Inter-element variation in the bone histology of *Anteosaurus* (Dinocephalia, Anteosauridae) from the *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa

Mohd Shafi Bhat[1], Christen D. Shelton[1,2,3] and Anusuya Chinsamy[1]

[1] Department of Biological Sciences, University of Cape Town, Cape Town, South Africa
[2] Natural History Department, New Jersey State Museum, Trenton, New Jersey, United States
[3] Biology/Mathematics & Physical Science Departments, Rogers State University, Claremore, Oklahoma, USA

Corresponding author
Mohd Shafi Bhat,
shafialig@gmail.com

ABSTRACT

Despite its abundance in the Permian fossil record of South Africa, little is known about the life history of *Anteosaurus*. Here we examine the bone microstructure of multiple skeletal elements of *Anteosaurus* from the *Tapinocephalus* Assemblage Zone of the Karoo Basin. The bone histology of *Anteosaurus magnificus* reveals that the cortex is composed of highly vascularized, uninterrupted fibrolamellar bone tissue surrounding the inner spongy medullary region. However, the histology of two ribs and a previously described femur of another *Anteosaurus* taxon revealed an interrupted growth pattern with lines of arrested growth and peripheral rest lines occurring in the compacta, indicating periodic pauses in growth possibly linked to the slowing down of growth during maturity. Given that the fibula of the same individual has well-vascularised fibrolamellar bone tissue without any growth marks in the cortex; this suggests variation in skeletal growth. Based on our histological results, three growth dynamic stages are deduced for the genus *Anteosaurus*: (i) the earliest growth stage is represented by the predominance of highly vascularized, uninterrupted fibrolamellar bone tissue in the inner cortex, which suggests rapid periosteal bone deposition during early ontogeny; (ii) the next stage of growth shows periodic interruptions in the bone deposition as indicated by the deposition of lines of arrested growth; (iii) the third stage shows the development of lamellar bone tissue with rest lines in the peripheral part of the cortex suggesting a slowing down of growth prior to death. Most of the skeletal elements are characterized by thick bone walls, extensive secondary reconstruction and the complete infilling of the medullary cavity. However, the radius and a previously studied femur have open medullary cavities with struts of bony trabeculae. Based on histologic structures and comparisons with extant taxa, it is likely that *Anteosaurus* may have been more terrestrial as its osteology point towards terrestriality, but it may have occasionally inhabited ephemeral pools like modern semi-aquatic *Hippopotamus*.

INTRODUCTION

The anteosaurs, a monophyletic group of dinocephalians (Therapsida: Dinocephalia: Anteosauria), first appeared during the Middle Permian (Guadalupian) and formed a key component of the terrestrial tetrapod fauna (*Rubidge, 1995*; *Rubidge & Sidor, 2001*; *Kammerer, 2011*; *Cisneros et al., 2012*; *Kemp, 1982, 2012*; *Smith, Rubidge & Walt, 2012*). The family Anteosauridae comprises two major clades, Syodontinae (*Australosyodon, Notosyodon* and *Syodon*) and Anteosaurinae (*Anteosaurus, Sinophoneus* and *Titanophoneus*) with Russian taxa *Archaeosyodon* and *Microsyodon* representing the most basal anteosaurs (*Kammerer, 2011*). *Liu (2013)* revised the phylogeny of Anteosauridae using the modified character lists and data matrices of *Kammerer (2011)* and *Cisneros et al. (2012)* and recovered *Sinophoneus* as a basal anteosaur, falling outside the clade Anteosaurinae. Anteosaurs are known from Middle Permian rocks of both Laurasia (*Efremov, 1954*; *Tchudinov, 1968*; *Ivachnenko, 1995*; *Li, Rubidge & Cheng, 1996*; *Cheng & Ji, 1996*; *Cheng & Li, 1997*; *Golubev, 2015*) and Gondwana (*Owen & Bain, 1845*; *Owen, 1879*; *Watson, 1921*; *Broom, 1929*; *Boonstra, 1954, 1969*; *Rubidge, 1994*; *Cisneros et al., 2012*; *Kruger, Rubidge & Abdala, 2018*). There are more than eight valid genera of anteosaurs (*King, 1988*; *Kammerer, 2011*; *Kemp, 2012*; *Cisneros et al., 2012*; *Liu, 2013*) but only two, *Australosyodon* and *Anteosaurus*, are represented in the Beaufort Group of the Karoo Supergroup of South Africa (*Boonstra, 1969*; *King, 1988*; *Rubidge, 1994*; *Kemp, 2012*; *Kruger, Rubidge & Abdala, 2018*). They were the largest apex predators during the Middle Permian Period; however, by the end of the *Tapinocephalus* Assemblage Zone (*Smith & Keyser, 1995*; *Kemp, 2012*; *Day & Rubidge, 2020*; *Day & Smith, 2020*), they along with other dinocephalians completely disappear from the fossil record leaving no descendants (*Boonstra, 1971*; *Kemp, 1982, 2005, 2012*). Their extinction within the Karoo Basin is linked either to the increasing aridification or to the loss of their food sources (*Bond et al., 2010*; *Rey et al., 2018*; *Day & Rubidge, 2021*). Anteosaurs are characterized by large pachyostotic skulls, which range in length from 280 to 805 mm (*Boonstra, 1954*; *Kemp, 1982*; *Kammerer, 2011*; *Kruger, Rubidge & Abdala, 2018*). The members of the family Anteosauridae are diagnosed by combined synapomorphic features: anterodorsally canted premaxilla, convex ventral maxillary margin, 'scroll' vomers, quadrate rami of the pterygoid that bifurcate the anterior margin of the basisphenoid, a ridge on the jugal-lacrimal suture, and a 'scoop'-shaped (strongly anteroventrally curved) postorbital bar (*Kemp, 1982*; *Ivakhnenko, 2008*; *Kammerer, 2011*).

Anteosaurs were fully terrestrial animals feeding on large tapinocephalid dinocephalians, bull-sized armored pareiasaurs and even scavenging on kills made by the lycosuchid and scylacosaurid therocephalians (*Boonstra, 1955*; *Rubidge, 1995*; *Lee, 1997*; *Nicolas & Rubidge, 2010*; *Kammerer, 2011*; *Kemp, 2012*; *Canoville, Thomas & Chinsamy, 2014*). They have also been considered riparian, obligate fish-eaters (*Boonstra, 1955, 1962*; *Ivakhnenko, 2001, 2003, 2008*), or even amphibious (*Olson, 1962*; *King, 1988*;

Ivakhnenko, 2008). *Kammerer (2011)* supported a fully terrestrial lifestyle for anteosaurs as they possessed the heaviest skulls of all the carnivorous synapsids, and were equipped with large canines and incisors, that would have been effective for preying on large land animals (*Sennikov, 1996*; *Van Valkenburgh & Jenkins, 2002*). *Canoville, Thomas & Chinsamy (2014)* performed isotopic analysis of the teeth of dinocephalians and pointed out that most of the dinocephalians had lower oxygen isotope compositions than contemporaneous pareiasaurs and therocephalians. They further suggested that dinocephalians and pareiasaurs inhabited different ecological niches and that the herbivorous pareiasaurs may have shared a terrestrial habitat with carnivorous therocephalians. However, their isotopic differences also reflected higher water turnover rates for dinocephalians suggesting niche partitioning (*Canoville, Thomas & Chinsamy, 2014*). Later, *Rey et al. (2020)* supported a terrestrial adaptation for *Anteosaurus* even though their oxygen values point towards water dependency. Since their sample size was small, they were unable to confirm whether anteosaurs were riparian or more in-land dwellers. Recently *Benoit et al. (2021)* concluded that anteosaurs were agile predators, based on the enlarged fossa for the floccular lobe of the cerebellum and semicircular canals of the inner ear.

Bone microanatomical studies of tetrapods have demonstrated that bone architecture (microanatomy) and internal tissue structure (histology) varies according to lifestyle adaptations (*Wall, 1983*; *Chinsamy, 1991*; *Ray, Chinsamy & Bandyopadhyay, 2005*; *Gray et al., 2007*; *Hayashi et al., 2013*; *Houssaye et al., 2016*; *Canoville, de Buffrénil & Laurin, 2016*; *Canoville & Chinsamy, 2017*). Furthermore, bone histology of extant and extinct vertebrates provides direct assessment of life history and the biology of an animal (*de Ricqlès, 1969*, *1972*; *Francillon-Vieillot et al., 1990*; *Chinsamy, 1997*; *Horner, de Ricqlès & Padian, 1999*, *2000*; *Chinsamy-Turan, 2005*, *2012*; *Klein & Sander, 2008*; *Chinsamy et al., 2013*, *2019*, *2020*; *Woodward, Horner & Farlow, 2014*; *Woodward et al., 2015*; *Woodward et al., 2020*; *Huttenlocker & Botha-Brink, 2014*; *Botha-Brink, Soares & Martinelli, 2018*; *Cullen et al., 2020*; *Huttenlocker & Shelton, 2020*; *Botha, 2020*). Several studies have examined the bone histology of the non-mammalian therapsids (see *Chinsamy-Turan, 2012* and references therein), however, except for the early work of *de Ricqlès (1972)*, dinocephalians have been relatively under-studied. Recent histology research on *Titanosuchus* led to the identification of osteomyelitis in a femur of *Jonkeria parva* (*Shelton, Chinsamy & Rothschild, 2019*). More recently, additional bone histology studies have been conducted on *Jonkeria* (*Bhat, Shelton & Chinsamy, in press (a)*) and have shown that these fast growing omnivorous animals were adapted for a semi-aquatic lifestyle, like modern graviportal *Hippopotamus*. Subsequently, a comprehensive histological study of various limb bones of several herbivorous dinocephalian taxa found richly vascularized fibrolamellar bone tissue, as well as extensively developed medullary spongiosa, and supported the semi-aquatic lifestyle hypothesis for herbivorous dinocephalian taxa *Bhat, Shelton & Chinsamy, in press (b)*.

Since tetrapods display a wide range of histological characteristics (*e.g.*, *Horner, de Ricqlès & Padian, 1999*, *2000*; *Ray & Chinsamy, 2004*; *Ray, Botha & Chinsamy, 2004*; *Chinsamy-Turan, 2005*, *2012*), as well as bone depositional rates (*e.g.*, *Amprino, 1947*; *de*

Margerie, Cubo & Castanet, 2002; *de Margerie et al., 2004*; *Starck & Chinsamy, 2002*), multi-element studies of individuals of a particular species provide a better assessment of their growth patterns, lifestyle habits and various aspects of their life history (*Horner, de Ricqlès & Padian, 1999*, *2000*; *Botha & Chinsamy, 2004*, *2005*; *Chinsamy-Turan, 2005*, *2012*; *Ray, Mukherjee & Bandyopadhyay, 2009*; *Woodward et al., 2015*). This study represents the first histological and microanatomical study of multiple skeletal elements of two *Anteosaurus* taxa. Our study aims to assess the inter-elemental variation in their bone histology as well as to shed light on their lifestyle adaptations.

MATERIALS & METHODS

The specimens studied here were excavated from the *Tapinocephalus* Assemblage Zone of the South African Karoo Basin (*Boonstra, 1969*). For our analysis, several skeletal elements (femora, radius, ulnae, fibula, and ribs; Fig. 1) were examined to assess inter-elemental histological variability. These skeletal elements are positively identified at species or generic levels (Table 1; references therein). In the text, different elements of the same individual have the same specimen numbers but are differentiated by the suffixes of a/b/c. The skeletal elements with specimen number SAM-PK-12088 belong to *Anteosaurus magnificus* whereas the fibula (BP/1/5591b) and ribs (BP/1/5591c–d) belong to another *Anteosaurus* taxon. All specimens were obtained from Iziko South African Museums, Cape Town, and Evolutionary Studies Institute (formerly the Bernard Price Institute) at the University of the Witwatersrand, Johannesburg, South Africa. Permission to section the fossils was obtained from the South African Heritage Resources Agency (SAHRA; Permits 2076, 2131, and 3752–4658).

Transverse sections were prepared from midshaft levels wherever possible as these are the regions of the bone that undergo the least amount of secondary remodeling (*Enlow, 1963*; *Chinsamy, 1995*; *Chinsamy-Turan, 2005*) and limb bones were preferentially selected because they retain the best record of growth (*Francillon-Vieillot et al., 1990*; *Chinsamy-Turan, 2005*; *Bhat, Chinsamy & Parkington, 2019*). Both stylopodial (femur) and zeugopodial (radius, ulna; fibula) bones were sampled as they can show different ecological signals and respond differently to any change in the habitat (*de Buffrénil & Schoevaert, 1989*; *de Margerie et al., 2005*; *Canoville & Laurin, 2010*; *Quemeneur, de Buffrénil & Laurin, 2013*). We also sectioned non-weight bearing bones (ribs) to investigate whether they exhibit a better growth mark record in their proximal ends like those of sauropod dinosaurs (*Stein & Sander, 2009*; *Waskow & Sander, 2014*). The destructive nature of histological analyses and the scarcity of complete specimens prohibited the sectioning of a large number of bones; however, an optimal sample was obtained by selecting diagnostic though incomplete skeletal elements.

Thin sections of long bones were petrographically prepared using cutting and grinding techniques following *Chinsamy & Raath (1992)*. Considering the technical challenge of sectioning large dinocephalian skeletal elements, limb bones were sampled by the hydraulic coring method using a drill with a one cm diamond encrusted coring bit or cut using a Dremel Precision Tool, following the standard procedures outlined in *Stein & Sander (2009)*. Core drilling was preferentially performed in an area that would cause the

Figure 1 Skeletal elements of *Anteosaurus* specimens studied. (A) Proximal femur (SAM-PK-12088a). (B) Proximal radius (SAM-PK-12088b). (C) Ulna (SAM-PK-12088c). (D) Ulna head (SAM-PK-12088d). (E) Fibula fragment (BP/1/5591b). (F) Proximal rib (BP/1/5591c). (G) Rib (BP/1/5591d). The dotted lines and circles indicate the histological section planes and transverse cores.

least amount of damage to the anatomy of the element. Note that permission was granted to section skeletal elements only in clearly specified areas (*e.g.*, ends of the bone/broken regions) and therefore this prevented us from sectioning both proximal and midshaft regions from the same element. After the cores were obtained, the holes were infilled with
Table 1 Skeletal elements of *Anteosaurus* specimens studied.

Specimen number		Skeletal element	Taxon	Locality	Section type
SAM-PK-12088	a	Femur	*Anteosaurus magnificus*	Sewefontein, Prince Albert, *Tapinocephalus* Assemblage Zone, Beaufort Group, Karoo Supergroup, South Africa.	Transverse
	b	Proximal radius			Transverse
	c	Ulna			Transverse core
	d	Ulna head			Transverse core
BP/1/5591	b	Fibula	*Anteosaurus* sp.	Rheboksfontein *Tapinocephalus* Assemblage Zone, Beaufort Group, Karoo Supergroup, South Africa.	Transverse core
	c	Proximal rib			Transverse
	d	Rib midshaft			

Notes:

All the material was recovered from the *Tapinocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa.
Abbreviations: SAM, Iziko South African Museums Cape Town, South Africa; BP, Evolutionary Sciences Institute (previously Bernard Price Institute);University of the Witwatersrand, Johannesburg, South Africa. Source of information: *Boonstra (1955, 1969)*; *King (1988)*.

plaster to preserve the overall morphology of the bone. Depending on the fossil itself, each core was either embedded in an epoxy resin (EpoxAcast 690 and/or Struers Epofix; *Chinsamy & Raath, 1992*; *Chinsamy-Turan, 2005*) or subjected to direct cutting/slicing along the preferred direction. The coring, sectioning, embedding and thin sectioning, as well as the microscopy were performed in the thin sectioning laboratory of the Palaeobiology Research Group at the Department of Biological Sciences, University of Cape Town. The embedded bones were mounted on frosted glass slides and thin sectioned using a Struers Accutom-50 and ground and polished using carborundum (silicon carbide) discs of various grit sizes (400–1,200 μm). This was followed by a final polish on a lap wheel with a velvet cloth using aluminium oxide (Al_2O_3) solution. The final thickness of the section was between 45–50 microns; this proved to be optimum for our analyses. Bones were processed in serial sections in case of slide breakages or loss of slide.

All prepared sections were studied and photographed using a digital compact camera Nikon DS-Fi1 mounted on Carl Zeiss Axio Lab A1 polarizing microscope. Histological nomenclature follows that of *Francillon-Vieillot et al. (1990)* and *Chinsamy-Turan (2005, 2012)*.

RESULTS

The femur (SAM-PK-12088a; Fig. 1A) belongs to *A. magnificus* (Table 1). The histology is well preserved even though the section is damaged by numerous cracks (Fig. 2A). The maximum diameter of the cross-section is approximately 73 mm. It has a distinct, outer cortex and medullary region partially infilled by trabeculae (Fig. 2A). The bone wall is thick, but the extensive resorption of vascular canals gives the inner cortex a spongy aspect. The overall cross-section is divided into three regions: inner spongy bone, a middle plexiform layer and an outer band of circumferential fibrolamellar bone.
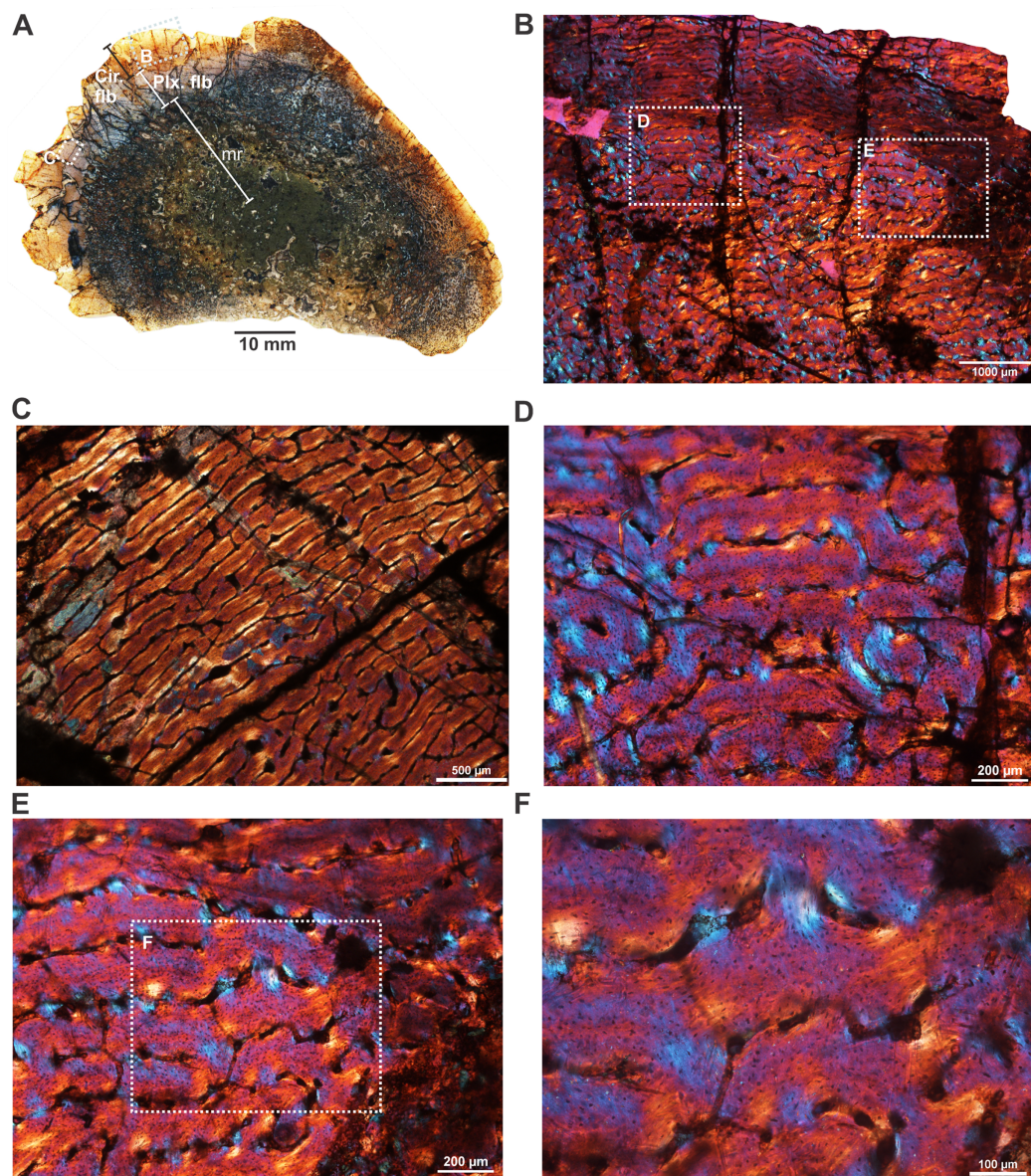
Figure 2 Transverse sections of the femur (SAM-PK-12088a) of *Anteosaurus magnificus*. Figs. 1B–1F were imaged under cross-polarized light with lambda compensator. (A) Transverse section showing the thick outer cortex and medullary spongiosa. (B) Magnified view of framed area in 'A' showing highly vascularized circumferential fibrolamellar bone. (C) Magnified view of framed area in 'A' showing plexiform fibrolamellar bone. (D) Magnified view of framed area in 'B' showing fibrolamellar bone tissue with woven matrix in the outer cortex. (E) Magnified view of framed area in 'B' showing the transition between inner plexiform and outer continuous circumferential vascular canals. (F) Magnified view of framed area in 'E' showing woven bone with dense lacunae. Abbreviations: cir. flb, circumferential fibrolamellar bone; plx. flb, plexiform fibrolamellar bone; mr, medullary region.

The medullary region is large, and the perimedullary region consists of unevenly distributed cancellous bone that grades into the more compacted mid-cortex (Fig. 2A). The predominant bone tissue of the outer cortex is highly vascularized uninterrupted fibrolamellar bone tissue (Figs. 2B–2F) with a woven matrix as defined by fiber orientation,

globular and randomly distributed osteocyte lacunae (Figs. 2D–2F). Fibrolamellar bone deposition continues up to the peripheral margin of the bone without any decrease in vascularization or change in the tissue type (Fig. 2B). The primary osteons in the peripheral cortex have a circumferential orientation (Figs. 2B, 2D–2F). A change in vascularity to a more plexiform pattern with radial and circumferential channels is observed in the inner mid-cortex (Figs. 2A, 2C). Growth marks are not present in the compacta.

A transverse section of the *A. magnificus* radius (SAM-PK-12088b; Fig. 1B) displays an open medullary cavity with thick struts of trabeculae (Fig. 3A). Given that the section is from the epiphyseal region, the medullary cavity is quite irregular and resorptive (Fig. 3A). Like the femur SAM-PK-12088a (Fig. 2A), the outer cortex is comprised of highly vascularized fibrolamellar bone tissue (Figs. 3C–3D) with a woven matrix as shown by the orientation of the collagen fibers and the profuse, globular, haphazardly oriented osteocyte lacunae. The vascular channels within the outer cortex are mostly longitudinally orientated and arranged circumferentially (Figs. 3B–3C), and they are surrounded by osteonal deposits forming primary osteons (Fig. 3C). The size and density of vascular canals are mostly consistent throughout the compacta (Fig. 3B), although, secondary reconstruction is extensive in the perimedullary region and has resulted in numerous enlarged cavities (Fig. 3D). Many of these erosional spaces are secondarily infilled by centripetally deposited lamellar bone (Fig. 3E).

Two ulnae (SAM-PK-12088c–d; Figs. 1C–1D) of *A. magnificus* were sectioned at the distal epiphyseal (Figs. 4A–4C) and midshaft regions (Figs. 4D–4F). They exhibited similar histological features as both are composed of highly vascularized cortex with an inner medullary region infilled by a dense network of bony trabeculae. Near the distal epiphyseal end (Fig. 4A), the bone is highly remodeled with many secondarily enlarged erosional cavities showing centripetal deposits of lamellar bone tissue (Figs. 4B–4C). The cross-section of the ulna at midshaft region (Fig. 4D) shows a compact bone with a large, partially filled medullary region. The medullary region has numerous islands of bony trabeculae. Circumferentially arranged longitudinal vascular canals are abundant in the compacta (Figs. 4E–4F).

The fibula (BP/1/5591b; Fig. 1E) of another *Anteosaurus* taxon shows an inner medullary region infilled by a dense network of bony trabeculae (Fig. 5A) while the pore spaces are occupied by diagenetic minerals (Fig. 5A, 5F). The outer margin of the medullary cavity and the inner medullary region have islands of trabeculae with a woven matrix (Fig. 5F). Resorption is intense in the inner cortex resulting in large erosional cavities (Fig. 5A). The size of the eroded cavities decreases from the inner cortex to the peripheral cortex (Fig. 5A). Overall, the compact bone tissue is laminar fibrolamellar with woven matrix (Figs. 5D–5E). The vascularization pattern is laminar towards the inner cortex whereas subperiosteally there tends to be more radial anastomoses between the circumferentially organized vascular canals (Figs. 5B–5C).

Two ribs (BP/1/5591c–d; Figs. 1F–1G) of *Anteosaurus* from the same individual were sectioned; one rib (BP/1/5591c; Fig. 1F) was sectioned at the proximal end (Figs. 6A–6F) and the other rib (BP/1/5591d; Fig. 1G) at the midshaft region (Figs. 6G–6K).
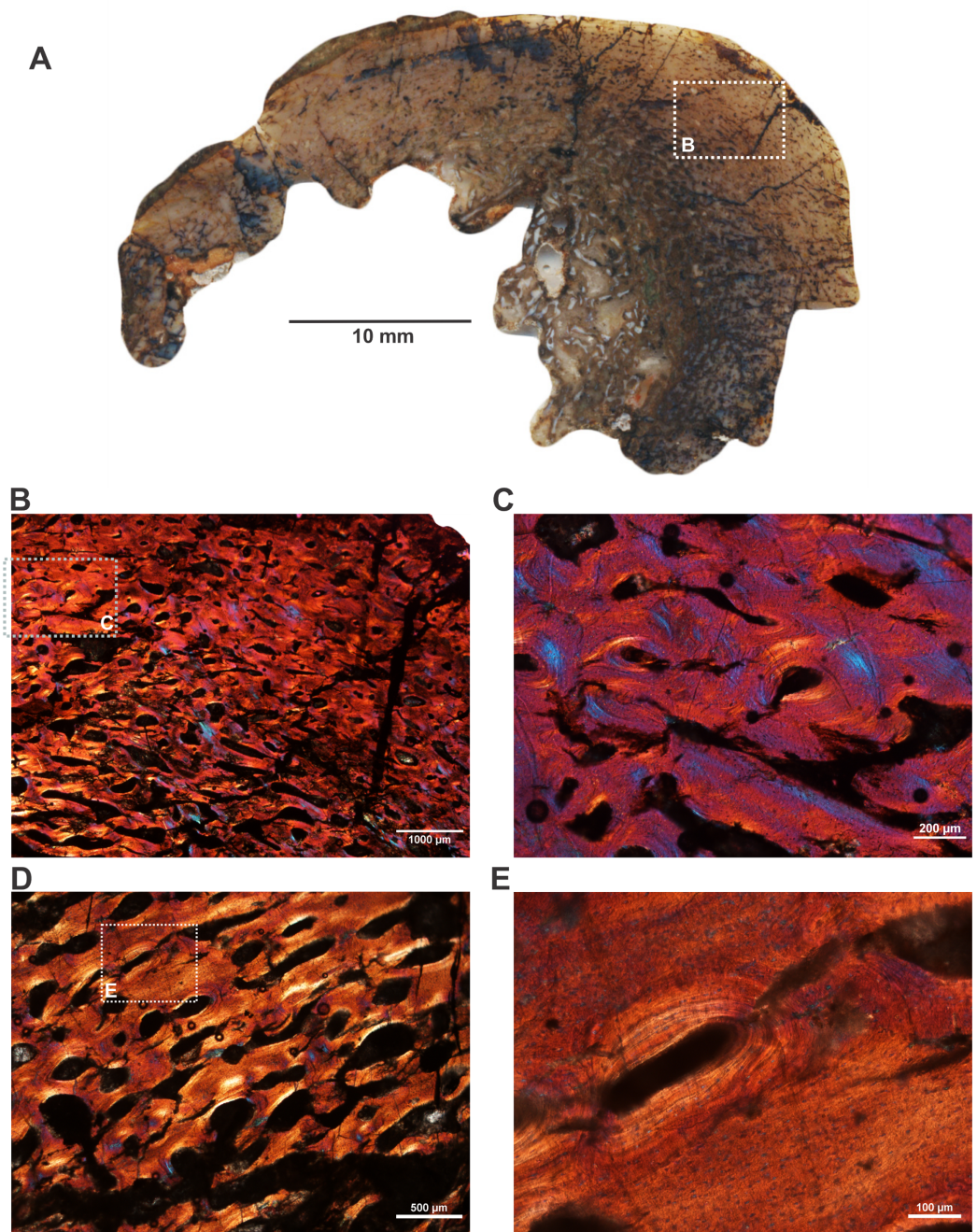
Figure 3 Transverse sections of the proximal radius (SAM-PK-12088b) of *Anteosaurus magnificus*. Figs. 2B–2E were imaged under cross-polarized light with lambda compensator. (A), transverse section of the radius under ordinary light showing a thick outer cortex and an open medullary cavity with thick struts of trabeculae. (B) Magnified view of framed area in 'A' showing highly porous outer cortex. (C) Magnified view of framed area in 'B' showing woven bone matrix and numerous primary osteons. (D) Large erosional spaces and centripetal bone deposition. (E) Magnified view of framed area in 'D' showing deposition of lamellar bone around the vascular canals.
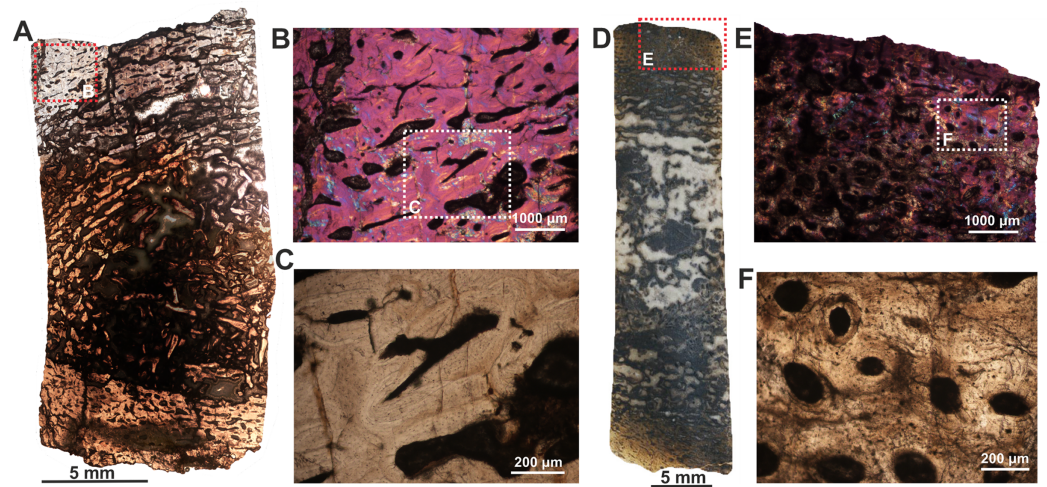
Figure 4 Histological thin section of a core of the ulnae (SAM-PK-12088c–d) of *Anteosaurus magnificus* under ordinary light (A, C, D, F) and under cross-polarized light with lambda compensator (B, E). (A) Overall view of the core showing highly vascularized outer cortex surrounding infilled medullary region. (B) Magnified view of framed area in 'A' showing circumferentially arranged vascular canals and large resorption cavities. (C) Magnified view of framed area in 'B' showing large erosional spaces encircled by lamellar bone tissue. (D) Overall view of the core showing highly vascularized outer cortex surrounding partially infilled medullary region. (E) Magnified view of framed area in 'D' showing circumferential arranged longitudinal vascular canals. (F) Magnified view of framed area in 'E' showing large vascular canals encircled by lamellar bone tissue.

The cortical thickness and overall shape of the section varies in different regions of the rib shaft (Figs. 6A, 6G). Near the proximal end (Fig. 6A), the bone is highly remodeled with many secondarily enlarged erosional cavities (Fig. 6B). Narrow bands of lamellar bone tissue occur between open spaces in the inner cortex (Figs. 6B–6C) whereas subperiosteally fibrolamellar bone tissue forms a thin peripheral layer (Figs. 6D, 6F). Several closely spaced rest lines and a few primary osteons are present in the subperiosteal region (Fig. 6E). The cross-section of rib BP/1/5591d taken at the midshaft level (Fig. 6G) displays a thick outer cortex of highly vascularized fibrolamellar bone tissue. However, like the proximal section, the inner cortex is spongy comprising of bony trabeculae (Fig. 6G). The outer cortex has numerous longitudinal primary osteons arranged circumferentially within the fibrolamellar bone preserving dense randomly organized globular osteocyte lacunae (Figs. 6H–6K). Circumferentially oriented longitudinal canals are dominant in the compacta (Figs. 6H–6K). A few localized radial and reticular organized vascular canals are visible (Figs. 6H, 6K). A line of arrested growth (LAG) is present in the outer peripheral cortex (Figs. 6J–6K).

DISCUSSION

Growth dynamics

Except for the proximal rib BP/1/5591c, all the bones exhibited fibrolamellar tissue to varying degrees in the inner cortices, suggesting that the early stage of growth was fast and resulted in the deposition of a more rapidly formed bone tissue (*Amprino, 1947*;
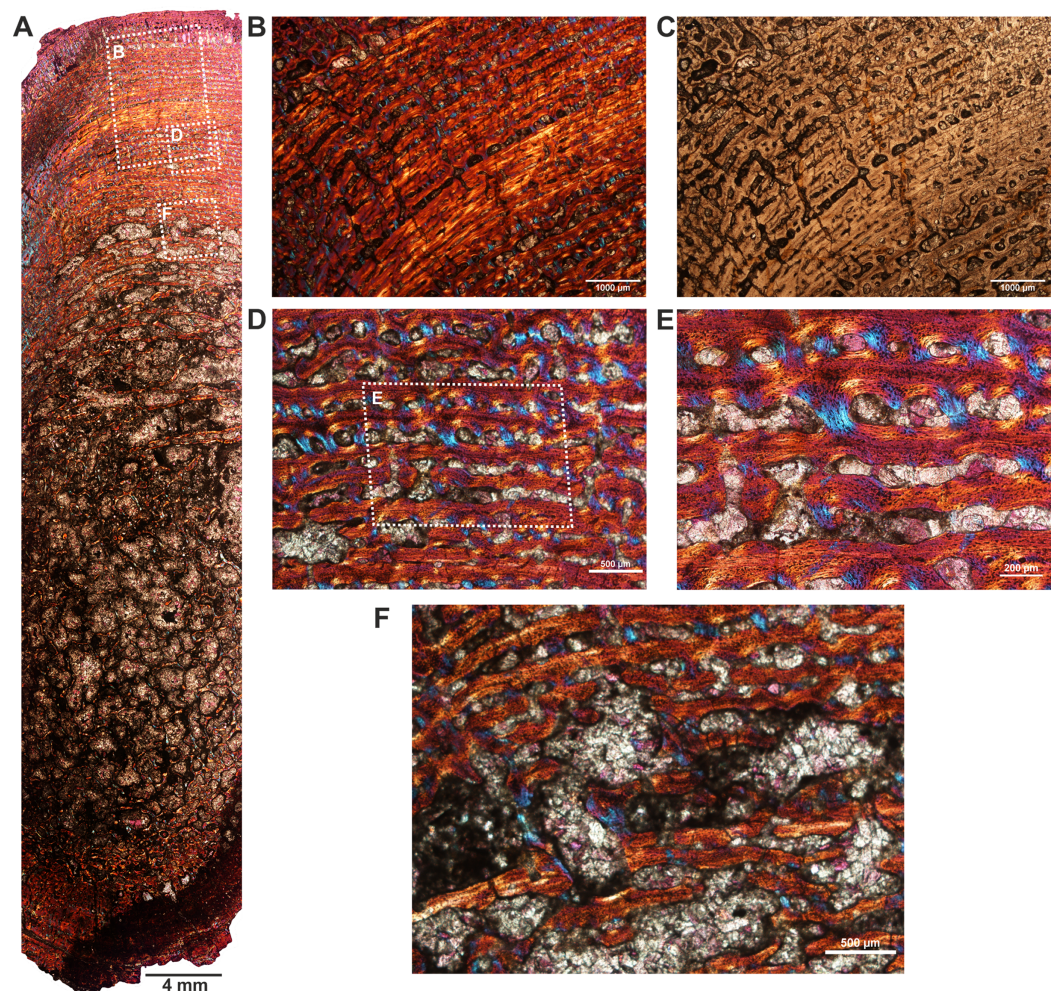
Figure 5 Histological thin section of a core of the fibula (BP/1/5591b) of *Anteosaurus* under cross-polarized light with lambda compensator (A, B, D, E, F), and under ordinary light (C). (A) Overall view of the core showing highly vascularized fibrolamellar bone tissue in the outer cortex surrounding infilled medullary cavity. Note: the trabecular density in the perimedullary region and mineral cement filling the large open spaces. (B) Magnified view of framed area in 'A' showing circumferentially oriented laminar vascular canals. (C) Same as previous image, but under ordinary light. (D) Magnified view of framed area in 'A' showing circumferential vascular canals and resorption between individual channels. (E) Magnified view of framed area in 'D' showing high density of osteocyte lacunae and large resorption between channels. (F) Magnified view of framed area in 'A' showing large resorption cavities with mineral cement.

Francillon-Vieillot et al., 1990; *Starck & Chinsamy, 2002*; *de Margerie, Cubo & Castanet, 2002*; *de Margerie et al., 2004*; *Chinsamy-Turan, 2005*). In most of the long bones, fibrolamellar bone deposition continues right up to the periphery of the cortex indicating continuous fast growth at the time of death (*Botha & Chinsamy, 2004*; *de Margerie et al., 2004*; *Bhat, Chinsamy & Parkington, 2019*). Except for the ribs, growth marks or lines of arrested growth (*Francillon-Vieillot et al., 1990*; *Castanet et al., 1993*; *Chinsamy et al., 1995*) are absent within the fibrolamellar bone tissue suggesting uninterrupted rapid osteogenesis and fast growth early in ontogeny (*Amprino, 1947*; *Francillon-Vieillot et al., 1990*;
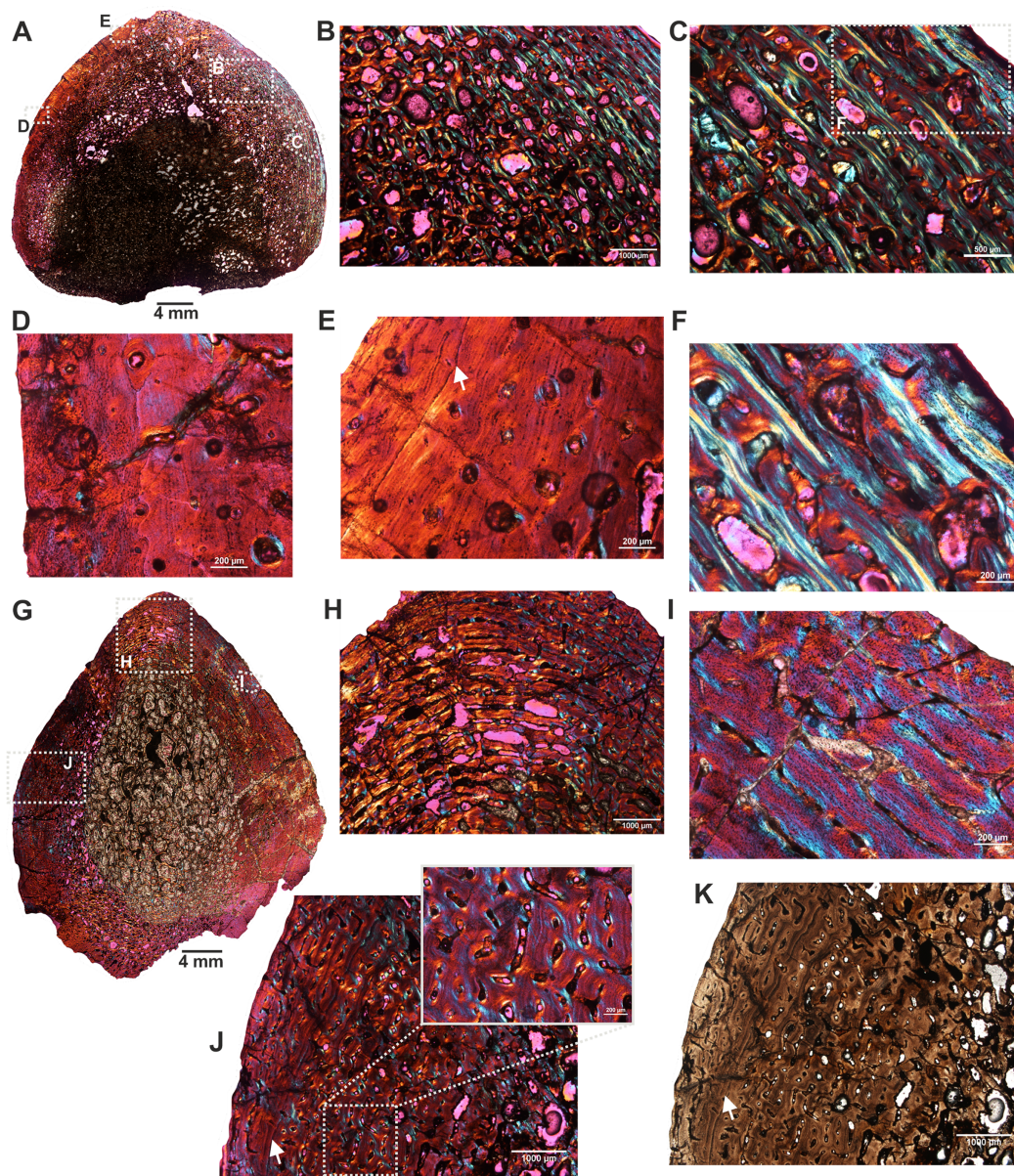
Figure 6 Transverse sections of the ribs (BP/1/5591c-d) of *Anteosaurus* under cross-polarized light with lambda compensator (A–J), and under ordinary light (K). (A) Diaphyseal cross-section at proximal end of the rib (BP/1/5591c) showing highly remodeled cortex surrounding cancellous medullary region. Note: the progressive transition from interior thin trabeculae to thick outer but porous cortex. (B) Magnified view of framed area in 'A' showing large erosional spaces. (C) Magnified view of framed area in 'A' showing lamellar bone tissue in between erosional spaces. (D) Magnified view of framed area in 'A' showing thin layer of fibrolamellar bone tissue towards the periphery (*i.e.*, left side of the image) and inner lamellar bone tissue (*i.e.*, right side of the image). (E) Magnified view of framed area in 'A' showing inner lamellar bone tissue with numerous rest lines. Note: a LAG (white arrow) towards peripheral cortex. (F) Highly vascularized fibrolamellar bone tissue with woven matrix in the outer cortex. Note: the density of osteocyte lacunae towards periphery and lamellar bone tissue between open spaces. (G) Diaphyseal cross-section at midshaft level (BP/1/5591d) showing highly vascular fibrola-mellar outer cortex surrounding cancellous medullary region. Note: the variation of bone tissue and cortical porosity between sections of the two ribs of the same individual at different levels of the shaft. (H) Magnified view of framed area in 'G' showing large erosional spaces and circumferential laminar vascular

Figure 6 (continued)
canals. (I) Magnified view of framed area in 'G' showing fibrolamellar bone tissue with primary osteons. (J) Magnified view of framed area in 'G' showing highly vascular fibrolamellar bone tissue with woven matrix (inset). Note: a LAG (white arrow) towards peripheral cortex and the density of osteocyte lacunae towards periphery. (K) Same as previous image, but under ordinary light.

Starck & Chinsamy, 2002; *de Margerie, Cubo & Castanet, 2002*; *de Margerie et al., 2004*; *Chinsamy-Turan, 2005*, *2012*). However, in a recent study on *Anteosaurus*, *Bhat, Shelton & Chinsamy, in press (b)* reported four LAGs in an *Anteosaurus* femur BP/1/5591a. Absence/ presence of growth marks/LAGs indicate a variable response to prevailing environmental conditions (*Köhler et al., 2012*; *Chinsamy & Warburton, 2021*) and give an indication of the ontogenetic status of the element (*Chinsamy-Turan, 2005*). The presence of multiple growth lines/marks indicates cyclical bone depositional rates during ontogeny (*e.g.*, *Amprino, 1947*; *de Margerie, Cubo & Castanet, 2002*; *de Margerie et al., 2004*; *Starck & Chinsamy, 2002*). The proximal section of the rib BP/1/5591c has several rest lines in the outer periphery. These rest lines were also noticed in the femur SAM-PK-K291 of *Anteosaurus magnificus* by *Bhat, Shelton & Chinsamy, in press (b)*. Presence of these peripheral rest lines indicate that the growth has significantly slowed down or periodically stopped at the time of death of the animal (*Francillon-Vieillot et al., 1990*; *Castanet et al., 1993*; *Chinsamy et al., 1995*; *Starck & Chinsamy, 2002*; *Chinsamy-Turan, 2005*; *Erickson, 2005*). These rest lines are related to the attainment of sexual and/or skeletal maturity (*Horner, de Ricqlès & Padian, 1999*, *2000*; *Chinsamy-Turan, 2005*; *Erickson, 2005*; *Cerda et al., 2017*).

The cortex of *Anteosaurus magnificus* is composed of highly vascularized, uninterrupted fibrolamellar bone tissue surrounding the inner spongy medullary region, suggesting rapid growth early in ontogeny. However, the histology of two ribs and a previously described femur of another *Anteosaurus* taxon revealed interrupted growth pattern with the lines of arrested growth and peripheral rest lines, suggesting periodic interruptions in growth in this taxon, which may be correlated with an overall slowing down of growth during later stages of ontogeny. The absence of growth marks in the fibula of the same *Anteosaurus* sp. individual suggests intra-skeletal variability in growth. Peripheral rest lines were also noticed in the femur SAM-PK-K291 of *Anteosaurus magnificus* (*Bhat, Shelton & Chinsamy, in press (b)*). Thus, considering bone microstructure of the various skeletal elements studied from two *Anteosaurus* taxa, three stages of growth are noted for the genus *Anteosaurus*. The earliest stage of growth shows the deposition of highly vascularized fibrolamellar bone with woven matrix and numerous primary osteons. The presence of uninterrupted fibrolamellar bone tissue right up to the peripheral cortex in most of our specimens indicate a young ontogenetic status for the individuals from which the skeletal elements were sampled (*e.g.*, *Ray, Chinsamy & Bandyopadhyay, 2005*). During this stage, *Anteosaurus* had rapid growth without any interruption; however, textural shifts in the vascularization pattern occurred. Bone growth marks and secondary osteons are absent at this stage, further supporting their immature or sub-adult status (*Ray, Chinsamy & Bandyopadhyay, 2005*; *Chinsamy-Turan, 2005*). The second phase of growth was interrupted, which resulted in the deposition of LAGs as seen in *Anteosaurus* femur BP/1/

5591a (*Bhat, Shelton & Chinsamy, in press (b)*). In this femur there is no associated change in degree or pattern of vascularization prior to or after the LAGs, *i.e.*, LAGs were followed by resumption of bone deposition in the form of wide zones of rapidly formed fibrolamellar bone (*Chinsamy & Rubidge, 1993*; *Horner, de Ricqlès & Padian, 2000*). Growth slowed down significantly in the third phase as indicated by the deposition of numerous rest lines in the peripheral cortex which are accompanied by lamellar bone. Such changes in the histology are evident in rib BP/1/5591c as well as in femur SAM-PK-K291 of *Anteosaurus magnificus* (*Kammerer, 2011*) where the peripheral bone has just a few isolated primary osteons (*Bhat, Shelton & Chinsamy, in press (b)*). The differences in the histology of the different skeletal elements from single individuals suggests that *Anteosaurus* exhibited variability in how different parts of its skeleton grew.

Fibrolamellar bone tissue has been described in a wide variety of extinct and extant vertebrates (*e.g.*, *Enlow & Brown, 1957*; *Enlow, 1969*; *de Ricqlès, 1983*; *Chinsamy, 1990*, *1995*; *Curry, 1999*; *Horner, de Ricqlès & Padian, 1999*, *2000*; *de Ricqlès et al., 2000*; *Chinsamy-Turan, 2005*; *Chinsamy & Abdala, 2008*, *Chinsamy, Codorniú & Chiappe, 2009*; *Cerda & Chinsamy, 2012*; *Prondvai & Stein, 2014*; *Cerda, Chinsamy & Pol, 2014*; *Cerda et al., 2017*), and has also been reported in the long bones of pelycosaurian-grade synapsids (*Enlow & Brown, 1956*, *1957*, *1958*; *Enlow, 1969*; *de Ricqlès, 1974*; *Huttenlocker, Rega & Sumida, 2010*; *Shelton, 2015*; *Shelton et al., 2013*; *Shelton & Sander, 2017*; *Agliano, Sander & Wintrich, 2021*), as well as in the limb elements of various therapsids (*e.g.*, *de Ricqlès, 1969*, *1972*, *1976*; *Chinsamy & Rubidge, 1993*; *Botha & Chinsamy, 2000*; *Ray, Botha & Chinsamy, 2004*; *Ray, Chinsamy & Bandyopadhyay, 2005*; *Ray, Mukherjee & Bandyopadhyay, 2009*; *Chinsamy-Turan, 2012*; *Botha, 2020*). These findings suggest that this tissue appeared early in synapsid evolution, well before the origin of mammals.

Histological variability

Bone histology of the multiple long bones of two *Anteosaurus* species revealed substantial variation in terms of degree of vascularization, tissue organization, amount of cancellous bone, presence/absence of peripheral lamellar bone tissue and incidence of lines of arrested growth. Such histological variation could be related to variations in the rate of periosteal deposition of different bones, ontogenetic age, varying amounts of cortical drift and remodeling, as well as to local conditions of growth within a single skeletal element (*Enlow, 1963*; *de Margerie, Cubo & Castanet, 2002*; *de Margerie et al., 2004*; *Chinsamy-Turan, 2005*; *Cerda & Chinsamy, 2012*). Since bone histology is influenced by phylogenetic, ontogenetic, functional and/or biomechanical constraints, such histological variations are expected and therefore indicate variable growth rates of skeletal elements (*de Ricqlès, 1972*; *Chinsamy, 1990*, *1995*; *de Ricqlès et al., 1991*; *Reid, 1996*; *Curry, 1999*; *Starck & Chinsamy, 2002*; *Chinsamy-Turan, 2005*, *2012*). When several elements of the same individual were examined, we had the opportunity to observe intra-skeletal variation. In all the bones, the medullary regions were secondarily remodeled and comprised of cancellous bone tissue, whereas the thick outer cortex consists of essentially primary fibrolamellar bone and subperiosteally lamellar bone. The cortex of femur SAM-PK-12088a is composed of a middle plexiform layer and a band of circumferential

fibrolamellar bone. The latter is restricted to the outer periphery. Such a textural shift in vascularization may be related to dietary change during ontogeny, linked to increased ontogenetic age of the animal (*Chinsamy et al., 2012*; *Cerda et al., 2017*; *Krupandan, Chinsamy-Turan & Pol, 2018*). Differences in the vascular pattern have also been reported to be related to regional variation in the growth rate (*de Margerie, Cubo & Castanet, 2002*; *de Margerie et al., 2004*; *de Margerie et al., 2005*; *de Cerff, Krupandan & Chinsamy, 2020*). Another notable feature is the varying degree of secondary remodeling as well as the extent and distribution of cancellous bone among the different skeletal elements as well as within a single cross-section. The radius of *Anteosaurus magnificus* has an open medullary cavity with the least amount of cancellous tissue whereas the fibula and ribs of another *Anteosaurus* taxon has highly remodeled medullary regions, and the cortex of the proximal rib is completely porous. On the other hand, the midshaft section of another rib of the same individual displayed highly vascularized fibrolamellar bone tissue. These differences in the rib histology are most likely related to the location of the thin sections. In contrast to sauropod dinosaurs which exhibit a better growth mark record at the proximal end of the rib (*Stein & Sander, 2009*; *Waskow & Sander, 2014*), in anteosaurs the growth mark record at the diaphyseal and proximal regions remains consistent.

Lifestyle adaptations

In addition to relative bone wall thickness and bone density, osteohistological characteristics have been used to deduce lifestyle adaptation of a variety of tetrapods (*e.g. Wall, 1983*; *Chinsamy, 1997*; *de Ricqlès & de Buffrénil, 2001*; *Germain & Laurin, 2005*; *Gray et al., 2007*; *Houssaye, 2009*; *Canoville & Laurin, 2009, 2010*; *Laurin, Canoville & Germain, 2011*; *Hayashi et al., 2013*; *Nakajima, Hirayama & Endo, 2014*; *Houssaye et al., 2016*; *Canoville & Chinsamy, 2017*; *Montoya-Sanhueza & Chinsamy, 2018*; *Botha, 2020*). Associated with semi-aquatic and aquatic lifestyles there is an increase in bone density, which counterbalances buoyancy (*e.g. Chinsamy, 1991*; *Gray et al., 2007*; *Hayashi et al., 2013*) and this is often reflected as a greater bone wall thickness (*Wall, 1983*). Interestingly, burrowing/fossorial animals also have thick bone walls (*Bramble, 1982*; *Ultsch & Anderson, 1988*; *Lips, 1991*; *Magwene, 1993*; *Ray & Chinsamy, 2004*; *Botha & Chinsamy, 2004, 2005*; *Chinsamy & Abdala, 2008*; *Lyson et al., 2016*; *Montoya-Sanhueza & Chinsamy, 2017*; *Legendre & Botha-Brink, 2018*; *Bhat, Chinsamy & Parkington, 2019*) as compared to terrestrial animals, which have lower relative bone thickness (RBT) values (<30%; *sensu Wall, 1983*), but given their large bulk, it is highly unlikely that anteosaurs were fossorial.

Among the anteosaur specimens studied here, except for the radius and the previously described femur (*Bhat, Shelton & Chinsamy, in press (b)*), most of the skeletal elements are characterized by thick bone walls and an extensive development of medullary spongiosa. However, femur SAM-PK-12088a does not have an extensively developed spongy medullary region, and the same applies to the radius (SAM-PK-12088b) of the same species which has a rather open medullary cavity with bone trabeculae. Similar bone

tissues present in SAM-PK-12088a have been reported in the femur BP/1/5591a of the *Anteosaurus* by *Bhat, Shelton & Chinsamy, in press (b)*.

The dicynodont *Lystrosaurus* has a very similar bone histology to the anteosaurs described here, and on the basis of its histology, *Ray, Chinsamy & Bandyopadhyay (2005)* proposed that it had a semi-aquatic/aquatic lifestyle. More recently using the same histological features, *Botha (2020)* proposed a fully terrestrial mode of life for *Lystrosaurus*. *Botha (2020)* further suggested biomechanical constraints to support the large body weight as the cause of the extensive development of medullary spongiosa. However, in a study of graviportal and aquatic tetrapods *Houssaye et al. (2016)* reported that the stylopodial bones and ribs increase bone compactness by reducing medullary cavity space. In particular, ribs showed more pronounced changes in compactness associated with aquatic behaviour than with graviportality, which supports the hypothesis that this microanatomical organization has a role in buoyancy control in shallow waters (*Chinsamy, 1991*; *Gray et al., 2007*; *Hayashi et al., 2013*; *Houssaye et al., 2016*), contra *Botha (2020)*. Furthermore, contra *Botha (2020)*, elephants (*Houssaye et al., 2016*), giraffes (*Smith, 2020*), and bison (*Sander & Andrassy, 2006*; *Houssaye et al., 2016*; *Canoville, de Buffrénil & Laurin, 2016*), which are large, graviportal terrestrial animals do not have medullary cavities infilled with spongious bone tissue as a biomechanical adaption for their bulk. However, as in *Anteosaurus*, the ribs of the known aquatic reptile, *Claudiosaurus* (*de Buffrénil & Mazin, 1989*) show a complete infilling of the medullary region by cancellous bone and are considered pachyostotic as an adaptation for their semi-aquatic lifestyles (*de Ricqlès & de Buffrénil, 2001*).

It is also worth mentioning that Middle Permian pareiasaurs, which were equally large extinct tetrapods contemporaneous with dinocephalians, exhibited medullary spongiosa and thin compact cortices (*Canoville & Chinsamy, 2017*). Isotopic analysis of the teeth of dinocephalians and pareiasaurs has shown that these large graviportal animals inhabited different ecological niches during Middle and Late Permian times with pareiasaurs sharing a terrestrial habitat with therocephalians. (*Canoville, Thomas & Chinsamy, 2014*), although *Rey et al. (2020)* subsequently reported low oxygen values for anteosaurs which point towards water dependency. However, they further suggested that a larger sample size is needed to verify their lower isotopic signatures (*Rey et al., 2020*) and supported a previously proposed terrestrial lifestyle for anteosaurs. Thus, based on the osteological features and oxygen isotopic signatures of teeth and bones, *Anteosaurus* is regarded as a fully terrestrial animal (*Kammerer, 2011*; *Sennikov, 1996*; *Van Valkenburgh & Jenkins, 2002*; *Rey et al., 2020*). However, the mixed histological features present in the skeletal elements and especially the ribs point towards aquatic tendencies. We cautiously propose that it is likely that *Anteosaurus* may have occasionally inhabited ephemeral water ponds like modern semi-aquatic *Hippopotamus* (*Houssaye et al., 2016*), but we suggest that in future more comprehensive sampling should be undertaken to verify our conclusions.

CONCLUSIONS

Three stages of growth dynamics are deduced for the genus *Anteosaurus*: the first stage during early ontogeny is rapid, the second stage has periodic interruptions (LAGs) in

the bone deposition, while the third stage shows a marked slowing down of bone deposition and overall growth as indicated by the presence of several peripheral rest lines. Most of the skeletal elements are characterized by thick bone walls, extensive secondary reconstruction and the complete infilling of the medullary cavity. The radius of *Anteosaurus magnificus* and previously studied femur of *Anteosaurus* sp. have open medullary cavities with struts of bony trabeculae. Based on the mixed histological features evident in the skeletal elements studied (*i.e.*, complete infilling of medullary cavity in some elements and open medullae in others), and considering the previous oxygen isotopic studies (*Canoville, Thomas & Chinsamy, 2014*), we propose that *Anteosaurus* may have been primarily terrestrial but it may have occasionally occupied ephemeral ponds as compared to the contemporaneous fully terrestrial pareiasaurs.

ACKNOWLEDGEMENTS

We are grateful to Iziko South African Museums, Cape Town, and Evolutionary Studies Institute (formerly the Bernard Price Institute) at the University of the Witwatersrand, Johannesburg, South Africa for providing access to the specimens used in the current study. The constructive comments by the Editor Brandon P. Hedrick, and reviewers, A. R. Tumarkin-Deratzian and Y. Nakajima are gratefully acknowledged.

Funding

The DST-NRF Centre of Excellence in Palaeosciences (CoE in Palaeosciences) provided postdoctoral support to Mohd Shafi Bhat (grants numbers COE2018-12POST, COE2019-PD09 and COE2020-PD09). The Claude Leon Foundation provided financial support to Christen D. Shelton (grant number 98813). Anusuya Chinsamy is supported by the NRF African Origins Platform (grant number 117716). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
DST-NRF Centre of Excellence in Palaeosciences: COE2018-12POST, COE2019-PD09 and COE2020-PD09.
Claude Leon Foundation: 98813.
NRF African Origins Platform: 117716.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Mohd Shafi Bhat conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

- Christen D. Shelton conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Anusuya Chinsamy conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Field Study Permissions

The following information was supplied relating to field study approvals (*i.e.*, approving body and any reference numbers):

Permission to section the fossils was obtained from the South African Heritage Resources Agency (SAHRA; Permits 2076, 2131, and 3752-4658).

Data Availability

All the specimens and the resulting thin section slides are housed in the Iziko Museums of Cape Town, and the Evolutionary Studies Institute (formerly the Bernard Price Institute) at the University of the Witwatersrand, Johannesburg, South Africa:

SAM-PK-12088a, SAM-PK-12088b, SAM-PK-12088c, SAM-PK-12088d, BP/1/5591b, BP/1/5591c, BP/1/5591d.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.12082#supplemental-information.

REFERENCES

Agliano A, Sander PM, Wintrich T. 2021. Bone histology and microanatomy of *Edaphosaurus* and *Dimetrodon* (Amniota, Synapsida) vertebrae from the Lower Permian of Texas. *The Anatomical Record* **304**:570–583.

Amprino R. 1947. La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l'accroissement. *Archives de Biologie* **58**:315–330.

Benoit J, Kruger A, Jirah S, Fernandez V, Rubidge BS. 2021. Palaeoneurology and palaeobiology of the dinocephalian therapsid *Anteosaurus magnificus*. *Acta Palaeontologica Polonica* **66**:29–39.

Bhat MS, Chinsamy A, Parkington J. 2019. Long bone histology of *Chersina angulata*: interelement variation and life history data. *Journal of Morphology* **280**:1881–1899.

Bhat MS, Shelton CD, Chinsamy A. Bone histology of the graviportal dinocephalian Jonkeria from the Middle Permian Tapinocephalus Assemblage Zone of the Karoo Basin of South Africa. *Acta Palaeontologica Polonica* in press (a).

Bhat MS, Shelton CD, Chinsamy A. Bone histology of dinocephalians (Therapsida, Dinocephalia): palaeobiological and palaeoecological inferences. *Papers in Palaeontology* in press (b).

Bond DPG, Hilton J, Wignall PB, Ali JR, Stevens LG, Sun Y, Lai X. 2010. The middle Permian (Capitanian) mass extinction on land and in the oceans. *Earth Science Reviews* **102**:100–116.

Boonstra LD. 1954. The cranial structure of the titanosuchian: *Anteosaurus*. *Annals of the South African Museum* **42**:108–148.

Boonstra LD. 1955. The girdles and limb bones of the South African Deinocephalia. *South African Journal of Science* **42**:185–326.

Boonstra LD. 1962. The dentition of the titanosuchian dinocephalians. *Annals of the South African Museum* **46**:57–112.

Boonstra LD. 1969. The fauna of the *Tapinocephalus*-zone. *Annals of the South African Museum* **56**:1–73.

Boonstra LD. 1971. The early therapsids. *Annals of the South African Museum* **59**:17–46.

Botha J. 2020. The paleobiology and paleoecology of South African *Lystrosaurus*. *PeerJ* **8(1)**:e10408 DOI 10.7717/peerj.10408.

Botha J, Chinsamy A. 2000. Growth patterns from the bone histology of the cynodonts *Diademodon* and *Cynognathus*. *Journal of Vertebrate Paleontology* **20**:705–711.

Botha J, Chinsamy A. 2004. Growth and life habits of the Triassic cynodont *Trirachodon*, inferred from bone histology. *Acta Palaeontologica Polonica* **49**:619–627.

Botha J, Chinsamy A. 2005. Growth patterns of *Thrinaxodon liorhinus*, a non-mammalian cynodont from the Lower Triassic of South Africa. *Palaeontology* **48**:385–394.

Botha-Brink J, Soares MB, Martinelli AG. 2018. Osteohistology of Late Triassic prozostrodontian cynodonts from Brazil. *PeerJ* **6(1)**:e5029 DOI 10.7717/peerj.5029.

Bramble DM. 1982. *Scaptochelys*: generic revision and evolution of gopher tortoises. *Copeia* **4**:852–867.

Broom R. 1929. On the carnivorous mammal-like reptiles of the family Titanosuchidae. *Annals of the Transvaal Museum* **13**:9–36.

Canoville A, Laurin M. 2009. Microanatomical diversity of the humerus and lifestyle in lissamphibians. *Acta Zoologica* **90**:110–122.

Canoville A, Laurin M. 2010. Evolution of humeral microanatomy and lifestyle in amniotes, and some comments on palaeobiological inferences. *Biological Journal of the Linnean Society* **100**:384–406.

Canoville A, Chinsamy A. 2017. Bone microstructure of pareiasaurs (Parareptilia) from the Karoo Basin, South Africa: implications for growth strategies and lifestyle habits. *The Anatomical Record* **300**:1039–1066.

Canoville A, Thomas DB, Chinsamy A. 2014. Insights into the habitat of Middle Permian pareiasaurs (Parareptilia) from preliminary isotopic analyses. *Lethaia* **47**:266–274.

Canoville A, de Buffrénil V, Laurin M. 2016. Microanatomical diversity of amniote ribs: an exploratory quantitative study. *Biological Journal of the Linnean Society* **118**:706–733.

Castanet J, Francillon-Vieillot HV, Meunier F, de Ricqlès A. 1993. Bone and individual aging. In: Hall BK, ed. *Bone Growth-B*. Vol. 7. Boca Raton, Florida: CRC Press, 245–283.

Cerda IA, Chinsamy A. 2012. Biological implications of the bone microstructure of the Late Cretaceous ornithopod dinosaur *Gasparinisaura cincosaltensis*. *Journal of Vertebrate Paleontology* **32**:355–368.

Cerda IA, Chinsamy A, Pol D. 2014. Unusual endosteally formed bone tissue in a Patagonian basal sauropodomorph dinosaur. *The Anatomical Record* **297**:1385–1391.

Cerda I, Chinsamy A, Pol D, Apaldetti C, Otero A, Powell J, Martinez R. 2017. Novel insight into the origin of the growth dynamics of sauropod dinosaurs, and the attainment of gigantism. *PLOS ONE* **12**:e0179707.

Cheng ZW, Ji S. 1996. First record of a primitive anteosaurid dinocephalian from the Upper Permian of Gansu, China. *Vertebrata PalAsiatica* **34**:123–134.

Cheng Z, Li J. 1997. A new genus of primitive dinocephalian: the third report on Late Permian Dashankou lower tetrapod fauna. *Vertebrate PalAsiatica* **35**:35–43.

Chinsamy A. 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). *Palaeontologia Africana* **27**:77–82.

Chinsamy A. 1991. The osteohistology of femoral growth within a clade: a comparison of the crocodile Crocodylus niloticus, the dinosaurs Massospondylus and Syntarsus, and the birds, Struthio and Sagittarius. Johannesburg: University of Witwatersr and Unpublished Ph.D. dissertation, 200.

Chinsamy A. 1995. Ontogenetic changes in the bone histology of the Late Jurassic ornithopod *Dryosaurus lettowvorbecki*. *Journal of Vertebrate Paleontology* **15**:96–104.

Chinsamy A. 1997. Assessing the biology of fossil vertebrates through bone histology. *Palaeontologia Africana* **33**:29–35.

Chinsamy A, Raath M. 1992. Preparation of fossil bone for histological examination. *Palaeontologia Africana* **29**:39–44.

Chinsamy A, Rubidge BS. 1993. Dicynodont (Therapsida) bone histology: phylogenetic and physiological implications. *Palaeontologia Africana* **30**:97–102.

Chinsamy A, Abdala F. 2008. Palaeobiological implications of the bone microstructure of South American traversodontids (Therapsida: Cynodontia). *South African Journal of Science* **104**:225–230.

Chinsamy A, Warburton N. 2021. Ontogenetic growth and the development of a unique fibrocartilage entheses in *Macropus fuliginosus*. *Zoology* **144(5)**:125860 DOI 10.1016/j.zool.2020.125860.

Chinsamy A, Hanrahan SA, Neto RM, Seely M. 1995. Skeletochronological assessment of age in *Angolosaurus skoogi*, a cordylid lizard living in an aseasonal environment. *Journal of Herpetology* **29**:457–460.

Chinsamy A, Codorniú L, Chiappe L. 2009. Palaeobiological implications of the bone histology of *Pterodaustro guinazui*. *The Anatomical Record* **292**:1462–1477.

Chinsamy A, Thomas DB, Tumarkin-Deratzian AR, Fiorillo AR. 2012. Hadrosaurs were perennial polar residents. *The Anatomical Record* **295**:610–614.

Chinsamy A, Chiappe LM, Marugán-Lobón J, Chunling G, Fengjiao Z. 2013. Gender identification of the Mesozoic bird *Confuciusornis sanctus*. *Nature Communications* **4(1381)**:1–5.

Chinsamy A, Marugán-Lobón J, Serrano F, Chiappe L. 2019. Osteohistology and life history of the basal pygostylian, *Confuciusornis sanctus*. *The Anatomical Record* **303**:949–962.

Chinsamy A, Angst D, Canoville A, Göhlich UB. 2020. Bone histology yields insights into the biology of the extinct elephant birds (Aepyornithidae) from Madagascar. *Biological Journal of the Linnean Society* **130**:268–295.

Chinsamy-Turan A. 2005. *The microstructure of dinosaur bone: deciphering biology with fine-scale techniques*. Baltimore: The John Hopkins University Press, 216.

Chinsamy-Turan A. 2012. *Forerunners of mammals. Radiation, histology, biology*. Bloomington: Indiana University Press, 372.

Cisneros JC, Abdala F, Atayman-Guven S, Rubidge BS, Celâl Şengör AM, Shultz CL. 2012. Carnivorous dinocephalian from the Middle Permian of Brazil and tetrapod dispersal in Pangaea. *Proceedings of the National Academy of Science* **109(5)**:1584–1588.

Cullen TM, Canale JI, Apesteguía S, Smith ND, Hu D, Makovicky PJ. 2020. Osteohistological analyses reveal diverse strategies of theropod dinosaur body-size evolution. *Proceedings of the Royal Society B* **287**:20202258.

Curry KA. 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. *Journal of Vertebrate Paleontology* **19**:654–665.

Day MO, Rubidge BS. 2020. Biostratigraphy of the *Tapinocephalus* assemblage zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**:149–164.

Day MO, Smith RMH. 2020. Biostratigraphy of the *Endothiodon* assemblage zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**:165–180.

Day MO, Rubidge BS. 2021. The Late Capitanian mass extinction of terrestrial vertebrates in the Karoo Basin of South Africa. *Frontiers in Earth Science* **9**:631198 DOI 10.3389/feart.2021.631198.

de Buffrénil V, Mazin J-M. 1989. Bone histology of *Claudiosaurus germaini* (Reptilia, Claudiosauridae) and the problem of pachyostosis in aquatic tetrapods. *Historical Biology* **2**:311–322.

de Buffrénil V, Schoevaert D. 1989. Données quantitatives etobservations histologiques sur la pachyostose du squelette dudugong, *Dugong dugon* (Müller) (Sirenia, Dugongidae). *Canadian Journal of Zoology* **67**:2107–2119.

de Cerff C, Krupandan E, Chinsamy A. 2020. Palaeobioloegical implications of the osteohistology of a basal sauropodomorph dinosaur from South Africa. In: *Historical Biology*. UK: Taylor & Francis.

de Margerie E, Cubo J, Castanet J. 2002. Bone typology and growth rate: testing and quantifying 'Amprino's rule' in the mallard (*Anas platyrhynchos*). *Les Comptes Rendus de l' Académie des sciences, Série Biologies* **325**:221–230.

de Margerie E, Robin J, Verrier D, Cubo J, Groscolas R, Castanet J. 2004. Assessing a relationship between bone microstructure and growth rate: a fluorescent labelling study in the king penguin chick (*Aptenodytes patagonicus*). *Journal of Experimental Biology* **207**:869–879.

de Margerie E, Sanchez S, Cubo J, Castanet J. 2005. Torsional resistance as a principal component of the structural design of long bones: comparative multivariate evidence in birds. *The Anatomical Record* **282**:49–66.

de Ricqlès A. 1969. Recherches paléohistologiques sur les os longs des Tétrapodes. II, Quelques observations sur la structure des longs des Thériodontes. *Annales de Paléontologie (Vertebres)* **55**:1–52.

de Ricqlès A. 1972. Recherches paléohistologiques sur les os longs des Tétrapodes. III, Titanosuchiens Dinocéphales et Dicynodontes. *Annales de Paléontologie (Vertébrés)* **58**:17–60.

de Ricqlès A. 1974. Evolution of endothermy: histological evidence. *Evolutionary Theory* **1**:51–80.

de Ricqlès A. 1976. On bone histology of fossil and living reptiles, with comments on its functional and evolutionary significance. In: Bellairs ADA, Cox CB, eds. *Morphology and Biology of Reptiles. Linnean Society Symposium Series*. London: Academic Press, 126–150.

de Ricqlès A. 1983. Cyclical growth in the long limb bones of a sauropod dinosaur. *Acta Palaeontologia Polonica* **28**:225–232.

de Ricqlès A, de Buffrénil V. 2001. Bone histology, heterochronies and the return of tetrapods to life in water: w[h]ere are we? In: Mazin J-M, de Buffrénil V, eds. *Secondary Adaptation of Tetrapods to Life in Water*. München, Germany: Pfeil Verlag, 289–306.

de Ricqlès A, Meunier FJ, Castanet J, Francilon-Vieillot H. 1991. Comparative microstructure of bone. In: Hall BK, ed. *Bone 3: Bone Matrix and Bone Specific Products*. Boca Raton: CRC Press Inc., 1–77.

de Ricqlès A, Padian K, Horner JR, Francillon-Vieillot H. 2000. Palaeohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications.

Zoological Journal of the Linnean Society **129(3)**:349–385
DOI 10.1111/j.1096-3642.2000.tb00016.x.

Efremov IA. 1954. The terrestrial vertebrate fauna from the Permian copper sandstones of the western Fore-Urals: Trudy Paleontologicheskogo Instituta. *Akademiya Nauk SSSR* **54**:1–416.

Enlow DH. 1963. Principles of bone remodeling. An account of post-natal growth and remodeling processes in long bones and the mandible. In: *American Lecture Series in Anatomy, Monograph.* Vol. 531. Springfield: Charles C Thomas, 131.

Enlow DH. 1969. The bones of reptiles. In: Gans C, ed. *Biology of the Reptilia.* New York: Academic Press, 45–80.

Enlow DH, Brown SO. 1956. A comparative histological study of fossil and recent bone tissues. Part I. *The Texas Journal of Science* **8**:405–443.

Enlow DH, Brown SO. 1957. A comparative histological study of fossil and recent bone tissues. Part II. *The Texas Journal of Science* **9**:136–214.

Enlow DH, Brown SO. 1958. A comparative histological study of fossil and recent bone tissues. Part 3. *The Texas Journal of Science* **10**:18–230.

Erickson GM. 2005. Assessing dinosaur growth patterns: a microscopic revolution. *Trends in Ecology and Evolution* **20(12)**:677–684 DOI 10.1016/j.tree.2005.08.012.

Francillon-Vieillot H, de Buffrénil V, Castanet J, Géraudie J, Meunier FJ, Sire JY, Zylberberg L, de Ricqlès A. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: Carter JG, ed. *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends.* New York: Van Nostrand Reinhold, 471–547.

Germain D, Laurin M. 2005. Microanatomy of the radius and lifestyle in amniotes (Vertebrata Tetrapoda). *Zoologica Scripta* **34(4)**:335–350 DOI 10.1111/j.1463-6409.2005.00198.x.

Golubev VK. 2015. Dinocephalian stage in the history of the Permian tetrapod fauna of Eastern Europe. *Paleontological Journal* **49(12)**:1346–1352 DOI 10.1134/S0031030115120059.

Gray NM, Kainec K, Madar S, Tomko L, Wolfe S. 2007. Sink or swim? bone density as a mechanism for buoyancy control in early cetaceans. *The Anatomical Record* **290**:638–653 DOI 10.1002/(ISSN)1932-8494.

Hayashi S, Houssaye A, Nakajima Y, Chiba K, Ando T, Sawamura H, Inuzuka N, Kaneko N, Osaki T. 2013. Bone inner structure suggests increasing aquatic adaptations in Desmostylia (Mammalia, Afrotheria). *PLOS ONE* **8(4)**:e59146.

Horner JR, de Ricqlès A, Padian K. 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. *Paleobiology* **25**:295–304.

Horner JR, de Ricqlès A, Padian K. 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: Growth dynamics and physiology of an ontogenetic series of skeletal elements. *Journal of Vertebrate Paleontology* **20**:115–129.

Houssaye A. 2009. Pachyostosis' in aquatic amniotes: a review. *Integrative Zoology* **4**:325–340.

Houssaye A, Waskow K, Hayashi S, Cornette R, Lee AH, Hutchinson JR. 2016. Biomechanical evolution of solid bones in large animals: a microanatomical investigation. *Biological Journal of the Linnean Society* **117**:350–371.

Huttenlocker AK, Rega E, Sumida S. 2010. Comparative anatomy and osteohistology of hyperelongate neural spines in the sphenacodontids *Sphenacodon* and *Dimetrodon* (Amniota: Synapsida). *Journal of Morphology* **271**:1407–1421.

Huttenlocker AK, Botha-Brink J. 2014. Bone microstructure and the evolution of growth patterns in Permo-Triassic therocephalians (Amniota, Therapsida) of South Africa. *PeerJ* **2**:e325.

Huttenlocker AK, Shelton CD. 2020. Bone histology of varanopids (Synapsida) from Richards Spur, Oklahoma, sheds light on growth patterns and lifestyle in early terrestrial colonizers. *Philosophical Transactions of the Royal Society B* **375**:20190142.

Ivachnenko MF. 1995. Primitive Late Permian dinocephalian-titanosuchids of Eastern Europe. *Paleontological Journal* **29**:120–129.

Ivakhnenko MF. 2001. Tetrapods from the East European Placket—Late Paleozoic natural territorial complex. *Trudy Paleontologicheskogo Instituta, Rossiiskaya Akademiya Nauk* **283**:1–200.

Ivakhnenko MF. 2003. Eotherapsids from the East European Placket (Late Permian). *Paleontological Journal* **37**:S339–S465.

Ivakhnenko MF. 2008. Cranial morphology and evolution of Permian Dinomorpha (Eotherapsida) of Eastern Europe. *Paleontological Journal* **42(9)**:859–995 DOI 10.1134/S0031030108090013.

Kammerer CF. 2011. Systematics of the Anteosauria (Therapsida: Dinocephalia). *Journal of Systematic Palaeontology* **9(2)**:261–304 DOI 10.1080/14772019.2010.492645.

Kemp TS. 1982. *Mammal-like reptiles and the origin of mammals*. London: Academic Press, 363.

Kemp TS. 2005. *The origin and evolution of mammals*. Oxford: Oxford University Press, 331.

Kemp TS. 2012. The origin and radiation of therapsids. In: Chinsamy-Turan A, ed. *Forerunners of Mammals: Radiation, Histology, Biology*. Bloomington and Indianapolis: Indiana University Press, 3–28.

King GM. 1988. Anomodontia. In: Wellnhofer P, ed. *Encyclopaedia of Paleoherpetology Volume 17C*. Stuttgart: Gustav Fischer, 1–174.

Klein N, Sander M. 2008. Ontogenetic stages in the long bone histology of sauropod dinosaurs. *Paleobiology* **34(2)**:247–263 DOI 10.1666/0094-8373(2008)034[0247:OSITLB]2.0.CO;2.

Köhler M, Marín-Moratalla N, Jordana X, Aanes R. 2012. Seasonal bone growth and physiology in endotherms shed light on dinosaur physiology. *Nature* **487(7407)**:358–361 DOI 10.1038/nature11264.

Kruger A, Rubidge BS, Abdala F. 2018. A juvenile specimen of *Anteosaurus magnificus* Watson, 1921 (Therapsida: Dinocephalia) from the South African Karoo, and its implications for understanding dinocephalian ontogeny. *Journal of Systematic Palaeontology* **16**:139–158.

Krupandan E, Chinsamy-Turan A, Pol D. 2018. The long bone histology of the sauropodomorph, *Antetonitrus ingenipes*. *The Anatomical Record* **301**:1506–1518.

Laurin M, Canoville A, Germain D. 2011. Bone microanatomy and lifestyle: a descriptive approach. *Comptes Rendus Palevol* **10**:381–402.

Lee MSY. 1997. A taxonomic revision of pareiasaurian reptiles: implications for Permian terrestrial palaeoecology. *Modern Geology* **21**:231–298.

Legendre LJ, Botha-Brink J. 2018. Digging the compromise: investigating the link between limb bone histology and fossoriality in the aardvark (*Orycteropus afer*). *PeerJ* **6**:e5216.

Li J, Rubidge BS, Cheng Z. 1996. A primitive anteosaurid dinocephalian from China–implications for the distribution of earliest therapsid faunas. *South African Journal of Science* **92**:252–253.

Lips KR. 1991. Vertebrates associated with tortoise (*Gopherus polyphemus*) burrows in four habitats in south-central Florida. *Journal of Herpetology* **25**:477–481.

Liu J. 2013. Osteology, ontogeny, and phylogenetic position of *Sinophoneus yumenensis* (Therapsida, Dinocephalia) from the Middle Permian Dashankou Fauna of China. *Journal of Vertebrate Paleontology* **33**:1394–1407.

Lyson TR, Rubidge BS, Scheyer TM, de Queiroz K, Schachner ER, Smith RMH, Botha-Brink J, Bever GS. 2016. Fossorial origin of the turtle shell. *Current Biology* **26**:1887–1894.

Magwene PM. 1993. What's bred in the bone: histology and cross-sectional geometry of mammal−like reptile long bones-evidence of changing physiological and biomechanical demands. M.Sc. dissertation, Harvard University, Cambridge. 54.

Montoya-Sanhueza G, Chinsamy A. 2017. Long bone histology of the subterranean rodent *Bathyergus suillus* (Bathyergidae): ontogenetic pattern of cortical bone thickening. *Journal of Anatomy* **230**:203–233.

Montoya-Sanhueza G, Chinsamy A. 2018. Cortical bone adaptation and mineral mobilization in the subterranean mammal *Bathyergus suillus* (Rodentia: Bathyergidae): effects of age and sex. *PeerJ* **6**:e4944.

Nakajima Y, Hirayama R, Endo H. 2014. Turtle humeral microanatomy and its relationship to lifestyle. *Biological Journal of the Linnean Society* **112**:719–734.

Nicolas M, Rubidge BS. 2010. Changes in Permo–Triassic terrestrial tetrapod ecological representation in the Beaufort Group (Karoo Supergroup) of South Africa. *Lethaia* **43**:45–59.

Olson EC. 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R. *Transactions of the American Philosophical Society, New Series* **52**:1–224.

Owen R, Bain G. 1845. Report on the reptilian fossils of South Africa. Part I. Description of certain fossil crania, discovered by A, Esq., in sandstone rocks at the south-eastern extremity of Africa, referable to different species of an extinct genus of Reptilia (*Dicynodon*), and indicative of a new tribe or suborder of *Sauria*. *Transactions of the Geological Society of London, Second Series* **7**:59–84.

Owen R. 1879. Description of fragmentary indications of a huge kind of theriodont reptile (*Titanosuchus ferox*, Ow.) from Beaufort West, Gough Tract, Cape of Good Hope. *Quarterly Journal of the Geological Society* **35**:189–199.

Prondvai E, Stein K. 2014. Medullary bone-like tissue in the mandibular symphyses of a pterosaur suggests non-reproductive significance. *Scientific Reports* **4(1)**:6253 DOI 10.1038/srep06253.

Quemeneur S, de Buffrénil V, Laurin M. 2013. Microanatomy of the amniote femur and inference of lifestyle in limbed vertebrates. *Biological Journal of the Linnean Society* **109**:644–655.

Ray S, Chinsamy A. 2004. *Diictodon feliceps* (Therapsida, Dicynodontia): bone histology, growth and biomechanics. *Journal of Vertebrate Paleontology* **24**:180–194.

Ray S, Botha J, Chinsamy A. 2004. Bone histology and growth patterns of some non-mammalian therapsids. *Journal of Vertebrate Paleontology* **24**:634–648.

Ray S, Chinsamy A, Bandyopadhyay S. 2005. *Lystrosaurus murrayi* (Therapsida, Dicyndontia): bone histology, growth and lifestyle adaptations. *Palaeontology* **48**:1169–1185.

Ray S, Mukherjee D, Bandyopadhyay S. 2009. Growth patterns of fossil vertebrates as deduced from bone microstructure: case studies from India. *Journal of Biosciences* **34**:661–672.

Reid REH. 1996. Bone histology of the Cleveland–Lloyd dinosaurs and of dinosaurs in general, part I: introduction: introduction to bone tissues. *Geology Studies* **41**:25–71.

Rey K, Day MO, Amiot R, Goedert J, Lécuyer C, Sealy J, Rubidge BS. 2018. Stable isotope record implicates aridification without warming during the late Capitanian mass extinction. *Gondwana Research* **59**:1–8.

Rey K, Day MO, Amiot R, Fourel F, Luyt J, Lécuyer C, Rubidge BS. 2020. Stable isotopes (δ18O and δ13C) give new perspective on the ecology and diet of *Endothiodon bathystoma* (Therapsida, Dicynodontia) from the late Permian of the South African Karoo Basin.

Palaeogeography Palaeoclimatology Palaeoecology **556**:109882
DOI 10.1016/j.palaeo.2020.109882.

Rubidge BS. 1994. *Australosyodon*, the first primitive anteosaurid dinocephalian from the Upper Permian of Gondwana. *Palaeontology* **37**:579–594.

Rubidge BS. 1995. *Biostratigraphy of the Beaufort group (Karoo Supergroup).* Pretoria: South African Committee for Stratigraphy, Biostratigraphic Series 1 Council for Geoscience, 46.

Rubidge BS, Sidor CA. 2001. Evolutionary patterns among Permo–Triassic therapsids. *Annual Reviews of Ecology and Systematics* **32**:449–480.

Sander PM, Andrassy P. 2006. Lines of arrested growth and long bone histology in Pleistocene large mammals from Germany: what do they tell us about dinosaur physiology? *Palaeontographica Abteilung A* **277**:143–159.

Sennikov AG. 1996. Evolution of the Permian and Triassic tetrapod communities of Eastern Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* **120**:331–351.

Shelton CD, Sander PM, Stein K, Winkelhorst H. 2013. Long bone histology indicates sympatric species of *Dimetrodon* (Lower Permian, Sphenacodontidae). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **103**:217–236.

Shelton CD. 2015. Origins of endothermy in the mammalian lineage. PhD dissertation, Universitäts und Landesbibliothek Bonn.

Shelton CD, Sander PM. 2017. Long bone histology of *Ophiacodon* reveals the geologically earliest occurrence of fibrolamellar bone in the mammalian stem lineage. *Comptes Rendus Palevol* **16**:397–424.

Shelton CD, Chinsamy A, Rothschild BM. 2019. Osteomyelitis in a 265-million-year-old titanosuchid (Dinocephalia, Therapsida). *Historical Biology* **31**:1093–1096.

Smith CCD. 2020. Giraffa camelopardalis: Limb Bone Histology Through Ontogeny. Masters dissertation. University of Cape Town.

Smith R, Rubidge B, Walt M. 2012. Therapsid biodiversity patterns and paleoenvironments of the Karoo Basin, South Africa. In: Chinsamy-Turan A, ed. *Forerunners of Mammals: Radiation, Histology, Biology*. Bloomington: Indiana University Press, 31–62.

Smith RMH, Keyser AW. 1995. Biostratigraphy of the Tapinocephalus assemblage zone. In: Rubidge BS, ed. *Biostratigraphic Series, Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. Pretoria: South African Committee for Stratigraphy Biostratigraphic Series, 1: Council for Geoscience, 8–12.

Starck JM, Chinsamy A. 2002. Bone microstructure and developmental plasticity in birds and other dinosaurs. *Journal of Morphology* **254**:232–246.

Stein K, Sander PM. 2009. Histological core drilling: a less destructive method for studying bone histology. In: Brown MA, Kane JF, Parker WG, eds. *Methods in Fossil Preparation. Proceedings of the first annual Fossil Preparation and Collections Symposium*. Berlin: Springer, 69–80.

Tchudinov PK. 1968. A new dinocephalian from the Cisuralian Region (Reptilia, Therapsida; Upper Permian). *Postilla* **121**:1–20.

Ultsch GR, Anderson JF. 1988. Gas exchange during hypoxia and hypercarbia of terrestrial turtles: a comparison of a fossorial species (*Gopherus polyphemus*) with a sympatric nonfossorial species (*Terrapene carolina*). *Physiological Zoology* **61**:142–152.

Van Valkenburgh B, Jenkins I. 2002. Evolutionary patterns in the history of Permo–Triassic and Cenozoic synapsid predators. *The Paleontological Society Papers* **8**:267–288.

Wall WP. 1983. The correlation between high limb bone density and aquatic habits in recent mammals. *Journal of Paleontology* **57**:197–207.

Waskow K, Sander PM. 2014. Growth record and histological variation in the dorsal ribs of *Camarasaurus* sp. (Sauropoda). *Journal of Vertebrate Paleontology* **34**:852–869.

Watson DMS. 1921. The bases of classification of the Theriodontia. In: *Proceedings of the Zoological Society of London.* 35–98.

Woodward HN, Horner JR, Farlow JO. 2014. Quantification of intraskeletal histovariability in *Alligator mississippiensis* and implications for vertebrate osteohistology. *PeerJ* **2**:e422.

Woodward HN, Freedman Fowler EA, Farlow JO, Horner JR. 2015. *Maiasaura*, a model organism for extinct vertebrate population biology: a large sample statistical assessment of growth dynamics and survivorship. *Paleobiology* **41**:503–527.

Woodward HN, Tremaine K, Williams SA, Zanno LE, Horner JR, Myhrvold N. 2020. Growing up *Tyrannosaurus rex*: Osteohistology refutes the pygmy *Nanotyrannus* and supports ontogenetic niche partitioning in juvenile *Tyrannosaurus*. *Science Advances* **6**:eaax6250.