Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia

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Abstract: Many tyrannosaurid skeletons have been collected in Canada, the United States, and Mongolia. These fossils tend to represent mature individuals, but juveniles are also known. Skeletons of five genera of tyrannosaurids representing two distinct clades (albertosaurines and tyrannosaurines) were measured, and bivariate analysis was done on 85 dimensions. Allometric differences among mature specimens of different species are shown to be trivial when compared with the allometric differences associated with growth. Nevertheless, albertosaurines tend to be more lightly built than tyrannosaurines. When compared with a tyrannosaurine of the same absolute size, albertosaurines had slightly shorter, lower skulls, shorter ilia, longer tibiae, longer metatarsals, and longer toes. The arms of albertosaurines and tyrannosaurines are the same size, with the exception of *Tarbosaurus*, which has shorter front limb elements. Tooth counts show individual and interspecific variation, but there is no evidence that tooth numbers are controlled by the size or age of an animal. *Dinotyrannus*, *Jenghizkhan*, *Maleevosaurus*, *Shanshanosaurus*, *Stygivenator*, and possibly *Nanotyrannus* have proportions that suggest they are ontogenetic stages of either *Tarbosaurus* or *Tyrannosaurus*.

Résumé : Plusieurs squelettes de tyrannosauridés ont été recueillis au Canada, aux États-Unis et en Mongolie. Ces fossiles tendent à représenter des individus adultes, mais des juvéniles sont aussi reconnus. Les squelettes de cinq genres de tyrannosauridés représentant deux clades distincts (albertosaurines et tyrannosaurines) ont été mesurés et des analyses à deux variables ont été effectuées sur 85 dimensions. Des différences allométriques entre les spécimens adultes de différentes espèces se sont montrées peu significatives lorsque comparées aux différences allométriques associées à la croissance. Néanmoins, les albertosaurines tendent à être de construction plus frêle que les tyrannosaurines. Lorsque comparés à un tyrannosaurine de même taille absolue, les albertosaurines ont un crâne légèrement plus court et plus bas, des iliaques plus courts, des tibias plus longs, des métatarses plus longs et des orteils plus longs. Les bras des albertosaurines et des tyrannosaurines sont de même taille à l'exception de *Tarbosaurus*, qui a les éléments des membres antérieurs plus courts. Le compte des dents montre des variations individuelles et interspécifiques, mais il n'y a aucune évidence que le nombre de dents est contrôlé par la taille ou l'âge d'un animal. *Dinotyrannus*, *Jenghizkhan*, *Maleevosaurus*, *Shanshanosaurus*, Stygivenator et probablement *Nanotyrannus* ont des proportions qui suggèrent qu'ils soient des stades ontogéniques de *Tarbosaurus* ou de *Tyrannosaurus*.

[Traduit par la Rédaction]

Introduction

To understand what a fossil species represents, it is important to know the changes that take place during growth. This is especially important in dinosaurs, which undergo considerable change in absolute size and proportions (Rozhdestvensky 1965). Proportional differences are often used in palaeontology to distinguish genera or species. But limited numbers of complete specimens usually make it impossible to determine whether these represent taxonomic differences, or individual, ontogenetic or sexual variation. Failing to understand these types of variation in fossils leads to the description of too many species, which in turn distorts our understanding of diversity in palaeoecosystems. Fortunately, there are at least a few dinosaurs where enough specimens exist or have been studied to make such studies possible. These include species of small theropods (Colbert 1990; Raath 1990), prosauropods (Rozhdestvensky 1965), hadrosaurs (Rozhdestvensky 1965; Dodson 1975), protoceratopsians (Brown and Schlaikjer 1940; Dodson 1976), and ceratopsids (Ryan et al. 2001).

Non-avian theropods are a generally homogenous group in terms of anatomy and proportions. Christiansen (1999) found that in some proportions non-avian theropods were even more conservative than modern mammals.

Long bone scaling in non-avian theropods has been examined closely in recent years. Gatesy (1991) determined from the long bone scaling of the hind limbs that birds were biomechanically different than non-avian theropods. Carrano (1998) and Christiansen (1999, 2002) showed that mammals (especially ungulates and carnivores) are much better analogues

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Fig. 1. Skulls of described tyrannosaurid genera and species, showing (in gray) what is known for each specimen. Teeth, palatal bones, and mandibles are excluded. (*a*) *Gorgosaurus libratus* (TMP 91.36.500); (*b*) *Albertosaurus sarcophagus* (TMP 81.10.1); (*c*) *Alectrosaurus olseni* (GIN 100/50-51, after Perle 1977); (*d*) *Alioramus remotus* (PIN 552/2, after Kurzanov 1976); (*e*) *Daspletosaurus torosus* (composite of NMC 8506, TMP 2001.36.1); (*f*) *Nanotyrannus lancensis* (CMNH 7541); (*g*) *Tarbosaurus bataar* (IVPP V4878, holotype of "Shanshanosaurus *huoyanshanensis*"); (*h*) *Tyrannosaurus rex* (LACM 28471, holotype of "*Stygivenator molnari*," after drawing by Tracy Ford in Olshevsky 1995); (*i*) *Tarbosaurus bataar* (PIN 552-3, holotype of "*Maleevosaurus novojilovi*," after Maleev 1974); (*j*) *Tyrannosaurus rex* (OMNH 10131, "*Aublysodon mirandus*," after Lehman and Carpenter 1990); (*k*) *Tarbosaurus bataar* (PIN 551-1, holotype of "*Jenghizkhan bataar*," after Maleev 1974); (*l*) *Tyrannosaurus rex* (LACM 28345, holotype of "*Dinotyrannus megagracilis*," after drawing by Tracy Ford in Olshevsky 1995); (*m*) *Tarbosaurus bataar* (after Hurum and Sabath in press); (*n*) *Tyrannosaurus rex* (BHI 3033). Not to scale.

than birds for understanding the locomotion of non-avian theropods.

Tyrannosaurids are amongst the most famous and best known dinosaurs. Most specimens are generally large mature individuals, and tyrannosaurid juveniles tend to be poorly represented in the fossil record. Many species have been described (Fig. 1; Tables 1, 2), although the only genera universally accepted are *Albertosaurus* and *Tyrannosaurus*, both established by Osborn (1905).

The purpose of this paper is to supplement what we know about osteological differences by focusing on allometric changes in skeletal (including cranial) proportions. There is no intention to describe here the osteological changes that occur in tyrannosaurids during growth because these have been adequately described in other papers (Carr 1999; Currie in review). Carpenter (1990) examined individual variation of the maxilla, dentary, and ischium bones in *Tyrannosaurus rex*, but worked only with mature specimens. Nor does this paper attempt to analyze the biomechanical implications of changing limb proportions, which is a subject that is at least partly covered by Coombs (1978), Gatesy (1991), Carrano (1998), Christiansen (1999, 2000), and others.

Rozhdestvensky (1965) and Russell (1970) established the general trends for ontogenetic changes in proportions in tyrannosaurids. Rozhdestvensky (1965) examined the four species described by Maleev (1955*a*, 1955*b*) from the Nemegt formation of Mongolia and determined that they were different ontogenetic stages of one animal — *Tarbosaurus bataar.* Russell (1970) based his study on six specimens of *Gorgosaurus libratus*, in which the femur of the smallest specimen was 57% of the length of the largest. Allometric changes were observed by plotting the lengths of different skeletal elements against femur length. Although based on a small number of specimens, Russell (1970) was able to demonstrate that as tyrannosaurs matured, the presacral vertebral column, ribs, scapulocoracoid, pubis, and ischium increased in size more rapidly than the femur, whereas the skull, sacrum, humerus, and forearm grew isometrically when compared with the femur. The tail, hand, tibia, metatarsus, and pes experienced negative allometric growth in comparison with the femur. He suspected that the growth rates could change as an animal grew, but still used the trends to calculate the lengths of bones in a hypothetical individual with a femur length of 100 mm. These measurements were then used to produce a drawing of a reconstructed, juvenile skeleton (fig. 4 of Russell 1970). This was the first good evidence that small tyrannosaurs were large-eyed, slender, long-legged animals that looked very different from the adults.

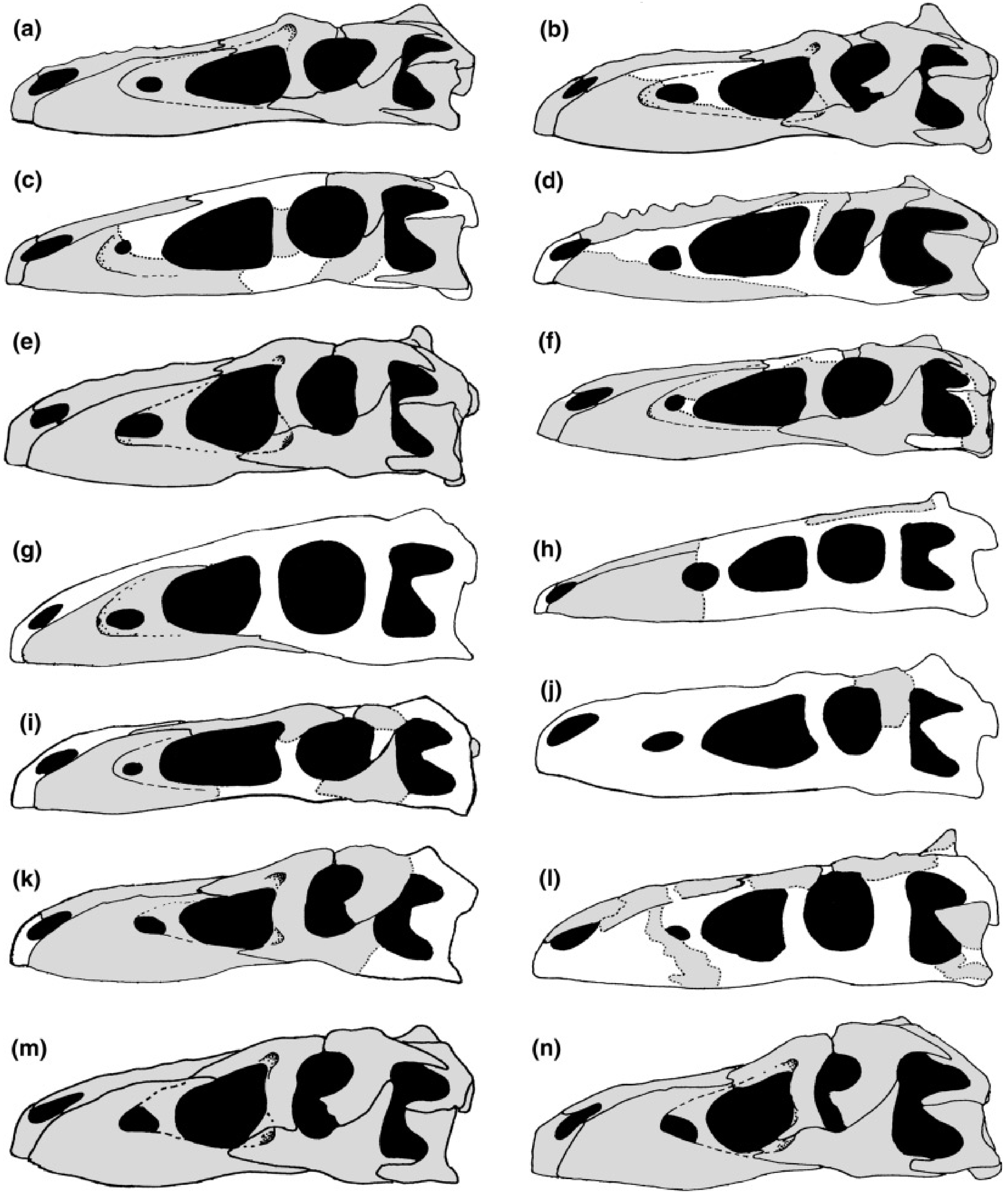
Carr (1999) describes the cranial ontogeny of tyrannosaurids. Although it is an excellent analysis for the most part, several character changes are considered as indications of ontogenetic stage, whereas they are in fact simply controlled by the absolute size of the animal, regardless of its ontogenetic stage.

Materials and methods

Over a period of more than ten years, more than 250 catalogued tyrannosaurid specimens have been measured by the author. Although many of these are isolated bones, more than half of the specimens represent partial to nearly complete skeletons. Measurements greater than 15 cm were generally made with a flexible metric tape measure. Those under 15 cm were taken with calipers. Because up to 75 measurements could be taken from the vertebral column, and 125 from skull and limbs, each measurement was usually only made once. Fernando Novas and Philip J. Currie will eventually publish these measurements in a book on theropod dinosaurs, which is currently being written for Johns Hopkins University Press.

Taxa included in this study are *Albertosaurus sarcophagus*, *Daspletosaurus torosus*, *Daspletosaurus* n. sp., *Gorgosaurus libratus*, *Nanotyrannus lancensis*, *Tarbosaurus bataar*, and *Tyrannosaurus rex*. *Nanotyrannus lancensis* (Bakker et al. 1988) is considered to be a juvenile *Tyrannosaurus rex* by some authors (Carpenter 1992; Carr 1999), although a strong case can be made for it being distinct at the species level (Currie in press). Paul (1988) lumped all of these taxa into only two genera — *Albertosaurus* and *Tyrannosaurus* — and many other authors follow this practice. *Tarbosaurus* is sometimes split into multiple genera (Maleev 1955*a*, 1955*b*; Carpenter 1992; Olshevsky 1995), although this practice is not universally accepted (Rozhdestvensky 1965; Currie 2000). LACM 28345 (designated as *Albertosaurus megagracilis* by Paul 1988 and renamed *Dinotyrannus megagracilis* by Olshevsky 1995) and LACM 28471 (*Aublysodon molnari* of Paul 1988; *Aublysodon mirandus* of Molnar and Carpenter 1990; *Stygivenator molnari* of Olshevsky 1995) are considered as juveniles of *Tyrannosaurus rex* in this study. Following Currie and Dong (2001), *Shanshanosaurus* is regarded as a juvenile *Tarbosaurus bataar.* The reassignment of *Aublysodon* and *Shanshanosaurus* specimens to *Tyrannosaurus* and *Tarbosaurus* removes the need for a subfamily designated by Paul (1988) as the Aublysodontinae and by Olshevsky (1995) as the Shanshanosaurinae (derived from Shanshanosauridae Dong 1977). Olshevsky (1995) subdivided the Tyrannosaurinae into the Alioramini, Tarbosaurini, Albertosaurini, and Tyrannosaurini.

Regardless of the instability of tyrannosaurid generic and



specific taxonomy (Tables 1, 2), it is universally agreed that these animals are a tight knit group in terms of size and morphology. All classification schemes other than Olshevsky (1995) organize the species used in this study into two clades within a monophyletic Tyrannosauridae. *Albertosaurus sarcophagus* and *Gorgosaurus libratus* form a clade that is referred to informally in this paper as the albertosaurines, whereas *Daspletosaurus torosus*,

Table 1. Tyrannosaurid taxa dealt with in this paper.

Taxa considered valid	Synonyms
Albertosaurus sarcophagus	*Albertosaurus arctunguis*
Alectrosaurus olseni	*Albertosaurus olseni*
Alioramus remotus	
Daspletosaurus torosus	*Tyrannosaurus torosus*
Gorgosaurus libratus	*Albertosaurus libratus*
Nanotyrannus lancensis	*Albertosaurus lancensis*
Tarbosaurus bataar	*Gorgosaurus lancinator, Gorgosaurus novojilovi, Jenghizkhan bataar, Maleevosaurus novojilovi, Shanshanosaurus huoyanshanensis, Tarbosaurus efremovi, Tyrannosaurus bataar*
Tyrannosaurus rex	*Albertosaurus megagracilis, Aublysodon mirandus, Aublysodon molnari, Dinotyrannus megagracilis, Dynamosaurus imperiosus, Manospondylus gigas, Stygivenator molnari*

Daspletosaurus n. sp., *Nanotyrannus lancensis*, *Tarbosaurus bataar*, and *Tyrannosaurus rex* make up the Tyrannosaurinae. These subfamilies are being defined formally on the basis of morphological differences (Currie et al. in press), although Holtz (2001) has already alluded to the albertosaurine clade. *Alectrosaurus olseni* may be an albertosaurine, as suggested by Paul (1988), but is excluded from this study because of insufficient information. *Alioramus remotus* (Kurzanov 1976) is also excluded, but is probably closely related to *Tarbosaurus* (Currie in press). Quantitative analysis alone usually cannot resolve taxonomic disputes, although the results will have an impact on the way that some of the characters are used in diagnoses.

Eighty-five bivariate comparisons were made (Table 3), in most cases using femur length as the standard against which other elements are judged. In theropods and many other animals, this seems to be one of the least variable lengths in the body (Russell 1970; Currie and Zhao 1993; Holtz 1994; Rosenberg and Dodson 1996) when it is compared with a wide suite of measurements. Femoral length is also highly correlated with body mass amongst extant mammals (Christiansen 1999). Tyrannosaurids maintained the relative length of the femur found in much smaller theropods, rather than evolving shorter, thicker bones that were more resistant to mechanical failure as the largest mammals do (Christiansen 1999). Many of the tyrannosaurid specimens consist solely of skulls, or lack the femur. Because both skull length and the length of the maxillary tooth row are well represented in the sample and are isometric with femur length (Table 3), these measurements were sometimes used as the basis for comparison with other elements and dimensions.

Measurements were transformed logarithmically to normalize the distribution of the dependent variable. Regressions were calculated using the least squares method. Each regression line is therefore defined as $\mathrm{Log}(y) = b + k\mathrm{Log}(x)$, which is an expression of the simple power equation $y = bx^k$. The sum of the error terms was not included in the calculation. Confidence limits (95% level) were calculated for the allometric coefficient (k) to determine whether or not the increase in size is likely to be isometric. The relative size increase of one element versus a standard unit (usually the length of the femur) is considered to be isometric when $k = 1.0$ or when 1.0 falls within the 95% confidence interval of the calculated value of k. Negative allometry is demonstrated when the calculated value of k is significantly less than 1.0, and positive allometry has a value of more than 1.0.

Ontogenetically, tyrannosaurids increased in length by as much as 25 times and in weight by more than 2000 times, and of necessity their body proportions changed dramatically. Nevertheless, there is no evidence to suggest that there were any postural changes as they grew up. And if there were, the family is uniform enough that such changes must have affected all species in the same way.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, U.S.A.; BHI, Black Hills Institute of Geological Research, Hill City, South Dakota, U.S.A.; BM, British Museum (Natural History), London, U.K.; CM, Carnegie Museum, Pittsburgh, U.S.A.; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, U.S.A.; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; GIN, Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; LACM, Los Angeles County Museum, Los Angeles, California, U.S.A.; NMC, Canadian Museum of Nature, Ottawa, Ontario, Canada; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, U.S.A.; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Results

Although the database includes more than 250 catalogued specimens, few of these are complete skeletons. Combine this with the inability to measure many dimensions accurately because of crushing, distortion and other factors, and the net result is that less than 10% of the specimens could be used in most bivariate comparisons. The most robust analysis is the comparison between dentary height and the length of the dentary tooth row, which includes 43 specimens. In spite of the fact that only 30% of the tyrannosaurid comparisons are based on twenty or more specimens, statistically significant comparisons can nevertheless be made with suites of fewer specimens when there is a substantial size range, when individual variation is low, and when specimens are well preserved. Almost half of the tyrannosaurid comparisons are well correlated with coefficients of determination (R^2) with values of 0.90 or greater, even though as few as six specimens were being analyzed in some cases.

The primary analysis looked at proportional changes in size within the Tyrannosauridae. Ontogenetic and interspecific size differences do not scale the same way (Currie 1978),

Table 2. Genera and species of Tyrannosauridae referred to in this paper, and the specimens to which the names have been applied.

Designation Here	Synonym	Reference	Specimen
Albertosaurus sarcophagus	*Albertosaurus sarcophagus*	Osborn 1905	TMP 81.10.1
Alectosaurus olseni	*Alectrosaurus olseni*	Perle 1977	GIN 100/50
Alioramus remotus	*Alioramus remotus*	Kurzanov 1976	PIN 552/2
Daspletosaurus torosus	*Daspletosaurus torosus*	Russell 1970	NMC 8506
Gorgosaurus libratus	*Gorgosaurus libratus*	Lambe 1914	TMP 91.36.500
Nanotyrannus lancensis	*Nanotyrannus lancensis*	Bakker et al. 1988	CMNH 7541
Tarbosaurus bataar	*Gorgosaurus lancinator*	Maleev 1974	PIN 553-1
Tarbosaurus bataar	*Jenghizkhan bataar*	Olshevsky 1995	PIN 551-1
Tarbosaurus bataar	*Maleevosaurus novojilovi*	Carpenter 1992	PIN 552-2
Tarbosaurus bataar	*Shanshanosaurus huoyanshanensis*	Dong 1977	IVPP V4878
Tarbosaurus bataar	*Tarbosaurus bataar*	Rozhdestvensky 1965	ZPAL MgD-I/4
Tarbosaurus bataar	*Tarbosaurus efremovi*	Maleev 1974	PIN 551-3
Tyrannosaurus rex	*Albertosaurus megagracilis*	Paul 1988	LACM 23845
Tyrannosaurus rex	*Aublysodon mirandus*	Lehman and Carpenter 1990	OMNH 10131
Tyrannosaurus rex	*Aublysodon molnari*	Paul 1988	LACM 28471
Tyrannosaurus rex	*Dinotyrannus megagracilis*	Olshevsky 1995	LACM 28345
Tyrannosaurus rex	*Dynamosaurus imperiosus*	Osborn 1905	BM 7994
Tyrannosaurus rex	*Stygivenator molnari*	Olshevsky 1995	LACM 28471
Tyrannosaurus rex	*Tyrannosaurus rex*	Osborn 1905	BHI 3033

Note: For a complete list and history of the multitude of names, their combinations, and synonyms refer to Olshevsky (1995). The first column lists the identifications as they are used in this paper. The second are alternative names proposed in the references listed in the third column. The specimens listed are not necessarily the type specimens, but are key to understanding the taxon.

and tyrannosaur species grow to different adult sizes. Skull length suggests that *Albertosaurus* (TMP 81.10.1 has a 0.98 m long skull) and *Gorgosaurus* (AMNH 5458 is 0.99 m) are about the same size, and that *Daspletosaurus* is about 10% larger at maturity (FMHN PR308 is 1.12 m long). *Tarbosaurus* is even larger (the skull of PIN 551-1 is 1.35 m in length), and *Tyrannosaurus* is the largest (the FMHN PR2081 skull is 1.53 m). Skulls are often highly variable in length even amongst closely related vertebrates, but the skull lengths of tyrannosaurids are consistent in that limb elements produce almost the same size relationships. For example, femur length suggests that *Albertosaurus* (ROM 807 has a 1.02 m long femur), *Daspletosaurus* (femur length of 1.02 in TMP 85.62.1) and *Gorgosaurus* (NMC 2120's femur is 1.04 m) are almost the same size at maturity, but are slightly smaller than *Tarbosaurus* (GIN 107/2 includes a l.12 m femur). The largest species is *Tyrannosaurus rex*, the largest femur of which is 1.34 m long (BHI 3033).

Currie (1978) demonstrates that the allometry expressed during growth within a species can be different than the allometry expressed among closely related species of different adult sizes. Within pelycosaurs, for example, growth can generally be considered as isometric when the allometric coefficient is 1.0 (i.e., k = 1.0). However, size increases between the adults of different but closely related species are isometric when the allometric coefficient is 0.67, when the x-variable (such as vertebral width) is weight dependent, and when the adults have different absolute sizes. For certain variables, the differences between growth and interspecific allometries are probably also present in tyrannosaurids. However, *Tyrannosaurus* is only 30% larger than *Albertosaurus* at maturity, whereas all of the tyrannosaur species increase in length by over 1000% as they grow from hatchlings to adults. Because of this great disparity between the two types of size increases, the effects of interspecific allometry are negligible compared with those of allometric growth. At the outset of this study, it was necessary to generally ignore interspecific allometry, even though there is no doubt that it has some influence on the coefficient of allometry. Some interspecific allometric differences did become evident during the course of the study, and it is clear that there would still be proportional differences between *Gorgosaurus* and *Tyrannosaurus*, even if a 13 m *Gorgosaurus* specimen was found. This indicates that it may be possible to better determine the magnitude of interspecific allometry when more mature specimens of the different tyrannosaurid species are discovered.

It is generally assumed (Paul 1988) that the albertosaurine clade is more gracile than the tyrannosaurine clade. This would be expected considering the fact that they are somewhat smaller at maturity. To test this hypothesis, and to see if there are differences in body proportions between the two clades, bivariate comparisons were also done for the albertosaurines and tyrannosaurines (Table 3). In some cases, analysis was also done at the generic–species level when there was evidence of a significant difference in size. For example, as pointed out by Holtz (2001), the arms of *Tarbosaurus* are shorter than those of any other tyrannosaurids, whereas those of the other tyrannosaurines scale with albertosaurines.

Cranial analysis

In tyrannosaurids, the lengths of the skull (k = 0.99 in albertosaurines, k = 1.08 in tyrannosaurines), maxillary tooth

Table 3. Analysis of size differences in Tyrannosauridae.

		Tyrannosauridae				Albertosaurinae				Tyrannosaurinae			
y	*x*	*n*	R^2	*k*	*b*	*n*	R^2	*k*	*b*	*n*	R^2	*k*	*b*
Skull length	Femur length	26	0.96	1.10	–0.29	12	0.95	0.99	–0.01	14	0.98	1.08	–0.20
Skull length	Max tooth row	32	0.95	0.99	0.36	10	0.93	0.96	0.43	22	0.96	0.98	0.40
Skull height	Femur length	12	0.94	1.33	–1.43	4	0.88	0.81	–0.01	8	0.82	1.14	–0.84
Skull height	Max tooth row	23	0.96	1.33	–1.00	9	0.95	1.13	–0.51	14	0.94	1.27	–0.84
Antorbital length	Skull length	22	0.98	1.00	–0.20	9	0.96	1.00	–0.20	13	0.97	0.99	–0.17
Antorbital length	Max tooth row	17	0.94	1.05	0.02	6	0.94	0.92	0.33	11	0.92	1.00	0.14
Antorbital length	Femur length	11	0.90	0.98	–0.12	5	0.90	0.54	1.10	6	0.79	0.85	0.29
Postorbital length	Max tooth row	15	0.90	1.48	–1.49	5	0.97	1.30	–1.05	10	0.82	1.42	–1.33
Skull height (front of orbit)	Max tooth row	20	0.94	1.34	–1.02	6	0.97	1.31	–0.97	14	0.94	1.24	–0.08
Maxillary tooth row	Femur length	27	0.95	1.05	–0.49	11	0.98	1.11	–0.66	16	0.94	1.03	–0.40
Maxilla, height at 6th alveolus	Max tooth row	36	0.90	1.31	–1.11	14	0.85	1.39	–1.35	22	0.92	1.20	–0.78
Max maxillary height	Max tooth row	15	0.94	1.14	–0.63	7	0.86	1.25	–0.93	8	0.97	1.11	–0.51
Maxilla, largest tooth height	Max tooth row	20	0.91	1.31	–1.49	7	0.89	1.41	–1.77	13	0.91	1.23	–1.27
Maxilla, largest tooth height	Min dentary height	18	0.88	0.84	0.26	8	0.7	0.73	0.46	10	0.88	0.82	0.31
Nasal length	Max tooth row	14	0.93	1.02	0.10	8	0.92	1.34	–0.73	6	0.99	0.90	0.41
Frontal width	Max tooth row	6	0.78	1.09	–0.70	3	0.995	1.09	–0.69	3	0.999	2.73	–4.70
Frontal width	Skull length	10	0.92	1.30	–1.65	6	0.96	0.96	–0.70	4	0.92	1.62	–2.56
Frontal length	Frontal width	22	0.82	0.51	1.14	11	0.75	0.50	1.16	11	0.83	0.51	1.15
Orbit length	Femur length	10	0.62	0.38	0.89	5	0.24	0.18	1.45	5	0.66	0.98	–0.94
Orbit length	Max tooth row	16	0.34	0.36	1.10	6	0.58	0.54	0.62	10	0.24	0.29	1.26
Orbit height	Max tooth row	16	0.87	1.26	–1.01	4	0.99	1.42	–1.49	12	0.92	1.00	–0.29
Orbit height	Femur length	9	0.93	1.40	–1.85	3	0.997	0.62	0.29	6	0.74	1.05	–0.78
Quadrate height	Max tooth row	7	0.92	1.30	–1.07	2	1.00	2.13	–3.18	5	0.94	1.24	–0.91
Occipital condyle	Max tooth row	14	0.95	1.42	–1.89	4	0.94	2.04	–3.48	10	0.96	1.36	–1.73
Foramen magnum	Skull length	10	0.76	0.87	–1.11	3	0.97	2.25	–5.15	7	0.79	0.74	–0.73
Foramen magnum	Max tooth row	11	0.79	0.95	–1.03	4	0.89	1.87	–3.40	7	0.84	0.82	–0.66
Foramen magnum	Occipital condyle	12	0.74	0.61	0.35	5	0.50	0.78	0.05	7	0.79	0.58	0.41
Mandible length	Femur length	17	0.97	0.95	0.14	7	0.98	0.72	0.80	10	0.99	0.96	0.11
Mandible length	Max tooth row	17	0.97	0.99	0.34	5	0.98	1.09	0.09	12	0.96	0.99	0.34
Mandible length	Skull length	29	0.99	0.95	0.11	12	0.99	1.00	–0.01	17	0.98	0.94	0.14
Dentary length	Skull length	25	0.98	0.93	0.02	9	0.96	0.98	–0.12	16	0.98	0.89	0.15
Dentary tooth tow	Max tooth row	28	0.97	0.88	0.29	9	0.98	0.79	0.50	19	0.97	0.87	0.31
Dentary, min height	Dent tooth row	43	0.93	1.45	–1.77	24	0.93	1.53	–1.95	19	0.92	1.41	–1.65
Dentary, min height	Femur length	15	0.97	1.41	–2.18	4	0.99	1.64	–2.85	11	0.97	1.38	–2.06
Scapula length	Femur length	12	0.98	1.32	–1.10	3	0.97	1.44	–1.43	9	0.98	1.31	–1.06
Scapula sw	Femur length	11	0.99	1.23	–1.97	4	0.98	1.27	–2.05	7	0.997	1.23	–1.99
Scapula dw	Femur length	7	0.81	1.37	–1.98	2	1.00	1.16	–1.25	5	0.89	1.51	–2.44
Coracoid height	Femur length	6	0.90	1.10	–1.04	2	1.00	0.84	–0.34	4	0.96	1.03	–0.79
Coracoid length	Femur length	8	0.88	1.69	–2.68	3	0.93	0.79	–0.04	5	0.95	1.93	–3.38
Humerus length	Femur length	20	0.88	0.91	–0.25	7	0.81	0.91	–0.28	13	0.88	0.89	–0.20
Humerus pw	Femur length	13	0.74	1.27	–2.01	4	0.27	0.32	0.71	9	0.84	1.35	–2.22
Humerus transverse sw	Femur length	14	0.92	1.35	–2.45	4	0.64	1.35	–2.47	10	0.95	1.34	–2.43
Humerus dw	Femur length	13	0.94	1.53	–2.80	4	0.68	1.00	–1.25	9	0.96	1.57	–2.92
Radius length	Femur length	10	0.77	0.84	–0.41	5	0.81	0.99	–0.85	5	0.72	0.81	–0.32
Radius pw	Femur length	8	0.70	1.31	–2.44	4	0.79	0.98	–1.44	4	0.83	1.73	–3.76
Radius sw	Femur length	7	0.66	1.08	–1.96	4	0.92	0.32	0.22	3	0.67	1.17	–2.26
Radius dw	Femur length	7	0.52	0.91	–1.27	4	0.81	1.05	–1.65	3	0.80	2.60	–6.50
Ulna length	Femur length	12	0.65	0.83	–0.29	6	0.81	0.87	–0.40	6	0.66	0.89	–0.50
Ulna pw	Femur length	10	0.88	1.44	–2.65	5	0.81	1.45	–2.65	5	0.98	1.61	–3.18
Ulna sw	Femur length	10	0.91	1.56	–3.32	5	0.91	1.94	–4.43	5	0.99	1.26	–2.41
Ulna dw	Femur length	10	0.81	1.24	–2.18	5	0.75	1.07	–1.68	5	0.84	1.40	–2.68
Metacarpal II	Femur length	14	0.73	0.78	–0.45	7	0.73	0.74	–0.30	7	0.81	0.87	–0.72
Manual I-1	Femur length	10	0.29	0.43	0.62	5	0.21	0.23	1.25	5	0.70	0.65	–0.08
Manual I-2	Femur length	6	0.63	1.19	–1.60	4	0.94	0.52	0.41	2	1.00	9.10	–23.88
Manual II-1	Femur length	10	0.43	0.66	–0.34	4	0.52	0.69	–0.41	6	0.42	0.66	–0.33
Manual II-2	Femur length	9	0.57	0.73	–0.38	4	0.14	0.31	0.89	5	0.90	0.94	–1.03
Manual II-3	Femur length	6	0.67	1.10	–1.36	4	0.68	0.73	–0.25	2	1.00	10.84	–28.75
Ilium length	Femur length	23	0.95	1.11	–0.31	10	0.99	0.98	0.04	13	0.99	1.06	–0.13
Ilium height	Femur length	15	0.93	1.34	–1.33	6	0.85	0.84	0.11	9	0.98	1.32	–1.22
Pubis length	Femur length	15	0.97	1.19	–0.62	8	0.93	1.34	–1.06	7	0.98	1.16	–0.51
Pubis boot length	Femur length	6	0.97	1.37	–1.35	3	0.95	2.04	–3.34	3	0.98	1.40	–1.41
Ischium length	Femur length	18	0.91	1.25	–0.87	9	0.87	1.20	–0.73	9	0.93	1.14	–0.51
Femur pw	Femur length	25	0.89	1.23	–1.28	8	0.88	1.47	–1.99	17	0.87	1.16	–1.07
Femur sw	Femur Length	22	0.96	1.41	–2.12	10	0.91	1.74	–3.11	12	0.98	1.37	–1.98
Femur sc	Femur Length	23	0.94	1.29	–1.30	12	0.93	1.27	–1.26	11	0.97	1.22	–1.06
Femur dw	Femur Length	29	0.87	1.12	–1.01	10	0.59	1.17	–1.17	19	0.92	1.10	–0.94

Table 3. (*concluded*).

		Tyrannosauridae				Albertosaurinae				Tyrannosaurinae			
y	*x*	*n*	R^2	*k*	*b*	*n*	R^2	*k*	*b*	*n*	R^2	*k*	*b*
Tibia length	Femur Length	35	0.96	0.78	0.63	12	0.91	0.70	0.87	23	0.96	0.80	0.57
Tibia pw	Femur length	25	0.86	1.12	–0.93	10	0.73	0.68	0.30	15	0.91	1.18	–1.09
Tibia sw	Femur length	32	0.93	1.19	–1.50	13	0.88	1.21	–1.55	19	0.94	1.17	–1.42
Tibia dw	Femur length	29	0.88	1.33	–1.60	11	0.89	1.48	–2.04	18	0.87	1.26	–1.39
Fibula length	Femur length	24	0.92	0.71	0.80	9	0.91	0.51	1.38	15	0.97	0.79	0.54
Fibula pw	Femur length	30	0.86	1.18	–1.30	15	0.82	1.20	–1.35	15	0.82	1.13	–1.14
Fibula sw	Femur length	19	0.85	1.30	–2.18	9	0.91	1.33	–2.37	10	0.82	1.03	–1.43
Fibula dw	Femur length	19	0.82	1.44	–2.53	8	0.81	1.18	–1.80	11	0.85	1.36	–2.25
Astragalus width	Femur length	13	0.86	0.93	–0.50	3	0.997	1.25	–1.41	10	0.85	0.90	–0.40
Astragalus height	Femur length	16	0.70	0.71	0.28	6	0.68	1.20	–1.18	10	0.85	0.64	0.51
Calcaneum height	Femur length	11	0.96	1.23	–1.71	4	0.33	0.46	0.47	7	0.97	1.26	–1.80
Metatarsus length	Femur length	25	0.93	0.62	0.90	11	0.97	0.65	0.83	14	0.96	0.62	0.89
Metatarsal I	Femur length	16	0.84	1.03	–1.04	8	0.90	1.13	–1.34	8	0.80	0.98	–0.90
Metatarsal II	Femur length	34	0.84	0.57	0.99	16	0.74	0.53	1.11	18	0.89	0.61	0.86
Metatarsal IV	Femur length	34	0.87	0.54	1.11	18	0.86	0.57	1.02	16	0.93	0.56	1.02
Metatarsal V	Femur length	13	0.96	0.84	–0.18	6	0.92	0.85	–0.22	7	0.97	0.84	–0.17
Pedal phalanx III-1	Femur length	19	0.80	0.88	–0.42	8	0.89	0.89	–0.42	11	0.84	0.90	–0.52
Pedal phalanx III-2	Femur length	19	0.87	0.92	–0.70	8	0.93	0.87	–0.55	11	0.87	0.94	–0.79
Pedal phalanx III-3	Femur length	17	0.88	1.04	–1.15	7	0.91	0.82	–0.51	10	0.89	1.12	–1.39
Pedal phalanx III-4	Femur length	15	0.70	1.10	–1.18	6	0.63	1.32	–1.81	9	0.76	1.06	–1.08

Note: The constants *b* and *k* of the power equation $y = bx^k$ have been solved using the least squares method. In most cases, size differences are isometric when $k = 1.00$, and there is positive allometry when *k* is greater than 1.00. *k*, coefficient of allometry; *n*, size of sample; R^2, coefficient of determination; x and y, the parts being compared; Max, maximum; min, minimum; dw, distal width; pw, proximal width; sw, shaft width; sc, shaft circumference.

row (Fig. 2), nasal, and antorbital region (Fig. 3) scale isometrically with the length of the femur and each other (Table 3). This is a peculiarity of most theropods, and is different than most herbivorous dinosaurs, which show strong positive allometry in the facial region (and total skull length as a consequence) as they increase in size. In ceratopsians and hadrosaurs (Dodson 1975; Horner and Currie 1994), the longer face correlates with an increase in the number of tooth rows, whereas tyrannosaurs maintain the same number of tooth sockets throughout life. Tyrannosaurids show positive allometry in cranial height (Fig. 3), and mature animals have skulls that are relatively much deeper than the juveniles. This correlates with a relative increase in skull height ($k > 1.33$), in maximum height of the maxilla ($k > 1.11$), and in quadrate height ($k > 1.24$).

The anteroposterior length of the orbit increases in size with negative allometry ($k < 0.38$ when compared with either femur or the maxillary tooth row), which reflects the decrease in size of the eyeball relative to the overall skull length. The correlation (*R*) and determination (R^2) coefficients are relatively low, presumably because the orbit tends to be a region that is easily distorted during the fossilization process. In contrast, the height of the orbit shows positive allometry ($k > 1.25$) during growth and interspecific size increase. This correlates with increased skull height.

Within individual bones, different dimensions grow at different rates. Maxillary tooth row length, as we have already seen, is isometric in comparison with skull length, snout (antorbital) length, and femur length. Maximum height of the maxilla (measured from the back of the lacrimal process to the closest point on the alveolar margin) increases with positive allometry ($k = 1.14$). However, height at the level of the sixth alveolus (where there is usually a pronounced step in the dorsal margin of the tyrannosaurid maxilla) increases at a faster rate ($k = 1.31$). Differential growth accounts for the transformation of the elongate, low, triangular maxilla of a juvenile tyrannosaurid into the deep, robust, almost quadrangular maxilla of an adult.

Fig. 2. Comparison of the length of the femur with the length of the skull (upper graph) and maxillary tooth row (lower graph). Diamonds represent albertosaurines; open squares are tyrannosaurine points.

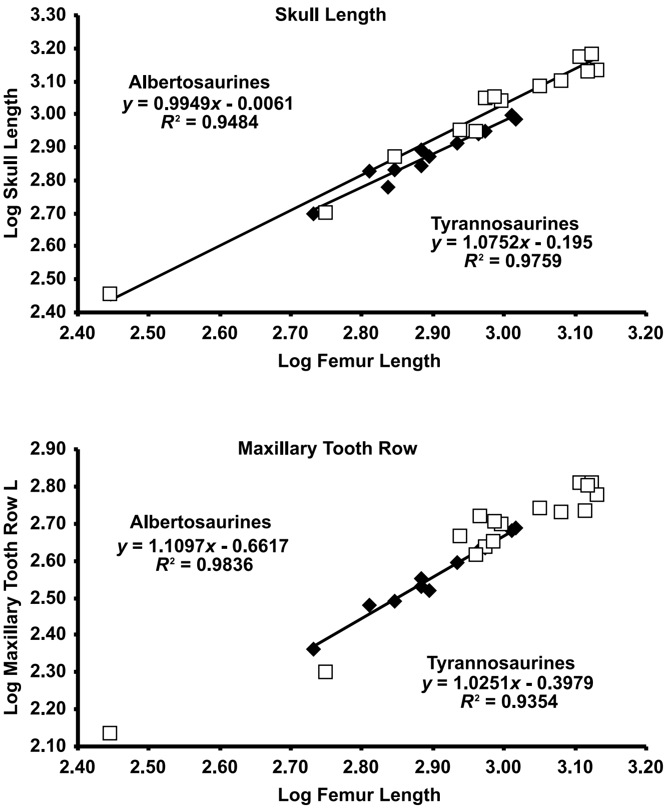


Fig. 3. Snout length compared with skull height (upper graph). Skull height (in front of orbits) compared with the length of the maxillary tooth row (lower graph). Diamonds represent albertosaurines; open squares are tyrannosaurine points.

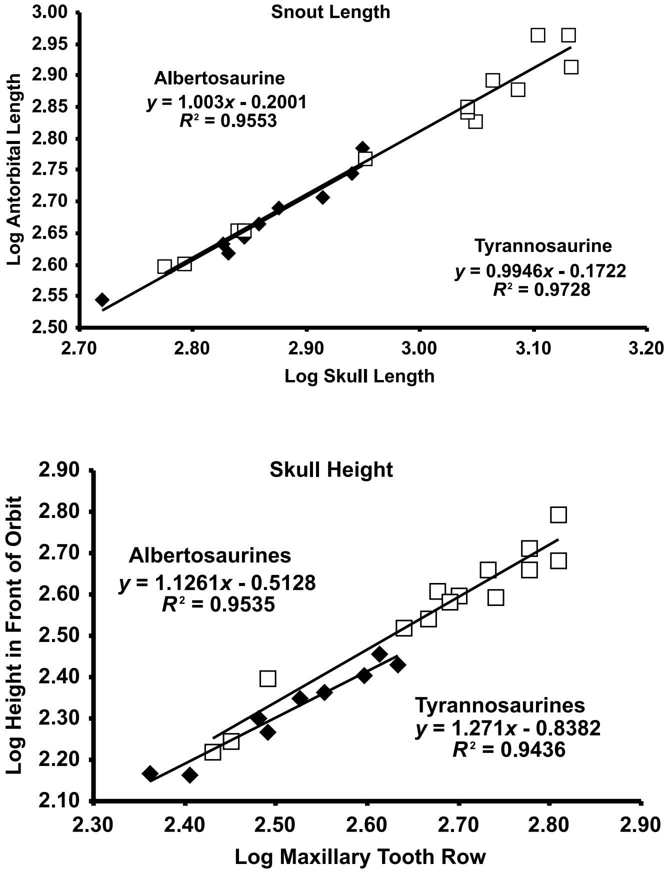


Fig. 4. Tyrannosaurid frontals. Frontal width (measured between the orbital slots, which separate the articulations on the frontal for the prefrontal and postorbital bones) compared with the length (measured from the most posterior point on the frontoparietal suture to the dorsal junction of the frontal, nasal, and prefrontal bones). Diamonds represent albertosaurines; open squares are tyrannosaurine points.

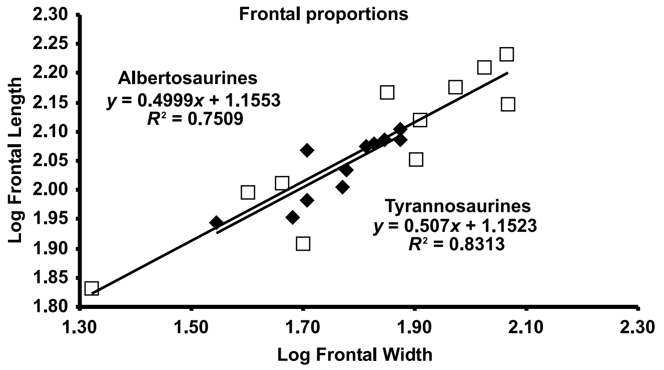
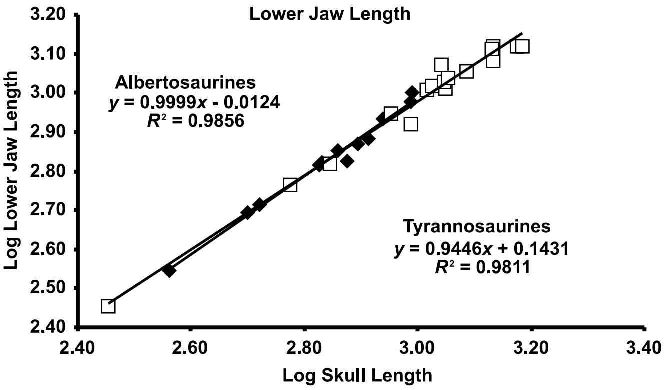


Fig. 5. Mandibular length compared with skull length in tyrannosaurids. Diamonds represent albertosaurines; open squares are tyrannosaurine points.



On the back of the skull, the foramen magnum decreases in relative size ($k = 0.87$ when compared with skull length, $k = 0.61$ in comparison with the occipital condyle), and reflects the negative allometry associated with growth of brain and spinal chord diameters. On the other hand, the occipital condyle increases with strong positive allometry ($k = 1.42$) to support the disproportionate increases in skull weight.

The frontal is a long narrow bone in small tyrannosaurids. Frontal width increases with positive allometry (in comparison with skull length), whereas the length (when compared with the width) is strongly negative in its allometry (Fig. 4). The latter is almost certainly scaling with the length of the brain and size of the orbit, which are relatively smaller in larger animals. Because of the differences in the allometry in the two dimensions, the frontals of large tyrannosaurids look very different than those of small individuals.

The lower jaw is isometric in its pattern of increasing length when compared with the lengths of the femur, skull (Fig. 5), and maxillary tooth row (Table 3). The length of the dentary shows a weak tendency towards negative allometry in comparison to skull length, as does the dentary tooth row (Fig. 6) in comparison with the maxillary tooth row. Some of the strongest positive allometric rates are to be found in the relative height increase of the dentary. Even the minimum height of the dentary has a coefficient of allometry greater than 1.40 when compared with femur length or with the length of the dentary tooth row (Fig. 6). In mature individuals, the high allometry results in a deep jaw adapted for a very powerful bite (Hurum and Currie 2000).

The teeth of tyrannosaurids are highly specialized, and set these animals apart from other theropods because they are disproportionately tall and thick. The longest maxillary tooth increases in size with positive allometry ($k > 1.23$) when compared with the length of the maxillary tooth row (Table 3). Because of the increased depth of the skull in larger individuals, the teeth can appear to be relatively smaller (for example, the height of the tallest maxillary tooth actually experiences negative allometry when compared with the increase in height of the dentary).

All tyrannosaurids have four premaxillary teeth, but the numbers of maxillary and dentary teeth are variable. The numbers can vary within individuals from one side of the mouth to the other. Different tyrannosaurid genera have different tooth counts, although their ranges overlap. However, statistically there is no evidence to indicate that tooth counts vary with the size and (or) age of the animals (Fig. 7).

Fig. 6. Dentary tooth row length compared with maxillary tooth row length (upper graph) and minimum dentary height (about one third of the distance from the front of the bone) (lower graph). Diamonds represent albertosaurines; open squares are tyrannosaurine points.

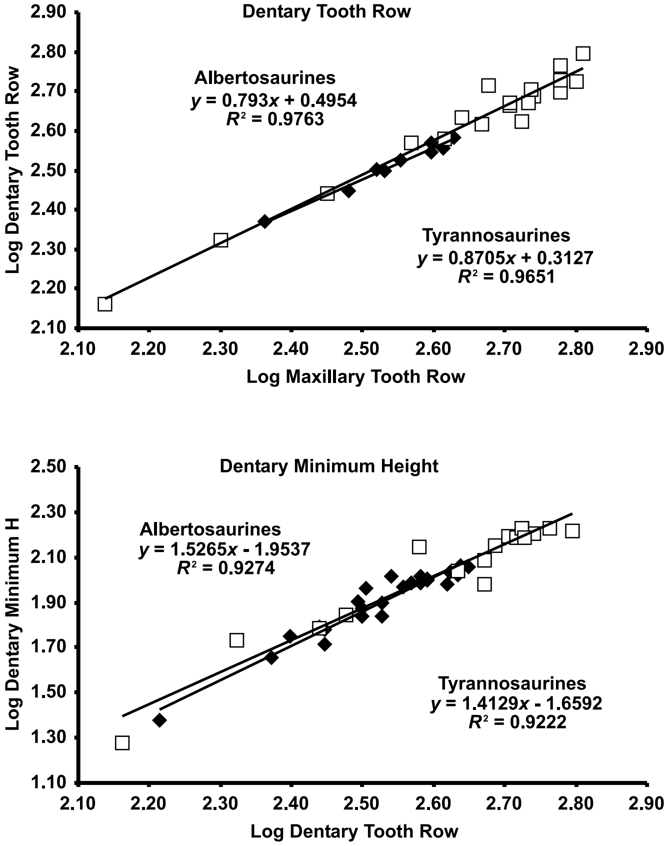


Fig. 7. Comparison between numbers of maxillary teeth and the size (represented by length of maxillary tooth row) of tyrannosaurid genera. Symbols: diamonds, *Albertosaurus*; squares, *Daspletosaurus*; triangles, *Gorgosaurus*; open circle, *Nanotyrannus*; +, *Tarbosaurus*; x with vertical bar, *Tyrannosaurus*.

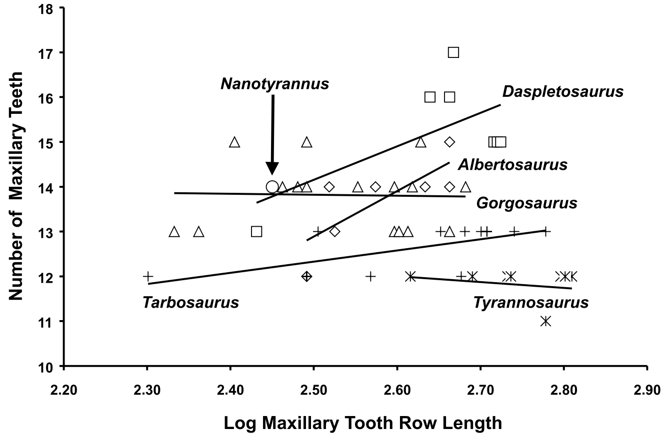
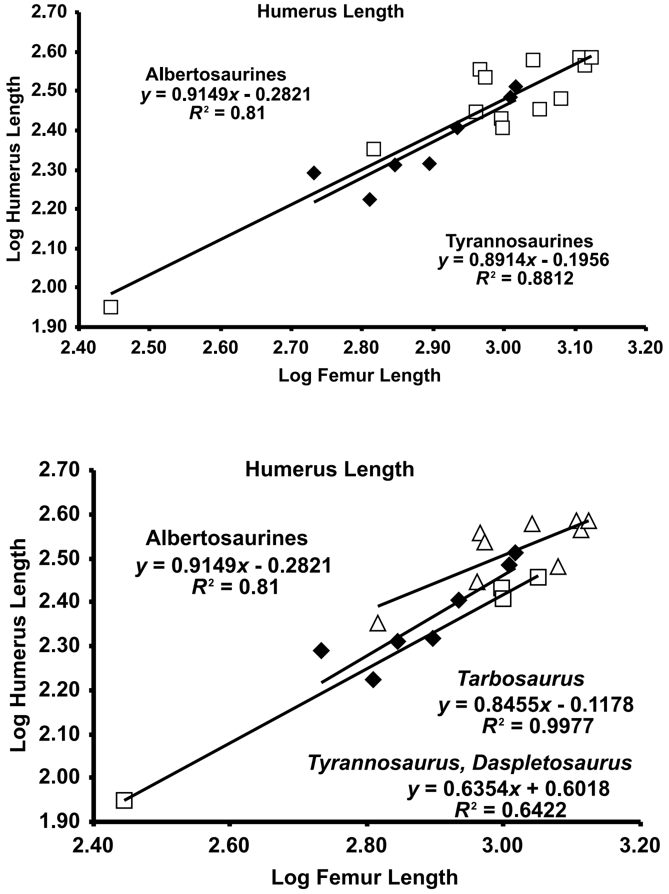


Fig. 8. Humerus length compared with femur length. In both graphs, diamonds represent albertosaurines. In the upper graph, open squares are tyrannosaurines. In lower graph, *Tarbosaurus* (open squares) has been separated from the other tyrannosaurines (open triangles).



Postcranial analysis

The length of the scapula increases with positive allometry, and there seems to be little difference between albertosaurines and tyrannosaurines (Table 3). Albertosaurine scapulae seem to be wider at their narrowest point of the shafts and at the distal ends than those of tyrannosaurines. Coracoid height is isometric, but length is positively allometric ($k > 1.6$) in at least tyrannosaurines.

The humerus is a highly variable bone amongst the Tyrannosauridae (Fig. 8), and much of this variability seems to be related to generic differences. These differences are generally not statistically significant because of the small number of humeri know for each genus, although the humerus of *Daspletosaurus* is significantly longer than that of *Tarbosaurus*. One albertosaurine specimen (*Albertosaurus sarcophagus*, TMP 86.64.1) has a relatively shorter humerus than any other tyrannosaurid, although all other specimens of this species had relatively longer humeri that were intermediate in size between *Daspletosaurus* and *Tarbosaurus*. The humerus of *Tyrannosaurus* seems to be closer to that of *Daspletosaurus* in length although the absence of knowledge of juvenile *Tyrannosaurus rex* humeri gives this animal a low correlation coefficient. In contrast with humeral length, the shaft width and distal widths are tightly correlated with femur length amongst the Tyrannosauridae (Table 3).

The ulna (including the olecranon) increases in length with negative allometry. When albertosaurines are compared with tyrannosaurines, the latter appear to have a shorter ulna (Fig. 9). At any particular size, ulnar length (Fig. 9) and proximal width are higher in albertosaurines than they are in tyrannosaurines, although there are no significant differences in either shaft or distal widths. As with the humerus, however, further division of the database shows that *Daspletosaurus* and *Tyrannosaurus* have ulnae that are as long as or longer than those of albertosaurines (Fig. 9), whereas the ulnae of *Tarbosaurus* are shorter.

The metacarpus (represented by the length of Metacarpal II) shows negative allometry with relation to size increase. When analyzed as a family, the tyrannosaurids have low correlation and determination coefficients (Table 3). The coefficients improve when the analysis is broken down to separate albertosaurines from tyrannosaurines. However, it improves considerably when *Tarbosaurus* is separated out from all other tyrannosaurids (Fig. 10). It appears that this genus has a metacarpus that is considerably shorter than the others, although the only specimen of *Daspletosaurus* (NMC 11315) that can be used in the comparison has a metacarpus that is almost as short. *Tyrannosaurus rex* seems to line up better with *Albertosaurus* and *Gorgosaurus* in terms of metacarpal length.

The manual phalanges correlate poorly amongst the tyrannosaurids, mostly because of the low number of known, measurable specimens. Nevertheless, there is a tendency for albertosaurines to scale higher than tyrannosaurines (Table 3), which suggests that their hands may be longer.

Ilium length is isometric. However, the length of the ilium is consistently longer (compared with the femur) in tyrannosaurines (Fig. 11). Ilium height above the pubic peduncle increases with positive allometry in tyrannosaurines, but is statistically isometric in albertosaurines. Pubic length shows slightly positive allometry, and the length of the pubic boot increases with stronger positive allometry. Ischial allometry is also positive, and the length tends to be higher in tyrannosaurines (Fig. 11).

Hind limb bones are relatively massive in tyrannosaurs, and therefore are more common as fossils. Proximal (mediolateral), shaft (transverse) and distal (mediolateral) widths all tend to be positively allometric, as does the circumference (Fig. 12). As tyrannosaurines are larger animals than albertosaurines, it is not surprising that all these measurements, which are related to the strength of the bones, are larger at any given size.

Tibial and fibular lengths show clear negative allometry in comparison with femur growth in the Tyrannosauridae (Table 3). Proximal (anteroposterior), shaft (transverse in the tibia, long axis of the cross-section of the fibula) and distal (mediolateral) widths all increase in size with positive allometry. As in the femora, the width measurements of the epipodials tend to be greater at any given size in tyrannosaurines than albertosaurines.

Fig. 9. Length of ulna compared with femur length. In both graphs, diamonds represent albertosaurines. In the upper graph, open squares are tyrannosaurine points. In lower graph, *Tarbosaurus* (open triangles) has been separated from the other tyrannosaurines (open squares).

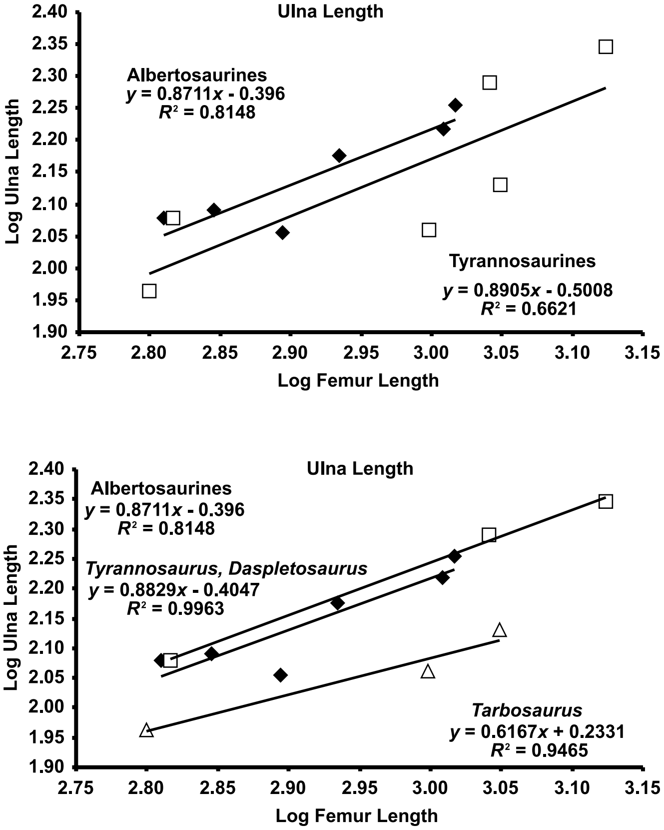
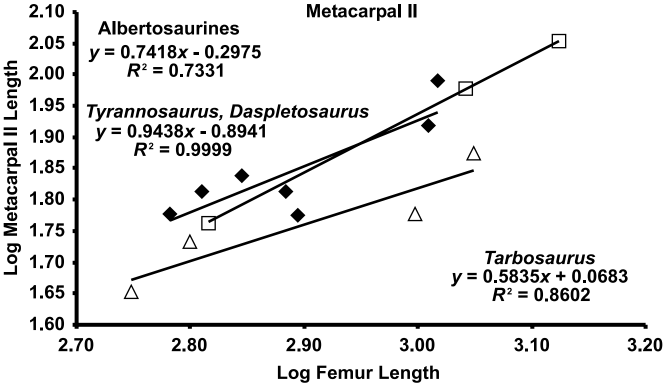


Fig. 10. Length of Metacarpal II compared with femur length. *Tarbosaurus* (open triangles) has been separated from *Daspletosaurus* and *Tyrannosaurus* (open squares). Diamonds represent *Albertosaurus* and *Gorgosaurus*.



Correlation coefficients of astragalar measurements are low, partially because of a relatively small number of specimens, but mostly because this bone is usually damaged in specimens. Both height and width increase with negative allometry. Calcaneum height, which can be equated with the size of the articulation with the metatarsus, increases with slight positive allometry in tyrannosaurids.

With the exception of the first metatarsal, which is isometric, the metatarsals all increase in size with negative allometry (the average coefficients of allometry for the second to fourth metatarsals are 0.57 for tyrannosaurids overall, 0.58

Fig. 11. Femur length compared with ilium length (upper graph) and ischium length (lower graph). Diamonds represent albertosaurines; open squares are tyrannosaurine points.

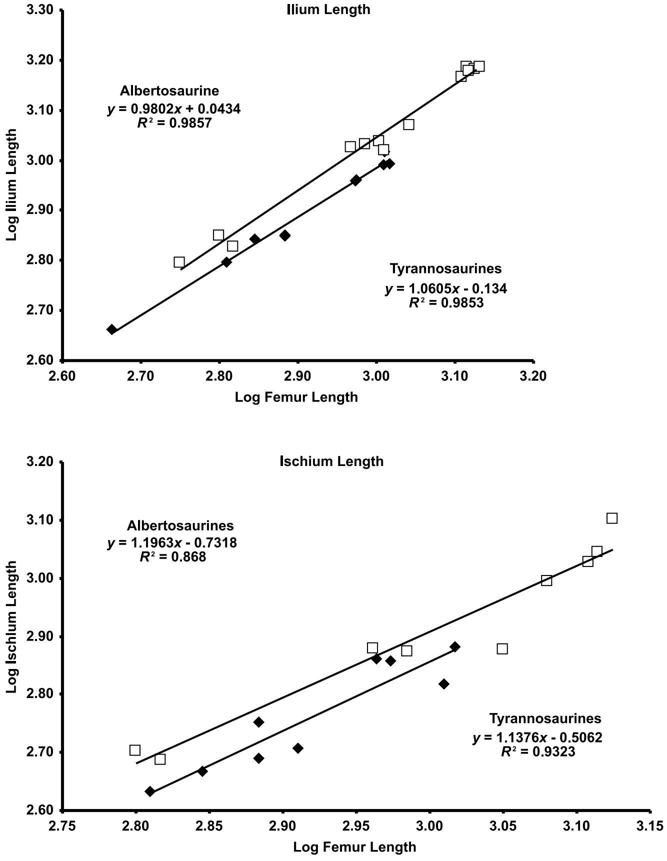
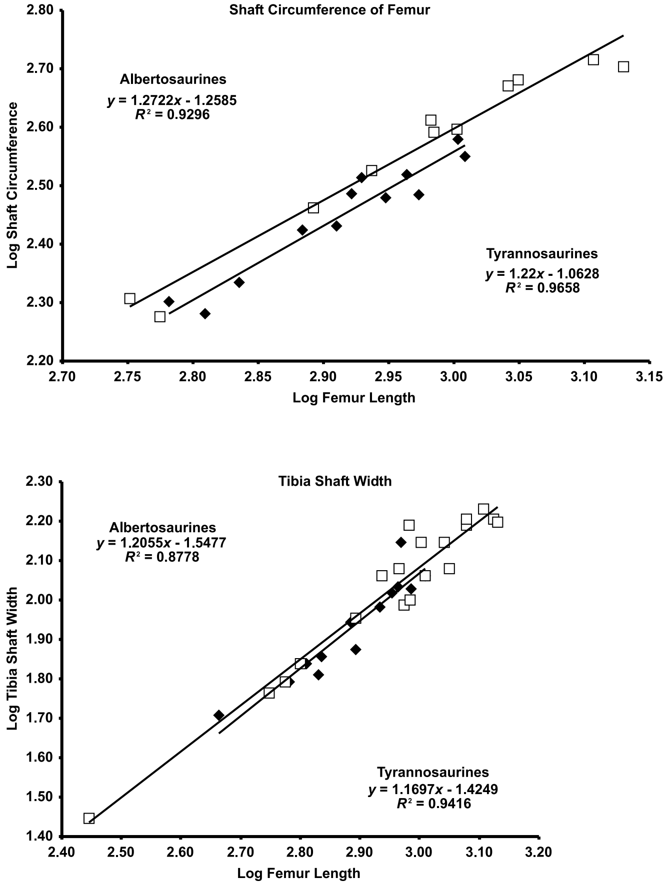


Fig. 12. Comparison of the shaft circumference of the femur (upper graph) and tibial shaft width (lower graph) with the length of the femur. Diamonds represent albertosaurines; open squares are tyrannosaurine points.



for albertosaurines, and 0.60 for tyrannosaurines). The fifth metatarsal also shows negative allometric growth, but it has a higher coefficient of allometry ($k = 0.84$) than the metatarsals that supported the body weight. Albertosaurines tend to have absolutely longer metatarsals and pedal phalanges than tyrannosaurines (Fig. 13) for any given body size. When separated at the generic level, it seems that both *Daspletosaurus* and *Tarbosaurus* have relatively shorter metatarsi than *Albertosaurus*, *Gorgosaurus*, and *Tyrannosaurus*. Pedal phalanges tend to increase their sizes with negative allometry, but not to the degree seen in the metatarsals.

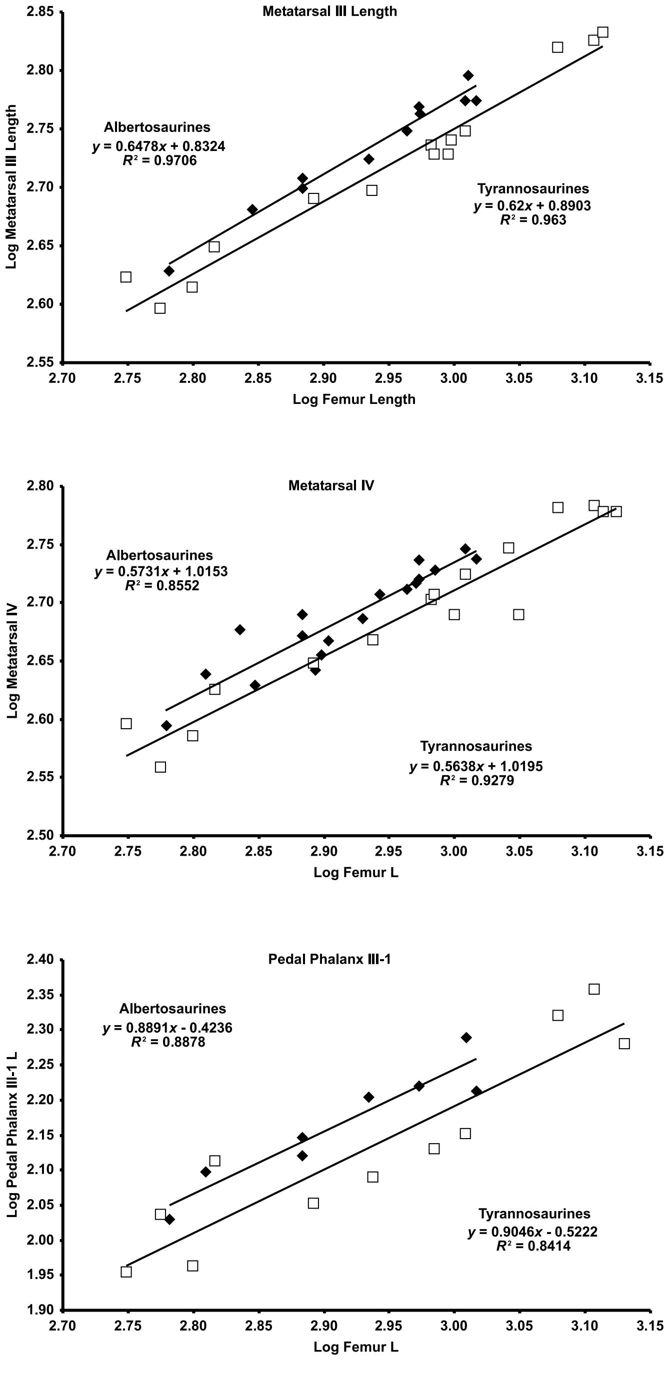
Discussion

The selection of femur as the standard of measurement seems to be appropriate for tyrannosaurids. If femur length had become shorter or longer in either albertosaurines or tyrannosaurines, one would expect to see the results skewed in one direction (i.e., albertosaurines would always align themselves on the same side of the trend lines for tyrannosaurines). The albertosaurine and tyrannosaurine points generally line up on the same trend line, or separate into two trend lines that do not always have the same relationship to each other. This suggests that femur length is a neutral unit of measurement that probably had a consistent relationship with total body weight in tyrannosaurids.

In tyrannosaurids, the length of the skull is isometric with femur length, and the two measurements are approximately the same in any individual. One can, therefore, easily estimate the length of a missing skull if femur length is known, and vice versa.

Tyrannosaurids are highly conservative in skeletal morphology and had body parts that functioned in the same manner. However, the albertosaurines used in this study are smaller than the tyrannosaurines, and one would expect them to be more lightly built because they did not have to carry as much weight. This manifests itself in at least the circumference and shaft width of the femur and tibia (Fig. 12; Table 3). The separation of the trend lines shows that allometry cannot be attributed strictly to growth because there is also a component related to the absolute size of the adult animals. In many of the size comparisons not connected directly with body support, albertosaurines and tyrannosaurines do not seem to be significantly different. Snout length (Fig. 3), frontal proportions (Fig. 4), mandibular length (Fig. 5), and dentary tooth row length (Fig. 6) are some examples of this category. For any given femur length, albertosaurines appear to have slightly shorter (Fig. 2), lower (Fig. 3) skulls, and shorter ilia and ischia (Fig. 11) than tyrannosaurines, but have longer metatarsals and pedal phalanges (Fig. 13). These differences also suggest that the dimensions of these bones have interspecific components related to the sizes of the animals

Fig. 13. Metatarsals III and IV, and Pedal Phalanx III–1 (upper, middle, and lower graphs, respectively) compared with femur length. Diamonds represent albertosaurines; open squares are tyrannosaurine points.



at maturity. Both individual and interspecific variation can be seen in the number of maxillary tooth positions (Fig. 7), but there is no evidence of any ontogenetic control. Finally, there are some characters that are specific to a genus or species. For example, the front limbs of *Tarbosaurus* at any given absolute size are shorter than the arms of the other tyrannosaurids examined (Figs. 8–10).

The findings of this analysis generally agree with what other authors have previously observed, with some notable exceptions. Paul (1988) remarked on the relative reduction of tooth size in an ontogenetic series of tyrannosaurids. In fact, the maximum heights of the largest maxillary teeth show positive allometry during growth. The reason that the teeth look smaller in larger individuals is because the height of the skull and the depth of the lower jaw show even greater positive allometry during growth.

Although Paul (1988) was correct is saying the snout length does not increase in more mature animals, he was in error when he speculated that snout height did not change during growth. Olshevsky (1995) stated that "*Jenghizkhan*" (PIN 551-1), treated here as *Tarbosaurus*, was different from *Tyrannosaurus* in having a relatively longer, more slender muzzle. Although the width was not covered in this study because of its high preservational variability, antorbital length increases isometrically (k = 1.00, R^2 = 0.98) with skull length. The snout of PIN 551-1 is not significantly different in dimensions from other tyrannosaurids. The long, low snout has also been used incorrectly as a character in the diagnosis of *Nanotyrannus* (Bakker et al. 1988).

The low, round orbit has frequently been used to characterize tyrannosaurids as distinct genera and (or) species (Bakker et al. 1988; Carpenter 1992; Olshevsky 1995), but this would be found in any juvenile tyrannosaurid.

Russell (1970) speculated that the number of tooth positions increased with maturity, whereas Carr (1999) suggested that the number might decrease with age. Statistically, there is no support for either hypothesis when maxillary tooth count is compared with maxillary tooth row length (Fig. 7) in *Albertosaurus* (k = 0.02, n (number of samples) = 5), *Daspletosaurus* (k = 0.01, n = 5), *Gorgosaurus* (k = 0.0002, n = 13), *Tarbosaurus* (k = 0.003, n = 13) or *Tyrannosaurus* (k = –0.008, n = 8). Although the number of tooth positions can vary somewhat in any tyrannosaurid species, there is no evidence to support this being an age or size dependent trait.

The maximum sizes of the maxillary teeth of all tyrannosaurids are controlled by the absolute size of the animal and a high coefficient of allometry (k = 1.31). However, in animals of equal size, *Tyrannosaurus* does not have larger teeth than *Daspletosaurus* (as proposed by Russell 1970) and neither does *Albertosaurus* (Paul 1988) or *Gorgosaurus* (Olshevsky 1995). Statistically, "aublysodontines" (= "shanshanosaurines") do not have teeth that are shorter (Olshevsky 1995) — they are exactly the size expected for juvenile tyrannosaurids.

"Aublysodontines" (= "shanshanosaurines") are supposedly distinguishable from tyrannosaurines on the basis of long, low, narrow skulls, and long, narrow frontals (Olshevsky 1995). As we have already seen, long, low skulls are expected in small tyrannosaurids. Skull width measurements were not analyzed here because distortion affects this dimension more than any other in most skulls. Regression analysis shows that long, narrow frontals are characteristic for small tyrannosaurids, but they became relatively short and wide at maturity. The elongate frontals of "*Stygivenator*" and "*Dinotyrannus*" (Olshevsky 1995) are statistically immature stages of the short broad frontals of *Tyrannosaurus*.

"*Maleevosaurus*" was in part separated from *Tarbosaurus* by its low, slender maxilla, long, low antorbital fenestra, large orbit and low dentary (Carpenter 1992). Olshevsky (1995) used the slenderness of the dentaries (presumably referring to the height) of "*Jenghizkhan*" as a character distinguishing it from *Tyrannosaurus*. Overall, the heights of the skulls and jaws of the holotypes of both "*Maleevosaurus*" and "*Jenghizkhan*" are almost directly on the trend lines for all tyrannosaurids, and the characters cited are not useful for diagnosing genera. As pointed out by Carr (1999), the same can be said about many of the characters used by Bakker et al. (1988) in diagnosing *Nanotyrannus*.

One of the characters used by Russell (1970) in his diagnosis of *Gorgosaurus libratus* is that the dentary tooth row is 71% the length of metatarsal IV. Although that may be true for two specimens (NMC 2120, USNM 12814), the allometric coefficients are different for these two elements, and the proportion is not valid for either larger or smaller specimens.

"*Stygivenator*" (LACM 28471) is diagnosed in part (Molnar 1978; Molnar and Carpenter 1989; Olshevsky 1995) by its relatively tall anterior maxillary and dentary teeth, with the height of the longest maxillary tooth exceeding the depth of the dentary. This cannot be used as a diagnostic character in tyrannosaurids because the dentaries are always lower than the longest teeth in small individuals (Currie and Dong 2001) because the teeth increase in size at a lower rate than dentary height.

Russell (1970) found that the humerus and forearm increased in size at the same rate as the femur. However, the wider suite of specimens indicates that only the humerus increases isometrically with the femur, whereas the forearm (radius and ulna) undergoes negative allometry. Concerning the front limbs, Paul (1988) was correct in assuming that *Tyrannosaurus rex* has relatively longer front limbs than *Gorgosaurus* and *Albertosaurus*. However, he considered both *Daspletosaurus* and *Tarbosaurus* as junior synonyms of *Tyrannosaurus*. The former has relatively long arms like *Tyrannosaurus rex*, but the latter has the shortest arms of any tyrannosaurid.

The coefficients in Table 3 can be used to calculate the approximate measurements (with confidence intervals) for missing bones in existing skeletons or even hypothetical animals of given size. Hatchling tyrannosaurs are not known at present. However, based on the largest known theropod eggs (*Macroelongatoolithus xixiaensis* Li et al. 1995), one can assume that a half-metre-long egg could hold an embryo up to 1.5 m in length. An embryo inside one of these eggs (Currie 1996) has a femur 57 mm long. Russell (1970) hypothesized a hatchling *Albertosaurus libratus* with a femur length of 100 mm, and calculated the sizes of different elements of the body. Recalculation and comparison (Table 4) produces similar results for some elements, but wildly different dimensions for others. For the hatchling to have a tibia more than twice as long as the femur is unlikely and unrealistic, although the true length probably does fall within the 95% confidence interval. The exercise shows there are limitations to what can be done in extrapolating this data.

Table 4. Estimated sizes of some bones of a hatchling tyrannosaur using power equations from Table 3.

Element	Length	Russell 1970
Skull	95	88
Presacral vertebral column	Not done	210
Sacrum	Not done	70
Tail, first 24 caudals	Not done	390
Scapulocoracoid	47	63
Humerus	43	26
Ulna	31	20
Manus	Not done	48
Metacarpal II	18	7
Ilium	70	100
Pubis	46	68
Ischium	32	54
Femur length	100	100
Femur circumference	14	28
Tibia-astragalus	224	140
Metatarsal III	273	85
Third digit, pes	59	56

Note: Generally, the more robust equations for the Tyrannosauridae were used unless there was a statistically significant difference between albertosaurines and tyrannosaurines. In those cases, the albertosaurine power equations were used preferentially. The column labeled "Russell 1970" gives the figures calculated from six specimens of *Gorgosaurus libratus*.

Conclusions

Tyrannosauridae is a rather conservative family of mostly Upper Cretaceous theropods from the Northern Hemisphere. In general, the allometric size changes that occurred in tyrannosaurid skeletons are similar in trends to those found in most other terrestrial vertebrates.

Two clades, termed here albertosaurines and tyrannosaurines, are well established by osteological differences. The former includes *Albertosaurus* and *Gorgosaurus*, whereas the latter is made up of *Daspletosaurus*, *Tarbosaurus*, *Tyrannosaurus*, and probably *Nanotyrannus* and *Alioramus*. However, other genera and species of tyrannosaurids have been established largely on the basis of proportional differences that on analysis turn out to reflect ontogenetic trends. *Maleevosaurus*, *Jenghizkhan*, and *Shanshanosaurus* are probably all junior synonyms of *Tarbosaurus*, whereas *Dinotyrannus*, *Stygivenator*, and possibly *Nanotyrannus* are ontogenetic stages of *Tyrannosaurus*.

Analysis of the allometric coefficients shows that in most cases allometric differences among mature specimens of different species are trivial when compared with the allometric differences associated with growth. This is not surprising considering tyrannosaurids increase in linear dimensions by more than 1000% during their lifetimes, whereas the largest mature tyrannosaurid is only 30% larger than the smallest. Nevertheless, albertosaurines tend to be more lightly built than tyrannosaurines in dimensions associated with weight bearing (such as the diameters of hind limb bones). The analysis also suggests that albertosaurines of the same absolute size as any tyrannosaurine had shorter, lower skulls, shorter ilia, longer tibiae, longer metatarsals and longer toes. The arms of albertosaurines and tyrannosaurines are the same relative size, with the exception of *Tarbosaurus*, which has shorter front limb elements. Tooth counts show some individual variation, but there is no evidence to suggest the number of teeth is controlled by the size and (or) age of the animal. In the case of *Nanotyrannus*, quantitative analysis cannot distinguish this genus from other tyrannosaurids, but tooth counts suggest that it is not a juvenile *Tyrannosaurus*.

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