Examples of past usage: Benton (1985), Merck (1997:109), Dilkes (1998), Müller (2004:83), Nesbitt (2011), Pritchard et al. (2015:2), Nesbitt et al. (in press:2).

Justification/Ontology:

Most early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, BP/1 2871) and saurians (e.g., *Protorosaurus speneri*, USNM 442453; *Azendohsaurus madagaskarensis*, UA 9-9-98-560) exhibit a premaxillary dentigerous margin that is in line with the dentigerous margin of the maxilla (Fig. 4A). By contrast, a number of archosauromorphs exhibit an anteroventrally inclined dentigerous margin. In some of these taxa, the ventral margin of the premaxilla is less steeply inclined than the posterodorsal process of the premaxilla (e.g., *Garjainia prima*, PIN 2334/5-1; *Erythrosuchus africanus*, NHMUK R3592). An absurd development of this character occurs in taxa traditionally referred to Proterosuchidae (e.g., Charig and Reig, 1970; Charig and Sues, 1976). In such taxa, the premaxilla is even more steeply inflected relative to the posterodorsal process of the premaxilla (e.g., *Chasmatosaurus yuani*, IVPP 36315; *Proterosuchus fergusi*, BP/1 3393) (Fig. 4B).

The extremely inclined premaxilla has long been recognized as a characteristic of *Proterosuchus* and its close relatives (e.g., Haughton, 1924; Broili and Schroeder, 1934; Young, 1936). Although some authors suggested that the downturned premaxillae in these specimens were the result of postmortem damage (e.g., Broom, 1932), the presence of the condition in all undistorted proterosuchid skulls (e.g., Young, 1936; Welman, 1998; Ezcurra and Butler, 2015) suggests that it is genuine.

A more slight incline to the dentigerous margin in *Erythrosuchus* and related forms has been considered homologous to the extreme condition in Proterosuchidae (Charig and Reig, 1970). This feature was incorporated into many early systematic studies of Permo-Triassic diapsids. Although not included as a discrete character in his analysis, Gauthier (1984) made note of the downturned premaxillary rostrum in describing Proterosuchidae. Benton (1985) argued that the downturned premaxilla was shared between *Proterosuchus* and *Prolacerta broomi*, and Dilkes (1998) concurred with this interpretation. Modesto and Sues (2004) argued that premaxillary downturn in specimens of *Prolacerta* was the result of distortion, an interpretation with which I concur (UCMP 37151, BP/1 5880). Our coding scheme thus recognizes slight downturn of the premaxilla in erythrosuchids and proterochampsids and the extreme condition in proterosuchids. This formulation is the first to involve a discrete distinction between the morphologies in proterosuchids and other early archosauriforms.

CHARACTER 3: Premaxilla, anterodorsal process: (0) present, contributing to separation of narial openings; (1) absent or reduced.

Examples of past usage: Benton (1985:M2), Gauthier et al (1988a:18), Benton and Allen (1997:1), Dilkes (1998:10), Müller (2004:84), Pritchard et al. (2015:3), Nesbitt et al. (in press:3).

Justification/Ontology: In most Permo-Triassic diapsid reptiles, the premaxilla contributes to an internarial bar (e.g., *Youngina capensis*, BP/1 2871; *Protorosaurus speneri*, USNM 442453; *Chasmatosaurus yuani*, IVPP 36315) (Fig. 4B). By contrast, some archosauromorph groups lack a projection at the anterodorsal corner of the premaxilla, creating a confluent external naris (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2751, UA 9-9-98-560; *Mesosuchus browni*, Dilkes, 1998) (Fig. 4A). A confluent naris also occurs in kuehneosaurids (e.g., *Icarosaurus siefkeri*, AMNH FARB 7101; *Kuehneosaurus latus*, Robinson, 1962).

For this study, I recognized a weak or absent development of the premaxilla in a number of additional archosauromorph taxa. The tanystropheid specimens I studied appear to lack such a process or exhibit a weak development of the condition (e.g., *Macrocnemus bassanii*, PIMUZ T/4822; *Tanystropheus longobardicus*, MCSN BES SC 1018), although these are usually reconstructed as exhibiting a septated naris with an elongate anterodorsal process of the premaxilla (e.g., Rieppel, 1989; Nosotti, 2007; Jiang et al., 2011). The process may be similarly weakly developed in *Prolacerta broomi* (best typified by BP/1 5880 and UCMP 37151). However, this does not necessarily correlate to a confluent external naris, as the nasals in some of these taxa extend anteriorly to meet the premaxillae (e.g., *Tanystropheus longobardicus*, PIMUZ T/2790). Wild (1973) accurately reported this condition in *Tanystropheus*.

Nearly all formulations of a similar character incorporate the role of the premaxilla in septating the external nares, reflecting the condition in rhynchosaurs. As these formulations do not describe the condition in tanystropheids, we focus our formulation solely on this process of the premaxilla. As a result, our formulation is comparable to that of Reisz et al. (2010) and Ezcurra et al. (2014), which ignore the external naris in the description.

CHARACTER 4: Premaxilla, posterodorsal process (=maxillary process, = subnarial process): (0) absent, such that premaxilla contributes a small ventral margin for the naris; (1) present, framing the posteroventral margin of the naris.

Examples of past usage: Benton (1985:C1), Laurin (1991:F2), Rieppel (1994), Jalil (1997:25), Dilkes (1998:8), Müller (2004:2), Senter (2004:3), Renesto et al. (2010:1), Pritchard et al. (2015:4), Nesbitt et al. (in press:4).

Justification/Ontology: The presence of a substantial process of the premaxilla framing the posterior margin of the external naris has long been recognized as a characteristic of archosaur-line reptiles (e.g., von Huene, 1936; Gauthier, 1984). In typical non-archosauromorph reptiles, the premaxilla exhibits a short margin that meets a small, sub-narial process of the maxilla (e.g., *Captorhinus aguti*, see Heaton, 1979; *Araeoscelis gracilis*, MCZ 4830; *Claudiosaurus germaini*, SAM K8263). The nature of this contact seems quite variable, some taxa exhibiting a poorly ossified, possibly ligamentous contact (e.g., *Czatkowiella harae*, Borsuk-Bialynicka and Evans, 2009). Others exhibit well-defined facets for the premaxilla-maxilla contact (e.g., *Captorhinus aguti*, Heaton, 1979) or a well-defined overlapping contact evident in articulated materials (e.g., *Youngina capensi*s, BP/1 2871; *Protorosaurus speneri*, USNM 442453).

Throughout Archosauromorpha, the premaxilla exhibits a prominent posterodorsal process that fits across the anterior, narial surface of the maxilla (e.g., *Prolacerta broomi*, BP/1 471; *Proterosuchus fergusi*, BP/1 3393; *Tanystropheus longobardicus*, MCSN BES SC 1018; *Azendohsaurus madagaskarensis*, UA 9-9-98-560) (Fig. 4A). Some subsequent reversals are recognized in derived archosaurs, including some poposauroids (e.g., Nesbitt, 2011). A similar process occurs in Kuehneosauridae (e.g., *Kuehneosaurus latus*, Evans, 2009; possibly *Pamelina polonica*, ZPAL RV1082) and in the rhynchocephalian genus *Clevosaurus* (e.g., *C. bairdi*, Sues et al., 1994; *C. hudsoni*, Fraser, 1988).

In discussing the "archosauromorph premaxilla," Gauthier (1984) drew attention to the relatively larger contribution of that element to the rostrum. Most early numerical phylogenies optimized the posterodorsal process of the premaxilla as a synapomorphy uniting all archosauromorphs (e.g., Gauthier, 1984; Evans, 1988; Dilkes, 1998). Müller (2004) recovered the character as a synapomorphy of Sauria and a non-saurian clade including Kuehneosauridae and Drepanosauridae. The distribution of this feature was complicated by the recognition that the Permian archosauromorph *Protorosaurus speneri* exhibited the plesiomorphic condition, although the modified Dilkes (1998) study by Gottmann-Quesada and Sander (2009) suggested that the condition in *P. speneri* was a reversal.

CHARACTER 5: Premaxilla, posterodorsal process (=maxillary process, = subnarial process): (0) short, failing to exclude maxilla from narial margin; (1) long, excluding maxilla from narial margin; (2) extremely long, reaching the anteriormost part of the prefrontal. ORDERED.

Examples of past usage: Merck (1997:93 & 108), Dilkes (1998:7), Pritchard et al. (2015:5), Nesbitt et al. (in press:5).

Justification/Ontology: The relative length of the posterodorsal process of the premaxilla is quite variable among those taxa that exhibit this structure. Among taxa with such a process, a short process that does not completely obscure the maxilla from the narial margin occurs in *Teraterpeton hrynewichorum* (Sues, 2003) and possibly the drepanosaurid *Megalancosaurus preonensis* (MFSN 1769). In most of the taxa that possess a posterodorsal process, the structure extends across the anterior border of the maxilla, meeting the nasal at its tip (e.g., *Garjainia prima*, PIN 2394/5; *Prolacerta broomi*, BP/1 471; *Tanystropheus longobardicus*, PIMUZ T/3901).

Taxa within Rhynchosauria exhibit particularly elongate posterodorsal processes that extend over the dorsal margin of the maxilla to meet the anterior tip of the prefrontal. Dilkes (1995) was the first to codify this variation in his phylogenetic analyses of Rhynchosauria. This contact can be seen in *Mesosuchus browni* (SAM-PK-K6536), *Rhynchosaurus articeps* (e.g., Benton, 1990), and taxa referred to *Hyperodapedon* (e.g., *H. gordoni*, Benton, 1983; *Teyumbaita sulcognathus*, Montefeltro et al., 2010). Although the premaxilla is not preserved in *Howesia browni*, Dilkes (1995) reports a separate contact surface on the anterior tip of the prefrontal for the premaxilla. Both Dilkes (1998) and Ezcurra et al. (2014) found the development of the premaxilla-prefrontal contact to be a synapomorphy of Rhynchosauria.

We unite these varied character states here, as each represents a consequence of the relative elongation of the posterodorsal process of the premaxilla. We order this character, as state 1 represents a necessary intermediate condition to bridge states 0 and 2. This character is coded as inapplicable ("-") if a taxon is coded as "0" for character 4, indicating the absence of a posterodorsal process of the premaxilla.

CHARACTER 6: Premaxilla, posterodorsal process, contact with maxilla: (0) simple, straight margin; (1) knob on the posterior margin of the posterodorsal process of the premaxilla fits into notch in the anterior surface of the maxilla.

Examples of past usage: Dilkes (1998:17), Müller (2004:88), Pritchard et al. (2015:6), Nesbitt et al. (in press:6).

Justification/Ontology: In most reptiles with a posterodorsal process of the premaxilla, the posterior margin of that structure is straight. It fits against a corresponding slot on the anterior margin of the maxilla. Examples of such contacts are evident in *Tanystropheus longobardicus* (e.g., PIMUZ T/3901), *Kuehneosaurus latus* (Evans, 2009), and *Prolacerta broomi* (e.g., BP/1 5066). By contrast, some archosauromorphs exhibit a small, posteriorly directed tab on the posterior margin of the premaxilla that corresponds to a notch in the anterior surface of the maxilla (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2751, UA 9-9-98-560; *Erythrosuchus africanus*, NHMUK R 3592) (Fig. 4A). In the two aforementioned examples, the premaxillary tab is positioned posteroventral to a prominent groove in the lateral surface of the premaxilla. This groove is typically positioned anterior to a large foramen on the maxilla.

This character is complicated by some archosauromorph taxa that exhibit gaps within the premaxilla-maxilla contact. In *Proterosuchus fergusi* (BP/1 3393) and "Chasmatosaurus" *yuani* (IVPP 36315), the gap occurs at the ventral base of the contact, terminating further dorsally. The gap is positioned anterior to the anterior maxillary foramen. In these taxa, the rest of the premaxilla-maxilla contact is straight.

It is possible that the tab-groove articulation in certain Archosauromorpha is correlate of the lateral groove on the surface of the premaxilla in these taxa. If the groove does correspond to the outlet of the anterior maxillary foramen, this could explain its absence in *Prot. fergusi* and "C." *yuani*. However, such a determination would require a more robust understanding of the cranial neurovasculature of early Archosauromorpha. I recommend further study of these structures in order to more fully assess possible character correlations in Permo-Triassic diapsids. This character is coded as inapplicable ("-") if a taxon is coded as "0" for character 4, indicating the absence of a posterodorsal process of the premaxilla.

CHARACTER 7: Maxilla, orientation of ventral margin: (0) linear, oriented anteroposteriorly; (1) convex ventrally.

Examples of past usage: Parrish (1992), Dilkes (1998:16), Ezcurra et al. (2014), Pritchard et al. (2015:7), Nesbitt et al. (in press:7).

Justification/Ontology: In most early reptiles and early diapsids, the ventral margin of the maxilla is straight in lateral view. It is typically directly in line with the ventral margins of the premaxilla and jugal (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, BP/1 2871; *Tanystropheus longobardicus*, MCSN BES SC 1018). By contrast, some archosauromorph lineages develop a prominent, convex curvature to the ventral margin of maxilla when viewed laterally. Parrish (1992) considered this to be a synapomorphy of Erythrosuchidae, in which the anteroventral surface of the maxilla is most prominently convex (e.g., *Erythrosuchus africanus*, BP/1 5207; *Garjainia prima*, PIN 2394/5). In these taxa, the convexity corresponds in position to a prominent notch at the premaxilla-maxilla contact. A similar condition occurs in certain derived rhynchosaurs. The early rhynchosaur *Mesosuchus browni* resembles other early diapsids, with a straight alveolar margin of the maxilla. However, in later taxa (e.g., *Rhynchosaurus articeps*, NHMUK R1236; *Teyumbaita sulcognathus*, Montefeltro et al., 2010), the anteroventral portion of the maxilla is prominently convex.

Parrish (1992) recovered this character as a synapomorphy of Erythrosuchidae. Dilkes (1995, 1998) recovered this character as an apomorphy of a clade including *Howesia*+Rhynchosauridae (excluding only the early taxon *Mesosuchus browni*). The latter is somewhat problematic due to the incomplete nature of the available maxilla of *Howesia* (SAM-PK-K5884).

CHARACTER 8: Maxilla, posterolateral surface: (0) directly adjacent to alveolar margin; (1) lateral process of maxilla present, creating distinct space between maxillary alveoli and posterolateral surface of the maxilla.

Examples of past usage: Pritchard et al. (2015:8), Nesbitt et al. (in press:8).

Justification/Ontology: This character addresses an intriguing morphology of the maxilla in *Trilophosaurus*. In these taxa, the lateralmost portion of the maxilla angles posterolaterally from the posteriormost teeth. This condition occurs in *T. buettneri* (TMM 31025-140) and *T. jacobsi* (NMMNH P41400). Pritchard et al. (2015) coded this character as present for *Teraterpeton hrynewichorum*. However, this condition is not apparent based on Sues (2003), which formed the basis of the coding. As such, I coded the taxon as "?" pending firsthand study.

CHARACTER 9: Nasal, prefrontal contact, orientation: (0) parasagittal, (1) anterolateral.

Examples of past usage: Gauthier et al. (1988a:59), Evans (1991), Laurin (1991:E1), Jalil (1997:1), Merck (1997:121), Senter (2004:11), Ezcurra et al. (2014), Pritchard et al. (2015:9), Nesbitt et al. (in press:9).

Justification/Ontology: Among early diapsids such as *Petrolacosaurus kansensis* (Reisz, 1981) and some *Youngina capensis* (AMNH FARB 5561), the nasal-prefrontal suture, as seen in dorsal view, run in parallel to the long axis of the skull. This condition is also prevalent in early archosauromorph taxa (e.g., *Prolacerta broomi*, BP/1 5375; *Proterosuchus alexanderi*, NMQR 1484). Among archosauromorphs, some rhynchosaurs exhibit parasagittal sutures (e.g., *Mesosuchus browni*, SAM-PK-K6536; *Rhynchosaurus articeps*, Benton, 1990), whereas others exhibit an anterolaterally inclined contact (e.g., *Bentonyx sidensis*, Hone and Benton, 2008; *Teyumbaita sulcognathus*, Montefeltro et al., 2010). This condition also occurs in

Kuehneosauridae (e.g., *Icarosaurus siefkeri*, AMNH FARB 2101). I also note anterolaterally inclined contacts in some *Youngina capensis* (e.g., SAM K6205) (Fig. 5A).

An anterolateral inclination to the contact has long been recognized in derived lepidosauromorphs (e.g., Squamata, Gauthier et al., 1988a; *Clevosaurus bairdi*, Sues et al., 1994; *Sphenodon punctatum*, Evans, 2008). Gauthier (1984) and Gauthier et al. (1988a) reported this character as a synapomorphy linking Kuehneosauridae to Lepidosauria.

CHARACTER 10: Prefrontal, contact with contralateral prefrontal: (0) absent, due to fronto-nasal contact; (1) prefrontals approach medially, constricting fronto-nasal contact; (2) present.

Examples of past usage: Dilkes (1998:125), Pritchard et al. (2015:10), Nesbitt et al. (in press:10).

Justification/Ontology: In most amniotes, the prefrontals contribute to the roof of the rostrum. The contributions of the two elements are separated by the contact of the nasals and frontals in the midline. Examples include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Icarosaurus siefkeri* (AMNH FARB 2101), *Macrocnemus bassanii* (PIMUZ T/4822), *Ctenosaura pectinata* (Oelrich, 1956), and *Alligator mississippiensis* (Iordansky, 1973). In choristoderes, the rostral contributions of the prefrontals meet at a midline suture. This separates the posterior portions of the nasals and the anterior tips of the frontals. Examples include *Lazarussuchus* sp. (Matsumoto et al., 2013) and *Hyphalosaurus baitaigouensis* (Gao and Ksepka, 2008).

CHARACTER 11: Lacrimal, facial contribution: (0) forms a portion of lateral surface of the face, reaching anteriorly to the external naris; (1) forms a portion of the lateral surface of the face, but does not reach naris; (0) limited to orbital margin.

Examples of past usage: Benton (1985:B1), Gauthier et al (1988a:1), Laurin (1991:B2), Benton and Allen (1997:6), Jalil (1997:15), Merck (1997:77), Dilkes (1998:15), Müller (2004:6), Senter (2004:5), Pritchard et al. (2015:11), Nesbitt et al. (in press:11).

Justification/Ontology: Among early amniotes and many early diapsid lineages, the lacrimal is a substantial contributor to the lateral surface of the rostrum. In these taxa, it intercedes between the ventrolateral margin of the nasal and the dorsal margin of the maxilla, extending from the anterior margin of the orbit to the posterior margin of the external naris. Examples of this condition include *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (MCZ 4830), and *Orovenator mayorum* (Reisz et al., 2011).

In most species considered to be Neodiapsida, the maxilla becomes dorsoventrally taller, such that the lacrimal only encounters the posterior margin of the maxilla. Among Permo-Triassic neodiapsids, the lacrimal still exhibits a prominent facial lamina, such that it forms much of the lateral surface of the rostrum. Examples of this condition include *Youngina capensis* (BP/1 2871; 3859), *Prolacerta broomi* (BP/1 5880), *Icarosaurus siefkeri* (AMNH FARB 2101) (Fig. 6A). Such a condition is also common among Archosauriformes, with the lacrimal contributing to much of the posterodorsal margin of the antorbital fossa (e.g., *Proterosuchus goweri*, NMQR 880; *Garjainia prima*, PIN 2394/5).

A third condition is noted among early lepidosauromorphs, in which the facial contribution of the lacrimal is further reduced. In these taxa, the contribution to the rostrum is all but absent, with the lacrimal forming only a tiny portion of the anteroventral margin of the orbit. Such a condition occurs in lacrimals referred to *Gephyrosaurus bridensis* (Evans, 1980), *Marmoretta oxoniensis* (Evans, 1991) and in many modern squamates (e.g., Conrad, 2004, 2008). As the progressive reduction in the facial lamina of the lacrimal forms a logical transformative series with state 1 serving as a necessary intermediate, we have ordered this character.

CHARACTER 12: Lacrimal, anterior extension: (0) lacrimal extends dorsally to reach the ventral margin of the nasal externally, (1) lacrimal fails to reach nasal.

Examples of past usage: Benton and Allen (1997:5), Jalil (1997:50), Dilkes (1998:15), Müller (2004:179), Pritchard et al. (2015:12), Nesbitt et al. (in press:12).

Justification/Ontology: No comments.

CHARACTER 13: Antorbital fenestra: (0) absent, (1) present.

Examples of past usage: Benton (1985:I1), Merck (1997:1), Dilkes (1998:5), Senter (2004:4), Nesbitt (2011), Pritchard et al. (2015:13), Nesbitt et al. (in press:13).

Justification/Ontology: The antorbital fenestra is a prominent cavity in the lateral surface of the face, connecting the lateral surface to the nasal cavity. It is framed by the maxilla anteroventrally, the lacrimal posterodorsally, and sometimes a contribution from the anterior process of the jugal posteroventrally. Witmer (1997) reviewed the anatomy and homology of the structure, presenting the hypothesis that it developed in tandem with an expansion of the paranasal air sinus. The feature has long been recognized as a characteristic of archosaurs (e.g., Cruickshank, 1972; Benton, 1985), and cladistic hypotheses have recovered the structure as a synapomorphy of Archosauriformes (Gauthier, 1984; Benton, 1985; Dilkes, 1998; Nesbitt, 2011).

The plesiomorphic condition, in which the maxilla, lacrimal, and jugal do not frame a cavity in the face is prevalent throughout early reptiles (*Captorhinus aguti*, Heaton, 1979), diapsids (*Petrolacosaurus kansensis*, Reisz, 1981; *Orovenator mayorum*, Reisz et al., 2011; *Youngina capensis*, Gow, 1975, BP/1 3859), lepidosaurs (*Gephyrosaurus bridensis*, Evans, 1980; *Clevosaurus hudsoni*, Fraser, 1988; Squamata, Conrad, 2008), and early archosauromorphs (*Protorosaurus speneri*, USNM 442453; *Prolacerta broomi*, BP/1 5375; *Trilophosaurus buettneri*, TMM 31025-140) (Fig. 6A). The antorbital fenestra is prevalent in Archosauriformes, such as *Proterosuchus* (NMQR 880, 1484), "Chasmatosaurus" *yuani* (IVPP 36315), *Garjainia prima* (PIN 2394/5), *Batrachotomus kupferzellensis* (Gower, 1999), and *Tyrannosaurus rex* (AMNH FARB 5027) (Fig. 6C). However, multiple groups of archosauriforms do not exhibit an antorbital fenestra. Examples include *Vancleavea campi* (GR 138), *Alligator mississippiensis* (Iordansky, 1973), and *Prosaurolophus maximus* (McGarrity et al., 2013).

Calzavarra et al. (1980), in their initial description of the skull of *Megalancosaurus preonensis*, reported the presence of an antorbital fenestra. Renesto (1994c) considered the presence of this cavity equivocal. Later reconstructions of the skull consider this cavity to be absent in *Megalancosaurus* (e.g., Renesto et al., 2010), an interpretation with which I agree based on MFSN 1769.

CHARACTER 14: Frontals, degree of fusion: (0) unfused (suture patent), (1) fused in the midline.

Examples of past usage: Benton (1985:M3), Gauthier et al (1988a:65), Merck (1997:111), Pritchard et al. (2015:14), Nesbitt et al. (in press:14).

Justification/Ontology: In early reptiles, early diapsids, and many early saurian groups, the frontal bones retain a visible sutural contact throughout ontogeny. Examples of this condition occur in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 375), *Protorosaurus speneri* (USNM 442543), *Macrocnemus bassanii* (PIMUZ T/4822), *Kuehneosaurus latus* (AMNH FARB 7762), and *Trilophosaurus buettneri* (TMM 31025-140) (Fig. 5). Among lepidosaurs, the frontal bones become fused to one another. Examples of this condition include *Gephyrosaurus bridensis* (Evans, 1980), *Diphydontosaurus avonis* (Whiteside, 1986), and much of Squamata (Gauthier et al., 2012). A number of analyses (e.g., Conrad, 2008; Gauthier et al., 2012) have recovered subsequent reversals of this fusion. Examples of the probable reversed condition include *Sphenodon punctatum* (Evans, 2008), *Polyglyphanodon sternbergi* (Gilmore, 1942), and *Mosasaurus missouriensis* (Konishi et al., 2014).

CHARACTER 15: Frontals, shape in dorsal view: (0) lateral margins subparallel, frontal maintains similar transverse width throughout anteroposterior length; (1) lateral margins gradually diverge throughout anteroposterior length; (2) lateral margins abruptly diverge laterally at posteriormost margin; (3) lateral margins taper posteriorly, due to transverse expansion of postfrontals.

Examples of past usage: Pritchard et al. (2015:15), Nesbitt et al. (in press:15).

Justification/Ontology: The frontals in most early reptiles and early diapsids retain the same transverse breadth throughout most of their anteroposterior lengths. This condition is exemplified by *Captorhinus aguti* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1979), *Youngina capensis* (BP/1 3859, SAM K6205), *Gephyrosaurus bridensis* (Evans, 1980), *Kuehneosaurus latus* (AMNH FARB 7762), *Macrocnemus bassanii* (PIMUZ T/4822), and *Prolacerta broomi* (BP/1 471) (Fig. 6A). In some other saurian taxa, the dorsal exposure of the frontals tapers posteriorly, usually as a consequence of a transverse expansive exposure of the postfrontal bones. Such a condition occurs in *Mesosuchus browni* (SAM-PK-K6536), *Rhynchosaurus articeps* (Benton, 1990), *Trilophosaurus buettneri* (TMM-31025-140), and *Azendohsaurus madagaskarensis* (UA 7-20-99-653) (Fig. 6C, D).

The frontals in a number of saurian groups exhibit distinctive transverse expansions posteriorly. In many squamate (e.g., *Scincus scincus*, *Shinisaurus crocodilurus*), the frontal exhibits a smooth, continuous expansion that begins around the anteroposterior midpoint of the bone (Conrad, 2004; Conrad, 2008). A distinct expansion of the frontals occurs in some archosauromorphs. In *Proterosuchus alexanderi* (NMQR 1484), *Erythrosuchus africanus* (NHMUK R3592), *Osmolskina czatkowicensis* (ZPAL RV/90), and *Plateosaurus engelhardti* (Prieto-Marquez and Norell, 2011) (Fig. 6B). In these taxa, the transverse expansion can co-occur with a reduction in the transverse breadth of the postfrontal, or its total absence in Dinosauria (Nesbitt, 2011).

CHARACTER 16: Frontal, shape of contact with parietal in dorsal view: (0) roughly straight in transverse plane; (1) frontal exhibits posterolateral processes, forming anteriorly curved U-shaped contact.

Examples of past usage: Benton and Allen (1997:3), Merck (1997:114), Müller (2004:10), Pritchard et al. (2015:16), Nesbitt et al. (in press:16).

Justification/Ontology: Throughout most early reptile groups, early diapsids, and a number of saurian taxa, the frontoparietal suture is distinctly "U"-shaped in dorsal view, with the primary convexity facing anteriorly. This occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 5389, SAM K6205), *Sphenodon punctatum* (Evans, 2008), *Macrocnemus bassanii* (PIMUZ T/4822), a drepanosaurid from the *Coelophysis quarry* (AMNH FARB 30834), *Teraterpeton hrynewichorum* (Sues, 2003), *Euparkeria capensis* (Ewer, 1965), and *Osmolskina czatkowicensis* (ZPAL RV/90) (Fig. 6A).

In many other early saurians, the suture lacks this anterior convexity is more weakly developed or transversely straight. This condition is exemplified in *Protorosaurus speneri* (USNM 442543), *Tanystropheus longobardicus* (PIMUZ T/2819), *Proterosuchus fergusi* (BP/1 3393), *Erythrosuchus africanus* (BP/1 5207), *Batrachotomus kupferzellensis* (Gower, 1999), and many squamate species (Conrad, 2008; Evans, 2008) (Fig. 6B).

In *Tanystropheus longobardicus*, an early saurian taxon which is known from a growth series ranging from ~1 meter to 6 meters in total length, this contact undergoes a slight change through ontogeny (noted by Wild, 1973). In small individuals, the suture is subtly convex posteriorly (PIMUZ T/2484). However, in larger individuals (e.g., PIMUZ T/2819), the contact is straight and transversely oriented. As the transverse condition among early saurian groups is largely restricted to large-bodied reptiles, I caution that small juveniles of these taxa may exhibit a distinct morphology of the frontoparietal contact from adults.

CHARACTER 17: Frontal and postfrontal, surface texture: (0) relatively smooth, (1) dorsal marked by distinct pitting.

Examples of past usage: Dilkes (1998:20 & 21), Pritchard et al. (2015:17), Nesbitt et al. (in press:17).

Justification/Ontology: In most early reptiles, diapsids, and saurian taxa, the frontal and postfrontal bones are either smooth or marked by limited sculpturing. This condition occurs in *Captorhinus aguti* (Heaton, 1979), *Araeoscelis gracilis* (MCZ 4380), *Protorosaurus speneri* (USNM 442543), *Trilophosaurus buettneri* (TMM 31025-140), and *Gephyrosaurus bridensis* (Evans, 2008) (Fig. 6A, B, D). However, in *Mesosuchus browni* (SAM-PK-K6536) and *Howesia browni* (SAM-PK-K5885), the dorsal surfaces of the frontal and postfrontal are marked by prominent depressions framed by thin bony ridges (Fig. 6C).

Dilkes (1995) first reported these features in early rhynchosaurs, considering them as separate characters in his 1995 and 1998 analyses. Pritchard et al. (2015) considered them as a single character, as the depressions always appear to co-occur and are very similar in morphology. Dilkes (1998) recovered the character as a synapomorphy of Rhynchosauria.

CHARACTER 18: Postorbital, medial contact with frontal and parietal: (0) present, (1) absent with postfrontal fitted in between.

Examples of past usage: Gauthier et al (1988a:41), Dilkes (1998:22), Müller (2004:89).

Justification/Ontology: The postorbital in early reptiles and most saurians exhibits a varying degree of contact with the midline elements of the skull table. In *Captorhinus aguti* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), *Protorosaurus speneri* (USNM 442543), *Prolacerta broomi* (BP/1 5375), and *Proterosuchus fergusi* (BP/1 3393) the postorbital is fitted posteroventral to the postfrontal such that it meets the parietal (Fig. 6B, C, D). Certain archosauriform taxa, including Proterochampsidae (e.g., MCZ 4037) and Dinosauria (Nesbitt, 2011) lack a postfrontal entirely, such that the postorbital always contacts the medial elements (coded as character 28). These animals are coded as "-" for this character.

In a number of non-saurian diapsids, the postfrontal completely intersects between the postorbital and the medial elements. This state occurs in the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Coelurosauravus jaekeli* (SMNS 53349; Evans and Haubold, 1987), *Youngina capensis* (BP/1 3859, SAM K6205), and *Hovasaurus boulei* (Currie, 1981) (Fig. 6A). Pritchard et al. (2015) erroneously coded for a similar condition in *Teraterpeton hrynewichorum*;

this is incorrect, as Sues (2003) reports the medial process making contact with the parietal in that taxon.

CHARACTER 19: Parietals, degree of fusion: (0) unfused (patent suture), (1) fused at midline.

Examples of past usage: Benton (1985), Gauthier et al (1988a:63), Merck (1997:128), Dilkes (1998:25), Müller (2004:11), Pritchard et al. (2015:19), Nesbitt et al. (in press:19).

Justification/Ontology: In early reptiles, early diapsids, and some early saurians, the parietals retain their ancestral condition as paired elements. This occurs in *Captorhinus aguti* (Heaton, 1979), *Araeoscelis gracilis* (MCZ 4830), *Youngina capensis* (BP/1 3589), *Megalancosaurus preonensis* (MPUM 8437), *Hovasaurus boulei* (Currie, 1980), *Macrocnemus bassanii* (PIMUZ T/4822), *Boreopricea funerea* (cast of PIN 3708/1), *Prolacerta broomi* (BP/1 471), *Azendohsaurus madagaskarensis* (UA 7-20-99-653) *Proterosuchus fergusi* (BP/1 3393), and *Osmolskina czatkowicensis* (ZPAL RV/98) (Fig. 6A, B). By contrast, a large number of early saurians and lepidosaurs exhibit co-ossification of the two parietals. In fossil taxa, I code this taxa when the interparietal suture is not apparent on the dorsal surface of the bones. This condition is present in *Protorosaurus speneri* (USNM 442543), *Tanystropheus longobardicus* (PIMUZ T/2819), *Mesosuchus browni* (SAM-PK-K6536), *Trilophosaurus buettneri* (TMM 31025-140), *Gephyrosaurus bridensis* (Evans, 1980), and most Squamata (Conrad, 2008) (Fig. 6C).

Gauthier et al. (1988a) included a similar character (63): “Parietals fused in embryo,” noting that modern squamates exhibit this fusion prior to hatching. Unfortunately, we cannot currently speak to the timing of this fusion event in the ontogeny of most of the fossil diapsid taxa noted above. The one taxon for which an extensive growth series is preserved, *Tanystropheus longobardicus*, does exhibit parietal fusion in the smallest specimens. For the moment, I exclude an ontogenetic component to this character due to the prevalence of fossil taxa, following the analysis of Conrad (2008).

CHARACTER 20: Parietal, dorsal surface: (0) flattened without lateral excavations; (1) flattened, elevated above prominent lateral excavations for jaw adductor musculature; (2) thin, blade-like sagittal crest. ORDERED.

Examples of past usage: Benton (1985:B2), Laurin (1991:D1 & G2), Merck (1997:135), Dilkes (1998:26), Müller (2004:13), Pritchard et al. (2015:20), Nesbitt et al. (in press:20).

Justification/Ontology: The dorsal surface of the parietal in early diapsid species is flat throughout its transverse breadth. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Megalancosaurus preonensis* (MPUM 8437), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Youngina capensis* (BP/1 3859, SAM K6205), and *Rautiania* spp. (PIN 5130/1, 5130/2) (Fig. 6A). In most saurian taxa, however, there exist prominent excavations in the lateral surface of the parietal, along the margin of the supratemporal fenestra, suggesting expansion of the attachment sites for jaw adductor musculature (Rieppel, 1994). This condition occurs in *Protorosaurus speneri* (USNM 442453), *Mesosuchus browni* (SAM-PK-K6536), *Proterosuchus fergusi* (BP/1 3393), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Gephyrosaurus bridensis* (Evans, 1980), and many squamate taxa (Conrad, 2004, 2008) (Fig. 6B, C). In other taxa, these excavated surfaces meet at the midline, resulting in a transversely narrow sagittal crest. This occurs in *Trilophosaurus buettneri* (TMM 31025-140), *Sphenodon punctatum* (Evans, 2008), *Rhynchosaurus articeps* (NHMUK R1237), and *Teyumbaita sulcognathus* (Montefeltro et al., 2010) (Fig. 6D).

Following Rieppel (1994), we consider the presence of small lateral excavations and that of a sagittal crest to be homologous. As the sagittal crest represents a hypertrophy of the adductor musculature, we order this character to represent the intermediate state in the transition. The degree of excavation by the adductor musculature appears similar throughout the growth series of *Tanystropheus longobardicus* (Wild, 1973). By contrast, in hatchling *Sphenodon punctatum* the excavations appear poorly developed, suggesting substantial change through ontogeny (Rieppel, 1992).

CHARACTER 21: Parietal, orientation of post-temporal process: (0) perpendicular to anteroposterior plane , (1) angled posterolaterally (~45 degree angle from midline).

Examples of past usage: Senter (2004:10), Nesbitt (2011:61), Pritchard et al. (2015:21), Nesbitt et al. (in press:21).

Justification/Ontology: The parietal of reptiles with upper temporal fenestrae exhibits a slender process that contacts either the squamosal or the squamosal and supratemporal to form the complete posterior margin of the supratemporal fenestra. In early diapsids , the long axis of this process is canted posterolaterally at roughly a 45 degree angle from the sagittal plane. Examples of this condition include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 5389, SAM K6205), and *Megalancosaurus preonensis* (MPUM 8437) (Fig. 6A). A similar condition is widespread among early saurians, including *Mesosuchus browni* (SAM-PK-K6536), *Macrocnemus* spp. (GMPKU-P-3001; PIMUZ T/2819), *Proterosuchus alexanderi* (NMQR 1484), *Gephyrosaurus bridensis* (Evans, 1980), and *Clevosaurus hudsoni* (Fraser, 1988) (Fig. 6C, D). In contrast, some other taxa exhibit transversely oriented post-temporal processes. Such a condition occurs in *Protorosaurus speneri* (USNM 442543), *Tanystropheus longobardicus* (PIMUZ T/2819), *Rhynchosaurus articeps* (NHMUK R1237), and *Teyumbaita sulcognathus* (Montefeltro et al., 2010).

CHARACTER 22: Pineal foramen: (0) present, (1) absent.

Examples of past usage: Benton (1985:N2), Laurin (1991:G3), Benton and Allen (1997:4), Merck (1997:129), Dilkes (1998:27), Senter (2004:9), Pritchard et al. (2015:22), Nesbitt et al. (in press:22).

Justification/Ontology: Early reptiles and early diapsids almost ubiquitously exhibit a prominent foramen in the midline of the skull table, representing the position of a light-sensitive organ linked to the pineal gland (e.g., Spencer, 1886). This condition can be found in *Captorhinus aguti* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), *Azendohsaurus* *madagaskarensis* (UA 7-20-99-653), *Tanystropheus longobardicus* (PIMUZ T/2819), and *Gephyrosaurus bridensis* (Evans, 1980) (Fig. 6A, B). The foramen has been reported in *Proterosuchus* (e.g., Cruickshank, 1972) and *Kuehneosaurus* (e.g., Robinson, 1962). However, I could not identify the foramen in the former, and the foramen is difficult to interpret in the latter due to the disarticulated nature of skull materials. See the figured skull roof of *Proterosuchus fergusi* (SAM K10203 in Fig. 6B).

The pineal foramen is absent in a large number of diapsid groups. There is no opening in *Rhynchosaurus articeps* (NHMUK R1237), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus fergusi* (NMQR 1484), and other known Archosauriformes (Nesbitt, 2011) (Fig. 6D). Gauthier et al. (2012) reported that the foramen was widespread in Squamata ancestrally, but lost in a large number of independent clades.

Prolacerta broomi is polymorphic for the pineal foramen, based on the specimens currently referred to the taxon. Gow (1975) and Modesto and Sues (2004) noted this variability in the taxon. Bhullar et al. (2011) noted the substantial homoplasy in the presence/absence of the pineal foramen in their analysis, suggesting the presence of a zone of variability within the species *Prolacerta broomi*. However, a taxonomic revision of the materials referred to *Prolacerta broomi* would be of use in further addressing this hypothesis.

CHARACTER 23: Pineal foramen, position: (0) margins formed entirely by parietals, (1) situated within the frontoparietal suture.

Examples of past usage: Gauthier et al (1988a:4), Merck (1997:131), Müller (2004:12), Pritchard et al. (2015:23), Nesbitt et al. (in press:23).

Justification/Ontology: The pineal foramen is enclosed entirely by the parietals ancestrally among reptiles. This condition is exemplified by *Captorhinus aguti* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), *Hovasaurus boulei* (Currie, 1980), *Youngina capensis* (BP/1 3859), *Gephyrosaurus bridensis* (Evans, 1980), specimens of *Prolacerta broomi* bearing a foramen (BP/1 5375, NMQR 3763), and *Tanystropheus longobardicus* (PIMUZ T/2819) (Fig. 6A, C). Among modern lepidosaurs included in this study, *Shinisaurus crocodilurus* (Conrad, 2004) and *Sphenodon punctatum* exhibit foramina enclosed by the parietals.

Alternatively, some saurians exhibit parietal foramina positioned within the frontoparietal suture. This condition is exemplified by *Azendohsaurus madagaskarensis* (UA 7-20-99-653) and *Uromastyx* sp. (Gauthier et al., 2012). This condition also occurs in a number of modern squamate clades, and is widespread in Iguania (Gauthier et al., 2012). Some squamates also exhibit a parietal foramen enclosed entirely within the frontals, but no such taxa are currently integrated into this matrix.

CHARACTER 24: Postparietals: (0) absent, (1) present.

Examples of past usage: Benton (1985:L1 & X5), Gauthier et al (1988a:5), Laurin (1991:E2), Jalil (1997:14), Dilkes (1998:29), Müller (2004:14), Pritchard et al. (2015:24), Nesbitt et al. (in press:24).

Justification/Ontology: Early reptiles and diapsids exhibit a paired ossification positioned posterior to the parietal bones, the postparietals (Romer, 1956; Berman et al., 2000). This condition is evident in *Petrolacosaurus kansensis* (Reisz, 1981) and *Youngina capensis* (Carroll, 1981). By contrast, these bones are not present in most early Sauria. They are absent in *Protorosaurus speneri* (USNM 442453), *Trilophosaurus buettneri* (TMM 31025-140), *Mesosuchus browni* (SAM K6536), and *Azendohsaurus madagaskarensis* (UA 7-20-99-653). A midline ossification in an identical position has been described for *Proterosuchus* (Cruickshank, 1972) and *Euparkeria* (Ewer, 1965), which I consider homologous to the postparietals. In most diapsids the postparietal4 bones tend to be quite small, which makes coding on small or distorted skulls difficult.

CHARACTER 25: Postparietals, degree of fusion: (0) unfused to one another fused as a midline interparietal.

Examples of past usage: Merck (1997:116), Pritchard et al. (2015:25), Nesbitt et al. (in press:25).

Justification/Ontology: Some early archosauromorphs exhibit a narrow midline ossification positioned in the midline, posterior to the appressed parietals. This condition has been described for *Proterosuchus* (Cruickshank, 1972), *Erythrosuchus* (Gower, 2003), and *Euparkeria* (1965). Borsuk-Bialynicka and Evans (2009) described an isolated, triangular bone as the interparietal of *Czatkowiella harae*.

Merck (1997) codified this structure independent of the postparietals, considering the two structures to be non-homologous, citing the morphological distinctions between the two and the likelihood of a reversal in Archosauriformes. However, developmental research on modern Mammalia (Koyabu et al., 2012) suggests that a midline interparietal in those taxa derives from paired ossifications in the embryo. A similar fused element in juvenile Crocodylia has been described and considered homologous to the ancestral postparietal (Mook, 1921). Considering these data and the topological similarities between the postparietal and interparietal ossification in Diapsida, I consider the structures to be homologous.

CHARACTER 26: Postorbital, presence of medial process: (0) absent, with contributions of the frontal, parietal or postfrontal forming the posterodorsal orbital margin; (1) present, postorbital contributing to posterodorsal orbital margin.

Examples of past usage: Pritchard et al. (2015:26), Nesbitt et al. (in press:26).

Justification/Ontology: The medial process of the postorbital is a nigh-ubiquitous feature in early diapsids and saurians. Examples are found in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Protorosaurus speneri* (USNM 442453), *Macrocnemus fuyuanensis* (GMPKU-P3001), *Mesosuchus browni* (SAM-PK-K6536), and *Erythrosuchus africanus* (NHMUK R3592). Pritchard et al. (2015) erroneously reported the absence of such a process in *Teraterpeton hrynewichorum*, although it is present.

The medial process of the postorbital is absent in the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834). Such a process does appear to be present in another drepanosauromorph, *Vallesaurus cenensis* (MCSNB 4751). Unfortunately, these are the only drepanosauromorphs for which this character can be coded currently.

CHARACTER 27: Postorbital, posterior process, length: (0) contributes to lateral margin of supratemporal fenestra, but does not reach the posterior aspect of that opening; (1) contributes to the entire length of the supratemporal fenestra, reaching the posterior aspect of that opening.

Examples of past usage: Gauthier et al (1988a:42), Benton and Allen (1997:8), deBraga and Rieppel (1997), Merck (1997:88), Müller (2004:131), Pritchard et al. (2015:28), Nesbitt et al. (in press:28).

Justification/Ontology: The posterior process of the postorbital in some early diapsids contributes to the bony bar separating the infratemporal and supratemporal fenestrae. In certain taxa, the lateral exposure of this process terminates anterior to the posterior margin of the supratemporal fenestra . Such a condition is found in *Petrolacosaurus kansensis* (Reisz, 1981), *Prolacerta broomi* (BP/1 471), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Mesosuchus browni* (SAM-PK-K6536), *Clevosaurus bairdi* (Sues et al., 1994), and *Shinisaurus crocodilurus* (Conrad, 2004).

In a number of early diapsid taxa, the postorbital posterior process is proportionally more elongate, extending well beyond the posterior aspect of the supratemporal fenestra (Fig 5A, 6A). These elongate processes are evident in *Youngina capensis* (BP/1 3859, SAM K6205, K7710), *Hovasaurus boulei* (Currie, 1980), and *Acerosodontosaurus piveteaui* (Bickelmann et al., 2009), and have been reported in other early amniote groups, such as Lanthanosuchoidea and Synapsida (DeBraga and Rieppel, 1997). Multiple gains and losses of this elongate process were reported within Diapsids by Müller (2004). We note the presence of exceptionally elongated postorbitals in *Proterosuchus* spp. (NMQR 1484; Broili and Schroeder, 1934).

CHARACTER 28: Postfrontal: (0) present, (1) absent.

Examples of past usage: Gauthier (1986:17).

Justification/Ontology: The postfrontal bone is an element that is ancestrally present within tetrapods (Romer, 1956). Within early diapsids, it contributes to the posterodorsal corner of the orbit. Postfrontals are present in nearly all diapsids throughout the early history (e.g., Reisz, 1981; Gow, 1975). The elements are present, although comparatively smaller in size in early archosauriforms (e.g., *Proterosuchus fergusi*, BP/1 3393; *Erythrosuchus africanus*, NHMUK R3592) and archosaurs (e.g., *Batrachotomus kupferzellensis*, Gower, 1999; *Neoaetosauroides engaeus*, Desojo and Báez, 2007). The postfrontal is lost in Proterochampsidae (e.g., *Chanaresuchus bonapartei*, MCZ 4037), *Doswellia kaltenbachi* (Dilkes and Sues, 2009), and Dinosauria (e.g., Gauthier, 1986; Nesbitt, 2011).

Among lepidosauromorphs, the postfrontal is lost as a distinct element in a number of groups (Conrad, 2008; Gauthier et al., 2012). It is absent as a discrete element in the squamate taxa in this study (*Uromastyx* sp., *Shinisaurus crocodilurus*), which are therefore coded as "1." However, I caution that the mechanism for the loss of the bone within Archosauriformes and Lepidosauria may be distinct and require further developmental study.

CHARACTER 29: Postfrontal, shape in dorsal view: (0) forms a right triangle, with right angle situated posteromedially; (1) anteroposteriorly broad, posterior margin posteromedially inclined**.**

Examples of past usage: Benton (1985:R1), Gauthier et al (1988a:7), Laurin (1991:B3), Benton and Allen (1997:7), Merck (1997:82), Dilkes (1998:24), Müller (2004:90), Senter (2004:7), Pritchard et al. (2015:27), Nesbitt et al. (in press:27).

Justification/Ontology: Among early diapsids and some early saurian taxa, the posterior margin of the postorbital is transversely oriented. This often exposes the medial process of the postorbital in dorsal view, such that the postorbital contributes to the anterior margin of the supratemporal fenestra in dorsal view. Examples of this include *Petrolacosaurus kansensis* (Reisz, 1981), *Protorosaurus speneri* (USNM 442453), *Prolacerta broomi* (BP/1 5375), *Proterosuchus alexanderi* (NMQR 1484), and *Garjainia prima* (PIN 2334/5) (Fig. 6B). The posterior margin of the bone also appears roughly transverse in *Acerosodontosaurus piveteaui* (Bickelmann et al., 2009).

The postfrontal is anteroposteriorly broader in most near-saurian diapsids and several distinct saurian lineages, such that the postfrontal overlies the postorbital medial process (Fig. 6A, C, D). This condition occurs in *Youngina capensis* (BP/1 3859), *Mesosuchus browni* (SAM-PK-K6536), *Macrocnemus bassanii* (PIMUZ T/4822), and *Trilophosaurus buettneri* (TMM 31025-140). Note that this character is independent of the postorbital contact with the midline skull bones; *Youngina capensis* is the only taxon in the above list to lack a postorbital-parietal contact. Also, an elongate postfrontal contact does not always require the postorbital to be overlain; the postorbital medial process overlies the postfrontal in some Rhynchocephalia (e.g., Gauthier et al., 1988a).

CHARACTER 30: Infratemporal fenestrae, conformation: (0) present, distinct opening framed by squamosal, postorbital and jugal; (1) absent, with squamosal extending anteriorly to slot into a notch on the jugal.

Examples of past usage: Dilkes (1998:4), Müller (2004:17), Pritchard et al. (2015:29), Nesbitt et al. (in press:29).

Justification/Ontology: An infratemporal fenestra framed by the jugal, quadratojugal, squamosal, and postorbital is present in many diapsid reptiles. Indeed, the presence of two temporal fenestrae has long been recognized as characteristic of Diapsida (e.g., Osborn, 1903). However, a number of diapsids have independently closed this opening by expanding the bones framing the cavity (Fig. 5D). Such a closure occurs in *Araeoscelis gracilis* (Vaughn, 1955), *Doswellia kaltenbachi* (Dilkes and Sues, 2009), and Sauropterygia (Rieppel, 1994). The sutural contacts between these elements should be taken into account in analyses addressing closure of the infratemporal fenestra.

State “1” describes the condition in the taxa in our analyses to exhibit closed lateral temporal fenestrae, based largely off of the sutures apparent in NMMNH P41400, the best specimen of the skull in *Trilophosaurus jacobsi*. These taxa include *T. buettneri* (TMM 31025-

140), *T. jacobsi*, and *Teraterpeton hrynewichorum* (Sues, 2003). Further detail on the skull elements in *Trilophosaurus buettneri* will benefit from descriptions of CT scans of the taxon (Merck, 1995).

CHARACTER 31: Jugal, ornamentation of lateral surface: (0) absent, lateral surface smooth, (1) distinct anteroposteriorly trending shelf present.

Examples of past usage: Benton (1985:Q2), Merck (1997:72), Dilkes (1998:33), Pritchard et al. (2015:30), Nesbitt et al. (in press:30).

Justification/Ontology: In most early diapsids and saurians, the jugal bone is unornamented laterally (Fig. 5B, CD). Smooth jugals occur in *Petrolacosaurus kansensis* (Reisz, 1981), *Protorosaurus speneri* (USNM 442453), *Tanystropheus longobardicus* (PIMUZ T/2819), *Trilophosaurus buettneri* (TMM 31025-140), and *Proterosuchus fergusi* (BP/1 3393). By contrast, an anteroposteriorly running shelf, usually with a slight dorsal incline at its anterior tip, is present in a number of early diapsids (Fig. 5A). This shelf occurs in *Youngina capensis* (BP/1 3859), *Rhynchosaurus articeps* (Benton, 1990), and *Teyumbaita sulcognathus* (Montefeltro et al., 2010).

Sill (1971) suggested that this crest in rhynchosaurs represented an attachment site for *levator anguli oris*. Benton (1983) described this structure in *Hyperodapedon gordoni*, but suggested that it did not represent a site of muscle attachment. He noted the possibility that it represented a support structure for a fleshy cheek. This assessment is not widely accepted, as other recent authors have dubbed this structure the *anguli oris* crest (e.g., Langer and Schultz, 2000; Montefeltro et al., 2010). I elect not to use this name until further details on its possible homology can be ascertained.

CHARACTER 32: Jugal, dorsal process, squamosal contact: (0) absent, (1) present.

Examples of past usage: Merck (1997:69), Pritchard et al. (2015:31), Nesbitt et al. (in press:31).

Justification/Ontology: The jugal in early diapsids slots posterior to the ventral base of the ventral process of the postorbital (Fig. 5). It does not extend far enough dorsally to contact the anterior process of the squamosal. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561), *Protorosaurus speneri* (USNM 442453), *Macrocnemus fuyuanensis* (GMPKU-P3001), *Proterosuchus alexanderi* (NMQR 1484), and *Coelophysis bauri* (Colbert, 1989).

Contact between the jugal and squamosal is commonplace among Lepidosauria. It occurs in *Gephyrosaurus bridensis* (codings of both Evans, 1980 and Conrad, 2008), *Clevosaurus hudsoni* (Fraser, 1988), but not *Sphenodon punctatum* (Evans, 2008). It is present in *Uromastyx* sp., but absent in *Shinisaurus crocodilurus* (Conrad, 2008). Among archosauromorphs, contact between these bones occurs in *Dinocephalosaurus orientalis* (Rieppel et al., 2008) and possibly *Boreopricea funerea* (cast of 3708/1; Benton and Allen, 1997). It is also present in *Trilophosaurus jacobsi* (NMMNH P41400), where the contact contributes to the broad, infratemporal plate.

CHARACTER 33: Jugal, posterior process: (0) absent; (1) present, but failing to contact the quadratojugal posteriorly; (2) present, contacting the quadratojugal posteriorly.

Examples of past usage: Benton (1985:E1), Gauthier et al (1988a:10 & 11), Benton and Allen (1997:10), Jalil (1997:13 & 28), Merck (1997:70 & 71), Dilkes (1998:4), Müller (2004:16), Senter (2004:6), Pritchard et al. (2015:32), Nesbitt et al. (in press:32).

Justification/Ontology: The earliest diapsid reptiles possess a lower temporal fenestra that is bounded ventrally by a lower temporal bar formed anteriorly by the posterior process of the jugal and posteriorly by the anterior process of the quadratojugal (state 2). This condition is evident in *Petrolacosaurus kansensis* (Reisz, 1981) and *Youngina capensis* (AMNH FARB 5561, BP/1 3859) (Fig. 5A), although the condition is unfortunately unknown in nearly all other early diapsid taxa that possess a lower temporal opening. The lower temporal bar is similarly constructed throughout Archosauriformes, examples including "Chasmatosaurus" *yuani* (IVPP V4067), *Proterosuchus alexanderi* (NMQR 1484, see Fig. 5C), *Erythrosuchus africanus* (BP/1 5207), *Batrachotomus kupferzellensis* (Gower, 1999), and *Plateosaurus engelhardti* (Prieto-Marquez and Norell, 2011). Among lepidosaurs, the lower temporal bar is very rarely complete. It occurs in *Sphenodon punctatum* (Evans, 2008), although the quadratojugal is positioned posterior to the fenestra in that taxon. A similar bar was reported in the Late Cretaceous lizard *Tianyusaurus zhengi* (Lü et al., 2008), although the quadratojugal is completely absent in that taxon.

In contrast, most early saurians exhibit a gap between the posterior tip of the jugal and the quadratojugal. This occurs in *Protorosaurus speneri* (USNM 442453), *Prolacerta broomi* (BP/1 5375, see Fig. 5B), *Macrocnemus basanii* (MCSN BES SC 111), *Mesosuchus browni* (SAM-PK-K6536), *Azendohsaurus madagaskarensis* (FMNH PR 2751), *Gephyrosaurus bridensis* (Evans, 1980), and *Clevosaurus hudsoni* (Fraser, 1988). The jugal posterior process in these taxa tapers to a point at its posterior margin. The bar is even less developed in some other diapsid groups, in which the jugal exhibits no posterior process at all, terminating in either a posteroventrally curved or squared-off margin. This condition occurs in Drepanosauromorpha (e.g., *Vallesaurus cenensis*, MCSNB 4751; *Megalancosaurus preonensis*, MFSN 1769; *Coelophysis* Quarry drepanosaurid, AMNH FARB 30834), and *Kuehneosaurus latus* (AMNH FARB 7767). In most squamates, there is either no posterior process or a tiny posteroventral projects (Conrad, 2008).

The lower temporal bar has long been considered a critical feature in understanding diapsid relationships and the origin of Lepidosauria (e.g., Parrington, 1935; Robinson, 1967a). In many nineteenth and early twentieth century studies of reptile relationships, an incomplete lower temporal bar was considered grounds for considering a fossil taxon close to the origin of modern squamates. However, studies in the latter half of the twentieth century (e.g., Gow, 1975; Dilkes, 1998) suggested that many Permian and Triassic reptiles with incomplete bars were in fact closer to Archosauria than to Lepidosauria. This hypothesis was born out by cladistic studies incorporating a broad sample of Diapsida (e.g., Gauthier, 1984; Benton, 1985; Evans, 1988; Dilkes, 1998; Müller, 2004), and recent discoveries suggest that an incomplete lower temporal bar was common among non-saurian diapsids as well (e.g., Modesto and Reisz, 2003) Indeed, Müller (2003) recognized multiple gains and losses of the bar in his phylogenetic analysis, and he noted that the bar appears incomplete in early embryos of modern taxa that exhibit complete bars after hatching (e.g., *Sphenodon punctatum*, *Alligator mississippiensis*).

CHARACTER 34: Squamosal, lateral (=descending) process/lamina: (0) anteroposteriorly broad, largely covering quadrate in lateral view; (1) anteroposteriorly narrow, bracing the lateral margin of the quadrate; (2) absent, quadrate is not braced laterally.

Examples of past usage: Benton (1985:B5 & Y7), Gauthier et al (1988a:15 & 40), Laurin (1991:B5 & E4), Benton and Allen (1997:9), Jalil (1997:4 & 54), Merck (1997:152 & 153), Dilkes (1998:36), Müller (2004:27), Pritchard et al. (2015:33 & 34), Nesbitt et al. (in press:33 & 34).

Justification/Ontology: Ancestrally, diapsids exhibit an anteroposteriorly broad lamina that masks the quadrate from view laterally. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981) and *Araeoscelis gracilis* (Reisz et al., 1984). A similarly broad lamina occurs in *Youngina capensis* (AMNH FARB 5561; SAM K7578). By contrast, many early saurians exhibit a descending lamina that is anteroposteriorly narrow, to the point that the quadrate is broadly exposed laterally. This condition occurs in *Protorosaurus speneri* (USNM 442453), *Macrocnemus bassanii* (PIMUZ T/4822), *Mesosuchus browni* (SAM K6536), and *Clevosaurus hudsoni* (Fraser, 1988), in which the lamina typically fits alongside the lateral margin of the lateral crest. A similarly narrow lamina occurs in the non-saurian diapsid *Hovasaurus boulei*, as reconstructed by Currie (1981).

In a number of other saurian taxa, the squamosal lacks a lateral lamina altogether. This condition is prevalent in modern Squamata (e.g., Jollie, 1960; Conrad, 2008), but it also occurs in *Tanystropheus longobardicus* (Nosotti, 2007) and Kuehneosauridae (AMNH FARB 2101; Robinson, 1962). I elected to combine these states into a single ordered character, as the dimensions of the lateral lamina appears to form a continuum ranging from an anteroposteriorly broad structure to the complete absence of the structure. Some past iterations of this character (e.g., Dilkes, 1998, character 36) describe only the covering of the quadrate in lateral view, without reference to the bones forming the covering. Other iterations make reference to the squamosal and quadratojugal forming the cover (e.g., Müller, 2004, character 27).

CHARACTER 35: Squamosal, posterior lamina: (0) posterior lamina present, covering much of posterior aspect of quadrate; (1) posterior lamina absent, posterior aspect of quadrate exposed in occipital view.

Examples of past usage: deBraga and Rieppel (1997), Müller (2004:132).

Justification/Ontology: Ancestrally, reptilian squamosals exhibit a prominent posterior flange that covers much of the quadrate in occipital view (e.g., Romer, 1956; Heaton, 1979). Among diapsids, such a construction is present in *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (MCZ 4830), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), and possibly *Claudiosaurus germaini* (Carroll, 1981). This flange is absent in most Permo-Triassic diapsids, such that the quadrate is only framed by a lateral flange of the squamosal. The posterior lamina is absent in *Youngina capensis* (SAM K7578), *Prolacerta broomi* (BP/1 5375), *Czatkowiella harae* (ZPAL RV/27) *Proterosuchus fergusi* (BP/1 3393), and known lepidosaurs (Evans, 1980; Jollie, 1960).

CHARACTER 36: Supratemporals: (0) present, (1) absent.

Examples of past usage: Benton (1985: J3 & Z3), Gauthier et al (1988a:12), Benton and Allen (1997:13), Merck (1997:157), Dilkes (1998:31), Müller (2004:21), Pritchard et al. (2015:36), Nesbitt et al. (in press:36).

Justification/Ontology: The supratemporal bone is a small dermal ossification that is positioned between the posterolateral portion of the parietal and the posteromedial portion of the squamosal in ancestral reptiles (Parrington, 1937; Romer, 1956). The supratemporal is posteriorly in contact with the tabular bone, if that element is present (see character 37). Examples of taxa that retain a supratemporal ossification include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561, SAM K6205, see Fig. 5A), *Prolacerta broomi* (Modesto and Sues, 2004), *Mesosuchus browni* (SAM PK-K6536, and *Proterosuchus fergusi* (BP/1 3393). The bone is absent in *Sphenodon punctatum*, but present and very small in some squamates, such as *Iguana* and Macrostomata, with multiple losses reported throughout Squamata (e.g., Gauthier et al., 2012).

By contrast, there is no apparent supratemporal bone in a number of early diapsid taxa. It has not been identified in the otherwise complete skulls of the *Coelophysis* Quarry Drepanosaurid (AMNH FARB 30834), *Trilophosaurus buettneri* (TMM 31025-140, see Fig. 5D), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Erythrosuchus africanus* (BP/1 5207), and *Chanaresuchus bonapartei* (MCZ 4037). Among Archosauriformes, the bone has only been reported in Proterosuchidae (Cruickshank, 1972; Nesbitt, 2011; Ezcurra and Butler, 2014).

The exact identity of the bone identified here as the supratemporal in fossil reptiles has been debated (e.g., Thyng, 1906; Broom, 1913; Evans, 2008). I follow Romer (1956) in the taxonomy of this ossification and that referred to as the tabular (see character 37). Also, as per Nesbitt (2011), I caution care in coding the absence of such a small bone based on anything but fully articulated skull materials.

CHARACTER 37: Tabulars: (0) present, (1) absent.

Examples of past usage: Benton (1985:C4 & X5), Gauthier et al (1988a:6), Laurin (1991:E3), Jalil (1997:2), Dilkes (1998:30), Müller (2004:15), Pritchard et al. (2015:37), Nesbitt et al. (in press:37).

Justification/Ontology: The tabular bone is a small ossification in early reptiles, positioned posterior to the supratemporal on the occipital face of the skull (Romer, 1956). This bone is present in *Petrolacosaurus kansensis* (Reisz, 1981) and *Araeoscelis gracilis* (Vaughn, 1955). It is absent in known Archosauromorpha (e.g., Dilkes, 1998) and Lepidosauromorpha, with the possible exception of *Paliguana whitei* (Gauthier et al., 1988a). Tabulars are not recognized in the articulated skulls of drepanosauromorphs (e.g., the *Coelophysis* Quarry drepanosaurid, AMNH FARB 30834) or weigeltisaurids (e.g., *Weigeltisaurus jaekeli*, Evans and Haubold, 1987). However, the distribution of this element in other taxa outside of Sauria is poorly understood, owing to incomplete fossil materials and conflicting interpretations.

Broom (1914) reported the presence of a tabular in *Youngina capensis*, positioned between the parietal and squamosal. By contrast, Parrington (1937) reported a supratemporal between the parietal and squamosal as well as a transversely broad bone appressed to the post-temporal process of the parietal as the tabular, an interpretation followed by Gow (1975). Carroll (1981) described a much smaller tabular on the occipital face of the skull in *Youngina*, sandwiched between a small supratemporal laterally and a smaller postparietal medially. Thus, although broad consensus exists that the tabulars are present in *Youngina*, there is no consensus whatsoever about the construction, position, or morphology of the bone. Tabulars have not been reported in other near-saurian diapsids, such as *Hovasaurus boulei* (Currie, 1981) and *Acerosodontosaurus piveteaui* (Bickelmann et al., 2009). I currently code the tabular as present in *Youngina capensis*, but it is important to reassess this character in the taxon.

CHARACTER 38: Quadratojugal: (0) present, (1) absent.

Examples of past usage: Benton (1985:F1 & Y9), Gauthier et al (1988a:12), Benton and Allen (1997:12), Merck (1997:142), Dilkes (1998:35), Müller (2004:19), Pritchard et al. (2015:38), Nesbitt et al. (in press:38).

Justification/Ontology: The quadratojugal is a dermal ossification that is ancestrally present in reptiles on the lateral surface of the face, lateral to the quadrate (Romer, 1956). Its contribution to the boundaries of the infratemporal fenestra is described above (Character 33). It is present broadly in early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, AMNH FARB 5561; *Rautiania* sp.; PIN 5130/18), archosauromorphs (e.g., *Macrocnemus bassanii*, PIMUZ T/2819; *Proterosuchus alexanderi*, NMQR 1484; Crocodylia, Iordansky, 1973), and Rhynchocephalia (e.g., *Gephyrosaurus bridensis*, Evans, 1980; *Sphenodon punctatum*, Evans, 2008). In early rhynchocephalians, the quadratojugal is quite small and strongly articulated to the quadrate, producing a structure reminiscent of the "quadrate conch" of squamates (Robinson, 1973).

The absence of the quadratojugal has long been noted in Squamata (e.g., Benton, 1985; Gauthier et al., 1988a; Gauthier et al., 2012), and it has also been reported in Kuehneosauridae (Robinson, 1962, 1967a). I did not identify a quadratojugal during study of *Icarosaurus siefkeri* (AMNH FARB 2101) or *Kuehneosaurus* materials at the NHMUK. However, the quadratojugals in certain early lepidosauromorphs (e.g., *Gephyrosaurus bridensis*; Evans, 1980) and archosauromorphs (e.g., *Macrocnemus bassanii*, PIMUZ T/4822) are extremely small, such that restudy of articulated kuehneosaurid material should be a priority to confirm this character. For the moment, both *Icarosaurus siefkeri* and *Kuehneosaurus* sp. are coded as "1."

CHARACTER 39: Quadratojugal, anterior process: (0) present, (1) absent.

Examples of past usage: Gauthier et al (1988a:9), Benton and Allen (1997:11), Jalil (1997:27), Merck (1997:143), Dilkes (1998:35), Müller (2004:20).

Justification/Ontology: Early diapsids exhibit a quadratojugal that is roughly "L"-shaped, with a prominent anteroventrally positioned process that contacts the posterior process of the jugal. This condition is evident in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561, possibly SAM K7710), and *Thadeosaurus colcanapi* (Currie and Carroll, 1984). Such anterior processes also occur in *Erythrosuchus africanus* (BP/1 5207), *Euparkeria capensis* (Ewer, 1965), and known Triassic archosaurs (e.g., Nesbitt, 2011). These processes are typically absent in taxa that lack a complete lower temporal bar (e.g., *Rautiania* sp., PIN 5130/18; *Protorosaurus speneri*, USNM 442453; *Tanystropheus longobardicus*, PIMUZ T/2819; *Gephyrosaurus bridensis* (Evans, 1980).

The absence of this process is not completely coincident with the absence of a lower temporal bar. In some specimens of *Proterosuchus* (e.g., NMQR 1484, see Fig. 5C), the quadratojugal does not exhibit an anterior process despite its contact with the posterior process of the jugal (Ezcurra and Butler, 2014). Although the details differ, a similar combination of an absent anterior process and a complete lower temporal bar can be found in *Sphenodon punctatum* (Evans, 2008).

CHARACTER 40: Quadratojugal, shape of anterior process: (0) paralleling dorsal and ventral borders, (1) dorsal and ventral margins converge anteriorly.

Examples of past usage: Merck (1997:141), Pritchard et al. (2015:40), Nesbitt et al. (in press:40).

Justification/Ontology: In early diapsids known to possess a quadratojugal anterior process, the process typically tapers anteriorly. Examples of this condition include *Petrolacosaurus kansensis* (Reisz, 1981), *Thadeosaurus colcanapi* (Currie and Carroll, 1984), and possibly *Youngina capensis* (SAM K7710). In contrast, the process in most later saurians exhibits parallel dorsal and ventral margins. This condition occurs in *Erythrosuchus africanus* (BP/1 5207) and most archosauriforms (e.g., *Plateosaurus engelhardti*, Prieto-Marquez and Norell, 2011; *Eoraptor lunensis*, Sereno et al., 2013). Merck (1997) reported this character as synapomorphy of Younginiformes, due to its presence in *Youngina capensis* and *Acerosodontosaurus piveteaui*, considering it absent in *Petrolacosaurus kansensis*. Based on Reisz (1981), we disagree with this characterization of *Petrolacosaurus*.

CHARACTER 41: Quadratojugal, extent of dorsal process: (0) dorsoventrally tall, (1) dorsoventrally short or absent.

Examples of past usage: Merck (1997:145), Müller (2004:182).

Justification/Ontology: In most early diapsids and non-diapsid reptiles, the quadratojugal is a dorsoventrally short element, contributing to substantially less of the dorsoventral height of the skull than does the squamosal. This condition is found in *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (MCZ 4830), and *Captorhinus aguti* (Heaton, 1979). Most reconstructions of the quadratojugal in *Youngina capensis* illustrate a similarly short bone (e.g., Gow, 1975; Carroll, 1981). However, restudy of the quadratojugal in the *Y. capensis* holotype suggests that this interpretation requires revision (NM Gardner, pers. comm., 2014). For the moment, we retain a coding of "1" for *Y. capensis*.

In contrast, the quadratojugals in most early saurians are taller bones, contributing to much of the dorsoventral height of the post-temporal region of the skull. Such tall quadratojugals can be found in *Clevosaurus hudsoni* (Robinson, 1973), *Prolacerta broomi* (BP/1 5375), *Macrocnemus bassanii* (PIMUZ T/4822), *Tanystropheus longobardicus* (PIMUZ T/2819), *Azendohsaurus madagaskarensis* (FMNH PR 2751), and *Proterosuchus alexanderi* (NMQR 1484).

CHARACTER 42: Quadrate, shape of posterior margin: (0) straight, oriented dorsoventrally; (1) concave posteriorly.

Examples of past usage: Benton (1985:B6 & Z4), Gauthier et al (1988a:36), Laurin (1991:E7), Jalil (1997:5), Merck (1997:19 & 59), Dilkes (1998:37), Pritchard et al. (2015:41), Nesbitt et al. (in press:41).

Justification/Ontology: In typical early reptiles and non-saurian diapsids, the posterior surface of the quadrate is vertically oriented. This condition occurs in *Captorhinus laticeps* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), *Rautiania* sp. (PIN 5130/18), and the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834). By contrast, the posterior aspect of the quadrate is concave in nearly all saurian diapsids. This can be seen in *Prolacerta broomi* (UCMP 37151), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Kuehneosaurus latus* (Robinson, 1962; Evans, 2009), *Gephyrosaurus bridensis* (Evans, 1980), and Squamata (e.g., Jollie, 1960). Embayed quadrates are illustrated in Figure 5B, C, D, E.

Although some systematic studies describe this character in tandem with the presence and absence of a lateral (=tympanic) crest (e.g., Dilkes, 1998), I elect to consider them independently in this study. For nearly all taxa, these character states do co-occur. However, in some specimens of *Youngina capensis* (e.g., AMNH FARB 5561), the condylar portion of the quadrate appears to be posteriorly positioned relative to the dorsal process of the quadrate. Unfortunately, the sutural relationships of the posterior suspensory region in *Y. capensis* are unclear in many specimens (e.g., AMNH FARB 5561). For the moment, we retain a coding as state "0," but further reconstruction is needed. The quadrate condition is illustrated by BP/1 3859 in figure 5A.

CHARACTER 43: Quadrate, lateral flange (=tympanic crest): (0) absent, quadrate has no lateral expansion; (1) present, flattened lateral crest projects from lateral surface of quadrate.

Examples of past usage: Gauthier et al (1988a:19), Jalil (1997:16), Merck (1997:60), Dilkes (1998:37), Müller (2004:29), Pritchard et al. (2015:43), Nesbitt et al. (in press:43).

Justification/Ontology: As discussed above, a lateral crest occurs in most saurian reptiles. Per Gauthier et al. (1988a), this structure supports a tympanic membrane in modern taxa. They also suggested the possible co-occurrence of this character with a reduction in the robusticity of the stapes.

Gauthier (1984) argued that a lateral conch was absent from the quadrate in *Prolacerta broomi*. Modesto and Sues (2004) also agreed that there was a tympanic crest in *P. broomi* but no lateral conch on the element. Evans (2008:22) however describes the pronounced lateral crest in squamates as "a concave conch," the lateral edge of which can be developed into a "raised edge, the tympanic crest." This terminology is forever in flux. For this character, I code for the presence of a lateral crest on the quadrate, considering the crest in archosauromorphs and lepidosauromorphs as homologous.

CHARACTER 44: Palatal teeth: (0) present, (1) absent.

Examples of past usage: Benton (1985:L3), Senter (2004:25), Pritchard et al. (2015:44), Nesbitt et al. (in press:44).

Justification/Ontology: The palate in early reptiles and early diapsids is a complex structure, bearing a large number of teeth ancestrally on multiple palatal bones. The degree and complexity of these arrangements will be discussed below. However, this character is included to account for the possibility of a relatively small genetic change producing the complete absence of palatal teeth. As summarized by Davit-Béal et al. (2009), multiple developmental experiments have shown that a small number of gene expression changes seem to be responsible for the arrest of tooth development in modern birds. Such a pattern could also hold true for palatal tooth development, such that a simple change could deactivate tooth generation across the entire palate. If this character were not employed, a total loss of palatal teeth in an OTU would require changes to every character describing the presence/absence of teeth in a region of the palate. For every character coded as "1" for this character, every character describing the regional presence of palatal teeth and the morphology of these teeth are coded as "-."

Among Permo-Triassic diapsids, palatal teeth are rarely completely absent. No palatal teeth occur in the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Trilophosaurus buettneri* (TMM 31025-140), *Dinocephalosaurus orientalis* (Rieppel et al., 2008), and many early archosaurs (e.g., *Batrachotomus kupferzellensis*, Gower, 1999; *Plateosaurus engelhardti*, Prieto-Marquez and Norell, 2011).

CHARACTER 45: Vomer, palatal teeth: (0) present, (1) absent.

Examples of past usage: Gauthier et al (1988a:22), Merck (1997:191), Dilkes (1998:66), Pritchard et al. (2015:45), Nesbitt et al. (in press:45).

Justification/Ontology: In early reptiles and ancestral diapsids, the vomer exhibits one to two rows of palatal teeth. A double row may be found in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561), *Macrocnemus bassanii* (MCSN V 457), and *Mesosuchus browni* (SAM K6536). A single row of vomer teeth occur in *Tanystropheus longobardicus* (Wild, 1973), *Proterosuchus alexanderi* (Cruickshank, 1972), and *Azendohsaurus madagaskarensis* (UA 9-8-98-519). Vomer teeth are completely absent in some modern lepidosaurs (e.g., *Shinisaurus crocodilurus*, Conrad, 2004; *Sphenodon punctatum*, Evans, 2008).

CHARACTER 46: Vomer, contact with maxilla: (0) absent, vomer only contacts premaxilla; (1) present, vomer-premaxilla contact expands onto maxilla.

Examples of past usage: Merck (1997:192), Dilkes (1998:38), Müller (2004:92), Pritchard et al. (2015:46), Nesbitt et al. (in press:46).

Justification/Ontology: In most early reptiles and Permo-Triassic diapsids, the vomer meets the posterior aspect of the premaxillae anteriorly at a transversely narrow contact surface. Examples of this contact include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 2871), *Gephyrosaurus bridensis* (Evans, 1980), *Prolacerta broomi* (UCMP 37151), *Proterosuchus alexanderi* (Cruickshank, 1972), and *Azendohsaurus madagaskarensis* (UA 9-8-98-519). The contact surfaces on the premaxilla is transversely broader in a number of archosauromorph taxa, such that the bone makes contact with the anteromedial surface of the maxilla. This contact is evident in *Mesosuchus browni* (SAM K6536) and *Teyumbaita sulcognathus* (Montefeltro et al., 2010). Borsuk-Bialynicka and Evans (2009) reconstructed a similar contact for *Czatkowiella harae*, based on disarticulated skull elements.

Dilkes (1998) reported a contact between the vomer and maxilla in *Proterosuchus fergusi*. Ezcurra and Butler (2014) do not report such a contact in their redescription of the type specimen, and I concur that this is absent based on study of BP/1 4016. Contacts do occur between the vomers and maxillae on some archosauriform taxa that possess a palatal process of the maxilla (e.g., *Euparkeria capensis*, Dilkes, 1998; *Plateosaurus engelhardti*, Prieto-Marquez and Norell, 2011; *Postosuchus kirkpatricki*, Weinbaum, 2011). However, these contacts differ markedly from those reported in rhynchosaurs and *Czatkowiella*.

CHARACTER 47: Palatine, palatal teeth: (0) present, (1) absent.

Examples of past usage: Dilkes (1998:67), Müller (2004:99), Pritchard et al. (2015:47), Nesbitt et al. (in press:47).

Justification/Ontology: The palatines in early reptiles typically exhibits one or more rows of palatal teeth. These are typically continuous with the anterolateral row of teeth on the palatal surface of the pterygoid. Examples of this condition include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561), *Prolacerta broomi* (BP/1 2675), *Gephyrosaurus bridensis* (Evans, 1980), *Mesosuchus browni* (SAM K6536), *Teraterpeton hrynewichorum* (Sues, 2003), and *Proterosuchus fergusi* (Cruickshank, 1972). Although distinctly arranged, the palatines in most rhynchocephalians also exhibit teeth (e.g., *Sphenodon punctatum*, Evans, 2008; *Clevosaurus hudsoni*, Fraser, 1988). Among those diapsids with palatal teeth, palatine teeth are absent in many squamates (e.g., *Shinisaurus crocodilurus*, Conrad, 2004) and in some archosauriforms (e.g., *Eoraptor lunensis*, Sereno et al., 2013). Gauthier et al. (2012) reconstructed the absence of palatine teeth as a synapomorphy of Squamata, although multiple reacquisitions were also noted.

CHARACTER 48: Pterygoid, anterior process, medially positioned tooth row: (0) absent, (1) present.

Examples of past usage: Merck (1997:181), Dilkes (1998:69), Müller (2004:101), Pritchard et al. (2015:48 & 49), Nesbitt et al. (in press:48 & 49).

Justification/Ontology: The anterior process of the pterygoid typically bears two rows of pterygoid teeth in early reptiles. One is positioned near the medial margin of the palatal exposure of the pterygoid, and is often continuous with the posterior portion of the tooth row of the vomer (accounted for in character 48). The second row is more laterally positioned, anterolaterally oriented, and usually continuous with a row of palatine teeth (accounted for in character 49). These were accounted for as a single character in Pritchard et al. (2015), which described the number of fields of dentition on the anterior process of the pterygoid. However, as the positions of the rows on the anterior process are quite consistent among early diapsids, I consider it reasonable to describe each field as a separate character.

The medial row of pterygoid teeth is present in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/375), *Thadeosaurus colcanapi* (Currie and Carroll, 1981), *Prolacerta broomi* (UCMP 37151), *Azendohsaurus madagaskarensis* (UA 7-16-99-619), *Mesosuchus browni* (SAM K6536), *Proterosuchus alexanderi* (NMQR 1484), *Eoraptor lunensis* (Sereno et al., 2013), *Clevosaurus hudsoni* (Fraser, 1988) and *Gephyrosaurus bridensis* (Evans, 1980). The medial tooth row is absent in *Tanystropheus longobardicus* (PIMUZ T/) and in some rhynchocephalians, such as *Sphenodon punctatum* (Evans, 2008) and *Zapatodon ejidoensis* (Reynoso and Clark, 1998).

CHARACTER 49: Pterygoid, anterior process, laterally positioned tooth row: (0) absent, (1) present.

Examples of past usage: Dilkes (1998:69), Müller (2004:101), Pritchard et al. (2015:48 & 49), Nesbitt et al. (in press:48 & 49).

Justification/Ontology: The anterolateral row of pterygoid is present in most early reptiles. Examples include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (Gow, 1975), *Prolacerta broomi* (UCMP 37151), *Azendohsaurus madagaskarensis* (UA 7-16-98-619), *Gephyrosaurus bridensis* (Evans, 1980), and *Proterosuchus alexanderi* (NMQR 1484). Among taxa with palatal teeth, this row is absent in *Clevosaurus hudsoni* (Fraser, 1988), *Shinisaurus crocodilurus* (Conrad, 2004), *Tanystropheus longobardicus* (Fraser, 1988), and *Eoraptor lunensis* (Sereno et al., 2013). This row may also be absent in *Thadeosaurus colcanapi* (Currie and Carroll, 1984).

CHARACTER 50: Pterygoid, transverse process dentition (0) present, (1) absent.

Examples of past usage: Gauthier et al (1988a:24), Laurin (1991:E5), Benton and Allen (1997:16), Merck (1997:190), Dilkes (1998:69), Müller (2004:163), Pritchard et al. (2015:50), Nesbitt et al. (in press:50).

Justification/Ontology: Many early reptile clades exhibit dentition along the posterior margin of the transverse process of the pterygoid. This field of dentition can exhibit varying numbers of transversely oriented rows or a single row. Examples of this morphology occur in *Captorhinus aguti* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 70), *Prolacerta broomi* (BP/1 2675), and *Proterosuchus alexanderi* (NMQR 1484). Such a field of teeth is absent in *Gephyrosaurus bridensis* (Evans, 1980), *Mesosuchus browni* (SAM K6536), *Tanystropheus longobardicus* (MCSN BES SC 1018), *Azendohsaurus madagaskarensis* (FMNH PR 2751, contra Flynn et al., 2010), and *Clevosaurus hudsoni* (Fraser, 1988). The transverse tooth row may also be absent in *Boreopricea funerea* (cast of PIN 3708/1) and *Thadeosaurus colcanapi* (Currie and Carroll, 1984)

Gauthier (1984) and Gauthier et al. (1988a) both consider the loss of teeth on the transverse flange of the pterygoid a synapomorphy of a clade including Kuehneosauridae and Lepidosauria. However, in his broader analysis of early Sauria, Dilkes (1998) recovered the absence of teeth on the transverse process as a synapomorphy of Sauria as a whole. Müller (2004) noted several independent losses of transverse process teeth within Diapsida. In some analyses (e.g., Ezcurra et al., 2014), the distribution of this character did not allow for an unambiguous transition along any branch.

CHARACTER 51: Pterygoid, number of tooth rows on transverse process: (0) multiple rows, (1) one row.

Examples of past usage: Dilkes (1998:69), Müller (2004:163), Pritchard et al. (2015:51), Nesbitt et al. (in press:51).

Justification/Ontology: The pterygoid transverse process in early reptiles and araeoscelids exhibits numerous, transversely running rows on the transverse process of the pterygoid. This condition is exemplified by *Captorhinus aguti* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), and *Araeoscelis gracilis* (Vaughn, 1955). In near-saurian and early saurian diapsids, only a single transverse row is present at the very posterior edge of the transverse process. This morphology is evident in *Youngina capensis* (BP/1 70), *Prolacerta broomi* (BP/1 2675), and *Proterosuchus alexanderi* (NMQR 1484).

In many past analyses, the morphologies described in this character and the total absence of the pterygoid tooth row are integrated into a single, unordered character (e.g., Dilkes, 1998; Ezcurra et al., 2014). This unfortunately removes the homology suggested by the presence of teeth on the transverse process, regardless of the number of rows. Accordingly, we have split the two into separate characters. I suggest that future studies might reintegrate the two and order the states such that the single tooth row is intermediate between the other states.

CHARACTER 52: Pterygoid, midline contact with contralateral pterygoid: (0) absent; (1) present, small contact anteriorly; (2) present, broad contact throughout length. ORDERED.

Examples of past usage: Benton (1985:L2 & Y4), Merck (1997:168 & 169), Dilkes (1998:126), Pritchard et al. (2015:52), Nesbitt et al. (in press:52).

Justification/Ontology: In early reptiles and most Permo-Triassic diapsids, the contralateral pterygoids make contact with one another at their anterior tips, which forms an anteroposteriorly elongate interpterygoid vacuity. Examples include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 375), *Prolacerta broomi* (BP/1 5880), *Proterosuchus alexanderi* (NMQR 1484), *Chanaresuchus bonapartei* (MCZ 4037), and *Sphenodon punctatum* (Evans, 1980). In some early archosauromorphs, the pterygoids meet along the anteroposterior lengths of their palatal exposures. This occurs in a number of rhynchosaurs, such as *Mesosuchus browni* (SAM K6536), *Rhynchosaurus articeps* (Benton, 1990), and *Teyumbaita sulcognathus* (Montefeltro et al. 2010). A third condition occurs in some Squamata (e.g., *Shinisaurus crocodilurus*, Conrad, 2004*)* and the *Coelophysis* Quarry drepanosaur (AMNH FARB 30834), in which the palatal exposures of the pterygoids do not make contact on the palate.

I order this character, as each state represents a varying degree of pterygoid contact on the palatal surface of the animal. State 1 represents a clear intermediate between states 0 and 2.

CHARACTER 53: Pterygoid, orientation of transverse process in ventral view: (0) lateral, (1) anterolateral.

Examples of past usage: Müller (2004:140), Pritchard et al. (2015:53), Nesbitt et al. (in press:53).

Justification/Ontology: Transverse processes of the pterygoid occur throughout Diapsida. Among early diapsids and Permo-Triassic saurians, the long axes of these processes are oriented in a transverse plane. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 70), *Prolacerta broomi* (BP/1 2675), *Mesosuchus browni* (SAM K6536), *Proterosuchus alexanderi* (NMQR 1484), *Erythrosuchus africanus* (NHMUK R3592), *Kuehneosaurus latus* (Robinson, 1962), *Gephyrosaurus bridensis* (Evans, 1980), and *Sphenodon punctatum* (Evans, 2008). In some squamate groups, the long axes of the processes are oriented anterolaterally. Examples include *Shinisaurus crocodilurus* (Conrad, 2004) and *Uromastyx hardwickii* (Gauthier et al., 2012).

CHARACTER 54: Pterygoid, shape of interpterygoid vacuity: (0) anteriorly tapering space, (1) anteriorly curved space.

Examples of past usage: Müller (2004:162), Pritchard et al. (2015:54), Nesbitt et al. (in press:54).

Justification/Ontology: In nearly all diapsids that exhibit a midline contact between the pterygoids, the bones meet to form an anteriorly tapering interpterygoid vacuity. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561), *Prolacerta broomi* (BP/1 5880), *Tanystropheus longobardicus* (Wild, 1973), *Rhynchosaurus articeps* (Benton, 1990), *Proterosuchus alexanderi* (NMQR 1484), *Chanaresuchus bonapartei* (MCZ 4037), and *Sphenodon punctatum* (Evans, 2008). By contrast, the vacuity in some rhynchosaurs, the contact between the bones produces a vacuity that is curved at its anterior tip.

Examples include *Teyumbaita sulcognathus* (Montefeltro et al., 2010) and *Hyperodapedon* sp. (MCZ 1636).

CHARACTER 55: Supraoccipital, texture of posterior surface: (0) smooth, (1) distinct dorsoventrally running crest in the midline.

Examples of past usage: Pritchard et al. (2015:55), Nesbitt et al. (in press:55).

Justification/Ontology: Throughout much of the diversity of early reptiles and early Diapsida, the supraoccipital features a dorsoventrally oriented midline crest on its posterior surface. Examples are found in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (Gardner et al., 2010), materials referred to *Czatkowiella harae* (ZPAL RV/421), *Azendohsaurus madagaskarensis* (FMNH PR 2675, see Fig. 7C), *Teyumbaita sulcognathus* (Montefeltro et al., 2010), *Sphenodon punctatum* (Evans, 2008), *Shinisaurus crocodilurus* (Conrad, 2004), and many archosaurs (e.g., *Batrachotomus kupferzellensis*, Gower, 2002). By contrast, the supraoccipital is smoothly sculptured in a number of non-saurians (e.g., Drepanosauridae n. gen., n. sp., AMNH FARB 30834, see Fig. 7A) and early saurians. These occur in *Prolacerta broomi* (NMQR 3763), *Trilophosaurus buettneri* (TMM 31025-443, fig. 7B), and likely *Erythrosuchus africanus* (Gower, 1997).

CHARACTER 56: Supraoccipital, shape: (0) anteroposteriorly flattened lamina, (1) pillar-like, with posteriorly convex lamina.

Examples of past usage: Dilkes (1998:54), Pritchard et al. (2015:56), Nesbitt et al. (in press:56).

Justification/Ontology: In most early diapsids and saurians, the supraoccipital is a transversely broad anteroposteriorly flattened structure that meets the opisthotic ventrally and the prootic anteroventrally. Examples include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (Gardner et al., 2010), *Tanystropheus longobardicus* (PIMUZ T/2484), *Azendohsaurus* *madagaskarensis* (FMNH FR 2765), *Proterosuchus fergusi* (BP/1 3393), and *Sphenodon punctatum* (Säve-Söderbergh, 1947). In contrast, the supraoccipital is a posteriorly convex structure and columnar structure in *Rhynchosaurus articeps* (Benton, 1990) and *Teyumbaita sulcognathus* (Montefeltro et al., 2010).

CHARACTER 57: Opisthotic, shape of ventral ramus: (0) slender process, (1) process exhibits distinct club-shaped expansion ventrally.

Examples of past usage: Merck (1997:44), Dilkes (1998:46), Pritchard et al. (2015:57), Nesbitt et al. (in press:57).

Justification/Ontology: Throughout Reptilia, the ovale window for the reception of the stapedial footplate and the metotic fissure are separated by a ventral ramus of the opisthotic. In *Captorhinus aguti* (Price, 1935), *Araeoscelis gracilis* (Vaughn, 1955), and the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834) this ramus retains its transverse slenderness throughout its length. In these taxa, the ramus exhibits a prominent, posteriorly facing surface that sits lateral to the basioccipital. Unfortunately, very little is known about the basicranial anatomy in other non-saurian diapsids. In *Youngina capensis* (Gardner et al., 2010), the ventral ramus is slender throughout its length, but its distal tip is poorly understood. For the moment we retain these taxa as exhibiting state "0," pending further detail on early diapsid skulls. Slender ventral rami also occur in *Sphenodon punctatum* (Gower and Weber, 1998) and

In Archosauromorpha, the distal end of the ventral ramus expands distally. This has been termed a club-shaped ventral ramus by Evans (1986), Dilkes (1998), and Gower and Weber (1998). This structure is apparent in *Azendohsaurus madagaskarensis* (FMNH PR 2765, Fig. 7C), *Prolacerta broomi* (UCMP 37151), *Macrocnemus bassanii* (PIMUZ T/2477), *Mesosuchus browni* (SAM K6536), *Trilophosaurus buettneri* (TMM 31025-443, Fig. 7B), *Proterosuchus fergusi* (BP/1 3393), and *Erythrosuchus africanus* (NHMUK R3592).

CHARACTER 58: Opisthotic, paroccipital process contact with suspensorium: (0) absent, ends freely; (1) present.

Examples of past usage: Laurin (1991:A4), Jalil (1997:7), Merck (1997:38), Dilkes (1998:52), Müller (2004:98), Pritchard et al. (2015:58), Nesbitt et al. (in press:58).

Justification/Ontology: In most early reptiles and diapsids, the distal tip of the paroccipital process does not make a bony contact with the squamosal or any other elements of the suspensorium. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981) and *Captorhinus laticeps* (Heaton, 1979). However, in the case of *Captorhinus* the distal tip of the process exhibits a "triangular projection that bore a small, intercalary cartilage joining the opisthotic to the occipital flange of the squamosal" (Heaton, 1979:56).

Non-saurian diapsids from the Permian exhibit a variety of conditions of the paroccipital process. Gardner et al. (2010) reported a prominent contact of the process with the quadrate, but they were uncertain over contacts of the process with the supratemporal as reported by Gow (1975). By contrast, Evans (1987) reported a very limited contact in Tangasauridae.

Pritchard et al. (2015) defined this character as exclusively involving a contact between the paroccipital process and the squamosal. However, considering the diversity of bony elements that the paroccipital process meets (e.g., the squamosal in *Mesosuchus browni,* SAM K6536; the supratemporal in *Youngina capensis*, AMNH FARB 5561; the quadrate in *Clevosaurus hudsoni*, Robinson, 1973), I modified the character state to describe a generalized contact with the suspensorium. Although this broadens the number of taxa that can be coded for the character, I caution that it may homologize too many contacts. This character should be further developed by describing the specifics of the contact surfaces.

CHARACTER 59: Exoccipital, dorsal contact with occipital elements: (0) transversely narrow dorsal contact with more dorsal occipital elements, exoccipital transversely narrow and columnar throughout its dorsoventral height; (1) transversely broad contact that does not meet its opposite in the midline, dorsal portion of exoccipital exhibits dorsomedially inclined process; (2)

transversely broad contact that meets its opposite in the midline, dorsal portion of exoccipital exhibits dorsomedially inclined process. ORDERED.

Examples of past usage: Pritchard et al. (2015:59 & 60), Nesbitt et al. (in press:59 & 60).

Justification/Ontology: Among early reptiles and diapsids, the exoccipitals manifest as dorsoventrally tall, transversely narrow struts that meet the supraoccipital at their dorsal tips. This morphology occurs in *Captorhinus aguti* (Price, 1935), *Araeoscelis gracilis* (Vaughn, 1955), *Youngina capensis* (Gardner et al., 2010), and the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834, see Fig. 7A). Among some saurian reptiles, the exoccipitals develop a dorsomedially inclined process that creates a transversely broad contact between the exoccipitals and the supraoccipital. These processes occur in *Proterosuchus alexanderi* (NMQR 1484), *Mesosuchus browni* (SAM K6536), *Azendohsaurus madagaskarensis* (FMNH PR 2765, see Fig 7C), and *Trilophosaurus buettneri* (TMM 31025-443, see Fig 7C). These processes contact one another in the midline to exclude the supraoccipital from the foramen magnum in other archosauriforms. These include *Prolacerta broomi* (BP/1 2675; NMQR 3763) and *Erythrosuchus africanus* (Gower and Sennikov, 1997).

Among adult squamates, the exoccipitals and opisthotics fused such that the relationship described above cannot be determined clearly. For the moment, we code squamates as state “0,” as the supraoccipital broadly contributes to the foramen magnum in these taxa. Still, developmental data would be advantageous for confirming this hypothesis.

In Pritchard et al. (2015), two separate characters accommodated the presence of a dorsomedial process and the exclusion of the supraoccipital from the foramen magnum. I have elected to combine those into a singe ordered character, as the development of dorsomedial processes appears to be a necessary prerequisite to exclusion of the supraoccipital from the foramen magnum. The character is ordered, as the incipient development of the dorsomedial processes is an intermediate state.

CHARACTER 60: Exoccipital, contralateral contact on floor of foramen magnum: (0) absent, basioccipital contributes to floor of foramen magnum; (1) present, excluding basioccipital from floor of the foramen magnum.

Examples of past usage: Merck (1997:34), Müller (2004:23), Pritchard et al. (2015:61), Nesbitt et al. (in press:61).

Justification/Ontology: The exoccipitals in early reptiles are typically strongly separated on the ventral aspect of the foramen magnum (e.g., *Hovasaurus boulei*, Currie, 1980: *Prolacerta broomi*, UCMP 37151). The aforementioned taxa do not exhibit fusion between the basioccipital and exoccipitals, but in some taxa with these elements fused that outlines of the exoccipitals can be seen allowing coding of the foramen magnum exposure. The floor of the foramen magnum is obscured by the exoccipitals in *Azendohsaurus madagaskarensis* (FMNH PR 2765, see Fig 7C), *Teyumbaita sulcognathus* (Montefeltro et al., 2010), and *Proterosuchus alexanderi* (NMQR 1484).

CHARACTER 61: Exoccipitals: (0) unfused to other braincase elements (sutures with basioccipital and opisthotic patent), (1) exoccipital fused to opisthotic, (2) exoccipital fused to basioccipital.

Examples of past usage: Gauthier et al (1988a:64), Gower and Sennikov (1996:25), Merck (1997:36), Pritchard et al. (2015:62), Nesbitt et al. (in press:62).

Justification/Ontology: Co-ossification of braincase elements is common throughout Diapsida, particularly with regards to the exoccipital. In *Petrolacosaurus kansensis* (Reisz, 1981) and *Hovasaurus boulei* (Currie, 1981), the exoccipitals remain unfused to other braincase elements. Vaughn (1955) reports vague sutures between the exoccipitals and the basioccipital in *Araeoscelis gracilis*, suggesting some degree of fusion. Fusion also occurs between the basioccipital and exoccipitals in *Youngina capensis* (Gardner et al., 2010), *Kuehneosaurus latus*

(AMNH FARB 7770), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834, see Fig. 7A), *Prolacerta broomi* (BP/1 2675), and *Diphydontosaurus avonis* (Whiteside, 1986).

A second type of fusion occurs in certain archosauromorphs and lepidosaurs, in which the opisthotic and exoccipital fuse indistinguishably. This condition occurs in *Teraterpeton hrynewichorum* (Sues, 2003), *Azendohsaurus madagaskarensis* (FMNH PR 2765), *Erythrosuchus africanus* (NHMUK R3592), *Osmolskina czatkowicensis* (ZPAL RV/4222), and *Euparkeria capensis* (Gower and Weber, 1998). A similar fusion occurs in many squamates (e.g., *Shinisaurus crocodilurus*, Bever et al., 2005), and this has been recovered as a synapomorphy of Squamata at a whole (Gauthier et al., 1988a, 2012).

Gower and Sennikov (1996) noted variation in the level of fusion between the exoccipitals and opisthotics in Archosauriformes, although they did not use this character in their systematic study. They cited the insufficiency of published descriptions and the necessity of well-preserved fossil materials. Although I have studied a number of specimens firsthand, I consider these fusions of braincase elements difficult to assess. Although I code these taxa based on externally visible sutures, I think it would be ideal to examine braincase ossifications using CT data to assess the comparability of the degrees of fusion. The timing of fusion is also worthy of study; in *Prolacerta broomi*, one small individual (UCMP 37151) exhibits a lack of fusion between exoccipitals and basioccipital, whereas a larger individual (BP/1 2675) exhibits such a fusion. By contrast, fusion between the exoccipital and opisthotic in modern squamates is noted to occur very early in ontogeny (e.g., Bever et al., 2005). This character could be improved through further understanding of the degree of fusion in these animals.

CHARACTER 62: Opisthotic, paroccipital process morphology: (0) unflattened and tapered, (1) anteroposteriorly-flattened distally.

Examples of past usage: Merck (1997:42), Pritchard et al. (2015:63), Nesbitt et al. (in press:63).

Justification/Ontology: The paroccipital processes taper from their medial base along their transverse lengths in most early reptiles and early diapsids. This condition is apparent in *Captorhinus aguti* (Price, 1935), *Youngina capensis* (Gardner et al., 2010), and the *Coelophysis*

Quarry drepanosaurid (AMNH FARB 30834, see Fig. 7A). Among saurian reptiles, tapered paroccipital processes occur in *Sphenodon punctatum* (Evans, 2008), large *Tanystropheus longobardicus* (PIMUZ T/2819), *Trilophosaurus buettneri* (TMM 31025-140), and possibly *Protorosaurus speneri* (USNM 442453).

Among other archosauromorphs, the paroccipital processes are anteroposteriorly flattened and somewhat dorsoventrally taller than in other taxa. This flattening occurs in *Azendohsaurus madagaskarensis* (FMNH PR 2765, see Fig. 7C), *Proterosuchus fergusi* (BP/1 3393), *Erythrosuchus africanus* (NHMUK R3592), and *Mesosuchus browni* (SAM K6536). This condition is also present in modern squamates, such as *Shinisaurus crocodilurus* (Bever et al., 2005) and *Uromastyx* sp. The latter coding is modified from Pritchard et al. (2015) and Nesbitt et al. (in press), in which *Uromastyx* sp. is coded as "0."

CHARACTER 63: Basioccipital, basal tubera: (0) poorly developed, not extending well ventral of occipital condyle; (1) well developed, extending ventral to level of occipital condyle'

Examples of past usage: Merck (1997:23), Müller (2004:136), Pritchard et al. (2015:64), Nesbitt et al. (in press:64).

Justification/Ontology: This character is dependent on the definition of basal tubera employed by the authors in question. As described by deBraga and Rieppel (1997) and coded by Müller (2004), early diapsids (e.g., *Petrolacosaurus kansensis*) lack basal tubera, which developed either near the base of Sauria (per deBraga and Rieppel) or multiple times within Neodiapsida. However, there are robust tubera on the ventral surface of the basioccipital in both early reptile (e.g., *Captorhinus aguti*, Price, 1935) and early diapsid (*Petrolacosaurus kansensis*, Reisz, 1981) taxa. Following Pritchard et al. (2015), it may be more appropriate to consider a character state in which the basal tubera of the basioccipital do not extend far ventrally relative to the occipital condyle. We also find this state in the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834, see Fig. 7A).

By contrast, the condition in most Neodiapsida is basioccipital tubera that extend well ventral of the occipital condyle. This condition may be found in *Youngina capensis* (Gardner et al., 2010 *contra* Carroll, 1981), *Trilophosaurus buettneri* (TMM 31025-443, see Fig. 7B), *Azendohsaurus madagaskarensis* (FMNH PR 2765, see Fig. 7C), *Prolacerta broomi* (BP/1 2675), *Proterosuchus fergusi* (BP/1 3393), *Sphenodon punctatum* (Gower and Weber, 1998), and *Ctenosaura pectinata* (Oelrich, 1956). I note that the relative development of the basal tubera appears linked to the development of a broad, unossified concavity ventral to the ventral ramus of the opisthotic in Archosauromorpha (e.g., *Azendohsaurus madagaskarensis*, *Prolacerta broomi*) and potentially in earlier taxa (e.g., *Youngina capensis* based on models of Gardner et al., 2010).

CHARACTER 64: Parabasisphenoid, dentition on cultriform process: (0) absent, (1) present.

Examples of past usage: Benton (1985:C10), Gauthier et al. (1988a:31), Merck (1997:47), Dilkes (1998:44), Müller (2004:97), Pritchard et al. (2015:65), Nesbitt et al. (in press:65).

Justification/Ontology: Teeth are present on the ventral surface of the parasphenoid ancestrally within reptiles. In *Captorhinus aguti* (Fox and Bowman, 1966), *Petrolacosaurus kansensis* (Reisz, 1981), *Orovenator mayorum* (Reisz et al., 2011), and *Lanthanolania ivakhnenkoi* (Modesto and Reisz, 2003) there are small denticles arranged near the posterior base of the cultriform process and along the posterior portion of the process. Similar teeth are present at the base of the rostrum in *Kuehneosaurus latus* (AMNH FARB 7771) and *Icarosaurus siefkeri* (AMNH FARB 2101).

Throughout most Permian diapsids and early saurians, the parasphenoid is edentulous. Toothless parasphenoids occur in *Coelurosauravus elivensis* (MNHN MAP 317), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Youngina capensis* (Gardner et al., 2010), *Tanystropheus longobardicus* (Wild, 1973), *Azendohsaurus madagaskarensis* (FMNH PR 2765), and *Proterosuchus fergusi* (BP/1 3393). Multiple analyses consider the absence of parasphenoid teeth characteristic of Lepidosauria (Benton, 1985; Gauthier et al., 1988a). Gauthier et al. (1988a) considered parasphenoid teeth to be independently lost in a monophyletic Younginiformes and Lepidosauria. Evans (1988) and Laurin (1991) considered the absence of such teeth characteristic of a wider sample of Diapsida.

CHARACTER 65: Parabasisphenoid, parasphenoid crests: (0) absent such that there is no ventral floor for the vidian canal; (1) present as prominent ventrolateral extensions of the caudoventral processes, framing the ventromedial floor of the vidian canal.

Examples of past usage: Merck (1997:33), Pritchard et al. (2015:66), Nesbitt et al. (in press:66).

Justification/Ontology: Throughout most early reptiles and Permo-Triassic diapsid, the dermal portion of the parasphenoid contributes ventrolaterally oriented flanges to the ventral surface of the bone. These flanges usually cover the foramina for the internal carotid arteries in ventral view. This condition occurs in *Youngina capensis* (BP/1 2871), *Prolacerta broomi* (UCMP 37151), and *Proterosuchus alexanderi* (NMQR 1484). In a number of other archosauromorphs, the parasphenoid does not exhibit ventral crests. This condition occurs in *Hyperodapedon sanjuanensis* (MCZ 3640), *Trilophosaurus buettneri* (TMM 31025-244), and *Azendohsaurus madagaskarensis* (FMNH PR 2765).

CHARACTER 66: Parabasisphenoid, passage for internal carotid arteries: (0) within lateral wall of braincase, (1) within ventral surface of the parabasisphenoid.

Examples of past usage: Dilkes (1998:45), Pritchard et al. (2015:67), Nesbitt et al. (in press:67).

Justification/Ontology: Throughout early reptiles and most early saurians, the foramina for the internal carotid arteries are positioned on the ventral surface of the parabasisphenoid. This occurs in *Youngina capensis* (Gardner et al., 2010), *Prolacerta broomi* (BP/1 2675), *Trilophosaurus buettneri* (TMM 31025-244), *Xilousuchus sapingensis* (Gower and Sennikov, 1996), and *Sphenodon punctatum* (Gower and Weber, 1998). By contrast, some derived archosaurs and lepidosaurs exhibit internal carotid foramina on the lateral surfaces of their braincases. This occurs in *Massospondylus carinatus* (Gow, 1990), *Shinisaurus crocodilurus* (Bever et al., 2005), and numerous squamate taxa (Säve-Söderbergh, 1947).

CHARACTER 67: Parabasisphenoid, conformation of ventral surface: (0) roughly planar, (1) distinct depression at the suture between the basioccipital and the parabasisphenoid, (2) distinct depression within the parabasisphenoid.

Examples of past usage: Pritchard et al. (2015:68), Nesbitt et al. (in press:68).

Justification/Ontology: Ancestrally among reptiles and Diapsida, the ventral surface of the parabasisphenoid is relatively planar. This condition occurs in *Captorhinus aguti* (Price, 1935), *Petrolacosaurus kansensis* (Reisz, 1981), and *Youngina capensis*. Among saurians, examples of flat surfaces include *Hyperodapedon sanjuanensis* (MCZ 3640), *Sphenodon punctatum* (Gower and Weber, 1998). By contrast, a prominent depression is present at the junction between the basioccipital and the parabasisphenoid. This condition occurs in *Trilophosaurus buettneri* (TMM 31025-443), *Prolacerta broomi* (BP/1 2675), *Euparkeria capensis* (Gower and Weber, 1998), and *Batrachotomus kupferzellensis* (Gower, 2002). A similar depression, entirely enclosed within the ventral surface of the parabasisphenoid occurs in *Azendohsaurus madagaskarensis* (FMNH PR 2765), *Pamelaria dolichotrachela*, Sen, 2003), and possibly *Amotosaurus rotfeldensis* (SMNS unnumbered specimen).

For the moment, I retain these states within a single character. However, I have noted the possible co-occurrence of these depressions in a single specimen. A small depression in the parabasisphenoid may be present in UCMP 37151, a specimen of *Prolacerta broomi* with a distinct depression at the suture with the basioccipital. A distinct depression appears present in both positions in *Blomosuchus georgii* (PIN 1025/348). It may be advantageous to include each depression as a separate character.

CHARACTER 68: Parabasisphenoid, cultriform process: (0) extremely elongate, reaching to the level of the internal nares; (1) shorter, failing to reach internal nares.

Examples of past usage: Müller (2004:141), Pritchard et al. (2015:69), Nesbitt et al. (in press:69).

Justification/Ontology: The cultriform process in most early reptiles and early diapsids is extremely elongate, reaching anteriorly to the level of the external nares. Such a condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (Gardner et al., 2010), and several saurians including *Tanystropheus longobardicus* (PIMUZ T/2482) and *Amotosaurus rotfeldensis* (SMNS unnumbered specimen). By contrast, the cultriform process is more abbreviated in *Trilophosaurus buettneri* (TMM 31025-140), *Mesosuchus browni* (SAM K6536), and modern taxa (e.g., *Sphenodon punctatum*, Evans, 2008; *Shinisaurus crocodilurus*, Bever et al., 2005). Note that this character is difficult to assess with disarticulated materials, which should be treated with caution.

CHARACTER 69: Parabasisphenoid, basipterygoid process orientation in transverse plane: (0) anterolateral, (1) lateral.

Examples of past usage: Dilkes (1998:43), Müller (2004:96), Pritchard et al. (2015:70), Nesbitt et al. (in press:70).

Justification/Ontology: Early reptiles and the earliest diapsids typically exhibit basipterygoid processes that are strongly directed anteriorly. This condition occurs in *Captorhinus aguti* (Price, 1935) and *Araeoscelis gracilis* (Vaughn, 1955). In most Permian diapsids and early saurian taxa, the basipterygoid processes are laterally directed. This condition occurs in *Prolacerta broomi* (BP/1 2765), *Youngina capensis* (Gardner et al., 2010), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), and *Trilophosaurus buettneri* (TMM 31025-244). A slight anterolateral inclination occurs in *Azendohsaurus madagaskarensis* (FMNH PR 2765), *Shinisaurus crocodilurus* (Bever et al., 2005), and most other squamates as well (Säve-Söderbergh, 1947).

CHARACTER 70: Parabasisphenoid, position of abducens foramina: (0) within the dorsum sella, (1) track across dorsal surface of dorsum sella.

Examples of past usage: Gauthier et al (1988a:29), Merck (1997:29), Dilkes (1998:49), Pritchard et al. (2015:71), Nesbitt et al. (in press:71).

Justification/Ontology: The abducens foramina pass out of the braincase anteriorly. In *Youngina capensis*, these foramina track across the dorsal surface of the dorsum sellae of the parabasisphenoid (Gardner et al., 2010). In early archosauromorphs, the course is similar as in *Prolacerta broomi* (BP/1 2675) and *Trilophosaurus buettneri* (TMM 31025-244). By contrast, there are distinct foramina for these nerves pass through the dorsum sellae in *Gephyrosaurus bridensis* (Evans, 1980), *Sphenodon punctatum* (Gower and Weber, 1998), and commonly in squamates (e.g., Bever et al., 2005). Borsuk-Bialynicka and Evans (2009) referred some parabasisphenoids to an early archosauromorph, *Czatkowiella harae*, which also exhibit abducens foramina (ZPAL RV/396).

In some archosauriforms, the prootics converge medially over the dorsal surface of the parabasisphenoid contribution to the dorsum sellae. This condition, seen in *Shansisuchus shansisuchus* (Gower and Sennikov, 1996) and phytosaurs (Case, 1928b), commonly involves the abducens foramina passing through the prootics. I code this condition as equivalent to state 1, as transmission of the foramina through the prootics still involves passage of the nerves dorsal to the dorsum sellae. Unfortunately, the distribution of a medial contact of the prootics has yet to be fully assessed.

CHARACTER 71: Laterosphenoid ossification: (0) absent; (1) present, but fails to reach ventral surface of frontals; (2) present, reaching ventral surface of frontals. ORDERED.

Examples of past usage: Benton (1985:L4), Dilkes (1998:50), Pritchard et al. (2015:72), Nesbitt et al. (in press:72).

Justification/Ontology: In most early reptiles, early saurians, and lepidosaurs, the ossified portion of the braincase terminates anteriorly with the prootic, the remainder of the structure presumably finished in cartilage as in modern lepidosaurs (Säve-Söderbergh, 1947). This morphology is exemplified by *Youngina capensis* (Gardner et al., 2010), *Prolacerta broomi* (BP/1 2675), *Trilophosaurus buettneri* (TMM 31025-244, see Fig. 8A), and *Pamelaria dolichotrachela* (Sen, 2003). By contrast, some other archosauromorphs exhibit a laterosphenoid (=pleurosphenoid, sensu Benton, 1985 and Gaffney, 1990) ossification that articulates with the anterior surface of the prootic. It usually articulates to the anterior margin framing the anterior semicircular canal dorsally and the anterior inferior process ventrally.

A small laterosphenoid, consisting of a single, laterally facing lamina occurs in *Azendohsaurus madagaskarensis* (FMNH PR 2765, see Fig. 8B). This element is shorter than other laterosphenoid ossifications, and fails to reach the ventral surface of the frontal. By contrast, the laterosphenoid in most Archosauriformes exhibits two distal laminae (one facing posterolaterally and one facing anterolaterally) and extends to contact the frontals. This condition occurs in *Proterosuchus goweri* (NMQR 880, see Fig. 8C), *Erythrosuchus africanus* (NHMUK R3592), *Euparkeria capensis* (Gower and Weber, 1998), and nearly all archosaurs (e.g., Nesbitt, 2011). Quite often, the impression of the laterosphenoid can be seen on the ventral surface of the frontal (e.g., *Archosaurus rossicus*, PIN 1100/84). Bhullar and Bever (2009) noted the similarity between the pleurosphenoid ossification in the early turtle *Proganochelys quentstedti* (reported by Gaffney, 1990) and those in early archosauriforms. I concur that the condition in *Proganochelys* closely resembles the condition described by state 2 (SMNS 15789).

A laterosphenoid ossification has long been considered a characteristic of archosaurs and their closest relatives (e.g., Gauthier, 1984; Benton, 1985; Clark et al., 1994; Dilkes, 1998). Flynn et al. (2010) reported the presence of a laterosphenoid in *Azendohsaurus madagaskarensis*, a taxon otherwise lacking clear archosauriform apomorphies. They hypothesized that this trait was evidence of a closer relationship between *Azendohsaurus* and Archosauriformes than to other archosauromorph groups. However, the analysis of Nesbitt et al. (in press) resolved this character as an independent derivation of a laterosphenoid ossification.

CHARACTER 72: Prootic, crista prootica: (0) present, (1) absent

Examples of past usage: Jalil (1997:70), Merck (1997:48), Dilkes (1998:47), Pritchard et al. (2015:73), Nesbitt et al. (in press:73).

Justification/Ontology: In early reptiles, the lateral surface of the prootic is overall smooth, marked only by the convexity of the lateral semicircular canal. This morphology is evident in *Captorhinus aguti* (Price, 1935), *Youngina capensis* (Gardner et al., 2010), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), and *Azendohsaurus madagaskarensis* (FMNH PR 2765, see Fig. 8B). A contrasting condition is found in many early saurian taxa, in which the prootic exhibits a sharply defined crest on its lateral surface that extends from the level of the lateral semicircular canal overtop of the foramen for the facial nerve (=crista prootica). Such a crest occurs in *Prolacerta broomi* (BP/1 2675), *Trilophosaurus buettneri* (TMM 31025-244, see Fig. 8A), *Proterosuchus goweri* (NMQR 880, see Fig. 8C), *Erythrosuchus africanus* (NHMUK R3592), and *Euparkeria capensis* (Gower and Weber, 1998). A similar condition occurs in *Ctenosaura pectinata* (Oelrich, 1956), *Shinisaurus crocodilurus* (Bever et al., 2005), and *Sphenodon punctatum* (Säve-Söderbergh, 1947).

CHARACTER 73: Prootic, anterior inferior process: (0) process present, sitting anterior to trigeminal foramen; (1) absent, trigeminal foramen unframed anteriorly.

Examples of past usage: Dilkes (1998:48), Pritchard et al. (2015:74), Nesbitt et al. (in press:74).

Justification/Ontology: In early reptiles the gap in the anteroventral face of the prootic for the trigeminal nerve is open anteriorly, lacking any anterior border formed by the prootic. This condition occurs in *Captorhinus aguti* (Price, 1935), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Youngina capensis* (Gardner et al., 2010), *Trilophosaurus buettneri* (TMM 31025-244, see Fig. 8A), and *Hyperodapedon sanjuanensis* (MCZ 3640). By contrast, the prootic exhibits a prominent anterior inferior process in many saurian taxa. This process projects anterodorsally and forms an anterior border for the trigeminal gap. Such a process occurs in *Sphenodon punctatum* (Gower and Weber, 1998), *Tanystropheus longobardicus* (PIMUZ

T/2482), *Mesosuchus browni* (SAM K6536), and *Proterosuchus goweri* (NMQR 880, see Fig. 8C).

CHARACTER 74: Prootic, contribution to paroccipital process: (0) absent, no contribution to anterior face of paroccipital process, (1) present, contributing tapering lamina to the anterior surface of the prootic.

Examples of past usage: Merck (1997:49), Dilkes (1998), Pritchard et al. (2015:75), Nesbitt et al. (in press:75).

Justification/Ontology: Posteriorly, the prootic is in contact with the anterior surface of the opisthotic. In some taxa, this contact is transversely narrow, not extending onto the anterior surface of the paroccipital process of the opisthotic. Such a contribution appears to be absent in the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834) and *Youngina capensis* (Gardner et al., 2010). By contrast, most saurian reptiles exhibit a slender lamina of the prootic that fits across the paroccipital process. This can be seen in *Sphenodon punctatum* (Gower and Weber, 1998), *Shinisaurus crocodilurus* (Bever et al., 2005), *Trilophosaurus buettneri* (TMM 31025-244, see Fig. 8A), *Proterosuchus goweri* (NMQR 880, see Fig. 8C), and *Teyumbaita sulcognathus* (Montefeltro et al., 2010). The degree of contribution in Rhynchosauria appears more extensive than in other diapsids (e.g., Benton, 1983; Montefeltro et al., 2010).

CHARACTER 75: Stapes, ossified dorsal process: (0) absent, (1) present.

Examples of past usage: Merck (1997:221), Müller (2004:134), Pritchard et al. (2015:76), Nesbitt et al. (in press:76).

Justification/Ontology: In early reptiles and the earliest diapsids, the stapes exhibits a prominent dorsal process. In articulated braincases of *Captorhinus aguti*, this process clearly articulates with the ventrolateral surfaces of the prootic. The stapes in *Petrolacosaurus kansensis*

(Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), and *Orovenator mayorum* (Reisz et al., 2011) all exhibit some form of this dorsal process. By contrast, this ossified dorsal process is absent in most Permo-Triassic diapsids and modern reptiles (e.g., Romer, 1956). It is absent in *Youngina capensis* (Gardner et al., 2010), *Prolacerta broomi* (BP/1 2675), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Proganochelys quentstedti* (Gaffney, 1990), *Mesosuchus browni* (SAM K6536), and *Sphenodon punctatum* (Evans, 2008).

It should be noted that the distal tip of the cartilaginous extrastapes in squamates *does* exhibit a dorsal process with a ligamentous attachment to the paroccipital process (Olson, 1966; Baird, 1970). It seems likely that this structure is the homolog of the osseous dorsal process in archaic reptiles, based on the position and relationships of the structure (Olson, 1966). Therefore, note that this character describes the absence of the osseous dorsal process (contra Pritchard et al., 2015), which is all that can be confidently assessed in the current taxon sample

CHARACTER 76: Stapes, foramen within shaft: (0) present, (1) absent.

Examples of past usage: Benton (1985:C5), Gauthier et al (1988a:35), Laurin (1991:E9), Jalil (1997:6), Merck (1997:222), Pritchard et al. (2015:77), Nesbitt et al. (in press:77).

Justification/Ontology: Early reptiles and early diapsids typically exhibit a prominent foramen within the shaft of the stapes. Examples include *Captorhinus aguti* (Price, 1935), *Youngina capensis* (Gardner et al., 2010), *Hovasaurus boulei* (Currie, 1981), and *Orovenator mayorum* (Reisz et al., 2011). Among modern reptiles, a similar foramen occurs in a small number of lepidosaurs (e.g., some Gekkota, *Dibamus* per Greer, 1965). In these taxa, the stapedial artery passes through this foramen, which most authors suggest occurred in early reptiles (e.g., Romer, 1956; Greer, 1965). By contrast, the stapes is imperforate in most early saurians. Imperforate stapes are known in *Prolacerta broomi* (BP/1 2675), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), and *Plateosaurus engelhardti* (Olson, 1966). They also occur in *Sphenodon punctatum* and most modern lepidosaurs (Greer, 1965).

It should be noted that the imperforate stapedial shafts in modern lepidosaurs may not necessarily be homologous. Greer (1965) reviewed the anatomical relationship of the imperforate stapedial shafts in modern taxa to the stapedial artery. In some cases, the stapedial artery sits anterior to the stapedial shaft (e.g., *Sphenodon punctatum*, Serpentes, most gekkonids), whereas other squamates exhibit a stapedial artery posterior to the stapedial shaft (most non-gekkonid lizards). This may suggest distinct developmental paths for the imperforate stapes in lepidosaurs. Although I code all taxa with an imperforate stapes as "1," further study is needed to understand patterns of loss of the stapedial foramen.

CHARACTER 77: Prootic, contribution to paroccipital process: (0) absent, no contribution to anterior face of paroccipital process, (1) present, contributing tapering lamina to the anterior surface of the prootic.

Examples of past usage: Dilkes (1998:72), Pritchard et al. (2015:78), Nesbitt et al. (in press:78).

Justification/Ontology: The dentaries in most reptiles and diapsids meet at their anterior tips, forming a symphyseal surface of varying levels of ossification (Holliday and Nesbitt, 2013). By contrast, the edentulous anterior tips of the dentaries in some rhynchosaurs diverge from one another at their tips. Examples of this condition include *Rhynchosaurus articeps* (Benton, 1990) and *Teyumbaita sulcognathus* (Montefeltro et al., 2010).

CHARACTER 78: Coronoid process: (0) absent, (1) present.

Examples of past usage: Merck (1997:197), Dilkes (1998:73), Pritchard et al. (2015:79), Nesbitt et al. (in press:79).

Justification/Ontology: I define a coronoid process as a dorsally directed flange constructed from the coronoid and adjacent dermal elements of the mandible positioned posterior to the tooth row. There is no coronoid process in early reptiles such as *Captorhinus laticeps* (Heaton, 1979), early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, AMNH FARB 5561), and many early saurian taxa (e.g., *Protorosaurus speneri*, USNM 442453; *Prolacerta broomi*, BP/1 5375; and *Azendohsaurus madagaskarensis*, FMNH PR 2751). Coronoid processes do occur in *Gephyrosaurus bridensis* (Evans, 1980), *Clevosaurus hudsoni* (Fraser, 1988), *Shinisaurus crocodilurus* (Conrad, 2004), *Trilophosaurus buettneri* (TMM 31025-140), and *Langobardisaurus pandolfii* (MFSN 1921).

CHARACTER 79: Surangular, lateral surface, foramen positioned near surangular-dentary contact: (0) absent, (1) present.

Examples of past usage: Modesto and Sues (2004:144), Pritchard et al. (2015:80), Nesbitt et al. (in press:80).

Justification/Ontology: A small foramen at this point on the surangular was first codified in systematic analysis by Modesto and Sues (2004), in reference to a structure they noted on *Prolacerta broomi* but not in rhynchosaurian archosauromorphs (e.g., *Mesosuchus browni*) and early lepidosauromorphs (e.g., *Gephyrosaurus bridensis*). They noted the presence of this structure in Squamata based on Oelrich (1956).

CHARACTER 80: Surangular, lateral surface, foramen positioned directly anterolateral to glenoid fossa: (0) absent, (1) present.

Examples of past usage: Modesto and Sues (2004:145), Pritchard et al. (2015:81), Nesbitt et al. (in press:81).

Justification/Ontology: A small foramen at this point on the surangular was first codified in systematic analysis by Modesto and Sues (2004), in reference to a structure they noted on *Prolacerta broomi*, many Triassic archosauromorphs, and modern squamates (e.g., Oelrich, 1956). Coding this structure requires careful study, preferably using light microscopy of mandibular elements in most small, early taxa.

CHARACTER 81: Angular, exposure on lateral mandibular surface: (0) dorsoventrally broad, (1) limited to dorsoventrally narrow, posteroventral sliver by dentary and surangular.

Examples of past usage: Gauthier et al (1988a:71), Jalil (1997), Merck (1997:193) Müller (2004:167), Senter (2004:18), Pritchard et al. (2015:82), Nesbitt et al. (in press:82).

Justification/Ontology: In most early reptiles and diapsids, the angular forms a substantial contribution to the lateral surface of the mandible. This condition persists through most early Archosauromorpha (e.g., *Macrocnemus bassanii*, PIMUZ T/4822; *Proterosuchus fergusi*, BP/1 3393). By contrast, *Kuehneosaurus latus* (as reconstructed by Robinson, 1962) and Lepidosauria (e.g., *Gephyrosaurus bridensis,* Evans, 1980; Squamata, Evans, 2008) exhibit a dorsoventrally narrow lateral exposure of the angular. Gauthier et al. (1988a: character 71) defined the latter state in terms of the angular extending more or less than one-third up the dorsoventral height of the mandible.

CHARACTER 82: Angular, exposure on lateral mandibular surface: (0) terminates anterior to the glenoid, (1) extends to the glenoid.

Examples of past usage: Gauthier (1984), Gauthier et al. (1988a:70), Merck (1997:194) Pritchard et al. (2015:83), Nesbitt et al. (in press:83).

Justification/Ontology: Throughout early reptiles and Diapsida, the lateral exposure of the angular extends posteriorly on the mandible to a point equivalent to the anteroposterior level of the quadrate articulation. This condition occurs in *Captorhinus laticeps* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 2871), and likely the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834). A similar condition occurs in most early archosauromorphs (e.g., *Protorosaurus speneri*, USNM 442453; *Trilophosaurus buettneri*, TMM 31025-140; *Proterosuchus fergusi*, BP/1 3393). Among lepidosauromorphs, the angular extends this far posteriorly in putative rhynchocephalians (e.g., *Gephyrosaurus bridensis*, Evans, 1980, *Oenosaurus muehlheimensis*, Rauhut et al., 2012; *Sphenodon punctatum*, Evans, 2008).

A contrasting condition occurs in some Squamata, in which the lateral exposure of the angular is well separated anteroposteriorly from the level of the quadrate articulation. This condition is seen in most modern squamates (e.g., *Shinisaurus crocodilurus,* Conrad, 2004). Gauthier et al. (2012) resolved the shortened angular as a synapomorphy of the clade including *Huehuecuetzpalli mixtecus* and all other Squamata; they recognized a reversal in Amphisbaenidae.

CHARACTER 83: External mandibular fenestra (EMF): (0) absent; (1) present as opening framed anteriorly by the dentary, dorsally by the surangular, and ventrally by the angular.

Examples of past usage: Benton (1985:J4), Dilkes (1998:76), Senter (2004:24), Pritchard et al. (2015:84), Nesbitt et al. (in press:84).

Justification/Ontology: The mandible in early reptiles and Permo-Triassic diapsids does not typically exhibit any fenestration of its lateral surface, the dentary, angular, and surangular fitting solidly together. Examples of unfenstrated mandibles include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561), *Protorosaurus speneri* (USNM 442453), *Mesosuchus browni* (SAM K6536), and *Trilophosaurus buettneri* (TMM 31025-5). In contrast, taxa within Archosauriformes typically exhibit a large opening in the lateral surface of the mandible, framed as described above. This opening is present in *Proterosuchus alexanderi* (NMQR 1484), “Chasmatosaurus” *yuani* (IVPP V4067), *Erythrosuchus africanus* (BP/1 5207), *Euparkeria capensis* (Ewer, 1965), and *Chanaresuchus bonapartei* (Romer, 1971).

The external mandibular fenestra has long been recognized as an important feature in interpreting archosauriform relationships. It has been recognized as synapomorphic of Archosauriformes (e.g., Dilkes, 1998; Ezcurra et al., 2014) or a more inclusive clade without *Proterosuchus* (e.g., Gauthier, 1984; Benton, 1985). My codings differ from this interpretation in that I code *Prolacerta broomi* as having this fenestra. In UCMP 37151 and BP/1 5880, two specimens that preserve the mandibles in articulation, there is a small gap between the anterior tips of the surangular and angular. This structure is smaller than most archosauriform external mandibular fenestrae, but it is positioned identically to those.

CHARACTER 84: Splenial, contribution to mandibular symphysis: (0) present, (1) absent.

Examples of past usage: Merck (1997:215), Müller (2004:37),, Pritchard et al. (2015:85), Nesbitt et al. (in press:85).

Justification/Ontology: The evolution of the mandibular symphysis in Diapsida is complex, which complicates the coding of this character. In a number of Archosauromorpha, the splenial may easily be seen entering the symphysis. In such taxa (e.g., *Trilophosaurus buettneri*, TMM 31025-140; *Hyperodapedon gordoni*, Benton, 1983), the symphysis forms a complex interdigitating suture such that the contacts between the splenials can be easily seen. Holliday and Nesbitt (2013) described this structure of symphysis as Class III.

Most early Diapsida and Sauria exhibit a mandibular symphysis of either Class I (a non-interdigitating, abutting contact) or II (a weakly interdigitating contact) following the classification of Holliday and Nesbitt (2013). As such, it is exceptionally difficult to assess the contribution of the splenial in articulated or distorted specimens without the aid of CT data. As such, many taxa are coded as "?" for this character, unless the splenial does not extend far enough anteriorly to reach the symphyseal region. I note that CT data could substantially improve codings for these codings.

CHARACTER 85: Retroarticular process: (0) present as extension of articular and adjacent bones posterior to quadrate articulation, (1) absent.

Examples of past usage: Benton (1985:B10), Gauthier et al (1988a:73), Jalil (1997:8), Laurin (1991:B6), Merck (1997:212), Dilkes (1998:74), Müller (2004:35), Senter (2004:20), Pritchard et al. (2015:86), Nesbitt et al. (in press:86).

Justification/Ontology: In the earliest known diapsids, the anteroposterior length of the mandible terminates at the level of the quadrate articulation. There is no posterior process in *Araeoscelis gracilis* (Vaughn, 1955) or *Petrolacosaurus kansensis* (Reisz, 1981). However, both of these taxa exhibit a small, medially inclined process near to the quadrate articulation, which may be homologous with the retroarticular process.

In most Neodiapsida, there is a retroarticular process present, extending posteriorly from the quadrate articulation. Such a process occurs in *Youngina capensis* (AMNH FARB 5561), *Rautiania* sp. (PIN 5130/47), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Protorosaurus speneri* (USNM 442453), *Proterosuchus alexanderi* (NMQR 1484), and Lepidosauria (e.g., Evans, 2008). Similar processes are also found in some early reptile groups, including *Captorhinus laticeps* (Heaton, 1979).

CHARACTER 86: Retroarticular process, composition: (0) articular only, (1) fused articular-prearticular.

Examples of past usage: Pritchard et al. (2015:87), Nesbitt et al. (in press:87).

Justification/Ontology: In most reptiles that bear a retroarticular process, the process itself is made from a posterior extension of the articular bone. The prearticular, if present does not contribute, as seen in “Chasmatosaurus” *yuani* (IVPP V4067), *Prolacerta broomi* (UCMP 37151), and *Tanystropheus longobardicus* (MCSN BES SC 265). By contrast, the prearticular and articular are fused such that the prearticular contributes to the retroarticular process in many lepidosaurs. This occurs in *Gephyrosaurus bridensis* (Evans, 1980), *Diphydontosaurus avonis* (Whiteside, 1986), and Squamata (e.g., Benton, 1985; Conrad, 2008). Benton (1985) suggested this character as a squamate synapomorphy, but later workers recover it as a lepidosaur synapomorphy.

CHARACTER 87: Marginal dentition on anteriormost portions of premaxilla and dentary: (0) present, (1) absent

Examples of past usage: Benton (1985:M1 & N1), Laurin (1991:G1), Merck (1997:200), Dilkes (1998:9), Müller (2004:152), Pritchard et al. (2015:88), Nesbitt et al. (in press:88).

Justification/Ontology: The premaxillae and the anterior tips of the dentaries house teeth in most Permo-Triassic reptiles and diapsids. Teeth are absent in the tips of the jaw of *Teraterpeton hrynewichorum* (Sues, 2003) and *Trilophosaurus buettneri* (TMM 31025-1, see Fig. 9A; 31025-207). The loss of teeth in the tips of the jaws also occurs in some Aetosauria (e.g., Desojo et al., 2013). Complete tooth loss is known in a few Triassic reptiles (e.g., Shuvosauridae, Nesbitt and Norell, 2006; *Lotosaurus adentus*, Zhang, 1975; Nesbitt et al., 2013; *Proganochelys quentstedti*, Gaffney, 1990), but among the taxa in this analysis it only occurs in the *Coelophysis* Quarry drepanosaurid.

CHARACTER 88: Marginal dentition, enlarged caniniform teeth in maxilla: (0) present, (1) absent, maxillary teeth subequal in size.

Examples of past usage: Benton (1985:B3), Laurin (1991:B1), Merck (1997:240), Dilkes (1998:56), Senter (2004:26), Pritchard et al. (2015:89), Nesbitt et al. (in press:89).

Justification/Ontology: In early diapsids and their closest relatives, the maxilla exhibits prominent and elongate teeth near the level of the premaxilla-maxilla suture. Such teeth occur in *Protorothyris archeri* (Clark and Carroll, 1973) and *Petrolacosaurus kansensis* (Reisz, 1981). These are not universal in early reptiles (e.g., *Captorhinus aguti*, Fox and Bowman, 1966; *Araeoscelis gracilis*, Vaughn, 1955). Among Neodiapsida, the maxillary teeth are typically subequal in size. Examples include *Protorosaurus speneri* (USNM 442453), *Macrocnemus* *bassanii* (PIMUZ T/2477), *Azendohsaurus madagaskarensis* (FMNH PR 2751), and *Proterosuchus fergusi* (BP/1 3393).

CHARACTER 89: Marginal dentition, serrations: (0) non-serrated, (1) serrated.

Examples of past usage: Dilkes (1998:57), Senter (2004:15), Pritchard et al. (2015:90), Nesbitt et al. (in press:90).

Justification/Ontology: The teeth in most early diapsids, archosauromorphs, and lepidosaurs do not exhibit serration on either their labial or lingual surfaces (Fig. 10A). By contrast, Triassic Archosauriformes nearly always exhibit serrated margins (e.g., *Proterosuchus fergusi*, BP/1 3393; *Erythrosuchus africanus*, BP/1 5207). *Azendohsaurus madagaskarensis* (FMNH PR 2751) and *Azendohsaurus laaroussii* (MNHN ALM 360, see Fig. 10C) exhibit much coarser serrations, but they are also coded as "1."

Brink and Reisz (2014) described extensive dental diversity in early synapsid taxa. They noted serrations on an extremely small scale in species of *Dimetrodon*, only visible using microscopy. Histological sections also revealed that all serrations were not equal; some were made up of inflections of the enamel, whereas others incorporated dentine as well. My studies of most early saurian fossils involved study using light microscopy and gross morphological study, and as such determination of these fine variations has not yet occurred. In order to fully assess this character and its variations within early diapsids, histological sectioning is needed.

CHARACTER 90: Marginal dentition, shape of the posterior margin of tooth: (0) convex or straight, (1) concave.

Examples of past usage: Benton (1985:D4), Jalil (1997:63), Merck (1997:233), Dilkes (1998:58), Senter (2004:15), Pritchard et al. (2015:91), Nesbitt et al. (in press:91).

Justification/Ontology: The teeth in many early diapsids form simple, conical pegs or pyramidal shapes. This occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Vallesaurus cenensis* (MCSNB 4751), *Claudiosaurus germaini* (SAM 8263), *Protorosaurus speneri* (USNM 442453), *Teraterpeton hrynewichorum* (Sues, 2003), and *Trilophosaurus buettneri* (TMM 31025-1, see Fig 9A). By contrast, the teeth in some early saurian reptiles are recurved posteriorly. This condition occurs in *Boreopricea funerea* (PIN 3708/1), *Prolacerta broomi* (BP/1 2675), *Proterosuchus alexanderi* (NMQR 1484), *Coelophysis bauri* (Colbert, 1989), and *Vancleavea campi* (GR 138, see Fig. 10B).

In the known sample of *Prolacerta broomi*, there is actually some variability with regards to this trait. Some small specimens of the taxon (e.g., AMNH FARB 9520, UCMP 37151), exhibit narrow and conical teeth similar to those in *Protorosaurus speneri*. By contrast, some larger individuals exhibit strongly recurved teeth that exhibit some degree of labiolingual compression (e.g., BP/1 2675, 5375). Substantial changes in dental morphology, concurrent with changes in niche occupation, are noted in modern *Alligator* (Gignac et al., 2014). It is certainly possible that similar changes occur in early saurian taxa as well. I recommend caution in coding taxa for this and other characters relating to dental form, as ontogenetic state must be a consideration.

CHARACTER 91: Marginal dentition, arrangement: (0) single row of marginal teeth, (1) multiple zahnreihen in maxilla.

Examples of past usage: Benton (1985:N4), Merck (1997:242), Dilkes (1998: multiple characters), Pritchard et al. (2015:92), Nesbitt et al. (in press:92).

Justification/Ontology: Among modern reptile taxa, each tooth position contains a single tooth in position at any one time (Edmund, 1960). By contrast, a number of fossil reptile groups exhibit multiple rows of teeth for each tooth position. These include Captorhinomorpha (Modesto et al., 2014; LeBlanc and Reisz, 2015) and Rhynchosauria (Benton, 1984; Dilkes, 1995). We use the term "zahnreihen" to note the presence of several "waves" of tooth replacement within a single jaw in the taxa in question, although LeBlanc and Reisz (2015) argue that this term denotes a developmental phenomenon that is not evidenced by fossils.

As noted by Malan (1963), the early rhynchosaur *Mesosuchus browni* exhibits a slight irregularity of tooth positions. Although multiple tooth positions were not noted in the taxon, this was considered a possible incipient condition of the arrested tooth replacement in later rhynchosaurs. It would be valuable to determine the tooth replacement strategy of both *Mesosuchus browni* and *Howesia browni* using CT imaging to determine if this irregularity does reflect the multiple zahnreihen of most rhynchosaurs.

CHARACTER 92: Marginal dentition, morphology of crown base: (0) single, pointed crown, (1) flattened platform with pointed cusps, (2) mesiodistally arranged cusps.

Examples of past usage: Merck (1997:244), Dilkes (1998:136), Pritchard et al. (2015:93), Nesbitt et al. (in press:93).

Justification/Ontology: The teeth in most early reptiles and Permo-Triassic diapsids exhibit only a single pointed tip to the crown. By contrast, the teeth in a small subset of archosauromorphs are overall flattened structures with cusps (Fig. 9B). Following Pritchard et al. (2015), I employ this character state to describe the condition in *Teraterpeton hrynewichorum* (Sues, 2003) and the species of *Trilophosaurus* (Spielmann et al., 2008). However, I note that the shape of the cusps in *Teraterpeton* is quite distinct from *Trilophosaurus*, such that one could argue for a coding of "0" for the taxon as well.

The third state describes the large, mesiodistally arranged cusps present in small individuals of *Tanystropheus longobardicus* (MCSN BES SC 1018) and in the mid-maxillary teeth of *Langobardisaurus pandolfii* (MCSNB 2883). In the former, a single middle cusp is framed two, slightly smaller mesial and distal cusps. In the latter, the tooth exhibits a single middle cusp and very slight mesial and distal cusps. The homology of these structures could be argued, as the three-dimensional construction of the tooth in *Langobardisaurus* is not clearly the same as in *Tanystropheus*.

CHARACTER 93: Marginal dentition, implantation: (0) teeth situated in shallow groove (pleurodonty + thecodonty), (1) teeth on dorsal surface of tooth-bearing bones (acrodonty).

Examples of past usage: Benton (1985:Z5), Gauthier et al (1988a:75), Dilkes (1998:55), Müller (2004:38), Pritchard et al. (2015:94), Nesbitt et al. (in press:94).

Justification/Ontology: In past analyses of early Sauria, tooth implantation is coded as a single character with states for acrodonty, thecodonty, pleurodonty, and ankylothecodonty. However, all of these conditions describe complex interactions of dental tissues with teeth (e.g., Luan et al., 2009; Zaher and Rieppel, 2009; LeBlanc and Reisz, 2013), involving multiple tissue types. For this character, we describe the depth of the tooth root relative to the tooth-bearing elements.

In most early reptiles and saurian reptiles, the teeth exhibit roots of varying depths that sit in a groove within the tooth-bearing bones. This condition occurs in *Youngina capensis* (SAM K10777), *Prolacerta broomi* (BP/1 2675), *Azendohsaurus madagaskarensis* (UA 7-16-99-612), *Kuehneosaurus latus* (AMNH FARB 7775), *Tanystropheus longobardicus* (MCSN BES SC 265), and *Shinisaurus crocodilurus* (Conrad, 2004). These taxa all exhibit a condition that would variably be considered pleurodonty, thecodont, subthecodonty, or ankylothecodonty (e.g., Chatterjee, 1974; Dilkes, 1998). By contrast, the teeth in taxa considered acrodont (e.g., *Sphenodon punctatum*, *Uromastyx aegyptia*, Robinson, 1976), the teeth do not have roots at all but are directly attached to apical portion of the tooth-bearing bones. Fraser and Shelton (1988) employed X-rays to examine implantation in a number of Triassic rhynchocephalians, noting that both rooted and superficial attachment co-occurred in some taxa (e.g., *Diphydontosaurus avonis*). Future iterations of this character should incorporate some measure of the relative length/depth of the rooting, although this would require data on dental variation within many diapsid species.

CHARACTER 94: Marginal dentition, lingual surface: (0) teeth walled by minimal lingual wall, (1) no lingual wall (=pleurodonty).

Examples of past usage: Merck (1997:239), Dilkes (1998:55), Müller (2004:38), Pritchard et al. (2015:95), Nesbitt et al. (in press:95).

Justification/Ontology: In a number of early diapsid and saurian taxa with rooted teeth, the lingual aspect of tooth-bearing elements exhibit a small, anteroposteriorly running shelf that borders the basalmost portion of the root. A structure like this is apparent in *Youngina capensis* (SAM K10777), possibly *Kuehneosaurus latus* (AMNH FARB 9974), and *Prolacerta broomi* (BP/1 2675). Zaher and Rieppel (1999:Fig. 1C) illustrated a similar shelf extending apically in a mosasaur jaw. The absence of this shelf exposes the entire medial/lingual aspect of the tooth root, as in many pleurodonty lepidosaurs (e.g., *Gephyrosaurus bridensis*, Evans, 1980; *Shinisaurus crocodilurus*, Conrad, 2006).

CHARACTER 95: Marginal dentition, lingual surface: (0) teeth walled by minimal lingual wall only, (1) interdental plates are present.

Examples of past usage: Merck (1997:238), Nesbitt (2011), Pritchard et al. (2015:96), Nesbitt et al. (in press:96).

Justification/Ontology: In most early reptiles, teeth are situated within some sort of alveolar groove but there is no septation dividing the positions for the alveoli (e.g., *Youngina capensis*, SAM K10777; *Petrolacosaurus kansensis*, Reisz, 1981; possibly *Kuehneosaurus latus*, AMNH FARB 9974). By contrast, some derived saurian taxa exhibit distinct bony ridges that divide tooth positions from one another. These remain intact during tooth replacement events (pers. obs.). Zaher and Rieppel (1999) noted such structures in both modern and fossil snakes, although Luan et al. (2009) questioned the comparability of the interdental ridges in those taxa with the alveolar bone forming interdental ridges in modern Crocodylia, taxa universally regarded as thecodont. LeBlanc and Reisz (2013) drew attention to the histological differences between bony attachment tissues in early tetrapods, suggesting that the homology of many tissues was open to question.

In light of the need for histological determination of the exact tissues present in early diapsids, I chose to retain the term “interdental plate” to describe any distinct bony tissue that separates the individual alveoli of a taxon with rooted teeth. Among archosauromorphs, these usually manifest as distinct ridges between tooth positions that are expanded into flat plates in lingual view. This condition is best seen in *Tanystropheus longobardicus* (MCSN BES SC 265, see Fig. 11), *Erythrosuchus africanus* (NHMUK R3592), *Azendohsaurus madagaskarensis* (UA 8-29-97-160), and *Euparkeria capensis* (Senter, 2003). In *Prolacerta broomi* (UCMP 37151; BP/1 2675), *Boreopricea funerea* (PIN 3708/2), and *Macrocnemus bassanii* (PIMUZ T/2472), this character is quite difficult to code; all specimens of these taxa exhibit some tissues in this region, but the separation of this into interdental ossifications is not easily apparent. These should be a priority for histological sampling. Of them, only *Prolacerta broomi* is coded as “1,” owing to slight thickenings in the tissue apparent between tooth positions in UCMP 37151.

CHARACTER 96: Marginal dentition, rooting: (0) tooth crowns are not attached to dentigerous bones, (1) teeth ankylosed to tooth-bearing element.

Examples of past usage: Benton (1985:N3), Merck (1997:235), Dilkes (1998), Pritchard et al. (2015:97), Nesbitt et al. (in press:97).

Justification/Ontology: Mineralized tissues are often present as a collar of bony tissue surrounding part or all of the root of a tooth, linking it to the tooth-bearing element. As noted by LeBlanc and Reisz (2013), this tissue has long been dubbed bone of attachment. Histologically, Luan et al. (2009) described this mineralization in mosasaurs as a combination of bony cementum and mineralized periodontal ligament. LeBlanc and Reisz (2013) emphasized that “bone of attachment” as a term required further contextualization, especially considering its apparent widespread presence in early amniotes. As described by LeBlanc and Reisz (2015), the tooth attachment in captorhinomorphs reptiles involves a type of alveolar bone that ankyloses the teeth into the jaw and breaks down during replacement events. I elect to code this tissue as present if a collar of bone is noted around the root of a tooth, linking it to a tooth-bearing bone.

Among early diapsids, some degree of ankylosis of the tooth occurs in *Youngina capensis* (SAM K10777), *Prolacerta broomi* (UCMP 37151), *Azendohsaurus madagaskarensis* (UA 9-9-98-560, see fig. 4A), *Mesosuchus browni* (SAM K6536), *Trilophosaurus buettneri* (TMM 31025-5), and "Chasmatosaurus" *yuani* (casts of IVPP 36315). Among Archosauria, ankylosis of the tooth into its alveolus is only known in silesaurid dinosauromorphs (Nesbitt, 2011). Ankylosing tissues are not apparent in *Tanystropheus longobardicus* (MCSN BES SC 265, see fig. 11), *Erythrosuchus africanus* (NHMUK R3592), and *Euparkeria capensis* (Senter, 2003).

CHARACTER 97: Marginal dentition, tooth shape at crown base: (0) circular, (1) labiolingually compressed, (2) labiolingually wider than mesiodistally long.

Examples of past usage: Benton (1985:I3), Jalil (1997:63), Merck (1997:234), Dilkes (1998:59), Pritchard et al. (2015:98), Nesbitt et al. (in press:98).

Justification/Ontology: Teeth crowns in most early diapsids and saurians are roughly circular at their bases. This condition is apparent in *Protorosaurus speneri* (USNM 442453), some specimens of *Prolacerta broomi* (UCMP 37151), *Mesosuchus browni* (SAM K6536), and *Gephyrosaurus bridensis* (Evans, 1980). Subcircular crowns are also present in the anteriormost teeth of *Azendohsaurus madagaskarensis* (UA 9-9-98-560) and "Chasmatosaurus" *yuani* (IVPP V/4067), although the remainder of their teeth are labiolingually compressed.

Other early saurians exhibit labiolingually compressed teeth that are substantially longer mesiodistally than they are wide labiolingually. This condition occurs in *Macrocnemus bassanii* (PIMUZ T/4822), *Boreopricea funerea* (BP/1 3708/2), some specimens of *Prolacerta broomi* (BP/1 5375), *Proterosuchus fergusi* (BP/1 3393), and nearly all Triassic archosauriforms (e.g., Edmund, 1969). In a small subset of saurian reptiles, the opposite condition occurs, in which the teeth are much broader transversely. This condition is evident in both species of *Trilophosaurus* (TMM 31025-140, NMMNH P41400, TTU P10411, see fig. 9B) and *Coelodontognathus ricovi* (PIN 4173/127).

CHARACTER 98: Palatal dentition, morphology: (0) small, button-like teeth, (1) small, conical teeth.

Examples of past usage: Pritchard et al. (2015:99), Nesbitt et al. (in press:99).

Justification/Ontology: No comments.

CHARACTER 99: Marginal dentition, procumbency: (0) anteriormost marginal teeth have similar apicobasal orientation to posterior teeth, (1) anteriormost teeth are procumbent.

Examples of past usage: Merck (1997:247), Müller (2004:117), Pritchard et al. (2015:100), Nesbitt et al. (in press:100).

Justification/Ontology: Broadly among early reptiles and diapsids, the anteriormost teeth of the jaws are similar in apicobasal orientation to the other teeth. Initial reconstructions of the jaws in *Langobardisaurus pandolfii* (Renesto, 1994b) suggested that the teeth were procumbent, although Saller et al. (2013) suggested that the "premaxillary teeth" were actually anteroventral striations on the surface of an edentulous premaxilla (see character 1). Procumbent teeth, such as those described, above can be found in a number of sauropterygians clades (Rieppel, 1994).

CHARACTER 100: Presacral vertebrae, shape of anterior articular surface: (0) planar, (1) concave.

Examples of past usage: Müller (2004:41),Pritchard et al. (2015:101), Nesbitt et al. (in press:101).

Justification/Ontology: No comments.

CHARACTER 101: Presacral vertebrae, shape of posterior articular surface: (0) planar, (1) concave, (2) convex.

Examples of past usage: Benton (1985:Y17), Gauthier et al (1988a:184), Merck (1997:258), Müller (2004:41), Pritchard et al. (2015:102), Nesbitt et al. (in press:102).

Justification/Ontology: The posterior articular surface in most early diapsids exhibits some degree of concavity. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Protorosaurus speneri* (Gottmann-Quesada and Sander, 2009), *Proterosuchus fergusi* (BP/1 3393), *Sphenodon punctatum* (Hoffstetter and Gasc, 1969), and *Gephyrosaurus bridensis* (Evans, 1981). By contrast, the posterior articular surface of some saurian taxa is convex, forming a stronger bony articulation with anterior surface of the next vertebra. This occurs in squamates (Conrad, 2006; Gauthier et al., 2012), a subset of Tanystropheidae (Pritchard et al., 2015), and in anterior vertebrae of *Trilophosaurus buettneri* (TMM 31025-140). In the latter taxon, some vertebrae exhibit an amphicoelous condition instead, but at this point this sort of serial variation is not accounted for in this study.

CHARACTER 102: Presacral vertebrae, development of posterior articular surface convexity: (0) moderate, (1) ball-like.

Examples of past usage:

Justification/Ontology: Among taxa with procoelous vertebrae, the morphology of the posterior condyle is quite variable. Squamates with procoelous vertebrae exhibit smoothly curved posterior condyles that are roughly hemispherical (e.g., Hoffstetter and Gasc, 1969). The shape is quite similar in *Tanytrachelos* (AMNH FARB 7206), tanystropheid vertebrae from the Hayden Quarry (Pritchard et al., 2015), and *Langobardisaurus pandolfii* (MSCNB 2883). This morphology contrasts with that in *Trilophosaurus buettneri* (TMM 31025-140) and *Spinosuchus caseanus* (Spielmann et al., 2008), in which procoelous centra exhibit posterior convexities with a flattened posterior "tip."

CHARACTER 103: Anterior cervical ribs, shaft shape: (0) triangular in lateral view, tapering rapidly; (1) elongate and splint-like in lateral view, ribs tapering gradually.

Examples of past usage: Benton (1985:C6), Benton and Allen (1997:22), Jalil (1997:36 & 41), Merck (1997:292), Dilkes (1998:77), Müller (2004:102), Senter (2004:38), Pritchard et al. (2015:104), Nesbitt et al. (in press:104).

Justification/Ontology: The ribs in the necks of early reptiles and early diapsids are typically robust elements. This morphology occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Petrolacosaurus kansensis* (Reisz, 1981), *Claudiosaurus germaini* (Carroll, 1981), *Hovasaurus boulei* (Currie, 1981), *Sphenodon punctatum* (Hoffstetter and Gasc, 1969), and *Erythrosuchus africanus* (NMQR 3765). Within early Archosauromorpha, nearly all taxa exhibit proportionally more elongate and slender cervical ribs. This occurs in *Protorosaurus speneri* (SMNS cast of WMsN P47361, see fig. 12A), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus fergusi* (BP/1 4016), *Macrocnemus fuyuanensis* (GMPKU P3001), and *Tanystropheus longobardicus* (PIMUZ T/1270, see fig. 12B). Although the rib shafts are incomplete in *Mesosuchus browni* (SAM K6046), they definitely appear oriented much as in other long-ribbed archosauromorphs (noted by Dilkes, 1998).

Low and elongate cervical ribs have long been considered a synapomorphy of Prolacertiformes or Protorosauria (e.g., Gauthier, 1984; Benton and Allen, 1997; Jalil, 1997). However, recent restudy of archosauromorph phylogeny suggests that the trait is far more widespread. Dilkes (1998) recovered the character as a synapomorphy of Archosauromorpha. I note that, among archosauromorphs, the relative elongation and slenderness of the cervical ribs appears coincident with elongate and slender post-axial cervical centra.

CHARACTER 104: Anterior post-axial cervical ribs, anterior process: (0) absent, (1) present.

Examples of past usage: Benton (1985:C6), Jalil (1997:37), Merck (1997:291), Dilkes (1998:78), Müller (2004:48), Pritchard et al. (2015:105), Nesbitt et al. (in press:105).

Justification/Ontology: In most early reptiles and early diapsids, cervical ribs consist of an elongate shaft attached to a process for the costal facets. This condition occurs in *Captorhinus laticeps* (Dilkes and Reisz, 1986), *Petrolacosaurus kansensis* (Reisz, 1981), *Hovasaurus boulei* (Currie, 1981), *Sphenodon punctatum*, and known squamate taxa (Hoffstetter and Gasc, 1969). Throughout Archosauromorpha, the cervical ribs bear a small anterior process that extends anteriorly from the junction between the costal articulations and the primary shaft of the rib. This can be seen in *Protorosaurus speneri* (SMNS cast of WMsN 47361, see fig. 12A), *Prolacerta broomi* (BP/1 2675), *Proterosuchus alexanderi* (NMQR 1484), *Erythrosuchus africanus* (NMQR 3765), and Triassic Archosauria (e.g., *Batrachotomus kupferzellensis,* Gower and Schoch, 2009). This process also appears present in *Claudiosaurus germaini* (Carroll, 1981).

CHARACTER 105: Intercentra in the post-axial cervical column: (0) present, (1) absent.

Examples of past usage: Benton (1985:L5), Merck (1997:278), Dilkes (1998:79), Müller (2004:43), Pritchard et al. (2015:106), Nesbitt et al. (in press:106).

Justification/Ontology: Intercentra are present between the cervical centra among early reptiles and diapsids. The structures are evident in *Captorhinus laticeps* (Dilkes and Reisz, 1986), *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), *Claudiosaurus germaini* (Carroll, 1981), and *Proterosuchus fergusi* (Cruickshank, 1972; BP/1 4016. These structures are also present in some portion of the cervical column in *Youngina capensis* (Gow, 1975) and *Acerosodontosaurus piveteaui* (Curie, 1980). In modern taxa, there are cervical intercentra in *Sphenodon punctatum* and many modern squamates (Hoffstetter and Gasc, 1969). Cervical intercentra appear to be absent in the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Coelurosauravus elivensis* (MNHN IP 1908-11), *Protorosaurus speneri* (USNM 442453), *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Prolacerta broomi* (UCMP 37151), and *Erythrosuchus africanus* (Gower, 2003).

CHARACTER 106: Anterior post-axial cervical vertebrae, shape of anterior articular surface: (0) subcircular, roughly equivalent in dorsoventral height and transverse width; (1) compressed, with a greater transverse width than dorsoventral height.

Examples of past usage: Pritchard et al. (2015:107), Nesbitt et al. (in press:107).

Justification/Ontology: The primary articular facets in cervical vertebrae in nearly all reptiles and diapsids are roughly circular, such that they are roughly equivalent in dorsoventral height and transverse breadth. Examples include *Captorhinus laticeps* (Dilkes and Reisz, 1986), *Araeoscelis gracilis* (Vaughn, 1955), *Youngina capensis* (BP/1 3859), *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Tanystropheus longobardicus* (PIMUZ T/2819), *Proterosuchus alexanderi* (NMQR 1484), *Erythrosuchus africanus* (NHMUK R3592), *Batrachotomus* (Gower and Schoch, 2009), and most archosaurs (e.g., Hoffstetter and Gasc, 1969). By contrast, the cervical articular facets are transversely broader than they are dorsoventrally tall in a small group of archosauromorphs. This occurs in *Tanytrachelos ahynis* (AMNH FARB 7206), a tanystropheid from the Hayden Quarry (Pritchard et al., 2015), and possibly *Langobardisaurus pandolfii* (MCSNB 2883).

CHARACTER 107: Cervical vertebrae, ventral keel: (0) present, (1) absent.

Examples of past usage: Merck (1997:275), Pritchard et al. (2015:108), Nesbitt et al. (in press:108).

Justification/Ontology: The ventral surface of the cervical centra in most early and modern Diapsida is marked by a thin ridge of bone that usually runs the full length of the centrum. This keel occurs in *Araeoscelis gracilis* (Vaughn, 1955), *Trilophosaurus buettneri* (TMM 31025-140), *Tanystropheus longobardicus* (MFSN 31579), *Prolacerta broomi* (BP/1 2675), *Erythrosuchus africanus* (Gower, 2003), and ubiquitously in Archosauria (Nesbitt, 2011). These are also common in modern Lepidosauria (Hoffstetter and Gasc, 1969) and in some fossil taxa (e.g., *Clevosaurus hudsoni*, Fraser, 1988).

A mid-ventral keel is absent in *Captorhinus laticeps* (Dilkes and Reisz, 1986) and *Proterosuchus alexanderi* (NMQR 1484). Fox and Bowman (1966) reported midventral keels in captorhinomorphs, noting that the centrum is beveled ventrolaterally. Dilkes and Reisz (1986) noted that this is not the same as the midline ridge in other taxa. Dilkes (1998) reported that no cervical keels were present in *Mesosuchus browni*, although the cortical bone in these specimens is heavily weathered (SAM K6536). Keels also appear absent in *Gephyrosaurus bridensis* (Evans, 1981).

CHARACTER 108: Anterior post-axial cervical vertebrae, shape of ventral surface excluding keel: (0) ventrally rounded, (1) flattened.

Examples of past usage: Pritchard et al. (2015:109), Nesbitt et al. (in press:109).

Justification/Ontology: The ventral surfaces of the cervical centra are ventrally convex in cross-section in most early reptiles and Permo-Triassic diapsids. Convex, rounded ventral surfaces occur in *Captorhinus laticeps* (Dilkes and Reisz, 1986), *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Proterosuchus fergusi* (BP/1 3393), *Erythrosuchus africanus* (Gower, 2003), *Gephyrosaurus bridensis* (Evans, 1980), and most modern reptiles (e.g., Hoffstetter and Gasc, 1969). In contrast, the ventral surface of the cervical centra in *Tanystropheus longobardicus* (MFSN 31579), *Tanystropheus conspicuus* (Wild, 1973), *Tanytrachelos ahynis* (AMNH FARB 7206), and *Langobardisaurus pandolfii* (MCSNB 2883). Our definition of this character specifically excludes the midline keel, which represents an interruption of the primary ventral surface.

CHARACTER 109: Cervical vertebrae, number of costal facets: (0) one, (1) two.

Examples of past usage: Gauthier et al (1988a:86), Laurin (1991:F4), Jalil (1997:29), Merck (1997:287), Pritchard et al. (2015:110), Nesbitt et al. (in press:110).

Justification/Ontology: Ancestrally, diapsid reptiles exhibit two costal facets within the cervical column. This condition is best known in *Araeoscelis gracilis* (Vaughn, 1955). By contrast, there is a single costal facet in *Youngina capensis* (Gow, 1975), *Gephyrosaurus bridensis* (Evans, 1980), and modern lepidosaurs (e.g., Conrad, 2006). Double costal facets also occur within most early archosauromorphs (*Protorosaurus speneri*, USNM 442453; *Trilophosaurus buettneri*, TMM 31025-140; *Azendohsaurus madagaskarensis* (UA 7-20-99-653).

CHARACTER 110: Anterior post-axial cervical vertebrae, position of diapophysis (or dorsal margin of synapophyses): (0) at or near dorsoventral level of pedicles; (1) further ventrally, near the dorsoventral midpoint of the centrum.

Examples of past usage: Pritchard et al. (2015:111), Nesbitt et al. (in press:111).

Justification/Ontology: Among early diapsids such as *Araeoscelis gracilis* (Vaughn, 1955), the costal facets are positioned far at the anteroventral margin of the cervical vertebrae. A similar condition is present throughout early archosauromorphs such as *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), and *Proterosuchus fergusi* (BP/1 3393). By contrast, the costal facets in *Youngina capensis* (BP/1 3859), *Hovasaurus boulei* (Currie, 1981), *Icarosaurus siefkeri* (AMNH FARB 2101), *Erythrosuchus africanus* (Gower, 2003), *Gephyrosaurus bridensis* (Evans, 1981), and modern lepidosaurs (Hoffstetter and Gasc, 1969) are much more dorsally positioned on the centra. It should be noted that this condition may be linked closely to the relative length of the centra, with longer centra co-occurring with anteroventrally placed facets.

CHARACTER 111: Anterior post-axial cervical vertebrae, relative location of costal facets: (0) distinctly offset from one another, (1) very closely appressed to one another with little or no finished bone separation.

Examples of past usage: Pritchard et al. (2015:112), Nesbitt et al. (in press:112).

Justification/Ontology: In early diapsid taxa with non-confluent costal facets in the cervical region, the facets are very closely appressed in most early archosauromorphs. This condition occurs in *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Prolacerta broomi* (BP/1 2675), *Trilophosaurus buettneri* (TMM 31025-140), and *Proterosuchus fergusi* (BP/1 3393). In contrast, the facets are well offset in *Kuehneosaurus latus* (AMNH FARB 7791), *Icarosaurus siefkeri* (Colbert, 1970), *Erythrosuchus africanus* (NHMUK R3592), and *Batrachotomus kupferzellensis* (Gower and Schoch, 2009).

I note that closely appressed cervical costal facets are nearly universally found in early archosauromorph taxa with elongated cervical centra (e.g., *Prolacerta broomi*). The taxa that possess this character state with the shortest centra include *Boreopricea funerea* (PIN 3708/1) and vertebrae referred to *Archosaurus rossicus* (PIN 1100/66). For the time being, I retain these as separate characters, but with the caveat that serial variation in the early diapsid vertebral column should be a priority for anatomists.

CHARACTER 112: Anterior post-axial cervical vertebrae, shape of neural spine: base: (0) elongate, subequal in length to the neural arch; (1) short, spine restricted to posterior half of neural arch.

Examples of past usage: Benton and Allen (1997:20), Pritchard et al. (2015:113), Nesbitt et al. (in press:113).

Justification/Ontology: No comments.

CHARACTER 113: Anterior post-axial cervical vertebrae, neural spine shape in cross-section: (0) transversely narrow, (1) elliptical or circular.

Examples of past usage: Pritchard et al. (2015:114), Nesbitt et al. (in press:114).

Justification/Ontology: No comments.

CHARACTER 114: Anterior post-axial cervical vertebrae, shape of anterior margin of neural spine in lateral view: (0) straight and linear, (1) anterodorsal process present forming an anterior notch.

Examples of past usage: Dilkes (1998:134), Senter (2004:30), Pritchard et al. (2015:115), Nesbitt et al. (in press:115).

Justification/Ontology: No comments.

CHARACTER 115: Anterior post-axial cervical vertebrae, anterior margin of neural spine, direction of inclination: (0) posterodorsal, (1) anterodorsal.

Examples of past usage: Pritchard et al. (2015:116), Nesbitt et al. (in press:116).

Justification/Ontology: In most early diapsids and lepidosauromorphs, the anterior cervical neural spines exhibit a posterodorsal inclination. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 33859), *Sphenodon punctatum* (Hoffstetter and Gasc, 1969) and most extant squamates (Hoffstetter and Gasc, 1969). By contrast, the equivalent spines are anterodorsally inclined in most early archosauromorphs, such as *Protorosaurus speneri* (USNM 442453), *Macrocnemus bassanii* (PIMUZ T/4822), *Mesosuchus* *browni* (SAM K6536), *Trilophosaurus buettneri* (TMM 31025-140), and *Proterosuchus alexanderi* (NMQR 1484).

CHARACTER 116: Anterior cervical vertebra, transverse width of dorsal tip of neural spine: (0) transversely slender, (1) expanded transversely.

Examples of past usage: Dilkes (1998), Renesto et al. (2010:7), Pritchard et al. (2015:117), Nesbitt et al. (in press:117).

Justification/Ontology: No comments.

CHARACTER 117: Mid-cervical vertebrae, dorsoventral depression of neural spines at anteroposterior midpoint: (0) absent, spines are roughly equal in dorsoventral height throughout anteroposterior length; (1) present, spines are dorsoventrally depressed at their anteroposterior midpoints, leaving them little more than midline dorsal ridges.

Examples of past usage: Pritchard et al. (2015:118), Nesbitt et al. (in press:118).

Justification/Ontology: In most early reptiles and Permo-Triassic diapsids, the dorsal margin of the mid-cervical neural spines are roughly straight or subtly convex dorsally. This shape is evident in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (SAM K7710), *Protorosaurus speneri* (SMNS cast of WMsN P47361, see fig. 12A), *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (UA 8-28-98-306), and *Proterosuchus alexanderi* (NMQR 1484). This is also the condition in most modern reptiles and Lepidosauria (e.g., Hoffstetter and Gasc, 1969; Evans, 1981).

In contrast, the cervical neural spines in the mid-cervical region of *Tanystropheus longobardicus* (PIMUZ T/1270, see fig. 12B, T/2819) and in vertebrae referred to *Tanystropheus conspicuus* (Wild, 1973) are dorsoventrally depressed near the anteroposterior midpoint. At this level, the spines are so short as to be roughly continuous with the dorsal margin of the neural canal. Pritchard et al. (2015) reported this condition in *Amotosaurus rotfeldensis*, based on illustrations in Rieppel and Fraser (2006;fig. 5). However, study of SMNS 54783 suggests that the dorsum of the spine was straight in *Amotosaurus*.

CHARACTER 118: Cervical vertebra, dorsal surface of postzygapophyses: (0) smooth and rounded, (1) posteriorly pointed projections (epipophyses) present.

Examples of past usage: Pritchard et al. (2015:119), Nesbitt et al. (in press:119).

Justification/Ontology: The dorsal surfaces of the postzygapophyses in early diapsids are relatively smooth, with a subtle dorsal convexity. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), *Youngina capensis* (BP/1 3859; possibly SAM K7710), and *Hovasaurus boulei* (Currie, 1981). Among early saurians, this condition occurs in *Protorosaurus speneri* (SMNS cast of WMsN 47361, see fig. 12A, USNM 442453), *Prolacerta broomi* (UCMP 37151; NMQR 3763), and *Proterosuchus fergusi* (BP/1 3393). By contrast, small and posterodorsally pointed projections are situated on the dorsal portions of the postzygapophyses. This condition occurs in *Mesosuchus browni* (SAM K5882), *Tanystropheus longobardicus* (PIMUZ T/2819), *Trilophosaurus buettneri* (TMM 31025-140, see fig. 13B), and *Teraterpeton hrynewichorum* (Sues, 2003).

I note that some taxa exhibit strongly domed postzygapophyses (e.g., *Prolacerta broomi*, BP/1 2675; *Azendohsaurus madagaskarensis*, UA 8-28-98-306). This condition may be a homolog of the projecting epipophyses in some other archosauromorphs, but further study is needed to understand the development of this feature.

CHARACTER 119: Anterior dorsal vertebrae, position of parapophysis (or ventral margin of dorsal synapophysis): (0) lateral surface of centrum, (1) entirely on neural arch.

Examples of past usage: Pritchard et al. (2015:120), Nesbitt et al. (in press:120).

Justification/Ontology: In most early diapsids and saurians, the lowermost costal articulation on anterior dorsal vertebrae is positioned on the vertebral centrum. This may be seen in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Boreopricea funerea* (PIN 3708/1), and *Erythrosuchus africanus* (Gower, 2003). A more dorsally positioned parapophyseal articulation occurs in rhynchosaurs, such as *Mesosuchus browni* (SAM K6046) and *Hyperodapedon gordoni* (Benton, 1983).

CHARACTER 120: Posterior dorsal vertebra, position of parapophysis (or ventral margin of dorsal synapophysis) in trunk vertebrae: (0) lateral surface of centrum, (1) entirely on neural arch.

Examples of past usage: Merck (1997:313), Pritchard et al. (2015:121), Nesbitt et al. (in press:121).

Justification/Ontology: In most early diapsids and saurians, the lower portion of the costal articulation in the posterior dorsal vertebrae is positioned partially on the centrum. In *Mesosuchus browni*, the parapophysis is partially positioned on the centrum (SAM K6046). In contrast, the parapophysis is positioned further dorsally on the neural arch in some other rhynchosaurs (e.g., *Hyperodapedon gordoni*, Benton, 1983).

CHARACTER 121: Anterior dorsal vertebra, number of pectoral costal facets: (0) one (holocephaly), (1) two (dichocephaly), (2) three (tricephaly).

Examples of past usage: Laurin (1991:D3), Jalil (1997:19), Merck (1997:310), Dilkes (1998:86), Müller (2004:104), Pritchard et al. (2015:122), Nesbitt et al. (in press:122).

Justification/Ontology: Diapsids ancestrally exhibit a dorsoventrally tall but confluent costal facet in the anterior dorsal vertebrae. This condition occurs in *Captorhinus laticeps* (Dilkes and Reisz, 1986) *Petrolacosaurus kansensis* (Reisz, 1981), and *Youngina capensis* (BP/1 3859). A similar construction occurs in Lepidosauromorpha (Hoffstetter and Gasc, 1969) and some Rhynchosauria (e.g., *Mesosuchus browni*, Dilkes, 1998; *Hyperodapedon gordoni*, Benton, 1983). In most early Archosauromorpha, there are two costal facets on anterior dorsal vertebrae. This condition occurs in *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Tanystropheus longobardicus* (MCSN BES SC 265), and *Azendohsaurus madagaskarensis* (Nesbitt et al., in press).

In a small number of early archosauromorphs, the anteriormost dorsal vertebrae exhibit an additional costal facet. This condition occurs in *Erythrosuchus africanus* (Gower, 2003), *Guchengosuchus shiguaiensis* (IVPP V8808), and possibly *Euparkeria capensis* (Ewer, 1965). Borsuk-Bialynicka and Evans (2009) reported tricephalous ribs from the Lower Triassic Czatkowice Quarry of Poland, which they referred to the “protorosaur” *Czatkowiella harae*.

CHARACTER 122: Posterior dorsal vertebrae, costal facets: (0) single rib facet, (1) 'inverse-L rib facet (suggesting partial confluence of diapophysis and parapophysis), (1) double rib facet.

Examples of past usage: Dilkes (1998:86), Senter (2004:39), Pritchard et al. (2015:123), Nesbitt et al. (in press:123).

Justification/Ontology: No comments.

CHARACTER 123: Posterior dorsal vertebra, ribs and vertebrae: (0) unfused, (1) fused.

Examples of past usage: Benton and Allen (1997:25), Jalil (1997:57), Merck (1997:309), Dilkes (1998:137), Renesto et al. (2010:11), Pritchard et al. (2015:124), Nesbitt et al. (in press:124).

Justification/Ontology: In many early reptiles and most early diapsids, the ribs associated with the posteriormost dorsal vertebrae do not co-ossify to their respective costal articulations. This condition occurs in *Captorhinus laticeps* (Dilkes and Reisz, 1986), *Araeoscelis gracilis* (Reisz et al., 1984), *Thadeosaurus colcanapi*, and *Claudiosaurus germaini* (Carroll, 1981). Among Sauria, there is no apparent co-ossification in *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Trilophosaurus buettneri* (TMM 31025-140), *Macrocnemus bassanii* (PIMUZ T/4822), *Boreopricea funerea* (PIN 3708/1, and *Euparkeria capensis* (Ewer, 1965). No co-ossified ribs are known in described materials of *Gephyrosaurus bridensis* (Evans, 1980) and *Clevosaurus hudsoni* (Fraser, 1988).

Among Sauria, the posterior dorsal vertebrae exhibit co-ossified ribs in a number of groups. Examples of this include *Tanystropheus longobardicus* (Wild, 1973), *Azendohsaurus madagaskarensis* (UA 7-20-99-654), *Proterosuchus alexanderi* (NMQR 1484), and possibly *Erythrosuchus africanus* (NMQR 3765). Hoffstetter and Gasc (1969) note occasional fusion of the posteriormost ribs with dorsal vertebrae in *Sphenodon punctatum* (it is coded as "1" here).

A number of modern squamate taxa also exhibit a differentiated posterior trunk region with either fused ribs or the absence of ribs (e.g., *Shinisaurus crocodilurus*, *Ctenosaura pectinata*, Hoffstetter and Gasc, 1969). Hoffstetter and Gasc (1969) note that a true lumber region lack ossified costal elements, so we elect to describe our anatomical understanding of this region in fossil taxa, rather than employ the term "lumbar."

CHARACTER 124: Dorsal vertebrae, neural spine, dorsal portion: (0) similar width as the more distal portion of the neural spine, (1) expanded transversely into a flattened tip (=spine table).

Examples of past usage: Merck (1997:302), Pritchard et al. (2015:125), Nesbitt et al. (in press:125).

Justification/Ontology: The dorsal tips of the neural spines in the dorsal region do not expand transversely in most early diapsids and some early saurians. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (SAM K7710), *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Trilophosaurus buettneri* (TMM 31025-140), and most lepidosaurs (Hoffstetter and Gasc, 1969). By contrast, the neural spines are transversely expanded in a number of early saurian taxa. This occurs in *Kuehneosaurus latus* (AMNH FARB 7794), *Proterosuchus* spp. (NMQR 1484; Cruickshank, 1972; Ezcurra and Butler, 2015), *Macrocnemus bassanii* (PIMUZ T/4822), *Tanystropheus longobardicus* (MCSN BES SC 265; Wild, 1973), *Erythrosuchus africanus* (Gower, 2003), and *Euparkeria capensis* (Ewer, 1965).

CHARACTER 125: Dorsal vertebra, breadth of neural spine expansion: (0) little lateral expansion relative to the neural spine base, (1) transversely broad, much wider than neural spine base.

Examples of past usage: Pritchard et al. (2015:126), Nesbitt et al. (in press:126).

Justification/Ontology: Among those taxa with transversely broadened dorsal neural spines, there is substantial variation in the relative breadth of the spine tip. In most taxa the expansion is limited, little broader than the ventral base of the spine. This condition occurs in *Kuehneosaurus latus* (AMNH FARB 7794), *Macrocnemus bassanii* (PIMUZ T/4822), and *Tanystropheus longobardicus* (PIMUZ T/1277). By contrast, the spine tip is broadened into a dorsally flattened table in the vertebrae of the Hayden Quarry tanystropheid (GR 275) and *Proterosuchus* sp. (Ezcurra et al., 2014).

This character is complicated by the presence of mammillary processes, small ovoid structures positioned lateral to tips of the dorsal neural spines in some reptiles. These structures have been described in *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), and *Prolacerta broomi* (Gow, 1975). Ezcurra and Butler (2015) noted lateral expansions in the dorsal spines of some *Proterosuchus* specimens as well. However, I note that the rounded structures in basal diapsids (e.g., *Araeoscelis gracilis*, MCZ 2043) appear quite different from the purported mammillary structures described for *Prolacerta broomi* (BP/1 2676) and *Proterosuchus alexanderi* (NMQR 1484), which more closely resemble lateral outgrowths of the neural spines. Further study is needed to fully assess the homologies of these structures, but I consider the expansions in *Prolacerta*, *Proterosuchus* and other archosauromorphs to be non-homologous with the rounded structures present in Araeoscelida.

CHARACTER 126: Dorsal vertebra, texturing on dorsum of neural spine expansion: (0) marked by irregular rugosities, (1) marked by transverse striations.

Examples of past usage: Merck (1997:303), Pritchard et al. (2015:127), Nesbitt et al. (in press:127).

Justification/Ontology: No comments.

CHARACTER 127: Dorsal vertebrae, intercentra: (0) present, (1) absent.

Examples of past usage: Benton (1985:L5 & Y19), Gauthier et al. (1988a:83), Benton and Allen (1997:24), Jalil (1997:67), Merck (1997:297), Dilkes (1998:80), Müller (2004:42), Pritchard et al. (2015:128), Nesbitt et al. (in press:128).

Justification/Ontology: Intercentra are present throughout the trunk region of early reptiles and early diapsids, and they are quite common in early saurians as well. Trunk intercentra occur in *Captorhinus laticeps* (Dilkes and Reisz, 1986), *Araeoscelis gracilis* (Vaughn, 1955), *Youngina capensis* (AMNH FARB 5561), *Thadeosaurus colcanapi* (Carroll, 1981), *Claudiosaurus germaini* (Carroll, 1981), *Trilophosaurus buettneri* (TMM 31025-140), *Prolacerta broomi* (BP/1 2676), *Proterosuchus alexander* (NMQR 1484), and *Erythrosuchus africanus* (Gower, 2003). Nesbitt (2011) notes that some specimens of *Euparkeria* exhibit intercentra, but that these occur "sporadically throughout the presacral column," (Nesbitt, 2011:108). He likewise cautions that early archosauriforms may bear intercentra in the absence of beveling of the dorsal centra. Among lepidosaurs, examples of trunk intercentra are known in the trunk region of *Sphenodon punctatum* (Hoffstetter and Gasc, 1969) and the Jurassic rhynchocephalians *Pleurosaurus goldfussi* and *Kallimodon cerinensis* (Cocude-Michel, 1968).

Ossified intercentra are unknown in the trunk regions in a number of distinct early diapsid groups. They are not present in *Drepanosaurus unguicaudatus* (MCSNB 5728), *Macrocnemus bassanii* (Peyer, 1937), *Tanystropheus longobardicus* (PIMUZ and GMPKU), *Azendohsaurus madagaskarensis* (Nesbitt et al., in press), and derived archosaurs (e.g., Nesbitt, 2011). Trunk intercentra have also not been reported in early rhynchocephalians (e.g., *Diphydontosaurus* sp., Renesto, 1995), although the incomplete, disarticulated nature of their remains makes such determinations problematic. Squamates lack trunk intercentra entirely, and this trait is often noted as a synapomorphy for the group (e.g., Gauthier et al., 1988).

CHARACTER 128: Dorsal vertebrae, height of neural spines: (0) tall, greater in dorsoventral height than anteroposterior length; (1) long and low, lesser in dorsoventral height than anteroposterior length.

Examples of past usage: Laurin (1991:C1), Dilkes (1998:85), Senter (2004:32), Pritchard et al. (2015:129), Nesbitt et al. (in press:129).

Justification/Ontology: The dorsal neural spines in most diapsid reptiles are anteroposteriorly elongate and dorsoventrally tall. Although the shape changes from the anterior trunk to posterior trunk regions in many taxa (e.g., *Azendohsaurus madagaskarensis*, Nesbitt et al., in press), the height/length ratio of the spine remains roughly consistent throughout the column. Vertebrae with such a ratio occur in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859; Currie, 1981b), *Hovasaurus boulei* (Currie, 1981a), *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Mesosuchus browni* (SAM K6536), *Trilophosaurus buettneri* (TMM 31025-140), and "*Chasmatosaurus*" *yuani* (IVPP V4067).

In contrast, the dorsal neural spines in some early lepidosaurs and squamates are quite distinct in shape. These are anteroposteriorly elongate with a small, posteriorly positioned apex. These spines are substantially longer anteroposteriorly than their maximum dorsoventral height. Examples of this state are found in *Coelurosauravus elivensis* (Evans and Haubold, 1987), *Gephyrosaurus bridensis* (Evans, 1981), *Planocephalosaurus robinsonae* (Fraser and Walkden, 1984), and many modern squamates (Hoffstetter and Gasc, 1969), such as *Shinisaurus crocodilurus* (Conrad, 2006).

CHARACTER 129: Dorsal vertebra, accessory zygosphene-zygantrum articulations: (0) absent, (1) present.

Examples of past usage: Gauthier et al. (1988a:78), Jalil (1997:20), Merck (1997:255), Müller (2004:44), Pritchard et al. (2015:130), Nesbitt et al. (in press:130).

Justification/Ontology: The zygapophyses in most early reptiles and diapsids exhibit flattened articular facets that make for a single articular contact on each side of the vertebra. This is present ubiquitously in early reptiles (e.g., *Captorhinus laticeps*, Dilkes and Reisz, 1986), early diapsids (e.g., *Araeoscelis gracilis*, Vaughn, 1955) and archosauromorphs (e.g., *Trilophosaurus buettneri*, TMM 31025-140). By contrast, some saurians develop a prominent gap between the postzygapophyses (zygantrum), which receives a small articular facet that is formed by an apparent anterodorsal inflection of the medial aspect of the prezygapophyseal facet (zygosphene). This accessory contact is evident in *Gephyrosaurus bridensis* (Evans, 1981), *Sphenodon punctatum* (Hoffstetter and Gasc, 1969), and many squamate taxa (Conrad, 2008; Gauthier et al., 2012). Both Conrad (2008) and Gauthier et al. (2012) differentiate between multiple types of zygosphene-zygantrum complexes of questionable homology. We retain a single character state, as all of the taxa in this analysis to exhibit these articular contacts exhibit similar, small dorsomedially inclined structures, as in Gauthier et al. (1988), Müller (2004), and Ezcurra et al. (2014).

CHARACTER 130: Second sacral rib, shape: (0) rib is a single unit, (1) rib bifurcates posteriorly into anterior and posterior processes.

Examples of past usage: Gauthier et al (1988a:88), Merck (1997:322), Dilkes (1998:87), Müller (2004:105), Pritchard et al. (2015:131), Nesbitt et al. (in press:131).

Justification/Ontology: In most early reptiles and diapsids, the distal portion of the second sacral rib (=pleurapophysis) does not bifurcate. Its entire lateral terminus thus forms an articular contact for the ilium. This state occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis* *gracilis* (Vaughn, 1955), *Claudiosaurus germaini* (Carroll, 1981), *Protorosaurus speneri* (Gottmann-Quesada and Sander, 2009), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexander* (NMQR 1484), and *Erythrosuchus africanus* (NMQR 3765). Some modern squamates also exhibit an unbifurcated second sacral rib.

In contrast, some saurian reptiles exhibit a bifurcation of the second sacral rib; the posterior surface of the articular process exhibits a prominent, flattened projection that projects posterolaterally. Examples of this condition include *Macrocnemus bassanii* (PIMUZ T/2472), *Amotosaurus rotfeldensis* (SMNS 50830), *Prolacerta broomi* (BP/1 2676), *Mesosuchus browni* (SAM 6046), *Pamelaria robinsonae* (Sen, 2003), *Planocephalosaurus robinsonae* (Fraser and Walkden, 1984), *Sphenodon punctatum* (Hoffstetter and Gasc, 1969), and some squamates (Hoffstetter and Gasc, 1969). Pritchard et al. (2015) erroneously coded a bifid second sacral transverse process in *Tanystropheus longobardicus*; no process is evident as noted by Wild (1973).

CHARACTER 131: Second sacral rib, morphology of posterior process: (0) terminally blunted, (1) sharp distally.

Examples of past usage: Dilkes (1998:87), Müller (2004:105), Ezcurra et al. (2014), Pritchard et al. (2015:132), Nesbitt et al. (in press:132).

Justification/Ontology: The morphology of the posterior projection of the second sacral rib (described in character 131) is variable within saurians. The projection in *Mesosuchus browni* (SAM K6046) and *Prolacerta broomi* (BP/1 2676) are blunted at their distal tips, being either subtly rounded or squared off. By contrast, the tips of the processes in *Macrocnemus bassanii* (PIMUZ T/2472), *Amotosaurus rotfeldensis* (SMNS 50830), *Planocephalosaurus robinsonae* (Fraser and Walkden, 1984), and *Sphenodon punctatum* (Hoffstetter and Gasc, 1969) are sharply pointed at their distal tips. Taxa coded as “0“ for character 131 are coded as “-“ for this character.

CHARACTER 132: Anterior caudal vertebrae, shape of transverse processes: (0) curved posterolaterally, (1) straight, (2) curved anterolaterally).

Examples of past usage: Merck (1997:332), Dilkes (1998:90), Pritchard et al. (2015:133), Nesbitt et al. (in press:133).

Justification/Ontology: The transverse processes and ribs (or the compound structure resulting from their fusion) of the caudal vertebrae in many early reptiles and early diapsids curve posterolaterally. This condition occurs in *Captorhinus laticeps* (Dilkes and Reisz, 1986), *Petrolacosaurus kansensis* (Reisz, 1981), and *Araeoscelis gracilis* (MCZ 4830). By contrast, the processes are straight in most near-saurian and saurian diapsids, such as *Youngina capensis* (AMNH FARB 5561, BP/1 5389), drepanosauromorphs from the Cromhall Quarry (Fraser and Renesto, 2005), *Prolacerta broomi* (BP/1 2676), *Proterosuchus alexanderi* (NMQR 1484), and most lepidosaurs (Hoffstetter and Gasc, 1969). The transverse processes curve anterolaterally in *Claudiosaurus germaini* (Carroll, 1981) and *Sphenodon punctatum* (Hoffstetter and Gasc, 1969). The original version of this character employed by Pritchard et al. (2015) and Nesbitt et al. (in press) only included states “0” and “1,” with the third state added for the current study.

CHARACTER 133: Anterior caudal vertebrae, orientation of transverse processes: (0) base of process perpendicular to the long axis of the vertebra, (1) base angled posterolaterally.

Examples of past usage: Pritchard et al. (2015:134), Nesbitt et al. (in press:134).

Justification/Ontology: Distinct from the curvature of the transverse processes in the caudal region is the primary inclination of the base of said processes. In most early reptiles and diapsids, the medial bases of said processes are roughly perpendicular to the long axis of the centrum. Examples include *Captorhinus laticeps* (Dilkes and Reisz, 1986), *Petrolacosaurus kansensis* (Reisz, 1981), *Claudiosaurus germaini* (Carroll, 1981), *Youngina capensis* (AMNH FARB 5561), *Icarosaurus siefkeri* (AMNH FARB 2101), *Protorosaurus speneri* (SMNS cast of WMsN P47361), and *Proterosuchus alexanderi* (NMQR 1484). In contrast, the bases of the processes are posterolaterally inclined in *Macrocnemus basanii* (PIMUZ T/2427), *Mesosuchus browni* (SAM K6046), *Langobardisaurus pandolfii* (MCSNB 2883), *Gephyrosaurus bridensis* (Evans, 1981a), and a number of squamates

CHARACTER 134: Caudal vertebrae, autotomic septa within the centrum: (0) absent, (1) present.

Examples of past usage: Gauthier et al (1988a:80), Merck (1997:323), Pritchard et al. (2015:135), Nesbitt et al. (in press:135).

Justification/Ontology: Lepidosauria exhibit a seemingly unique adaptation in their caudal vertebrae, resulting from apparently incomplete fusion of adjacent sclerotome elements in the caudal region (Winchester and Bellairs, 1977). These incompletely fused regions result in caudal vertebrae with pre-made fracture planes that allow the loss of portions of the tail. These are present in a number of early lepidosaurian fossil taxa, including *Gephyrosaurus bridensis* (Evans, 1981b), *Planocephalosaurus robinsonae* (Fraser and Walkden, 1984), and *Clevosaurus bairdi* (MCZ 9106). This character has long been recognized as a lepidosaurian synapomorphy (Gauthier et al., 1988a).

Caudal autotomy has been recognized in a number of different fossil taxa. Wild (1980) reported an apparently autotomized tail in the archosauromorph *Tanystropheus longobardicus*. However, I have not recognized any autotomy septa in any specimen of *Tanystropheus longobardicus* at MCSN or PIMUZ, and thus the taxon is coded “0.” Price (1940) reported autotomy septa in the Permian non-diapsid genera *Captorhinus*, *Labidosaurus*, and a then-unnamed taxon, and Dilkes and Reisz (1986) corroborated this observation. However, the absence of such septa in any early diapsids suggests and independent derivation of this morphology.

CHARACTER 135: Chevron, shape of hemal spine: (0) tapers along its proximodistal length; (1) broadens slightly along its length; (2) broadens distally, forming inverted T shape; (3) broadens distally, forming subcircular expansion.

Examples of past usage: Benton (1985:W4), Merck (1997:334), Müller (2004:108), Pritchard et al. (2015:136), Nesbitt et al. (in press:136).

Justification/Ontology: Among known early diapsids, the chevron bones tend to taper slightly along their proximodistal lengths. These chevrons occur in *Petrolacosaurus kansensis* (Reisz, 1981) and *Claudiosaurus germaini* (Carroll, 1981). By contrast, most Permo-Triassic diapsids exhibit a subtle anteroposterior broadening of the distal tip of the chevrons. This condition is apparent in *Youngina capensis* (Gow, 1975), *Thadeosaurus colcanapi* (Currie and Carroll, 1984), *Protorosaurus speneri* (SMNS cast of WMsN 47361, see fig. 15A, USNM 442453), *Proterosuchus alexanderi* (NMQR 1484), and *Erythrosuchus africanus* (NHMUK R3592). A distinct anteroposterior broadening, producing an inverted "T" shape, occurs in *Trilophosaurus buettneri* (TMM 31025-140) and *Coelurosauravus jaekeli* (Evans, 1982). A third type of anteroposterior broadening occurs in the tanystropheid *Langobardisaurus pandolfii* (MFSN 1921). Pritchard et al. (2015) originally included a state that described chevrons that remained consistent in anteroposterior length. However, such a condition is not apparent in most early diapsids.

CHARACTER 136: Gastralia, pairs of lateral gastralia: (0) two, (1) one.

Examples of past usage: Merck (1997:341), Pritchard et al. (2015:138), Nesbitt et al. (in press:138).

Justification/Ontology: Merck (1997) reported that one pair of lateral gastralia are present in most early Sauria, with a subsequent reversal to two pairs in Archosauriformes. However, the distribution of this feature is highly ambiguous in this analysis, due to the limited number of taxa for which the feature could be coded. I also note that both *Tanystropheus longobardicus* (MCSN

BES SC 1018) and *Proterosuchus alexanderi* (NMQR 1484) appear to exhibit a single pair of lateral gastralia, the latter in contrast to Merck (1997).

CHARACTER 137: Epiphyses of limb elements, secondary ossification centers: (0) absent, (1) present.

Examples of past usage: Benton (1985), Merck (1997:346), Gauthier et al (1988a:137), Pritchard et al. (2015:139), Nesbitt et al. (in press:139).

Justification/Ontology: In known early reptiles and non-saurian diapsids, the long bones of the limbs do not exhibit secondary ossification at the articular surfaces. As noted by Haines (1969) and Gauthier et al. (1988a), secondary ossification of the epiphyses occurs in modern Lepidosauria. Although difficult to assess in fossil taxa, I agree with Gauthier et al. (1988a) that this character can be assessed for fossil taxa known from articulated material, preferably of multiple ontogenetic states. Among archosauromorphs, such secondary ossification appears to be absent in *Macrocnemus bassanii*, *Tanystropheus longobardicus*, and *Tanytrachelos ahynis*, which are all known from multiple partially articulated limb skeletons at multiple states of growth. Among Triassic taxa, the Italian putative lepidosauromorph *Megachirella wachtleri* may exhibit a separate ossification of the olecranon process (Renesto and Bernardi, 2013).

CHARACTER 138: Cleithrum: (0) present, (1) absent.

Examples of past usage: Benton (1985), Gauthier et al (1988a:94), Laurin (1991:E11), Jalil (1997:9), Merck (1997:356), Dilkes (1998:93), Müller (2004:51), Pritchard et al. (2015:140), Nesbitt et al. (in press:140).

Justification/Ontology: The cleithrum is a dermal ossification that sits across the anterodorsal face of the scapular blade just dorsal to the dorsal stem of the clavicle (Romer, 1956). This bone is present throughout the earliest reptiles and in the earliest diapsids. Cleithra are present in

Petrolacosaurus kansensis (Reisz, 1981) and *Araeoscelis gracilis* (Vaughn, 1955). Currie (1981) noted cleithra in many specimens of *Hovasaurus boulei*. Evans (1982) tentatively considered a cleithrum present in *Coelurosauravus*, although this is difficult to assess due to the disarticulated materials in the taxon. Cleithra are absent throughout most other diapsids (the drepanosaurid GR 113; *Youngina capensis*, BP/1 3859; *Macrocnemus fuyuanensis*, GMPKU P3001; *Prolacerta broomi*, BP/1 2675; *Proterosuchus alexanderi*, NMQR 1484; *Iguana iguana*, Russell and Bauer, 2008; *Shinisaurus crocodilurus*, Conrad, 2006).

Cleithra have long been held to be absent in modern reptiles (Romer, 1956). However, Lyson et al. (2013) presented developmental and anatomical data that suggest that the anterormedian element in the turtle carapace, the nuchal, is homologous with the cleithra. If this interpretation stands, and Testudines are nested within Sauria (e.g., Kumazawa and Nishida, 2009; Chiari et al., 2012; Crawford et al., 2012), this would represent the only current evidence of ossified cleithra among crown reptiles.

CHARACTER 139: Clavicle, portion articulated with the interclavicle: (0) anteroposteriorly broader than distal portion of clavicle, (1) similar in narrowness to the distal portion of the clavicle.

Examples of past usage: Dilkes (1998:95), Müller (2004:52), Pritchard et al. (2015:141), Nesbitt et al. (in press:141).

Justification/Ontology: In the earliest reptiles and diapsids, the portion of the clavicle that articulates with the interclavicle is substantially broader anteroposteriorly relative to the dorsal portion that articulates with the anterior surface of the scapular blade. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Petrolacosaurus kansensis* (Reisz, 1981), and *Araeoscelis gracilis* (Vaughn, 1955)

CHARACTER 140: Interclavicle, shape: (0) transversely robust, forming broad diamond anteriorly; (1) transversely gracile anteriorly, forming anchor-like shape anteriorly.

Examples of past usage: Gauthier et al (1988a:93), Merck (1997:357), Dilkes (1998:96), Pritchard et al. (2015:142), Nesbitt et al. (in press:142).

Justification/Ontology: The interclavicle is anteriorly massive and roughly diamond-shaped anteriorly in a number of early reptiles, including *Captorhinus aguti* (Holmes, 1977) and *Claudiosaurus germaini* (Carroll, 1981). Similarly massive interclavicles occur *Proterosuchus alexanderi* (NMQR 1484) and "*Chasmatosaurus*" *yuani* (IVPP V4067). By contrast, anteriorly narrow interclavicles occur broadly in other early diapsid and early saurian groups, including *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Azendohsaurus madagaskarensis* (Nesbitt et al., in press), and Hyperodapedontinae (Benton, 1983).

CHARACTER 141: Interclavicle, shape of anterior surface anteromedial to clavicular articulations: (0) smooth margin, (1) prominent notch in margin.

Examples of past usage: Merck (1997:362), Dilkes (1998:97), Müller (2004:111), Pritchard et al. (2015:143), Nesbitt et al. (in press:143).

Justification/Ontology: In most early diapsids, the anterior margin of the interclavicle is subtly convex between the clavicular articular surfaces. This condition occurs in *Youngina capensis* (BP/1 3859) and *Claudiosaurus germaini* (SAM K8266). Lepidosauromorphs typically exhibit this morphology as well (e.g., Sphenodontia, Carroll, 1985).

A contrasting morphology occurs throughout early archosauromorphs, in which there is an anteriorly concave notch between the clavicular articulations. This condition occurs in *Protorosaurus speneri* (Gottmann-Quesada and Sander, 2009), *Mesosuchus browni* (Dilkes, 1998), *Prolacerta broomi* (BP/1 2675), and *Proterosuchus alexanderi* (NMQR 1484). There is no anterior notch in the interclavicle of *Trilophosaurus buettneri* (TMM 31025-144).

CHARACTER 142: Interclavicle, shape of posterior stem: (0) slender, tapering; (1) marked transverse expansion near anteroposterior midpoint.

Examples of past usage: Dilkes (1998:98), Müller (2004:112), Pritchard et al. (2015:144), Nesbitt et al. (in press:144).

Justification/Ontology: The posterior stem of the interclavicle in most early reptiles and diapsids is transversely narrow throughout its length. This condition occurs in *Araeoscelis gracilis* (Vaughn, 1955), *Petrolacosaurus kansensis* (Reisz, 1981), and *Thadeosaurus colcanapi* (Carroll, 1981). A similar shape occurs in the interclavicles of some rhynchocephalians, such as *Sphenodon punctatus* and *Palaeopleurosaurus posidonae* (Carroll, 1985), and most squamates (e.g., Conrad, 2006; Gauthier et al., 2012).

Archosauromorphs exhibit a diversity of conditions of the posterior stem. In *Protorosaurus speneri* (Gottmann-Quesada and Sander, 2009) and *Macrocnemus bassanii* (PIMUZ T/2475). In contrast, the posterior stem of the interclavicle is transversely expanded near its anteroposterior midpoint in *Proterosuchus alexanderi* (NMQR 1484), "*Chasmatosaurus*" *yuani* (IVPP V4067), *Azendohsaurus madagaskarensis* (UA 8-27-98-271), and *Mesosuchus browni* (SAM K6536). This expansion can be quite subtle in some taxa, such as *Prolacerta broomi* (BP/1 2675), and further quantification of this character may be in order to best understand its variation.

CHARACTER 143: Scapula, scapular blade, shape: (0) flattened blade directed dorsally, (1) flattened blade exhibits large posterior concavity, (2) blade curves anterodorsally.

Examples of past usage: Benton and Allen (1997:26), Merck (1997:374), Senter (2004:44), Pritchard et al. (2015:145), Nesbitt et al. (in press:145).

Justification/Ontology: The three states of this character describe apparent changes in the inclination of the dorsalmost portion of the scapular blade. Typically, in early reptiles, diapsids, and nearly all early saurians, the scapular blade is a rectangular structure with a long axis that is roughly vertical. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexanderi* (NMQR 1484), and *Gephyrosaurus bridensis* (Evans, 1980). By contrast, the dorsal portion of the scapular blade arcs posterodorsally in Tanystropheidae. This condition occurs in *Macrocnemus bassanii* (MCSN BES SC 111), *Tanystropheus longobardicus* (PIMUZ T/1277), *Tanytrachelos ahynis* (VMNH 120046), and *Fuyuansaurus acutirostris* (Fraser et al., 2013). It is interesting to note that a similar scapular shape, with a prominent posterior concavity in the blade, occurs in Thalattosauria (Li and Rieppel, 2005; Liu, 2007) and some mosasaurs (Romer, 1956).

A third condition occurs in some drepanosauromorphs. In these taxa, the scapular blade arcs anterodorsally along its dorsoventral height. This condition occurs in *Vallesaurus cenensis* (MCSNB 4751), *Megalancosaurus preonensis* (MFSN 1721), and *Drepanosaurus unguicaudatus* (MCSNB 5287).

CHARACTER 144: Scapula, supraglenoid morphology:' (0) prominent tubercle developed superior to glenoid fossa; (1) smooth bone dorsal to glenoid, lacking tubercle.

Examples of past usage: Pritchard et al. (2015:146), Nesbitt et al. (in press:146).

Justification/Ontology: An example of this tubercle occurs in *Trilophosaurus buettneri* (TMM 31025-140, see fig. 16B). The smoothened bone in other taxa is evident in *Tanystropheus longobardicus* (PIMUZ T/1277, see fig. 16C).

CHARACTER 145: Coracoid, number of ossifications: (0) two, (1) one.

Examples of past usage: Merck (1997:373), Müller (2004:123), Pritchard et al. (2015:147), Nesbitt et al. (in press:147).

Justification/Ontology: In most early reptiles and the earliest diapsids, the coracoid manifests as two distinct ossifications, one positioned anterior to the other. These are separated by a slender, dorsoventrally oriented suture. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Petrolacosaurus kansensis* (Reisz, 1981), and *Araeoscelis gracilis* (Vaughn, 1955). By contrast, the coracoid forms a single ossification in most non-saurian diapsids (e.g., *Megalancosaurus preonensis*, MPUM 6008; *Youngina capensis*, BP/1 3859) and early Sauria (e.g., *Tanystropheus longobardicus*, PIMUZ T/1277; *Proterosuchus alexanderi*, NMQR 1484).

CHARACTER 146: Coracoid, infraglenoid morphology: (0) no development of coracoid posteroventral to glenoid, (1) prominent post-glenoid process on coracoid, terminating in thickened margin.

Examples of past usage: Benton (1985:Q8), Merck (1997:324), Dilkes (1998:94), Müller (2004:110), Pritchard et al. (2015:148), Nesbitt et al. (in press:148).

Justification/Ontology: In most early reptiles and non-saurian diapsids, the coracoid extends well posteriorly of the glenoid fossa. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), and *Megalancosaurus preonensis* (MPUM 6008). Variable development of this process is seen in early archosauromorphs, although all taxa basal to *Erythrosuchus*+Archosauria exhibit some development of a process posterior to the glenoid. Among lepidosauromorphs (e.g., *Gephyrosaurus bridensis*, Evans, 1981; *Shinisaurus crocodilurus*, Conrad, 2006), some development of the coracoid posterior to the glenoid is commonplace. It should be noted that the development of the post-glenoid process in Archosauromorpha is quite variable which this character fails to capture; for example, the process only extends slightly posterior to the glenoid in *Protorosaurus speneri* (SMNS cast of WMsN P 47361) and *Proterosuchus alexanderi* (NMQR 1484), whereas the coracoid is substantially more elongate in *Trilophosaurus buettneri* (TMM 31025-140).

CHARACTER 147: Sternum, ossification of sternal plates: (0) absent, (1) present.

Examples of past usage: Laurin (1991:A5), Merck (1997:379), Müller (2004:81), Pritchard et al. (2015:149), Nesbitt et al. (in press:149).

Justification/Ontology: The sternum has not been recognized as a distinct, ossified structure in most early reptiles and diapsids. It is unrecognized in *Captorhinus aguti* (Holmes, 1977) and *Araeoscelis gracilis* (Vaughn, 1955). This also occurs in known early archosauromorphs (e.g., *Protorosaurus speneri*, SMNS cast of WMsN P 47361; *Tanystropheus longobardicus*, PIMUZ T/1287). Distinct, ossified sternal plates are known in the early diapsids *Thadeosaurus colcanapi* (Currie and Carroll, 1984), *Hovasaurus boulei* (Currie, 1981), and *Youngina capensis* (Gow, 1975). Although unknown in early lepidosaurs (e.g., *Clevosaurus hudsoni,* Fraser, 1988), the sternal plates are not ossified in modern lepidosaurs (Lécuru, 1968; Russell and Bauer, 2008). They are strongly mineralized in these taxa.

Note that Pritchard et al. (2015) included a similar character, describing "mineralized" sternal plates, such that the Permian diapsids noted above were coded in the same way as modern lepidosaurs. However, it is unclear if such mineralized sterna would be preserved in the fossil record. As such, I have altered the character here to describe true ossification of the sternal plates. It must be noted that the nature of sternal ossification in fossil tetrapods is poorly understood and warrants further investigation.

CHARACTER 148: Humerus, ectepicondyle, presence of radial nerve groove: (0) absent, (1) present.

Examples of past usage: Merck (1997:390), Pritchard et al. (2015:150), Nesbitt et al. (in press:150).

Justification/Ontology: In nearly all early reptiles, diapsids, and early saurians, there is a prominent groove on the preaxial aspect of the distal radius. In modern taxa, this structure provides a passage for the radial neurovasculature (Romer, 1956). However, some archosauromorphs exhibit a weakly developed or absent radial nerve groove. This condition occurs in *Dinocephalosaurus orientalis* (Rieppel et al., 2008).

CHARACTER 149: Humerus, ectepicondyle, morphology of radial nerve groove: (0) no roof; (1) roofed, forming ectepicondylar foramen.

Examples of past usage: Jalil (1997:21), Dilkes (1998:108), Merck (1997:390), Müller (2004:64), Pritchard et al. (2015:151), Nesbitt et al. (in press:151).

Justification/Ontology: The groove for the radial neurovasculature is roofed by a prominent bony ridge to form an ectepicondylar foramen in most early reptiles (e.g., *Captorhinus aguti*, Holmes, 1977). This condition is variable in later diapsids. A foramen is present in large individuals of *Youngina capensis* (BP/1 3859), *Thadeosaurus colcanapi* (Carroll, 1981), and *Claudiosaurus germaini* (Carroll, 1981). However, these features are not present in smaller individuals (Caldwell, 1994). Among early Sauria, there is no roof to the ectepicondylar foramen in *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Tanystropheus longobardicus* (PIMUZ T/1277), and *Trilophosaurus buettneri* (TMM 31025-140). A foramen is present in *Kuehneosaurus latus* (AMNH FARB 7786), *Gephyrosaurus bridensis* (Evans, 1981), and most modern Squamata (Lécuru, 1969).

CHARACTER 150: Humerus, ectepicondyle morphology: (0) prominent preaxial crest, (1) no crest.

Examples of past usage: Müller (2004:63), Pritchard et al. (2015:152), Nesbitt et al. (in press:152).

Justification/Ontology: The preaxial aspect of the humerus projects well beyond the level of the capitellum of the humerus in most early reptiles and diapsids, forming a prominent ectepicondylar crest. This condition occurs in *Captorhinus aguti* (Holmes, 1977), *Araeoscelis* *gracilis* (Vaughn, 1955), *Kuehneosaurus latus* (AMNH FARB 7786), *Sphenodon punctatum* (Carroll, 1985), and many squamates (Lécuru, 1969). By contrast, the preaxial aspect of the humerus is barely raised beyond the margin of the condyle in many early diapsids and saurians. This condition is evident in *Claudiosaurus germaini* (SAM K8266), *Thadeosaurus colcanapi* (MNHN MAP 360), *Tanystropheus longobardicus* (PIMUZ T/1277), and *Proterosuchus alexanderi* (NMQR 1484).

CHARACTER 151: Humerus, entepicondyle morphology: (0) foramen absent, (1) foramen present.

Examples of past usage: Benton (1985:Y22), Gauthier et al (1988a:98), Laurin (1991:F6), Benton and Allen (1997:27), Jalil (1997:32), Merck (1997:393), Dilkes (1998:107), Müller (2004:65), Senter (2004:46), Pritchard et al. (2015:153), Nesbitt et al. (in press:153).

Justification/Ontology: In most early reptiles and diapsids, there is a prominent foramen in the post-axial aspect of the humerus. In many basal taxa, this foramen sits atop a prominent entepicondylar crest, which extends beyond the level of the ulnar condylar (see character 152). This condition occurs in *Captorhinus aguti* (Holmes, 1977), *Petrolacosaurus kansensis* (Reisz, 1981), and *Thadeosaurus colcanapi* (MNHN MAP 360). In some taxa that lack a prominent crest, the foramen is situated along the post-axial aspect of the humeral shaft. This condition occurs in *Youngina capensis* (BP/1 3859) and *Claudiosaurus germaini* (SAM K8266).

In most early Sauria, there is no entepicondylar foramen, regardless of the presence or absence of an entepicondylar crest. This is evident in *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Tanystropheus longobardicus* (PIMUZ T/1277), *Kuehneosaurus latus* (AMNH FARB 7786), and *Trilophosaurus buettneri* (TMM 31025-140). There is an entepicondylar foramen in "*Chasmatosaurus*" *yuani* (IVPP V4067), *Gephyrosaurus bridensis* (Evans, 1981), and many Squamata (Lécuru, 1969).

CHARACTER 152: Humerus, entepicondyle morphology: (0) smooth margin between shaft and post-axial condyle, (1) prominent entepicondylar crest present.

Examples of past usage: Benton (1985:S4), Gauthier et al (1988a:109), Merck (1997:391), Müller (2004:63), Pritchard et al. (2015:154), Nesbitt et al. (in press:154).

Justification/Ontology: Entepicondylar crests are typically well developed in early diapsids and saurians (e.g., Fig. 17A, B, C, D, E). Among early archosauromorphs, the crest is weakly developed in Tanystropheidae (e.g., Fig. 17F).

CHARACTER 153: Humerus, entepicondylar crest morphology: (0) crest exhibits a curved proximal margin, (1) crest exhibits a prominently angled proximal margin.

Examples of past usage: Pritchard et al. (2015:155), Nesbitt et al. (in press:155).

Justification/Ontology: Among most early reptiles and Diapsida that possess a prominent entepicondylar crest, the proximal margin of the crest is sharply angled. This condition occurs in *Captorhinus aguti* (Holmes, 1977), *Araeoscelis gracilis* (Vaughn, 1955), and *Thadeosaurus colcanapi* (MNHN MAP 360). Among early Sauria, a similarly sharp crest occurs in *Trilophosaurus buettneri* (TMM 31025-140). Sharp crests also occur in a number of Lepidosauria (Lécuru, 1969). The proximal crests are subtly curved in *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Proterosuchus alexanderi* (NMQR 1484), and *Erythrosuchus africanus* (NHMUK R3592).

CHARACTER 154: Humerus, distal condyle morphology: (0) distinct trochlear and capitular articulations; (1) low, double condyle.

Examples of past usage: Müller (2004:146), Pritchard et al. (2015:156), Nesbitt et al. (in press:156).

Justification/Ontology: Throughout early reptiles and Diapsida, the bony distal condyles of the humerus are extremely well defined, forming elliptical trochleae and capitella. This is seen in *Captorhinus aguti* (Holmes, 1977), *Araeoscelis gracilis* (MCZ 2043), *Thadeosaurus colcanapi* (Carroll, 1981), and *Drepanosaurus unguicaudatus* (MCSNB 5728). Well-defined condyles also occur in *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Trilophosaurus buettneri* (TMM 31025-140), *Kuehneosaurus latus* (AMNH FARB 7786), and throughout Lepidosauria (Lécuru, 1969; Carroll, 1985). By contrast, the distal condylar surface is poorly defined in many archosauromorphs. This condition occurs in *Tanystropheus longobardicus* (PIMUZ T/1277), *Batrachotomus kupferzellensis* (Gower and Schoch, 2009), and *Euparkeria capensis* (Ewer, 1965).

CHARACTER 155: Ulna, ossified olecranon process: (0) present, (1) absent.

Examples of past usage: Benton (1985:B11), Gauthier et al (1988a:107), Laurin (1991:C2), Merck (1997:402), Senter (2004:48), Müller (2004:147), Pritchard et al. (2015:157), Nesbitt et al. (in press:157).

Justification/Ontology: In early reptiles and Diapsida, the ulna exhibits a well-ossified, proximally projecting olecranon process. This process occurs in *Captorhinus aguti* (Holmes, 1977), *Petrolacosaurus kansensis* (Reisz, 1981), *Coelurosauravus elivensis* (MNHN MAP 317), and *Megalancosaurus preonensis* (MPUM 8437). Among Permian Diapsida typically considered close relatives of *Youngina capensis*, an ossified olecranon process is comparatively rare. There is no well-defined process in *Youngina capensis* (BP/1 3859; SAM K7710), *Thadeosaurus colcanapi* (MNHN MAP 360), and *Claudiosaurus germaini* (Carroll, 1981).

CHARACTER 156: Medial centrale of hand: (0) absent, (1) present.

Examples of past usage: Benton and Allen (1997:30), Laurin (1991: F7), Jalil (1997:33 &51), Merck (1997:425), Dilkes (1998:109), Pritchard et al. (2015:158), Nesbitt et al. (in press:158).

Justification/Ontology: No comments.

CHARACTER 157: Distal carpal five: (0) absent, (1) present.

Examples of past usage: Pritchard et al. (2015:159), Nesbitt et al. (in press:159).

Justification/Ontology: A fifth distal carpal ossification is present in early reptiles and early Diapsida, including *Captorhinus aguti* (Holmes, 1977), *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), *Thadeosaurus colcanapi* (Carroll, 1981), *Coelurosauravus jaekeli* (Evans and Haubold, 1987), and *Hovasaurus boulei* (Caldwell, 1994). Among Triassic taxa in this study, such ossifications are only known in Drepanosauromorpha (Renesto et al., 2010). By contrast, fifth distal carpals are absent in *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Tanystropheus longobardicus* (GMPKU-P-1527; MCSN BES SC 1018), *Azendohsaurus madagaskarensis* (Nesbitt et al., in press), and *Erythrosuchus africanus* (NMQR 3765). They are also absent in modern Lepidosauria (e.g., Russell and Bauer, 2008; Nesbitt et al., in press).

Ossification sequences from series of early diapsids from the Upper Permian Sakamena Formation of Madagascar show that the fifth distal carpal appears after the proximal carpal series, centralia, and the fourth distal carpal (Caldwell, 1994). As such, caution should be used in coding for the absence of this character. Ideally, an OTU should be represented by a number of different size classes (e.g., samples of *Tanystropheus longobardicus* described by Wild, 1973) to allow robust assessment of the absence of this ossification.

CHARACTER 158: Manual intermedium: (0) present, (1) absent.

Examples of past usage: Gauthier et al (1988a:101), Benton and Allen (1997:29), Jalil (1997:47), Merck (1997:426), Dilkes (1998), Pritchard et al. (2015:160), Nesbitt et al. (in press:160).

Justification/Ontology: A manual intermedium is commonplace in early reptiles, diapsids, and most early Sauria. This bone occurs in *Captorhinus aguti* (Holmes, 1977), *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (SAM K7710), *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Tanystropheus longobardicus* (MCSN BES SC 1018), *Trilophosaurus buettneri* (Nesbitt et al., in press), *Azendohsaurus madagaskarensis* (Nesbitt et al., in press), and *Sphenodon punctatum* (Rénous-Lécuru, 1973). The intermedium is heavily reduced in most squamates, including *Uromastyx aegyptia* (El-Toubi, 1949), *Shinisaurus crocodilurus* (Conrad 2006), and a number of scincids (Stokely, 1950).

CHARACTER 159: Ulnare and intermedium, perforating foramen between elements: (0) present, (1) absent.

Examples of past usage: Benton (1985:C10), Merck (1997:427), Pritchard et al. (2015:161), Nesbitt et al. (in press:161).

Justification/Ontology: Ancestrally, early reptiles and Diapsida exhibit a prominent, gap between the ulnare and intermedium. This feature is typically present in all saurian reptiles with well-ossified intermedia (e.g., *Protorosaurus speneri*, SMNS cast of WMsN P 47361; *Trilophosaurus buettneri*, Nesbitt et al., in press). This foramen is absent between the intermedium and ulnare in *Sphenodon punctatus* (Rénous-Lécuru, 1973) and those squamates that retain an intermedium (Stokely, 1950).

CHARACTER 160: Manual digit four, phalangeal formula: (0) five, (1) four.

Examples of past usage: Merck (1997:414), Pritchard et al. (2015:162), Nesbitt et al. (in press:162).

Justification/Ontology: The manual formula of ancestral reptiles and most Permo-Triassic Diapsida is 2-3-4-5-3. The phalangeal formula for the fourth digit is reduced to four in *Tanystropheus longobardicus* (MCSN BES SC 1018) and *Tanytrachelos ahynis* (Olsen, 1979). In Drepanosauromorpha, the manual phalangeal formula is reduced across the manus in *Drepanosaurus unguicaudatus* and *Megalancosaurus preonensis* (Renesto et al., 2010) to two phalanges.

CHARACTER 161: Puboischiadic plate, fenestration: (0) no fenestra, (1) thyroid fenestra within plate.

Examples of past usage: Benton (1985:x9), Gauthier et al (1988a:121), Benton and Allen (1997:36), Jalil (1997:22), Merck (1997:448), Dilkes (1998:100), Müller (2004:68), Senter (2004:59), Pritchard et al. (2015:163), Nesbitt et al. (in press:163).

Justification/Ontology: The pubis and ischium form a continuous bony plate in nearly all early reptiles and Diapsida. This condition occurs in *Labidosaurus hamatus* (Sumida, 1989), *Petrolacosaurus kansensis* (Reisz, 1981), and *Thadeosaurus colcanapi* (Carroll, 1981). A similar, continuous plate occurs in *Protorosaurus speneri* (SMNS 55387), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexanderi* (NMQR 1484). By contrast, a number of reptiles exhibit a gap in the lateral surface of the puboischiadic plate, which is typically dubbed the thyroid fenestra (e.g., Romer, 1956; Gauthier et al., 1988a). This condition has been noted in *Hypuronector limnaios* (AMNH FARB 7759), *Drepanosaurus unguicaudatus* (MCSNB 5728), *Macrocnemus bassanii* (MCSN V 457), *Tanystropheus longobardicus* (PIMUZ T/2817), *Gephyrosaurus bridensis* (Evans, 1981), and modern Lepidosauria (e.g., Russell and Bauer, 2008).

The presence or absence of a thyroid fenestra is debatable in some fossil taxa. Gow (1975) described the first postcranium of *Youngina capensis* (BP/1 3895), and indicated the presence of a ventrally pointed, subtriangular gap within the puboischiadic plate. I concur that this structure is present and framed by well-defined margins, suggestive of a true thyroid fenestra. However, thyroid fenestrae are absent in the skeletons referred to *Youngina capensis* by Smith and Evans (1992). However, I consider it likely that these materials represent a distinct taxon from the *Y. capensis* type material, albeit a close relative.

Dilkes (1998) reconstructed the skeleton of *Mesosuchus browni* with a small gap in the puboischiadic plate. However, I note that the gap evident in SAM K7416 is quite irregular and may be pathological. Regardless, I do not consider a thyroid fenestra to be present in *M. browni*.

CHARACTER 162: Ilium, iliac blade, orientation of long axis: (0) horizontal, (1) posterodorsal, (2) anterodorsal.

Examples of past usage: Gauthier et al (1988a:120), Merck (1997:433), Renesto et al. (2010:)22, Pritchard et al. (2015:164), Nesbitt et al. (in press:164).

Justification/Ontology: In many Permian reptiles and early Diapsida, the long axis of the narrow structure that forms the blade of the ilium is oriented posterodorsally. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966) and *Petrolacosaurus kansensis* (Reisz, 1981). By contrast, the narrow blade in *Araeoscelis gracilis* is horizontally oriented (MCZ 2043).

In most Permian diapsids, the long axis of the blade is oriented horizontally. This occurs in *Youngina capensis* (SAM K7710), *Coelurosauravus elivensis* (Evans, 1982), and *Thadeosaurus colcanapi* (MNHN MAP 360). A similar condition occurs throughout early Archosauromorpha. Horizontal ilia occur in *Tanystropheus longobardicus* (PIMUZ T/1277), *Trilophosaurus buettneri* (TMM 31025-140), "*Chasmatosaurus*" *yuani* (IVPP V4067), and *Erythrosuchus africanus* (NHMUK R3592). By contrast, the ilium is posterodorsally inclined in known Lepidosauria. This occurs in *Sphenodon punctatum* and several extinct rhynchocephalians (e.g., Fraser, 1988; Russell and Bauer, 2008) and Squamata (Russell and Bauer, 2008).

CHARACTER 163: Ilium, anteroventral process extending from anterior margin of pubic peduncle: (0) absent; (1) present, process draping across anterior surface of pubis

Examples of past usage: Gauthier et al (1988a:117), Merck (1997:432), Dilkes (1998:144), Pritchard et al. (2015:165), Nesbitt et al. (in press:165).

Justification/Ontology: In most early diapsids, the anteroventral margin of the ilium is flattened ventrally. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Trilophosaurus buettneri* (TMM 31025-73), *Kuehneosaurus latus* (AMNH FARB 7781), *Drepanosaurus unguicaudatus* (MCSNB 5728), and "*Chasmatosaurus*" *yuani* (IVPP V4067). By contrast, the anteroventral margin of the bone is drawn into an anteroventrally oriented process that overlies the anterodorsal portion of the pubis in other taxa. This occurs in many Lepidosauria (e.g., Fraser, 1988; Russell and Bauer, 2008). Ilia referred to the putative Early Triassic lepidosauromorph *Sophineta czatkowicensis* from Czatkowice, Poland exhibit a pubic process (ZPAL V/950).

CHARACTER 164: Ilium, supra-acetabular crest: (0) absent, posterodorsal margin of acetabulum similar in development of anterodorsal margin; (1) present as prominent anterodorsal bony lamina framing anterodorsal margin of acetabulum.

Examples of past usage: Benton and Allen (1997:35), Pritchard et al. (2015:166), Nesbitt et al. (in press:166).

Justification/Ontology: Among early diapsids and saurians, most taxa exhibit a well-defined buttress framing the acetabulum anterodorsally (e.g., Fig. 18B, Fig. 19). However, drepanosauromorphs exhibit a poorly defined anterodorsal margin to the ilium (e.g., MCSNB 5728, see fig. 18A).

CHARACTER 165: Ilium, shape of supra-acetabular margin: (0) dorsalmost margin of acetabulum is unsculptured, (1) prominent, bulbous rugosity superior to acetabulum.

Examples of past usage: Pritchard et al. (2015:167), Nesbitt et al. (in press:167).

Justification/Ontology: No comments.

CHARACTER 166: Ilium, acetabulum shape: (0) irregular, marked by posterodorsal invasion by finished bone; (1) roughly circular, no posterodorsal invasion.

Examples of past usage: Pritchard et al. (2015:168), Nesbitt et al. (in press:168).

Justification/Ontology: No comments.

CHARACTER 167: Ilium, anterior margin of iliac blade, anterior process or tuber: (0) absent, smooth anterior margin; (1) present.

Examples of past usage: Benton (1985:J12), Dilkes (1998:102), Müller (2004:113), Pritchard et al. (2015:169), Nesbitt et al. (in press:169).

Justification/Ontology: No comments.

CHARACTER 168: Ilium, anterior process/tuber of ilium: (0) anterior process/tuber small, with anterodorsal margin of ilium curving smoothly into dorsal margin of iliac blade; (1) large and anteriorly projecting tuber, with dorsal margin of tuber nearly continuous with dorsal margin of iliac blade.

Examples of past usage: Dilkes (1998:102), Senter (2004:54), Pritchard et al. (2015:170), Nesbitt et al. (in press:170).

Justification/Ontology: No comments.

CHARACTER 169: Ilium, development of posterior process: (0) weakly developed, failing to extend well posterior of acetabulum; (1) strongly developed, extending well posterior to the acetabulum.

Examples of past usage: Merck (1997:434), Dilkes (1998:102), Pritchard et al. (2015:171), Nesbitt et al. (in press:171).

Justification/Ontology: No comments.

CHARACTER 170: Ilium, morphology of dorsal blade margin: (0) smoothly textured dorsal border, (1) distinct dorsoventral striations running from acetabulum to dorsal margin of iliac blade.

Examples of past usage: Pritchard et al. (2015:172), Nesbitt et al. (in press:172).

Justification/Ontology: No comments.

CHARACTER 171: Pubis, morphology of symphysis: (0) pubic apron present, with distinct anteroventral downturn of the symphyseal region; (1) pubic apron absent, symphyseal region only in coronal plane.

Examples of past usage: Benton (1985:J11), Dilkes (1998:104), Pritchard et al. (2015:173), Nesbitt et al. (in press:173).

Justification/Ontology: No comments.

CHARACTER 172: Pubis, tubercle at the anteroventral corner of the pubis: (0) present, (1) absent, pubis is tapered anterolaterally.

Examples of past usage: Merck (1997:445), Pritchard et al. (2015:174), Nesbitt et al. (in press:174).

Justification/Ontology: No comments.

CHARACTER 173: Pubis, anterolateral surface: (0) lateral pubic tubercle (sensu Vaughn, 1955) present, appearing as rounded tuberosity; (1) prominent, transversely narrow ambiens flange present; (2) anterolateral surface of pubis marked by rugose bone.

Examples of past usage: Pritchard et al. (2015:175), Nesbitt et al. (in press:175).

Justification/Ontology: In the earliest diapsid reptiles, the anterolateral surface of the pubis, just anterior to the acetabulum, is marked by a dorsally rounded, bulbous tuberosity. It occurs in *Araeoscelis gracilis* (Vaughn, 1955) and *Petrolacosaurus kansensis* (Reisz, 1981). This was dubbed the lateral pubic tubercle by Vaughn (1955) in his description of *Araeoscelis*, who later speculated that it might be homologous with the pubic tubercle in modern squamates (Vaughn, 1956). I consider this interpretation problematic, as there is an anteroventrally facing tuberosity in these taxa as well, which matches the position of the pubic tubercle in later diapsids (e.g., *Youngina capensis*, BP/1 3859; *Prolacerta broomi*, BP/1 2676, see fig. 18B) more closely.

In most Permo-Triassic diapsids, the bone surface anterolateral to the acetabulum is marked by a transversely narrow crest. This structure can be seen in *Youngina capensis* (BP/1 3859), *Prolacerta broomi* (BP/1 2676), *Azendohsaurus madagaskarensis* (UA 8-30-98-375), *Icarosaurus siefkeri* (AMNH FARB 2101), and *Mesosuchus browni* (SAM K6046). In contrast, the anterolateral surface of the pubis is marked by a thick, rugose surface (e.g., *Erythrosuchus africanus*, NHMUK R3592; *Batrachotomus kupferzellensis*, Gower and Schoch, 2009; *Osmolskina czatkowicensis*, Borsuk-Bialynicka and Sennikov, 2009).

This character is substantially modified from Pritchard et al. (2015), which merely described the presence and absence of the lateral pubic tubercle. I elect to include more states to fully address the range of morphologies present on the anterolateral face of the pubis.

CHARACTER 174: Ischium, shape of posterior margin: (0) straight, (1) interrupted by posterior process extending from posterodorsal ischiadic margin (spina ischii sensu El-Toubi, 1949).

Examples of past usage: Gauthier et al (1988a:122), Pritchard et al. (2015:176), Nesbitt et al. (in press:176).

Justification/Ontology: In most early reptiles and Diapsida, the posterior surface of the ilium is a straight, vertically oriented margin. This condition is seen in *Araeoscelis gracilis* (MCZ 2043), *Youngina capensis* (SAM K7710), *Trilophosaurus buettneri* (TMM 31025-140), and *Proterosuchus alexanderi* (NMQR 1484). In contrast, some Sauria exhibit a posteriorly projecting process at the posterodorsal corner of the ischium. This occurs in *Protorosaurus speneri* (SMNS 55387), *Macrocnemus bassanii* (MCSN V 457), *Langobardisaurus pandolfii* (MCSNB 2883), *Gephyrosaurus bridensis* (Evans, 1981), and *Uromastyx aegyptia* (El-Toubi, 1949).

The impact of ontogeny on this character is unclear. There is a similar posterior process in small individuals of *Tanystropheus longobardicus* (Wild, 1973). However, the process becomes less pronounced throughout ontogeny, as the portion of the ilium below the process “fills in” with bones, ultimately disappearing in the largest individuals (PIMUZ T/2817; Wild, 1973). This ontogenetic trajectory is quite different from that known for *Macrocnemus bassanii*, in which the process does not disappear in the largest individuals.

CHARACTER 175: Femur, profile in pre-axial view: (0) sigmoidally curved, (1) linear with slight ventrodistal curvature.

Examples of past usage: Benton (1985:13), Benton and Allen (1997:38), Merck (1997:451), Müller (2004:70), Renesto et al. (2010:23), Pritchard et al. (2015:177), Nesbitt et al. (in press:177).

Justification/Ontology: Sigmoid curvature of the femur has long been considered a characteristic of some subdivision of Diapsida. Benton (1985) considered this a characteristic of Neodiapsida. I consider a sigmoid femur to be more widespread among Diapsida. I note it in *Araeoscelis gracilis* (MCZ 2043), *Youngina capensis* (BP/1 3859), *Thadeosaurus colcanapi* (MNHN MAP 360), *Protorosaurus speneri* (SMNS 55387), *Trilophosaurus buettneri* (TMM 31025-140), "*Chasmatosaurus*" *yuani* (IVPP V4067), and *Tanystropheus longobardicus* (GMPKU-P-1527). By contrast the femoral shaft is straight except for its distalmost end in a number of Sauria. This occurs in *Tanytrachelos ahynis* (VMNH 120015), *Langobardisaurus pandolfii* (MCSNB 2883), *Kuehneosaurus latus* (AMNH FARB 7776), and *Icarosaurus siefkeri* (AMNH FARB 2101).

CHARACTER 176: Femur, morphology of proximal end of head: (0) well-ossified and hemispherical, (1) concave with groove.

Examples of past usage: Pritchard et al. (2015:178), Nesbitt et al. (in press:178).

Justification/Ontology: In most early reptiles and Diapsida, the proximal femoral head is strongly convex and smoothened. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Araeoscelis gracilis* (Vaughn, 1955), and *Petrolacosaurus kansensis* (Reisz, 1981). A similarly convex head occurs in *Coelurosauravus elivensis* (MNHN MAP 325) and *Hypuronector limnaios* (AMNH FARB 7759). A slightly different condition occurs in *Claudiosaurus germaini* (SAM K 8266), which exhibits a subtly convex head.

Most early Sauria and near-saurian diapsids exhibit a slightly concave femoral head with a grooved proximal surface. This condition occurs in *Youngina capensis* (BP/1 3859), *Tanystropheus longobardicus* (PIMUZ T/1277), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexanderi* (NMQR 1484), and *Erythrosuchus africanus* (NHMUK R3592). In contrast, subtly convex heads occur in *Kuehneosaurus latus* (AMNH FARB 7776) and *Azendohsaurus madagaskarensis* (Nesbitt et al., in press).

CHARACTER 177: Femur, development of internal trochanter crest: (0) trochanteric crest does not reach femoral head; (1) trochanteric crest reaches far proximally, continuous with the femoral head.

Examples of past usage: Pritchard et al. (2015:179), Nesbitt et al. (in press:179).

Justification/Ontology: No comments.

CHARACTER 178: Femur, size of distal condyles (medial and lateral), comparison: (0) about equal in size, (1) unequal, lateral condyle larger than the medial condyle.

Examples of past usage: Benton (1985:A14), Laurin (1991:B8), Dilkes (1998:110), Müller (2004:73), Pritchard et al. (2015:180), Nesbitt et al. (in press:180).

Justification/Ontology: In most early reptiles and Diapsida, the lateral (post-axial) femoral condyle projects further distally than does the medial (preaxial) condyle. This condition occurs in *Labidosaurus hamatus* (Sumida, 1989), *Captorhinus aguti* (Fox and Bowman 1966), *Petrolacosaurus kansensis* (Reisz, 1981), and *Araeoscelis gracilis* (Vaughn, 1955). By contrast, most Permian diapsids and Sauria exhibit femoral condyles that project distally to a similar degree. This condition occurs in *Youngina capensis* (BP/1 3859), *Claudiosaurus germaini* (SAM K8266), *Protorosaurus speneri* (SMNS 55387), *Trilophosaurus buettneri* (TMM 31025-140), and *Proterosuchus alexanderi* (NMQR 1484).

CHARACTER 179: Femur, expansion of distal condyles relative to femoral shaft: (0) distinct expansion beyond the circumference of the femoral shaft, (1) limited expansion beyond the circumference of the femoral shaft.

Examples of past usage: Müller (2004:72), Nesbitt (2011), Pritchard et al. (2015:181), Nesbitt et al. (in press:181).

Justification/Ontology: No comments.

CHARACTER 180: Femur, shape of tibial condyle in distal view: (0) medial surface is rounded and mound-like, (1) medial surface is triangular and sharply pointed.

Examples of past usage: Pritchard et al. (2015:182), Nesbitt et al. (in press:182).

Justification/Ontology: No comments.

CHARACTER 181: Femur, fibular (=medial) condyle, shape of ventral surface: (0) flattened and planar, (1) rounded and mound-like.

Examples of past usage: Pritchard et al. (2015:183), Nesbitt et al. (in press:183).

Justification/Ontology: No comments.

CHARACTER 182: Pedal centrale: (0) absent as distinct ossification, fused to astragalus; (1) present as distinct ossification.

Examples of past usage: Benton (1985:J14, M4, & X11), Benton and Allen (1997:42), Merck (1997:472), Dilkes (1998:112), Müller (2004:151), Pritchard et al. (2015:184), Nesbitt et al. (in press:184).

Justification/Ontology: No comments.

CHARACTER 183: Astragalus-calcaneum, extent of co-ossification: (0) present as distinct ossifications, (1) co-ossified.

Examples of past usage: Benton (1985), Gauthier et al (1988a:126), Jalil (1997:23), Merck (1997:467),Müller (2004:171), Renesto et al. (2010: 26), Pritchard et al. (2015:185), Nesbitt et al. (in press:185).

Justification/Ontology: In most early Diapsida and Sauria, the astragalus and calcaneum are separate ossifications throughout ontogeny (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Youngina capensis*, BP/1 3859; *Tanystropheus longobardicus*, MCSN BES SC 1018; *Erythrosuchus africanus*, Gower, 1996). By contrast, Lepidosauria exhibit a compound astragalocalcaneum: a single proximal tarsal element (e.g., *Gephyrosaurus bridensis*, Evans, 1981; Squamata, Russell and Bauer, 2008). Developmental studies support the hypothesis that this structure is a derivative of the ancestral astragalar and calcaneal ossification centers (Maisano, 2002; Leal et al., 2010). The co-ossification is complete at hatching, such that an ontogenetic sequence may be less important for coding this character.

CHARACTER 184: Astragalus-calcaneum, perforating foramen at contact: (0) present, positioned between astragalus and calcaneum, (1) absent, no foramen evident between astragalus and calcaneum.

Examples of past usage: Benton and Allen (1997:40), Merck (1997:473), Dilkes (1998:115), Müller (2004:74), Pritchard et al. (2015:186), Nesbitt et al. (in press:186).

Justification/Ontology: Early reptiles and Diapsida typically exhibit a distinct foramen between the astragalus and calcaneum, for the passage of an artery (Romer, 1956). This condition is widespread in early Archosauromorpha. In Lepidosauria (e.g. *Gephyrosaurus bridensis*, Evans, 1981; *Clevosaurus hudsoni*, Fraser, 1988; Squamata, Russell and Bauer, 2008), there is no distinct foramen present. It should be noted that the absence of a foramen is coincident with the fusion of the astragalus and calcaneum. The foramen is also lost in Archosauromorpha more derived that *Erythrosuchus africanus* (e.g., *Euparkeria capensis*, Ewer, 1965).

CHARACTER 185: Calcaneum, distal facet: (0) little broader dorsoventrally than is the proximal facet; (1) markedly expanded dorsoventrally, more than twice the breadth of the distal facet.

Examples of past usage: Pritchard et al. (2015:187), Nesbitt et al. (in press:187).

Justification/Ontology: In most reptiles, including early Sauria, the distal facet of the calcaneum is not much broader than the proximal facet surface. Such tarsi can be seen in *Youngina capensis* (BP/1 3859), *Macrocnemus bassanii* (PIMUZ T/4822), *Trilophosaurus buettneri* (TMM 31025-140), and *Erythrosuchus africanus* (Gower, 1996). By contrast, *Tanytrachelos ahynis* (AMNH FARB 7206) and calcanei from the Hayden Quarry (GR 306) exhibit substantially broader calcaneal facets, twice as wide as the proximal facet in a dorsal-plantar plane.

CHARACTER 186: Calcaneum, lateral margin: (0) calcaneum terminating in unthickened margin, (1) roughened tuberosity present laterally.

Examples of past usage: Benton (1985:C11), Laurin (1991:F9), Benton and Allen (1997:41), Jalil (1997:35), Merck (1997:469), Dilkes (1998:116), Müller (2004:75), Senter (2004:64), Renesto et al. (2010: 25), Pritchard et al. (2015:188), Nesbitt et al. (in press:188).

Justification/Ontology: No comments.

CHARACTER 187: Calcaneum, expansion of lateral margin: (0) limited, calcaneum less than twice as broad as the distal calcaneal facet, (1) pronounced, lateral wing of calcaneum is twice as broad or broader than the distal calcaneal facet.

Examples of past usage: Laurin (1991:F9), Dilkes (1998:116), Merck (1997:469), Müller (2004:75), Senter (2004:64), Renesto et al. (2010: 25), Pritchard et al. (2015:189), Nesbitt et al. (in press:189).

Justification/Ontology: No comments.

CHARACTER 188: Calcaneum, lateral projection: (0) ventrolateral margin of calcaneum projection coplanar with dorsolateral margin of projection, (1) ventrolateral margin of calcaneum "curls" externally.

Examples of past usage: Pritchard et al. (2015:190), Nesbitt et al. (in press:190).

Justification/Ontology: The entirety of the lateral (=postaxial) portion of the calcaneum sits in a single plane in most early reptiles, diapsids, and saurians. This condition occurs in *Araeoscelis gracilis* (Vaughn, 1955), *Youngina capensis* (SAM K7710), and *Protorosaurus speneri* (SMNS 55387). By contrast, the tip of the lateral portion curves towards the dorsal aspect of the pes in *Tanytrachelos ahynis* (AMNH FARB 7206) and the Hayden Quarry tanystropheid material (Pritchard et al., 2015).

CHARACTER 189: Distal tarsal four, morphology of proximal contact: (0) smooth contact surface for proximal tarsals, (1) prominent process for contact with proximal tarsals.

Examples of past usage: Jalil (1997:24), Merck (1997:461), Dilkes (1998:114), Pritchard et al. (2015:191), Nesbitt et al. (in press:191).

Justification/Ontology: In most early reptiles and Diapsida, for which the three-dimensional structure of the tarsus is known, the fourth distal tarsal abuts the proximal tarsal row at a relatively smooth contact. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Claudiosaurus germaini* (MNHN MAP 1), and *Protorosaurus speneri* (SMNS 55387). By contrast, Lepidosauria exhibit a complex articulation between the calcaneum and the fourth distal tarsal, in which a process on the latter fits into a notch on the former (Brinkman, 1980). However, there may be substantial additional complexity to this character, as evidenced by the possibly intermediate tarsal condition in the Permian *Saurosternon bainii* (Brinkman, 1980). Note that this character has been described as a "lepidosaurian ankle joint" by some past authors (e.g., Gauthier, 1984; Dilkes, 1998).

CHARACTER 190: Pedal centrale, contact with tibia: (0) absent, (1) present.

Examples of past usage: Merck (1997:470), Dilkes (1998:117), Pritchard et al. (2015:192), Nesbitt et al. (in press:192).

Justification/Ontology: No comments.

CHARACTER 191: First distal tarsal: (0) present, (1) absent.

Examples of past usage: Benton (1985:J14 & X12), Gauthier et al (1988a:128), Benton and Allen (1997:43), Jalil (1997:58), Dilkes (1998:119), Müller (2004:76), Senter (2004:73), Pritchard et al. (2015:193), Nesbitt et al. (in press:193).

Justification/Ontology: No comments.

CHARACTER 192: Second distal tarsal: (0) present, (1) absent.

Examples of past usage: Benton (1985:J14), Gauthier et al (1988a:129), Benton and Allen (1997:44), Dilkes (1998:120), Müller (2004:77), Pritchard et al. (2015:194), Nesbitt et al. (in press:194).

Justification/Ontology: No comments.

CHARACTER 193: Fifth distal tarsal: (0) present, (1) absent.

Examples of past usage: Benton (1985:C13 & U4), Gauthier et al (1988a:130), Laurin (1991:E13), Jalil (1997:11), Merck (1997:460), Dilkes (1998:121), Pritchard et al. (2015:195), Nesbitt et al. (in press:195).

Justification/Ontology: Most early reptiles and some early diapsids exhibit a full complement of five distal tarsal ossifications, each positioned proximal to the respective metatarsal. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Petrolacosaurus kansensis* (Reisz, 1981), *Claudiosaurus germaini* (MNHN MAP 1), and *Drepanosaurus unguicaudatus* (MCSNB 5728). A tiny fifth distal tarsal may occur in *Youngina capensis* (Goodrich, 1942) and *Hovasaurus boulei* (Caldwell, 1994). However, in both cases, the tarsal is apparently partially fused to the fourth distal tarsal. Unfortunately, the only specimen of *Youngina capensis* described as exhibiting this condition is now lost (Goodrich, 1942). Fifth distal tarsals are unknown in Sauria (e.g., *Protorosaurus speneri*, SMNS 55387; *Sphenodon punctatus*, Russell and Bauer, 2008).

As with all character involving ossifications that appear later in post-natal ontogeny, caution should be exercised in coding. Caldwell (1994) described a fifth distal tarsal in both *Hovasaurus boulei* and *Claudiosaurus germaini* as the last tarsal ossification to appear. Its possible fusion to the fourth distal tarsal complicates the coding further.

CHARACTER 194: Metatarsal five, shape of proximal postaxial margin: (0) smooth, curved margin; (1) prominent, pointed process (outer process sensu Robinson, 1975).

Examples of past usage: Pritchard et al. (2015:196), Nesbitt et al. (in press:196).

Justification/Ontology: In most early reptiles and some early Diapsida, the fifth metatarsal exhibits a similar proximal articular surface to the other metatarsals. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Petrolacosaurus kansensis* (Reisz, 1981), and *Araeoscelis gracilis* (Reisz et al., 1984). This condition also occurs in Drepanosauromorpha (e.g., Renesto et al., 2010). By contrast, a number of other Permian Diapsida exhibit a prominent "outer process" (following the terminology of Goodrich, 1942), situated at the post-axial margin of the proximal articular surface. This condition occurs in *Youngina capensis* (Goodrich, 1942), *Hovasaurus boulei* (Currie, 1981), and *Claudiosaurus germaini* (MNHN MAP 1). This condition is also prevalent in Sauria (Goodrich, 1916, 1942; Robinson, 1975)

CHARACTER 195: Metatarsal five, angling of primary shaft with proximal tarsal articulation: (0) straight, with proximal tarsal articulation forming straight line with primary shaft; (1) hooked, with proximal tarsal articulation forming right angle with primary shaft.

Examples of past usage: Benton (1985: several characters), Gauthier et al (1988a:132), Laurin (1991:E14), Jalil (1997), Merck (1997:466), Dilkes (1998:122), Müller (2004:80), Senter (2004:70), Ezcurra et al. (2014), Pritchard et al. (2015:197), Nesbitt et al. (in press:197).

Justification/Ontology: In most early reptiles and early Diapsida, the fifth metatarsal is a straight shafted structure, with the proximal tarsal articulation and the distal phalangeal articulation sitting in parallel planes. This condition occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Araeoscelis gracilis* (Reisz et al., 1984), *Youngina capensis* (SAM K7710), *Thadeosaurus colcanapi* (MNHN MAP 360), and *Drepanosaurus unguicaudatus* (MCSNB 5728). Evans (1981) coded *Kuehneosaurus* as exhibiting a straight-shafted fifth metatarsal, which has been followed by Gauthier (1984) and is followed herein. In contrast, the fifth metatarsal is "hooked" in most saurian taxa, with the proximal tarsal articulation situated in a plane perpendicular to that of the distal phalangeal articulation. This condition occurs in *Gephyrosaurus bridensis* (Evans, 1981), *Protorosaurus speneri* (SMNS 55387), *Macrocnemus bassanii* (PIMUZ T/4822), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexanderi* (NMQR 1484), and *Euparkeria capensis* (Ewer, 1965). A similar morphology occurs in *Proganochelys quentstedti* and is commonplace among turtles (Gaffney, 1990).

Goodrich (1916) first described the distribution of hooked fifth metatarsals in fossil and extant reptiles, which he considered characteristic of sauropsid reptiles. Robinson (1975) described the construction of this character in Lepidosauria in detail, equivocating on the possible homology of the structure in Lepidosauria, Archosauria, and Testudines. Some authors (e.g., Benton, 1985) have noted that the fifth metatarsal in lepidosaurs exhibits a second inflection in a dorsal-plantar plane. Further study of this character would benefit from developmental data on the on the form of the hooking in lepidosaurs and archosaurs.

CHARACTER 196: Metatarsal five, concavity along preaxial margin: (0) present; (1) absent, creating blocky metatarsal five.

Examples of past usage: Benton (1985:G3), Benton and Allen (1997:47), Jalil (71), Pritchard et al. (2015:198), Nesbitt et al. (in press:198).

Justification/Ontology: In most saurian reptiles that exhibit a hooked fifth metatarsal, the pre-axial surface of the bone is concave. This produces a distinctly L-shaped ossification, as seen in *Protorosaurus speneri* (SMNS 55387), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexanderi* (NMQR 1484), and *Gephyrosaurus bridensis* (Evans, 1981). By contrast, some Tanystropheidae lack this concavity, producing a roughly quadrangular fifth metatarsal. This condition occurs in *Tanystropheus longobardicus* (MCSN BES SC 1018), *Amotosaurus rotfeldensis* (SMNS 54810), *Langobardisaurus pandolfii* (MCSNB 2883), and *Tanytrachelos ahynis* (YPM VP 8600).

CHARACTER 197: Pedal digits, morphology of digit five: (0) proximodistally shorter than proximal phalanx of digit four; (1) proximodistally elongate, longer than all other proximal phalanges.

Examples of past usage: Benton (1985), Benton and Allen (1997), Jalil (1997), Merck (1997:459), Dilkes (1998:138), Pritchard et al. (2015:199), Nesbitt et al. (in press:199).

Justification/Ontology: No comments.

CHARACTER 198: Heterotopic ossifications: (0) absent in a minimum of 5 individuals, (1) present.

Examples of past usage: Benton (1985:G2), Benton and Allen (1997:48), Jalil (1997:60), Merck (1997:338), Pritchard et al. (2015:200), Nesbitt et al. (in press:200).

Justification/Ontology: A small number of Triassic reptiles exhibit two pairs of broad, anterolaterally pointed ossifications lateral to the first few caudal vertebrae. These elements occur in some specimens of *Tanystropheus longobardicus* (e.g., PIMUZ T/2817; Wild, 1973; Rieppel, 1976) and *Tanytrachelos ahynis* (e.g., VMNH 120048; Olsen, 1979). The presence and absence of these elements in a roughly equal proportion of both *Tanystropheus* and *Tanytrachelos* (Casey, 2005; Casey et al., 2007) has led to the hypothesis that they are a sexually dimorphic feature.

The exact function of these elements remains unknown. Wild (1973:123) tentatively dubbed them “peniselemente.” He later considered these features in *Tanystropheus* potential homologs to similar ossifications in some squamate groups (reviewed by Rieppel, 1976). However, Kluge (1982) noted that even within Squamata, these bones are diverse in shape and topology and may not be homologous with one another. For the moment, I retain this character without further morphological description, as the two taxa incorporated that exhibit these ossifications present them in a very similar way. Following Pritchard et al. (2015), these bones are only coded as “0” if they are not present in at least five relevant specimens, allowing >95% probability that members of both sexes are present in the sample.

CHARACTER 199: Maxilla, medial surface dorsal to tooth row: (0) smooth, (1) prominent anteroposteriorly oriented ridge present.

Examples of past usage: Nesbitt et al. (in press:201).

Justification/Ontology: The maxilla in most early reptiles and Permo-Triassic diapsids is smooth dorsal to the articulations for the palatal elements (e.g., *Captorhinus aguti*, Fox and Bowman, 1966; *Youngina capensis*, AMNH FARB 5561; *Tanystropheus longobardicus*, MCSN BES SC 265). By contrast, there is a prominent anteroposteriorly running keel on the medial surface of the maxilla just ventral to the base of the ascending process of that element in *Azendohsaurus madagaskarensis* (Flynn et al., 2010) and *Azendohsaurus laaroussii* (Gauffre, 1993). This structure is distinct from the palatal processes of the maxillae developed in derived archosauriforms (e.g., *Euparkeria capensis*, Ewer, 1965; *Batrachotomus kupferzellensis*, Gower, 1999; *Sphenosuchus acutus*, Walker, 1990).

CHARACTER 200: Maxilla, dorsal portion, shape: (0) dorsal process simply tapers to point dorsally; (1) dorsal process of the maxilla has a posteriorly concave margin.

Examples of past usage: Nesbitt et al. (in press:202).

Justification/Ontology: Primitively among reptiles and Diapsida, the portion of the maxilla dorsal to the alveoli is a relatively simple, dorsally convex structure. The height of this dorsal process is directly related to the contribution of the lacrimal to the lateral surface of the face, but the shape remains relatively consistent. Simple, dorsally convex dorsal processes occur in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561), *Protorosaurus speneri* (USNM 442453), *Czatkowiella harae* (Borsuk-Bialynicka and Evans, 2009), *Sphenodon punctatum* (Evans, 2008), and possibly *Trilophosaurus buettneri* (Parks, 1969).

A contrasting condition occurs in subset of Archosauromorpha, in which the dorsal process of the maxilla is deeply concave on its posterior margin. This condition occurs in *Macrocnemus bassanii* (PIMUZ T/4822), *Tanystropheus longobardicus* (MCSN BES SC 1018; PIMUZ T/2819), *Azendohsaurus madagaskarensis* (UA 8-29-97-160), and *Azendohsaurus laaroussii* (MNHN ALM 365). This condition may also occur in *Prolacerta broomi* (e.g., BP/1 5880). This condition also occurs in Archosauriformes, where the concave portion of the maxilla forms that bone's contribution to the antorbital fenestra (e.g., *Proterosuchus fergusi*, BP/1 4016; *Garjainia prima*, PIN 2334/5).

Nesbitt et al. (in press) first employed this character to describe the comparable shape of the maxilla in *Azendohsaurus* and Archosauriformes, with the second state describing a "distinct, dorsal process of the maxilla." However, this dorsal expansion of the bone is not particularly different from the condition in other saurians (e.g., *Protorosaurus speneri*, USNM 442453; *Trilophosaurus buettneri*, TMM 31025-207), aside from the posterior concavity in the bone.

The ontogenetic series in *Tanystropheus longobardicus* provides context for the development of the dorsal process. In juveniles (e.g., MCSN BES SC 1018), the process is very similar in shape to *Azendohsaurus madagaskarensis*. However, the process becomes proportionally much shorter through the ontogeny of *Tanystropheus* (e.g., PIMUZ T/2819), but retaining the prominent posterior concavity. Thus, we have modified this character to accommodate this morphology.

CHARACTER 201: Maxilla, anterolateral surface, large anteriorly opening foramen: (0) present, positioned just anterodorsal to primary row of neurovascular foramina; (1) absent.

Examples of past usage: Nesbitt et al. (in press:203).

Justification/Ontology: No comments.

CHARACTER 202: Maxilla, anteromedial surface, palatal process: (0) absent, (1) present but fails to reach the midline, (2) present and touches its antimere at the midline.

Examples of past usage: Nesbitt (2011), Nesbitt et al. (in press:204).

Justification/Ontology: No comments.

CHARACTER 203: Jugal, anterior process: (0) slender and tapering, (1) broad and expanded anteriorly.

Examples of past usage: Nesbitt (2011), Nesbitt et al. (in press:205).

Justification/Ontology: The anterior process of the jugal in most early diapsids is a slender, tapering structure that frames the anteroventral margin of the orbit. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Orovenator mayorum* (Reisz et al., 2011), *Youngina capensis* (BP/1 3859, see fig. 6A), *Protorosaurus speneri* (USNM 442453), *Vallesaurus cenensis* (MCSNB 4751), *Prolacerta broomi* (BP/1 2675), *Mesosuchus browni* (SAM K6536), and *Azendohsaurus madagaskarensis* (FMNH PR 2751). Similar jugals occur in most lepidosaurs (e.g., *Gephyrosaurus bridensis*, Evans, 1980; *Sphenodon punctatum*, Evans, 2008; *Shinisaurus crocodilurus*, Conrad, 2004). The process in *Proterosuchus alexanderi* (NMQR 1484, see fig. 6C) and "Chasmatosaurus" *yuani* (IVPP V4067) is also anteriorly tapering, although it seems to arc slightly anteromedially against the maxilla.

The anterior process of the jugal expands dorsoventrally in some archosauriforms, such that it forms more of the lateral surface of the face. This is evident in *Erythrosuchus africanus* (BP/1 5207), *Osmolskina czatkowicensis* (ZPAL RV/484), *Chanaresuchus bonapartei* (MCZ 4037, see fig. 6E), and *Batrachotomus kupferzellensis* (Gower, 1999). Similarly broadened anterior processes occur in early reptiles (e.g., *Captorhinus aguti*, Fox and Bowman, 1966) and some rhynchosaurs (*Bentonyx sidensis*, Hone and Benton, 2008; *Teyumbaita sulcognathus*, Montefeltro et al., 2010).

CHARACTER 204: Ectopterygoid, articulation with the pterygoid: (0) contacts part of the lateral edge of the pterygoid, (1) contacts the entire lateral edge of the pterygoid.

Examples of past usage: Dilkes (1998:42), Müller (2004:93), Nesbitt (2011), Nesbitt et al. (in press:206).

Justification/Ontology: In most early diapsids, the medial portion of the ectopterygoid contacts on a small portion of the anterolateral surface of the transvers process of the pterygoid. This condition occurs in *Youngina capensis* (Gow, 1975), *Azendohsaurus madagaskarensis* (FMNH PR 2751), *Mesosuchus browni* (SAM K6536), *Trilophosaurus buettneri* (TMM 31025-140), and *Gephyrosaurus bridensis* (Evans, 1980). By contrast, an anteroposteriorly elongate contact in which the ectopterygoid fits against the entire lateral margin of the transverse process occurs in *Proterosuchus fergusi* (BP/1 3393), *Erythrosuchus africanus* (Gower, 2003)*, Teyumbaita sulcognathus* (Montefeltro et al., 2010), and *Clevosaurus hudsoni* (Fraser, 1988).

CHARACTER 205: Quadrate, proximal portion, posterior side: (0) continuous with the shaft, (1) expanded and hooked.

Examples of past usage: Nesbitt et al. (in press:207).

Justification/Ontology: In most early diapsids and saurians, the posterodorsal aspect of the quadrate is smoothly continuous with the lower portion or "shaft" of the element. This condition may be see in basal taxa (e.g., *Youngina capensis*, SAM K7578; the *Coelophysis* Quarry drepanosaurid, AMNH FARB 30834) and most saurians, such as *Protorosaurus speneri* (USNM 442453), *Prolacerta broomi* (BP/1 5375, see fig. 6B), *Proterosuchus alexanderi* (NQMR 1484, see fig. 6C), *Shinisaurus crocodilurus* (Conrad, 2004), and *Sphenodon punctatum* (Evans, 2008). A distinct condition occurs in *Teraterpeton hrynewichorum* (Sues, 2003), *Trilophosaurus buettneri* (TMM 31025-140, see fig. 6D), and *Azendohsaurus madagaskarensis* (FMNH PR 2751), in which the posterodorsal portion of the quadrate hooks posteriorly such that it dorsally overlies the shaft of the bone. This condition does not occur *Pamelaria dolichotrachela*, a purported close relative of the aforementioned taxa (Sen, 2003). This condition may also occur in *Langobardisaurus pandolfii* (MFSN 1921) and a specimen of *Tanystropheus* (PIMUZ T/3901) established as the type of *Tanystropheus meridensis* by Wild (1980a). However, the crushed nature of both specimens makes study of the elements difficult.

CHARACTER 206: Parabasisphenoid, orientation: (0) horizontal, (1) more vertical.

Examples of past usage: Gower and Sennikov (1996:7), Nesbitt (2011), Nesbitt et al. (in press:208).

Justification/Ontology: In most early reptiles, the parabasisphenoid is a horizontally oriented structure. Following Gower and Sennikov (1996), this involves the parabasisphenoid contribution to the ventral surface of the braincase being roughly in line with the basipterygoid processes. This condition occurs in *Captorhinus aguti* (Price, 1935), *Youngina capensis* (Gardner et al., 2010), *Prolacerta broomi* (BP/1 2675), and *Proterosuchus fergusi* (BP/1 3393). In contrast, the bone is more vertically oriented in other taxa, such that the origins of the basipterygoid processes are ventrally positioned relative to the ventral surface of the braincase. This condition occurs in *Trilophosaurus buettneri* (TMM 31025-244), *Azendohsaurus madagaskarensis* (FMNH PR 2765), and *Erythrosuchus africanus* (NHMUK R3592). As noted by Gower and Sennikov (1996), the degree of verticalization in derived archosaurs is subject to much continuous variation. This character would benefit from morphometric study of the braincase throughout Archosauromorpha.

CHARACTER 207: Parabasisphenoid, semilunar depression on the lateral surface of the basal tubera: (0) present, (1) absent.

Examples of past usage: Gower and Sennikov (1996:11), Nesbitt (2011), Nesbitt et al. (in press:209).

Justification/Ontology: The semilunar depression is an anteroventrally curved concavity in the posterolateral surface of the parabasisphenoid. Gower and Sennikov (1996:897) noted that the function of the structure was unknown. No such depression is present in *Youngina capensis* (Gardner et al., 2010) and likely the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834). The semilunar depression is noted in *Trilophosaurus buettneri* (TMM 31025-244), *Azendohsaurus madagaskarensis* (FMNH PR 2765), *Prolacerta broomi* (BP/1 2675), *Proterosuchus fergusi* (BP/1 3393), and *Erythrosuchus africanus* (Gower, 1997). No such depression occurs in extant lepidosaurs (e.g., *Shinisaurus crocodilurus*, Bever et al., 2005; *Sphenodon punctatum*, Gower and Weber, 1998) or archosaurs (Gower and Sennikov, 1996).

CHARACTER 208: Dentary, posteroventral portion: (0) just meets the angular, (1) laterally overlaps the anteroventral portion of the angular.

Examples of past usage: Nesbitt (2011:164), Nesbitt et al. (in press:210).

Justification/Ontology: The dentary meets the anterodorsal margin of the angular in most early reptiles and early diapsids. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Protorosaurus speneri* (USNM 442453), *Tanystropheus longobardicus* (MCSN BES SC 1018), *Mesosuchus browni* (SAM K6536), *Trilophosaurus buettneri* (TMM 31025-5), *Prolacerta broomi* (UCMP 37151), and *Proterosuchus alexanderi* (NMQR 1484). In contrast, the posteroventral portion of the dentary laps over the anterolateral surface of the angular in *Erythrosuchus* (Gower, 2003), and Archosauria (e.g., *Batrachotomus kupferzellensis*, Gower, 1999; *Coelophysis bauri*, Colbert, 1989).

CHARACTER 209: Dentition, crown height of the upper dentition compared with lower dentition: (0) similar tooth crown height, (1) the upper dentition is shorter relative to the taller lower dentition.

Examples of past usage: Nesbitt et al. (in press:211).

Justification/Ontology: As described in Nesbitt et al. (in press), the maxillary and dentary dentition in *Azendohsaurus madagaskarensis* and *A. laaroussii* are of different sizes. This led Flynn et al. (1999) to consider there to be two "prosauropod" dinosaur taxa in the *Azendohsaurus* bonebed.

CHARACTER 210: Antorbital fossa: (0) restricted to the lacrimal; (1) restricted to the lacrimal and dorsal process of the maxilla; (1) present on the lacrimal, dorsal process of the maxilla and the dorsal margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra).

Examples of past usage: Nesbitt (2011), Nesbitt et al. (in press:212).

Justification/Ontology: Nesbitt (2011) described this character in detail. The antorbital fossa is a small, restricted structure in the earliest archosauriforms (e.g., *Proterosuchus alexanderi*, NMQR 1484; "Chasmatosaurus" *yuani*, IVPP 36315).

CHARACTER 211: Anterior cervical vertebrae (presacral vertebrae 3-5), postzygapophyses: (0) separated posteriorly, (1) connected through a horizontal lamina (=transpostzygapophyseal lamina) with a notch at the midline.

Examples of past usage: Nesbitt et al. (in press:213).

Justification/Ontology: The distribution of this lamina is discussed in Nesbitt et al. (in press). Since the submission of that publication, I have recognized nearly identical transpostzygapophyseal laminae in two early archosauromorphs: the tanystropheid *Augustaburiania vatagini* (PIN 1043/587) and the basal taxon *Czatkowiella harae* (ZPAL unnumbered specimen from Czatkowice quarry).

CHARACTER 212: Cervical centra 3-5, length versus height: (0) length greater than height, (1) subequal.

Examples of past usage: Benton and Allen (1997:19), Dilkes (1998:81), Müller (2004:174), Senter (2004:28), Nesbitt et al. (in press:214).

Justification/Ontology: The dorsoventral height/anteroposterior length ratio in the anterior cervical centra early reptiles and diapsids show a high degree of variability. In captorhinomorphs, the ratio is roughly subequal (Dilkes and Reisz, 1986). Among the early diapsids, *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), and *Claudiosaurus germaini* (Carroll, 1981) have centra that are substantially longer than dorsoventrally tall. *Youngina capensis* (BP/1 3859), *Hovasaurus boulei* (Currie, 1981), and *Thadeosaurus colcanapi* (Carroll, 1981) exhibit shorter centra.

Among saurian reptiles, many early archosauromorphs exhibit proportionally elongate cervical centra. These include *Protorosaurus speneri* (USNM 442453), *Trilophosaurus buettneri* (TMM 31025-140, see fig. 13B), *Azendohsaurus madagaskarensis* (UA 7-20-99-653, 8-28-98-306), *Tanystropheus longobardicus* (MCSN BES SC 1018), *Boreopricea funerea* (PIN 3708/1), and *Proterosuchus fergusi* (BP/1 3393). Shorter centra occur in *Gephyrosaurus bridensis* (Evans, 1981), *Sphenodon punctatum* (Hoffstetter and Gasc, 1969), *Erythrosuchus africanus* (NMQR 3765, see fig. 13A), and *Sarmatosuchus otschevi* (PIN 2865/68). As noted in my discussion of character 104, the relative elongation of the cervical centra may correlate closely to the length and slenderness of the cervical ribs.

CHARACTER 213: Dorsal vertebrae, diapophysis, position: (0) anterior portion of the neural arch/centrum, (1) anteroposterior middle of the neural arch/centrum.

Examples of past usage: Nesbitt et al. (in press:215).

Justification/Ontology: As noted in Nesbitt et al. (in press), the costal articulations in the dorsal vertebrae of *Trilophosaurus buettneri* (TMM 31025-140), *Trilophosaurus jacobsi* (Spielmann et al., 2008), and *Spinosuchus caseanus* (Spielmann et al., 2009) are positioned near the anteroposterior midpoint of the centrum. I note that a similar condition is reported by Renesto (2005) in a juvenile specimen of *Tanystropheus longobardicus*. This variation needs further study, as the dorsal vertebrae in PIMUZ T/2787 seem to be positioned anteriorly on the dorsal vertebrae.

CHARACTER 214: Sacral ribs, anteroposterior length of the first primordial sacral rib versus the second primordial sacral rib, dorsal view: (0) primordial sacral rib one is longer anteroposteriorly than primordial sacral rib two, (1) primordial sacral rib two is about the same length or longer anteroposteriorly than primordial sacral rib one.

Examples of past usage: Nesbitt et al. (in press:216).

Justification/Ontology: Among known diapsid taxa, the latter condition is found in the sacra of *Pamelaria dolichotrachela*, *Azendohsaurus*, and *Trilophosaurus* (Nesbitt et al., in press). To the description by Nesbitt et al. (in press), I note that the sacral ribs in *Rautiania* sp. (of which there are three in PIN 5130/53) are all of roughly equal length, such that the taxon should be coded as "1." Also, *Icarosaurus siefkeri* (AMNH FARB 2101) exhibits sacral ribs of roughly equal anteroposterior lengths.

CHARACTER 215: Anterior caudal vertebrae, neural spines: (0) inclined posteriorly, (1) vertical.

Examples of past usage: Nesbitt et al. (in press:217).

Justification/Ontology: The anterior caudal neural spines in most early reptiles and early diapsids are vertically inclined. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), and *Hovasaurus boulei* (Currie, 1981a). This condition also occurs in a range of early saurian taxa (e.g., *Trilophosaurus buettneri*, TMM 31025-140; *Prolacerta broomi*, BP/1 2676; *Protorosaurus speneri*, SMNS cast of WMsN P 47361). By contrast, a number of other saurian taxa exhibit posterodorsally inclined neural spines in *Proterosuchus alexanderi* (NMQR 1484), *Azendohsaurus madagaskarensis* (UA 8-29-97-172), *Langobardisaurus pandolfii* (MFSN 1921), and *Mesosuchus browni* (SAM K6046). Nesbitt et al. (in press) erroneously noted that this character was employed by Dilkes (1998).

CHARACTER 216: Caudal vertebrae, length of the anterior caudal vertebrae (caudal vertebrae 1-10) relative to posterior caudal vertebrae (25+): (0) nearly the same length, (1) posterior caudal vertebrae much longer.

Examples of past usage: Nesbitt et al. (in press:218).

Justification/Ontology: As noted by Nesbitt et al. (in press), elongation of the posterior caudal centra occurs in the two species of *Trilophosaurus*. I have noted the same condition in *Boreopricea funerea* (PIN 3708/1), although the exact position of a specimen within the column is more difficult to determine in that taxon due to its disarticulation.

CHARACTER 217: Scapula, entire anterior margin: (0) straight/convex or partially concave, (1) markedly concave.

Examples of past usage: Merck (1997:372), Nesbitt (2011:217), Nesbitt et al. (in press:219).

Justification/Ontology: No comments.

CHARACTER 218: Humerus, distal end, transverse width: (0) less than 2.5 times the minimum width of the shaft, (1) equal or more than 2.5 times the minimum width of the shaft.

Examples of past usage: Laurin (1991:D4), Senter (2004:47), Nesbitt et al. (in press:221).

Justification/Ontology: No comments.

CHARACTER 219: Manual ungual, length: (0) about the same length or shorter than the last phalanx of the same digit, (1) distinctly longer than the last phalanx of the same digit.

Examples of past usage: Nesbitt et al. (in press:222).

Justification/Ontology: No comments.

CHARACTER 220: Ilium, ventral margin of the acetabulum: (0) convex, (1) concave.

Examples of past usage: Senter (2004:56), Nesbitt et al. (in press:223).

Justification/Ontology: No comments.

CHARACTER 221: Ilium, iliac blade, maximum length: (0) less 3 times its maximum height, (1) more than 3 times its maximum height.

Examples of past usage: Nesbitt et al. (in press:224).

Justification/Ontology: No comments.

CHARACTER 222: Ischium length: (0) about the same length or shorter than the dorsal margin of iliac blade, (1) markedly longer than the dorsal margin of iliac blade.

Examples of past usage: Benton (1985:D4), Benton and Allen (1997:34), Nesbitt et al. (in press:225).

Justification/Ontology: No comments.

CHARACTER 223: Femur, ridge of attachment of the *M. caudifemoralis*: (0) bladelike with a distinct asymmetric apex located medially, (1) low and without a distinct medial asymmetrical apex (= fourth trochanter).

Examples of past usage: Benton (1985:I4), Senter (2004:62), Nesbitt et al. (in press:226).

Justification/Ontology: No comments.

CHARACTER 224: Femur, anterior trochanter (M. iliofemoralis cranialis insertion): (0) absent, (1) present.

Examples of past usage: Nesbitt et al. (in press:227).

Justification/Ontology: No comments.

CHARACTER 225: Astragalus, tibial and fibular articulations: (0) separated by a gap (or notch of Gower, 1996), (1) continuous.

Examples of past usage: Nesbitt et al. (in press:228).

Justification/Ontology: No comments.

CHARACTER 226: Calcaneum, calcaneal tuber, shaft proportions at the midshaft of the tuber: (0) taller than broad, (1) about the same or broader than tall.

Examples of past usage: Nesbitt et al. (in press:229).

Justification/Ontology: No comments.

CHARACTER 227: Calcaneum, articular surfaces for fibula and distal tarsal IV: (0) separated by a nonarticular surface, (1) continuous.

Examples of past usage: Nesbitt et al. (in press:230).

Justification/Ontology: No comments.

CHARACTER 228: Calcaneum, calcaneal tuber, orientation relative to the transverse plane: (0) lateral, less the 20 degrees posteriorly; (1) deflected between 21-49 degrees posterolaterally; (2) between 50-90 degrees posteriorly.

Examples of past usage: Nesbitt et al. (in press:231).

Justification/Ontology: No comments.

CHARACTER 229: Metatarsal IV: (0) longer than metatarsal III, (1) about the same length or shorter than metatarsal III.

Examples of past usage: Dilkes (1998:124), Senter (2004:68), Nesbitt et al. (in press:232).

Justification/Ontology: No comments.

CHARACTER 230: Pes, unguals, ventral tubercle: (0) absent or small, (1) well developed and extended ventral to the articular portion of the ungual.

Examples of past usage: Nesbitt et al. (in press:233).

Justification/Ontology: No comments.

CHARACTER 231: Distal pedal phalanges, distal articular portion: (0) lateral and medial sides parallel or near parallel, (1) lateral and medial sides converging anteriorly.

Examples of past usage: Nesbitt et al. (in press:234).

Justification/Ontology: No comments.

CHARACTER 232: Pes, penultimate phalanx (last phalanx before the ungual): (0) shorter than the more proximal phalanx, (1) significantly longer than the more proximal phalanx.

Examples of past usage: Renesto et al. (2010:20), Nesbitt et al. (in press:235).

Justification/Ontology: No comments.

CHARACTER 233: Osteoderms: (0) absent, (1) present.

Examples of past usage: Nesbitt et al. (in press:236).

Justification/Ontology: No comments.

CHARACTER 234: Prefrontal, orbital margin, lateral surface: (0) smooth or slight grooves present, (1) rugose sculpturing present.

Examples of past usage: Nesbitt et al. (in press:237).

Justification/Ontology: In most early diapsids and saurian reptiles, the orbital margin of the prefrontal bone is smoothly sculptured, similar to the condition of the other bones of the orbital margin. This condition occurs in *Youngina capensis* (AMNH FARB 5561), *Prolacerta broomi* (BP/1 2675), *Macrocnemus bassanii* (PIMUZ T/4822), and *Protorosaurus speneri* (USNM 442453). By contrast, a number of other early saurians exhibit thick, rugose ridges on the orbital margin of the prefrontal bone. This occurs in *Azendohsaurus madagaskarensis* (Flynn et al., 2010), *Kuehneosaurus latus* (AMNH FARB 7764).

CHARACTER 235: Gastralia: (0) abundant, with individual gastral elements nearly contacting, (1) small in number (= well separated) or unossified.

Examples of past usage: Gauthier et al (1988a:136), Merck (1997:339), Dilkes (1998:92), Müller (2004:109), Renesto et al. (2010:14), Pritchard et al. (2015: 137), Nesbitt et al. (in press:238).

Justification/Ontology: Reptiles ancestrally exhibit a series of small, slender, dermal ossifications that line the ventral surface of the trunk region. These small, delicate elements form a "gastral basket," of bones interlocking near the midline. Gastralia are reported in *Petrolacosaurus kansensis* (Reisz, 1981), *Thadeosaurus colcanapi* (Currie and Carroll, 1984), *Claudiosaurus germaini* (Carroll, 1981), *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Tanystropheus longobardicus* (MCSN BES SC 1018), *Proterosuchus alexanderi*

(NMQR 1484), *Erythrosuchus africanus* (NMQR 3765), and many archosaurs (e.g., Romer 1956).

Rather than simply code for the absence of gastralia (as in Pritchard et al., 2015), I follow Nesbitt et al. (in press) in coding for the rarity or apparent absence of gastralia. This is only done for fossil material that preserves substantial portions of the trunk, regardless of articulation. Gastralia are extremely weakly ossified or absent in *Azendohsaurus madagaskarensis* (Nesbitt et al., in press), *Trilophosaurus buettneri* (TMM skeletal materials), known drepanosauromorphs (e.g., *Hypuronector limnaios*, AMNH FARB 7759; *Drepanosaurus unguicaudatus*, MCSNB 5728), and squamates (e.g., Gauthier et al., 1988a). The absence of gastralia is commonly recovered as a squamate synapomorphy (e.g., Gauthier et al., 1988a).

CHARACTER 236: Astragalus, margin between tibial and fibular facets: (0) margin grades smoothly into anterior hollow, (1) prominent ridge separates margin from anterior hollow.

Examples of past usage: Nesbitt et al. (in press:239).

Justification/Ontology: In early reptiles and early diapsids, the anterior hollow of the astragalus and the gap between the tibial and fibular facets is smoothly continuous. This can be seen in *Araeoscelis gracilis* (MCZ 412), *Tanystropheus longobardicus* (MCSN V 3730), *Prolacerta broomi* (BP/1 2676), and *Trilophosaurus buettneri* (TMM 31025-140). By contrast, a ridge running between the dorsal surfaces of the tibial and fibular facets separates these two cavities in some archosauromorphs. I note this condition in *Protorosaurus speneri* (SMNS 55387, see fig. 21C), *Azendohsaurus madagaskarensis* (Nesbitt et al., in press), and *Proterosuchus alexanderi* (NMQR 1484).

It is critical to note that at least one taxon is polymorphic for this character. In the NMMNH collections of *Trilophosaurus jacobs*i from the Kahle Quarry bonebed, the sample of astragali can exhibit either condition. Comparison with other taxa known from a larger sample suggest that polymorphism is not typical. As such, *Trilophosaurus jacobsi* is the only taxon coded as polymorphic, and codings based on a small sample of specimens should be treated with caution.

It should also be noted that some derived archosauriforms exhibit no gap between the facets, and these are coded as "-" for this character (e.g., *Euparkeria capensis*, Ewer, 1965). It is not clear if the ridge separating the two cavities described above is a predecessor of the convergence of facets described above.

CHARACTER 237: Dentary, anterior portion in lateral view: (0) in the same horizontal plane as the middle portion of the dentary, (1) anteroventrally deflected.

Examples of past usage: Nesbitt et al. (in press:241).

Justification/Ontology: As noted in Nesbitt et al. (in press), characters describing the anteroventral deflection of the anterior tip of the dentary were first used in archosaur datasets. For that study, they noted slight anteroventral deflection in the jaw of *Azendohsaurus madagaskarensis* (FMNH PR 2751), *Trilophosaurus buettneri* (TMM 31025-140), and *Tanystropheus longobardicus* (MCSN BES SC 1018). They also suggested that this downturn might occur in *Protorosaurus speneri*, but study of USNM 442453 and SMNS 55387 strongly suggests that this character state is not present in that taxon.

CHARACTER 238: Quadrate, posterior margin, distal half, lateral view: (0) concave, (1) convex.

Examples of past usage: Nesbitt et al. (in press:242).

Justification/Ontology: Nesbitt et al. (in press) noted a prominent convexity on the posterior surface of the ventral half of the quadrate. This produces a sigmoid shape in lateral view among those reptiles with a posterior concavity to the quadrate. This character state is noted in *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (FMNH PR 2751), and *Proterosuchus fergusi* (BP/1 3393). Nesbitt et al. (in press) coded *Prolacerta broomi* as exhibiting this convexity, which does occur in BP/1 5375. However, this character state is less apparent in a smaller individual of *Prolacerta broomi* (UCMP 37151). As a result, I change this coding for *Prolacerta* to polymorphic.

CHARACTER 239: Atlas, centrum: (0) separate from axial intercentrum, (1) fused to axial intercentrum.

Examples of past usage: Nesbitt et al. (in press:243).

Justification/Ontology: No comments.

CHARACTER 240: Axis, neural spine, shape: (0) dorsal margin inclined anteroventrally, (1) dorsal margin inclined anterodorsally.

Examples of past usage: Nesbitt et al. (in press:244).

Justification/Ontology: In some early reptiles, early diapsids, and in most early saurians, the neural spine of the axis is horizontalized posteriorly before curving strongly anteroventrally. This occurs in *Captorhinus aguti* (Fox and Bowman, 1966), *Hovasaurus boulei* (Currie, 1981), possibly in *Youngina capensis* (SAM K7710), *Protorosaurus speneri* (USNM 442453), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexanderi* (NMQR 1484), and *Erythrosuchus africanus* (NMQR 3765). By contrast, the axial neural spine slopes strongly anterodorsally in other early diapsids (e.g., *Petrolacosaurus kansensis*, Reisz, 1981; *Claudiosaurus germaini*, Carroll, 1981) and Tanystropheidae (e.g., *Macrocnemus bassanii*, MCSN V 457; *Tanystropheus longobardicus*, MCSN BES SC 1018). A substantially weaker anterodorsal incline occurs in some specimens of *Prolacerta broomi* (BP/1 2675) and *Czatkowiella harae* (Borsuk-Bialynicka and Evans, 2009).

CHARACTER 241: Presacral vertebrae, 5th vertebra to the sacrum, neural arch, posterior edge: (0) spinopostzygapophyseal laminae absent, (1) spinopostzygapophyseal laminae present.

Examples of past usage: Nesbitt et al. (in press:245).

Justification/Ontology: No comments.

CHARACTER 242: Dentary, lateral exposure, posterior extent: (0) posteriormost extent of dentary on dorsum of mandible, (1) posteriormost extent of dentary positioned ventral to surangular.

Examples of past usage: Nesbitt et al. (in press:246).

Justification/Ontology: No comments.

CHARACTER 243: Premaxilla, contribution to palate: (0) absent, (1) flattened palatal processes present.

Examples of past usage: Nesbitt et al. (in press:247).

Justification/Ontology: The premaxillae in many early reptiles do not exhibit any contribution to the ventral face of the palate. The vomer extends anteriorly to just posterior to the alveolar portion. This occurs in *Petrolacosaurus kansensis* (Reisz, 1981), likely the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Azendohsaurus madagaskarensis* (UA 9-9-98-560), *Ctenosaura pectinata* (Oelrich, 1956), *Gephyrosaurus bridensis* (Evans, 1980), and *Sphenodon punctatum* (Evans, 2008). By contrast, the premaxilla exhibits prominent, medially directed plates of bone in some saurian taxa, forming a bony palate. This condition occurs in *Prolacerta broomi* (UCMP 37151), *Proterosuchus goweri* (NMQR 880), "Chasmatosaurus" *yuani* (IVPP 36315), *Boreopricea funerea* (PIN 3708/2), and *Trilophosaurus buettneri* (TMM 31025-207). A similar process occurs in the putative early kuehneosaurids *Pamelina polonica* (Evans, 2009). *Youngina capensis* (BP/1 2871) also appears to exhibit a similar condition.

There is diversity in the shape of the palatal contributions of the premaxillae. In *Pamelina polonica*, the palatal process has its base at the posteromedial margin of the premaxilla, framing a prominent choanal incisure laterally. By contrast, prominent, flattened plates fill the entire palatal space framed by the premaxillae in *Trilophosaurus buettneri* (TMM 31025-207) and *Boreopricea funerea* (PIN 3708/2). In *Prolacerta broomi* and *Proterosuchus* spp., the plates are even more pronounced, extending posteriorly beyond the premaxilla-maxilla suture (Gow, 1975). Further study of these structures, especially in Archosauromorpha, is needed to fully understand the homologies of these structures. For the time being, I consider palatal processes to be homologous.

CHARACTER 244: Cervical vertebrae, hypapophysis: (0) absent, ventral surface of centrum unexpanded posteroventrally; (1) posteroventral surface of centrum exhibits massive, posteroventrally projecting crest.

Examples of past usage: Benton (1985), Gauthier et al (1988a:79), Renesto et al. (2010:4).

Justification/Ontology: In most early diapsid reptiles and early Sauria, the posteroventral surface of the cervical centra is equivalent in depth to the remainder of the centrum. This condition occurs in *Araeoscelis gracilis* (Vaughn, 1955), *Youngina capensis* (BP/1 3859), *Protorosaurus speneri* (USNM 442453), *Tanystropheus longobardicus* (MCSN BES SC 1018), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Proterosuchus fergusi* (BP/1 3393), and most Triassic archosaurs (e.g., *Batrachotomus kupferzellensis*, Gower and Schoch, 2009; *Coelophysis bauri*, Colbert, 1989). By contrast, some saurians exhibit a prominent, transversely flattened crest that expands posteroventrally from the centrum. This can be seen in some modern squamates (e.g., Hoffstetter and Gasc, 1969; Conrad, 2006) and drepanosauromorphs (e.g., *Vallesaurus cenensis*, MCSNB 4751; *Megalancosaurus preonensis*, MPUM 8437).

CHARACTER 245: Terminal caudal vertebra(e): (0) similar in morphology to other posterior caudal vertebrae, (1) modified into claw-like element.

Examples of past usage: Senter (2004:37), Renesto et al. (2010:40).

Justification/Ontology: In most reptiles, the distal tip of the tail is formed by a continuously tapering series of caudal vertebrae. The tip of the tail is rarely preserved in fossil reptiles, but in most cases this tapering is present (e.g., *Protorosaurus speneri*, Gottmann-Quesada and Sander, 2009; *Langobardisaurus pandolfii*, MFSN 1921; *Hypuronector limnaios*, AMNH FARB 7759; *Vallesaurus cenensis*, MCSNB 4751). In contrast, the distal tip of the tail in some drepanosaurid diapsids exhibits a large ossification that closely resembles and ungual, complete with a lateral groove. This structure occurs in *Megalancosaurus preonensis* (MFSN 18443, see fig. 15C) and *Drepanosaurus unguicaudatus* (MCSNB 5728). This may be a modification of the terminal caudal vertebra(e), but hey, it's a drepanosaur. Who the hell knows?

CHARACTER 246: Anterior chevrons, hemal spine morphology: (0) element forms single spine, (1) element bifurcates ventrally.

Examples of past usage: Merck (1997:337), Senter (2004:41), Renesto et al. (2010:37).

Justification/Ontology: Chevron bones in most early diapsids and reptiles remain a single, elongate shaft throughout their proximodistal lengths. In some drepanosauromorphs, the distal shaft of the chevron bifurcates in the anterior portion of the tail. This occurs in *Drepanosaurus unguicaudatus* (MCSNB 5728), *Megalancosaurus preonensis* (MFSN 18443, see fig. 15C), and a specimen from the Argilliti di Riva di Solto of Italy referred to *Drepanosaurus* sp. (Renesto and Paganoni, 1995).

CHARACTER 247: Anteriormost chevrons, hemal spine morphology: (0) bifid spines remain separate ventrally, (1) bifid spines recontact ventrally, forming foramen.

Examples of past usage: Merck (1997:337), Senter (2004:41), Renesto et al. (2010:37).

Justification/Ontology: Among those diapsids with distally bifid chevrons in the anterior caudal region, a yet-smaller number of taxa exhibit a reconnection between the bifurcate portions of the shaft. This condition is present in *Megalancosaurus preonensis* (MPUM 8437). Renesto et al. (2010) considered there to be two species of *Megalancosaurus*: *M. preonensis* and *M. endennae*. Although I disagree with this taxonomy (Pritchard et al., in prep.), this character is included to allow testing of the monophyly of the genus *Megalancosaurus*.

CHARACTER 248: Posterior chevrons, proximal articulation: (0) articulate intervertebrally, (1) contact anteroventral margin of centrum.

Examples of past usage: Renesto et al. (2010:39).

Justification/Ontology: In most Permo-Triassic reptiles, chevrons exist as intervertebral ossification positioned at the ventral margin of caudal intervertebral articulations. However, a small number of drepanosaurids exhibit chevrons that articulate to the anteroventral surfaces of the centra in the posterior caudal region. These are most often fused onto those centra. This condition occurs in *Dolabrosaurus aquatilis* (CMNH 28589, see fig. 15B), *Megalancosaurus preonensis* (MFSN 1801), and *Drepanosaurus unguicaudatus* (MCSNB 5728).

CHARACTER 249: Chevrons, proximal articular morphology: (0) chevrons remain separate from centra, (1) chevrons fuse to centra.

Examples of past usage: NOVEL character.

Justification/Ontology: In most early reptiles, chevrons remain as distinct ossifications from the caudal centra. However, drepanosauromorphs exhibit co-ossification of the chevrons with their respective centra. This occurs in *Hypuronector limnaios* (AMNH FARB), *Vallesaurus cenensis* (MCSNB 4751), *Megalancosaurus preonensis* (MPUM 8537), *Dolabrosaurus aquatilis* (CMNH 28589), and *Drepanosaurus unguicaudatus* (MCSNB 5728). This characteristic was noted by Fraser and Renesto (2005) in a number of drepanosauromorph caudal vertebrae from the Cromhall Quarry of England.

CHARACTER 250: Chevrons, hemal spine length: (0) similar in length or shorter than caudal neural spines, (1) substantially longer than caudal neural spines.

Examples of past usage: Senter (2004:40), Renesto et al. (2010:38).

Justification/Ontology: The chevron ossifications in most early reptiles are typically similar in proximodistal length than the neural spines of their respective vertebrae. This can be seen in *Thadeosaurus colcanapi* (Currie and Carroll, 1984), *Mesosuchus browni* (SAM K7416), and *Tanystropheus longobardicus* (GMPKU-P1527). In contrast, the chevrons in drepanosauromorphs are substantially longer proximodistally than their respective neural spines. Examples include *Hypuronector limnaios* (AMNH FARB 7759), *Vallesaurus cenensis* (MCSNB 4751), and *Dolabrosaurus aquatilis* (CMNH 28589, see fig. 15C).

CHARACTER 251: Caudal vertebrae, anterior neural spines: (0) unexpanded dorsally; (1) exhibit slender anterior/posterior projections, forming T-shape.

Examples of past usage: Dilkes (1998:139), Senter (2004:36), Renesto et al. (2010:33)

Justification/Ontology: The tips of the caudal neural spines in most diapsid reptiles are of equivalent anteroposterior length throughout their dorsoventral heights. This can be seen in *Youngina capensis* (AMNH FARB 5561), *Tanystropheus longobardicus* (GMPKU-P1527), *Langobardisaurus pandolfii* (MFSN 1921), and *Prolacerta broomi* (BP/1 2676). This is also the condition in some drepanosauromorphs (e.g., *Hypuronector limnaios*, AMNH 7759; *Vallesaurus* *cenensis*, MCSNB 4751). By contrast, other drepanosauromorphs exhibit anterior and posterior extensions of the tips of the caudal neural spines. This occurs in *Dolabrosaurus aquatilis* (CMNH 28589, see fig. 15B), *Megalancosaurus preonensis* (MFSN 18443, see fig. 15C, MPUM 8437), and *Drepanosaurus unguicaudatus* (MCSNB 5728). These expansions were recovered as a synapomorphy of a clade including *Megalancosaurus* and *Dolabrosaurus* in Senter (2004), but he did not recognize the character in *Drepanosaurus unguicaudatus*.

CHARACTER 252: Anterior dorsal vertebrae, pedicel height: (0) substantially shorter than respective centra, (1) taller than respective centra.

Examples of past usage: Renesto et al. (2010:8).

Justification/Ontology: In nearly all Permo-Triassic reptiles, the pedicels of the anterodorsal vertebrae are relatively shorter than their respective centra. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Gephyrosaurus bridensis* (Evans, 1981a), *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Trilophosaurus buettneri* (TMM 31025-140), and *Proterosuchus alexanderi* (NMQR 1484). This condition appears to occur in one drepanosauromorph, *Hypuronector limnaios*, based on the partial dorsal vertebrae of AMNH FARB 1721. By contrast, the pedicels are substantially taller than the centra in *Vallesaurus cenensis* (MCSNB 4751), *Megalancosaurus preonensis* (MFSN 1769), and *Drepanosaurus unguicaudatus* (MCSNB 5728).

CHARACTER 253: Anterior dorsal vertebrae, neural spine expansion: (0) similar in morphology to posterior dorsal neural spines; (1) dorsally broader anteroposteriorly than spine base; (2) fourth? expanded into anteroposteriorly broad hatchet shape. ORDERED.

Examples of past usage: Merck (1997:301), Dilkes (1998:130), Senter (2004:31), Renesto et al. (2010:9).

Justification/Ontology: In most early diapsids and early reptiles, the neural spines of the dorsal series are all subequal in dimensions. This condition occurs in *Youngina capensis* (BP/1 3859), *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Tanystropheus longobardicus* (MCSN BES SC 265), *Trilophosaurus buettneri* (TMM 31025-140), *Erythrosuchus africanus* (NMQR 3765), and modern lepidosaurs (e.g., Hoffstetter and Gasc, 1969). By contrast, the anterior dorsal neural spines expand anteroposteriorly at their dorsal tips in *Vallesaurus cenensis* (MCSNB 4751). An extreme development is noted in *Megalancosaurus preonensis* (MPUM 6008) and *Drepanosaurus unguicaudatus* (MCSNB 5728), in which the spines are not only anteroposteriorly expanded, but the fourth spine is broadened to form a dorsally convex hatchet shape.

CHARACTER 254: Second manual ungual: (0) similar in morphology to other manual unguals, (1) substantially taller and more massive than other manual unguals.

Examples of past usage: Renesto et al. (2010:21).

Justification/Ontology: The second manual ungual in nearly all reptiles is similar in proportion to the adjacent manual unguals. This similarity in shape occurs in *Thadeosaurus colcanapi* (MNHN MAP 360), *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Tanystropheus longobardicus* (MCSN BES SC 1018), “Chasmatosaurus” *yuani* (IVPP V/4067), *Vallesaurus cenensis* (MCSNB 4751), and *Megalancosaurus preonensis* (MPUMP 6008). In contrast, the second manual ungual in the type specimen of *Drepanosaurus unguicaudatus* (MCSNB 5728) and referred material from the Hayden Quarry (chapter 3 of this dissertation) is massively expanded dorsoventrally and proximodistally relative to the other unguals. It should be noted that the claws in these animals are substantially larger than the ulna in the same specimens.

CHARACTER 255: Ulna, shape: (0) similar to radius, with elongate shaft; (1) flattened in pre-axial-post-axial plane, forming enormous crescent.

Examples of past usage: Renesto et al. (2010:18).

Justification/Ontology: The ulna in nearly all tetrapods is a proximodistally elongate structure with a shaft that runs parallel to the radius. However, in the type specimen of *Drepanosaurus unguicaudatus* (MCSNB 5728) and several forelimb specimens from the Hayden Quarry of New Mexico, the ulna is a flattened and crescent-shaped bone. Its long axis is nearly perpendicular to that of the radius (Pritchard, 2015).

CHARACTER 256: Radius, proximal tab for articulation with ulna: (0) absent, (1) present.

Examples of past usage: NOVEL character.

Justification/Ontology: The proximal surface of the radius in most diapsids is a simple concavity that receives the radial condyle of the humerus. This condition can be seen in *Petrolacosaurus kansensis* (Reisz, 1981), *Boreopricea funerea* (PIN 3708/1), and *Prolacerta broomi* (BP/1 2675). A similar proximal surface with a slight inflection occurs in *Azendohsaurus madagaskarensis* (UA 7-13-99-577) and *Trilophosaurus buettneri* (TMM 31025-140). By contrast in the type specimen of *Drepanosaurus unguicaudatus* (MCSNB 5728) and several forelimb specimens from the Hayden Quarry of New Mexico the proximal end of the radius exhibits a flattened, proximally convex articular tab that fits into a corresponding notch on the ulna.

CHARACTER 257: (0) Proximal femur, dorsal surface: (0) unornamented, (1) marked by prominent tuberosity.

Examples of past usage: NOVEL character.

Justification/Ontology: In some early reptile and early diapsid lineages, the dorsal surface of the proximal femur is marked by a distinct rugosity. This occurs in *Captorhinus aguti* (Fox and

Bowman, 1966) and *Petrolacosaurus kansensis* (Reisz, 1981). Such a tuberosity is absent in *Coelurosauravus elivensis* (Evans, 1982), *Youngina capensis* (BP/1 3859), *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Gephyrosaurus bridensis* (Evans, 1981), and *Proterosuchus alexanderi* (NMQR 1484).

CHARACTER 258: Mid dorsal ribs, fusion to respective centra: (0) absent, (1) present.

Examples of past usage: Merck (1997:309).

Justification/Ontology: In contrast to nearly all diapsid and saurian reptiles, the ribs in the dorsal region are fused onto their respective vertebrae. This condition occurs in the drepanosauromorphs *Hypuronector limnaios* (AMNH FARB 1721), *Megalancosaurus preonensis* (Renesto, 2000), and *Dolabrosaurus aquatilis* (CMNH 28589). The condition is note universal, as it is absent in *Drepanosaurus unguicaudatus* (MCSNB 5728) and *Vallesaurus cenensis* (MCSNB 4751).

CHARACTER 259: Femur, morphology of internal trochanter: (0) elongate, slender crest, (1) rounded tuberosity.

Examples of past usage: NOVEL character.

Justification/Ontology: In nearly all early reptiles and diapsids, the internal and/or fourth trochanter is a transversely narrow crest. In sharp contrast, there does not appear to be a crest in drepanosauromorphs and weigeltisaurids for which the three-dimensional osteology of the femur is preserved. In *Hypuronector limnaios* (AMNH FARB 7759) and *Coelurosauravus elivensis* (MNHN MAP 325, see fig. 19A), there is a prominent tuberosity on the ventral surface of the femur. A similar shape is found in the crushed femur of *Vallesaurus cenensis* (MCSNB 4751).

CHARACTER 260: Proximal tarsals, morphology of perforating foramen: (0) broad, marked by finished bone on astragalus and calcaneum; (1) pinched, marked by extremely constricted space between astragalus and calcaneum.

Examples of past usage: Jalil (1997).

Justification/Ontology: In the earliest diapsid reptiles, the perforating foramen between the astragalus and calcaneum is a very narrow opening with a pinched appearance. This condition occurs in *Araeoscelis gracilis* (MCZ 412) and *Petrolacosaurus kansensis* (Reisz, 1981). By contrast, the opening is broader and elliptical in most early saurians (e.g., *Protorosaurus speneri*, SMNS 55387; *Trilophosaurus buettneri*, TMM 31025-140; *Proterosuchus alexanderi*, NMQR 1484) and some non saurian diapsids (e.g., *Drepanosaurus unguicaudatus*, MCSNB 5728; *Claudiosaurus germaini*, SAM K8266). An apparent reversal to the plesiomorphic condition occurs in some archosauromorphs (e.g., *Tanystropheus longobardicus*, MCSN V 3730; *Tanytrachelos ahynis*, AMNH FARB 7206, Pritchard et al., 2015).

CHARACTER 261: Calcaneum, lateral projection, ventral margin: (0) convex and continuous with the lateral margin of the projection; (1) concave, sharply angled relative to lateral margin of the projection.

Examples of past usage: NOVEL character.

Justification/Ontology: In nearly all early reptiles, the distolateral margin of the calcaneum is smoothly concave. This condition is widespread, occurring in *Araeoscelis gracilis* (MCZ 412), *Thadeosaurus colcanapi* (MNHN MAP 360), *Claudiosaurus germaini* (SAM K8266), *Protorosaurus speneri* (SMNS 55387, see fig 21C), *Macrocnemus bassanii* (PIMUZ T/4822), *Trilophosaurus buettneri* (TMM 31025-140), and *Proterosuchus* sp. (AMNH FARB 2237). By contrast, the calcaneum in *Drepanosaurus unguicaudatus* (MCSNB 5728, see fig. 21B) and *Azendohsaurus madagaskarensis* (Nesbitt et al., in press) exhibits a concave ventral margin.

In a number of derived archosaurs, the surface of the calcaneum that is homologous to this one is unclear due to the radical rearrangement of the tarsus (e.g., Brinkman, 1980; Chatterjee, 1982). As a result *Coelophysis bauri* (Colbert, 1989), *Batrachotomus kupferzellensis* (Gower and Schoch, 2009) and other archosaurs are coded as "?."

CHARACTER 262: Ilium, bone between acetabulum and iliac blade: (0) bone broadens smoothly into blade, (1) bone exhibits anteroposterior constriction between blade and acetabulum.

Examples of past usage: NOVEL character.

Justification/Ontology: In nearly all early reptiles and diapsids, the ilium broadens dorsally from the acetabulum without any anteroposterior constriction. This occurs in *Youngina capensis* (BP/1 3859), *Shinisaurus crocodilurus* (Conrad, 2006), *Hypuronector limnaios* (AMNH FARB 7759), *Prolacerta broomi* (BP/1 2676), "*Chasmatosaurus*" *yuani* (IVPP V4067), and *Erythrosuchus africanus* (NHMUK R3592). By contrast, the ilium is strongly constricted anteroposteriorly in *Drepanosaurus unguicaudatus* (MCSNB 5728, see fig. 19A) and very close relatives.

CHARACTER 263: Chevrons, hemal spine curvature: (0) spines roughly straight, (1) spines concave anteriorly.

Examples of past usage: Dilkes (1998:141).

Justification/Ontology: In most diapsid reptiles, the anterior surface of each chevron bone is straight. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561), *Protorosaurus speneri* (SMNS cast of WMsN P47361, see fig. 15A), *Azendohsaurus madagaskarensis* (Nesbitt et al., in press), *Proterosuchus alexanderi* (NMQR 1484), and *Shinisaurus crocodilurus* (Conrad, 2006). By contrast, the chevrons arc posteroventrally along their proximodistal lengths in most drepanosauromorphs, producing an anterior concavity. This condition occurs in *Vallesaurus cenensis* (MCSNB 4751), *Megalancosaurus preonensis* (MFSN 18443), *Drepanosaurus unguicaudatus* (MCSNB 5728), and *Dolabrosaurus aquatilis* (CMNH 28589, see fig. 15B). This condition does not occur in *Hypuronector limnaios* (AMNH FARB 7759), recovered by Renesto et al. (2010) as the earliest-diverging drepanosauromorph.

CHARACTER 264: Dorsal ribs, orientation: (0) ribs curve to frame trunk; (1) ribs splay laterally, forming patagium.

Examples of past usage: NOVEL character.

Justification/Ontology: In the kuehneosaurid diapsids, the ribs are elongate and straight throughout their proximodistal lengths. This condition occurs in *Icarosaurus siefkeri* (AMNH FARB 2101, see fig. 14B) and *Kuehneosaurus latus* (Robinson, 1962). This contrasts with the condition in the gliding weigeltisaurids (e.g., *Coelurosauravus elivensis*, *C. jaekeli*), in which the ribs are typically curved like other diapsids (Evans, 1982). The patagium in those forms is instead formed by elongate, straight ossifications that attach to the distal tips of the dorsal ribs (see character 290).

CHARACTER 265: Posterior cranial table, ornamentation: (0) absent, (1) prominent horns on squamosal and quadratojugal.

Examples of past usage: Merck (1997:156), Senter (2004:23).

Justification/Ontology: In contrast to the smooth cranial tables in nearly all early diapsids and saurians, weigeltisaurids exhibit prominent and laterally facing horns on the posterolateral margins of the squamosal and quadratojugal bones. This can be seen in *Coelurosauravus elivensis* (MNHN MAP 317), *Coelurosauravus jaekeli* (SMNS 53349), and *Rautiania* spp.

(Bulanov and Sennikov, 2006). In *Rautiania* sp., a horn is also noted on the lateral surface of the postdentary complex (PIN 5130/47).

CHARACTER 266: Ulnare and intermedium, elongation: (0) longer proximodistally than in pre-axial-post-axial plane; (1) short proximodistally, equivalent in proximodistal and pre-axial-post-axial length.

Examples of past usage: Merck (1997:430), Senter (2004:50), Renesto et al. (2010:27).

Justification/Ontology: In the earliest diapsids and a number of Triassic taxa, the post-axial proximal carpal elements, the ulnare and intermedium, are anteroposteriorly elongated relative to their width in an axial plane. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), and *Megalancosaurus preonensis* (MPUM 8437). In *Drepanosaurus unguicaudatus*, this condition reaches its greatest extreme, with these carpal elements being longer proximodistally than the bones of the zeugopodium (see chapter 2 of this dissertation). By contrast, the carpal elements are proportionally shorter than their breadths in *Youngina capensis* (BP/1 3859), *Acerosodontosaurus piveteaui* (Bickelmann et al., 2009), and saurian reptiles (see chapter 2 of this dissertation).

CHARACTER 267: Metatarsal I, proximal articular surface, proportions: (0) similar in pre-axial-post-axial breadth to other metatarsals, (1) broader in pre-axial-post-axial breadth than other metatarsals.

Examples of past usage: NOVEL character.

Justification/Ontology: In most early Diapsida and Sauria, the proximal articular surface of the first metatarsal is similar in pre-axial-postaxial breadth to the other metatarsals. This condition occurs in *Araeoscelis gracilis* (Reisz et al., 1984), *Protorosaurus speneri* (USNM 442453), and *Youngina capensis* (SAM K7710). A contrasting condition occurs in some drepanosauromorphs, in which the proximal surface of the first metatarsal is substantially broader than the other metatarsals.

In *Dolabrosaurus aquatilis* (CMNH 28589), specimens of *Megalancosaurus* referred to *M. endennae* by Renesto et al. (2010), and *Vallesaurus cenensis* (MCSNB 4751), the proximal articular surface of the first metatarsal is substantially broader than those of the other metatarsals. This broadened metatarsal supports a massive, curved first phalanx of the first pedal digit in *Megalancosaurus* and *Vallesaurus cenensis* (Renesto et al., 2010). However, this condition is not found in *Drepanosaurs unguicaudatus* (MCSNB 5728), specimens of *Megalancosaurus* referred to *M. preonensis* by Renesto et al. (2010), and specimens referred to *Vallesaurus zorzinensis* by Renesto et al. (2010), all of which exhibit a narrow first metatarsal.

As noted in chapter 3 of this dissertation, I do not accept the specific distinctions between the species of *Megalancosaurus* and *Vallesaurus* described by Renesto et al. (2010). One of the characters used to support these distinctions is the apparent differences in the morphology of the first pedal digit. However, I note that the first pedal digits differ substantially in the bonebed of drepanosaurid specimens described by Chure et al. (2013), which may suggest dimorphism in the anatomy of the first digit. For the moment, *Dolabrosaurus aquatilis*, *Megalancosaurus preonensis*, and *Vallesaurus cenensis* are coded as “1” for this character, although I will likely change the codings to polymorphism in future studies.

CHARACTER 268: Tooth-bearing surface of maxilla: (0) ungrooved, (1) single anteroposteriorly running groove, (2) double anteroposteriorly running groove. ORDERED

Examples of past usage: Benton (1985:Q3), Dilkes (1998:62).

Justification/Ontology: Rhynchosauria exhibit complex and transversely broad maxillae with numerous tooth rows. In some taxa, this occlusal surface exhibits an anteroposteriorly running groove that separates the tooth surface into two separate fields. This condition occurs in *Rhynchosaurus articeps* (Benton, 1990), *Fodonyx spenceri* (Hone and Benton, 2008), and *Hyperodapedon tikiensis* (Mukherjee and Ray, 2014). A more complex construction occurs in other rhynchosaurs (e.g., *Teyumbaita sulcognathus*, Montefeltro et al., 2010). This character is ordered, as a single groove is logically intermediate.

CHARACTER 269: Basioccipital, occipital condyle: (0) exhibits elliptical depression that occupies much of posterior surface of condyle, (1) exhibits narrow "pinprick" notochordal pit within posterior surface, (2) exhibits smoothly convex surface. ORDERED.

Examples of past usage: Merck (1997:24).

Justification/Ontology: In early reptiles and some diapsid groups, the posterior surface of the occipital condyle is marked by a prominent depression that occupies much of the breadth of the bone. This is a developmental remnant of the notochord and is thus termed the notochordal pit. Broad notochordal depressions occur in *Captorhinus aguti* (Price, 1935), *Youngina capensis* (Gardner et al., 2010), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834, see 7A), and *Gephyrosaurus bridensis* (Evans, 1980).

Notochordal depressions also occur in a large number of early saurian taxa. However, these are typically transversely narrow structures relative to the early taxa. In light of this distinction, I introduce an intermediate condition relative to the broad depressions in early taxa. Narrow notochordal pits can be seen in *Trilophosaurus buettneri* (TMM 31025-443, see fig. 7B), *Proterosuchus fergusi* (BP/1 3393), and *Garjainia madiba* (Gower et al., 2014). Notochordal pits are completely obliterated in other saurian taxa (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 2765, see fig. 7B; *Ctenosaura pectinata*, Oelrich, 1956; *Shinisaurus crocodilurus*, Bever et al., 2005). The development of the pit can be difficult to assess in some archosauriforms, in which the pit has become extremely small relative to the size of the condyle (e.g., *Erythrosuchus africanus*, Gower, 1996). I have ordered this character, as the incipient condition seems a logical intermediate between the broad pit and the smooth occipital surface.

CHARACTER 270: Parabasisphenoid, cultriform process dentition: (0) teeth run anteroposteriorly on process, (1) teeth clustered at base of process.

Examples of past usage: NOVEL character.

Justification/Ontology: In many early reptile groups and the earliest diapsids, teeth on the cultriform process are arranged anteroposteriorly along the bone. This may be seen in *Captorhinus aguti* (Fox and Bowman, 1966) and *Petrolacosaurus kansensis* (Reisz, 1981). By contrast the teeth of the parasphenoid are located in a small cluster at the posterior base of the cultriform process in *Kuehneosaurus latus* (AMNH FARB 7771) and in *Icarosaurus siefkeri* (AMNH FARB 2101).

CHARACTER 271: Humerus, internal tuberosity: (0) continuous with humeral shaft; (1) prominent projection, offset from humeral shaft.

Examples of past usage: NOVEL character.

Justification/Ontology: The internal tuberosity in most early reptiles is present as an expansion on the post-axial surface of the humeral head. In most taxa, the post-axial margin of the tuberosity is roughly continuous with the post-axial margin of the shaft. This condition occurs in *Youngina capensis* (BP/1 3859), modern lepidosaurs (Lécuru, 1969), *Protorosaurus speneri* (SMNS cast of WMsN P47361, see fig. 17E), *Azendohsaurus madagaskarensis* (UA 8-29-97-121), *Trilophosaurus buettneri* (TMM 31025-140), *Boreopricea funerea* (PIN 3708/1), and “Chasmatosaurus” *yuani* (IVPP V4067). By contrast, the internal tuberosity is off set on a small pedicel from the remainder of the humeral shaft in *Icarosaurus siefkeri* (AMNH FARB 2101) and *Kuehneosaurus latus* (AMNH FARB 7784, see fig. 17B).

CHARACTER 272: Third manual digit, phalangeal formula: (0) multiple phalanges, (1) single, non-ungual phalanx.

Examples of past usage: Merck (1997:413), Senter (2004:53).

Justification/Ontology: The typical manual phalangeal formula in diapsid reptiles is 2-3-4-5-3 (e.g., Romer, 1956), as is common to nearly all animals in this study (but see Character 161). However, in some drepanosauromorphs, this formula has been drastically reduced in nearly all manual digits. For this character, I chose to focus on the third manual digit as it is discernable in nearly all drepanosauromorph taxa. In *Dolabrosaurus aquatilis*, in which three fragmentary digits of a manus are preserved (CMNH 28589), only the third can be known to be present with certainty. In that taxon, multiple phalanges are present. However, in *Drepanosaurus unguicaudatus* (MCSNB 5728) and *Megalancosaurus preonensis* (MPUM 6008) the third digit exhibits only a single non-ungual phalanx.

CHARACTER 273: Cervical ribs: (0) present, (1) absent.

Examples of past usage: Renesto et al. (2010:5).

Justification/Ontology: Cervical ribs are present as distinct ossifications throughout nearly all reptiles, including all modern diapsids with discrete cervical regions (e.g., Hoffstetter and Gasc, 1969). By contrast, no distinct intercentra have ever been recognized in any articulated drepanosauromorph skeleton (e.g., *Hypuronector limnaios*, AMNH FARB 7759; *Megalancosaurus preonensis*, Renesto et al., 2010). Indeed, the cervical vertebrae in the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834) exhibit broad transverse foramina, framed presumably by fused cervical ribs, akin to the condition in Mammalia. I code drepanosauromorphs with articulated cervical regions as lacking cervical ribs.

CHARACTER 274: Pedal digit three (III), number of phalanges: (0) four, (1) three.

Examples of past usage: Merck (1997:420), Senter (2004:66), Renesto et al. (2010:28).

Justification/Ontology: The typical pes in Diapsida exhibits a phalangeal formula of 2-3-4-5-4 (e.g., Romer, 1956), a condition found in the third pedal digit of nearly all taxa included in this analysis. By contrast, *Megalancosaurus preonensis* (Renesto et al., 2010) and *Drepanosaurus unguicaudatus* (MCSNB 5728) exhibit three phalanges in the third pedal digit.

CHARACTER 275: Post-axial cervical vertebra, morphology of intervertebral articulations (for amphicoelous taxa): (0) circular/elliptical articulations appressed to one another (traditional amphicoely), (1) saddle-shaped articulations (heterocoely).

Examples of past usage: NOVEL character.

Justification/Ontology: Vertebral articulations in which an anterior concave surface meets a posterior concave surface of the next-most anterior vertebra is typical for nearly all reptiles. In drepanosauromorphs, the cervical vertebrae exhibit distinctly saddle-shaped articular surfaces. In these taxa, the anterior articular surface exhibits anteriorly projecting “lips” laterally which fit together with dorsal and ventral “lips” framing the posterior articular surface. This form of articulation distinctly resembles the condition in modern birds (e.g., Baumel et al., 1993). Examples of this vertebral articulation can be found in *Megalancosaurus preonensis* (MPUM 6008), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), and a cervical vertebra from the Upper Triassic Cromhall Quarry in the United Kingdom (Renesto and Fraser, 2003).

CHARACTER 276: Vertebrae, notochordal canal: (0) present, (1) absent.

Examples of past usage: Benton (1985:C6), Laurin (1991:F3), Jalil (1997:29), Merck (1997:259), Dilkes (1998:83), Müller (2004:40).

Justification/Ontology: The notochordal canal is an anteroposteriorly running, cylindrical canal within the vertebral centrum present throughout early reptiles (e.g., Romer, 1956). Among early diapsids, a notochordal canal occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis* *gracilis* (Vaughn, 1955), *Youngina capensis* (BP/1 5389), and *Claudiosaurus germaini* (SAM K8580). In saurians, notochordal canals are common within early Lepidosauria. They occur in *Gephyrosaurus bridensis* (Evans, 1981) and *Clevosaurus hudsoni* (Fraser, 1988). In modern taxa, this canal occurs in some Gekkota and *Sphenodon punctatum* (Hoffstetter and Gasc, 1969).

Notochordal canals are obliterated in a number of early saurian taxa. They are absent in all animals typically considered Archosauromorpha (e.g., *Tanystropheus longobardicus*, PIMUZ T/1277; *Trilophosaurus buettneri*, TMM 31025-140; *Azendohsaurus madagaskarensis*, UA 8-28-98-306). The only possible exception is *Aenigmastropheus parringtoni*, a fragmentary reptile from the Late Permian of Tanzania named by Ezcurra et al. (2014). They are also absent in procoelous members of modern Squamata (e.g., Hoffstetter and Gasc, 1969). Gauthier et al. (2012) linked their character for procoely and the absence of a notochordal canal, which I do not follow. In the mid-Mesozoic squamate *Parviraptor* cf. *P. estesi*, described by Evans (1994), a notochordal canal co-occurs with a convex posterior articular surface, suggesting that the characters are not necessarily correlated.

Characters describing the presence or absence of a notochordal canal often make reference to the ontogenetic maturity of the taxon coded (e.g., Dilkes, 1998; Ezcurra et al., 2014). Winchester and Bellairs (1977) do note the presence of notochordal canals in the embryonic squamates they studied, but these are obliterated near the birth of the animals. Although I have not been able to study growth series of many of the fossil taxa in my sample, I have not recognized variation in the presence of absence of notochordal canals in any taxa.

CHARACTER 277: Anterior caudal vertebrae, neural spines, dorsoventral height: (0) similar in height or shorter than sacral neural spines, (1) taller than sacral neural spines.

Examples of past usage: Dilkes (1998:88); Müller (2004:106).

Justification/Ontology: The difference in the absolute heights of the neural spines of the sacral and anterior caudal neural spines is usually negligible in most early diapsids. This condition can be seen in *Petrolacosaurus kansensis* (Reisz, 1981), *Hovasaurus boulei* (Currie, 1981), *Protorosaurus speneri* (SMNS cast of WMsN P 47361), *Tanystropheus longobardicus* (MCSN

BES SC 1018), and "Chasmatosaurus" *yuani* (IVPP V4067). A contrasting condition occurs in some rhynchosaurs, in which the anteriormost neural spines are dorsoventrally taller than the sacral spines. This condition occurs in *Noteosuchus colletti* (Carroll, 1976), *Mesosuchus browni* (SAM K6046), and *Rhynchosaurus articeps* (Benton, 1990). Dilkes (1998) employed a distinct character that captured the same morphological variation within Rhynchosauria, describing the height/length ratio of the caudal neural spines.

CHARACTER 278: Humerus, ectepicondyle morphology: (0) squared off pre-axially, (1) pointed, triangular pre-axially.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: In those diapsid reptiles with an ectepicondylar crest that extends beyond the margins of the humeral shaft, that structure is often quadrangular and squared off at its lateral margin. This occurs in *Drepanosaurus unguicaudatus* (MCSNB 5728, H3-053-08, see fig. 17C), *Sphenodon punctatum* (Carroll, 1985), and modern lepidosaurs (e.g., Lécuru, 1969). By contrast, in the kuehneosaurids this crest is notably triangular in shape and pointed laterally. This condition is evident in *Icarosaurus siefkeri* (AMNH FARB 2101) and *Kuehneosaurus latus* (AMNH FARB 7786, see fig. 17B).

CHARACTER 279: Articular, retroarticular process, shape in lateral view: (0) shallow, dorsal margin positioned posteroventral to quadrate articulation; (1) deep, dorsal margin at dorsoventral level equivalent to quadrate articulation.

Examples of past usage: Laurin (1991:E10), Gauthier et al (1988a:72), Merck (1997:210).

Justification/Ontology: In most early reptiles and non-saurian diapsids, the dorsal margin of the retroarticular process is positioned well ventral of the quadrate articulation. This condition usually co-occurs with an anteroposteriorly short retroarticular process, as in *Captorhinus aguti*

(Fox and Bowman, 1966), *Youngina capensis* (AMNH FARB 5561), and *Megalancosaurus preonensis* (MFSN 1769). By contrast, the retroarticular processes in most saurians is substantially taller dorsoventrally, such that the dorsal margin is roughly on the same dorsoventral level as the quadrate articulation. This condition can be seen in the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), *Protorosaurus speneri* (USNM 442453), *Prolacerta broomi* (NMQR 3763), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexanderi* (NMQR 1484), *Gephyrosaurus bridensis* (Evans, 1980), and Triassic archosaurs (e.g., *Batrachotomus kupferzellensis*, Gower, 1999).

CHARACTER 280: Humerus, distalmost end: (0) collinear with proximal shaft, (1) long axis of shaft curves towards flexor surface at distal end.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: The humeral shaft is straight in nearly all early reptiles and diapsids. In contrast, the shaft seems to curve slightly towards the anterior surface of the humerus in *Drepanosaurus unguicaudatus*, both in the holotype (MCSNB 5728) and the referred material from the Hayden Quarry (chapter 2 of this dissertation). This can be seen in the former case with the surprising curvature of the ectepicondyle.

CHARACTER 281: Humerus, entepicondyle: (0) terminates proximal to the distal margin of the ulnar condyle, (1) extends distally relative to ulnar condyle.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: In most early diapsid reptiles, the distal end of the entepicondyle is positioned at or near the distal margin of the ulnar condyle. This condition may be seen in *Petrolacosaurus kansensis* (Reisz, 1981), *Thadeosaurus colcanapi* (MNHN MAP 360), *Claudiosaurus germaini* (SAM K8580), *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (UA 8-29-97-151), "*Chasmatosaurus*" *yuani* (IVPP V4067), *Gephyrosaurus bridensis* (Evans, 1980), modern Squamata (Lécuru, 1969), and *Drepanosaurus unguicaudatus* (MCSNB 5728). By contrast, the entepicondyle extends distally relative to the ulnar condyle in *Rautiania* sp. (PIN 5130/54), *Coelurosauravus elivensis* (MNHN MAP 327), and *Sphenodon punctatum* (Carroll, 1985).

CHARACTER 282: Ilium, iliac blade, post-acetabular portion: (0) relatively planar or lightly sculptured; (1) marked by posterodorsally running ridge, extending from posterior margin of supraacetabular margin.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: The iliac blade posterior to the acetabulum is typically a laterally flattened structure. This condition occurs in *Youngina capensis* (BP/1 3859), *Gephyrosaurus bridensis* (Evans, 1981a), lepidosaurs (Russell and Bauer, 2008), *Prolacerta broomi* (BP/1 2676), *Trilophosaurus buettneri* (TMM 31025-73), *Azendohsaurus madagaskarensis* (UA 8-30-98-375), and "Chasmatosaurus" *yuani* (IVPP V4067). By contrast *Macrocnemus bassanii* (PIMUZ T/2477, see fig. 19; T/4822), *Tanystropheus longobardicus* (MFSN 34739), and *Tanytrachelos ahynis* (AMNH FARB 7206) exhibit a distinct posterodorsally running ridge on the lateral surface of the post-acetabular portion of the ilium.

CHARACTER 283: Palatine, anterior transverse expansion: (0) absent, producing anteriorly curved suborbital fenestrae; (1) present, producing anteriorly tapered suborbital fenestrae.

Examples of past usage: Gauthier et al (1988a:49).

Justification/Ontology: The palatine in most Diapsida frames the anterior margin of the suborbital fenestra. In most taxa, the palatines are concave posterolaterally such that the anterior margin of the cavity is curved. This condition occurs in *Youngina capensis* (Gow, 1975), *Prolacerta broomi* (UCMP 37151), *Proterosuchus alexanderi* (NMQR 1484), and *Ctenosaura pectinata* (Oelrich, 1956). In contrast, Rhynchocephalia exhibit a prominent transverse expansion of the palatine that constricts the anterior tip of the suborbital fenestra. This condition occurs in *Gephyrosaurus bridensis* (Evans, 1980), *Clevosaurus hudsoni* (Fraser, 1988), *Diphydontosaurus avonis* (Whiteside, 1986), and *Sphenodon punctatum* (Evans, 2008).

CHARACTER 284: Scapula & coracoid, position of glenoid fossa: (0) at or near base of scapular blade, (1) located far ventral of base of scapular blade.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: The ventral portion of the scapular blade in most diapsids is equivalent in position to the dorsal portion of the glenoid fossa. By contrast, a small number of drepanosaurids exhibit a glenoid fossa that is positioned well ventrally relative to the base of the scapular blade. This is noted in *Drepanosaurus unguicaudatus* (MCSNB 5728), the *Coelophysis* Quarry drepanosaurid pectoral girdle (GR 1113, see fig. 16D), and a pectoral girdle from the Dockum Group of Texas (Martz et al., 2013).

CHARACTER 285: Humerus, epicondyles, proximal origination: (0) positioned distal to midshaft, (1) positioned at/near midshaft.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: In most early reptiles, ect- and entepicondyles are developed to some degree or another. However, in *Petrolacosaurus kansensis* (Reisz, 1981), *Azendohsaurus madagaskarensis* (UA 8-29-97-151), "*Chasmatosaurus*" *yuani* (IVPP V4067), *Gephyrosaurus bridensis* (Evans, 1980), and most squamates (Lécuru, 1969), the proximal portion of the epicondyles project from the humeral shaft distal to midshaft. By contrast, the epicondyles in

Drepanosaurus unguicaudatus (MCSNB 5278) and a drepanosaurid from the Hayden Quarry referred to *D. unguicaudatus* (chapter 2 of this dissertation).

CHARACTER 286: Supraneural ossification, bone growth positioned anterodorsal to anterior dorsal neural spines: (0) absent, (1) present.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: In a small number of Triassic diapsids, an accessory ossification is developed anterodorsal to the anterior dorsal neural spines. As reconstructed by Renesto et al. (2010), this supraneural ossification is anteriorly convex and articulated one or more of the anterior neural spine tips. Such a structure is evident in *Megalancosaurus preonensis* (MPUM 6008), and *Drepanosaurus unguicaudatus* (MCSNB 5728). A similar supraneural ossification is present in *Vallesaurus cenensis* (Renesto and Binelli, 2006), although the reconstruction of Renesto et al. (2010) positions the supraneural ossification further posteriorly in the trunk than in *Megalancosaurus* and *Drepanosaurus*. For the moment, we code these as homologous structures (“1”), but it will be important to assess the construction of supraneural ossifications in further drepanosauromorphs. We only code the presence or absence of a supraneural ossification when the anterior trunk region is completely preserved.

CHARACTER 287: Scapulacoracoid, glenoid fossa, construction: (0) oriented posterolaterally, ventral margin extends posterior of dorsal margin; (1) oriented laterally, ventral margin positioned directly underneath to dorsal margin.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: Among early diapsid reptiles, the glenoid fossa exhibits a distinct posterolateral orientation. The dorsal margin of the glenoid is positioned well anteriorly relative to the ventral lip. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina* *capensis* (BP/1 3859), *Protorosaurus speneri* (SMNS cast WMsN P47361), *Trilophosaurus buettneri* (TMM 31025-140), *Proterosuchus alexanderi* (NMQR 1484), *Gephyrosaurus bridensis* (Evans, 1981), early lepidosaurs (e.g., Russell and Bauer, 2008), *Hypuronector limnaios* (AMNH FARB 1721), and *Megalancosaurus preonensis* (MPUM 8437). This inclination is somewhat less developed in *Azendohsaurus madagaskarensis* (UA 8-29-97-168) and early archosaurs (e.g., *Batrachotomus kupferzellensis*, Rainer and Schoch, 2009; *Coelophysis bauri*, Colbert, 1989). These taxa exhibit a dorsal margin of the glenoid positioned only slightly anteriorly relative to the ventral margin and are still coded as “0.”

In contrast, the pectoral girdle in some derived drepanosauromorphs is distinctly constructed such that the dorsal and ventral lips of the glenoid sit one dorsal to the other, with the facet itself facing strongly laterally. This occurs in *Drepanosaurus unguicaudatus* (MCSNB 5728), a pectoral girdle from the *Coelophysis* Quarry (GR 1113, see fig. 16D), and the drepanosaurid from the Hayden Quarry (GR H3-037-080527).

CHARACTER 288: Scapula, blade, anteroposterior length-dorsoventral height (at base of blade) ratio: (0) >.4, (1) .4–.25, (2) .25–0. ORDERED.

Examples of past usage: Benton (1985), Merck (1997:376), Dilkes (1998:99), Müller (2004:119), Senter (2004:43), Renesto et al. (2010:15), Nesbitt et al. (in press:220).

Justification/Ontology: The scapular blade in early reptiles is an anteroposteriorly broad structure, with a high length/height ratio (state 1). This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Protorosaurus speneri* (SMNS cast of WMsN P47361), *Tanystropheus longobardicus* (PIMUZ T/1277, see fig. 16B) *Azendohsaurus madagaskarensis* (UA 8-29-97-168), and “Chasmatosaurus” *yuani* (IVPP V4067). An intermediate length/height ratio occurs in *Trilophosaurus buettneri* (TMM 31025-140, see fig. 16C), *Teraterpeton hrynewichorum* (Sues, 2003), and the early-diverging drepanosauromorph *Hypuronector limnaios* (AMNH FARB 1721). Finally, extremely slender scapular blades occur in derived drepanosaurids such as *Vallesaurus cenensis* (MCSNB 4751), *Megalancosaurus preonensis* (MFSN 1769), *Drepanosaurus unguicaudatus* (MCSN 5728), and an isolated drepanosaurid pectoral girdle from the *Coelophysis* Quarry (GR 1113, see fig. 16D). Nesbitt et al. (in press) character 220 described a state equivalent to state 1 of this character, in order to code for the relatively narrow scapulae in *Trilophosaurus buettneri* and *T. jacobsi*.

CHARACTER 289: Dentary, lateral/labial surface along alveolar margin: (0) remains unchanged during tooth replacement events, (1) develops labial resorption pits during tooth replacement events.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: Tooth replacement in early reptiles typically involves the weathering of attachment tissues ankylosing the tooth root within a dentigerous element. This can involve the breakdown of both non-mineralized and mineralized periodontal ligament tissues, which can link the tooth root to permanent alveolar tissues (Luan et al., 2009). It must be noted that the individual tissue types that form the alveoli and periodontal ligament tissues in extinct tetrapods exhibit a surprising degree of variation (e.g., LeBlanc and Reisz, 2013, 2015). Pending further investigation of the histology of the dental attachment tissues throughout early Sauria, we describe the gross morphology of these replacement events.

The weathering of dental attachment tissues and tooth roots in early diapsids can be seen on the lingual aspect of the tooth-bearing bones. Examples of this condition can be seen in *Gephyrosaurus bridensis* (Evans, 1985), a dentary referred to *Archosaurus rossicus* (PIN 1100/78), *Azendohsaurus madagaskarensis* (FMNH PR 2751), and *Tanystropheus longobardicus* (MCSN BES SC 265). In these examples, these tissues are below the margin of the actual tooth-bearing element, such that they cannot be seen in lateral/labial view.

In *Trilophosaurus buettneri*, the dental attachment tissues are quite distinct from other early diapsids. In *T. buettneri* the dental attachment tissues appear to rise dorsal to the cortical bone of the dentary. This manifests itself in some specimens as a roughened bone texture around the lateral surfaces of the teeth, quite distinct from the cortical bone of the dentary (visible in TMM 31025-1, see fig. 9A). As an apparent consequence of the elevation of these tissues, both the labial and lingual surfaces of the attachment tissues wear through during tooth replacement.

Thus far, I have identified this condition in *T. buettneri* (TMM 31025-140) and the Early Triassic *Coelodontognathus ricovi* (PIN 4173/127). Unfortunately, none of the teeth in the referred skull of *Trilophosaurus jacobsi* (NMMNH P41400) appear to be undergoing replacement.

CHARACTER 290: Patagial ossification: (0) absent, (1) present as distinct distally tapering rod articulated to distal tip of dorsal rib.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: In weigeltisaurid diapsids, the ribs of the trunk articulate with an additional elongate and slender strut that forms the patagium. This condition is known in *Coelurosauravus elivensis* and *Coelurosauravus jaekeli* (Evans, 1982; Evans and Haubold, 1987), but it has not been reported in the disarticulated material of *Rautiania* spp. (Bulanov and Sennikov, 2010). Romer (1956) notes that the trunk ribs in reptiles articulate with multiple cartilaginous segments that link them to the sternum. It is possible that the patagial structure in weigeltisaurids is a derivative of one of these structures, or that it is a neomorphic structure. For the moment, I describe these as "patagial ossifications," and describe their general morphology.

CHARACTER 291: Quadrate, pterygoid ramus: (0) ventral margin of posterior base of ramus in line with quadrate condylar surface, (1) posterior base of ramus elevated dorsally relative to quadrate condylar surface.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: The pterygoid ramus of the quadrate is a transversely narrow flange of bone that is ventrally in line with the quadrate condyles. *Captorhinus laticeps* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), and *Rautiania* sp. (PIN 5130/31). Other diapsids, in particular saurians, typically exhibit a ventral margin of the pterygoid ramus elevated dorsally above the condyles. This construction occurs in *Sphenodon punctatum* (Evans, 2008), *Youngina capensis* (AMNH FARB 5561), *Gephyrosaurus bridensis* (Evans, 2008), *Protorosaurus speneri* (USNM 442453), *Azendohsaurus madagaskarensis* (FMNH PR 2751), *Proterosuchus fergusi* (BP/1 3393), and *Erythrosuchus africanus* (NHMUK R3592).

CHARACTER 292: Parietal, post-temporal processes: (0) slender and tapering; (1) anteroposteriorly flattened, such that parietal contributes prominently to occipital face of skull.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: Throughout early diapsids, the post-temporal processes are slender and tapering in both anteroposterior and dorsoventral planes. This morphology is evident in *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (AMNH FARB 5561), the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834), and *Megalancosaurus preonensis* (MPUM 8437), *Gephyrosaurus bridensis* (Evans, 1980), *Shinisaurus crocodilurus* (Conrad, 2004), and *Eublepharis macularis* (Gauthier et al., 2012). In the weigeltisaurids, the post-temporal processes tend to be broad anteroposteriorly, but they appear dorsoventrally narrow as in the aforementioned taxa (e.g., *Rautiania* spp., 5130/1 and 5130/2).

The post-temporal processes in most archosauromorphs are dorsoventrally tall and flattened posteriorly. This shape is evident in *Protorosaurus speneri* (USNM 442453), *Proterosuchus alexanderi* (NMQR 1484), *Trilophosaurus buettneri* (TMM 31025-227), *Mesosuchus browni* (SAM K6536), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), and *Erythrosuchus africanus* (BP/1 5207). Among lepidosaurs, this shape also occurs in *Sphenodon punctatum* (Evans, 2008). This character appears to be closely linked to the dimensions of the post-temporal fenestra, with the breadth of the post-temporal processes compressing the post-temporal fenestrae [compare *Youngina capensis* (AMNH FARB 5561) to *Erythrosuchus africanus* (BP/1 5207)]. For the moment, we prefer this character relative to any describing the post-temporal fenestrae as the latter requires articulated skull materials.

CHARACTER 293: Stapes, stapedial shaft, robusticity; (0) robust, with thick shaft; (1) slender, with rod-like shaft.

Examples of past usage: Gauthier et al (1988a:35), Laurin (1991:E8), Merck (1997:223), Müller (2004:133), Reisz et al. (2010).

Justification/Ontology: The ancestral reptilian and diapsid stapes appear to have been massive and robust, with similar in breadth to the paroccipital process. Such massive stapes occur in *Petrolacosaurus kansensis* (Reisz, 1981), *Araeoscelis gracilis* (Vaughn, 1955), possibly *Hovasaurus boulei* (Currie, 1981), and the *Coelophysis* Quarry drepanosaurid (AMNH FARB 30834). In contrast, the stapedial shaft is much slenderer in most Permo-Triassic diapsids and throughout Sauria. This occurs in *Youngina capensis* (Gardner et al., 2010), *Prolacerta broomi* (BP/1 2675), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Mesosuchus bronwi* (SAM K6536), *Sphenodon punctatum* (Evans, 2008), and most Squamata (e.g., Olson, 1966).

CHARACTER 294: Surangular, dorsolateral surface: (0) transversely narrow, (1) exhibits transversely wide shelf.

Examples of past usage: Müller (2004:166), Ezcurra et al. (2014).

Justification/Ontology: The dorsal surface of the surangular is transversely narrow in early diapsids and most Permo-Triassic diapsids. This condition occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Protorosaurus speneri* (USNM 442453), *Trilophosaurus buettneri* (TMM 31025-5), *Prolacerta broomi* (BP/1 5375), and *Gephyrosaurus bridensis* (Evans, 1980). In *Mesosuchus browni*, the surangular is transversely narrow at its dorsal margin, although the bone does exhibit a prominent lateral crest (SAM K6536). It is coded as "0" in this analysis.

A prominent transverse expansion (=lateral shelf of Ezcurra et al., 2014) is present on the dorsum of the surangular in some Archosauriformes. This occurs in *Proterosuchus fergusi* (BP/1 3393), *Erythrosuchus africanus* (NHMUK R3592), and *Euparkeria capensis* (Ewer, 1965). This also occurs in many derived archosaurs, including *Decuriasuchus quartacolonia* (de Franca et al., 2013), *Batrachotomus kupferzellensis* (SMNS 80260), and *Silesaurus opolensis* (Dzik, 2003). Other archosaurs (e.g., *Plateosaurus engelhardti*, Prieto-Marquez and Norell, 2011; *Herrerasaurus ischigualastensis*, Sereno and Novas, 1993) appear to lack the shelf.

CHARACTER 295: Premaxilla, fusion to contralateral premaxilla: (0) absent, (1) present.

Examples of past usage: Benton (1985:Y1), Gauthier et al (1988a:62), Merck (1997:102), Conrad (2008:11).

Justification/Ontology: In early reptiles and throughout most Permo-Triassic diapsid taxa, the premaxillae remain separate ossifications throughout ontogeny. Examples of separate premaxillae include *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 2871), *Protorosaurus speneri* (USNM 442453), *Trilophosaurus buettneri* (TMM 31025-207), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Proterosuchus fergusi* (BP/1 3393), *Batrachotomus kupferzellensis* (Gower, 1999), *Diphydontosaurus avonis* (Whiteside, 1986), and *Sphenodon punctatum* (Evans, 2008). By contrast, the premaxillae are fused in some early lepidosauromorphs, including *Gephyrosaurus bridensis* (Evans, 1980). Gauthier et al. (2012) recovered fused premaxillae as a synapomorphy of Squamata, whereas Conrad (2008) recovered the character as independently derived in Iguania and Autarchoglossa.

We follow Conrad (2008) in not including an ontogenetic component to this character. As originally defined by Estes et al. (1988), the premaxillary fusion event occurred in very early ontogeny. Conrad (2008) notes that such ontogenetic data is very rarely available in fossils, but that caution should be taken in coding fossils from individuals with indicators of somatic immaturity.

CHARACTER 296: Metatarsal I, shaft, proximodistal length relative to proximodistal length of metatarsal IV: (0) >.42, (1) .42–.32, (2) .32<. ORDERED.

Examples of past usage: Dilkes (1998), Ezcurra et al. (2014).

Justification/Ontology: The ratio of the length of the metatarsals to one another vary substantially throughout Diapsida. Although I have worked to avoid large numbers of non-continuous proportional characters in this analysis, this one is particularly valuable in its linking *Noteosuchus colletti* to Rhynchosauria. The proportional values described above are taken from Ezcurra et al. (2014).

The comparatively elongate first metatarsal is most common among the taxa included in this analysis. It occurs in *Petrolacosaurus kansensis* (Reisz, 1981), *Azendohsaurus madagaskarensis* (UA 8-25-98-231), *Trilophosaurus buettneri* (TMM 31025-140), and *Macrocnemus bassanii* (PIMUZ T/4822). The intermediate length is known in *Youngina capensis* (Smith and Evans, 1992) and *Thadeosaurus colcanapi* (Carroll, 1981). The proportionally shortest metatarsals occur in *Noteosuchus colletti* (Carroll, 1976), *Mesosuchus browni* (SAM K6046), and *Rhynchosaurus articeps* (Benton, 1990).

CHARACTER 297: Nasals, anterior margins: (0) appressed nasals form anteriorly pointed structure visible dorsally, with the point in the midline; (1) appressed nasals form anteriorly flattened surface visible dorsally.

Examples of past usage: Dilkes (1998:13).

Justification/Ontology: In most early reptiles and many saurians, the appressed nasals form an anterior point that meets the appressed anterodorsal processes of the premaxillae. The two structures thus form an internarial bar that forms the two narial openings. Such a condition is present in *Captorhinus aguti* (Heaton, 1979), *Petrolacosaurus kansensis* (Reisz, 1981), *Youngina capensis* (BP/1 2871), *Protorosaurus speneri* (USNM 442453), and *Proterosuchus goweri* (NMQR 880).

Some saurian reptiles exhibit the anteriorly pointed nasal bones, although they lack the prominent anterodorsal processes of the premaxillae. In some of these taxa, the nasals extend far enough anteriorly to form a complete internarial bar (e.g., *Tanystropheus longobardicus*, PIMUZ T/2790). The sutures are difficult to see in *Macrocnemus*, but the construction of the premaxilla and nasal apparent in PIMUZ T/2477 and PIMUZ T/4822 suggests a similar combination of anatomies to *Tanystropheus*. By contrast, the narial opening in *Mesosuchus browni* is confluent, although it has anteriorly pointed nasals. In a number of taxa with confluent external nares, the anterior surface of the nasals is flattened in dorsal view. This condition is evident in derived rhynchosaurs (e.g., *Howesia browni*, SAM-PK K5884; *Rhynchosaurus articeps*, Benton, 1990), *Icarosaurus siefkeri* (AMNH FARB 2101), and likely *Azendohsaurus madagaskarensis* (FMNH PR 2751).

Classically, a confluent naris has been coded as a single character (e.g., Dilkes, 1998), without addressing the elements that contribute to that opening. Pritchard et al. (2015) described the confluence of the nares in the context of the absence of the anterodorsal process of the premaxilla. However, restudy of tanystropheid material noted above illustrates the finer variations that exist in the narial anatomy of early saurians. As such, we address the confluence of the nares by describing both the anterodorsal process of the premaxilla and the anterior portion of the nasal bone.

CHARACTER 298: Ilium, posterior process, ventral surface: (0) smoothly textured, (1) exhibits prominent elliptical depression.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: In most early reptiles and saurians, the posterior process of the ilium is flattened on its lateral surface. Examples include *Youngina capensis* (BP/1 3859), *Trilophosaurus buettneri* (TMM 31025-73, 31025-140), and *Azendohsaurus madagaskarensis* (UA 8-30-98-375). However, a small number of early saurian taxa exhibit a very prominent, elliptical depression in the ventral portion of the lateral surface of the posterior process. These include *Prolacerta broomi* (BP/1 2676, see fig. 18B; NMQR 3763) and *Mesosuchus browni* (SAM K7416, see fig. 19C).

The lateral surface of the posterior process of the ilium in certain other saurians (e.g., *Macrocnemus bassanii*, *Tanystropheus longobardicus*) exhibits a posterodorsally running ridge (codified in character 282), which produces a small fossa in lateral view. However, this condition appears independent of the elliptical cavity described above. In taxa with the elliptical cavity, the fossa is framed by distinctive curved margins anteriorly and posteriorly which are entirely absent in Tanystropheidae. Also, both conditions appear to be present in *Prolacerta broomi* (e.g., BP/1 2676).

CHARACTER 299: Articular, retroarticular process, fossa posterior to quadrate articulation: (0) fossa anteroposteriorly elongate, broader than quadrate articulation; (1) fossa anteroposteriorly constricted, shorter than quadrate articulation.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: Among early saurians, the retroarticular process exhibits a greater complexity than in non-saurian diapsids, which exhibits a dorsally concave fossa posterior to the glenoid fossa (see character). In most early archosauromorphs, this fossa subequal in anteroposterior length to the glenoid fossa. Examples include *Youngina capensis* (AMNH FARB 5561), *Prolacerta broomi* (e.g., NMQR 3763), *Macrocnemus bassanii* (PIMUZ T/2472), *Mesosuchus browni* (SAM K6536) and *Trilophosaurus buettneri* (TMM 31025-140). In certain other taxa, this fossa is anteroposteriorly constricted relative to the glenoid fossa. This condition is found primarily in Archosauriformes. Examples include *Sphenodon punctatum* (Evans, 2008), *Proterosuchus alexanderi* (NMQR 1484), *Erythrosuchus africanus* (NHMUK R3592), and *Batrachotomus kupferzellensis* (SMNS 80260). In archosauromorphs, an abbreviated fossa is usually posteriorly bounded by a robust, upturned tip to the retroarticular process, but this is not ubiquitous; *Sphenodon punctatum* exhibits a very short fossa and a small, posteriorly directed tip to its retroarticular.

CHARACTER 300: Articular, retroarticular process, posterior tip: (0) oriented posteriorly, (1) oriented posterodorsally.

Examples of past usage: Merck (1997:211), Dilkes (1998:75), Müller (2004:101).

Justification/Ontology: Among early reptile taxa that possess a retroarticular process, the tip of the process is directed posteriorly subparallel to the dentigerous margin of the dentary. Examples include *Captorhinus aguti* (Heaton, 1979), *Youngina capensis* (AMNH FARB 5561), and *Rautiania* sp. (PIN 5130/49). This condition is uncommon in archosauromorphs, present in *Protorosaurus speneri* (USNM 442453). In many archosauromorph species, the tip of the process is upturned such that it is directed dorsally. This condition occurs in *Macrocnemus bassanii* (PIMUZ T/2472), *Mesosuchus browni* (SAM K6536), *Prolacerta broomi* (NMQR 3763), *Proterosuchus alexanderi* (NMQR 1484), *Erythrosuchus africanus* (NHMUK R3592), and *Batrachotomus kupferzellensis* (SMNS 80260).

CHARACTER 301: Dorsal vertebrae, neural arches, surface dorsolateral to zygapophyses: (0) smooth or convex, (1) marked by deep concavities.

Examples of past usage: Dilkes (1998:84), Müller (2004:103).

Justification/Ontology: In most early reptiles and diapsids, the lateral surface of the neural arch is smooth dorsolateral to the zygapophyses just ventral to the base of the neural spine. This condition is present in *Youngina capensis* (BP/1 5389; Currie, 1981), *Gephyrosaurus bridensis* (Evans, 1981a), *Macrocnemus bassanii* (PIMUZ T/4822), *Prolacerta broomi* (BP/1 2765), and *Proterosuchus alexanderi* (NMQR 1484). In contrast, deep depressions occur in the dorsal neural spines of the early rhynchosaurs *Mesosuchus browni* (SAM K6046) and at least in the posterior dorsal region of *Howesia browni* (SAM-PK-K5886). This condition is also evident in some early archosauriforms, including *Erythrosuchus africanus* (Gow, 2003) and *Batrachotomus kupferzellensis* (Gower and Schoch, 2009). Such fossae are not developed in some derived rhynchosaurs (e.g., *Teyumbaita sulcognathus*, Montefeltro et al., 2013). In certain other early archosauromorphs, such as *Spinosuchus caseanus* (NMMNH P-57859) and *Augustaburiania vatagini* (PIN 1043/589) similarly positioned fossae are framed by extremely narrow laminae extending from the costal articulations. Similar fossae occur in araeoscelids (e.g., *Araeoscelis gracilis*, Vaughn, 1955; *Petrolacosaurus kansensis*, Reisz, 1981), although these are substantially more massive and bounded by thick rounded ridges. We coded these all as representing the same character state. Gower (2001) noted these fossae in *Erythrosuchus*, comparing them favorably to probable pneumatic structures in Ornithodira.

CHARACTER 302: Prootic, foramen for facial nerve: (0) exit sits within broad, open surface along anterior inferior process; (1) exit sandwiched between crista prootica anterodorsally and an additional thin plate of bone posteroventrally.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: Among most early reptiles, diapsids, and early saurians, the hyomandibular branch of the facial nerve exits the lateral surface of the braincase via a small foramen on the anterior, inferior process of the prootic. This is seen in *Captorhinus aguti* (Price, 1935), *Youngina capensis* (Gardner et al., 2010), *Prolacerta broomi* (BP/1 2675), *Ctenosaura pectinata* (Oelrich, 1956), *Azendohsaurus madagaskarensis* (FMNH PR 2765, see fig. 8B), *Sphenodon punctatum* (Evans, 2008), and *Osmolskina czatkowicensis* (ZPAL RV/539). A contrasting state occurs in some archosauriforms, in which the facial nerve foramen is compressed between two laminar bony plates. One, the crista prootica is situated anterodorsally, whereas the second plate is a slender expansion of the bony surface of the prootic posterior to the facial nerve opening. This “sandwiched” morphology can be seen in *Proterosuchus goweri* (NMQR 880, see fig. 8C), *Erythrosuchus africanus* (NHMUK R3592), *Batrachotomus kupferzellensis* (Gower, 2002), and *Fugusuchus hejiapensis* (Gower and Sennikov, 1996).

CHARACTER 303: Ilium, anteroventral margin of iliac blade: (0) inclined posterodorsally, (1) inclined vertically, (2) inclined anterodorsally.

Examples of past usage: NOVEL CHARACTER.

Justification/Ontology: The anteroventral margin of the iliac blade, anterodorsal to the acetabulum, is inclined posterodorsally in most early reptiles. This condition is found in

Petrolacosaurus kansensis (Reisz, 1981), *Youngina capensis* (BP/1 3859), *Thadeosaurus colcanapi* (MNHN PM 1908-11-19a), and modern lepidosaurs (e.g., Conrad, 2006; Russell and Bauer, 2008). In contrast, the anterior margin of the iliac blade is vertical in drepanosauromorphs (e.g., *Hypuronector limnaios*, AMNH FARB 7759) early saurians, including *Trilophosaurus buettneri* (TMM 31025-73) and *Noteosuchus colletti* (Carroll, 1976). In most archosauromorphs, the base of the iliac blade has an anterodorsal inclination, such that the anterior portion of the blade is positioned dorsal to the pubic peduncle. This inclination occurs in *Tanystropheus longobardicus* (PIMUZ T/1277), *Macrocnemus bassanii* (PIMUZ T/4822), *Prolacerta broomi* (BP/1 2676; SAM K10802), "Chasmatosaurus" *yuani* (IVPP V4067), *Azendohsaurus madagaskarensis* (Nesbitt et al., in press), and *Erythrosuchus africanus* (NHMUK R3592). *Kuehneosaurus latus* (AMNH FARB 7781) exhibits a similar condition, although it also has a slender lamina of bone between the pubic peduncle and the anterior surface of the blade that makes the anterior surface appear verticalized.

Phylogenetic Analysis

All of the phylogenetic analyses run as part of this study were performed using TNT v. 1.1 (Goloboff et al., 2008). We ran a heuristic search with 10,000 replicates of Wagner trees (using random addition sequences) followed tree-bisection and reconnection (TBR) branch swapping, holding 10 trees per replicate. The best trees obtained from this were subjected to a final round of TBR branch swapping. Zero-length branches were collapsed under rule one of Coddington and Scharff (1994).

For Bremer support values, we used the Bremer.run script available with TNT. We employed Jackknife resampling in TNT, using 10,000 replications with a 20% character removal probability. CI and RI were calculated using the STATS.run script available with TNT. Alternative topologies were constructed the tree editor window in Mesquite 3.02 (Maddison and Maddison, 2015). These were imported in TNT, where we enforced the topological constraints described below.

RESULTS

This iteration of this analysis presented includes all of the taxa and characters discussed above. The analysis produced 18 most-parsimonious trees (MPTs) of 945 steps, recovered in 3,416 out of 10,000 replicates. The consistency index (CI) is 0.350, and the retention index (RI) is 0.654. The strict consensus is present in Figure 4.

The recovered topology is broadly consistent with past hypotheses of the phylogeny of Diapsida, in terms of the taxa included in Neodiapsida, Lepidosauromorpha, and Archosauromorpha (e.g., Gauthier, 1984; Evans, 1988; Dilkes, 1998; Pritchard et al., 2015). The position of Drepanosauromorpha outside of Sauria was noted in chapter 4 of this dissertation, as previously recovered by Merck (2003), Senter (2004), and Müller (2004). The position of this clade, Weigeltisauridae, and those taxa traditionally grouped in Younginiformes (see Currie, 1981a; Gauthier et al., 1988a; Bickelmann et al., 2009) relative to Sauria is highly unstable. The additions to the character count from chapter 4 have altered the topology of non-Sauria diapsids, with "younginiforms" being more closely related to Sauria than either Drepanosauromorpha or Weigeltisauridae. However, this portion of the topology is highly unstable; the node supporting a "younginiform" + Sauria clade has a GC value of 25.

Sauria itself is substantially better supported than any of the other early-diverging nodes with a GC value of 70. Two of the characters unambiguously supporting this node are a posterior embayment to the quadrate (42.1) and a lateral crest on the quadrate (43.1), both of which likely relate to the development of a tympanic membrane linked to the quadrate (e.g., Robinson, 1973). Changes in the construction of the quadrate have been recognized in past analyses at the saurian node, consistent with the development of the tympanum. Laurin (1991) recovered a posterior emargination at that node. Other analyses have not recognized changes to the quadrate at this node unambiguously (e.g., Dilkes, 1998; Ezcurra et al., 2014). Further study is needed to assess the connection between a tympanum and the radiation of crown reptiles.

Within Sauria, a major topological change involves the position of Kuehneosauridae. Gauthier et al. (1988a), Waldman and Evans (1994), and Evans (2009) recovered Kuehneosauridae within Lepidosauromorpha but outside of Lepidosauria. By contrast, Müller (2004) recovered a Drepanosauridae + Kuehneosauridae clade near the base of Sauria. In contrast to the topology presented in chapter 3 of this dissertation, Kuehneosauridae is recovered deeply nested within Archosauromorpha as opposed to at its base. This may be a consequence of the addition of the Early Triassic Russian archosauromorph *Boreopricea funerea*. However, the node supporting a relationship between Kuehneosauridae and *Boreopricea* is extremely unstable.

The topology in this analysis differs from that in Nesbitt et al. (in press) in the position of Rhynchosauria. In that study Rhynchosauria was the sister taxon to Allokotosauria + Archosauriformes. By contrast, this analysis recovers a Kuehneosauridae + Allokotosauria clade as the sister taxon of Rhynchosauria + Archosauria clade. However, all of the major internodes on the stem of Archosauromorph are rife with contradictory data; the only major node supported by a GC value greater than 50 is Tanystropheidae + Archosauria. As such, the only statement that can be made without much ambiguity is that *Protorosaurus speneri* is the sister taxon of all other Archosauromorpha.

Neodiapsida Benton, 1985

Revised Definition: All taxa more closely related to *Sphenodon punctatum*, *Lacerta agilis*, *Passer domesticus*, and *Crocodylus niloticus* than to *Araeoscelis gracilis*.

Comments on Definition: Benton (1985) originally coined Neodiapsida to refer to Lepidosauria, Archosauria, and a number of taxa of indeterminate affinities (e.g., *Heleosaurus*, Kuehneosauridae). Gauthier et al. (1988b) offered a stem-based definition that excluded Araeoscelida. I follow this definition here, albeit including species of modern and extinct diapsids as specifiers.

Weigeltisauridae Kuhn, 1939

Support Metrics: Bremer = 2, GC = 98.

Revised Definition: All taxa more closely related to *Coelurosauravus jaekeli* than to *Drepanosaurus unguicaudatus*, *Youngina capensis*, *Thadeosaurus colcanapi*, *Lacerta agilis*, *Sphenodon punctatum*, *Crocodylus niloticus*, and *Passer domesticus*.

Unambiguous Synapomorphies: Prominent horns on squamosal and quadratojugal (265.1); entepicondyle extends distally relative to humeral condyles (281.1).

Comments: A single genus-level taxon, *Coelurosauravus*, has been incorporated into a number of past analyses of diapsid phylogeny (e.g., Laurin, 1991; Müller, 2004). No other analysis has incorporated more than one weigeltisaurid taxon. I maintain the species-level separation between *C. jaekeli* and *C. elivensis* as suggested by Evans and Haubold (1987). One character that is not unambiguously optimized as a weigeltisaurid synapomorphy is the presence of accessory patagial spurs articulated with the distal tips of the dorsal ribs. This is a consequence of the disarticulated nature of the *Rautiania* spp. material coded in this study.

Drepanosauromorpha Renesto et al., 2010

Support Metrics: Bremer = 3, GC = 98.

Revised Definition: The most recent common ancestor of *Hypuronector limnaios* and *Drepanosaurus unguicaudatus* and all of its descendants.

Unambiguous Synapomorphies: Thyroid fenestra present (161.1); chevrons fused to respective caudal centra (249.1); chevrons more proximodistally elongate than caudal neural spines (250.1); absence of cervical ribs (273.1); heterocoely (saddle-shaped intervertebral articulations) in cervical column (275.1).

Comments: Most cladistic studies of diapsid relationships have incorporated a small number of drepanosauromorphs. Merck (1997) and Dilkes (1998) incorporated *Megalancosaurus* and *Drepanosaurus*, whereas Müller (2004) employed a concatenated Drepanosauridae based on Dilkes (1998) and descriptions of drepanosaurid fossils (e.g., Berman and Reisz, 1992; Renesto and Paganoni, 1995). Both Merck and Dilkes recovered the drepanosaurid taxa within a clade.

Senter (2004) published an analysis incorporating all named drepanosauromorph taxa at the time. That study recovered MCSNB 4751 (later named *Vallesaurus cenensis* by Renesto and

Binelli, 2006) as the earliest divergence within the lineage. Renesto et al. (2010) developed an independent analysis to test the ingroup affinities of drepanosaurs, recovering *Hypuronector limnaios* as the sister taxon of all other drepanosaurs. They named Drepanosauromorpha as a node-based taxon based on *Hypuronector* and all other named drepanosaurs.

Elyurosauria Renesto et al., 2010

Support Metrics: Bremer = 2, GC = 85.

Revised Definition: The most recent common ancestor of *Vallesaurus cenensis* and *Drepanosaurus unguicaudatus* and all of its descendants.

Comments on Definition: Renesto et al. (2010) defined this clade as the least inclusive including *Vallesaurus* and *Megalancosaurus*. I modify the definition here to include *Drepanosaurus*.

Unambiguous Synapomorphies: Scapular blade curves anterodorsally (143.1); anterior dorsal pedicels taller than respective centra (252.1); chevrons exhibit prominent anterior concavity (263.1); accessory supraneural ossification present anterodorsal to anterior dorsal vertebrae (286.1); scapular blade extremely anteroposteriorly narrow (ratio of anteroposterior length to dorsoventral height >1/4) (288.1).

Comments: I recover a pattern of divergences among Drepanosauromorpha identical to that suggested by Renesto et al. (2010). I maintain the clade name suggested by Renesto et al. (2010), Elyurosauria, for the node-based taxon of Drepanosauromorpha excluding *Hypuronector*.

Drepanosauridae Carroll, 1988

Support Metrics: Bremer = 2, GC = 87.

Revised Definition: The most recent common ancestor of *Dolabrosaurus aquatilis*, *Megalancosaurus preonensis*, and *Drepanosaurus unguicaudatus* and all of its descendants.

Unambiguous Synapomorphies: Calcaneum exhibits prominent lateral wing (187.1); posterior chevrons articulate with anteroventral surfaces of centra (248.1); anterior caudal neural spines expand into “T” shape dorsally (250.1).

Comments: I employ the definition offered by Dilkes (1998) for Drepanosauridae.

Unnamed Node (*Megalancosaurus* + *Drepanosaurus*)

Support Metrics: Bremer = 1, GC = 69.

Unambiguous Synapomorphies: One non-ungual phalanx in third manual digit (272.1).

Comments: This result differs from Senter (2004), in which *Megalancosaurus* and *Dolabrosaurus* are sister taxa. In contrast, Renesto et al. (2010) recovered the same branching pattern described here.

Unnamed Node (*Coelophysis* Quarry Drepanosaurid + *Drepanosaurus*)

Support Metrics: Bremer = 1, GC = 69.

Unambiguous Synapomorphies: Glenoid fossa shifted distally relative to scapular blade (284.1); glenoid fossa faces laterally (287.1).

Unnamed Node (*Youngina* + Sauria)

Support Metrics: Bremer = 2, GC = 25.

Unambiguous Synapomorphies: Posterior lamina of squamosal absent (35.1); limited development of ectepicondylar crest (150.1); internal trochanter reaches proximal surface of femur (177.1); pterygoid ramus of quadrate elevated above condylar margin (291.1).

Sauria MacCartney, 1802

Support Metrics: Bremer = 3, GC = 70.

Revised Definition: The most recent common ancestor of *Sphenodon punctatum*, *Lacerta agilis*, *Passer domesticus*, and *Crocodylus niloticus* and all of its descendants.

Unambiguous Synapomorphies: Quadrate embayed posteriorly (42.1); lateral flange (= tympanic crest) of quadrate present (43.1); posterior process on posterodorsal corner of ischium (173.1); fifth metatarsal hooked (195.1).

Archosauromorpha von Huene, 1946

Support Metrics: Bremer = 7, GC = 96.

Revised Definition: All taxa more closely related to *Crocodylus niloticus* and *Passer domesticus* than to *Sphenodon punctatum* and *Lacerta agilis*.

Comments on Definition: This definition follows that of Gauthier (1984) and has been employed in most modern analyses (e.g., Dilkes, 1998).

Unambiguous Synapomorphies: Postorbital makes contact with medial elements of skull table (18.0); pineal foramen absent (22.1); anterior cervical ribs elongate and parallel to long axis of cervical column (103.1); anterior process of cervical ribs (104.1); anterior cervical costal facets positioned anteroventrally on cervical centra (110.1); long axis of cervical neural spines inclined anterodorsally (115.1); two costal facets in anterior dorsal region (121.1); notch in anteromedian margin of interclavicle (141.1); no ectepicondylar crest (149.1); no roof to ectepicondylar groove for radial neurovasculature (151.1); absence of fifth distal carpal (157.1); long axis of iliac blade oriented horizontally (162.1); femoral head concave with prominent groove (176.1); absence of notochordal canal (276.1); post-temporal processes of parietal anteroposteriorly flattened.

Unnamed Node (Tanystropheidae + Archosauria)

Support Metrics: Bremer = 2, GC = 70.

Unambiguous Synapomorphies: Reduced anterodorsal process of premaxilla (2.1); posterodorsal process of premaxilla present (3.1); tibia contacts pedal centrale (189.1).

Tanystropheidae Gervais, 1859

Support Metrics: Bremer = 3, GC = 93.

Revised Definition: All taxa more closely related to *Tanystropheus conspicuus* than to *Protorosaurus speneri*, *Rhynchosaurus articeps*, *Trilophosaurus buettneri*, *Azendohsaurus madagaskarensis*, *Kuehneosaurus latus*, *Boreopricea funerea*, and *Proterosuchus fergusi*.

Unambiguous Synapomorphies: Lacrimal does not extend dorsally to meet nasal (12.1); conical palatal teeth (97.1); prominent anterodorsal process on anterior cervical neural spines (113.1); dorsal neural spines expanded anteroposteriorly and transversely at distal tips (124.1); posterior process of second sacral pleurapophysis terminally sharp (131.1); anterior caudal transverse processes angled posterolaterally (133.1); scapular blade curved posterodorsally (142.1); entepicondylar crest absent (152.0); thyroid fenestra present (161.1); supraacetabular crest exhibits bulbous expansion dorsal to acetabulum (165.1); outer process of fifth metatarsal absent (194.0); maxilla dorsal process concave posteriorly (199.0); axial neural spine inclined anterodorsally (239.1); post-acetabular portion of iliac blade exhibits anterodorsally running crest (282.1).

Macrocnemus Nopcsa, 1930
(*Macrocnemus bassanii* + *Macrocnemus fuyuanensis*)

Support Metrics: Bremer = 3, GC = 93.

Unambiguous Synapomorphies: Frontoparietal suture forms anteriorly convex "U" shape in dorsal view (16.1); marginal dentition recurved posteriorly (90.1).

Unnamed Node (*Amotosaurus* + *Tanytrachelos*)

Support Metrics: Bremer = 3, GC = 77.

Unambiguous Synapomorphies: Pedal centrale absent as distinct ossification (182.1); first distal tarsal absent (191.1); fifth metatarsal lacks preaxial concavity (196.1); first phalanx of fifth pedal digit elongate, similar in length to metatarsals (197.1).

Unnamed Node (*Tanystropheus* + *Tanytrachelos*)

Support Metrics: Bremer = 3, GC = 93.

Unambiguous Synapomorphies: Posterior dorsal ribs fused to transverse processes (123.1); posterodorsal portion of quadrate with a ventrally oriented hook (205.1); metatarsals IV similar in length to metatarsal III (229.1); perforating foramen in tarsus narrow and constricted (260.1).

Unnamed Node (*Langobardisaurus* + *Tanytrachelos*)

Support Metrics: Bremer = 1, GC = 48.

Unambiguous Synapomorphies: Procoelous vertebrae (101.2); cervical centra dorsoventrally compressed (106.1); anterior process of ilium anteroposteriorly elongate and dorsoventrally tall (168.1); femoral shaft straight with slight ventrodistal inclination (175.1).

Unnamed Node (Allokotosauria + Archosauria)

Support Metrics: Bremer = 1, not recovered in jackknife analysis.

Unambiguous Synapomorphies: Exoccipitals exhibit ventromedially inclined processes that do not exclude the supraoccipital from the foramen magnum (59.1); posterior surface of ilium straight (174.0); calcaneum exhibits prominent lateral wing, twice the breadth of the distal tarsal facet (186.1).

Unnamed Node (Kuehneosauridae + Allokotosauria)

Support Metrics: Bremer = 2, not recovered in jackknife analysis.

Unambiguous Synapomorphies: Depression on ventral surface of parabasisphenoid (67.2); lateral exposure of angular terminates anterior to articular (81.0); supraglenoid tubercle on scapula (144.0); prominent flexor tubercle on pedal unguals, expanded ventral to phalangeal articulation (230.1); gastralia small in number or absent (235.1), atlantal centrum fused to axial intercentrum (239.1).

Unnamed Node (*Boreopricea* + Kuehneosauridae)

Support Metrics: Bremer = 2, not recovered in jackknife analysis.

Unambiguous Synapomorphies: Frontoparietal suture anteriorly convex and "U"-shaped in dorsal view (16.1); posterior process of jugal absent (32.0); dorsal vertebral neural spines expanded anteroposteriorly and transversely (124.1); premaxilla exhibits palatal process (243.1).

Kuehneosauridae Robinson, 1962

Support Metrics: Bremer = 5, GC = 99.

Definition: All taxa more closely related to *Kuehneosaurus latus* than to *Protorosaurus speneri*, *Tanystropheus longobardicus*, *Boreopricea funerea*, *Trilophosaurus buettneri*, *Azendohsaurus laaroussii*, *Rhynchosaurus articeps*, *Prolacerta broomi*, *Crocodylus niloticus*, *Passer domesticus*, *Lacerta agilis*, *Sphenodon punctatum*, and *Drepanosaurus unguicaudatus*.

Comments on Definition: The definition provided for Kuehneosauridae is particularly speciose, owing to the large number of possible phylogenetic positions suggested for the group (e.g., archosauromorph, lepidosauromorph, non-saurian diapsid).

Unambiguous Synapomorphies: Squamosal lateral lamina absent (34.2); anterior cervical diapophysis near dorsoventral level of pedicels (110.0); ectepicondylar foramen (149.1); femoral shaft straight with ventrodistal downturn (175.1); centra of cervical vertebrae 3–5 with subequal length and height (212.1); costal articulations of dorsal vertebrae at anteroposterior midpoint of centrum (213.1); dorsal ribs oriented laterally to form patagium (264.1); elongate and projecting internal tuberosity of humerus (271.1).

Allokotosauria Nesbitt et al., in press

Support Metrics: Bremer = 1, GC = 31.

Definition: The least inclusive clade including *Azendohsaurus madagaskarensis* and *Trilophosaurus buettneri*, but not *Protorosaurus speneri*, *Tanystropheus longobardicus*, *Kuehneosaurus latus*, and *Proterosuchus fergusi*

Comments on Definition: This definition of Allokotosauria is congruent with that offered by Nesbitt et al. (in press). I have added *Kuehneosaurus* into the definition due to its deeply nested position within Archosauromorpha in this analysis.

Unambiguous Synapomorphies: Pointed, projecting tibial condyle of the femur (180.1); rounded and mound-like fibular condyle (181.1); posterodorsal portion of quadrate exhibits ventrally oriented hook (205.1); distal pedal phalanges, external margins of articular condyles converge distally (231.1); anterior tip of dentary deflected anteroventrally (237.1).

Comments: Nesbitt et al. (in press) was the first published analysis to incorporate *Azendohsaurus* into a phylogenetic study. They recovered a close relationship between *Trilophosaurus* and *Azendohsaurus*. A number of additional unambiguous synapomorphies were offered for the clade (e.g., distinct trochlear and capitular articulations of the humerus, rugose orbital margin, rugose orbital margin). However, the distributions of these characters have changed in this study due to the incorporation of new taxa and modifications to existing codings. As with Nesbitt et al. (in press), most of the characters diagnosing Allokotosauria are highly homoplastic, with multiple transitions recognized.

Azendohsauridae Nesbitt et al., in press

Support Metrics: Bremer = 1, GC = 16.

Revised Definition: All taxa more closely related to *Azendohsaurus laaroussii* than to *Protorosaurus speneri*, *Tanystropheus conspicuus*, *Rhynchosaurus articeps*, *Trilophosaurus buettneri*, and *Proterosuchus fergusi*.

Unambiguous Synapomorphies: Marginal dentition serrated (88.1); distal femoral condyles expanded beyond femoral shaft (179.0); metatarsal five without proximally projecting process (194.0).

Comments: Nesbitt et al. (in press) recovered *Pamelaria dolichotrachela* as the sister taxon to Allokotosauria, although they noted several apparent homoplasies shared between *P. dolichotrachela* and *Azendohsaurus*. One of these, the weak development of an anterodorsal process of the premaxilla, is now recognized as widespread in early archosauromorphs (e.g., *Boreopricea funerea*, PIN 3708/2; *Tanystropheus longobardicus*, PIMUZ T/2819). Another, the ventral depression on the parabasisphenoid, appears to be present in *Kuehneosaurus latus* (AMNH FARB 7771). The low Bremer value and the extremely low GC for this node suggest a great deal of instability in this portion of the tree.

Azendohsaurus Dutuit, 1972

(*Azendohsaurus laaroussii* + *Azendohsaurus madagaskarensis*)

Support Metrics: Bremer = 1, GC = 80.

Unambiguous Synapomorphies: Dentary teeth proportionally larger than upper dentition (209.1).

Comments: Nesbitt et al. (in press) recovered the two *Azendohsaurus* species as a clade, supported by three unambiguous synapomorphies. One, the medial ridge on the maxilla, is only scored for these two species within the ingroup sample. However, it is unknown in *Pamelaria dolichotrachela*, leaving its distribution ambiguous. Another, the ascending process of the maxilla being a separate and posteriorly concave process, is now evidenced in a number of other archosauromorph taxa (e.g., *Macrocnemus bassanii*, PIMUZ T/4822; *Amotosaurus rotfeldensis*, SMNS 90601).

Trilophosauridae Gregory, 1945

Support Metrics: Bremer = 1, GC = 47.

Revised Definition: All taxa more closely related to *Teraterpeton hrynewichorum* and *Trilophosaurus buettneri* than to *Protorosaurus speneri*, *Tanystropheus conspicuus*, *Rhynchosaurus articeps*, *Azendohsaurus laaroussii*, and *Proterosuchus fergusi*.

Comments on Definition: Following Nesbitt et al. (in press), I adopt a formal definition of Trilophosauridae incorporating *Trilophosaurus buettneri* and *Teraterpeton hrynewichorum*.

Unambiguous Synapomorphies: Anterodorsal process of premaxilla contributes to internarial bar (3.0); maxilla with lateral process projecting beyond alveoli (8.1); infratemporal fenestra closed due to expansion of lateral temporal bones (30.1); contact between dorsal process of jugal and squamosal present (32.1); marginal dentition absent on anterior portion of jaws (87.1); teeth consist of flattened platform with pointed cusps (92.1); scapular blade anteroposteriorly narrow (ratio of length/height 0.4 > 0.25) (288.1).

Comments: Sues (2003) presented a modification of the Dilkes (1998) analysis incorporating both *Teraterpeton hrynewichorum* and *Trilophosaurus buettneri*. These were recovered in a monophyletic grouping in this analysis and that of Pritchard et al. (2015).

Trilophosaurus Case, 1928

(*Trilophosaurus buettneri* + (*T. jacobsi* + *Spinosuchus caseanus*))

Support Metrics: Bremer = 1, GC = 62.

Revised Definition: The most recent common ancestor of *Trilophosaurus buettneri* and *Spinosuchus caseanus* and all of its descendants.

Unambiguous Synapomorphies: Facial contribution of lacrimal restricted to orbital margin (11.2); prominent coronoid process (78.1); marginal teeth broader labiolingually than mesiodistally (97.2); dorsal costal articulations positioned at anteroposterior center of centra (213.1); marginal teeth with lateral resorption pits (289.1).

Comments: Excluding the last unambiguous synapomorphy of this list, the characters listed above diagnosing *Trilophosaurus* are identical to those offered by Nesbitt et al. (in press). The latter character was not included in that study. Considering the high number of synapomorphies exclusive to the group, a low Bremer support value is initially surprising. However, this is likely a consequence of the limited nature of the available material of *Spinosuchus caseanus* (UMMP 7507), which does not include any cranial and appendicular elements. Excluding *Spinosuchus* results from an iteration of this analysis produces a *Trilophosaurus* node with a Bremer of 4.

Unnamed Node (*T. jacobsi* + *Spinosuchus*)

Support Metrics: Bremer = 1, GC = 47.

Unambiguous Synapomorphies: Spinopostzygapophyseal lamina present on fifth vertebra from sacrum (241.1).

Comments: The ambiguity regarding the synonymy of *Trilophosaurus jacobsi* and *Spinosuchus caseanus* is discussed above and by Nesbitt et al. (in press). This result and its character support is identical to that recovered by Nesbitt et al. (in press).

Unnamed Node (Rhynchosauria + Archosauria)

Support Metrics: Bremer = 2, GC = 15.

Unambiguous Synapomorphies: Paroccipital processes of opisthotic flattened anteroposteriorly (62.1); femoral condyles do not expand markedly beyond femoral shaft (179.0); prominent neurovascular opening on anterolateral surface of maxilla (201.0); posterior tip of retroarticular process upturned posterodorsally (300.1).

Comments: A number of different early archosauromorph groups have been resolved as the sister taxon to Archosauriformes in past cladistic studies. Gauthier (1984) recovered Trilophosauria, Protorosauria, and Archosauriformes in a polytomy. This result most closely mirrors that of Dilkes (1998) and Ezcurra et al. (2014), in which Rhynchosauria is recovered as the sister taxon to the clade *Prolacerta* + Archosauriformes.

Although a close relationship between Rhynchosauria and Archosauriformes has been recovered by past studies (noted above), I do not consider the question of which early archosauromorph clade is the sister taxon to Archosauriformes resolved. In Dilkes (1998), this node could be collapsed with a single additional step. The result is slightly more robust in this study, but the extremely low GC value suggests high levels of contradictory data in this portion of the phylogeny.

Rhynchosauria Osborn, 1903

Support Metrics: Bremer = 7, GC = 98.

Revised Definition: All taxa more closely related to *Rhynchosaurus articeps* than to *Protorosaurus speneri*, *Tanystropheus conspicuus*, *Trilophosaurus buettneri*, *Azendohsaurus madagaskarensis*, *Kuehneosaurus latus*, *Boreopricea funerea*, and *Proterosuchus fergusi*.

Comments on Definition: Dilkes (1998) offered a node-based definition of Rhynchosauria based on the common ancestor of *Mesosuchus browni*, *Howesia browni*, and all of its descendants. However, a node-based definition will allow incorporation of all taxa close to the rhynchosaur stem. We also incorporate the nominal taxon, *Rhynchosaurus articeps*, into the definition.

Unambiguous Synapomorphies: Posterodorsal process of premaxilla extends posteriorly to contact anterior tip of prefrontal (5.2); dorsal surface of frontal and prefrontal marked by distinct dorsal pits (16.1); vomer contacts maxilla (45.1); pterygoids make broad contact along anteroposterior length (52.2); exoccipitals do not fuse with basioccipital or opisthotic (60.0); splenials contribute mandibular symphysis (83.0); multiple zahnreihen in maxilla (90.1); anterior margin of scapula concave (217.1); anterior caudal neural spines dorsoventrally taller than sacral neural spines (277.1); metatarsal I proximodistally short (length ratio relative to metatarsal IV <0.32) (296.2).

Comments: A monophyletic Rhynchosauria was recovered by Dilkes (1998), Ezcurra et al. (2014), and Pritchard et al. (2015). Early phylogenetic studies offered a small number of synapomorphies supporting the clade (e.g., Benton, 1985, 1990; Evans, 1988), although Dilkes (1998) expanded the number of characters substantially. This list of synapomorphies is broadly congruent with that of Dilkes (1998).

Among the characters found to be diagnostic of Rhynchosauria in this analysis, two are worthy of further study: the lack of fusion of the exoccipitals with other braincase elements (60.0) and the contribution of the splenial to the mandibular symphysis (83.0). With regards to the former, it is based on the sutural distinctiveness of the exoccipital in *Mesosuchus browni* (SAM K6536) and other figured rhynchosaur skulls (e.g., Montefeltro et al., 2010), a relatively limited sample. With regards to the symphyseal character, a number of other archosauromorph taxa exhibit splenials near the level of the symphysis (e.g., *Prolacerta broomi*, UCMP 37151; *Tanystropheus longobardicus*, MCSN BES SC 1018). However, the symphyses in these taxa may be of class I or II as defined by Holliday and Nesbitt (2013), in which the symphysis is formed by limited rugosities and smooth, abutting contact sites. Without well-preserved and/or well disarticulated splenials, the relative contribution of that element to the symphysis would be difficult

Unnamed Node (*Howesia* + Rhynchosauridae)

Support Metrics: Bremer = 3, GC = 88.

Unambiguous Synapomorphies: Ventral margin of maxilla convex (7.1); parietal dorsal surface drawn into transversely narrow sagittal crest (20.2); appressed nasals form anteriorly flattened margin (297.1).

Rhynchosauridae Huxley, 1887

Support Metrics: Bremer = 7, GC = 99.

Revised Definition: The most recent common ancestor of *Rhynchosaurus articeps* and *Hyperodapedon gordoni* and all of its descendants.

Unambiguous Synapomorphies: Post-temporal processes of parietal oriented transversely (21.0); jugal exhibits anteroposteriorly running crest (31.1); posterior process of jugal contacts quadratojugal (33.2); palatal teeth absent (44.1); supraoccipital pillar-shaped (56.1); ectopterygoid contacts entire lateral surface of pterygoid (204.1); anteroposteriorly running groove in alveolar surface of maxilla (268.1); concavity in dorsolateral surfaces of dorsal neural arches absent (301.0).

Unnamed Node (*Prolacerta* + Archosauria)

Support Metrics: Bremer = 5, GC = 83

Unambiguous Synapomorphies: Anterodorsal process of premaxilla prominent and contributing to internarial bar (3.0); depression in ventral surface of parabasisphenoid (67.1); external mandibular fenestra present between postdentary elements (83.1); marginal dentition recurved posteriorly (90.1); marginal teeth labiolingually compressed (97.1); tibial condyle projecting and pointed (180.1); fibular condyle rounded and mound-like (181.1); margin between tibial and fibular facets of astragalus bridged by thin lamina (236.1); posteriormost portion of lateral surface of dentary positioned between surangular and angular (242.1); premaxilla palatal process present (243.1).

Comments: Dilkes (1998) developed the first cladistic analysis to both recover *Prolacerta broomi* outside of a monophyletic grouping of long-necked archosauromorphs and to find the species as the sister taxon to Archosauriformes. However, Benton (1985) did note many morphological characters that linked *Prolacerta* and *Proterosuchus*. Nesbitt (2011), Pritchard et al. (2015), and numerous modifications of Dilkes (1998) (e.g., Sues, 2003; Gottmann-Quesada and Sander, 2009) have also recovered this result.

This analysis is the first to recognize an external mandibular fenestra in the lateral surface of the mandible of *Prolacerta broomi*. This is a preliminary observation based primarily on two specimens (BP/1 5880 and UCMP 37151), which exhibit the best-preserved contacts between postdentary bones. In these specimens, there is a small but distinct gap situated between the anterior tips of the angular and surangular and the posteroventral portion of the dentary. It is possible that this gap is a preservational artifact in both of these specimens, but additional data is needed to disprove the presence of the opening.

Archosauriformes Gauthier et al., 1988b

Support Metrics: Bremer = 5, GC = 99.

Revised Definition: The most recent common ancestor of *Proterosuchus fergusi*, *Crocodylus niloticus*, and *Passer domesticus*.

Unambiguous Synapomorphies: Prefrontal-nasal suture oriented anteroposteriorly (8.0); antorbital fenestra present (13.1); frontals exhibit abrupt expansion posteriorly (15.2); postparietals present (24.1); posterior process of postorbital reaches posterior margin of supratemporal fenestra (27.1); jugal posterior process contacts quadratojugal (33.2); exoccipitals meet one another on floor of foramen magnum (60.1); laterosphenoid ossification present and contacting frontal (71.2); serrated marginal dentition (89.1); intercentra in cervical column (104.0); dorsal process of maxilla concave posteriorly (200.0); ectopterygoid articulates with entire lateral extent of pterygoid (204.1); surangular exhibits prominent lateral shelf (294.1); articular fossa posterior to glenoid anteroposteriorly narrow than glenoid fossa (299.1).

Comments: Gauthier et al. (1988b) coined Archosauriformes to describe a clade including Proterosuchidae + Archosauria. A similar grouping has been recovered in nearly all analyses of Archosauromorpha (e.g., Dilkes, 1998; Nesbitt, 2011; Ezcurra et al., 2015; Pritchard et al., 2015). That at least one Permian reptile, *Archosaurus rossicus*, falls within this clade based on a number of morphological characters (see Sennikov, 1988; Ezcurra et al., 2014) drives much of the discussion of the timing of the archosauromorph diversification within the Permian Period (e.g., Dilkes, 1998).

Proterosuchidae Broom, 1906

Support Metrics: Bremer = 5, GC = 99.

Revised Definition: All taxa more closely related to *Proterosuchus fergusi* than to *Prolacerta broomi*, *Erythrosuchus africanus*, *Chanaresuchus bonapartei*, *Euparkeria capensis*, *Crocodylus niloticus*, and *Passer domesticus*.

Unambiguous Synapomorphies: Ventral margin of premaxilla strongly downturn (2.2); ventral keel of cervical vertebrae absent (106.1); interclavicle broad anteriorly (140.0); posterior stem of interclavicle with transverse expansion (142.1); posterior margin of ventral half of quadrate convex (238.1).

Comments: This analysis is the second to incorporate multiple species referred to Proterosuchidae in the published literature (following Ezcurra et al., 2014). In the Ezcurra et al. (2014) analysis, a monophyletic Proterosuchidae was recovered including *Proterosuchus fergusi* and the holotype premaxilla of the Upper Permian taxon *Archosaurus rossicus*. We concur that the substantial anteroventral downturn is apomorphic for Proterosuchidae. However, the incorporation of further taxa with a similarly massive downturn (e.g., *Chalishevia cotburnata,* PIN 3852/104) may alter the distribution of this feature.

Unnamed Node (*Erythrosuchus* + Archosauria)

Support Metrics: Bremer = 5, GC = 99.

Unambiguous Synapomorphies: Premaxilla exhibits posterior knob fitted into corresponding notch on maxilla (6.1); postparietals fuse into midline interparietal (25.1); supratemporals absent (36.0); quadratojugal anterior process present (39.0); crests on ventral surface of parabasisphenoid reduced (65.0); teeth not ankylosed to tooth-bearing elements (96.0); anterior cervical ribs taper abruptly (103.0); posterior process of coracoid absent (146.0); anterior process of ilium prominent and anteriorly projecting (168.1); anterolateral surface of pubis marked by rugosity (173.2); distinct pedal centrale absent (182.0); prominent neurovascular opening on anterolateral surface of maxilla (201.0); anterior process of jugal dorsoventrally expanded (202.1); parabasisphenoid vertically oriented (206.1); posteroventral portion of maxilla overlies angular (208.0), cervical vertebrae centra 3–5 length and height subequal (212.1); iliac blade length greater than three times its height (221.1).

Comments: In all cladistic studies of Archosauriformes, *Proterosuchus* and its kin are resolved as the sister taxon of an *Erythrosuchus* + Archosauria clade (e.g., Benton, 1985; Ezcurra et al., 2010; Nesbitt, 2011). I also recover this relationship with very strong support.

Unnamed Node (*Chanaresuchus* + Archosauria)

Support Metrics: Bremer = 3, GC = 97.

Unambiguous Synapomorphies: Low attachment for caudifemoralis without asymmetric apex (= fourth trochanter) (223.1); tibial and fibular facets continuous (225.1); calcaneal tuber deflected posteriorly at angle 21 < 49 degrees posteriorly (228.1); osteoderms present (232.1).

Comments: The relative position of Proterochampsidae and *Euparkeria* to Archosauria is equivocal. Some analyses (e.g., Brusatte et al., 2010) recover the former as a closer relative of Archosauria than *Euparkeria*, whereas other studies (e.g., Nesbitt, 2011) find the opposite result. Here, as with Nesbitt (2011), we recover a closer connection between *Euparkeria* and Archosauria with relatively high support.

Unnamed Node (*Euparkeria* + Archosauria)

Support Metrics: Bremer =2, GC = 95.

Unambiguous Synapomorphies: Ischium markedly longer than iliac blade (222.1); calcaneal tuber equivalent in dimensions at mid shaft (226.1).

Archosauria Cope, 1869

Support Metrics: Bremer = 5, GC = 99.

Definition: The most recent common ancestor of *Crocodylus niloticus* and *Passer domesticus* and all of its descendants.

Comments on Definition: We employ a definition of Archosauria identical to that of Sereno (2005) and Nesbitt (2011).

Unambiguous Synapomorphies: Postparietals absent (24.0); posterior process of postorbital does not reach posterior margin of supratemporal fenestra (27.0); palatal teeth absent (44.1); carotid foramina in lateral surface of parabasisphenoid (66.0); abducens foramina positioned within dorsum sellae (70.0); lateral exposure of angular terminates anterior to glenoid fossa (82.0); intercentra absent in cervical region (105.1);,intercentra absent in dorsal region (127.1); ossified olecranon process (155.0); absence of perforating foramen between astragalus and calcaneum (184.1); palatal processes of maxilla present and contacting at midline (202.2); absence of semilunar depressions in lateral surface of parabasisphenoid (207.1); antorbital fossa expanded onto lacrimal and all portions of maxilla (210.2); articular facets for fibula and distal tarsal four confluent (227.1); scapular blade anteroposteriorly narrow (height/length ratio 0.4 > 0.25) (288.1).

Saurischia Seeley, 1887

Support Metrics: Bremer = 5, GC = 99.

Revised Definition: All taxa more closely related to *Passer domesticus* than to *Triceratops horridus*.

Unambiguous Synapomorphies: Frontals maintain transverse breadth throughout anteroposterior length (15.0); postfrontal absent (27.1); jugal with anteroposteriorly running shelft (31.1); opisthotic ventral ramus narrow ventrally (57.0); exoccipitals do not meet on floor of foramen magnum (59.0); anterior cervical ribs elongate and parallel to long axis of cervical column (103.1); posteriorly pointed projections on dorsal surfaces of cervical postzygapophyses (=epipophyses) (118.1); two costal facets in anterior dorsal region (121.1); neural spines of dorsal vertebrae dorsoventrally shorter than anteroposteriorly long (128.1); absence of groove for radial neurovasculature (148.0); dorsal margin of iliac blade smoothly textured (170.0); well-ossified, convex femoral head (176.0); fifth metatarsal lacks outer process (194.0); fifth metatarsal straight-shafted (195.0); jugal tapers anteriorly (203.0); anterior cervical centra anteroposteriorly longer than dorsoventrally tall (211.0); ventral margin of acetabulum concave (220.1); anterior trochanter of femur present (224.1); osteoderms absent (233.0); gastralia few in number or absent (235.1).

Comments: The two representative early dinosaurs in this analysis were selected for the expanded Pritchard et al. (2015) analysis in Nesbitt et al. (in press). Both *Coelophysis bauri* and *Plateosaurus engelhardti* are both known from a substantial number of complete and partial individuals from extensive bonebeds (e.g., Colbert, 1989; Sander, 1992). This definition of Saurischia follows Gauthier (1986). Based on extensive studies of early archosaur phylogeny (e.g., Nesbitt, 2011), some of these characters exhibit a more complex distribution within Ornithodira.

Lepidosauromorpha Benton, 1983

Revised Definition: All taxa more closely related to *Sphenodon punctatum* and *Lacerta agilis* than to *Crocodylus niloticus* and *Passer domesticus*.

Lepidosauria Haeckel, 1866

Support Metrics: Bremer = 10, GC = 99.

Revised Definition: The most recent common ancestor of *Sphenodon punctatum* and *Lacerta agilis* and all of its descendants.

Unambiguous Synapomorphies: Abducens foramina positioned within dorsum sellae (70.0); coronoid process present (78.1); lateral exposure of angular dorsoventrally narrow (81.1); retroarticular process made up of fused prearticular and articular (86.1); marginal teeth with no lingual border (= pleurodonty) (94.1); dorsal vertebral neural spines dorsoventrally shorter than anteroposteriorly long (128.1); accessory zygosphene-zygantrum articulations in dorsal vertebral column (129.1); autotomy septa within caudal vertebrae (134.1); no perforating foramen within carpus (159.1); iliac blade posterodorsally inclined (161.1); pubic process of ilium drapes across anterodorsal margin of pubis (163.1); distinct pedal centrale absent (182.1); astragalus and calcaneum co-ossified (183.1); perforating foramen within astragalocalcaneum absent (184.1); centra of cervical vertebrae 3–5 length and height subequal (212.1).

Comments: For this analysis, we incorporated a sample of "younginiform" and kuehneosaurid diapsids, both of which have been considered divergences from the stem of Lepidosauria (e.g., Gauthier, 1984; Benton, 1985; Evans, 1988; Gauthier et al., 1988a). Most recent cladistic studies have considered "younginiforms" to be earlier divergences from the stem to Sauria (e.g., Laurin, 1991; Dilkes, 1998; Bickelmann et al., 2009). Kuehneosaurids have been recovered as the sister taxon to Lepidosauria (Gauthier et al., 1988a; Evans, 1991) and as the sister taxon of Drepanosauromorpha outside of Sauria (Müller, 2004).

In this analysis, none of these taxa are recovered as the sister taxon to Lepidosauria. Thus, the diagnosis offered for Lepidosauria equally applies to Lepidosauromorpha. Unfortunately, this produces a ghost lineage for Lepidosauromorpha that extends from the Middle Triassic deep into the Permian (Jones et al., 2013). However, this study does not yet incorporate any "paliguanids," small, lizard-like diapsids from the Lower Triassic deposits of the Karoo Basin of South Africa (e.g., Carroll, 1975). Ezcurra et al. (2014) recovered *Paliguana* in a polytomy with Rhynchocephalia and Squamata at the base of Lepidosauria. I am currently collaborating on a study of the complete postcranium of *Saurosternon bainii* (NHMUK R1235) in order to more fully assess the osteology of a "paliguanid" before incorporating such an animal into this analysis.

Rhynchocephalia Günther, 1867 or **Sphenodontia Williston, 1925**

Support Metrics: Bremer = 1, GC = 23.

Revised Definition: All taxa more closely related to *Sphenodon punctatum* than to *Lacerta agilis*.

Comments on Definition: Although both Estes et al. (1988) and Gauthier et al. (1988a) employ a node-based definition of these two clades, I follow Conrad (2008) in suggesting a stem-based definition for both Rhynchocephalia and Squamata.

Unambiguous Synapomorphies: Dorsal process of jugal contacts squamosal (32.1); prominent conical palatal teeth (98.1); posteriormost portion of lateral surface of dentary positioned between surangular and angular (242.1).

Comments: In nearly all phylogenies of early lepidosaurs, *Gephyrosaurus* and *Diphydontosaurus* form successive sister taxa to the rest of sphenodontidans (e.g., Fraser and Benton, 1989; Wilkinson and Benton, 1996). Benton (1985) preferred the name Sphenodontia over Rhynchocephalia for the clade including *Sphenodon* and its extinct relatives. Gauthier et al. (1988a) considered Sphenodontida to include all taxa more derived than *Gephyrosaurus bridensis*; they dubbed the clade including both taxa Rhynchocephalia.

This analysis follows Benton (1985) in recovering *Gephyrosaurus bridensis* outside of Sphenodontia, and closer to Squamata. This result is quite poorly supported, and further sampling of crown lepidosaur characters may shift the species back to its broadly accepted position as the sister taxon of Sphenodontia (e.g., Gauthier et al., 1988a; Fraser and Benton, 1989; Jones et al., 2013).

Unnamed Node (*Clevosaurus* + *Sphenodon*)

Support Metrics: Bremer = 1, GC = 42.

Unambiguous Synapomorphies: Jugal posterior process contacts quadratojugal (33.2); exoccipitals unfused to other braincase elements (61.0); dorsal process of maxilla with distinct, concave posterior margin (200.0).

Comments: Phylogenies of early Lepidosauria typically recover *Clevosaurus* as a closer relative of *Sphenodon* than either is of *Diphydontosaurus* (e.g., Fraser and Benton, 1989; Jones et al., 2013).

Squamata Oppel, 1811

Support Metrics: Bremer = 1, GC = 10.

Revised Definition: All taxa more closely related to *Lacerta agilis* than to *Sphenodon punctatum*.

Comments on Definition: The definition of Squamata offered by Estes et al (1988) and Gauthier et al. (1988a) is node-based, concentrated on the two major subclades recovered by their morphological analyses: Iguania and Autarchoglossa. Conrad (2008) instead suggested a stem-based definition, including all non-rhynchocephalian lepidosaurs. I follow this definition.

Unambiguous Synapomorphies: Parietals indistinguishably fused (19.1); prominent ectepicondylar crest (150.0); internal trochanter does not reach proximal femoral surface (177.0); premaxillae indistinguishably fused (295.1).

Comments: This analysis recovers *Gephyrosaurus* as the outgroup to a clade including the two extant squamates in the study, *Uromastyx* and *Shinisaurus*. The postcranial characters recovered as apomorphies of Squamata exhibit substantial homoplasy within Sauria, which could easily destabilize this relationship if further taxa are incorporated. However, the cranial fusions noted in *Gephyrosaurus* are characters otherwise only shared with squamates in this analysis. A similar result was noted by Benton (1985), although nearly all lepidosaur-focused studies unite *Gephyrosaurus* with Sphenodontida (e.g., Gauthier et al., 1988a; Jones et al., 2013).

Unnamed Node (*Shinisaurus* + *Uromastyx*)

Support Metrics: Bremer = 8, GC = 98.

Unambiguous Synapomorphies: Frontals expand gradually along anteroposterior length (15.1); posterior process of jugal absent (33.0), squamosal lateral lamina absent (34.2); quadratojugal absent (38.1); pterygoid midline contact absent (52.0); pterygoid transverse processes anterolaterally oriented (53.1); exoccipitals fused to opisthotic (61.1); carotid foramina within lateral surface of parabasisphenoid (66.0); cervical neural spines restricted to posterior half of neural arch (112.1); cervical centra exhibit posteroventrally oriented crest (= hypapophysis) (244.1); notochordal pit of occipital condyle absent (269.2); notochordal canal absent (276.1).

Comments: The two modern squamates in this analysis are recovered as a clade, as expected based on past studies of modern lepidosaur phylogeny (e.g., Gauthier et al., 1988b; Conrad, 2008; Gauthier et al, 2012). The taxonomic selections made here were based on the fundamental division between *Iguana*-line taxa and those closer to scincomorphs, gekkotans, and anguimorphs (referred to as Scincogekkonomorpha by Conrad, 2008). However, molecular studies (e.g., Wiens et al., 2012) suggest that other squamate groups represent early divergences within the group (e.g., *Dibamus*, Gekkota). Future expansions of this study should include these taxa and their fossil relatives.

DISCUSSION

Stratigraphy

The distinction between the Permian and Triassic records of diapsid reptiles is a stark one (e.g., Ezcurra et al., 2014), with the Triassic seeing a rapid increase in diapsid taxonomic and morphological diversity in the Early Triassic (e.g., Borsuk-Bialynicka and Evans, 2009; Nesbitt et al., 2011) that would continue throughout the Mesozoic Era. In a way, this rapid radiation in the wake of the Permo-Triassic Extinction (PTE) mirrors the evolution of other major vertebrate groups in the wake of mass extinction events [e.g., crown birds (Zhang et al., 2014) and placental mammals (O'Leary et al., 2013)]. However, as in both of those prior cases, it is unclear how much taxonomic and morphological diversification occurred among crown diapsids prior to the PTE.

Dilkes (1998) noted that his phylogenetic hypothesis demanded a great deal of taxonomic diversification of Sauria prior to the PTE, with long ghost lineages for *Prolacerta*, *Trilophosaurus*, rhynchosaurs, and the clade Drepanosauridae + Tanystropheidae. He argued that the poor terrestrial vertebrate record during the Early Triassic and Late Permian was likely responsible for these sizeable gaps. Although other phylogenetic hypotheses for early Sauria differ from Dilkes (1998) topologically, virtually every hypothesis requires a large number of diapsid ghost lineages extending into the Late Permian (e.g., Gauthier, 1984; Müller, 2004). Ezcurra et al. (2014) suggested an even earlier divergence for many of these taxa, driven by the hypothesis that the fragmentary Middle Permian diapsid *Eorasaurus olsoni* is an archosauriform.

The topology produced here, as with that in chapter 4, is consistent with this pattern (Fig. 22, 23). In this analysis, Tanystropheidae, Rhynchosauria, *Prolacerta*, Proterosuchidae, the clade *Erythrosuchus* + Archosauria, and the clade Kuehneosauridae + Allokotosauria must originate within the Late Permian. However, as in Nesbitt et al. (in press), only the stem of Kuehneosauridae + Allokotosauria must diverge prior to the Permo-Triassic extinction. Within this clade, an origin for Allokotosauria and Kuehneosauridae is suggested by the Early Triassic based on the position of *Boreopricea funerea* (Benton and Allen, 1997). The divergence between *Trilophosaurus* and *Azendohsaurus* is suggested by the late Middle Triassic, based on the position of *Azendohsaurus madagaskarensis*. This grouping suggests that substantial taxonomic diversification was still underway among early saurian lineages during the Triassic.

In order to best understand the time of origination for these major early saurian lineages, the discovery and phylogenetic study of purported Early Triassic saurians should be a priority. Unfortunately, these taxa are often extremely fragmentary (e.g., Sennikov, 2011) or based on disarticulated materials (e.g., Borsuk-Bialynicka and Evans, 2009; Evans, 2009; Evans and Borsuk-Bialynicka, 2009). This analysis, incorporating the widest range of partial and complete skeletal material from early Sauria, will serve as a critical framework for the interpretation of such taxa.

The support metrics at the internodes within early Archosauromorpha (e.g., between *Protorosaurus* and Archosauriformes) suggest caution in interpreting the pattern of divergence among these lineages. Although low Bremer supports suggest that only limited character data supports this pattern, the very low GC values resulting from the Jackknife analysis suggest that even a slightly different selection of characters produces contradictory topologies. Indeed, past iterations of this analysis presented in Pritchard et al. (2015) and Nesbitt et al. (in press), produce contradictory branching patterns within Archosauromorpha. Interestingly, each analysis suggests that a similar number of taxonomic divergences had occurred prior to the PTE. However, a lack of understanding of the plesiomorphic character states within Archosauromorpha continues to hamper our understanding of character evolution within the group (as noted by Nesbitt et al. in press).

As more and more members of the major clades of early archosauromorph become known, it has become clear that each represents a complex radiation in its own right. As noted by Pritchard et al. (2015), Tanystropheidae includes a number of small clades with incredibly varied vertebral anatomies and craniofacial constructions (e.g., Renesto and Dalla Vecchia, 2000). The discovery of *Teraterpeton hrynewichorum* suggested a wide range of dental and cranial anatomies within a clade previously only known from *Trilophosaurus buettneri* (Sues, 2003). Indeed, one non-saurian diapsid group, drepanosauromorphs, radiated substantially during the Late Triassic (chapters 3 and 4 of this dissertation). If we are to fully understand the distribution of characters along the stem of Archosauromorpha, it is essential to understand the distribution of characters within each of these early saurian radiations. It will be especially important to find early members of each of these taxa from near the time of the Permo-Triassic Extinction (PTE).

The polyphyly of Protorosauria

Since the recognition that *Prolacerta* and other long-necked archosauromorphs shared more in common with Archosauromorpha than lizards (Gow, 1975), a group containing these reptiles has been the subject of extensive study. Most analyses (e.g., Gauthier, 1984) have incorporated a combined OTU to describe this taxon. Other studies (e.g., Evans, 1987; Benton and Allen, 1997; Jalil, 1997) have considered the possible ingroup relationships of this group. However, the recognition that a wide sample of early saurians produces a polyphyletic "protorosaur" group (e.g., Dilkes, 1998; Gottmann-Quesada and Sander, 2009) suggests that continued sampling of constituent members is critical to a broader understanding of the Permo-Triassic diapsid diversification.

In this analysis, the following taxa have been referred to Prolacertiformes or Protorosauria in cladistic studies: *Protorosaurus speneri*, Drepanosauromorpha, Tanystropheidae, *Boreopricea funerea*, *Pamelaria dolichotrachela*, and *Prolacerta broomi*. In this analysis, every of these taxa is recovered as a distinct lineage of diapsid reptile in this analysis, none of which is the sister taxon of any other "protorosaur" group (Fig. 24). Of the core of archosauromorph taxa previously considered to be "protorosaurs," only Tanystropheidae is strongly supported as a clade.

The relative elongation of the cervical vertebrae and cervical ribs have long been considered characteristic of Prolacertiformes or Protorosauria (e.g., Evans, 1987; Benton and Allen, 1997; Dilkes, 1998). Gauthier (1984), Benton and Allen (1997), Jalil (1997) also suggested that an incomplete lower temporal bar was independently acquired within this group. However, the character optimizations of Dilkes (1998), and Müller, 2004, Ezcurra et al. (2014) suggest that both cervical elongation and an incomplete lower temporal bar are more widespread within Sauria. The extensive sampling of this study allows for a new study of these characters.

The character distribution recovered by this analysis strong supports the hypothesis of Borsuk-Bialynicka and Evans (2009) that the "protorosaur" characters represent a grade within Archosauromorpha. The elongate cervical vertebrae and slender, tapering cervical ribs are recovered as plesiomorphic for the clade. These persist through many of the early-diverging lineages, although there is some ambiguity as to the presence or absence of such ribs in some clades (e.g., Kuehneosauridae, early Rhynchosauria). However, this does not represent the distribution of the body proportions noted in "protorosaurs," in which the neck is proportionally elongate relative to the skull and trunk. Mapping such proportions onto this topology will be an ideal way to resolve the distribution of these features.

The distribution of an incomplete lower temporal bar is even more complex. Among non-saurian diapsids incorporated into this study, a complete lower temporal bar is only noted in *Petrolacosaurus kansensis* and *Youngina capensis*. The bar appears to be incomplete in *Acerosodontosaurus piveteaui* (Bickelmann et al., 2009), drepanosauromorphs (see chapter 5 of this dissertation), and weigeltisaurids (Evans and Haubold, 1987). An incomplete lower temporal bar is also noted in several other problematic early saurians, such as *Claudiosaurus germaini* (MNHN MAP 1) and *Lanthanolania ivakhnenkoi* (Modesto and Reisz, 2003). This result corroborates the analysis of Müller (2003), which noted the absence of an osseous lower temporal bar as commonplace within early Diapsida and Sauria. Dilkes (1998) recovered an incomplete lower temporal bar as a synapomorphy of Sauria.

CONCLUSIONS

It is hoped this work will serve as a foundation for future studies on the phylogeny and early radiation of Diapsida and Sauria during the Permian and Triassic Periods. I envisioned three primary utilities for the phylogenetic data matrix constructed here:

1. A mechanism for understanding the distribution of morphological characters in Permo-Triassic diapsids and providing an apomorphy-based framework for interpreting new and/or fragmentary fossils (e.g., Pritchard et al., 2015; chapter 2 of this dissertation).
2. A preliminary framework for interpreting the phylogenetic position of problematic lineages (e.g., Sauropterygia, Testudines, and Thalattosauria). See chapter 4 of this dissertation.
3. A topological basis for studies of character evolution within the early diapsid radiation (e.g., Turner and Nesbitt, 2013).

The poor support metrics recognized for the major internodes within early Sauria recovered in this analysis does suggest some courses of action to improve the quality of this phylogeny, in order to improve the results to allow for the aforementioned utilities. Problematically, most of the early saurian lineages recovered as Permian divergences do not appear in the fossil record until the Middle Triassic (e.g., Rhynchosauria) or Late Triassic (e.g., Trilophosauridae, Kuehneosauridae). Improving the poor record of Late Permian and Early Triassic vertebrates should be a priority for elucidating the plesiomorphic morphologies within each major lineage. It will also be important to further describe the osteology of many early saurian groups. With recent improvements in CT technology, it is possible to produce high-resolution three-dimensional models of small, friable bony elements that were previously inaccessible through mechanical preparation (see Gardner et al., 2010; chapters 4 and 5 of this dissertation). If models of similar quality can be produced for many Permo-Triassic diapsids, especially those with small body size, the substantial amount of missing data in this phylogenetic data matrix could be drastically reduced.

LITERATURE CITED

Ahl E. (1930) Beitrage zur Lurch und Kriechtierfauna Kwangsi: section 5, Eideschen. Sitz Ges Nat Fr Berl 1930:326–331.

Australasian Reptile & Amphibian Specialist Group. 1996. *Sphenodon punctatus*. The IUCN red list of threatened species. Version 2015.2. www.iucnredlist.org Downloaded August 10, 2015.

Azevedo SA and Schultz CL. (1987) *Scaphonyx sulcognathus* (sp. nov.), um novo rincossaurideo do neotriássico do Rio Grande do Sul, Brasil. X Congreso Brasileiro de Paleontologia. (Sociedade Brasileira de Paleontologia), pp. 99–113.

Baird IL. (1970) The anatomy of the reptilian ear. Biology of the Reptilia, Volume 2 Morphology B. C Gans and T Parsons (eds). (Academic Press, London and NewYork), pp. 193–272.

Bartholomai A. (1979) New lizard-like reptiles from the Early Triassic of Queensland. Alcheringa 3:225–234.

Bassani F. (1886) Sui fossili e sull'età degli schist bituminosi triasici di Besano in Lombara. Atti Soc Italian di Sci Nat Milano 29:15–72.

Baumel JJ. (1993) Handbook of avian anatomy: Nomina Anatomica Avium, 2nd Edition. Pub of the Nuttall Ornitho Club 23:1–779.

Baur G. (1887) On the phylogenetic arrangement of the Sauropsida. J Morphology 1:93-104.

Benton MJ. (1983) The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. Phil Trans Roy Soc B 302:605–717.

Benton MJ. (1984) Tooth form, growth, and function in Triassic rhynchosaurs (Reptilia, Diapsida) Palaeo 27:66–68.

Benton MJ. (1985) Classification and phylogeny of the diapsid reptiles. Zool J Linn Soc 84:97–164.

Benton MJ. (1990) The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. Phil Trans Roy Soc B 328:213–306.

Benton MJ, Allen JL. (1997) *Boreopricea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles.

Benton MJ, Clark JM. (1988) Archosaur phylogeny and the relationships of the Crocodylia. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 295–338.

Berman DS, Reisz RR. (1992) *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. J Paleo 66:1001–1009.

Berman DS, Henrici AC, Sumida SC, Martens T. (2000) Redescription of *Seymouria sanjuanensis* (Seymouriamorpha) from the Lower Permian of Germany based on complete, mature specimens with a discussion of paleoecology of the Bromacker locality assemblage. J Vert Paleo 20:253–268.

Bever GS, Bell CJ, Maisano JA. (2005) The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). Palaeontologia Electronica 8, 4A:1–36.

Bhullar B-A, Bever GS. (2009) An archosaur-like laterosphenoid in early turtles (Reptilia: Pantestudines). Breviora 518:1–11.

Bhullar B-A, Bever GS, Merck J, Lyson T, Gauthier JA. (2011) Uniting microevolution and macroevolution in deep time: the zone of variability in Archosauromorpha

Bickelmann C, Müller J, Reisz RR. (2009) The enigmatic diapsid *Acerosodontosaurus piveteaui* (Reptilia: Neodiapsida) from the Upper Permian of Madagascar and the paraphyly of "younginiform" reptiles. Can J Earth Sci 46:651–661.

Bonaparte JF. (1976) *Pisanosaurus mertii* Casamiquela and the origin of the Ornithischia. Palaeo 50: 808–820.

Bonaparte JF, Sues H-D. (2006) A new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the Upper Triassic of Rio Grande do Sul, Brazil. Palaeo 49:917–923.

Borsuk-Bialynicka M, Evans SE. (2009) A long-necked archosauromorph from the Early Triassic of Poland. Paleo Pol 65:203–234.

Borsuk-Bialynicka M, Sennikov AG. Archosauriform postcranial remains from the Early Triassic kart deposits of southern Poland. Paleo Pol 65:283–328.

Brink AS. (1955) Notes on some thecodonts. Res National Mus 1:141–148.

Brink D. (1981) The origin of the crocodiloid tarsus and the interrelationships of thecodontian archosaurs. Breviora 464:1–23.

Brink KS, Reisz RR. (2013) Hidden dental diversity in the oldest terrestrial apex predator *Dimetrodon*. Nat Comm 5, 3269:1–5.

Brinkman D. (1980) Structural correlates of tarsal and metatarsal functioning in *Iguana* (Lacertilia; Iguanidae) and other lizards. Can J Zool 58:277–289.

Broili F, Schröder J. (1934) Beobachtungen an wirbeltieren der Karrooformation V. Über *Chasmatosaurus* van hoepeni Haughton. Sitz Bayer Akad Wiss München 1934:225–264.

Broom R. (1903) On a new reptile (*Proterosuchus fergusi*) from the Karroo beds of Tarkastad, South Africa. Annals South African Mus 4:159–164.

Broom R. (1905) Notice of some new fossil reptiles from the Karroo beds of South Africa. Rec Albany Mus 1:331–337.

Broom R. (1906) On the South African diaptosaurian reptile *Howesia*. Proc Zool Soc London 1906:591–600.

Broom R. (1913) Note on *Mesosuchus browni*, Watson and on a new South African Triassic pseudosuchian (*Euparkeria capensis*). Rec Albany Mus 2:394–396.

Broom R. (1914) A new thecodont reptile. Proc Zool Soc London 84:1072–1077.

Broom R. (1932) On some South African pseudosuchians. Annals Natal Mus 7:55–59.

Broom R, Robinson PGL. (1948) Some new reptiles from the Karroo Beds of South Africa. Proc Zool Soc London B 118:392–407.

Brusatte SL, Benton MJ, Desojo JB, Langer MC. (2010) The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). J Sys Palaeo 8:3–47.

Bulanov VV, Sennikov AG. (2006) The first gliding reptiles form the Upper Permian of Russia. Paleontological Journal 40:S567–S570.

Bulanov VV, Sennikov AG. (2010) New data on the morphology of Permian gliding weigeltisaurid reptiles of eastern Europe. Paleontological Journal 44:682–694.

Caldwell MW. (1994) Developmental constraints and limb evolution in Permian and extant lepidosauromorph diapsids. J Vert Paleo 14:459–471.

Calzavara M, Muscio G, Wild R. (1980) *Megalancosaurus preonensis* n. g., n. sp., a new reptile from the Norian of Friuli, Italy. Gortiana 2:49–64.

Camp CL. (1945a) *Prolacerta* and the protorosaurian reptiles, part I. Am J Sci 243:17–32.

Camp CL. (1945b) *Prolacerta* and the protorosaurian reptiles, part II. Am J Sci 243:84–101.

Carroll RL. (1969) Origin of reptiles. Biology of the Reptilia, Vol. 1 Morphology A, ed. C Gans (Academic Press, London and New York), pp. 1–44.

Carroll RL. (1975) Permo-Triassic “lizards” from the Karroo. Palaeo Afr 18:71–87.

Carroll RL. (1978) Permo-Triassic ‘lizards’ from the Karoo system. Part 2. A gliding reptile from the Upper Permian of Madagascar. Paleo Africana21:143–159.

Carroll RL. (1981) Plesiosaur ancestors from the Upper Permian of Madagascar. Phil Trans Roy Soc London B 293:315–383.

Carroll RL. (1985) A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Palaeontographica Abt A 189:1–28.

Case EC. (1927) The vertebral column of *Coelophysis* Cope. Cont Mus Geol, U of MI 2:209–222.

Case EC. (1928a) Indications of a cotylosaur and of a new form of fish from the Triassic beds of Texas, with remarks on the Shinarump Conglomerate. Cont Mus Geol, U of MI 3:1–14.

Case EC. (1928b) An endocranial cast of a phytosaur from the upper Triassic beds of west Texas. J Comp Neuro 45:161–168.

Casey MM. (2005) Multivariate morphometrics and allometry of the Triassic reptile *Tanytrachelos ahynis*. Abstracts of the Annual Meeting of the Geological Society of America, Salt Lake City.

Casey MM, Fraser NC, Kowalewski M. (2007) Quantitative taphonomy of a Triassic reptile *Tanytrachelos ahynis* from the Cow Branch Formation, Dan River Basin, Solite Quarry, Virginia. Palaios 22:598–611.

Charig AJ, Reig OA. (1970) The classification of the Proterosuchia. Bio J Linn Soc 2:125–171.

Charig AJ, Sues H-D. (1976) Suborder Proterosuchia Broom 1906b. Handbuch der Paläoherpetologie 13. Kuhn O (ed). (Verlag Fischer, Stuttgart), pp. 11–40.

Chatterjee S. (1974) A rhynchosaur from the Upper Triassic Maleri Formation of India. Phil Trans Roy Soc B 267:209–261.

Chatterjee S. (1982) Phylogeny and classification of thecodontian reptiles. Nature 295:317–320.

Chiari Y, Cahais V, Galtier N, Delsuc F. (2012) Phylogenomic analyses support the position of turtles as the sister group of birds and crocodiles (Archosauria). BMC Biology 10:65 doi:10.1186/1741-7007-10-65.

Chure DJ, Britt B, Engelmann G, Andrus A, Scheetz R. (2013) Drepanosaurs in the desert: multiple skeletons of a new drepanosaurid from the Eolian Nugget Sandstone (?Late Triassic–Early Jurassic), Saints and Sinners Quarry, Utah: morphology, relationships, and biostratigraphic implications. Abstracts of the 2013 Annual Meeting of the Society of Vertebrate Paleontology, Los Angeles. Journal of Vertebrate Paleontology 43:106A.

Clark J, Carroll RL. (1973) Romeriid reptiles from the Lower Permian. Bull Mus Comp Zool 144:353–407.

Clark JM, Welman J, Gauthier JA, Parrish JM. (1993) The laterosphenoid bone of early archosauriforms. J Vert Paleo 13:48–57.

Cocude-Michel M. (1968). Les rhynchocéphales et les saurians des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. Ph.D. Thesis, Université de Nancy.

Coddington J, Scharff N. (1994) Problems with zero-length branches. Cladistics 10:415–423.

Colbert EH. (1966) A gliding reptile from the Triassic of New Jersey. Am Mus Nov 2246:1–23.

Colbert EH. (1970) The Triassic gliding reptile *Icarosaurus*. Bull American Mus Nat History 143:85–142.

Colbert EH. (1987) The Triassic reptile *Prolacerta* in Antarctica. Am Mus Nov 2882:1-19.

Colbert EH. (1989) The Triassic dinosaur *Coelophysis*. Bulletin of the Museum of Northern Arizona 57:1–160.

Colbert EH and Olsen PJ. (2001) A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). Am Mus Novitates 3334:1–24.

Conrad JL. (2004) Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). Zool J Linn Soc 141:399–434.

Conrad JL. (2006) Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). J Morph 267:769–775.

Conrad JL. (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology Bull Am Mus Nat History 310:1–182.

Cope ED. (1869) Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Trans Amer Phil Soc 14:1–252.

Cope ED. (1885) On the evolution of the Vertebrata, progressive and retrogressive (continued). American Naturalist 19:234–247.

Cope ED. (1887) The dinosaurian genus *Coelurus*. Am Naturalist 21:367–369.

Crawford NG, Faircloth BC, McCormack JE, Brumfield RT, Winker K, Glenn TC. (2012). More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs. Biology Letters 8:783–786.

Currie PJ. (1979) The osteology of haptodontine sphenacodonts (Reptilia: Pelycosauria). Palaeontographica Abt A 163:130–168.

Currie PJ. (1980). A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. Can J Earth Sci 17:500–511.

Currie PJ. (1981a) *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeontologia Africana 24:99–168.

Currie PJ. (1981b) The vertebrae of *Youngina* (Reptilia: Eosuchia) Can J Earth Sci 18:815–818.

Currie PJ. (1982) The osteology and relationships of *Tangasaurus mennelli* Haughton. Annals South Afr Mus 86:247–265.

Cruickshank ARI. (1972) The proterosuchian thecodonts. *Studies in Vertebrate Evolution: Essays presented to F. R. Parrington*, eds KA Joysey, TS Kemp. (Winchester Press, New York).

Davit-Béal T, Tucker AS, Sire J-Y. (2009) Loss of teeth and enamel in tetrapods: fossil record, genetic data and morphological adaptations. J Anat 214:477–501.

deBraga M, Rieppel O. (1997) Reptile phylogeny and the interrelationships of turtles. Zool J Linn Soc 120:281–385.

de Franca MAG, Langer MC, Ferigolo J. (2013) The skull anatomy of *Decuriasuchus quartacolonia* (Pseudosuchia: Suchia: Loricata) from the Middle Triassic of Brazil. Geol Soc London, Spec Pub 379:469–501.

Desojo JB, Báez AM. (2007) Cranial morphology of the Late Triassic South American archosaur *Neoaetosauroides engaeus*: evidence for aetosaurian diversity. Palaeo 50:267–276.

Desojo JB, Heckert AB, Martz JW, Parker WG, Schoch RR, Small BJ, Sulej T. (2013) Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. Geol Soc London, Spec Pub 379:203–239.

Dilkes DW. (1995) The rhynchosaur *Howesia browni* from the Lower Triassic of South Africa. Palaeo 30:665–685.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Proc Roy Soc B 353:501–541.

Dilkes DW, Reisz RR. (1986) The axial skeleton of the Early Permian reptile *Eocaptorhinus laticeps* (Williston). Can J Earth Sci 23:1288–1296.

Dilkes DW, Sues H-D. (2009) Redescription and phylogenetic relationships of *Doswellia kaltenbachi* (Diapsida: Archosauriformes) from the Upper Triassic of Virginia. J Vert Paleo 29:58–79.

Dutuit MJ-M. (1982) Découverte d'un orintischien dans le Trias supérieur de l'Atlas occidental marocain. Comptes rendus Acad. Sci. Paris 275:2841–2844.

Dzik J. (2003) A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. J Vert Paleo 23:556–574.

Edmund AG. (1960) Tooth replacement phenomena in the lower vertebrates. Royal Ontario Mus, Life Sci Cont 52:1–190.

Edmund AG. (1969) Dentition. Biology of the Reptilia Volume 1, Morphology A. C Gans, A Bellairs, TS Parsons. (Academic Press, London and New York), pp. 117–200.

El-Toubi MR. (1949) The post-cranial osteology of the lizard, *Uromastyx aegyptia* (Forskal). J Morph 84:281–292.

Evans SE. (1980) The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool J Linn Soc 70:203–264.

Evans SE. (1981a) The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. Zool J Linn Soc 73:81–116.

Evans SE. (1981b) Caudal autotomy in a Lower Jurassic eosuchian. Copeia 1981:883–884.

Evans SE. (1982) The gliding reptiles of the Upper Permian. Zool J Linn Soc 76:97–123.

Evans SE. (1985) Tooth replacement in the Lower Jurassic lepidosaur *Gephyrosaurus bridensis*. Neues Jahr für Geol und Paläo Mh 1985:411–420.

Evans SE. (1987) The braincase of *Youngina capensis* (Reptilia: Diapsida; Permian). Neues Jahr für Geol Paläo Mon 1984:193–203.

Evans SE. (1988) The early history and relationships of the Diapsida. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 221–260.

Evans SE. (1991) A new lizard-like reptile (Diapsida: Lepidosauromorpha) from the Middle Jurassic of England. Zool J Linn Soc 103:391–412.

Evans SE. (2008) The skull of lizards and tuatara. *Biology of the Reptilia Volume 20*, ed C Gans (Society for the Study of Amphibians and Reptiles), pp. 1–347.

Evans SE. (2009) An early kuehneosaurids reptile from the Early Triassic of Poland. Palaeontologia Polonica 65:145–178.

Evans SE, Borsuk-Bialynicka M. (2009) Cranial and mandibular osteology of the Early Triassic archosauriform *Osmolskina czatkowicensis* from Poland. Paleo Pol 65:235–281.

Evans SE, Haubold H. (1987) A review of the Upper Permian genera *Coelurosauravus*, *Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). Zool J Linn Soc 90:275–303.

Evans SE, King MS. (1993) A new specimen of *Protorosaurus* (Reptilia: Diapsida) from the Marl Slate (late Permian) of Britain. Proc Yorkshire Geol Soc 49:229–234.

Evans SE, Jones MEH. (2009) The origin, early history, and diversification of lepidosauromorph reptiles. Lecture Notes in Earth Sci 132:27–44.

Ewer RF. (1965) The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil Trans Roy Soc B 248:379–435.

Ezcurra MD, Butler RI. (2015) Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early archosauriform radiation. Palaeontology 58:141–170.

Ezcurra MD, Scheyer TM, Butler RJ. (2014) The origin and early evolution of Sauria: the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS One 9:e89165.

Ezcurra MD, Lecuona A, Martinelli A. (2010) A new basal archosauriform diapsid from the Lower Triassic of Argentina. J Vert Paleo 30:1433–1450.

Flynn JJ, Nesbitt SJ, Parrish JM, Ranivoharimanana L, Wyss AR. (2010) A new species of *Azendohsaurus* (Diapsida: Archosauromorpha) from the Triassic Isalo Group of southwestern Madagascar: cranium and mandible. Palaeo 53:669–688.

Flynn JJ, Parrish JM, Rakotosamimanana B, Simpson WF, Whatley RL, Wyss AR. (1999) A Triassic fauna from Madagascar, including early dinosaurs. Science 286:763–765.

Fox RC, Bowman MC. (1966) Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). University of Kansas Paleo Contributions 11:1–79.

Fraser NC. (1988). The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). Phil Trans Roy Soc London B 321:125–178.

Fraser NC, Benton MJ. (1989) The Triassic reptiles *Brachyrhinodon* and *Polysphenodon* and the relationships of the sphenodontids. Zool J Linn Soc 96:413–445.

Fraser NC, Renesto S. (2003) Drepanosaurid (Reptilia: Diapsida) remains from a Late Triassic fissure infilling at Cromhall Quarry (Avon, Great Britain). J Vert Paleo 23:703–705.

Fraser NC, Rieppel O. (2006) A new protorosaur (Diapsida) from the Upper Buntsandstein of the Black Forest, Germany. J Vert Paleo 26:866–871.

Fraser NC, Walkden GM. (1984) The postcranial skeleton of the Upper Triassic sphenodontid *Planocephalosaurus robinsonae*. Palaeo 27:575–595.

Fraser NC, Shelton CG. (1988) Studies of tooth implantation in fossil tetrapods using high-resolution X-radiography. Geo Mag 125:117–122.

Fraser NC, Rieppel O, Chun L. (2013) A long-snouted protorosaur from the Middle Triassic of southeastern China. J Vert Paleo 33:1120–1126.

Fraser NC, Grimaldi DA, Olsen PE, Axsmith B. (1996) A Triassic lagerstätte from eastern North America. Nature 380:615–619.

Gaffney ES. (1990) The comparative osteology of the Triassic turtle *Proganochelys*. Bull American Mus Nat History 194:1–263.

Galton PM. Comment on *Plateosaurus* Meyer, 1837 (Dinosauria, Sauropodomorpha): proposed replacement of unidentifiable name-bearing type by a neotype (Case 3560). Bull Zool Nom 70:205–206.

Gao K-Q, Ksepka DT. (2008) Osteology and taxonomic revision of *Hyphalosaurus* (Diapsida: Choristodera) from the Lower Cretaceous of Liaoning, China. J Anat 212:747–768.

Gardner NM, Holliday CM, O'Keefe FR. (2010) The braincase of *Youngina capensis* (Reptilia, Diapsida): new insights from high-resolution CT scanning of the holotype. Palaeontologia Electronica 13: 16 pp.

Gauffre F-X. (1993) The prosauropod dinosaur *Azendohsaurus laaroussii* from the Upper Triassic of Morocco. Palaeo 36:897–908.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, University of California Berkeley.

Gauthier JA. (1986) Saurischian monophyly and the origin of birds. The Origin of Birds and the Evolution of Flight. Padian K (ed). Mem CA Acad Sci 8, pp. 1–55.

Gauthier JA, Kluge AG, Row T. (1988b) The early evolution of the Amniota. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 103–155.

Gauthier JA, Estes R, de Queiroz K. (1988a) A phylogenetic analysis of Lepidosauromorpha. *Phylogenetic Relationships of the Lizard Families*, eds R Estes, G Pregill (Stanford University Press, Stanford), pp. 15–98.

Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB. (2012) Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bull Peabody Mus Nat Hist 53:3–308.

Gervais P. (1859 Zoologie et Paléontologie Françaises, 2nd Edition. (Bertrand, Paris), 544 pp.

Gignac PM, Erickson GM. (2014) Ontogenetic changes in dental form and tooth pressures facilitate developmental niche shifts in American alligators. J Zool 295:132–142.

Gilmore CW. (1942) Osteology of *Polyglyphanodon*, and Upper Cretaceous lizard from Utah. Proc US Nat Mus 92:229–265.

Goloboff PA, Farris JS, Nixon KC. (2008) TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Goodrich ES. (1916) On the classification of the Reptilia. Proc Roy Soc B 89:261–276.

Goodrich ES. (1942) The hind foot of *Youngina* and fifth metatarsal in Reptilia. J Anat 76:308–312.

Gottmann-Quesada A, Sander PM. (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. Palaeontographica Abteilung A 287:123–220.

Gow CE. (1990) Morphology and growth of the *Massospondylus* braincase (Dinosauria Prosauropoda). Palaeo Afr 27:59–75.

Gower DJ. (1997) The braincase of the early archosaurian reptile *Erythrosuchus africanus*. J Zool Soc London 242:557–576.

Gower DJ. (1999) The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. Stuttgarter Beit Nat B 280:1–49.

Gower DJ. (2002) Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. Zool J Linn Soc 136:49–76.

Gower DJ. (2003) Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. Annal S Afr Mus 110:1–88.

Gower DJ, Schoch RR. (2009) Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. J Vert Paleo 29:103–122.

Gower DJ, Sennikov AG. (1996) Morphology and phylogenetic informativeness of early archosaur braincases. Palaeontology 39:883–906.

Gower DJ, Weber E. (1998) The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. Biol Rev 73:367–411.

Greer AE. (1976) One the occurrence of a stapedial foramen in living non-gekkonid lepidosaurs. Copeia 1976:591–592.

Gregory JT. (1945) Osteology and relationships of *Trilophosaurus*. University of Texas Publication 4401:273–359.

Günther A. (1867) Contribution to the anatomy of *Hatteria* (*Rhynchocephalus*, Owen). Phil Trans Roy Soc 157:595–629.

Haeckel E. (1866) Allgemeine Morphologie der Organismen, Vol 1, 2. (G. Reimer, Berlin).

Haines RW. (1969). Epiphyses and bony sesamoids. *Biology of the Reptilia, Volume 1: Morphology*, ed. C. Gans. (Academic Press, London and New York), pp. 81–15

Halstead BL, Nicoll PG. (1971) Fossilized caves on Mendip. Stud Speleol 2:93–102.

Haughton SH. (1924) On a new type of thecodont from the middle Beaufort Beds. Annals Trans Mus 20:343–346.

Heaton MJ. (1979) Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian Oklahoma and Texas. Bulletin of the Oklahoma Geological Society 127:1–84.

Hennig W. (1965) Phylogenetic systematics. Ann Rev Entomol 10:97–116.

Hone DWE, Benton MJ. (2008) A new genus of rhynchosaur from the Middle Triassic of south-west England. Palaeo 51:95–115.

Hoffstetter R, Gasc J-P. 1969. Vertebrae and ribs of modern reptiles. Biology of the Reptilia, Volume 1: Morphology A. C. Gans (ed.) (Academic Press, London and New York), pp. 209–301

Holliday CM, Nesbitt SJ. (2013) Morphology and diversity of the mandibular symphysis of archosauriforms. Geol Soc London, Spec Pub 379:555–571.

Huene FR von. (1905) Über der Trias-dinosaurier Europas. Zentr. Deut. Geol. Gess. 57: 345–349.

Huene FR von. (1926) Zur beurteilung von *Protorosaurus*. Centr für Mineral, Geol, Paläo Abt. B 1926:469–475.

Huene FR von. (1931) Über *Tanystropheus* und verwandte formen. Neues Jahr für Mineral, Geol, Paläo Beilageband 67:65–86.

Huene FR von. (1932) Die fossile reptil-ordung Saurischia. Ihre Entwicklung und Gescichte. Monograph zur Geol Palaeo, Serie 1 4:1–361.

Huene FR von. (1936) The constitution of the Thecodontia. 207–217. Amer J Sci series 5 32:207–217.

Huene FR von. (1944) Die zwieteilung des reptistammes. Neues Jahr für Mineral, Geol, Paläo Abh 88:427–440.

Huene FR von. (1946) Die grossen Stämme der tetrapoden in den geologischen Zeiten. Biol Zentralbl 65:268–275.

Huene FR von. (1956) Paläontologie und Phylogenie der niederen Tetrapoden. (Gustav Fischer, Jena).

Huxley TH. (1871) A manual of Vertebrate Animals. (J. and A. Churchill, London).

Iordansky NN. (1973) The skull of the Crocodylia. *Biology the Reptilia, Volume 4 Morphology B*, eds C Gans, TS Parsons. (Academic Press, London and New York), pp. 201–262.

Irmis, R. B., S. J. Nesbitt, K. Padian, N. D. Smith, A. H. Turner, D. Woody, and A. Downs. (2007) A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317:358–361.

Jalil N-E. (1997) A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. J Vert Paleo 17:506–525.

Jalil, N.-E., and F. Knoll. (2002) Is *Azendohsaurus laaroussii* (Carnian, Morocco) a dinosaur? J Vert Paleo 22:70A.

Jiang, D.-Y., O. Rieppel, N. C. Fraser, R. Motani, W.-H. Hao, A. Tintori, Y.-L. Sun and Z.-Y. Sun. (2011) New information on the protorosaurian reptile *Macrocnemus fuyuanensis* Li et al., 2007, from the Middle/Upper Triassic of Yunnan, China. Journal of Vertebrate Paleontology 31:1230–1237.

Jollie MT. (1960) The head skeleton of the lizard. Acta Zool 41:1–64.

Jones MEH. (2006) The Early Jurassic clevosaurs from China (Diapsida: Lepidosauria). NM Mus Nat Hist Bull 37:548–562.

Jones MEH, Anderson CL, Hipsley CA, Müller JA, Evans SE, Schoch RR. (2013) Integration of molecules and new fossils supports a Triassic origin for Lepidosauria (lizards, snakes, and tuatara). BMC Evolutionary Biology 13:208.

Kluge AG. (1982) Cloacal bones and sacs as evidence of gekkonoid lizard relationships. Herpetologica 38:348–355.

Konishi T, Newbrey MG, Caldwell MW. (2014) A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the Bearpaw Formation, western Canada, and the first stomach contents for the genus. J Vert Paleo 34:802–819.

Koyabu D, Maier W, Sánchez-Villagra MR. (2012) Paleontological and developmental evidence resolve the homology and dual embryonic origin of a mammalian skull bone, the interparietal. Proc Nat Acad Sci 109:14075–14080.

Kuhn O. (1939) Schädelbau und systematische Stellung von *Weigeltisaurus*. Paläo Zeit 21:163–167.

Kumazawa Y, Nishida M. (1999) Complete mitochondrial DNA sequences of the green turtle and blue-tailed mole skink: statistical evidence for archosaurian affinity of turtles. Molec Bio & Evo 16:784–792.

Lane HH. (1945) New mid-Pennsylvanian reptiles from Kansas. Trans KS Acad Sci 47:381–390.

Langer MC, Schultz CL. (2000) Rincossauros—herbívoros cosmopolitas do Tríassico. Palaeontologia do Rio Grande do Sul. (Ediçao CIGO/UFRGS, Porto Alegre), pp. 246–272.

Laurin M. (1991) The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. Zool J Linn Soc 101:59–95.

Laurin M, Reisz RR. (1995) A reevaluation of early amniote phylogeny. Zool J Linn Soc 113:165–223.

Leal F, Tarazona, OA, Ramírez-Pinilla MP. (2010) Limb development in the gekkonid lizard *Gonatodes albogularis*: a reconsideration of homology in the lizard carpus and tarsus. J Morph 271:1328–1341.

LeBlanc ARH, Reisz RR. (2013) Periodontal ligament, cementum, and alveolar bone in the oldest herbivorous tetrapods, and their evolutionary significance. PLoS One e74697.

LeBlanc ARH, Reisz RR. (2015) Patterns of tooth development and replacement in captorhinids reptiles: a comparative approach for understanding the origin of multiple tooth rows. J Vert Paleo DOI: 10.1080/02724634.2014.919928.

Lécuru S. (1969) Étude morphologique de l'humérus des lacertiliens. Annales Sci Natu, Zool Paris 12e Série 9:515–558.

Li, C., Zhao L. J., Wang L. T. 2007. A new species of *Macrocnemus* (Reptilia: Protorosauria) from the Middle Triassic of southwestern China and its palaeogeographical implication. Science in China Series D, Earth Sciences 50:1601–1605.

Lü J-C, Ji S-A, Dong Z-M, Wu X-C. (2008). An Upper Cretaceous lizard with a lower temporal arcade. Naturwiss 95:663–669.

Luan X, Walker C, Dangaria S, Ito Y, Druzinsky R, Jasorius K, Lesot H, Rieppel O. The mosasaur tooth attachment apparatus as paradigm for the evolution of the gnathostome periodontum. Evo & Devo 11:247–259.

Lyson TR, Bhullar B-AS, Bever GS, Joyce WG, de Queiroz K, Abzhanov A, Gauthier JA. (2013) Homology of the enigmatic nuchal bone reveals novel reorganization of the shoulder girdle in the evolution of the turtle shell. Evo & Devo 15:317–325.

MacCartney J. (1802) Preface and Table III. Lectures on Comparative Anatomy, translated from William Ross. G. Cuvier (ed) (Oriental Press, London).

Maisano JA. (2002) Postnatal skeletal ontogeny in five xantusiids (Squamata: Scleroglossa). J Morphology 254:1–38.Malan ME. (1963) The dentitions of the South African Rhynchocephalia and their bearing on the origin of the rhynchosaurs. S Afr J Sci 59:214–220.

Martz JW, Mueller B, Nesbitt SJ, Stocker MR, Parker WG, Atanassov M, Fraser NC, Weinbaum J, Lehane J. (2013) A taxonomic and biostratigraphic re-evaluation of the Post Quarry vertebrate assemblage from the Cooper Canyon Formation (Dockum Group, Upper Triassic) of southern Garza County, western Texas. Earth Env Sci Trans Roy Soc Edin 103:339–364.

Matsumoto R, Buffetaut E, Escuillie F, Hervet S, Evans SE. (2013). New material of the choristodere *Lazarussuchus* (Diapsida, Choristodera) form the Paleocene of France. J Vert Paleo 33:319–339.

McGarrity CT, Campione NE, Evans DC. (2013) Cranial anatomy and variation in *Prosaurolophus maximus* (Dinosauria: Hadrosauridae). Zool J Linn Soc 167:531–568.

Merck JA. (1995) The cranial anatomy of *Trilophosaurus buettneri* as revealed by high-resolution computer-aided tomography. Abstracts of the 1995 Annual Meeting of the Society of Vertebrate Paleontology, Pittsburgh. J Vert Paleo 15:44A.

Merck JA. (1997) A phylogenetic analysis of the euryapsid reptiles. Ph.D. thesis, University of Texas at Austin.

Merck JA. (2003). An arboreal radiation of non-saurian diapsids. Abstracts of the Society of Vertebrate Paleontology Annual Meeting, St. Paul. Journal of Vertebrate Paleontology 33:78A.

Meyer H von. (1837) Mitteilung an Prof. Bronn. Neues Jahr für Geol und Paläo Abh 1837:316.

Meyer H von. (1832) Palaeologica zur Geschichte der Erde und ihrer Geschöpfe (Verlag Sigmund Schmerber, Frankfurt), 560 pp.

Meyer H von. (1847–1855) Die saurier des Muschelkalkes: mit Rücksicht auf die saurier aus buntem sandstein und Keuper. Zur Fauna der Vorwelt, zweite abtheilung. (Heinrich Keller, Frankfurt).

Modesto SP, Reisz RR. (2003) An enigmatic new diapsid reptile from the Upper Pemian of eastern Europe. J Vert Paleo 22:851–855.

Modesto SP, Sues H-D. (2004) The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. Zool J Linn Soc 140:335–351.

Modesto SP, Lamb AJ, Reisz RR. (2014) The captorhinids reptile *Captorhinikos valensis* from the lower Permian Vale Formation of Texas, and the evolution of herbivory in eureptiles. J Vert Paleo 34:291–302.

Montefeltro FC, Langer MC, Schultz CL. (2010) Cranial anatomy of a new genus of hyperodapedontine rhynchosaur (Diapsida, Archosauromorpha) from the Upper Triassic of Brazil. Earth Env Sci Trans Roy Soc Edin 101:27–52.

Montefeltro FC, Bittencourt JS, Langer MC, Schultz CL. (2013) Postcranial anatomy of the hyperodapedontine rhynchosaur *Teyumbaita sulcognathus* (Azevedo and Schultz, 1987) from the Late Triassic of southern Brazil. J Vert Paleo 33:67–84.

Mook CC. (1921) The dermo-supraoccipital bone in the Crocodilia. Am Mus Nov 44:101–103.

Mukherjee D, Ray S. (2014) A new *Hyperodapedon* (Archosauromorpha, Rhynchosauria) from the Upper Triassic of India: implications for rhynchosaur phylogeny. Palaeo 57:1241–1276.

Müller J. (2003) Early loss and multiple return of the lower temporal arcade in diapsid reptiles. Naturwiss 90:473–476.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Murry PA. (1987) New reptiles from the Upper Triassic Chinle Formation of Arizona. J Vert Paleo 61:773–786.

Muscio B. (1999) *Sphenodon punctatus*. Available at http://animaldiversity.org/accounts/Sphenodon_punctatus/. Accessed June 13, 2015.

Muscio G. (1996) Preliminary note on a specimen of prolacertiform (Reptilia) from the Norian (Late Triassic) of Preone (Udine, north-eastern Italy). Gortiana 18:33–40.

Nesbitt SJ. (2011) The early evolution of archosaurs: relationships and the origin of major clades. Bull Am Mus Nat Hist 352:1–292.

Nesbitt SJ, Norell MA. (2006) Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda) Proc Roy Soc B 273:1045–1048.

Nesbitt SJ, Flynn JJ, Pritchard AC, Parrish JM, Ranivoharimanana L, Wyss A. (in press) Postcranial anatomy and relationships of *Azendohsaurus madagaskarensis*. Bull Am Mus Nat Hist.

Nesbitt SJ, Brusatte SL, Desojo JB, Liparini A, de França MAG, Weinbaum JC, Gower DJ. (2013) Rauisuchia. Geol Soc London, Spec Pub 379:241–274.

Nguyen TQ, Hamilton P, Ziegler T. 2014. *Shinisaurus crocodilurus*. The IUCN red list of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded August 10, 2015.

Nopcsa F. (1930) Notizen über *Macrochemus Bassanii* nov. gen. et spec. Cent für Mineral, Geol und Paläo B 1930:252–255.

Nosotti S. (2007). *Tanystropheus longobardicus* (Reptilia, Protorosauria): re-interpretations of the anatomy based on new specimens from the Middle Triassic of Besano (Lombardy, northern Italy). Mem. Mus Civ Storia Nat Milano 35:1–88.

O'Leary MA, et al. (2013) The placental mammalian ancestor and the post-K-Pg radiation of placentals. Science 339:662–667.

Oelrich TM. (1956) The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Misc Pub Mus Zool, U of Mich 94:1–122.

Olsen, P. E. 1979. A new aquatic eosuchian from the Newark Supergroup (Late Triassic-Early Jurassic) of North Carolina and Virginia. Postilla 176:1–14.

Olsen PE. (1980) A comparison of the vertebrate assemblages from the Newark and Hartford basins (early Mesozoic, Newark Supergroup) of eastern North America. *Aspects of Vertebrate Evolution: Essays in Honor of Edwin Harris Colbert*, ed LL Jacobs. (Northern Arizona Press, Flagstaff), pp. 35–53.

Olsen PE, Kent DV, Whiteside JH. (2011) Implications of the Newark Supergroup-based astrochronology and geomagmatic polarity time scale (Newark-APTS) for the tempo and mode of the early diversification of the Dinosauria. Earth Env Sci Trans Roy Soc Edin 101:201–229.

Olson EC. (1966) The middle ear—morphological types in amphibians and reptiles. Amer Zool 6:399–416.

Osborn HF. (1903a) On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. Science 17:275, 276.

Osborn HF. (1903b) The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. Mem American Mus Nat Hist 1:449-519.

Owen R. (1842) Description of an extinct lacertilian, *Rhynchosaurus articeps*, Owen, of which the bones and foot-prints characterize the upper New Red Sandstone at Grinshill, near Shrewsbury. Trans Camb Phil Soc 7:355–369.

Parks P. (1969) Cranial anatomy and mastication of the Triassic reptile *Trilophosaurus*. M.S. Thesis, University of Texas at Austin

Parrington FR. (1935) On *Prolacerta broomi* gen. et sp. nov. and the origin of lizards. Annals Mag of Nat Hist 16:197–205.

Parrington FR. (1937) On the supratemporal and tabular bones in reptiles. J Nat Hist 69–76.

Peyer B. (1937) Die Triasfauna der Tessiner Kalkalpen XII. *Macrocnemus bassanii* Nopcsa. Schweizerische Paläo Abhandlungen 59:1–140.

Piveteau J. (1926) Paléontologie de Madagascar XIII. Amphibiens et reptiles Permiens. Annales de Paléo 15:55–179.

Pinna G. (1980) *Drepanosaurus unguicaudatus*, nuovo genere e nuova specie di lepidosauro del Trias alpino. Atti della Soc ital di sci nat del mus civ di storia nat di Milano 121:181–192.

Pinna G. (1984) Osteologia di *Drepanosaurus unguicaudatus*, lepidosauro triassico del sottordine Lacertilia. Mem della Soc ital. di sci nat e del Mus civ di storia nat di Milano 24:7–28.

Pinna G. (1986) On *Drepanosaurus unguicaudatus*, an Upper Triassic lepidosaurian from the Italian Alps. J Paleo 60:1127–1132.

Price LI. (1935) Notes on the brain case of *Captorhinus*. Proc Boston Soc Nat History 40:377–386.

Prieto-Márquez A, Norell MA. (2011) Redescription of a nearly complete skull of *Plateosaurus* (Dinosauria: Sauropodomorpha) from the Late Triassic of Trossingen (Germany). Am Mus Novitates 3727:1–58.

Pritchard AC. (2015) Extreme modification of the tetrapod forelimb in a Triassic reptile. Abstracts of the 2015 Society of Int & Comp Bio Annual Meeting, West Palm Beach:E147.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2015). Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. Journal of Vertebrate Paleontology 35: e911186.

Reisz RR. (1977) *Petrolacosaurus*, the oldest known diapsid reptile. Science 196:1091–1093.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Special Publication of the Museum of Natural History, University of Kansas 7:1–74.

Reisz RR, Laurin M, Marjanovic D. (2010) *Apsisaurus witteri* from the Lower Permian of Texas: yet another small varanopid synapsid, not a diapsid. J Vert Paleo 30:1628–1631.

Reisz RR, Berman DS, Scott D. (1984) The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. J Vert Paleo 4:57–67.

Reisz RR, Modesto SP, and Scott MD. (2011) A new Early Permian reptile and its significance in early diapsid evolution. Proc Roy Soc B 278:3731–3737.

Renesto S. (1994a) The shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the upper Triassic (Norian) of northern Italy. Zool J Linn Soc 111:247–264.

Renesto S. (1994b) A new prolacertiform reptile from the Late Triassic of northern Italy. Riv Ital Paleo Strat 100:285–306.

Renesto S. (1994c) *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. J Vert Paleo 14:38–52.

Renesto S. (1995) A sphenodontid from the Norian (Late Triassic) of Lombardy (northern Italy): a preliminary note. Modern Geol 20:149–158.

Renesto S. (2000) Bird-like head on a chameleon body: new specimens of the enigmatic diapsid reptile *Megalancosaurus* from the Late Triassic of northern Italy. Riv Ital Paleo Strat 106:157–180.

Renesto S. (2005) A new specimen of *Tanystropheus* (Reptilia Protorosauria) from the Middle Triassic of Switzerland and the ecology of the genus. Riv Ital Paleo Strat 111:577–594.

Renesto S. (2006) A reappraisal of the diversity and biogeographic significance of the Norian (Late Triassic) reptiles from the Calcare di Zorzino. NM Mus Nat Hist Bull 37:445–456.

Renesto S, Avanzini M. (2002) Skin remains in a juvenile *Macrocnemus bassanii* Nopcsa (Reptilia, Prolacertiformes) from the Middle Triassic of northern Italy. Neues Jahr für Geol und Paläo Abh 224:31–48.

Renesto S, Bernardi M. (2014) Redescription and phylogenetic relationships of *Megachirella wachtleri* Renesto et Posenato, 2003 (Reptilia, Diapsida) Paläo Zeit 88:197–210.

Renesto S and Binelli G. (2006) *Vallesaurus cenensis* Wild, 1991, a drepanosaurid (Reptilia, Diapsida) from the Late Triassic of northern Italy. Riv Ital Paleo Stat 112:77–94.

Renesto S, Dalla Vecchia FM. (2000) The unusual dentition and feeding habits of the prolacertiform reptile *Langobardisaurus* (Late Triassic, northern Italy). J Vert Paleo 20:622–627.

Renesto S, Paganoni A. (1995) A new *Drepanosaurus* (Reptilia, Neodiapsida) from the Upper Triassic of northern Italy. Neues Jahr für Geol Paläo Abh 197:87–99.

Renesto S, Spielmann JA, Lucas SG, and Spagnoli GT. (2010) The taxonomy and paleobiology of the Late Triassic (Carnian–Norian: Adamanian–Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha). Bull NM Mus Nat Hist Sci 46:1–81.

Rénous-Lécuru S. (1973) Morophologie comparée du carpe chez des Lepidosauriens actuels (Rhynchocéphales, Lacertiliens, Amphisbéniens). Gegenbaurs morphologisches Jahrbuch 119:727–766.

Reynoso V-H, Clark JM. (1998) A dwarf sphenodontian from the Jurassic La Boca Formation of Tamaulipas, México. J Vert Paleo 18:333–339.

Rieppel O. (1976) On the presence and function of postcloacal bones in the Lacertilia. Mon Zool Ital 10:7–13.

Rieppel O. (1989) The hind limb of *Macrocnemus bassanii* (Nopcsa) (Reptilia, Diapsida): development and functional anatomy. J Vert Palo 9:373–387.

Rieppel O. (1992) The skull in a hatchling of *Sphenodon punctatus*. J Herp 26:80–84.

Rieppel O. (1994) Osteology of *Simosaurus gaillardoti* and the relationships of stem-group Sauropterygia. Fieldiana, Geology 28:1–83.

Rieppel O, Fraser NC, Nosotti S. (2003) The monophyly of Protorosauria (Reptilia, Archosauromorpha): a preliminary analysis. Atti Soc It Sci Nat Mus Civ Stor Nat Milano 144:359–382.

Rieppel O, Li C, Fraser NC. (2008) The skeletal anatomy of the Triassic protorosaur *Dinocephalosaurus orientalis* Li, from the Middle Triassic of Guizhou Province, southern China. J Vert Paleo 28:95–110.

Rieppel O, Jiang D-Y, Fraser NC, Hao W-C, Motani R, Sun Y-L, Sun Z-Y. (2010) *Tanystropheus* cf. *T. longobardicus* from the early Late Triassic of Guizhou Province, southwestern China

Robinson PGL. (1967a) The evolution of the Lacertilia. Problèms actuels de paléontologie (evolution des vertébrés). Colloques Internationaux du Centre National de la REcherche Scientifique 163:395–407.

Robinson PGL. (1967b) Triassic vertebrates from lowland and upland. Sci & Cult 33:169–173.

Robinson PGL. (1973) A problematic reptile from the British Upper Trias. J Geol Soc London 129:457–479.

Robinson PGL. (1975) The functions of the hooked fifth metatarsal in lepidosaurian reptiles. Colloque International C.N.R.S. 218:461–483.Robinson PGL. (1976) How *Sphenodon* and *Uromastyx* grow their teeth and use them. Morphology and Biology of Reptiles. A d'A Bellairs and CB Cox (eds) Linnean Symposium Series 3:43–64.

Romer AS. (1933) Vertebrate Paleontology, 1st Edition. (University of Chicago Press, Chicago).

Romer AS. (1947) The relationships of the Permian reptile *Protorosaurus*. Am J Sci 245:19–30.

Romer AS. (1956). Osteology of the Reptiles. (University of Chicago Press, Chicago), 772 pp.

Romer AS. (1967) Early reptilian evolution re-viewed. Evolution 21:821–833.

Romer AS. (1971) The Chañares (Argentina) Triassic reptile fauna. XI. Two new long-snouted thecodonts, *Chanaresuchus* and *Gualosuchus*. Breviora 379:1–22.

Russell, A. P., and A. M. Bauer. 2008. The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates; pp. 1–466 in C. Gans, A. S. Gaunt, and K. Adler (eds.), Biology of the Reptilia, Volume 21: The Skull and Appendicular Locomotor Apparatus of Lepidosauria. Academic Press, London and New York.

Saller F, Renesto S, Dalla Vecchia FM. (2013) First record of *Langobardisaurus* (Diapsida, Protorosauria) from the Norian (Late Triassic) of Austria, and a revision of the genus. Neues Jahr für Geol Paläo Abh 268:83–95.

Sander PM. (1992) The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. Palaeogeo, Palaeoclim, Palaeoeco 93:255–299.

Säve-Söderbergh G. (1947) Notes on the brain-case in *Sphenodon* and certain Lacertilia. Zool Bidrag Uppsala 25:489–516.

Schaumberg G, Unwin DM, Brandt S. (2007) New information on the anatomy of the Late Permian gliding reptile *Coelurosauravus*. Paläo Zeit 81:160–173.

Seeley HG. (1887) Researches on the structure, organization and classification of the fossil Reptilia. I. One *Protorosaurus speneri* (von Meyer). Phil Trans Roy Soc B 178:187–213.

Sen K. (2003) *Pamelaria dolichotrachela*, a new prolacertid reptile from the Middle Triassic of India. J Asia Earth Sci 21:663–681.

Sennikov AG. (1988) The role of the oldest thecodonts in vertebrate assemblages of eastern Europe. Paleo Journal 1988:74–82.

Senter PJ. (2003) New information on cranial and dental features of the Triassic archosauriform reptile *Euparkeria capensis*. Palaeo 46:613–621.

Senter PJ. (2004) Phylogeny of Drepanosauridae (Reptilia: Diapsida). Journal of Systematic Palaeontology 2:257–268.

Sereno PC, Novas FE. (1993) The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. J Vert Paleo 13:451–476.

Sereno PC, Martínez RN, Alcober OA. (2012) Osteology of *Eoraptor lunensis* (Dinosauria, Sauropodomorpha). Mem Soc Vert Paleo 12:83–179.

Sill WD. (1971) Functional morphology of the rhynchosaur skull. Form Funct 4:303–318.

Smith REH, Evans SE. (1992) New material of *Youngina*: evidence of juvenile aggregation in Permian diapsid reptiles. Palaeo 39:289–303.

Smith ND, Crandall JR, Hellert SM, Hammer WL, Makovicky PJ. (2011) Anatomy and affinities of large archosauromorphs from the lower Fremouw Formation (Early Triassic) of Antarctica. J Vert Paleo 31:784–797.

Sookias RB, Butler RJ. (2013). Euparkeriidae. Geol Soc London, Spec Pub 379:35–48.

Spielmann JA, Lucas SG, Rinehart LF, Heckert AB. 2008. The Late Triassic archosauromorph *Trilophosaurus*. New Mexico Museum of Natural History and Science Bulletin 43:1–177.

Spielmann JA, Lucas SG, Heckert AB, Rinehart LF, Hunt AP. (2007) Taxonomy and biostratigraphy of the Late Triassic archosauromorph *Trilophosaurus*. NM Mus Nat His Bull 40:231–240.

Spielmann JA, Lucas SG, Heckert AB, Rinehart LF, Richards HR. (2009) Redescription of *Spinosuchus caseanus* (Archosauromorpha: Trilophosauridae) from the Upper Triassic of North America. Palaeodiv 2:283–313.

Stein K, Palmer C, Gill PG, Benton MJ. (2008) The aerodynamics of the British Late Triassic Kuehneosauridae. Palaeo 51:967–981.

Stokely PS. (1950) The occurrence of an intermedium in izards. Am Midl Nat 43:179–182.

Sues H-D. (2003) An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. Canadian Journal Earth Sci 40:635–649.

Sues H-D and Fraser NC. (2013) Triassic Life on Land. (Columbia University Press, New York) 236 pp.

Sues H-D, Olsen PE. (1993) A new procolophonid and a new tetrapod of uncertain, possibly procolophonian affinities from the Upper Triassic of Virginia. J Vert Paleo 13:282–286.

Sues H-D, Olsen PE. (2015) Stratigraphic and temporal context and faunal diversity of Permian–Jurassic continental tetrapod assemblages from the Fundy rift basin, eastern Canada. Atlantic Geo 51:139–205.

Sues H-D, Reisz RR. (1995) First record of the early Mesozoic sphenodontian *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the southern hemisphere. J Paleo 69:123–126.

Sues H-D, Shubin NH, Olsen PE. (1994) A new sphenodontian (Lepidosauria: Rhynchocephalia) from the McCoy Brook Formation (Lower Jurassic) of Nova Scotia, Canada. J Vert Paleo 327–340.

Sumida SS. (1989) The appendicular skeleton of the Early Permian genus *Labidosaurus* (Reptilia, Captorhinomorpha, Captorhinidae) and the hind limb musculature of captorhinid reptiles. J Vert Paleo 9:295–313.

Swinton WE. (1939) A new Triassic rhynchocephalians from Gloucestershire. J Nat Hist 4:591–594.

Tatarinov LP. (1960) [Pseudosuchians in the Upper Permian of the USSR]. Paleo Journal 1960:74–80.

Tatarinov LP. (1978) Triassic prolacertilians of the USSR. Paleo J 1978:505–514.

Thulborn RA. (1973) Teeth of ornithischian dinosaurs from the Upper Jurassic of Portugal. Serv Geol Portugal, Mem 22:89–134.

Thulborn RA. (1974) A new heterodontosaurid dinosaur (Reptilia: Ornithischia) from the Upper Triassic Red Beds of Lesotho. Zool J Linn Soc 55:151–175.

Thyng FW. (1906) Squamosal bone in tetrapodous Vertebrata. Proc Boston Nat Hist Soc 32:387–425.

Vaughn PP. (1955) The Permian reptile *Araeoscelis* restudied. Bull Mus Comp Zool 113:305–467.

Vaughn PP. (1956) The phylogenetic migrations of the ambiens muscle. J Mitchell Soc 77:243–262.

Waldman M, Evans SE. (1994) Lepidosauromorph reptiles from the Middle Jurassic of Skye. Zool J Linn Soc 112:135–150.

Walker AD. (1990) A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (Late Triassic) of South Africa. Phil Trans Roy Soc B 330:1–120.

Watson DMS. (1912) *Mesosuchus browni*, gen. et spec. nov. Rec Albany Mus 2:296–297.

Watson DMS. (1957) On *Millerosaurus* and the early history of the sauropsid reptiles. Phil Trans Roy Soc B 240:325–400.

Weigelt K. (1930). *Palaeochameleo jaekeli nov. gen. nov sp.* Ein neuer Rhynchocephale aus dem Mansfelder Kupferschiefer. Leopoldina 6:625–642.

Weinbaum JC. (2011) The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. PaleoBios 30:18–44.

Welman J. (1998) The taxonomy of the South African proterosuchids (Reptilia, Archosauromorpha). J Vert Paleo 18:340–347.

Welman J, Fleming A. (1993) Statistical analysis of the skulls of Triassic proterosuchids. Palaeo Afr 30:113–123.

Wescott WA, Diggens JN. (1998) Depositional history and stratigraphical evolution of the Sakamena group (Middle Karoo Supergroup) in the southern Morondava Basin, Madagascar. J Afr Earth Sci 27:461–479.

Whatley RL. (2005) Phylogenetic relationships of *Isalorhynchus genovefae*, the rhynchosaur (Reptilia, Archosauromorpha). Ph.D. thesis, University of California at Santa Barbara.

Whiteside DI. (1986) The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et sp. nov. and the modernizing of a living fossil. Phil Trans Roy Soc B 312:379–430.

Whiteside DI, Marshall JEA. (2008) The age, fauna and paleoenvironment of the Late Triassic fissure deposits of Tytherington, south Gloucestershire, UK. Geol Mag 145:105–147.

Wiens JJ, Hutter CR, Mulcahy DG, Noonan BP, Townsend TM, Sites JW, Reeder TW. Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. Bio Letters 6:1043–1046.

Wild R. (1973) Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergenbisse). Abhand der Schweizer Paläo Gesellschaft 95:1–162.

Wild R. (1980a) Die Triasfauna der Tessiner Kalkalpen. XXIV. Neue funde von *Tanystropheus* (Reptilia, Squamata). Abhand der Schweizer Paläo Gesellschaft 102:1–43.

Wild R. (1980b) *Tanystropheus* (Reptilia, Squamata) and its importance for stratigraphy. Mem Soc Geol France 139:201–206.

Wild R. (1990) *Aetosaurus* (Reptilia Thecodontia) from the Upper Triassic (Norian) of Cene near Bergamo, Italy with a revision of the genus. Riv Mus Civ Sci Nat Bergamo 14:1–24.

Wilkinson M, Benton MJ. (1996) Sphenodontid phylogeny and the problems of multiple trees. Phil Trans Roy Soc B 351:1–16.

Williston SW. (1904) The temporal arches of the Reptilia. Biol Bull 7:175–192.

Williston SW. (1917) The phylogeny and classification of reptiles. J Geol 25:411–421.

Winchester L, Bellairs Ad'A. (1977) Aspects of vertebral development in lizards and snakes. J Zool Soc London 181:495–525.

Witmer LM. (1997) The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Soc Vert Paleo, Mem 3:1–73.

Yates AM. (2003) The species taxonomy of the sauropodomorph dinosaurs from the Löwenstein Formation (Norian, Late Triassic) of Germany. Palaeo 46:317–337.

Young CC. (1936) On a new *Chasmatosaurus* from Sinkiang. Bull Geol Soc China 15:291–311.

Young CC. (1963) Additional remains of *Chasmatosaurus yuani* Young from Sinkiang, China. Vertebrate PalAsiatica 13:215–222.

Zaher H, Rieppel O. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. Amer Mus Nov 3271:1–19.

Zhang F-K. (1975) A new thecodont *Lotosaurus*, from the Middle Triassic of Hunan. Vertebrata PalAsiatica 13:144–147.

Zhang G, et al. (2014) Comparative genomics reveals insights into avian genomes and adaptation. Science 346:1311–1320.

SUPPLEMENTARY DATA

SUPPLEMENTARY APPENDIX 1. Institutional abbreviations employed in text.

AMNH FARB–American Museum of Natural History, Fossil Amphibian, Reptiles and Birds (New York, NY, USA)
BP–Evolutionary Studies Institute (formerly Bernard Price Institute; Johannesburg, South Africa)
CMNH–Carnegie Museum of Natural History (Pittsburgh, PA, USA)
FMNH–Field Museum of Natural History (Chicago, IL, USA)
GMPKU–Geological Museum of Peking University (Beijing, China)
GR–Ruth Hall Museum of Paleontology at Ghost Ranch (Abiquiu, NM, USA)
IVPP–Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China)
MCSN–Museo Civico di Storia Naturali (Milano, Italy)
MCSNB–Museo Civico di Storia Naturali Enrico Caffi (Bergamo, Italy)
MFSN–Museo Friulano di Scienze Naturali (Udine, Italy)
MNHN–Muséum National d'Histoire Naturelle (Paris, France)
MPUM–Museo di Paleontologia Univeristà degli Studi di Milano (Milano, Italy)
NHMUK–Natural History Museum of the United Kingdom (London, United Kingdom)
NMK–Naturkundmuseum im Ottoneum (Kassel, Germany)
NMMNHS–New Mexico Museum of Natural History and Science (Albuquerque, NM, USA)
NMQR–National Museum (Bloemfontein, South Africa)
PIMUZ–Paleontological Institute and Museum, University of Zürich (Zürich, Switzerland)
PIN–Paleontological Institute (Moscow, Russia)
SAM–Iziko Museum of South Africa (Cape Town, South Africa)
SMNS–Staaliches Museum fur Naturkunde Stuttgart (Stuttgart, Germany).
SSGW–Sektion Geologie, Ernst-Moritz-Arndt Universistät (Greifswald, Germany)
TMM–Texas Memorial Museum (Austin, TX, USA)
TTU–Museum of Texas Tech University (Lubbock, TX, USA)
UA–Université d'Antannanarivo (Antannanarivo, Madagascar)
UCMP–University of California Museum of Paleontology (Berkeley, CA, USA)
UMMP–University of Michigan Museum of Paleontology (Ann Arbor, MI, USA)
USNM–United States National Museum (Washington, DC, USA)
VMNH–Virginia Museum of Natural History (Martinsville, VA, USA)
WMsN–Westfäliches Museum für Naturkunde (Münster, Germany)
YPM–Yale Peabody Museum (New Haven, CT, USA)

TABLE 6.1 Phylogenetic data matrix employed to analyze the affinities of Permo-Triassic Diapsida.

Petrolacosaurus kansasensis
0000--00000000010000000101000000200110011000000111010000000000010111000?0???1000
0001011-000000000000011-00000010?1000000000100--0000-0001?000100010?010011000110
0?0100000-0-110000010?-100000000000-0-0?00100000?00-000010000000000-0-000000?00-0
10000?0-00000000000100000000?[0,1]0000000-000000000000?00

***Uromastyx* sp.**
0000--00102-01100?101010-0???001021001---111-0-----01-11010-01010100100011001011010
01010100001---0-002100000000-1000000000000--1110-1011-11110001100100111001101011
10?11-10111100001000110000 1-1111100000100?00?0?-010010?00?000?0-0-00000010000000
0100-00000000000-000001002-00?0010000000000000010101?

Azendohsaurus madagaskarensis
00111000001000000000010010-1001000111000 1?0010000110-?001?1?10111101-210111010100
1100011-0010000001100011-1110001100001001001110--1100-1103-011111001101010100110
0000001111?11011000000110000?1101001010001100001100 1-0000001110[1,0]00000000110
01111110000000-000000000000100001002-000?01-1000000?00011100?

Azendohsaurus laaroussii
00111-00??0????????
01100000110?0???
??????????????????????????11?0??????1-????????????????????????1?1????00????????????????
???????0????????????????????????0?

Trilophosaurus buettneri
00011001102-0000000201-0-1001101-[0,1]1000???111-0-----10?01111011?1001111100010101
?101000011000100?12--1201110001110001001011010--0000-1002?0111010011010101100100
0000011110110110011011110001100100111 00?00100011000-10101110000000000000 1110110
11100010?0-00000?000000000001001-000?01-10000000010111000

Trilophosaurus jacobsi
0?0???01002-000?000101??0100?101?11??0??0?1??????????????????????????????????01??0?0
0??11000100?12?-110???0001110001?01???????????0-??0?????????0?11?10101100??00?00010
1101?1?100110111?0001100?????????0010-0???00-10?0?1?0?000000000?1110??01?1?1?00??
??0?000?0?0000??001?0??000?01-?000?00?010??????

Pamelaria dolichotrachela
??1???00?0??0???00?0?????10000001?1??01???100?011?????????00???1???2?????????01??0?
010001100000101011-???000110000100100 11?0--??00-??0??0?????0010?10101000????0000

1?1101????0011001110001 1??????010??????0?10?00-00000?00100000000???001????000000
?0-?0000000000000000?001-000?01-1000000?0001???0?

Spinosuchus caseanus
??
????????????110???00011100??001001100--?00???
??????????????????????????????????????101?0?????????????????0???????1??0???????????????
????????????0?01????????0??0??????

Prolacerta broomi
0001100010100001000 10[0,1]00-10000001111001-01100001111100[0,1]01111001101110110
0010100110101000101000011 10011-1110001100001000 00?100--000101[1,0]01??1001001100
10100-11???00001010010011001100111000110010011100?00000000000-0001100000000000
000???00?101000110?0-000000??00000000001002-0?0001-100000?0000111001

Teraterpeton hrynewichorum
00010001101?000000001??0?1001101?01000???110?0000?????10?100010?0???11?00????00?
1000?0011000100?10?-11-?1101010?0001001????0???100????????111?00???????????????????
?????????????????????????????????????01?0010?00-??0???1?1?????????????01??10?????0????
???000??0?????0???0???0??01??????0?0?10?1??0?

Protorosaurus speneri
0000--0000100000001101-??10000001111001-0110???1??????10??000?0??????????????001?0
10?0001000000000?010-1110??111000100000 1000--0000-?001??1?11000110101010 0?100000
00?????1?111101100??100000000001?1000?0100?0??00-?0001000000000000000000000000?
0?000-0000000000000000001001?000001-100??00000011?000

Proterosuchus fergusi
0201100000101020000111-101100000201100[1,0]-01100001?1100-10111011110111111 2000?
?0011011?0001110000111 0010-1100101100000000??2?1110000101 0010?1001101100101010?
1????000111?1111110010001110001100100111 00?01000100000-00010?00?000000000?0000
?0101000110?0-000000?0?00000000?001-??0?01-1000000?00011?10?

“Chasmatosaurus” yuani
0201100000101020000111-1?110000020110 01-0110?0??????0??????????1?????????????00??0
11?0001110000?1100?1-????101??????00?0???010000?0-1001?0100?1011101011100??00?00
010?1?111110011001110?011001??10100?0100010???0-?0011001100000000011?000?101???1
10?0-00000000000?00000100??00??01-1000?00000011??0?

Youngina capensis
0000--00001000010100000101101000201110010000000111110000010 0?[0,1]0101100010110
0000??0?0?000101000001000 10-??001000-0100000000000--000101001??111000?111101110?
0110001101010-1?111001100??10000000000010-0??0100000?00-00001?100000000-0000?010
?00-??0010?0-0000000000??000001000-000000-00000000000101001

Gephyrosaurus bridensis

0000--00002-01000110100001?010001110001-1110000110-100????0000?10110?000?????01?0
??0?0101000001-100010-00?0?000-00000?000?000--?11101111??111000010?11011?????????1
110011-10111?000010?01100?01????110??00000000?10-0111??01?000000-0-?1?????000100?
00?0-00??0??0?00-?0000??00-??0?00?1000100?00?10?01?

Mesosuchus browni
00112?00111-000010[0,1]11000-10010001111001-0110010110-20?1011100011011011000?0
100?011000001001000?100010-?1101011?000100110?000--0001011010?101100?110??101011
0000?100??10011111001100001000110010011100?00000000000-0001001000000000000000000
10000000000?0-00000000000?00000?00?-?00001-1000000?000111002

Rhynchosaurus articeps
02112010111-0000101101-0-100101021110000011 1-?-----20?????????11001011100????11??0
?00001100100??10--10-??00?0100110100011?000--?000-10010?1111101100101010110?00000
0?01111111001?-0??1000??0010010100??0000100?00-01010010000000000000000000000??0
000?0-0000??00?00?00000?01?-000001-?00000?0000?1?002

Teyumbaita sulcognathus
02112010111-0000001201-0-1101010211?00000111-1-----2011101100011 0????1?000???10011
00-001100100??10--11-??10001001?0000101?0?0--100????0??01????0110?10100-1??????????
???????????1010??10??????1?????????0000100?00-011???11????000???????00?00000?000???
????00???000????0??22-0?0?01-0?0?00??00??1?00?

Langobardisaurus pandolfii
1011?00???1?000?????????????0?000?11???1??1??????????????????????????????0?????01????0?
0?01000200?00?01211111?1111001?101????1?????0111103001111 0???010100-11?00?0100?
11111?111111101?0100?1?0011110111???1?0?1???0-?00000?000000?0???1??0000000??0??00
000000??00000?00000?00??0000?1-?00??0?0??0???000

Tanystropheus longobardicus
001110000011000000110 01??11000001211001?0110000100-1001???0001010??001?00?1?100
??01010001000[0,2]001001011-111001111001?011011111011000-1101001111011110101 00-1
10000110011110111 11[1,0]011010000001000-111011110110 0010?00-10[1,0]100000000000?0
-1?0000001001 0000?0-0000000000001000000001?000001-100100?000001?000

Tanytrachelos ahynis
0011?000?01?00000000?01??1??0?0012???????11000???0-100???????0?????????????????????0?
0?0?01000000?0000121111101??10011?01????11?110?0-100?00?????1?11010100-11????1100
?111111111111101??0001??1??11?0111100?00?????0-?0001000?0000?00001??00?0?0??1???0
???00?000?0?00100?00?00??0000?1-?001?0?0000?????0

Macrocnemus bassanii
0011100010110001000111???1001000111?001?01100?0110-??????????????0??001?0?????01?1
01010?010100000?01011-1110?01110011000-???01?01001111010011110111101 0100-11?00?0
1001111 0111?1101101?010000?0010110100?00?00?00?00-?00?10000010000???0?000000000
1?000??????????????0??????0?????0001-1001?0?000011?000

Amotosaurus rotfeldensis
00?1??00??1?0????????????????000[1,0]?1??????1?01?0110-?0???????????0??201???????00??
??0???0100000???01001-11100?1110011?010?1?0???10011?10????????1?11010?????0????010
0???101?1?1001101??000???0?-101?111?01100?00?00-?0000000?010000?000???0?0?10?1?0?
0??????000?0000000?00?00??000001?10???0?00001?????

Erythrosuchus africanus
0001111000101020000111-11110000020110000010??0?????100001?111111001?0112001??00
1101110001110000101-010-0?000011010000000012100--0000-100100111100?10010101011???
??000111111101100100000100??1000???1??00?0111110101010101?011?0100000000???01?10
0?00110?0-000?00?0000?00000??02-0?0?01-10?000??00011?100

Shinisaurus crocodilurus
0000--00101-01100?101000---??000021101?--110101000-01-10010001110100110000101011 1
100101010100001-000012100001000-1000000000000--1100-101111111000110010011100110 1
01100010-10111000010000110 10?1?001010000?1?0100100-000?001010000?0-0-10001010001
0000100-00100000000-000001002-0000-10000000?0000001010

Euparkeria capensis
000111000010102100 01?1-11110100021100000011 0?00110?100??1?1?11110?11?11210?0100
11011?00011100001010011-010000100?00?000??2??1100000-??0??11??00??0???1?0-11????
?0001?11111??1?01-011100001100-11111000010111010101010110000011101101100 0100-00
??01?0???????00?0000?00?00?002-000001-1000?0?0000?1?100

Batrachotomus kupferzellensis
000101101010100000111-0-100000020100000011 1-0---0-1001011101011?001?1020?1??00?1
0010000111000010 1-011-011000110[0,1]00110111210100 1000-??010011???0010010100010?
????000101111101100 1-01?1001011?0-???110??0112110111020101 1?00?01110?1121?0?1?0-
00?10110?0-000000?000--00000??02-0?0?01-100000??01011?00?

Coelophysis bauri
0101-100001010000001 11-0-101-0102110000001111?10-0-100100?1001110?0111?21?10100?
?0011000111000010 1-011-1110001110001001111100--1100-1001?01----011000-1000100011-
0001011110011000-01110[0,1]10---0-11100--00112010111020001?1001111111-1-1000001-00
010??0???????????????????????0001-?00000?0010????0?

Plateosaurus_engelhardti
0001-100001010000001 11-0-101-0102110000001111?10-0-?00100?1001110001110[1,2]10101
00?100110001100000100-011-1110001100001001111100--1100-1001?01?---011000-10001000
11-0001011110011?00-01110010---0-11100--00112010111020001000111111 11-1-1000011-00
000110??????????????????????2???0001-100000?001011??0?

Macrocnemus fuyuanensis
00111000101100010 01111-??10000001110 00???110???11????????????????????????????0???0
10?0?0101000???0?011-1110??1110011?0000100 1??10011110?00111??111??101?0-1000??01

001011010111101101001000000010110100??01?0?0??00-?000?00000000?00000??0000000?1?0?0??????????????0??????0?????0001-100??0?0000???000

Hovasaurus boulei
??????00?????00101??1001?1101000?1111????000???111110010??00?00001?0?1?????????????????0???0000??????11-000000???0000?00?01000??000??1?0???01101011111111110111000010?010-1?1110000?1??10000100000[1,0]10?00???????0?????00?10000000000001??00?00??00???0?0-00000000?000000001000-0001000?000?000000?00??0

Thadeosaurus colcanapi
?????????????00??????????1???0????????????0?0??0110-?0????????0010110?1???????????010????????????????11-00?0?0?????????0000000??0000-10001?1?1?0011111111110011000010???0-1?111000101??100??100000?10?00???????0?????100100000000?00?01??00?00?-?????0?0-0000000000000000010?0?00000?0?00??0000?0?????1

Coelurosauravus elivensis
??????00??2?00010?00100??0?00?00000?001?100????????????????????0??0?1???????????????????100000???0??11-0011?0?0?0000?00?0??00--110????02??00??00????11001000110??0?????111?111?000?1??10???0??100000-??00?00?00???-?00??000????0?0-??????0?0??-?????0?0-000?00?0001?0?001100??000?000001???0???1?0?00?

Coelurosauravus jaekeli
0000--00??2-0000?000100??1000000?0???0?????0?0?000000??????0?????1???????????00??0?0???11?????02????????????1?011?00110?0??????????????00?01??10???????0000000??0??0?????0-?01??0?00?????0??????0000?0??????0?0-00????00?0????0?1100??00000??001???0???1?0?00?

***Rautiania* spp.**
0000--00????00????0?100??????0???00??01-100?????????????????????????????????00?1010?0001000001-10?0??????????????????????????????0-????????????????1101100?????0???????????????????????????????????????0?0??0???0????0???00????????????????0-????0??????????0?????????1??0??00?????001???0????00?00?

Dolabrosaurus aquatilis
??11-????????????????????110??000-??01???00??100?10000-0???????????????111?????????00?01??????0???????????1111??0??1?01?10??1????0???0????????????0?????0

***Coelophysis* Quarry Drepanosaur**
??????00????0001010001-0-1001000000?0????001-?-----00-000000000000?010?011?0100????0?0?1?????????????11-??1?0??????0100?????????????????1???00??0?001???00??????????????????????0-?????1????11?????????????0???0???1?10?1???01??12?0?001?

Drepanosaurus unguicaudatus

???
???????????????????????????????0?001???10?0-??01-???????2?1????0???00??0?-1200010-?011
10000????100??10?000000-0???????????????11100?00?0??00?01??10?-0????????11011111211
1?101110?01????111??0?100?111120?????0

Hypuronector limnaios
??0???
1?00000?????-11-????????????????????01???100??1101-?11???0111????????????120???0-001
111000???????????????????????????????????0??100???00?????????0?1?0???????00-01100??0?
11??000???????01?10????0?0?0010??????

Icarosaurus siefkeri
??????001010000100011?????000000021?0????1100?01??????0????????0111?210???????00???
?0???010000???000011-??10??1000001?000?1?1???1000-100???1?????1?1?0110?0??1?????100
?????1?1??0?0?01????????????????????0100?00?00-?111??0000000?????????00??0010?0?0???
????00?000?????10??0211?0?011?00???00?00?1??0?

***Kuehneosaurus* sp.**
0011100010100001000111-??1?00000021??1???110??01111?0????110?0011112?110?????0?1
1100?0001000001-100011-???00010000010000111?10??000-100????1???0?11?1100100??????
1001010-10????1000100?0????????????0???0??00?00????1111??00?0000?????????01??00?01?1
0???????01???00??0?10??0211?0?0111000000?00011?00?

Megalancosaurus preonensis
000???00??1?00110?00?1-??1???00000???????0????????????????????????????????????00??0?0?
0?0100?0???0??011-??1?0????000100000??10??100????01???????2?11??????00??0??120???0
??????00??????1001?1???00000?00?0??0??????0-?0??100?0?0??00?01??10?100???0?1111111
1120001??1010001????1111??0000?001020?0???0

Vallesaurus cenensis
0000--00??1?00??0?0????????000000???00????0?
0?0100000?????01????1?0??--??????000??00??10?????01-?1????2?11????????11?0001?0?????
??1???0001???10???0??1???00-0?????0?????0-?1??1010000???????1??10?1?0??????100-01101
100001??010011???0010?0??0???0?1020????00

FIG. 6-1. Hypotheses for the phylogeny of diapsid reptiles based on the strict consensuses of A) a composite of the archosauromorph and lepidosauromorph topologies offered by Gauthier (1984), B) Benton (1985), and C) Evans (1988). Lowercase taxa indicate supraspecific OTUs as described in these analyses, whereas capitalized taxa indicate taxa represented by multiple OTUs.

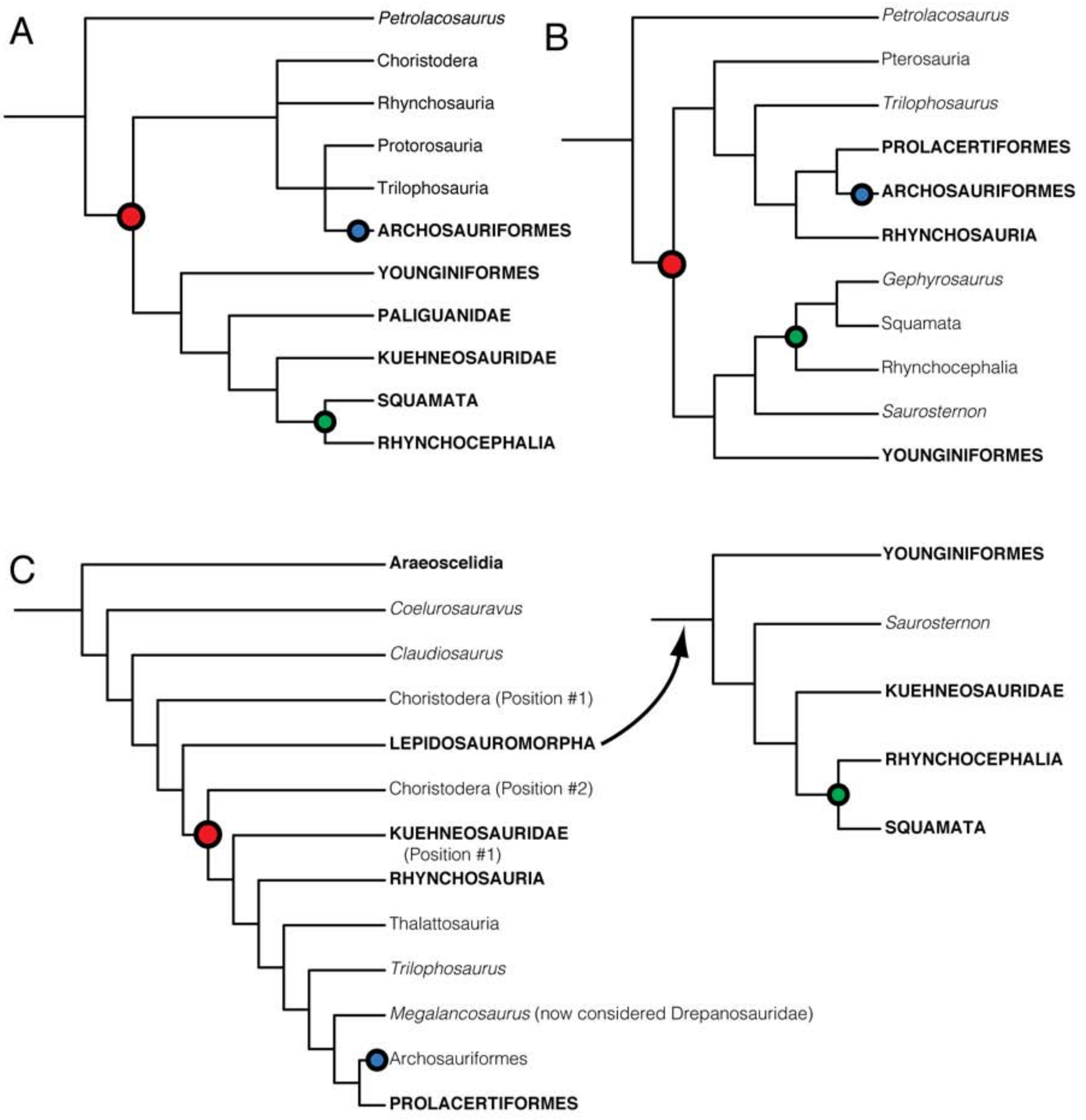

A
Petrolacosaurus
Choristodera
Rhynchosauria
Protorosauria
Trilophosauria
ARCHOSAURIFORMES
YOUNGINIFORMES
PALIGUANIDAE
KUEHNEOSAURIDAE
SQUAMATA
RHYNCHOCEPHALIA
B
Petrolacosaurus
Pterosauria
Trilophosaurus
PROLACERTIFORMES
ARCHOSAURIFORMES
RHYNCHOSAURIA
Gephyrosaurus
Squamata
Rhynchocephalia
Saurosternon
YOUNGINIFORMES
C
Araeoscelidia
Coelurosauravus
Claudiosaurus
Choristodera (Position #1)
LEPIDOSAUROMORPHA
Choristodera (Position #2)
KUEHNEOSAURIDAE
(Position #1)
RHYNCHOSAURIA
Thalattosauria
Trilophosaurus
Megalancosaurus (now considered Drepanosauridae)
Archosauriformes
PROLACERTIFORMES
YOUNGINIFORMES
Saurosternon
KUEHNEOSAURIDAE
RHYNCHOCEPHALIA
SQUAMATA

FIG. 6-2. Hypotheses for the phylogeny of diapsid reptiles based on the strict consensuses of A) Laurin (1991), B) Rieppel (1994), C) Merck (1997) and D) Dilkes (1998).

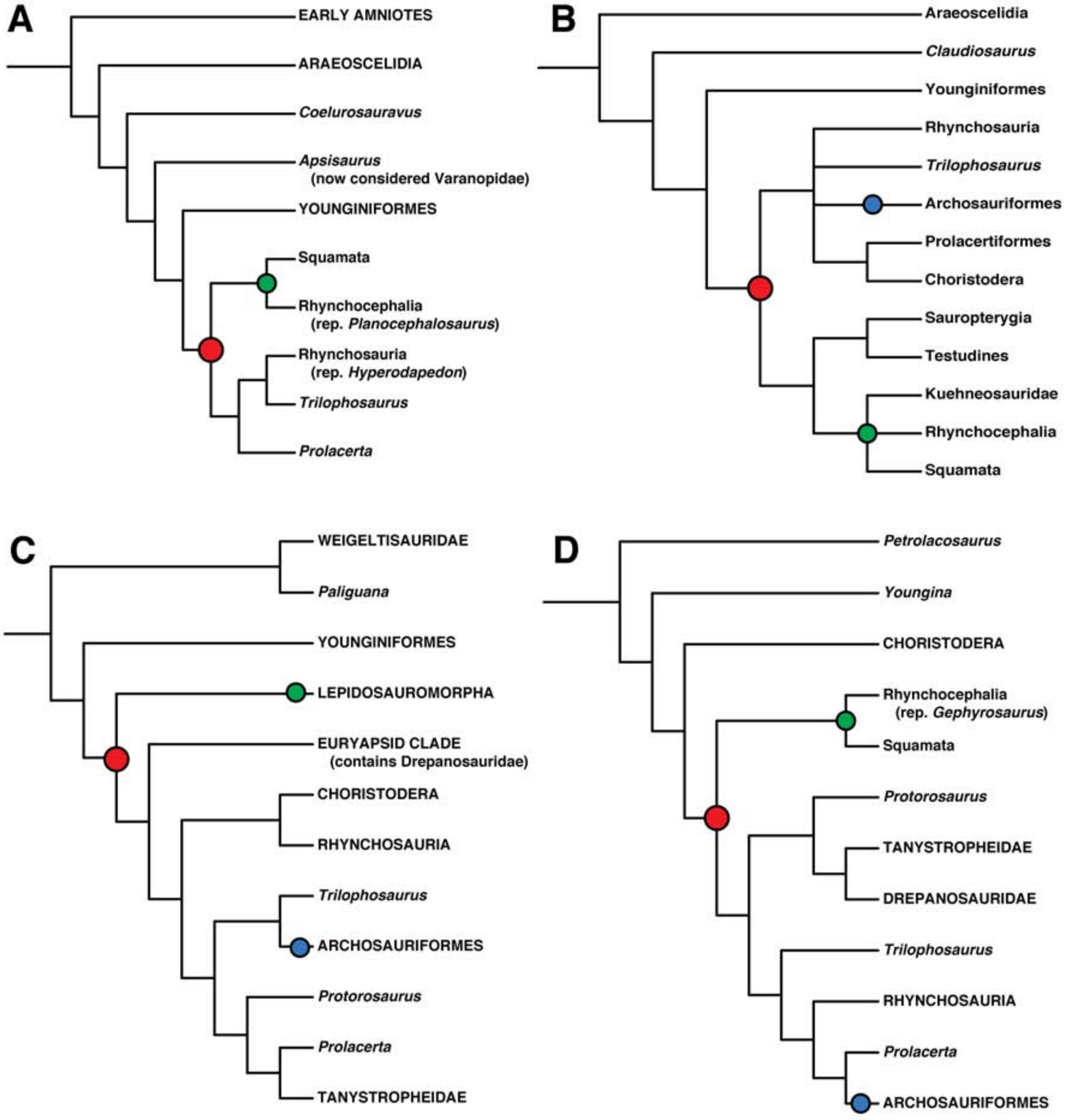

A
EARLY AMNIOTES
ARAEOSCELIDIA
Coelurosauravus
Apsisaurus
(now considered Varanopidae)
YOUNGINIFORMES
Squamata
Rhynchocephalia
(rep. Planocephalosaurus)
Rhynchosauria
(rep. Hyperodapedon)
Trilophosaurus
Prolacerta
B
Araeoscelidia
Claudiosaurus
Younginiformes
Rhynchosauria
Trilophosaurus
Archosauriformes
Prolacertiformes
Choristodera
Sauropterygia
Testudines
Kuehneosauridae
Rhynchocephalia
Squamata
C
WEIGELTISAURIDAE
Paliguana
YOUNGINIFORMES
LEPIDOSAUROMORPHA
EURYAPSID CLADE
(contains Drepanosauridae)
CHORISTODERA
RHYNCHOSAURIA
Trilophosaurus
ARCHOSAURIFORMES
Protorosaurus
Prolacerta
TANYSTROPHEIDAE
D
Petrolacosaurus
Youngina
CHORISTODERA
Rhynchocephalia
(rep. Gephyrosaurus)
Squamata
Protorosaurus
TANYSTROPHEIDAE
DREPANOSAURIDAE
Trilophosaurus
RHYNCHOSAURIA
Prolacerta
ARCHOSAURIFORMES

FIG. 6-3. Hypotheses for the phylogeny of diapsid reptiles based on the strict consensuses of A) Müller (2004), Senter (2004), Ezcurra et al. (2014), and Pritchard et al. (2015).

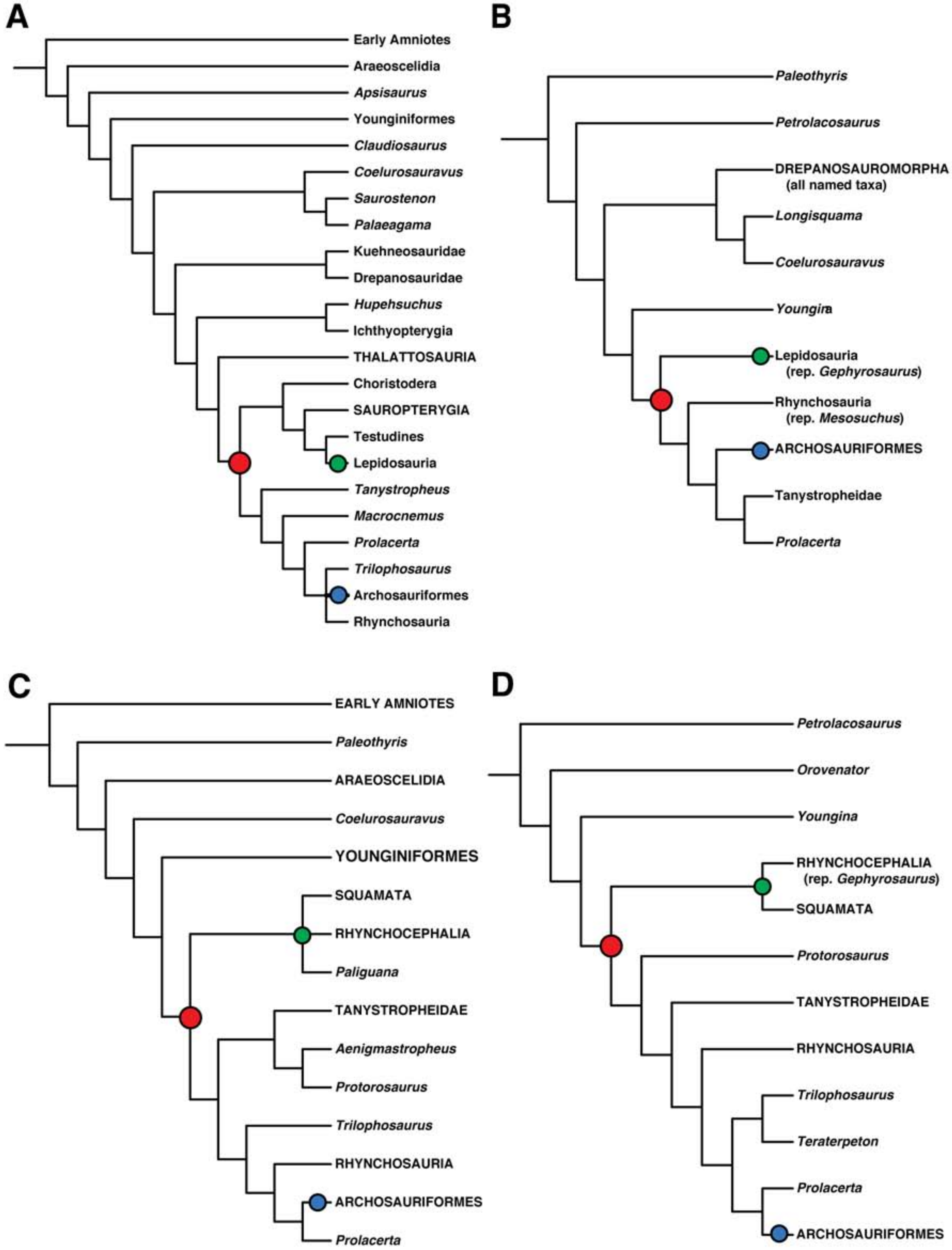

A
Early Amniotes
Araeoscelidia
Apsisaurus
Younginiformes
Claudiosaurus
Coelurosauravus
Saurostenon
Palaeagama
Kuehneosauridae
Drepanosauridae
Hupehsuchus
Ichthyopterygia
THALATTOSAURIA
Choristodera
SAUROPTERYGIA
Testudines
Lepidosauria
Tanystropheus
Macrocnemus
Prolacerta
Trilophosaurus
Archosauriformes
Rhynchosauria
B
Paleothyris
Petrolacosaurus
DREPANOSAUROMORPHA
(all named taxa)
Longisquama
Coelurosauravus
Youngina
Lepidosauria
(rep. Gephyrosaurus)
Rhynchosauria
(rep. Mesosuchus)
ARCHOSAURIFORMES
Tanystropheidae
Prolacerta
C
EARLY AMNIOTES
Paleothyris
ARAEOSCELIDIA
Coelurosauravus
YOUNGINIFORMES
SQUAMATA
RHYNCHOCEPHALIA
Paliguana
TANYSTROPHEIDAE
Aenigmastropheus
Protorosaurus
Trilophosaurus
RHYNCHOSAURIA
ARCHOSAURIFORMES
Prolacerta
D
Petrolacosaurus
Orovenator
Youngina
RHYNCHOCEPHALIA
(rep. Gephyrosaurus)
SQUAMATA
Protorosaurus
TANYSTROPHEIDAE
RHYNCHOSAURIA
Trilophosaurus
Teraterpeton
Prolacerta
ARCHOSAURIFORMES

FIG. 6-4. **A**, right premaxillae of *Azendohsaurus madagaskarensis* (UA 9-9-98-560) and **B**, “Chasmatosaurus” *yuani* (cast of IVPP 36315) in lateral view. Numbers indicate a character, whereas values in parentheses indicate the state represented in the indicated taxon.

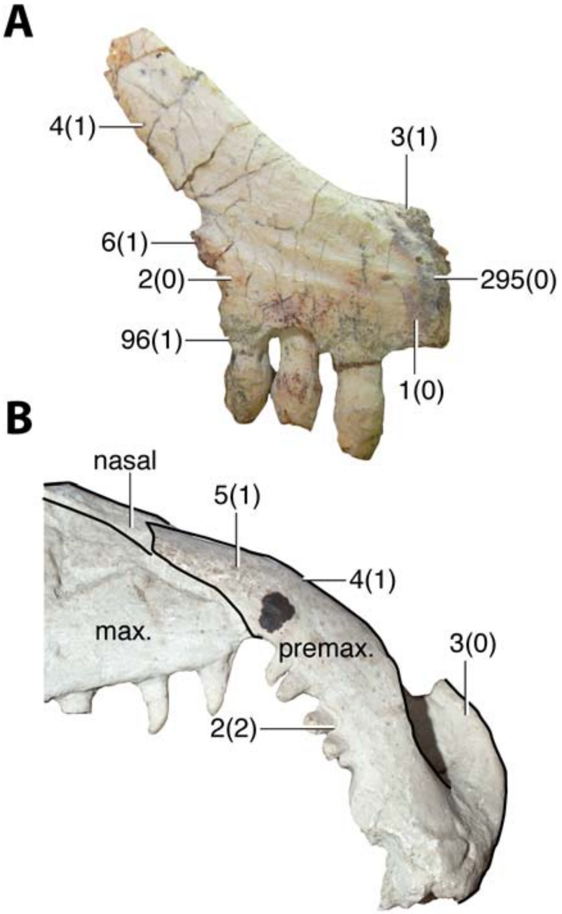

A
4(1)
3(1)
6(1)
2(0)
295(0)
96(1)
1(0)
B
nasal
5(1)
4(1)
max.
premax.
3(0)
2(2)

FIG. 6-5. Skull roofs from a series of early diapsid reptiles in dorsal view. **A**, cf. *Youngina capensis* (SAM K6205). **B**, *Proterosuchus fergusi* (SAM K10603). **C**, *Mesosuchus browni* (SAM K6536). **D**, *Trilophosaurus buettneri* (TMM 31025-140).

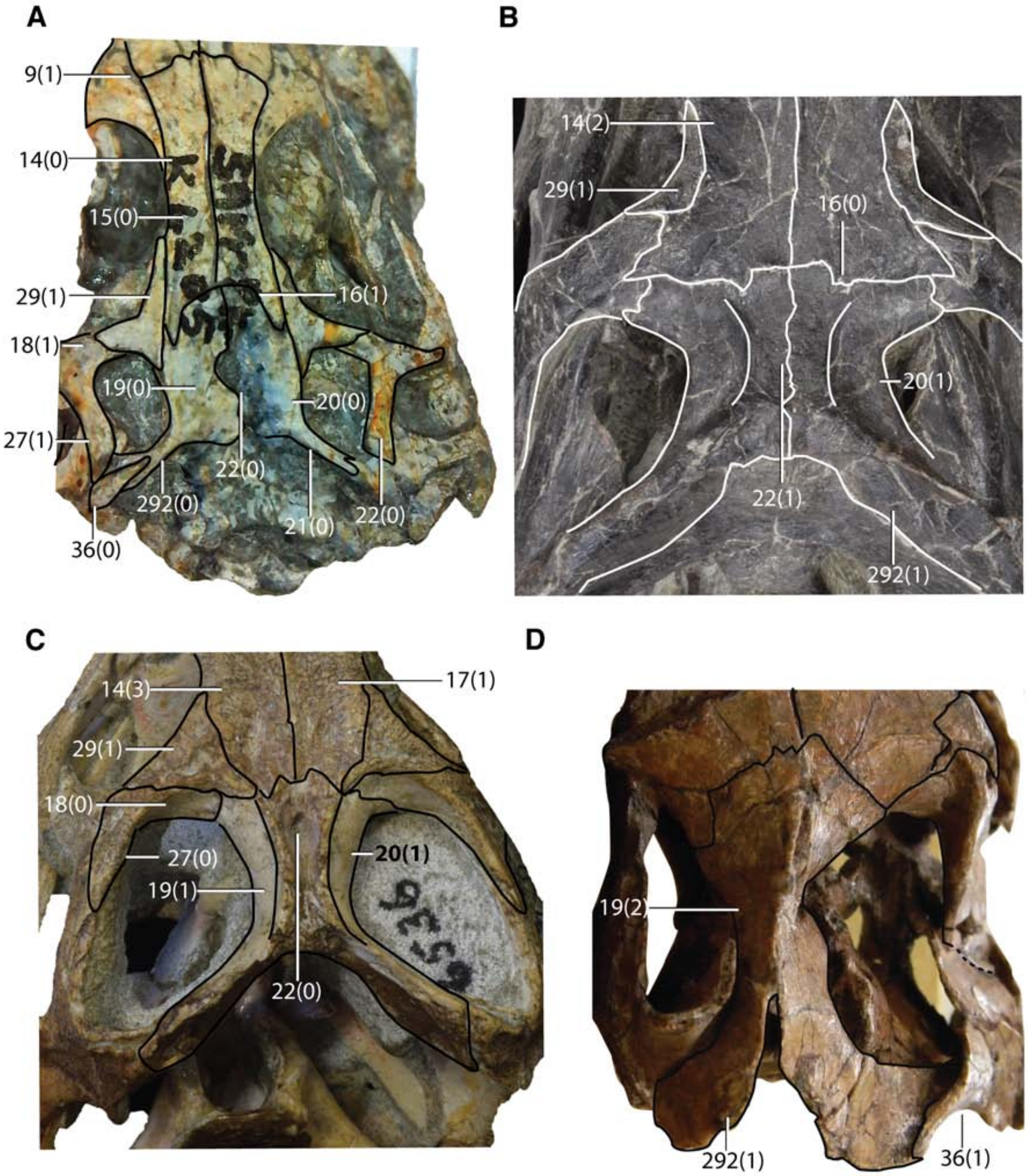

A
9(1)
14(0)
15(0)
29(1)
16(1)
18(1)
19(0)
20(0)
27(1)
22(0)
292(0)
21(0)
22(0)
36(0)
B
14(2)
29(1)
16(0)
20(1)
22(1)
292(1)
C
14(3)
17(1)
29(1)
18(0)
27(0)
20(1)
19(1)
22(0)
D
19(2)
292(1)
36(1)

FIG. 6-6. Temporal regions of a series of early diapsid reptiles in lateral view. A) *Youngina capensis* (BP/1 3859), B) *Prolacerta broomi* (BP/1 5375), C) *Proterosuchus alexanderi* (NMQR 1484), D) *Trilophosaurus buettneri* (TMM 31025-140), and E) *Chanaresuchus bonapartei* (MCZ 4037). C and D have been mirrored from the original photographs.

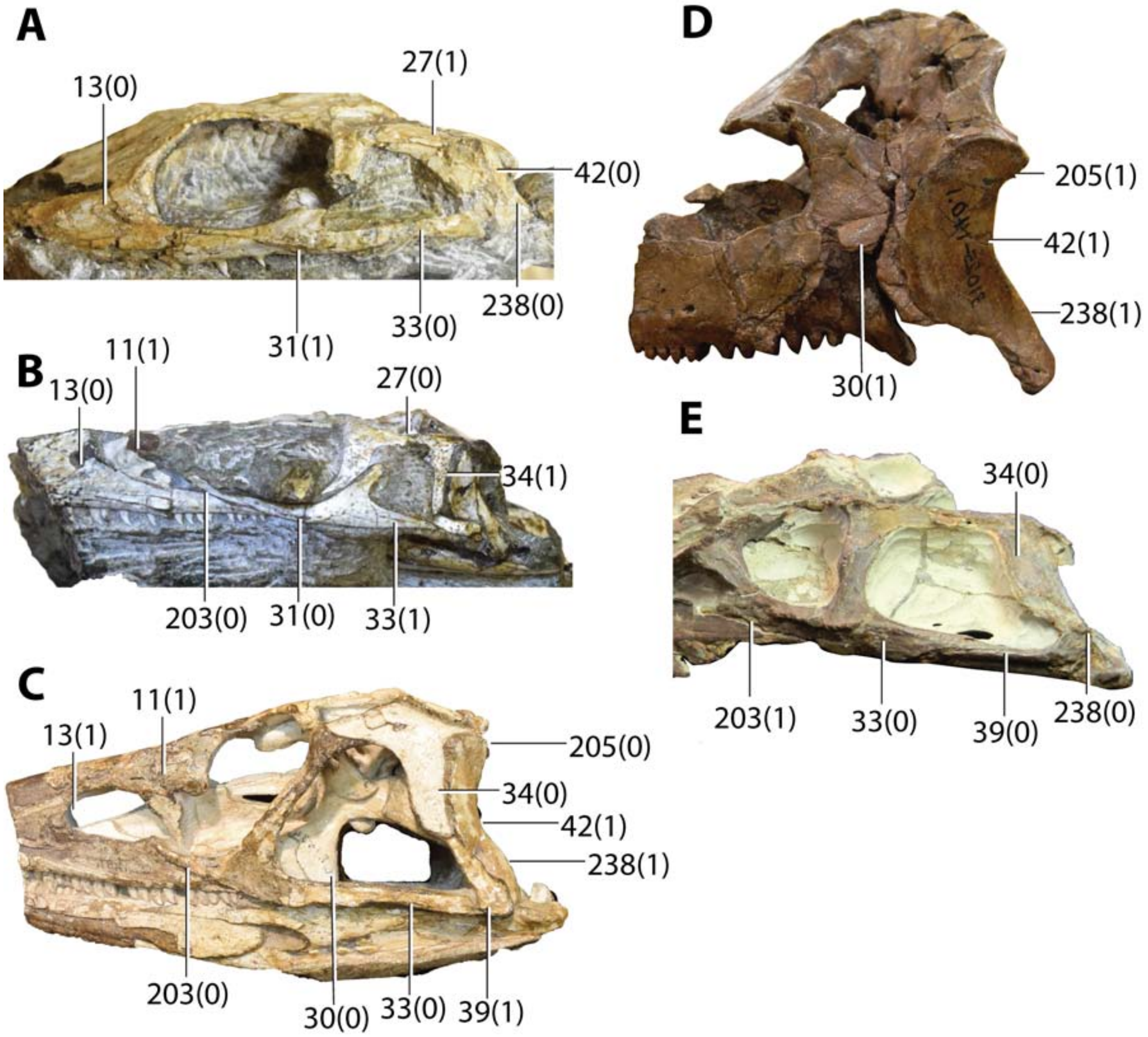

A
13(0)
27(1)
42(0)
31(1)
33(0)
238(0)
B
13(0)
11(1)
27(0)
34(1)
203(0)
31(0)
33(1)
C
13(1)
11(1)
205(0)
34(0)
42(1)
238(1)
203(0)
30(0)
33(0)
39(1)
D
205(1)
42(1)
238(1)
30(1)
E
34(0)
203(1)
33(0)
39(0)
238(0)

FIG. 6-7. Braincases of a series of early diapsid reptiles in posterior view. A, Three-dimensional reconstruction of Drepanosauridae n. gen., n. sp. (AMNH FARB 30834); B, *Trilophosaurus buettneri* (TMM 31025-443); C, *Azendohsaurus madagaskarensis* (FMNH PR 2765).

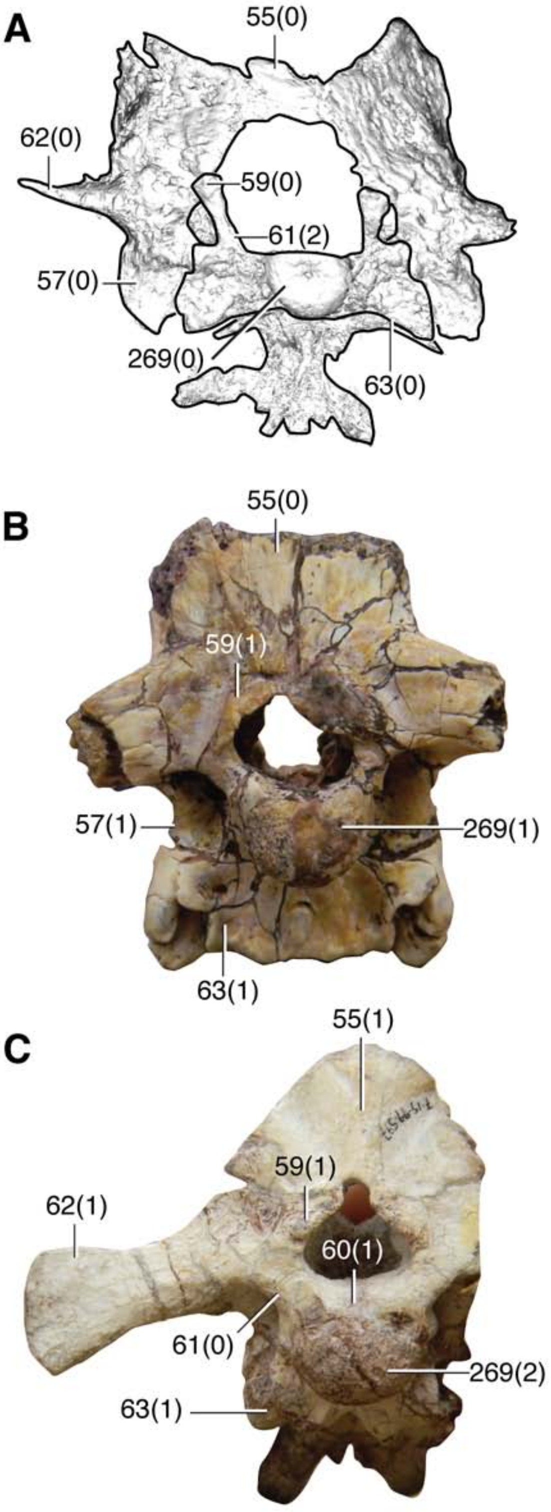

A
55(0)
62(0)
59(0)
61(2)
57(0)
269(0)
63(0)
B
55(0)
59(1)
57(1)
269(1)
63(1)
C
55(1)
59(1)
62(1)
60(1)
61(0)
269(2)
63(1)

FIG. 6-8. Braincases of a series of early diapsid reptiles in lateral view. A, *Trilophosaurus buettneri* (TMM 31025-244) in right lateral view; B, *Azendohsaurus madagaskarensis* (FMNH PR 2765) in left lateral view; C, *Proterosuchus goweri* (NMQR 880) in left lateral view. A has been mirrored from the original photograph.

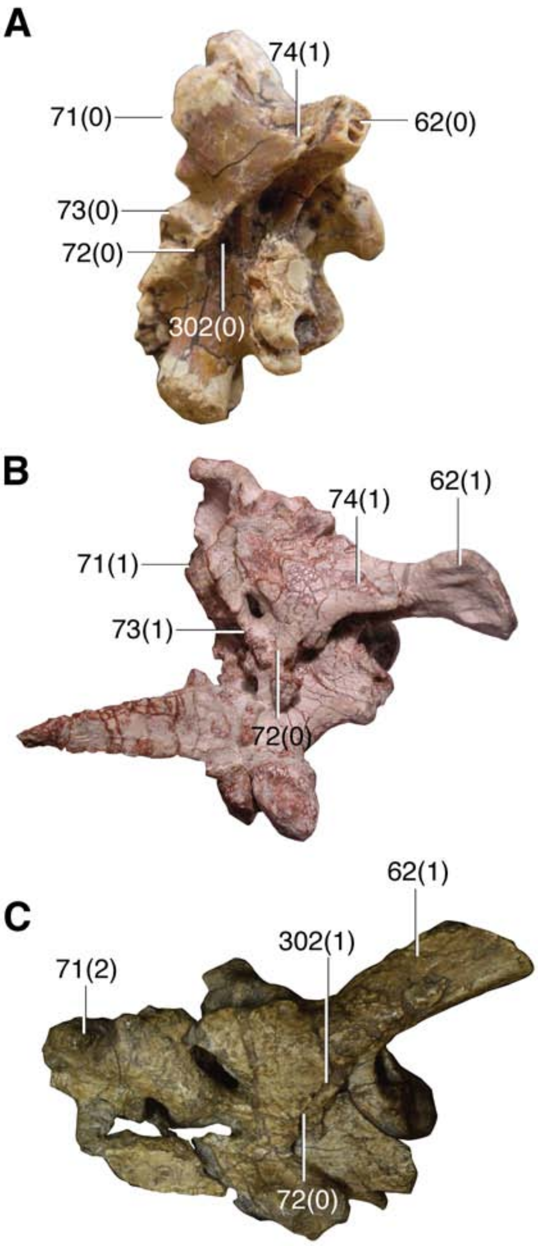

A
74(1)
71(0)
62(0)
73(0)
72(0)
302(0)
B
74(1)
62(1)
71(1)
73(1)
72(0)
62(1)
C
302(1)
71(2)
72(0)

FIG. 6-9. A, Right dentary of *Trilophosaurus buettneri* (TMM 31025-1) in lateral view. B, complete tooth of *Trilophosaurus* sp. (TTU P10411) in mesial view.

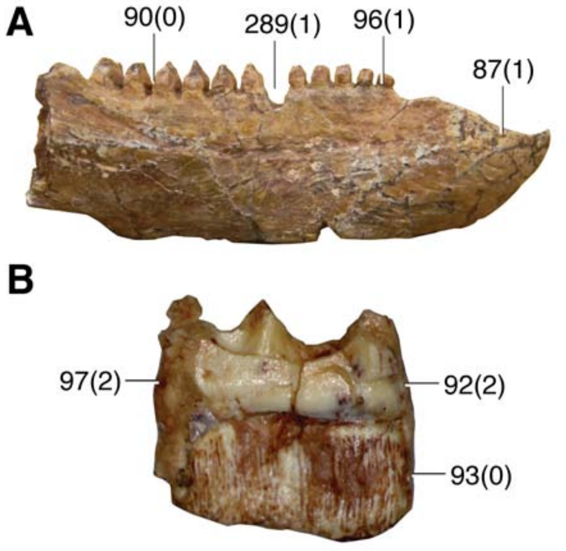

A
90(0)
289(1)
96(1)
87(1)
B
97(2)
92(2)
93(0)

FIG. 6-10. Tooth-bearing jaw elements from a series of early diapsid reptiles. A, anterior fragment of right maxilla of *Czatkowiella harae* (ZPAL RV/1115) in lateral view; left maxilla and dentary of *Vancleavea campi* (GR 138) in lateral view; partial right dentary of *Azendohsaurus laaroussii* (MNHN ALM 360) in medial view. C has been mirrored from the original photograph.

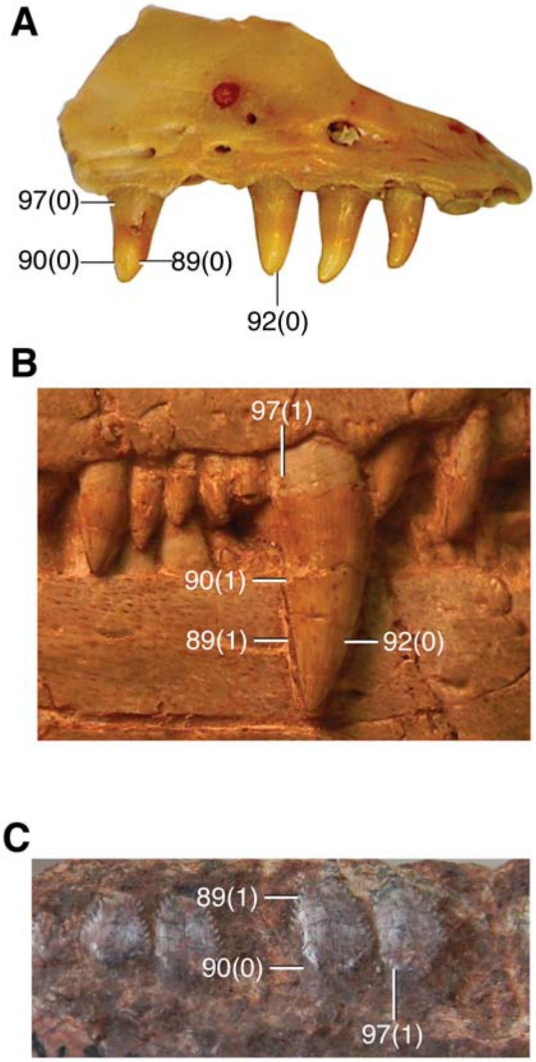

A
97(0)
90(0)
89(0)
92(0)
B
97(1)
90(1)
89(1)
92(0)
C
89(1)
90(0)
97(1)

FIG. 6-11. Partial skull and lower jaws of *Tanystropheus longobardicus* (MCSN BES SC 265) in ventrolateral view.

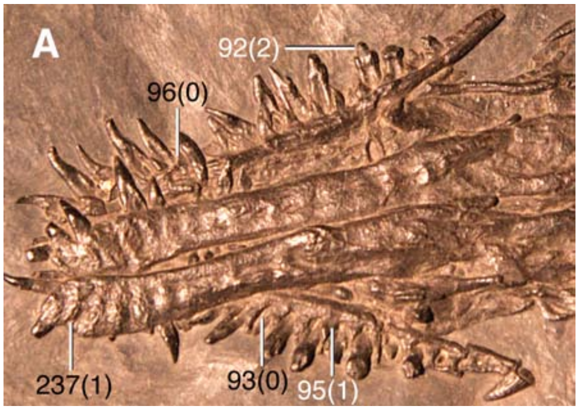

A
92(2)
96(0)
237(1)
93(0)
95(1)

FIG. 6-12. Cervical vertebral series of A, *Protorosaurus speneri* (SMNS cast of WMsN P47361) and B, *Tanystropheus longobardicus* (PIMUZ T/1270) in right lateral view.

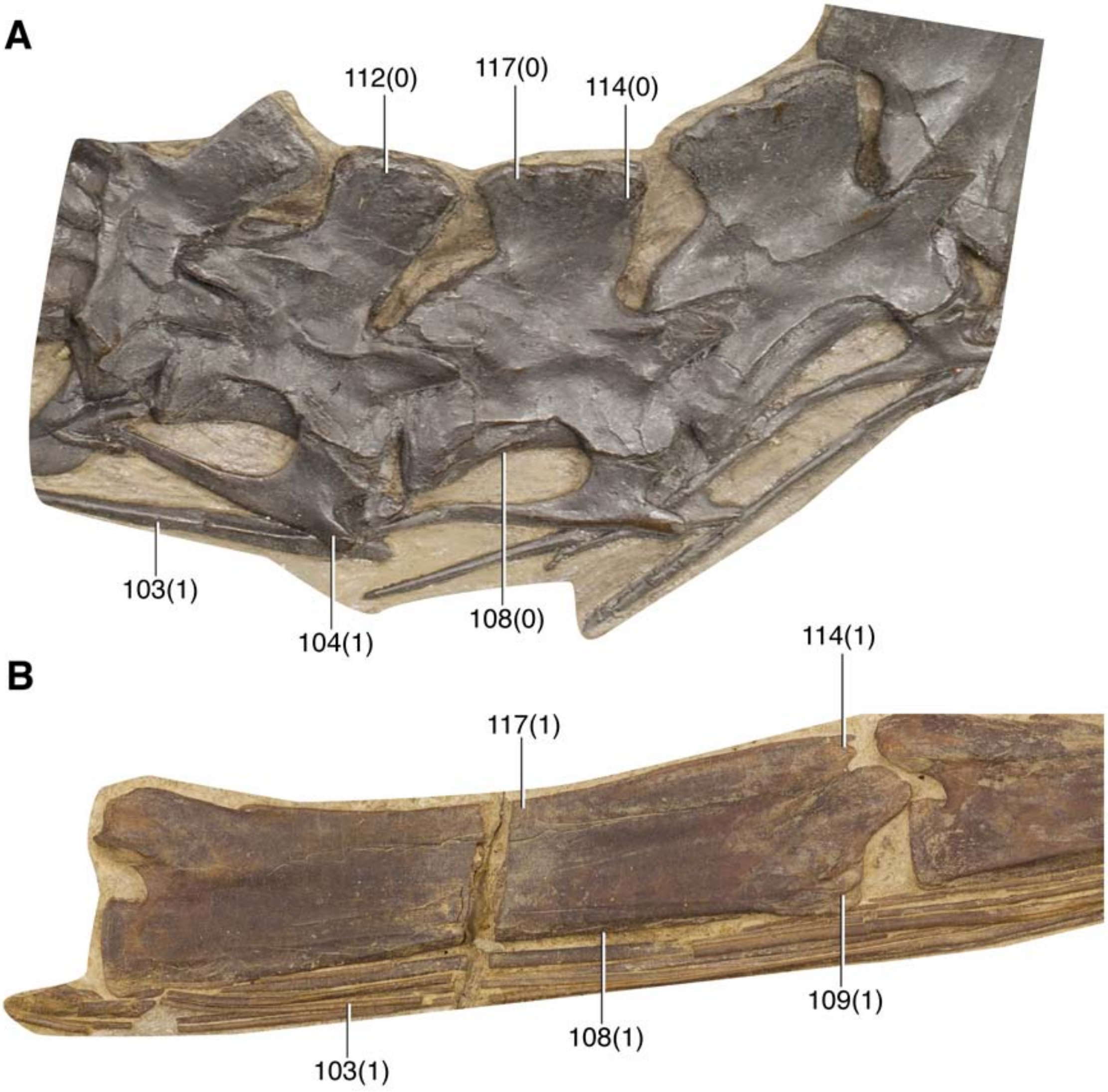

A
112(0)
117(0)
114(0)
103(1)
104(1)
108(0)
B
114(1)
117(1)
109(1)
108(1)
103(1)

FIG. 6-13. A, atlas-axis complex and anterior cervical vertebrae of *Erythrosuchus africanus* (NMQR 3765) in right lateral view. B, axis and third cervical vertebra of *Trilophosaurus buettneri* (TMM 31025-140) in right lateral view. C, axis of *Tanystropheus longobardicus* (PIMUZ T/2819) in left lateral view. C has been mirrored from the original photograph.

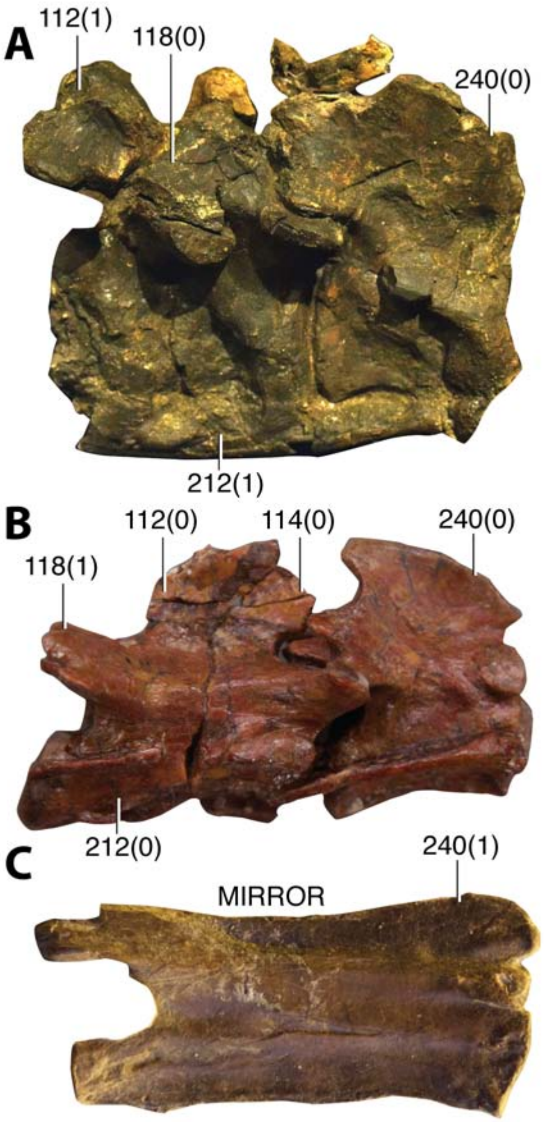

A
112(1)
118(0)
240(0)
212(1)
B
118(1)
112(0)
114(0)
240(0)
212(0)
C
240(1)
MIRROR

FIG. 6-14. Dorsal vertebral series of selected diapsid reptiles. A, *Mesosuchus browni* (SAM K7416) in ventral view. B, *Icarosaurus siefkeri* (AMNH FARB 2101) in dorsal view. C, *Megalancosaurus preonensis* (MPUM 8437) in ventral view. Note that C has been mirrored from the original photograph.

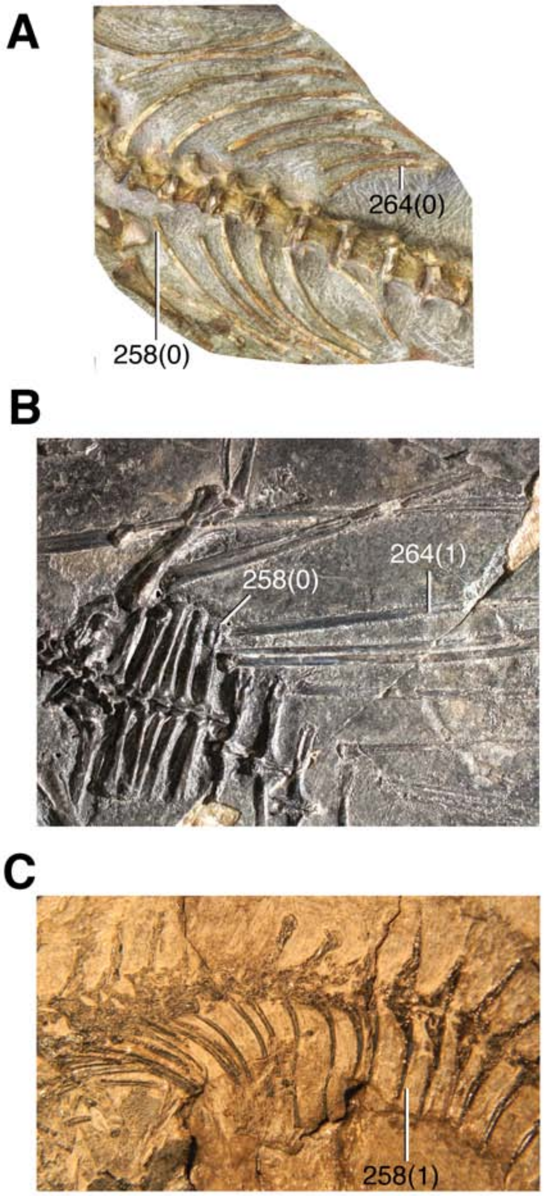

A
264(0)
258(0)
B
264(1)
258(0)
C
258(1)

FIG. 6-15. Caudal series from a series of early diapsid reptiles. A, *Protorosaurus speneri* (SMNS cast of WMsN 47361) in right lateral view. B, *Dolabrosaurus aquatilis* (CMNH 28589) in left lateral view. C, *Megalancosaurus preonensis* (MFSN 18443) in left lateral view. Note that A has been mirrored from the original photograph.

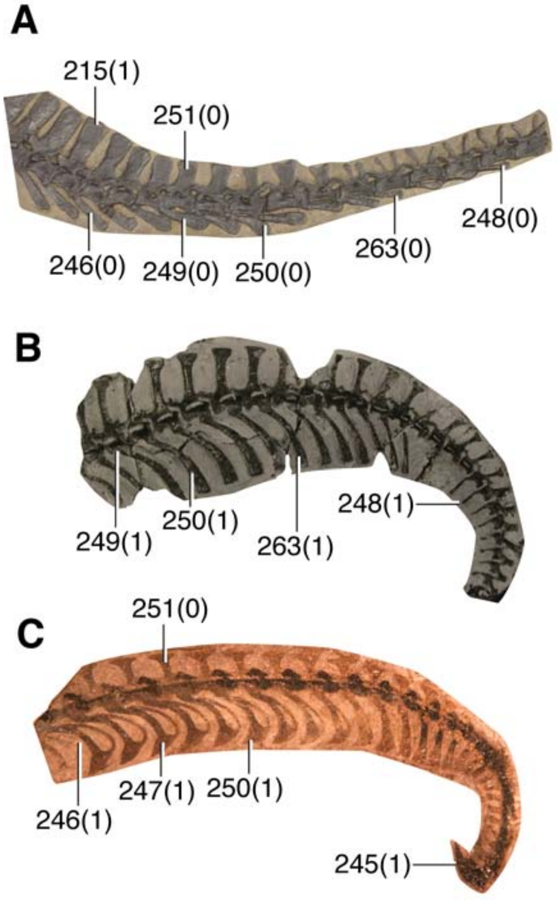

A
215(1)
251(0)
246(0)
249(0)
250(0)
263(0)
248(0)
B
249(1)
250(1)
263(1)
248(1)
C
251(0)
246(1)
247(1)
250(1)
245(1)

FIG. 6-16. Scapulacoracoids from a series of early diapsid reptiles in lateral view. A, left of *Mesosuchus browni* (SAM K5882). B, right of *Tanystropheus longobardicus* (PIMUZ T/1277). C, right of *Trilophosaurus buettneri* (TMM 31025-140). D, cartoon illustration of unnamed drepanosaurid (based on GR 1113).

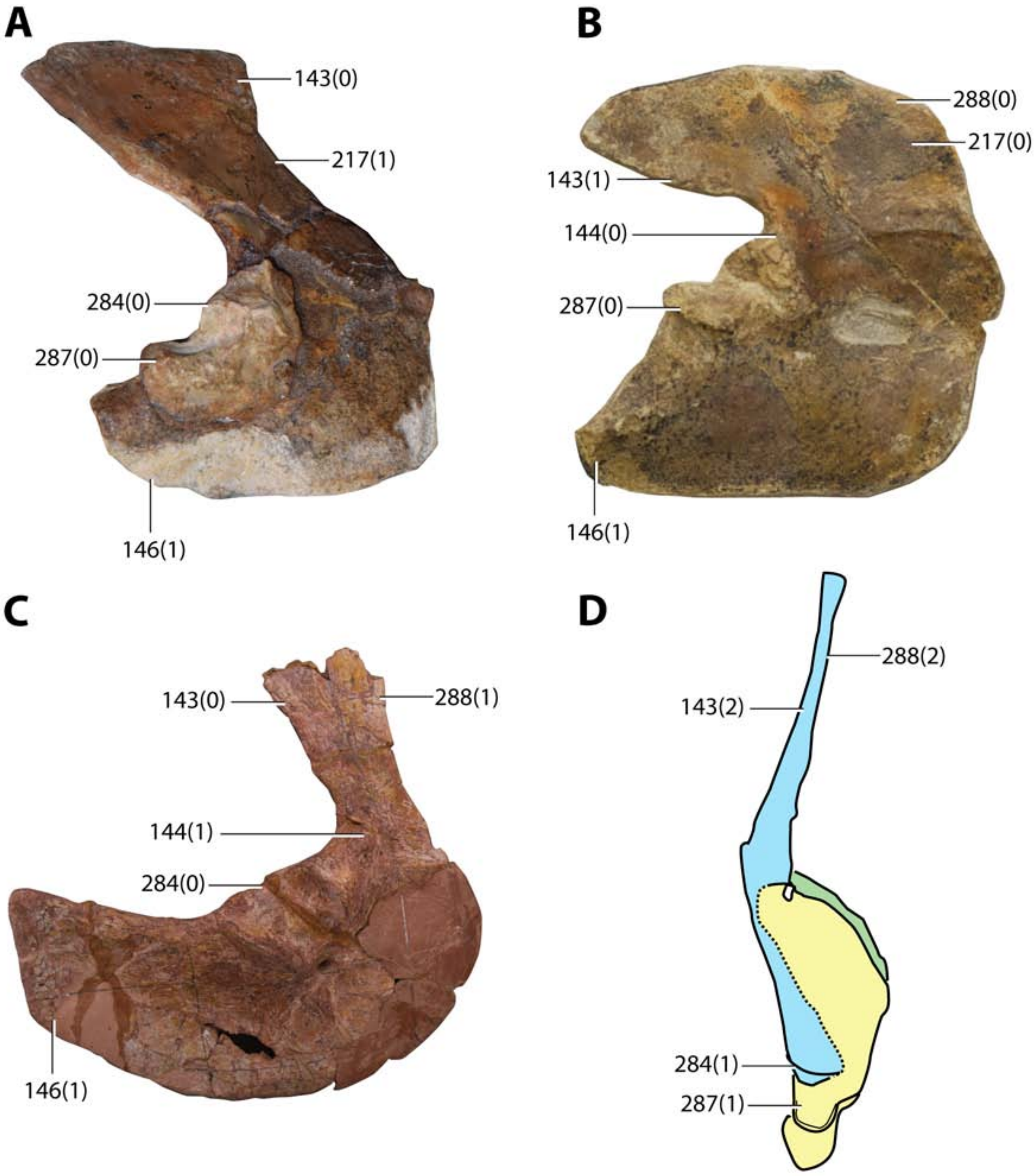

A
143(0)
217(1)
284(0)
287(0)
146(1)
B
288(0)
217(0)
143(1)
144(0)
287(0)
146(1)
C
143(0)
288(1)
144(1)
284(0)
146(1)
D
288(2)
143(2)
284(1)
287(1)

FIG. 6-17. Humeri from a series of early diapsid reptiles. A) *Thadeosaurus colcanapi* (MNHN MAP 360) in posterior view, B) *Kuehneosaurus latus* [AMNH FARB 7784 (proximal) and 7786 (distal)] in anterior view, C) 3D reconstruction of *Drepanosaurus unguicaudatus* (H3-037-080527) in anterior view, D) *Trilophosaurus buettneri* in anterior view (TMM 31025-66A), E) *Protorosaurus speneri* in anterior view (SMNS cast of WMsN 47361), and *Tanystropheus longobardicus* in posterior view (PIMUZ T/1277). B and C have been mirrored.

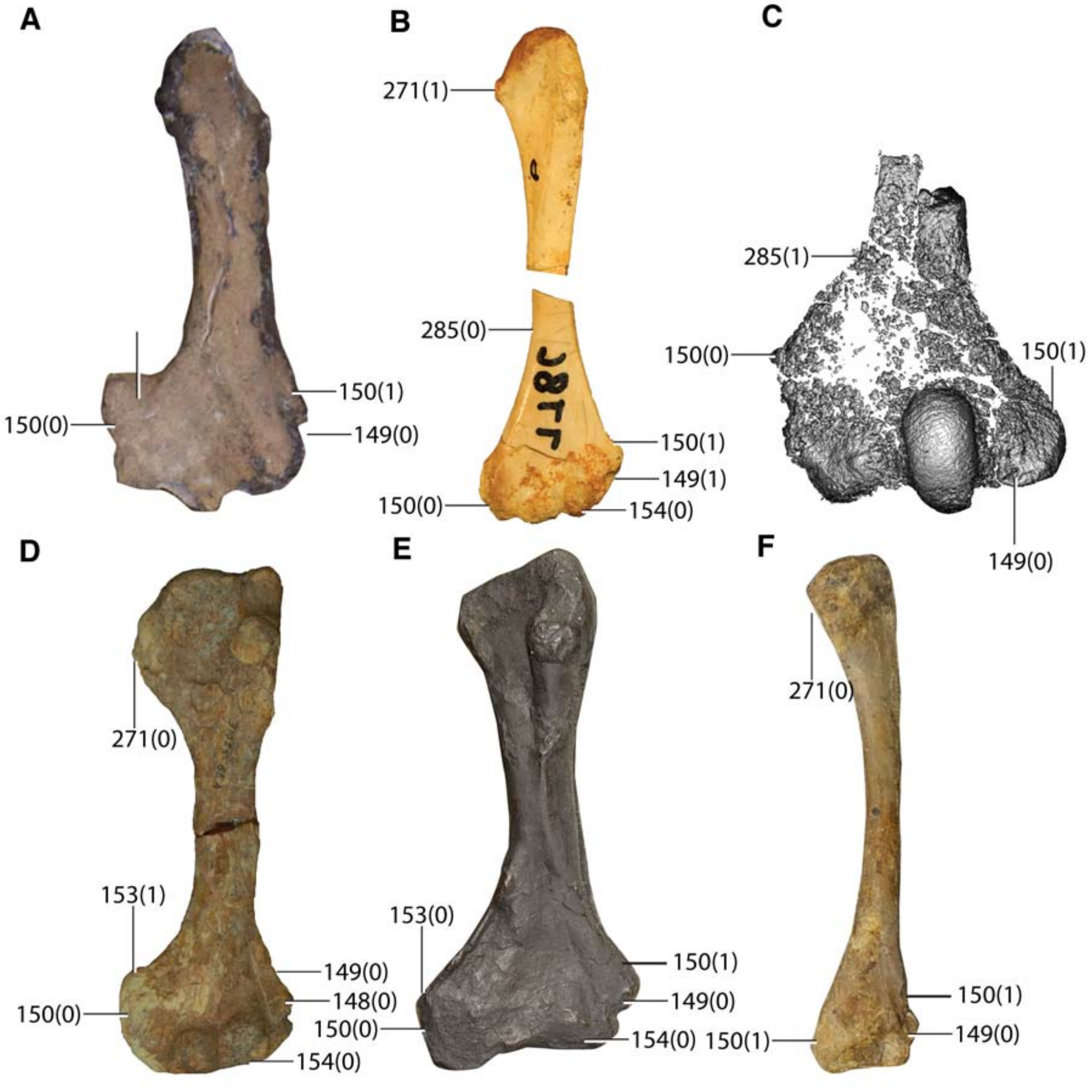

A
150(1)
150(0)
149(0)
B
271(1)
285(0)
150(1)
149(1)
150(0)
154(0)
C
285(1)
150(0)
150(1)
149(0)
D
271(0)
153(1)
149(0)
148(0)
150(0)
154(0)
E
153(0)
150(1)
149(0)
150(0)
154(0)
F
271(0)
150(1)
150(1)
149(0)

FIG. 6-18. Right pelves of A, *Drepanosaurus unguicaudatus* (MCSNB 5728) and B, *Prolacerta broomi* (BP/1 2676) in lateral view.

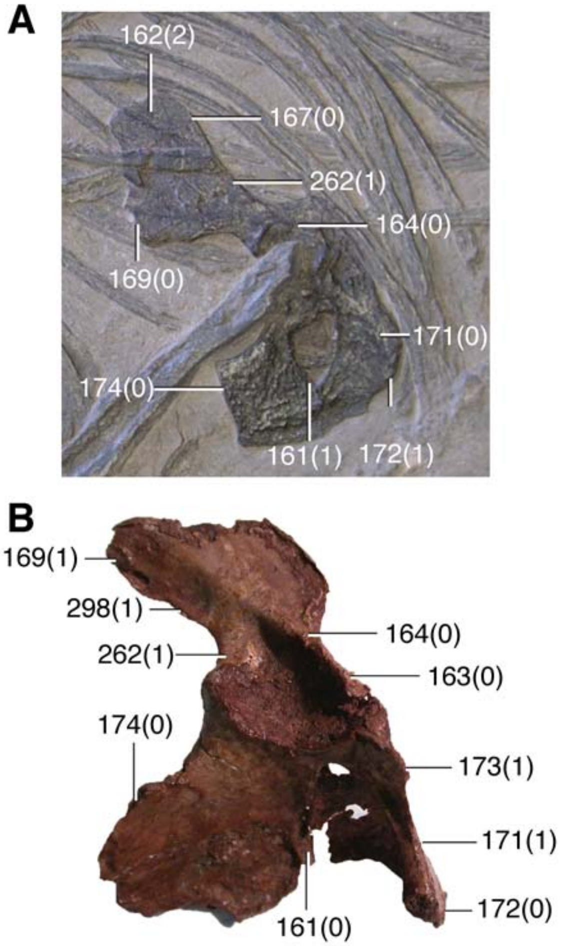

A
162(2)
167(0)
262(1)
164(0)
169(0)
171(0)
174(0)
161(1)
172(1)
B
169(1)
298(1)
262(1)
164(0)
163(0)
174(0)
173(1)
171(1)
172(0)
161(0)

FIG. 6-19. Ilia from a series of early diapsid reptiles in lateral view. A) *Sophineta cracoviensis* (ZPAL RV/1063), B) *Trilophosaurus buettneri* (TMM 31025-73), C) *Mesosuchus browni* (SAM K7046), D) *Macrocnemus bassanii* (PIMUZ T/2477), and E) *Erythrosuchus africanus* (NHMUK R3592). B and C are mirrored.

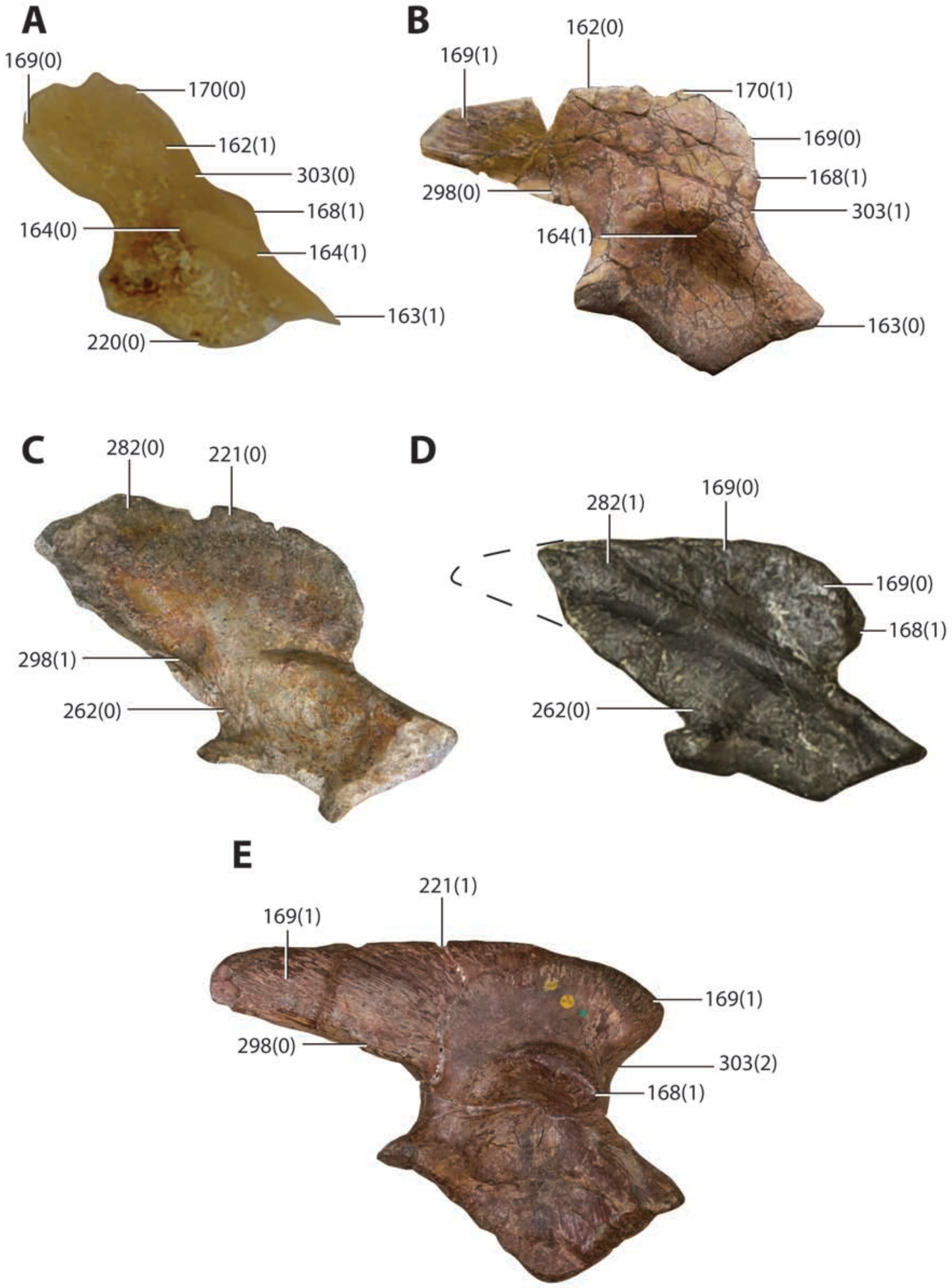

A
169(0)
170(0)
162(1)
303(0)
168(1)
164(0)
164(1)
163(1)
220(0)
B
162(0)
169(1)
170(1)
169(0)
168(1)
298(0)
303(1)
164(1)
163(0)
C
282(0)
221(0)
298(1)
262(0)
D
169(0)
282(1)
169(0)
168(1)
262(0)
E
221(1)
169(1)
169(1)
298(0)
303(2)
168(1)

FIG. 6-20. Left femora of selected early diapsid reptiles. A, *Coelurosauravus elivensis* (MNHN MAP 325) in ventromedial view. B, *Claudiosaurus germaini* (SAM K8266) in medial view. C, *Mesosuchus browni* (SAM K7416) in medial view.

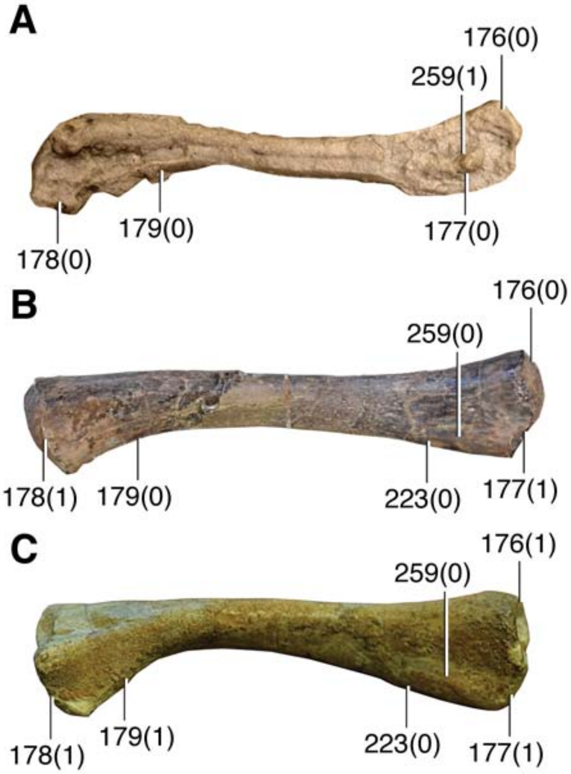

A
176(0)
259(1)
179(0)
178(0)
177(0)
B
176(0)
259(0)
178(1)
179(0)
223(0)
177(1)
C
176(1)
259(0)
178(1)
179(1)
223(0)
177(1)

FIG. 6-21. Tarsus and metatarsus from a series of early diapsid reptiles in dorsal view. A, Right of *Claudiosaurus germaini* (MNHN MAP 1a). B, left of *Drepanosaurus unguicaudatus* (MCSNB 5728). C, left of *Protorosaurus speneri* (SMNS 55387). D, right of *Tanystropheus longobardicus* (MCSN BES SC 1018). Note that B and C have been mirrored from the original photographs.

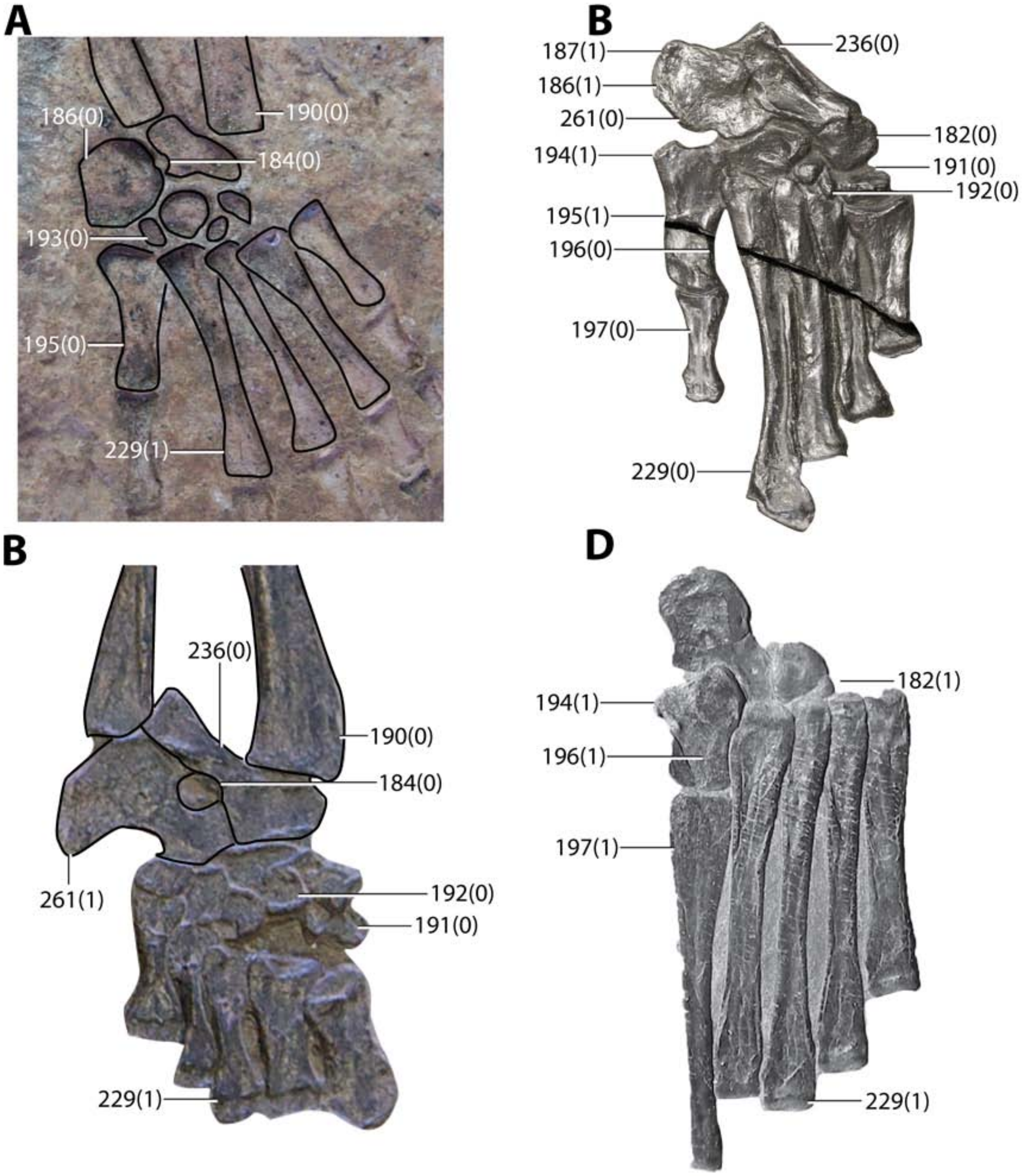

A
186(0)
190(0)
184(0)
193(0)
195(0)
229(1)
B
187(1)
186(1)
261(0)
194(1)
195(1)
196(0)
197(0)
229(0)
236(0)
182(0)
191(0)
192(0)
B
236(0)
190(0)
184(0)
261(1)
192(0)
191(0)
229(1)
D
194(1)
196(1)
197(1)
182(1)
229(1)

FIG. 6-22. Strict consensus phylogeny resulting from the current analysis.

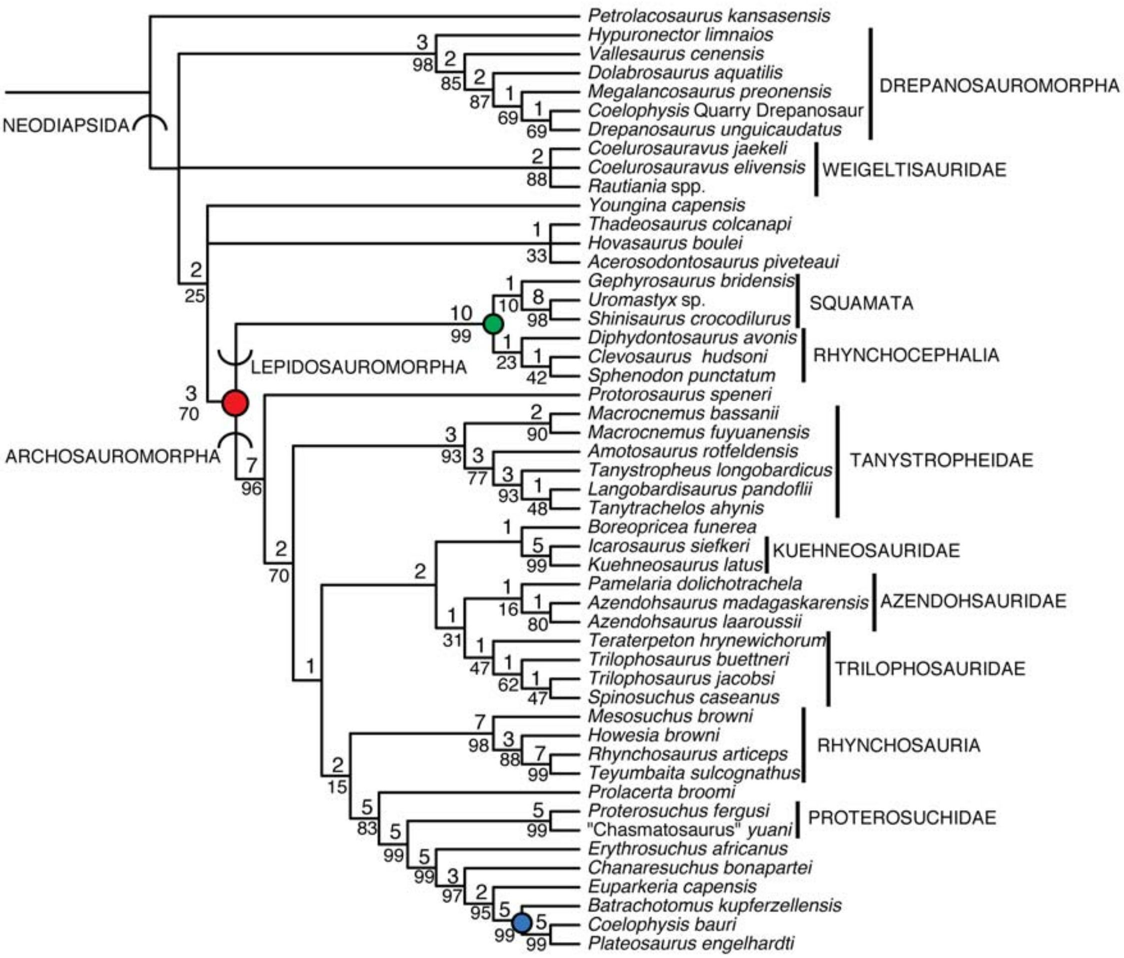

Petrolacosaurus kansasensis
Hypuronector limnaios
Vallesaurus cenensis
Dolabrosaurus aquatilis
Megalancosaurus preonensis
Coelophysis Quarry Drepanosaur
Drepanosaurus unguicaudatus
DREPANOSAUROMORPHA
Coelurosauravus jaekeli
Coelurosauravus elivensis
Rautiania spp.
WEIGELTISAURIDAE
NEODIAPSIDA
Youngina capensis
Thadeosaurus colcanapi
Hovasaurus boulei
Acerosodontosaurus piveteaui
Gephyrosaurus bridensis
Uromastyx sp.
Shinisaurus crocodilurus
SQUAMATA
Diphydontosaurus avonis
Clevosaurus hudsoni
Sphenodon punctatum
RHYNCHOCEPHALIA
LEPIDOSAUROMORPHA
ARCHOSAUROMORPHA
Protorosaurus speneri
Macrocnemus bassanii
Macrocnemus fuyuanensis
Amotosaurus rotfeldensis
Tanystropheus longobardicus
Langobardisaurus pandoflii
Tanytrachelos ahynis
TANYSTROPHEIDAE
Boreopricea funerea
Icarosaurus siefkeri
Kuehneosaurus latus
KUEHNEOSAURIDAE
Pamelaria dolichotrachela
Azendohsaurus madagaskarensis
Azendohsaurus laaroussii
AZENDOHSAURIDAE
Teraterpeton hrynewichorum
Trilophosaurus buettneri
Trilophosaurus jacobsi
Spinosuchus caseanus
TRILOPHOSAURIDAE
Mesosuchus browni
Howesia browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
RHYNCHOSAURIA
Prolacerta broomi
Proterosuchus fergusi
"Chasmatosaurus" yuani
PROTEROSUCHIDAE
Erythrosuchus africanus
Chanaresuchus bonapartei
Euparkeria capensis
Batrachotomus kupferzellensis
Coelophysis bauri
Plateosaurus engelhardti

FIG. 6-23. Stratigraphically calibrated strict consensus topology resulting from the current analysis. Dots indicate stratigraphic occurrences of included taxa, whereas brackets indicate occurrences of uncertain duration.

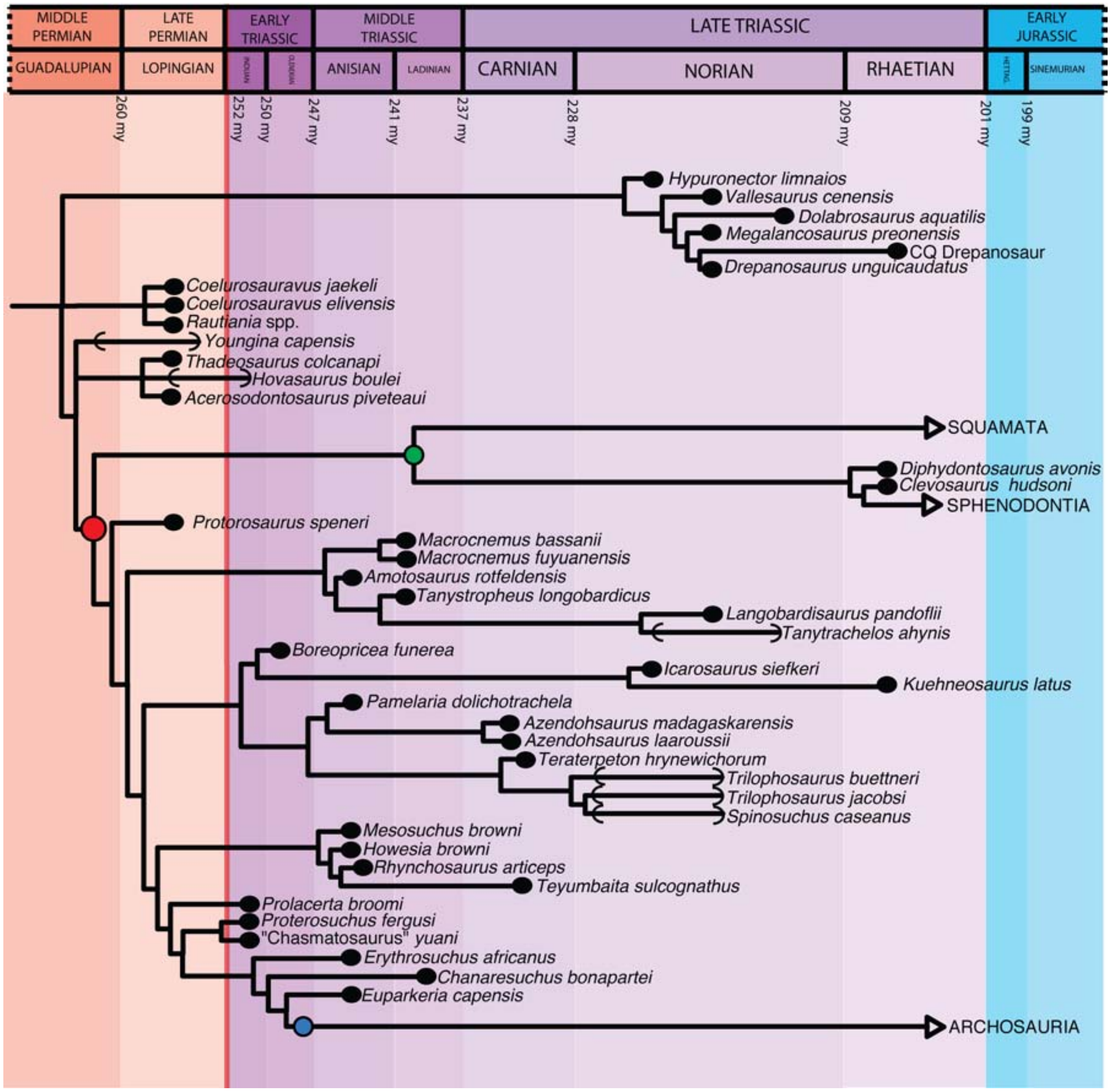
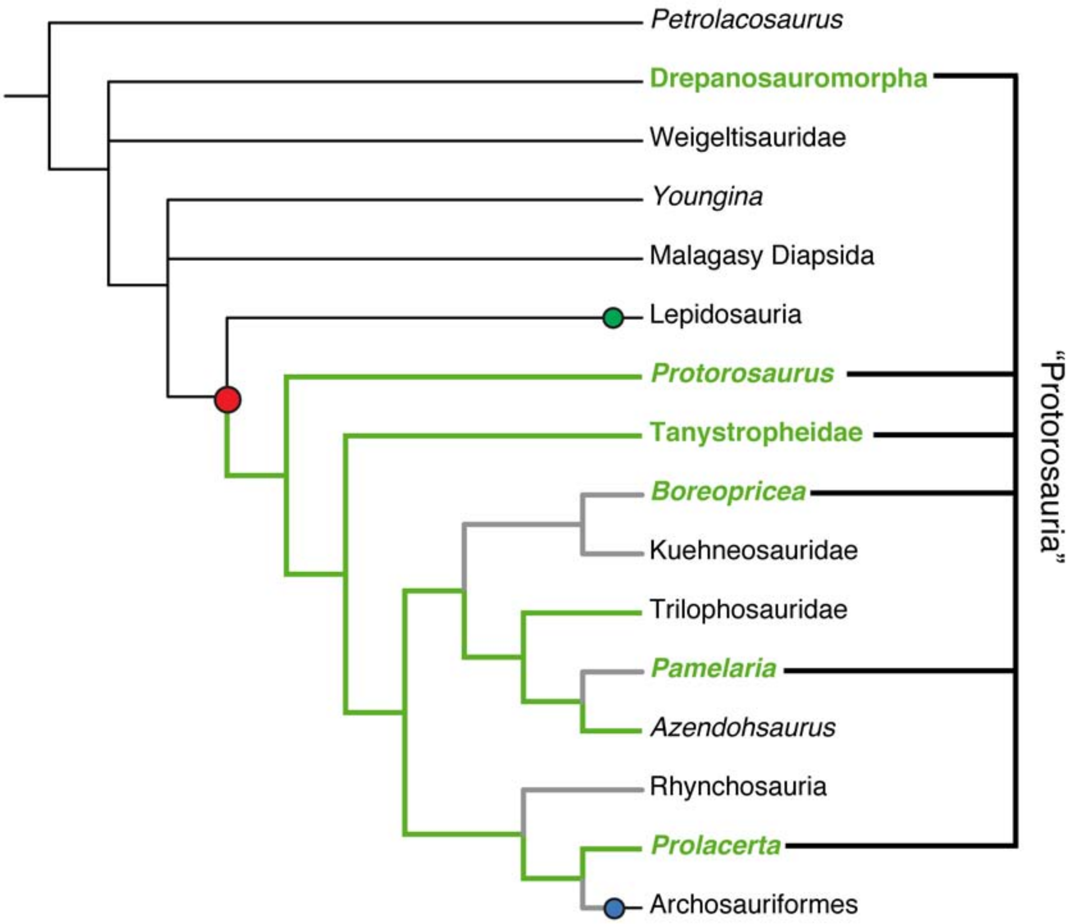

MIDDLE PERMIAN
LATE PERMIAN
EARLY TRIASSIC
MIDDLE TRIASSIC
LATE TRIASSIC
EARLY JURASSIC
GUADALUPIAN
LOPINGIAN
INDUAN
OLENEKIAN
ANISIAN
LADINIAN
CARNIAN
NORIAN
RHAETIAN
HETTANG.
SINEMURIAN
260 my
252 my
250 my
247 my
241 my
237 my
228 my
209 my
201 my
199 my
Hypuronector limnaios
Vallesaurus cenensis
Dolabrosaurus aquatilis
Megalancosaurus preonensis
CQ Drepanosaur
Drepanosaurus unguicaudatus
Coelurosauravus jaekeli
Coelurosauravus elivensis
Rautiania spp.
Youngina capensis
Thadeosaurus colcanapi
Hovasaurus boulei
Acerosodontosaurus piveteaui
SQUAMATA
Diphydontosaurus avonis
Clevosaurus hudsoni
SPHENODONTIA
Protorosaurus speneri
Macrocnemus bassanii
Macrocnemus fuyuanensis
Amotosaurus rotfeldensis
Tanystropheus longobardicus
Langobardisaurus pandoflii
Tanytrachelos ahynis
Boreopricea funerea
Icarosaurus siefkeri
Kuehneosaurus latus
Pamelaria dolichotrachela
Azendohsaurus madagaskarensis
Azendohsaurus laaroussii
Teraterpeton hrynewichorum
Trilophosaurus buettneri
Trilophosaurus jacobsi
Spinosuchus caseanus
Mesosuchus browni
Howesia browni
Rhynchosaurus articeps
Teyumbaita sulcognathus
Prolacerta broomi
Proterosuchus fergusi
"Chasmatosaurus" yuani
Erythrosuchus africanus
Chanaresuchus bonapartei
Euparkeria capensis
ARCHOSAURIA

FIG. 6-24. Simplified strict consensus phylogeny resulting from the current analysis. The outer brackets indicate taxa that have been considered a part of Protorosauria or Prolacertiformes. The green branches indicate taxa optimized as exhibiting the combination of elongate cervical vertebrate and cervical ribs considered to be characteristic of the taxon.


Petrolacosaurus
Drepanosauromorpha
Weigeltisauridae
Youngina
Malagasy Diapsida
Lepidosauria
Protorosaurus
Tanystropheidae
Boreopricea
Kuehneosauridae
Trilophosauridae
Pamelaria
Azendohsaurus
Rhynchosauria
Prolacerta
Archosauriformes
"Protorosauria"

Chapter 7

Conclusion and Prospectus

SUMMARY

In the course of this dissertation I employed a phylogenetic framework to address the diversification of Permian and Triassic Diapsida in multiple ways:

Chapter 2—I identify a series of isolated vertebrae and appendicular bones from the Upper Triassic Hayden Quarry (~212 my) from the Chinle Formation (Petrified Forest Member) of New Mexico as the first definitive record of Tanystropheidae from western North America. I base the identification on a series of apomorphies, informed by an iteration of my phylogeny. The vertebrae are procoelous, with a distinctive dorsal expansion of the neural spines marked by complex, striated bone, which is interpreted as bracing mechanism to keep the column from falling into flexion. The femora and calcaneum are comparable to those in other plesiomorphic archosauromorphs. A number of synapomorphies link the materials to *Tanytrachelos ahynis*, a smaller taxon from the Late Triassic of eastern North America. The apomorphy-based criterion for identifying the Hayden materials allowed me to note the presence of the group in a number of western localities, suggesting that they were far more abundant than previously recognized.

Chapter 3—I describe a series of forelimb elements from the Upper Triassic Hayden Quarry of New Mexico and refer them to *Drepanosaurus unguicaudatus*, a bizarre reptile otherwise known from the Late Triassic of Italy. The high-quality, three-dimensionally preserved bones allow me to make homology statements for the bizarre limb elements. The ulna is flattened and crescent shape. Its long axis is roughly perpendicular to that of the radius. The proximal, post-axial carpal elements are proximodistally longer than the radius. The second manual digit is massive, terminating in an ungual that is larger than any other forelimb element. The second manual digit also exhibits only a single, non-ungual phalanx. The taxa resolved as the closest relatives of *D. unguicaudatus* among drepanosaurids exhibit slightly elongated carpals and a reduction in the

manual phalangeal count. These seem to be transitional stages in the evolution from the primitive diapsid forelimb condition to the derived states seen in *Drepanosaurus*.

Chapters 4 & 5—These chapters focus on the first three-dimensionally preserved cranial material described from a drepanosaurid, discovered in a matrix block from the Upper Triassic *Coelophysis* Quarry of New Mexico. Through high-resolution μCT scans and three-dimensional reconstruction of all preserved skull elements, I develop the first detailed osteological description for the taxon. For the fourth chapter, I briefly described the osteology and presented the results of a phylogenetic study incorporating the taxon. The taxon exhibits primitive anatomical traits for a diapsid such as a verticalized quadrate, a posterior lamina of the squamosal, and a massive stapes. The taxon also exhibits several autapomorphies including complete edentulousness, a transversely broad anterior portion of the braincase, and dorsally inflated frontal and parietal contributions to the braincase. In the phylogenetic study, drepanosauromorphs are positioned outside of Sauria, diverging from other diapsids deep in the Permian Period. I tested past phylogenetic positions for drepanosauromorphs, positioning them closer to archosauromorph taxa, finding these to be substantially less parsimonious. In the fifth chapter, I describe the individual skull elements of the new drepanosaurid in detail, comparing the animal to other Permo-Triassic reptiles.

Chapter 6—In this chapter, I address past phylogenetic hypotheses of Permo-Triassic diapsid reptiles from pre-cladistic and modern cladistic perspectives. Although some consensus has emerged regarding which Permo-Triassic taxa are a part of the early saurian radiation, there is no consistent hypothesis for the interrelationships of these taxa. I present a novel phylogenetic hypothesis incorporating a larger taxonomic sample (51) of near-saurian and early saurian taxa than previously studied with a novel dataset of 303 morphological characters. The resultant topology differs substantially from most past studies. Kuehneosauridae, long regarded as the sister taxon of Lepidosauria, are recovered deeply nested within Archosauromorpha. The long-necked archosauromorphs that are traditionally considered part of a monophyletic clade (dubbed either Prolacertiformes or Protorosauria) are recovered as a polyphyletic grouping. Character distributions suggest that most early archosauromorphs were long-necked taxa with lizard-like postcranial skeletons. The branching pattern within early archosauromorphs is well resolved but very poorly supported. Although Bremer support values at some nodes are moderate, the results of a jackknife analysis suggest substantial character conflict. Examining the topology from a stratigraphic perspective suggests that a substantial amount of taxonomic diversification among near-saurian and early saurian reptiles had occurred prior to the Permo-Triassic Extinction (PTE).

PROSPECTUS

Expanded Material Sampling—It is the common clarion call of systematists to increase taxon sampling to improve the accuracy of phylogenetic analyses. While I definitely intend to increase the sample of Permo-Triassic reptiles incorporated into this study, I argue that improving the types of fossil material sampled for certain taxa will be important to increasing the amount of useful phylogenetic data. As discussed in chapter four, past systematic studies produced extremely inconsistent hypotheses for the position of drepanosauromorphs among Permo-Triassic diapsids. This owed in some part to the types of fossils incorporated into those studies; past described drepanosauromorph fossils included articulated, but badly crushed and distorted skeletons. The incorporation of these fossil materials and the three-dimensional skull material from the *Coelophysis* Quarry resulted in a highly stable position for drepanosauromorphs outside of Sauria. However, several other fossil taxa in this analysis are represented by badly distorted materials (e.g., most Tanystropheidae, *Protorosaurus speneri*, many younginiform diapsids.) CT scanning represents a critical step in understanding the anatomy of these taxa, most of which are represented by extremely small skeletons that cannot be mechanically prepared. Three-dimensional reconstruction of such specimens can provide detail on the osteology of fossil diapsids to rival that available for modern lepidosaurs (e.g., Gauthier et al., 2012). There are substantial numbers of well-preserved fossils of small-bodied diapsids from Permian and Triassic deposits that are difficult or impossible to prepare mechanically (e.g., Benton and Allen, 1997; Jalil, 1997) that could be subject to such study.

Improved Character Sampling—Although the character presented in this analysis sample all areas of the skeleton in Permo-Triassic Diapsida, they encompass only a small part of the variation evident in the skeletons I have studied. Some specimens preserve exceptionally detailed muscle scars that could be used to develop complete muscle maps for a range of early saurian and near-saurian taxa. Studies in other diapsid groups (e.g., Hutchinson, 2001a, 2001b; Schachner et al., 2011), suggest that some muscle groups undergo substantial transitions within extinct taxa and that useful phylogenetic data could be obtained through such study. Employing the muscle reconstruction algorithms of Burch (2014), combined with novel context from modern reptile groups could provide new and biologically informed character data for ancient reptile groups. This morphological sampling would also be well informed by modern reptile biology.

LITERATURE CITED

Benton MJ, Allen JL. (1997) *Boreopricea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles.

Burch SH. (2014) Complete forelimb myology of the basal theropod dinosaur *Tawa hallae* based on a novel robust muscle reconstruction method. J Anat 225:271–297.

Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB. (2012) Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bull Peabody Mus Nat Hist 53:3–308.

Hutchinson JR. (2001a) The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). Zool J Linn Soc 131:123–168.

Hutchinson JR. (2001b) The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). Zool J Linn Soc 131:169–197.

Jalil N-E. (1997) A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. J Vert Paleo 17:506–525.

Schachner ER, Manning PL, Dodson P. (2011) Pelvic and hindlimb myology of the basal archosaur *Poposaurus gracilis* (Archosauria: Poposauroidea). J Morph 272:1464–149.

COMPLETE BIBLIOGRAPHY

Ahl E. (1930) Beitrage zur Lurch und Kriechtierfauna Kwangsi: section 5, Eideschen. Sitz Ges Nat Fr Berl 1930:326–331.

Alifanov VR, Kurochkin EN. (2011). *Kyrgyzsaurus bukhanchenkoi*, gen. et sp. nov., a new reptile from the Triassic of southwestern Kyrgyzstan. Paleontological Journal 45:639–647.

Alonso PD, Milner AC, Ketcham RA, Cookson MJ, Rowe TB. 2004. The avian nature of the brain and inner ear of *Archaeopteryx*. Nature 430:666–669.

Atanassov MN. (2001). Two new archosauromorphs from the Late Triassic of Texas. J Vert Paleo 21(3 Supplement):30A.

Azevedo SA and Schultz CL. (1987) *Scaphonyx sulcognathus* (sp. nov.), um novo rincossaurideo do neotriássico do Rio Grande do Sul, Brasil. X Congreso Brasileiro de Paleontologia. (Sociedade Brasileira de Paleontologia), pp. 99–113.

Baird IL. (1970) The anatomy of the reptilian ear. Biology of the Reptilia, Volume 2 Morphology B. C Gans and T Parsons (eds). (Academic Press, London and New York), pp. 193–272.

Balanoff AM, Norell MA. (2012) Osteology of *Khaan mckennai* (Oviraptorosauria: Theropoda). Bull Am Mus Nat Hist 372:1–77.

Balanoff AM, Xing X, Kobayashi Y, Matsufune Y, Norell MA. (2009) Cranial osteology of the theropod dinosaur *Incisivosaurus gauthieri* (Theropoda: Oviraptorosauria). American Mus Nov 3651:1–35.

Balanoff AM, Bever GS, Rowe TB, Norell MA. (2013) Evolutionary origins of the avian brain. Nature 501:93–96.

Bartholomai A. (1979) New lizard-like reptiles from the Early Triassic of Queensland. Alcheringa 3:225–234

Bassani F. (1886) Sui fossili e sull'età degli schist bituminosi triasici di Besano in Lombara. Atti Soc Italian di Sci Nat Milano 29:15–72.

Baumel JJ. (1993) Handbook of avian anatomy: Nomina Anatomica Avium, 2nd Edition. Pub of the Nuttall Ornitho Club 23:1–779

Baur G. (1887) On the phylogenetic arrangement of the Sauropsida. J Morphology 1:93-104.

Bell CJ, Gauthier JA, Bever GS. (2010) Covert biases, circularity, and apomorphies: a critical look at the American Quaternary herpetofaunal stability hypothesis. Quat Int 217:30–36.

Bell CJ, Head JJ, Mead JI. (2004) Synopsis of the herpetofauna from Porcupine Cave. *Biodiversity Response to Climate Change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado*, ed. AD Barnosky (University of California Press, Berkeley, California) pp. 117–126

Benton MJ. (1983) The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. Phil Trans Roy Soc B 302:605–717.

Benton MJ. (1984) Tooth form, growth, and function in Triassic rhynchosaurs (Reptilia, Diapsida) Palaeo 27:66–68.

Benton MJ. (1985) Classification and phylogeny of the diapsid reptiles. Zool J Linn Soc 84:97–164.

Benton MJ. (1990) The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. Phil Trans Roy Soc B 328:213–306.

Benton MJ, Allen JL. (1997) *Boreopricea* from the Lower Triassic of Russia, and the relationships of the prolacertiform reptiles.

Benton MJ, Clark JM. (1988) Archosaur phylogeny and the relationships of the Crocodylia. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 295–338.

Benton MJ, Walker AD. (1996) *Rhombopholis*, a prolacertiform reptile from the Middle Triassic of England. Palaeo 39:763–789.

Benton MJ, Zhang Q, Hu S, Chen Z-Q, Wen W, Liu J, Huang J, Zhou C, Xie T, Tong J, Choo B. (2013) Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. Earth-Sci Rev 125:199–243.

Berman DS, Reisz RR. (1992) *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile from the Upper Triassic Chinle Formation of north-central New Mexico. J Paleo 66:1001–1009.

Berman DS, Henrici AC, Sumida SC, Martens T. (2000) Redescription of *Seymouria sanjuanensis* (Seymouriamorpha) from the Lower Permian of Germany based on complete, mature specimens with a discussion of paleoecology of the Bromacker locality assemblage. J Vert Paleo 20:253–268.

Berra F, Jadoul F, Anelli A. (2010) Environmental control on the end of the Dolomia Principale/Hauptdolomit depositional system in the central Alps: coupling sea-level and climate changes. Palaeogeo, Palaeoclimat, Palaeoeco 290:138–150.

Bever GS, Bell CJ, Maisano JA. (2005) The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). Palaeontologia Electronica 8, 4A:1–36.

Bhullar B-A, Bever GS. (2009) An archosaur-like laterosphenoid in early turtles (Reptilia: Pantestudines). Breviora 518:1–11.

Bhullar B-A, Bever GS, Merck J, Lyson T, Gauthier JA. (2011) Uniting microevolution and macroevolution in deep time: the zone of variability in Archosauromorpha

Bickelmann C, Müller J, Reisz RR. (2009) The enigmatic diapsid *Acerosodontosaurus piveteaui* (Reptilia: Neodiapsida) from the Upper Permian of Madagascar and the paraphyly of "younginiform" reptiles. Can J Earth Sci 46:651–661.

Bock W. (1945) A new small reptile from the Triassic of Pennsylvania. Notulae Naturae Acad Nat Sci Philadelphia 154:1–8.

Bonaparte JF. (1976) *Pisanosaurus mertii* Casamiquela and the origin of the Ornithischai. Palaeo 50: 808–820.

Bonaparte JF, Sues H-D. (2006) A new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the Upper Triassic of Rio Grande do Sul, Brazil. Palaeo 49:917–923.

Borsuk-Bialynicka M, Evans SE. (2009a) A long-necked archosauromorph from the Early Triassic of Poland. Paleo Pol 65:203–234.

Borsuk-Bialynicka M, Evans SE. (2009b) Cranial and mandibular osteology of the Early Triassic archosauriform *Osmolskina czatkowicensis* from Poland. Paleontologia Polonica 65:235–281.

Borsuk-Bialynicka M, Sennikov AG. Archosauriform postcranial remains from the Early Triassic kart deposits of southern Poland. Paleo Pol 65:283–328.

Brink AS. (1955) Notes on some thecodonts. Res National Mus 1:141–148.

Brink D. (1981) The origin of the crocodiloid tarsus and the interrelationships of thecodontian archosaurs. Breviora 464:1–23.

Brink KS, Reisz RR. (2013) Hidden dental diversity in the oldest terrestrial apex predator *Dimetrodon*. Nat Comm 5, 3269:1–5.

Brinkman D. (1980) Structural correlates of tarsal and metatarsal functioning in *Iguana* (Lacertilia; Iguanidae) and other lizards. Can J Zool 58:277–289.

Broili F, Schröder J. (1934) Beobachtungen an wirbeltieren der Karrooformation V. Über *Chasmatosaurus* van hoepeni Haughton. Sitz Bayer Akad Wiss München 1934:225–264.

Broom R. (1903) On a new reptile (*Proterosuchus fergusi*) from the Karroo beds of Tarkastad, South Africa. Annals South African Mus 4:159–164.

Broom R. (1905) Notice of some new fossil reptiles from the Karroo beds of South Africa. Rec Albany Mus 1:331–337.

Broom R. (1906) On the South African diaptosaurian reptile *Howesia*. Proc Zool Soc London 1906:591–600.

Broom R. (1913) Note on *Mesosuchus browni*, Watson and on a new South African Triassic pseudosuchian (*Euparkeria capensis*). Rec Albany Mus 2:394–396.

Broom R. (1914) A new thecodont reptile. Proc Zool Soc London 84:1072–1077.

Broom R. (1924) On the origin of lizards. Proc Zool Soc London 1925:1–16.

Broom R. (1932) On some South African pseudosuchians. Annals Natal Mus 7:55–59.

Broom R, Robinson PGL. (1948) Some new reptiles from the Karroo Beds of South Africa. Proc Zool Soc London B 118:392–407.

Brusatte SL, Benton MJ, Desojo JB, Langer MC. (2010) The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). J Sys Palaeo 8:3–47.

Buck-Gramcko D. (2004) Congenital disorders: radial and ulnar club hand. *Hand Surgery*, eds RA Berger, APC Weiss (Lippincott Williams & Williams), pp. 1453–1464.

Bulanov VV, Sennikov AG. (2006) The first gliding reptiles form the Upper Permian of Russia. Paleontological Journal 40:S567–S570.

Bulanov VV, Sennikov AG. (2010) New data on the morphology of Permian gliding weigeltisaurid reptiles of eastern Europe. Paleontological Journal 44:682–694.

Burch SH. (2014) Complete forelimb myology of the basal theropod dinosaur *Tawa hallae* based on a novel robust muscle reconstruction method. J Anat 225:271–297.

Burch SH, Carrano MT. (2012) An articulated pectoral girdle and forelimb of the abelisaurid theropod *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 32:1–16.

Caldwell MW. (1994) Developmental constraints and limb evolution in Permian and extant lepidosauromorph diapsids. J Vert Paleo 14:459–471.

Calzavara M, Muscio G, Wild R. (1980) *Megalancosaurus preonensis* n. g., n. sp., a new reptile from the Norian of Friuli, Italy. Gortiana 2:49–64.

Camp CL. (1945a) *Prolacerta* and the protorosaurian reptiles, part I. Am J Sci 243:17–32.

Camp CL. (1945b) *Prolacerta* and the protorosaurian reptiles, part II. Am J Sci 243:84–101.

Carroll RL. (1969) Origin of reptiles. Biology of the Reptilia, Vol. 1 Morphology A, ed. C Gans (Academic Press, London and New York), pp. 1–44.

Carroll RL. (1975) Permo-Triassic "lizards" from the Karroo. Palaeo Afr 18:71–87.

Carroll RL. (1976) *Noteosuchus*—the oldest known rhynchosaur. Annals S Afr Mus 72:37–57.

Carroll RL. (1978) Permo-Triassic 'lizards' from the Karoo system. Part 2. A gliding reptile from the Upper Permian of Madagascar. Paleo Africana21:143–159.

Carroll RL. (1981) Plesiosaur ancestors from the Upper Permian of Madagascar. Phil Trans Roy Soc London B 293:315–383.

Carroll RL. (1985) A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Palaeontographica Abt A 189:1–28.

Carroll RL (1988). *Vertebrate Paleontology and Evolution*. WH Freeman.

Case EC. (1927) The vertebral column of *Coelophysis* Cope. Cont Mus Geol, U of MI 2:209–222.

Case EC. (1928a) Indications of a cotylosaur and of a new form of fish from the Triassic beds of Texas, with remarks on the Shinarump Conglomerate. Cont Mus Geol, U of MI 3:1–14.

Case EC. (1928b) An endocranial cast of a phytosaur from the upper Triassic beds of west Texas. J Comp Neuro 45:161–168.

Case EC. (1932) On the caudal region of *Coelophysis* sp. and on some new or little known forms from the Upper Triassic of western Texas. Cont Mus Paleo, U MI 4:81–91.

Casey MM. (2005) Multivariate morphometrics and allometry of the Triassic reptile *Tanytrachelos ahynis*. Abstracts of the Annual Meeting of the Geological Society of America, Salt Lake City.

Casey MM, Fraser NC, Kowalewski M. (2007) Quantitative taphonomy of a Triassic reptile *Tanytrachelos ahynis* from the Cow Branch Formation, Dan River Basin, Solite Quarry, Virginia. Palaios 22:598–611.

Charig AJ, Reig OA. (1970) The classification of the Proterosuchia. Bio J Linn Soc 2:125–171.

Charig AJ, Sues H-D. (1976) Suborder Proterosuchia Broom 1906b. Handbuch der Paläoherpetologie 13. Kuhn O (ed). (Verlag Fischer, Sttutgart), pp. 11–40.

Chatterjee S. (1974) A rhynchosaur from the Upper Triassic Maleri Formation of India. Phil Trans Roy Soc B 267:209–261.

Chatterjee S. (1982) Phylogeny and classification of thecodontian reptiles. Nature 295:317–320.

Chatterjee S. (1993) *Shuvosaurus*, a new theropod. National Geographic Research & Exploration 9:274–285.

Chiari Y, Cahais V, Galtier N, Delsuc F. (2012) Phylogenomic analyses support the position of turtles as the sister group of birds and crocodiles (Archosauria). BMC Biology 10:65 doi:10.1186/1741-7007-10-65.

Chure DJ, Britt B, Engelmann G, Andrus A, Scheetz R. (2013) Drepanosaurs in the desert: multiple skeletons of a new drepanosaurid from the Eolian Nugget Sandstone (?Late Triassic–Early Jurassic), Saints and Sinners Quarry, Utah: morphology, relationships, and biostratigraphic implications. Abstracts of the 2013 Annual Meeting of the Society of Vertebrate Paleontology, Los Angeles. J Vert Paleo 43:106A.

Clark J, Carroll RL. (1973) Romeriid reptiles from the Lower Permian. Bull Mus Comp Zool 144:353–407.

Clark JM, Welman J, Gauthier JA, Parrish JM. (1993) The laterosphenoid bone of early archosauriforms. J Vert Paleo 13:48–57.

Coates MI. (1996) The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, tetrapod interrelationships, and patterns of skeletal evolution. Trans Roy Soc Edinburgh 87:363–421.

Cocude-Michel M. (1968). Les rhynchocéphales et les saurians des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. Ph.D. Thesis, Université de Nancy.

Coddington J, Scharff N. (1994) Problems with zero-length branches. Cladistics 10:415–423.

Colbert EH. (1966) A gliding reptile from the Triassic of New Jersedy. Am Mus Nov 2246:1–23.

Colbert EH. (1970) The Triassic gliding reptile *Icarosaurus*. Bull American Mus Nat History 143:85–142.

Colbert EH. (1987) The Triassic reptile *Prolacerta* in Antarctica. Am Mus Nov 2882:1-19.

Colbert EH. (1989) The Triassic dinosaur *Coelophysis*. Bulletin of the Museum of Northern Arizona 57:1–160.

Colbert EH and Olsen PJ. (2001) A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). Am Mus Novitates 3334:1–24.

Conrad JL. (2004) Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). Zool J Linn Soc 141:399–434.

Conrad JL. (2006) Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). J Morph 267:769–775.

Conrad JL. (2008) Phylogeny and systematics of Squamata (Reptilia) based on morphology Bull Am Mus Nat History 310:1–182.

Cope ED. (1866) Meeting Report from October 23rd. Proc Acad Nat Sci Philadelphia 180:290.

Cope ED. (1869) Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Trans Amer Phil Soc 14:1–252.

Cope ED. (1885) On the evolution of the Vertebrata, progressive and retrogressive (continued). American Naturalist 19:234–247.

Cope ED. (1887) The dinosaurian genus *Coelurus*. Am Naturalist 21:367–369.

Crawford NG, Faircloth BC, McCormack JE, Brumfield RT, Winker K, Glenn TC. (2012). More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs. Biology Letters 8:783–786.

Currie PJ. (1979) The osteology of haptodontine sphenacodonts (Reptilia: Pelycosauria). Palaeontographica Abt A 163:130–168.

Currie PJ. (1980). A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. Can J Earth Sci 17:500–511.

Currie PJ. (1981a) *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeontologia Africana 24:99–168.

Currie PJ. (1981b) The vertebrae of *Youngina* (Reptilia: Eosuchia) Can J Earth Sci 18:815–818.

Currie PJ. (1982) The osteology and relationships of *Tangasaurus mennelli* Haughton. Annals South Afr Mus 86:247–265.

Cruickshank ARI. (1972) The proterosuchian thecodonts. *Studies in Vertebrate Evolution: Essays presented to F. R. Parrington*, eds KA Joysey, TS Kemp. (Winchester Press, New York).

Dalla Vecchia FM. (2006) The tetrapod fossil record from the Norian–Rhaetian of Friuli (northeastern Italy). Bull NM Mus Nat Hist Sci 37:432–444.

Dalla Vecchia FM. (2008) Vertebrati fossili del Friuli. Pub Mus Friulano Storia Naturale 50:1–303.

Davit-Béal T, Tucker AS, Sire J-Y. (2009) Loss of teeth and enamel in tetrapods: fossil record, genetic data and morphological adaptations. J Anat 214:477–501.

deBraga M, Rieppel O. (1997) Reptile phylogeny and the interrelationships of turtles. Zool J Linn Soc 120:281–385.

de Franca MAG, Langer MC, Ferigolo J. (2013) The skull anatomy of *Decuriasuchus quartacolonia* (Pseudosuchia: Suchia: Loricata) from the Middle Triassic of Brazil. Geol Soc London, Spec Pub 379:469–501.

Desojo JB, Báez AM. (2007) Cranial morphology of the Late Triassic South American archosaur *Neoaetosauroides engaeus*: evidence for aetosaurian diversity. Palaeo 50:267–276.

Desojo JB, Heckert AB, Martz JW, Parker WG, Schoch RR, Small BJ, Sulej T. (2013) Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. Geol Soc London, Spec Pub 379:203–239.

Dilkes DW. (1995) The rhynchosaur *Howesia browni* from the Lower Triassic of South Africa. Palaeo 30:665–685.

Dilkes DW. (1998) The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. Phil Trans Roy Soc B 353:501–541.

Dilkes DW (2000) Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Trans Roy Soc Edin Earth Sci 90:87–125.

Dilkes DW, Reisz RR. (1986) The axial skeleton of the Early Permian reptile *Eocaptorhinus laticeps* (Williston). Can J Earth Sci 23:1288–1296.

Dilkes DW, Sues H-D. (2009) Redescription and phylogenetic relationships of *Doswellia kaltenbachi* (Diapsida: Archosauriformes) from the Upper Triassic of Virginia. J Vert Paleo 29:58–79.

Downs A. (2005) The Hayden Quarry, a new Upper Triassic fossil locality at Ghost Ranch, New Mexico. NM Geo Soc Guidebook 56:339–340.

Dubiel RF. (1989) Depositional environments of the Upper Triassic Chinle Formation in the eastern San Juan Basin and vicinity, New Mexico. U.S. Geo Survey Bull 1808-B:1–22.

Dutuit MJ-M. (1982) Découverte d'un orintischien dans le Trias supérieur de l'Atlas occidental marocain. Comptes rendus Acad. Sci. Paris 275:2841–2844.

Dzik J. (2003) A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. J Vert Paleo 23:556–574.

Edmund AG. (1960) Tooth replacement phenomena in the lower vertebrates. Royal Ontario Mus, Life Sci Cont 52:1–190.

Edmund AG. (1969) Dentition. Biology of the Reptilia Volume 1, Morphology A. C Gans, A Bellairs, TS Parsons. (Academic Press, London and New York), pp. 117–200.

El-Toubi MR. (1949) The post-cranial osteology of the lizard, *Uromastyx aegyptia* (Forskal). J Morph 84:281–292.

Estes R, deQueiroz K, Gauthier JA. (1988) Phylogenetic relationships within Squamata. Eds R Estes and G Pregill (Stanford University Press, Palo Alto), pp. 119–281.

Evans SE. (1980) The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zool J Linn Soc 70:203–264.

Evans SE. (1981a) The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. Zool J Linn Soc 73:81–116.

Evans SE. (1981b) Caudal autotomy in a Lower Jurassic eosuchian. Copeia 1981:883–884.

Evans SE. (1982) The gliding reptiles of the Upper Permian. Zool J Linn Soc 76:97–123.

Evans SE. (1985) Tooth replacement in the Lower Jurassic lepidosaur *Gephyrosaurus bridensis*. Neues Jahr für Geol und Paläo Mh 1985:411–420.

Evans SE. (1986) The braincase of *Prolacerta broomi* (Reptilia: Triassic). N Jarh fur Geo Paleo 173:181–200.

Evans SE. (1987a) The phylogeny of Prolacertiformes. *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Drumheller, Alberta, Short Papers*, eds. PJ Currie and E Koppelhus. Tyrrell Museum of Paleontology, Occasional Papers 3:117–126.

Evans SE. (1987b) The braincase of *Youngina capensis* (Reptilia: Diapsida; Permian). Neues Jahr für Geol Paläo Mon 1984:193–203.

Evans SE. (1988) The early history and relationships of the Diapsida. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 221–260.

Evans SE. (1991a) A new lizard-like reptile (Diapsida: Lepidosauromorpha) from the Middle Jurassic of England. Zool J Linn Soc 103:391–412.

Evans SE. (1991b) The postcranial skeleton of the choristodere *Cteniogenys* (Reptilia: Diapsida) from the Middle Jurassic of England. Geobios 24:187–199.

Evans SE. (2008) The skull of lizards and tuatara. *Biology of the Reptilia Volume 20*, ed C Gans (Society for the Study of Amphibians and Reptiles), pp. 1–347.

Evans SE. (2009) An early kuehneosaurids reptile from the Early Triassic of Poland. Palaeontologia Polonica 65:145–178.

Evans SE, Borsuk-Bialynicka M. (2009) Cranial and mandibular osteology of the Early Triassic archosauriform *Osmolskina czatkowicensis* from Poland. Paleo Pol 65:235–281.

Evans SE, Haubold H. (1987) A review of the Upper Permian genera *Coelurosauravus*, *Weigeltisaurus* and *Gracilisaurus* (Reptilia: Diapsida). Zool J Linn Soc 90:275–303.

Evans SE, King MS. (1993) A new specimen of *Protorosaurus* (Reptilia: Diapsida) from the Marl Slate (late Permian) of Britain. Proc Yorkshire Geol Soc 49:229–234.

Evans SE, Jones MEH. (2009) The origin, early history, and diversification of lepidosauromorph reptiles. Lecture Notes in Earth Sci 132:27–44.

Ewer RF. (1965) The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil Trans Roy Soc B 248:379–435.

Ezcurra MD. (2006) A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. Geodiversitas 28:649–684.

Ezcurra MD, Butler RI. (2015) Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early archosauriform radiation. Palaeontology 58:141–170.

Ezcurra MD, Scheyer TM, Butler RJ. (2014) The origin and early evolution of Sauria: the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS One 9:e89165.

Ezcurra MD, Lecuona A, Martinelli A. (2010) A new basal archosauriform diapsid from the Lower Triassic of Argentina. J Vert Paleo 30:1433–1450.

Feduccia A. (1999). *The Origin and Evolution of Birds*. Yale University Press.

Flynn JJ, Nesbitt SJ, Parrish JM, Ranivoharimanana L, Wyss AR. (2010) A new species of *Azendohsaurus* (Diapsida: Archosauromorpha) from the Triassic Isalo Group of southwestern Madagascar: cranium and mandible. Palaeo 53:669–688.

Flynn JJ, Parrish JM, Rakotosamimanana B, Simpson WF, Whatley RL, Wyss AR. (1999) A Triassic fauna from Madagascar, including early dinosaurs. Science 286:763–765.

Fordyce RE, Barnes LG. (1994). The evolutionary history of whales and dolphins. Ann Rev Earth Planet Sci 22:419–455.

Fox RC, Bowman MC. (1966) Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). University of Kansas Paleo Contributions 11:1–79.

Fraser NC. (1988). The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). Phil Trans Roy Soc London B 321:125–178.

Fraser NC, Benton MJ. (1989) The Triassic reptiles *Brachyrhinodon* and *Polysphenodon* and the relationships of the sphenodontids. Zool J Linn Soc 96:413–445.

Fraser NC, Renesto S. (2003) Drepanosaurid (Reptilia: Diapsida) remains from a Late Triassic fissure infilling at Cromhall Quarry (Avon, Great Britain). J Vert Paleo 23:703–705.

Fraser NC, Rieppel O. (2006) A new protorosaur (Diapsida) from the Upper Buntsandstein of the Black Forest, Germany. J Vert Paleo 26:866–871.

Fraser NC, Walkden GM. (1984) The postcranial skeleton of the Upper Triassic sphenodontid *Planocephalosaurus robinsonae*. Palaeo 27:575–595.

Fraser NC, Shelton CG. (1988) Studies of tooth implantation in fossil tetrapods using high-resolution X-radiography. Geo Mag 125:117–122.

Fraser NC, Irmis RB, Elliott DK. (2005) A procolophonid (Parareptilia) from the Owl Rock Member, Chinle Formation of Utah, U.S.A. Palaeo Elect 8:1–7.

Fraser NC, Nosotti S, Rieppel O. (2004) A re-evaluation of two species of *Tanystropheus* (Diapsida, Protorosauria) from Monte San Giorgio, southern Alps. J Vert Paleo 24(Supplement):60.

Fraser NC, Rieppel O, Chun L. (2013) A long-snouted protorosaur from the Middle Triassic of southeastern China. J Vert Paleo 33:1120–1126.

Fraser NC, Grimaldi DA, Olsen PE, Axsmith B. (1996) A Triassic lagerstätte from eastern North America. Nature 380:615–619.

Fraser NC, Olsen PE, Dooley AC, Ryan TR. (2007) A new gliding tetrapod (Diapsida: ?Archosauromorpha) from the Upper Triassic (Carnian) of Virginia. J Vert Paleo 27:261–265.

Frey E. (1988).Anatomie des Körperstammes von *Alligator mississippiensis* Daudin. Stuttgarter Beiträge zur Naturkunde: Serie A (Biologie) 424:1–60.

Gaffney ES. (1990) The comparative osteology of the Triassic turtle *Proganochelys*. Bull American Mus Nat History 194:1–263.

Galton PM. Comment on *Plateosaurus* Meyer, 1837 (Dinosauria, Sauropodomorpha): proposed replacement of unidentifiable name-bearing type by a neotype (Case 3560). Bull Zool Nom 70:205–206.

Gao K-Q, Ksepka DT. (2008) Osteology and taxonomic revision of *Hyphalosaurus* (Diapsida: Choristodera) from the Lower Cretaceous of Liaoning, China. J Anat 212:747–768.

Gardner NM, Holliday CM, O'Keefe FR. (2010) The braincase of *Youngina capensis* (Reptilia, Diapsida): new insights from high-resolution CT scanning of the holotype. Palaeontologia Electronica 13: 16 pp.

Gauffre F-X. (1993) The prosauropod dinosaur *Azendohsaurus laaroussii* from the Upper Triassic of Morocco. Palaeo 36:897–908.

Gauthier JA. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, University of California Berkeley.

Gauthier JA. (1986) Saurischian monophyly and the origin of birds. The Origin of Birds and the Evolution of Flight. Padian K (ed). Mem CA Acad Sci 8, pp. 1–55.

Gauthier JA, Estes R, de Queiroz K. (1988a) A phylogenetic analysis of Lepidosauromorpha. *Phylogenetic Relationships of the Lizard Families*, eds R Estes, G Pregill (Stanford University Press, Stanford), pp. 15–98.

Gauthier JA, Kluge AG, Rowe T. (1988b) Amniote phylogeny and the importance of fossils. Cladistics 4:105–209.

Gauthier JA, Kluge AG, Row T. (1988c) The early evolution of the Amniota. *The Phylogeny and Classification of the Tetrapoda, Volume 1*, ed M Benton (Clarendon Press, Oxford), pp. 103–155.

Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB. (2012) Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bull Peabody Mus Nat Hist 53:3–308.

Gervais P. (1859 Zoologie et Paléontologie Françaises, 2nd Edititon. (Bertrand, Paris), 544 pp.

Gignac PM, Erickson GM. (2014) Ontogenetic changes in dental form and tooth pressures facilitate developmental niche shifts in American alligators. J Zool 295:132–142.

Gilmore CW. (1942) Osteology of *Polyglyphanodon*, and Upper Cretaceous lizard from Utah. Proc US Nat Mus 92:229–265.

Goloboff PA, Farris JS, Nixon KC. (2008a). TNT: tree analysis using new technology, vers. 1.1. Willi Hennig Society. Available at http://www.zmuc.dk/public/phylogeny/tnt. Accessed February, 2, 2013.

Goloboff PA, Farris JS, Nixon KC. (2008b) TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Goodrich ES. (1916) On the classification of the Reptilia. Proc Roy Soc B 89:261–276.

Goodrich ES. (1942) The hind foot of *Youngina* and fifth metatarsal in Reptilia. J Anat 76:308–312.

Gottmann-Quesada A, Sander PM. (2009) A redescription of the early archosauromorph *Protorosaurus speneri* Meyer, 1832, and its phylogenetic relationships. Palaeontographica Abteilung A 287:123–220.

Gow CE. (1972) The osteology and relationships of the Millerettidae (Reptilia: Cotylosauria). J Zool Soc London 167:219–264.

Gow CE. (1975) The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeontologia Africana 18:89–131.

Gow CE. (1990) Morphology and growth of the *Massospondylus* braincase (Dinosauria Prosauropoda). Palaeo Afr 27:59–75.

Gower DJ. (1996) The tarsus of erythrosuchid archosaurs, and implications for early diapsid phylogeny. Zool J Linn Soc 116:347–375.

Gower DJ. (1997) The braincase of the early archosaurian reptile *Erythrosuchus africanus*. J Zool Soc London 242:557–576.

Gower DJ. (1999) The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of souther Germany. Stuttgarter Beit Nat B 280:1–49.

Gower DJ. (2002) Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian *Batrachotomus kupferzellensis*. Zool J Linn Soc 136:49–76.

Gower DJ. (2003) Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. Annal S Afr Mus 110:1–88.

Gower DJ, Nesbitt SJ. (2008) The braincase of *Arizonasaurus babbitti*—further evidence for the non-monophyly of 'rauisuchian' archosaurs. J Vert Palo 26:79–87.

Gower DJ, Schoch RR. (2009) Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. J Vert Paleo 29:103–122.

Gower DJ, Sennikov AG. (1996) Morphology and phylogenetic informativeness of early archosaur braincases. Palaeontology 39:883–906.

Gower DJ, Weber E. (1998) The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. Biol Rev 73:367–411.

Greer AE. (1976) One the occurrence of a stapedial foramen in living non-gekkonid lepidosaurs. Copeia 1976:591–592.

Gregory JT. (1945) Osteology and relationships of *Trilophosaurus*. University of Texas Publication 4401:273–359.

Grimaldi D. (1999) The co-radiations of pollinating insects and angiosperms in the Cretaceous. Annals MS Bot Garden 86:373–406.

Günther A. (1867) Contribution to the anatomy of *Hatteria* (*Rhynchocephalus*, Owen). Phil Trans Roy Soc 157:595–629.

Haeckel E. (1866) Allgemeine Morphologie der Organismen, Vol 1, 2. (G. Reimer, Berlin).

Haines RW. (1969). Epiphyses and bony sesamoids. *Biology of the Reptilia, Volume 1: Morphology*, ed. C. Gans. (Academic Press, London and New York), pp. 81–15

Halstead BL, Nicoll PG. (1971) Fossilized caves on Mendip. Stud Speleol 2:93–102.

Harris JD, Downs A. (2002) A drepanosaurid pectoral girdle from the Ghost Ranch (Whitaker) Coelophysis Quarry (Chinle Group, Rock Point Formation, Rhaetian), New Mexico. J Vert Paleo 22:70–75.

Hasiotis ST. (1997) Abuzz before flowers…. Plateau, J Mus N AZ 1:20–27.

Hasiotis ST, Dubeil RF, Kay PT, Demko TM, Kowalska K, McDaniel D. (1998) *National Park Service Paleontological Research. Technical Report NPS/NRGRD/GRDTR-90/01*, eds Santucci VL, McClelland L, pp. 116–121.

Haughton SH. (1924) On a new type of thecodont from the middle Beaufort Beds. Annals Trans Mus 20:343–346.

Hayssen V, Miranda F, Pasch B. (2012) *Cyclopes didactylus* (Pilosa: Cyclopeidae). Mammalian Species 44:51–48.

Heaton MJ. (1979) Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian Oklahoma and Texas. Bulletin of the Oklahoma Geological Society 127:1–84.

Heckert AB. (2004) Late Triassic microvertebrates from the Upper Triassic Chinle Group (Otischalkian–Adamanian, Carnian), southwestern U.S.A. Bull NM Mus Nat Hist Sci 27:1–170.

Heckert AB, Lucas SG, Spielmann JA. (2012) A new species of the enigmatic archosauromorph *Doswellia* from the Upper Triassic Bluewater Creek Formation, New Mexico, U.S.A. Palaeo 55:1333–1348.

Hennig W. (1965) Phylogenetic systematics. Ann Rev Entomol 10:97–116.

Hildebrand M, Goslow GE. (2001). *Analysis of Vertebrate Structure, Fifth Edition*. John Wiley & Sons.

Hirschfield S. (1976) A new fossil anteater (Edentata, Mammalia) from the Miocene of Columbia, S.A. and evolution of the Vermilingua. J Paleo 50:419–432.

Hoffstetter R, Gasc J-P. 1969. Vertebrae and ribs of modern reptiles. Biology of the Reptilia, Volume 1: Morphology A. C. Gans (ed.) (Academic Press, London and New York), pp. 209–301

Holliday CM, Nesbitt SJ. (2013) Morphology and diversity of the mandibular symphysis of archosauriforms. Geol Soc London, Spec Pub 379:555–571.

Holmes R. (1977) The osteology and musculature of the pectoral limb of small captorhinids. J Morphology 152:101–140.

Hone DWE, Benton MJ. (2008) A new genus of rhynchosaur from the Middle Triassic of south-west England. Palaeo 51:95–115.

Hopkins SSB, Davis EB. (2009). Quantitative morphological proxies for fossoriality in small mammals. Journal of Mammalogy 90:1449–1460.

Hopson JA. (1979) Paleoneurology. *Biology of the Reptilia, Vol 9*, ed C Gans (Academic Press, London), pp. 39–146.

Howes GB, Swinnerton HH. (1901) On the development of the skeleton of the tuatara, *Sphenodon punctatus*; with remarks on the egg, on the hatching, and on the hatched young. Transactions of the Zoological Society of London 16:1–85.

Huene FR von. (1905) Über der Trias-dinosaurier Europas. Zentr. Deut. Geol. Gess. 57: 345–349.

Huene FR von. (1926) Zur beurteilung von *Protorosaurus*. Centr für Mineral, Geol, Paläo Abt. B 1926:469–475.

Huene FR von. (1931) Über *Tanystropheus* und verwandte formen. Neues Jahr für Mineral, Geol, Paläo Beilageband 67:65–86.

Huene FR von. (1932) Die fossile reptil-ordung Saurischia. Ihre Entwicklung und Gescichte. Monograph zur Geol Palaeo, Serie 1 4:1–361.

Huene FR von. (1936) The constitution of the Thecodontia. 207–217. Amer J Sci series 5 32:207–217.

Huene FR von. (1944) Die zwieteilung des reptistammes. Neues Jahr für Mineral, Geol, Paläo Abh 88:427–440.

Huene FR von. (1946) Die grossen Stämme der tetrapoden in den geologischen Zeiten. Biol Zentralbl 65:268–275.

Huene F von. (1948) Notes on *Gwyneddosaurus*. Amer J Sci 246:208–213.

Huene FR von. (1956) Paläontologie und Phylogenie der niederen Tetrapoden. (Gustav Fischer, Jena).

Hughes B. (1963) The earliest archosaurian reptiles. S Afr J Sci 59:221–241.

Hutchinson JR. (2001b). The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). Zool J Linn Soc 131:169–197.

Hutchinson MN, Skinner A, Lee MSY. (2012) *Tikiguania* and the antiquity of squamate reptiles (lizards and snakes). Bio Lett 8:665–669.

Huxley TH. (1871) A manual of Vertebrate Animals. (J. and A. Churchill, London).

Iordansky NN. (1973) The skull of the Crocodylia. *Biology the Reptilia, Volume 4 Morphology B*, eds C Gans, TS Parsons. (Academic Press, London and New York), pp. 201–262.

Irmis R B. 2005. The vertebrate fauna of the Upper Triassic Chinle Formation in northern Arizona. *Guidebook of the Triassic Formations of the Colorado Plateau*, eds. SJ Nesbitt, WG Parker, RB Irmis. Mesa Southwest Museum 9:63–88.

Irmis RB, Nesbitt SJ. (2012) The evolution of early crocodylomorph disparity and locomotor styles: new evidence from the latest Triassic of New Mexico. Abstracts of the Society of Vertebrate Paleontology Annual Meeting, Raleigh. Journal of Vertebrate Paleontology 42:115A.

Irmis RB, Whiteside JH. (2012) Delayed recovery of non-marine tetrapods after the end-Permian mass extinction tracks global carbon cycle. Proc Roy Soc B 279:1310–1318.

Irmis RB, Mundil R, Martz JW, Parker WG. (2011). High-resolution U-Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. Earth Planet Sci Letters 309:258–267.

Irmis RB, Nesbitt SJ, Padian K, Smith ND, Turner AH, Woody D, Downs A. (2007) A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317:358–361.

Jacobs L, Murry PA. (1980) The vertebrate community of the Triassic Chinle Formation near St. Johns, Arizona. *Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert*, ed. LL Jacobs. (Museum of Northern Arizona Press: Flagstaff), pp. 55–71.

Jalil N-E. (1997) A new prolacertiform diapsid from the Triassic of North Africa and the interrelationships of the Prolacertiformes. J Vert Paleo 17:506–525.

Jalil N-E, Knoll F. (2002) Is *Azendohsaurus laaroussii* (Carnian, Morocco) a dinosaur? J Vert Paleo 22:70A.

Jarvik E. (1996) The Devonian tetrapod *Ichthyostega*. Fossils & Strata 40:1–213.

Jiang D-Y, Rieppel O, Fraser NC, Motani R, Hao W-H, Tintori A, Sun Y-L, Sun Z-Y. (2011) New information on the protorosaurian reptile *Macrocnemus fuyuanensis* Li et al., 2007, from the Middle/Upper Triassic of Yunnan, China. J Vert Paleo 31:1230–1237.

Jollie MT. (1960) The head skeleton of the lizard. Acta Zool 41:1–64.

Jones MEH. (2006) The Early Jurassic clevosaurs from China (Diapsida: Lepidosauria). NM Mus Nat Hist Bull 37:548–562.

Jones MEH, Anderson CL, Hipsley CA, Müller JA, Evans SE, Schoch RR. (2013) Integration of molecules and new fossils supports a Triassic origin for Lepidosauria (lizards, snakes, and tuatara). BMC Evolutionary Biology 13:208.

Jurcsák T. (1975). *Tanystropheus biharicus* n. sp. (Reptilia, Squamata) o noua specie pentru fauna Triasica Romaniei. Nymphaea 3:45–52.

Kaye FT, Padian K. (1994) Microvertebrates from the *Placerias* Quarry: a window on Late Triassic vertebrate diversity in the American Southwest. *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, eds. NC Fraser, H-D Sues. (Cambridge University Press, Cambridge, U.K.), pp. 171–196.

Kent DV, Tauxe L. (2005) Corrected Late Triassic latitudes for continents adjacent to the North Atlantic. Science 307:240–244.

Klembara J, Welman J. (2009) The anatomy of the palatoquadrate in the Lower Triassic *Proterosuchus fergusi* (Reptilia, Archosauromorpha) and its morphological transformation within the archosauriform clade. Acta Zool 90:275–284.

Kluge AG. (1982) Cloacal bones and sacs as evidence of gekkonoid lizard relationships. Herpetologica 38:348–355.

Knoll AH, Bamback RK, Payne JL, Pruss S, Fischer WW. (2007) Paleophysiology and end-Permian mass extinction. Earth * Planet Sci Lett 256:295–313.

Konishi T, Newbrey MG, Caldwell MW. (2014) A small, exquisitely preserved specimen of *Mosasaurus missouriensis* (Squamata, Mosasauridae) from the upper Campanian of the Bearpaw Formation, western Canada, and the first stomach contents for the genus. J Vert Paleo 34:802–819.

Koyabu D, Maier W, Sánchez-Villagra MR. (2012) Paleontological and developmental evidence resolve the homology and dual embryonic origin of a mammalian skull bone, the interparietal. Proc Nat Acad Sci 109:14075–14080.

Kuhn O. (1939) Schädelbau und systematische Stellung von *Weigeltisaurus*. Paläo Zeit 21:163–167.

Kuhn-Schnyder VE. (1959) Hand und Fuss von *Tanystropheus longobardicus* (Bassani). Eclogae Geologicae Helvetiae 52:921–941.

Kumazawa Y, Nishida M. (1999) Complete mitochondrial DNA sequences of the green turtle and blue-tailed mole skink: statistical evidence for archosaurian affinity of turtles. Molec Bio & Evo 16:784–792.

Landsmeer JMF. (1983) The mechanism of forearm rotation in *Varanus exanthematicus*. J Morphology 175:119–130.

Lane HH. (1945) New mid-Pennsylvanian reptiles from Kansas. Trans KS Acad Sci 47:381–390.

Langer MC, Schultz CL. (2000) Rincossauros—herbívoros cosmopolitas do Tríassico. Palaeontologia do Rio Grande do Sul. (Ediçao CIGO/UFRGS, Porto Alegre), pp. 246–272.

Laurin M. (1991) The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. Zool J Linn Soc 101:59–95.

Laurin M, Reisz RR. (1995) A reevaluation of early amniote phylogeny. Zool J Linn Soc 113:165–223.

Leal F, Tarazona, OA, Ramírez-Pinilla MP. (2010) Limb development in the gekkonid lizard *Gonatodes albogularis*: a reconsideration of homology in the lizard carpus and tarsus. J Morph 271:1328–1341.

LeBlanc ARH, Reisz RR. (2013) Periodontal ligament, cementum, and alveolar bone in the oldest herbivorous tetrapods, and their evolutionary significance. PLoS One e74697.

LeBlanc ARH, Reisz RR. (2015) Patterns of tooth development and replacement in captorhinids reptiles: a comparative approach for understanding the origin of multiple tooth rows. J Vert Paleo DOI: 10.1080/02724634.2014.919928.

Lécuru S. (1969) Étude morphologique de l'humérus des lacertiliens. Annales Sci Natu, Zool Paris 12e Série 9:515–558.

Li C, Zhao L, Wang L. (2007) A new species of *Macrocnemus* (Reptilia: Protorosauria) from the Middle Triassic of southwestern China and its palaeogeographical implication5. Sci in China D 50:1601–1605.

Long RA, Murry PA. (1995) Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. NM Mus Nat Hist Bull 4:1–254.

Lü J-C, Ji S-A, Dong Z-M, Wu X-C. (2008). An Upper Cretaceous lizard with a lower temporal arcade. Naturwiss 95:663–669.

Luan X, Walker C, Dangaria S, Ito Y, Druzinsky R, Jasorius K, Lesot H, Rieppel O. The mosasaur tooth attachment apparatus as paradigm for the evolution of the gnathostome periodontum. Evo & Devo 11:247–259.

Lucas SG, Minter NJ, Hunt AP. (2010) Re-evaluation of alleged bees' nests from the Upper Triassic of Arizona. Palaeogeo, Palaeoclimat, Palaeoeco 286:194–201.

Luo Z-X, Meng Q-J, Ji Q, Liu D, Zhang Y-G, Neander AI. (2015) Evolutionary development in basal mammaliaforms as revealed by a docodontan. Science 347:760–764.

Lyson TR, Bhullar B-AS, Bever GS, Joyce WG, de Queiroz K, Abzhanov A, Gauthier JA. (2013) Homology of the enigmatic nuchal bone reveals novel reorganization of the shoulder girdle in the evolution of the turtle shell. Evo & Devo 15:317–325.

MacCartney J. (1802) Preface and Table III. Lectures on Comparative Anatomy, translated from William Ross. G. Cuvier (ed) (Oriental Press, London).

Maddison WP, Maddison DR. (2015) Mesquite: a modular system for evolutionary analysis. Version 3.02. http://mesquiteproject.org

Maisano JA. (2002) Postnatal skeletal ontogeny in five xantusiids (Squamata: Scleroglossa). J Morphology 254:1–38.

Malan ME. (1963) The dentitions of the South African Rhynchocephalia and their bearing on the origin of the rhynchosaurs. S Afr J Sci 59:214–220.

Martz JW, Mueller B, Nesbitt SJ, Stocker MR, Parker WG, Atanassov M, Fraser NC, Weinbaum J, Lehane J. (2013) A taxonomic and biostratigraphic re-evaluation of the Post Quarry vertebrate assemblage from the Cooper Canyon Formation (Dockum Group, Upper Triassic) of southern Garza County, western Texas. Earth Env Sci Trans Roy Soc Edin 103:339–364.

Matsumoto R, Buffetaut E, Escuillie F, Hervet S, Evans SE. (2013). New material of the choristodere *Lazarussuchus* (Diapsida, Choristodera) form the Paleocene of France. J Vert Paleo 33:319–339.

Maxwell EE, Larsson HCE. (2009) Comparative ossification sequence and skeletal development of the postcranium of palaeognathous birds (Aves: Palaeognathae). Zoological Journal of the Linnean Society 157:169–196.

McGarrity CT, Campione NE, Evans DC. (2013) Cranial anatomy and variation in *Prosaurolophus maximus* (Dinosauria: Hadrosauridae). Zool J Linn Soc 167:531–568.

McGregor JH. (1906) The Phytosauria, with especial reference to *Mystriosuchus* and *Rhytidodon*. Mem Amer Mus Nat Hist 9:87–100.

Meers MB. (2003) Crocodylian forelimb musculature and its relevance to Archosauria. Anat Rec 274A:891–916.

Merck JA. (1995) The cranial anatomy of *Trilophosaurus buettneri* as revealed by high-resolution computer-aided tomography. Abstracts of the 1995 Annual Meeting of the Society of Vertebrate Paleontology, Pittsburgh. J Vert Paleo 15:44A.

Merck JA. (1997) A phylogenetic analysis of the euryapsid reptiles. Ph.D. thesis, University of Texas at Austin.

Merck JA. (2003). An arboreal radiation of non-saurian diapsids. Abstracts of the Society of Vertebrate Paleontology Annual Meeting, St. Paul. Journal of Vertebrate Paleontology 33:78A.

Meyer H von. (1837) Mitteilung an Prof. Bronn. Neues Jahr für Geol und Paläo Abh 1837:316.

Meyer H von. (1832) Palaeologica zur Geschichte der Erde und ihrer Geschöpfe (Verlag Sigmund Schmerber, Frankfurt), 560 pp.

Meyer H von. (1847–1855) Die saurier des Muschelkalkes: mit Rücksicht auf die saurier aus buntem sandstein und Keuper. Zur Fauna der Vorwelt, zweite abtheilung. (Heinrich Keller, Frankfurt).

Miner RW. (1925) The pectoral limb of *Eryops* and other primitive tetrapods. Bulletin of the American Museum of Natural History 51:145–312.

Modesto SP, Reisz RR. (2003) An enigmatic new diapsid reptile from the Upper Pemian of eastern Europe. J Vert Paleo 22:851–855.

Modesto SP, Sues H-D. (2004) The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. Zool J Linn Soc 140:335–351.

Modesto SP, Lamb AJ, Reisz RR. (2014) The captorhinids reptile *Captorhinikos valensis* from the lower Permian Vale Formation of Texas, and the evolution of herbivory in eureptiles. J Vert Paleo 34:291–302.

Montefeltro FC, Langer MC, Schultz CL. (2010) Cranial anatomy of a new genus of hyperodapedontine rhynchosaur (Diapsida, Archosauromorpha) from the Upper Triassic of Brazil. Earth Env Sci Trans Roy Soc Edin 101:27–52.

Montefeltro FC, Bittencourt JS, Langer MC, Schultz CL. (2013) Postcranial anatomy of the hyperodapedontine rhynchosaur *Teyumbaita sulcognathus* (Azevedo and Schultz, 1987) from the Late Triassic of southern Brazil. J Vert Paleo 33:67–84.

Mook CC. (1921) The dermo-supraoccipital bone in the Crocodilia. Am Mus Nov 44:101–103.

Motani R. (1999) On the evolution and homology of ichthyosaur forefins. J Vert Paleo 19:28–41.

Mukherjee D, Ray S. (2014) A new *Hyperodapedon* (Archosauromorpha, Rhynchosauria) from the Upper Triassic of India: implications for rhynchosaur phylogeny. Palaeo 57:1241–1276.

Müller J. (2003) Early loss and multiple return of the lower temporal arcade in diapsid reptiles. Naturwiss 90:473–476.

Müller J. (2004) The relationships among diapsid reptiles and the influence of taxon selection. *Recent Advances in the Origin and Early Evolution of Vertebrates*, eds MVH Wilson, G Arratia, R Cloutier (Verlag Dr. Friedrich Pfeil), pp. 379–408.

Murry PA. (1987) New reptiles from the Upper Triassic Chinle Formation of Arizona. J Vert Paleo 61:773–786.

Murry PA. (1989) Microvertebrate fossils from the Petrified Forest and Owl Rock members (Chinle Formation) in Petrified Forest National Park and vicinity, Arizona. *Dawn of the Age of Dinosaurs in the American Southwest*, eds. SG Lucas and AP Hunt. (New Mexico Museum of Natural History, Albuquerque), pp. 249–277.

Muscio B. (1999) *Sphenodon punctatus*. Available at http://animaldiversity.org/accounts/Sphenodon_punctatus/. Accessed June 13, 2015.

Muscio G. (1996) Preliminary note on a specimen of prolacertiform (Reptilia) from the Norian (Late Triassic) of Preone (Udine, north-eastern Italy). Gortiana 18:33–40.

Nesbitt SJ. (2011) The early evolution of archosaurs: relationships and the origin of major clades. Bull Am Mus Nat Hist 352:1–292.

Nesbitt SJ, Chatterjee S. (2008) Late Triassic dinosauriforms from the Post Quarry and surrounding areas, west Texas, U.S.A. Neues Jahr für Geol und Paläo Abh 249:143–156.

Nesbitt SJ, Norell MA. (2006) Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda) Proc Roy Soc B 273:1045–1048.

Nesbitt SJ, Stocker MR. (2008) The vertebrate assemblage of the Late Triassic Canjilon Quarry (northern New Mexico, USA) and the importance of apomorphy-based assemblage comparisons. J Vert Paleo 28:1063–1072.

Nesbitt SJ, Butler RJ, Gower DJ. (2013). A new archosauriform (Reptilia: Diapsida) from the Manda Beds (Middle Triassic) of southwestern Tanzania. PLoS One 8:e72753. doi:10.1371/journal.pone.0072753.

Nesbitt SJ, Stocker MR, Small BJ, Downs A. (2009a). The osteology and relationships of *Vancleavea campi* (Reptilia: Archosauriformes). Zool J Linn Soc 157:814–864.

Nesbitt SJ, Flynn JJ, Pritchard AC, Parrish JM, Ranivoharimanana L, Wyss A. (in press) Postcranial anatomy and relationships of *Azendohsaurus madagaskarensis*. Bull Am Mus Nat Hist.

Nesbitt SJ, Irmis RB, Parker WG, Smith ND, Turner AH, Rowe T. (2009b). Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. J Vert Paleo 29:498–516.

Nesbitt SJ, Brusatte SL, Desojo JB, Liparini A, de França MAG, Weinbaum JC, Gower DJ. (2013) Rauisuchia. Geol Soc London, Spec Pub 379:241–274.

Nguyen TQ, Hamilton P, Ziegler T. 2014. *Shinisaurus crocodilurus*. The IUCN red list of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded August 10, 2015.

Nopcsa F. (1930) Notizen über *Macrochemus Bassanii* nov. gen. et spec. Cent für Mineral, Geol und Paläo B 1930:252–255.

Nosotti S. (2007). *Tanystropheus longobardicus* (Reptilia, Protorosauria): re-interpretations of the anatomy based on new specimens from the Middle Triassic of Besano (Lombardy, northern Italy). Mem. Mus Civ Storia Nat Milano 35:1–88.

O'Leary MA, Kaufman SG. (2007). Morphobank 2.5: web application for morphological phylogenetics and taxonomy. http://morphobank.org.

O'Leary MA, et al. (2013) The placental mammalian ancestor and the post-K-Pg radiation of placentals. Science 339:662–667.

Oelrich TM. (1956) The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Misc Pub Mus Zool, U of Mich 94:1–122.

Olsen PE. (1979). A new aquatic eosuchian from the Newark Supergroup (Late Triassic-Early Jurassic) of North Carolina and Virginia. Postilla 176:1–14.

Olsen PE. (1980) A comparison of the vertebrate assemblages from the Newark and Hartford basins (early Mesozoic, Newark Supergroup) of eastern North America. *Aspects of Vertebrate Evolution: Essays in Honor of Edwin Harris Colbert*, ed LL Jacobs. (Northern Arizona Press, Flagstaff), pp. 35–53.

Olsen PE. (1990). Tectonic, climatic, and biotic modulation of lacustrine ecosystems—examples from Newark Supergroup of eastern North America. *Lacustrine Basin Exploration: Case Studies and modern Analogs*, ed. BJ Katz. AAPG Memoir 50:209–224.

Olsen PE, Kent DV, Whiteside JH. (2011) Implications of the Newark Supergrou-based astrochronology and geomagmatic polarity time scale (Newark-APTS) for the tempo and mode of the early diversification of the Dinosauria. Earth Env Sci Trans Roy Soc Edin 101:201–229.

Olson EC. (1966) The middle ear—morphological types in amphibians and reptiles. Amer Zool 6:399–416.

Ortlam D. (1967). Fossile Böden als Leithoriztone für die Gliederung des Höheren Butsandsteins im nördlichen Schwarzwald und südlichen Odenwald. Geol Jahrbuch 84:485–590.

Osborn HF. (1903a) On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. Science 17:275, 276.

Osborn HF. (1903b) The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. Mem American Mus Nat Hist 1:449-519.

Osmólska H, Currie PJ, Barsbold R. (2004) Oviraptorosauria. *Dinosauria, 2nd Edtion,* eds D Weishampel, P Dodson, H Osmólska (University of California Press, Berkeley), pp. 165–183.

Osmólska H, Roniewicz E, Barsbold R. (1972) A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. Paleontologia Polonica 27:103–143.

Owen R. (1842) Description of an extinct lacertilian, *Rhynchosaurus articeps*, Owen, of which the bones and foot-prints characterize the upper New Red Sandstone at Grinshill, near Shrewsbury. Trans Camb Phil Soc 7:355–369.

Padian K, Rayner JMV. (1993) The wings of pterosaurs. Amer J Science 293A:91-166.

Parker WG. (2008) Description of new material of the aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*. PaleoBios 28:1–40.

Parker WG, Irmis RB, Nesbitt SJ , Martz JW, Browne LS. (2005). The Late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs. Proc Roy Soc B 272:963–969.

Parks P. (1969) Cranial anatomy and mastication of the Triassic reptile *Trilophosaurus*. M.S. Thesis, University of Texas at Austin

Parrington FR. (1935) On *Prolacerta broomi* gen. et sp. nov. and the origin of lizards. Annals Mag of Nat Hist 16:197–205.

Parrington FR. (1937) On the supratemporal and tabular bones in reptiles. J Nat Hist 69–76.

Peterson JA. (1984) The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. J Zool London 202:1–42.

Peyer B. (1937) Die Triasfauna der Tessiner Kalkalpen XII. *Macrocnemus bassanii* Nopcsa. Schweizerische Paläo Abhandlungen 59:1–140.

Peyer K, Carter JG, Sues H-D, Novak SE, Olsen PE. (2008). A new suchian archosaur from the Upper Triassic of North Carolina. J Vert Paleo 28:363–381.

Piveteau J. (1926) Paléontologie de Madagascar XIII. Amphibiens et reptiles Permiens. Annales de Paléo 15:55–179.

Pinna G. (1980) *Drepanosaurus unguicaudatus*, nuovo genere e nuova specie di lepidosauro del Trias alpino. Atti della Soc ital di sci nat del mus civ di storia nat di Milano 121:181–192.

Pinna G. (1984) Osteologia di *Drepanosaurus unguicaudatus*, lepidosauro triassico del sottordine Lacertilia. Mem della Soc ital. di sci nat e del Mus civ di storia nat di Milano 24:7–28.

Pinna G. (1986) On *Drepanosaurus unguicaudatus*, an Upper Triassic lepidosaurian from the Italian Alps. J Paleo 60:1127–1132.

Prendini L. (2001). Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. Sys Bio 50:290–300.

Price LI. (1935) Notes on the brain case of *Captorhinus*. Proc Boston Soc Nat History 40:377–386.

Prieto-Márquez A, Norell MA. (2011) Redescription of a nearly complete skull of *Plateosaurus* (Dinosauria: Sauropodomorpha) from the Late Triassic of Trossingen (Germany). Am Mus Novitates 3727:1–58.

Pritchard AC. (2015) Extreme modification of the tetrapod forelimb in a Triassic reptile. Abstracts of the 2015 Society of Int & Comp Bio Annual Meeting, West Palm Beach:E147.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2012). A new drepanosaurid from the Late Triassic of New Mexico: insights into the forelimb evolution and biogeography of drepanosaurs. J Vert Paleo 32(3, Supplement):158–159.

Pritchard AC, Turner AH, Nesbitt SJ, Irmis RB, Smith ND. (2015). Late Triassic tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified Forest Member, Chinle Formation) and the biogeography, functional morphology, and evolution of Tanystropheidae. Journal of Vertebrate Paleontology 35: e911186.

Ramezani J, Hoke GD, Fastovsky DE, Bowring SA, Therrien S, Dworkin SI, Atchley SC, and LC Nordt. (2011) High-precision U-Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): temporal constraints on the early evolution of dinosaurs. Geo Soc Amer Bull 123:2142–2159.

Reig O. (1967) Archosaurian reptiles: a new hypothesis on their origins. Science 157:565–568.

Reisz RR. (1977) *Petrolacosaurus*, the oldest known diapsid reptile. Science 196:1091–1093.

Reisz RR. (1981) A diapsid reptile from the Pennsylvanian of Kansas. Special Publication of the Museum of Natural History, University of Kansas 7:1–74.

Reisz RR, Laurin M, Marjanovic D. (2010) *Apsisaurus witteri* from the Lower Permian of Texas: yet another small varanopid synapsid, not a diapsid. J Vert Paleo 30:1628–1631.

Reisz RR, Berman DS, Scott D. (1984) The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. J Vert Paleo 4:57–67.

Reisz RR, Modesto SP, and Scott MD. (2011) A new Early Permian reptile and its significance in early diapsid evolution. Proc Roy Soc B 278:3731–3737.

Renesto S. (1994a) The shoulder girdle and anterior limb of *Drepanosaurus unguicaudatus* (Reptilia, Neodiapsida) from the upper Triassic (Norian) of northern Italy. Zool J Linn Soc 111:247–264.

Renesto S. (1994b) A new prolacertiform reptile from the Late Triassic of northern Italy. Riv Ital Paleo Strat 100:285–306.

Renesto S. (1994c) *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. J Vert Paleo 14:38–52.

Renesto S. (1995) A sphenodontid from the Norian (Late Triassic) of Lombardy (northern Italy): a preliminary note. Modern Geol 20:149–158.

Renesto S. (2000) Bird-like head on a chameleon body: new specimens of the enigmatic diapsid reptile *Megalancosaurus* from the Late Triassic of northern Italy. Riv Ital Paleo Strat 106:157–180.

Renesto S. (2005) A new specimen of *Tanystropheus* (Reptilia Protorosauria) from the Middle Triassic of Switzerland and the ecology of the genus. Riv Ital Paleo Strat 111:577–594.

Renesto S. (2006) A reappraisal of the diversity and biogeographic significance of the Norian (Late Triassic) reptiles from the Calcare di Zorzino. NM Mus Nat Hist Bull 37:445–456.

Renesto S, Avanzini M. (2002) Skin remains in a juvenile *Macrocnemus bassanii* Nopcsa (Reptilia, Prolacertiformes) from the Middle Triassic of northern Italy. Neues Jahr für Geol und Paläo Abh 224:31–48.

Renesto S, Bernardi M. (2014) Redescription and phylogenetic relationships of *Megachirella wachtleri* Renesto et Posenato, 2003 (Reptilia, Diapsida) Paläo Zeit 88:197–210.

Renesto S, Binelli G. (2006) *Vallesaurus cenensis* Wild, 1991, a drepanosaurid (Reptilia, Diapsida) from the Late Triassic of northern Italy. Riv Ital Paleo Stat 112:77–94.

Renesto S, Dalla Vecchia FM. (2000) The unusual dentition and feeding habits of the prolacertiform reptile *Langobardisaurus* (Late Triassic, northern Italy). J Vert Paleo 20:622–627.

Renesto S and Dalla Vecchia FM. (2005) The skull and lower jaw of the holotype of *Megalancosaurus preonensis* (Diapsida, Drepanosauridae) from the Upper Triassic of Italy. Riv Ital Paleo Stat 111:247–257.

Renesto S, Paganoni A. (1995) A new *Drepanosaurus* (Reptilia, Neodiapsida) from the Upper Triassic of northern Italy. Neues Jahr für Geol Paläo Abh 197:87–99.

Renesto S, Spielmann JA, Lucas SG. (2009). The oldest record of drepanosaurids (Reptilia, Diapsida) from the Late Triassic (Adamanian Placerias Quarry, Arizona, USA) and the stratigraphic range of the Drepanosauridae. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 252:315–325.

Renesto S, Spielmann JA, Lucas SG, and Spagnoli GT. (2010) The taxonomy and paleobiology of the Late Triassic (Carnian–Norian: Adamanian–Apachean) drepanosaurs (Diapsida: Archosauromorpha: Drepanosauromorpha). Bull NM Mus Nat Hist Sci 46:1–81.

Rénous-Lécuru S. (1973) Morophologie comparée du carpe chez des Lepidosauriens actuels (Rhynchocéphales, Lacertiliens, Amphisbéniens). Gegenbaurs morphologisches Jahrbuch 119:727–766.

Reynoso V-H, Clark JM. (1998) A dwarf sphenodontian from the Jurassic La Boca Formation of Tamaulipas, México. J Vert Paleo 18:333–339.

de Ricqlès A, Padian KA, Horner JR, Francillon-Viellot H. (2000) Paleohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications. Zool J Linn Soc 129:349–385.

Rieppel O. (1976) On the presence and function of postcloacal bones in the Lacertilia. Mon Zool Ital 10:7–13.

Rieppel O. (1989) The hind limb of *Macrocnemus bassanii* (Nopcsa) (Reptilia, Diapsida): development and functional anatomy. J Vert Palo 9:373–387.

Rieppel O. (1992) The skull in a hatchling of *Sphenodon punctatus*. J Herp 26:80–84.

Rieppel O (1993a) Studies on skeleton formation in reptiles. V. Patterns of ossification in the skeleton of *Alligator mississippiensis* Daudin (Reptilia, Crocodylia). Zoological Journal of the Linnean Society 109:301–325.

Rieppel O (1993b) Studies on skeleton formation in reptiles. II. *Chamaeleo hoehnelii* (Squamata: Chamaeleoninae), with comments on the homology of carpal and tarsal bones. Herpetologica 49:66-78.

Rieppel O. (1994) Studies on skeleton formation in reptiles. Patterns of formation in the skeleton of *Lacerta agilis exigua* Eichwald (Reptilia, Squamata). Journal of Herpetology 28:145–153.

Rieppel O. (1994) Osteology of *Simosaurus gaillardoti* and the relationships of stem-group Sauropterygia. Fieldiana, Geology 28:1–83.

Rieppel O. (2001) A new species of *Tanystropheus* (Reptilia: Protorosauria) from the Middle Triassic Makhtesh, Ramon, Israel. N Jahr fur Geo Paleo Abh 221:271–287.

Rieppel O, Fraser NC, Nosotti S. (2003) The monophyly of Protorosauria (Reptilia, Archosauromorpha): a preliminary analysis. Atti Soc It Sci Nat Mus Civ Stor Nat Milano 144:359–382.

Rieppel O, Li C, Fraser NC. (2008) The skeletal anatomy of the Triassic protorosaur *Dinocephalosaurus orientalis* Li, from the Middle Triassic of Guizhou Province, southern China. J Vert Paleo 28:95–110.

Rieppel O, Mazin J-M, Tchernov E. 1999. Sauropterygia from the Middle Triassic of Makhtesh Ramon, Negev, Israel. Fieldiana Geology 40:1–85.

Rieppel O, Jiang D-Y, Fraser NC, Hao W-C, Motani R, Sun Y-L, Sun Z-Y. (2010) *Tanystropheus* cf. *T. longobardicus* from the early Late Triassic of Guizhou Province, southwestern China

Robinson PGL. (1967a) The evolution of the Lacertilia. Problèms actuels de paléontologie (evolution des vertébrés). Colloques Internationaux du Centre National de la Recherche Scientifique 163:395–407.

Robinson PGL. (1967b) Triassic vertebrates from lowland and upland. Sci & Cult 33:169–173.

Robinson PGL. (1973) A problematic reptile from the British Upper Trias. J Geol Soc London 129:457–479.

Robinson PGL. (1975) The functions of the hooked fifth metatarsal in lepidosaurian reptiles. Colloque International C.N.R.S. 218:461–483.

Robinson PGL. (1976) How *Sphenodon* and *Uromastyx* grow their teeth and use them. Morphology and Biology of Reptiles. A d'A Bellairs and CB Cox (eds) Linnean Symposium Series 3:43–64.

Rogers JV. (2003) *Pachycheilosuchus trinquei*, a new procoelous crocodyliform from the Lower Cretaceous (Albian) Glen Rose Formation of Texas. J Vert Paleo 23:128–145.

Romer AS. (1933) Vertebrate Paleontology, 1st Edition. (University of Chicago Press, Chicago).

Romer AS. (1947) The relationships of the Permian reptile *Protorosaurus*. Am J Sci 245:19–30.

Romer AS. (1956). Osteology of the Reptiles. (University of Chicago Press, Chicago), 772 pp.

Romer AS. (1967) Early reptilian evolution re-viewed. Evolution 21:821–833.

Romer AS. (1971) The Chañares (Argentina) Triassic reptile fauna. XI. Two new long-snouted thecodonts, *Chanaresuchus* and *Gualosuchus*. Breviora 379:1–22.

Rose KD, Emry RJ. (1983) Extraordinary fossorial adaptations in the Oligocene palaeanodonts *Epoicotherium* and *Xenocranium* (Mammalia). Journal of Morphology 175:33–56.

Rovereto C. (1914) Los Estratos Araucanos y sus Fósiles. Anales del Museo Nacional de Historia Natural de Buenos Aires 25:1–250.

Russell AP, Bauer AM. (2008) The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. *Biology of the Reptilia, Volume 21: The Skull and Appendicular Locomotor Apparatus of Lepidosauria*, eds. C Gans, AS Gaunt, K Adler. (Academic Press, London and New York), pp. 1–466.

Rybczynski N. (2000) Cranial anatomy and phylogenetic position of *Suminia getmanovi*, a basal anomodont (Amniota: Therapsida) from the Late Permian of eastern Europe. Zool J Linn Soc 130:329–373.

Salisbury SW, Frey E, Martill DM, Buchy M-C. (2003) A new crocodilian from the Lower Cretaceous Crato Formation of north-eastern Brazil. Palaeontographica Abteilung A 270:3–47.

Salisbury SW, Molnar RE, Frey E, Willis PMA. (2006) The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. Proc B 273:2439–2448.

Saller F, Renesto S, Dalla Vecchia FM. (2013) First record of *Langobardisaurus* (Diapsida, Protorosauria) from the Norian (Late Triassic) of Austria, and a revision of the genus. Neues Jahr für Geol Paläo Abh 268:83–95.

Sander PM. (1992) The Norian *Plateosaurus* bonebeds of central Europe and their tapnohomy. Palaeogeo, Palaeoclim, Palaeoeco 93:255–299.

Säve-Söderbergh G. (1947) Notes on the brain-case in *Sphenodon* and certain Lacertilia. Zool Bidrag Uppsala 25:489–516.

Schaumberg G, Unwin DM, Brandt S. (2007) New information on the anatomy of the Late Permian gliding reptile *Coelurosauravus*. Paläo Zeit 81:160–173.

Schoch RR, Nesbitt SJ, Müller J, Lucas SG, Boy JA. (2010) The reptile assemblage from the Moenkopi Formation (Middle Triassic) of New Mexico. N Jahr fur Geo Paleo Abh 255:345–369.

Schwartz HL, Gillette DD. (1994) Geology and taphonomy of the Coelophysis Quarry, Upper Triassic Chinle Formation, Ghost Ranch, New Mexico. J Paleo 68:1118–1130.

Schwarz D, Meyer CA, Frey E. (2005) New frontiers in reconstructing sauropods. Abstracts of the 3rd Swiss Geosciences Meetings:59–60.

Schwarz D, Frey E, Meyer CA. (2007) Pneumaticity and soft tissue reconstruction in the neck of diplodocid and dicraeosaurid sauropods. Acta Paleo Pol 52:167–188.

Schwarz-Wings D, Frey E, Martin T. (2009) Reconstruction of the bracing system of the trunk and tail in hyposaurine dyrosaurids (Crocodylomorpha; Mesoeucrocodylia). J Vert Paleo 29:453–472.

Seeley HG. (1887) Researches on the structure, organization and classification of the fossil Reptilia. I. One *Protorosaurus speneri* (von Meyer). Phil Trans Roy Soc B 178:187–213.

Seidel MR. (1978) The somatic musculature of the cervical and occipital regions of *Alligator mississippiensis*. Ph.D. dissertation, City University of New York, New York, New York, 327 pp.

Sen K. (2003) *Pamelaria dolichotrachela*, a new prolacertid reptile from the Middle Triassic of India. J Asia Earth Sci 21:663–681.

Sennikov AG. (1988) The role of the oldest thecodonts in vertebrate assemblages of eastern Europe. Paleo Journal 1988:74–82.

Sennikov AG. (2011). New tanystropheids (Reptilia: Archosauromorpha) from the Triassic of Europe. Paleo J 45:90–104.

Senter PJ. (2003) New information on cranial and dental features of the Triassic archosauriform reptile *Euparkeria capensis*. Palaeo 46:613–621.

Senter PJ. (2004) Phylogeny of Drepanosauridae (Reptilia: Diapsida). Journal of Systematic Palaeontology 2:257–268.

Sereno PC. (1991) Basal archosaurs: phylogenetic relationships and functional implications. Soc Vert Paleo Mem 2:1–53.

Sereno PC, Arcucci AB. (1994) Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. J Vert Paleo 14:53–73.

Sereno PC, Chenggang R. (1992). Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. Science 255:845–848.

Sereno PC, Novas FE. (1993) The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. J Vert Paleo 13:451–476.

Sereno PC, Martínez RN, Alcober OA. (2012) Osteology of *Eoraptor lunensis* (Dinosauria, Sauropodomorpha). Mem Soc Vert Paleo 12:83–179.

Sertich JJW, and Groenke JR. (2010). The postcranial appendicular skeleton of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar, eds DW Krause, NJ Kley. Society of Vertebrate Paleontology Memoir 30:177–236.

Shedlock AM, Edwards SV. (2009) Amniotes (Amniota). The Timetree of Life. SB Hedges, S Kumar (eds.) (Oxford University Press, Oxford), pp. 375–379.

Sheil CA. (2003) Osteology and skeletal development of *Apalone spinifera* (Reptilia: Testudines: Trionychidae). J Morph 256:42–78.

Sheil CA, Portik D. (2008) Formation and ossification of limb elements in *Trachemys scripta* and a discussion of autopodial elements in turtles. Zool Sci 25:622–641.

Shen S-Z, Bowring SA. (2015) The end-Permian mass extinction: a still-unexplained catastrophe. Nat Sci Rev 2014:492–495.

Shubin NH, Alberch P. (1985) A morphogenetic approach to the organization of the tetrapod limb. *Evolutionary Biology, Vol. 20*, eds MK Hecht, B Wallace, GT Prance (Springer US), pp. 319–387.

Shubin NH, Sues H-D. (1991) Biogeography of early Mesozoic continental tetrapods: patterns and implications. Paleobio 17:214–230.

Shubin NH, Daeschler EB, and Jenkins FA. (2006) The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. Nature 440:764–771.

Sill WD. (1971) Functional morphology of the rhynchosaur skull. Form Funct 4:303–318.

Simmons NB, Seymour KL, Habersetzer J, Gunnell GF. (2008). Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451:818–821.

Smith REH, Evans SE. (1992) New material of *Youngina*: evidence of juvenile aggregation in Permian diapsid reptiles. Palaeo 39:289–303.

Smith ND, Crandall JR, Hellert SM, Hammer WL, Makovicky PJ. (2011) Anatomy and affinities of large archosauromorphs from the lower Fremouw Formation (Early Triassic) of Antarctica. J Vert Paleo 31:784–797.

Snyder RC. (1954) The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. Amer J Anat 95:1–45.

Sookias RB, Butler RJ. (2013). Euparkeriidae. Geol Soc London, Spec Pub 379:35–48.

Spielmann JA, Lucas SG, Rinehart LF, Heckert AB. 2008. The Late Triassic archosauromorph *Trilophosaurus*. Bull NM Mus Nat Hist Sci 43:1–177.

Spielmann JA, Lucas SG, Heckert AB, Rinehart LF, Hunt AP. (2007) Taxonomy and biostratigraphy of the Late Triassic archosauromorph *Trilophosaurus*. Bull NM Mus Nat Hist Sci 40:231–240.

Spielmann JA, Lucas SG, Heckert AB, Rinehart LF, Richards HR. (2009) Redescription of *Spinosuchus caseanus* (Archosauromorpha: Trilophosauridae) from the Upper Triassic of North America. Palaeodiv 2:283–313.

Stein K, Palmer C, Gill PG, Benton MJ. (2008) The aerodynamics of the British Late Triassic Kuehneosauridae. Palaeo 51:967–981.

Stokely PS. (1950) The occurrence of an intermedium in lizards. Am Midl Nat 43:179–182.

Sues H-D. (2003) An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. Canadian Journal Earth Sci 40:635–649.

Sues H-D and Fraser NC. (2013) *Triassic Life on Land*. (Columbia University Press, New York) 236 pp.

Sues H-D, Olsen PE. (1993) A new procolophonid and a new tetrapod of uncertain, possibly procolophonian affinities from the Upper Triassic of Virginia. J Vert Paleo 13:282–286.

Sues H-D, Olsen PE. (2015) Stratigraphic and temporal context and faunal diversity of Permian–Jurassic continental tetrapod assemblages from the Fundy rift basin, eastern Canada. Atlantic Geo 51:139–205.

Sues H-D, Reisz RR. (1995) First record of the early Mesozoic sphenodontian *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the southern hemisphere. J Paleo 69:123–126.

Sues H-D, Shubin NH, Olsen PE. (1994) A new sphenodontian (Lepidosauria: Rhynchocephalia) from the McCoy Brook Formation (Lower Jurassic) of Nova Scotia, Canada. J Vert Paleo 327–340.

Sumida SS. (1989) The appendicular skeleton of the Early Permian genus *Labidosaurus* (Reptilia, Captorhinomorpha, Captorhinidae) and the hind limb musculature of captorhinid reptiles. Journal of Vertebrate Paleontology 9:295–313

Surahya S. (1989) *Atlas Komodo: studi anatomi dan kedudukannya dalam sistematik hewan*. (Gadjah Mada University Press, Gadjah Mada, India), 419 pp.

Susaita D, Pouydebat E, Manzano A, Abdala V, Hertel F, Herrel A. (2011). Getting a grip on tetrapod grasping: form, function, and evolution. Biological Reviews 88:380–405.

Swinton WE. (1939) A new Triassic rhynchocephalians from Gloucestershire. J Nat Hist 4:591–594.

Swofford DI. (2003) PAUP*. Phylogenetic analysis using parsimony (* and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tatarinov LP. (1960) [Pseudosuchians in the Upper Permian of the USSR]. Paleo Journal 1960:74–80.

Tatarinov LP. (1978) Triassic prolacertilians of the USSR. Paleo J 1978:505–514.

Taylor BK. (1978) The anatomy of the forelimb in the anteater (*Tamandua*) and its functional implications. J Morph 157:347–368.

Taylor BK. (1985) Functional anatomy of the forelimb in Vermilinguas (anteaters). *The Evolution and Ecology or Armadillos, Sloths, and Vermilinguas*, eds GG Montgomery (Smithsonian Institution Press), pp. 163–171.

Thulborn RA. (1973) Teeth of ornithischian dinosaurs from the Upper Jurassic of Portugal. Serv Geol Portugal, Mem 22:89–134.

Thulborn RA. (1974) A new heterodontosaurid dinosaur (Reptilia: Ornithischia) from the Upper Triassic Red Beds of Lesotho. Zool J Linn Soc 55:151–175.

Thulborn RA. (1979) A proterosuchian thecodont from the Rewan Formation of Queensland. Mem Queens Mus 19:331–355.

Thyng FW. (1906) Squamosal bone in tetrapodous Vertebrata. Proc Boston Nat Hist Soc 32:387–425.

Tschanz K. (1985) *Tanystropheus*—an unusual reptilian construction. Konstruktionsprin Lebender und Austgestorbener Reptilien. Konz Sonderforschungsbereich 230:169–178.

Tsuihiji T. (2004) The ligament system in the neck of *Rhea americana* and its implications for the bifurcated neural spines in sauropod dinosaurs. J Vert Paleo 24:165–172.

Tsuihiji T. (2005). Homologies of the transversospinalis muscles in the presacral region of Sauria (crown Diapsida). J Morph 263:151–178.

Tsuji LA. (2006) Cranial anatomy and phylogenetic affinities of the Permian parareptiles *Macroleter poezicus*. J Vert Paleo 26:849–865.

Tulli MJ, Cruz FB, Herrel A, Vanhooydonck B, Abdala V. (2009) The interplay between claw morphology and microhabitat use in neotropical iguanian lizards. Zoology 112:379–392.

Vaughn PP. (1955) The Permian reptile *Araeoscelis* restudied. Bull Mus Comp Zool 113:305–467.

Vaughn PP. (1956) The phylogenetic migrations of the ambiens muscle. J Mitchell Soc 77:243–262.

Vickers-Rich P, Rich TH, Rieppel O, Thulborn RA, McClure HA. (1999). A Middle Triassic vertebrate fauna from the Jihl Formation, Saudi Arabia. N Jahr fur Geo Paleo Abh 213:201–232.

Waldman M, Evans SE. (1994) Lepidosauromorph reptiles from the Middle Jurassic of Skye. Zool J Linn Soc 112:135–150.

Walker AD. (1961) Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. Phil Trans Roy Soc B 244:103–204.

Walker AD. (1990) A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (Late Triassic) of South Africa. Phil Trans Roy Soc B 330:1–120.

Ward PD, Botha J, Buick R, de Kock MO, Erwin DH, Garrison GH, Kirschvink JL, Smith R. (2005) Abrupt and gradual extinction among Late Permian land vertebrates in the Karoo basin, South Africa. Science 307:709–714.

Watson DMS. (1912) *Mesosuchus browni*, gen. et spec. nov. Rec Albany Mus 2:296–297.

Watson DMS. (1957) On *Millerosaurus* and the early history of the sauropsid reptiles. Phil Trans Roy Soc B 240:325–400.

Weigelt K. (1930). *Palaeochamaeleo jaekeli nov. gen. nov sp.* Ein neuer Rhynchocephale aus dem Mansfelder Kupferschiefer. Leopoldina 6:625–642.

Weinbaum JC. (2011) The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. PaleoBios 30:18–44.

Welman J. (1998) The taxonomy of the South African proterosuchids (Reptilia, Archosauromorpha). J Vert Paleo 18:340–347.

Welman J, Fleming A. (1993) Statistical analysis of the skulls of Triassic proterosuchids. Palaeo Afr 30:113–123.

Wescott WA, Diggens JN. (1998) Depositional history and stratigraphical evolution of the Sakamena group (Middle Karoo Supergroup) in the southern Morondava Basin, Madagascar. J Afr Earth Sci 27:461–479.

Whatley RL. (2005) Phylogenetic relationships of *Isalorhynchus genovefae*, the rhynchosaur (Reptilia, Archosauromorpha). Ph.D. thesis, University of California at Santa Barbara.

Whiteside DI. (1986) The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et sp. nov. and the modernizing of a living fossil. Phil Trans Roy Soc B 312:379–430.

Whiteside DI, Marshall JEA. (2008) The age, fauna and paleoenvironment of the Late Triassic fissure deposits of Tytherington, south Gloucestershire, UK. Geol Mag 145:105–147.

Whiteside JH, Grogan DS, Olsen PE, Kent DV. (2011) Climatically driven biogeographic provinces of Late Triassic tropical Pangea. Proc Nat Acad Sci 108:8972–8977.

Wiens JJ, Hutter CR, Mulcahy DG, Noonan BP, Townsend TM, Sites JW, Reeder TW. Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. Bio Letters 6:1043–1046.

Wild R. (1973) Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergenbisse). Abhand der Schweizer Paläo Gesellschaft 95:1–162.

Wild R. (1980a) Die Triasfauna der Tessiner Kalkalpen. XXIV. Neue funde von *Tanystropheus* (Reptilia, Squamata). Abhand der Schweizer Paläo Gesellschaft 102:1–43.

Wild R. (1980b) *Tanystropheus* (Reptilia, Squamata) and its importance for stratigraphy. Mem Soc Geol France 139:201–206.

Wild, R. (1980c). The fossil deposits of Kupferzell, southwest Germany. Mesozoic Vertebrate Life 1:15–18.

Wild R. (1990) *Aetosaurus* (Reptilia Thecodontia) from the Upper Triassic (Norian) of Cene near Bergamo, Italy with a revision of the genus. Riv Mus Civ Sci Nat Bergamo 14:1–24.

Wilkinson M, Benton MJ. (1996) Sphenodontid phylogeny and the problems of multiple trees. Phil Trans Roy Soc B 351:1–16.

Williston SW. (1904) The temporal arches of the Reptilia. Biol Bull 7:175–192.

Williston SW. (1917) The phylogeny and classification of reptiles. J Geol 25:411–421.

Winchester L, Bellairs Ad'A. (1977) Aspects of vertebral development in lizards and snakes. J Zool Soc London 181:495–525.

Witmer LM. (1997) The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Soc Vert Paleo, Mem 3:1–73.

Witmer LM, Chatterjee S, Franzosa J, Rowe T. (2003) Neuroanatomy of flying reptiles and implications for flight, posture and behavior. Nature 425:950–953.

Xu X, et al. (2011) A monodactyl nonavian dinosaur and the complex evolution of the alvarezsauroid hand. Proc Nat Acad Sci 108:2338–2342.

Yates AM. (2003) The species taxonomy of the sauropodomorph dinosaurs from the Löwenstein Formation (Norian, Late Triassic) of Germany. Palaeo 46:317–337.

Young CC. (1936) On a new *Chasmatosaurus* from Sinkiang. Bull Geol Soc China 15:291–311.

Young CC. (1963) Additional remains of *Chasmatosaurus yuani* Young from Sinkiang, China. Vertebrate PalAsiatica 13:215–222.

Zaher H, Rieppel O. Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. Amer Mus Nov 3271:1–19.

Zani PA. (2000) The comparative evolution of lizard claw and toe morphology and clinging performance. Journal of Evolutionary Biology 13:316–325.

Zanno L, Makovicky PJ. (2010) Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. Proc Nat Acad Sci 108:232–237.

Zeigler KE, Lucas SG, Morgan VL. (2005). Vertebrate fauna of the upper Triassic Mesa Montosa Member (Petrified Forest Formation, Chinle Group), Chama Basin, northern New Mexico. NM Geol Soc Guidebook 56:335–340.

Zhang F-K. (1975) A new thecodont *Lotosaurus*, from the Middle Triassic of Hunan. Vertebrata PalAsiatica 13:144–147.

Zhang G, et al. (2014) Comparative genomics reveals insights into avian genomes and adaptation. Science 346:1311–1320.

Zhou Z, Zhang F. (2002) A long-tailed, seed-eating bird from the Early Cretaceous of China. Nature 418:405–409.