associated error as the sum of terms arising from nonlinear interactions between parameter perturbations and noise (natural variability) in the model simulations used to construct the predictions. Both error terms were assumed to be independent of location in parameter space (and hence climate sensitivity). The first term was estimated by verifying our statistical predictions against simulations made with 13 model versions containing multiple parameter perturbations and simulating climate sensitivities in the range 3.1–4.9 °C. The second term was estimated from the long STD experiment (See Supplementary Information). Each of our $21 \times 4 \times 10^6$ predictions of λ was then expressed as a gaussian distribution accounting for its expected error. A PDF of feedback strength was derived by combining the resulting $21 \times 4 \times 10^6$ distributions, each weighted according to the probability of the relevant value of λ_{std}.This was converted into a PDF of climate sensitivity using $\Delta T = \Delta Q/\lambda$, giving the blue PDF in Fig. 3. The red PDF was derived in the same manner, except that a further weighting of $\exp(-0.5\mathrm{CPI}^2)$ was applied to each of the gaussian distributions of λ. Results from our 13 verifying multiple perturbation experiments showed that our statistical predictions of CPI were close to the simulated values and that the predictions of λ carried a standard error of about $0.15\,\mathrm{W\,m^{-2}\,K^{-1}}$, arising mainly from the nonlinear effects of combining parameter perturbations[29].

Received 29 March; accepted 16 June 2004; doi:10.1038/nature02771.

1. Gordon, C. *et al.* The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Clim. Dyn.* **16,** 147–168 (2000).
2. Giorgi, F. & Francisco, R. Evaluating uncertainties in the prediction of regional climate change. *Geophys. Res. Lett.* **27,** 1295–1298 (2000).
3. Allen, M. R. & Ingram, W. J. Constraints on future changes in climate and the hydrological cycle. *Nature* **419,** 224–232 (2002).
4. Cubasch, U. *et al.* in *Climate Change 2001, The Science of Climate Change* Ch. 9 (eds Houghton, J. T. *et al.*) 527–582 (Cambridge Univ. Press, Cambridge, 2001).
5. Allen, M. R., Stott, P. A., Mitchell, J. F. B., Schnur, R. & Delworth, T. L. Quantifying the uncertainty in forecasts of anthropogenic climate change. *Nature* **417,** 617–620 (2000).
6. Mearns, L. O. *et al.* in *Climate Change 2001, The Science of Climate Change* Ch. 13 (eds Houghton, J. T. *et al.*) 739–768 (Cambridge Univ. Press, Cambridge, 2001).
7. Meehl, G. A. *et al.* Trends in extreme weather and climate events: issues related to modelling extremes in projections of future climate change. *Bull. Am. Meteorol. Soc.* **81,** 427–436 (2000).
8. Stocker, T. F. *et al.* in *Climate Change 2001, The Science of Climate Change* Ch. 7 (eds Houghton, J. T. *et al.*) 417–470 (Cambridge Univ. Press, Cambridge, 2001).
9. Randall, D. A. & Wielicki, B. A. Measurements, models and hypotheses in the atmospheric sciences. *Bull. Am. Meteorol. Soc.* **78,** 399–406 (1997).
10. Wigley, T. M. L. & Raper, S. C. B. Interpretation of high projections for global-mean warming. *Science* **293,** 451–454 (2001).
11. Palmer, T. N. A nonlinear dynamical perspective on model error: A proposal for non-local stochastic-dynamic parametrization in weather and climate prediction models. *Q.J.R. Meteorol. Soc.* **127,** 279–303 (2001).
12. Pope, V. D., Gallani, M., Rowntree, P. R. & Stratton, R. A. The impact of new physical parameterisations in the Hadley Centre climate model—HadAM3. *Clim. Dyn.* **16,** 123–146 (2000).
13. Keen, A. B. & Murphy, J. M. Influence of natural variability and the cold start problem on the simulated transient response to increasing CO_2. *Clim. Dyn.* **13,** 847–864 (1997).
14. Palmer, T. N. & Räisänen, J. Quantifying the risk of extreme seasonal precipitation events in a changing climate. *Nature* **415,** 514–517 (2002).
15. Leroy, S. S. Detecting climate signals: Some Bayesian aspects. *J. Clim.* **11,** 640–651 (1998).
16. Stott, P. A. & Kettleborough, J. A. Origins and estimates of uncertainty in predictions of twenty-first century temperature rise. *Nature* **416,** 723–726 (2002).
17. Giorgi, F. & Mearns, L. O. Calculation of average, uncertainty range, and reliability of regional climate changes from AOGCM simulations via the "Reliability Ensemble Averaging" (REA) method. *J. Clim.* **15,** 1141–1158 (2002).
18. Giorgi, F. & Mearns, L. O. Probability of regional climate change based on the Reliability Ensemble Averaging (REA) method. *Geophys. Res. Lett.* **30,** 1629 (2003).
19. Andronova, N. G. & Schlesinger, M. E. Objective estimation of the probability density function for climate sensitivity. *J. Geophys. Res.* **106,** 22605–22612 (2001).
20. Forest, C. E., Stone, P. H., Sokolov, A. P., Allen, M. R. & Webster, M. D. Quantifying uncertainties in climate system properties with the use of recent climate observations. *Science* **295,** 113–117 (2002).
21. Knutti, R., Stocker, T. F., Joos, F. & Plattner, G. K. Constraints on radiative forcing and future climate change from observations and climate model ensembles. *Nature* **416,** 719–723 (2002).
22. Gregory, J. M., Stouffer, R. J., Raper, S. C. B., Stott, P. A. & Rayner, N. A. An observationally based estimate of the climate sensitivity. *J. Clim.* **15,** 3117–3121 (2002).
23. Anderson, T. L. *et al.* Climate forcing by aerosols—a hazy picture. *Science* **300,** 110–111 (2003).
24. Barnett, T. P., Pierce, D. W. & Schnur, R. Detection of anthropogenic climate change in the world's oceans. *Science* **292,** 270–274 (2001).
25. Boer, G. J. & Yu, B. Dynamical aspects of climate sensitivity. *Geophys. Res. Lett.* **30,** 1135 (2003).
26. Stouffer, R. J. & Manabe, S. Response of a coupled ocean-atmosphere model to increasing atmospheric carbon dioxide: sensitivity to the rate of increase. *J. Clim.* **12,** 2224–2237 (1999).
27. Watterson, I. G. Interpretation of simulated global warming using a simple model. *J. Clim.* **13,** 202–215 (2000).
28. Senior, C. A. & Mitchell, J. F. B. The time-dependence of climate sensitivity. *Geophys. Res. Lett.* **27,** 2685–2689 (2000).
29. Stainforth, D. A. *et al.* Evaluating uncertainty in the climate response to changing levels of greenhouse gases. *Nature* (submitted).
30. Allen, M. R. & Stainforth, D. A. Towards objective probabilistic climate forecasting. *Nature* **419,** 228 (2002).

Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank A. Thorpe and M. Allen for encouraging the development of this project. We also acknowledge many Hadley Centre colleagues for their advice on model parameters and their uncertainty ranges, and for comments on earlier versions of the manuscript. This work was supported by the UK Department of the Environment, Food and Rural Affairs. D.A.S. was funded by the NERC COAPEC thematic programme.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to J.M.M. (james.murphy@metoffice.com).

Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs

Gregory M. Erickson[1,2], **Peter J. Makovicky**[3], **Philip J. Currie**[4], **Mark A. Norell**[2], **Scott A. Yerby**[5] & **Christopher A. Brochu**[6]

[1] *Department of Biological Science, Florida State University, Tallahassee, Florida 32306-1100, USA*
[2] *Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA*
[3] *Department of Geology, The Field Museum, 1400 S. Lake Shore Drive, Chicago, Illinois 60605, USA*
[4] *Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta T0J 0Y0, Canada*
[5] *Department of Biomechanical Engineering, Stanford University, Stanford, California 94305, USA*
[6] *Department of Geoscience, University of Iowa, Iowa City, Iowa 52242, USA*

How evolutionary changes in body size are brought about by variance in developmental timing and/or growth rates (also known as heterochrony) is a topic of considerable interest in evolutionary biology[1]. In particular, extreme size change leading to gigantism occurred within the dinosaurs on multiple occasions[2]. Whether this change was brought about by accelerated growth, delayed maturity or a combination of both processes is unknown. A better understanding of relationships between non-avian dinosaur groups and the newfound capacity to reconstruct their growth curves make it possible to address these questions quantitatively[3]. Here we study growth patterns within the Tyrannosauridae, the best known group of large carnivorous dinosaurs, and determine the developmental means by which *Tyrannosaurus rex*, weighing 5,000 kg and more, grew to be one of the most enormous terrestrial carnivorous animals ever. *T. rex* had a maximal growth rate of 2.1 kg d^{-1}, reached skeletal maturity in two decades and lived for up to 28 years. *T. rex*'s great stature was primarily attained by accelerating growth rates beyond that of its closest relatives.

Stemming from more than a century of investigation, considerable understanding of tyrannosaurid osteology[4], myology[5], neurology[6], behaviour[7,8], physiology[3,9], physical capabilities[10,11] and phylogeny[12,13] have been gained. Lacking are empirical data on tyrannosaurid life history such as growth rates, longevity and somatic maturity (adult size) from which the developmental possibilities for how *T. rex* attained gigantism can be formally tested.

Recent advances in techniques for determining the ages at death of dinosaurs by using skeletal growth line counts[3,14], coupled with developmental size estimates[3], make quantitative growth-curve reconstructions for dinosaurs feasible. These methods have been used to study growth rates in two small theropods, a small and a large ornithischian and a medium-sized and a gigantic sauropodomorph[3]. These data were used to derive a regression of body mass against growth rate and to generalize broadly about non-avian dinosaur growth[3]. However, because of the phylogenetically disparate nature of these data (that is, none are close outgroups to one another) it has not been possible to use them to infer how specific cases of size change occurred within dinosaurian sub-clades such as the Tyrannosauridae. Such an understanding requires multi-species sampling at low taxonomic levels (that is, among closely related species) and access to growth series spanning juvenile through adult stages, a rarity among extinct dinosaurs[15]. Furthermore, it requires the capacity to account for growth line losses due to medullar cavity hollowing and cortical remodelling[16], two processes that are pervasive in the major weight-bearing bones from large theropods such as tyrannosaurids.

The sampling problem has been overcome in North American tyrannosaurids. A flurry of recent discoveries has greatly increased the number of substantially complete specimens representing various growth stages available for study. For example, more than 30 *T. rex* specimens are known[4,17], compared with only 11 reported in 1993 (ref. 18; see Supplementary Information). Recent work has broadened the developmental representation of these animals by showing that several purported 'dwarf' tyrannosaur species are juveniles of larger, previously recognized forms such as *T. rex*[12,13,19,20]. Finally, preliminary analyses for this research revealed that several non-weight-bearing bones in tyrannosaurids (for example pubes, fibulae, ribs, gastralia and postorbitals) did not develop hollow medullar cavities and showed negligible intracortical remodelling during their entire life history (Fig. 1). Like major long bones, these elements are effective for assessing longevity in living reptiles (Fig. 1)[21,22] and hence provide a viable alternative method for determining the age at death of extinct reptiles such as tyrannosaurids.

Here we exploit these findings to determine the pattern of growth in *T. rex* and three of its close tyrannosaurid relatives. We then use character optimization methods[23] to infer how *T. rex* attained giant proportions among tyrannosaurids. Finally, this new evidence is used to further our understanding of tyrannosaurid biology. In performing these analyses, we sampled several amedullar bones from adolescent, juvenile, sub-adult and adult representatives of the North American Late Cretaceous tyrannosaurids *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, *Daspletosaurus torosus* and *T. rex*. Longevity in each of the 20 specimens was assessed from line counts in histological sections by using polarizing, dissecting and reflected-light microscopy (Fig. 1)[3,14]. Conservative estimates of body mass (see Supplementary Information) were made by using femoral circumference measures[24]. Longevity and size data were plotted and least-squares regression was used to determine the first empirical growth curves for tyrannosaurids[3]. The length and timing of the various developmental stages and the maximal growth rates for each taxon were compared[25]. The results were examined in an evolutionary context[23] by using two competing phylogenetic hypotheses for the Tyrannosauridae[12,13].

Sampled longevities for *T. rex* ranged from 2 to 28 years and corresponding body mass estimates ranged from 29.9 to 5,654 kg (Table 1). The transition to somatic maturity in this taxon seems to have begun at about 18.5 years of age (Fig. 2). At least one individual (exemplified by FMNH (The Field Museum) PR 2081), showed evidence for prolonged senescence in the form of conspicuously narrow pericortical growth-line spacing (Fig. 1). Maximal growth rates in *T. rex* were $2.07\,\mathrm{kg\,d^{-1}}$ and such exponential rates were maintained for about 4 years (Fig. 2). The longevity estimates for *T. rex* outgroups ranged from 2 to 24 years and corresponding body sizes spanned from 50.3 to 1,791 kg (Table 1). Somatic maturity occurred at between 14 and 16 years in these taxa (Fig. 2). Like *T. rex*, at least some exceptionally large individuals of *A. sarcophagus* and *D. torosus* showed narrow pericortical growth-line spacing indicative of the onset of senescence. The maximal growth rates for the three smaller tyrannosaurid taxa ranged from 0.31 to $0.48\,\mathrm{kg\,d^{-1}}$; such exponential stage rates were also maintained for about 4 years (Fig. 2). Optimization of growth rates onto the two current phylogenetic hypotheses of tyrannosaurid relationships suggests that a 1.5-fold acceleration in maximal growth rate might diagnose Tyrannosaurinae (the clade comprising *Daspletosaurus and Tyrannosaurus*[13,19], Fig. 2). A second substantial increase in growth rate optimizes as a physiological autapomorphy of *Tyrannosaurus* irrespective of phylogenetic hypothesis and optimization criterion.

T. rex is notable for its great size, which is at least 15-fold greater than the largest living terrestrial carnivorous animals today and second only to *Giganotosaurus*[26] among theropod dinosaurs. How did it attain such great proportions within the Tyrannosauridae? From the two competing hypotheses of tyrannosaurid phylogeny it is most parsimonious to conclude that *T. rex* acquired the majority of its giant proportions after diverging from the common ancestor of itself and *D. torosus*, a species with an optimized body mass of about 1,800 kg. Direct comparison between the tyrannosaurid growth curves shows that the transition to the exponential and stationary phases of development occurred about 2–4 years later in *T. rex* (Fig. 2). However, such temporal post-displacement had little to do with the evolution of its gigantism because the exponential

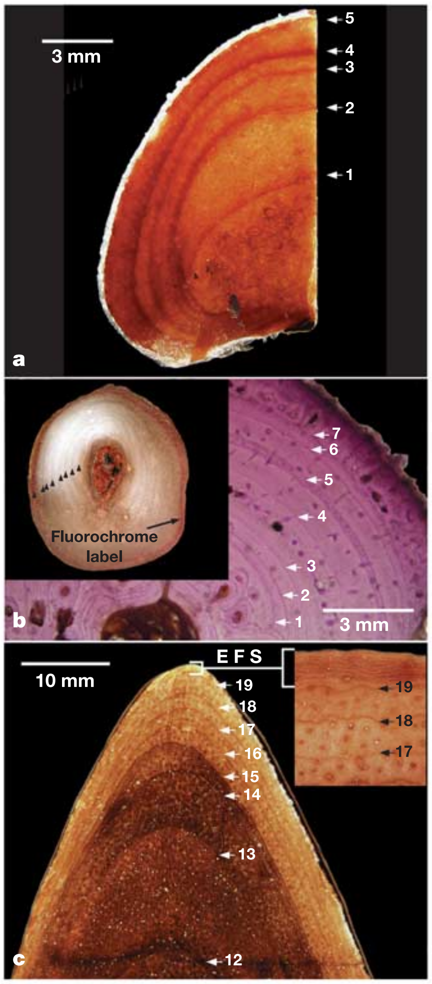

Figure 1 Growth-line counts in tyrannosaurids and reptiles of known ages. **a**, Thin-sectioned *Gorgosaurus* fibula (FMNH PR 2211). The growth record in this element is complete and shows five growth lines (arrows), indicating that it died early in its sixth year of life. **b**, Haematoxylin-stained fibula from an 8-year-old alligator (*Alligator mississippiensis*) showing the expected seven growth lines. Inset, gastralia (unstained) from 9-year-old *A. mississippiensis* showing the expected eight growth lines and the chemical label used to verify the periodicity of ring formation. **c**, *Tyrannosaurus* rib (FMNH PR 2081) showing the 15th to 19th growth lines. Inset, external fundamental system[16] with nine tightly spaced growth lines, indicating late-adulthood senescence and growth-rate attenuation.

Table 1 **Specimens, size measures, and longevity data**

Taxon	Specimen no.	Elements examined	Femoral length (cm)	Body mass (kg)	Longevity (years); no. of growth lines in EFS
Tyrannosaurus rex	FMNH PR 2081	G, R, F, OLB	134.5	5654	28; 9
	RTMP 81.12.1	R, OLB	128.4 est.	5040	22
	RTMP 81.6.1	G, R, OLB	120	3230	18
	ICM 2001.90.1	G, R	116.8 est.	2984	16
	LACM 23845	P, OLB	98.9	1807	14
	AMNH 30564	G, R, F	98	1761	15
	LACM 28471	R, C	25.2 est.	29.9	2
Gorgosaurus libratus	RTMP 94.12.602	R, G, OLB	91.6	1105	18
	RTMP 73.30.1	F, OLB	80.4 est.	747	14
	RTMP 99.33.1	G, F, OLB	75	607	14
	RTMP 86.144.1	R, F, OLB	54.2	229	7
	FMNH PR 2211	G, R, F, OLB	44.5	127	5
Albertosaurus sarcophagus	RTMP 81.10.1	G, R, F, OLB	89.5	1142	24; 2
	AMNH 5432	P, F	99.3 est.	1282	22
	USNM 12814/AMNH 5428	R	86.0 est.	1013	18
	RTMP 86.64.01	R, F, OLB	78.2 est.	762	15
	RTMP 2002.45.46	F, OLB	31.6 est.	50.3	2
Daspletosaurus torosus	FMNH PR 308	G, R	96.0 est.	1791	21; 5
	AMNH 5438	R	84.1 est.	1518	17
	RTMP 94.143.1	G, OLB	62.6 est.	496	10

FMNH, The Field Museum; RTMP, Royal Tyrrell Museum of Palaeontology; ICM, Indianapolis Children's Museum; LACM, Los Angeles County Museum; AMNH, American Museum of Natural History; USNM, United States National Museum. R, rib; G, gastralia; F, fibula; P, pubis; C, dermal skull bones; OLB, other long bones; est., estimated; EFS, external fundamental system[16].

stage, during which most body size is accrued[25], was not extended beyond the ancestral, 4-year condition observed in other tyrannosaurids. Rather, the key developmental modification that propelled *T. rex* to giant proportions was primarily through evolutionary acceleration in the exponential stage growth rate and the transition zones bounding it. This is reflected in the regions of maximal slope on the growth curves depicted in Fig. 2 and holds true regardless of which evolutionary hypothesis is correct and how the maximum growth rates are optimized. Notably, this method of attaining gigantism contrasts with that in the largest crocodilians and lizards, where ancestral growth rates were retained and the exponential stages lengthened[27]. How other dinosaurs attained gigantism within their respective sub-clades will serve as an interesting line of inquiry in the future. Does the same pattern of acceleratory growth seen here characterize the means by which all or most members of the Dinosauria attained great size?

Besides revealing how the evolution of *T. rex* gigantism was obtained, the data garnered here provide for a more comprehensive understanding of tyrannosaurid biology. For instance the presence of thin, tightly packed growth lines late in development (Fig. 1) shows that these animals, like nearly all (if not all) dinosaurs, had determinate growth[3,14]. They would not have gained an appreciably greater size than the largest specimens studied here and could spend nearly 30% of their lives as full-grown adults (Fig. 2). In addition, the maximal growth rates for these tyrannosaurid species are only 33–52% of the rates expected for non-avian dinosaurs of their size when compared with the more broadly sampled data of Erickson *et al.*[3]. This provides the first evidence of its kind pointing to major differences in whole body growth rates among a non-avian dinosaur sub-clade. Such findings are not unexpected because similar patterns (for example primates within Eutheria) occur within living vertebrate groups[28]. Our findings also have a bearing on the

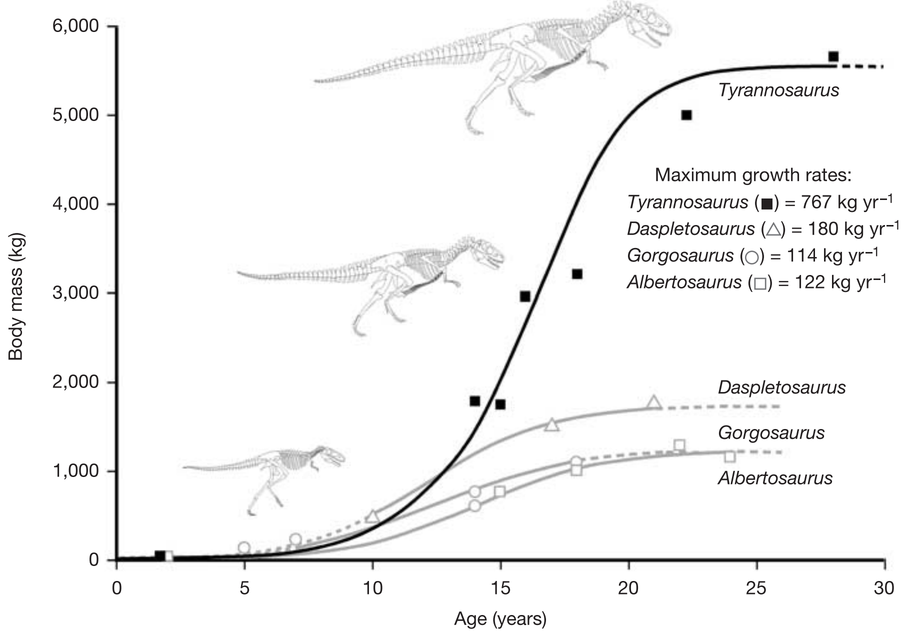

Figure 2 Logistic growth curves for *Tyrannosaurus* and three related tyrannosaurids. Note that the exponential stages (the regions of maximal slope) are similar in duration but differ in slope (that is, growth rates). Regression equations (mass in kg, age in years) are as follows: *T. rex*, $\text{mass} = \{5{,}551/[1 + e^{-0.57(\text{age} - 16.1)}]\} + 5$, $r^2 = 0.953$; *D. torosus*, $\text{mass} = \{1{,}728/[1 + e^{-0.44(\text{age} - 12.1)}]\} + 5$, $r^2 = 0.992$; *G. libratus*, $\text{mass} = \{1{,}234/[1 + e^{-0.38(\text{age} - 12.4)}]\} + 5$, $r^2 = 0.950$; *A. sarcophagus*, $\text{mass} = \{1{,}218/[1 + e^{-0.43(\text{age} - 14.1)}]\} + 5$; $r^2 = 0.985$.

biomechanical capacities of tyrannosaurids. *T. rex*'s capacity for 'fast running' was biomechanially infeasible after a body mass of about 1,000 kg was attained[11]. This corresponds to a juvenile-sized animal just 13 years of age on the basis of our longevity data and conservative estimates of body mass (Fig. 2). If we assume that the same relationship held true for the smaller tyrannosaurid species studied here, such locomotory limitations would not have emerged until these animals were much closer to adult size (Fig. 2). Finally, a glimpse into the potential population age structure for a dinosaur is also afforded from these data. Currie[7] has described a catastrophic death assemblage consisting of eight or nine *A. sarcophagus* specimens thought to represent an entire pack or a subset of one. On the basis of femoral lengths, the age and developmental stage of each animal can now be estimated. The group seems to have consisted of two or three older adults ~21 or more years of age, one ~17-year-old young adult, four ~12–17-year-old sub-adults that were undergoing exponential stage growth at the time of death, and one ~10-year-old juvenile that was beginning the transition to exponential stage growth. A reopening of the site has revealed at least one more specimen (RTMP (Royal Tyrrell Museum of Palaeontology) 2002.45.46) shown here to be only 2 years old (Table 1). This indicates that *A. sarcophagus* groups, whether temporary or permanent, might have been composed of individuals spanning the age spectrum from adolescents to very old, senescent adults, a finding consistent with trackway evidence for other theropod dinosaurs[7]. □

Methods

Assessments of tyrannosaurid longevity

Growth lines have been shown to form throughout the cranial and post-cranial skeletons of living tetrapods[16,21,22,27] and their annual formative rhythms have been shown in lepidosaurian and archosaurian (that is crocodilian) outgroups to dinosaurs[21,22,27]. This indicates that similar annual genesis might have occurred in non-avian dinosaurs such as tyrannosaurids[3]. Here we used fibulae, pubes, gastralia, ribs and cranial bones and a few selected long-bone elements in which medullar cavity expansion and remodelling was not pervasive. Bones such as these have been shown to have excellent efficacy for assessing longevity in snakes[21] and lizards[22], and our own multi-element histological studies on lizards and crocodilians of known ages from the Florida Museum of Natural History, Gainesville, and the Florida Fish and Wildlife Conservation Commission, Gainesville, confirm this (Fig. 1). In cases where some of the earliest-forming tyrannosaur growth rings were remodelled, losses were accounted for by examining younger individuals in which the rings were still present or through back-calculation methods[3]. Inter-elemental comparisons revealed longevity estimates to within 1 year in all cases, the higher values of which were used in the longevity assessments.

Body size estimates

To permit comparisons of growth rates between tyrannosaurids and living taxa and to negate the effects of shape differences, the data were standardized to body mass[3] by using a femoral circumference/body mass regression equation[24]. This method produces conservative estimates of body mass[29] (see Supplementary Information). Subadult sizes were determined with the Developmental Mass Extrapolation femoral scaling principle[3]. In cases in which the femora were not preserved, the tyrannosaurid long-bone regression equations of Currie[30] were used to estimate the missing measurements.

Reconstruction of growth curves

Age and mass data were contrasted to reveal growth curves for the four tyrannosaurid species (Fig. 2). All vertebrates show logistic (S-shaped) growth patterns such as these during post-parturition/hatching development[3,25]. Hence a logistic equation and least-squares regression analysis were used to describe the relationship between the data. The terminology used to refer to the various stages of development is as follows[25]. The initial, slow growth phase is referred to as the lag stage. This is followed by the linear exponential stage during which maximal slope is observed and maximal growth rates occur. Finally, growth reaches a plateau during the stationary stage. Here we refer to animals in the lag stage as adolescents, those in transition to the exponential stage as juveniles, those in the exponential stage as sub-adults, those in transition to the stationary stage as young adults, and finally animals in the stationary stage as senescent adults. Here, adulthood refers to the onset of somatic maturity whereby adult size is first attained. Is not known when sexual maturity for non-avian dinosaurs occurred, because gender has not been established with certainty for any taxon.

Character evolution analysis

Maximum growth rates were optimized as a continuous character onto two competing phylogenies for the Tyrannosauridae[12,13]. The topologies as they pertain to the taxa sampled are (*Albertosaurus*, *Gorgosaurus* (*Daspletosaurus*, *Tyrannosaurus*))[12] and ((*Albertosaurus*, *Gorgosaurus*) (*Daspletosaurus*, *Tyrannosaurus*))[13]. Because no basal tyrannosaurids have been sampled, the basal theropod *Syntarsus*[3] was used to root the trees. Both linear and squared-changes optimizations were applied[23]. Both optimality criteria and all possible topologies suggest that a large increase in growth rate is diagnostic of the *Daspletosaurus*–*Tyrannosaurus* clade (Tyrannosaurinae)[13], and a second large increment in growth rate optimizes as unique to *T. rex*. The actual magnitude of the growth rate change reconstructed at ancestral nodes differs with topology and more drastically with the optimization method. Linear parsimony yields a punctuated pattern with higher changes at individual nodes, whereas squared-changes parsimony forces a 'smoother' distribution on the data but also incurs some counterintuitive deceleration in growth for the slower-growing basal taxa.

Received 3 March; accepted 26 May 2004; doi:10.1038/nature02699.

---

1. Gould, S. J. *Ontogeny and Phylogeny* (Harvard Univ. Press, Cambridge, Massachusetts, 1977).
2. Carrano, M. T. in *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles* (eds Carrano, M. T., Blob, R. W., Gaudin, T. & Wible, J.) (Univ. Chicago Press, Chicago, in the press).
3. Erickson, G. M., Curry-Rogers, K. & Yerby, S. Dinosaur growth patterns and rapid avian growth rates. *Nature* **412,** 429–433 (2001).
4. Brochu, C. A. Osteology of *Tyrannosaurus rex*: Insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *J. Vert. Paleontol. Mem.* **22**(7), 1–138 (2003).
5. Carrano, M. T. & Hutchinson, J. R. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *J. Morphol.* **253,** 207–228 (2002).
6. Brochu, C. A. A digitally rendered endocast for *Tyrannosaurus rex*. *J. Vert. Paleontol.* **20,** 1–6 (2003).
7. Currie, P. J. Possible evidence of gregarious behavior in tyrannosaurids. *GAIA* **15,** 271–277 (1998).
8. Erickson, G. M. Breathing life into *Tyrannosaurus rex*. *Scient. Am.* **9,** 42–49 (1999).
9. Chin, K., Tokaryk, T. T., Erickson, G. M. & Calk, L. C. A king-sized theropod coprolite. *Nature* **393,** 680–682 (1998).
10. Erickson, G. M. *et al.* Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature* **382,** 706–708 (1996).
11. Hutchinson, J. & Garcia, M. *Tyrannosaurus* was not a fast runner. *Nature* **415,** 1018–1021 (2002).
12. Holtz, T. R. in *Mesozoic Vertebrate Life* (eds Tanke, D. & Carpenter, K.) 64–83 (Indiana Univ. Press, Bloomington, 2001).
13. Currie, P. J. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontol. Pol.* **48,** 191–226 (2003).
14. Chinsamy, A. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia: Theropoda). *Palaeontol. Afr.* **27,** 77–82 (1993).
15. Weishampel, D. B. & Horner, J. R. in *Dinosaur Eggs and Babies* (eds Carpenter, K., Hirsch, K. F. & Horner, J. R.) 229–243 (Cambridge Univ. Press, Cambridge, 1994).
16. Francillon-Viellot, H., *et al.* in *Biomineralization: Patterns and Evolutionary Trends* (ed. Carter, J. G.) 471–530 (Van Nostrand Reinhold, New York, 1990).
17. Larson, P. & Donnan, K. *Rex Appeal* (Invisible Cities Press, Montpelier, 2002).
18. Horner, J. R. & Lessem, D. *The Complete T. rex* (Simon & Schuster, New York, 1993).
19. Currie, P. J., Hurum, J. H. & Sabath, K. Skull structure and evolution in tyrannosaurid dinosaurs. *Acta Palaeontol. Pol.* **48,** 227–234 (2003).
20. Carr, T. D. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *J. Vert. Paleontol.* **19,** 497–520 (1999).
21. Castanet, J. & Naulleau, G. Données expérimentales sur la valeur des marques squelettiques comme indicateur de l' age chez *Vipera aspis* (L.) (Ophidia, Viperidae). *Zool. Scripta* **3,** 201–208 (1974).
22. de Buffrenil, V. & Castanet, J. Age estimation by skeletochronology in the Nile monitor (*Varanus niloticus*), a highly exploited species. *J. Herpetol.* **34,** 414–424 (2000).
23. Maddison, W. P. & Maddison, D. R. *MacClade Version 3; Analysis of Phylogeny and Character Evolution* (Sinauer Associates, Sunderland, MA, 1992).
24. Anderson, J. F., Hall-Martin, A. & Russell, D. A. Long bone circumference and weight in mammals, birds, and dinosaurs. *J. Zool. A* **207,** 53–61 (1985).
25. Sussman, M. *Growth and Development* (Prentice-Hall, Englewood Cliffs, New Jersey, 1964).
26. Coria, R. A. & Salgado, L. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* **377,** 224–226 (1995).
27. Erickson, G. M., de Ricqles, A., de Buffrenil, V., Molnar, R. E. & Bayless, M. A. Vermiform bones and the evolution of gigantism in *Megalania*—how a reptilian fox became a lion. *J. Vert. Paleontol.* **23,** 966–970 (2003).
28. Case, T. E. On the evolution and adaptive significance of post-natal growth rates in the terrestrial vertebrates. *Q. Rev. Biol.* **53,** 243–282 (1978).
29. Seebacher, F. A new method to calculate allometric length-mass relationships of dinosaurs. *J. Vert. Paleontol.* **21,** 51–60 (2001).
30. Currie, P. J. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. *Can. J. Earth Sci* **40,** 651–665 (2003).

Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank O. Rieppel and B. Simpson (The Field Museum), L. Chiappe (Los Angeles County Museum of Natural History), P. Larson and N. Larson (Black Hills Institute), B. Stein and M. Triebold (Triebold Paleontology), D. Evans (Indianapolis Children's Museum), C. Mehling (American Museum of Natural History), S. Williams, M. Henderson and L. Cranford (Burpee Museum of Natural History), J. Gardner, D. Tanke and D. Brinkman (Royal Tyrrell Museum of Palaeontology), T. Carr (University of Toronto), F. W. King and K. Krysco (Florida Museum of Natural History), K. Womble (Florida State University), M. Bayless (Berkeley, California) and A. Woodward (Florida Fish and Wildlife Conservation Commission) for assistance with this research. The NSF and the College of Arts and Sciences of Florida State University generously funded this project.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to G.M.E. (gerickson@bio.fsu.edu).