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To cite this article: G.J. Windholz, R. González, I.A. Cerda, F. Bellardini, J.C.G. Silva, T.S. Marinho, L.C.B. Ribeiro & A.G. Martinelli (2023): Osteohistology of *Uberabatitan ribeiroi* (Dinosauria, Sauropoda) provides insight into the life history of titanosaurs, Historical Biology, DOI: [10.1080/08912963.2023.2253257](https://doi.org/10.1080/08912963.2023.2253257)

To link to this article: <https://doi.org/10.1080/08912963.2023.2253257>



Published online: 07 Sep 2023.



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# Osteohistology of *Uberabatitan ribeiroi* (Dinosauria, Sauropoda) provides insight into the life history of titanosaurs

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## ABSTRACT

The Serra da Galga Formation is a geological unit that has provided a taxonomically diverse fossil record for the Late Cretaceous of Brazil. The formation highlights the richest evidence of titanosaurs in this country, with a handful of described species, (e.g. *Uberabatitan ribeiroi*). Over time, palaeobiological works based on the osteohistology of fossils are becoming more frequent. However, *U. ribeiroi* has never been the subject of a purely histological study. We performed osteohistological descriptions of specimens referred to this species. The results support that the hyper-elongated cervical ribs of *U. ribeiroi* are tendons that have developed through metaplasia, as occur in other neosauropods. Further, samples show rapid and uninterrupted growth, evidenced by a continuous deposit of fibrolamellar tissue. Subsequently, growth would have ceased with the appearance of periodic interruptions (at least in appendicular bones), in the most advanced stages of development. The variable presence of an external fundamental system reveals that not all the specimens studied here reached somatic maturity. Finally, the high degree of bone remodelling described in the samples, especially in the ribs, is higher than expected for other neosauropods in the same ontogenetic stages. This supports the previous idea that this feature would be typical of Titanosauria.

## ARTICLE HISTORY

Received 25 June 2023  
Accepted 25 August 2023

## KEYWORDS

*Uberabatitan ribeiroi*;  
palaeobiology; sauropod  
growth dynamic; Serra da  
Galga Formation; Bauru  
group; Late Cretaceous

## Introduction

Titanosauria was a diverse and iconic lineage of sauropod dinosaurs whose main records come from South America (Upchurch et al. 2004; D'Emic 2012; Gorscak and O'Connor 2016; Carballido et al. 2017; Hechenleitner et al. 2020). Among them, *U. ribeiroi* was described based on several postcranial elements, (putatively assigned as three individuals), coming from the site known as BR-050 km 153 from the Serra da Galga Formation (Maastrichtian) of southeastern Brazil, and recently recovered as a rinconsaurian titanosaur (Hechenleitner et al. 2020; Navarro et al. 2022; Silva Junior et al. 2022). Later, more skeletal remains were discovered and described (Silva Junior et al. 2019), indicating the presence of more individuals in the unearthed quarry. This fossil assemblage is dominated by several specimens of *U. ribeiroi* in different ontogenetic stages (Salgado and Carvalho 2008; Silva Junior et al. 2019).

With the advancement of scientific knowledge and the appearance of new technologies, palaeohistological investigations of fossil vertebrate forms are becoming more frequent. Among sauropod dinosaurs, *U. ribeiroi* is no exception, since a pair of previous palaeobiological studies were carried out in specimens assigned to this species. The first study concerns the presence of palaeopathologies in caudal elements (two fused vertebrae and a healing fracture callus in a haemal arch) (Martinelli et al. 2015), while, the second provides evidence of osseous tissue related to the presence of pneumatic diverticula extending from the respiratory system (the

so-called pneumosteam) in a cervical vertebra, and highlights how taphonomy can play an important role in providing evidence of vertebral pneumaticity (Aureliano et al. 2019). We highlight that despite that histological sections of *U. ribeiroi* specimens have been the subject of a previous investigation, that investigation had a different focus from that of the present paper. To date, *U. ribeiroi* has never been microstructurally described in detail.

Considering that palaeohistology has become a widely used tool to elucidate palaeobiological aspects among fossil forms, including sauropod dinosaurs (e.g. Sander 2000; Chinsamy Turan 2005; Castanet 2006; Ricqlès de 2006; Klein and Sander 2008; Erickson 2014; Waskow and Sander 2014; Cerda et al. 2017; Woodruff et al. 2017), a detailed osteohistological description of the axial and appendicular elements referred to titanosaur *U. ribeiroi* is presented here. Our goal is to identify the osteohistological ontogenetic stages of the sampled specimens. Additionally, this study aims to increase our knowledge of cervical rib genesis and growth dynamics in sauropod dinosaurs, especially titanosaurs.

## Geological setting

The Serra da Galga Formation is the geological unit of the Bauru Group that has the richest fossil record of titanosaurs in the Late Cretaceous of Brazil (e.g. Martinelli and Teixeira 2015; Soares et al.

2020; Silva Junior et al. 2022). This unit crops out in the east portion of the Triângulo Mineiro region, Minas Gerais State, and was before considered as a member within the extensive Marília Formation (Fernandes and Coimbra 2000; Soares et al. 2020). After this new lithostratigraphic proposal, the Marília Formation remained with a relatively low fossil record (see Iori et al. 2021).

The Serra da Galga Formation has provided a taxonomically diverse fossil biota, including remains of plants, invertebrates, and disparate groups of vertebrates (e.g. Candeiro et al. 2006; Martinelli and Teixeira 2015; Menegazzo et al. 2016). Among vertebrate groups in this formation there exists a considerably large diversity of fishes, anurans, lizards, chelonians, crocodylians and saurischian dinosaurs (e.g. França and Langer 2005; Novas et al. 2008; Báez et al. 2012; Martinelli and Teixeira 2015; Silva Junior et al. 2022). In particular, the sauropod diversity of this unit is represented by three species of titanosaurs: *Baurutitan britoi* (Kellner et al. 2005), *Caieiria allocaudata* (Silva Junior et al. 2022), and *Uberabatitan ribeiroi* (Salgado and Carvalho 2008) plus several remains of Titanosauria indet (e.g. Campos and Kellner 1999; Santucci 2002; Powell 2003; Santucci and Bertini 2006; Martinelli et al. 2011, 2015; Silva Junior et al. 2017).

## Material and methods

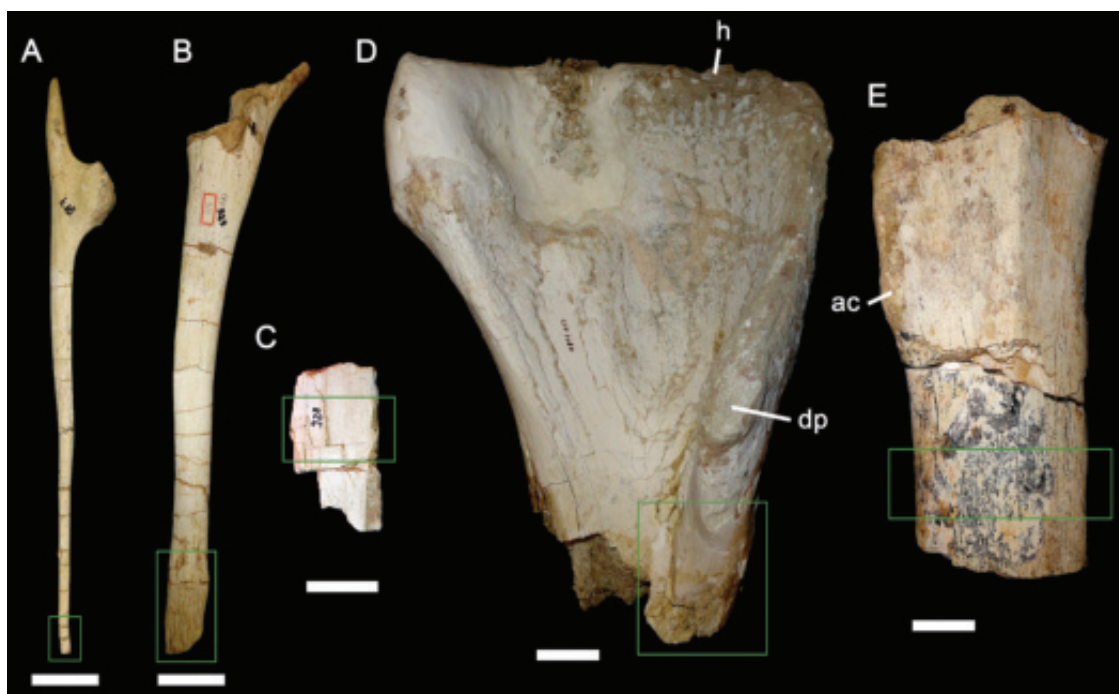
The materials here studied are housed at the Centro de Pesquisas Paleontológicas Lewellyn Price (CPPLIP), Complexo Cultural e Científico Peirópolis, Universidade Federal do Triângulo Mineiro, Peirópolis, Uberaba, Minas Gerais, Brazil. The studied samples are: the distal portion of a cervical rib (CPPLIP-917); the distal end (CPPLIP-925) and middle portion of dorsal ribs (CPPLIP-928); a portion of the left humerus below the level of the deltopectoral crest (CPPLIP-1030); and the diaphysis of a right femur (CPPLIP-1687) (Figure 1). These elements come from a single quarry and are referred to as *U. ribeiroi*; the cervical rib and humerus were previously assigned as part of the holotype specimen.

Complete cross-sections were obtained from all samples, except the diaphysis of the humerus, for which only a small fragment was sampled. A Dremel rotatory tool equipped with a thin diamond-edge saw was used in order to obtain all histological thin-sections. The samples were processed in the Palaeohistological Laboratory of 'Museo Provincial Carlos Ameghino' (Cipolletti, Río Negro Province, Argentina) following standard procedures (Chinsamy Turan and Raath 1992; Cerda et al. 2020). Finally, the samples were examined using a petrographic cross-polarising microscope (BestScope and Nikon E200 POL). The histological nomenclature and terminology employed in this contribution follow Francillon-Vieillot et al. (1990) and Ricqlès de et al. (1991).

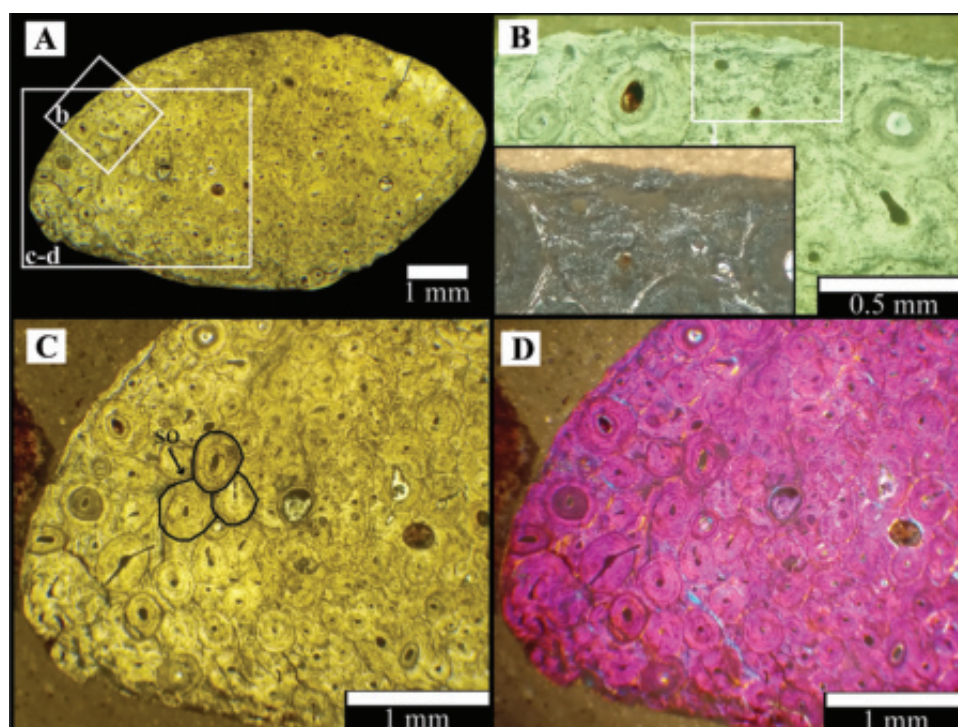
## Results

### Cervical rib

The cervical rib CPPLIP-917 is elliptical and symmetrical in cross-section, being slightly dorsoventrally compressed. The microanatomy consists of a compact bone without medullary cavity (Figure 2A). The compacta mainly consists of secondary bone and only a small portion of primary bone is localised near the outer cortex. At least three generations of secondary osteons can be observed (Figure 2B). In most cases the secondary osteons are completely filled with a high amount of lamellar bone and exhibit narrow vascular spaces. Remains of interstitial primary bone can be observed between the secondary osteons (Figure 2C,D). The primary bone contains a high density of coarse bundles of mineralised collagenous fibres. These fibres bundles have a diamond-shape in cross section under cross-polarised light, and they are enclosed by a distinct sheath (Figure 2B). The vascularisation is profuse and consists of small vascular spaces which mostly exhibit longitudinal orientation. Sharpey's fibres and cyclical growth marks (CGMs) were not recorded in the primary bone.



**Figure 1.** Specimens of *Uberabatitan ribeiroi* (Late Cretaceous, Serra da Galga Formation, Bauru group) selected for histological studies; the square indicates the region that was sampled. (A) distal portion of cervical rib (CPPLIP-917, holotype). (B) distal end of dorsal rib (CPPLIP-925). (C) middle portion of dorsal rib (CPPLIP-928). (D) proximal portion of left humerus in anterior view (CPPLIP-1030, holotype). (E) diaphysis of right femur in anterior view (CPPLIP-1687). Abbreviations: ac, adductor crest; dp, deltopectoral crest; h, head. Scale bars equal 5 cm.



**Figure 2.** Bone microstructure of the cervical rib (CPPLIP-917) of *Uberabatitan ribeiroi*. (A) complete histological section. (B) detail of primary bone matrix in the outer cortex. (C) secondary osteons and remains of interstitial primary tissue, under normal transmitted light. (D) secondary osteons under polarised light with a lambda compensator. Abbreviation: so, secondary osteons.

### Dorsal ribs

The portions of the two dorsal ribs have similar histological features, thus we describe them together, highlighting the differences where applicable. The dorsal rib CPPLIP-925 has a large medullary cavity (Figure 3A) bordered by trabecular bone (Figure 3B), while in CPPLIP-928 the medullary cavity reveals trabecular spaces struts, which is formed by lamellar tissue (Figure 4A-C). The cortical regions in both dorsal ribs are mostly composed of dense Haversian tissue, with at least four generations of overlapping secondary osteons identified. Indeed, in some instances the secondary osteons reach the subperiosteal border (Figures 3C and 4D,E). The primary bone matrix is composed of fibrolamellar bone tissue, with globular osteocyte lacunae embedded in a matrix formed by haphazardly arranged fibres (with a low level of birefringence) (Figures 3D,E and Figures 4F,G). Vascular canals are mainly longitudinally oriented. Sharpey's fibres are oriented perpendicularly or slightly obliquely in the outer region of bone (Figure 3F,G). The outermost cortex exhibits an almost avascular layer of parallel fibred bone, with at least six closely spaced LAGs in CPPLIP-925 (Figure 3H,I) and at least three in CPPLIP-928 (Figure 3F-I). Some vascular canals open to the subperiosteal margin in CPPLIP-925.

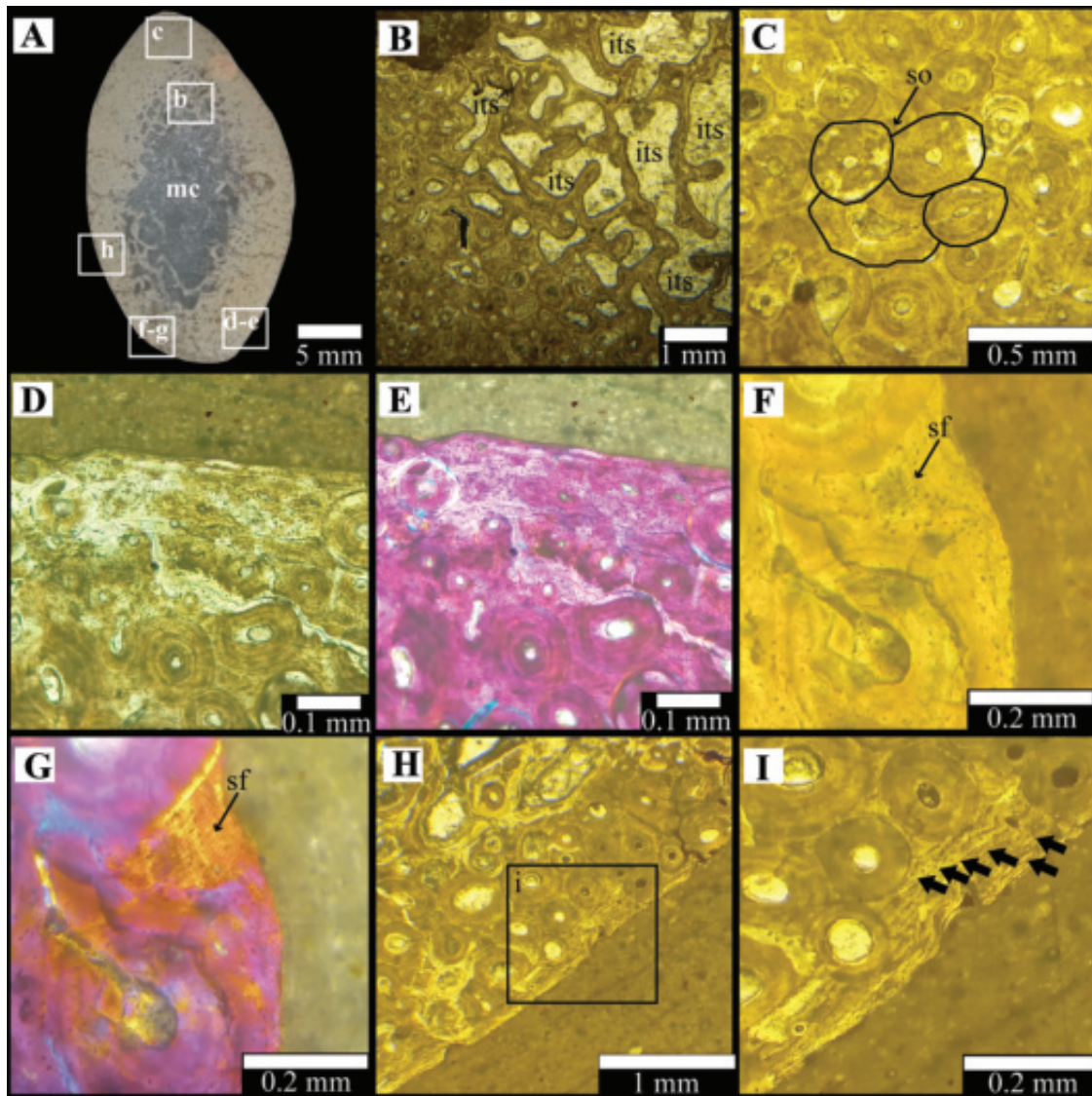
### Humerus

The medullary region of the humerus CPPLIP-1030 is formed by trabeculae with large intertrabecular spaces (Figure 5A-C). Trabecular bone is composed of secondary tissue (Figure 5C). Bone remodelling is extensive (Figure 5D,E), with abundant secondary osteons (at least three generations). Some of them reach the outermost cortex of the sample. The compacta is composed of fibrolamellar tissue with a poor ordering of

intrinsic fibres, which is inferred from the low degree of birefringence (Figure 5F,G). The osteocyte lacunae are generally globular in shape. The primary bone is highly vascularised. The vascular spaces exhibit a laminar to plexiform pattern (Figure 5F-I). Towards the external cortex, CGMs are evident on the humerus, with at least four LAGs. Three of them generate planes of weakness in some areas (Figure 5I).

### Femur

The thin section includes tissue from the entire shaft of the femur CPPLIP-1687. While the bone histology is not perfectly preserved, some areas still retain well-distinguishable microstructural characteristics. The specimen has a wide medullary cavity filled with sediment (Figure 6A) and bordered by trabecular bone. The trabecular tissue is composed of secondarily formed lamellar bone, including remains of Haversian osteons (Figure 6B). Large and irregularly distributed erosion cavities extend from the inner to the middle regions of the cortex (Figure 6C). The compacta mostly exhibits highly vascularised fibrolamellar bone. The vascularisation pattern is laminar, but occasional oblique anastomoses occur (Figure 6D-J). The osteocyte lacunae are mainly round in shape. The matrix exhibits a low to moderate degree of birefringence in some parts. The sample presents abundant concentric bands of secondary osteons (Figure 6F,G). These bands, in two cases coincide with very regular fractures that laterally follow a clear plane of weakness (Figure 6H), indicating the presence of at least two CGMs. The sample has a high degree of bone remodelling (especially in the anterior region), with at least three generations of secondary osteons (Figure 6K). Secondary osteons are randomly distributed in the diaphysis, from the inner to the outer portions of the cortex.



**Figure 3.** Bone microstructure of the dorsal rib (CPPLIP-925) of *Uberabatitan ribeiroi*. (A) general view of the complete cross-section, note the large medullary cavity. (B) detailed view of the transition between compact and trabecular bone in the perimedullary region. (C) dense Haversian tissue showing four generations of overlapping secondary osteons. (D) (E) dense Haversian tissue with interstitial remains of fibrolamellar primary bone, note the mass monorefringence (D) and cross-polarised light with a lambda compensator (E). (F) (G) detailed view of the external cortex showing Sharpey's fibres under normal (F) and cross-polarised light using a lambda compensator (G). (H) outermost cortex with an avascular layer of parallel fibred bone. (I) detail of six closely spaced LAGs. Abbreviations: its, intertrabecular space; sf, Sharpey's fibres; so, secondary osteons.

## Discussion

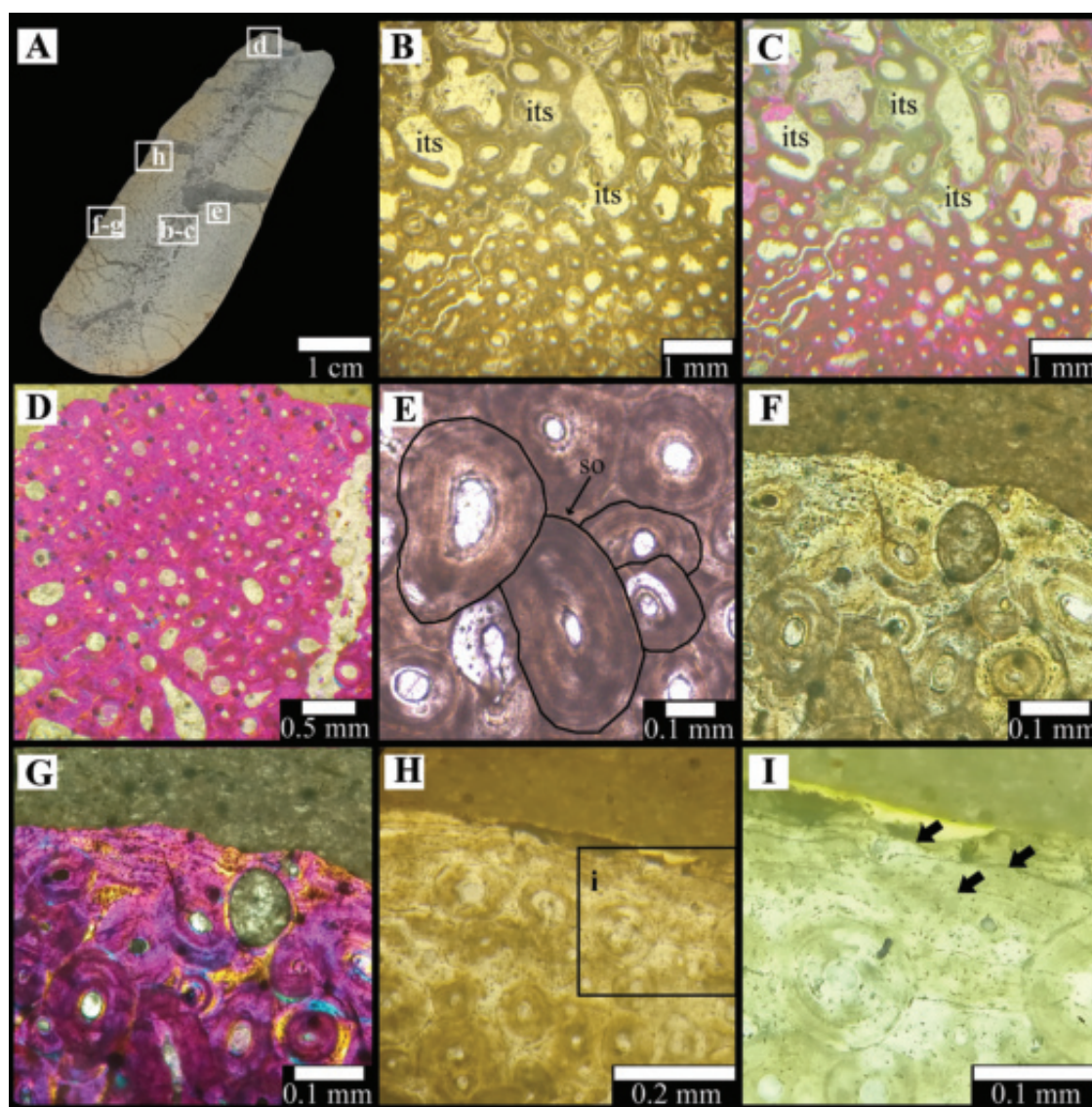
### Cervical rib genesis

It is previously known that the hyper-elongated cervical ribs present in sauropods correspond at the histological level with bone tissue formed from metaplasia of previous ossified tendons (e.g. Cerda 2009, 2022; Gallina 2012; Klein et al. 2012a; Martínez et al. 2016; Díez Díaz et al. 2018). Thus, the histology of these elements is characterised by the presence of dense clusters of mineralised collagen fibres that align in parallel with the main axis of the ribs (Cerda 2022). Comparable structures are also present in the cervical rib sample of *U. ribeiroi* CPPLIP-917 here studied, strengthening the previous hypothesis for cervical rib origin of some sauropods. At the same time, the high degree of bone remodelling described in CPPLIP-917 and cervical ribs of other titanosaur sauropods such as *Aeolosaurini* indet. DGM 198-R, *Bonitasaura salgadoi*, *Gondwanatitan faustoi*, *Maxakalisaurus topai*, *Sarmientosaurus musacchioi* and Titanosauria indet. MUCPh 138-142 (Cerda

2009; Gallina 2012; Martínez et al. 2016; Brum et al. 2021, 2022) account for a rapid replacement of primary metaplastic bone tissue by secondary tissue.

### Minimum age of *Uberabatitan* specimens

The titanosaurian fossil record of South America shows a taxonomic diversification and a wide geographic dispersion, especially in Argentina and Brazil (Otero et al. 2022). This high diversity has allowed for several palaeohistological investigations (e.g. Company 2011; Klein et al. 2012b; Cerda et al. 2015; García et al. 2015; Carballido et al. 2017; Curry Rogers and Kulik 2018; Aureliano et al. 2019; González et al. 2020; Brum et al. 2021, 2022); however, numerous palaeobiological aspects of titanosaurs are still shrouded in mystery. The specimens described here of *U. ribeiroi*, in general terms, exhibit a series of features also present in other previously studied titanosaur sauropods (e.g. *Pellegrinisaurus*) (Cerda et al. 2021). These are:



**Figure 4.** Bone microstructure of the dorsal rib (CPPLIP-928) of *Uberabatitan ribeiroi*. (A) general view of the complete cross-section. (B) (C) trabecular bone under normal transmitted light (B) and under polarised light with a lambda compensator (C). (D) compact bone formed by dense Haversian tissue. E, detail of the four generations of secondary osteons. (F) (G) dense Haversian tissue with interstitial remains of fibrolamellar bone viewed under plane (F) and cross-polarised light with a lambda compensator (G). (H) outermost cortex shows an avascular layer of parallel fibred bone. (I) detail of three closely spaced LAGs. Abbreviations: its, intertrabecular space; so, secondary osteons.

abundant Haversian tissue, with a small amount of primary tissue limited to the outer cortex, and primary bone composed of fibrolamellar bone (in some cases interrupted by cyclical growth marks).

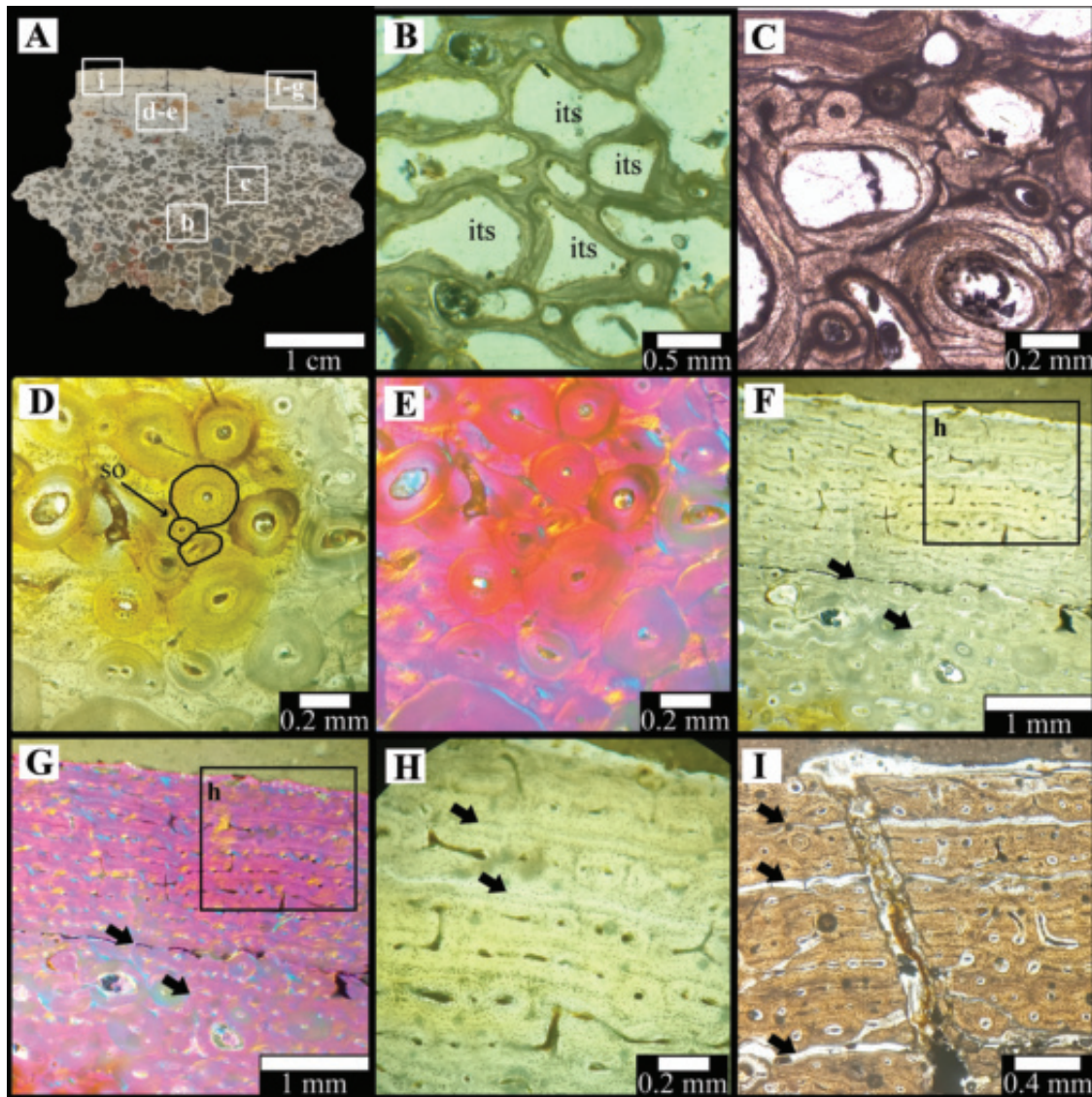
Despite that the high degree of remodelling obliterated most of primary bone in ribs (CPPLIP-917/CPPLIP-925/CPPLIP-928), four CGMs in the fibrolamellar bone tissue of the humerus (CPPLIP-1030) were identified, as were two in the femur (CPPLIP-1687) (Table 1). Assuming an annual periodicity of these histological structures (Castanet et al. 1993; Chinsamy Turan 2005; Curry Rogers and Erickson 2005; Castanet 2006), each stylopodial specimen would have reached a minimum age of four years and two years, respectively, before perishing.

#### **Growth dynamics and bone remodelling**

The growth dynamics of extinct forms, including sauropodomorph dinosaurs, is perhaps the most explored topic in palaeohistological

studies in vertebrates (Sander et al. 2011). Studies to date indicate that early-branching sauropodomorphs ('prosauropods') produced growth markings throughout their ontogeny; suggesting a relatively slow growth, with marked seasonal interruptions throughout its ontogeny. As for the sauropods, these marks only appeared in the most advanced stages of their development, evidencing an accelerated and continuous growth during most of the ontogeny in Sauropoda (Sander et al. 2004, 2011).

Based on the appendicular bones, we interpret that the growth dynamics of *U. ribeiroi*, like other titanosaurs, is comparable to that of other neosauropods (Sander 2000; Sander et al. 2004, 2011; Klein and Sander 2008), with rapid and uninterrupted growth (evidenced by a continuous deposit of fibrolamellar tissue) (Figure 7). Subsequently, growth would have ceased in the most advanced stages of development, with the appearance of periodic interruptions (cyclical growth marks obliterated in axial elements, but present in appendicular bones). The presence of CGMs would indicate that the specimens studied experienced growth slowdowns due to growth interruptions,

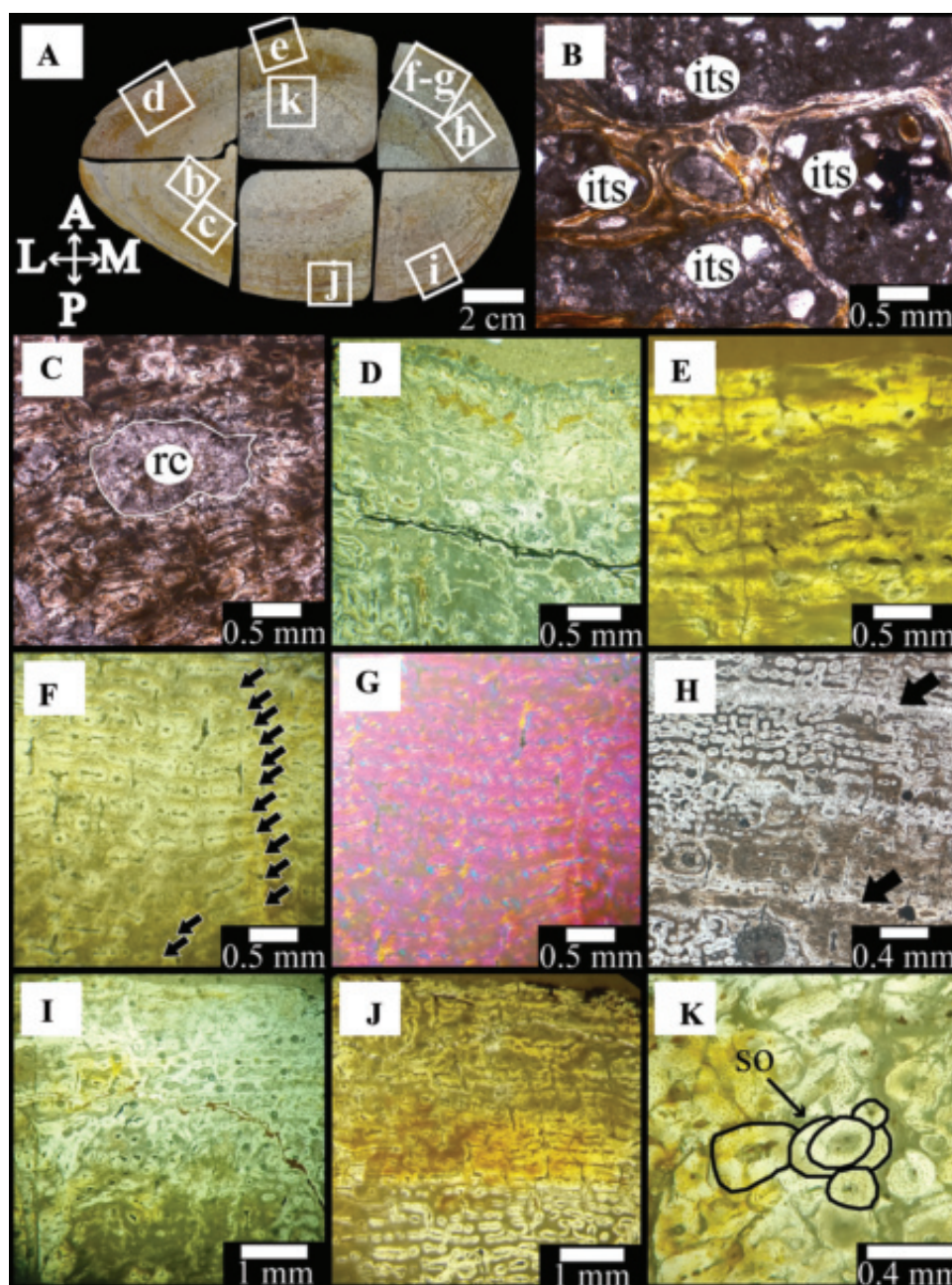


**Figure 5.** Bone microstructure of the humerus (CPPLIP-1030) of *Uberabatitan ribeiroi*. (A) general view of the sampled cross-section. (B), (C) general view of trabecular bone (B) showing remains of secondary osteons in the trabeculae (C). (D), (E) extensive bone remodelling showing at least three generations of overlapping secondary osteons viewed under plane (D) and cross-polarised light with a lambda compensator (E). (F), (G) outermost cortex shows primary fibrolamellar tissue with CGMs viewed under plane (F) and cross-polarised light with a lambda compensator (G). (H) detail of two CGMs. (I), CGMs coinciding laterally with planes of weakness. Abbreviations: so, secondary osteons.

as was described for other titanosaurs such as *Lirainosaurus* and *Magyarosaurus*, and even other non-titanosaurian neosauropods, such as *Amargasaurus*, *Barosaurus*, *Europasaurus* and *Katapsaurus* (Sander 2000; Sander et al. 2006; Klein and Sander 2008; Klein et al. 2009, 2012b; Stein et al. 2010; Company 2011; Ibiricu et al. 2017; Windholz and Cerda 2021). This pattern contrasts with that inferred for early-branching sauropodomorphs, which exhibited cyclical growth even from the early stages of development (Sander et al. 2011; Cerda et al. 2017; Botha et al. 2022).

Histological differences may be linked to physiological variations specific to each clade. Consequently, it is expected that certain histological features will vary between different lineages (Sander 2000; Klein and Sander 2008). Thus, in some cases it is possible to recognise histological features that are unique to different groups (Sander 2000). Specifically, current knowledge of titanosaur histology indicates that there is a trend in this

group towards higher bone remodelling (Woodward and Lehman 2009; Company 2011; García et al. 2015; González et al. 2020). The high degree of remodelling observed in the elements studied here, especially in the ribs, supports the premise that the members of the Titanosauria clade had a higher remodelling rate than the rest of the sauropodomorphs; supporting the previous idea that this characteristic would be typical of Titanosauria. Similarly, certain features of the bone microstructure (such as the degree of secondary remodelling, among others) vary during the ontogeny of sauropods, providing further evidence of the ontogenetic stages based on the osteohistology of individuals (Klein and Sander 2008). However, the high degree of bone remodelling described in the samples studied here, as well as in other titanosaurs (e.g. *Magyarosaurus*), is higher than expected for other neosauropods in the same ontogenetic stages (Mitchell et al. 2017).

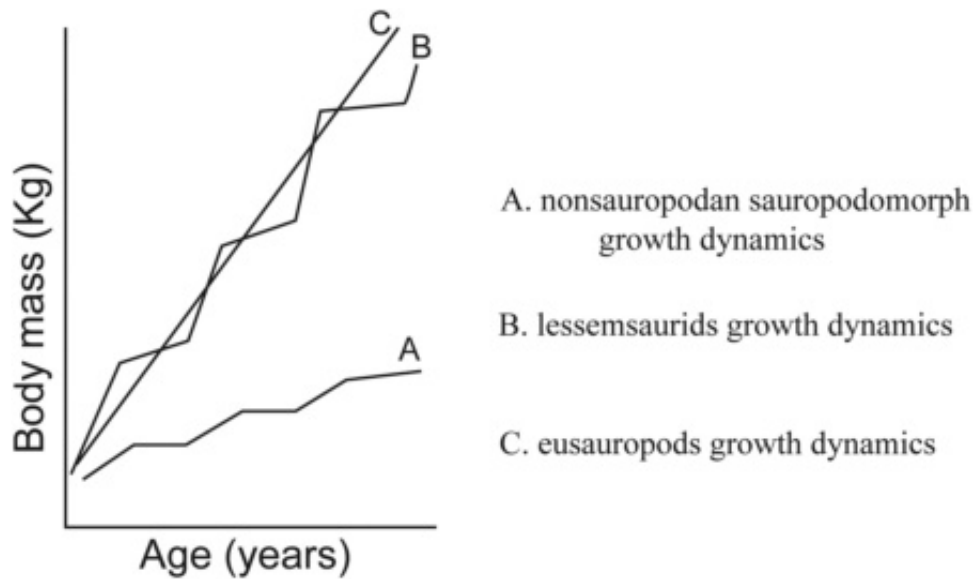


**Figure 6.** Bone microstructure of the femur of *Uberabatitan ribeiroi* (CPPLIP-1687). (A) complete histological section of the diaphysis. (B) detail of trabecular bone. (C) detail of erosion cavities. (D) outermost cortex shows primary bone in anterolateral region. (E) primary bone with a laminar vascularisation pattern. (F), (G) concentric bands of secondary osteons under plane (arrowheads) (F) and cross-polarised light with a lambda compensator (G). (H) detail of two CGMs, notes that the same generate weakness planes that provoke regular fractures. (I), (J) lamina vascularisation pattern with occasional oblique anastomoses at posteromedial (I) and posterior region (J). (K) detail of secondary osteons. Abbreviations: its, intertrabecular space; rc, resorption cavity; so, secondary osteons.

**Table 1.** Histological features of sampled materials of *Uberabatitan ribeiroi*.

Anatomical element	Specimen number	Specimen type	CGMs	EFS	HOS
Cervical rib	CPPLIP-917	Referred specimen (previously holotype specimen)	0	no	not applicable
Dorsal rib	CPPLIP-925	Referred specimen	0	yes	not applicable
Dorsal rib	CPPLIP-928	Referred specimen	0	yes	not applicable
Humerus	CPPLIP-1030	Referred specimen (previously holotype specimen)	4	no	9/10
Femur	CPPLIP-1687	Referred specimen	2	no	9/10





**Figure 7.** Scheme showing different growth strategies among sauropodomorphs: slow and interrupted growth (A) rapid and interrupted growth (B) rapid and uninterrupted growth (C). The growth dynamics of the specimens studied here conforms to 'C'. Modified after Apaldetti et al., (2018).

### Ontogenetic stage assignment

The time at which sexual maturation is reached varies among living vertebrates. While in certain groups of reptiles (such as squamates and crocodylians), sexual maturation occurs prior to somatic maturation, the opposite occurs in most birds (Erickson et al. 2007; Lee and Werning 2008; Ikejiri 2012). Among fossil forms, identification of sexual maturation is often more difficult. However, in the specific case of sauropod dinosaurs there is some consensus that this event takes place prior to somatic maturation (Sander 2000; Sander and Klein 2005; Klein and Sander 2008). In this sense, different criteria have been used to investigate sexual maturation of sauropod individuals. One of these involves the recognition of 'histologic ontogenetic stages' (HOS) proposed by Klein and Sander (2008). According to these authors, 13 HOS may be identified on the basis of a combination of seven different types of bone tissues. Each tissue type is characterised by several features, such as vascularisation pattern, degree of secondary remodelling, presence of growth marks, type of bone matrix and its degree of organisation. The onset of sexual maturation was reached around HOS 8.

Osteohistological characteristics observed in stylopodial bones of *U. ribeiroi* (i.e. the humerus and femur) show certain similarities between them. Both cases are composed of fibrolamellar bone with medium-size vascular canals representing a still fast-growing tissue. Also, these vascular spaces show a mainly laminar organisation. Secondary osteons are mainly deposited at inner and middle areas of compacta, although in some cases it reaches outer cortex. Finally, CGMs in both appendicular elements were preserved (Table 1). Following the criteria of Klein and Sander (2008), the histology of the long bones studied here shows mainly type E bone tissue (primarily fibrolamellar bone, with medium-size vascular spaces; secondary osteons may extend up to the middle of the primary cortex; and growth marks may occur), which predominates in the HOS 9 and 10, which, in turn, suggests that the individual reached sexual maturation.

When an individual reaches sexual maturity it begins to grow more slowly; and, consequently, it will show changes in the degree of organisation of the intrinsic fibres that make up their bone

matrix (Sander 2000). Thus, an individual that has reached sexual maturation is expected to show a lower degree of organisation in the medullary region and transitional changes to a higher degree of organisation in the cortical region of the bone (Francillon-Vieillot et al. 1990; Chinsamy Turan 2005). A slowdown in bony apposition rates also tends to be accompanied by CGMs; a reduction in the spacing between these histological structures towards the most cortical region of the bone can be linked to sexual maturation (Castanet and Baez 1991; Khonsue et al. 2010). Surprisingly, the histological sections taken from both appendicular elements of *U. ribeiroi* show quite a homogeneous degree of organisation (fibrolamellar bone), and the distance of the CGMs appears to be similar throughout the sample of the humerus (CPPLIP-1030). These features yield conflicting results with the HOS criteria of Klein and Sander (2008), since they account for individuals that did not reach sexual maturation. However, the determination of HOS so far seems to be a good tool to deal with the scarce growth marks in stylopodium of some neosauropods, especially titanosaurs, whose bone remodelling advances in early ontogenetic stages (e.g. Woodward and Lehman 2009; Stein et al. 2010).

According to the literature, an external fundamental system (EFS), also called outer circumferential layer, is a type of bone that consists of avascular or poorly vascularised parallel fibred or lamellar bone. This structure is typically found on the outermost part of the histological section and contains numerous closely spaced LAGs (Sander 2000; Sander and Klein 2005; Erickson et al. 2007; Klein and Sander 2007, 2008). Most samples studied here lack EFS, as occurs in individuals assigned to different titanosaur taxa, such as *Lirainosaurus*, *Magyarosaurus* and *Ampelosaurus* (Klein et al. 2012b); evidencing that the specimens of *U. ribeiroi* studied here died in an active phase of growth. However, the outer cortex of dorsal ribs CPPLIP-925/CPPLIP-928 displays an avascular layer of parallel fibred bone that contains at least six and three closely spaced CGMs, respectively. We interpret this structure as EFS, which suggests that the individual was indeed a fully grown individual. Among titanosaurs, this histological structure is also present in, for example, *Epachthosaurus* and *Neuquensaurus* specimens studied by Cerda et al. (2015) and García et al. (2015), respectively.

## Conclusions

The first study based exclusively on the osteohistology of the Brazilian titanosaur *Uberabatitan ribeiroi* is presented here. This investigation shows that hyper-elongated cervical ribs of this species correspond with tendons that have developed through metaplasia, like in other Neosauropoda members. *U. ribeiroi* shows a rapid and uninterrupted growth, with periodic interruptions in the most advanced stages of development (at least in appendicular bones). Whereas some of the specimens studied died in an active phase of growth, others appear to have reached somatic maturation (EFS in dorsal ribs). Finally, studied samples show a high degree of bone remodelling (typical feature of Titanosauria), especially in the ribs, compared to what is expected for other neosauropods in comparable ontogenetic stages.

## Acknowledgments

We would like to thank the Centro de Pesquisas Paleontológicas Llewellyn Ivor Price, and Universidade Federal do Triângulo Mineiro, for providing the specimens studied here and to the staff for the field and lab assistance provided over the years. We thank the Sci-hub library and Wikipaleo group for sharing with us the relevant bibliography. This research received support from Agencia Nacional de Promoción Científica y Tecnológica (PICT-2015-1021 to I.A.C.).

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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