

Research



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Osteohistological analyses reveal diverse strategies of theropod dinosaur body-size evolution

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The independent evolution of gigantism among dinosaurs has been a topic of long-standing interest, but it remains unclear if gigantic theropods, the largest bipeds in the fossil record, all achieved massive sizes in the same manner, or through different strategies. We perform multi-element histological analyses on a phylogenetically broad dataset sampled from eight theropod families, with a focus on gigantic tyrannosaurids and carcharodontosaurids, to reconstruct the growth strategies of these lineages and test if particular bones consistently preserve the most complete growth record. We find that in skeletally mature gigantic theropods, weight-bearing bones consistently preserve extensive growth records, whereas non-weight-bearing bones are remodelled and less useful for growth reconstruction, contrary to the pattern observed in smaller theropods and some other dinosaur clades. We find a heterochronic pattern of growth fitting an acceleration model in tyrannosaurids, with allosauroid carcharodontosaurids better fitting a model of hypermorphosis. These divergent growth patterns appear phylogenetically constrained, representing extreme versions of the growth patterns present in smaller coelurosaurs and allosauroids, respectively. This provides the first evidence of a lack of strong mechanistic or physiological constraints on size evolution in the largest bipeds in the fossil record and evidence of one of the longest-living individual dinosaurs ever documented.

1. Introduction

Histological analyses of fossil tetrapod bones are commonly used to investigate their palaeobiology, and the applications of these methods to dinosaurs have yielded insights into their growth rates, thermophysiology, taxonomic identification and maturity [1–5]. *Tyrannosaurus rex*, one of the largest terrestrial carnivores and bipeds known, has been the focus of several studies elucidating life-history parameters through bone histology [6–9]. Nevertheless, these studies have sampled different bones of the skeleton, generating questions as to whether the largest growth stages of *T. rex* have been sampled [6] or not [10], and also

whether weight-bearing bones (WBB) present a more or less reliable record of growth than non-weight-bearing elements (NWB) (e.g. [1,6,7,11]). To the latter issue, while previous research on small theropods has suggested that NWB such as fibulae provide a more complete record when compared with WBB of the same individuals [12,13], it remains unclear how well this holds in large theropods [6,7,9], and in other large dinosaurs, there are varying patterns, with hadrosaurs appearing to generally preserve the most complete growth record in WBB [14], while in sauropods NWBs preserve the most complete and less remodelled growth records [15]. Furthermore, while it was shown that *T. rex* achieved greater body mass through growth acceleration when compared with related tyrannosaurids [6], comparable data are lacking for other large theropods such as carcharodontosaurids, which achieved body masses rivalling those of many large tyrannosaurids. In this histological study, we have undertaken the hitherto broadest phylogenetic sampling of non-avian theropods, including multi-element comparisons for 8 of our 11 total sampled species, to address two fundamental questions in the study of dinosaur growth and life-history parameters:

- (i) Given documented inter-elemental variability in preserved growth mark records in hadrosaurid [14] and sauropod [15] dinosaurs, how variable is the growth mark record across commonly sampled bones in the theropod skeleton, and do WBB or NWB preserve a more complete growth record?
- (ii) Theropod dinosaurs such as *Tyrannosaurus* and carcharodontosaurids independently evolved gigantic sizes (greater than 1–4.5 tonnes), converging on mass estimates of 7–8 tonnes for large individuals via most methods, and up to or greater than 10 tonnes in the case of some estimation methods [6,16–19]. Did all lineages exhibiting gigantism follow a common growth strategy of growth acceleration as already shown for *T. rex* [6], or is there evidence for a diversity of strategies with modulation of life-history parameters other than the growth rate, such as longevity?

Related to our first question, individual, intra- and inter-specific variability in growth marks between different bones remains somewhat poorly quantified in non-avian theropod dinosaurs due to a paucity of multi-element analyses compared with the number of studies using a single bone [12–15,20,21]. Without detailed data to address these uncertainties, palaeohistologists have debated the selection of WBB versus NWB as the primary source of data for growth and age reconstructions (e.g. [1,6–8,11,14,21–24]). Arguments favouring the use of WBB rely on their more symmetrical growth, because they support the whole body mass and are thus less influenced by differential allometric patterns than NWB [7]. The counterargument in favour of using NWB is that they are less likely to experience stress-induced microfractures and consequently less likely to be remodelled [16]. As an additional benefit, they may have more complete growth records resulting from a lack of large medullary cavities [6]. Further investigation of within-specimen histovariability is necessary to quantify the uncertainty in preserved growth signals across individual skeletons and species samples and allow for more accurate comparisons of growth records between taxa.

Understanding the macroevolutionary pressures driving repeated independent evolution of gigantism in theropods, and the mechanisms by which it was attained, is of great interest to understanding how dinosaurian ecosystems were structured [25]. If the considerable increase in growth rate over a constrained growth period, as seen in tyrannosaurids [6,7], is the sole strategy by which theropods achieved large body sizes, it could suggest that metabolic or mechanistic constraints may have influenced the evolution of gigantism in these bipeds. Alternatively, independent evolution of large body size in theropods resulting from divergent growth strategies might suggest that differing selective regimes related to extrinsic factors, or phylogenetic constraints, played a larger role in these evolutionary patterns.

In this study, specific comparisons focus on variation in recorded cyclical growth mark (CGM) or line of arrested growth (LAG) counts, growth zone thickness and vascularization patterns, as preserved in the bone microstructure of thin-sectioned fossil bones. Changes in vascularization patterns have been shown to relate to metabolism and growth rate, whereas changes in LAG circumference and growth zone thickness can be used to assess the amount of body-size change in a given year [3,4,6,22,26–30]. Additionally, each sampled specimen is assessed for skeletal maturity, which can be determined through the presence or absence of an ‘external fundamental system’ (EFS [14], also referred to as an outer circumferential layer or OCL [26]) in the periosteal margin of the bone cortex. These combined metrics and traits allow for relative differences in the growth patterns of the sampled taxa to be compared and assessed. Furthermore, proportional annual bone circumference changes were compared for a broad sample of theropods, and model-based age retrocalculation and growth curve reconstructions performed on representatives of two gigantic theropod taxa as an additional comparison and quantification of growth pattern differences.

2. Results

(a) Element choice is most critical in large-bodied taxa

All thin-sectioned elements predominantly exhibit fibrolamellar bone as a woven-parallel complex tissue [21,28]. Vascular patterns and density are consistent with a laminar to plexiform arrangement over much of the primary bone, although localized areas of more complex reticular or longitudinal vascularization occur and are more prevalent in small-bodied coelurosaurs, consistent with other studies of theropod osteohistology [5–7,12,13,31,32]. Histological comparisons from a wide range of theropods (figures 1 and 2; electronic supplementary material, table S1) reveal several broad patterns. First, in smaller-bodied (less than 1 tonne) taxa, growth mark count varies only slightly between sampled elements of the same individuals, with NWB often preserving more growth marks (typically approximately 1 additional LAG; electronic supplementary material, table S1). A different pattern is seen in *Cryolophosaurus ellioti*, where considerably more LAGs are identifiable in the fibula, gastralia and rib when compared with the femur. The femur of this specimen is cracked and re-crystallized, however, so determination of LAGs is hampered.

Unlike the pattern seen in these smaller theropods, the gigantic taxa *Tyrannosaurus rex* and an unnamed Campanas

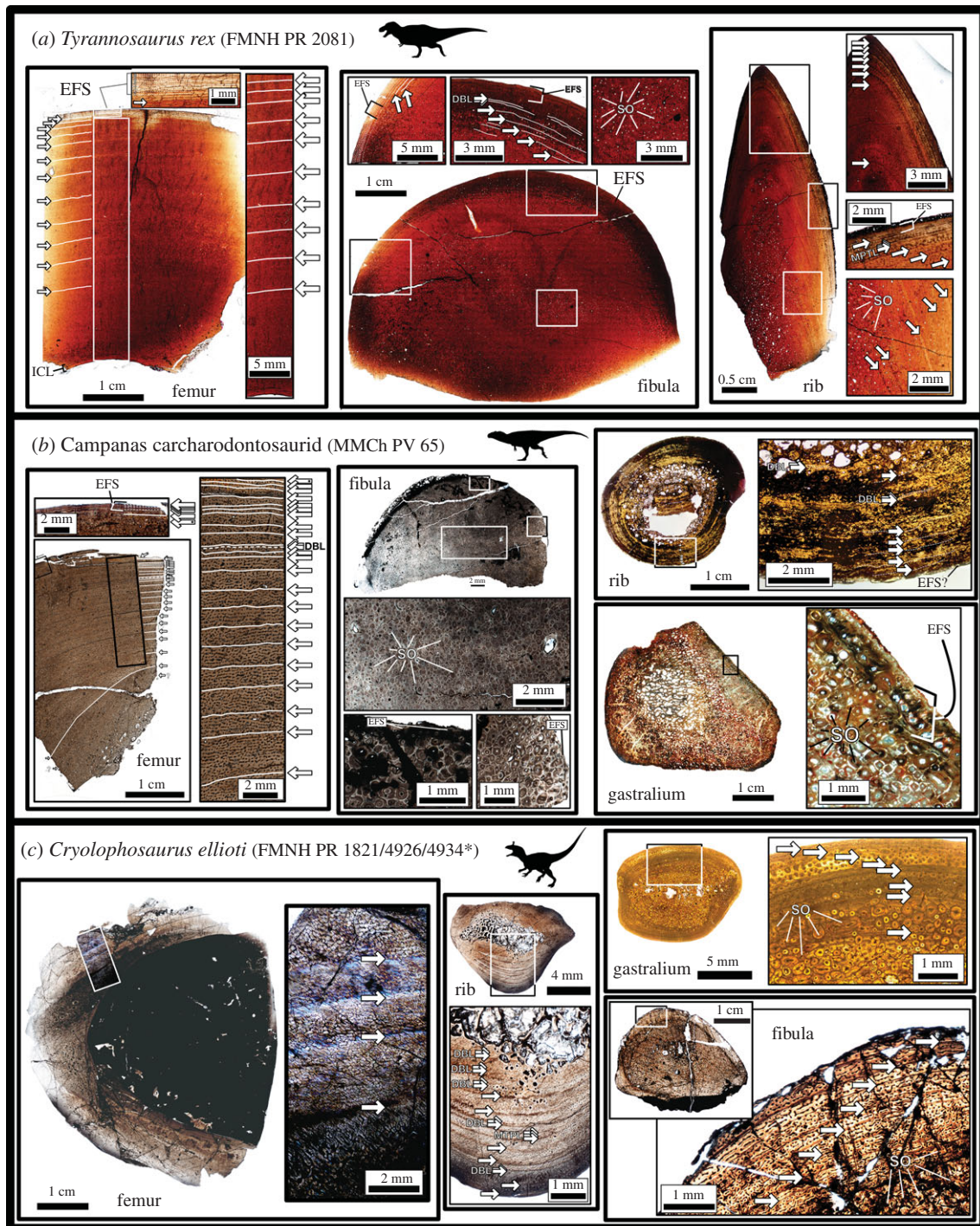


Figure 1. Multi-element osteohistological comparisons of (a) *Tyrannosaurus rex*, (b) the Campanas carcharodontosaurid and (c) *Cryolophosaurus ellioti*. In the case of the latter, all bones are from same individual but represented by multiple specimen numbers based on collection history (see electronic supplementary material, methods S1). Growth marks indicated by arrows and solid traced lines. Double or multiple growth marks indicated by multiple stacked arrows and dashed lines. Abbreviations: DBL, double growth mark; EFS, external fundamental system; ICL, inner circumferential layer; MPTL, multiple growth mark; SO, secondary osteons. See electronic supplementary material, results S1 and Dryad [60] for additional histological comparisons and images. (Online version in colour.)

carcharodontosaurid (see electronic supplementary material, methods S1) exhibit marked differences in preserved bone tissue and LAG counts between WBB and NWB (figure 1). In these gigantic taxa, the weight-bearing femora consistently preserve excellent growth records as LAGs and primary tissue, with a relatively little remodelling. By contrast, the fibulae of both taxa are heavily remodelled, to the point of preserving few if any discernable growth marks beside the EFS in the outermost cortex. Among other sampled elements, ribs appear to preserve more primary tissue than fibulae, but have higher rates of remodelling than the femora, and

sampled gastralia are heavily remodelled, similar to fibulae (figure 1; electronic supplementary material, table S1).

(b) Distinct patterns of growth exist in taxa that independently evolved gigantic size

Comparisons of the femoral sections of *T. rex* and the Campanas carcharodontosaurid reveal distinct differences in growth mark count and distribution. In *T. rex*, 23 growth marks are observable (12 in the primary cortex, 11 in the EFS), with growth zone thickness varying but generally transitioning

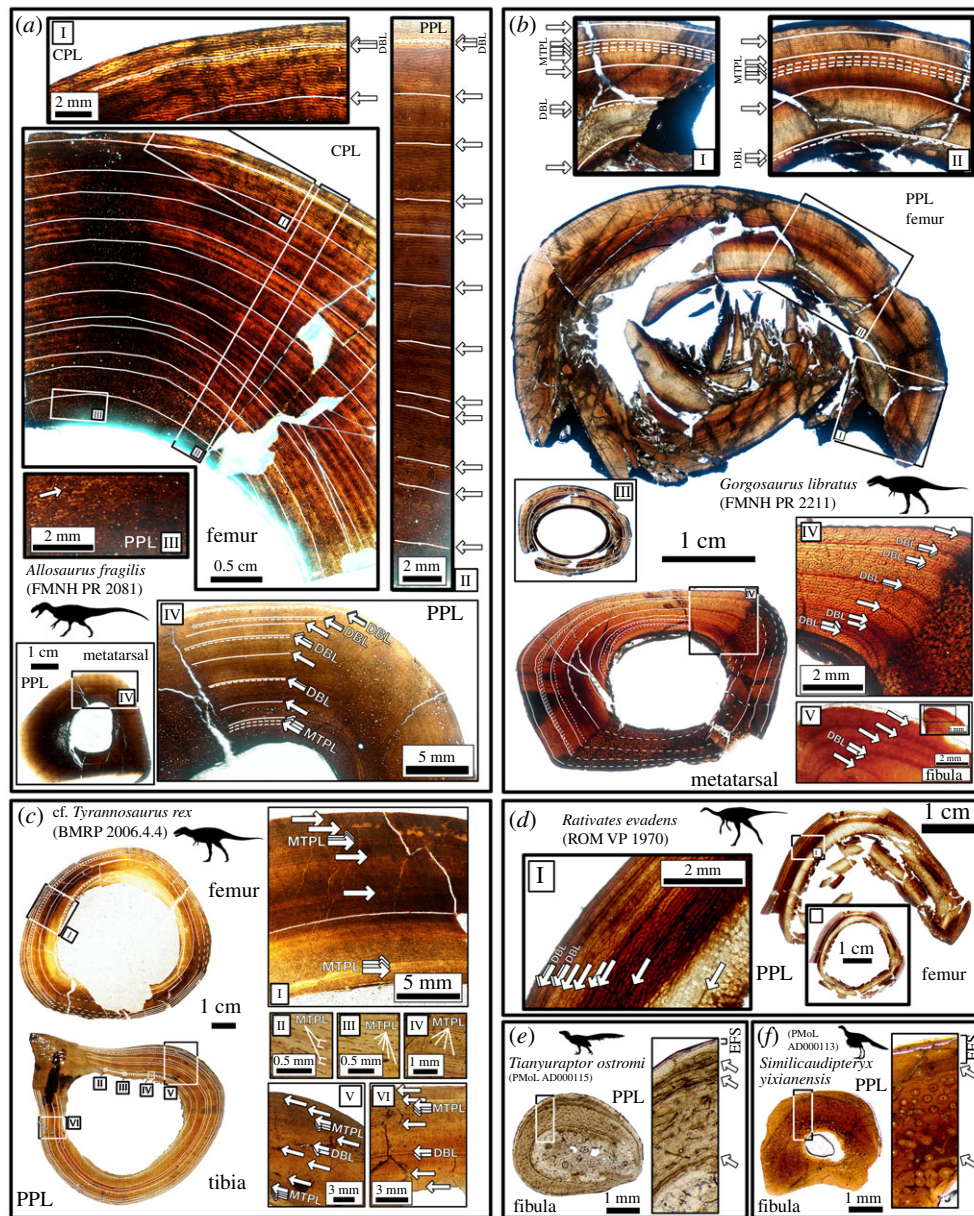


Figure 2. Osteohistological overview of (a) *Allosaurus fragilis*, (b) *Gorgosaurus libratus*, (c) cf. *Tyrannosaurus rex*, (d) *Rativates evadens*, (e) *Tianyuraptor ostromi* and (f) *Similicaudipteryx yixianensis*. Where multiple inset images exist for a single specimen, inset associations are indicated by roman numerals. Growth marks indicated by arrows and solid traced lines. Double or multiple growth marks indicated by multiple stacked arrows and closely dashed lines. Broadly dashed lines indicate inferred location of circumferential growth marks, based on observed presence elsewhere in specimen. Abbreviations: CPL, circular polarized light; DBL, double growth mark; EFS, external fundamental system; MPTL, multiple growth mark; PPL, plane polarized light. See electronic supplementary material, results S1 and Dryad [60] for additional histological comparisons and images, and discussion of multiple growth marks and re-interpretation of juvenile *T. rex* ages. (Online version in colour.)

abruptly from broad growth zones in the inner cortex to thin zones in the outer cortex, just prior to the onset of the EFS (figure 1a; electronic supplementary material, table S1). By contrast, in the Campanian carcharodontosaurid, there are 28 growth marks observed (24 in primary cortex, 4 in EFS), with growth zone thickness gradually decreasing in the absence of any abrupt shifts (figure 1b; electronic supplementary material, table S1). Cortical thickness and medullary cavity size are proportionally similar in both taxa, though the *T. rex* specimen is approximately 10% larger than the carcharodontosaurid.

These distinct patterns are reflected in the model-based growth curve reconstructions of both taxa and related age retrocalculations (figure 3a,b), where *T. rex* exhibits rapid sub-adult growth increases, which quickly level off to skeletal

maturity under all fitted models, and the carcharodontosaurid exhibits a far more drawn out growth pattern with considerably more shallow slope (and resulting growth rates). Depending on the model applied, *T. rex* is reconstructed with age at death of 27–33 and skeletal maturity achieved after 16–22 years, which is for most models older, but overall broadly consistent with previously published estimates for this taxon based on estimates from a rib section [6], and together with Persons *et al.*'s fibula data [8] also conclusively demonstrates that we have sampled the largest/eldest growth stages for *T. rex* (contra [10]). The model with the best fit (logistic) for the recorded growth in this mature *T. rex* specimen is also consistent with recent analyses of two juvenile specimens referred to *T. rex*, which hypothesized a period of smaller size in early ontogeny followed by a

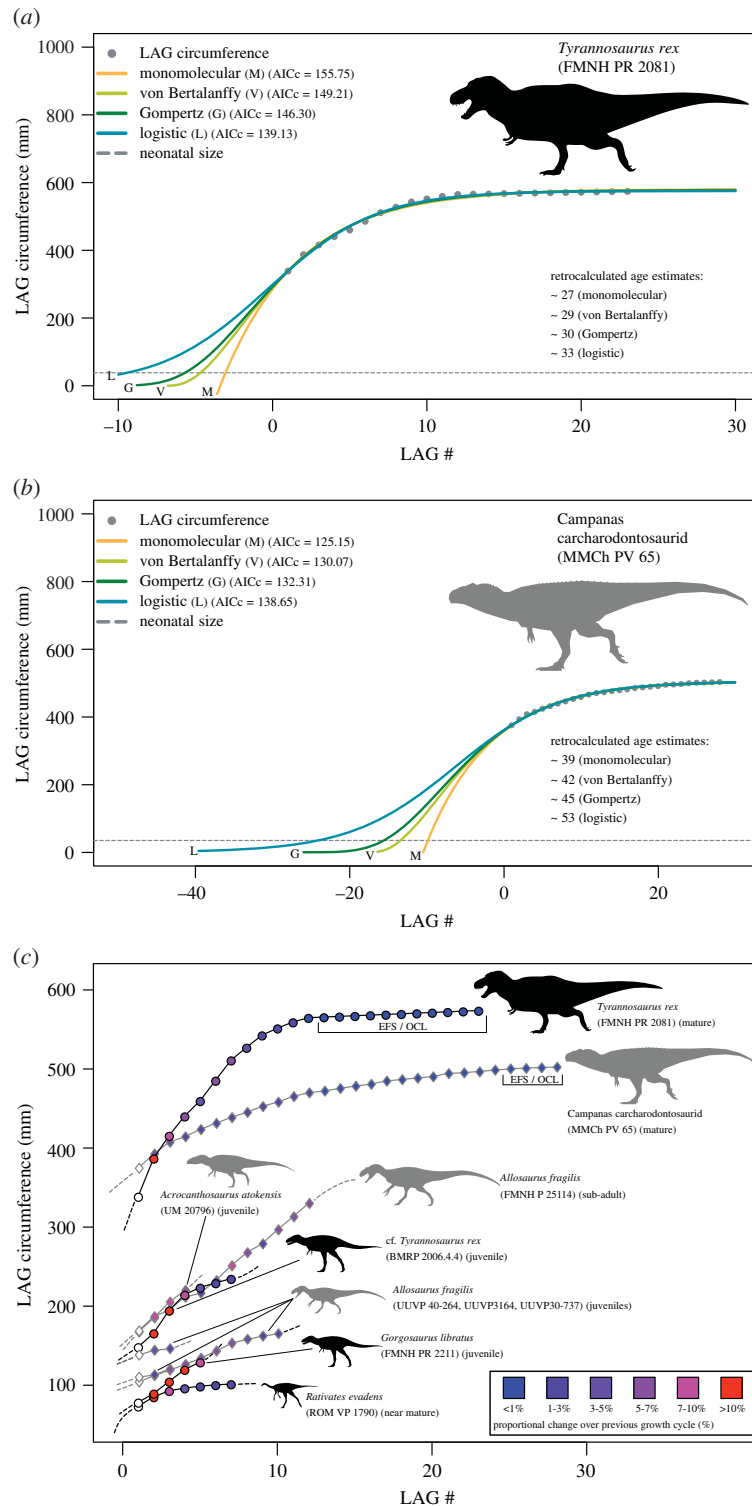


Figure 3. Growth curve reconstructions and retrocalculated ages for (a) FMNH PR 2081 (*Tyrannosaurus rex*), and (b) MMCh PV 65 (*Campanas carcharodontosaurid*), with (c) superimposed growth mark circumferences and associated LAG counts for these specimens and a broad sample of theropod dinosaurs (see electronic supplementary material, tables S1 and S2). For each specimen in (c), proportional change in circumference over the previous growth cycle (in %) was calculated and plotted in colours for each point based on six possible categories (noted on the figure). In (c), circles denote coelurosaurs and diamonds denote allosauroids.

massive increase in growth in ‘teenage’ years to achieve adult body size [9]. Retrocalculated ages for the *Campanas carcharodontosaurid* range from 39 to 53 years, with skeletal maturity achieved after 35–49 years. The age estimates for this carcharodontosaurid also place it as one of the oldest known dinosaur specimens, certainly among the oldest estimates for a large theropod [33], and similar to estimated ages for mature large sauropod taxa [34], with a caveat that even the upper bound estimate falls short of the maximal age estimates proposed for some sauropods [35].

(c) Increased growth rates distinguish sampled coelurosaurs from non-coelurosaurs

The pattern of growth observed in *T. rex* [6,7,9], with major increases in growth rate (via growth zone thicknesses) in early to mid-ontogeny, followed by abrupt shifts to growth cessation and maturity, is also observed in the other sampled coelurosaurs, both qualitatively (figure 2) and quantitatively via differences in proportional annual changes in femoral circumference (figure 3c; wherein only coelurosaurs record

proportional annual changes greater than 10%). This includes juvenile specimens of tyrannosaurids such as *Gorgosaurus libratus* (figures 2b and 3c) and *T. rex* (figures 2c and 3c), but also small to medium-sized coelurosaurs such as the ornithomimids *Rativates evadens* (figures 2d and 3c) and *Ornithomimus edmontonicus* [12], the caenagnathid *Anzu wyliei* [13], and even in the very rapid growth and fast maturation of small taxa like the caudipterid *Similicaudipteryx yixianensis* (figure 2f) and the microraptorine *Tianyuraptor ostromi* (figure 2e). The pattern of growth in *T. rex* thus appears to represent an extreme, or ‘end-member’, variant of the general growth pattern observed across non-avian Coelurosauria. Similarly, the more gradual and extended periods of relatively rapid growth in the Campanas carcharodontosaurid (figures 1 and 3) is an extended variant of the pattern of growth observed in other, smaller (though still relatively large) non-coelurosaurs, such as *Cryolophosaurus ellioti* (figure 1c), *Allosaurus fragilis* (figures 2a and 3c) and *Acrocanthosaurus atokensis* (figure 3c), which display many narrow, but relatively similarly spaced growth zones, rather than the broad inner zones and abrupt shift to thinner outer zones at the onset of maturation seen in coelurosaurs. Our *Allosaurus fragilis* sample records and extends a growth pattern broadly consistent with other specimens of *Allosaurus* [31], and represents the largest histologically examined individual (figure 3c; electronic supplementary material, table S1). As well, double/multiple growth marks are prevalent throughout the sampled theropod taxa (figures 1 and 2), occurring in specimens of various ontogenetic stages and in different sampled elements. See electronic supplementary material, results S1 for expanded histological and growth comparisons of sampled theropod specimens, including additional multi-element comparisons and discussion of ‘double’/‘multiple’ growth mark distribution. Expanding these comparisons to include an even broader sample of coelurosaurs and non-coelurosaurs from the literature recovers a similar pattern, with coelurosaurs exhibiting higher growth rates when compared to non-coelurosaur taxa of similar size (electronic supplementary material, table S3, results S2).

3. Discussion

(a) Multi-element sampling crucial for studies of theropod osteohistology

Our multi-element comparisons across a phylogenetically broad sample of theropods, representing taxa and individuals from a wide variety of body sizes and ontogenetic stages, suggest that element choice is crucial in histological examinations of gigantic theropods. Particularly in the case of mature individuals of large to gigantic taxa such as *T. rex*, carcharodontosaurids, and even *Allosaurus*, NWB preserves less of the growth and age record than WBB of the same individuals (figure 1). Combined with the benefit of using more symmetrically growing weight-bearing elements in body mass estimation equations [19] and growth curve reconstructions [2,27,36], it is recommended that weight-bearing elements such as femora or tibiae be used for histological analyses of gigantic theropod dinosaur species. In all specimens with EFS, WBB have greater LAG counts than NWB. This relationship also holds for larger/older specimens without an EFS, but where moderate to large degrees of remodelling especially in NWB have erased a greater part of the growth

record. Conversely, in younger specimens exhibiting no EFS and only slight to moderate remodelling, NWB retain a greater number of LAGs and may thus have a higher fidelity with respect to age than WBB, although variances are small. Taking this into account alongside the small to moderate variability that exists in growth zone thickness patterns between elements, we strongly recommend that multi-elemental sampling be used whenever possible, but emphasize that for larger and mature animals the inclusion of weight-bearing elements is crucial.

Our results demonstrating that WBB are less remodelled than NWB in gigantic taxa may seem counterintuitive given greater biomechanical stress on WBB. Nevertheless, this pattern matches hypothetical predictions that in large-bodied taxa with a comparatively rapid and massive overall body-size increase, the main weight-bearing limb bones need to increase in size at a rate greater than would allow considerable remodelling to occur [37]. Smaller NWB without such constraints would likely slow or cease their growth at an earlier growth stage and would then begin to experience considerable secondary bone remodelling [37]. Our results provide empirical support for this hypothesis in giant theropods and underscore our conclusion that WBB be examined preferentially when studying the growth of extremely large bipedal organisms. These results differ in varying degrees from those published for other dinosaurs. For example, in a multi-element sampling of *Camarasaurus* [15], ribs were found to preserve a more extensive growth record than limb bones. On the other hand, Horner *et al.* [14] also found that in a mature specimen of the hadrosaurid *Hypacrosaurus*, hind limb bones including the femur preserved a better growth record than rib samples. Taken together, these empirical results suggest that growth patterns are unique to clades and perhaps even species, precluding a single sampling approach for all non-avian dinosaurs and emphasizing the need for multi-element sampling.

(b) Macroevolution of gigantic body size not constrained to a single growth strategy

Our results suggest that divergent growth strategies exist in theropods and are particularly identifiable in ‘gigantic’ taxa (figure 3). While slight to moderate variability exists in growth from year to year in the sampled specimens, consistent with other studies of theropod histovariability [9,12], it does not fundamentally impact the overall macroevolutionary patterns we observe. Indeed, the relative growth patterns preserved for the gigantic representatives of the sampled clades are very similar to those of their respective smaller sized relatives, but taken to a relative extreme. Whereas the heterochronic pattern of growth in tyrannosaurs has been ascribed to acceleration [6] that observed in allosauroid carcharodontosaurids may better fit a model of hypermorphosis [38]. This suggests that gigantic body size in theropods can be achieved through multiple changes to life-history parameters and is not mechanically or physiologically constrained to a single growth strategy.

From these results, we would also predict that, barring the identification of an additional distinct strategy for attaining large body size, a suitable null hypothesis for the growth patterns of other large to gigantic non-coelurosaurian theropod taxa would most closely fit a hypermorphosis model. Small to medium abelisaurid taxa have been found to display

a range of moderate to relatively slow growth rates [39], and although complicated by a lack of mature specimens, the limited histological data from spinosaurids suggests an extended period of growth [40]. While the allosauroid *Acrocantiosaurus* has been hypothesized to achieve large body size through growth rate acceleration [41], proportional circumference changes in femoral sections from juveniles of this taxon follow the pattern seen in other non-coelurosaurs (figure 3c).

Multiple growth strategies for achieving gigantism have also been identified in sauropodomorph dinosaurs [42], suggesting that body-size evolution by modulating growth was common in dinosaurs. Whereas LAGs/CGMs are present throughout growth in most non-sauropod sauropodomorphs, sauropods only appear to develop LAGs in limb bones close to somatic maturity suggesting that protracted continuous growth during early ontogeny explains their generally greater body sizes, including the largest terrestrial animals to have lived. Such marked differences in tissue organization are as yet unknown among non-avian theropods, in which similar maximum body sizes are attained by both slow-growing and fast-growing clades, all of which show LAG/CGM throughout ontogeny (figure 3; electronic supplementary material, results S1 and S2).

The phylogenetic distribution of growth patterns in the available theropod data, with representatives of earlier diverging clades (e.g. *Cryolophosaurus* and allosauroids such as *Allosaurus*, *Acrocantiosaurus* and the Campanas carcharodontosaurid) primarily achieving larger size via steady growth over extended periods somewhat similar to those seen in crocodylians [43], and coelurosaurs like the tyrannosaurids (e.g. *Gorgosaurus*, *Tyrannosaurus*) achieving large body size through the acceleration of growth rate, it is conceivable that the latter strategy was selected for as a result of the greater metabolic and growth rates synapomorphic to coelurosaurs generally [2,7,11,16,17,24,29,44]. This inference is supported by the presence of similar growth patterns, albeit not as extreme, observed in the histological record of many non-tyrannosaur coelurosaurs, including ornithomimids (figures 2d and 3c; see also [12,45–47]), oviraptorosaurs (figure 2f) [13,17,48], troodontids [49,50], dromaeosaurids (figure 2e) [51] and of course, birds [29,52,53]. This may also suggest a physiological mechanism for how, if not why, previously small-bodied tyrannosaurs had the capacity to evolve rapidly into the top predator niche vacated by large allosauroid theropods following the ‘mid-late’-Cretaceous dinosaur faunal turnover in western North America [44,54–56].

4. Methods

Institutional abbreviations: CMN FV, Canadian Museum of Nature; FMNH, Field Museum of Natural History; MMCh, Museo Municipal ‘Ernesto Bachmann’; PMoL, Paleontological Museum of Liaoning; ROM VP, Royal Ontario Museum; UM, University of Michigan Museum of Paleontology; UUVU, University of Utah Vertebrate Paleontology.

Taxonomic, element and catalogue number identifications of sampled specimens are provided in figures 1 and 2, and electronic supplementary material, table S1. Prior to palaeohistological sampling, specimens were photographed and/or three-dimensionally scanned. Transverse sections were obtained from the bones and processed into thin sections for analysis using standard palaeohistological methods, as outlined by Cullen *et al.*

[12]. Core samples were obtained using a modified version of the methods detailed by Woodruff [23] (see electronic supplementary material, methods S1). Sampled cores were then prepared into thin sections following the same methods noted above for transverse sections. After sectioning and/or coring, casts of sampled material were made and integrated with specimens to restore lost morphological and measurement information.

LAG circumferences were estimated for the *Tyrannosaurus rex* (FMNH PR 2081) and the Campanas carcharodontosaurid (unnamed carcharodontosaurid taxon from the Huincul Formation of Argentina; MMCh PV 65) samples using growth zone radii from cores and measured circumferential dimensions of the whole bones, with LAG circumferences for other specimens directly measured from full-sections and/or retrodeformed sections (electronic supplementary material, table S2). While growth zone radii cannot be considered directly equivalent to full measures of zonal area/LAG circumference, the roughly circular to elliptical and relatively constrained growth pattern of the femur in other theropods suggests that the patterns observed here should be broadly consistent with the overall pattern of femur growth in this individual. Care was taken to sample all cores/wedges from similar locations on the anterior surface to maximize comparability, with additional comparisons made to theropod full-sections to better account for intra-cortical variability. Neonatal mass for each individual was estimated following the method outlined by Grady *et al.* [57] (and references therein) and combined with adult body mass estimations, obtained from femur circumferences of mature specimens, using the methods of Campione & Evans [58] and Campione *et al.* [19], in order to estimate neonatal femur circumferences using the ‘developmental mass extrapolation’ approach of Erickson and Tumanova [59]. Finally, these data, and the LAG circumference estimates, were used to compute model-based age retrocalculations and growth curve fitting following the methods introduced by Cooper *et al.* [2] and Lee & O’Connor [36]. Growth mark circumferences from measured taxa and literature sources were compared, and proportional annual changes (i.e. from LAG to LAG) calculated for figure 3 analyses, with source data available in electronic supplementary material, table S2 and expanded method details in electronic supplementary material, methods S1.

Data accessibility. Analytical data contained in figures/tables and attached electronic supplementary materials. All project data, including high-resolution thin-section images from sampled specimens, are archived in Dryad Digital Repository [60].

Authors’ contributions. T.M.C. conceived the project, made thin sections, performed histological analyses, performed growth curve analyses, wrote the manuscript and made the figures/tables; J.I.C. collected fossil material, assisted in histological analyses and in writing the manuscript; S.A. collected fossil material and assisted in writing the manuscript; N.D.S. collected fossil material, assisted in histological analyses and in writing the manuscript; D.H. assisted in histological analyses and in writing the manuscript; P.J.M. conceived the project, assisted in histological analyses and wrote the manuscript.

Competing interests. The authors declare no competing interests.

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