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Osteohistology of hyperodapedontine rhynchosaurs from the Upper Triassic of Southern Brazil

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The first osteohistological study focused exclusively on rhynchosaurs (non-archosauriform archosauromorphs), based on the hyperodapedontines *Teyumbaita sulcognathus* and *Hyperodapedon* sp., from the Upper Triassic of Southern Brazil, indicates a relatively rapid growth rate in early ontogeny shown by the fibrolamellar complex, with a change to slow intermittent growth during late ontogeny represented by parallel-fibred bone with several growth marks. Contrary to previous studies, which described a typical non-archosaur reptilian bone tissue pattern for rhynchosaurs, with growth marks extending across the entire cortex, we demonstrate that, in both studied taxa, the initial growth rate was faster in comparison to the later. This suggests that the ability of rapid growth at high rates was already present in basal non-archosauriform archosauromorphs.

Key words: Diapsida, Archosauromorpha, Rhynchosauria, Hyperodapedontinae, bone histology, growth pattern, Triassic, Brazil.

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Introduction

Bone microstructure gives important information about the paleobiology of extinct animals, such as age of the individuals, sexual maturity, and bone growth rates and patterns. From these data it is also possible to deduce many aspects of physiology, ontogeny and phylogeny of fossil vertebrates (Erickson and Tumanova 2000; Horner et al. 2000; Chinsamy 2005). As such, research describing bone histology and growth patterns of fossil vertebrates has become recurrent in the literature in the last years, mainly focusing on the Archosauria clade, which includes crocodiles, birds and their extinct relatives (e.g., pterosaurs, dinosaurs) (Ricqlès 1983; Chinsamy 1993a, b, 1995; Horner et al. 2000, 2001; Padian et al. 2001; Ricqlès et al. 2003). However, there are still gaps in the knowledge concerning bone histology, including the growth patterns of basal members of archosauromorphs/archosauriforms. Recently, Ricqlès et al. (2008) and Botha-Brink and Smith (2011) described the bone histology of some archosauromorphs, archosauriforms and basal archosaurs using a comparative approach. These studies have shown that

the capacity to achieve high growth rates may be plesiomorphic for archosaurs, i.e., a condition already present in basal archosauriforms. Non-archosauriform archosauromorphs, on the other hand, are accepted as displaying a non-archosaur reptilian pattern of slow and intermittent growth. Yet, according to Ricqlès et al. (2008), these results must be interpreted as preliminary, given the small analyzed sample and the lack of ontogenetic control.

Rhynchosauria were herbivorous non-archosauriform archosauromorphs, recorded in Triassic continental beds (Chatterjee 1980; Langer and Schultz 2002; Lucas et al. 2002). They include Early Triassic basal forms such as *Mesosuchus browni* Watson, 1912 and *Howesia browni* Broom, 1906; “intermediate” Middle Triassic taxa, represented by the paraphyletic “Rhynchosauridae”; and the more derived Late Triassic rhynchosaurs, the Hyperodapedontinae clade, which includes *Isalorhynchus genovefae* Buffetaut, 1983, *Teyumbaita sulcognathus* Montefeltro, Langer and Schultz, 2010 and *Hyperodapedon* spp. Huxley, 1859 (Langer et al. 2000; Langer and Schultz 2000; Schultz 2009; Montefeltro et al. 2010). During the Late Triassic, rhynchosaurs, especially the genus *Hyperodapedon*, became the main components

of many terrestrial faunas, with a cosmopolitan distribution (Langer et al. 2000; Langer and Schultz 2000; Schultz 2009; Lucas et al. 2002; Langer 2005).

Despite the abundance of rhynchosaurs in Triassic rocks, little is known about their bone histology and growth patterns. The only available descriptions (e.g., Enlow and Brown 1957; Ricqlès 1976; Ricqlès et al. 2008) were based solely on ribs and unidentified bones from the Ischigualasto Formation, Upper Triassic of Argentina, all related to *Hyperodapedon* (sensu Langer and Schultz 2000).

Here, we provide detailed descriptions of the bone histology of *Teyumbaita sulcognathus* and *Hyperodapedon* sp. from the Upper Triassic of Brazil, based on several elements (i.e., femur, tibiae, humerus, radii, and ribs; Table 1). In addition, we discuss the growth patterns of non-archosauria archosauromorphs, and the possibility of rapid growth rates in these animals.

Table 1. Specimens thin sectioned in this study.

Species	Specimen number	Skeletal element	Portion sectioned	Diameter (mm)
<i>Teyumbaita sulcognathus</i>	UFRGS-PV-0298-T	radius	proximal	24.20
	UFRGS-PV-0298-T	rib		15.25
	UFRGS-PV-0298-T	humerus	proximal	41.40
	UFRGS-PV-0232-T	tibia	midshaft	20.60
	UFRGS-PV-0290-T	tibia	midshaft	37.70
<i>Hyperodapedon</i> sp.	UFRGS-PV-0247-T	rib		14.35
	UFRGS-PV-0247-T	tibia	proximal	63.60
	UFRGS-PV-0247-T	humerus	midshaft	40.75
	UFRGS-PV-1217-T	radius	midshaft	16.90
	UFRGS-PV-0271-T	femur	proximal fragments	44.45
	UFRGS-PV-0293-T	tibia	midshaft	29.40
	UFRGS-PV-0408-T	humerus	midshaft	48.80
	MMACR-PV-018	humerus	proximal	85.80

Institutional abbreviations.—MMACR, Museu Municipal Aristides Carlos Rodrigues, Candelária, Rio Grande do Sul, Brazil; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil.

Other abbreviations.—LAG, line of arrested growth; EFS, external fundamental system.

Material and methods

All studied materials come from the *Hyperodapedon* Assemblage Zone (AZ), Santa Maria Supersequence, Santa Maria 2 Sequence (Upper Triassic) of Rio Grande do Sul, Brazil (Zerfass et al. 2003; Soares et al. 2011). Long bones were preferentially selected because they contain the least secondary remodeling in the midshaft region, and better record the entire growth of the animals (Francillon-Vieillot et al. 1990; Horner et al. 1999).

Thin-sections were performed at the Laboratório de Preparação de Amostras, Instituto de Geociências of Universidade Federal do Rio Grande do Sul, Brazil, following the procedures of Chinsamy and Raath (1992). All elements were measured with a calliper rule and photographed with a Canon Power Shot SX 110 IS digital camera prior to thin-sectioning. The materials were embedded in an epoxy resin (Aradur® HY 951 and Araldite© GY279), sectioned in the required direction, ground down and polished. The resulting petrographic slides were examined under ordinary and polarized light optical microscopes (LEICA DMLP). Terminology follows Francillon-Vieillot et al. (1990) and Reid (1996). The term “growth mark” is used for annuli and lines of arrested growth (LAGs). Annuli represent a temporary decrease in growth, whereas LAGs indicate a temporary complete cessation of growth (Francillon-Vieillot et al. 1990; Chinsamy-Turan 2012).

Systematic paleontology

Subclass Diapsida Osborn, 1903

Infraclass Archosauromorpha Huene, 1946

Order Rhynchosauria (Gervais, 1859) Osborn, 1903

Family Hyperodapedontidae Lydekker, 1885

Genus *Teyumbaita* Montefeltro, Langer, and Schultz, 2010

Type species: *Scaphonyx sulcognathus* Azevedo and Schultz, 1987; Candelária, Brazil, Upper Triassic.

Teyumbaita sulcognathus Montefeltro, Langer, and Schultz, 2010

Fig. 1A–C.

Holotype: UFRGS-PV-0232-T, complete skull, complete mandibles, atlas, axis, and following four cervical vertebrae, four disarticulated trunk vertebrae, sixteen disarticulated caudal vertebrae, partial gastralia, complete left scapulocoracoid, partial right scapulocoracoid, left humerus, right femur, right tibia, and two isolated phalanges.

Type locality: Candelária, Rio Grande do Sul, Brazil.

Type horizon: *Hyperodapedon* Assemblage Zone (AZ), Santa Maria Supersequence, Santa Maria 2 Sequence, Upper Triassic.

Material.—UFRGS-PV-0298-T, radius; UFRGS-PV-0298-T, rib; UFRGS-PV-0298-T, humerus; UFRGS-PV-0232-T; UFRGS-PV-0290-T, tibia; from the type locality.

Description.—*Radius (UFRGS-PV-0298-T):* The radius shaft (Fig. 1A,) has a large medullary cavity surrounded by a narrow cortex. Secondary remodeling in the perimedullary region is extensive, as recorded by large resorption cavities. In the innermost cortex, the vascular canals are arranged mostly as longitudinally oriented primary osteons with a decrease in density toward the periphery. The cortex is formed by parallel-fibred complex. Highly organized flattened osteocyte lacunae, parallel to one another, occur mainly in the mid- and the outer cortex. Growth marks are absent.

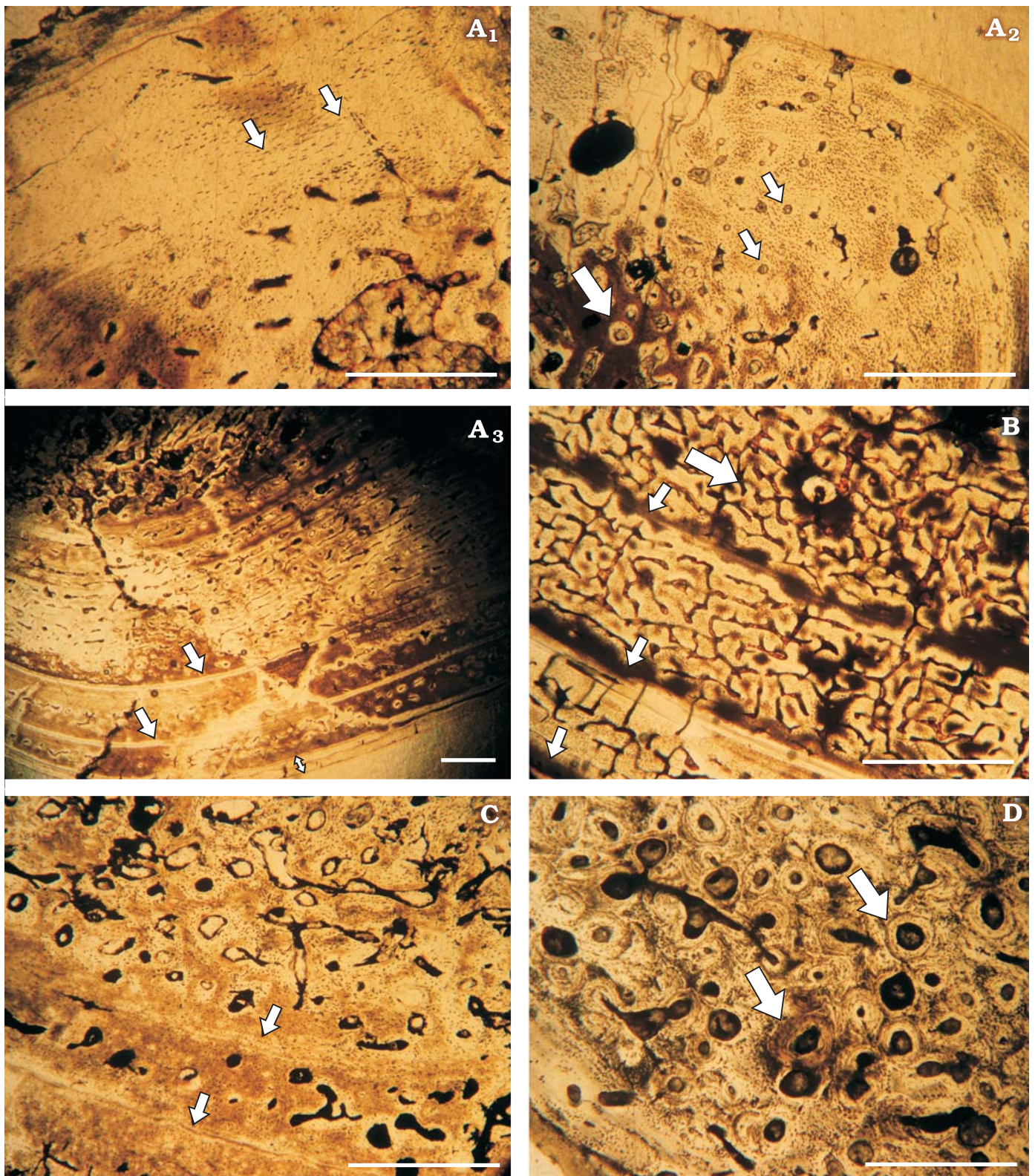


Fig. 1. Transverse section of hyperodapedontine rhynchosaurs *Teyumbaita sulcognathus* Montefeltro, Langer and Schultz, 2010 (A–C) and *Hyperodapedon* sp. (D) from Santa Maria Supersequence, Santa Maria 2 Sequence, Rio Grande do Sul, Brazil, Upper Triassic. A. UFRGS-PV-0298-T, radius, cortex showing a more organized parallel-fibred region (arrows) (A₁); rib, cortex showing primary (arrows) and secondary (big arrow) osteons (A₂); humerus, lamellar-zonal bone with growth marks (arrows) and the EFS (double-headed arrow) on the external surface of the cortex (A₃). B. UFRGS-PV-0232-T, tibia, fibrolamellar bone tissue in the perimedullary region (big arrow) and three growth marks (arrows) near the periosteal surface. C. UFRGS-PV-0290-T, tibia showing the growth marks present in the parallel-fibred region (arrows). D. UFRGS-PV-0247-T, rib showing the secondary osteons (big arrows) in the perimedullary region. Scale bars 1 mm.

Rib (UFRGS-PV-0298-T): The rib (Fig. 1A₂) microstructure is similar to that of the radius. Longitudinal primary osteons are extensive and concentrated in the perimedullary region (secondary osteons are also present). The osteocyte lacunae are more globular in shape and mostly arranged haphazardly in the innermost cortex, around the primary osteons. Toward the periphery, the primary osteons are sparser and the osteocyte lacunae tend to be more organized, forming a parallel-fibred bone tissue. Canaliculi are extensive and radiate out in all directions from the osteocyte lacunae. A very thin avascular layer at the periosteal surface suggests the presence of an EFS, with one internal LAG. The presence of an EFS (see Cormack 1987) at the outer surface of the cortex indicates that the growth of UFRGSPV-0298-T slowed in comparison to that of earlier stages and that the specimen had reached somatic maturity.

Humerus (UFRGS-PV-0298-T): The humerus (Fig. 1A₃) was sectioned near its proximal end. The secondary remodeling in the perimedullary region is extensive with enlarged resorption cavities. The cortex is highly vascularized and varies from a mixture of longitudinal and circular-oriented primary osteons (in its innermost portion) to longitudinal primary osteons organized in circular rows (in the outer cortex). The primary bone tissue comprises lamellar-zonal bone with organized osteocyte lacunae arranged parallel to one another. Canaliculi are not preserved. Two to three annuli occur in the cortex, and are more concentrated in the outer cortex. An EFS is also present at the periosteal surface of the cortex, confirming somatic maturity.

Tibia (UFRGS-PV-0232-T): Transverse sections of the tibia (Fig. 1B) reveal secondary remodeling in the perimedullary region, with the formation of large resorption cavities and the presence of primary and secondary osteons. In the innermost cortex, the vascular canals are organized in a plexiform pattern, with osteocyte lacunae distributed haphazardly around the primary osteons, indicating the presence of fibrolamellar bone tissue. The same vascularization pattern remains toward the periphery; but the primary bone tissue changes to a parallel-fibred pattern, where the osteocyte lacunae are highly organized and lie parallel to one another. Three growth marks are present near the periosteal surface.

UFRGS-PV-0290-T: The secondary remodeling (Fig. 1C) is extensive with enlarged resorption cavities in the perimedullary region, extending across the cortex. The cortex is highly vascularized in the innermost region and tends to become more avascular in the periosteal area, formed by primary and secondary osteons organized in a sub-plexiform pattern. Osteocyte lacunae are abundant, globular and arranged haphazardly around the vascular canals in the innermost cortex, becoming more organized toward the outer cortex. This organization indicates fibrolamellar bone tissue in the perimedullary region, which becomes parallel-fibred tissue periosteally. Three growth marks are present in the cortex, but are more concentrated in the outer cortex.

Stratigraphic and geographic range.—*Hyperodapedon* Assemblage Zone (AZ), Santa Maria Supersequence, Santa Maria 2 Sequence (Upper Triassic) of Rio Grande do Sul, Brazil.

Order Rhynchosauria (Gervais, 1859) Osborn, 1903

Family Hyperodapedontidae Lydekker, 1885

Genus *Hyperodapedon* Huxley, 1859

Type species: Hyperodapedon gordonii Huxley, 1859; Scotland, Upper Triassic.

Hyperodapedon sp.

Figs. 1D, 2.

Material.—UFRGS-PV-0247-T, rib; UFRGS-PV-0247-T, UFRGS-PV-0293-T, tibia; UFRGS-PV-0247-T, humerus; UFRGS-PV-1217-T, radius; UFRGS-PV-0271-T, femur;—from Santa Maria Supersequence, Santa Maria 2 Sequence, Rio Grande do Sul, Brazil, Upper Triassic.

Description.—*Rib (UFRGS-PV-0247-T)*: The rib (Fig. 1D) has a small medullary cavity surrounded by a relatively thick cortex. The secondary remodeling in the perimedullary region is extensive, with large resorption cavities. Vascular canals are numerous and arranged as longitudinally-oriented secondary osteons, mainly in the innermost cortex. The primary bone tissue consists of a parallel-fibred bone matrix with highly organized globular osteocyte lacunae. Canaliculi are extensive and radiate out in all directions from the osteocyte lacunae. Toward the periphery, the vascular canals decrease in abundance and tend to be arranged in circular rows. Two growth marks are seen in the outer cortex.

Tibia (UFRGS-PV-0247-T): The tibia (Fig. 2A₁) has a large medullary cavity surrounded by a narrow cortex with some secondary remodeling in the perimedullary region. The cortex is highly vascularized by longitudinal primary and secondary osteons, without decreasing in size and abundance toward the periosteal surface. In some areas, the vascular canals are arranged as circular rows with anastomoses. The osteocyte lacunae in the innermost cortex are globular and arranged randomly around the vascular canals, indicating a fibrolamellar complex. The tissue changes toward the periosteal surface into parallel-fibred bone and the osteocyte lacunae become more organized, indicating a slight decrease in growth rate. One annulus interrupts the cortex near the periosteal surface.

UFRGS-PV-0293-T: The tibia (Fig. 2C) has a relatively narrow cortex surrounding a large medullary cavity. Secondary remodeling is extensive in the perimedullary region and extends to the mid-cortex. The cortex is moderately vascularized and contains mostly longitudinally-oriented primary osteons, with a decrease in vascularization toward the periphery. The osteocyte lacunae are abundant and globular, and arranged haphazardly around the primary osteons, indicating a fibrolamellar complex. However, toward the periphery, the osteocyte lacunae become more organized, in a parallel arrangement. Canaliculi are extensive and radiate out in all directions from the osteocyte lacunae. Two growth marks are present, one in the mid- and another in the outer cortex.

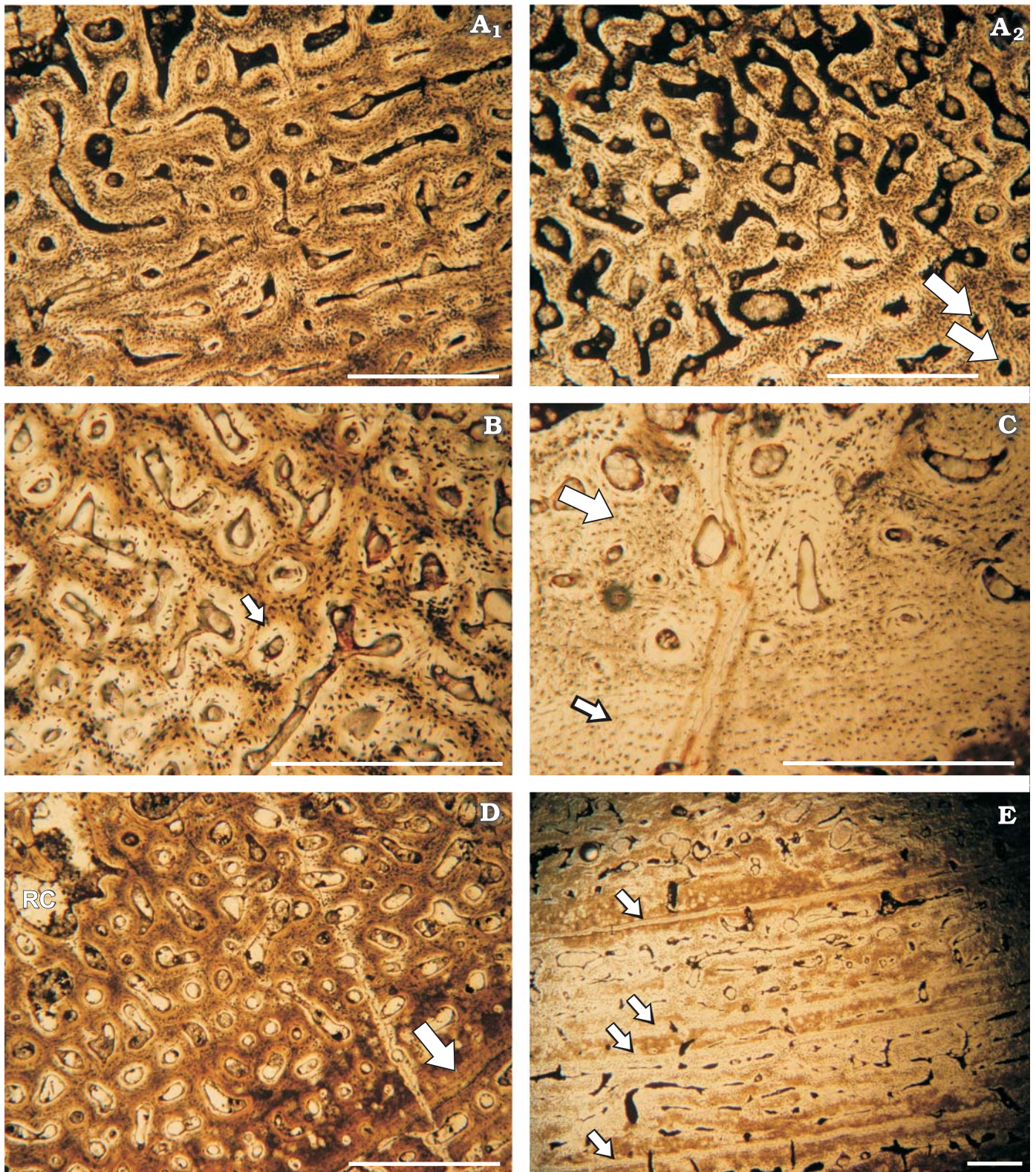


Fig. 2. Transverse section of hyperodapedontine rhynchosaurs *Hyperodapedon* sp. from Santa Maria Supersequence, Santa Maria 2 Sequence, Rio Grande do Sul, Brazil, Upper Triassic. **A.** UFRGS-PV-0247-T, tibia showing the fibrolamellar bone tissue in the perimedullary region (A_1); humerus showing the fibrolamellar bone tissue with primary osteons (big arrows) (A_2). **B.** UFRGS-PV-1217-T, radius showing uninterrupted fibrolamellar bone tissue with longitudinal oriented vascular canals (arrow). **C.** UFRGS-PV-0293-T, tibia showing a poorly defined fibrolamellar bone tissue in the perimedullary region (big arrow) and a parallel-fibred bone tissue (arrow) towards the periphery. **D.** MMACR-PV-018, humerus with resorption cavities (RC) in the perimedullary region and a growth mark (big arrow) in the mid-cortex. **E.** UFRGS-PV-408-T, humerus showing the lamellar-zonal bone tissue with growth marks (arrows). Scale bars 1 mm.

Humerus (UFRGS-PV-0247-T): The humerus (Fig. 2A₂) shows extensive secondary remodeling, with large resorption cavities in the perimedullary region. This region contains globular osteocyte lacunae haphazardly distributed around the vascular canals, mostly primary osteons organized in a plexiform arrangement, indicating a fibrolamellar complex. Toward the periphery the osteocyte lacunae tend to be more organized and the primary bone tissue changes to parallel-fibred bone with the vascular canals arranged as longitudinal primary osteons. Canaliculi are extensive and radiate out in all directions from the osteocyte lacunae. One annulus is present in the mid-cortex.

MMACR-PV-018: The humerus (Fig. 2D) has a narrow cortex and a large medullary cavity. Secondary remodeling is extensive and large resorption cavities occur in the perimedullary region, extending periosteally. The narrow cortex is not well preserved, having suffered some diagenetic alteration. The cortex is highly vascularized and mostly contains primary osteons oriented longitudinally and arranged in circular rows. Osteocyte lacunae are abundant and globular, arranged haphazardly around the primary osteons, indicating a fibrolamellar complex in the perimedullary region. Toward the periphery, the osteocyte lacunae become more flattened and organized and are arranged parallel to one another, suggesting a change from fibrolamellar to parallel-fibred bone. One growth mark is present in the mid-cortex.

UFRGS-PV-0408-T: The humerus (Fig. 2E) has a relatively narrow cortex that surrounds a large medullary cavity. In the perimedullary region resorption cavities are extensive and extend to the outer cortex. The cortex is slightly vascularized with longitudinally-oriented primary and secondary osteons. The osteocyte lacunae are mostly flattened and organized parallel to one another. These features indicate the presence of parallel-fibred bone. Four to five closely spaced growth marks are observed near to the outer cortex, which indicates a decrease in growth rate. The presence of EFS at the periosteal surface of the cortex indicates that UFRGS-PV-0408-T, had reached somatic maturity.

Radius (UFRGS-PV-1217-T): Secondary remodeling is not extensive in the radius (Fig. 2B). The primary bone tissue consists of fibrolamellar bone comprising a woven-fibred matrix with abundant longitudinal and radial primary osteons. The osteocyte lacunae are abundant and globular, distributed haphazardly around the primary osteons. There is no decrease in their size or abundance toward the periphery. Canaliculi are extensive and radiate out in all directions from the osteocyte lacunae. Growth marks are absent.

Femur (UFRGS-PV-0271-T): The femur is diagenetically modified, particularly in the inner and mid-cortex. The cortex is narrow with some secondary remodeling and has vascular canals arranged as longitudinally-oriented primary and secondary osteons, with a decrease in vascularization toward the periphery. The globular osteocyte lacunae are haphazardly distributed around the vascular canals, in a pattern compatible with that of a fibrolamellar complex. Growth marks are absent.

Discussion

Recent studies on non-archosaur archosauromorph bone histology have provided important information about the growth patterns of these taxa (e.g., Ricqlès et al. 2008; Nesbitt et al. 2009; Botha-Brink and Smith 2011). Botha-Brink and Smith (2011) revealed a relatively fast, uninterrupted growth for derived non-archosauriform archosauromorph *Prolacerta broomi* Parrington, 1935. Bones of *Prolacerta* are characterized by parallel-fibred tissue with longitudinal primary osteons, with laicly woven matrix. The growth patterns of the more derived non-archosaur archosauriforms *Proterosuchus fergusi* Broom, 1903 (Botha-Brink and Smith 2011) and *Chanaresuchus* sp. (Ricqlès et al. 2008) are similar and include a relatively rapid and continuous early growth, change to a slow and interrupted growth late in ontogeny. The non-archosaur archosauriform *Erythrosuchus africanus* Broom, 1905, has an uninterrupted rapid growth similar to that of fast growing dinosaurs, as revealed by the relatively highly vascularized fibrolamellar bone (Gross 1934; Ricqlès 1976; Ricqlès et al. 2008; Botha-Brink and Smith 2011). According to Ricqlès et al. (2008) and Botha-Brink and Smith (2011), there appears to be an increase in growth rate with predominance of rapidly fibrolamellar bone within archosauriforms. De Ricqlès et al. (2008) suggested that the ability to growth at high rates was plesiomorphic for archosauriforms. However, derived non-archosaur archosauriforms, such as *Euparkeria capensis* Broom, 1913 (Botha-Brink and Smith 2011) and *Vancleavea campi* Long and Murry, 1995 (Nesbitt et al. 2009) deviate from this pattern, showing a slow growth rate (Botha-Brink and Smith 2011). These data suggest a relatively weak phylogenetic signal and that others factors must be considered when analyzed the growth patterns of archosauriforms (Botha-Brink and Smith 2011; Ricqlès et al. 2008).

Previous observations (e.g., Enlow and Brown 1957; Ricqlès 1976; Ricqlès et al. 2008) described rhynchosaur bone histology as lamellar-zonal, characterized by slow growth throughout ontogeny, a typical non-archosaur reptilian pattern.

Our study of *Teyumbaita sulcognathus* and *Hyperodapedon* sp. indicates the presence of fibrolamellar bone tissue in the perimedullary region with globular osteocyte lacunae arranged haphazardly around the vascular canals. Fibrolamellar bone is indicative of rapid osteogenesis (Amprino 1947; Chinsamy 1997; Ray et al. 2012), which suggests a relatively rapid growth in this region. Toward the periphery, tissue changes to a parallel-fibred or lamellar-zonal bone, with fewer primary osteons and more organized flattened osteocyte lacunae, suggesting a decrease in growth rate decreased. It is clear from both gross morphology and bone microstructure that all sampled specimens of *T. sulcognathus* had reached adulthood at their time of death, which indicates that the overall growth rate decreased, possibly with the onset of reproductive maturity (Sander 2000; Ray et al. 2012). As done for *T. sulcognathus*, the dimensions and bone microstructure of the *Hyperodapedon* bones used in the present

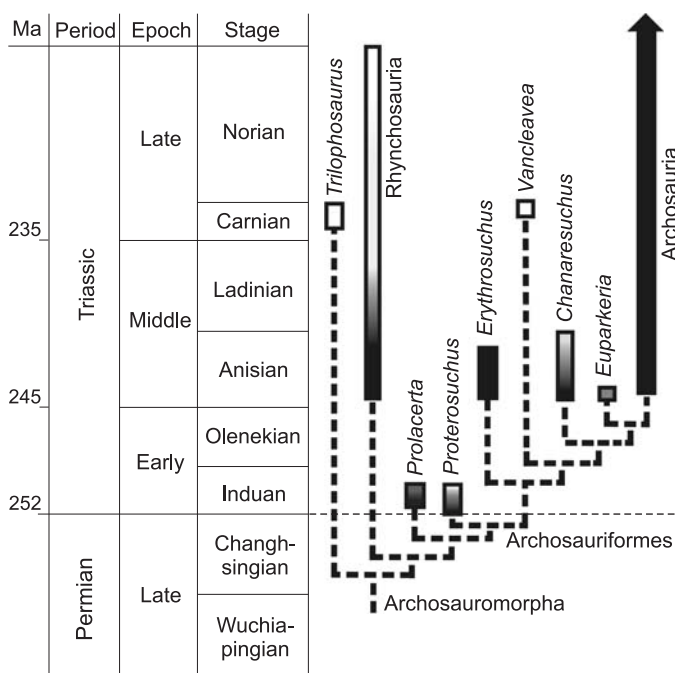


Fig. 3. Stratocladogram of archosauromorph bone histology modified from Botha-Brink and Smith (2011) with the new data from the present study. Lamellar-zonal and parallel-fibred bone indicates slowest growth, represented by white and grey shading, respectively. Black shading indicates rapid growing of fibrolamellar bone. In the Rhynchosauria it occurs during the early ontogenetic stages, similarly to *Proterosuchus* and *Chanaresuchus*. Phylogeny from Sues (2003), Dilkes and Sues (2009), and Nesbitt et al. (2009). Histological information from Ricqlès et al. (2008), Nesbitt et al. (2009), Werning and Irmis (2010), and Botha-Brink and Smith (2011). Time scale from Walker and Geissman (2009).

study were a priori considered as belonging to adult individuals, except UFRGS-PV-1217-T, which has fibrolamellar bone throughout the entire cortex, without growth marks or changes in the vascularization. Accordingly, this specimen may represent a juvenile. The presence of an EFS indicates that UFRGS-PV-0298-T (*T. sulcognathus*) and PV-0408-T (*Hyperodapedon* sp.) had reached somatic adulthood and, confirms the presence of determinate growth in both the hyperodapedontine rhynchosaur analyzed in this study. This feature has been positively identified in birds (e.g., Ponton et al. 2004) and non-avian dinosaurs (e.g., Erickson et al. 2004; Horner and Padian 2004; Padian et al. 2004) and also observed in some pseudosuchians (e.g., Castanet et al. 1988; Buffrénil and Castanet 2000; Ricqlès et al. 2003) and the non-archosaurian archosauriform *Erythrosuchus* (e.g., Ricqlès et al. 2008).

Conclusions

The new data from the hyperodapedontine rhynchosaurs *Hyperodapedon* sp. and *Teyumbaita sulcognathus* presented here indicate, contrary to Botha-Brink and Smith (2011), a relatively rapid growth during early ontogeny, which then slowed down during the subadult stage with periodic inter-

ruptions. This scenario reveals that the ability to growth at high rates was already present in basal archosauromorphs (Fig. 3).

The sample used in this study is small, and considering the extensive secondary remodeling of the perimedullary region, our results should be received as preliminary. Analysis of more specimens, including other rhynchosaur taxa, with a better ontogeny control, is required to confirm these conclusions.

Additionally, the confirmation of determinate growth in the non-archosaur archosauriform *Erythrosuchus* and the results reported herein should encourage additional osteohistological studies with the aim of establishing the extent of determinate growth within basal members of the more inclusive groups related to Archosauria.

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