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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
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 & Laredi 2015; Laredi 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 Mesoeucrocodilia (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 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-af 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), thermomtabolism (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 Ocaçu 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 Gemo-

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 | | |
| Steneosaurus Geoffroy, 1825 (Jurassic) | Quadruped marine | | |
| Susisuchus anatoceps Salisbury, Frey, Martill & Buchy, 2003 (Cretaceous) | Quadruped semi-aquatic | | |
| Pepesuchus diegae Campos, Oliveira, Figueiredo, Riff, Azevedo, Carvalho & Kellner, 2011 (Cretaceous) | Quadruped terrestrial | | |
| Iberosuchus macrodon Antunes, 1975 (Eocene) | Quadruped semi-aquatic | | |
| Recent crocodylian, Alligator mississippiensis Daudin, 1802 | Quadruped semi-aquatic | | |
| Aenigmastropheus parringtoni Ezcurra, Scheyer & Butler, 2014 (Permian) | Quadruped terrestrial | | |
| Terrestrisuchus Crush, 1984 (Triassic) | Quadruped terrestrial | | |
| Proterosuchus Broom, 1903 (Triassic) | Quadruped terrestrial | | |
| Stenauorhynchus stockleyi/ Haughton, 1932 (Triassic) | Quadruped semi-aquatic | | |
| Pepesuchus diegae | Quadruped semi-aquatic | Alternate fast and moderate growth rates | Sena et al. 2018 Company & Pereira-Suberbiola 2017 |
| Acrodon sp. Buscalioni, Ortega & Vasse, 1997 (Cretaceous) | Quadruped semi-aquatic | | |
| Extinct and recent Caimaninae | | | |
| Alligator mississippiensis | | | |
| 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 | | |
| Lewisuchus admixtus Romer, 1972 (Triassic) | Quadruped terrestrial | | |
| Lesothosaurus Galton, 1978 (Jurassic) | Biped terrestrial | | |

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 longitudi-
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

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**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.
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 endostal 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.
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**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, 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 ARCHOASAUROMORPHS

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 & Irims 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 Archosauromorphs 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 protorochampsian *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 *Battachotosuchus 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 annual changes in the environment (Castanet et al. 1995). 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 *Guanisuchus munizii* 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 *Battachotosuchus 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 *Guanisuchus munizii* (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.