

Comparative bone microstructure of three archosauromorphs from the Carnian, Late Triassic Chañares Formation of Argentina

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Marsà, J.A.G., Agnolín, F.L., and Novas, F.E. 2020. Comparative bone microstructure of three archosauromorphs from the Carnian, Late Triassic Chañares Formation of Argentina. *Acta Palaeontologica Polonica* 65 (2): 387–398.

The Chañares Formation exhibits one of the most important archosauriform records of early Carnian ecosystems. Here we present new data on the palaeohistology of Chañares archosauriforms and provide new insights into their paleobiology, as well as possible phylogenetically informative traits. Bone microstructure of *Lagerpeton chanarensis* and *Tropidosuchus romeri* is dominated by fibro-lamellar tissue and dense vascularization. On the other hand, *Chanaresuchus bonapartei* is more densely vascularized, but with cyclical growth characterized by alternate fibro-lamellar, parallel-fibered and lamellar-zonal tissues. Dense vascularization and fibro-lamellar tissue imply fast growth and high metabolic rates for all these taxa. These histological traits may be tentatively interpreted as a possible adaptive advantage in front of Chañares Formation environmental conditions.

Key words: Archosauromorpha, Lagerpeton, Tropidosuchus, paleobiology, paleohistology, Mesozoic, South America.

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Received 27 May 2019, accepted 11 February 2020, available online 7 April 2020.

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Introduction

The taxonomic and ecological diversity of Chañares Formation vertebrates, combined with its relatively short temporal span of deposition (236–234 Ma) (Marsicano et al. 2016) and its well-documented paleoenvironmental setting provide an ideal framework for investigating disparity growth dynamics of related taxa that span a pivotal stage in the evolution of terrestrial vertebrates, which represent the best record of tetrapod evolution immediately prior to the Late Triassic diversification of dinosaurs, advanced cynodonts, and mammals (Romer and Jensen 1966; Romer 1973; Bonaparte 1982).

Lagerpeton chanarensis and *Chanaresuchus bonapartei* were described by Romer (1971a, b) on the basis of partially articulated skeletons. *Tropidosuchus romeri* was described on the basis of several articulated and nearly complete individuals by Arcucci (1990). All available specimens from

Lagerpeton, *Chanaresuchus*, and *Tropidosuchus* specimens come from the Late Triassic Chañares Formation (Carnian), at La Rioja province, in Argentina (Marsicano et al. 2016).

Romer (1971a) described *Lagerpeton chanarensis* as a new slender-limbed archosaur, based on an articulated right hind-limb that exhibited remarkable dinosaur-like traits. Subsequent expeditions recovered new *Lagerpeton* specimens, which reinforced its similarities to dinosaurs (Bonaparte 1984; Arcucci 1986; Sereno and Arcucci 1993), being currently considered the sister taxon of Dinosauriformes (Sereno and Arcucci 1993; Novas 1996; Ezcurra 2006; Nesbitt 2011; Cabreira et al. 2016). *Lagerpeton chanarensis* was the only known lagerpetid for decades until the discovery of *Dromomeron* and *Ixalerpeton* (Irmis et al. 2007; Nesbitt et al. 2009a; Small 2009; Martínez et al. 2012; Cabreira et al. 2016). In contrast, *Chanaresuchus* and *Tropidosuchus* have been included within Proterochampsidae, a group of crocodile-like basal archosauriforms (Sereno and Arcucci 1990;

Sereno 1991; Dilkes and Sues 2009; Ezcurra et al. 2010). This clade is endemic to the Late Triassic beds of South America (Trotteyn et al. 2013).

Arcucci (1986) noted that several anatomical traits of *Lagerpeton* may be indicative of possible proterochampsid affinities. In this sense, Arcucci (1990) remarked that the pelvis of *Tropidosuchus* possesses characters that are similar to *Lagerpeton* and *Herrerasaurus* (presence of a supratabular crest, a ventral opening between pubis and ischium, a posterodorsal notch in acetabulum) and tarsal adaptations similar to basal dinosauromorphs as *Lagosuchus* and *Lagerpeton*. More recently, Novas and Agnolín (2015) indicated similarities between *Lagerpeton* and proterochampsids, particularly with *Tropidosuchus*. *Lagerpeton* resembles proterochampsids in several features, having a proximal pubis with a robust ambiens process, a pubic margin of pubis sigmoid in anterior view, a cup-like and ellipsoidal-shaped acetabulum, transverse processes on caudal vertebrae that are long and narrow, a femoral 4th trochanter that is proximodistally expanded, a middle tubercle surrounded by two shallow concavities on the caudal surface of the distal end of the tibia, an astragalus with an acute anteromedial corner, and a transversely thick metatarsal II. Furthermore, *Lagerpeton* and *Tropidosuchus* share an elongate and compact metatarsus with a metatarsal V that is reduced and devoid of phalanges, with articular surface for distal tarsal 4 subparallel to the longitudinal axis of shaft, and metatarsal IV longer than III. If we follow this proposal, lagerpetids and proterochampsids may be more closely related than previously thought.

Some authors made previous histological descriptions of selected proterochampsians from Northwestern Argentina. Ricqlès et al. (2008) described an indeterminate long bone of *Chanaresuchus* (MCZ 4036). This bone shows a fibro-lamellar tissue, but toward the periphery, the tissue progressively changes to lamellar-zonal, indicating active growth during a great part of early ontogeny. Cerda et al. (2015) described osteoderm histology of *Chanaresuchus* and *Pseudochampsia*. The osteoderms of *Pseudochampsia* are avascular and consist of parallel-fibered bone, which suggests that these elements grew at a constant, low rate. Conversely, the osteoderms of *Chanaresuchus* are well-vascularized structures composed of zones of woven-fibered bone and annuli of parallel-fibered bone. Arcucci et al. (2019) analyzed indeterminate proterochampsian specimens that revealed a predominance of fibro-lamellar tissue, suggesting fast bone growth.

The aim of the present contribution is to describe in detail and make comparisons between the bone histology of several archosauriforms from the Los Chañares Formation. These analyses may be useful to infer details on the behavior, ecology, and the growth patterns of roughly coeval proterochampsids and lagerpetids. On this basis, the disparity in growth strategies and the diverse ecological strategies carried out by several archosauromorphs of the Los Chañares Formation are compared in some detail. We also analyze the paleohistological data in the light of the varied phylogenetic proposals performed by different au-

thors (Bonaparte 1984; Arcucci 1986; Sereno and Arcucci 1990, 1993; Sereno 1991; Dilkes and Sues 2009; Ezcurra et al. 2010; Novas and Agnolín 2015).

Institutional abbreviations.— MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts, USA; PULR, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Fundacion Miguel Lillo, San Miguel de Tucuman, Argentina.

Other abbreviations.—CCCB, Compact Coarse Cancellous Bone; EFS, External Fundamental System; ICL, Inner Circumferential Layer; LAG, Lines of Arrested Growth.

Material and methods

Bone tissue samples were extracted from mid-shaft of long bones (Fig. 1) belonging to: *Lagerpeton chanarensis*, femur (PULR-V 124) and femur and tibia (PVL-4625); one femur of *Chanaresuchus bonapartei* (PULR-V 125) and one femur of *Tropidosuchus romeri* (PVL-4604), all from the Los Chañares Formation, in the Rioja Province, Argentina. The specimens are confidently referred to the respective taxa carrying out a bibliographic review of Romer (1971a, b), Sereno and Arcucci (1993) and Arcucci (1990).

PVL-4625 is an incomplete *Lagerpeton* skeleton, previously reported by Sereno and Arcucci (1993). This specimen is referred to *Lagerpeton chanarensis* on the basis of a unique combination of characters, including posterior dorsal vertebrae with anterodorsally inclined neural spines, first sacral vertebra with fan-shaped rib extending anterodorsally to the tip of the preacetabular process of the ilium, iliac blade with sinuous dorsal margin, preacetabular process laterally convex with anterior end directed anteromedially, ischial peduncle of ilium recessed, band-shaped eminence passing posterodorsally across lateral surface of postacetabular process, ischium with broad convex ventromedial flange and vertically deep puboischial suture, distal ischial blades horizontal, proximal end of pubis with subtriangular lateral fossa, pubic shaft deflected medially distal to ambiens process (Romer 1971a; Sereno and Arcucci 1993). The femur PULR-V 124 is referred to *Lagerpeton* and characterized by proximal end of femur with flat anteromedial surface, deep femoral head with hook-shaped medial extension, elongate aliform fourth trochanter, distal end of femur with large fibular condyle, among other traits (Müller et al. 2018).

PVL-4604 is a nearly complete skeleton previously described by Arcucci (1990), as belonging to *Tropidosuchus romeri*. The specimen shares with *Tropidosuchus* a unique combination of derived features, including relatively large orbit, curved premaxilla at the distal tip, quadrate shaft subvertically oriented, skull roof with ornamentation formed by longitudinal crests, cervical vertebrae notably elongate and distinct from dorsal elements, being parallelogram-shaped in lateral view (see Trotteyn et al. 2013).



Fig. 1. Long bones of archosauromorphs from La Rioja province, NW Argentina; Chañares Formation, Carnian (Late Triassic). **A, B.** *Lagerpeton chanaensis* Romer, 1971 (PVL-4625) femur in posteromedial view (**A**) and tibia in lateral view (**B**). **C.** *Chanaresuchus bonapartei* Romer, 1971 (PULR-V 125), femur in posteromedial view. **D.** *Tropidosuchus romeri* Arcucci, 1990 (PVL-4604), femur in posteromedial view. Arrows indicate place of the mid-shaft extraction of bone tissue samples. Scale bars 10 mm.

PULR-V 125 is represented by a nearly complete skeleton belonging to *Chanaresuchus bonapartei*. The specimen shares with *Chanaresuchus* skull with reduced antorbital fenestra, slit-like external nares placed close together dorsally and distant from the tip of the snout; parietals swing sharply outwards posteriorly, suspensorium far back from the posterior margin of the occiput, lateral fenestra anteroposteriorly elongate, and notably long choanae (Romer 1971b; Trotteyn et al. 2013).

Thin sections were prepared following the method outlined by Chinsamy and Raath (1992). 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). Samples were studied using a Zeiss Axio Scope.A1 petrographic polarizing microscope under normal, polarized, and lambda light regimes.

Vascularization in the samples have not been quantified. Therefore, the relative densities of vascular canals are assessed visually and described qualitatively, we follow the terminology of Warshaw (2008), with modifications. The following three terms are used: (i) sparse vascularization, vascu-

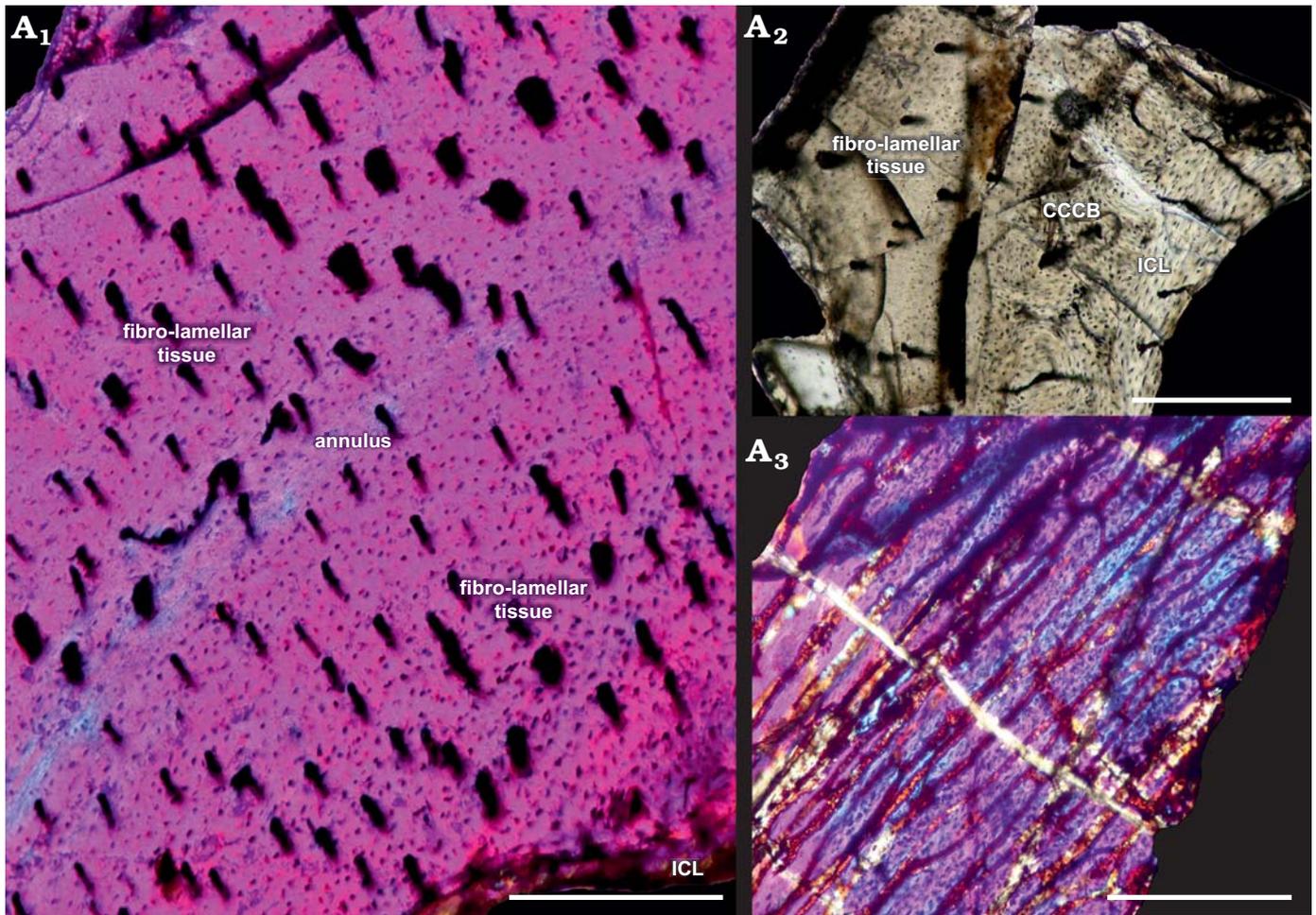


Fig. 2. Femur of archosauriform *Lagerpeton chanarensis* Romer, 1971 (PULR-V 124, in lambda light) from La Rioja province, NW Argentina; Chañares Formation, Carnian (Late Triassic). Section showing the inner circumferential layer and the cortex (A₁), detail of the compact coarse cancellous bone (A₂), oblique section of the same femur (A₃). Abbreviations: CCCB, Compact Coarse Cancellous Bone; ICL, Inner Circumferential Layer. Scale bars 300 μ m.

lar canals are irregularly distributed, with avascular stretches between them that generally exceed three times the diameter of the canals; (ii) moderate vascularization, vascular canals are more regularly distributed, with the distance between canals frequently less than three times the diameter of the canals; (iii) dense vascularization, vascular canals are separated from each other by less than the diameter of two canals.

Results

***Lagerpeton chanarensis* Romer, 1971.—Femur (PULR-V 124):** Two samples were extracted from this femur. The first sample is eroded on its anterolateral surface and its posterior edge is broken off. However, this has not affected the main features of bone microstructure and medullar cavity (Fig. 2A₁). The second sample corresponds to a small broken portion of a femur in oblique section.

In the first sample, the compacta is densely vascularized is composed of fibro-lamellar tissue, with an annulus in the compacta midway. The vascular canals are longitudinally oriented, and there are some primary osteons in the inner cortex.

The medullary cavity is surrounded by a thin layer of endosteally deposited lamellar bone tissue that forms the inner circumferential layer (ICL). An external fundamental system (EFS) was not observed. A high density of circular osteocyte lacunae are present throughout the cortex. In the inner circumferential lamellae the osteocyte lacunae are elongated.

Restricted to the medial portion of the shaft of the femur, there is an area where the perimedullar region is sharply separated of the compacta by a thin layer of compact coarse cancellous bone (CCCB). The CCCB does not expand beyond this limited area situated between the inner-middle cortex (Fig. 2A₂). CCCB is formed through the compaction of trabeculae in the metaphysis, subsequently incorporated into the diaphyseal cortex during longitudinal growth and presents a characteristic structure of compacted lamellar trabeculae (Enlow 1962).

In the second sample corresponds to a small broken portion of a femur. There is dense vascularization in the cortex, preserved in oblique section (Fig. 2A₃). The vascular canals, conformed as primary osteons, are interconnected by Volkman's canals.

Femur (PVL-4625): This femur is broken and partially

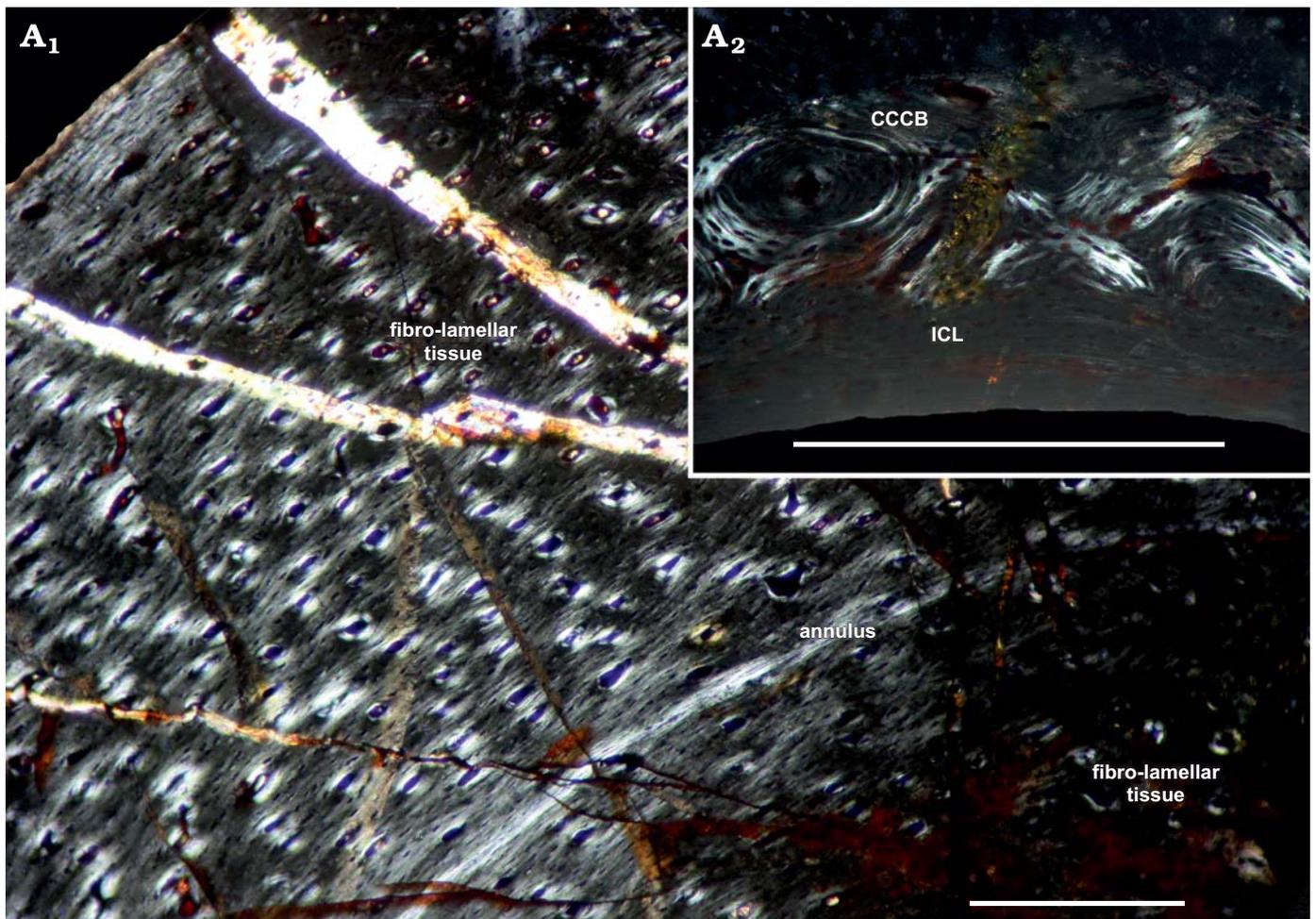


Fig. 3. Femur of archosauromorph *Lagerpeton chanarensis* Romer, 1971 (PVL-4625, in polarized light) from La Rioja province, NW Argentina; Chañares Formation, Carnian (Late Triassic). Section showing the inner circumferential layer and the cortex (A_1), detail of the compact coarse cancellous bone (A_2). Abbreviations: CCCB, Compact Coarse Cancellous Bone; ICL, Inner Circumferential Layer. Scale bars 300 μm .

collapsed on its anterior surface, whereas the posterior half is totally broken. This does not affect the main features of the preserved bone microstructure as well as the medullary cavity (Fig. 3A₁)

The compacta is densely vascularized and is constituted of fibro-lamellar tissue with an annulus in the inner compacta. Vascular canals are conformed as primary osteons and are longitudinally oriented, with some anastomoses present. There are some Volkman's canals between primary osteons. The medullary cavity is surrounded by a thin layer of endosteally deposited lamellar bone tissue that forms the ICL. The subperiosteum is composed by parallel-fibered tissue. A high density of subcircular osteocyte lacunae are present throughout the cortex. In the inner circumferential lamellae the osteocyte lacunae are elongated. Restricted to the anterior portion of the shaft of the femur the perimedullar region is sharply separated of the compacta by a thin layer of CCCB (Fig. 3A₂), which presents a characteristic structure of compacted lamellar trabeculae. The CCCB does not expand beyond of this limited area situated between the inner-middle cortex.

Tibia (PVL-4625): The tibia of this specimen is partially broken on its posteromedial surface. This does not affect the

main features of bone microstructure as well as the medullary cavity (Fig. 4).

The compacta is densely vascularized and is constituted of fibro-lamellar tissue, with the presence of a LAG in the compacta midway. The vascular canals are radially oriented, some of these canals are primary osteons in the inner cortex. Longitudinal and reticular canals are sparse, but they are scattered throughout the cortex. There are some Volkman's canals. The medullary cavity is surrounded by a layer of endosteally deposited lamellar bone tissue, which forms the ICL. An EFS was not observed. A high density of subcircular osteocyte lacunae are present throughout the cortex. In the inner cortex some osteocyte lacunae have canaliculi. In the inner circumferential lamellae, the osteocyte lacunae are elongated.

Chanaresuchus bonapartei Romer, 1971.—*Femur* (PULR-V 125): The transverse section of the bone has been partially deformed by diagenetic processes and the medullary cavity is filled with sediment and bone cortex fragments. The outer cortex and subperiosteum are partially broken. This does

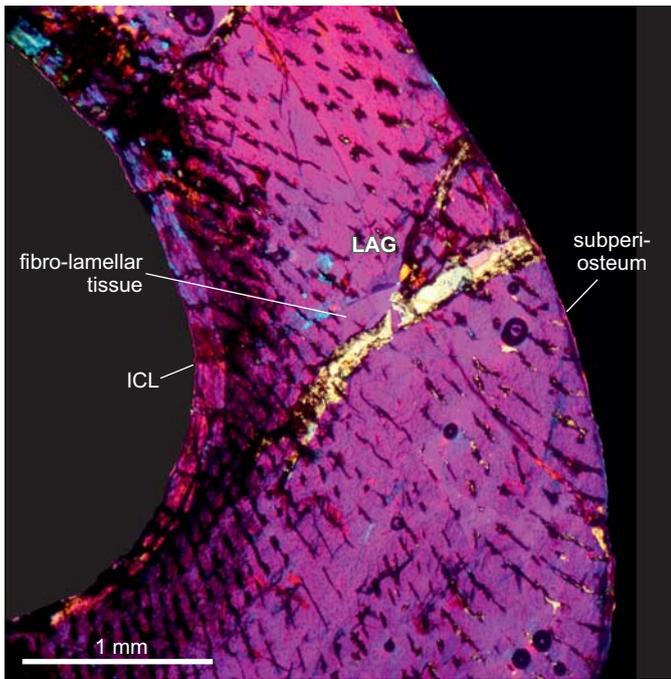


Fig. 4. Tibia of archosauromorph *Lagerpeton chanarensis* Romer, 1971 (PVL-4625, in lambda light) from La Rioja province, NW Argentina; Chañares Formation, Carnian (Late Triassic). Section showing the main features of the tibia bone microstructure. Abbreviations: ICL, Inner Circumferential Layer; LAG, line of arrested growth.

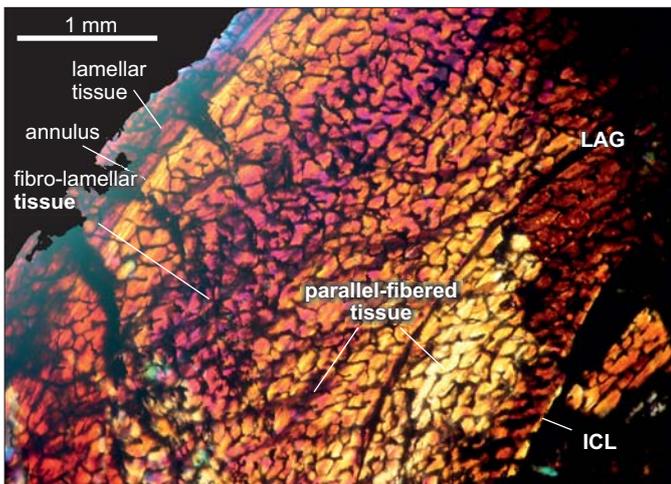


Fig. 5. Femur of archosauromorph *Chanaresuchus bonapartei* Romer, 1971 (PULR-V 125, in lambda light) from La Rioja province, NW Argentina; Chañares Formation, Carnian (Late Triassic). Section showing the main features of the femur bone microstructure. Abbreviations: ICL, Inner Circumferential Layer; LAG, line of arrested growth.

not affect the main features of bone microstructure and bone marrow (Fig. 5).

The compacta is densely vascularized. The fibro-lamellar compacta shows a cyclical growth with the presence of a LAG and annulus. In the first zone, from the ICL to the LAG the tissue is conformed as parallel-fibered. In a second zone, there are two subdivisions: from the LAG to the middle of the cortex the tissue is parallel-fibered. In contrast, from the

middle of the cortex to the annulus the tissue is fibro-lamellar. At the third zone, starting from the avascular lamellar-zonal annulus, the tissue is parallel-fibered, comprising a thin layer compared with the previous zone, which ends in a thin avascular lamellar layer. Vascular canals are reticular and longitudinal oriented, there are some primary osteons in the inner cortex. The medullary cavity is surrounded by a layer of endosteally deposited lamellar bone tissue, that forms the ICL. The subperiosteum is composed of lamellar-zonal tissue. A high density of circular osteocyte lacunae are present throughout the cortex. In the inner circumferential lamellae the osteocyte lacunae are elongated.

***Tropidosuchus romeri* Arcucci, 1990.—Femur (PVL-4604):** The cross-section of the bone is well preserved (Fig. 6).

The compacta is densely vascularized and conformed into fibro-lamellar tissue. The cortex is uninterrupted by growth marks. Vascular canals are represented by primary osteons and are mainly disposed as longitudinal canals, though more scarce reticular canals are present. The medullary cavity is surrounded by a layer of endosteally deposited lamellar bone tissue that forms the ICL.

Towards the outer cortex the fibro-lamellar tissue changed

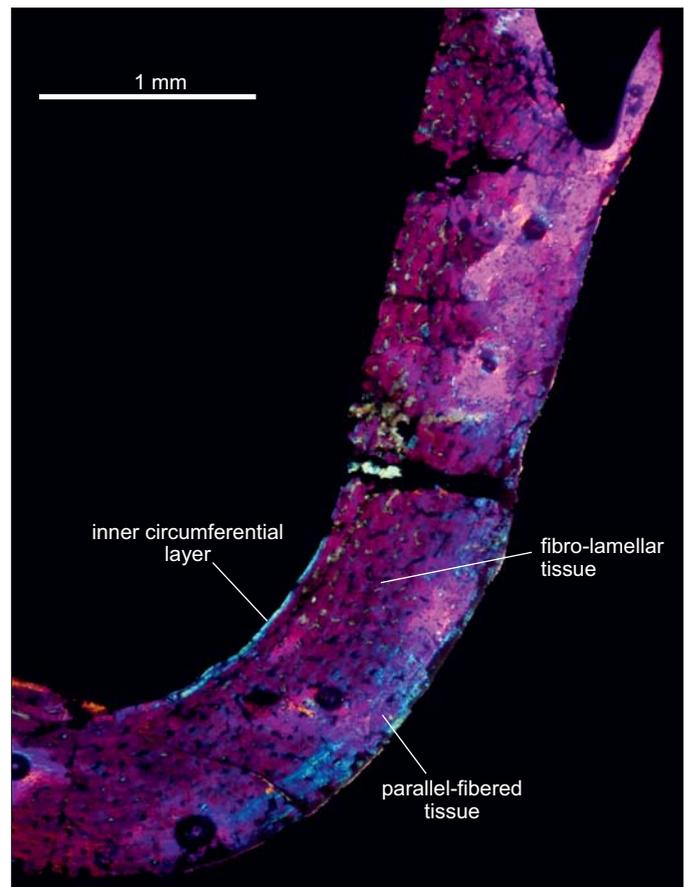


Fig. 6. Femur of archosauromorph *Tropidosuchus romeri* Arcucci, 1990 (PVL-4604, in lambda light) from La Rioja province, NW Argentina; Chañares Formation, Carnian (Late Triassic). Section showing the main features of the femur bone microstructure.

in some places by patches of parallel-fibered tissue. The subperiosteum is composed of parallel-fibered tissue.

The osteocyte lacunae are less abundant than in *Chanaresuchus* and *Lagerpeton*, and are subcircular in contour and present throughout the cortex and the inner circumferential lamellae.

Discussion

Ontogenetic age of the studied specimens.—In bone tissues of tetrapods, reduced vascularization, predominance of longitudinal canals and lack of anastomoses, narrowing of zones deposited between successive LAGs, and formation of an EFS at the bone perimeter are all indicative of a slowing growth rate in an individual (e.g., Horner et al. 1999; Horner et al. 2000; Padian and Horner 2004; Fostowicz-Frelik and Sulej 2010; Knoll et al. 2010; Marsà et al. 2017). Some of these traits are present in the material here reported.

The absence of an EFS suggests that the growth had not completely ceased in *Lagerpeton* individuals, indicating that the described specimens had not reached somatic maturity. The annulus in the two available femora (PVL-4625 and PULR-V 124) and the LAG in the tibia appear not to be related to an overall decrease in growth rate. The vascularization in *Lagerpeton* does not decrease in external portions of the cortex and the bone bears a fast-growing aspect, lacking lamellar or pseudo-lamellar tissues. Annuli and LAGs in *Lagerpeton* specimens could represent an annual/seasonal pattern of growth cessation, triggered whether the environment happened to be stressful that year.

In contrast with *Lagerpeton*, in the *Chanaresuchus* hindlimb the vascularization decreases towards the periphery. Growth zones of the cortex decreases in width towards the subperiosteum. The subperiosteum is composed of a thin, avascular lamellar-zonal layer without internal LAGs, but in a similar position of an EFS. These features indicate a strong decrease in growth rate, which would suggest that the specimen has nearly reached its somatic maturity.

In *Tropidosuchus*, towards the outer cortex the fibro-lamellar tissue is replaced in some places by parallel-fibered tissue patches, indicating a decrease in growth rate. In the subperiosteum a thin, avascular parallel-fibered layer is present in a similar position of an EFS. This also indicates a decrease in growth rate, suggesting that the specimen had nearly reached somatic maturity.

The absence of an EFS is shared with indeterminate proterochampsian specimens studied by Arcucci et al. (2019), indicating that these specimens were still growing, and were not fully-grown adults, at the time of death.

In some archosaurs, although the closure of the neurocentral suture is not an unambiguous indicator of maturity, for many groups of archosaurs it has been shown to be a morphological evidence of adult age (Brochu 1996; Irmis 2007). In all studied specimens, with the exception of PULR-V 124 that consists of an isolated femur, the neurocentral sutures

are closed in the available cervical, dorsal and caudal vertebrae, indicating at least some degree of somatic maturity if this taxon follows pseudosuchian fusion pattern (Brochu 1996; Irmis 2007).

The EFS is an informative feature in palaeohistological studies because it indicates skeletal maturation and slowing down in the rate of bone deposition (e.g., Chinsamy-Turan 2005; Woodward et al. 2011). It is typical of taxa with determinate growth and consists of completely avascular lamellar or parallel-fibered bone, that may or may not have annuli or LAGs (Chinsamy-Turan 2005). In our sample, although the arrangement of the collagen fibers in the outer cortex of some specimens becomes parallel, the bone tissue is never avascular. Therefore, no fully-grown specimens are present in our sample of Chañares Formation archosauriforms. The well-vascularized nature of the external cortex (which also contains vascular spaces open to the subperiosteal surface) is indicative of active bone deposition, suggesting that even our largest individuals were actively growing at the time of death (e.g., Chinsamy-Turan 2005; Erickson 2005; Cerda and Chinsamy-Turan 2012).

Proterochampsid growth patterns.—The evolution of bone growth rates and metabolic rates in Archosauromorpha represents an area of active research (e.g., Horner et al. 2000; Starck and Chinsamy 2002; Padian et al. 2004; Ricqlès et al. 2003, 2008; Erickson 2005; Fostowicz-Frelik and Sulej 2010; Griffin and Nesbitt 2016; Marsà et al. 2017; Griffin et al. 2019; Veiga et al. 2019). Bone microstructure reflects growth rate, in agreement with the Amprino's Rule (Padian and Horner 2004; Ricqlès et al. 2008). Bone tissues of *Lagerpeton* and *Tropidosuchus* suggest a fast growth rate, significantly higher than most crurotarsans. The fibro-lamellar tissue of these taxa is characterized by dense vascularization mainly with longitudinal vascular canals, with radial and reticular canals also present, and zonation of the cortex is not evident. This combination of traits also occurs in some crurotarsans, including *Terrestrisuchus gracilis* (Crush, 1984), *Postosuchus kirkpatricki* (Chatterjee, 1985), as well as dinosauriforms (Ricqlès et al. 2003, 2008; Padian and Horner 2004). Notably, the samples of *Lagerpeton* and *Tropidosuchus* show less vascularized tissues than in dinosaurs (Horner et al. 2000; Starck and Chinsamy 2002; Ricqlès et al. 2003; Padian and Horner 2004), being most comparable to basal dinosauriforms (e.g., *Silesaurus*, *Asilisaurus*, *Lewisuchus*; Fostowicz-Frelik and Sulej 2010; Griffin and Nesbitt 2016; Marsà et al. 2017).

In the proterochampsid *Chanaresuchus*, the compacta is more densely vascularized than in *Lagerpeton* and *Tropidosuchus* and fibro-lamellar, parallel-fibered and lamellar-zonal tissues are present. Contrary to *Lagerpeton* and *Tropidosuchus*, the cyclical growth of *Chanaresuchus* shows the presence of LAG, annuli and a thin avascular layer (in an EFS-equivalent position), which would indicate a notable decrease in the growth rate. In concordance, Ricqlès et al. (2008) studied a section of an indeterminate long bone shaft attributed to *Chanaresuchus*. This bone shows a well-

developed reticulum of short vascular anastomoses uniting longitudinally oriented vascular canals. These authors noted an early rapid growth rate (based on an inner thick region of fibro-lamellar bone), which dramatically decreased later in ontogeny (based on the presence of peripheral lamellar-zonal bone; Ricqlès et al. 2008). The histology of the specimen described by Ricqlès et al. (2008) is very similar to the femur of *Chanaresuchus* here described, but in the latter the vascularization is even greater. Previously, Arcucci et al. (2019) conducted a histological examination of indeterminate proterochampsian specimens that revealed a predominance of fibrolamellar bone tissue, suggesting rapid periosteal osteogenesis and therefore overall fast bone growth.

The absence of an EFS in *Chanaresuchus*, *Tropidosuchus*, and *Lagerpeton*, as well as the proterochampsians studied by Arcucci et al. (2019) indicates that they were still growing, and that they were not fully-grown adults (Klein and Sander 2008). Fibro-lamellar tissue is shared between *Chanaresuchus*, *Tropidosuchus*, and *Lagerpeton*, whereas the presence of LAGs is shared by *Chanaresuchus* and *Lagerpeton*. The abundance of fibrolamellar cortical tissue and the existence of LAGs was documented in the indeterminate proterochampsian analyzed by Arcucci et al. (2019). An exception to this fibro-lamellar tissue is the proterochampsid *Pseudochampsia ischigualastensis* Trotteyn and Ezcurra, 2014, which shows a low growth rate (Cerdeña et al. 2015). These diverse growth patterns and rates suggest a deep variation of metabolism within Proterochampsia, a condition previously unknown in any non-archosaurian archosauriform clade. Along the same line of thought, the bone histology of *Dromomeron romeri* (Griffin et al. 2019) is similar to that of *Lagerpeton chanarensis* (woven-bone tissue, moderate to dense vascular canals in longitudinal configuration), but with higher LAGs numbers in *Dromomeron*.

Growth patterns here described differ from that seen in other archosauromorphs, as for example, in archosauromorphs from the Triassic faunas of Karoo, South Africa (see Botha-Brink and Smith 2011; e.g., *Prolacerta brommi* Parrington, 1935, *Proterosuchus fergusi*, Broom, 1903, *Erythrosuchus africanus* Broom, 1905, *Euparkeria capensis* Broom, 1913). The growth pattern of the early Triassic *Prolacerta broomi* exhibits a vascular pattern with longitudinally-oriented primary osteons, with anastomoses in some vascular canals, and with the prevalence of a mixture of weakly developed fibrolamellar and parallel-fibered tissue (Botha-Brink and Smith 2011). These features suggest notably lower growth rates than in Chañares archosauromorphs. Similar-aged *Proterosuchus fergusi*, a medium-sized proterosuchid, possesses radiating vascular canals within fibrolamellar bone tissue during early ontogeny, but its growth decreases dramatically during late ontogeny, with the onset of poorly vascularized lamellar-zonal bone tissue (Botha-Brink and Smith 2011). This contrasts with Chañares archosauromorphs which shows active growth.

The early Middle Triassic *Erythrosuchus africanus* (Gross 1934; Ricqlès 1976; Ricqlès et al. 2008; Botha-Brink

and Smith 2011) exhibits uninterrupted growth and a variety of vascular patterns including laminar, reticular and radial, all within fibro-lamellar bone tissue, indicating rapid growth rates, similar to those found in fast-growing dinosaurs. The growth rates of *Lagerpeton* and *Tropidosuchus* are less than those of *Erythrosuchus*. *Chanaresuchus* shows a fast growth with a complex pattern of vascular canals, but with cyclical growth. *Euparkeria capensis* exhibits sparse to moderate vascular canals embedded in parallel-fibered bone (Botha-Brink and Smith 2011). *Euparkeria* shows low growth rates compared with Chañares Formation archosauromorphs.

The histology of *Teleocrater rhadinus* Nesbitt, Butler, Ezcurra, Barrett, Stocker, Angielczyk, Smith, Sidor, Niedźwiedzki, and Charig, 2017, sister taxon of Ornithodira, resembles *Lagerpeton* and *Tropidosuchus*. In these taxa the cortex consists of woven bone tissue with longitudinal vascular canals and primary osteons, but in *Teleocrater* the number of anastomoses is higher (Nesbitt et al. 2017). *Chanaresuchus* shows growth patterns similar to *Teleocrater*, with a high number of anastomosis, but in *Teleocrater* the growth is uninterrupted.

The histology of hindlimb bones described here suggests that *Lagerpeton* and *Tropidosuchus* show similar growth rates, and together with *Chanaresuchus* exhibited a fast growth. This implies that these taxa possessed a relatively high metabolic rate, comparable to that seen in other archosaurs, including non-dinosaurian Dinosauriformes (Fostowicz-Frelik and Sulej 2010; Griffin and Nesbitt 2016; Marsà et al. 2017; Veiga et al. 2019). The osteohistology of *Sacisaurus*, *Silesaurus*, *Asilisaurus*, and *Lewisuchus* exhibit predominantly longitudinally-oriented primary osteons with few or no anastomoses. This simple vascular pattern is common to all silesaurids studied to date and indicates relatively slower growth rates when compared to most Dinosauria (Fostowicz-Frelik and Sulej 2010; Griffin and Nesbitt 2016; Marsà et al. 2017; Veiga et al. 2019).

The bone histology of the dinosauriform *Nyasasaurus parringtoni* Nesbitt, Barrett, Werning, Sidor, and Charig, 2012 is constituted by vascular canals configured as primary osteons, many of these canals are longitudinal canals, but at least half of these anastomose with other canals (in all directions), and locally, short radial canals may dominate. The outermost cortex shows transition from woven-fibered to parallel-fibered bone. The bone histology of *Nyasasaurus* is similar to that of early dinosaurs, with plexiform and laminar vascular patterns (e.g., *Herrerasaurus ischigualastensis* Reig, 1963; Ricqlès et al. 2003; Padian et al. 2004; *Tawa hallae* Nesbitt, Smith, Irmis, Turner, Downs, and Norell 2009; Werning 2013; *Coelophysis bauri* Cope, 1887; Colbert 1995; Nesbitt et al. 2006; *Megapnosaurus rhodesiensis* Ivie, Slipinski, and Wegrzynowicz, 2001; Chinsamy 1990; Werning 2013; *Lesothosaurus diagnosticus* Galton, 1978; Knoll et al. 2010; *Plateosaurus engelhardti* Meyer, 1837; Klein and Sander 2007; *Mussaurus patagonicus* Bonaparte and Vince, 1979; Cerdeña et al. 2014; *Massospondylus carinatus* Owen, 1854; Chinsamy 1993). These features indicate

that early saurischian dinosaurs had higher growth rates than Chañares archosauromorphs.

In contrast, the growth rate and levels of tissue disorganization are higher in Chañares archosauromorphs than in early ornithischians such as *Fruitadens haagorum* Butler, Richard, Galton, Porro, Chiappe, Henderson, and Erickson, 2010 and *Scutellosaurus lawleri* Colbert, 1981, which exhibit slower rates of tissue deposition (Butler et al. 2010; Padian et al. 2004). In this sense, *Fruitadens* exhibits parallel-fibered bone tissue (Butler et al. 2010) and *Scutellosaurus* contains few fibrolamellar bone during early ontogeny and entirely lamellar-zonal bone tissue during adulthood (Padian et al. 2004).

The Late Triassic pterosaur *Eudimorphodon ranzii* Zambelli, 1973 shows moderate vascularization and a woven-fibered tissue cortex to parallel-fibered bone tissue later in ontogeny, with some anastomoses in few vascular canals (Padian et al. 2004; Werning 2013). *Dimorphodon* Owen, 1859, an Early Jurassic pterosaur, possesses fibro-lamellar bone tissue with some areas of more parallel-fibered bone, but with anastomosing vascular canals (Ricqlès et al. 2000; Padian et al. 2004; Werning 2013). The Early Jurassic pterosaur *Dorygnathus banthensis* Wagner, 1860 (Gross 1934), has more typical fibro-lamellar cortical tissues. *Tropidosuchus* and *Lagerpeton* show growth patterns similar to *Dimorphodon* and *Dorygnathus*, but with a lesser vascularity and anastomosis. *Eudimorphodon* shows a low growth pattern when compared with Chañares archosauromorphs.

Behavioral implications of paleohistological analysis.—

Reig (1959) proposed semiaquatic habits for the proterochampsid *Proterochampsia barrionuevoi* Reig, 1959 based on the elongated and triangular snout and dorsally flattened head, a distinctive pattern of dermal ornamentation of the skull, and dorsally located orbits and external nares. These morphological characteristics resemble those of Recent crocodylians, which led several authors to suggest a probable aquatic lifestyle for proterochampsians, a hypothesis that was accepted by later authors and extrapolated to other members of the clade (Sill 1967; Romer 1971b, 1972; Bonaparte 1978). Cerda et al. (2015) studied osteoderm histology of proterochampsids, and concluded that the compact nature of their osteoderms fits with an increase in bone mass (sensu Houssaye 2013) supporting aquatic or semiaquatic lifestyle. However, Cerda et al. (2015) also indicated that given the diminutive size and low number of osteoderms in each individual (just a single row of osteoderms dorsal to the vertebral column), it is improbable that osteoderm compactness actually modifies the whole skeletal mass.

More recently, Arcucci (2011) noted that the proterochampsids *Chanaresuchus bonapartei*, *Gualosuchus reigi* Romer, 1971, and *Tropidosuchus romeri*, may have had a more terrestrial lifestyle than the genus *Proterochampsia*. Arcucci's (2011) proposal rests on the fact that Chañares proterochampsids (i.e., *Chanaresuchus*, *Gualosuchus*, *Tropidosuchus*) lack anatomical features typical of aquatic taxa (e.g.,

absence of secondary palate, laterally compressed teeth, limbs long and slender, lacking signs of digit reduction or enlargement of the distal elements, subvertically positioned limbs, and tail not dorsoventrally tall, but transversely wide). In contrast, Arcucci et al. (2019) argued that anatomical features recognized in proterochampsians, such as marginal dentition, palatal teeth, morphology of the tail, limb modification, and dermal armor suggest a more terrestrial life style.

Several studies have demonstrated that modifications in bone microanatomy in tetrapods are correlated with lifestyle (Ricqlès and Buffrénil 2001; Houssaye 2009). In this regard, adaptation to aquatic life may be inferred on the basis of bone microstructure (Houssaye 2009; Canoville and Laurin 2010). Extant and extinct vertebrates secondarily adapted to aquatic life show four major bone types: osteoporotic, pachyostotic, osteosclerotic and pachy-osteosclerotic (Ricqlès and Buffrénil 2001; Houssaye 2009). Osteoporotic-like type consists of a lightening of the bones by decreasing the thickness of the compact cortical bone and increasing the osseous porosity. Conversely, pachyostosis (sensu stricto) corresponds to a hyperplasia (increase of deposit) of periosteal cortices that leads to an alteration of the bone morphology by increasing its volume (Ricqlès and Buffrénil 2001; Houssaye 2009). Osteosclerosis is an increase of bone inner compactness either as a result of incomplete endochondral ossification, inhibition of secondary remodelling and/or the filling of inner cavities, with no effect on the external dimensions of the bone. Finally, pachyosteosclerosis corresponds to the combination of the pachyostotic and osteosclerotic states in the same bone (Ricqlès and Buffrénil 2001; Houssaye 2009).

Chanaresuchus shows a pachyostotic femur, with a relatively reduced medullary cavity and wide cortex, being consistent with semiaquatic habits proposed by previous authors (in fact, the increase of the skeletal mass in pachyostotic bones is interpreted as an adaptation to reduce buoyancy; Taylor 2000). The pachyostotic condition of *Chanaresuchus* contrasts with *Tropidosuchus*, which shows a very thin cortex and wide medullary cavity, consistent with terrestrial habits. Conversely, *Lagerpeton* has been invariably considered as having terrestrial habits (Serenó and Arcucci 1993).

The cortex compactness and reduced medullary cavity recorded for the indeterminate proterochampsians studied by Arcucci et al. (2019), support an amphibious/terrestrial life style.

Palaeoecological implications.—The paleohistological analysis of proterochampsids and *Lagerpeton* show two different growth strategies: on one hand a rapid growth with one or any growth mark in *Lagerpeton* and *Tropidosuchus*; on the other hand, *Chanaresuchus* was characterized by a marked cyclical growth, with fast growth intercalated with seasonal interruptions (sensu Chinsamy and Hurum 2006), showing a decrease in the growth rate to the subperiosteum.

The depositional environment in which the specimens of *Lagerpeton*, *Tropidosuchus*, and *Chanaresuchus* were found suggests a warm climate with variable rainfall, with humid

periods alternating with extensive and harsh drier periods (Tucker and Benton 1982; Rogers et al. 2001; Mancuso et al. 2014). Their rapid early growth reflects a plesiomorphic growth strategy for archosauriforms (Ricqlès et al. 2008), including proterochampsids and *Lagerpeton*. Fast growth rates at early age may have improved juvenile survivorship in Chañares Formation environmental conditions (e.g., Tinkle 1969; Gasser et al. 2000; Curtin et al. 2009). The growth strategy observed in *Tropidosuchus* and *Lagerpeton* contrasts with that of *Chanaresuchus*, which is characterized by seasonal interruptions. In agreement with de Ricqlès et al. (2008), we posit that *Chanaresuchus* possesses progressively increased growth rates, exhibiting rapid early growth, but slow and cyclical late growth.

Phylogenetic implications.—Some authors have asserted that histological features may express “individual histories” but do not shed light on phylogenetic relationships (Castanet et al. 2001; Cubo et al. 2005; Ricqlès et al. 2004). However, recent authors (e.g., Padian et al. 2001, 2004; Padian and Horner 2004; Ricqlès et al. 2003, 2008; Fostowicz-Frelik and Sulej 2010; Legendre et al. 2014; Marsà et al. 2017; Veiga et al. 2019) agree in that histological characters may reflect phylogenetic signal.

Most non-avian archosauriforms show relatively slow growth rates (e.g., Ricqlès et al. 2003; Botha and Smith 2011). Some taxa, as *Terrestrisuchus*, erythrosuchians and *Proterosuchus* show a growth rate that is higher than in most crurotarsans, with bone microstructure that is highly similar to that observed in small dinosaurs (Ricqlès et al. 2003, 2008; Botha and Smith 2011). Ricqlès et al. (2008) suggested that the ability to reach and maintain rapid growth rates during at least early and mid-ontogenetic stages is plesiomorphic for archosauriforms and that the Triassic was a time of experimentation in growth strategies. Pseudosuchians more derived than sphenosuchian *Terrestrisuchus*, secondarily reverted to a poorly vascularized matrix, and an indeterminate cyclical growth that persists in living crocodiles (Ricqlès 1978; Schweitzer and Marshall 2001; Botha and Smith 2011).

In this sense, the bone microstructure of *Lagerpeton*, *Tropidosuchus* and *Chanaresuchus* indicates notably high growth rates, congruent with previous studies indicating fast growth rates is plesiomorphic for archosauriforms (Ricqlès et al. 2003, 2008; Fostowicz-Frelik and Sulej 2010; Marsà et al. 2017).

Lagerpeton and *Tropidosuchus* resemble each other in the distribution and abundance of vascular canals composed by longitudinal primary osteons, some anastomoses, and the fibro-lamellar matrix throughout the cortex. This pattern differs from other basal archosauromorphs, and resemble non-dinosaurian dinosauriforms (Fostowicz-Frelik and Sulej 2010; Griffin and Nesbitt 2016; Marsà et al. 2017). Similar histological features suggest that these two taxa shared similar life history strategies and could indicate a possible close phylogenetic relationships, as was previously proposed by Novas and Agnolín (2015).

Conclusions

Lagerpeton and *Tropidosuchus* show a rapid growth rate, and the sampled individuals both lack evidence of a decrease in their growth rate. These two taxa resemble each other in the distribution of primary osteons, presence of anastomosis and fibro-lamellar bone tissues throughout the cortex. This suggests that these two taxa shared similar life history strategies (as growth rates, growth patterns, and ontogenetic stages) and also possible close phylogenetic relationships (Novas and Agnolín 2015; Fechner 2009; Arcucci 1986, 1990). *Chanaresuchus*, with a reduced medullary cavity related to a terrestrial/amphibious life style, exhibits a denser vascularization with a reticular pattern, with a cyclical growth conformed by an alternate fibro-lamellar, parallel-fibered and lamellar-zonal tissues. This is strongly different from the condition exhibited by *Lagerpeton* and *Tropidosuchus*. It is remarkable the disparity in growth strategies evolved among archosauromorphs of Chañares at the same paleoenvironment. However, it is not particularly surprising that different growth strategies exist within the same environment—all through vertebrate history there have been a diversity of successful growth strategies in the same environment.

Fast early growth and acquisition could represent an advantageous plesiomorphic trait to the low juvenile survivorship hypothesized for the Chañares Formation environment, as previously suggested for the coeval basal dinosauriform *Lewisuchus* (Marsà et al. 2017).

Acknowledgements

We thank Ignacio Cerda (Museo Carlos Ameghino, Cipolletti, Río Negro province, Argentina) for his advice, assistance, and comments on paleohistological techniques. We thank Federico Brisson Egli, Sebastian Rozadilla, Mauricio Alexis Rolando, Mattia Motta, Julia Soledad D'Angelo, Nicolas Chimento and Gabriel Lio (all Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Autonomous City of Buenos Aires, Argentina) for comments and discussion. Special thanks to Mirtha González (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Autonomous City of Buenos Aires, Argentina) for your assistance in the use of petrographic microscope. The research here presented has been supported by CONICET.

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