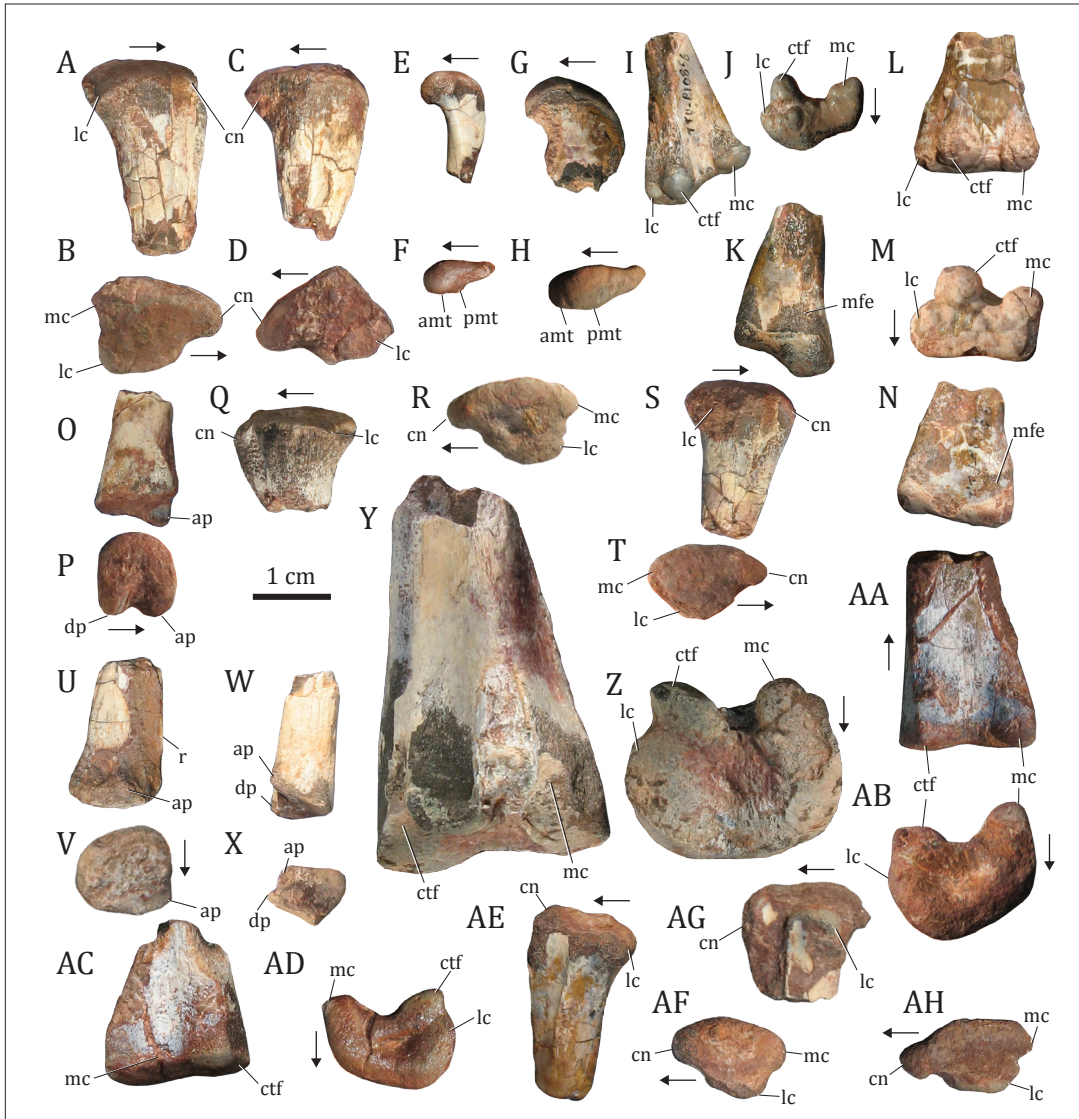# *PaleoBios*

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EMILY J. LESSNER, WILLIAM G. PARKER, ADAM D. MARSH, STERLING J. NESBITT, RANDALL B. IRMIS & BILL D. MUELLER (2018). New insights into Late Triassic dinosauromorph-bearing assemblages from Texas using apomorphy-based identifications.

Cover illustration: Dinosauromorph limb bones from the Late Triassic Dockum Group of Texas. See Figure 10 for details.
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New insights into Late Triassic dinosauromorph-bearing assemblages from Texas using apomorphy-based identifications

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The Upper Triassic Dockum Group of Garza County, Texas (lower, middle, and upper Cooper Canyon Formation) captures the radiation of Triassic non-marine tetrapods by preserving a variety of Late Triassic taxa from the southwestern United States. Our understanding of the vertebrate assemblage from these strata largely comes from a single site, the Post Quarry (lower Cooper Canyon Formation), with previous research documenting a variety of temnospondyls, sphenodontians, non-archosauriform archosauromorphs, and archosauriforms including a phytosaur, three species of aetosaurs, a poposauroid, a rauisuchid, a crocodylomorph, and several dinosauromorphs. To more completely reconstruct the vertebrate assemblage of the Dockum Group of Garza County we use an apomorphy-based approach to identify morphologically similar disarticulated and fragmentary elements from a variety of localities that span the entire Cooper Canyon Formation (Norian-Rhaetian), allowing assignments from the large clade level to the species level. Many skeletal elements are incomplete yet diagnostic and are assigned to the least inclusive clade if discrete character states do not allow for an unambiguous species-level identification. We identify new specimens referable to numerous clades including Tanystropheidae, Allokotosauria + *Prolacerta* + Archosauriformes, *Vancleavea* + *Litorosuchus*, Phytosauria, Paracrocodylomorpha, Dinosauriformes, and Saurischia, in addition to additional species identifications of the aetosaur *Scutarx deltatlyus*, and the dinosauromorph *Drommeron gregorii*. Our study of this material demonstrates the utility of an apomorphy-based approach in making testable and repeatable observations for identifying small, isolated fragmentary fossil tetrapod material to reconstruct a more accurate faunal hypothesis for a portion of the Late Triassic of Texas. Previous claims of the earliest dinosaurs from near the base of the Dockum Group do not pass the apomorphy-based identification test, and the question of whether the oldest known North American dinosaurs are present in the Chinle Formation or Dockum Group can be resolved by utilizing vertebrate biostratigraphic correlation. Our revision of these fossil assemblages supports the hypothesis that early diapsids, early archosauromorphs, and non-dinosaurian dinosauromorphs were more common, diverse, and widespread in low latitudes during this time than previously thought.

Keywords: Upper Triassic, Dockum Group, Diapsida, Archosauromorpha, Dinosauromorpha

INTRODUCTION

The radiation and diversification of terrestrial diapsids during the Triassic Period led to the appearance of taxa characterized by unique suites of morphologies in addition to the emergence of present-day clades (Fraser and Sues 2010). Key discoveries emphasizing the diversity of Late Triassic taxa include the recognition of small diapsids (Senter 2004, Pritchard et al. 2016), early archosauromorphs (Murry 1986, 1989a, b, Nesbitt et al. 2015, Pritchard et al. 2015), shuvosaurid poposauroids (Long and Murry 1995, Nesbitt and Norell 2006, Nesbitt, 2007), as well as the discovery of abundant non-dinosaurian dinosauromorphs and dinosauriforms from Upper Triassic strata (Dzik 2003, Ferigolo and Langer 2007, Irmis et al. 2007a, Nesbitt et al. 2007, 2009c, 2010, Kammerer et al. 2012, Martinez et al. 2016). What is significant is that discovery of relatively complete material prompted workers to re-evaluate specimens already in collections, allowing the identification of these clades in material collected over the past seven decades.

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For example, the description of the non-dinosaurian dinosauriform *Silesaurus opolensis* Dzik, 2003 resulted in a paradigm shift towards the discoveries of large, possibly globally-distributed dinosauriforms with unexpected morphologies, which was needed to highlight the significance of less complete, previously collected material. Along with the subsequent discovery of skeletal material that could unambiguously be assigned to the tooth-taxon *Revueltosaurus callenderi* Hunt, 1989, this spurred apomorphy-based investigations (Parker 2005b, Irmis et al. 2007b, Nesbitt et al. 2007) of the Late Triassic dinosaur record of North America. These studies found that many of the Late Triassic fossils previously assigned to the Dinosauria were not referable to that clade based on discrete character states present in the specimens and that Triassic dinosaurs in North America were rarer and less diverse than previously hypothesized. A similar apomorphy-based study provided critical new paleoecological insights by overturning the long standing hypothesis that juvenile dinosaurian gut contents in an adult specimen of *Coelophysis bauri* Colbert, 1989 was evidence for cannibalism (e. g., Colbert 1989, 1995) by determining that the gut contents belonged instead to a pseudosuchian archosaur (Nesbitt et al. 2006).

Such studies have illuminated that although avemetatarsalians and pseudosuchians are distinct phylogenetically, their postcrania can be morphologically similar, anatomical convergence is common, and that apomorphy-based identification, utilizing character state distributions from up-to-date phylogenetic analyses, is essential to determining taxonomic assignments (Nesbitt and Stocker 2008, Nesbitt et al. 2017b). A striking example of this issue is the discovery that some members of Avemetatarsalia such as *Asilisaurus* Nesbitt et al., 2010 and *Teleocrater* Charig, 1956 possessed a crocodylian-like tarsus, a character that was traditionally used to separate avemetatarsalians and pseudosuchians (Nesbitt et al. 2010, 2017a). Other key recent studies regarding the anatomy of Late Triassic reptiles include expanded understanding of the phylogenetic relationships and stratigraphic occurrences of the archosauriform *Vancleavea campi* Long and Murry, 1995 (Parker and Barton 2008, Nesbitt et al. 2009a), the first definitive records of tanystropheids from western North America (Pritchard et al. 2015), the discovery of three-dimensionally preserved drepanosaurids (Pritchard et al. 2016), and the recognition of a diversity of allokotosaurid archosauromorphs other than *Trilophosaurus* Case, 1928 (Spielmann et al. 2006, Spielmann et al. 2009, Flynn et al. 2010, Nesbitt et al. 2015, 2017b, Marsh et al. 2017).

Voucher specimens with discrete apomorphic character states allow for the verification of taxonomic assignments when describing vertebrate faunal assemblages (Nesbitt and Stocker 2008, Bell et al. 2010). This paper follows those recommendations and demonstrates the utility of an apomorphy-based approach in identifying isolated and fragmentary small limb material from a variety of sites from the Dockum Group of Texas to report a tetrapod assemblage whose taxonomy is both testable and repeatable.

GEOLOGIC SETTING AND AGE

All of the specimens discussed here were collected from localities within the Upper Triassic Dockum Group of western Texas by field crews from Texas Tech University (Table 1, 2). The stratigraphic relationships and nomenclature of the Dockum Group has been the subject of debate (Chatterjee 1986a, Lucas 1993, 1994, Lehman 1994a, b, Lucas et al. 1994, Long and Murry 1995, Carpenter 1997, Lehman and Chatterjee 2005); however, subsequent detailed fieldwork has elucidated the stratigraphic relationships between many of the vertebrate quarries from the type section of the Cooper Canyon Formation of the Dockum Group in southern Garza County, Texas (Martz 2007, 2008, Martz et al. 2013, Martz and Parker 2017; Fig. 1). Those studies divided the type section of the Cooper Canyon Formation (Lehman 1992) into three units that correlate with formations in eastern New Mexico: a lower mudstone unit that is correlated with the Tecovas Formation, a middle unit that is correlated with the Trujillo Formation, and an upper unit that is correlated with the Bull Canyon Formation (and possibly the Redonda Formation). This scheme places the Post Quarry (MOTT 3624) stratigraphically lower than previously hypothesized (i.e., in the lower part of the Cooper Canyon Formation rather than the upper part of the Cooper Canyon Formation), as it is within Martz's lower mudstone unit along with, but slightly higher than, the Boren (=Neyland) Quarry (MOTT 3869) (Martz et al. 2013). Additional localities in the lower part of the Cooper Canyon Formation include the McCarty Ranch (MOTT 0690) and Kirkpatrick Quarry (MOTT 3628) sites (Martz et al. 2013).

Other specimens discussed in this paper are from localities in the middle part of the Cooper Canyon Formation including the Headquarters (MOTT 3892), Headquarters South (MOTT 3898), Headquarters NW (MOTT 3899), Headquarters N (MOTT 3900) and Green Tooth Arroyo (MOTT 3901). Those from the upper part of the Cooper Canyon Formation include Patty East Quarry

Table 1. List of voucher specimens.

Taxon	Voucher (TTU-P)	Elements	MOTT Locality	Figure
Tetrapoda	11409F	Distal end of L femur	3898	3A, B
	11403	Distal end of R femur	3892	3C, D
	11273	Distal end of R femur	3892	3E, F
	11278	Distal end of L femur	3898	3G, H
	11390A	Distal end of L femur	3892	3I, J
	11390B	Distal end of R femur	3892	3K, L
	11410B	Proximal end of L humerus	3898	3M, N
	11410C	Proximal end of R humerus	3898	3O, P
Reptilia	11287	Complete R femur	3892	4A–C
Diapsida	11407A	Proximal end of L femur	3892	4D, E
	11407B	Proximal end of L femur	3892	4F, G
	11408A	Proximal end of R femur	3898	4H, I
	11408B	Proximal end of R femur	3899	4J, K
	11408C	Proximal end of L femur	3900	4L, M
	11408D	Proximal end of L femur	3901	4N, O
	11288	Proximal end of L femur	3892	4P, Q
	11404A	Distal end of L humerus	3898	4R, S
	11404B	Distal end of L humerus	3898	4T, U
	11404C	Distal end of R humerus	3898	4V, W
	11404D	Distal end of R humerus	3898	4X-Y
	11404E	Distal end of R humerus	3898	4Z, AA
	11394	Distal end of R humerus	3892	4AB, AC
	11410A	Distal end of L humerus	3898	4AD, AE
	11401	Distal end of L humerus	3898	4AF, AG
Sauria	11280	Proximal end of R femur	3898	5A, B
Archosauromorpha	11410E	Distal end of R humerus Distal	3898	5C, D
	11277	end of R? humerus	3898	5E, F
	11386	Proximal end of L ulna	3869	5G
Tanystropheidae	11344	Complete R femur	3869	5H–J
	11281	Distal end of R femur	3628	5K, L
Allokotosauria+*Prolacerta broomi* +Archosauriformes	11409E	Distal end of L femur	3898	5M, N
	11275	Distal end of L femur	3898	5O, P
	11276	Distal end of R femur	3898	5Q, R
	11286	Distal end of L femur	3898	5S, T
	11384	Proximal end of R humerus	3624	5U, V
Archosauriformes	11400	Proximal end of L humerus	3628	6A, B
	11410D	Proximal end of R humerus	3898	6C
	11391	Distal end of R humerus	3880	6D, E
	11392	Distal end of L humerus	3880	6F
Vancleavea campi + Litorosuchus somnii	11382	Complete R humerus	3628	6G–I
	11385	Complete L humerus	3624	6J

Table 1 (continued). List of voucher specimens.

Taxon	Voucher (TTU-P)	Elements	MOTT Locality	Figure
Phytosauria	11395	Complete L femur	0690	6K, L
Archosauria	11399	Distal end of L pubis	3898	7A–C
Pseudosuchia	11393	Proximal end of R tibia	3892	7D
	11290	Proximal end of R tibia	3898	7E, F
	11396A	Proximal end of L tibia	3898	7G, H
	11396B	Proximal end of R tibia	3898	7I, J
	11412F	Proximal end of R tibia	3898	7K, L
	11412G	Proximal end of R tibia	3898	7M, N
	11398	Proximal end of L tibia	3898	7O, P
	11397B	Distal end of R tibia	3898	7Q, R
Aetosauria *Scutarx deltatylus*	10195	L paramedian osteoderm	3899	8A–C
Paracrocodylomorpha	11411E	Proximal end of R femur	3898	9A, B
	11409A	Distal end of L femur	3898	9C, D
	11409B	Distal end of R femur	3898	9E, F
	11048	Distal end of L femur	3902	9G, H
	11283	Distal end of L femur	3898	9I, J
	11284	Distal end of L femur	3898	9K, L
	10845	Distal end of L femur	3898	9M, N
Poposauroidea Shuvosauridae	11411A	Proximal end of L femur	3898	9O, P
	11411B	Proximal end of L femur	3898	9Q, R
	11411C	Proximal end of L femur	3898	9S, T
	11402	Proximal end of L femur	3899	9U, V
	11272	Proximal end of R femur	3898	9W, X
Ornithodira=Avemetatarsalia Dinosauromorpha	11412A	Proximal end of R tibia	3898	10A, B
	11412E	Proximal end of L tibia	3898	10C, D
Lagerpetidae	11877	Proximal end of R femur Proximal end of R femur	3898	10E, F
	11282		3898	10G,H
	10866	Distal end of L femur	3898	10I–K
Dromomeron gregorii	11186	Distal end of L femur	3869	10L, M
Dinosauriformes	11412B	Distal end of L tibia	3898	10O, P
Dinosauria	11289	Proximal end of L tibia	3898	10Q, R
	11412D	Proximal end of R tibia	3898	10S, T
	11405B	Distal end of R tibia	3898	10U, V
Saurischia	11412C	Distal end of R tibia	3898	10W, X
	11139	Distal end of L femur	3899	10Y, Z
	11409C	Distal end of L femur	3898	10AA, AB
	11274	Distal end of R femur	3898	10AC, AD
Theropoda	11405A	Proximal end of L tibia	3898	10AE, AF
	11397A	Proximal end of L tibia	3898	10AG, AH

Table 2. Voucher specimens listed by locality.

Locality	Formation	TTU-P#	Apomorphy-based identification
Patty East MOTT 3880	Upper Cooper Canyon Fm.	11391 11392	Archosauriformes Archosauriformes
Lower Far East MOTT 3902	Upper Cooper Canyon Fm.	11048	Paracrocodylomorpha
Headquarters S MOTT 3898	Middle Cooper Canyon Fm.	11409F	Tetrapoda
		11278	Tetrapoda
		11410B	Tetrapoda
		11410C	Tetrapoda
		11408A	Diapsida
		11404A	Diapsida
		11404B	Diapsida
		11404C	Diapsida
		11404D	Diapsida
		11410E	Diapsida
		11410A	Diapsida
		11401	Diapsida
		11280	Sauria
		11410E	Archosauromorpha
		11277	Archosauromorpha
		11409E	Allokotosauria+*Prolacerta broomi*+Archosauriformes
		11275	Allokotosauria+*Prolacerta broomi*+Archosauriformes
		11276	Allokotosauria+*Prolacerta broomi*+Archosauriformes
		11286	Allokotosauria+*Prolacerta broomi*+Archosauriformes
		11410D	Archosauriformes
		11399	Archosauria
		11290	Pseudosuchia
		11396A	Pseudosuchia
		11396B	Pseudosuchia
		11412F	Pseudosuchia
		11412G	Pseudosuchia
		11398	Pseudosuchia
		11397B	Pseudosuchia
		11411E	Paracrocodylomorpha
		11409A	Paracrocodylomorpha
		11409B	Paracrocodylomorpha
		11283	Paracrocodylomorpha
		11284	Paracrocodylomorpha
		10845	Paracrocodylomorpha
		11411A	Shuvosauridae
		11411B	Shuvosauridae
		11411C	Shuvosauridae
		11272	Shuvosauridae
		11412A	Dinosauromorpha
		11412E	Dinosauromorpha
		11877	Lagerpetidae
		11282	Lagerpetidae
		10866	Lagerpetidae
		11412B	Dinosauriformes
		11289	Dinosauria
		11412D	Dinosauria
		11405B	Dinosauria
		11412C	Saurischia
		11409C	Saurischia
		11274	Saurischia
		11405A	Theropoda
		11397A	Theropoda

Table 2 (continued)**.** Voucher specimens listed by locality.

| Locality	Formation	TTU-P#	Apomorphy-based identification
Headquarters MOTT 3892	Middle Cooper Canyon Fm.	11403	Tetrapoda
		11273	Tetrapoda
		11390A	Tetrapoda
		11390B	Tetrapoda
		11287	Reptilia
		11407A	Diapsida
		11407B	Diapsida
		11288	Diapsida
		11394	Diapsida
		11393	Pseudosuchia
Headquarters NW MOTT 3899	Middle Cooper Canyon Fm.	11408B	Diapsida
		10195	*Scutarx deltatylus*
		11402	Shuvosauridae
		11139	Saurischia
Headquarters N MOTT 3900	Middle Cooper Canyon Fm.	11408C	Diapsida
Green Tooth Arroyo MOTT 3901	Middle Cooper Canyon Fm.	11408D	Diapsida
Post Quarry MOTT 3624	Lower Cooper Canyon Fm. (Upper part)	11384	Allokotosauria+*Prolacerta broomi*+Archosauriformes
		11385	*Vancleavea campi*+*Litorosuchus somnii*
		09472	Clevosauridae (lepidosaur)
		09497	*Trilophosaurus dornorum*
		09604	Simiosauria
		09606	Simiosauria
		09231	Phytosauria
		09236	Phytosauria
	Additional taxa assigned with an apomorphy-based method (Martz et al. 2013)	09234	*Leptosuchus* (phytosaur)
		09420	*Calyptosuchus wellesi* (aetosaur)
		09214	*Typothorax coccinarum* (aetosaur)
		09416	*Paratypothorax* (aetosaur)
		09204	*Desmatosuchus smalli* (aetosaur)
		09280+	*Shuvosaurus inexpectatus*
		09000/2	*Postosuchus kirkpatrickorum*
		11443	Crocodylomorpha
		11282	*Dromomeron gregorii*
		11127	Dinosauriformes
		09021	*Technosaurus smalli* (silesaurid)
		10082	Herrerasauridae (theropod)
		11044	Neotheropoda
		10071	Neotheropoda
Kirkpatrick Quarry MOTT 3628	Lower Cooper Canyon Fm. (Middle part)	11281	Tanystropheidae
		11400	Archosauriformes
		11382	*Vancleavea campi*+*Litorosuchus somnii*
McCarty Ranch MOTT 0690	Lower Cooper Canyon Fm. (Middle part)	11395	Phytosauria
Boren Quarry MOTT 3869	Lower Cooper Canyon Fm. (Lower part)	11386	Archosauromorpha
		11344	Tanystropheidae
		11186	*Dromomeron gregorii*
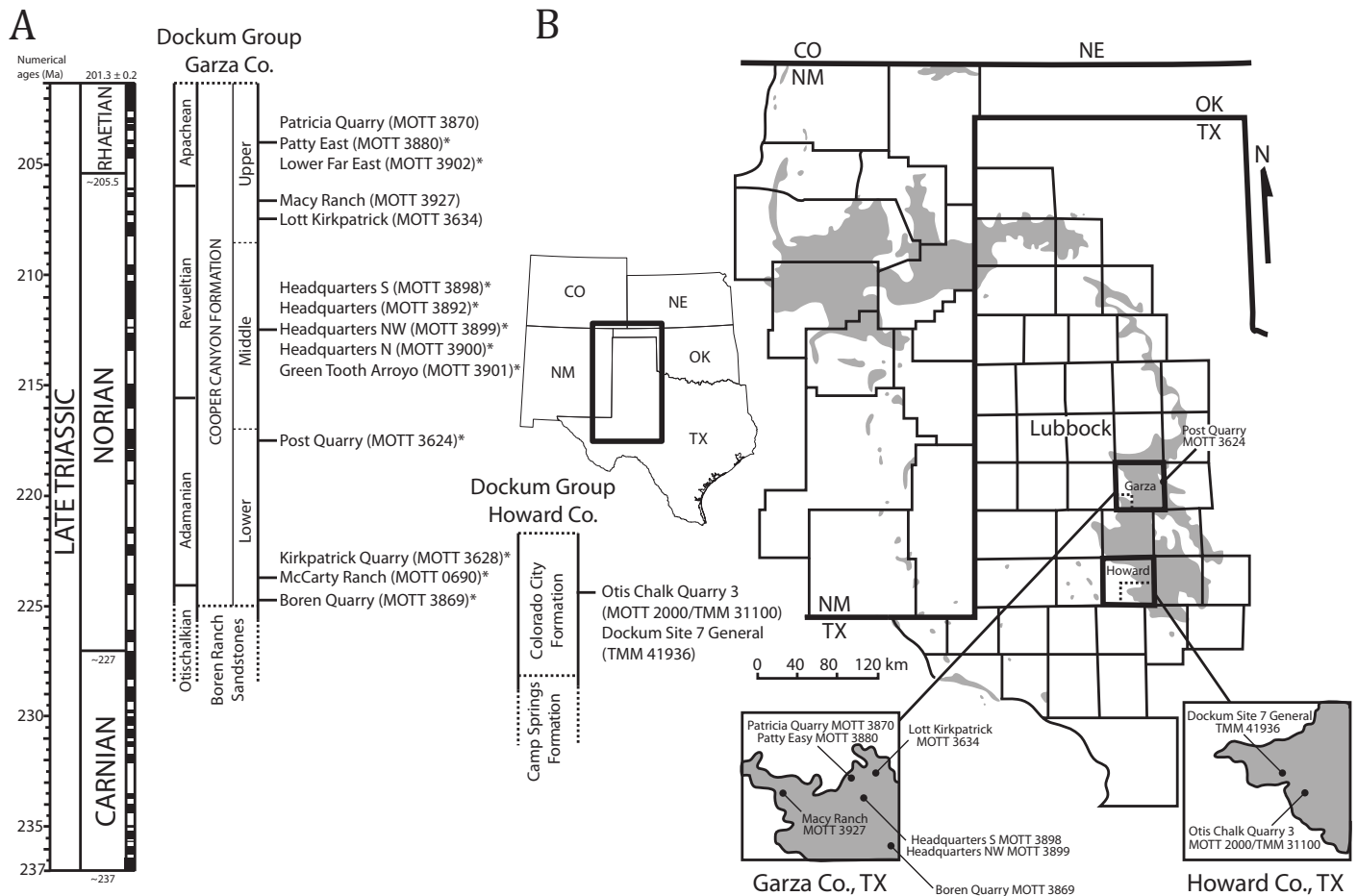
Figure 1. Relative stratigraphic (**A**) and geographic (**B**) locations of fossil localities (adapted from Heckert et al. 2006, Martz 2008, Mueller et al. 2016, Sarigül, 2016, 2017a, 2017b, and Kent et al. 2017). Asterisks indicate localities with described specimens.

(MOTT 3880) and Lower Far East (MOTT 3902) (Fig. 1).

The exact ages of these quarries are unknown. However, the Tecovas Formation and lower part of the Cooper Canyon Formation have a similar tetrapod assemblage to the Blue Mesa Member and lower part of the Sonsela Member of the Chinle Formation in northern Arizona and western New Mexico (Parker and Martz 2011, Martz et al. 2013, Martz and Parker 2017), which are now dated to between 217 Ma and 225 Ma (Irmis and Mundil 2008, Irmis et al. 2011, Ramezani et al. 2011, 2014, Nordt et al. 2015). According to all recent versions of the Late Triassic timescale (e.g., Ogg 2012, Kent et al. 2017) these U-Pb zircon ages fall within the Norian, thus all of the Dockum localities discussed here are likely Norian in age.

The lowest known occurrence of a phytosaur in the Dockum Group is the holotype skull of *Wannia scurriensis* Langston, 1949 (TTU-P00539) from MOTT 0696 in Scurry County (Stocker 2013a). This locality is in the Camp Springs Conglomerate and is Otischalkian in age (Martz and Parker 2017). This includes the top of the

Boren Ranch sandstone beds and almost all of the lower part of the Cooper Canyon Formation (Martz 2008, Martz and Parker 2017).

The lowest known occurrence of a leptosuchomorph phytosaur (*sensu* Stocker 2010) is a skull (TTU-P09234) referred to *Leptosuchus* Case, 1922 from the Post Quarry (MOTT 3624) in the middle of the Cooper Canyon Formation and diagnoses the base of the Adamanian teilzone in Garza County (Martz and Parker 2017). The Adamanian teilzone includes the uppermost part of the lower Cooper Canyon Formation and the lower half of the middle Cooper Canyon Formation (Martz 2008, Martz and Parker 2017).

The lowest known occurrence of the phytosaur *Machaeroprosopus* Mehl, 1916 in the Dockum Group of Texas is an isolated squamosal (TTU-P11880) from the Headquarters locality (MOTT 3892; Martz 2008). Thus, the top of the middle part of the Cooper Canyon Formation and at least most of the uppermost part of the Cooper Canyon Formation are Revueltian in age (Lucas and Hunt

1993, Martz and Parker 2017). The base of the Revueltian corresponds to ~215 Ma in northeastern Arizona (Parker and Martz 2011, Martz and Parker 2017, Kent et al. 2018).

The lowest known occurrence of a phytosaur referable to a monophyletic "*Redondasaurus*" Hunt and Lucas, 1993 (*sensu* Martz et al. 2014) is a referred specimen of *Machaeroprosopus lottorum* Hungerbühler et al., 2013 (TTU-P10077) from the Patricia Quarry (MOTT 3870; Hungerbühler et al. 2013). This specimen diagnoses the base of the local Apachean teilzone in Garza County (Martz and Parker 2017).

Therefore, because precise radioisotopic and magnetostratigraphic age constraints are not available for the Dockum Group, the best age estimates for the various vertebrate localities in Garza County are based on vertebrate biostratigraphic correlations to the Chinle Formation of Arizona and New Mexico where such geochronologic data exist. The Boren (Neyland) Quarry (MOTT 3869) from the lower part of the Cooper Canyon Formation is latest Otischalkian in age, likely between 227–224 Ma (Martz and Parker 2017) and roughly equivalent in age to the Otis Chalk quarries. The Kirkpatrick (MOTT 3628) and McCarty Ranch (MOTT 0690) sites are latest Otischalkian or earliest Adamanian in age (approximately 224–225 Ma). The Post Quarry (MOTT 3624) from the middle of the Cooper Canyon Formation is late Adamanian in age, between 215–220 Ma (Martz et al. 2013, Martz and Parker 2017). The various Headquarters localities (MOTT 3892, 3898, 3899, 3900), Green Tooth Arroyo (MOTT 3901), Macy Ranch (MOTT 3927), and Lott Kirkpatrick (MOTT 3634) in the upper part of the middle Cooper Canyon Formation and the lower part of the uppermost Cooper Canyon Formation are Revueltian in age, between 215–207 Ma (Martz and Parker 2017; Kent et al. 2018). The Patricia Quarry (MOTT 3870), Patty East locality (MOTT 3880), and Lower Far East locality (MOTT 3902) in the upper Cooper Canyon Formation are Apachean in age, thought to be between 207–202 Ma (Fig. 1) (Martz 2008, Martz and Parker 2017). Nevertheless, the assignment of numerical ages from Arizona to these Dockum strata should be taken with great caution. They are based on long-distance vertebrate biostratigraphic correlations, which can be problematic because taxa do not necessarily have the same first and last appearance across their entire biogeographic range (e.g., Irmis et al. 2010, Martz and Parker 2017, pg. 12 in Parker and Martz 2017).

Institutional Abbreviations—BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; **ISIR**, Indian Statistical Institute, Kolkata, India; **MCN**, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MOTT**, Museum of Texas Tech Locality; **MoTTU**, Museum of Texas Tech University, Lubbock, Texas; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico; **PEFO**, Petrified Forest National Park, Arizona; **PFV**, Petrified Forest National Park vertebrate fossil locality; **TMM**, Vertebrate Paleontology Laboratory, University of Texas, Austin, Texas; **TTU-P**, Museum of Texas Tech University Paleontology, Lubbock, Texas; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan.

MATERIALS AND METHODS

The majority of the material in this study was collected by one of the authors (BDM) and Texas Tech fossil preparator Douglas Cunningham through an ongoing, intensive field study of fossil localities in the Dockum Group of Garza County (Martz 2008, Mueller et al. 2016). These fossils are reposited in the MoTTU in Lubbock, Texas. Other material collected from this study has been or will be published elsewhere (e.g., Mueller and Parker 2006, Martz 2008, Nesbitt and Chatterjee 2008, Martz et al. 2013, Sarigül 2016, 2017a, b). The collection presented here highlights the diversity of small reptiles (predominantly archosauromorphs) from these localities.

The majority of the material was collected on the surface and prepared using Paraloid B-72 as a consolidant and an adhesive. Cellulose powder mixed with pH neutral polyvinal acetate adhesive was used as a filler for some bones.

All specimens consist of fragmentary limb elements (with the exception of the aetosaur plate, TTU-P10195) and were identified using discrete apomorphies and assigned to the least inclusive clade using the technique recommended by Nesbitt and Stocker (2008) following Bell et al. (2004, 2010). Furthermore, much of this material is from small individuals (<1m–3m), and in all cases ontogenetic age could not be assessed based on single elements, as size alone is not a reliable indicator of skeletal maturity (Brochu 1996, Irmis 2007, Griffin and Nesbitt 2016a). Past studies have been hindered by a lack of good comparative specimens and an understanding of the interspecific morphological variation within the limb bones of Late Triassic archosauromorphs. This has been remedied by recent anatomical studies of a variety of archosauromorphs (e.g., Irmis et al. 2007b, Nesbitt et al. 2009a, 2015, Nesbitt 2011, Pritchard 2015, and Pritchard et al. 2015). Anatomical orientation follows the relevant publications listed previously. Apomorphies used to identify the fossils in this study are based

on character states that are optimized in phylogenetic analyses in these and other recent publications (Table 3). Generally, the character states cited are consistent across multiple analyses. Relationships of the described taxa are provided in Figure 2.

SYSTEMATIC PALEONTOLOGY

TETRAPODA Goodrich, 1930

Referred Specimens—*Femora:* TTU-P11409F, distal end of left femur (Fig. 3A, B); TTU-P11403, distal end of right femur (Fig 3C, D); TTU-P11273, distal end of right femur (Fig. 3E, F); TTU-P11278, distal end of left femur (Fig. 3G, H); TTU-P11390A, distal end of left femur (Fig. 3I, J); TTU-P11390B, distal end of right femur (Fig. 3K, L). *Humeri:* TTU-P11410B, proximal end of left humerus (Fig. 3M, N); TTU-P11410C, proximal end of right humerus (Fig. 3O, P).

Figure 2. Phylogenetic relationships of taxa and clades discussed in the text with those present in the described fossil assemblage highlighted. Based on Rubidge and Sidor 2011, Nesbitt 2011, Nesbitt and Ezcurra 2015, Nesbitt et al. 2015, Cabreira et al. 2016, Ezcurra 2016, Parker 2016a, Nesbitt et al. 2017a, and Pritchard and Nesbitt 2017.

Table 3. Phylogenetic analyses consulted, by clade and element.

TETRAPODA	Femora	Benton 1985 Panchen and Smithson 1987
	Humeri	Gauthier et al. 1988
REPTILIA	Femur	Pritchard 2015
DIAPSIDA	Femur	Pritchard 2015
	Humeri	Senter 2004
SAURIA	Femur	Gauthier et al. 1988
ARCHOSAUROMORPHA	Humeri	Senter 2004 Pritchard et al. 2015
	Ulna	Ezcurra 2016 Nesbitt 2011
TANYSTROPHEIDAE	Femora	Pritchard et al. 2015
ALLOKOTOSAURIA + *PROLACERTA BROOMI* + ARCHOSAURIFORMES	Femora	Ezcurra 2016 Nesbitt et al. 2015 Nesbitt 2011
	Humerus	Ezcurra 2016 Nesbitt et al. 2015
ARCHOSAURIFORMES	Humeri	Ezcurra 2016 Nesbitt 2011
VANCLEAVEA CAMPI + LITOROSUCHUS SOMNII	Humeri	Li et al. 2016 Ezcurra 2016
PHYTOSAURIA	Femur	Nesbitt 2011
ARCHOSAURIA	Pubis	Nesbitt 2011
PSEUDOSUCHIA	Tibiae	Nesbitt 2011
SCUTARX DELTATYLUS	Osteoderm	Parker 2016a
PARACROCODYLOMORPHA	Femora	Nesbitt 2011
SHUVOSARIDAE	Femora	Nesbitt 2011
DINOSAUROMORPHA	Tibiae	Novas 1996 Nesbitt 2011
LAGERPETIDAE	Femora	Nesbitt 2011
DROMOMERON GREGORII	Femur	Nesbitt 2011 Nesbitt et al. 2009c
DINOSAURIFORMES	Tibia	Nesbitt 2011
DINOSAURIA	Tibiae	Novas 1992
SAURISCHIA	Tibia	Nesbitt 2011
	Femora	Nesbitt 2011
THEROPODA	Tibiae	Novas 1992 Nesbitt 2011
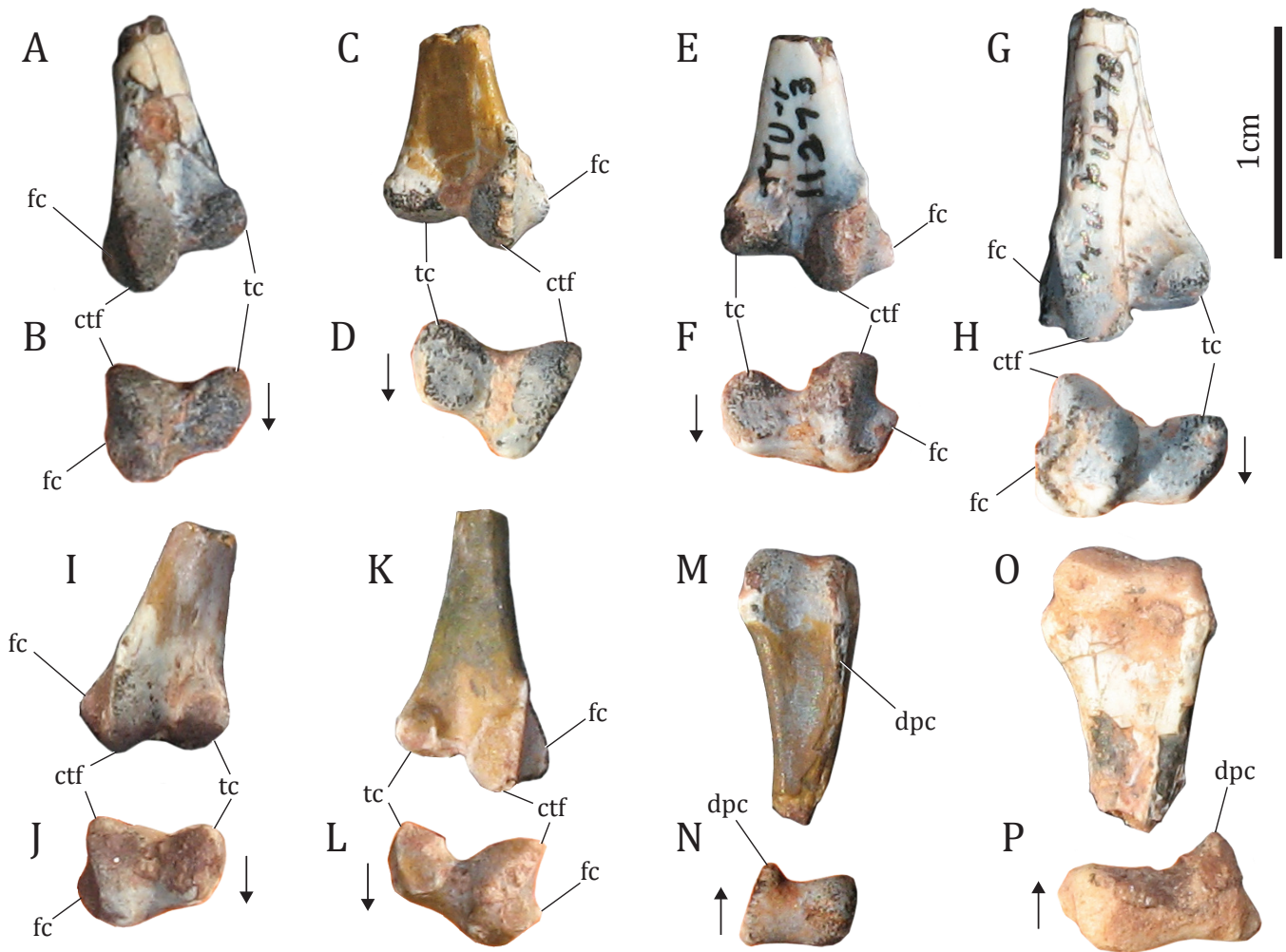
Figure 3. A–L. Tetrapod femora in posterior (A, C, E, G, I, K) and distal (B, D, F, H, J, L) views. **A, B.** TTU-P11409F. **C, D.** TTU-P11403. **E, F.** TTU-P11273. **G, H.** TTU-P11278. **I, J.** TTU-P11390A. **K, L**. TTU-P11390B. **M–P.** Tetrapod humeri in anterior (M), proximal (N, P), and posterior (O) views. M, N. TTU-P11410B. O, P. TTU-P11410C. Scale bar 1 cm. Abbreviations: **ctf**, crista tibiofibularis; **dpc**, deltopectoral crest; **fc**, fibular condyle; **tc**, tibial condyle. Arrows point anteriorly.

Localities—*Femora:* MOTT 3898 (Headquarters South); MOTT 3892 (Headquarters). *Humeri:* MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—

Femora—The distal ends of the femora (TTU-P11409F, TTU-P11403, TTU-P11273, TTU-P11278, TTU-P11390A-B) preserve the distal expansions of each element as well as small portions of the midshafts proximally (Fig. 3A–L). The specimens are nearly identical, and therefore we describe them together. The femur preserves two distal condyles and the crista tibiofibularis (Fig. 3A–L). The fibular condyle is present as a small lateral crest on the anterolateral margin of the crista tibiofibularis. The crista tibiofibularis is circular in lateral view and extends

further distally than the smaller medial, tibial condyle (Fig. 3A, C, E, G, I, K). This is in contrast to the neodiapsid character state of level distal articular surfaces (Benton 1985; character B: state 14). The distal surface of the tibial condyle is flat, whereas the distal surface of the crista tibiofibularis is convex, with an anteroposteriorly-trending ridge on the lateral margin (Fig. 3B, D, F, H, J, L). There is a wide groove separating the crista tibiofibularis and the tibial condyle that continues onto the dorsal surface. This combination of femoral characters is similar to that of the drepanosauromorphs *Hypuronector limnaios* Colbert and Olsen, 2001 and *Vallesaurus cenensis* Wild, 1991 (Renesto et al. 2010). However, the absence of apomorphies specific to Reptilia, Diapsida,
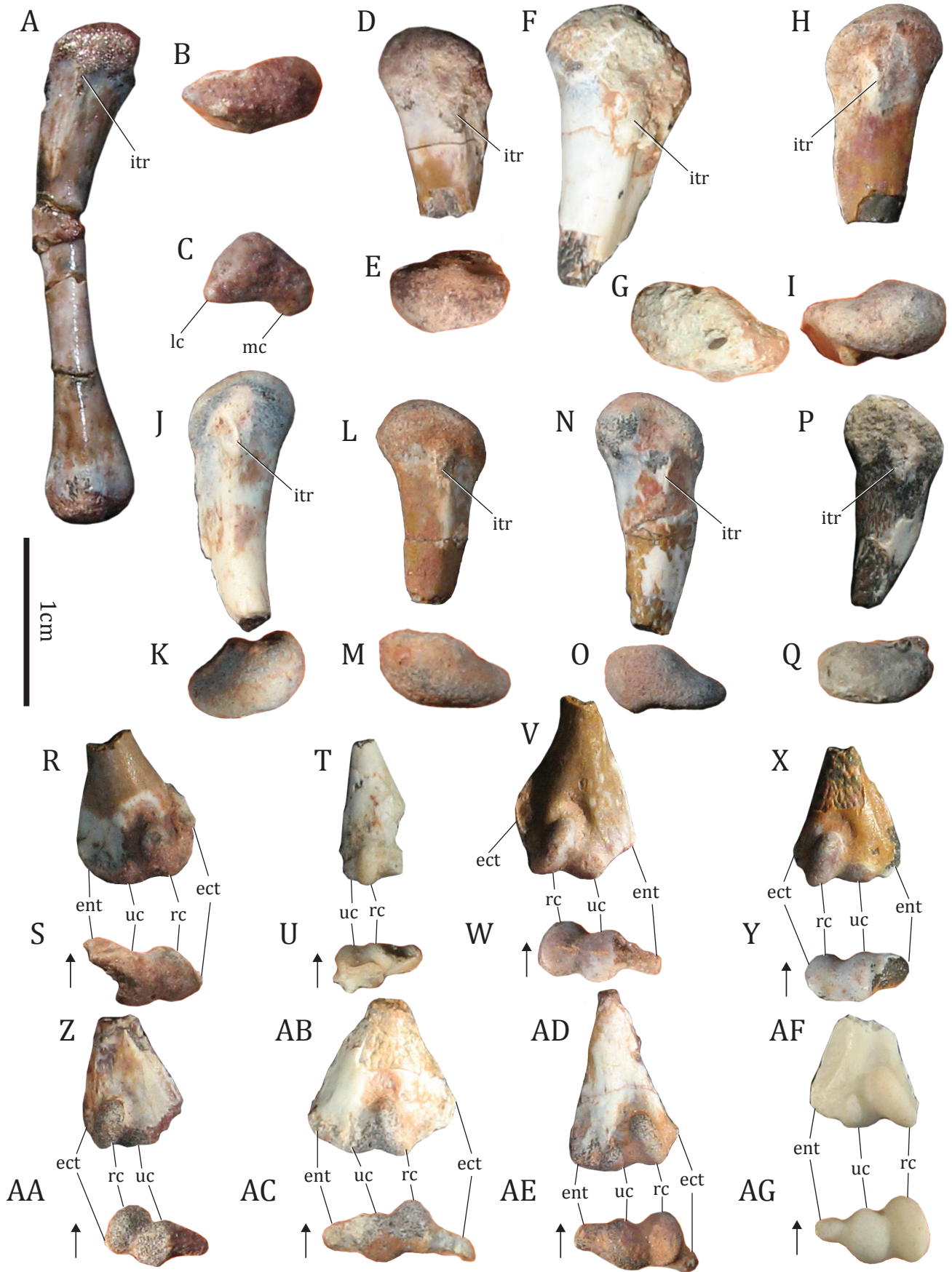
Sauria, or Drepanosauromorpha precludes referral to a more specific clade than Tetrapoda; however, this is the most-inclusive assignment and is based on the presence of distal condyles indicating a hinged knee-joint in the hindlimb (Panchen and Smithson 1987; character 62).

Humeri—The proximal ends of the humeri (TTU-P11410B-C) preserve the proximal expansion and a small portion of the midshaft (Fig. 3M–P). TTU-P11410B is smaller and more gracile than TTU-P11410C, but otherwise the two specimens are identical and are therefore described together. The humerus is subrectangular in proximal view with slightly concave posterior and anterior margins (Fig. 3N, P). The concave anterior margin is formed by a triangular fossa on the anterior surface that tapers distally towards the midshaft. This fossa is bordered laterally by the deltopectoral crest, an anterolateral ridge extending along the length of the proximal end of the humerus from the proximal articular surface onto the midshaft distally (Fig. 3M, N, P). There is a small anteromedial protuberance just distal to the proximal end of the humerus. The lateral surface is flat, rounded proximally, and tapers distally in lateral view. There is another ridge along the posterolateral length of the proximal end of the humerus from the proximal end extending onto the midshaft distally. The ridge-like morphology of the deltopectoral crest and the combination of characters described above are similar to *Hypuronector*, *Vallesaurus*, *Megalancosaurus* Calzavara et al., 1980, and *Drepanosaurus* Pinna, 1980 (Pritchard 2015). We assign TTU-P11410B-C to Tetrapoda based the presence of a distinct humeral shaft (Gauthier et al. 1988), and the absence of apomorphies specific to a more inclusive clade.

<div align="center">

REPTILIA Linnaeus, 1758
sensu Gauthier et al., 1988

</div>

Referred Specimen—TTU-P11287, complete right femur (Fig. 4A–C).

Locality—MOTT 3892 (Headquarters).

Description and Rationale for Assignment—TTU-P11287 is rounded proximally and medially, lacks distinct proximal condyles, and tapers laterally in proximal view (Fig. 4A–C). The laterally tapering portion of the proximal end extends distally as a ridge on the lateral margin of the

midshaft, expanding dorsally into a rounded hump. The ventral surface of the femur preserves a ridge (=internal trochanter) that originates just distal to the proximal surface and extends distally (Fig. 4A). This ridge is present in nearly all early reptiles and diapsids (Pritchard 2015; 259:0). The proximal end of TTU-P11287 is very similar to the proximal ends of other diapsid femora described later, although the internal trochanter is present as a ridge in TTU-P11287, rather than a rounded knob as in the other specimens. However, the distal end of TTU-P11287 is unique among the sample; two distal condyles are preserved, a larger lateral, fibular condyle and a smaller medial, tibial condyle (Fig. 4C). The lateral condyle extends slightly further distally than the medial condyle, similar to the condition in the early reptile *Petrolacosaurus* Reisz, 1981. We assign TTU-P11287 to Reptilia because of the presence of the ridge-like internal trochanter and the absence of apomorphies specific to a more inclusive clade.

<div align="center">

DIAPSIDA Osborn, 1903
sensu Laurin, 1991

</div>

Referred Specimens—*Femora:* TTU-P11407A, proximal end of left femur (Fig. 4D, E); TTU-P11407B, proximal end of left femur (Fig. 4F, G); TTU-P11408A, proximal end of right femur (Fig. 4H, I); TTU-P11408B, proximal end of right femur (Fig. 4J, K); TTU-P11408C, proximal end of left femur (Fig. 4L, M); TTU-P11408D, proximal end of left femur (Fig. 4N, O); TTU-P11288, proximal end of left femur (Fig. 4P, Q). *Humeri*: TTU-P11404A, distal end of left humerus (Fig. 4R, S); TTU-P11404B, distal end of left humerus (Fig. 4T, U); TTU-P11404C, distal end of right humerus (Fig. 4V, W); TTU-P11404D, distal end of right humerus (Fig. 4X, Y); TTU-P11404E, distal end of right humerus (Fig. 4Z, AA); TTU-P11394, distal end of right humerus (Fig. 4AB, AC); TTU-P11410A, distal end of left humerus (Fig. 4AD, AE); TTU-P11401, distal end of left humerus (Fig. 4AF, AG).

Localities—*Femora:* MOTT 3898 (Headquarters South); MOTT 3892 (Headquarters); MOTT 3900 (Headquarters North); MOTT 3901 (Green Tooth Arroyo). *Humeri:* MOTT 3898 (Headquarters South); MOTT 3892 (Headquarters).

< Figure 4. A. Reptilian femur in ventral (A), proximal (B), and distal (C) views. **A–C**. TTU-P11287. **D–Q**. Diapsid femora in ventral (D, F, H, J, L, N, P) and proximal (E, G, I, K, M, O, Q) views. **D,E**. TTU-P11407A. **F, G**. TTU-P11407B. **H, I**. TTU-P11408A. **J, K**. TTU-P11408B. **L, M**. TTU-P11408C. **N, O**. TTU-P11408D. **P, Q**. TTU-P11288. **R–AG**. Diapsid humeri in anterior (R, T, V, X, Z, AB, AD, AF) and distal (S, U, W, Y, AA, AC, AE, AG) views. **R, S**. TTU-P11404A. **T, U**. TTU-P11404B. **V, W**.TTU-P11404C. **X, Y**. TTU-P11404D. **Z, AA**. TTU-P11404E. **AB, AC**. TTU-P11394. **AD, AE**. TTU-P11410A. A**F, AG**. TTU-P11401. Scale bar 1 cm. Abbreviations: **ect**, ectepicondyle; **ent**, entepicondyle; **itr**, internal trochanter; **rc**, radial condyle; **uc**, ulnar condyle. Arrows point anteriorly.
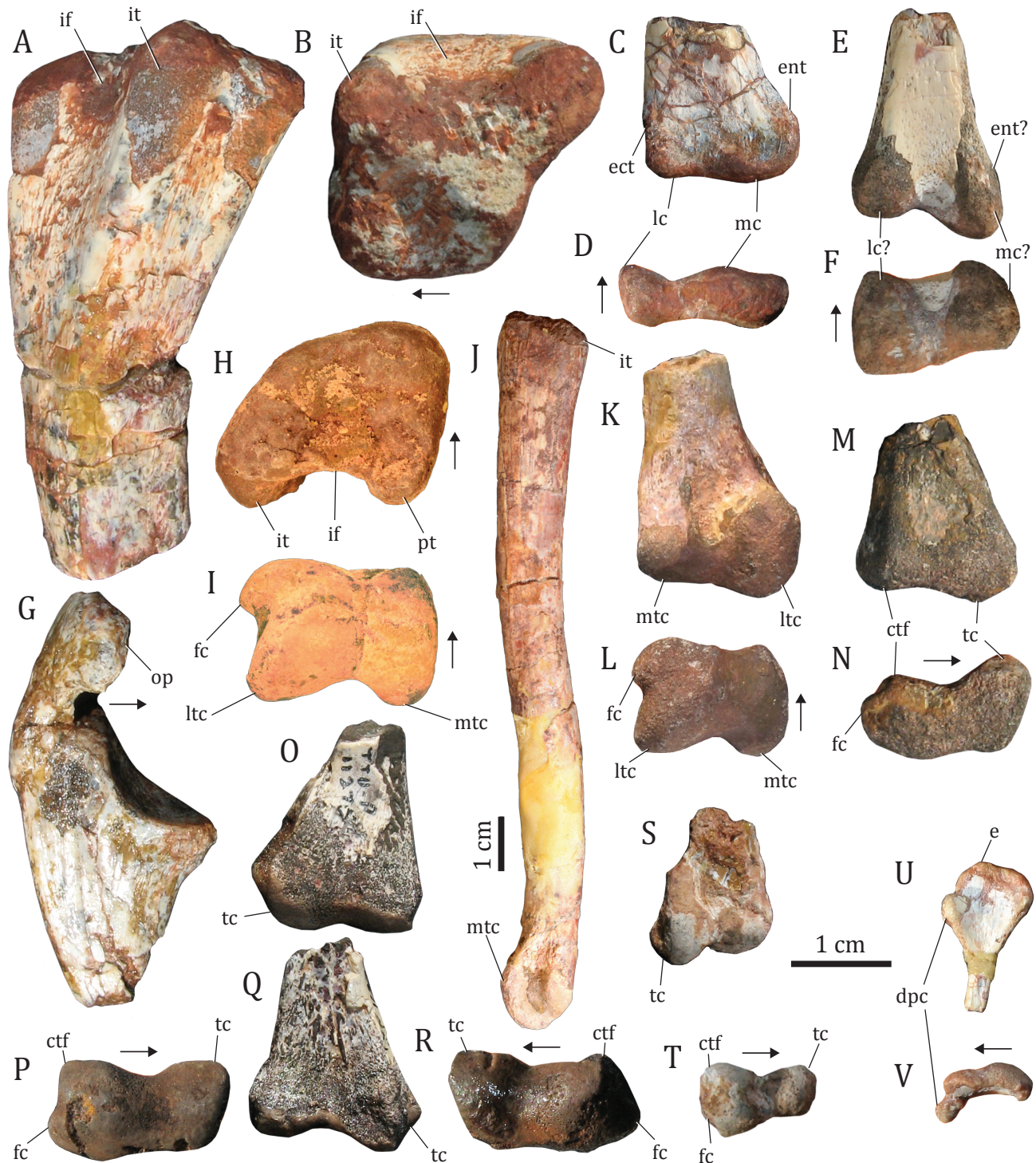
Figure 5. A, B. Saurian femur in ventral (A) and proximal (B) views; TTU-P11280. **C–F**. Archosauromorph humeri in anterior (C, E) and distal (D, F) views. **C, D**.TTU-P11410E. **E, F**. TTU-P11277. **G.** Archosauromorph ulna in medial view; TTU-P11386. **H–K.** Tanystropheid femora in proximal (H), distal (I, L), lateral (J), and posterior (K) views. **H–J**. TTU-P11344, **K, L**. TTU-P11281. **M–T.** Allokotosaurian + *Prolacerta* + archosauriform femora in posteroventral (M), distal (N), anterodorsal (O, Q, S), and distal (P, R, T) views. **M, N**. TTU-P11409E. **O, P**. TTU-P11275. **Q, R**. TTU-P11276. **S, T**. TTU-P11286. **U, V.** Allokotosaurian humerus in ventral (U) and proximal (V) views; TTU-P11384. Scale bars 1 cm (smaller scale bar for J only). Abbreviations: **ctf**, crista tibiofibularis; **dpc**, deltopectoral crest; **e**, expansion; **ect**, ectepicondyle; **ent**, entepicondyle; **fc**, fibular condyle; **if**, intertrochanteric fossa; **it**, internal trochanter; **lc**, lateral condyle; **ltc**, lateral tibial condyle; **mc**, medial condyle; **mtc**, medial tibial condyle; **op**, olecranon process; **pt**, posterior trochanter; **tc**, tibial condyle. Arrows point anteriorly.

Description and Rationale for Assignment—

Femora—The specimens (TTU-P11407A-B, TTU-P11408A-D, TTU-P11288) preserve the proximal expansions of the femora as well as a small portion of the midshafts distally (Fig. 4D–Q). The specimens are nearly identical, and therefore we describe them together. The femur is rounded proximally and medially, lacks distinct proximal condyles, and tapers laterally in proximal view (Fig. 4E, G, I, K, L, O, Q). The laterally-tapering portion extends distally as a ridge on the lateral margin of the midshaft, expanding dorsally into a rounded hump. The ventral surface of the femur preserves a rounded tuberosity, marking the internal trochanter, that originates just distal to the proximal end and extends distally as a ridge (Fig. 4D, F, H, J, L, N, P). The internal trochanter is observed as a rounded tuberosity in drepanosauromorphs and weigeltisaurids (Pritchard 2015; 259:1). Therefore, we assign TTU-P11407A-B, TTU-P11408A-D, and TTU-P11288 to Diapsida, the least inclusive clade that includes Drepanosauromorpha and Weigeltisauridae.

Humeri—The distal ends of the humeri (TTU-P11404A-E, TTU-P11394, TTU-P11410A, TTU-P11401) preserve the distal expansion and a small portion of the midshaft in all specimens (Fig. 4R–AG). TTU-P11410A and TTU-P11404B are transversely narrow with less extensive epicondyles in comparison with the other specimens (Fig. 4T, AD). Otherwise, all specimens are nearly identical and are therefore described together. The entepicondyle originates on the medial side of the midshaft slightly more proximally than the ectepicondyle originates on the lateral side of the midshaft (Fig. 4R, T, V, X, Y, AB, AD, AF). Only TTU-P11404C preserves an ectepicondylar foramen The ectepicondyle is broken away to differing degrees in some specimens, but it is complete in TTU-P11404A, TTU-P11404D, TTU-P11410A, and TTU-P11401, all of which lack an entepicondylar foramen, similar to the condition in drepanosaurs and archosauromorphs (Senter 2004; 63:1). There are two distal condyles: the large, lateral radial condyle and the smaller, medial ulnar condyle (Fig. 4S, U, W, Y, AA, AC, AE, AG). In anterior view, the radial condyle is elliptical and extends distally from the proximal end. The majority of the radial condyle is located on the anterior surface of the distal end of the humerus, and the condyle extends as a sharp ridge onto the distal surface. The ulnar condyle is elliptical in distal view and sits on the distal end of the humerus, slightly overhanging the posterior surface. A shallow groove separates the two condyles anterodistally and ends in a fossa just proximal to the radial condyle. The morphology and proportions of the ectepicondyle,

entepicondyle, and radial condyle are comparable to *Drepanosaurus*, but because of incomplete preservation of our specimens and the compressed preservation of most drepanosauromorph specimens, we assign these specimens to Diapsida on the basis of the absence of an entepicondylar foramen and the absence of apomorphies specific to a more inclusive clade. The distal ends of the humeri discussed above compare favorably with a left distal end of a humerus (NMMNH P-29044) from the Snyder Quarry in New Mexico, which was assigned to Cynodontia without using apomorphies (Zeigler et al. 2003).

SAURIA McCartney, 1802

Referred Specimen—TTU-P11280, proximal end of right femur (Fig. 5A, B).

Locality—MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—The proximal end of the right femur, TTU-P11280, preserves the expanded proximal condyles and a small portion of the midshaft (Fig. 5A, B). The element is trapezoidal in proximal view, square anteriorly and dorsally, and tapers slightly posteriorly, very similar to *Trilophosaurus buettneri* Case, 1928 (TMM 31025-140). The portion that tapers posteriorly extends distally as a ridge. In proximal view, the internal trochanter is present ventrally as a robust ridge (Fig. 5B). The dorsal portion of the proximal surface is raised above the proximal extent of the internal trochanter on the ventral surface, similar to *Malerisaurus robinsonae* Chatterjee, 1980, *Trilophosaurus buettneri*, *Pamelaria dolichotrachela* Sen, 2003 (ISIR 316/55), and *Prolacerta broomi* Parrington, 1935 (BP/1/2676) (Chatterjee 1980, Chatterjee 1986b, Sen 2003, Spielmann et al. 2008). In anterior and posterior views, the proximal border of the internal trochanter slopes proximally to meet the proximal surface of the femur as in *Malerisaurus* (Chatterjee 1980, 1986b). The internal trochanter of TTU-P11280 extends distally as a ridge on the ventral surface of the midshaft. A shallow, smooth intertrochanteric fossa is present, bordered by the internal trochanter ventrally and the posteriorly tapering ridge dorsally (Fig. 5A, B). A shallow intertrochanteric fossa is present in Sauria (Gauthier et al. 1988; 81:1). A rugose intertrochanteric fossa occurs only in *Azendohsaurus madagaskarensis* Flynn et al., 2010, *Erythrosuchus africanus* Broom, 1905, *Proterosuchus alexanderi* Hoffman, 1965, and *Prolacerta broomi* (Nesbitt et al. 2015), and these are deeper than that of TTU-P11280. The morphology of the intertrochanteric fossa and absence of apomorphies specific to the taxa

listed above leads us to assign TTU-P11280 to Sauria.

ARCHOSAUROMORPHA Huene, 1946
sensu Benton, 1985

Referred Specimens—*Humeri*: TTU-P11410E, distal end of right humerus (Fig. 5C, D); TTU-P11277, distal end of (right?) humerus (Fig. 5E, F). *Ulna*: TTU-P11386, proximal end of left ulna (Fig. 5G).

Localities—*Humer*i: MOTT 3898 (Headquarters South). *Ulna*: MOTT 3869 (Boren Quarry).

Description and Rationale for Assignment—
Humeri—TTU-P11410E and TTU-P11277 preserve distal ends of humeri and are described below individually (Fig. 5C–F).

TTU-P11410E preserves the distal end of a right humerus and a portion of the midshaft (Fig. 5C, D. It is likely that this specimen is associated with TTU-P11410D described below (Fig. 6C), the proximal end of a right humerus assigned to Archosauriformes because the specimens are from the same locality, of similar preservation and size, and the midshafts have similar cross sections. The distal end of the humerus is mediolaterally elongate in distal view (Fig. 5D). The distal end expands medially, whereas the lateral edge is vertical. The distal end preserves two condyles, the larger medial condyle (=ulnar) and the smaller lateral condyle (=radial). The lateral condyle tapers anterolaterally. The medial condyle expands slightly anteriorly and is rounded from the proximal surface onto the medial edge. The ectepicondyle is flat, whereas the entepicondyle is present as a flange proximal to the medial condyle (Fig. 5C). The absence of an entepicondylar foramen is a character state shared by drepanosaurs and archosauromorphs (Senter 2004; 46:1). The obvious difference in morphology from the specialized drepanosauromorph humeri (e.g., the distal condyles are elliptical and the epicondyles are blade-like in drepanosauromorph humeri) and the absence of a preaxial crest on the lateral surface precludes referral to Drepanosauromorpha (Pritchard et al. 2015; 152:1). Therefore, we assign TTU-P11410E to Archosauromorpha.

TTU-P11277 preserves the distal end of a (right?) humerus and a portion of the midshaft (Fig. 5E, F). Our description of this specimen is preliminary because we are unable to determine its exact medial-lateral orientation. The distal end of the humerus expands mediolaterally and posteriorly and has two condyles, one descending further distally than the other (Fig. 5E). The descending condyle (=medial/ulnar?) is smaller and triangular in distal view, whereas the more proximal condyle (=lateral/ radial?) is larger and rectangular in distal view (Fig. 5F).

There is an intercondylar groove that shallows anteroposteriorly and widens mediolaterally from the posterior edge of the distal surface onto the anterior surface. The non-descending condyle has a flat epicondyle, but there is a small ridge on the posterolateral edge of the descending condyle (=entepicondyle?) (Fig. 5E). The posterior surface is concave on the distally descending condyle. Because of the absence of any epicondylar foramina and the obvious difference in morphology from drepanosauromorph humeri (e.g., the distal condyles are elliptical and the epicondyles are blade-like in drepanosauromorph humeri) we assign TTU-P11277 to Archosauromorpha. This humerus is identical to the known distal end of a humerus (UMMP 10604) that has been assigned both to *Hesperosuchus agilis* Colbert, 1952 (Long and Murry 1995) and a phytosaur (Case 1929) but is now believed to be shuvosaurid on the basis of an associated femur (personal observation, e.g., proximal end of femur with posteriorly-projecting hook on anteromedial tuber and the absence of an anterolateral tuber on proximal end of femur; Nesbitt 2011; 300:3, 302:1).

Ulna—TTU-P11386 preserves the expanded proximal end of a left ulna (Fig. 5G). The olecranon process is elongate and projects further proximally than the rest of the element. The olecranon process is firmly co-ossified to the rest of the ulna, but a suture is visible, indicating that the process is a separate ossification. The large olecranon process is similar to the condition in the stem-sauropodomorph dinosaur *Saturnalia tupiniquim* Langer et al., 1999 (Langer et al. 2007). A separately-ossified olecranon process is present in the archosauromorphs *Protorosaurus speneri* Meyer, 1832 and *Amotosaurus rotfeldensis* Fraser and Rieppel, 2006 (Ezcurra 2016; 423:1). It is also present in some kannemeyeriiform dicynodonts (e.g., Maisch 2001; 33:1), including the Late Triassic, North American taxon *Placerias* Camp and Welles, 1956 (Camp and Welles 1956: fig. 33). However, these taxa differ from TTU-P11386 because the separate ossification of the olecranon is proportionally much larger than that of TTU-P11386, comprising more than half the length of the proximal ulna. This ossification in dicynodonts also possesses a large fossa on the medial surface (Camp and Welles 1956: fig. 33b), whereas this surface is convex in TTU-P11386. However, a poorly developed or absent olecranon process is the more basal synapsid morphology (Reisz 1986). In TTU-P11386, the olecranon is attached on the posterior surface of the proximal end at the same level as of the anterodorsally-facing articular surfaces. The olecranon process is convex posteriorly and thickens proximally on the medial edge

(Fig. 5G). There is no lateral tuber (=radius tuber) present on the proximal end of the ulna. Distinct lateral tubera are present in aetosaurs, *Revueltosaurus*, most paracrocodylomorphs, and early dinosauriforms (Nesbitt 2011; 237). The proximal surface of the element is divisible into three sections: a proximally raised, rounded posterior section, a flat anterolateral surface, and a proximally concave anteromedial surface. The two anterior proximal surfaces are separated by an anteroposteriorly trending ridge. The posterolateral edge of the ulna is rounded, whereas the posteromedial edge of the ulna is formed by a proximodistal ridge. The medial surface of TTU-P11386 is flat. TTU-P11386 is triangular in distal view, tapering anteriorly. A proportionately small, separately-ossified olecranon is only present in some archosauromorphs and so we assign TTU-P11386 to Archosauromorpha.

TANYSTROPHEIDAE Gervais, 1859
sensu Pritchard et al., 2015

Referred Specimens—*Femora:* TTU-P11344, complete right femur (Fig. 5H–J); TTU-P11281, distal end of right femur (Fig. 5K, L).

Localities—MOTT 3869 (Boren Quarry); MOTT 3628 (Kirkpatrick Quarry).

Description and Rationale for Assignment—The complete femur (TTU-P11344) is approximately 129 mm in length, and when viewed in medial and lateral perspective TTU-P11344 is nearly straight with only the slightest sigmoid curvature (Fig. 5H–J). The lack of a proximodorsal incline in the proximal head of the femur is a character state diagnosing a clade comprising the tanystropheids *Langobardisaurus* Renesto, 1994, *Tanytrachelos* Olsen, 1979, and the Hayden Quarry taxon (Pritchard et al. 2015; 177:1). The proximal surface of TTU-P11344 is slightly concave (Fig. 5H). The internal trochanter projects from the proximal end and tapers distally along the ventromedial surface of the shaft of TTU-P11344 (Fig. 5J). The posterior trochanter of TTU-P11344 does not extend as far distally along the ventrolateral shaft as the internal trochanter and is not as wide mediolaterally as the internal trochanter. The posterior and internal trochanters comprise the borders for the intertrochanteric fossa on the ventral surface of the proximal end of TTU-P11344 (Fig. 5H). The element tapers distally and both TTU-P11344 and TTU-P11281 broaden mediolaterally just proximal to three distal condyles (Fig. 5K). Both specimens preserve a medial and lateral tibial condyle on the ventral side of the distal femur and a fibular condyle on the dorsolateral surface of the lateral tibial condyle (Fig. 5I, L). There is a fossa present

on the medial distal surface of both TTU-P11344 and TTU-P11281, between the lateral tibial condyle and the fibular condyle; this depression that extends proximally onto the medial shaft. The lateral tibial condyle is larger than both the medial tibial and fibular condyles in both specimens, and the fibular condyle in both specimens has a flat ventral surface. These character states (e.g., larger lateral tibial condyle and flat ventral surface of fibular condyle) are shared with the Hayden Quarry femora assigned to Archosauromorpha by Pritchard et al. (2015) and are not present in most early archosauriforms. We assign TTU-P11344 to Tanystropheidae based on the lack of curvature discussed above and tentatively assign TTU-P11281 to the clade based on the character states present on the distal end.

ALLOKOTOSAURIA + *PROLACERTA BROOMI* + ARCHOSAURIFORMES Nesbitt et al., 2015

Referred Specimens—*Femora:* TTU-P11409E, distal end of left femur (Fig. 5M, N); TTU-P11275, distal end of left femur (Fig. 5O, P); TTU-P11276, distal end of right femur (Fig. 5Q, R); TTU-P11286, distal end of left femur (Fig. 5S, T). *Humerus:* TTU-P11384, proximal end of right humerus (Fig. 5U, V).

Localities—*Femora:* MOTT 3898 (Headquarters South). *Humerus:* MOTT 3624 (Post Quarry).

Description and Rationale for Assignment—
Femora—The distal ends of the femora (TTU-P11409E, TTU-P11275, TTU-P11276, TTU-P11286) are nearly identical, though TTU-P11286 is noticeably smaller than the other specimens (Fig. 5M–T). Therefore, we describe them together noting the few differences. The distal end comprises uneven distal articular surfaces, with the lateral, fibular condyle projecting further distally than the medial, tibial condyle (especially noticeable in TTU-P11286, Fig. 5S), which is characteristic of *Petrolacosaurus kansensis*, allokotosaurians, *Prolacerta broomi*, *Jaxtasuchus salomoni* Schoch and Sues, 2014, phytosaurs, ornithosuchids, *Nundasuchus songeaensis* Nesbitt et al., 2014, and suchian archosaurs (Ezcurra 2016; 512:0). The distal condyles in the specimens are otherwise equal in size (Fig. 5N, P, R, T), a character state not present in *Petrolacosaurus kansensis*, but shared by *Prolacerta broomi* and allokotosaurians (Nesbitt et al. 2015; 180:0). In addition, the distal end of the femur expands dorsoventrally, a character not present in *Vancleavea*, *Euparkeria* Broom, 1913, proterochampsians, and Archosauria (Nesbitt 2011; 318:0). There is a shallow intercondylar groove on the distal surface of the femur. The posterior border of the distal end is concave
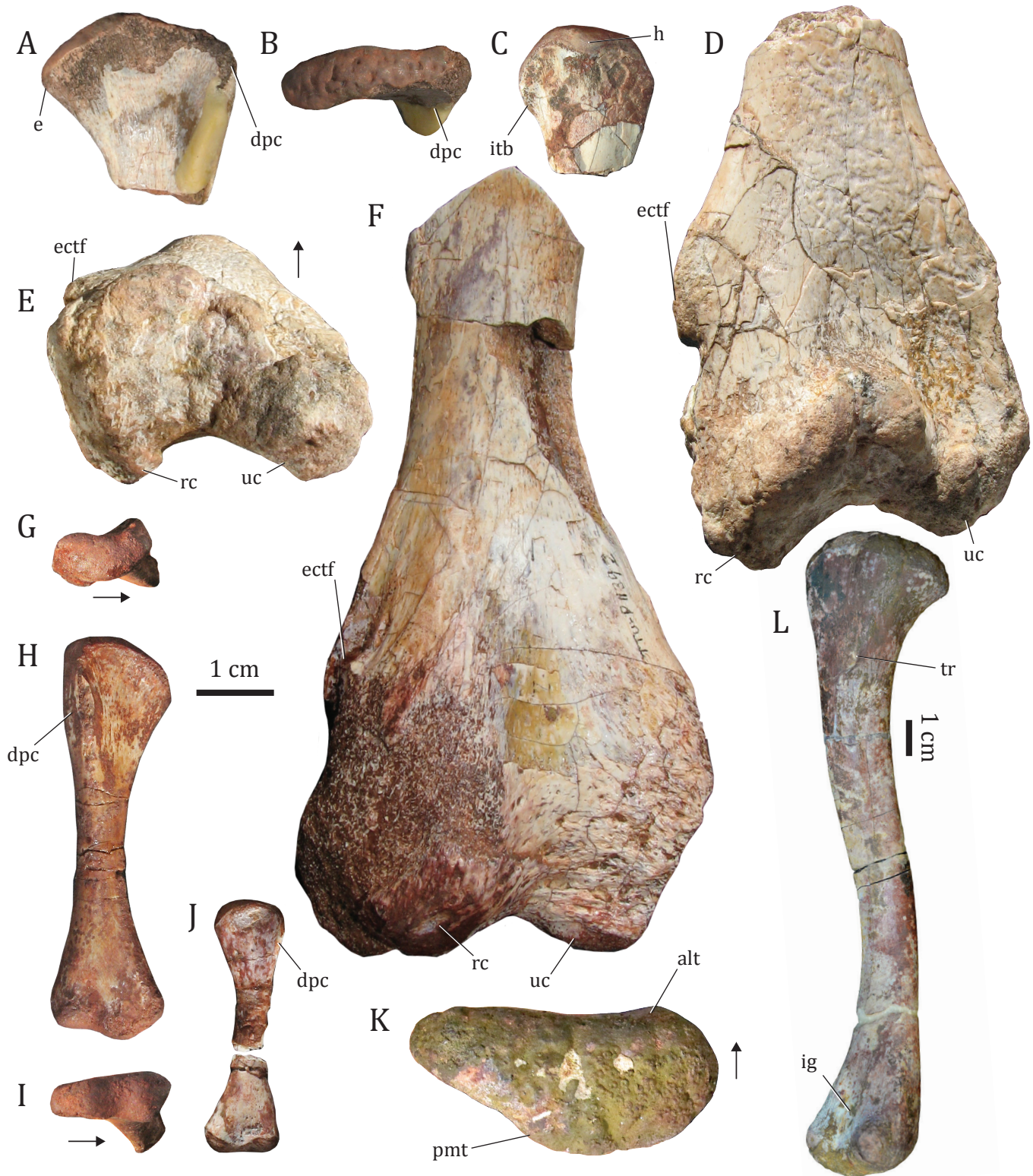
Figure 6. A–F. Archosauriform humeri in anterior (A, D), proximal (B), posterior (C, F), and distal (E) views. **A, B.** TTU-P11400. **C.** TTU-P11410D. **D, E.** TTU-P11391. **F.** TTU-P11392. **G–J.** *Litorosuchus + Vancleavea* humeri in proximal (G), ventral (H, J), and distal (I) views. **G–I.** TTU-P11382. **J.** TTU-P11385. **K, L.** Phytosaur femur in proximal (K) and posterior (L) views; **K, L** TTU-P11395. Scale bars 1 cm (smaller scale bar for L only). Abbreviations: **alt**, anterolateral tuber; **dpc**, deltopectoral crest; **ectf**, ectepicondylar flange; **h**, hook; **ig**, intercondylar groove; **itb**, internal tuberosity; **pmt**, posteromedial tuber; **rc**, radial condyle; **tr**, trochanter; **uc**, ulnar condyle. Arrows point anteriorly.

in distal view because there is a groove on the posterior surface of the femur separating the fibular condyle and the crista tibiofibularis (less noticeable in TTU-P11286 and TTU-P11409E because of lack of preservation) (Fig. 5P, R). This posterior groove, for articulation for the tibia, is present in *Malerisaurus* spp., *Trilophosaurus buettneri*, and *Azendohsaurus madagaskarensis* and overall, the character distributions of these specimens are consistent with allokotosaurids (Chatterjee 1980, Chatterjee 1986b, Spielmann et al. 2006, 2007, 2008, 2009, Nesbitt et al. 2015). Based on the morphology and expansion of the distal articular surface, we assign these specimens to the clade that includes Allokotosauria, *Prolacerta broomi*, and Archosauriformes.

Humerus—TTU-P11384 preserves the proximal expansion of the right humerus as well as a small portion of the midshaft (Fig. 5U, V). The anteroventral surface is concave and bounded anterolaterally by the deltopectoral crest and posteromedially by a ridge. The deltopectoral crest is robust, projects anteroventrally, has a fossa on the ventral surface, is concave on the dorsal surface, and is continuous with the midshaft. The deltopectoral crest of TTU-P11384 is not continuous with the proximal surface of the humerus (Fig. 5U). The proximal end of the humerus is crescent-shaped and anteroventrally-concave in proximal view (Fig. 5V). There is a small expansion on the proximal surface of the humerus (Fig. 5U) that resembles the conical process described by Ezcurra (2016; 420:1), which is present in *Pamelaria dolichotrachela*, *Azendohsaurus madagaskarensis*, and *Prolacerta broomi*. There is a ridge present on the anterodorsal surface extending from dorsal to the deltopectoral crest to the midshaft, which does not occur in *Prolacerta broomi* or *Trilophosaurus buettneri* (Nesbitt et al. 2015). A shallow fossa is present posterior to this ridge, and the fossa extends to the proximal surface of the humerus. A proximodistally trending groove is present on the posterodorsal surface just distal to the proximal end. This feature is present in *Azendohsaurus madagaskarensis*, where Nesbitt et al. (2015) described it as a fossa distally bounded by a hump. Because of the incomplete preservation of the specimen, it is difficult to determine whether TTU-P11384 preserves a distinct muscle scar on the dorsal surface, proximal to the midshaft, which was also mentioned by Nesbitt et al. (2015) as a characteristic of *A. madagaskarensis*. Based on the presence of the conical process on the proximal surface of the humerus and the absence of apomorphies specific to *Pamelaria*, *Prolacerta*, and *Azendohsaurus*, we assign TTU-P11384 to the least inclusive clade that includes these taxa.

The position of *Pamelaria dolichotrachela* as the outgroup of Azendohsauridae + Trilophosauridae is not well supported; *Pamelaria* shares a number of derived character states with Azendohsauridae yet may not be a member of Allokotosauria (Nesbitt et al. 2015). Overall, the character distributions of TTU-P11384 are most consistent with allokotosaurian azendohsaurids.

ARCHOSAURIFORMES Gauthier et al., 1988

Referred Specimens—*Humeri:* TTU-P11400, proximal end of left humerus (Fig. 6A, B); TTU-P11410D, proximal end of right humerus (Fig. 6C); TTU-P11391, distal end of right humerus (Fig. 6D, E); TTU-P11392, distal end of left humerus (Fig. 6F).

Localities—MOTT 3628 (Kirkpatrick Quarry); MOTT 3898 (Headquarters South); MOTT 3880 (Patty East Quarry).

Description and Rationale for Assignment—TTU-P11400 preserves the proximal expansion of a left humerus (Fig. 6A, B). The cross section just below the proximal expansion is ovate. There is a slight depression on the posterior surface of TTU-P11400, but the surface is otherwise flat and featureless. The proximal end of the humerus is asymmetric and is expanded more medially than laterally (Fig. 6A), a characteristic of some proterochampsids, doswelliids, phytosaurs, ornithosuchids, and avemetatarsalians (Ezcurra 2016; 419:1). The proximal surface is rounded with a rugose texture and is continuous with the deltopectoral crest (Fig. 6B). There is a small anteriorly-extending ridge of bone on the lateral edge just distal to the proximal end of the element. This is all that remains preserved of the deltopectoral crest, and there is an artificially reconstructed ridge that extends the preserved ridge of bone distally and anteriorly (Fig. 6A). Because of the absence of any apomorphies specific to clades listed above that share a medially expanded proximal end of the humerus, we assign TTU-P11400 to Archosauriformes.

TTU-P11410D preserves the proximal end of a right humerus and a portion of the midshaft (Fig. 6C). It is likely that this specimen is associated with TTU-P11410E described previously (Fig. 5C, D) because the specimens are from the same locality, of similar preservation and size, and the midshafts have similar cross sections. The humerus tapers medially and laterally in proximal view and has a convex proximal surface. The articular surface of the head of TTU-P11410D is expanded posteriorly, and this posterior expansion is convex and therefore hooked slightly distally (Fig. 6C). This is similar to the posteriorly-expanded and hooked proximal surface of the

humerus that is observed in various members of Loricata (Nesbitt 2011; 232:1). The proximal articular surface slopes gently medially to the internal tuberosity, rather than the abrupt change in slope present in loricatans (Ezcurra 2016; 421:0). The internal tuberosity is rounded and expanded medially (Fig. 6C). The medial portion of the proximal end of the humerus is expanded anteriorly. The thin lateral edge of the proximal end of the humerus is angled slightly anteriorly (=deltopectoral crest) and is continuous with the proximal articular surface, characteristic of most archosauriforms (Nesbitt 2011; 233:0). Therefore, we assign TTU-P11410D to Archosauriformes.

TTU-P11391 and TTU-P11392 preserve the expanded distal ends of humeri as well as portions of the midshafts (Fig. 6D–F). These specimens are largely identical and therefore described together with differences noted. The midshaft is round and slightly anteroposteriorly flattened in cross section at the distal end. The distal end preserves two condyles, a smaller, medial ulnar condyle and a larger, lateral radial condyle (Fig. 6E). The ulnar condyle is not completely preserved on its medial surface, but there appears to be a proximodistally-oriented ridge where the medial condyle angles into the anteromedial surface of the midshaft. This ridge is more prominent in TTU-P11392 than TTU-P11391. Distally, the radial condyle narrows to an anteroposteriorly trending ridge. On the posterior surface of the humerus, the radial condyle continues proximally as a proximodistal ridge that forms the posterolateral border of the midshaft. The distal surface of the humerus is concave, and the condyles are separated by a wide, shallow groove. On the center of the distal posterior surface there is some pitting adjacent to the radial condyle. In TTU-P11391, the pitting is more extensive. There is a proximodistally-oriented lateral groove and adjacent anterolateral ridge on the anterolateral surface of the distal end of the humerus, just distal and lateral to the radial condyle (Fig. 6D, F). The groove is deeper in TTU-P11392 than in TTU-P11391. This ectepicondylar flange and groove (=supinator process and groove of Ezcurra (2016)) are present in phytosaurs, aetosaurs, *Batrachotomus* Gower, 1999, *Postosuchus* Chatterjee, 1985, *Stagonosuchus* Huene, 1938, and *Poposaurus* Mehl, 1915 (Nesbitt 2011; 234:0). On the center of the anterior surface of the distal end of the humerus, there is a process that extends anteriorly and appears to be a continuation of the radial condyle (Fig. 6E). There is some pitting just proximal to this process in TTU-P11392. We assign TTU-P11391 and TTU-P11392 to Archosauriformes, the least inclusive clade containing Phytosauria and Pseudosuchia because of the presence of the ectepicondylar flange and groove.

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VANCLEAVEA CAMPI Long and Murry, 1995 +
LITOROSUCHUS SOMNII Li et al., 2016

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Referred Specimens—*Humeri:* TTU-P11382, complete right humerus (Fig. 6G–I) TTU-P11385, complete left humerus (Fig. 6J).

Localities—MOTT 3628 (Kirkpatrick Quarry); MOTT 3624 (Post Quarry).

Description and Rationale for Assignment—TTU-P11382 and TTU-P11385 are nearly identical, complete humeri and are therefore described together with differences noted (Fig. 6G–J). The proximal end of the humerus is thickened dorsoventrally (Fig. 6G). The deltopectoral crest is located high on the lateroventral margin proximal to the midshaft (Fig. 6H, J). In TTU-P11385 the midshaft is nearly circular and thick in cross-section. The two condyles on the distal end of the humerus expand equally anteriorly and posteriorly (Fig. 6I). The ulnar condyle is larger than the radial condyle, and the condyles are separated on the lateral surface side by a small fossa that does not extend dorsally onto the shaft. The medial surface of the distal end of the humerus is flat. The absence of the ectepicondylar flange is a synapomorphy for archosauriforms, and the specimen, the humerus of *Vancleavea campi*, and the humerus of *Litorosuchus somnii* lack an ectepicondylar flange (Li et al. 2016; 234:1). TTU-P11382 is approximately 49.5 mm in length and the proximal and distal ends form an angle of approximately 45°. TTU-P11385 has been deformed during preservation, so we are unable to acquire these measurements though there is obvious torsion between the proximal and distal ends (Fig. 6G, I). A high angle of torsion between the proximal and distal ends of the humerus is present in the non-archosauromorph diapsids *Petrolacosaurus kansensis*, *Youngina capensis* Broom, 1914, *Planocephalosaurus robinsonae* Fraser, 1982, *Gephyrosaurus bridensis* Evans, 1980, and *Simoedosaurus lemoinei* Gervais, 1877 and the archosauromorphs *Prolacerta broomi*, *Boreopricea funereal* Tatarinov, 1978, "*Chasmatosaurus*" *yuani* Young, 1936, and *Vancleavea campi* (Ezcurra 2016; 415:0). *Litorosuchus* has not been scored for a high angle of torsion between the proximal and distal ends of the humerus, but the proximal head is oriented posteromedially with respect to the humeral shaft (Li et al. 2016). On the basis of this character state, the absence of an ectepicondylar flange, and the absence of synapomorphies specific to *Litorosuchus* or *Vancleavea*, we assign TTU-P11382 and TTU-P11385 to the clade that includes these two taxa.

ARCHOSAURIA Cope, 1869
sensu Gauthier & Padian, 1985

Referred Specimen—TTU-P11399, distal end of left pubis (Fig. 7A–C).

Locality—MOTT 3898 (Headquarters South).

Description and Rationale for Assignment —TTU-P11399 preserves the posteriorly expanded distal end of the left pubis as well as a portion of the pubic shaft (Fig. 7A–C). A posteriorly expanded distal end of the pubis is present among paracrocodylomorphs and saurischians
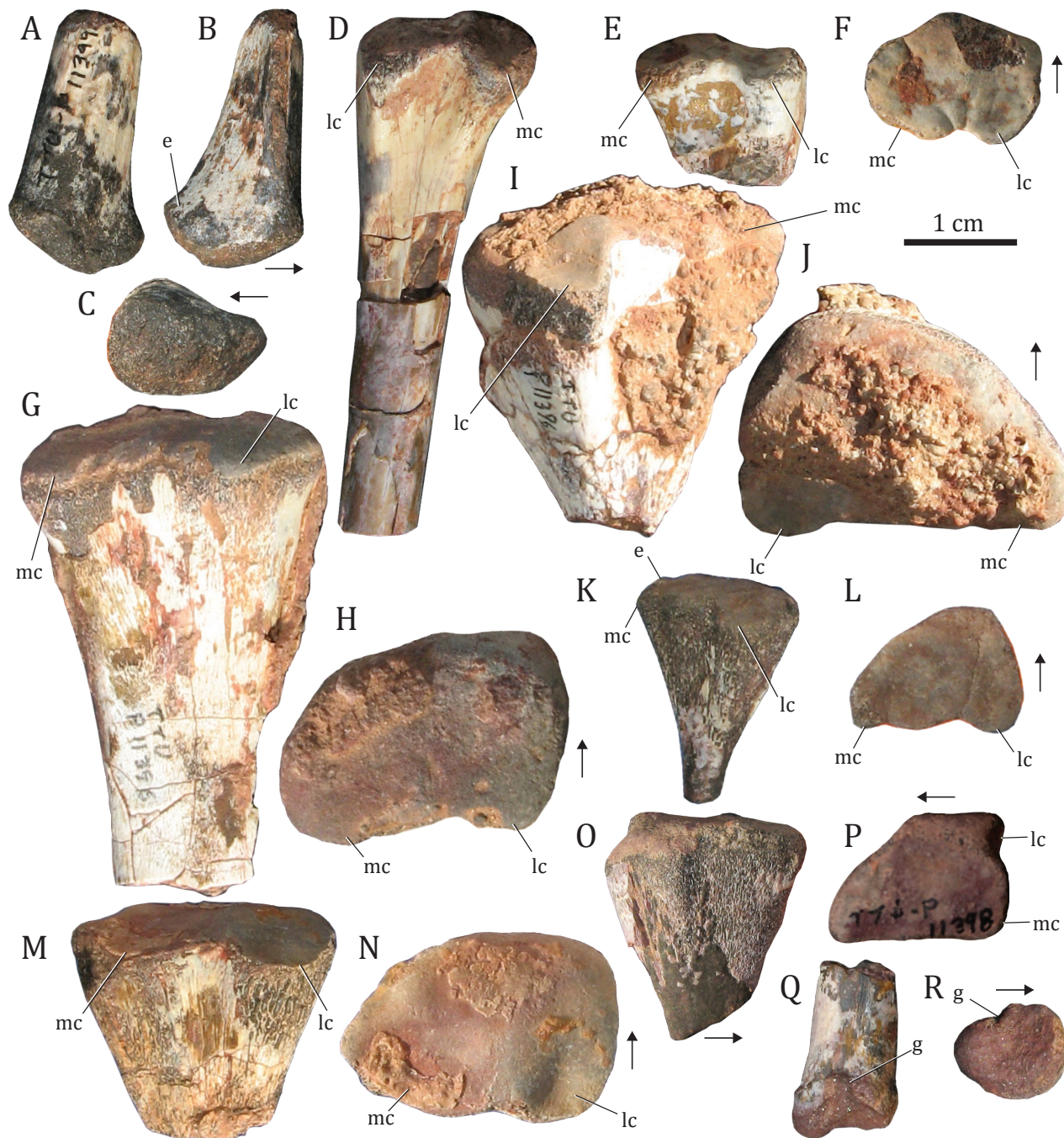

Figure 7. A–C. Archosaur pubis in anterolateral (A), medial (B), distal (C) views. TTU-P11399. **D–R.** Pseudosuchian tibiae in posterior (D, E, G, M), proximal (F, H, J, L, N, P), lateral (O, Q), posterolateral (I, K), and distal (R) views. **D**. TTU-P11393. **E, F**. TTU-P11290. **G, H**. TTU-P11396A. **I, J**. TTU-P11396B. **K, L**. TTU-P11412F. **M, N**. TTU-P11412G. **O, P**. TTU-P11398. **Q, R**. TTU-P11397B. Scale bar 1 cm. Abbreviations: **e**, expansion; **g**, groove; **lc**, lateral condyle; **mc**, medial condyle. Arrows point anteriorly.

(Nesbitt 2011; 283:1). The pubic shaft is crescentic in cross-section, narrows more medially than laterally, and is convex anterolaterally and concave posteromedially (Fig. 7B). The medially-narrowing portion (=midline contact) of the pubic shaft extends distally, forming the anteromedial border of the distal end of the pubis. The area of midline contact does not extend to the distal most end of the pubis and the distal expansions of the pubes would likely not contact when articulated. The specimen is rectangular in anterior view. In lateral view, the pubic shaft widens anteroposteriorly towards the convex, rugose distal end of the pubis. The anterior corner of the distal expansion is just wider than 90° in lateral view, and the posterior border of the distal expansion narrows to a posterodorsally-hooking point (Fig. 7B). In distal view, TTU-P11399 is wide anteriorly, tapers posteriorly, and is slightly concave laterally and convex medially (Fig. 7C). TTU-P11399 most closely resembles the pubis of *Coelophysis bauri* (Padian 1986: fig. 5.3), in that there is little dorsal inflection of the posterior tip of the distal end of the pubis, whereas the paracrocodylomorphs such as *Poposaurus* and *Postosuchus* have large, sharp dorsal inflections of the posterior tip (Schachner et al. 2011, Parker and Nesbitt 2013, Weinbaum 2013). However, in the absence of any apomorphies specific to Paracrocodylomorpha or Saurischia, we assign TTU-P11399 to Archosauria on the basis of the posteriorly expanded distal end.

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PSEUDOSUCHIA Zittel, 1890
sensu Gauthier & Padian, 1985

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Referred Specimens—*Tibiae:* TTU-P11393, proximal end of left tibia (Fig. 7D); TTU-P11290, proximal end of right tibia (Fig. 7E, F); TTU-P11396A, proximal end of right tibia (Fig. 7G, H); TTU-P11396B, proximal end of left tibia (Fig. 7I, J); TTU-P11412F, proximal end of right tibia (Fig. 7K, L); TTU-P11412G, proximal end of right tibia (Fig. 7M, N); TTU-P11398, proximal end of left tibia (Fig. 7O, P); TTU-P11397B, distal end of right tibia (Fig. 7Q, R).

Localities—MOTT 3892 (Headquarters); MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—TTU-P11393, TTU-P11290, TTU-P11396A-B, TTU-P11412F-G, and TTU-P11398 preserve the proximal ends of tibiae as well as portions of the midshafts. There are five distinct morphs of tibiae among these six specimens. TTU-P11396A (Fig. 7G, H), TTU-P11393 (Fig. 7D), TTU-P11290 (Fig. 7E, F), and TTU-P11398 (Fig. 7O, P) represent distinct morphologies, whereas TTU-P11412F-G are identical to TTU-P11396B, and these latter three

specimens are described together (Fig. 7I–N).

TTU-P11393 preserves a large portion of the midshaft that is circular in cross section (Fig. 7D). The proximal end of the tibia is subcircular with a flat posterior border in proximal view. Anteriorly, the tibia is rounded, and there are two posterior condyles that are the same length at their posterior borders. The posterolateral margin of the proximal end appears to be square; however, the lateral posterior condyle is worn, presumably as a result of taphonomy. The proximal surface of the lateral condyle is depressed (Fig. 7D). This is similar to the condition in *Euparkeria* and pseudosuchian archosaurs, though the depression in *Euparkeria* is not to the same degree as in pseudosuchians (Nesbitt 2011; 330:1). The medial posterior condyle is rounded posteromedially, and the medial surface is slightly concave. Because the specimen has a depressed lateral condyle, we assign TTU-P11393 to Pseudosuchia.

The posterior portion of the proximal end of TTU-P11290 comprises a larger medial condyle and a smaller lateral condyle (Fig. 7E, F). The posterior border of the condyles is level in proximal view, and the condyles are separated by a small groove on the posterior surface that widens distally to form a fossa (Fig. 7F). The proximal surface of the lateral condyle is depressed in comparison to the concave medial condyle (Fig. 7E), which is characteristic of *Euparkeria* and crocodylian-line archosaurs, though the proximal surface is not as depressed in *Euparkeria* as it is in pseudosuchians (Nesbitt 2011; 330:1). The posteromedial margin of the proximal end of the tibia is formed by a proximodistally-oriented ridge originating just distal to the medial condyle and continuing onto the midshaft. In proximal view, the anterolateral border is flat and the anteromedial border angles towards the rounded medial condyle (Fig. 7F). The specimen has a depressed lateral condyle, so we assign TTU-P11290 to Pseudosuchia.

The midshaft of TTU-P11396A is elliptical in cross section and is widest in the posteromedial-anterolateral axis (Fig. 7G, H). TTU-11396A expands slightly towards the proximal end in comparison with the other tibiae, and is rounded anteriorly with a flat lateral border in proximal view (Fig. 7H). TTU-P11396A has two posterior condyles on the proximal end. The medial condyle is rounded posteromedially. The lateral condyle of TTU-P11396A expands posteriorly to a lesser extent than TTU-P11396B and TTU-P11412F and is depressed (Fig. 7G). Again, this is a characteristic of *Euparkeria* and pseudosuchians, though the proximal surface is not as depressed in *Euparkeria* as it is in pseudosuchians (Nesbitt 2011; 330:1).
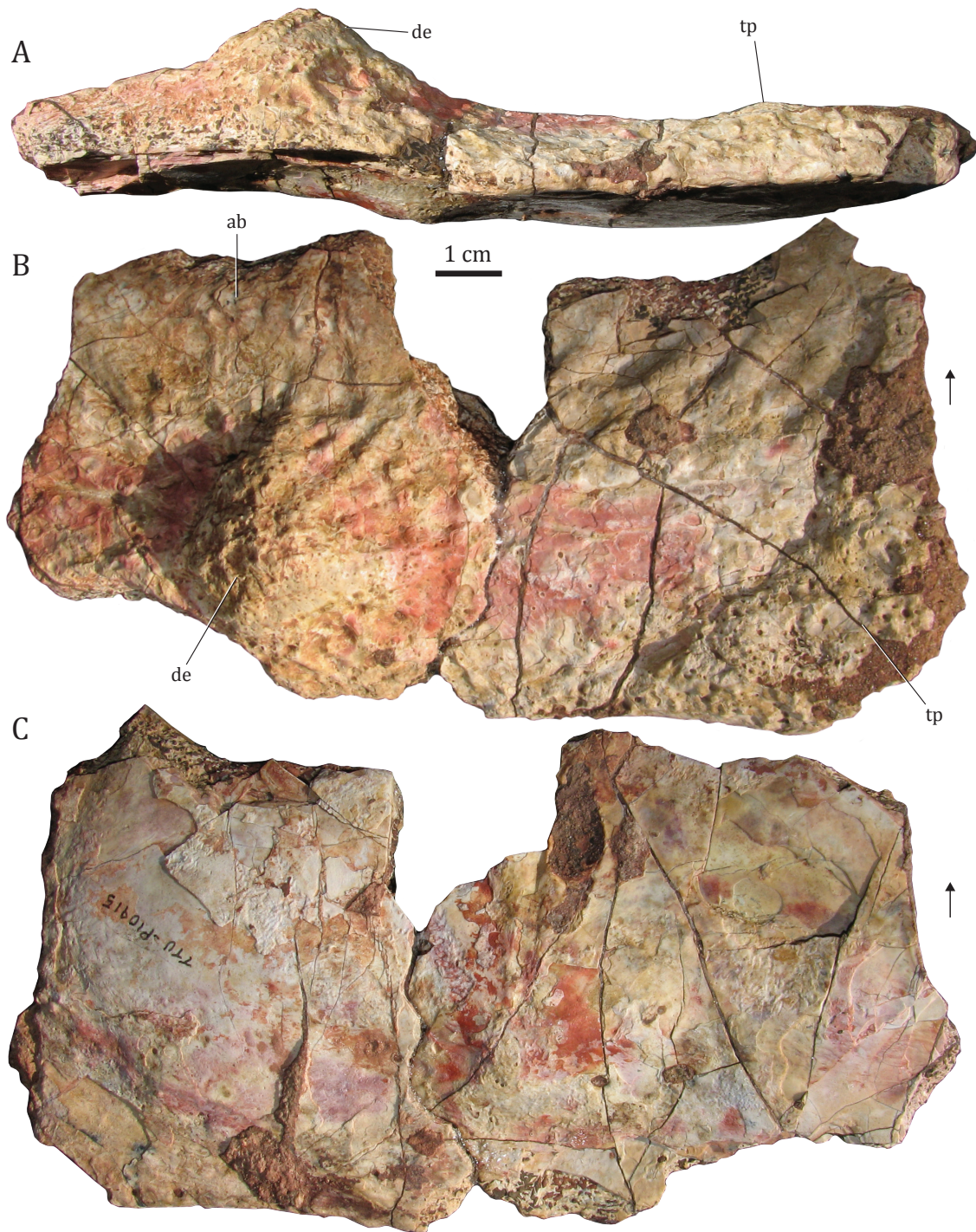
Figure 8. A–C. *Scutarx deltatylus* paramedian osteoderm in posterior (A), dorsal (B), and ventral (C) views; TTU-P10195. Scale bar 1 cm. Abbreviations: **ab**, anterior bar; **de**, dorsal eminence; **tp**, triangular protuberance. Arrows point anteriorly.

The lateral condyle is level with the medial condyle in TTU-P11396A, and the two condyles are separated by a wide proximodistally-trending groove (Fig. 7G, H). TTU-P11396A has a round fossa on the posterior surface distal to the medial condyle. The specimen has a depressed lateral condyle, and therefore we assign TTU-P11396A to Pseudosuchia.

The midshaft of TTU-P11412F is elliptical in cross section and is widest in the posteromedial-anterolateral axis. TTU-P11412F-G and TTU-P11396B are triangular

in anterior view and expand greatly from the midshaft to the proximal end (Fig. 7I–N). Both TTU-P11412F-G and TTU-P11396B are rounded anteriorly and have flat lateral borders in proximal view (Fig. 7J, L, N). TTU-P11412F tapers slightly anterolaterally in proximal view, whereas TTU-P11396B and TTU-P11412G are rounded in proximal view. All three specimens have two posterior condyles on the proximal end. The medial condyle in both TTU-P11412F and TTU-P11396B is rounded posteromedially, and it is worn in TTU-P11412G. In TTU-P11412F-G, the proximal surface of the medial condyle is concave, whereas this surface is obscured by matrix in TTU-P11396B. The proximal surface of the lateral condyle is concave in all three specimens (Fig. 7I, K, M), again a characteristic of *Euparkeria* and pseudosuchians, though the proximal surface is not as depressed in *Euparkeria* as it is in pseudosuchians (Nesbitt 2011; 330:1). The surface between the two concavities on the proximal surface of TTU-P11412F-G is convex. There is a rounded expansion just anteromedial to the concavity on the surface of the medial condyle in TTU-P11412F (Fig. 7K). The lateral condyle in TTU-P11396B and TTU-P11412F-G expands posteriorly from the proximal end and is concave proximally (Fig. 7J, L, N). The lateral condyle is level with the medial condyle in all specimens, and the two condyles are separated by a wide proximodistally-trending groove. The groove is wider and shallower in TTU-P11396A. The anterior border of the proximal end is angled anterodistally in TTU-P11412G and TTU-P11396A. TTU-P11412F-G and TTU-P11396B have depressed lateral condyles, so we assign them to Pseudosuchia.

TTU-P11398 preserves the expanded proximal end of the tibia as well as a small portion of the midshaft (Fig. 7O, P). The proximal end is flat and preserves two posterior condyles. In proximal view, the medial and posterolateral borders are flat (Fig. 7P). On the anterior border of the proximal surface, the tibia tapers anteromedially. The anteromedially-tapering portion is distinct from the cnemial crest observed in dinosauromorphs in that it does not form a distinct angle with the shaft of the tibia (Novas 1996). On the posterior border of the proximal surface, the lateral posterior condyle tapers posteriorly and the medial posterior condyle is rounded and forms much of the posterior border (Fig. 7P). There is a distally-trending groove separating the posterior condyles that extend from the proximal surface onto the midshaft distally. In proximal view this groove appears as a small concavity between the posterior condyles. The posterior condyles are level at their posterior borders. The lateral posterior condyle forms a rounded ridge on the posterolateral

surface that does not extend distally onto the midshaft. The anteromedially-tapering portion forms a sharp ridge on the anterior surface of the proximal end of the tibia that extends distally onto the midshaft. The lateral and medial posterior condyles are depressed distally. A depressed lateral condyle on the proximal surface of the tibia is a characteristic of *Euparkeria* and pseudosuchian archosaurs, though the proximal surface is not as depressed in *Euparkeria* as it is in pseudosuchians (Nesbitt 2011; 330:1), and based on this character state, we assign TTU-P11398 to Pseudosuchia.

TTU-P11397B preserves the distal end of a right tibia as well as a portion of the midshaft (Fig. 7Q, R). The tibia is hollow, and the midshaft is convex medially and slightly concave laterally because of a groove on the lateral surface (Fig. 7Q). This groove is present in most crocodylian-line archosaurs (Nesbitt 2011; 337:1). The distal end of the tibia expands anteroposteriorly and preserves two articular surfaces for the astragalus. The distally rounded posterolateral surface is extended further distally than the distally concave anterolateral surface, identical to the condition in *Effigia* Nesbitt and Norell, 2006 (Nesbitt 2007: fig. 45). The anterolateral articular surface slants medially, whereas the posterolateral articular surface slants laterally as in shuvosaurids, *Postosuchus*, stagonolepidids, and crocodylomorphs (Nesbitt 2007). We therefore assign TTU-P11397B to Pseudosuchia based on the presence of a groove on the lateral surface.

AETOSAURIA Marsh, 1884 *sensu* Parker, 2007
SCUTARX DELTATYLUS Parker, 2016a

Referred Specimen—TTU-P10195, left paramedian osteoderm (Fig. 8A–C).

Locality—MOTT 3899 (Headquarters NW).

Description and Rationale for Assignment—TTU-P10195 is incomplete but still possesses diagnostic character states allowing a precise taxonomic assignment (Fig. 8A–C). The weakly-raised anterior bar and a radial ornamentation of grooves and ridges (Fig. 8B) allow assignment as a non-desmatosuchin desmatosuchine aetosaur (Parker 2016a; 52:2, 53:1). This specimen is a paramedian osteoderm, as it is mediolaterally longer than anterolaterally wide, and an anteromedial projection of the anterior bar places this osteoderm on the left side of the carapace. No distinct pitting is present as ornament surrounding the eminence. The osteoderm is dorsoventrally-thickened with a slight ventral strut similar to that found in *Calyptosuchus wellesi* Long and Ballew, 1985, *Scutarx deltatylus*, and typothoracisine aetosaurs (Martz 2002; Parker 2016a; 56:1). A prominent dorsal
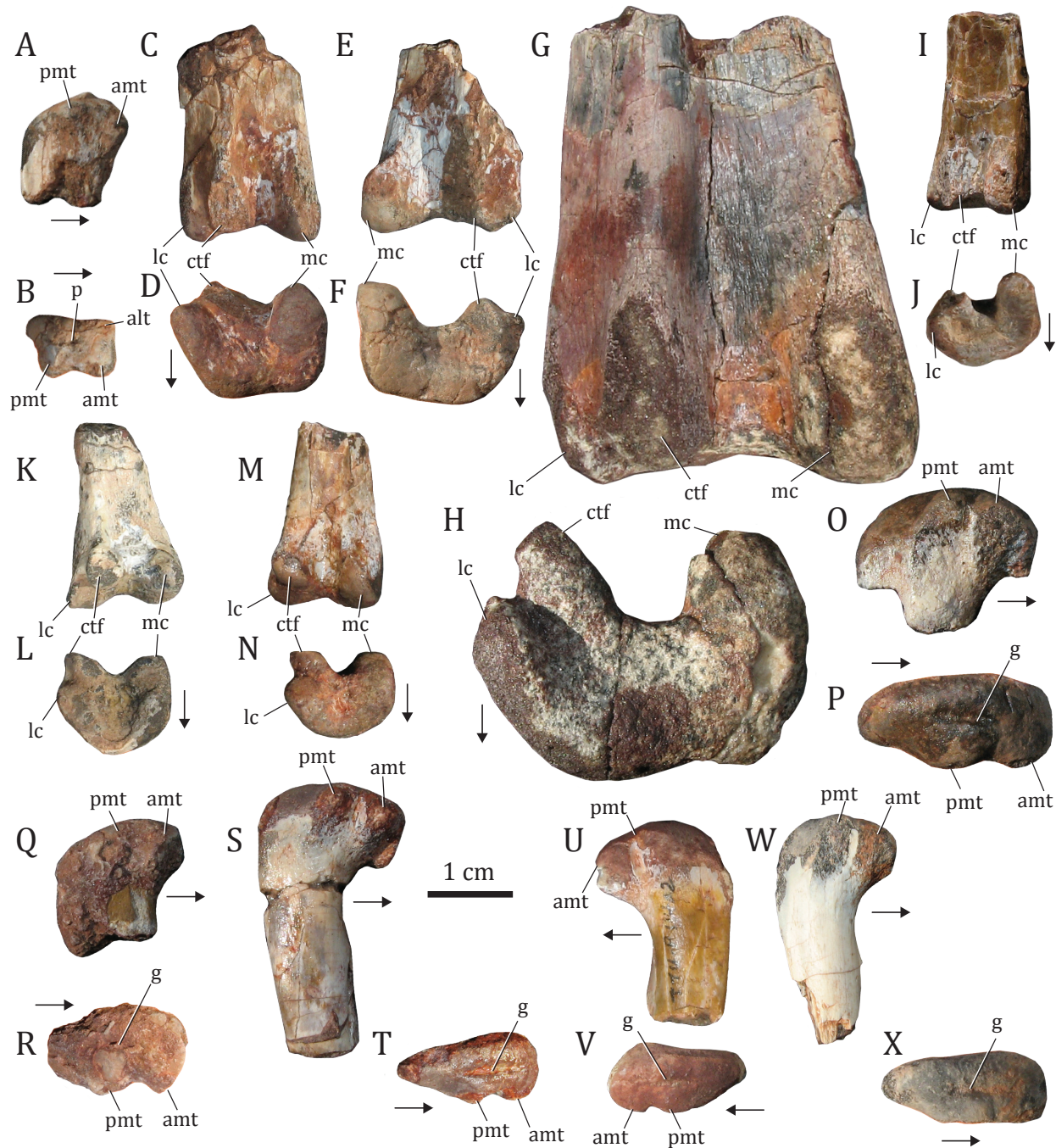
Figure 9. A–N. Paracrocodylomorph femora in medial (A), proximal (B), posterior (B, E, G, I, K, M), and distal (D, F, H, J, L, N) views. **A, B**. TTU-P11411E. **C, D**. TTU-P11409A. **E, F**. TTU-P11409B. **G, H**. TTU-P11048. **I, J**. TTU-P11283. **K, L**. TTU-P11284. **M, N**. TTU-P10845. **O–X**. Shuvosaurid femora in medial (O, Q, S, U, W) and proximal (P, R, T, V, X) views. **O, P**. TTU-P11411A. **Q, R**. TTU-P11411B. **S, T**. TTU-P11411C. **U, V**. TTU-P11402. **W, X**. TTU-P11272. Scale bar 1 cm. Abbreviations: **alt**, anterolateral tuber; **amt**, anteromedial tuber; **ctf**, crista tibiofibularis; **g**, groove; **lc**, lateral condyle; **mc**, medial condyle; **p**, pit; **pmt**, posteromedial tuber. Arrows point anteriorly.

eminence that does not contact the posterior margin of the plate (Fig. 8B) and a slightly beveled posterior margin are characteristics of paratypothoracisin aetosaurs (Heckert and Lucas 2000, Martz and Small 2006, Parker 2007, Parker 2016a; 54:0, 55:1). The posteromedial corner of the plate preserves a raised triangular rugose protuberance (Fig. 8A, B) that is autapomorphic for *S. deltatylus* (Parker 2016a, b). The ventral surface is smooth (Fig. 8C) with the exception of a series of longitudinal striations near the posterior margin, which is present in

most aetosaurs, and is the area that dorsally overlaps the anterior margin of the subsequent plate (Parker 2008). Two small foramina are present in the slight ventral surface emargination ventral to the dorsal eminence. The dorsoventral thickening, anteriorly-situated eminence, and the triangular raised rugose posteromedial margin suggest this plate is from the anterior trunk region. The presence of the triangular protuberance at the postero-medial margin allows assignment of this specimen to *S. deltatylus* (Parker 2016a, b).

PARACROCODYLOMORPHA Parrish, 1993
sensu Weinbaum and Hungerbühler, 2007

Referred Specimens—*Femora:* TTU-P11411E, proxi-mal end of right femur (Fig. 9A, B); TTU-P11409A, distal end of left femur (Fig. 9C, D); TTU-P11409B, distal end of right femur (Fig. 9E, F); TTU-P11048, distal end of left femur (Fig. 9G, H); TTU-P11283, distal end of left femur (Fig. 9I, J); TTU-P11284, distal end of left femur (Fig. 9K, L); TTU-P10845, distal end of left femur (Fig. 9M, N).

Localities—MOTT 3898 (Headquarters South); MOTT 3902 (Lower Far East).

Description and Rationale for Assignment—TTU-P11411E comprises the expanded proximal end of a right femur (Fig. 9A, B). The proximal surface of the femur is convex and has a small pit (Fig. 9B) that may correspond to the anteroposteriorly-trending groove present in shu-vosaurids (Nesbitt 2011; 314:1). The anterior portion of the femoral head is expanded anteriorly but does not project markedly from the shaft (Fig. 9A). The anterior surface is flat, and the medial surface bears an expansion with two distinct, medially-rounded tubera (anterior and posterior). These tubera are separated by a shal-low groove and are equal in size (Fig. 9B). The antero-medial and posteromedial tubera are similar in size to crocodylomorphs and most taxa previously categorized as 'rauisuchians' (e.g., rauisuchids and poposauroids) (Nesbitt and Stocker 2008). The lateral margin is concave in proximal view, and there is a small, anterolaterally-rounded anterolateral tubera (Fig. 9B). The presence of three tubera is characteristic of all suchians (Nesbitt 2011; 300–302). The area where a proximal condylar fold might be present is worn and therefore prevents a more specific assignment of TTU-P11411E (e.g., to Crocodylomorpha; see Nesbitt et al. 2006). Therefore we assign this specimen to Paracrocodylomorpha.

TTU-P11409A-B, TTU-P11048, TTU-P11283, TTU-P11284, and TTU-P10845 preserve the distal ends of femora and portions of the midshafts (Fig. 9C–N). These specimens are nearly identical and are described

together with differences noted. In cross section, the shaft is rounded laterally and tapers medially to varying de-grees. The femur is anteriorly convex and posteriorly con-cave in distal view. The distal end of the femur preserves three condyles, a large, posteriorly-rounded medial, tibial condyle, a small, posterolaterally-tapering lateral, fibular condyle, and a laterally-rounded crista tibiofibularis (Fig. 9D, F, H, J, L, N). The crista tibiofibularis is separated from the lateral condyle by a deep groove on the distal surface, a character state present in dinosauromorphs, *Effigia*, *Poposaurus*, *Fasolasuchus* Bonaparte, 1981, *Postosuchus*, and crocodylomorphs (Parker and Irmis 2005: pg. 52; Nesbitt 2011; 322:1). The angle between the lateral con-dyle and crista tibiofibularis in distal view is about 90° in these specimens, a character shared by *Effigia*, *Batracho-tomus*, *Fasolasuchus*, *Postosuchus*, and crocodylomorphs (Nesbitt 2011; 319:1). The intercondylar groove is deep on the posterior surface in all specimens and continues onto the distal end of TTU-P11284 and TTU-P11283 (Fig. 9D, F, H, J, L, N). In the smaller TTU-P11284 and TTU-P10845 the posterolateral margin of the distal end is formed by a proximodistally-oriented ridge (Fig. 9K, M). In the larger TTU-P11048, this posterolateral margin is formed by a flattened surface that originates between the lateral condyle and crista tibiofibularis and extends proximally (Fig. 9G). TTU-P11283 and TTU-P11409A-B are not preserved well enough to describe this feature. The anteromedial border is similar in TTU-P11284 and TTU-P409A, whereas TTU-P11048 and TTU-P11283 pre-serve a proximodistally-oriented groove just proximal to the medial condyle. The combination of the presence of a groove and the 90° angle between the crista tibiofibu-laris and lateral condyle supports assignment of these specimens to Paracrocodylomorpha.

POPOSAUROIDEA Nopsca, 1928
sensu Weinbaum & Hungerbühler, 2007
SHUVOSAURIDAE Chatterjee, 1993
sensu Nesbitt, 2007

Referred Specimens—*Femora:* TTU-P11411A, proxi-mal end of left femur (Fig. 9O, P); TTU-P11411B, proximal end of left femur (Fig. 9Q, R); TTU-P11411C, proximal end of left femur (Fig. 9S, T); TTU-P11402, proximal end of left femur (Fig. 9U, V); TTU-P11272, proximal end of right femur (Fig. 9W, X).

Localities— MOTT 3898 (Headquarters South); MOTT 3899 (Headquarters NW).

Description and Rationale for Assignment —TTU -P11402, TTU-P11272, and TTU-P11411A-C preserve the femoral head and the uncrushed proximal portion
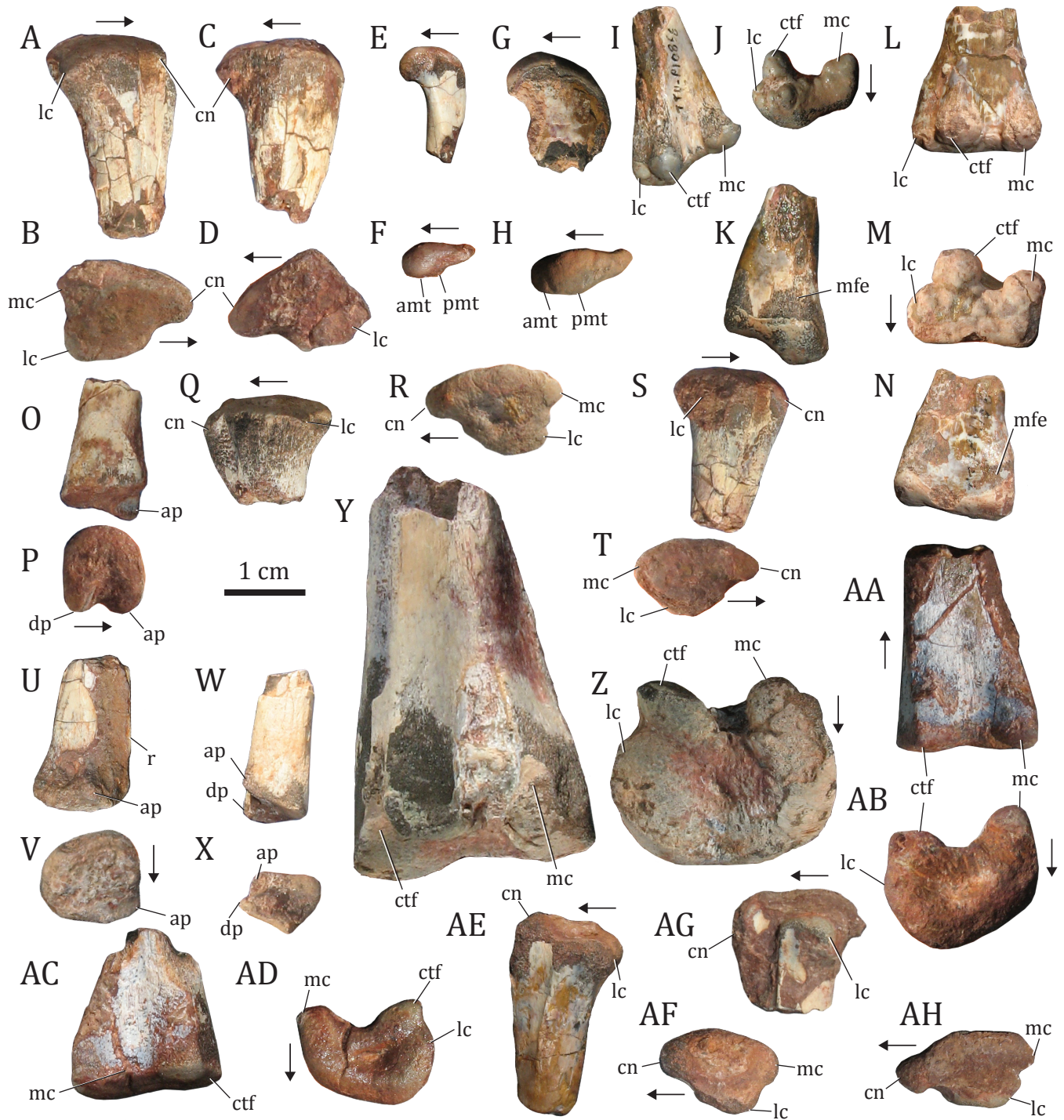
Figure 10. A–D. Dinosauromorph tibiae in lateral (A), proximal (B, D), and medial (C) views. **A, B**. TTU-P11412A. C, D. TTU-P11412E. **E–K.** Lagerpetid femora in medial (E, G), proximal (F, H), posterior (I), distal (J), and anterior (K) views; **E, F**. TTU-P11877. **G, H**. TTU-P11282. **I–K**. TTU-P10866. **L–N**. *Dromomeron gregorii* femur in posterior (L), distal (M), and anterior (N) views; TTU-P11186. **O, P.** Dinosauriform tibia in anterior (O) and distal (P) views; TTU-P11412B. **Q–V.** Dinosaur tibiae in lateral (Q), proximal (R, T), posterolateral (S), anterolateral (U), and distal (V) views. **Q, R**. TTU-P11289. **S, T**. TTU-P11412D. **U, V**. TTU-P11405B. **W, X**. Saurischian tibia in anterior (W) and distal (X) views; TTU-P11412C. **Y–AD.** Saurischian femora in posterior (Y, AA, AC) and distal (Z, AB, AD) views. **Y, Z**. TTU-P11139. **AA, AB**. TTU-P11409C. **AC, AD**. TTU-P11274. **AE–AH.** Theropod tibiae in lateral (AE, AG) and proximal (AF, AH) views. **AE, AF**. TTU-P11405A. **AG, AH**. TTU-P11397A. Scale bar 1 cm. Abbreviations: **ap**, astragalar process; **amt**, anteromedial tuber; **cn**, cnemial crest; **ctf**, crista tibio-fibularis; **dp**, descending process; **lc**, lateral condyle; **mc**, medial condyle; **mfe**, distal origin of *M. femorotibialis externus*; **pmt**, posterome-dial tuber; **r**, ridge. Arrows point anteriorly.

of the femoral shaft (Fig. 9O–X). The femora are nearly identical and are subsequently described together with any differences noted. The broken cross-section of the femur reveals that the midshaft is ovate and hollow. The proximal surface of the femur possesses a prominent anteroposteriorly-trending groove (Fig. 9P, R, T, V, X) as in the dinosauriform *Eucoelophysis* Sullivan and Lucas, 1999 and shuvosaurids, though this character is not restricted to these taxa (Nesbitt 2011; 314:1). The posterior portion of the proximal surface of the femur slopes posteromedially as in theropods and the anterior portion of the femoral head projects markedly from the shaft providing a distinct neck (Fig. 9O, Q, S, U, W). However, there is no pronounced ligament sulcus on the ventral surface of the femoral head and therefore it is not "offset" in the same manner as in members of Dinosauria (Novas 1992; character 11). The anteromedial and posteromedial tubera are separated by a pronounced sulcus in TTU-P11402 and TTU-P11411B-C (Fig. 9Q–V). TTU-P11272 and TTU-P11411A are worn and missing both of the medial tubers, although broken areas show that they were present (Fig. 9O, P, W, X). The anteromedial tuber has a posteriorly-projecting apex that forms a hook in proximal view. This hook is most evident in TTU-P11402 and TTU-P11411B (Fig. 9R, V), and is a character shared by *Effigia* and *Shuvosaurus* Chatterjee, 1993 (Nesbitt 2011; 300:3). The lateral margin is slightly convex in proximal view and there is no distinct anterolateral tuber (Fig. 9P, R, T, V, X) as in most pseudosuchian archosaurs (Nesbitt 2011; 302:1). These are all characteristics of shuvosaurids (Nesbitt 2007: fig. 44, Nesbitt 2011: fig. 38). The medial surface of the shaft lacks the distinct ridge or trochanter found in *Arizonasaurus* Welles, 1947 and *Effigia* (Nesbitt 2005: fig. 26, 2007: fig. 44). Nevertheless, these specimens cannot be assigned to a specific genus and therefore we assign the listed partial femora to Shuvosauridae.

ORNITHODIRA Gauthier, 1986
=AVEMETATARSALIA Benton, 1999
DINOSAUROMORPHA Benton, 1985
sensu Sereno, 1991

Referred Specimens—Tibiae:* TTU-P11412A, proximal end of right tibia (Fig. 10A, B); TTU-P11412E, proximal end of left tibia (Fig. 10C, D).

Locality—MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—TTU-P11412A and E preserve the proximal ends of tibiae and portions of the midshafts (Fig. 10A–D). The specimens are nearly identical and therefore described together, noting any differences. The proximal end is flat and preserves a cnemial crest anteriorly. TTU-P11412A preserves two posterior condyles that taper posteriorly and are equal in size, and the medial posterior condyle is worn in both TTU-P11412A and E (Fig. 10B, D). Because the medial posterior condyle is worn, we cannot tell if the posterior condyles are level at their posterior borders. The posterior border is concave between the posterior condyles in TTU-P11412A (Fig. 10B). The lateral posterior condyle is separated from the cnemial crest by a groove on the lateral surface that extends from the proximal end onto the midshaft (Fig. 10A). The groove does not extend further distally, and the medial surface of the midshaft is flat and featureless. The cnemial crest tapers anteriorly and forms a rounded ridge on the anterior surface of the proximal end of the tibia that extends distally onto the midshaft (Fig. 10A, C). An anteriorly-tapered cnemial crest is a characteristic of Avemetatarsalia (Novas 1996; 10:1), and an anteriorly straight cnemial crest is a characteristic of non-dinosaurian dinosauromorphs (Nesbitt 2011; 328:1). Therefore, we assign TTU-P11412A and E to Dinosauromorpha.

LAGERPETIDAE Arcucci, 1986
sensu Nesbitt et al., 2009c

Referred Specimens—Femora:* TTU-P11877, proximal end of right femur (Fig. 10E, F); TTU-P11282, proximal end of right femur (Fig. 10G, H); TTU-P10866, distal end of left femur (Fig. 10I–K).

Locality—MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—TTU-P11877 and TTU-P11282 preserve the proximal ends of right femora and portions of the midshaft (Fig. 10E–H). They were briefly described by Nesbitt et al. (2009c: pg. 508) and assigned to Lagerpetidae. These specimens are identical and are described together. The proximal surface of the femur is convex and smooth. The anterior portion of the femoral head projects from the shaft with a smooth transition, and the femoral head is hook shaped in medial and lateral views (Fig. 10E, G). This is characteristic of lagerpetid dinosauromorphs (Irmis et al. 2007a; Nesbitt et al. 2009c; Nesbitt 2011; 306:1). The medial surface of the femur is smooth except for the small, worn, medially-projecting posteromedial tuber at the proximal end (Fig. 10F, H), also shared by lagerpetids (Nesbitt et al. 2009c). The lateral margin is convex anteriorly at the small anteromedial tuber and concave posteriorly. The anterior border of the femur is rounded in proximal view at the small, rounded anteromedial tuber (Fig. 10F, H). A small anteromedial tuber is characteristic of all avemetatarsalians (Nesbitt 2011: pg. 146). The posterior border

of the shaft is a sharp, proximodistally-trending ridge, a character of many dinosauriforms (Nesbitt 2011; 301:1). The posterolateral surface of the proximal end is lower distally than the anterolateral portion of the proximal surface of the femur, a dinosauromorph character state (Nesbitt 2011; 313:1). TTU-P11877 and TTU-P11282 do not have an anterior trochanter or a trochanteric shelf, unlike the condition in *Dromomeron gregorii* (Nesbitt et al. 2009c: fig. 2), although the development of the anterior trochanter and trochanteric shelf is ontogenetically variable in dinosauromorphs (Nesbitt et al. 2009c, Griffin and Nesbitt 2016a, b). We are unable to assign TTU-P11877 and TTU-P11282 to *Lagerpeton* Romer, 1971, *Ixalerpeton* Cabreira et al. 2016, or *D. romeri* Irmis et al., 2007a and therefore we assign both specimens to Lagerpetidae.

TTU-P10866 preserves the robust distal end of a femur that gradually expands distally from the shaft and was briefly assigned to Lagerpetidae by Nesbitt et al. (2009c: pg. 508) (Fig. 10I–K). The anterior surface of TTU-P10866 preserves a mediolaterally-oriented ridge that arcs proximally onto the lateral side of the femur. The ridge separates unfinished bone (dorsally) from finished bone (ventrally) (Fig. 10K), and Nesbitt et al. (2009c) identify this ridge as the distal origin of the *M. femorotibialis externus*. The medial surface is flat in the specimen, and the anteromedial corner is obtuse (Fig. 10J). In distal view, the anterior edge of TTU-P10866 is sigmoidal. The crista tibiofibularis is as large as the medial, tibial condyle in the specimen and is separated from the lateral, fibular condyle on the distal surface by a distinct groove (Fig. 10J). The presence of a large crista tibiofibularis places TTU-P10866 within Lagerpetidae (Nesbitt 2011; 326:1). The medial condyle of the specimen is robust and square in distal view and the lateral condyle is gracile and rounded. The distal articular surface of the lateral condyle of TTU-P10866 is covered with small grooves and ridges. Based on the morphology of the crista tibiofibularis, we assign TTU-P10866 to Lagerpetidae.

DROMOMERON GREGORII Nesbitt et al., 2009c

Referred Specimen—TTU-P11186, distal end of left femur (Fig. 10L–N).

Locality—MOTT 3869 (Boren Quarry).

Description and Rationale for Assignment—TTU-P11186 preserves the robust distal end of a femur and was briefly assigned to Lagerpetidae by Nesbitt et al. (2009c: pg. 508) (Fig. 10L–N). The anterior surface of TTU-P11186 preserves a mediolaterally-oriented ridge

that arcs proximally onto the lateral side of the femur, though this ridge is less defined in TTU-P11186 than in TTU-P10866, described above. The ridge separates unfinished bone (dorsally) from finished bone (ventrally) (Fig. 10N), and Nesbitt et al. (2009c) identify this ridge as the distal origin of the *M. femorotibialis externus*. The medial surface is flat in the specimen, and the anteromedial corner is about 90° (Fig. 10M). On the distal end of the femur, the presence of the concave posterolateral surface of the crista tibiofibularis, the scar on the anterior surface for the origin of the *M. femorotibialis externus* and the 90° anteromedial corner are autapomorphic for *Dromomeron* (Nesbitt et al. 2009c, Nesbitt 2011; 327:1) (modification to the placement within Lagerpetidae by Nesbitt et al. (2009c)).. In distal view, the anterior edge of TTU-P11186 is flat (Fig. 10M). The crista tibiofibularis is larger than the medial, tibial condyle in TTU-P11186, is broad mediolaterally, and is separated from the lateral, fibular condyle on the distal surface by a distinct groove. The presence of a large crista tibiofibularis is autapomorphic for Lagerpetidae (Nesbitt 2011; 326:1), and the inflated morphology of the crista tibiofibularis is more similar to that of *Dromomeron* (Irmis et al. 2007a). The medial condyles of the specimen are square in distal view and the lateral condyle is rounded (Fig. 10M). The distal articular surface of the lateral condyle of TTU-P11186 is covered with small grooves and ridges that are less defined than that of TTU-P10866. TTU-P11186 lacks autapomorphies of the distal end of the femur of *D. romeri*, including the presence of a sharp, flaring ridge on the anteromedial edge and a lateral tuberosity on the anterolateral edge (Nesbitt et al. 2009c; 130:1). We assign this specimen to *D. gregorii* on the basis of the scar on the anterior surface, the 90° anteromedial corner, and the absence of the anteromedial flare present in *D. romeri*.

DINOSAURIFORMES Novas, 1992

Referred Specimen—TTU-P11412B, distal end of left tibia (Fig. 10O, P).

Locality—MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—TTU-P11412B preserves the distal end of a left tibia and the portion of a midshaft (Fig. 10O, P). The specimen is rounded posteriorly and has two laterally extending processes in distal view (Fig. 10P). The posterolateral process (=descending process of Langer 2004) tapers to a point laterally in distal view, extends proximally, but stops just distal to the midshaft. The anterolateral process (=astragalar process of Langer (2004)) is rounded anteriorly in distal view. The posterolateral process of

the distal end is slightly concave and extends farther distally than the anterolateral process (Fig. 10O); this is a dinosauriform apomorphy (Nesbitt 2011; 334:1). On the lateral surface of TTU-P11412B, the processes are separated by a proximodistally-oriented groove that does not extend onto the midshaft, a character state present in some dinosauriforms and all dinosaurs (Nesbitt 2011; 338:1). The anterior and posterior margins of the distal end of the tibia are straight. The medial face of the distal end of the tibia is rounded, smooth, and featureless. Based on the morphology of the posterolateral process and the presence of a proximodistally-oriented groove on the lateral surface, we assign TTU-P11412B to Dinosauriformes.

<div align="center">

DINOSAURIA Owen, 1842
sensu Padian & May, 1993

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Referred Specimens—*Tibiae:* TTU-P11289, proximal end of left tibia (Fig. 10Q, R); TTU-P11412D, proximal end of right tibia (Fig. 10S, T); TTU-P11405B, distal end of right tibia (Fig. 10U, V).

Locality—MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—TTU-P11289 and TTU-P11412D preserve the proximal ends of tibiae and TTU-P11412D preserves a portion of the midshaft as well (Fig 10Q–T). The midshaft of TTU-P11412D is subelliptical in cross-section and tapers anteriorly. The specimens are nearly identical and therefore described together, noting any differences. The proximal end is slightly convex and preserves a cnemial crest anteriorly and two posterior condyles that taper posteriorly and are equal in size (Fig. 10R, T). A prominent cnemial crest is an apomorphic trait of Dinosauriformes (Novas 1992; 4:1). The posterolateral condyle is worn in TTU-P11412D (Fig. 10R). Like other early dinosaurs (*Scutellosaurus* Colbert, 1981, *Saturnalia*, *Tawa* Nesbitt et al., 2009b, *Dilophosaurus* Welles, 1954, *Coelophysis*) the posterolateral condyle is offset anteriorly relative to the posteromedial condyle (Langer and Benton 2006: fig. 13, Nesbitt 2011; 331:1). The posterolateral condyle is rounded laterally in TTU-P11289 and separated from the cnemial crest by a groove on the lateral surface that extends from the distal end onto the midshaft in both specimens (Fig. 10Q-T). The medial surface is flat and featureless, lacking the fibular crest of many theropods. The cnemial crest tapers anterolaterally and forms a sharp ridge on the anterior surface of the proximal end of the tibia that extends distally onto the midshaft (Fig. 10Q, S). An anterolaterally-tapering cnemial crest is a character shared by all dinosaurs (Nesbitt 2011; 328:2).

Therefore, based on the presence of this character and absence of theropod apomorphies discussed below, we assign TTU-P11289 and TTU-P11412D to Dinosauria.

TTU-P11405B preserves the distal end of the right tibia and a portion of the midshaft. The midshaft is almost circular in cross section with the exception of a flat anterolateral side (Fig. 10U, V). TTU-P11405B is subrectangular in distal view (Fig. 10V), a synapomorphy of Dinosauromorpha (Sereno 1991: pg. 37). The posteromedial edge of the midshaft is rounded, whereas the anteromedial surface has a sharp, proximodistally-oriented ridge that terminates just proximal to the distal end (Fig. 10S). This is a character state present in ornithischians, sauropodomorphs, and neotheropods (Nesbitt 2011; 336:1). The medial border is rounded and the anteromedial corner of the proximal surface is downturned. The lateral portion of TTU-P11405B preserves two surfaces for articulation that are level at their lateral border (Fig. 10V). The proximal surface of the anterior articular surface (=astragalar process) is slightly depressed distally in comparison to the proximal surface of the posterior articular surface (descending process). Based on the ridge on the anteromedial surface, we assign TTU-P11405B to Dinosauria.

<div align="center">

SAURISCHIA Seeley, 1887
sensu Gauthier, 1986

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Referred Specimens—*Tibia:* TTU-P11412C, distal end of right tibia (Fig. 10W, X). *Femora:* TTU-P11139, distal end of left femur (Fig. 10Y, Z); TTU-P11409C, distal end of left femur (Fig. 10AA, AB); TTU-P11274, distal end of right femur (Fig. 10AC, AD).

Localities—*Tibia:* MOTT 3898 (Headquarters South). *Femora*: MOTT 3899 (Headquarters NW); MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—*Tibia*—TTU-P11412C preserves the distal end of a right tibia as well as a portion of the midshaft (Fig. 10W, X). Upon initial inspection, TTU-P11412C is very similar to TTU-P11412B (assigned to Dinosauriformes above, Fig. 10O, P), though slight but important differences are discussed below. The tibia is nearly square in distal view. The posterolateral surface (=descending process of Langer (2004)) of the distal end extends further distally than the anterolateral surface (=astragalar process of Langer (2004)), and the two surfaces level out on the medial surface of the distal end (Fig. 10W). The posterior margin of the distal end of the tibia is slightly concave (Fig. 10X), an apomorphy of saurischians (Nesbitt 2011; 335:1). The anterolateral and anteromedial margins

are rounded, whereas the posteromedial margin of the distal end is formed by a proximodistally-oriented ridge, which is a dinosaur character state (Nesbitt 2011; 336:1). The medial side of the distal end of the tibia is smooth and featureless. The lateral side of the distal end has a proximodistally-oriented groove between the descending and astragalar processes (Fig. 10X), a plesiomorphy of dinosaurs (Nesbitt 2011; 338:1). Based on this combination of characters found in dinosaurs and saurischians, we assign TTU-P11412C to Saurischia.

Femora—TTU-P11139, TTU-P11274, and TTU-P11409C preserve the distal ends of femora, and TTU-P11139 and TTU-P11409C also preserve a portion of the midshaft (Fig. 10Y–AD). These specimens are otherwise identical and therefore described together. In distal view, the femur is concave posteriorly and convex anteriorly (Fig. 10Z, AB, AD). The femur preserves a medial, tibial condyle on the posteromedial surface of the distal end that tapers posteriorly (worn in TTU-P11139), a rounded lateral, fibular condyle on the anterolateral surface of the distal end, and a small, square crista tibiofibularis on the posterolateral surface of the distal end (Fig. 10Z, AB, AD). The crista tibiofibularis and lateral condyle are separated on the distal surface by a groove that deepens to a fossa in the center of the distal end. The presence of the groove is a character state of dinosauromorphs, *Effigia*, *Poposaurus*, *Fasolasuchus*, *Postosuchus*, and crocodylomorphs (Nesbitt 2011; 322:1). Among dinosauromorphs this character state is shared by *Dromomeron* (which exhibits a squared anteromedial corner and an inflated crista tibiofibularis) and saurischians (Nesbitt 2011). The distal surface of the femur is otherwise flat. In distal view, the angle between the lateral condyle and the crista tibiofibularis on the lateral surface of the distal end is obtuse (Fig. 10Z, AB, AD) as in avian-line archosaurs, whereas this angle is about 90° in *Effigia*, *Batrachotomus*, *Fasolasuchus*, *Postosuchus*, and crocodylomorphs (Nesbitt 2011; 319:1). As in avian-line archosaurs the obtuse angle between the lateral condyle and crista tibiofibularis in this femur is accompanied by a semicircular, rounded lateral condyle (Nesbitt 2011; 319:1). On the posterior surface, there is a wide intercondylar groove created by the medial condyle medially and the crista tibiofibularis laterally that extends from the distal end and shallows proximally onto the midshaft (Fig. 10AA–AD). The medial condyle extends proximally, ending in a roughened surface angling onto the posteromedial side of the midshaft. The crista tibiofibularis extends proximally as well, though less proximally than the medial condyle, and ends proximally in a distinct step onto the midshaft (Fig. 10Y,

AA, AC). The anterior surface of the distal end of the femur is smooth. TTU-P11139, TTU-P11409C, and TTU-P11274 are very similar to *Tawa hallae* (GR 244, Nesbitt et al. 2009b) though they do not preserve any apomorphies specific to *Tawa*. We assign these specimens to Saurischia based on the groove and angle between the lateral condyle and crista tibiofibularis.

<div align="center">

THEROPODA Marsh, 1881
sensu Gauthier, 1986

</div>

Referred Specimens—*Tibiae:* TTU-P11405A, proximal end of left tibia (Fig. 10AE, AF); TTU-P11397A, proximal end of left tibia (Fig. 10AG, AH).

Locality—MOTT 3898 (Headquarters South).

Description and Rationale for Assignment—TTU-P11405A and TTU-P11397A preserve the proximal ends of left tibiae as well as portions of the midshaft (Fig. 10AE–AH). TTU-P397A is smaller and preserves more of the midshaft than TTU-P11405A. The midshaft of TTU-P11397 is nearly oval in cross section. The proximal ends of both tibiae preserve the cnemial crest anteriorly and two posterior condyles (Fig. 10AF, AH). A prominent cnemial crest is a derived trait of Dinosauriformes (Novas 1992; 4:1). The proximal surface of TTU-P11405A has a slight concavity posterior to the cnemial crest and anterior to the medial posterior condyle, and in TTU-P11397A the proximal surface is slightly concave as well. Among theropods, *Coelophysis* has a shallow concavity on the proximal surface of the tibia, whereas the surface is deeply concave in some other theropods (e.g., *Allosaurus* Marsh, 1877) (Nesbitt 2011; 329:1). The cnemial crest in both specimens tapers and curves anterolaterally in proximal view (Fig. 10AF, AH), a character state shared by all dinosaurs (Nesbitt 2011; 328:2). In TTU-P11397A, the lateral and medial posterior condyles are rounded, whereas in TTU-P11405A the medial condyle tapers posteriorly and the lateral condyle is rounded. In both specimens, the lateral and medial condyles each form half of the posterior border in proximal view and are separated by a groove that originates on the proximal end and continues onto the posterior surface. In proximal view, the lateral condyle is offset anteriorly relative to the medial condyle (Fig. 10AF, AH), which is plesiomorphic for theropods (Nesbitt 2011; 331:1). The lateral margin of the lateral condyle in TTU-P11405A is flat as in theropods (Nesbitt 2011; 332:1), and this surface is nearly flat, but worn, in TTU-P11397A. The medial surface of the proximal end is smooth in TTU-P11405A and expands slightly laterally on the cnemial crest just distal to the proximal surface of TTU-P11397A. On the anterolateral

surface of both TTU-P11405A and TTU-P11397A, there is a wide groove paralleled posteriorly by a sharp, dorso-ventrally-oriented ridge originating at the proximal end and ending on the midshaft (Fig. 10AE, AG). This ridge (=fibular crest) is observed in *Saturnalia*, *Heterodontosaurus* Crompton and Charig, 1962, *Silesaurus*, *Sacisaurus* Ferigolo and Langer, 2007, and neotheropods (Nesbitt 2011; 333:1). The flat lateral margin of the lateral tibial condyle and the presence of a fibular crest lead us to assign TTU-P11405A and TTU-P11397 to Theropoda.

DISCUSSION

Revisions to the Dockum Vertebrate Assemblage

This work expands on recent studies of the Dockum Group vertebrate assemblage by Nesbitt and Chatterjee (2008), Hungerbühler et al. (2013), Martz et al. (2013), and Sarigül (2016, 2017a, 2017b), demonstrating a previously-unrecognized diversity of saurian taxa in these strata, which are otherwise typically found outside North America. This study and those of Sarigül (2016, 2017a) also demonstrate the widespread occurrence of dinosauromorphs in the Dockum Group that are part of an emerging ubiquitous Chinle Formation/Dockum Group assemblage during the Late Triassic. Our study reflects a new emphasis on smaller-bodied saurian records from these units, and combined with an apomorphy-based approach to identification (e.g., Nesbitt and Stocker 2008, Pritchard 2015, Pritchard et al. 2015), allows for the improved identification of specimens from these assemblages that was not possible previously.

We add to the known Dockum Group tetrapod assemblage members of the clade Tanystropheidae and the second species-level identification of *Scutarx deltatylus* (Parker 2016b). This occurrence of *Scutarx deltatylus* is significant because it is from the lowermost Revueltian teilzone, as it occurs at about the same level (MOTT 3899) of the lowest observed occurrence of *Machaeroprosopus* (*sensu* Parker et al. 2012), which diagnoses the local base of the Revueltian (Martz and Parker 2017). This further extends the record of non-desmatosuchin aetosaurs (Parker 2016a) into the Revueltian, with the only other record being a purported specimen of *Desmatosuchus smalli* from the earliest Revueltian of Arizona (Parker 2005a, b, 2006). Tanystropheid material from Texas is currently only identified from the lower part of the Cooper Canyon Formation although this is almost certainly a sampling issue, as material is known from the Revueltian of New Mexico (e.g., Pritchard et al. 2015) and the Adamanian of Arizona (e.g., Kaye and Padian 1994, Kligman

et al. 2017, 2018).

Our identifications of members of drepanosaurid-like diapsids concur with the unpublished (other than abstracts [Mueller and Chatterjee 2012, Mueller et al. 2016]) identifications of drepanosaurid material (Martz et al. 2013). Of interest is the stratigraphic restriction of the occurrence of this material to the middle of the Cooper Canyon Formation, and thus Revueltian, although a simiosaurian scapula has been documented from the Adamanian Post Quarry (Martz et al. 2013) and Adamanian occurrences are known from Arizona and from younger rocks in New Mexico (Renesto et al. 2010). We add voucher specimens from the lower part of the Cooper Canyon Formation for the clade that includes *Vancleavea campi* and *Litorosuchus somnii* (Li et al. 2016), previously only known from the Dockum by a single vertebra (UMMP 7278; Long and Murry 1995). Previous referral of vertebrae to *Vancleavea* from the lower part of the Cooper Canyon Formation using a non-apomorphy-based methodology (Lucas et al. 2017) are erroneous because these vertebrae lack the autapomorphies found in *Vancleavea* vertebrae, such as that sharp double paramedian ventral keels on the trunk vertebrae (Nesbitt et al. 2009a), and instead represent a different archosauriform. Members of Allokotosauria were already known from the Dockum Group (e.g., Case 1922, Gregory 1945, Chatterjee 1986b, Mueller and Parker 2006, Spielmann et al. 2008, 2009), but the clade was only named recently (Nesbitt et al. 2015) with broader recognition of its morphological disparity, allowing us to better classify the specimens from these assemblages. We identify members of clade Allokotosauria + *Prolacerta broomi* + Archosauriformes from the lower and middle parts of the Cooper Canyon Formation. Moreover, our data support evidence that non-trilophosaurid allokotosaurids are far more common in the Dockum assemblage than previously recognized (Spielmann et al. 2009, Stocker 2013a, Nesbitt et al. 2017a).

Overall, we report two species-level identifications and taxa from 21 clades (Table 1). Six of these clades and species identifications are terminal and exclusive of other taxa identified by this study (e.g., Tanystropheidae, *Vancleavea campi* + *Litorosuchus somnii*, Phytosauria, *Scutarx deltatylus*, Shuvosauridae, *Dromomeron gregorii*, Theropoda). In this study, most specimens were from the Headquarters South (MOTT 3989) site; we report taxa from 16 clades, three of which are terminal for this site (Table 2). Other sites contained taxa from one to four clades. We recognize at least five distinct taxa of Pseudosuchia and three distinct taxa of Dinosauromorpha

simply from morphological differences in the proximal ends of the tibiae. Also, multiple specimens described as identical (e.g., tetrapod, diapsid, *V. campi* + *L. somnii*, paracrocodylomorph, shuvosaurid, and saurischian femora and diapsid humeri) are distributed across multiple localities. However, with the exception of the *V. campi* + *L. somnii* and paracrocodylomorph femora, these identical specimens are limited to a single stratigraphic level within the Cooper Canyon Formation.

The Earliest Dinosaurs in Western North America

Compared with the recently published dinosaur records (Sarigül 2017a), those that are identified in this study, largely from the middle of the Cooper Canyon Headquarters South (MOTT 3898) site, do not comprise a range extension of the dinosaur fossil record in North America. However, the apomorphy-based identification method used here needs to be strictly applied to other fossils that are claimed to be from the oldest dinosaurs in North America. TTU-P10514 and TTU-P10517 (right dentaries) and TTU-P10515 (left dentary) were described as saurischians from the stratigraphically-low Boren Quarry (MOTT 3898, Fig. 1) (Sarigül 2017b), but in fact represent archosauromorphs belonging to the group Allokotosauria (Nesbitt et al. 2015), and this is supported by multiple character states. Unlike most archosauriforms, the Meckelian groove of TTU-P10514 and TTU-P10515 extends anteriorly through the mandibular symphysis; this feature is found in the silesaurids *Silesaurus* and *Sacisaurus* (Nesbitt 2011; 153:1) as well as azendohsaurid allokotosaurs (Flynn et al. 2010; Nesbitt et al. 2017a). In contrast, the Meckelian groove terminates posterior to the mandibular symphysis in early dinosaurs (e.g., *Scutellosaurus*, sauropodomorphs, *Tawa*, *Dilophosaurus*) (Nesbitt 2011; 153:0). Furthermore, the teeth of TTU-P10514, TTU-P10515, and TTU-P10516 are ankylosed to the dorsal surface of the dentary, which is a plesiomorphic feature of archosauromorphs present in the allokotosaurs *Teraterpeton* Sues, 2003, *Trilophosaurus*, and *Azendohsaurus* (Nesbitt et al. 2015; 97:1), as well as in silesaurids (Nesbitt 2011; 174:0). The teeth of early saurischians are rooted and implanted in the alveoli of the dentary in a complete thecodont condition (LeBlanc et al. 2017). The combination of an anteriorly-extending Meckelian groove and dentary teeth ankylosed to the top of the mandible is also found in the silesaurids *Silesaurus* and *Sacisaurus* (Dzik 2003, Langer and Ferigolo 2013). However, tooth morphology of the TTU-P dentaries does not resemble that of silesaurids in that the dentaries from the Boren Quarry have teeth that are smooth and recurved with serration on the anterior carina unlike those of *Sacisaurus* (MCN PV10041), which are not curved, are serrated on both the mesial and distal carina, and have longitudinal striations. Finally, the TTU-P dentaries are smoothly rounded anteriorly and lack the 'beak' found in most silesaurids (Nesbitt 2011; 155:1).

The removal of TTU-P10514, TTU-P10515, and TTU-P10517 from the dinosaur record of North America eliminates Dinosauria from the Boren Quarry and negates these specimens as the "lowest occurrence of dinosaurs in the Dockum Group and in North America" (contra Sarigül 2017b: pg. 11). This was already a questionable statement given the presence of TMM-31100-532, a proximal end of a femur referred to *Chindesaurus bryansmalli* Long and Murry 1995 and the recent recognition of the theropod *Lepidus praecisio* Nesbitt and Ezcurra, 2015 from the Colorado City Formation of the Dockum Group. Our identification of these three dentaries shortens the temporal range of Saurischia in the Dockum Group to the Otis Chalk Quarry 3 (MOTT 2000/TMM 31100) and TMM 41936, the holotype locality of the theropod *L. praecisio* (Nesbitt and Ezcurra, 2015). It remains unclear how those two quarries within the Colorado City Formation relate precisely to the preliminary Rb-Sr date of ~225 Ma taken just below the Boren Quarry (MOTT 3869) of the lower part of the Cooper Canyon Formation (Sarigül 2017b) and to the U-Pb age of approximately 223.036 ± 0.059 Ma near PFV 337 (Parker and Martz 2011, Ramezani et al. 2011), a locality bearing a proximal end of a theropod femur (PEFO 35117). Maximum depositional age determinations from detrital zircons (Riggs et al. 1996, Dickinson and Gehrels 2008) strongly suggest that the Santa Rosa Formation (Dockum Group) and Shinarump Member (Chinle Formation) were deposited by the same major drainage and roughly no earlier than ~227 Ma (Dickinson and Gehrels 2008, Atchley et al. 2013). Therefore, the occurrence of *L. praesicio* must be younger than that date, although how much younger cannot presently be determined. Because a non-phytosaurid phytosaur (*Wannia scurriensis*) is present in the Camp Springs Member, the local equivalent of the Santa Rosa Formation, this suggests this unit is older than the Blue Mesa Member of the Chinle Formation and the lower portion of the Cooper Canyon Formation (e.g., Lucas and Anderson 1993, Lucas et al. 1993, Stocker 2013a, b, Sarigul 2017a, b, Martz and Parker 2017.) Thus, the lowest occurrences of Dinosauria in North America are in the Dockum Group based on vertebrate biostratigraphic correlation.

CONCLUSIONS

Constructing faunal assemblage lists is a challenge affected by the quality of existing data for various taxonomic groups, as well as the differing methodologies used by previous investigators. Biostratigraphic biases also commonly come into play when stratigraphic position is used as part of the identification process (e.g., Long and Murry 1995). It is often difficult for the non-specialist to recognize when the precision of a taxonomic assignment exceeds the available data to make an accurate assignment, leading to flaws in larger scale studies (e.g., biostratigraphic, biogeographic, paleoecologic) that rely on these primary data. Apomorphy-based identifications are an attempt to standardize the process, removing the subjectivity as well as the inherent circularity of specimen description and comparison, ensuring that the identification process is testable and repeatable (e.g., Nesbitt and Stocker 2008, Bell et al. 2010).

However, because it is rooted in the process of phylogenetic inference, apomorphy-based identifications are also limited by the quality of existing phylogenetic data. For example, the study of this material was started more than a decade ago, but the phylogenetic data required to complete the study were not available until more recently. In particular, our understanding of discrete apomorphies for clades such as Allokotosauria and Drepanosauromorpha were lacking, and recent revisions of these groups (e.g., Flynn et al. 2010, Nesbitt et al. 2015, Pritchard 2015, Pritchard et al. 2015, 2016) allow us to finally identify these specimens beyond the clade Reptilia. Even still, apomorphies for these clades are in their infancy and relationships remain poorly resolved. We have identified the apomorphies that are available and detailed the observable variation among specimens.

Triassic workers are commonly faced with the difficult task of collecting fragmentary specimens from multi-taxic bonebed assemblages. A detailed understanding of postcranial apomorphies is critical to the accuracy of identifying these specimens to the finer taxonomic levels (e.g., genus and species) that are required for the detailed reconstruction of ecosystems (Nesbitt 2011, Pritchard et al. 2015, 2016) and allow for regional and global comparisons (Irmis et al. 2010, Parker and Martz 2017). Even so, a strict adherence to apomorphy-based identifications of fragmentary material limits species-level identifications.

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