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Paleohistology of the crocodyliform *Mariliasuchus amarali* Carvalho & Bertini, 1999 (Mesoeucrocodylia, Notosuchia) based on a new specimen from the Upper Cretaceous of Brazil

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Thin section of the radius from *Mariliasuchus amarali* (UFRPE 5311). Image taken with cross polarized light and lambda compensator.

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ABSTRACT

Mariliasuchus amarali Carvalho & Bertini, 1999 was a terrestrial quadruped crocodyliform from the Late Cretaceous of the Bauru Group, Brazil. In this paper we present the first study of the bone

KEY WORDS
Cretaceous,
Notosuchian,
Brazil,
bone histology,
Godwana.

histology of this species. Moderate growth rate, interspersed by growth marks, was observed in thin sections of a rib and appendicular bones; growth patterns observed in *M. amarali*s appear similar to those observed in Triassic archosauriforms. The *M. amarali* cross-sections indicate growth variability between both the axial and appendicular bones. Distinctive remodeling processes were found in the radius, which had extensive inner cortex remodeling composed of compacted coarse cancellous bone. Furthermore, the medullary region was infilled with spongy bone.

MOTS CLÉS
Crétacé,
Notosuchien,
Brésil,
Osteohistologie,
Gondwana.

RÉSUMÉ
Paléohistologie du crocodyliforme Mariliasuchus amarali *Carvalho & Bertini, 1999 (Mesoeucrocodylia, Notosuchia) fondée sur un nouveau spécimen du Crétacé supérieur du Brésil.*
Mariliasuchus amarali Carvalho & Bertini, 1999 était un crocodyliforme quadrupède terrestre du Crétacé supérieur du Groupe de Bauru, au Brésil. Dans cet article, nous présentons la première étude de l'ostéohistologie de cette espèce. Un taux de croissance modéré, entrecoupé de marques de croissance, a été observé dans des sections fines d'une côte et d'os appendiculaires ; les schémas de croissance observés chez *M. amaralis* semblent similaires à ceux observés chez les archosauriformes du Trias. Les coupes transversales de *M. amaralis* indiquent une variabilité de croissance entre les os axiaux et appendiculaires. Des processus de remodelage distincts ont été trouvés dans le radius qui présentait un remodelage important du cortex interne composé d'os spongieux grossier compacté. De plus, la région médullaire était remplie d'os spongieux.

INTRODUCTION

Archosauromorpha, a group of diapsids that are more closely related to birds and crocodylians than to squamates, has one of the most diverse fossil records within the Sauropsida. It radiated during the Triassic and gave rise to the crown group, Archosauria. Archosaurs diverged into two lineages, the Pseudosuchia (Crocodyliformes and relatives) and the Ornithodira (pterosaurs and dinosaurs, including birds) (Nesbitt 2011; Ezcurra 2016).

The Notosuchia were a diverse clade of crocodyliforms that thrived during the Cretaceous and whose remarkable diversity is mainly represented by the Neuquén Basin, Argentina (e.g. Pol & Leardi 2015; Leardi *et al.* 2018) and the Bauru Group, Brazil (e.g. Marinho & Carvalho 2009; Campos *et al.* 2011; Pol *et al.* 2014). Our knowledge of the early members of the Mesoeucrocodylia (*sensu stricto* Benton & Clark 1988) has been largely derived from notosuchian records in Africa and South America (Ortega *et al.* 2000). In Brazil, the Bauru Group has yielded a diverse notosuchian fauna, with more than 30 species reported (Iori & Campos 2016; Iori *et al.* 2016; Martinelli *et al.* 2018).

Mariliasuchus Carvalho & Bertini, 1999 belongs to the advanced notosuchians, a group of heterodont crocodyliforms found in the South American landmasses during the Cretaceous (Pol *et al.* 2014). The genus consisted of two species: *Mariliasuchus amarali* Carvalho & Bertini, 1999 and *Mariliasuchus robustus* Nobre, Carvalho, Vasconcellos & Nava, 2007, both from Marília County, Adamantina Formation, Bauru Group (Brusatte *et al.* 2017). This formation is a stratigraphic unit that dates from the Campanian-Maastrichtian and its paleoenvironment is classified as a warm semiarid system (Zaher *et al.* 2006; Andrade & Bertini 2008; Fernandes & Ribeiro 2015). *Mariliasuchus amarali* was a small-bodied notosuchian (Augusta & Zaher 2019) from this ecosystem. The species is considered terrestrial due to the presence of a short skull, lateral orbits, frontal external nares, and long, robust limbs indicating a quadrupedal posture (Vasconcellos & Carvalho 2005). *Mariliasuchus amarali* is characterized by anatomical features, such as the presence of four premaxillary teeth and fore-aft jaw movements (Pol *et al.* 2014). Additionally, *Notosuchus terrestris* Woodward, 1896 (Santonian, Neuquén group) and *Mariliasuchus* share more advanced traits such as the presence of quadrate and maxillo-palatine fenestrae (Andrade & Bertini 2008).

To date, several paleohistological studies on both extinct and extant taxa have been published that elucidate growth strategies in archosauromorphs (Veiga *et al.* 2019), thermometabolism (Legendre *et al.* 2016) and lifestyle (Ponce *et al.* 2017). In this study, we describe the osteohistology of the Archosauromorpha using the bones of *Mariliasuchus amarali* to compare growth strategies and lifestyle to other archosauromorphs taxa.

GEOLOGICAL SETTING

Mariliasuchus amarali UFRPE 5311 remains were collected in an outcrop of the Adamantina Formation on the right margin of the Água Formosa Creek, 10 km south of the Marília County. It is located 500 m from the secondary road between Marília and Ocauçu counties in the state of São Paulo, Brazil (Fernandes & Coimbra 2000; Brusatte *et al.* 2017). The age of this formation is uncertain, however, has been dated to late Campanian-early Maastrichtian ages (Santucci & Arruda-Campos 2011; Brusatte *et al.* 2017; Batezelli *et al.* 2018). The outcrops cover a broad range of the western part of the São Paulo and Minas Gerais states.

This formation overlaps the basalts of the Serra Geral Group which represents a significant volcanic event consequential of the separation of South America and Africa during the Early Cretaceous (Renne *et al.* 1992). The Adamantina Formation presents at its base reddish mudstone and sandstone layers intercalated on planar-parallel bedding. The desert lithologies decrease upwards through the formation and the lacustrine and fluvial clays and massive sandstones begin to appear in the middle-to-upper portion of the unit deposited in warm and humid conditions, with carbonatic nodules and root marks (Marsola *et al.* 2016; Brusatte *et al.* 2017). The specimen herein was found in a semi-arid paleoenvironment with a fluvial distributary system.

MATERIAL AND METHODS

Material

UFRPE 5311 is composed of the humerus, ulna, and radius from the right forelimb and three ribs (Fig. 1). These elements were assigned to *Mariliasuchus amarali* by association with other complete specimens that were diagnosed as *M. amarali* using cranial and post-cranial morphology. The specimen is housed in the paleontological collection at the Universidade Federal Rural de Pernambuco (UFRPE), Brazil. Osteohistological terminology follows Francillon-Vieillot *et al.* (1990) and Enlow (1969).

Sampling methods

Samples of 0.5 cm in thickness were removed from the diaphysis of each element, in order to prepare the histological slides. Thin sections were prepared at the Laboratório de Paleobiologia e Microestrutura, Centro Acadêmico de Vitória of the Universidade Federal de Pernambuco (CAV/UFPE) and at the Laboratório de Paleontologia e Sistemática of the Universidade Federal Rural de Pernambuco (LAPASI/UFRPE).

The specimens were hand-measured and photographed as per protocols proposed by Lamm (2013). Thin sections were then prepared using standard fossil histology techniques (Chinsamy & Raath 1992; Lamm 2013). Samples were embedded in clear epoxy resin Resapol T-208, catalyzed with Butanox M50, and cut with a diamond-tipped blade mounted on a saw. The mounting-side of the sections was wet-ground using a metallographic polishing machine (Aropol-E, ArotecLtda) with Arotec abrasive sandpapers of increasing grit size (60/P60, 120/P120, 320/P400, 1200/ P2500) until a 60 µm thick section was reached.

Image analysis

Thin sections were observed under normal light and cross-polarized light with lambda compensator using two optical microscopes. Images were obtained from an AxioCam digital sight camera (Zeiss Inc., Barcelona, Spain) mounted to an Axio Imager.M2 (Zeiss Inc. Barcelona, Spain) and an Olympus BX51 (Olympus Corporation, Tokyo, Japan), mounted to an Olympus DP26 (Olympus Corporation, Tokyo, Japan). The images were taken at CAV/UFPE and Laboratório de Geologia (LABGEM/UFPE). Cortical thickness was measured using straight-line tool on ImageJ. The final value was given by the arithmetic mean of the local thicknesses. They were taken from 10 distinct points of each thin section.

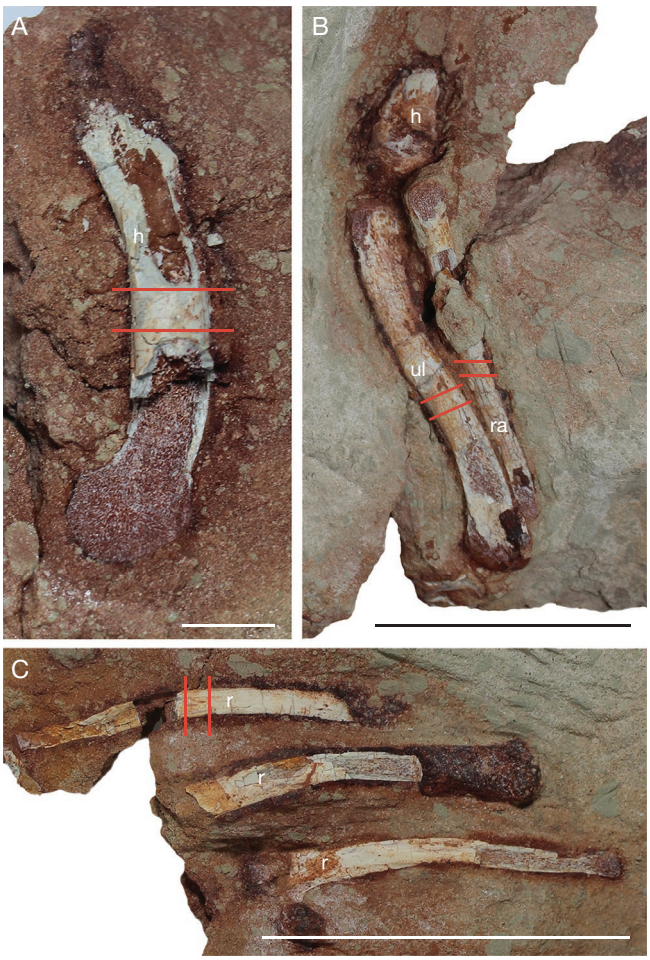

Fig. 1. — Bone elements of *Mariliasuchus amarali* Carvalho & Bertini, 1999 UFRPE 5311: **A**, right humerus, lateral view; **B**, right ulna and radius, lateral view; **C**, ribs. The **red lines** mark the sampling location. Abbreviations: **h**, humerus; **r**, rib; **ra**, radius; **ul**, ulna. Scale bars: A, 1 cm; B, C, 5 cm.

Bone compactness analysis was carried out for all bone elements. The photographs of the cross-sections were transformed into binary images in Adobe Photoshop® CS6 by marking bone in black and vascular spaces (medullary cavity, vascular canals, and resorption cavities) in white. The binary images (supplementary material) were analyzed quantitatively with the software Bone Profiler version 4.5.8 (Girondot & Laurin 2003) to infer on bone compactness profile from cross-sections.

Abbreviations

CCCB	compacted coarse cancellous bone;
CGM	cyclical growth marks;
EFS	external fundamental system;
LAG	line of arrested growth.

Repository and institutional abbreviation

UFRPE	Universidade Federal Rural de Pernambuco, Recife.

TABLE 1. — Bone histology of some Archosauromorpha taxa shows different growth patterns related to their lifestyle and posture.

Archosauromorpha species	Posture and lifestyle	Growth pattern and bone tissues	Studies
Vancleavea campi Long & Murry, 1995 (Triassic)	Quadruped aquatic	Slow growth rate – lamellar-zonal bone	Nesbitt *et al.* 2009; Ponce *et al.* 2017
Trilophosaurus buettneri Case, 1928 (Triassic)	Quadruped terrestrial		Spielmann *et al.* 2008; Werning & Irmis 2010; Grinham *et al.* 2019
Steneosaurus Geoffroy, 1825 (Jurassic)	Quadruped marine		Hua & Buffrénil 1996
Susisuchus anatoceps Salisbury, Frey, Martill & Buchy, 2003 (Cretaceous)	Quadruped semi-aquatic		Sayão *et al.* 2016
Pepesuchus deiseae Campos, Oliveira, Figueiredo, Riff, Azevedo, Carvalho & Kellner, 2011 (Cretaceous)			Riff *et al.* 2012; Sena *et al.* 2018
Iberosuchus macrodon Antunes, 1975 (Eocene)	Quadruped terrestrial		Ortega *et al.* 2000; Cubo *et al.* 2017
Recent crocodylian, *Alligator mississippiensis* Daudin, 1802	Quadruped semi-aquatic		Woodward *et al.* 2014
Aenigmastropheus parringtoni Ezcurra, Scheyer & Butler, 2014 (Permian)	Quadruped terrestrial	Early fast growth rates (fibrolamellar) and later slow growth rates (lamellar-zonal bone)	Ezcurra *et al.* 2014
Terrestrisuchus Crush, 1984 (Triassic)	Quadruped terrestrial		Cruickshank 1972; Allen 2003; Ricqlès *et al.* 2003, 2008; Brown *et al.* 2019; Grinham *et al.* 2019
Proterosuchus Broom, 1903 (Triassic)	Quadruped terrestrial or semi-aquatic		Ricqlès *et al.* 2003, 2008; Botha-Brink & Smith 2011
Stenaulorhynchus stockleyi Haughton, 1932 (Triassic)	Quadruped terrestrial		Mukherjee 2015; Werning & Nesbitt 2016
Pepesuchus deiseae	Quadruped semi-aquatic	Alternate fast and moderate growth rates	Sena *et al.* 2018
Acynodon sp. Buscalioni, Ortega & Vasse, 1997 (Cretaceous)			Company & Pereda-Suberbiola 2017
Extinct and recent Caimaninae			Andrade *et al.* 2018
Alligator mississippiensis			Woodward *et al.* 2011
Sacisaurus agudoensis Ferigolo & Langer, 2007 (Triassic)	Biped terrestrial	Unceasing fast growth composed of uninterrupted fibrolamellar	Ferigolo & Langer 2007; Grinham *et al.* 2019; Veiga *et al.* 2019
Erythrosuchus Broom, 1905 (Triassic)	Quadruped terrestrial		Ricqlès *et al.* 2008; Grinham *et al.* 2019
Lewisuchus admixtus Romer, 1972 (Triassic)	Quadruped terrestrial		Nesbitt *et al.* 2010; Marsà *et al.* 2019
Lesothosaurus Galton, 1978 (Jurassic)	Biped terrestrial		Ricqlès *et al.* 2008; Knoll *et al.* 2010; Grinham *et al.* 2019

RESULTS

RIB

Some remodeling processes in the perimedullary and medullary regions were observed, forming cancellous bone which is highlighted by trabeculae and resorption cavities (Fig. 2A, B). Cross-sections have a high level of bone compactness (0.89) with the cortical thickness of approximately 0.9 mm. The cortex is composed of parallel-fibered bone tissue interrupted by four single lines of arrested growth (LAGs) and one double LAG (Fig. 2B). These growth marks become closely spaced toward the periosteal margin (Fig. 2C, E) and these lines divide the cortex into five distinct growth zones, the third being the largest (Fig. 2E). The periosteal cortex shows simple vascular canals and primary osteons, but scattered secondary osteons are also present (Fig. 2D).

HUMERUS

The medullary cavity was infilled with iron oxides during the fossil diagenetic processes (Fig. 3A), also as this bone is fragmented compactness (0.58) must be underrated. Most of the endosteal region shows primary bone with no trace of remodeling (Fig. 3D). The primary bone (cortical thickness approximately 5 mm) appears to be a combination of lamellar and parallel-fibered bone tissue (Fig. 3B). The parallel-fibered bone tissue is highly vascularized and shows longitudinally oriented primary osteons and primary reticular canals branch up to the external bone surface (Fig. 3E).

In the mid-cortex, at least three LAGs are observed (Fig. 3F). The osteocyte lacunae exhibit either flat or globular shapes that are randomly spread out. Towards the outer margin, some Sharpey's fibers and four LAGs are visible in the outer cortex (Fig. 3C).

ULNA

The ulna contains iron oxides and some cracks derived from taphonomic processes (Fig. 4A). Bone remodeling is visible in the endosteal layer (Fig. 4B, C) and the cortical thickness is approximately 4 mm with a bone compactness of 0.88. This cortex exhibits a poorly organized parallel-fibered arrangement and contains at least five LAGs and the woven bone matrix is visible in some portions (Fig. 4D, E). The vascularization pattern is composed of longitu-

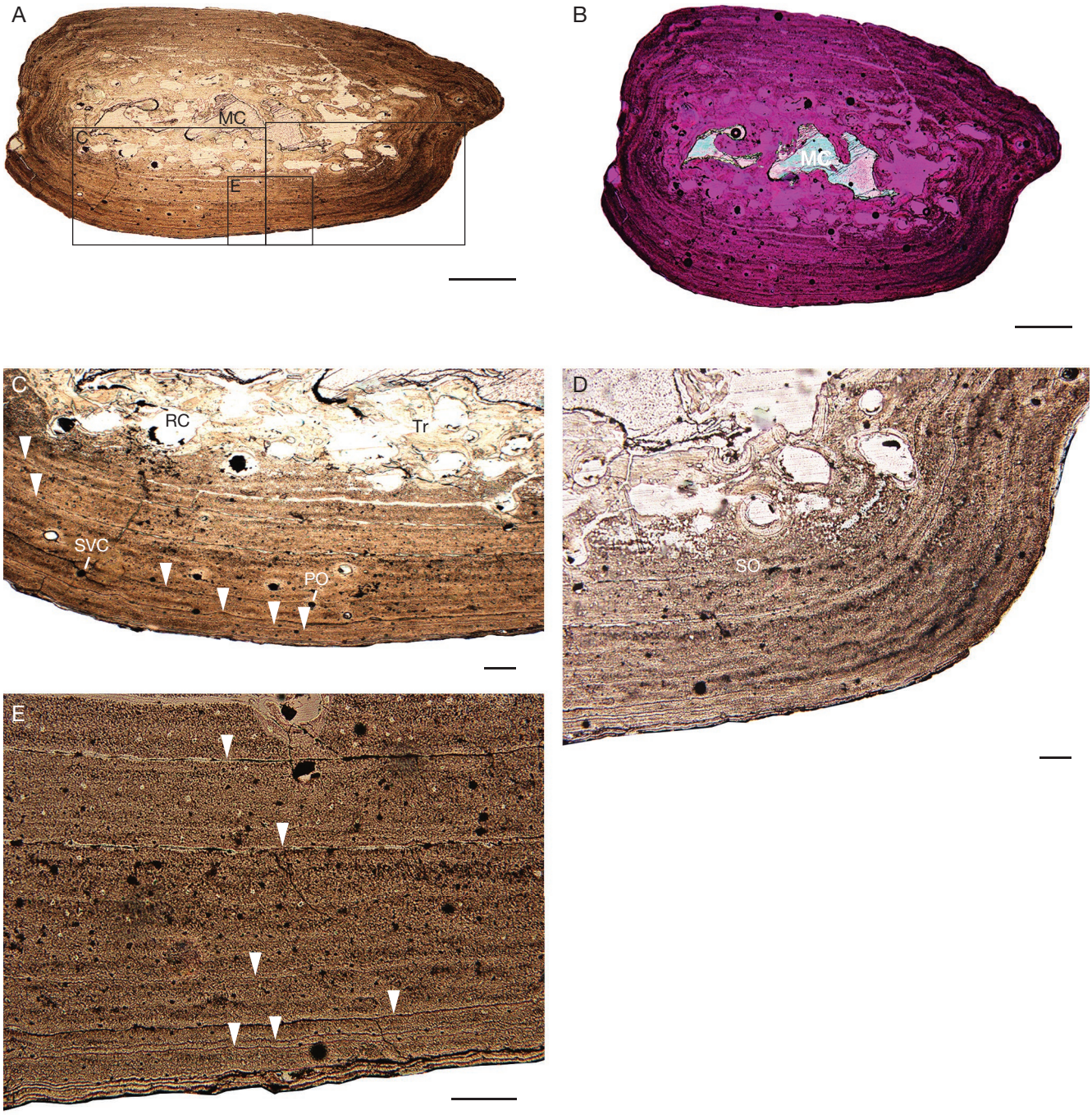

FIG. 2. — Transverse histological sections: **A**, **B**, microanatomical overview of the rib of *Mariliasuchus amarali* Carvalho & Bertini, 1999 UFRPE 5311; **C**, close-up of **A**, showing typical features of the cortex of the rib: parallel-fibered tissue and LAGs; **D**, close-up of **A**, the medullary region is marked by secondary trabeculae, resorption cavities and a secondary osteon; **E**, close-up of **A**, showing five distinct growth zones separated by LAGs in the cortex, the third zone is the largest. Abbreviations: **MC**, medullary cavity; **PO**, primary osteon; **RC**, resorption cavity; **SO**, secondary osteon; **SVC**, simple vascular canal; **Tr**, trabecula. The **white arrows** correspond to LAGs. Images: normal transmitted light (**A**, **C** and **D**) and cross polarized light with lambda compensator (**B**). Scale bars: A, B, 1 mm; C, 100 µm; D, E, 200 µm.

dinally-oriented vascular canals (Fig. 4D) which become radially-oriented toward the external bone surface (Fig. 4E). In the lamellar matrix osteocyte lacunae have a flat aspect distributed in concentric rows.

RADIUS

Remarkably this radius, found in articulation with the previously described humerus and ulna, exhibited a sharply different pattern in bone microstructure. Medullary cavity in the radius is infilled with spongy bone (Fig. 5A) and the cancellous bone is composed of resorption cavities surrounded by thin lamellar bone tissue (Fig. 5B). In the endosteal region, compacted coarse cancellous bone (CCCB) is constituted of sinuous convolutions of lamellae (Fig. 5C). A scalloped and conspicuous resorption line marks the boundary between the compacted coarse

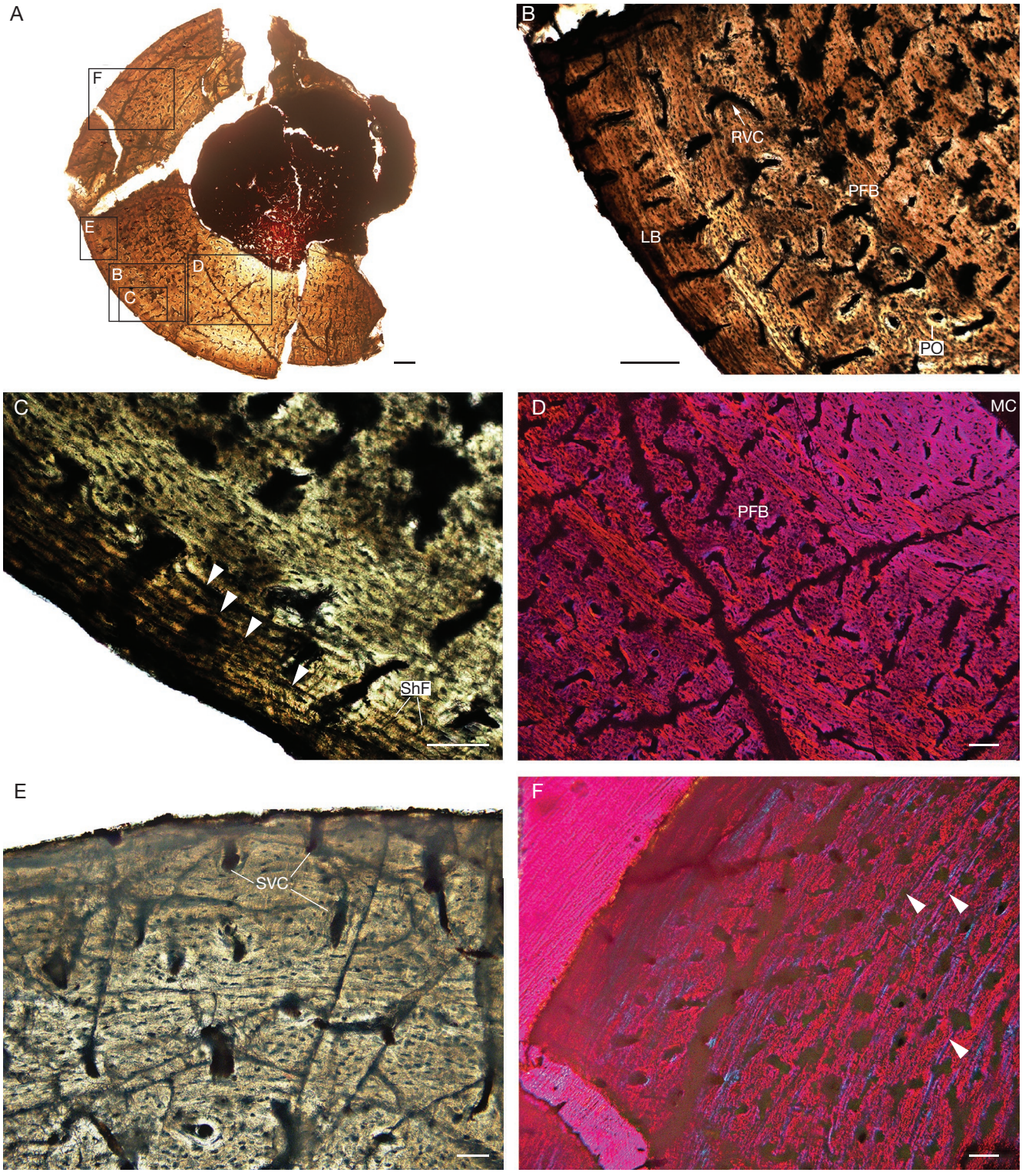

FIG. 3. — **A**-**D**, Transverse histological sections: **A**, microanatomical overview of the humerus of *Mariliasuchus amarali* Carvalho & Bertini, 1999 UFRPE 5311; **B**, close-up of **A**, showing the limit between parallel-fibered bone and lamellar bone; **C**, close-up of **A**, showing Sharpey's fibers on the periosteal surface; **D**, close-up of **A**, showing parallel-fibered bone filling endosteal region near medullary cavity; **E**, close-up of **A**, showing simple vascular canals in the outer cortex; **F**, close-up of **A**, showing LAGs in the mid-cortex. Abbreviations: **LB**, lamellar bone; **MC**, medullary cavity; **PFB**, parallel-fibered bone; **PO**, primary osteon; **RVC**, reticular vascular canal; **ShF**, Sharpey's fibers; **SVC**, simple vascular canal. The **white arrows** correspond to LAGs. Images: normal transmitted light (**A**-**C**) and cross polarized light with lambda compensator (**D** and **F**). Scale bars: A, 1 mm; B, D, F, 200 µm; C, 100 µm; E, 5 µm.

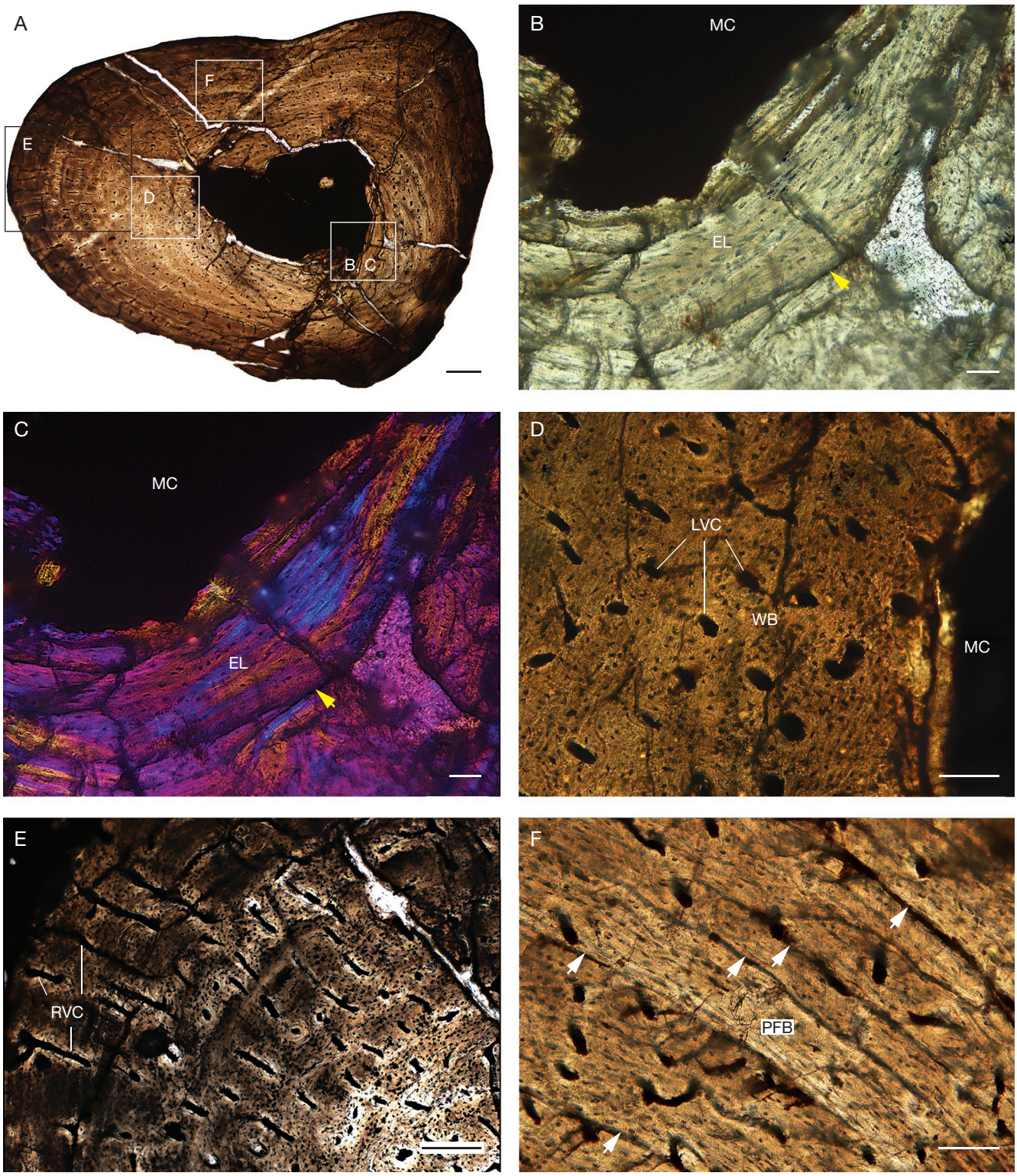

FIG. 4. — **A**, **B**, Transverse histological sections: **A**, microanatomical overview of the ulna of *Mariliasuchus amarali* Carvalho & Bertini, 1999 UFRPE 5311; **B**, **C**, close-up of **A**, showing lamellar bone surrounding the medullary cavity; **D**, close-up of **A**, showing most of the endosteal cortex formed by woven bone; **E**, close-up of **A**, showing radial vascular canals toward the bone periphery; **F**, close-up of **A**, showing lines of growth arrested interrupting the bone deposition. Abbreviations: **EL**, endosteal lamellae; **LVC**, longitudinal vascular canal; **MC**, medullary cavity; **PFB**, parallel-fibered bone; **RVC**, radial vascular canal; **yellow arrows**, resorption line; **WB**, woven bone. The **white arrows** correspond to LAGs. Images: normal transmitted light (**A**, **B**, **D** and **E**) and cross polarized light with lambda compensator (**C** and **F**). Scale bars: A, 1 mm; B, 5 µm; C-F, 200 µm.

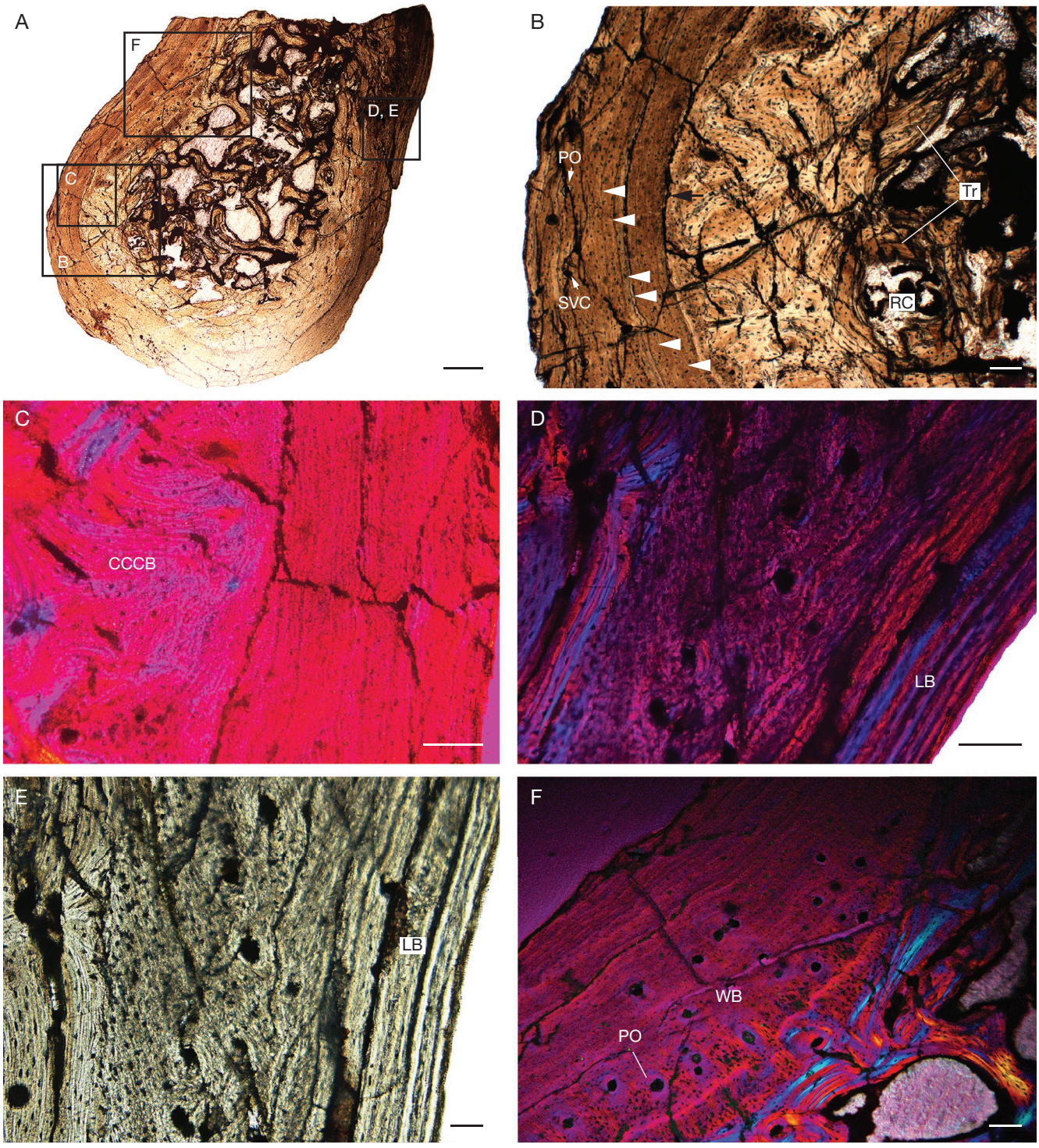

FIG. 5. — **A**-**D**, Transverse histological sections: **A**, microanatomical overview of the radius of *Mariliasuchus amarali* Carvalho & Bertini, 1999 UFRPE 5311; **B**-**F**, close-up of **A**, showing typical features of the cortex of the radius: lamellar-bone and LAGs. Midcortical woven bone vascularized by primary osteons. The endosteal region is formed by compacted coarse cancellous bone and the medullary region presents spongy tissue with several trabeculae and resorption cavities. Abbreviations: **CCCB**, compacted coarse cancellous bone; **LB**, lamellar bone; **PO**, primary osteon; **RC**, resorption cavity; **SVC**, simple vascular canal; **Tr**, trabecula; **WB**, woven bone. The **black arrow** corresponds to resorption line; the **white arrows** correspond to LAGs. Images: normal transmitted light (**A**, **B** and **E**) and cross polarized light with lambda compensator (**C**, **D** and **F**). Scale bars: A, 1 mm; B, 100 µm; C-F, 200 µm.

cancellous bone and the periosteal cortex (cortical thickness approximately 1 mm; bone compactness is 0.87) (Fig. 5B). The primary lamellar bone tissue is poorly vascularized and growth marks are featured by five LAGs and one double LAG (Fig. 5B, E). Parts of mid-cortex are comprised of woven bone tissue (Fig. 5F). This bone contains flattened and scarce osteocyte lacunae that follow the orientation of collagen fibers.

DISCUSSION

Comparing growth patterns and lifestyle in *Mariliasuchus amarali* to other archosauromorphs

Since the Late Permian, different lineages of Archosauromorpha exhibit very diverse growth patterns, and in archosauromorphs, bone growth appears to be related to posture (Werning & Irmis 2010; Ponce *et al.* 2017), lifestyle (Woodward *et al.* 2011; Company & Pereda-Suberbiola 2017; Andrade *et al.* 2018) or even to both (Ricqlès *et al.* 2003, 2008; Botha-Brink & Smith 2011; Ezcurra *et al.* 2014; Mukherjee 2015; Werning & Nesbitt 2016). In early ontogenetic stages, they appear to have higher growth rates, which seems to decrease over time, a pattern that is commonly observed in Permo-Triassic terrestrial archosauromorphs (Allen 2003; Ricqlès *et al.* 2003, 2008; Botha-Brink & Smith 2011; Ezcurra *et al.* 2014; Mukherjee 2015; Werning & Nesbitt 2016). On the other hand, terrestrial archosauriforms from the Triassic-Jurassic show continuous bone apposition, as evidenced by cortices composed of uninterrupted fibrolamellar tissue (Ferigolo & Langer 2007; Ricqlès *et al.* 2008; Knoll *et al.* 2010; Grinham *et al.* 2019; Marsà *et al.* 2019; Veiga *et al.* 2019). Slower growth rates as indicated by cortices composed of lamellar-zonal bone tissue are present in Archosauromorpha at least since the Permian. For example, this is a common growth strategy adopted by extinct and extant crocodyliforms with different lifestyles. Nevertheless, semi-aquatic crocodyliforms are capable of rapid growth for some periods (Table 1).

The bony elements of *Mariliasuchus amarali* showed differences in the types of the tissue deposited throughout life, a fact considered to be directly related to endogenous responses to biomechanical forces and lifestyle. In the humerus and ulna, growth was still active shortly before death, as indicated by vascular canals being open to the surface. However, the rib presents a slow growth that is evidenced by the poorly vascularized parallel-fibered bone. The bony tissues of the humerus and ulna of *M. amarali* have similarities to Triassic quadruped archosauriforms such as the proterochampsian *Chanaresuchus* Romer, 1971 (Ricqlès *et al.* 2008; Trotteyn *et al.* 2013; Ponce *et al.* 2017; Arcucci *et al.* 2019; Grinham *et al.* 2019) and the terrestrial pseudosuchian *Batrachotomus kupferzellensis* Gower, 1999 (Sues & Schoch 2013; Klein *et al.* 2017; Grinham *et al.* 2019). These species had fast to moderate appositional growth rates with temporary cessation of the bone growth during annual cycles (Ricqlès *et al.* 2008; Klein *et al.* 2017).

Growth marks in *Mariliasuchus amarali*

Both LAGs and annuli are cyclical growth marks (CGMs) driven by *circannual* changes in the environment (Castanet *et al.* 1993). However, the LAGs were the only CGMs present in *M. amarali* and varied in number among the bone elements. Such variability may be explained by the medullary expansion (Woodward *et al.* 2014) or different rhythms of osteogenesis (Cullen *et al.* 2014). The highest number of LAGs were observed in the UFRPE 5311 humerus, suggesting an age of seven years for this individual at time of death. The absence of an external fundamental system (EFS) indicates that growth had not completely ceased in the sampled bone elements, suggesting that skeletal maturity had not been attained by UFRPE 5311. Notwithstanding, the endosteal lamellae surrounding the medullary cavity in the ulna indicate cessation of medullary expansion (Chinsamy *et al.* 2008). These traits indicate a sub-adult ontogenetic state for this specimen.

Bone remodeling

The large amount of the CCCB in the perimedullary region suggests that the radius is the least resistant within the limb bones, this occurs because primary cortical bone is more resistant than the secondary bones (Ray & Chinsamy 2004). The compacted coarse cancellous bone formation occurred during the remodeling process when cancellous bone in the medullary region of the metaphysis was converted into compacted coarse cancellous bone as the metaphysis was relocated and became the diaphysis at an advanced ontogenetic stage (Enlow 1962a, b; Prondvai *et al.* 2012). The presence of this bone in the cortex has been reported in *Iberosuchus macrodon* Antunes, 1975 (2 m in total length; see Ortega *et al.* 2000) IPS 4932 in Cubo *et al.* (2017), and considered by the authors as a compacted spongiosa related to muscle insertion or as a radial fibrolamellar bone.

However, *Mariliasuchus amarali* (*c.* 1.4 m body length) shares with the neosuchian *Susisuchus anatoceps* Salisbury, Molnar, Frey & Willis, 2006 (*c.* 1.10 m body length) the remodeled trabecular bone in the ribs. In the case of the neosuchian *Guarinisuchus munizi* Barbosa, Kellner & Viana, 2008 (*c.* 2.79-3.43 m), the remodeling process in the rib forms Haversian systems (Hastings *et al.* 2010; Andrade *et al.* 2015; Sayão *et al.* 2016). The latter must repair microdamages caused by an intense biomechanical strain on the rib (Martin & Burr 1982; Lee *et al.* 2002). The osteohistology of rib described here suggest that the axial skeleton of *M. amarali* was affected by a low strain level, comparable with that seen in *Susisuchus anatoceps*.

CONCLUSIONS

Mariliasuchus amarali resembles *Chanaresuchus* (Arcucci *et al.* 2019) and *Batrachotomus kupferzellensis* (Klein *et al.* 2017) in growth patterns, with the presence of woven and parallel-fibered bone tissues periodically interrupted by growth marks throughout the cortex. This suggests that these Triassic quadruped archosauriforms shared similar growth rates. Bone microstructure of *Mariliasuchus amarali* (UFRPE 5311) indicates active growth.

The assessment of intraskeletal variability reveals variable appositional growth within the skeletal elements of *Mariliasuchus amarali*. The compacted coarse cancellous bone in the midshaft region of the radius highlights the hypothesis that this bone had the lowest resistance among limb bones. In the ribs of *Mariliasuchus amarali* and *Susisuchus anatoceps* (Sayão *et al.* 2016), the remodeling process forms trabecular bones, whereas in *Guarinisuchus munizi* (Andrade *et al.* 2015) it occurs through Haversian reconstruction.

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APPENDIX

APPENDIX 1. — Schematic **black** (bone) and **white** (vascular spaces and medullary cavities) drawings of the extinct *Mariliasuchus amarali* Carvalho & Bertini, 1999 (UFRPE 5311) prepared for use with bone profiler: **A**, rib; **B**, humerus; **C**, radius; **D**, ulna.