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Analyzing the Life History of Caimans: The Growth Dynamics of *Caiman latirostris* From an Osteohistological Approach

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ABSTRACT

Skeletochronology and growth dynamics are intensively investigated in vertebrate osteohistology. These techniques are particularly important for interpreting the life history of long-lived species, such as crocodilians. To understand the longevity, growth dynamics, sexual maturity, and sexual dimorphism of caimans we studied an almost complete ontogenetic series of captive and wild specimens of *Caiman latirostris* from different localities of Argentina. We identified both cyclical and noncyclical growth marks in juvenile caimans, and we suggest that the latter are associated with environmental stress. By overlapping the growth marks of different individuals, we were able to estimate the minimum age of each specimen. Variations in growth rate are evident in different bones, with the femur and scapula having the highest growth rates, while the fibula and pubis have much slower growth rates. We were able to determine the approximate age of sexual maturity from growth curves deduced from osteohistology, which concurred with those assessed in ecological studies. Additionally based on the growth curves we were able to document different growth dynamics which may be related to sexual dimorphism. This study provides valuable insights into the life history and ecological dynamics of crocodilians, shedding light on their growth patterns, attainment of sexual maturity, and the influence of environmental factors on growth. Furthermore it documents the intraspecific and interelemental osteohistological variation in crocodilians and has direct implications for studies that assess the life history of extinct archosaurs and other sauropsids.

1 | Introduction

Skeletochronology is widely used in modern and fossil vertebrates to determine the minimum age of the individuals in addition to understanding various aspects of their life history (e.g., Avens et al. 2009; Castanet and Baez 1991; Castanet et al. 1993; Chinsamy 2023; Snover and Rhodin 2007; Tucker 1997). Such studies are based on the identification of growth marks (GMs) that are deposited in the mineralized tissues, such as long bones, osteoderms, teeth, scales, and otoliths (e.g., Avens and Snover 2013; Castanet 1994; Castanet and Baez 1991; Castanet et al. 1993; Chinsamy-Turan 2005; Curtin et al. 2005; Klevezal 1996; Klinger and Musick 1995). Skeletochronology has been tested and validated as a reliable age estimation method through numerous techniques (e.g., capture and recapture, Bjorndal et al. 2003; Caetano and Castanet 1993; Castanet et al. 1993; Halliday and Verrell 1988; use

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of morphometric measurements, Mattox 1936; determination of the maturity of the gonads, Halliday and Verrell 1988; fluorochrome injections, Castanet et al. 1993; Cubo et al. 2008; de Buffrenil and Castanet 2000; known age specimens, Snover and Hohn 2004). This methodology has been applied to amphibians (e.g., Castanet and Smirina 1990; Erismis and Chinsamy 2010), reptiles (e.g., Castanet and Smirina 1990; Chinsamy and Valenzuela 2008; Peabody 1961), and mammals (e.g., Klevezal 1996; Köhler et al. 2012; Montoya-Sanhueza and Chinsamy 2017). Among extant crocodilians, skeletochronology has not been utilized extensively, although there are studies performed in *Alligator mississippiensis* (e.g., Garcia 2011; Rainwater et al. 2021; Roberts et al. 1988; Woodward, Horner, and Farlow 2014), *Crocodylus niloticus* (Hutton 1986), and *Crocodylus johnstoni* (Tucker 1997).

Growth marks are produced because of a variation in the rate of osteogenesis (e.g., Castanet et al. 1993; Chinsamy-Turan 2005; Woodward, Horner, and Farlow 2014). The periods of fast osteogenesis are represented by zones and the periods of slower osteogenesis are represented by annuli or/and lines of arrested growth (LAGs; e.g., Chinsamy-Turan 2005; de Ricqlès et al. 1991; Francillon-Vieillot et al. 1990; Ray, Mukherjee, and Bandyopadhyay 2009). Although GMs are generally considered to be annually formed, such periodicity is unsupported in some vertebrates, and it is still under study (e.g., Halliday and Verrell 1988; Klein, Scheyer, and Tütken 2009; Schucht, Klein, and Lambertz 2021; Smirina 1994). The deposition of GMs is linked to biological rhythms (intrinsic processes), which are synchronized and reinforced by environmental cues (extrinsic processes; e.g., Castanet et al. 2004; Guarino, Andreone, and Angelini 1998; Hemelaar 1980; Klevezal 1996; Köhler et al. 2012; Marín-Moratalla, Jordana, and Köhler 2013; Mattox 1936; Patnaik and Behera 1981; Peabody 1961; Roberts et al. 1988; Zug 1991). Some studies have demonstrated a correlation between the occurrence of GMs and environmental variations (e.g., Andrade et al. 2018; Chinsamy and Warburton 2021; de Buffrenil and Buffetaut 1981; Hutton 1986; Peabody 1961; Tucker 1997; Woodward, Horner, and Farlow 2014).

The growth dynamics of vertebrates can be reconstructed based on relative and/or absolute growth rates. The rate of osteogenesis is affected by the growth rate which is evident in the microstructural features in the cortex of the bones or/and on the spatial distribution of consecutive cyclical GMs (e.g., Castanet et al. 1993; Castanet et al. 2000; Chinsamy-Turan 2005; Chinsamy and Warburton 2021; Chinsamy 2023; Cullen et al. 2020; Francillon-Vieillot et al. 1990). Studying growth strategies is fundamental for understanding life history traits (such as hatching, attainment of sexual maturity, time of reproduction, and lifespan) of different species. Thus, by studying growth curves based on rates of osteogenesis as well as the bone microstructure of individuals it is possible to infer such life history events (e.g., Botha-Brink and Smith 2011; Castanet and Baez 1991; Chinsamy, Codorniu, and Chiappe 2009; Hugi and Sánchez-Villagra 2012; Waskow and Mateus 2017; Woodward et al. 2015).

In the case of long-lived animals, such as crocodilians, that have lifespans exceeding 50 years (Castanet 1994; Grigg and Kirshner 2015; Hutton 1986; Wilkinson et al. 2016), it is challenging to follow their life history. Since skeletochronology can provide information regarding ontogenetic age, longevity, and lifehistory strategies, as well as growth dynamics, it is a reliable methodology for understanding the biology and ecology of wild populations of crocodilians, as well as their evolutionary history (e.g., Audije-Gil, Barroso-Barcenilla, and Cambra-Moo 2023; Bailleul and Schweitzer 2023; Garcia 2011; Hutton 1986; Patnaik and Behera 1981; Peabody 1961; Roberts et al. 1988; Tucker 1997; Wilkinson et al. 2016; Woodward, Horner, and Farlow 2014; Zhao et al. 2019). It is worth noting that among crocodilians, growth rates directly impact on their body size and are therefore an important determinant of sexual dimorphism (e.g., Bona et al. 2017). Since sexual maturity in crocodilians is body size dependent, with males often growing faster and reaching larger sizes than females, growth rate therefore determines when males and females reach reproductive body sizes (e.g., Grigg and Kirshner 2015; Magnusson et al. 1990; Werning 2013). There are only a few studies that record the actual age at which sexual maturity was reached in crocodilians (e.g., Brazaitis 1973; Da Silveira et al. 2013; Eaton and Link 2011; Lance 2021; Larriera et al. 2006; Magnusson and Sanaiottio 1995; Verdade et al. 2003; Verdade and Sarkis 1998; Viotto, Navarro, and Piña 2020; Webb, Manolis, and Buckworth 1983; Wilkinson et al. 2016; Wilkinson and Rhodes 1997). Thus, although it is known at what size crocodilians reach sexual maturity, the age at which this is attained is poorly known (e.g., Larriera et al. 2006; Kofron 1990).

Crocodilians have variable growth rates which can be influenced by ontogeny, sex, habitat, and geographical location, among others (Hutton 1987; Jacobsen and Kushlan 1989; Magnusson and Taylor 1981; Webb, Manolis, and Buckworth 1983). Thus, among crocodilians substantial variation in growth rates occurs because of interspecific, intraspecific as well as sexual dimorphism (Campos et al. 2008; Thorbjarnarson 1996).

The aim of this study is to analyze the bone histology of *Caiman latirostris* to estimate the age of sexual maturity, decipher whether or not sexual dimorphism is detectable in the bone microstructure, and to obtain an estimation of body mass through ontogeny based on skeletochronology. As such, we estimate the minimum age of all individuals in the study, and we determine which of the long bones maintains the best record of growth, as well as evaluate the growth rate and growth dynamics of each bone to assess intraskeletal variation. The overarching aim of this study is to assess the intraspecific and interelemental osteohistological variation in crocodilians, which has direct implications for studies that attempt to decipher the life history of extinct archosaurs and other sauropsids.

2 | Materials and Methods

Specimens of *C. latirostris* from different localities of Argentina are housed in the collection of reptiles of the Museo de La Plata (MLPR). Seven of the specimens studied were captive individuals, while six specimens were wild (Table 1). The captive specimens were obtained from a rescue center in Santa Fé province called "La Esmeralda" (Proyecto Yacaré; Larriera, Imhof, and Siroski 2008). The wild specimens were collected from the provinces of Corrientes, Salta, and Chaco. The anterior and posterior appendicular bones (hindlimb, forelimb, anterior and posterior girdle) of all specimens were studied. The determination of the sex, defatting, and the calcified thin sectioning methods are as described in Pereyra et al. (2024) (Table 2). The cross-section studied here are the same ones which Pereyra et al. (2024) used to document their osteohistology. The sections were examined using a petrographic microscope, and micrographs were taken using a Nikon E200 microscope and a Zeiss petrographic microscope at the University of Cape Town. The analysis was done under transmitted light, cross-polarizer (530 nm), and 1/4 lambda filter under $\times 5$, $\times 10$, and $\times 20$ magnifications. The images were processed using different editing programs (Photoshop CC20, Illustrator 20, AutopanoGiga). The terminology and definitions of histological structures used in this study are from Francillon-Vieillot et al. (1990) and

 TABLE 1
 Locality of the studied specimens of Caiman latirostris.

Specimen	Locality
MLPR-6822	Captivity (known-age)- Proyecto
MLPR-6819	yacare - Santa Fe, Argentina
MLPR-6815	
MLPR-6817	
MLPR-6820	
MLPR-6818	
MLPR-6816	
MLPR-6810	Chevarria, Corrientes, Argentina
MLPR-6771	Salta, Argentina
MLPR-6809	Corrientes, Argentina
MLPR-6770	Cachape, Chaco, Argentina
MLPR-6813	
MLPR-6814	

Chinsamy-Turan (2005). The preparation of the histological sections was carried out in the Museo Provincial Carlos Ameghino (Rio Negro, Argentina) and Museo de La Plata (Buenos Aires, Argentina).

We used skeletochronology to estimate the minimum age of each specimen, based on the presence of GMs in the appendicular bones (Figure 1; Curtin et al. 2008; Hugi and Sánchez-Villagra 2012; Woodward, Horner, and Farlow 2014; Chinsamy 2023). Growth marks are counted from the perimedullary cavity to the subperiosteal margin and are identified according to the criteria described by Peabody (1961) and Castanet et al. (1993). Closely associated GMs, that is, double or triple GMs, are considered as a single growth interruption event (Francillon-Vieillot et al. 1990; Castanet et al. 1993; Castanet and Baez 1991; Cullen et al. 2020). In the cases when the GMs were not fully traceable around the entire compacta due to medullary expansion or secondary reconstruction, we extrapolated each GMs following Nacarino-Menesa, Jordana, and Köhler (2016); however, in the cases where the reconstruction of the GMs was impossible, we expressed these as non-traceable GM. Using the perimeter function of ImageJ (Rasband 2003), the perimeter of each GM, the perimedullary margin, and the subperiosteal margin of each thin section were measured. Additionally, the areas enclosing each GM were also calculated (Supporting Information S1: Figure S1). The ratio of the medullary cavity area to that of the cortex and the cortical-diaphyseal index were also calculated. All measurements were then recorded in Excel worksheets (Microsoft Office).

We used the surface perimeter of the 12-month-old specimens to distinguish between the cyclical and noncyclical GM in the juvenile specimens. Since we have a sample of captive specimens from 6 months to 1 year old, we calculated the perimeter of the surface of each of their bones as well as the perimeter of

TABLE 2 | List of the *Caiman latirostris* specimens studied. The juveniles and adult specimens were classified based on Leiva et al. (2018): Class I: < 25 cm SVL (hatchlings of the year); Class II: 25–67.9 cm SVL (juveniles); Class III: 68–99.9 cm SVL (reproductive male and females); and Class IV: \geq 99.9 cm SVL (reproductive males). Measurements of each of the bones is the maximum length. All the measurements, TL, SVL, and length of the bones are expressed in mm. The specimens MLPR-6822, MLPR-6819, MLPR-6815, MLPR-6817, MLPR-6820, MLPR-6818, MLPR-6816 are known-age captive individuals, while the rest of the specimens are wild with no information about their age.

Specimen	TL	SVL	J/A	Sex	Н	U	R	S	С	Fe	Т	Fi	Р
MLPR-6822	490	240	J	F	25	20.5	17.6	16.4	14	31.8	26.3	25.5	14.3
MLPR-6819	540	270	J	М	31.4	24.8	22.9	22.9	18.7	39	31.9	31	18.4
MLPR-6815	590	290	J	М	37.4	29	25.7	26.8	20.7	45.2	34.4	35.7	21.7
MLPR-6817	640	320	J	М	37.6	29.3	25.8	27.4	21.9	45	37	35.4	21.9
MLPR-6820	650	340	J	М	38	30.2	26.8	26.1	20.5	48	38.2	36.3	22.1
MLPR-6818	700	360	J	М	38.2	29.7	26.3	—	—	45.3	36.2	37	_
MLPR-6816	840	450	J	F	45.3	35.2	32.2	33.8	28.2	52.2	44.5	42.4	27.7
MLPR-6810	880	480	J		60.3	41.5	41	—	—	75	60	57	
MLPR-6771	—	~500	J		57	44	39	42	35	67	55.5	53.5	35
MLPR-6809	~1570	~690	А	—	98	79.5	69.5	—	—	~122	98	95	
MLPR-6770	—	900	А	F	108	82	71	98	79	137	108	100	82
MLPR-6813	~1850	~800	А		128.3	95.2	84.4	117	83.7	162.1	120	114.1	90.9
MLPR-6814	~1950	~930	А	—	125.5	92.3	77.6	94	77	154.3	110.7	108.5	76.2

Abbreviations: A, adult; F, female; Fi, fibula; Fe, femur; H, humerus; J, juvenile; M, male; P, pubis; R, radius; S, scapula; SVL, snout-vent length; T, Tibia; TL, total length; U, ulna.



FIGURE 1 | Growth marks in the long bone of *Caiman latirostris*. Note the preservation of the growth marks in the cross-section of the tibia (a) and radius (b) of adult specimens. The purple lines represent each growth mark. Note that growth marks are only drawn on one half of the cross-section image.

each of the GMs recorded in the compacta. The GMs observed in the specimens less than 1-year-old were considered noncyclical GM, and we have previously proposed that these may have been in response to other stress factors (Pereyra et al. 2024). In the current study, we also documented noncyclical GMs such as hatching lines (HL) and other GMs which may have been related to environmental stress (Pereyra et al. 2024). For clarity, we describe the HL, the noncyclical GM, and the cyclical GM separately.

The age of the wild specimens was deduced by comparing the perimeter of their bone surfaces with known-aged captive young specimens. Retrocalculation of the GMs was deduced by the superposition of the perimeter of the smallest specimen with the largest (e.g., Audije-Gil, Barroso-Barcenilla, and Cambra-Moo 2023; Woodward, Padian, and Lee 2013). Since we have several ontogenetic stages, we were able to evaluate which GM coincides with the ages of the different specimens (e.g., Castanet and Baez 1991; Woodward, Horner, and Farlow 2014). Although the growth rate and age of captive-bred individuals is generally higher than those of wild individuals, we believe that using GMs perimeter values of captive individuals is still useful in providing an estimate of the age of wild animals.

The thickness of each growth cycle was calculated, and the annual growth rate was determined by subtracting the growth cycle of year n from the growth cycle of year n + 1 (e.g., GM 2 -GM 1), and the daily growth rate was calculated by dividing the annual growth rate by 214 which are the number of days of the favorable season (in *A. mississippiensis*; Woodward, Horner, and Farlow 2014; Supporting Information S1: Figure S1). To be able to compare our results with studies where the growth rate was calculated based on the radius of

each GMs and not based on perimeter measurements, we used the formula: Radius = Perimeter/ $2 \times \pi$.

Since sexual maturity is correlated with a significant drop in the growth rate (e.g., Bernardo 1993; Castanet and Baez 1991; Hugi and Sánchez-Villagra 2012; Klein et al. 2015; Grigg and Kirshner 2015; Lance 2003), to estimate the age at which sexual maturity was reached, we generate the growth curves based on the superimposition of the perimeter of the GMs of each bone. Once the growth curves were constructed, sexual maturation was determined as the point when the growth rate showed a significant decrease (e.g., Li et al. 2023).

The body mass was calculated using the equation of Campione and Evans (2012): logBM = $2749 \times \log Ch + f - 1104$ (where Ch + f is the circumference of the diaphysis of the humerus and femur). The estimated age was then plotted against the body mass and the snout-vent length. Body mass was also calculated using the perimeter of each of the circumferential GMs using the equation proposed by Campione and Evans (2012): logBM = $2749 \times \log Ch + f - 1104$. To generate the growth curves based on SVL and body mass versus the maximum estimated age per individual, we use the "nlsr" package (Nash and Murdoch 2017) in Rstudio (R Core Team 2018) taken from Viotto, Navarro, and Piña (2020).

3 | Results

Table 3 lists the number of GMs in each of the caiman specimens, whereas perimeters and areas enclosing each GM as well as the growth rate of each bone are in the Supporting Information S2: Table S1, while Supporting Information S1:

TABLE 3	Τ	Number of growth marks in each specimen of Caiman latirostris studied. The specimens MLPR-6822, MLPR-6819, MLPR-6815
MLPR-6817	7, N	/LPR-6820, MLPR-6818, and MLPR-6816 are known-age captive individuals, while the rest of the specimens are wild with no
information	1 ał	bout their age.

	Skeletal element									
Specimen	Scapula	Coracoid	Humerus	Radius	Ulna	Pubis	Femur	Fibula	Tibia	
MLPR-6822				HL				HL		
MLPR-6819	HL		HL	HL	HL	HL		HL	HL	
MLPR-6815				HL	HL			HL		
MLPR-6817				HL				HL		
MLPR-6820				HL	HL			HL		
MLPR-6818				HL	HL			HL		
MLPR-6816	1		1	HL-1	1	1	1	HL-1	1	
MLPR-6771	2	2	2	HL-2	2	2	2	HL-2	2	
MLPR-6810			2	2	2		1	2	1	
MLPR-6809				10	13		10	11	12	
MLPR-6770	8	7	11	11	12	12	10	14	10	
MLPR-6813	15	13	14	15	16	15	13	17	15	
MLPR-6814	10	8	10	10	13	14	11	10	12	

Abbreviation: HL, hatching line.

Tables S2–S5 list the estimated body mass of each specimen. To exemplify the growth curves obtained for each individual we show the growth curves of the scapula in Figure 2, however, all the other growth curves are presented in the Supporting Information. Our results complement the data reported upon in the qualitative study of these bones (Pereyra et al. 2024). To streamline the results, we are presenting the data according to the skeletal element in the following sequence: scapulae, coracoids, humerus, radius, ulna, pubis, femur, fibula, and tibia.

3.1 | Scapula

Of all the scapulae studied, the largest ratio of the medullary cavity area to the compact cortex was observed in the juvenile MLPR-6822, while the smallest was in the adult MLPR-6813 (Supporting Information S2: Table S1). Of all the 6- to 8-month juveniles studied (five specimens in total), only MLPR-6819 and MLPR-6820 presented noncyclical GMs. Additionally, specimen MLPR-6819 records a HL. The 1-yearold or older juveniles (MLPR-6816 and MLPR-6771) exhibit at least one noncyclical GM, as well as two cyclical GMs. Among the adult scapulae, the individual MLPR-6813 has the highest number of GMs (Table 3). The three adult specimens exhibited double or triple GMs in different regions of their scapulae. Close to the outer cortex of MLPR-6813 there is a thick layer of unusual bone between GMs (Figure 3a). The GMs before the deposition of the unusual bone layer are triple GMs that are closely spaced, and some of them merge into one another (Figure 3a). The average annual growth rate of the adults studied is 1.44 mm/year in MLPR-6770, 1.71 mm/year in MLPR-6813, and 2.37 mm/year in MLPR-6814 (Supporting Information S2: Table S1). The annual growth rate of the scapula of the adult specimens shows a

more rapid rate of early growth, which tends to decrease as the individuals get older (Figure 2 and Supporting Information S2: Table S1). The only exception to this tendency is in specimens MLPR-6813 which shows an increase in the growth rate between the 12th and 14th GM that coincides with the occurrence of the unusual bone tissue (Figures 2d and 3a; Supporting Information S2: Table S1).

3.2 | Coracoid

As observed in the scapulae, the ratio of the medullary cavity area to the compact cortex is largest in the juveniles as compared with the adults (Supporting Information S2: Table S1). Among the captive juveniles (Table 1), only the coracoid of the specimen MLPR-6819 exhibits noncyclical GMs, while among the wild juveniles, MLPR-6771 presents one noncyclical GM and two cyclical GMs. The adult specimen MLPR-6813 has the highest number of GMs (Table 3), and the coracoid also shows the unusual bone layer (as described above in the scapula) and it shows triple GMs internally and externally to this layer (Figure 3b). The adult specimen MLPR-6770 also has double or triple GMs in different regions of the cortex, however those double or triple GMs are not related to a layer of unusual bone tissue. Both specimens MLPR-6770 and MLPR-6814 show a decrease in the annual growth rate after the fourth GMs. However, this decrease is not observed in MLPR-6813, which presents several high growth rate peaks. Particularly, the peak between the GM5 and GM8 is related to the thick layer of unusual bone (Supporting Information S2: Table S1; Supporting Information S1: Figure S2). The average growth rate of the coracoid of adult specimens varied between 1.92 mm/year (MLPR-6770) and 1.43 mm/year (MLPR-6813; Supporting Information S2: Table S1).



FIGURE 2 | Growth curves of the scapula of *Caiman latirostris*. (a), (c), (e) cumulative growth of MLPR-6770, MLPR-6813, and MLPR-6814, respectively. (b), (d), (f) annual growth rate of MLPR-6770, MLPR-6813, and MLPR-6814, respectively. GM, growth marks.

3.3 | Humerus

While the adult MLPR-6814 has the smallest ratio of the medullary cavity area to the cortex, the juvenile MLPR-6822 has the highest ratio (Supporting Information S2: Table S1). However, MLPR-6771 also has a small ratio (Supporting Information S2: Table S1). The captive specimens MLPR-6819 and MLPR-6820 have noncyclical GMs, respectively, and the juvenile MLPR-6819 has parts of the HL preserved. Both wild juveniles, MLPR-6771 and MLPR-6810, exhibit cyclical and noncyclical GMs. While the adult MLPR-6813 has the highest number of GMs, with several triple GMs, the adult MLPR-6814 has the lowest number of GMs, some of which are double GMs (Table 3 and Supporting Information S2: Table S1). However, the perimeter of each GM and the perimeter of the subperiosteal GM of the humerus MLPR-6814 is much higher as compared with the values of the other adult specimens (Supporting Information S2: Table S1; Supporting Information S1: Figures S3). While the annual growth rate between the first and the second GMs in the juvenile specimen MLPR-6771 is 2.59 mm/year, it is 0.98 mm/year in the juvenile MLPR-6810 (Supporting Information S2: Table S1). The adult specimens have similar average annual growth rates (between 1.03 and 1.41 mm/year; Supporting Information S2: Table S1). The humerus of the three



FIGURE 3 | Bone histology of postcranial bones of *Caiman latirostris*. Layer of unusual bone (green line) in the scapula of MLPR-6813 (a), the coracoid of MLPR-6813 (b), the radius of MLPR-6814 (c), the ulna of MLPR-6814 (d), the pubis of MLPR-6814 (e), and the femur of MLPR-6813 (f), (g) hatching line (arrowhead) in the radius of MLPR-6819, (h) increase in the organization of the collagen fibers and decrease of the vascularization density toward the outer cortex of the radius of MLPR-6770. (a), (b), (f), (g), (h) normal light; (c), (d), (e) cross-polarized light with ¼ lambda compensator.

adults shows a decrease in the annual growth rate between the fourth and the fifth GM (Supporting Information S2: Table S1; Supporting Information S1: Figure S3).

3.4 | Radius

Except for the juveniles MLPR-6815 and MLPR-6818, and the adult MLPR-6814 there is a tendency for a decrease in the ratio of the medullary cavity area to the cortex from juveniles to adult specimens (Supporting Information S2: Table S1). Most of the juveniles present noncyclical GMs. Except for MLPR-6810, all the juvenile specimens preserve partial HL. The juveniles MLPR-6816, MLPR-6771, and MLPR-6810 have one, two, and two cyclical GMs, respectively (Table 3). The annual growth rate (between the first and second GMs) of the juveniles MLPR-6771 and MLPR-6810 is 1.13 and 0.63 mm/year, respectively (Supporting Information S2: Table S1). Among the adult specimens, MLPR-6813 has the highest number of GMs (15 GMs; Table 3). Except for MLPR-6770, all other adult specimens have double or triple GMs in different regions of the cortex. Specimen MLPR-6814 has an unusual layer of bone with a higher-than-usual growth rate between the fourth and fifth GMs (Figure 3c and Supporting Information S1: Figure S4). At the external limit of this tissue, there are triple GMs. The lowest average annual growth rate is observed in the adult MLPR-6809 (0.91 mm/year) and the highest is in the adult MLPR-6770 (1.13 mm/year; Supporting Information S2: Table S1). The growth dynamic of the adults, MLPR-6770 and MLPR-6813 show a decrease in the annual growth rate after the fourth GM in, and MLPR-6814 shows this after the fifth GM, whereas MLPR-6809 does not show this decrease (Supporting Information S2: Table S1; Supporting Information S1: Figure S4).

3.5 | Ulna

The ulna of the juveniles tends to have a smaller ratio of the medullary cavity area to the compact cortex than the ulna of the adults (Supporting Information S2: Table S1). Most of the juveniles studied present noncyclical GMs, and only MLPR-6819, MLPR-6815, and MLPR-6820 also have partial HL preserved. The juveniles MLPR-6816, MLPR-6771, and MLPR-6810 have cyclical GM (Table 3). The growth rate between the first and second GMs in MLPR-6770 and MLPR-6810 is 1.28 and 0.66 mm/year, respectively (Supporting Information S2: Table S1). Most of the adult specimens have double or triple GMs and the specimen MLPR-6813 has the largest number of GMs (Table 3). As in the radius, the ulna of MLPR-6814 has a thick layer of unusually faster-formed bone tissue between the third and fourth GMs (Figure 3d and Supporting Information S1: Figure S5h). The average annual growth rate varies between 0.95 mm/year in MLPR-6809 and 1.31 mm/year in MLPR-6814 (Supporting Information S2: Table S1). The adult specimens show a decrease in growth rate after the seventh GM (in MLPR-6770) and after the fifth (in MLPR-6814). However, the specimens MLPR-6809 and MLPR-6813 do not show a clear decrease in the growth rate (Supporting Information S2: Table S1; Supporting Information S1: Figure S5).

3.6 | Pubis

The pubis of the specimens studied do not show a clear trend in the ratio of the medullary cavity area to the compact cortex, since some juveniles such as MLPR-6820 and MLPR-6771 have smaller values than the adults (Supporting Information S2: Table S1). The juveniles MLPR-6822, MLPR-6819, MLPR-6815, MLPR-6820, MLPR-6816, and MLPR-6771 show noncyclical GM. Only MLPR-6819 has some remnants of the HL, while the juveniles MLPR-6816 and MLPR-6771 all have cyclical GMs (Table 3). The growth rate between the first and second GM in MLPR-6771 is 0.89 mm/year (Table S1). The adult MLPR-6813 has the highest number of GMs (15; Table 3). The specimens MLPR-6770 and MLPR-6813 have double GMs associated with the sixth and seventh GMs, respectively (Supporting Information S2: Table S1). The adult MLPR-6814 shows an unusual bone tissue between the seventh and eighth GMs which coincides with a high growth rate (Supporting Information S2: Table S1; Figure 3e and Supporting Information S1: Figure S6). The lowest average annual growth rate is in the specimen MLPR-6813 (0.66 mm/year) and the highest is in MLPR-6814 (0.99 mm/year). In MLPR-6813 and MLPR-6814 there is a decrease in the growth rate after the fifth GM and fourth GM, respectively. On the other hand, the specimen MLPR-6770 shows a decrease only after the eighth GM (Supporting Information S2: Table S1; Supporting Information S1: Figure S6).

3.7 | Femur

The highest value of the ratio of the medullary cavity area to the compact cortex is in the juvenile MLPR-6822, while the lowest is in the adult MLPR-6813. Cyclical GMs are present in the captive juvenile MLPR-6816, as well as the wild juveniles MLPR-6771 and MLPR-6810 (Table 3). The femur of the specimen MLPR-6813 also shows the highest number of GMs among adults (Table 3). MLPR6809, MLPR-6813, and MLPR-6814 have double or triple GM in different femur regions (Supporting Information S2: Table S1). In the outermost part of the cortex (between the last LAG and the subperiosteal margin) of MLPR-6813 shows a thick band of unusual bone tissue (Figure 3f). Among the adults, the highest average growth rate is in the femur of MLPR-6813 (1.98 mm/year), and the lowest is in MLPR-6770 (1.43 mm/year) (Table S1). Among the adults, a decrease in the annual growth rate is observed after the fifth (MLPR-6809), the second (MLPR-6770), the sixth (MLPR-6813), and the second (MLPR-6814) GM (Supporting Information S2: Table S1; Supporting Information S1: Figure S7).

3.8 | Fibula

The fibulae studied do not show a clear trend in the ratio of the medullary cavity area to the compact cortex (Supporting Information S2: Table S1). All the juveniles have noncyclical GMs, and except for MLPR-6810 all show remnants of the HL (Table 3). The juveniles MLPR-6816, MLPR-6771, and MLPR-6810 also have cyclical GM (Table 3). The adult specimen MLPR-6813 has the highest number of GMs (Table 3), and all the adult specimens have double or triple GMs (Supporting Information S2: Table S1). The specimens MLPR-6809 and MLPR-6770 have a thick layer of unusually rapidly formed bone tissue in the inner cortex of the bone (Supporting Information S2: Table S1 and Supporting Information S1: Figure S8). The lowest average annual growth rate is present in MLPR-6813 (0.91 mm/year) and the highest is in MLPR-6814 (1.26 mm/year) (Supporting Information S2: Table S1). In MLPR-6809 and MLPR-6770, there is a decrease in the annual growth rate after the third GM, and this occurs after the fifth in MLPR-6813 (Supporting Information S2: Table S1; Supporting Information S1: Figure S8).

3.9 | Tibia

The ratio of the medullary cavity area to the compact cortex of the adult tibiae tends to be lower than the juveniles (Supporting Information S2: Table S1). Some juvenile specimens have noncvclical GMs, and only MLPR-6819 and MLPR-6820 have partial HL evident. The juveniles MLPR-6816, MLPR-6810, and MLPR-6771 have cyclical GMs. The growth rate between the first and second GMs in the juvenile MLPR-6771 is 2.40 mm/year (Supporting Information S2: Table S1). Among the adults, MLPR-6813 has the highest number of GMs (Table 3). The specimens MLPR-6809, MLPR-6770, and MLPR-6813 have double or triple GMs in different regions of the cortex (Supporting Information S2: Table S1). The specimens MLPR-6809 have the highest average annual growth rate (1.96 mm/year; Supporting Information S2: Table S1) and MLPR-6814 has the lowest (1.05 mm/year; Supporting Information S2: Table S1). In MLPR-6809, MLPR-6770, and MLPR-6814 there is a decrease in the annual growth rate after the third, the second, and the third GMs, respectively (Supporting Information S2: Table S1; Supporting Information S1: Figure S9). In MLPR-6814 the decrease of the growth rate starts after the third GM, and although there is another peak at the seventh GM, this does not reach the same value as at the third GM. On the other hand, in MLPR-6813, there is not a clear decrease in the annual growth rate (Supporting Information S2: Table S1; Supporting Information S1: Figure S9).

4 | Discussion

In Pereyra et al. (2024) we provided a comprehensive qualitative description of the osteohistology of the caiman specimens that we analyze here. In the current study, we quantitatively analyze the growth dynamics of *C. latirostris* derived from the GMs of nine skeletal elements of each differently sized individual. Based on the skeletochronological assessment, we also discuss other attributes linked to the life history of caimans, such as age, sexual maturity, and body size.

4.1 | Skeletochronology

Since the age of the captive individuals was known, we were able to discriminate between the noncyclical and cyclical GMs (Table 3). Cyclical GMs are generally related to annual/seasonal growth cycles (Castanet et al. 1993; Castanet and Smirina 1990;

Chinsamy-Turan 2005; Chinsamy 2023; Francillon-Vieillot et al. 1990; Klinger and Musick 1995; Peabody 1961; Snover and Hohn 2004; Zug, Chaloupka, and Balazs 2006; Zug 1991) whereas, noncyclical GM can be caused by a variety of events, such as hibernation (e.g., Chinsamy, Rich and Vickers-Rich 1996), birth/hatching (e.g., Bruce and Castanet 2006; Castanet and Baez 1991; Garrone, Cerda, and Tomassini 2019; Nacarino-Meneses and Köhler 2018), metamorphosis (e.g., Leary et al. 2005), weaning, and unusual climate variations (e.g., Castanet et al. 2004; Morris 1970; Snover and Hohn 2004). In the case of crocodilians, it is known that they are susceptible to environmental variations, such as temperature, humidity, and food availability (e.g., Hutton 1987; Jacobsen and Kushlan 1989; Magnusson and Taylor 1981; Webb, Manolis, and Buckworth 1983). Juveniles are particularly vulnerable (e.g., Hutton 1987; Larriera and Imhof 2006; Viotto et al. 2022). The noncyclical GMs observed in the juveniles we studied, could be related to environmental stress that these individuals experienced during the first few months of life after hatching, which in Argentina are autumn and winter, which are unfavorable conditions for crocodilian development (e.g., Larriera and Imhof 2006; Larriera, Imhof, and Siroski 2008; Parachú-Marcó, Piña, and Larriera 2009; Piña and Larriera 2002) One of the important noncyclical GMs identified in some of the juveniles was the presence of HLs (Figure 3g). Among all the juveniles. the radius and the fibula showed HLs, whereas the femur did not preserve any such traces of hatching. Additionally, when comparing similar aged wild and captive specimens, both the wild individuals MLPR-6771 and the captive individual MLPR-6816 present HLs in the same bones (radius and fibula). These findings suggest intraskeletal variation in terms of growth and remodeling (Table 3). Interestingly, specimen MLPR-6819 shows traces of HL in most of the skeletal elements we studied, whereas, in other juvenile specimens only remnants of the HL were evident in some bones (Table 3), that is intraspecific variation in terms of the preservation of HL. It is quite likely that these findings are related to remodeling changes during growth, such as the expansion of the medullary cavity (e.g., Castanet and Baez 1991; Chinsamy et al. 1995; Chinsamy-Turan 2005; Ehret 2007; Halliday and Verrell 1988, Nacarino-Meneses and Köhler 2018). This idea appears to be supported in that the perimeter of the medullary cavity of MLPR-6819 is the smallest among the juveniles studied here (Supporting Information S2: Table S1).

Neither the noncyclical GMs nor the HL were identifiable among the adult specimens of C. latirostris (Table 3). This might be related to the process of remodeling changes and the expansion of the medullary cavity (e.g., Chinsamy-Turan 2005; Erickson and Tumanova 2000; Horner, De Ricqlès, and Padian 2000; Klein and Sander 2007; Smirina 1994). This is evident in the perimeter measurements of the medullary cavity, which increases in larger individuals (Supporting Information S2: Table S1). Indeed, the perimeter of the medullary cavity of all the bones studied is larger in the adult specimens as compared with the juveniles (Supporting Information S2: Table S1). There were, however, some exceptions (e.g., the fibula of MLPR-6810, MLPR-6809, and MLPR-6770, and the radius of MLPR-6814), where the ratio of the medullary cavity area to the compact cortex decreased with ontogeny (Supporting Information S2: Table S1). This was also found to be the case in the

humerus of C. niloticus (Audije-Gil, Barroso-Barcenilla, and Cambra-Moo 2023) and long bones of dinosaurs such as Jeholosaurus shangyuanensis (Han et al. 2020). In the case of the adult specimens studied, different numbers of GMs are recorded in the different skeletal elements of each specimen, which suggests intraskeletal variation in C. latirostris. The bones that have the highest number of GMs are the ulna and fibula, while the coracoid in most of the adults least preserves an accurate account of GMs (Table 3). Such intraskeletal variability in the number of GMs has been reported in other vertebrates such as dinosaurs (e.g., Cullen et al. 2021; Horner, de Ricqlès, and Padian 1999; Waskow and Sander 2014), turtles (e.g., Bhat, Chinsamy, and Parkington 2019; Pereyra 2023), and crocodilians (e.g., Garcia Marsà et al. 2023; Ponce et al. 2021, 2022; Woodward, Horner, and Farlow 2014). As was established in previous studies, it is important to consider several bones in a skeleton to be able to get an overall understanding of the presence of GMs in each bone and to deduce which bone best preserves a track record of growth (e.g., Chinsamy and Hillenius 2004; Chinsamy-Turan 2005, Chinsamy 2023; Cullen et al.2021).

In most of the bones we studied, double or triple GMs were observed (Supporting Information S2: Table S1). This is not uncommon and has been reported in several other vertebrates (Andrade and Sayão 2014; Andrade et al. 2018; Caetano and Castanet 1993; Castanet and Baez 1991; Chinsamy et al. 1995; Chinsamy and Warburton 2021; Cullen et al. 2021; Curtin et al. 2005; Gee, Haridy, and Reisz 2020; Goshe et al. 2010; Han et al. 2020). The occurrence of double or triple GMs is often associated with hibernation, estivation or environmental stressors (Castanet et al. 1993; Castanet and Baez 1991; Goshe et al. 2010). Thus, the occurrence of double or triple GMs we observed in our specimens could be due to their vulnerability to environmental fluctuations. Additionally, in some cases, such as the scapula and coracoid of MLPR-6813, double or triple GMs were closely related to the presence of a layer of unusual bone tissue, which is likely pathological tissue (Figure 3). Thus, the double or triple GMs here could perhaps be related to a slow down in growth following the trauma.

To estimate the age of the adult specimens we used the overlap method based on the perimeter of each GM (see Section 2). Although in most of the cases, the values of the perimeters of the GMs are similar and straightforward to overlap (Figures 4 and 5), in a few cases there was not a clear overlap of the GM perimeter measurements, which could be related to intraspecific variation (e.g., the scapula; Supporting Information S2: Table S1; Supporting Information S1: Figure 4e). In a skeletochronological study of C. latirostris from Brazil, the spacing between GMs was consistent between 2- to 4-year-old individuals. However, in older individuals, the spacing between GMs was less well correlated (Mascarenhas-Junior, Bassetti, and Manso Sayão 2021). This variation is likely related to competition for food, as well as to growth plasticity within the sample. Curiously, eight captive specimens of C. niloticus from 1-year-old to 14 years old showed a good correlation of the perimeters of the GMs (Audije-Gil, Barroso-Barcenilla, and Cambra-Moo 2023). In our study, since not all bones preserved the same number of GM, we deduced the age suggested by each of the bones per individual, to obtain an estimated age range.

Furthermore, we estimated an age of 2 years for MLPR-6771 and MLPR-6710, 11-14 years for MLPR-6809, 11-17 years for MLPR-6770, 16-18 years for MLPR6813, and 13-23 years for MLPR-6814 (Figures 4 and 5). In all these cases the higher number of GMs is a closer approximation to the actual age of the individual. However, we are cognizant that these data are an estimation of age, and it is possible that the number of GMs in bones can differ from the actual age of the individual for a few reasons, including ontogenetic stage, sex and the fact that captive and wild specimens can express different growth rates (e.g., Heck and Woodward 2021; Schucht, Klein, and Lambertz 2021). In our study, the presence of thick layers of pathological bone tissue in some bones would have had a direct impact on the perimeter values of the GMs external to this layer, thus causing an overestimation of the age. It is worth noting that the specimens MLPR-6771 and MLPR-6770 present here have a younger estimated age than reported by Pereyra (2021) since here age estimation is based on the GMs perimeter values of known-age juvenile specimens. The age of MLPR-6814 (the largest adult based on SVL of ~93 cm) is estimated as 13-23 years old; whereas MLPR-6809 (the smallest adult with SVL of ~69 cm) is estimated to be between 11 and 14 years old (Table 2; Figures 4, 5 and Supporting Information S1: Figure S10). According to the growth curves deduced for wild C. latirostris from Brazil, a specimen with a SVL of 80 cm, would be about 15-20 years old (Moulton, Magnusson, and Melo 1999). However, reintroduced females (captive during the first year of life) from Santa Fé, Argentina, with a mean total length of 152.4 cm are 9.3 years old (Larriera et al. 2006). Additionally, wild and reintroduced caimans in Santa Fé, Argentina, with SVL of 68 cm are 7.9 years old (Viotto, Navarro, and Piña 2020). Although, there is substantial variation in the estimated age deduced from the different skeletal elements, the estimated age for the wild specimens of C. latirostris studied here is higher than the reintroduced Argentinian specimens. It is worth noting that generally wild animals (especially juveniles) take more years to reach a specific size than captive specimens (Viotto, Navarro, and Piña 2020). The latter is most likely because of captive environments providing optimal temperatures and a regular supply of food, which are conducive to faster growth. Indeed, juvenile crocodilians in captive environments often show fibro-lamellar bone tissue in their bones which is indicative of rapid rates of growth (e.g., Chinsamy 1991; 1993; Tumarkin-Deratzian 2007; Woodward, Horner, and Farlow 2014).

4.2 | Growth Rate and Growth Dynamic

Pereyra et al. (2024) reported substantial variations in the bone microstructure of *C. latirostris* in terms of the type of bone tissues that occurred in the different skeletal elements (Pereyra et al. 2024). The different types of bone tissues directly indicate variations in the rate at which bone was deposited. The current study quantified the growth rates of each skeletal element in each of the specimens, and we document considerable variations in the growth rate among the different individuals (Figures 4–7; Supporting Information S2: Table S1). It is well recognized that bone deposition rates can vary within the same bone (in different regions), as well as among different bones in the same individual (Chinsamy 1993; Chinsamy et al. 2019; de



FIGURE 4 | Cumulative growth of forelimb bones of specimens MLPR-6816, MLPR-6810, MLPR-6771, MLPR-6809, MLPR-6770, MLPR-6813, and MLPR-6814. (a) scapula, (b) cosacoid, (c) humerus, (d) radius, (e) ulna.

Margerie et al. 2004; de Ricqlès and Bolt 1983; de Ricqlès et al. 1991; Nacarino-Menesa, Jordana, and Köhler 2016; O'Connor et al. 2014; Smith and Clarke 2015; Starck and Chinsamy 2002; Watanabe 2018; Woodward, Horner, and Farlow 2014). We found that the femur, tibia, humerus, coracoid, and scapula have higher average annual growth rates, while the fibula, pubis, ulna, and radius generally have lower

growth rates (Supporting Information S2: Table S1). These results agree with similar studies on juvenile *A. mississippiensis* which found higher annual growth rates in the humerus, femur, and tibia, as opposed to the fibula, radius, and ulna (Woodward, Horner, and Farlow 2014). Mascarenhas-Junior, Bassetti and Manso Sayão (2021) found that the distance between LAGs in the humerus of *C. latirostris* from Brazil varies



FIGURE 5 | Cumulative growth of hindlimb bones of specimens MLPR-6816, MLPR-6810, MLPR-6771, MLPR-6809, MLPR-6770, MLPR-6813, and MLPR-6814. (a) pubis, (b) femur, (c) fibula, (d) tibia.



FIGURE 6 | Growth rates of forelimb bones of specimens MLPR-6810, MLPR-6809, MLPR-6771, MLPR-6770, MLPR-6813, and MLPR-6814. (a) scapula, (b) coracoid, (c) humerus, (d) radius, (e) ulna.

between 0.10 and 0.47 mm, which compares well with the annual growth rate we deduced for the humerus of the juvenile *C. latirostris* MLPR-6771 (0.41 mm/year; Supporting Information S2: Table S1). These results contrast with the daily growth rate deduced for the humerus of other species of crocodilians such as juvenile *A. mississippiensis* (2.87–11.39 mm/year), and juvenile *C. niloticus* (37.17 μ m/day) (Woodward, Horner, and Farlow 2014; Cubo et al. 2012).

We found that the different bones in the skeleton of the juvenile *C. latirostris* specimens (MLPR-6810 and MLPR-6771) showed variation: 0.73–1.92 μ m/day (humerus), 0.4–0.83 μ m/day (radius), 0.48–0.95 μ m/day (ulna), 2.11 μ m/day (femur), 0.56–0.64 μ m/day (fibula), and 1.78 μ m/day (tibia) (Supporting Information S2: Table S1). On the other hand, the daily growth rate of the adult specimens at their estimated 3 and 4 years age is variable: 0.41, 0.66, and 0.79 μ m/day (radius of MLPR-6809, MLPR-6770, and



FIGURE 7 | Growth rates of hindlimb bones of specimens MLPR-6810, MLPR-6809, MLPR-6771, MLPR-6770, MLPR-6813, and MLPR-6814. (a) pubis, (b) femur, (c) fibula, (d) tibia.

MLPR6813, respectively), 0.70, 1.33, and 1.81 µm/day (ulna of MLPR-6809, MLPR-6770, and MLPR6813), 2.22 µm/day (femur of MLPR-6809), 0.79 µm/day (fibula of MLPR-6813), 2.29, 2.86, and 1.41 µm/day (tibia of MLPR-6809, MLPR-6770, and MLPR6813) (Supporting Information S2: Table S1). These results also contrast with the daily growth rate deduced for other species of crocodilians. Woodward, Horner, and Farlow (2014) reported daily growth rate for juveniles of A. mississippiensis: 1.05-4.16 µm/day (humerus), 0.3-3.14 µm/day (radius) 0.58-1.81 µm/day (ulna), 1.05-6.8 µm/day (femur), $0.56-3.10 \,\mu\text{m/day}$ (fibula), and $0.93-4.44 \,\mu\text{m/day}$ (tibia) (based on 214 days; Woodward, Horner, and Farlow 2014). Cubo et al. (2012) also reported variation in the daily growth rate of postcranial bones of juvenile C. niloticus: 13.57 µm/day (humerus), 9.53 µm/day (femur), and 8.66 µm/day (tibia) (non-specification of the number of days). Interestingly in another juvenile C. niloticus, a daily growth rate of 2.48 µm/day (tibia) was reported (based on 121 days; Montes et al. 2010), which is much slower than that previously reported in the tibia by Cubo et al. (2012). Thus, it appears that the growth rate of C. latirostris is similar but a little slower than that estimated for A. mississippiensis and even slower than C. niloticus. These differences could be related to the different final sizes of these species (maximum size registered for C. latirostris is 2.5 m, for A. mississippiensis is 4.5 m, and for C. niloticus is 5.7 m; Cott 1961; Grigg and Kirshner 2015; Siroski et al. 2020). It is also worth noting that the measurements taken from other crocodilians specimens to calculate the annual or daily growth rates is calculated from the radius of cross sections of one or more bones (Cubo et al. 2012; Montes et al. 2010; Woodward, Horner, and Farlow 2014). In this study, we observed that there is an important difference between the bone appositional rates obtained from the radius of the GMs and that obtained from the perimeter of the GMs. Based on the irregular shape of the bones (i.e., few bones of crocodilians are circular in cross section; Figure 1a,b), therefore more information might be recovered when the perimeter is utilized instead of the radius of the cross section.

Growth curves based on measurements of GMs have been made in several vertebrates such as mammals (e.g., Chinsamy and Warburton 2021; Cullen et al. 2021; Nacarino-Meneses, Jordana, and Köhler 2016; Nacarino-Meneses et al. 2021), dinosaurs (e.g., Chinsamy 1993; Cooper et al. 2008; Cullen et al. 2021; Waskow and Mateus 2017; Woodward et al. 2015), tortoises (e.g., Bhat, Chinsamy, and Parkington 2023), lizards (e.g., Castanet and Baez 1991), and pseudosuchians (e.g., Taborda, Cerda, and Desojo 2013) among others. More specifically, among the crocodilians, growth curves have been deduced for the extant A. mississippiensis (e.g., Erickson and Brochu 1999; Klein, Scheyer, and Tütken 2009; Woodward, Horner, and Farlow 2014), C. niloticus (Audije-Gil, Barroso-Barcenilla, and Cambra-Moo 2023; Games 1990), Crocodylus porosus (Erickson and Brochu 1999) as well as in extinct species (e.g., Araripesuchus, Fernández Dumont et al. 2021; Leidyosuchus, Erickson and Brochu 1999; crocodylomorph, Waskow and Mateus 2017). Crocodilians and other reptiles are characterized by having relatively rapid growth until they reach sexual maturity, after which their growth rate decreases (e.g., Bernardo 1993; Castanet and Baez 1991; Hugi and Sánchez-Villagra 2012; Klein et al. 2015; Grigg and Kirshner 2015; Lance 2003). In the current study, we found that C. latirostris presented variations in its growth rates throughout ontogeny. The growth curves generated in this study show that generally,

the growth rate presents distinctively high growth rates during early ontogeny, which tends to slow down during the last cycles of growth (this can be clearly seen in the large specimens; Figures 1, 2, S5d,h and S6h). Curiously, we found that the growth rate of some bones (e.g., ulna, fibula, radius, tibia; Figures 6 and 7) was slower in the first year of life than in the subsequent years. This is also observed in the histology of these specimens (mostly lamellar or parallel fibered bone tissue; Pereyra et al. 2024). This was also the case in Cretaceous alligatoroids (Acynodon sp.; Company and Pereda-Suberbiola 2017) and modern crocodilians (A. mississippiensis; de Ricqlès, Padian, and Horner 2001 and C. niloticus; Audije-Gil, Barroso-Barcenilla, and Cambra-Moo 2023). The initial slower growth rates during the early stages of ontogeny could be related to difficulty in food acquisition which may be related to dietary changes that is juveniles crocodilians eat mainly invertebrates (principally insects), and after they are about 1 year old, they change their diets to incorporate more nutritionally rich vertebrates (Borteiro et al. 2009; Christianini and Cestari 2019; Coutinho et al. 2013; Dodson 1975; Farias et al. 2013; Magnusson, da Silva, and Lima 1987; Thorbjarnarson 1996; Tucker et al. 1996; Santos et al. 1996).

Regarding the adult specimens, although high and low growth rates are evident in the first few ontogenetic stages, the growth rates are relatively higher at first, and then decrease in some bones (such as the scapula of MLPR-6770 and MLPR-6814, the humerus of MLPR-6770, the radius of MLPR-6814) but remain consistently high in others (e.g., the tibia of MLPR-6813, the ulna and radio of MLPR6809; Supporting Information S1: Figures S2-S9; Supporting Information S2: Table S1). Similar growth dynamics were observed in the extinct Araripesuchus buitreraensis (Fernández Dumont et al. 2021) and modern specimens of C. niloticus (Audije-Gil, Barroso-Barcenilla, and Cambra-Moo 2023). Such variations were thought to be related to climatic variations or intrinsic individual differences (Audije-Gil, Barroso-Barcenilla, and Cambra-Moo 2023). In our caiman specimens, we found considerable variation among specific bones and individuals. For example, a decrease in the growth rate is more evident in the scapula of the adult MLPR-6814 (Figure 2f), the humerus of the adults MLPR-6770 and MLPR-6813 (Supporting Information S1: Figure S3b,d), the radii of the adults MLPR-6770, MLPR-6814 (Figure S4d,h), and the fibula of adult MLPR-6770 (Figure S8d). This decrease in growth is also reflected in an increase in the organization of fibers toward the external cortex and a decrease in the density of vascular canals (Figures 1b and 3h). The correlation between the organization of the bone matrix and the rate of bone deposition (growth dynamics) is well recognized (e.g., Chinsamy-Turan 2005; Chinsamy 2023; Francillon-Vieillot et al. 1990; Starck and Chinsamy 2002). This correlation has also been documented in crocodyliforms such as Alligator (Woodward, Horner, and Farlow Horner, and Farlow 2011, 2014), Crocodylus (Hutton 1986), Gavialis (de Buffrénil 1982), and Caiman (Andrade et al. 2018), and now in C. latirostris. Usually, during the winter season when temperatures are low, C. latirostris reduce their activity (which becomes limited to sun basking and staying in the water), and they do not feed (Larriera and Imhof 2006). These decreased levels of activity manifest in the bone tissues, as growth rings which may be associated with narrow bands of lamellar tissue (Pereyra et al. 2024).

As a general trend, non-avian reptiles reach sexual maturity long before somatic maturity, and this attainment is correlated with a decrease in growth rate (e.g., Andrews 1982; Bourdon et al. 2009; Chinsamy 1993; Castanet and Baez 1991; Chinsamy and Dodson 1995; Halliday and Verrell 1988; Li et al. 2023; Smirina 1994; Wilkinson et al. 2016). Usually, male and female vertebrates reach sexual maturity at different ages or body sizes, while in some female reptiles can be sexually mature earlier than males (e.g., Castanet et al. 1993; Misawa and Matsui 1999). The attainment of sexual maturity is variable in crocodilians since it is influenced by several endogenous and/or exogenous factors such as sex, temperature, and diet (e.g., Bernardo 1993; Grigg and Kirshner 2015; Lance 2003). However, females mature at a younger age and/or body size than males (see Supporting Information S1: Table S6; Chabreck and Joanen 1979; Magnusson and Lima 1991; Magnusson, Sanaiotti, and Sanaiotti 1995; Webb and Messel 1978). Among crocodilians, body size appears to be the determinant factor of sexual maturation, that is they reach sexual maturity when they are a specific body size (Grigg and Kirshner 2015; Montes et al. 2007; Rootes et al. 1991; Wilkinson et al. 2016). Studies on A. mississippiensis that have a wide latitudinal distribution, show that the size and age at which these species reach sexual maturity varies with the latitude since the mean temperatures and the food resources vary throughout their distribution. For example, when temperatures are high, like in Louisiana, they grow fast and reach sexual maturity earlier, however, when the temperatures are high but food is not abundant, like in the Everglades, they grow slowly and reach sexual maturity at smaller sizes and at younger ages (Grigg and Kirshner 2015; Jacobsen and Kushlan 1989; Lance 2003; 2021; Wilkinson et al. 2016; Wilkinson and Rhodes 1997; Supporting Information S1: Table S6). Other species, such as Caiman crocodilus (e.g., Campos et al. 2008; Magnusson, Sanaiotti, and Sanaiotti 1995), C. niloticus (Games 1990; Shine et al. 2001), C. johnstoni (Lance 2003; Tucker et al. 2006; Webb, Manolis, and Buckworth 1983), and Melanosuchus niger (Da Silveira et al. 2013) have different geographic distribution and growth rates that determine when they reach the particular body size that determines the attainment of sexual maturity. It should also be noted that captive specimens have controlled temperature and food availability, thus their body mass increases faster, and they reach sexual maturity earlier than wild specimens (e.g., Joanen and McNease 1987; Lance 1989, 2003; 2021; Viotto, Navarro, and Piña 2020). Thus, a benefit of growing in captivity is having all the resources needed to grow fast and therefore reach sexual maturity at an earlier age as compared with wild specimens (e.g., Lance 1989, 2003, 2021; Viotto, Navarro, and Piña 2020; Wilkinson et al. 2016). Since C. latirostris has a wide latitudinal distribution, it is expected that they would reach sexual maturity at different ages depending on where they are located (Supporting Information S1: Table S6; Larriera et al. 2006). Indeed, several studies have shown the attainment of sexual maturity in C. latirostris from different localities and conditions (wild or in captivity) (e.g., Larriera et al. 2006; Verdade and Sarkis 1998; Verdade et al. 2003; Viotto, Navarro, and Piña 2020). In general, females and males reach sexual maturity when they reach an SVL of between 60-81 and 60-100 cm, respectively (Supporting Information S1: Table S6).

At the osteohistological level, the attainment of sexual maturity can be inferred from a change in the bone tissue, a shorter distance between adjacent GMs, or a decrease in the growth rate (e.g., Chinsamy-Turan 2005, 2023; Games 1990; Klein and Sander 2007; Waskow and Sander 2014). Based on our results we observed that sexual maturity can be estimated: overall we were able to estimate that sexual maturity was attained at the age of 7 years for the specimens MLPR-6770 and MLPR-6813, and 10 years old for the specimen MLPR-6814 (Figures 6 and 7). These differences may be related to sexual dimorphism. Although the attainment of sexual maturity is variable and dependent on several factors, the ages recovered for sexual maturity using skeletochronology concurs with that reported for C. latirostris (i.e., 5 and 10 years old; Supporting Information S1: Table S6). However, the body masses estimated at the age of sexual maturity in our specimens were lower (e.g., 7 kg for MLPR-6770 and MLPR-6813 and 14 kg for MLPR-6814; Supporting Information S2: Tables S3 and S4, Figure S11) than those reported for captive or reintroduced females (15-30 kg; Supporting Information S1: Table S6). However, it should be noted that the mass values were calculated (see Section 2), which may be underestimated.

4.4 | Sexual Dimorphism

It is widely reported that male crocodilians grow faster and reach larger body sizes than females (e.g., Da Silveira et al. 2013; Games 1990; Grigg and Kirshner 2015; Joanen and McNease 1987; Lance 2021; McIlhenny 1934; Rootes et al. 1991; Webb, Manolis, and Buckworth 1983; Wilkinson and Rhodes 1997; Wilkinson et al. 2016). In A. mississippiensis, it was shown that both sexes grew 30 cm/year until they reached 5 years old, and thereafter, males continued to grow while the growth rate of females decreased (McIlhenny 1934). In crocodilians species where growth curves and/or the microstructure of long bones of individuals of both sexes have been studied, higher growth rates have been reported in males than in females (e.g., Eaton and Link 2011; Chabreck and Joanen 1979; Werning 2013). Additionally, it has been reported that the growth rate of male crocodilians decreases gradually after they reach sexual maturity, however, the growth of females decreases sharply (Chabreck and Joanene 1979; Hutton 1987). The scapula, humerus, ulna, femur, and tibia of the female specimen MLPR-6770 revealed an abrupt decrease in the growth rate after the attainment of sexual maturity, while the specimen MLPR-6813 expressed a gradual decrease (Figures 6 and 7). These findings suggest that while the former specimen is known to be a female, the latter is likely a male individual. Additionally, we observed that the estimated body mass for the juveniles and adult specimens is similar but slightly smaller than the one reported by other authors for the same species (Supporting Information S1: Table S2; Barboza et al. 2008; Larriera et al. 2006; Piña and Larriera 2002; Verdade et al. 2003). However, at the same estimated age (e.g., 13 years old) MLPR-6813 has a larger body mass than MLPR-6770 (15.94 vs. 17.76 kg; Supporting Information S1: Tables S3 and S4; Supporting Information S1: Figures S2–S4); therefore, since we know MLPR-6770 is a female, we can deduce that MLPR-6813 is likely a male. However, since we do not have many adult

specimens of both sexes this issue must be addressed with a more complete sample.

5 | Conclusions

In this study, we were able to analyze the skeletochronology and the growth dynamics of C. latirostris. We identified the presence of both cyclical and noncyclical GMs in juveniles of this species, with noncyclical GMs likely influenced by environmental stressors such as climate or food accessibility. We observed an intraskeletal and intraspecific variation regarding the deposition of the noncyclical GMs. In adult specimens, GMs vary across different bones, with the ulna and fibula showing more GMs compared with other postcranial bones. The overlap method was used to estimate the age of the specimens, revealing the estimated age of 23 years old for the oldest and largest adult individuals with a SVL of ~93 cm. Growth rates were generally higher in the femur, tibia, and scapula, and slower in the fibula, pubis, and radius. The growth curves permitted more information about the life history and the growth dynamics of this species, and we estimated the age of sexual maturity for the adult specimens as between 7 and 10 years old. Growth curves indicate a rapid growth phase during early life, which slows down after reaching sexual maturity, which is consistent with data derived from ecological studies of this species. Finally, based on the growth curves we estimated potential sexual dimorphism in the growth rate before and after the attainment of sexual maturity in males and females.

The data that supports the findings of this study are available in the supplementary material of this article.

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Data Availability Statement

The data that support the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.