Anais da Academia Brasileira de Ciências (2019) 91(Suppl. 2): e20180643
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
http://dx.doi.org/10.1590/0001-3765201920180643
www.scielo.br/aabc | www.fb.com/aabcjournal

Osteohistology of the silesaurid *Sacisaurus agudoensis* from southern Brazil (Late Triassic) and implications for growth in early dinosaurs

FÁBIO H. VEIGA[1], JENNIFER BOTHA-BRINK[2], ANA MARIA RIBEIRO[1,3], JORGE FERIGOLO[3] and MARINA B. SOARES[1,4]

[1]Programa de Pós-Graduação em Geociências, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, 91501-970 Porto Alegre, RS, Brazil
[2]Karoo Palaeontology Department, National Museum, Bloemfontein 9300, South Africa and Department of Zoology and Entomology, P.O. Box 266, University of the Free State, Bloemfontein 9300, South Africa
[3]Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Av. Salvador França, 1427, 90690-000 Porto Alegre, RS, Brazil
[4]Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, 91501-970 Porto Alegre, RS, Brazil

Manuscript received on June 23, 2018; accepted for publication on September 16, 2018

How to cite: VEIGA FH, BOTHA-BRINK J, RIBEIRO AM, FERIGOLO J AND SOARES MB. 2019. Osteohistology of the silesaurid *Sacisaurus agudoensis* from southern Brazil (Late Triassic) and implications for growth in early dinosaurs. An Acad Bras Cienc 91: e20180643. DOI 10.1590/0001-3765201920180643.

Abstract: The non-dinosaurian dinosauriform silesaurids are the closest relatives of crown-group dinosaurs and are thus, important for understanding the origins of that group. Here, we describe the limb bone histology of the Late Triassic silesaurid *Sacisaurus agudoensis* from the Candelária Sequence of the Santa Maria Supersequence, Rio Grande do Sul state, Brazil. The sampled bones comprise eight femora and one fibula from different individuals. The microscopic analysis of all elements reveals uninterrupted fibrolamellar bone tissue indicating rapid growth. A transition to slower growing peripheral parallel-fibered bone tissue in some individuals indicates a decrease in growth rate, suggesting ontogenetic variation within the sample. The osteohistology of *Sacisaurus agudoensis* is similar to that of other silesaurids and supports previous hypotheses that rapid growth was attained early in the dinosauromorph lineage. However, silesaurids lack the complex vascular arrangements seen in saurischian dinosaurs. Instead, they exhibit predominantly longitudinally-oriented primary osteons with few or no anastomoses, similar to those of some small early ornithischian dinosaurs. This simpler vascular pattern is common to all silesaurids studied to date and indicates relatively slower growth rates compared to most Dinosauria.

Key words: Archosauria, bone microstructure, dinosauriform, fibrolamellar bone, growth rates.

INTRODUCTION

Archosauria comprises extant crocodilians and birds, as well as their extinct relatives. The early diversification of Archosauria occurred during the Middle Triassic when they diverged into two lineages: the crocodilian-line (Crurotarsi or Pseudosuchia) and the avian-line (Ornithosuchia, Ornithodira or Avemetatarsalia; see Gauthier 1986, Sereno 1991, Benton 2004, Nesbitt et al.

Correspondence to: Fábio Hiratsuka Veiga
E-mail: fhveiga@gmail.com
ORCid: http://orcid.org/0000-0003-3493-8542
* Contribution to the centenary of the Brazilian Academy of Sciences.

2010). Ornithodira includes two clades, namely Pterosauromorpha and Dinosauromorpha (Langer and Benton 2006, Nesbitt 2011, Nesbitt et al. 2010). Within the latter, least inclusive clades, include the Dinosauriformes and the Dinosauria (Nesbitt 2011, Langer et al. 2013).

The Silesauridae (Langer et al. 2010, Nesbitt et al. 2010) were a diverse Middle to Late Triassic clade that are generally considered non-dinosaurian dinosauriforms (Ezcurra 2006, Irmis et al. 2007, Brusatte et al. 2010, Nesbitt et al. 2010, Nesbitt 2011). However, its phylogenetic relationships to Dinosauria is still debated in literature with the suggestion that all or some silesaurid taxa fall amongst the early members of the ornithischian lineage (Ferigolo and Langer 2007, Niedzwiedzki et al. 2009, Langer and Ferigolo 2013, Cabreira et al. 2016).

Given the discovery of new silesaurid specimens (Kammerer et al. 2012, Peecook et al. 2013, Barrett et al. 2015) and the current debate regarding their phylogenetic relationships to Dinosauria, data on the life history of these animals can provide important new information on their biology and shed light on their similarities/differences to Dinosauria. The analysis of bone microstructure or osteohistology of fossil bones can provide such life history data by revealing growth patterns and rates, ontogenetic stages and even biomechanical and hence lifestyle adaptations of extinct animals (e.g., Enlow and Brown 1956, 1957, 1958, Ricqlès 1976, Horner et al. 2000, Chinsamy-Turan 2012, Padian and Lamm 2013, Legendre et al. 2016).

Previous studies on the osteohistology of extant archosaurs and their extinct relatives have shown differences in the type of bone tissue deposition between the two lineages of the group. Within the Pseudosuchia, lamellar bone, indicative of slow growth, is preponderant (Ricqlès et al. 2003). In contrast, the bone tissues of the Ornithodira reveal predominantly fibrolamellar bone (Padian et al. 2001), which is defined here by the presence of a woven-fibered bone matrix associated with primary osteons, a tissue type that is indicative of relatively high rates of bone deposition and growth rates (Francillon-Vieillot et al. 1990). The presence of growth marks [annuli and Lines of Arrested Growth (LAGs) indicating a temporary decrease or cessation in growth, respectively, Francillon-Vieillot et al. 1990] varies considerably in both groups, but most pseudosuchians tend to exhibit cyclical growth from early ontogenetic stages (Ricqlès et al. 2003) whereas many derived ornithodirans only express growth marks during the latest ontogenetic stages (e.g., neosauropod dinosaurs, Klein and Sander 2008).

Studies on the osteohistology of dinosaurs have increased dramatically in recent years (e.g., Grady et al. 2014, Vanderven et al. 2014, Cerda et al. 2014, Bo et al. 2016, Mitchell et al. 2017, Skutschas et al. 2017). However, given the relative scarcity of material, fewer studies encompassing the taxa leading to crown-group dinosaurs have been conducted. Previous descriptions on silesaurid osteohistology include *Silesaurus opolensis* Dzik 2003 (Fostowicz-Frelik and Sulej 2010), *Asilisaurus kongwe* Nesbitt et al. 2010 (Griffin and Nesbitt 2016) and *Lewisuchus admixtus* Romer 1972 (Marsà et al. 2017). These studies reveal similar bone tissues amongst the studied taxa, where uninterrupted fibrolamellar bone with isolated primary osteons dominates. Griffin and Nesbitt (2016) suggested that the absence of LAGs may be widespread amongst silesaurids and Marsà et al. (2017) further proposed that these similarities indicated that silesaurids shared similar life history strategies.

Here, we present the first osteohistological description of the Late Triassic Brazilian silesaurid *Sacisaurus agudoensis* Ferigolo and Langer 2007. Given that few studies on the osteohistology of silesaurids have been conducted to date, the data obtained from *S. agudoensis* provides an important contribution towards understanding the presumed similarities in their life histories and more broadly, the acquisition of early dinosaur osteohistological characteristics and growth patterns.

MATERIALS AND METHODS

INSTITUTIONAL ABBREVIATIONS

MCN PV – Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Brazil, Paleovertebrates Collection.

MATERIAL, LOCALITY AND HORIZON

The holotype and referred material of *Sacisaurus agudoensis*, was recovered from the Santa Maria Supersequence, Rio Grande do Sul State, Brazil. The Late Triassic Santa Maria Supersequence is composed of four third order sequences, from the base to the top: Pinheiros-Chiniquá; Santa Cruz; Candelária and Mata (sensu Horn et al. 2014), the first three being remarkable for their rich vertebrate fossil record. All specimens referred to *S. agudoensis* were collected from a bone accumulation at a single outcrop located in the municipality of Agudo (Ferigolo and Langer 2007, Langer and Ferigolo 2013) assigned to the upper strata of the Candelária sequence and the *Riograndia* Assemblage Zone, Norian in age (Soares et al. 2011, Langer et al. 2018). The lithology of this sedimentary package mostly consists of sandstones with isolated layers of mudstone and mud intraclasts, which is associated with fluvial channel deposits (Zerfass et al. 2003, Horn et al. 2014).

Sacisaurus agudoensis is a small-bodied species (less than 1 meter in body length), with elongated distal hind limbs, an herbivorous/omnivorous diet and well-developed cursorial abilities (see Langer and Ferigolo 2013). The bone accumulation of *S. agudoensis* shows a peculiar preservation of over 30 nearly identical right femora with only one left femur (see Langer and Ferigolo 2013). The morphology of the taxon has already been described in detail in previous studies (see Ferigolo and Langer 2007, Langer and Ferigolo 2013).

We analyzed nine limb bones, which comprise eight right femora and one right incomplete fibula, all from different individuals. The complete femora in the bone accumulation range from 85 mm to 110 mm in length (Langer and Ferigolo 2013). We sectioned one nearly complete femur (85 mm length, without the head) and seven incomplete femora, where total length could not be measured (Table I). However, comparing the width of the epiphyses with more complete femora found at the study locality showed that all the bones in our sample fall within this size range. The narrow size range and similar morphology suggest that all femora represent individuals of a similar ontogenetic stage. To determine the ontogenetic stage of the elements in our sample, we compared the presence of femoral scars in *S. agudoensis* with the landmarks proposed by Griffin and Nesbitt (2016), who examined the development of bone scars across a femoral ontogenetic series of the silesaurid *Asilisaurus kongue*. All the known femora of *S. agudoensis* possess bone scars typical of skeletally mature individuals of *A. kongue*, with the exception of the trochanteric shelf, the linea intermuscularis cranialis and the linea intermuscularis caudalis, which are less developed in *S. agudoensis*. The modest development of these scars suggests that the femora of *S. agudoensis* do not belong to fully grown individuals. The morphology alone is an imprecise proxy in this case to determine the exact ontogenetic stage due to all the femora being isolated and fragmented in the bone accumulation. One of the aims of this paleohistological analysis is to verify if these femora do belong to a single ontogenetic stage.

TABLE I
Measurements, % vasc = percentage of vascularization, bone tissue type and preservation for the specimens examined in this study.

Element	Collection Number (MCN PV)	Proximal width (mm)	Distal width (mm)	Cross-sectional diameter (mm)	% vasc	Bone tissue type	Preservation
Fibula	10084	5.93	-	5.62	8.06	FLB	Proximal half
Femur	10071	-	12.87	8.02	-	FLB	Distal quarter
Femur	10228	4.20	-	3.44	12.74	FLB	Proximal half
Femur	10231	6.35	-	5.69	11.50	FLB	Proximal quarter
Femur	10022	4.03	-	3.21	12.91	FLB/PFB	Proximal three-fifths
Femur	10062	-	8.70	6.55	12.36	FLB/PFB	No head
Femur	10070	-	-	6.54	14.48	FLB/PFB	Proximal quarter
Femur	10230	8.90	-	5.97	10.55	FLB/PFB	Proximal quarter
Femur	10234	8.55	-	7.03	10.75	FLB/PFB	Proximal half

PALEOHISTOLOGICAL PROTOCOLS

Transverse thin sections were made as close to the midshaft as possible as this region undergoes the least secondary remodeling during growth and thus, provides the most complete growth record of the animal in long bones (Chinsamy 1990, Francillon-Vieillot et al. 1990, Chinsamy and Dodson 1995, Horner et al. 1999). Photographs were taken prior to thin sectioning and measurements (cross-sectional diameter, proximal/distal widths) are reported in Table I. The osteohistological thin sections were made at the Laboratório de Paleontologia de Vertebrados, Instituto de Geociências of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, following standard methodological procedures outlined by Chinsamy and Raath (1992), with adjustments. The bones were embedded in a clear epoxy resin (Araldite© GY 279, catalyzed with Aradur® HY 951) and left for 24 hours to set. They were cut into smaller blocks perpendicular to the long axis of the bone using a cut-off diamond-tipped saw within a Ken 9025 grinding machine. One surface of each resin block was then affixed to a frosted petrographic glass slide using the same resin that was used for embedding and left to set for a further 24 hours. The sections were wet-ground to approximately 60 µm thick and polished using a Prazis APL-S polishing machine with abrasive papers of increasing grit size (P80, P120, P320, P400, P600, P1200, P1500, P2000, P3000).

IMAGE ANALYSIS

The resulting thin sections were analyzed using a Leica DM 2500P microscope and photographed using an attached AxioCam ERc 5s camera. The image analysis program NIH ImageJ 1.52e (Schneider et al. 2012) was used to quantify the degree of vascularization of the mid-cortex of each element allowing a quantitative comparison between the study specimens and other related groups in which similar data is available. Channel area was measured in a field of view (FOV) taken from the mid-cortex, divided by the total FOV area and then converted into a percentage (Chinsamy 1993a). As already noted in the literature, although the channels includes lymph, nerves and vascular canals that extend through the bone tissue (Mckenzie and Klein 2000), the calculation provides an estimation of the maximum amount of vascularization within a given section. We repeated the procedure for every third FOV at 10X magnification resulting in eight to ten FOV per slide, providing a good average of a given section. Terminology adopted follows that of Francillon-Vieillot et al. (1990), Reid (1996), Chinsamy-Turan (2005, 2012) and Prondvai et al. (2014).

RESULTS

FEMORA

The transverse thin sections of all femora reveal a medullary cavity free of trabecular bone. Some elements (MCN PV 10022; PV 10062; PV 10228) are lateromedially compressed resulting in a flattened medullary cavity. This compression has caused numerous cracks to extend through the compact bone, but there are enough patches of well-preserved bone tissue to facilitate an assessment of the primary bone. A thick, irregular avascular endosteal layer of lamellar bone (Figure 1a-b) surrounds the medullary cavity in all femora.

The bone matrix exhibits regions of closely distributed haphazardly arranged globular osteocyte lacunae in a woven-fibered bone matrix between primary osteons (Figure 1c-f). This bone matrix indicates static osteogenesis and fast growth (Prondvai et al. 2014) and combined with the primary osteons acknoledges the presence of a fibrolamellar bone complex. The primary osteons are predominantly isolated longitudinally-oriented canals (Figure 2a), with some short radial and circumferential anastomoses (Figure 2b). The vascularization of the mid-cortex varies from 10.6% to 14.5% (Table I). Specimen MCN PV 10070 exhibits a more complex vascular arrangement, especially in the inner cortex, with radial and circumferential anastomoses reaching a sub-reticular arrangement (Figure 2c-d). Small, scattered secondary osteons were observed in most of the bones, but are mostly limited to the inner cortex. However, the specimens, MCN PV 10230, MCN PV 10231 and most notably MCN PV 10071, exhibit large, abundant secondary osteons, but not to the extent of forming multi-generational dense Haversian bone. In MCN PV 10230 and PV 10231 (Figure 3a and 3b, respectively) they appear locally, on the medial side of the bone, whereas in MCN PV 10071 (Figure 3c-d) they extend all around the medullary cavity and into the mid-cortex, occupying approximately half of the compact cortex. This region forms compacted coarse cancellous bone and is demarcated by a reversal line (Figure 3d). The high degree of remodeling in these three bones reflects the region in which the thin sections were taken, which are the proximal (MCN PV 10230 and PV 10231) and distal (MCN PV 10071) metaphyses where remodeling tends to be more prevalent.

Growth marks are absent from all the bones, resulting in an uninterrupted fibrolamellar bone complex. However, a peripheral area of slower forming parallel-fibered bone can be seen in some of the femora (MCN PV 10022; PV 10062; PV 10070; PV 10230; PV 10234). In these specimens, the osteocyte lacunae near the bone periphery are flattened and more evenly distributed, running parallel to one other (Figure 4a-h). The region also appears anisotropic in polarized light (Figure 4a-f). In these elements, there is a slight decrease in the size and amount of the vascular canals towards the peripheral region of the bone. The decreased vascularization and transition to a parallel-fibered

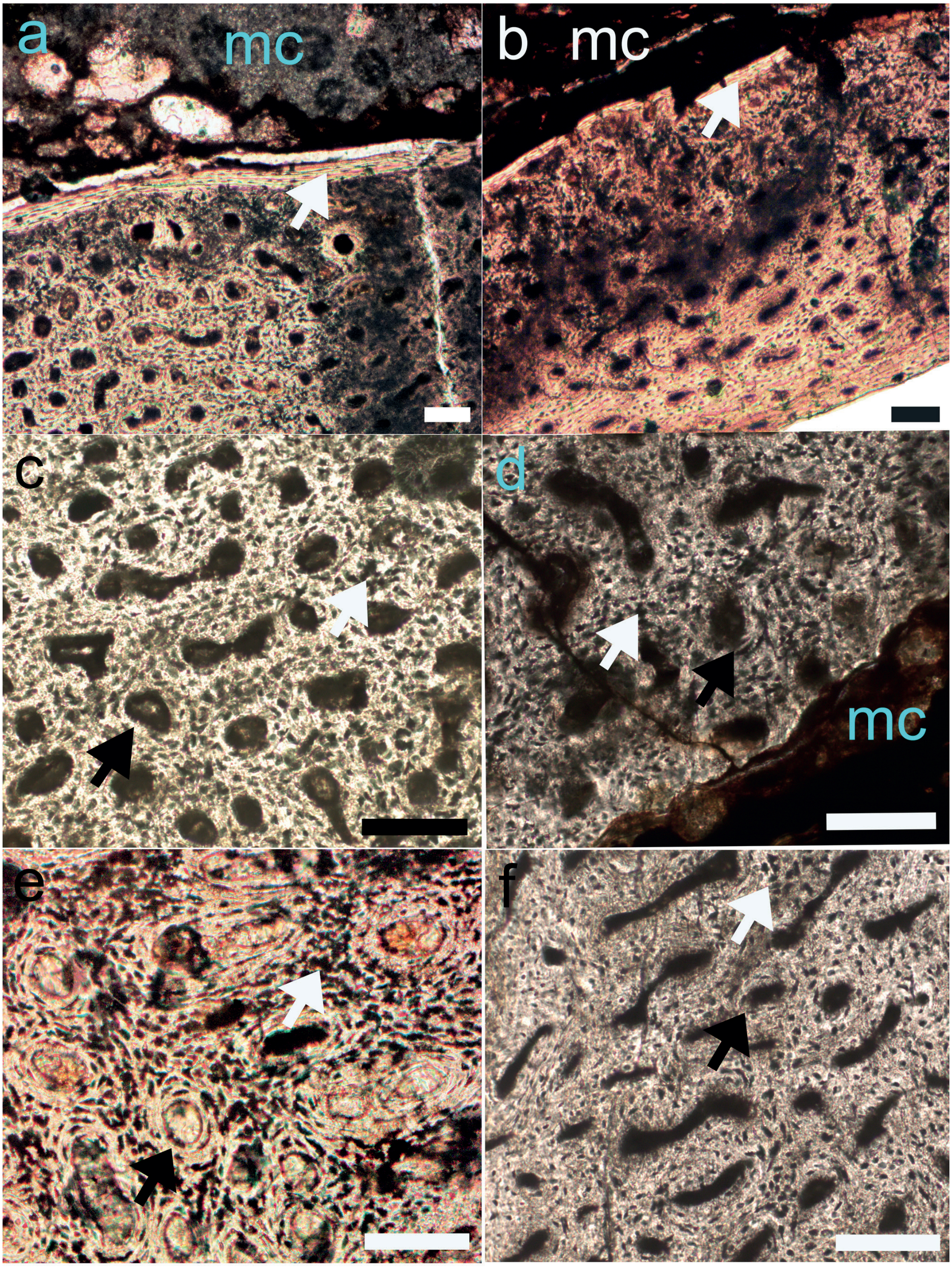

Figure 1 - Bone histology of femora of the Late Triassic *Sacisaurus agudoensis*. **a**, **b**: thin-sections of MCN PV 10228 and PV 10022 respectively, showing layers of endosteal bone (arrow) in the perimedullary region; **c**, **d**, **e** and **f**: higher magnification of MCN PV 10228, PV 10022, PV 10231 and PV10234 respectively, showing primary osteons (**black arrows**) associated with the woven bone matrix and haphazardly osteocyte lacunae (**white arrows**). *Abbreviations*: mc, medullary cavity. Scale bars equal 100 µm.

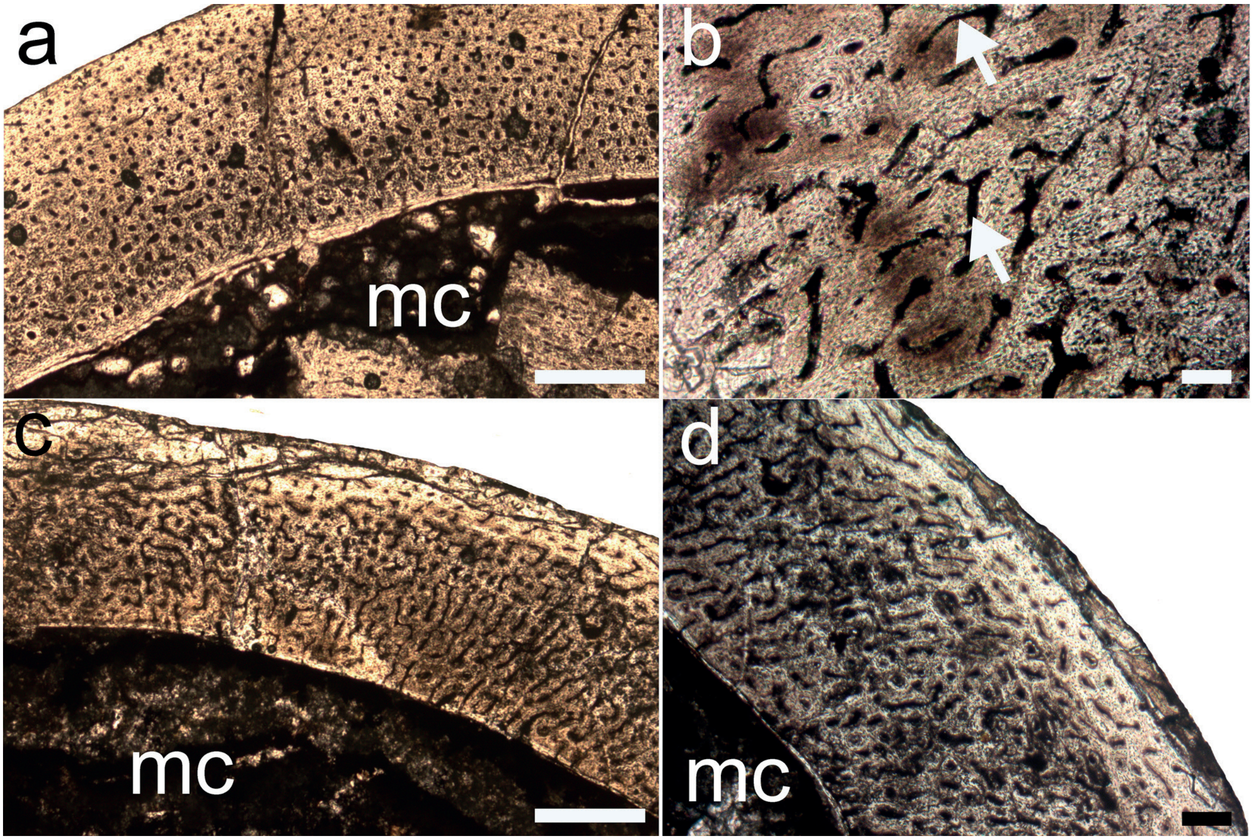

Figure 2 - Bone histology of femora of the Late Triassic *Sacisaurus agudoensis*. **a**: thin-section of MCN PV 10228 showing isolated primary osteons through the cortex; **b**: thin-section of MCN 10062 showing primary osteons with short anastomoses (**arrows**); **c**, **d**: thin-sections of MCN PV 10070 showing the sub-reticular arrangement. *Abbreviations*: mc, medullary cavity. Scale bars equal 500 µm in **a** and **c**; 100 µm in **b**; 200 µm in **d**.

bone matrix in the outer regions of the bone indicates an overall decrease in the growth rate. However, the absence of an External Fundamental System (EFS, sensu Cormack 1987) suggests that these bones were not fully grown as an EFS generally indicates the achievement of maximum size.

FIBULA

An incomplete fibula (MCN PV 10084, Figure 5a-d) was thin sectioned for this study. The most striking feature of the bone is a broad and rugose “tibial flange” extending obliquely from its cranioproximal corner (see Langer and Ferigolo 2013: Figure 19f).

Similar to the femora, the medullary cavity of the fibula is completely free of trabecular bone (Figure 5a). The compact cortex also comprises a fibrolamellar bone complex with longitudinally-oriented primary osteons in a woven bone matrix (Figure 5c). The primary osteons are mostly isolated with short anastomoses and the bone tissues are less vascularized (8.1%) than the femora (average = 12.2%). Vascularization remains constant throughout the cortex and there are no interruptions in the bone tissue (Figure 5d). Scattered secondary osteons are mostly limited to the inner cortex. As in the femora an EFS is absent. The most conspicuous difference between the bone tissues of the fibula and femora is the absence of an endosteal layer surrounding the medullary cavity in the fibula (Figure 5a and 5b).

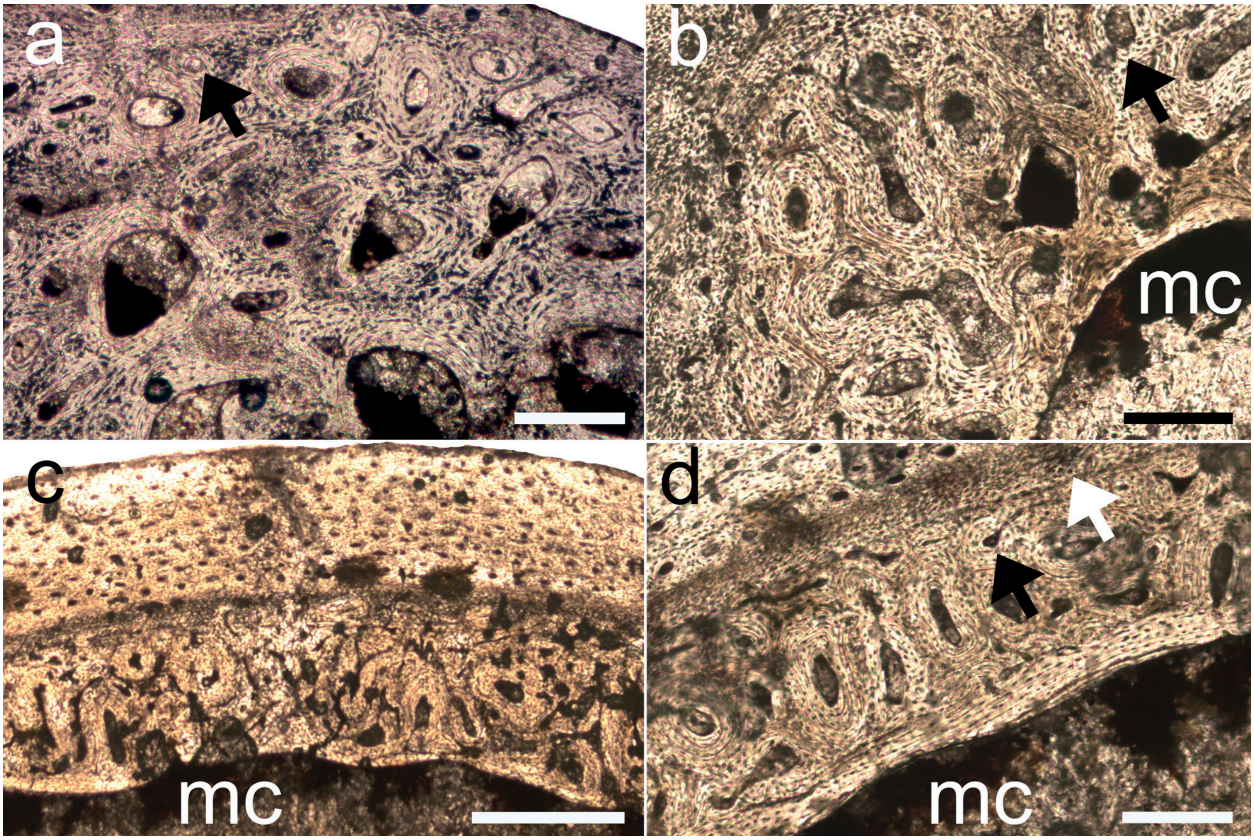

Figure 3 - Bone histology of femora of the Late Triassic *Sacisaurus agudoensis*. **a**, **b**: thin-sections of MCN PV 10230 and MCN PV 10231 respectively, showing compacted coarse cancellous bone and secondary osteons (**arrows**); **c**: thin section of MCN PV 10071 showing compacted coarse cancellous bone in the perimedullary region; **d**: higher magnification of MCN PV 10071 showing compacted coarse cancellous bone demarcated by a reversal line (**white arrow**) and secondary osteon (**black arrow**). *Abbreviation*: mc, medullary cavity. Scale bars equal 200 µm in **a**, **b** and **d**; 500 µm in **c**.

DISCUSSION

ONTOGENETIC STAGE OF THE STUDIED INDIVIDUALS

The analysis of the bone tissues of the study material reveals similar osteohistological features and thus suggests that the elements represent a similar ontogenetic stage. All elements, apart from the fibula, exhibit a thick avascular endosteal layer of lamellar bone surrounding the medullary cavity. This structure, as well as an EFS, has been observed in the femora of mature individuals of the silesaurid *Silesaurus opolensis* (Fostowicz-Frelik and Sulej 2010), indicating the cessation of medullar expansion and thus, a mature ontogenetic age (Chinsamy-Turan 2005). However, in the case of *S. agudoensis*, the absence of an EFS suggests that the circumferential endosteal lamellae indicates a temporary cessation in medullary expansion, after which growth would have resumed. The presence of fibrolamellar bone, even at the sub-periosteal surface in some elements, indicates that these animals were still growing at the time of death.

Some femora (MCN PV 10022; PV 10062; PV 10070; PV 10230; PV 10234) exhibit a transition from an inner woven bone matrix to an outer parallel-fibered bone matrix. This transition from fast to slower growing bone, as well the decrease in size and abundance of vascular canals towards the bone periphery is evidence of a decrease in growth rate, which indicates a departure from the juvenile stage into at least an early subadult stage for these individuals.

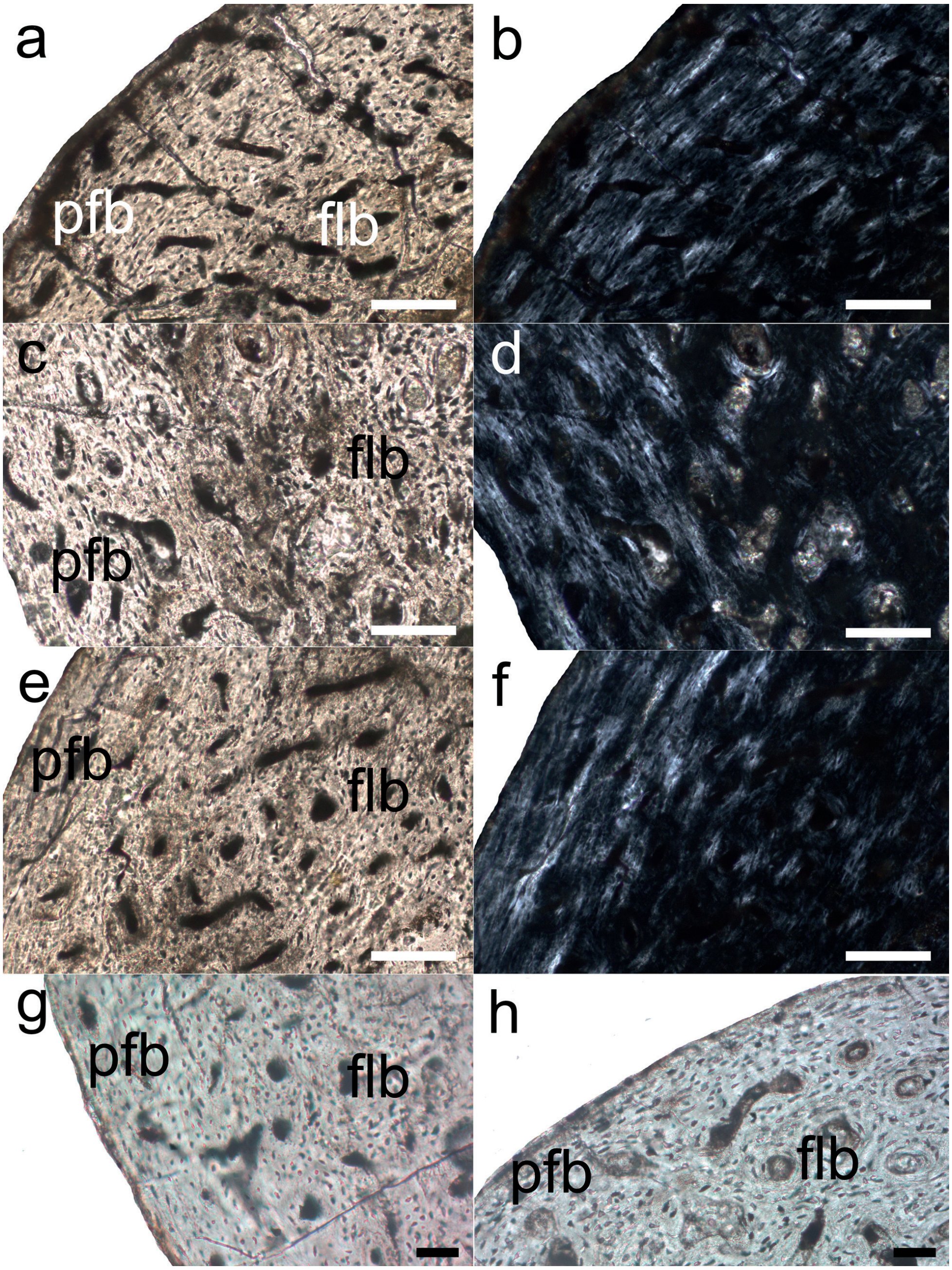

Figure 4 - Bone histology of femora of the Late Triassic *Sacisaurus agudoensis*. **a**: thin-section of MCN PV 10022 showing the transition from fibrolamellar bone in the inner cortex to parallel-fibered bone in the outer cortex; **b**: same region as **a** in polarized light highlighting the parallel-fibered bone; **c**: thin-section of MCN PV 10230 showing the transition from fibrolamellar bone to parallel-fibered bone; **d**: same region as **c** in polarized light highlighting the parallel-fibered bone; **e**: thin-section of MCN PV 10234 showing the transition from fibrolamellar bone to parallel-fibered bone; **f**: same region as **e** in polarized light highlighting the parallel-fibered bone; **g**: high magnification of MCN PV 10062 showing the transition from fibrolamellar bone to parallel-fibered bone; **h**: high magnification of MCN PV 10070 showing the transition from fibrolamellar bone to parallel-fibered bone. *Abbreviations*: flb, fibrolamellar bone; pfb, parallel-fibered bone. Scale bars equal 100 µm in **a**, **b**, **c**, **d**, **e** and **f**; 50 µm in **g** and **h**.

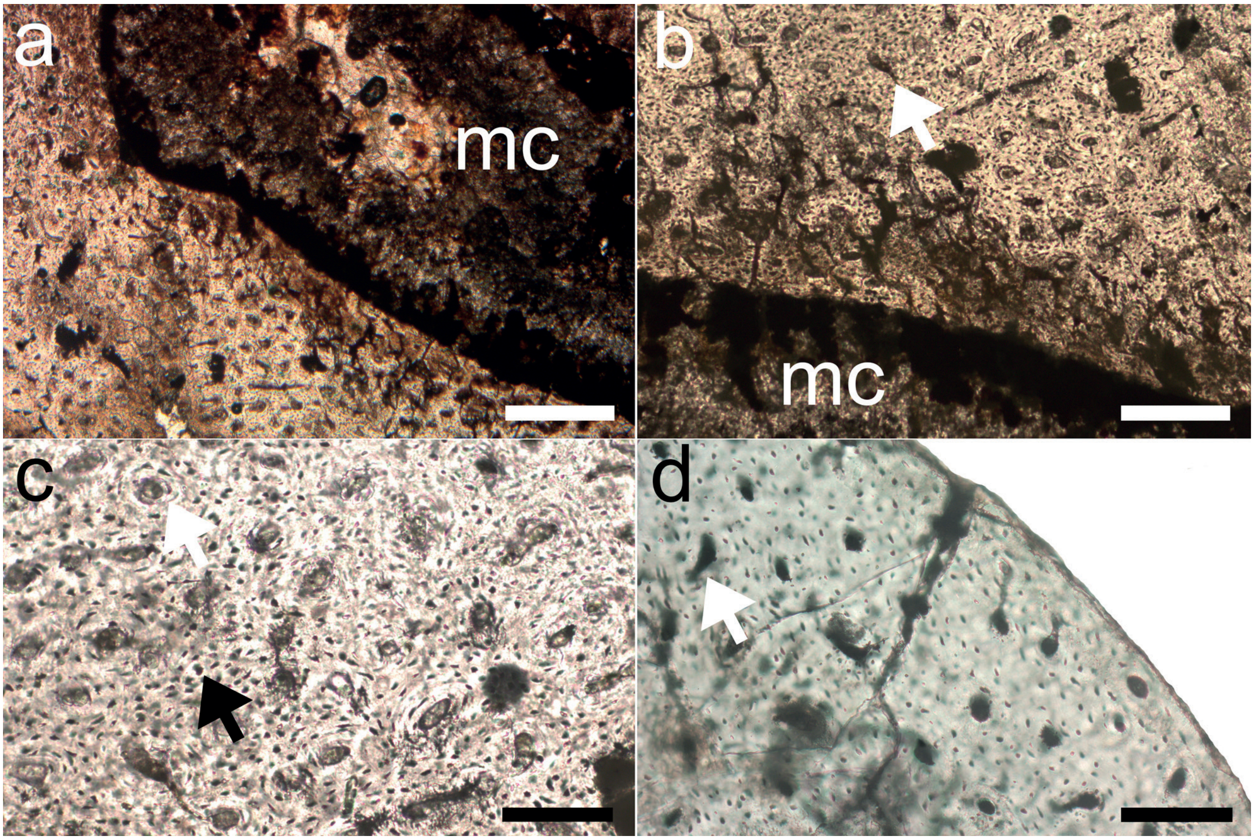

Figure 5 - Bone histology of a fibula (MCN PV 10084) of the Late Triassic *Sacisaurus agudoensis*. **a**: thin-section showing an open medullary cavity free of trabecular bone (note the absence of endosteal bone around the medullary cavity); **b**: high magnification showing primary osteons in the inner cortex (arrow); **c**: mid-cortical fibrolamellar bone with transversal osteocyte lacunae (**black arrow**) and primary osteons (**white arrow**); **d**: primary osteon (**arrow**) in the outer cortex (note how the vascularization is continuous and uniform towards the bone periphery). *Abbreviations*: mc, medullary cavity. Scale bars equal 400 μm in **a**; 200 μm in **b**; 100 μm in **c** and **d**.

The transverse thin section of the fibula MCN PV 10084 lacks all features indicating an older ontogenetic stage with only scattered secondary osteons appearing mainly in the inner cortex. There is no decrease in vascularization and no change to slower forming parallel-fibered bone towards the outer surface. Although vascularization is lower than in the femora, the uniformity of the rapidly forming fibrolamellar bone throughout the cortex supports a juvenile status for this individual.

GROWTH PATTERN AND COMPARISON WITH OTHER ARCHOSAUROMORPHA

The bone tissues of *Sacisaurus agudoensis* are primarily composed of uninterrupted fibrolamellar bone. The presence of this tissue type indicates relatively high rates of bone deposition and hence growth (Amprino 1947, Francillon-Vieillot et al. 1990, Margerie et al. 2002, Padian and Lamm 2013, Prondvai et al. 2014). The compact bone comprises isolated longitudinally-oriented primary osteons with some short anastomoses and a high density of globular osteocyte lacunae. Fibrolamellar bone has been found in all other silesaurids studied to date and the vascular pattern in *S. agudoensis* is similar to that observed in other taxa, such as *Silesaurus opolensis* (Fostowicz-Frelik and Sulej 2010), *Asilisaurus kongwe* (Griffin and Nesbitt 2016) and *Lewisuchus admixtus* (Marsà et al. 2017). However, it differs slightly from *S. opolensis* and

L.admixtus in having more anastomoses connecting the longitudinal primary osteons.

Given the onset of peripheral parallel-fibered bone in some individuals of *S. agudoensis* and absence of growth marks in all the bones studied, it is clear that it grew continuously (Padian and Lamm 2013) to at least the subadult stage of its ontogeny. Growth marks have been observed within peripheral parallel-fibered bone in the largest specimen of *Silesaurus opolensis*, however, (Fostowicz-Frelik and Sulej 2010) and thus, it is possible that *S. agudoensis* exhibited cyclical growth during later ontogenetic stages, but material from older individuals is required to test this.

The growth patterns of silesaurids differ from that seen in stem archosaurs, i.e., non-archosaurian archosauromorphs (Figure 6). For example, the osteohistology of the Late Triassic *Trilophosaurus buettneri* Case 1928, described by Werning and Irmis (unpublished data), comprises poorly vascularized lamellar bone with multiple LAGs throughout the cortex, indicating a slow growth rate. Rhynchosauria osteohistology also indicates slow growth rates. For example, Werning and Nesbitt (2015) described the osteohistology of a femur and tibia from a mature individual of the Middle Triassic *Stenaulorhynchus stockleyi* Haughton 1932 from Tanzania as moderate to poorly vascularized parallel-fibered bone tissue. Similar bone tissues have also been found in the ribs of *Hyperodapedon sanjuanensis* Langer and Schultz 2000 (previously *Scaphonyx sanjuanensis* Sill 1970) from the Late Triassic of Argentina (Ricqlès et al. 2008). Fast growing fibrolamellar bone has been observed in several elements of some Late Triassic rhynchosaurs, such as *Teyumbaita sulcognathus* Montefeltro, Langer and Schultz 2010 and *Hyperodapedon* sp. Huxley 1859 from southern Brazil (Veiga et al. 2015), and *Hyperodapedon* sp. from India (Mukherjee 2015). However, the fibrolamellar bone in these taxa is restricted to the innermost cortex, the rest of the cortex being comprised of slowly forming lamellar-zonal bone (Mukherjee 2015, Veiga et al. 2015). The tibia from an adult individual of the slightly more derived Early Triassic archosauromorph *Prolacerta broomi* Parrington 1935, exhibits a vascular pattern similar to that found in silesaurids in which the longitudinally-oriented primary osteons are mostly isolated with a few anastomoses (Botha-Brink and Smith 2011). However, the bone tissues are notably less vascularized (e.g. 2.2% compared to an average of 11% in *S. agudoensis*) and combined with the prevalence of a mixture of weakly developed fibrolamellar and parallel-fibered bone, these features suggest lower growth rates in *P. broomi* (Botha-Brink and Smith 2011).

Fibrolamellar bone becomes more prevalent in the non-archosaurian archosauriforms. *Proterosuchus fergusi* Broom 1903, a medium-sized proterosuchid (nearly 2 m in body length, Botha-Brink and Smith 2011), exhibits highly vascularized (e.g. femoral vascularity 15%) radiating vascular canals within fibrolamellar bone during early ontogeny. Growth decreases dramatically during late ontogeny, however, with the onset of poorly vascularized lamellar-zonal bone (Botha-Brink and Smith 2011). An unidentified long bone of the proterochampsid *Chanaresuchus bonapartei* Romer 1971 reveals similar bone tissues, but with a more sub-reticular vascular arrangement in the inner cortex (Ricqlès et al. 2008). Several elements from different individuals of the large-bodied Triassic erythrosuchids *Erythrosuchus africanus* Broom 1905 (Gross 1934, Ricqlès 1976, Ricqlès et al. 2008, Botha-Brink and Smith 2011) and *Garjainia madiba* Gower et al. 2014 (Gower et al. 2014) exhibit a variety of vascular arrangements including laminar, reticular and radial, within a fibrolamellar bone complex, indicating rapid growth rates, similar to those found in fast-growing dinosaurs. Although faster growing tissues become more prevalent among non-archosaurian archosauriforms, it should be

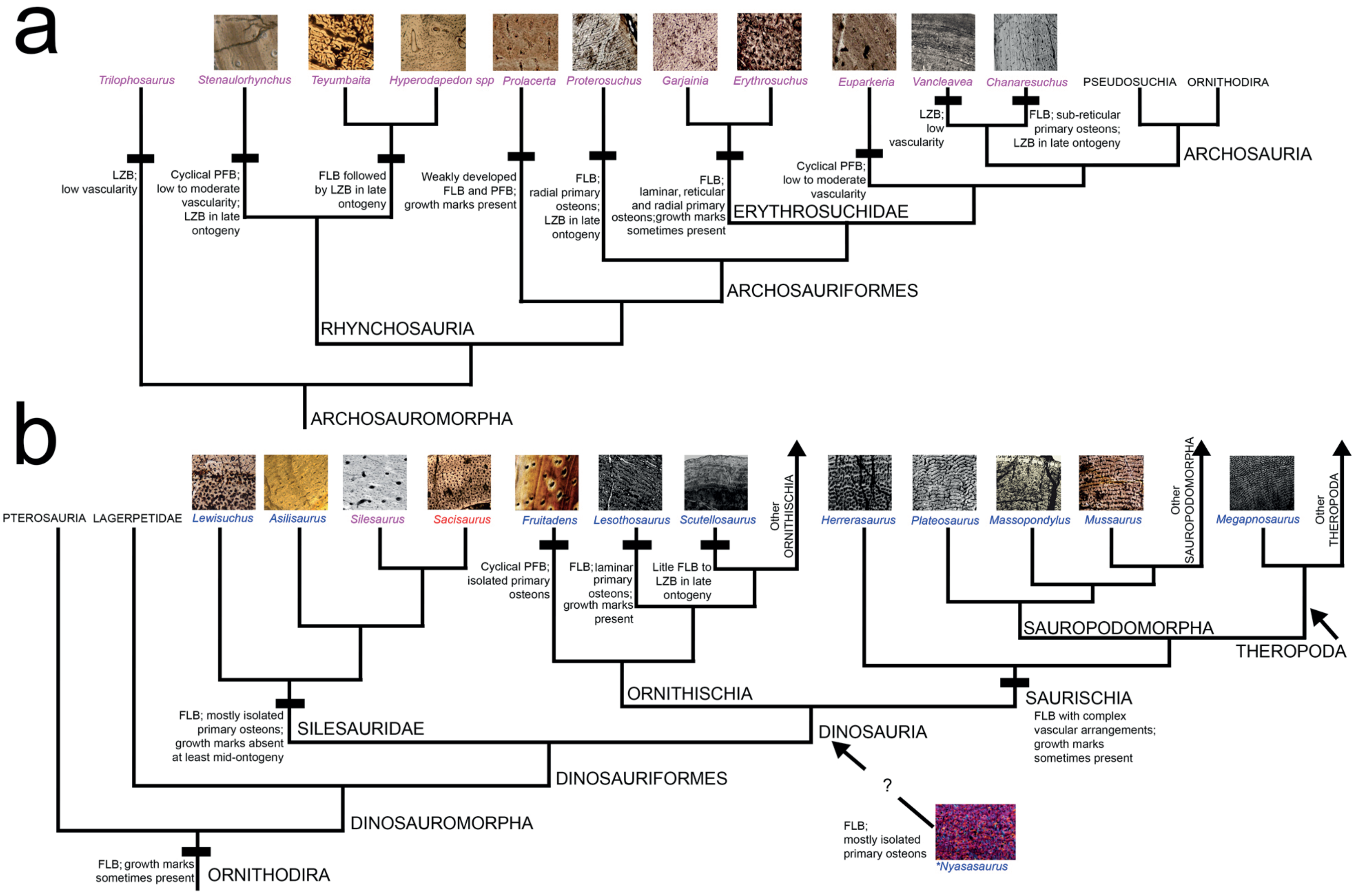

Figure 6 - Cladogram **a** and **b** (modified from Langer and Benton 2006, Nesbitt 2011, Otero et al. 2015, Ezcurra 2016) shows the microstructure of long bone along Archosauromorpha as revealed by bone histology. Taxa examined in this study appear in **red**. Taxa cited in the text appear in **blue**. * indicates the possible phylogenetic position of *Nyasasaurus*. *Abbreviations*: FLB, fibrolamellar bone; LZB, lamellar-zonal bone; PFB, parallel-fibered bone.

noted that there are exceptions. For example, the Middle Triassic *Euparkeria capensis* Broom 1913 exhibits predominantly low to moderately vascularized (3.3 to 5.4 %) parallel-fibered bone (Botha-Brink and Smith 2011) and the Late Triassic *Vancleavea campi* Long and Murry 1995 contains poorly vascularized lamellar-zonal bone tissue (Nesbitt et al. 2009). These taxa show that there was some degree of experimentation amongst the Triassic non-archosaurian archosauriforms as shown by the variety of bone tissue patterns in this group. However, the increasing prevalence of highly vascularized fibrolamellar bone shows that rapid growth rates evolved before the origin of Ornithodira (Ricqlès et al. 2008, Botha-Brink and Smith 2011, Gower et al. 2014) and is considered plesiomorphic for archosauriforms (Ricqlès et al. 2003).

The simpler vascular pattern seen in silesaurids differs from most early dinosaurs where the vascular arrangements tend to exhibit more complex anastomosing. For example, plexiform and laminar vascular patterns are typical of early saurischian dinosaurs [e.g., *Herrerasaurus ischigualastensis* Reig 1963, (Padian et al. 2001, 2004, Ricqlès et al. 2003)], early sauropodomorphs [e.g., *Plateosaurus engelhardti* Meyer 1837, *Mussaurus patagonicus* Bonaparte and Vince 1979, *Massospondylus carinatus* Owen 1854, (Klein and Sander 2007, Cerda et al. 2014, Chinsamy, 1993b, respectively)] and the coelophysid neotheropod (Chinsamy 1990, Ricqlès et al. 2003, Padian et al. 2004) *Megapnosaurus rhodesiensis* Ivie et al. 2001 (previously *Syntarsus rhodesiensis* Raath 1969), as well as the early ornithischian *Lesothosaurus diagnosticus* Galton 1978 (specimen NMQR 3076, Knoll et al. 2010).

In contrast, the osteohistology of some early ornithischians such as the heterodontosaurid *Fruitadens haagarorum* Butler et al. 2010 and the thyreophoran *Scutellosaurus lawleri* Colbert 1981 exhibit slower forming bone tissues. *F. haagarorum* exhibits parallel-fibered bone (Butler et al. 2010) and *S. lawleri* contains very little fibrolamellar bone during early ontogeny and entirely lamellar-zonal bone during adulthood (Padian et al. 2004). Both taxa contain predominantly longitudinally-oriented vascular canals with few anastomoses. These ornithischians are relatively small, with *F. haagarorum* only growing to a maximum length of 75 cm and *S. lawleri* less than 1.5 m (Padian et al. 2004, Butler et al. 2010) and thus, body size may have played a role in their relatively slower growth rates (Padian et al. 2004). For example, Padian et al. (2004) showed that the vascular arrangements of the bone tissues in small dinosaurs are simpler and less vascularized compared to their larger relatives (Singh et al. 1974, Case 1978). However, the fabrosaurid *L. diagnosticus*, was also relatively small with an approximate body length of 2 m (Knoll et al. 2010). It displays rapidly forming fibrolamellar bone with longitudinally-oriented primary osteons during early ontogeny and a laminar vascular arrangement during mid-ontogeny (Knoll et al. 2010), typical of other early saurischian dinosaurs. Thus, factors other than body size likely played a role in shaping ornithischian growth rates and more research is required to better understand the life histories of these taxa.

Although there are relatively few studies on the osteohistology of silesaurids and early dinosaurs, the data available to date suggest that a simpler vascular arrangement of longitudinally-oriented primary osteons is typical of silesaurids. In contrast, most early dinosaurs examined to date [apart from the contentious *Nyasasaurus parringtoni* (Nesbitt et al. 2013)] show a more complex vascular arrangement early in their life history. Given that more complex vascular patterns are associated with higher growth rates (Margerie et al. 2002, Padian and Lamm 2013), this implies that silesaurids grew relatively more slowly than the earliest crown-group dinosaurs (apart from some small ornithischians). Again, this may be related to body size because based on femoral length (sensu Irmis 2011, Turner and Nesbitt 2013, Piechowski et al. 2014, Barrett et al. 2015), all silesaurids studied to date were small-bodied species (body length of approximately 1.5 m or less, Barrett et al. 2015), whereas early sauropodomorph dinosaurs with more complex anastomoses were larger (Irmis 2011, Turner and Nesbitt 2013). However, as noted with *L. diagnosticus* some taxa do not show correlation between body size and vascularization. The coelophysid neotheropod *M. rhodesiensis* also exhibits highly vascularized, complex arrangements despite having a similar body size to *S. opolensis* (Padian et al. 2001, Irmis 2011, Turner and Nesbitt 2013).

Additionally, Barrett et al. (2015) described the first larger-bodied silesaurid (NHMUK R16303) from the Lifua Member of the Manda Beds of Tanzania, estimated to have had a femoral length of approximately 345 mm (body length estimated to be approximately 3 m), which according to the authors, may represent a large individual of *Asilisaurus kongwe*. The osteohistology of *A. kongwe* indicates that the specimens were still growing at the time of death and thus probably represent juveniles or subadult individuals (Griffin and Nesbitt 2016). The material we sampled here also indicates that the bones came from juveniles and subadult individuals that were still growing. This suggests that some silesaurids reached larger body sizes than previously thought. Further osteohistological descriptions of such large specimens will clarify the correlation between body size and vascular pattern among silesaurids.

CONCLUSIONS

The bone tissues of the non-dinosaurian dinosauriform silesaurid *S. agudoensis* exhibit rapidly forming fibrolamellar bone with longitudinally-oriented primary osteons and occasional anastomoses similar to that observed in other silesaurids. Our study supports previous studies in showing that high growth rates were already present prior the evolution of Ornithodira. However, the simpler vascular pattern of longitudinally-oriented primary osteons with few anastomoses differs from the complex arrangements generally found in crown-group dinosaurs. This suggests that silesaurids grew comparatively more slowly than most dinosaurs, which may be related to phylogeny or smaller body sizes. Further examination of more dinosauromorph taxa is required to confirm this hypothesis.

ACKNOWLEDGMENTS

We thank Dr. C.S. Vega from the Universidade Federal do Paraná (UFPR) and the Laboratório de Pesquisa em Microscopia of UFPR for access to imaging equipment. We also thank two anonymous reviewers for their suggestions and comments. The Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (FAPERGS) provided financial support to FHV, MBS and JBB (Grant number 0441-2551/14-7), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided financial support to FHV, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided financial support to MBS (Grant number 312387/2016-4), to AMR (Grant number 306951/2017-7) and the National Research Foundation (UID 98819 and 104688), the Palaeontological Scientific Trust (PAST), Johannesburg, South Africa, and DST-NRF Centre of Excellence in Palaeosciences (CoE-Pal) provided financial support to JBB.

AUTHOR CONTRIBUTIONS

Fábio Hiratsuka Veiga, Jennifer Botha-Brink and Marina Bento Soares are responsible for the study conception, data analysis and to the writing of the manuscript with input from the other authors. Fábio Hiratsuka Veiga, Ana Maria Ribeiro and Jorge

Ferigolo performed the acquisition of sampled bones. All authors discussed the results, provided critical revision of the manuscript and contributed to the final manuscript.

REFERENCES

AMPRINO R. 1947. La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l'accroissement. Arch Biol 58: 315-330.

BARRETT PM, NESBITT SJ AND PEECOOK BR. 2015. A large-bodied silesaurid from the Lifua Member of the Manda beds (Middle Triassic) of Tanzania and its implications for body-size evolution in Dinosauromorpha. Gondwana Res 27(3): 925-931.

BENTON MJ. 2004. Origin and relationships of Dinosauria. In: Weishampel DB et al. (Eds), Dinosauria, 2nd ed.,Berkeley: University of California Press, p. 7-24.

BO Z, HEDRICK BP, CHUNLING G, TUMARKIN-DERATZIAN AR, FENGJIAO Z, CAIZHI S AND DODSON P. 2016. Histologic examination of an assemblage of *Psittacosaurus* (Dinosauria: Ceratopsia) juveniles from the Yixian Formation (Liaoning, China). The Anat Rec 299(5): 601-612.

BOTHA-BRINK J AND SMITH RMH. 2011. Osteohistology of the Triassic Archosauromorphs *Prolacerta*, *Proterosuchus*, *Euparkeria*, and *Erythrosuchus* from the Karoo Basin of South Africa. J Vertebr Paleontol 31: 1238-1254.

BRUSATTE SL, BENTON MJ, DESOJO JB AND LANGER MC. 2010. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). J Syst Palaeontol 8: 3-47.

BUTLER RJ, GALTON PM, PORRO LB, CHIAPPE LM, HENDERSON DM AND ERICKSON GM. 2010. Lower limits of ornithischian dinosaur body size inferred from a new Upper Jurassic heterodontosaurid from North America. Proc R Soc B 277(1680): 375-381.

CABREIRA S ET AL. 2016. A unique Late Triassic dinosauromorph assemblage reveals dinosaur ancestral anatomy and diet. Curr Biol 26(22): 3090-3095.

CASE TJ. 1978. Speculations on the growth rate and reproduction of some dinosaurs. Paleobiology 4: 320-328.

CERDA IA, POL D AND CHINSAMY A. 2014. Osteohistological insight into the early stages of growth in *Mussaurus patagonicus* (Dinosauria, Sauropodomorpha). Hist Biol 26(1): 110-121.

CHINSAMY A. 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). Palaeontol Afr 27: 77-82.

CHINSAMY A. 1993a. Image analysis and the physiological implications of the vascularization of femora in archosaurs. Mod Geol 19: 101-108.

CHINSAMY A. 1993b. Bone histology and growth trajectory of the prosauropod dinosaur *Massospondylus carinatus* Owen. Mod Geol 18: 319-329.

CHINSAMY A AND DODSON P. 1995. Inside a dinosaur bone. Am Sci 83: 174-180.

CHINSAMY A AND RAATH MA. 1992. Preparation of fossil bone for histological examination. Palaeontol Afr 29: 39-44.

CHINSAMY-TURAN A. 2005. The microstructure of dinosaur bone: deciphering biology with fine scale techniques. Baltimore: Johns Hopkins University Press, 195 p.

CHINSAMY-TURAN A. 2012. The forerunners of mammals: radiation, histology, biology. Chinsamy-Turan A (Ed), Bloomington: Indiana University Press, 330 p.

CORMACK D. 1987. Ham`s histology. New York: Lippincott, 732 p.

ENLOW DH AND BROWN SO. 1956. A comparative histological study of fossil and recent bone tissue. Part I. Tex J Sci 8: 405-443.

ENLOW DH AND BROWN SO. 1957. A comparative histological study of fossil and recent bone tissue. Part II. Tex J Sci 9: 186-214.

ENLOW DH AND BROWN SO. 1958. A comparative histological study of fossil and recent bone tissue. Part III. Tex J Sci 10: 187-230.

EZCURRA MD. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis haldwini* Sullivan and Lucas, 1999 from the Upper Triassic of New Mexico, USA. Geodiversitas 28: 649-684.

EZCURRA MD. 2016. The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. PeerJ 4: e1778.

FERIGOLO J AND LANGER MC. 2007. A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian predentary bone. Hist Biol 19: 23-33.

FOSTOWICZ-FRELIK L AND SULEJ T. 2010. Bone histology of *Silesaurus opolensis* Dzik, 2003 from the Late Triassic of Poland. Lethaia 43: 137-148.

FRANCILLON-VIEILLOT H, BUFFRÉNIL V, CASTANET J, GÉRAUDIE J, MEUNIER FJ, SIRE JY, ZYLBERBERG L AND RICQLÈS A DE. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: Carter JG (Ed), Skeletal biomineralisation; patterns, processes and evolutionary trends. New York: Van Nostrand Reinhold, New York, USA, p. 471-530.

GAUTHIER JA. 1986. Saurischian monophyly and the origin of birds. In: Padian K (Ed), The origin of birds and the evolution of flight. Mem Calif Acad Sci, p. 1-56.

GOWER DJ, HANCOX PJ, BOTHA-BRINK J, SENNIKOV AG AND BUTLER RJ. 2014. A New Species of *Garjainia* Ochev, 1958 (Diapsida: Archosauriformes: Erythrosuchidae) from the Early Triassic of South Africa. PLoS ONE 9(11): e111154.

GRADY JM, ENQUIST BJ, DETTWEILER-ROBINSON E, WRIGHT NA AND SMITH FA. 2014. Evidence for mesothermy in dinosaurs. Science 344: 1268-1272.

GRIFFIN CT AND NESBITT SJ. 2016. The femoral ontogeny and long bone histology of the Middle Triassic (?late Anisian) dinosauriform *Asilisaurus kongwe* and implications for the growth of early dinosaurs. J Vertebr Paleontol 36(3): e1111224.

GROSS W. 1934. Die Typen des mikroskopischen Knochenbaues bei fossilen Stegocephalen und Reptilien. Z Anat Entwicklungs 203: 731-764.

HORN BLD, MELO TM, SCHULTZ CL, PHILIPP RP, KLOSS HP AND GOLDBERG K. 2014. A new third-order sequence stratigraphic framework applied to the Triassic of the Paraná Basin, Rio Grande do Sul, Brazil, based on structural, stratigraphic and paleontological data. J S Am Earth Sci 55: 123-132.

HORNER JR, RICQLÈS A DE AND PADIAN K. 1999. Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology. Paleobiology 25: 295-304.

HORNER JR, RICQLÈS A DE AND PADIAN K. 2000. Long bone histology of the hadrosaurid dinosaur *Maisaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. J Vertebr Paleontol 20: 115-129.

IRMIS RB. 2011. Evaluating hypotheses for the early diversification of dinosaurs. Earth Env Sci T R So 101: 397-426.

IRMIS RB, NESBITT SJ, PADIAN K, SMITH ND, TURNER AH, WOODY D AND DOWNS A. 2007. A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317: 358-36.

KAMMERER CF, NESBITT SJ AND SHUBIN NH. 2012. The first silesaurid dinosauriform from the Late Triassic of Morocco. Acta Palaeontol Pol 57(2): 277-284.

KLEIN N AND SANDER PM. 2007. Bone histology and growth of the prosauropod dinosaur *Plateosaurus engelhardti* Von Meyer, 1837 from the Norian bonebeds of Trossingen (Germany) and Frick (Switzerland). Spec Pap Palaeontol 77: 169-206.

KLEIN N AND SANDER PM. 2008. Ontogenetic stages in the long bone histology of sauropod dinosaurs. Paleobiology 34: 247-263.

KNOLL F, PADIAN K AND RICQLES A DE. 2010. Ontogenetic change and adult body size of the early ornithischian dinosaur *Lesothosaurus diagnosticus*: Implications for basal ornithischian taxonomy. Gondwana Res 17: 171-179.

LANGER MC AND BENTON MJ. 2006. Early dinosaurs: a phylogenetic study. J Syst Palaeontol 4: 309-358.

LANGER MC, EZCURRA MD, BITTENCOURT JS AND NOVAS FE. 2010. The origin and early evolution of dinosaurs. Biol Rev 85: 55-110.

LANGER MC AND FERIGOLO J. 2013. The Late Triassic dinosauromorph *Sacisaurus agudoensis* (Caturrita Formation; Rio Grande do Sul, Brazil): anatomy and affinities. In: Nesbitt SJ et al. (Eds), Anatomy, phylogeny, and palaeobiology of early Archosaurs and their kin, London: Geological Society, Special Publications, vol. 379, p. 353-392.

LANGER MC, NESBITT SJ, BITTENCOURT JS AND IRMIS RB. 2013. Non-dinosaurian Dinosauromorpha. In: Nesbitt SJ et al. (Eds), Anatomy, phylogeny and palaeobiology of early Archosaurs and their kin, London: Geological Society, Special Publications, vol. 379, p. 157-186.

LANGER MC, RAMEZANI J, DA ROSA A. 2018. U-Pb age constraints on dinosaur rise from south Brazil. Gondwana Res 57: 133-140.

LANGER MC AND SCHULTZ CL. 2000. A new species of the late Triassic rhynchosaur *Hyperodapedon* from the Santa Maria Formation of south Brazil. Palaeontology 43: 633-652.

LEGENDRE LJ, GUÈNARD G, BOTHA-BRINK J AND CUBO J. 2016. Evidence for ancestral high metabolic rate in archosaurs. Syst Biol 66: 989-996.

MARGERIE E, CUBO J AND CASTANET J. 2002. Bone typology and growth rate: testing and quantifying ‘Amprino’s rule’ in the mallard (*Anas platyrhynchos*). C R Biologies 325: 221-230.

MARSÀ JAG, AGNOLÍN FL AND NOVAS F. 2017. Bone microstructure of *Lewisuchus admixtus* Romer, 1972 (Archosauria, Dinosauriformes). Hist Biol 1-6.

MCKENZIE JC AND KLEIN RM. 2000. Basic concepts in cell biology and histology. New York: McGraw-Hill, 427 p.

MITCHELL J, SANDER PM AND STEIN K. 2017. Can secondary osteons be used as ontogenetic indicators in sauropods? Extending the histological ontogenetic stages into senescence. Paleobiology 43(2): 321-342.

MUKHERJEE D. 2015. New insights from bone microanatomy of the Late Triassic *Hyperodapedon* (Archosauromorpha, Rhynchosauria): implications for archosauromorph growth strategy. Palaeontology 58: 313-339.

NESBITT SJ. 2011. The early evolution of Archosauria: relationships and the origin of major clades. Bull Am Mus Nat Hist 352: 1-292.

NESBITT SJ, BARRETT PM, WERNING S, SIDOR CA AND CHARIG AJ. 2013. The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania. Biol Lett 9(1): 20120949.

NESBITT SJ, SIDOR CA, IRMIS RB, ANGIELCZYK KD, SMITH RMH AND TSUJI LA. 2010. Ecologically distinct dinosaurian sister-group shows early diversification of Ornithodira. Nature 464: 95-98.

NESBITT SJ, STOCKER MR, SMALL BJ AND DOWNS A. 2009. The osteology and relationships of *Vancleavea campi* (Reptilia: Archosauriformes). Zool J Linn Soc-Lond 157: 814-864.

NIEDZWIEDZKI G, PIECHOWSKI R AND SULEJ T. 2009. New data on the anatomy and phylogenetic position of *Silesaurus opolensis* from the late Carnian of Poland. J Vertebr Paleontol 29: 155A.

OTERO A, KRUPANDAN E, POL D, CHINSAMY A AND CHOINIERE J. 2015. A new basal sauropodiform from South Africa and the phylogenetic relationships of basal sauropodomorphs. Zool J Linn Soc Lond 174: 589-634.

PADIAN K, HORNER JR AND RICQLÈS A DE. 2004. Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies. J Vertebr Paleontol 24: 555-571.

PADIAN K AND LAMM ET. 2013. Bone histology of fossil tetrapods: advancing methods, analysis, and interpretation. Padian K and Lamm ET (Eds), Berkeley: University of California Press, 298 p.

PADIAN K, RICQLÈS A DE AND HORNER JR. 2001. Dinosaurian growth rates and bird origins. Nature 412: 405-408.

PEECOOK BR, SIDOR CA, NESBITT SJ, SMITH RMH, STEYER JS AND ANGIELCZYK KD. 2013. A new silesaurid from the Upper Ntawere Formation of Zambia (Middle Triassic) demonstrates the rapid diversification of Silesauridae (Avemetatarsalia, Dinosauriformes). J Vertebr Paleontol 33(5): 1127-1137.

PIECHOWSKI R, TALANDA M AND DZIK J. 2014. Skeletal variation and ontogeny of the Late Triassic dinosauriform *Silesaurus opolensis*. J Vertebr Paleontol 34: 1383-1393.

PRONDVAI E, STEIN K, RICQLÈS A DE, CUBO J. 2014. Development-based revision of bone tissue classification: the importance of semantics for science. Biol J Linn Soc 112: 799-816.

REID REH. 1996. Bone histology of the Cleveland-Lloyd dinosaurs and of the dinosaurs in general, Part I: introduction: introduction to bone tissues. Geol Stud 41: 25-71.

RICQLÈS A DE. 1976. On bone histology of living and fossil reptiles, with comments on its functional and evolutionary significance. In: Bellairs AD and Cox CB (Eds), Morphology and Biology of Reptiles, London: Academic Press, p. 123-150.

RICQLÈS A DE, PADIAN K AND HORNER JR. 2003. On the bone histology of some Triassic pseudosuchian archosaurs and related taxa. Ann Paleontol 89: 67-101.

RICQLÈS A DE, PADIAN K, KNOLL F AND HORNER JR. 2008. On the origin of high growth rates in archosaurs and their ancient relatives: complementary histological studies on Triassic archosauriforms and the problem of a “phylogenetic signal” in bone histology. Ann Paleontol 94: 57-76.

SCHNEIDER CA, RASBAND WS AND ELICEIRI KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9: 671-675.

SERENO PC. 1991. Basal archosaurs: phylogenetic relationships and functional implications. Mem Soc Vertebr Paleontol 2: 1-53.

SINGH IJ, TONNA EA AND GANDEL CP. 1974. A comparative histological study of mammalian bone. J Morphol 144: 421-438.

SKUTSCHAS PP, BOITSOVA EA, AVERIANOV AO AND SUES HD. 2017. Ontogenetic changes in long-bone histology of an ornithomimid theropod dinosaur from the Upper Cretaceous Bissekty Formation of Uzbekistan. Hist Biol 29(6): 715-729.

SOARES MB, SCHULTZ CL AND HORN B. 2011. New information on *Riograndia guaibensis* Bonaparte, Ferigolo and Ribeiro, 2001 (Eucynodontia, Tritheledontidae) from the Late Triassic of southern Brazil: anatomical and biostratigraphic implications. An Acad Bras Cienc 83: 329-354.

TURNER AH AND NESBITT SJ. 2013. Body size evolution during the Triassic archosauriform radiation. In: Nesbitt SJ et al. (Eds), Anatomy, phylogeny, and palaeobiology of early Archosaurs and their kin, London: Geological Society, Special Publications, vol. 379, p. 573-597.

VANDERVEN E, BURNS ME AND CURRIE PJ. 2014. Histological growth dynamic study of *Edmontosaurus regalis* (Dinosauria: Hadrosauridae) from a bonebed assemblage of the Upper Cretaceous Horseshoe Canyon Formation, Edmonton, Alberta, Canada. Can J Earth Sci 51(11): 1023-1033.

VEIGA FH, SOARES MB AND SAYÃO JM. 2015. Osteohistology of hyperodapedontine rhynchosaurs from the Upper Triassic of Southern Brazil. Acta Palaeontol Pol 60(4): 829-836.

WERNING S AND NESBITT SJ. 2015. Bone histology and growth in *Stenaulorhynchus stockleyi* (Archosauromorpha: Rhynchosauria) from the Middle Triassic of the Ruhuhu Basin of Tanzania. C R Palevol 15(1): 163-175.

ZERFASS H, LAVINA EL, SCHULTZ CL, GARCIA AJV, FACCINI UF AND CHEMALE JR F. 2003. Sequence stratigraphy of continental Triassic strata of southernmost Brazil: a contribution to southwestern Gondwana palaeogeography and palaeoclimate. Sediment Geol 161: 85-105.