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The femora of Drepanosauromorpha (Reptilia: Diapsida): Implications for the functional evolution of the thigh of Sauropsida

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Abstract

The femora of diapsids have undergone morphological changes related to shifts in postural and locomotor modes, such as the transition from plesiomorphic amniote and diapsid taxa to the apomorphic conditions related to a more erect posture within Archosauriformes. One remarkable clade of Triassic diapsids is the chameleon-like Drepanosauromorpha. This group is known from numerous articulated but heavily compressed skeletons that have the potential to further inform early reptile femoral evolution. For the first time, we describe the three-dimensional osteology of the femora of Drepanosauromorpha, based on undistorted fossils from the Upper Triassic Chinle Formation and Dockum Group of North America. We identify apomorphies and a combination of character states that link these femora to those in crushed specimens of drepanosauromorphs and compare our sample with a range of amniote taxa. Several characteristics of drepanosauromorph femora, including a hemispherical proximal articular surface, prominent asymmetry in the proximodistal length of the tibial condyles, and a deep intercondylar sulcus, are plesiomorphies shared with early diapsids. The femora contrast with those of most diapsids in lacking a crest-like, distally tapering internal trochanter. They bear a ventrolaterally positioned tuberosity on the femoral shaft, resembling the fourth trochanter in Archosauriformes. The reduction of an internal trochanter parallels independent reductions in therapsids and archosauriforms. The presence of a ventrolaterally positioned trochanter is also similar to that of chameleonid squamates. Collectively, these features demonstrate a unique femoral morphology for drepanosauromorphs, and suggest an increased capacity for femoral adduction and protraction relative to most other Permo-Triassic diapsids.

1 | INTRODUCTION

In limbed tetrapods, the femur plays a key role in hindlimb posture and locomotion. Therefore, its skeletal morphology provides important evidence for evolutionary transformations in the functional morphology of the tetrapod thigh. Major transitions in the anatomy of the femur are known in a wide range of tetrapod lineages, most notably therapsids and archosaurs. In both of these lineages, prior research has linked modifications to major muscle groups and osteological correlates for muscle attachments to large-scale changes in posture and locomotion (e.g., Blob, 2001; Hutchinson, 2001; Romer, 1922). Most notably, both lineages underwent modifications indicating a shift from an ancestrally sprawling condition similar to that of extant salamanders and lepidosaurs to an erect or semi-erect gait. These changes have been linked to shifts in the locomotor strategies and ecological roles occupied by these taxa. Analogous changes to the morphology of the femora in other tetrapod lineages are thus of interest to evolutionary biologists seeking further examples of changes in femoral trochanters and shifts in thigh muscle attachment sites. Herein, we document a specialized femur in the early diapsid clade Drepanosauromorpha, which is highly modified from the ancestral diapsid condition and distinct from that of any other known reptile. The modifications to the ventral trochanteric system bear distinct similarities to those in archosauriforms and therapsids.

Drepanosauromorpha are a clade of exclusively Triassic diapsid reptiles with bizarre morphologies that have been linked to arboreality (e.g., Pritchard et al., 2016; Renesto, 1994a, 1994b), specialized swimming (e.g., Britt et al., 2016; Colbert & Olsen, 2001), and possible fossoriality (e.g., Jenkins et al., 2020). Much of the present understanding of the group comes from a small number of complete to partial articulated skeletons from Upper Triassic marine deposits in Italy (Renesto et al., 2010) and lacustrine deposits in eastern North America (Colbert & Olsen, 2001). Most of these skeletons are heavily compressed, which has long inhibited interpretation of the three-dimensional osteology of the group. More recent discoveries of three-dimensionally preserved, largely undistorted drepanosauromorph fossils from fluvial deposits in western North America have substantially expanded our understanding of the cranial and appendicular osteology of the group and their phylogenetic position among Diapsida (e.g., Pritchard et al., 2016; Pritchard & Nesbitt, 2017). These include skulls, partially articulated forelimbs, dozens of isolated bones, and many unguals, which have revealed high morphological disparity in drepanosauromorphs from western North America (Gonçalves & Sidor, 2019; Harris & Downs, 2002; Jenkins et al., 2020; Pritchard et al., 2016).

In this contribution, we describe a series of femora from the Upper Triassic Chinle Formation and Dockum Group from the American southwest. The femora share a series of apomorphies with more complete drepanosauromorph specimens from the Triassic of Italy and eastern North America, supporting their referral to the clade. Their exquisite three-dimensional preservation allows a complete description of the femoral osteology of drepanosauromorphs for the first time. We compare these femora with a wide range of amniotes, noting points of homology shared among our sample taxa and surveying extant reptiles and extinct amniotes for possible shared functional similarities.

1.1 | Institutional abbreviations

AMNH FARB, American Museum of Natural History, Fossil Amphibians, Reptiles, and Birds, New York, NY, USA; **BP**, Evolutionary Studies Institute (formerly Bernard Price Institute), Johannesburg, South Africa; **CM**, Carnegie Museum of Natural History, Pittsburgh, PA, USA; **GR**, Ruth Hall Museum of Paleontology, Ghost Ranch, Abiquiu, NM, USA; **MCSNB**, Museo Civico di Scienze Naturale Enrico Caffi, Bergamo, Italy; **MCZ**, Museum of Comparative Zoology, Cambridge, MA, USA; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MPUM**, Museo di Paleontologia Universita degli Studi di Milano, Milano, Italy; **NHMUK**, Natural History Museum, London, United Kingdom; **PIMUZ**, Palaeontological Museum of the University of Zürich, Zürich, Switzerland; **SAM**, Iziko-South African Museum, Cape Town, South Africa; **TMM**, Texas Vertebrate Paleontology Collections, Jackson School of Geosciences, the University of Texas at Austin, Austin, TX, USA; **TTU**, Museum of Texas Tech, Lubbock, TX, USA; **UMNH**, Natural History Museum of Utah, Salt Lake City, UT, USA; **VMNH**, Virginia Museum of Natural History, Martinsville, VA, USA; **VTPE**, Virginia Tech Paleobiology Extant Collection (Geosciences), Blacksburg, VA, USA.

2 | MATERIALS AND METHODS

2.1 | Terminology and orientation

As with many sprawling tetrapods, the three-dimensional orientation of the femur in drepanosauromorphs would likely change considerably throughout a single stride (e.g., Fischer et al., 2010; Higham & Jayne, 2004). Comparisons to other amniotes that possess different postures are thus difficult. We choose to employ the terminology of Gower (2003) in his description of *Erythrosuchus africanus* and Russell and Bauer (2008) in their description of lepidosaur postcrania in which the long axis of the proximal end of the femur defines the transverse axis of the femur. In a sprawled posture at mid-stance, the anterior surface of the femur is defined as medial and the posterior surface of the femur is defined as lateral. Terminology for the distal femoral condyles follows

Russell and Bauer (2008) and Pritchard et al. (2015), defining lateral and medial tibial condyles and a fibular condyle.

2.2 | Geological context

A portion of the material described in this paper was collected from the Hayden Quarry (HQ) site, a fossil-rich deposit in the Petrified Forest Member of the Chinle Formation (Irmis et al., 2007). A middle Norian age for the HQ is inferred from a U–Pb radioisotopic date from one of the paleochannels suggesting a maximum age of 211.9 ± 0.7 Ma (Irmis et al., 2011). The drepanosauromorph fossils from the HQ include mostly isolated elements and a few partially articulated forelimbs (Pritchard et al., 2016), and all are three-dimensionally preserved and mostly uncrushed. The specimens were collected during summer field seasons that began in 2006. The other diverse vertebrate taxa represented in the HQ assemblage include phytosaurs, aetosaurs, ornithodirans, loricatans, temnospondyls, and actinopterygians (Irmis et al., 2007; Lessner et al., 2016; Nesbitt, Smith, et al., 2009). Pritchard et al. (2016) previously described drepanosauromorph forelimbs from the HQ comparable to those of *Drepanosaurus unguicaudatus*.

Specimens from the Dockum Group of Texas span nearly the entirety of the Norian, with material collected in the 1930s and 1940s by the Works Progress Administration representing Otischalkian (latest Carnian-earliest Norian) drepanosauromorphs from the Colorado City Formation (e.g., Stocker, 2013). The specimen described here (TMM 31100-1333) is from Quarry 3, which also preserves a diverse assemblage of temnospondyls, early archosauromorphs, phytosaurs, aetosaurs, poposauroids, and loricatans (Long & Murry, 1995; Stocker et al., 2016). Additional specimens of complete and partial femora from the Headquarters Locality (e.g., Lessner et al., 2018) in the middle–late Norian of the Cooper Canyon Formation were collected by teams from Virginia Tech.

2.3 | Specimen and scanning data availability

We present linear measurements of preserved features of all femora identified in our study in Table 1. Three-dimensional surface scans of three of the most complete drepanosauromorph femora (GR 1078, TMM 31100-1333, TTU- P24739) are presented as Supplemental files 1, 2, and 3. Mapped surface textures are included for TMM 31100-1333 and TTU- P24739. Three-dimensional surface scans of two chameleon femora with mapped surface textures are also presented as Supplemental files 4 and 5. Supplemental file 4 is a right femur of a Meller's Chameleon (*Trioceros melleri*) (VTPE.LA.0269), and Supplemental file 5 is a right femur of a Gracile Chameleon (*Chamaeleo gracilis*) (VTPE.LA.0144). These 3D scans were generated by an Artec Micro 1 model 3D scanner at the Virginia Tech University Library 3D Scanning Studio. The torsions of the femora discussed in the Description section were measured on photographs in the ImageJ 1.52 photographic utility using the angle tool (Schindelin et al., 2012).

TABLE 1 Linear measurements of drepanosauromorph femora sampled in this study. An asterisk indicates poor preservation of specimen, which may obscure the original measurement

SPECIMEN #	Locality	Proximodistal length (mm)	Transverse width of proximal end (mm)	Transverse width of distal end (mm)	Proximodistal length of FTA	Flexor-extensor dimension of lateral condyle	Flexor-extensor dimension of medial condyle
GR 387	Hayden Quarry (H4)	XX	7.8	8.4	3.8	5.9	3.6
GR 1078	Hayden Quarry (H2)	47.6	9.5	9.1	4.9	6.6	4.9
GR 1079	Hayden Quarry (H4)	45.4*	8.3	7.5	2.9*	7.1	4.6
GR 388	Hayden Quarry (H3)	X	X	X	3.7	X	X
GR 1080	Hayden Quarry (H4)	X	X	8.9		6.4	4.2
TMM 31100-1333	HO-3-Q3	43	8.7	10.4	5.8	6.7	4.6
TTU-P24739	Headquarters Locality	32.6	6.2	6.3	2.8	4.3	2.9
TTU-P24741	Headquarters Locality	X	5.8	X	3.3	X	X
TTU-P24746	Headquarters Locality	X	6.7	X	X	X	X
TTU-P24745	Headquarters Locality	X	6.9	X	X	X	X

Note: * indicates post-mortem damage to specimen that may obscure original dimensions.

A 3D surface file of a left femur of *Captorhinus* (UMNH VP 33627) from the Permian Richards Spur locality (Oklahoma, USA) is presented as Supplemental file 6. The specimen was imaged at the University of Utah Preclinical Imaging Core Facility on March 22, 2022. It was scanned using a Siemens INVEON µCT scanner at a voxel resolution of 47 µm, a voltage of 80 kVp, and a current of 250 µA, producing a total of 1,035 slices. The 3D model was generated using segmentation in the Avizo 7.0 software package. 3D surfaces and original µCT scans of all specimens are available for download as part of MorphoSource Project 000487630 (https://www.morphosource.org/projects/000487630).

3 | RESULTS

3.1 | Identification as Drepanosauromorpha

The three-dimensional femora in our sample exhibit an apomorphy and a unique combination of morphological character states shared with the crushed, articulated skeletons of known drepanosauromorphs, supporting the referral of the former to the clade. The proximal articular surface of the specimens in our sample (e.g., GR 1078, 1079, 1080; TMM 31100-1333) is hemispherical, as in the early-diverging drepanosauromorphs *Hypuronector limnaios* (AMNH FARB 7759) and *Vallesaurus cenensis* (MCSNB 4751) (Figure 1a–d). Assuming an early-branching position for Drepanosauromorpha among Diapsida (supported by Müller, 2004, Senter, 2004, Pritchard and Nesbitt, 2017), this is a plesiomorphic state shared with araeoscelids (Reisz, 1981; Vaughn, 1955) and weigeltisaurids (*Coelurosauravus elivensis* [MNHN. MAP327]; *Weigeltisaurus jaekeli* [SMNK PAL 2882; Pritchard et al., 2021]). *Drepanosaurus unguicaudatus* (MCSNB 5728) bears well-defined distal tibial condyles of the femora, which are separated medially by a deep central sulcus (Figure 1e,f). Similarly well-defined tibial condyles and a deep sulcus are present in the Chinle and Dockum femora. These are plesiomorphic states shared with other early diapsids (e.g., Reisz, 1981; Vaughn, 1955). The intercondylar sulcus is less pronounced in *V. cenensis* (MCSNB 4751).

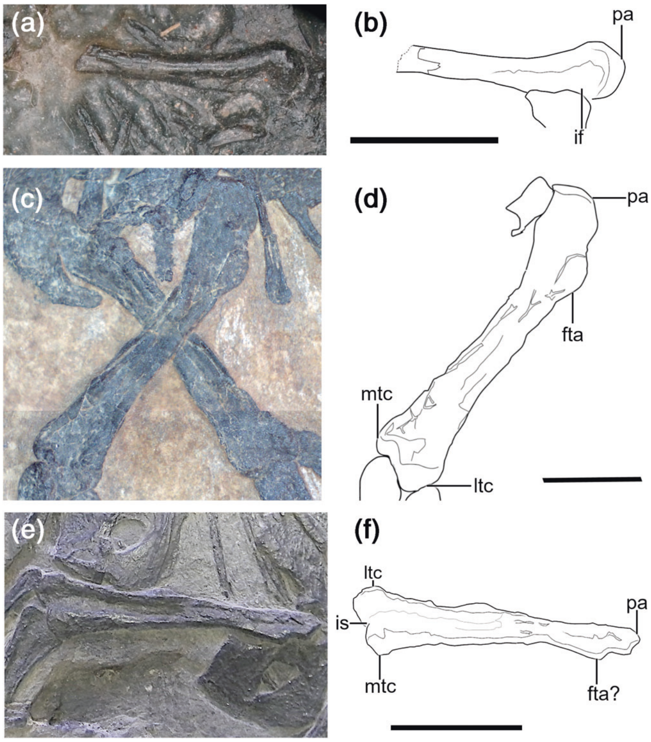

FIGURE 1 Femora of select drepanosauromorphs as photographs and line drawings. (a) Photograph and (b) interpretive illustration of the right femur of *Hypuronector limnaios* (AMNH FARB 7759) in medial view. (c) Photograph and (d) interpretive illustration of pelvis and thigh region of *Vallesaurus cenensis* (MCSNB 4751) in left anterolateral view. (e) Photograph and (f) interpretive illustration of the right femur region of *Drepanosaurus unguicaudatus* (MCSNB 5728) in dorsomedial view. Anatomical abbreviations: fta, fourth trochanter analogue; if, intertrochanteric fossa; is, intercondylar sulcus; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface. Scale bar = 5.0 mm for (b), 2.5 mm for (d), and 20.0 mm for (f).

The Chinle and Dockum femora lack a ventromedially positioned, distally tapering crest on the femoral shaft—an internal trochanter—as is present in most early amniote and diapsid taxa, such as *Captorhinus* (UMNH VP 33627), *Clevosaurus hudsoni* (Fraser, 1988), and *Trilophosaurus buettneri* (TMM 31025-1036, Gregory, 1945). The ventral surfaces of the femora in *Drepanosaurus unguicaudatus* (MCSNB 5728) and *Hypuronector limnaios* (AMNH FARB 7759) also lack a clear internal trochanter (Figure 1a,b,e,f). Instead, the North American drepanosauromorph femora in our sample bear an apomorphic, ventrolaterally positioned tuberosity. The ventrolateral surfaces of the femora in *Vallesaurus cenensis* (MCSNB 4751), *V. zorzinensis* (Renesto et al., 2010), and likely *Drepanosaurus unguicaudatus* (MCSNB 5728) bear a similar, ventrolaterally positioned tuberosity (Figure 1c–f).

This tuberosity in drepanosauromorphs is positioned similar to the primary *mm. caudofemoralis* attachment site on the femur—the fourth trochanter—of apomorphic archosauriforms (Hutchinson, 2001; Nesbitt, Irmis, et al., 2009; Parrish, 1986), and we refer to the drepanosauromorph structure as the "fourth trochanter analogue" throughout this contribution. We describe it as an analogue given its topological similarities to the structure in archosauriforms. In archosauriforms with a fourth trochanter, the structure manifests as a slender ridge or mound in contrast to the rounded tuberosity in available drepanosauromorphs. All recent hypotheses for drepanosauromorph relationships (e.g., Senter, 2004; multiple phylogenies in Renesto et al., 2010; Pritchard & Nesbitt, 2017; Simões et al., 2018) place the clade outside of Archosauriformes, indicating that this distally placed tuberosity must have been acquired independently of the archosauriform fourth trochanter.

Despite their topological and morphological distinctions, the internal trochanter of early reptiles and fourth trochanter of advanced archosauriforms may be partly homologous due to the attachments of similar, but not identical, sets of thigh muscles (e.g., Dilkes, 2000; Hutchinson, 2001; Romer, 1942). This hypothesis remains under investigation, and no clear intermediate stages within Archosauriformes have been described (e.g., Gower, 2003; Hutchinson, 2001; Nesbitt, Irmis, et al., 2009). The same transformation from an ancestral internal trochanter to the fourth trochanter analogue may have occurred in the early evolution of Drepanosauromorpha. It is also possible that the fourth trochanter and fourth trochanter analogue represent neomorphic structures, developed independently of the internal trochanter. In the absence of a clear homology hypothesis, we use the terms "internal trochanter" and "fourth trochanter" in our description section to specifically describe the topological and morphological distinctiveness of these structures. In referring to the absence or reduction of the internal trochanter, we refer specifically to the distally tapering, crest-like structure present on the ventromedial aspect of the femoral shaft in early amniote and diapsid taxa. In referring to the presence of the fourth trochanter (or fourth trochanter analogue), we refer to the more distolaterally positioned crest or tuberosity on the femoral shaft. Consideration of possible homology schema is reserved for Section 4.

SYSTEMATIC PALEONTOLOGY
AMNIOTA Haeckel (1866) *sensu* Gauthier et al. (1988)
DIAPSIDA Osborn (1903) *sensu* Gauthier et al. (1988)
NEODIAPSIDA Benton (1985)
DREPANOSAUROMORPHA Renesto et al. (2010)

3.2 | Referred material

GR 387, distal end of right femur; GR 388, weathered right femur; GR 1078, complete left femur; GR 1079, nearly complete right femur; GR 1080, distal end of left femur (Petrified Forest Member, Chinle Formation); TMM 31100–1333, complete right femur (Colorado City Formation, Dockum Group); TTU-P24739, complete left femur; TTU-P24741, proximal end of right femur; TTU-P24746, proximal end of left femur; TTU-P24745, proximal end of left femur (Cooper Canyon Formation, Dockum Group).

3.3 | Anatomical description

The numerous femora from the Chinle Formation and Dockum Group allow for a detailed description of the three-dimensional external morphology of the drepanosauromorph femur. However, we refrain from referring these specimens to a single species or distinct species. Femora from a large number of early diapsid and early saurian taxa have been described in detail (Gow, 1975; Gregory, 1945; Nesbitt et al., 2015; Reisz, 1981), but in none of these cases have the femora contributed to the species-level identification of the taxon described due to the absence of definitive autapomorphies. We focus our description on the three most complete femora identified thus far: GR 1078 from the Petrified Forest Member of the Chinle Formation (Figure 2), TMM 31100-1333 from the Colorado City Formation (Figure 3), and TTU-P24739 from the Cooper Canyon Formation (Figure 4).

The proximal articular surface of the femur is hemispherical, as in araeoscelids (e.g., Reisz, 1981; Vaughn, 1955) and weigeltisaurids (e.g., MNHN.F. MAP327) (Figure 5). Among other early neodiapsids, such as *Youngina capensis* (BP/1 3859) and *Claudiosaurus germaini* (SAM-PK-K8260, K8580), and archosauromorphs such as *Trilophosaurus buettneri* (TMM 31025-140, -1036) and *Macrocnemus bassanii* (PIMUZ T2477), the proximal articular surface is relatively flatter or marked by a concave groove (Figure 5d). In some extant lepidosaurs, the rounded proximal articular surface is present and part of an epiphyseal ossification that fits into a concavity on the proximal end of the diaphysis; these two elements may fuse during ontogeny (*Iguana iguana* VMNH 129477, Russell & Bauer, 2008) (Figure 5c). In the absence of an ontogenetic series, it is unclear if the proximal articular surfaces in drepanosauromorphs represent fused epiphyses similar to those in lepidosaurs. In pseudosuchian archosaurs, the proximal articular surface is convex and rounded, but it is not hemispherical (*Alligator mississippiensis* VMNH 129468, Gower & Schoch, 2009; Weinbaum, 2013) (Figure 5e).

In proximal view, the proximal articular surface in Drepanosauromorpha is roughly teardrop shaped with a tapered lateral edge. It is marked by a prominent posteromedial tuber on its dorsal surface, similar to that of some early archosauriforms—including erythrosuchids and

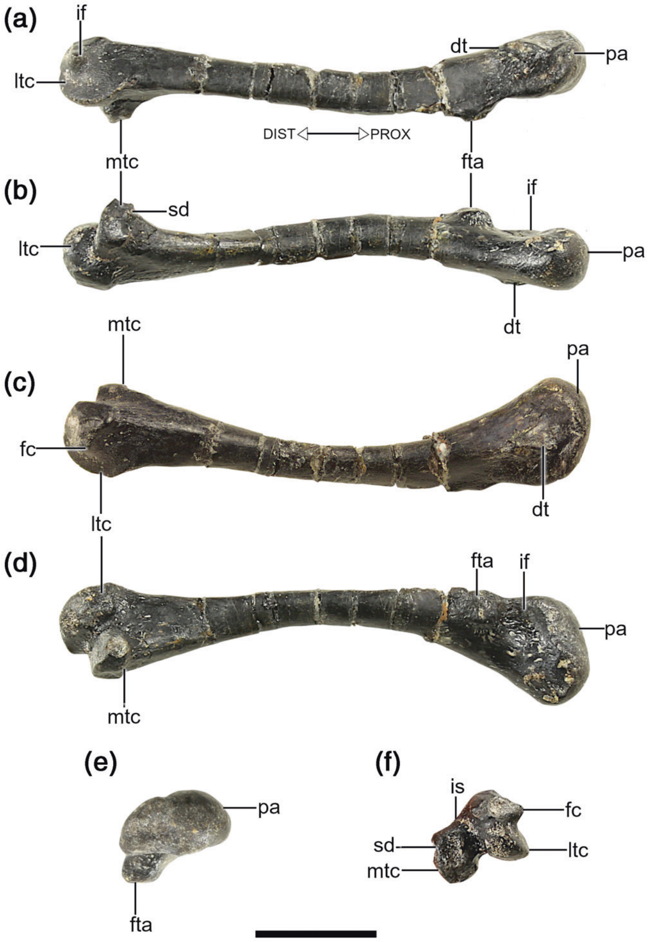

FIGURE 2 Photographs of left femur of Drepanosauromorpha from the Hayden Quarry site (GR 1078) in (a) lateral, (b) medial, (c) dorsal, (d) ventral, (e) proximal, and (f) distal views. Anatomical abbreviations: dist, distal; dt, dorsal tuberosity; fc, fibular condyle; fta, fourth trochanter analogue; if, intertrochanteric fossa; is, intercondylar sulcus; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface; prox, proximal; sd, small depression. Scale bar equals 1.0 cm.

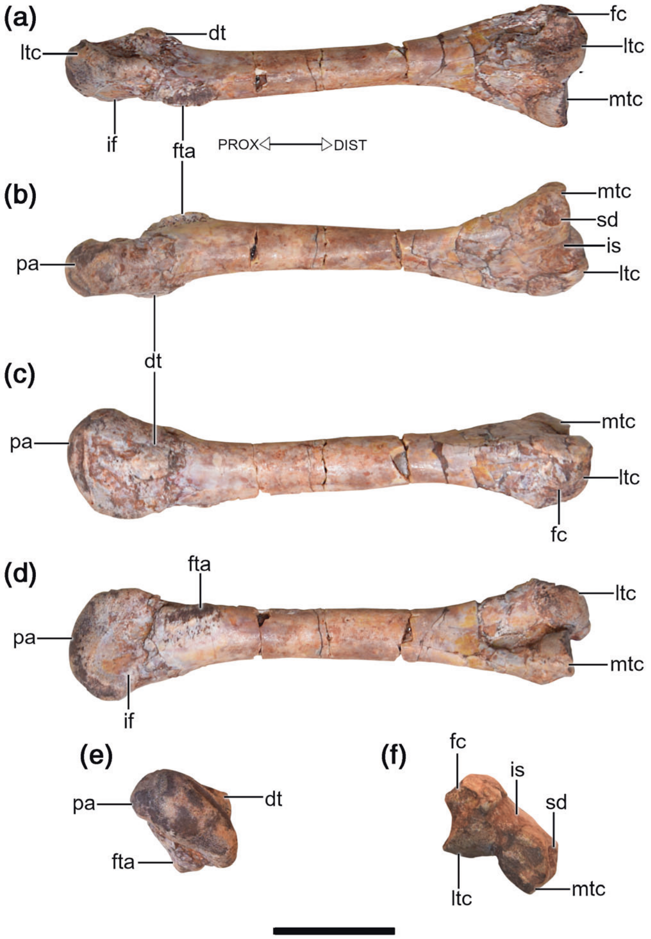

FIGURE 3 Photographs of right femur of Drepanosauromorpha from the Colorado City Formation (TMM 31100-1333) in (a) lateral, (b) medial, (c) dorsal, (d) ventral, (e) proximal, and (f) distal views. Anatomical abbreviations: dist, distal; dt, dorsal tuberosity; fc, fibular condyle; fta, fourth trochanter analogue; if, intertrochanteric fossa; is, intercondylar sulcus; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface; prox, proximal; sd, small depression. Scale bar equals 1.0 cm.

Euparkeria capensis (e.g., Nesbitt, 2011)—and many early archosaurs with well-ossified proximal femoral articular surfaces, such as early pseudosuchians (e.g., Nesbitt et al., 2014; von Baczko et al., 2019; Schachner et al., 2020) and dinosauromorphs (e.g., Kammerer et al., 2020; Nesbitt, Irmis, et al., 2009). In the HQ femora, the articular surface is a distinctly lighter gray color and more porous in texture than the black and smoothly textured femoral shaft (Figure 2). The articular surfaces are similarly porous in both Dockum femora. The shaft and articular surfaces of the Colorado City femur (TMM 31100-1333) are brown (Figure 3). In the Cooper Canyon femur, the shaft is cream colored, and the articular surfaces are red (TTU-P24739) (Figure 4).

The dorsal (=extensor) surface of the proximal end of the femur bears a prominent tuberosity, just distal to the proximal articular surface (Figures 2–4, and 6). This dorsal tuberosity is roughly trapezoidal in shape in GR 1078 and TMM 31100-1333. The same tuberosity is proportionally smaller with less defined margins in TTU-P24739. In all specimens, the dorsal tuberosity tapers distally, transitioning into a thin ridge that extends approximately one-quarter distally down the length of the femoral shaft. A similar dorsal tuberosity is present in many early amniotes and diapsids (e.g., CM 41704, Vaughn, 1955; Romer, 1956; Reisz, 1981) and some extant lepidosaurs (VMNH 129477, Russell & Bauer, 2008) (Figure 6a–c).

The ventral (=flexor) surface of the proximal end of the femur bears a distinct intertrochanteric fossa just distal to the proximal articular surface (Figures 2–4). The fossa is bounded laterally by a thin ridge that runs from

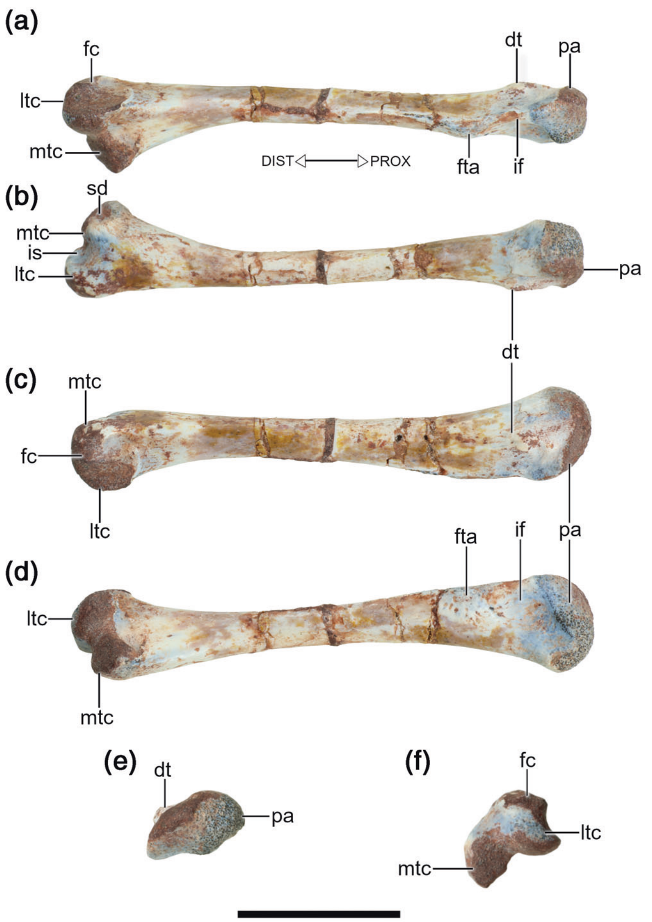

FIGURE 4 Photographs of left femur of Drepanosauromorpha (TTU-P24739) from the Cooper Canyon Formation of the Dockum Group in (a) lateral, (b) medial, (c) dorsal, (d) ventral, (e) proximal, and (f) distal views. Anatomical abbreviations: dist, distal; dt, dorsal tuberosity; fc, fibular condyle; fta, fourth trochanter analogue; if, intertrochanteric fossa; is, intercondylar sulcus; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface; prox, proximal; sd, small depression. Scale bar equals 1.0 cm.

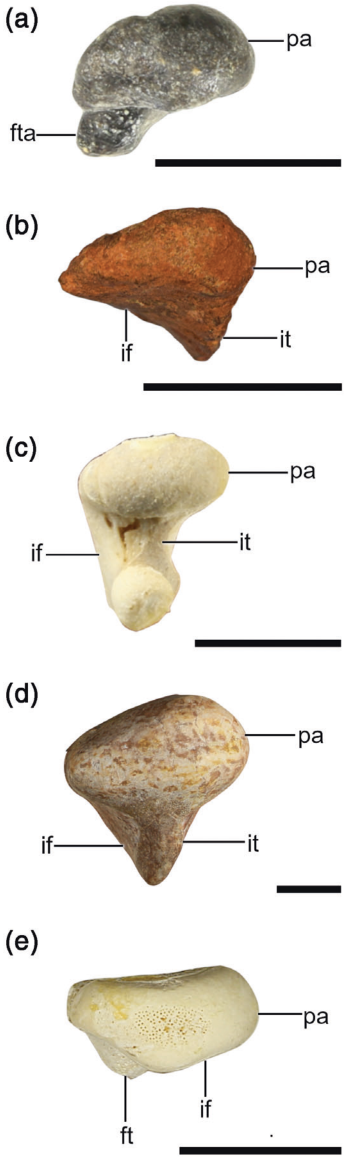

FIGURE 5 Photographs of femora of selected amniote taxa in proximal view. (a) Left femur of HQ Drepanosauromorpha (GR 1078), (b) left femur of *Zarcasaurus tanyderus* (CM 47104), (c) left femur of *Iguana iguana* (VMNH 129477), (d) right femur (mirrored) of *Trilophosaurus buettneri* (TMM 31025-1036), (e) and left femur of *Alligator mississippiensis* (VMNH 129468). Anatomical abbreviations: ft, fourth trochanter; fta, fourth trochanter analogue; if, intertrochanteric fossa; it, internal trochanter; pa, proximal articular surface. Scale bar equals 1.0 cm.

the proximal articular surface to a prominent tuberosity on the ventrolateral surface of the femur. This tuberosity marks the distal end of the ventral fossa (Figures 2d, 3d, and 4d). The ventral surface of the tuberosity is rugose and surrounded by a ring of thin ridges on its proximal, medial, and distal sides that trend away from its apex. The lateral surface of the tuberosity is smooth. Because of its distal position relative to the intertrochanteric fossa, and its ventrolateral position on the femoral shaft we consider this to be an analogue to the archosauriform fourth trochanter and describe it as the fourth trochanter analogue. The fourth trochanter analogue is more proximodistally elongate and roughly ovoid in shape in TMM 31100-1333, but proximodistally shorter and similarly wide transversely in GR 1078 and TTU-P24739. A similar ventrolaterally positioned tuberosity occurs in *Vallesaurus cenensis* (MCSNB 4751), *V. zorzinensis* (e.g., Renesto et al., 2010) and *Drepanosaurus unguicaudatus* (MCSNB 5728) (Figure 1c–f). This tuberosity may also be present in *Hypuronector limnaios* (AMNH FARB 7759), but this portion of the femur is obscured by other bones in the holotype.

In most early amniotes and diapsids, the ventral surface of the proximal end of the femur is marked by a

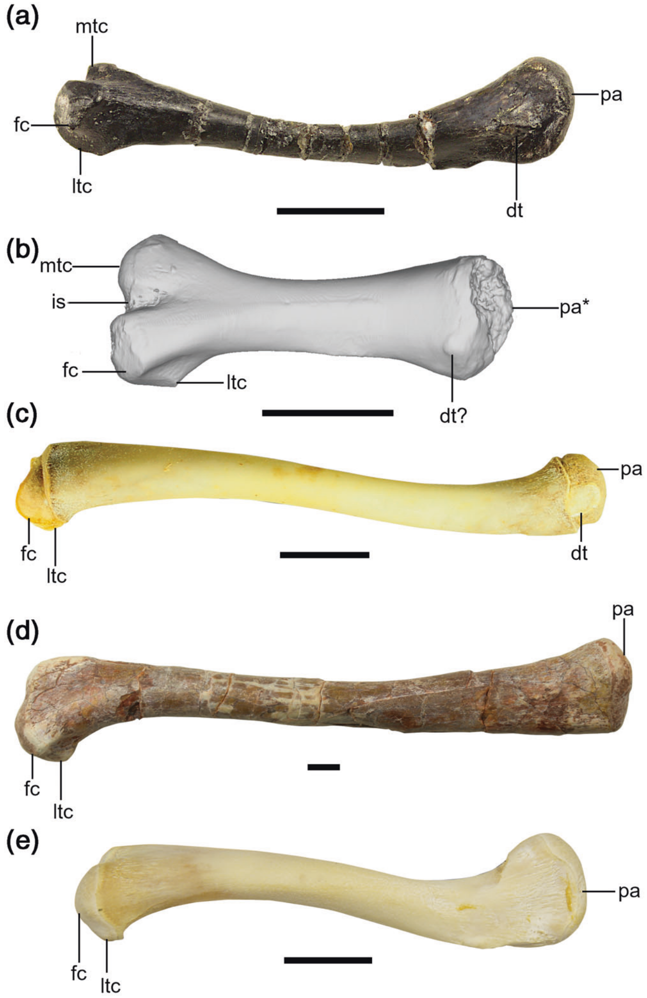

FIGURE 6 Photographs (a, c–e) and 3D surface generated from microCT data (b) of femora of selected amniote taxa in dorsal view. (a) Left femur of HQ Drepanosauromorpha (GR 1078), (b) right femur (mirrored) of *Captorhinus* (UMNH VP 33627), (c) left femur of *Iguana iguana* (VMNH 129477), (d) right femur (mirrored) of *Trilophosaurus buettneri* (TMM 31025-1036), (e) and left femur of *Alligator mississippiensis* (VMNH 129468). Anatomical abbreviations: dt, dorsal tuberosity; fc, fibular condyle; ft, fourth trochanter; fta, fourth trochanter analogue; if, intertrochanteric fossa; is, intercondylar sulcus; it, internal trochanter; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface. Scale bar equals 1.0 cm. * indicates incomplete preservation of this structure.

prominent ventromedially positioned, and distally tapering crest: the internal trochanter (9B—9D). This condition occurs widely in early amniotes (e.g., Holmes, 2003; Romer, 1956; Sumida, 1989), araeoscelids (e.g., Reisz, 1981; Vaughn, 1955), "younginiforms" (e.g., Carroll, 1981; Gow, 1975), early-diverging members of Sauria (e.g., Fraser, 1988; Nesbitt et al., 2015; Pritchard et al., 2015), and modern lepidosaurs (e.g., Russell & Bauer, 2008). In the non-drepanosauromorph neodiapsids, the internal trochanter is dorsoventrally tallest at its proximal end, tapering in height as it trends distally.

In contrast, the fourth trochanter of Archosauriformes, such as *Euparkeria capensis* (Ewer, 1965; Nesbitt, 2011) and *Alligator mississippiensis* (e.g., VMNH 129468, Nesbitt, 2011) manifests as a proximodistally running ridge or mound, positioned laterally on the ventral surface of the femoral shaft. This trochanter is topologically similar to that in the drepanosauromorph femora described here. As noted above, we distinguish between the internal and fourth trochanters on topological and morphological grounds, as the possible homology of the two structures remains unresolved (Hutchinson, 2001).

In the drepanosauromorph femora, the distal end of the fourth trochanter analogue is continuous with a very subtle adductor ridge that extends distally two-thirds the length of the femoral shaft. The adductor ridge is more robust and blade-like in early amniotes like *Captorhinus* (UMNH VP 33627, Holmes, 2003) (Figures 7b and 8b). A similarly blade-like adductor ridge is absent in diapsids, including Araeoscelida (e.g., MCZ 2043, Reisz, 1981), early neodiapsids such as *Claudiosaurus germaini* and *Thadeosaurus colcanapi* (SAM-PK-K8266, MNHN.F. MAP360), and early saurians such as *Clevosaurus hudsoni* and *Trilophosaurus buettneri* (NHMUK PLR 600a, TMM 31025-1036, Gregory, 1945) (Figures 7d). Similar low adductor ridges are present in extant diapsids, including lepidosaurs such as *Iguana iguana* (VMNH 129477) (Figure 7c) and archosaurs such as *Alligator mississippiensis* (VMNH 129468).

The torsion of the long axis of the proximal end of the femur relative to the distal end varies in our complete drepanosauromorphs. Torsion is approximately 40° in the Cooper Canyon femur (TTU-P24739), 45° in the Colorado City femur (TMM 31100-1333), and 47° in the Hayden Quarry femur (GR 1078). These angles are comparable to those of extant squamates. In our comparative sample of squamates, femoral torsion is 48° in *Iguana iguana* (VMNH 129468) and 49° in *Pogona vitticeps* (VMNH 68587). The same measure is 63° in *Alligator mississippiensis* (VMNH 129468).

The relative curvature of the femoral shaft is also variable among our sample of drepanosauromorph femora. The most complete of the HQ femora are sigmoidal (GR 377, 1078) (Figure 2), curving ventrolaterally proximal to the midshaft and then dorsomedially distal to the midshaft. The proximal articular end is canted slightly dorsomedially from the long axis of the shaft. By contrast, the shafts of the Dockum femora (TMM 31100-1333, TTU-P24739) are straight, with a slight dorsal incline distal to the dorsal tuberosity (Figures 3 and 4). Although they are distorted by crushing, the Italian

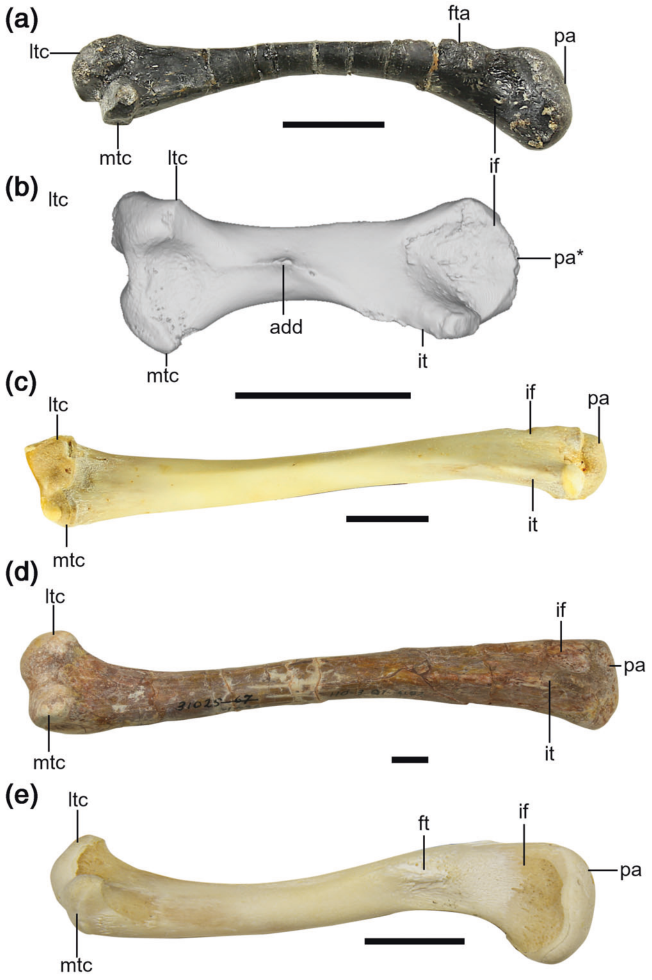

FIGURE 7 Photographs (a, c–e) and 3D surface generated from microCT data (b) of selected amniote taxa in ventral view. (a) Left femur of HQ Drepanosauromorpha (GR 1078), (b) right femur (mirrored) of *Captorhinus* (UMNH VP 33627), (c) left femur of *Iguana iguana* (VMNH 129477), (d) right femur (mirrored) of *Trilophosaurus buettneri* (TMM 31025-1036), (e) and left femur of *Alligator mississippiensis* (VMNH 129468). Anatomical abbreviations: add, adductor crest; ft, fourth trochanter; fta, fourth trochanter analogue; if, intertrochanteric fossa; it, internal trochanter; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface. Scale bar equals 1.0 cm. * indicates incomplete preservation of this structure.

drepanosauromorphs also preserve a variety of different femoral curvatures. A sigmoidal curvature characterizes *Vallesaurus cenensis* (MCSNB 4751) (Figure 1c,d) and *V. zorzinensis* (Renesto et al., 2010), whereas, in *Megalancosaurus endennae* and *Drepanosaurus unguicaudatus*, the femoral shafts are all straight along their lengths (Renesto et al., 2010) (Figure 1e,f). A possible intermediate condition occurs in a referred specimen of *Megalancosaurus preonensis* (MPUM 8437), in which the femoral shaft arcs dorsally just distal to the proximal end of the bone. However, there is no further curvature distally on the shaft in that specimen, unlike the more sigmoid curvature and ventral inclination to the distal articular surface in GR 1078.

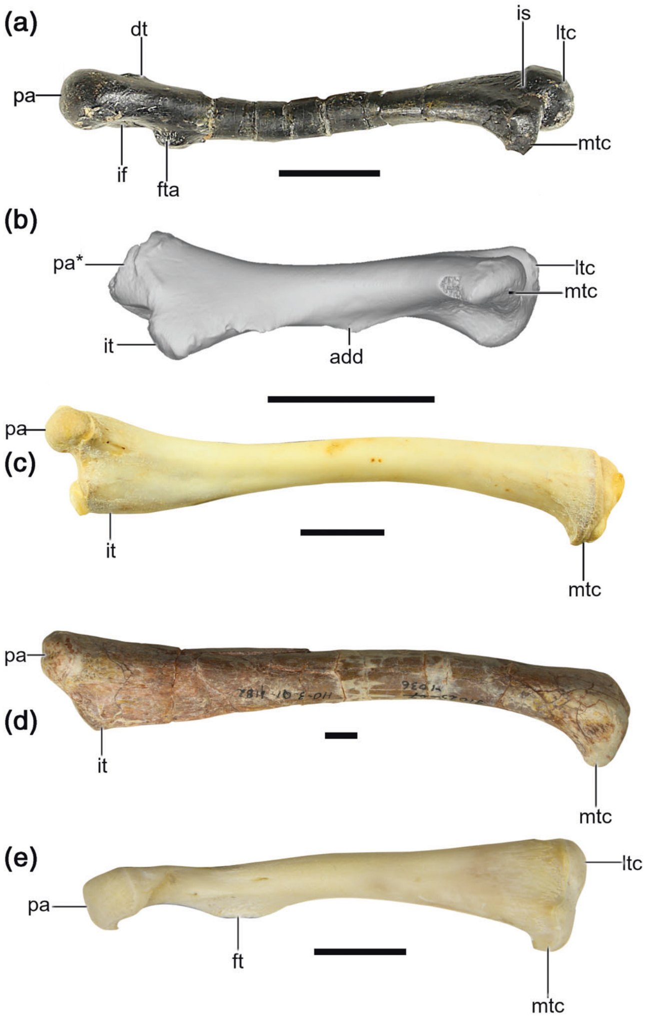

FIGURE 8 Photographs (a, c–e) and 3D surface generated from microCT data (b) of selected amniote taxa in medial view. (a) Left femur of HQ Drepanosauromorpha (GR 1078), (b) right femur (mirrored) of *Captorhinus* (UMNH VP 33627), (c) left femur of *Iguana iguana* (VMNH 129477), (d) right femur (mirrored) of *Trilophosaurus buettneri* (TMM 31025-1036), (e) and left femur of *Alligator mississippiensis* (VMNH 129468). Anatomical abbreviations: add, adductor crest; dt, dorsal tuberosity; ft, fourth trochanter; fta, fourth trochanter analogue; if, intertrochanteric fossa; is, intercondylar sulcus; it, internal trochanter; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface. Scale bar equals 1.0 cm. * indicates incomplete preservation of this structure.

The relative curvature of the femoral shaft has been recognized as a phylogenetically informative character state among early diapsids (Benton, 1985; Müller, 2004; Pritchard & Nesbitt, 2017; Spiekman et al., 2021). In the non-diapsid amniote *Captorhinus* (UMNH 33627) the femoral shaft is straight. This contrasts with the strong sigmoid curvature in *Araeoscelis gracilis* (MCZ 2043), *Thadeosaurus colcanapi* (MNHN.F.MAP 360, Carroll, 1981), *Protorosaurus speneri* (Gottmann-Quesada & Sander, 2009), *Trilophosaurus buettneri* (TMM 31025-1036), lepidosaurs such as *Iguana iguana* (VMNH 129477, Russell & Bauer, 2008), and archosaurs such as *Alligator mississippiensis* (VMNH 129468) (Figure 9a,c–f).

In our sample of drepanosauromorph femora, the shaft itself tapers to roughly one-half its proximal width near mid-shaft, before expanding again at its distal end. The distal end of the femur is comprised by of two tibial condyles, a fibular condyle, and an intercondylar sulcus (Figures 2–4 and 10). Following the terminology of Pritchard et al. (2015), the lateral tibial condyle is considered homologous with the *crista tibiofibularis* of archosauromorphs (e.g., Elzanowski, 2008; Nesbitt, 2011; Nesbitt, Irmis, et al., 2009). The tibial condyles are well-defined and robust in GR 1078 and TMM 31100-1333

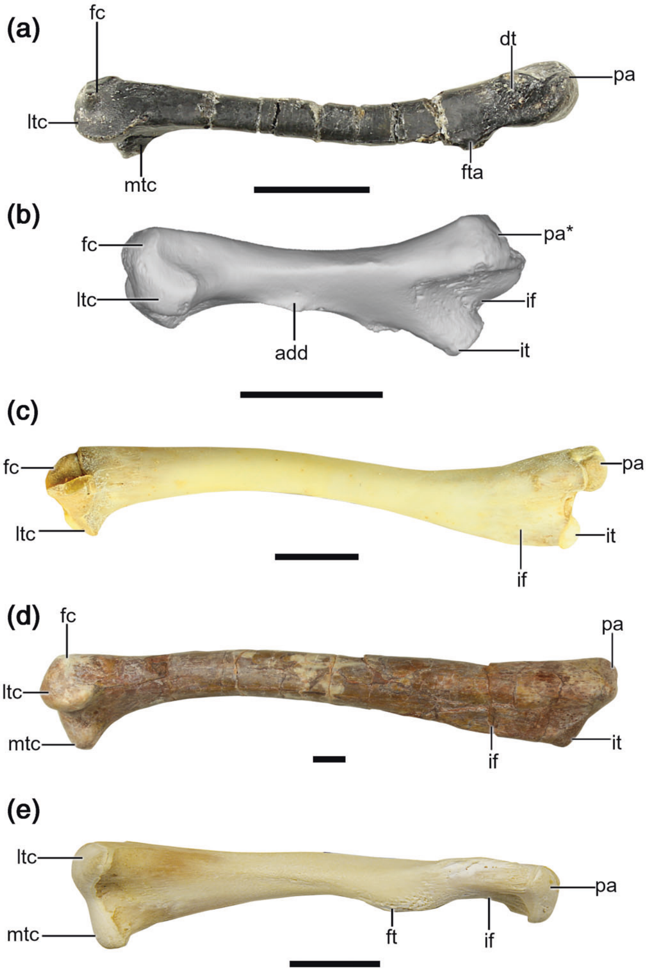

FIGURE 9 Photographs (a, c–e) and 3D surface generated from microCT data (b) of selected amniote taxa in lateral view. (a) Left femur of HQ Drepanosauromorpha(GR 1078), (b) right femur (mirrored) of *Captorhinus* (UMNH VP 33627), (c) left femur of *Iguana iguana* (VMNH 129477), (d) right femur (mirrored) of *Trilophosaurus buettneri* (TMM 31025-1036), (e) and left femur of *Alligator mississippiensis* (VMNH 129468). Anatomical abbreviations: add, adductor crest; dt, dorsal tuberosity; fc, fibular condyle; fta, fourth trochanter analogue; if, intertrochanteric fossa; is, intercondylar sulcus; it, internal trochanter; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface. Scale bar equals 1.0 cm. * indicates incomplete preservation of this structure.

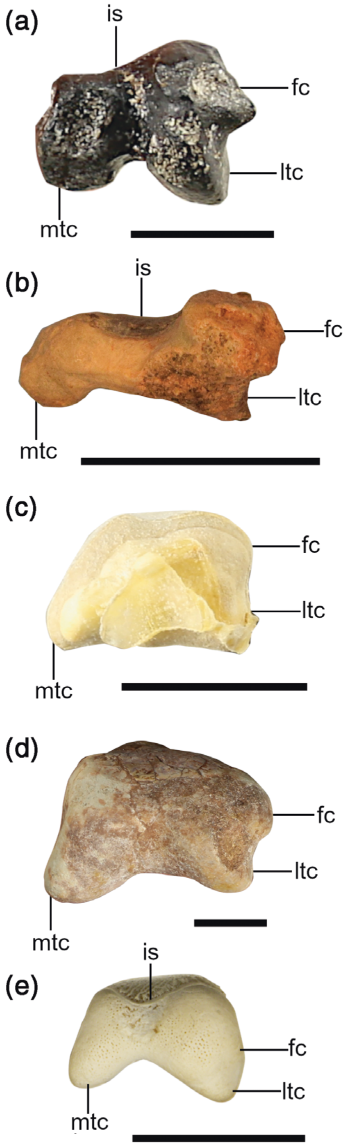

FIGURE 10 Photographs of femora of selected amniote taxa in distal view. (a) Left femur of HQ Drepanosauromorpha (GR 1078), (b) left femur of *Zarcasaurus tanyderus* (CM 41704), (c) left femur of *Iguana iguana* (VMNH 129477), (d) right femur (mirrored) of *Trilophosaurus buettneri* (TMM 31025-1036), and left femur of (E) *Alligator mississippiensis* (VMNH 129468). Anatomical abbreviations: fc, fibular condyle; is, intercondylar sulcus; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface. Scale bar (a) equals 0.5 cm and (b–e) equals 1.0 cm.

(Figures 2 and 3), but are relatively smaller with slightly less defined margins in TTU-P24739 (Figure 4).

In the Chinle and Dockum femora, the lateral tibial condyle extends much farther distally than the medial tibial condyle. The medial tibial condyle bears a prominent depression on its medial surface and tapers to a sharp point along its ventral surface. The distal surface of the medial tibial condyle is flat. The dorsal surface of the lateral tibial condyle is flat. In some specimens (e.g., TMM 31100-1333), it is raised dorsally as a distinct rectangular platform with proximal and medial borders separating it from the rest of the femoral shaft (Figure 3b,c). The lateral surface of the tibial condyle is interrupted near its dorsal margin by a very small, triangular, and laterally pointed fibular condyle. The fibular condyle projects laterally from the dorsal half of the lateral tibial condyle. The ventral half of the lateral surface of the lateral tibial condyle is flat.

The degree of condylar asymmetry observed in drepanosauromorphs is similar to early amniotes such as *Captorhinus* (UMNH VP 33627, Holmes, 2003), *Petrolacosaurus kansensis* (Reisz, 1981), and *Zarcasaurus tanyderus* (CM 41704) (Figures 6 and 10). This asymmetry is far less pronounced in neodiapsids, such as *Youngina capensis* (BP/1 3859), *Claudiosaurus germaini* (SAM-PK-K8266), *Clevosaurus hudsoni* (NHMUK PLR 600a), and *Trilophosaurus buettneri* (TMM 31025-140, -1036) (Figures 6 and 10). A deep cleft—the intercondylar sulcus—is present between the condyles in the drepanosauromorphs. The cleft is dorsoventrally deep in the HQ femora and TMM 31100-1333, whereas the sulcus is transversely narrower and less pronounced in TTU-P24739. Prominent intercondylar sulci occur in *Captorhinus* (UMNH VP 33627, Fox & Bowman, 1966), *Petrolacosaurus kansensis* (Reisz, 1981), and *Zarcasaurus tanyderus* (CM 47104, Brinkman et al., 1984). This feature may relate to the relative size and development of the cnemial crest of the tibia in early amniotes and early diapsids. In *Captorhinus aguti* (Fox & Bowman, 1966) and *Petrolacosaurus kansensis* (Reisz, 1981), the cnemial crest of the tibia is proximally inclined from the tibial cotyles that articulate with the distal tibial condyles of the femur. Such a crest could fit conformably in the sulcus between the distal tibial condyles. Due to the crushing of most associated skeletons, it is unclear whether any drepanosauromorphs possess a large, proximally inclined cnemial crest (e.g., *Vallesaurus cenensis*, MCSNB 4751; *Drepanosaurus unguicaudatus*, MCSNB 5728).

The morphology of the medial tibial condyle offers additional possible apomorphies distinguishing drepanosauromorph femora from those of other reptiles. The small depression on the medial surface of the medial tibial condyle and the flattened distal surface of that condyle differs from the smooth surface and rounded distal end present in other reptile femora, such as *Captorhinus* (UMNH VP 33627, Fox & Bowman, 1966), *Claudiosaurus germaini* (SAM-PK-K8266), *Trilophosaurus buettneri* (TMM 31025-1036), and *Iguana iguana* (VMNH 129477). The triangular and distally tapered fibular condyle also contrasts with the more rounded and mound-like condyles in other amniotes, such as *Zarcasaurus tanyderus* (CM 41704), *Clevosaurus hudsoni* (NHMUK PLR 600a), *Trilophosaurus buettneri* (TMM 31025-1036), and *Alligator mississippiensis* (VMNH 129478) (Figure 10).

4 | DISCUSSION

4.1 | Diagnostic features of the drepanosauromorph femur

To aid in the future identification of isolated drepanosauromorph femora in mixed taxonomic fossil assemblages such as those preserving the specimens described in this contribution, we provide a summary of diagnostic features of the bone. We identify a series of four apomorphies in the sampled femora. First, the ventral surface of the femur lacks the internal trochanter present in many early diapsid taxa, instead bearing a small and ventrolaterally positioned tuberosity: the fourth trochanter analogue. The fourth trochanter analogue differs from the traditional fourth trochanter of archosauriform femora in shape, manifesting as a roughly trapezoidal or ovoid tuberosity rather than a ridge or mound. Three additional apomorphies are seen in the distal end of the femora. These include a small, subcircular depression on the medial surface of the medial tibial condyle; a flattened distal surface of the medial tibial condyle; and a triangular and laterally tapered fibular condyle. These features are not present in any other known early amniote or Permo-Triassic diapsid (Figure 11).

Drepanosauromorph femora also possess a unique combination of characters, mixing plesiomorphic character states of early amniotes and diapsids and character states convergent on those in well-nested archosauriforms. The plesiomorphic states include a strongly convex and hemispherical proximal femoral head, a tuberosity on the dorsal surface of the shaft distal to the proximal articulation, a prominent intercondylar sulcus, and a more proximodistally elongated lateral tibial condyle relative to the medial tibial condyle. The ventral surface of the femoral shaft resembles the condition in advanced archosauriforms in lacking an internal trochanter and instead exhibiting a ventrolaterally placed rugosity topologically similar to the fourth trochanter. Morphological distinctions between the fourth trochanter

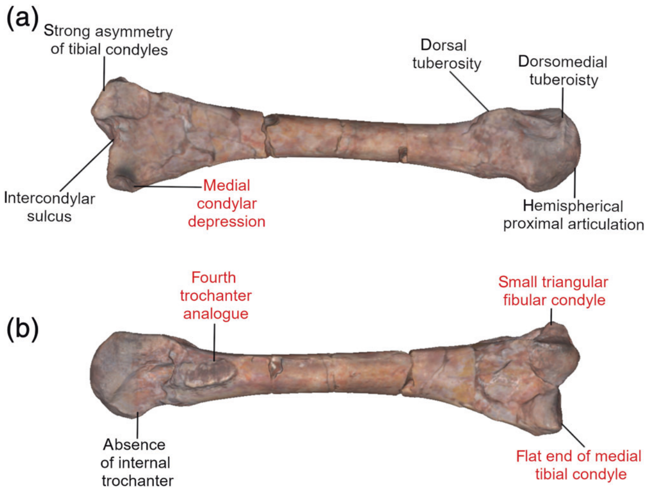

FIGURE 11 Three-dimensional (3D) scan reconstruction of right femur of a drepanosauromorph (TMM 31100-1333) in (a) dorsomedial and (b) ventrolateral views. Key identifying characters are noted, with probable apomorphies for the clade colored in red.

analogue and the fourth trochanter of Archosauriformes are noted in the preceding paragraph.

4.2 | The functional anatomy of the trochanteric system in Drepanosauromorpha

Drepanosauromorphs are distinctive among sauropsids in combining many plesiomorphic amniote character states with the apomorphic reduction of an internal trochanter and the acquisition of the fourth trochanter analogue. These major changes in the morphology of the proximoventral surface of the femoral shaft have implications for interpreting the functional anatomy of adduction, abduction, protraction, and retraction of the thigh. The homologies of the internal trochanter and fourth trochanter (and analogue) are worthy of further comment.

As noted above, the fourth trochanter analogue may represent a distolaterally shifted portion of the internal trochanter or neomorph structure. Similar hypotheses exist for the origin of the fourth trochanter in advanced archosauriforms, based partly on the muscle attachments present in extant taxa (e.g., Hutchinson, 2001).

In extant reptiles, both the internal and fourth trochanters serve as attachment sites for portions of the *mm. caudofemoralis* muscle complex. Still, there are significant differences between the two. In normal-limbed lepidosaurs (using the terminology of Russell & Bauer, 2008 to exclude snakes and other limb-reduced taxa), the *m. pubischiofemoralis externus* attaches to the proximal end of the internal trochanter (e.g., Dilkes, 2000; Hutchinson, 2001; Romer, 1942). By contrast this muscle attaches to the posterior side of the femoral head in extant archosauriforms with a fourth trochanter (e.g., Dilkes, 2000; Hutchinson, 2001). It is therefore possible that the fourth trochanter of archosauriforms also represents a reduced, distolaterally shifted remnant of the internal trochanter, but the evidence remains ambiguous (e.g., Gower, 2003; Nesbitt, Irmis et al., 2009). Further research and the recognition of intermediate states will be needed to resolve the possible homologies for the structures in both archosauromorphs and drepanosauromorphs.

Chameleons have long been considered ecomorphological analogues for drepanosauromorphs (e.g., Renesto, 1994a, 1994b, 2000; Renesto et al., 2010). Some of the features supporting that comparison included elongate slender digits with elongate claws, opposable manual digits in *Megalancosaurus*, and laterally flattened tails with a curled distal end. This latter feature has been compared favorably to the prehensile tails of chameleons, and it is modified into a claw-like bone at the posterior tip of the tail in *Megalancosaurus* and *Drepanosaurus* (Renesto, 1994a, 1994b, 2000). The unique femoral anatomy in drepanosauromorphs allows additional functional comparisons. Multiple studies have described chameleons as unique among normal-limbed squamates in possessing a reduced internal trochanter (e.g., Cope, 1892; Estes et al., 1988; Gauthier et al., 2012). However, some chameleons, including *Chamaeleo gracilis* (VTPE.LA.0144) and *Trioceros melleri* (VTPE.LA.0269) do indeed possess prominent, distally tapering internal trochanters that resemble the internal trochanters of other normal-limbed squamates (Figure 12). However, the crest of the trochanter in these chameleons is positioned nearer the ventrolateral edge of the proximal articular surface rather than the ventromedial position of the crest in the femora of other normal-limbed squamates. Although the ventral trochanters in chameleonids and drepanosauromorphs differ greatly in shape, their position on the lateral edge of the femoral shaft is similar.

Kinematic studies indicate that chameleons do not adduct their hindlimbs substantially differently from other squamates (Fischer et al., 2010; Peterson, 1984). In some studies, chameleons walking on a level surface actually possess a more abducted femur than other squamates (e.g., Higham & Jayne, 2004). However, chameleons are capable of a high degree of femoral protraction relative to other studied sprawling taxa, including squamates and turtles (Higham & Jayne, 2004). Based on XROMM (X-ray Reconstruction of Moving Morphology per Brainerd et al., 2010) studies of non-chameleonid squamate taxa (Arnold et al., 2014; Mayerl et al., 2019), this protraction may be limited by the presence of a large,

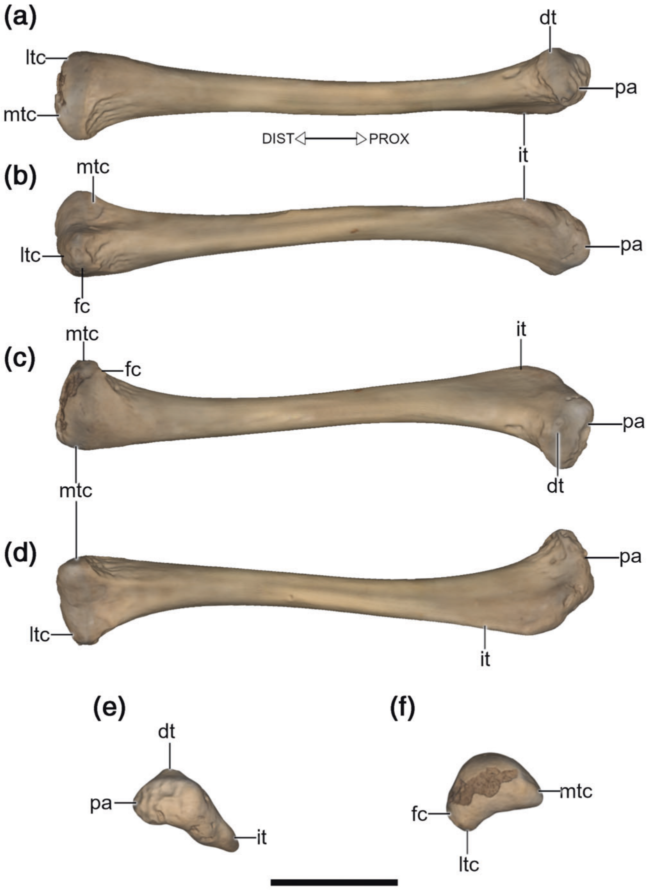

FIGURE 12 Three-dimensional (3D) scan reconstructions of right femur of *Trioceros melleri* (VTPE.LA.0269) in (a) medial, (b) lateral, (c) dorsal, (d) ventral, (e) proximal, and (f) distal views. Anatomical abbreviations: dist, distal; dt, dorsal tuberosity; fc, fibular condyle; it, internal trochanter; ltc, lateral tibial condyle; mtc, medial tibial condyle; pa, proximal articular surface; prox, proximal. Scale bar equals 1.0 cm.

ventromedially positioned internal trochanter. If the shift of the internal trochanter to the lateral edge of the femur in chameleons relates to their increased ability to protract the thigh, the same may be true of drepanosauromorphs. That said, the skeletal and myological consequences of the unique trochanter in chameleons and its functional significance for arboreal habits have not been studied in detail. As such, the similarities of chameleon femoral morphology to that of drepanosauromorphs may indicate functional similarities, but they do not provide additional support to the hypothesis of arboreality in drepanosauromorphs.

A reduction and subsequent loss of a crest-like internal trochanter occurred in both therapsid synapsids and archosauriforms (e.g., Anderson & Higham, 2014; Beck, 2004; Blob, 2001; Hutchinson, 2001; Kemp, 1978; Nesbitt, 2011; Russell & Bauer, 2008). The loss of a prominent proximoventral crest would eliminate an osseous limitation for the adduction of the femur and thus facilitate a more upright posture (as noted by Hutchinson, 2001; Sullivan, 2015). Thus, with the reduction of the internal trochanter, drepanosauromorphs may have been capable of a more parasagittal posture than other early diapsids and saurians. However, the functional implications of the reduction of the internal trochanter remain ambiguous in both therapsids and archosauriforms.

Despite differing homology schema for the internal trochanter and the mammalian lesser trochanter (Beck, 2004; Parrington, 1961; Romer, 1922, 1924), there is consensus that the internal trochanter of therapsids was reduced to a small, ventral ridge to varying degrees in different lineages. Owing in part to the reduction of this bony limitation to adduction, some of these therapsid taxa, including dicynodonts (Ray & Chinsamy, 2003) and therocephalians (Kemp, 1978; Parrington, 1961), are interpreted to have had an upright posture.

In Archosauriformes, the earliest-diverging forms (e.g., Proterosuchidae) possess a large internal trochanter comparable to the condition in non-archosauriform archosauromorphs. This structure is subsequently reduced in later-diverging archosauriform taxa (e.g., Erythrosuchidae) and seemingly absent in *Euparkeria capensis*, Phytosauria, and Archosauria (e.g., Ezcurra, 2016; Gower, 2003; Nesbitt, 2011). In concert with this reduction, a smaller and more distally positioned crest is present on the ventrolateral surface of the femoral shaft: the fourth trochanter. Although the homology of this structure with any portion of the internal trochanter is not well understood (e.g., Hutchinson, 2001), its distal position on the femoral shaft and the significant differences in shape indicate major differences in the functional anatomy of the thigh. This transition in femoral anatomy has been linked to the evolution of a semi-erect posture within Archosauriformes. Most studies indicate that this condition was intermediate to the erect postures in some pseudosuchians and ornithodirans like pterosaurs and dinosauromorphs (e.g., Hutchinson, 2001; Hutchinson & Gatesy, 2000).

The drepanosauromorph condition most closely resembles that of advanced archosauriforms, especially in the presence of a fourth trochanter analogue. However, the torsion of the femoral shaft and the orientation of the distal condyles in drepanosauromorph femora differ substantially from those in advanced archosauriforms interpreted to use or known to use erect or semi-erect gaits. If the reduction of the internal trochanter supported adduction of the femur, the drepanosauromorph hindlimb would still have been held in a posture radically different from that of any archosauriform. The femora of drepanosauromorphs sampled here have a much smaller torsional angle (<48°) relative to extant pseudosuchians

(∼63° in *Alligator mississippiensis*). When protracted and strongly adducted, the drepanosauromorph distal femoral condyles are oriented posteromedially towards the sagittal plane of the body. In this hypothetical adducted state, the leg would not have been oriented parasagittally at any point in the stride.

The major differences in the anatomy of the proximal end of the femur between drepanosauromorphs and other early diapsids present a number of functional hypotheses:

1. Drepanosauromorphs were capable of an increased range of thigh protraction, much as in living chameleonids. Support for this hypothesis would come from further study of the role of a laterally positioned trochanter in chameleon locomotion and better-preserved specimens, illustrating how the drepanosauromorph pelvis articulated with the femur.
2. Drepanosauromorphs could hold their hindlimbs in an adducted state because of the reduction of the internal trochanter. This condition is analogous to the reductions seen in Therapsida and Archosauriformes, but also quite distinct due to the lack of other femoral features indicative of a semi-erect gait. Support for this hypothesis would come from better-preserved drepanosauromorph hindlimbs with pelvic girdles, to illustrate more fully the articulations between elements; as well as the discovery of more plesiomorphic drepanosauromorph femora that preserve intermediate reductions to the internal trochanter and its possible homologies with the fourth trochanter analogue.

As is the case with other wholly extinct lineages, the drepanosauromorph thigh may also have had functions with no extant analogues. We will be able to further test those hypotheses with the discovery of additional fossils and functional studies in extant taxa.

5 | CONCLUSIONS

We describe three-dimensionally preserved drepanosauromorph femora for the first time, after decades of these taxa being known largely from crushed, distorted, or otherwise obscured specimens. We compare these femora to a wide range of early amniote, diapsid, and saurian femora. Apomorphic features of the drepanosauromorph femur include a ventrolateral tuberosity on the femoral shaft (the fourth trochanter analogue), a depression on the medial surface of the medial tibial condyle, a flattened distal surface of the medial tibial condyle, and a small and triangular fibular condyle. The drepanosauromorph femora also exhibit a combination of anatomical features characteristic of non-saurian diapsids and early amniotes. These include a well-defined and hemispherical femoral head, a tuberosity on the dorsal surface of the proximal femur, a deep sulcus between the distal femoral condyles, and a far greater distal extension of the lateral tibial condyle than the medial tibial condyle. Uniquely among non-archosauriform diapsids, there is no ventromedially positioned, crest-like internal trochanter. However, a ventrolaterally positioned tuberosity—the fourth trochanter analogue—is present. The structure is topologically very similar to the fourth trochanter of archosauriforms. The reduction of the internal trochanter on the proximoventral end of the femoral shaft resembles the condition in some therapsids—such as dicynodonts and therocephalians—and especially archosauriforms, suggesting the possibility of more adducted hindlimb postures in drepanosauromorphs. The position of a trochanter on the ventrolateral edge of the femoral shaft is also similar to that of extant chameleons, which may suggest similar functional capabilities and ranges of motion.

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DATA AVAILABILITY STATEMENT

The fossils first described in this contribution are reposited in the Ruth Hall Museum of Paleontology (Abiquiu, NM), the Texas Memorial Museum (Austin, TX), the Museum of Texas Tech (Lubbock, TX), the Natural History Museum of Utah (Salt Lake City, UT), and the Virginia Tech Osteological Collection (Geosciences) (Blacksburg, VA). All other fossils cited for comparisons in this study are available for study in their respective institutions. 3D surface files were generated for three of the drepanosauromorph femora, two chameleon femora, and a captorhinid femur described in this contribution, all of which will be available on the NSF-supported Morphosource data repository as Project 000487630.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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