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# Developmental growth patterns of the filter-feeder pterosaur, *Pterodaustro guiñazui*

**A. Chinsamy**[1,*], **L. Codorniú**[2] **and L. Chiappe**[3]

[1]*Zoology Department, University of Cape Town, Private Bag, Rondebosch 7701, Republic of South Africa*
[2]*Becario CONICET, Departamento de Geología, Universidad Nacional de San Luis, Chacabuco y Pedernera, CP 5700 San Luis, Argentina*
[3]*The Dinosaur Institute, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA*
**Author for correspondence (anusuya.chinsamy-turan@uct.ac.za).*

**Life-history parameters of pterosaurs such as growth and ontogenetic development represent an enigma. This aspect of pterosaur biology has remained perplexing because few pterosaur taxa are represented by complete ontogenetic series. Of these, *Pterodaustro* is unique in that besides being represented by hundreds of individuals with wing spans ranging from 0.3 to 2.5 m, it includes an embryo within an egg. Here we present a comprehensive osteohistological assessment of multiple skeletal elements of a range of ontogenetic sizes of *Pterodaustro*, and we provide unparalleled insight into its growth dynamics. We show that, upon hatching, *Pterodaustro* juveniles grew rapidly for approximately 2 years until they reached approximately 53% of their mature body size, whereupon they attained sexual maturity. Thereafter, growth continued for at least another 3–4 years at comparatively slower rates until larger adult body sizes were attained. Our analysis further provides definitive evidence that *Pterodaustro* had a determinate growth strategy.**

**Keywords:** Pterosauria; histology; development; growth

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## 1. INTRODUCTION

The peculiar filter-feeder *Pterodaustro guiñazui* is known from the Lower Cretaceous laminated shales of the Lagarcito Formation of central Argentina (Codorniú & Chiappe 2004). This pterodactyloid pterosaur is represented by a range of different sized individuals, and therefore appears to be more like the small Jurassic pterodactyloids such as *Pterodactylus* and *Rhamphorhynchus* (Bennett 1995), rather than the large pterodactyloids such as *Pteranodon* and *Nyctosaurus*, which have only small size differences between adults and juveniles (Bennett 1993*a*,*b*; de Ricqlès *et al.* 2000).

Owing to the limited number of pterosaurs represented by different growth stages, there are relatively few studies that have explored the developmental trajectories of pterosaurs. Landmark studies in this area include largely morphological analyses on *Pteranodon* (Bennett 1993*a*) and *Rhamphorhynchus* (Bennett 1995) to assess their ontogenetic growth. In *Pteranodon*, Bennett (1993*a*) found that the extent of fusion in the juvenile skeletons, and not absolute size, allowed a distinction between juveniles and adults, and he proposed that large immature specimens of *Pteranodon*, as well as *Nyctosaurus*, *Ornithocheirus* and *Anhanguera*/*Santanadactylus* grew rapidly to adult size and then virtually stopped growing (Bennett 1993*a*,*b*). In the case of *Rhamphorhynchus*, Bennett (1995) was able to separate the specimens into distinct size classes representing different aged individuals, which led him to suggest that *Rhamphorhynchus* had a much slower growth rate than the large pterodactyloids of the Upper Cretaceous (like *Pteranodon*) and that its growth rates were comparable to extant crocodilians (Bennett 1995).

More recent attempts to interpret pterosaur growth and life-history strategies involved the histological analyses of various pterosaurs (de Ricqlès *et al.* 2000; Padian *et al.* 2004). Although limited by the availability of different ontogenetic stages within single taxa, these studies provide important baseline information about pterosaur osteohistology and led to the deduction that Late Cretaceous pterodactyloids, with wingspans of 3–11 m, such as *Montanazhdarcho*, *Pteranodon* and *Quetzalcoatlus* had 'typical dinosaurian and even typical bird-like bone growth' (de Ricqlès *et al.* 2000; Padian *et al.* 2004). These researchers further suggested that some smaller basal pterosaurs of the Triassic and Jurassic (with wingspans up to 1.5 m), especially *Rhamphorhynchus*, appear to have grown more like smaller birds (de Ricqlès *et al.* 2000; Padian *et al.* 2004). The current study represents the first comprehensive assessment of osteohistological changes during ontogeny within a single pterosaur taxon.

## 2. MATERIAL AND METHODS

Our sample consisted of multiple examples of limb bones such as the humerus, tibia and femur of different sized individuals of *Pterodaustro* (table 1). In addition, different bones from single skeletons were also sampled to gain information about histological variability within single skeletons. Each skeletal element sampled was compared with the largest known specimen in order to determine its relative body size (table 1). After detailed anatomical study and casting of all the material to be studied histologically, samples were thin-sectioned according to the methodology outlined in Chinsamy-Turan (2005). Bones were preferentially cross sectioned in the midshaft region of the bone, while longitudinal sections were taken in the proximal or distal regions.

## 3. RESULTS

Although the bones of *Pterodaustro* were generally crushed, histological details were clearly discernible. The thin bone walls consisted of a varying mixture of periosteally derived primary bone and/or endosteally formed compacted coarse cancellous bone and/or lamellar bone, depending on the size of the individual and the region of the bones sectioned. From the multiple skeletal analyses, it was evident that the histological record is best studied in the femora, tibiae and radii, while the humeri appears to be fairly remodelled during early ontogeny and was therefore unreliable for skeletochronology, as were the ulnae and fibulae (table 1). However, the well-represented sample sizes of the humeri enabled deductions regarding the timing of medullary expansion and the development of the inner circumferential lamellae (ICL; figure 1*a*,*b*). By 51% of adult size (V89, table 1),

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Table 1. Tabulation of specimens studied, length and relative size of the individual elements when compared with the largest element known and number of growth rings counted. (Specimens from the collections of Museo de Historia Natural, Universidad Nacional de San Luis, Departamento de Geología, Vertebrados (MHIN-UNSL-GEO V) have the prefix 'V', and specimens from the collections of the Museo Municipal de Ciencias Naturales 'Galileo Scaglia', Mar del Plata, have the prefix MMP. —, none observed; X, poor histological preservation; ?, possibly; est., estimated.)

| | | | no. of growth rings | | | | | |
|---|---|---|---|---|---|---|---|---|
| specimen | element length (mm) | % of largest | humeri | femora | tibiae | radii | ulnae | fibulae |
| V237 | 16.93 | 13 | X | | | | | |
| MMP1207 | 59.62 | 45 | — | | | | | |
| MMP1207 | 85.58 | 49 | | | | | X | |
| MMP1207 | 84.93 | 53 | | | | 2 | | |
| V58 | 42.85 | 45 | | 3 | | | | |
| MMP1089 | 64.02 | 49 | X | | | | | |
| V89 | 66.92 | 51 | 3 | | | | | |
| V161 | 106.73 | 58 | | | 4 | | | |
| V231 | 117.42 | 67 | | | | | 2 | |
| V150 | 129.52 | 70 | | | 4 | | | |
| V150 | — | — | | | | | | 4? |
| V56 | 71.35 | 74 | | 4 | | | | |
| V16 | 122.28 | 77 | | | | 2 | | |
| V82 | 136.97 | 78 | | | | | X | |
| MMP1469 | 104.39 | 79 | 4 | | | | | |
| V28 | 168.6 | 91 | | | 5 | | | |
| V382 | est. 96.0 | 100 | | 5 | | | | |

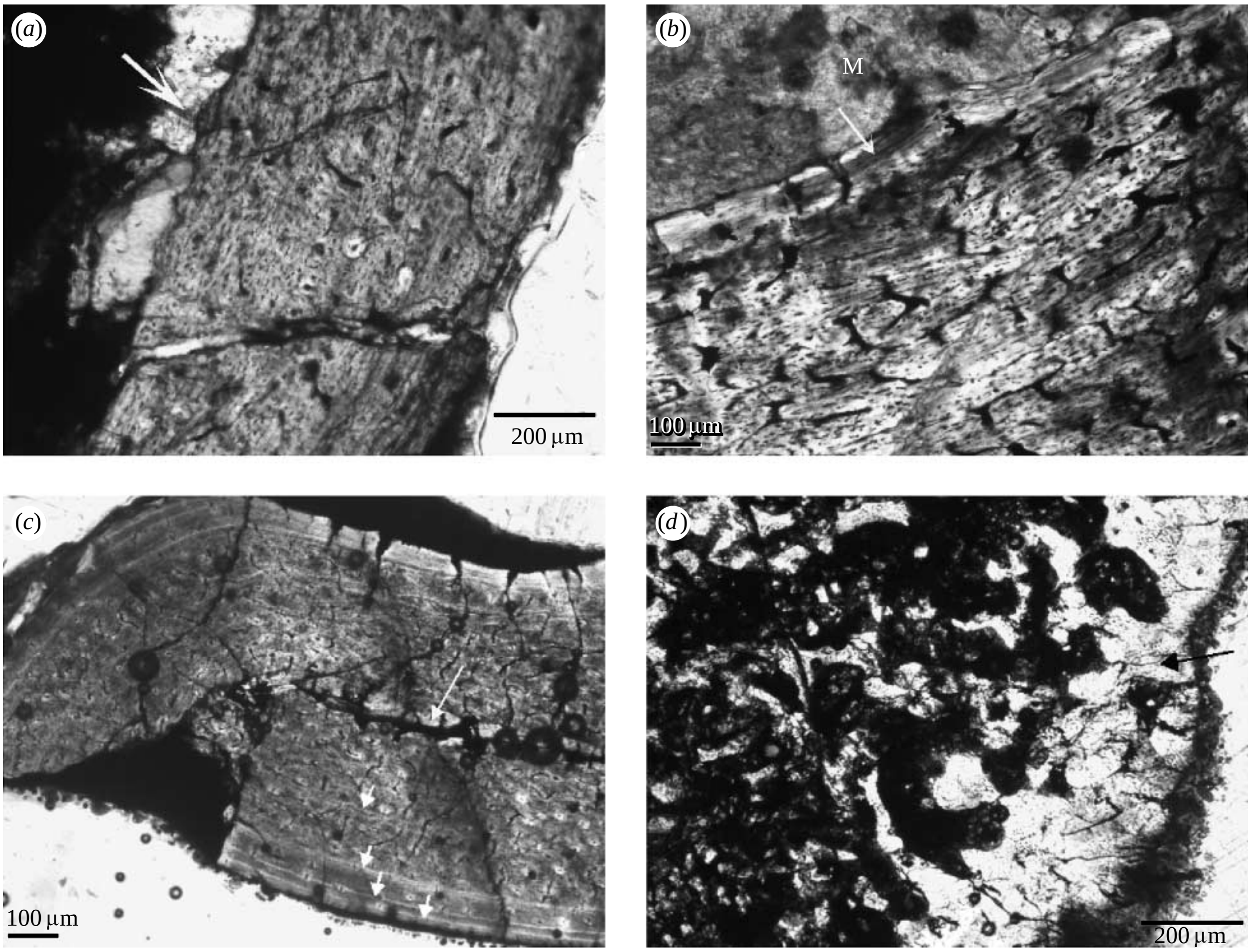

Figure 1. Bone microstructure of *Pterodaustro*. (*a*) Transverse section of humerus MMP1207 showing the resorptive medullary surface (arrow). (*b*) Oblique section of humerus MMP1469 showing the well-developed layer of inner circumferential lamellar (arrow) bone that lines the medullary cavity (M). (*c*) Transverse section of tibia V28. Black arrows indicate periodic interruptions in growth. Note the close spacing of the outer three growth marks and the gradual decrease in the number of 'blood vascular' channels towards the periphery. The medullary cavity is lined by an inner circumferential layer of bone (white arrow). (*d*) Longitudinal section of the proximal end of femur V382 (largest known femur of *Pterodaustro*). A distinct layer of bone lines the 'articular edge' of the bone (arrow).

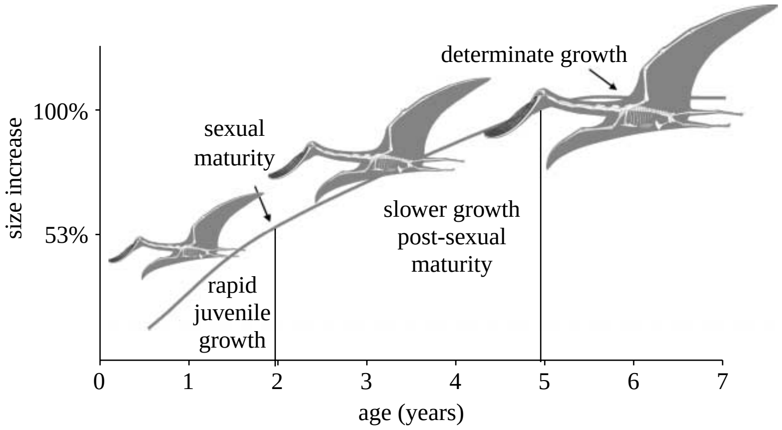

Figure 2. Schematic growth curve of *Pterodaustro* based on the analysis of the bone microstructure. It appears that early growth occurred rapidly for about 2 years until approximately 53% of adult size, when sexual maturity occurred. Thereafter, growth continued at a slower rate for 3–4 years until skeletal maturity was reached.

a thin layer of ICL lines the medullary cavity suggesting that medullary expansion had reached its maximum dimensions. By 79% of adult size (MMP1469, table 1), the medullary cavity is lined by a thick layer of ICL and no resorption lines were observed. These findings suggest that by the time *Pterodaustro* is 51% of adult size, humeral medullary expansion is already complete, and further increase in size does not involve the perimedullary region of the mid-diaphysis. The bone walls of *Pterodaustro*'s bones are richly inundated by a large number of channels wherein blood vessels and other connective tissue occurred in the living pterosaur (Starck & Chinsamy 2002). The channel orientation was predominantly longitudinal, with some reticular arrangements (figure 1*a*,*c*). This type of spatial arrangement of the channels occurred in the wing bones (humerus, radius and ulna) and leg bones (femur and tibia), and is characteristically unlike the predominantly circumferentially oriented 'vascular' channels present in the wing bones of most birds in response to torsional loading during flight (de Margerie 2002). The bone microstructure observed in *Pterodaustro* appears to be similar to that of Procellariiformes (albatrosses, petrels and relatives; de Margerie 2002), most of which are fairly large birds that tend to soar in strong winds on long narrow wings that are not specialized for consistent flapping flight (de Margerie 2002). The histological similarity between Procellariiformes and *Pterodaustro* may indicate that the latter had a similar flight mode, but it is also likely that other factors such as bone depositional rate and biomechanical properties of the bone influence its histological structure.

Erosion cavities are absent in *Pterodaustro*'s bones and only some isolated occurrences of secondary osteons. This seems to be a general characteristic of pterosaur cortical bone tissues (de Ricqlès *et al.* 2000; Padian *et al.* 2004), and the current study provides evidence that this is the case throughout ontogeny.

In the youngest individuals, the occurrence of fibrolamellar bone tissue suggests that bone deposition (and hence growth) was rapid. Thereafter, the deposition of a thin layer of lamellar bone tissue, the annulus, indicates a comparatively slower rate of bone formation. Such alternating fast (zones) and slow growth (annulus) cycles are known to form annually in lepidosaurs (Castanet *et al.* 1993) and crocodilians (Castanet *et al.* 1993; Erickson *et al.* 2004), and are also present and assumed to be annual in non-avian dinosaurs (Reid 1981; Chinsamy 1990; Erickson *et al.* 2004; Chinsamy-Turan 2005; Erickson 2005; Erickson *et al.* 2007) and Mesozoic basal birds (Chinsamy & Chiappe 1994). Thus, given that such annual growth patterns are present in the archosaurian out-groups of pterosaurs, it is reasonable to assume that they are also annual in *Pterodaustro*.

Two to three cycles of zones and annuli are observed in *Pterodaustro*. With increasing ontogeny, bone deposition periodically stopped, resulting in the formation of lines of arrested growth (LAGs), and the bone deposited in the zones changed to a parallel-fibred bone tissue with less channels for vascularization, suggesting an overall slower rate of bone formation when compared with early growth. Later, in ontogeny, the spacing of the LAGs tends to become visibly closer as a result of less bone being appositionally deposited (figure 1*c*).

Longitudinal sections of long bones of young individuals show large amounts of calcified cartilage at the ends of the bone. Bony trabeculae also extend into the metaphyseal area and, in many instances, islands of calcified cartilage occur in them. These characteristics suggest that elongation of the bone occurred rapidly during early stages of growth. However, in the larger individuals, the bony struts extend right to the 'articular' end of the bone, and in the largest individual studied, a distinct layer of bone is visible at that articular edge of the bone (figure 1*d*), directly implying that diaphyseal elongation had ceased, and that maximum skeletal size had been attained.

## 4. DISCUSSION

On the basis of these histological findings, it appears that *Pterodaustro* hatchlings grew rapidly for approximately 2 years, until they were approximately 53% of adult size. Thereafter, the change from fibrolamellar bone tissue to parallel-fibred bone tissue is possibly in response to energy being redirected from growth to reproduction (Chinsamy-Turan 2005; Erickson 2005; Erickson *et al.* 2007). This trend has been observed in extant lepidosaurs (Castanet *et al.* 1993) and it has been hypothesized for a variety of non-avian dinosaurs (Erickson *et al.* 2007). Thus, we suggest that the change in growth rate observed in the growth series of *Pterodaustro* marks the onset of sexual maturity at approximately 53% of adult size. Thereafter, growth in length and diameter occur at slower rates for another 4–5 years until larger body sizes were attained. In the largest individuals, the close spacing of the growth lines, and the lack of calcified cartilage in the long bones, directly suggests that overall growth had ceased.

These histological findings support the deductions made on the basis of morphology that Late Jurassic *Rhamphorynchus* and *Pterodactylus* represent multiple year classes and took several years before adulthood was attained (Bennett 1995). Thus, our findings are contrary to the suggestion that small basal pterosaurs of the Triassic and Jurassic (with wingspans up to 1.5 m) appear to have growth patterns more like smaller birds (Padian *et al.* 2004). We found that the growth patterns of *Pterodaustro* differs significantly from modern birds: firstly, *Pterodaustro* grew in periodic spurts and took several years to reach skeletal maturity and secondly, unlike modern birds that attain sexual maturity after reaching full adult size (Erickson *et al.* 2007), *Pterodaustro* appears to have attained sexual maturity and continued growing for a few more years before attaining full skeletal size (figure 2). Thus, the timing of sexual maturity in *Pterodaustro* is more similar to extant squamata and crocodilians (Chabreck & Joanen 1979; Wilkinson & Rhodes 1997) and a variety of non-avian dinosaurs (Chinsamy-Turan 2005).

Our investigation of skeletal and ontogenetic variation in *Pterodaustro* has directly revealed insight into the developmental growth dynamics of this unusual filter-feeding pterosaur from early ontogeny to adulthood. Our results provide novel information regarding the timing of medullary expansion in *Pterodaustro*, and suggest that this pterodactyloid pterosaur attained sexual maturity at approximately 2 years of age, and continued to grow for 3–4 years until it doubled in size and attained skeletal maturity (figure 2).

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