Age and growth dynamics of *Tyrannosaurus rex*†

John R. Horner[1][*] and Kevin Padian[2]

[1]*Museum of the Rockies, Bozeman, MT 59718, USA*
[2]*Museum of Paleontology, University of California, Berkeley, CA 94720-4780, USA*

Tyrannosaurus rex is the most commonly found North American latest Cretaceous theropod, but until the 1980s only five specimens had been discovered, and no more than six have received a full description. Consequently there has been little information on how old *Tyrannosaurus* specimens were at maturity or death. Histological analysis of seven individuals provided, for the first time, an opportunity to assess the age represented by the bone cortex, to estimate the average individual age of these skeletons, to determine whether they represented fully grown individuals, and to predict their individual longevity. Though a range of ages (15–25 years) was found for the specimens studied, the seven individuals demonstrate that *T. rex* reached effectively full size in less than 20 years. The growth rate of *T. rex* was comparable to that of the African elephant, which has a similar mass and time to maturity. Some of the known specimens of *T. rex* did not quite reach full size; others do not seem to have survived long after achieving it.

Keywords: dinosaurs; Tyrannosauridae; growth rates; bone histology; growth dynamics; life-history strategy

1. INTRODUCTION

Recent studies of bone microstructure have enabled researchers to chart growth curves for a variety of Mesozoic dinosaurs, including prosauropods (Chinsamy 1993), sauropods (Curry-Rogers 2000; Sander 2000), ornithopods (Horner *et al.* 2000), ceratopsians (Erickson & Tumanova 2000) and others (Erickson *et al.* 2001). These studies show that dinosaurs did not grow like typical reptiles, but rather more like large birds and mammals (Padian *et al.* 2001). Not all dinosaurs grew at the same rates, and small forms grew more slowly to adult size than larger forms did (Padian *et al.* 2004). Using known growth rates of bone tissues in living birds (Castanet *et al.* 1996, 2000), it is possible to estimate growth rates in extinct dinosaurs (Rimblot-Baly *et al.* 1995; Horner *et al.* 1999, 2001; Erickson & Tumanova 2000), a calculation independently tested by counting presumably annual growth rings in dinosaur bones (Chinsamy 1993; Horner *et al.* 1999, 2000; Erickson & Tumanova 2000).

We used standard bone thin sections from seven specimens of *Tyrannosaurus rex* in the Museum of the Rockies (MOR) to assess the age and growth dynamics of one of the largest carnivores ever known. We wanted to ask whether the largest specimens show evidence of cessation of growth, whether slightly smaller specimens were near full growth, and how old these specimens probably were at death.

Ages have been estimated for large (presumably mature) specimens of other dinosaurs, including the prosauropod *Massospondylus* at more than 15 years (Chinsamy 1993), the hadrosaur *Maiasaura* at 7–8 years (Horner *et al.* 2000) and the basal ceratopsian *Psittacosaurus* at 13–15 years (Erickson & Tumanova 2000). Age at maturity in dinosaurs, as in mammals, was apparently not strictly correlated with adult size. Several estimates of the age of maturity of large sauropods have included *Lapparentosaurus* at *ca.* 20

years (Rimblot-Baly *et al.* 1995), *Janenschia* at *ca.* 11 years (Sander 2000) and *Apatosaurus* at 8–10 years (Curry-Rogers 2000). The conclusion that *Massospondylus* had indeterminate growth (Chinsamy 1993) was based on the inference that a power curve best fits the distribution of femoral sizes. This result may be valid for *Massospondylus*; however, other studies have determined that growth in dinosaurs was rapid at juvenile stages, began to slow at an inflection point associated with sexual maturity and tapered for several years until growth virtually ceased. Because few specimens in the *Massospondylus* sample were relatively large, it is also possible that adults were not adequately represented in the available sample.

Nearly all *T. rex* specimens known are presumed on gross morphology to be adult or sub-adult. The smallest of this sample, MOR 009 and MOR 1125, have a tibial length of 107 cm and a cross-sectional diameter of 15.25 cm by 12.75 cm (major and minor axes). The larger MOR 555 has a tibia 120 cm long. In estimating the thickness between lines of arrested growth (LAGs), known to be annual in living tetrapods and inferred to be so in extinct dinosaurs (Horner *et al.* 1999), and hence the number of missing LAGs to complete the age assessment, three alternative assumptions could be made. The missing intervals could be on average thicker (if early growth was more rapid), the same thickness, or thinner (if early growth was the same) than intervals of the preserved inner cortex. We used all three assumptions (see § 2), but the first assumption generally appears most likely: appositional growth rates are inferred to be higher in young dinosaurs than in older ones (as in all other amniotes), because they deposited more highly vascularized tissue beginning in embryonic stages (Horner *et al.* 2000, 2001; Padian *et al.* 2001).

2. METHODS

To assess age and growth dynamics in *T. rex*, we took transverse thin sections at mid-shaft of the tibia, femur and fibula (and in

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† Both authors contributed in equal part to this work.
*Author for correspondence (kpadian@socrates.berkeley.edu).

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Table 1. Specimens of *Tyrannosaurus rex* analysed in this study.

(Specimen numbers are from the MOR, with catalogue numbers of labelled thin sections; tib, tibia; fem, femur; fib, fibula; *L*, length of bone (mm); *C*, circumference of bone (mm); Tcor, total cortical thickness; Tlag, cortical thickness with LAGs preserved; Tnon, cortical thickness without LAGs preserved; MR, medullary radius (marrow cavity from which bone has been eroded) = total radius minus cortical thickness; actual LAGs, number of LAGs that could be counted in Tlag; retroc LAGs, number of LAGs retrocalculated for Tnon. Methods of calculation: (i) maximum; (ii) penultimate; (iii) mean; (iv) parabolic; and (v) incremental; for explanation see § 2.)

specimen	section	L	C	Tcor	Tlag	Tnon	MR	actual LAGs	retroc LAGs	calibrated age methods of calculation and overall age estimates
009 tib	TI-1-C	1070	404	16	16	0	35	4	10–11	14–15±1 (i), 8–10 (ii), 10–12 (iii) →11–12
009 tib	TI-1-D	1070	404	20	20	0	45	3	10–11	13–14±1 (i), 9–11 (ii), 13–15 (iii) →11–12
555 tib	TI-1a	1200	ca. 500	26	26	0	43	7	4–14	11–12 (ii), 14 (iii), 16–18 (iv) →14±2
555 tib	TI-1b	1200	ca. 500	27	27	0	43	7	4–14	11–12 (ii), 14 (iii), 16–18 (iv) →14±2
1125 fem	Fe1-L2-B2a	1070	433	30	14	16	46	4	9–11	15–17 (i)
1125 fem	Fe1-L2-B2b	1070	433	22	12	10	38	7	10–15	17–18 (v), 20–22 (ii) →18±2
1156 tib	T2-1	—	—	38	18	20	—	7	—	—
1156 tib	T3-1	—	—	43	11	32	—	7	—	—
1198 tib	Fe-1-B-1	—	—	44	22	22	—	10	3–4	—
1198 tib	Fe-1-A-1	—	—	29	29	0	—	8	—	—
1128 tib	TI-1	1120	464	26	26	0	44	6–7	4–13	11–12 (v), 14–16 (ii), 18–20 (iii), 20–21 (i) →16±5
1128 tib	TI-2	1120	464	26	26	0	44	6–7	4–13	11–12 (v), 14–16 (ii), 18–20 (iii), 20–21 (i) →16±5
1152 fem	LBF2-1	—	—	44	22	22	—	10	3–4	—
1152 fem	F2-1	—	—	41	26	15	—	10	2–3	—
1152 fib	Fi-2	—	—	22	11	11	1	≫17	5–10	24–25 (ii), 27 (iii), 22 (v) →25±2

other long bones such as humerus, ulna and metatarsals for comparison as available) in seven specimens (see table 1). Although no single bone infallibly records growth dynamics, the tibial midshaft has a rounder cross-section (and therefore is less subject to cortical drift than other bones); its large size and rapid growth delays secondary erosion–reconstruction cycles of the cortex that obliterate primary bone records; and its record of LAGs agrees better with those of other less altered bones (Horner *et al.* 1999). The fibula, by contrast, is equally subject to secondary reconstruction in the inner cortex, but it has a very small marrow cavity. Moreover, whereas in other long bones, preserved LAG intervals of the outer cortex comprised only 20–40% of the entire radius, the fibula of MOR 152 preserved 56%, a 40–180% increase over the other long bones.

We measured or estimated the length, circumference and cortical thickness of each specimen where possible, and assessed the patterns of LAGs in the preserved cortex. We counted LAGs and measured successive distances between them (table 2). Histological observations were made through a Nikon petrographic Microscope; LAG intervals were measured and digitized with a Nikon DS-L1 camera to a resolution of 10 μm. By extrapolating these patterns into the marrow cavity, which formerly contained cortical bone now destroyed by erosion and remodelling, we could estimate the number of lines that had been erased. We assumed that the LAGs are annual (Chinsamy 1993), and that the diameter of the hatchling *T. rex* tibia was *ca.* 4 mm, based on inferred egg size. Most tibial cross-sections were complete, and centroids could be identified easily. For incomplete sections, we approximated centroids by comparison with more complete specimens.

Missing data for major and minor axes and circumferences of bones were calculated using Ramanujan's (1914) formula

$$C = \Pi \left[3(a+b) - \sqrt{(a+3b)(3a+b)} \right],$$

where C is the circumference and $2a$ and $2b$ are the lengths of the major and minor diametral axes, respectively (so the major and minor radii equal a and b). Bone deposition tends to be thicker along the major axis.

Retrocalculations were performed for the medullary cavity and the parts of the inner cortex where the LAGs were obscured by secondary osteons. The number of missing annual intervals was assessed in the following ways: (i) maximum; (ii) penultimate; (iii) mean intervals: the distance in question was divided by the width of the largest (usually innermost) LAG interval, the penultimate LAG interval or the mean of all preserved LAG intervals, respectively; (iv) incremental factor: a mean percentage increase in size of LAG intervals, moving centripetally, was calculated and extrapolated to account for the obscured and missing sections; and (v) parabolic: hypothesizing that LAG intervals were maximal at the innermost preserved LAG, the intervals of the series progressing centrifugally were applied to the missing centripetal series, producing a probable underestimate of growth rate (Erickson *et al.* 2001; Horner *et al.* 2001; Padian *et al.* 2001, 2004).

3. RESULTS

All bones sampled have LAGs throughout the outer cortex and inner cortex (when not obscured by secondary osteons) (figure 1). The LAGs are invariably very thin lines, no thicker than a vascular canal (*ca.* 20 μm). They are never associated with erosion of pre-existing bone or with rings of avascular bone, and therefore provide no evidence of temporary cessation in growth. The bone tissue in all sections is invariably of the fibro-lamellar complex, as seen in larger extant birds and mammals. Vascularization of the

Table 2. Widths of LAG intervals for each specimen and section of *Tyrannosaurus rex* examined.

(Element identifications are keyed to table 1. Intervals are listed from the outermost cortex inward, in millimetres; numbers in parentheses indicate cortical intervals in which LAGs were obscured from view and could not be counted (see text for extrapolations). inc, incomplete LAG intervals.)

MOR 009/TI-1-C: 0.55, 1.60, 3.33,.3.85, 6.44
MOR 009/TI-1-D: 1.88, 4.3, 3.46, (10.46)
MOR 555/TI-1a: 0.54,1.70, 2.60, 2.30, 3.20, 6.68, 9.11
MOR 555/TI-1b: 0.45, 0.83, 0.95, 2.50, 2.32, 3.22, 6.18, 9.30
MOR 1125/Fe1-L2-B2a: 0.71, 1.09, 3.23, 8.70, 16
MOR 1125/Fe1-L2-B2b: 0.66, 0.81, 0.94, 1.19, 1.24, 3.33, 3.66, (10)
MOR 1128/TI-1: 1.63, 2.10, 2.38, 2.98, 3.20, 4.15, 6.45, 3.29 inc
MOR 1128/TI-2: 1.61, 2.10, 2.45, 2.81, 3.10, 4.16, 6.73, 3.27 inc
MOR 1152/LBF2-1: 0.17, 0.98, 0.87, 1.71, 1.88, 2.19, 2.81, 3.24, 3.70, 4.22, (22)
MOR 1152/F2-1: 0.52, 0.84, 0.93, 1.72, 1.94, 2.34, 2.73, 3.18, 3.88, 8.03, (15)
MOR1152/Fi-2: 0.44 (EFS), 0.21, 0.21, 0.25, 0.23 ,0.15, 0.55, 0.20, 0.47, 0.41, 0.41, 0.78, 0.91, 1.14, 1.30, 1.10, 1.34, 1.42, (11.03)
MOR 1156/T2-1: 1.48, 1.69, 1.79, 2.77, 3.03, 3.59, 3.80, (20)
MOR 1156/T3-1: 0.41, 1.50, 1.13, 1.19, 1.29, 1.88, 4.11, (32)
MOR 1198/Fe-1-A-1: 1.67, 1.47, 1.63, 2.70, 5.68, 2.08, 4.12, 9.34
MOR 1198/Fe-1-B-1: 0.50, 1.25, 1.53, 1.68, 3.19, 4.06, 4.78, (25)

femora and tibiae is mostly circumferential, with frequent radial anastomoses and some longitudinal canals. The fibula contains mostly longitudinal canals, with some radial and circumferential canals. The thickness of the laminae in all bones is almost uniformly 0.17 mm, but in some local regions this is reduced to 0.15 mm or 0.13 mm, with no change in tissue; in no bone does the laminar thickness vary by more than ±7%. Similar thicknesses are recorded in thin sections of the long bones of the small theropod dinosaur *Troodon* (0.13 mm), the deer *Odocoileus* (0.13 mm), the elk *Cervus* (0.16 mm) and the moa *Dinornis* (0.17 mm) in the collections of the MOR.

As typical theropod long bones grow and the medullary cavities expand, bone deposited early in growth is eroded, so that the remaining bone records only about the last third of the individual's life history. The internal part of this remaining cortex, furthermore, is frequently remodelled by secondary (Haversian) osteons that obscure LAGs and other records of growth history. To estimate age, this lost information must be retrocalculated, which we carried out for each specimen using several methods (see below), according to the information available for each specimen.

The tibia of MOR 009 has a cortical section 16–20 mm thick that represents 4–6 years of fast-growing bone (4–5 LAGs) (see § 2 for all estimates). The radius of the medullary cavity is 35 mm, which could represent as few as 2 years' additional growth (using an incremental factor based on growth patterns of other specimens at similar size), or up to 10 ± 1 additional years (using a very conservative mean interval retrocalculation). The specimen was still actively growing at death, based on the thickness of the outermost LAG intervals; we estimate its actual age at *ca.* 11 years.

The tibia of MOR 555 has a major axis cortical section of 27.03 mm that represents just over 7 years' growth. The radius of the medullary cavity is 43 mm, which represents *ca.* 4.6 years (maximum interval), 7 years (penultimate interval) or 9–11 years (parabolic). During the broadest LAG intervals preserved, the tibia was growing at rates of 16.7–25 μm d^{-1}, comparable to the most rapid

developmental rates of wing bone growth in the mallard (Castanet *et al.* 1996). The estimated age range of the specimen is 12–18 years, of which 14 ± 2 years appears reasonable. The outermost LAG intervals are less than 1 mm thick, so the animal had effectively stopped actively growing for 2 or 3 years.

A femoral section of MOR 1125 taken along the minor axis is 21.83 mm thick, representing 10–11 years. The medullary radius of 38 mm represents 7 years (incremental factor) to 10–11 years (maximum interval), but the preserved maximum interval in this specimen is relatively low. The calculated age range of 17–22 years may be an overestimate; 18 ± 2 years is a more constrained estimate. The outermost two or three LAG intervals are less than 1 mm thick, so the animal had effectively stopped growing at 16 ± 2 years.

The tibial cross-sections of MOR 1156 and MOR 1198 are too incomplete for the retrocalculation of age; however, their preserved thicknesses suggest 11–16 years (average 14 ± 2) and at least 10 years (± 1), respectively. MOR 1198 is approximately the same size as MOR 555, but like MOR 1156 it appears to have been actively growing, depositing at least 1.5 mm per year of cortical thickness for several years before death.

The most completely preserved sequence of LAGs from the tibia is of MOR 1128. Six complete intervals separated by LAGs occur in a section 26.18 mm thick along a radius of *ca.* 70 mm. The number of LAGs in the space now occupied by the medullary cavity is estimated to represent from 4 years (incremental factor of 1.25) to 7–8 years (maximum interval), 11–12 years (penultimate interval) or 13 years (mean interval). Each of these figures can be added to 7–8 years of growth represented by the preserved cortex to yield age estimates of (i) 11–12, (ii) 14–16, (iii) 18–20 and (iv) 20–21 years, for a mean estimate of *ca.* 16 years. Although the outermost LAG intervals are smaller than inner ones, their thicknesses suggest that active growth would have continued for at least 2–3 years.

If *T. rex*'s growth was slowing at a consistent rate, at what age did it virtually stop growing? To extrapolate this, we
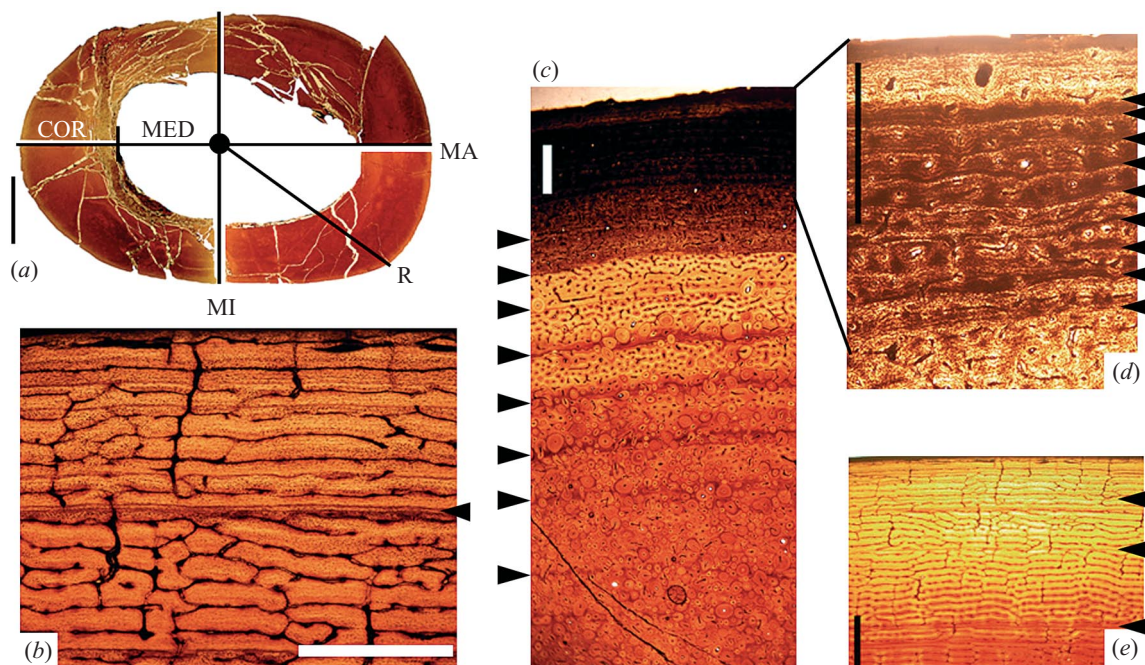
Figure 1. Bone histology of *Tyrannosaurus rex*. Transverse thin sections of long bone mid-shafts. (*a*) MOR 009, composite quadrants of tibia. COR, cortex; MA, major axis; MED, medullary cavity; MI, minor axis; R, radius. (*b*) MOR 1128, external cortex of tibia, showing typical fibro-lamellar bone and LAG (arrow). In this region the bone is growing at an average rate of 11.2–17.4 $\mu m\, d^{-1}$, comparable to very rapid growth in the developing mallard (Castanet *et al.* 1996). (*c*) MOR 1152, external cortex of fibula showing tight spacing of eight LAGs (arrows) throughout the cortex. The round structures with small centres interrupting the matrix are mature secondary osteons that progressively invade the cortex centrifugally. (*d*) Detail of (*c*) showing the outermost cortex with tighter spacing of nine more LAGs. External to these LAGs is a compact area of low vascularity that may reflect the final stages of very slow growth. (*e*) MOR 1152, outer cortex of femur showing the final closely spaced three LAGs that may correspond to the outermost layer of the fibula. Scale bars: (*a*) 2 cm; (*b*–*e*) 1 mm.
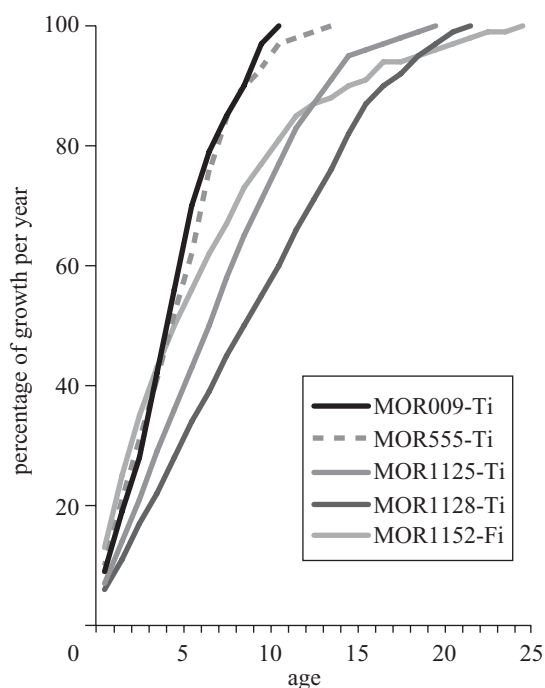

Figure 2. Growth trajectories of individual specimens of *Tyrannosaurus rex*. These are expressed as an annual percentage of attainment of full size (cortical radius of long bones). The variation results from the fact that different bones grow at different rates. The early trajectories of bone growth are estimated (see table 1).

applied a factor of 0.8, the inverse of the incremental factor of 1.25, to the preserved series of LAG intervals, calibrated from the last three preserved intervals. At this rate of growth decrease, within 5 years MOR 1128 would have deposited 0.5 mm of bone centrifugally per year, and after 8 years this would have decreased to $0.25\, mm\, yr^{-1}$. By the sixth year, projected growth is just over $1\, \mu m\, d^{-1}$, comparable to very slow growth in living tetrapods (see figure 2).

According to these estimates, a virtually fully grown *T. rex* would have been between 15 and 18 years old. (However, as the femur of MOR 1152 shows, growth can drop more precipitously than an incremental estimate suggests.) We have not found in any sectioned *T. rex* tibia or femur evidence of an outer acellular, nearly avascular layer similar to the external fundamental system (EFS) (Cormack 1957), that indicates effective cessation of growth. (An EFS has been identified in the ornithischian dinosaur *Maiasaura* (Horner *et al.* 2000).) The absence of an EFS in preserved specimens of *T. rex* could suggest that none of the animals had stopped growing, although growth was greatly slowing. Without an EFS, the near cessation of growth seems the most practical indicator of full size.

To test this hypothesis, we examined sections of a femur and fibula of MOR 1152. The preserved section of the femur allows an estimate of 12–14 years; the record represented by the missing eroded internal cortex cannot be estimated. The fibula from MOR 1152 is complete, however. Its transverse radius of 22.55 mm was measured from the perimeter to a small erosion room representing the centroid

of the bone. It comprises an outer, highly compressed section of 0.44 mm, 17 LAG intervals in a section of 11.08 mm, and an inner cortical area of 11.03 mm, where the record of primary bone structure has been completely erased by secondary osteons. Using the maximum and penultimate interval retrocalculations, the inner cortex could have been deposited in 7.5–10 years. However, the LAG intervals increase centripetally at a rate of *ca.* 1.17 mm, which incremental rate yields no more than 5 years to complete the inner cortex. According to this calculation, the age of the specimen is 22–27 years, plus the time represented by the outer, highly compressed section. Because the last three LAG intervals of the femur drop precipitously in width to less than 1 mm, we infer that the fibular LAG may represent those 3 years. The most likely estimate of the age of this fully grown *T. rex*, therefore, was 22–25 years, and full growth was reached at least 3 years before death. This estimate could be too high if the fibula grew at substantially higher rates earlier in life.

4. CONCLUSIONS

These results have several implications for the assessment of age and growth in large dinosaurs. Not all bones provide the same signal of age. Larger or more robust specimens are not necessarily older than smaller more gracile ones. The substantial variation seen in *T. rex* skeletons cannot yet reliably be attributed to either age, sexual dimorphism or anagenetic evolution through their known temporal range. Erosion and reconstruction of cortical bone obscure primary tissues useful in skeletochronology. Various methods can retrocalculate destroyed tissue, but none is *a priori* better than any other. Independent evidence of growth dynamics is needed from earlier growth stages, which are currently unavailable.

Three out of the seven specimens that we analysed appear to have effectively ceased active growth 2 or 3 years before death, although their cortical radius continued to increase annually by 0.5–0.7% (e.g. MOR 555). Four other specimens appear to have still been growing, but LAG interval decreases suggest that each of them would have reached effectively full size in another 1 to 3 years. Evidence from the femora and tibiae suggest, therefore, that *T. rex* reached full size by 16±3 years, but we caution that our sample is small and individual variation may have affected age at maturity. The fibula of MOR 1152 suggests a higher range of 22–27 years, although the rate of its inner cortical growth may be underestimated. In any case, within about two decades *T. rex* appears to have effectively stopped growing.

The growth profile of *Tyrannosaurus* is slightly more accelerated than that of the African elephant (*Loxodonta africana*), which matures and ceases active growth at 25–35 years (Laws *et al.* 1975). Estimates for the mass of an adult *T. rex* range from 5000 to 8000 kg (Alexander 1997). Adult male elephants weigh 4500–6000 kg (Laws *et al.* 1975), with some outliers reported up to 7300 kg (Nowak 1999), so the body masses of *T. rex* and African elephants at full size are similar. It follows that the dinosaur and the elephant would have grown at roughly similar rates, consistent with the well vascularized fibro-lamellar tissue that *T. rex* deposited (Castanet *et al.* 1996, 2000; Padian *et al.* 2001; figure 1). As Chinsamy (1993, p. 327) noted, the

predominant production of fibro-lamellar tissues in dinosaur bones throughout life 'would require and thus implies a high metabolic rate'. This metabolic rate was sustained throughout growth, diminishing with age as in all warm-blooded animals of today.

These findings should have implications for studies of palaeoecology and community structure of latest Cretaceous terrestrial environments (Farlow & Pianka 2002; Ruxton & Houston 2003; Sampson *et al.* 2003). Estimates of habitat partitioning and living space requirements have been based on the assumption that tyrannosaurids were ectothermic, because ecological models based on extrapolations from much smaller living guilds do not work if tyrannosaurids were endothermic. Our study indicates that *T. rex* grew quickly to adult size, and its growth dynamics suggest high basal metabolic rates to sustain this growth (Chinsamy 1993). The question of its food requirements is a different one from that of endothermy: tyrannosaurids may have grown rapidly but not continuously (as occurs in warm-blooded mammals and birds today). It may be that their food requirements lessened during periods when they were not growing so actively. If so, they may have required less food over the course of a year than living mammalian carnivores do. These questions, unfortunately, are unlikely ever to be answered but we stress that the ecological models in question must be viewed with caution, because they require such substantial extrapolations and assumptions. Tyrannosaurids had masses 30 times larger than those of African lions, the largest land carnivores today, and it is often difficult to interpret the ecological roles, habitat preferences and range requirements of extinct dinosaurs (Farlow & Pianka 2002).

Although tyrannosaurs grew at rates comparable to those of some large mammals, other dinosaurs grew even more rapidly, as noted above: *Maiasaura* reached adult size at 7–8 years (Horner *et al.* 2000) and large sauropods at 8–11 years (Curry-Rogers 2000; Sander 2000). This pattern is generally explained by the fact that large taxa grow more rapidly than smaller ones (Case 1978; Erickson *et al.* 2001; Padian *et al.* 2001, 2004), but another ecological factor may be considered: prey species such as hadrosaurs and sauropods may have found an advantage in growing as rapidly as possible, because large size is a defence against predation.

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