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LONG BONE SCALING AND LIMB POSTURE IN NON-AVIAN THEROPODS: EVIDENCE FOR DIFFERENTIAL ALLOMETRY

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ABSTRACT—Long bone allometry has been analyzed in a large sample of non-avian theropod dinosaurs spanning almost the entire size range of known adult species. Theropod long bone allometry closely parallels the trends observed in extant mammals. Like mammals, large theropods scale with significantly lower regression slopes than do smaller species. As in extant mammals non-avian theropods are neither geometrically nor elastically similar. Large non-avian theropods tend to be elastically similar, whereas small species approach geometric similarity. As in extant mammals non-avian theropods appear to show a size dependent change in limb posture, aligning the individual long bones more steeply to vertical with increasing size, thus probably reducing the mass specific amount of force necessary to counteract moments about the joints. The main difference between non-avian theropods and mammals appears to be the retention of very long limbs among large non-avian theropod species, which, however, is not unparalleled among extant large mammals.

INTRODUCTION

If animals scaled anatomically in a geometric fashion their body masses would be proportional to the cubes of their linear dimensions, whereas bone cross sectional area would be proportional to the squares. This relationship was recognized centuries ago by Galileo (1638), and implies that skeletal stress could be expected to increase proportionally to $M^{0.33}$ (Biewener, 1990; Alexander and Pond, 1992), where M is body mass.

For most of this century most anatomists have assumed that animals scaled their structures of support allometrically, becoming progressively stouter as size increased, but until Thomas McMahon's influential papers (McMahon, 1973, 1975a, b) no actual theory of exactly what degree of allometry would be required in order to maintain skeletal stress at uniform levels had been formulated. Peak skeletal stress during locomotion has empirically been found to vary remarkably little in animals spanning four orders of magnitude in mass (e.g., Biewener, 1990), and is on the order of 40–100 megapascals (MPa), which is 25–50% of the yield strength of bones. Thus, it would appear that structures of support are constrained to maintain peak stresses at uniform levels.

Animals which scale limb bone lengths to $M^{0.25}$ and least circumferences or diameters to $M^{0.375}$, implying bone lengths proportional to (circumference or diameter) $^{0.67}$, would be subjected to equal degrees of physical distortion, or buckling, under gravity (McMahon, 1973, 1975a). McMahon termed the theory elastic similarity, as animals thus constructed would be elastically similar. Alexander (1977) found reasonable agreement with the theory from his study of bovids, but Alexander et al. (1979a) and Biewener (1983) found that phylogenetically wider samples of mammals scaled closer to geometric similarity. However, Bou et al. (1987) and Christiansen (1999a,b) found that when analyzing large data sets, mammals conform to neither elastic nor geometric similarity.

As pointed out by Maloiy et al. (1979) one potential flaw with the theory of elastic similarity is that it predicts skeletal optimization under the static influence of gravity. One could reasonably expect skeletal optimization to follow the peak forces experienced, and these occur during fast locomotion (e.g., Alexander, 1977; Alexander et al., 1979b; Alexander and Jayes, 1983; Biewener, 1983, 1989a, b, 1990; Biewener et al., 1983a, b, 1988; Maloiy et al., 1979).

Both elastic and geometric similarity are too simplistic to

explain the scaling of the long bones in extant terrestrial mammals, as many factors other than bone allometry contribute to maintaining peak skeletal stress at uniform levels. A very important factor is a size dependent change in limb posture, progressively aligning the long bones more steeply to vertical as species size increases. This increases the effective mechanical advantage of the muscles, drastically reducing the mass specific amount of muscular force necessary to counteract moments about the joints during locomotion (Biewener, 1983, 1989a, b, 1990; Bertram and Biewener, 1990). This pattern is also observed in extant birds (Biewener, 1989b; Gatesy and Biewener, 1991). Postural changes only apply to animals up to about 300 kilograms in body mass, however. Around this size limb postures have become so vertical that further postural changes would lead to essentially pillar-like limbs, unfit for fast progression, as this would imply that speed during fast locomotion would increase proportionally to the square root of effective limb length in progressively larger species.

Instead, progressively more pronounced skeletal allometry and a decrease in locomotor performance among the largest taxa maintains peak skeletal stress at uniform levels (Alexander et al., 1979b; Biewener, 1989a, b, 1990; Prothero and Sereno, 1982). Some researchers have also suggested that the duty factors (the fraction of a stride where a foot is on the ground) grow progressively larger as species size increases (Alexander et al., 1977), implying that peak stress during fast locomotion will be lower multiples of body mass in large animals, but the evidence is ambiguous (Biewener, 1983).

The above implies that long bone allometry could be expected to show differential scaling among small to medium sized and large animals, which is indeed the case (Economos, 1983; Bertram and Biewener, 1990; Christiansen, 1999a,b). Large animals scale with significantly lower regression coefficients than smaller animals, which are actually often rather close to being geometrically similar (Bertram and Biewener, 1990; Christiansen, 1999a,b). Elastic and geometric similarity are too simplistic to account for long bone scaling across a large size spectrum of extant terrestrial mammals, and even McMahon's (1975b) data, which supposedly supported the theory of elastic similarity, are ambiguous (Christiansen, 1999b).

Long bone scaling in running birds has been claimed to conform fairly well to the theory of elastic similarity (Maloiy et al., 1979) but the evidence is ambiguous, as a substantial number of regression coefficients calculated by these authors appear

different from the predicted values. Unfortunately Maloiy et al. (1979) did not statistically compare their samples to elastic or geometric similarity. More volent species conform closer to geometric similarity (Bennett, 1996) but they also diverge on a number of points.

The recognition of the inability of these two theories to satisfactorily explain the scaling of the long bones in extant terrestrial vertebrates is important, as they have previously been used to predict locomotory ability among extinct taxa. For example, Paul (1988) noted that the long bones of ornithomimid and tyrannosaurid theropods were elastically similar, and argued that this was evidence of mechanical potential for rapid locomotion in large theropods. However, elastic similarity refers to static deformation under gravity, not locomotion. Furthermore, Paul's regression coefficient ($\text{Circumference} = \text{Length}^{1.28}$) is in fact significantly different from the predicted value ($C = L^{1.50}$), but rather similar to regression coefficients calculated for large samples of extant mammals (Bertram and Biewener, 1990; Biewener, 1983; Bou et al., 1987; Christiansen, 1999b).

Bakker (1980) also used the theory of elastic similarity to conclude that most dinosaur limbs, with the exception of sauropods, were as resistant to mechanical failure as those of extant ungulates capable of fast locomotion with a suspended phase. However, mechanical strength cannot be assessed from bivariate plots involving such different animals as elephants, rhinos, sauropods and ceratopsids as in Bakker's sample (1980:figs. 28, 30). For example, the difference in the location of the center of gravity among the above animals makes the seemingly very sturdy hind limb bones of sauropods about as strong as those of extant elephants (Christiansen, 1997a). Second moments of area are also important. Secondary moments about the diaphyses are far more important than simple axial compression (Alexander, 1984, 1989, 1991; Alexander et al., 1979b; Alexander and Pond, 1992).

When comparing dinosaurs to extant animals scaling analyses are more appropriate in evaluating whether or not the two groups follow the same trends with respects to differential allometry. Along with assessments of limb strengths and empirical observations of locomotory potential and adaptations for maintaining the capability for fast locomotion at large sizes among extant mammals, studies of allometry in dinosaurs can be used as a comparison of the nature of skeletal adaptations at various body sizes.

This author concurs with Carrano (1997) that mammals, and especially ungulates and carnivores with largely parasagittal limb kinematics, constitute an anatomically superior extant analog for theropod locomotion to birds, both due to the great size diversity of mammals, but also due to their similar limb kinematics, notably a longer, more vertically oriented femur (e.g., Gatesy, 1990, 1991). Joint morphology in both non-avian and avian theropods, as well as the above mentioned mammals, are largely identical, implying that all non-avian theropods also employed largely parasagittal limb kinematics.

Non-avian theropod dinosaurs constitute a very important group for scaling analyses. Their postcranial anatomy was rather similar and apparently they were all terrestrial animals employing alternate striding during locomotion. This implies that ecological specializations such as saltatoriality, fossoriality or arboreality, which often have profound influence on appendicular morphology among extant mammals (e.g., Casinos et al., 1993; Bennett and Taylor, 1995), should be of little relevance. Their appendicular skeleton should be primarily adapted for support of mass and locomotory purposes. Furthermore, they spanned an estimated four orders of magnitude in mass, constituting a suitable sample for testing differential allometry.

To date Gatesy (1991) has made the only detailed analysis of long bone scaling in non-avian theropods. However, his main conclusions were directed towards demonstrating that from a

biomechanical perspective, the completely avian limb posture claimed by some authors to have been present in non-avian theropods also (e.g., Padian and Olsen, 1989) was unfounded both from a biomechanical (Gatesy, 1991) and a functionally anatomical perspective (Gatesy, 1990).

This paper presents an analysis of long bone scaling in non-avian theropods, in order to evaluate if they scale their long bones in a comparable fashion to mammals, and whether they differ statistically from elastic or geometric similarity. As differential scaling is present among extant mammals which maintain the potential for fast locomotion at large sizes, this suggests that differential scaling may also be present among non-avian theropods. This is obviously an important factor in evaluating theropod biomechanics.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; CM, Carnegie Museum of Natural History, Pittsburgh; CN, Zoological Museum, Copenhagen; FMNH, Field Museum of Natural History, Chicago; GI, Museum of the Geological Institute, Ulan Bator; HMN, Museum für Naturkunde, Berlin; MCZ, Museum of Comparative Zoology, Harvard; MOR, Museum of the Rockies, Bozeman; TMP, Royal Tyrrell Museum of Paleontology, Drumheller; UCMP, University of California Museum of Paleontology, Berkeley.

MATERIALS AND METHODS

Long bone scaling in theropods was analyzed using a sample of 53 specimens, representing at least 26 species and spanning almost the entire size range of known adult non-avian theropod species (Table 1). Additionally, four unidentified ornithomimid specimens, five unidentified tyrannosaurid specimens and four unidentified theropod specimens were included. No values were obtained from the literature. Length is given as the greatest length of the bone and circumference as the least circumference of the diaphysis, usually located at midshaft in femora, but often slightly more distally in tibiae and fibulae. Tibial length is including the astragalus. In most cases this bone is fused to the tibia, but in some cases it is not (e.g., *Dryptosaurus* ANSP 9995). In these cases the astragalus was either fitted to the tibia, or the astragalus was measured dorsoventrally at various places, and the average value was added to tibial length. Length measurements up to 585 mm were taken with callipers, above this value a measuring tape was used.

Least circumference was chosen as opposed to diaphysial diameter, the parameter usually employed in analyses of long bone scaling, as the femoral diaphysis is usually more circular than the tibial diaphysis, and large species tend to have long bones slightly more ellipsoid in cross section than smaller species, as in extant mammals. Furthermore, slight crushing, which may not be readily detectable without CAT scanning the bone (e.g., Farlow et al., 1995) will probably have less influence on circumference than diameter.

As differential scaling could be expected the sample was divided into three subsamples according to the predicted masses of the specimens included. Masses of certain species had been found by weighing scale models in air and water (mass values and methods in Christiansen, in press). Incomplete specimens were placed into one of the three subsamples based on their linear dimensions. Femoral length appears to constitute a good parameter for size evaluation as it is highly correlated with body mass among extant mammals (Biewener, 1983; Christiansen, 1999a).

Small theropods included species up to about 300 kilograms in body mass, as it is around this size that postural changes in mammals decrease and skeletal allometry increases. Large theropods included species heavier than this. Accordingly, the two *Gallimimus* specimens from Table 1, which had been averaged

TABLE 1. List of specimens used in the analysis. All measurements are in mm. Systematics follows Holtz (1994), Carpenter et al. (1997), Makovicky and Sues (1997), and Padian and Hutchinson (1997).

Taxon	Femur		Tibia		Fibula	
	L	C	L	C	L	C
CERATOSAURIA						
<i>Coelophysis bauri</i> AMNH 2704	207	47	—	—	—	—
<i>Dilophosaurus wetherilli</i> UCMP 37302	551	185	537	128	517	57
<i>Elaphrosaurus bambergi</i> HMN dd	519	165	608	132	—	—
ALLOSAUROIDEA						
<i>Allosaurus fragilis</i> TMP ?	874	293	747	265	620	97
<i>Allosaurus fragilis</i> AMNH 680	981	375	848	313	734	126
<i>Allosaurus fragilis</i> AMNH 6125	884	340	757	280	680	107
<i>Allosaurus fragilis</i> AMNH 324	908	331	701	277	783	128
<i>Allosaurus fragilis</i> AMNH 290	899	345	—	—	—	—
<i>Allosaurus fragilis</i> FMNH UC1505	848	255	—	—	—	—
<i>Allosaurus fragilis</i> FMNH P25114	872	338	—	—	—	—
<i>Allosaurus fragilis</i> AMNH 408	—	—	743	258	—	—
<i>Allosaurus fragilis</i> AMNH 287	—	—	—	—	670	111
<i>Allosaurus fragilis</i> AMNH 5750	—	—	—	—	596	117
<i>Sinraptor dongi</i> TMP 90.300.1	884	283	815	232	681	88
COELUROSAURIA INCERTAE SEDIS						
<i>Coelosaurus antiquus</i> AMNH 11039	—	—	393	98	—	—
<i>Dryptosaurus aquilunguis</i> ANSP 9995	787	270	830	258	—	—
<i>Ornitholestes hermanni</i> AMNH 587	210	64	165	41	162	24
ORNITHOMIMIDAE						
<i>Anserimimus planinychus</i> G.A.AN. 100/300	433	145	472	125	427	29
<i>Archaeornithomimus asiaticus</i> AMNH 21800	326	106	—	—	—	—
<i>Archaeornithomimus asiaticus</i> AMNH 6570	301	103	—	—	—	—
<i>Archaeornithomimus asiaticus</i> AMNH 21801	—	—	403	89	—	—
<i>Archaeornithomimus asiaticus</i> AMNH 6576	—	—	305	89	—	—
<i>Archaeornithomimus asiaticus</i> AMNH 6570	—	—	463	115	—	—
<i>Archaeornithomimus asiaticus</i> AMNH ?	—	—	428	104	—	—
<i>Archaeornithomimus asiaticus</i> AMNH ?	—	—	421	102	—	—
<i>Dromiceiomimus brevitertius</i> AMNH 5201	392	100	436	92	—	—
<i>Dromiceiomimus brevitertius</i> TMP ?	451	132	537	113	507	30
<i>Gallimimus bullatus</i> G.I.DPS 100/11	673	216	737	193	679	60
<i>Gallimimus bullatus</i> ¹	504	153	537	146	486	39
<i>Ornithomimus edmontonensis</i> TMP ?	443	107	498	97	431	28
<i>Ornithomimus edmontonensis</i> AMNH 5884	497	143	—	—	—	—
<i>Struthiomimus altus</i> AMNH 5339	486	127	—	—	526	40
<i>Struthiomimus altus</i> AMNH 5385	372	99	419	90	—	—
<i>Ornithomimidae</i> sp. TMP 91.36.854	371	112	—	—	—	—
<i>Ornithomimidae</i> sp. TMP 91.36.569	372	106	—	—	—	—
<i>Ornithomimidae</i> sp. TMP 92.36.964	—	—	—	—	480	29
<i>Ornithomimidae</i> sp. TMP 91.121.1	—	—	—	—	379	22
TROODONTIDAE						
<i>Saurornithoides</i> sp. TMP 90.30.06	85	23	105	19.5	—	—
TYRANNOSAURIDAE						
<i>Alectrosaurus olseni</i> AMNH 6554	661	215	748	201	—	—
<i>Albertosaurus</i> sp. AMNH 5218	901	313	—	—	—	—
<i>Albertosaurus</i> sp. TMP 94.12.608	—	—	—	—	547	33
<i>Albertosaurus</i> sp. TMP 91.463	—	—	—	—	511	55
<i>Gorgosaurus libratus</i> TMP 91.36.500	654	188	689	191	690	63
<i>Gorgosaurus libratus</i> TMP 81.10.01	893	287	957	251	796	94
<i>Gorgosaurus libratus</i> TMP ?	905	298	987	268	801	101
<i>Gorgosaurus libratus</i> TMP ?	781	241	821	222	792	105
<i>Gorgosaurus libratus</i> FMNH PR308	—	—	984	264	—	—
<i>Tyrannosaurus bataar</i> ¹	854	312	799	281	724	95
<i>Tyrannosaurus bataar</i> ¹	771	281	767	261	681	84
<i>Tyrannosaurus rex</i> TMP 81.12.1	1289	497	1173	435	982	147
<i>Tyrannosaurus rex</i> CM 9780 (AMNH 5027)	1273	540	1199	468	1163	154
<i>Tyrannosaurus torosus</i> AMNH 5438	1006	389	1022	347	—	—
<i>Tyrannosauridae</i> sp. TMP 90.300.30	599	198	—	—	—	—
<i>Tyrannosauridae</i> sp. TMP 82.13.30	1007	382	—	—	—	—
<i>Tyrannosauridae</i> sp. TMP ?	702	205	—	—	—	—
<i>Tyrannosauridae</i> sp. TMP ?	—	—	799	199	—	—
<i>Tyrannosauridae</i> sp. TMP 82.13.5	—	—	—	—	856	112
OVIRAPTOROSAURIA						
<i>Microvenator celer</i> AMNH 3041	123	35	155	33	—	—
<i>Oviraptor philoceratops</i> ¹	303	93	388	83	—	—

TABLE 1. (Continued)

Taxon	Femur		Tibia		Fibula	
	L	C	L	C	L	C
DROMAEOSAURIDAE						
<i>Deinonychus antirrhopus</i> MCZ 4371	336	110	—	—	—	—
<i>Saurornitholestes langstoni</i> TMP 88.121.39	214	63	283	63	—	—
<i>Saurornitholestes langstoni</i> MOR 666	—	—	256	54	225	13
INCERTAE SEDIS						
Theropoda sp. AMNH 5255	688	228	—	—	—	—
Theropoda sp. FMNH ?	656	254	—	—	—	—
Theropoda sp. TMP ?	178	47	—	—	—	—
Theropoda sp. TMP 86.18.25	365	104	—	—	—	—

¹Bones part of original skeletal mounts of a mongolian exhibit. Apart from holotypes of *Gallimimus bullatus* [G.I.DPS 100/11] and *Anserimimus planinychus* [G.I. AN.100/300] no specimen numbers were available.

prior to analysis in the sample comprising all species, were included in the small and large subsample, respectively, due to the great size of the holotype G.I. DPS 100/11 (estimated mass 490 kg, see Christiansen, in press). Finally, the largest species from the subsample of large species were separated to form a

subsample of their own. They were identified as specimens weighing over one ton in body mass. Incomplete specimens were again assigned to the sample if their linear dimensions were comparable to animals in which masses had been found, e.g., the tyrannosaurid femur TMP 82.13.30 (Table 1), which is 1,007 mm long, corresponding to the femur in an adult *Tyrannosaurus torosus*.

Species with multiple specimens were averaged prior to analysis in order not to introduce intraspecific allometry into the samples. Unfortunately this is often neglected in analyses of scaling (Labarbera, 1989). It was assumed that specimens which were not identified to species level (e.g., *Albertosaurus* sp., *Ornithomimidae* sp.) constituted separate species, although this is not certain. These were thus all included. The data were logarithmically transformed to normalize the distribution of the dependent variable and regression lines were fitted to the data using both Least Squares linear regression analysis (Model I) and Reduced Major Axis and Major Axis analyses (Model II), the latter probably the more appropriate methods when comparing samples where dependence cannot be assigned to either variable with confidence. The model is thus of the appearance

$$\ln(y) = \ln(a) + b\ln(x) + e \quad (1)$$

which is mathematically similar to the standard power function

$$Y = aX^b + e \quad (2)$$

which describes an allometric relationship. The value e is the sum of the error terms and is assumed to be normally distributed with a mean of zero.

Zar (1968) pointed out that this procedure could create problems as (1) and (2), while mathematically identical, may not be statistically equivalent, as minimizing the sum of squared residuals, as in Model I analysis, may not be equivalent to minimizing the sum of squared residuals on log transformed data. However, it appears that it does not create any problems when analyzing broad allometry (Manaster and Manaster, 1975; Smith, 1984; Labarbera, 1989).

Confidence limits (95% CI) were calculated for the regression coefficients or slopes (b). Confidence limits for the regression coefficients obtained by Major Axis analysis are computed differently from the Least Squares method, but for the Reduced Major Axis analysis the standard error of the slope may be approximated by the standard error of the Least Squares regression slope (Sokal and Rohlf, 1981). Thus, it can be used to assign confidence limits to the regression coefficients calculated by the former method also.

The various regression coefficients were compared to each other using the t distribution. They were also compared to the regression coefficients obtained from a large data set on extant mammals from Christiansen (1999b), both the sample comprising all mammals (189 species), and the two subsamples of small

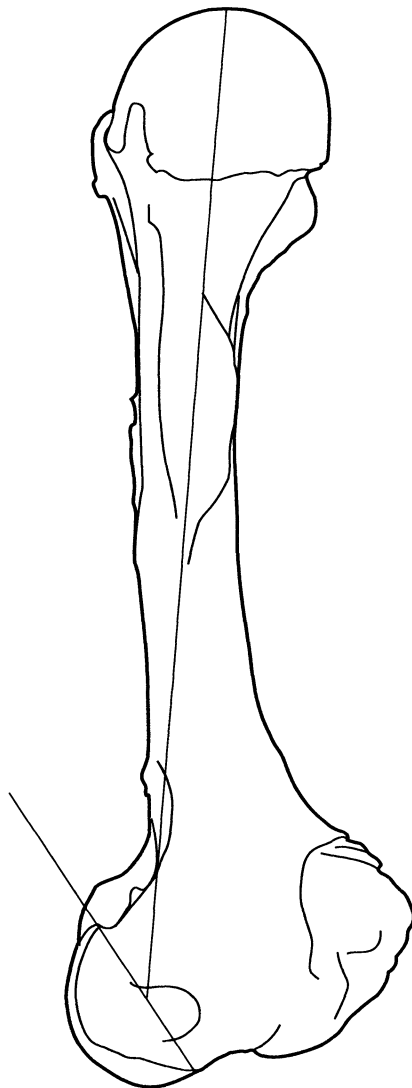


FIGURE 1. Femur of *Ceratotherium simum* bull CN 4324, illustrating the angulation of the distal femoral epiphysis to the long axis of the bone.

TABLE 2. Body mass, femoral length and calculated femoral distal epiphysial angulation to center of femoral caput in mammals and theropod dinosaurs. Theropod systematics follows Holtz (1994), Novas (1997), and Padian and Hutchinson (1997).

Taxon	Body mass	Femoral length	Angle
THEROPODA			
HERRERASAUROIDAE			
<i>Herrerasaurus ischigualastensis</i>	145 kg	345 mm	32°
CERATOSAURIA			
<i>Elaphrosaurus bambergi</i>	245 kg	519 mm	36°
<i>Carnotaurus sastrei</i>	2070 kg	1030 mm	38°
ALLOSAUROIDEA			
<i>Allosaurus fragilis</i>	1620 kg	884 mm	39.5°
<i>Sinraptor dongi</i>	1700 kg	884 mm	38°
ORNITHOMIMIDAE			
<i>Archaeornithomimus asiaticus</i>	—	326 mm	30°
<i>Gallimimus bullatus</i>	38 kg	270 mm	30°
TYRANNOSAURIDAE			
<i>Gorgosaurus libratus</i>	1815 kg	905 mm	39°
<i>Tyrannosaurus rex</i>	6250 kg	1273 mm	42°
DROMAEOSAURIDAE			
<i>Deinonychus antirrhopus</i>	73 kg	336 mm	26.5°
THEROPODA INCERTAE SEDIS			
<i>Avimimus portentosus</i>	14 kg	205 mm	27.5°
MAMMALIA			
ARTIODACTYLA			
<i>Alces alces</i>	410 kg	448 mm	23.5°
<i>Antidorcas marsupialis</i>	21.2 kg	183 mm	20.5°
<i>Bos taurus</i>	225 kg	305 mm	29°
<i>Bubalus bubalis</i>	382 kg	371 mm	23°
<i>Camelus dromedarius</i>	495 kg	541 mm	31°
<i>Capra ibex</i>	36 kg	192 mm	22°
<i>Cephalophus maxwelli</i>	7.8 kg	118 mm	21°
<i>Cervus nippon</i>	35.6 kg	221 mm	19°
<i>Cervus timorensis</i>	37 kg	255 mm	23°
<i>Choeropsis liberiensis</i>	250 kg	269 mm	24.5°
<i>Connochaetes gnou</i>	139 kg	267 mm	22°
<i>Dama dama</i>	45 kg	229 mm	22°
<i>Damaliscus dorcas</i>	43.5 kg	210 mm	20°
<i>Elaphurus davidianus</i>	194 kg	327 mm	21.5°
<i>Gazella dorcas</i>	19 kg	150 mm	17°
<i>Gazella granti</i>	34 kg	232 mm	16°
<i>Hemitragus jemlahicus</i>	43 kg	233 mm	26°
<i>Hippopotamus amphibius</i>	2400 kg	458 mm	30.5°
<i>Muntiacus muntjak</i>	34 kg	180 mm	20°
<i>Okapia johnstoni</i>	260 kg	368 mm	22°
<i>Oreamnos americanus</i>	120 kg	269 mm	19°
<i>Ovis dalli</i>	99 kg	261 mm	21°
<i>Phacochoerus aethiopicus</i>	88 kg	216 mm	18°
<i>Potamochoerus porcus</i>	76 kg	218 mm	29°
<i>Rangifer tarandus</i>	160 kg	289 mm	25.5°
<i>Rupicapra pyrenaica</i>	26.2 kg	205 mm	22°
<i>Saiga tartarica</i>	26.2 kg	185 mm	23.5°
<i>Sylvicapra grimmia</i>	13.7 kg	149 mm	21°
<i>Synerus caffer</i>	440 kg	396 mm	28°
<i>Tragelaphus spekei</i>	29.5 kg	214 mm	23.5°
<i>Tragelaphus strepsiceros</i>	190 kg	402 mm	21°
CARNIVORA			
<i>Ailurus fulgens</i>	4.4 kg	110 mm	22°
<i>Alopex lagopus</i>	4.5 kg	103 mm	15.5°
<i>Canis familiaris</i>	29 kg	205 mm	26.5°
<i>Canis lupus</i>	35 kg	225 mm	24°
<i>Felis concolor</i>	47 kg	274 mm	26°
<i>Felis pardalis</i>	13.9 kg	164 mm	22°
<i>Gulo gulo</i>	12 kg	133.5 mm	28.5°
<i>Hyaena hyaena</i>	32 kg	221 mm	21°
<i>Lycalopex vetulus</i>	4.2 kg	108 mm	19°
<i>Meles meles</i>	10 kg	116 mm	28°
<i>Nasua nasua</i>	3.4 kg	99 mm	22°
<i>Panthera leo</i>	170 kg	401 mm	21°
<i>Panthera onca</i>	67.4 kg	258 mm	21.5°
<i>Panthera pardus</i>	51 kg	233 mm	23.5°
<i>Panthera tigris</i>	145 kg	384 mm	27.5°
<i>Panthera uncia</i>	34.8 kg	225 mm	23.5°
<i>Ursus middendorffi</i>	496 kg	505 mm	37°

TABLE 2. (Continued)

Taxon	Body mass	Femoral length	Angle
HYRACOIDEA			
<i>Procavia capensis</i>	2.8 kg	73 mm	19°
PERISSODACTYLA			
<i>Ceratotherium simum</i>	1900 kg	548 mm	33.5°
<i>Diceros bicornis</i>	875 kg	470 mm	37°
<i>Equus burchelli</i>	136 kg	337 mm	21°
<i>Tapirus indicus</i>	317 kg	342 mm	24°
<i>Tapirus terrestris</i>	173 kg	322 mm	19.5°
PROBOSCIDEA			
<i>Elephas maximus</i>	3534 kg	996 mm	50.5°
<i>Loxodonta africana</i>	6250 kg	1172 mm	50°

(107 species) and large mammals (70 species), respectively. Finally, the regression coefficients were tested for significance against the theoretical slopes for elastic and geometric similarity, respectively.

A size dependent change in limb posture in mammals is a major contributing factor to maintaining peak stress in the long bones at uniform levels. Hence, it might be expected that non-avian theropod dinosaurs would follow this pattern also, evolving limb postures with individual long bones progressively more steeply inclined to vertical as linear dimensions increased. Apart from suggestions of Christiansen (1997b), based only on preliminary analyses, that this indeed appears to be the case, it has not previously been analyzed for theropod dinosaurs or compared to extant mammals.

Obviously it is not possible to compare actual limb posture in non-avian theropods to mammals, implying that the changes in limb posture discussed by Biewener (1983, 1989a, b, 1990) are not directly comparable. Hence, it was decided to give a measure of the angulation of the distal femoral epiphysis compared to the centre of the caput in medial view (Fig. 1). This would allow a more direct comparison with extant animals. The method is briefly discussed and figured in Paul and Chase (1989), in this case as a means of restoring limb posture in extinct tetrapods, and not as a quantifiable model.

Pictures were taken in direct medial view of the femora of nine species of theropods, where body masses had been found

by Christiansen (in press) for seven of these by weighing in air and water as noted above (Table 2). Masses of *Herrerasaurus*, *Deinonychus* and *Avimimus*, however, were not calculated by the author but were taken from Paul (1988). Additionally, drawn illustrations from Bonaparte et al. (1990) and Kurzanov (1987) were used instead of pictures for the femora of *Carnotaurus* and *Avimimus*, respectively, as these taxa were not examined. Hence, these values must be regarded as tentative. It was decided to include *Carnotaurus* as it is an almost complete and aberrant species and thus important. Body mass for *Carnotaurus* was taken from Paul (1997). *Avimimus* is small and usually depicted as distinctly avian in many respects (e.g., Kurzanov, 1982, 1985; Norman, 1985; Paul, 1988), but lately there have been suggestions that the material may represent different taxa (Holtz, 1996a,b; Hutchinson and Padian, 1997). The angulation values calculated from these illustrations fitted well with values obtained from the other theropods of comparable linear dimensions.

As any distortion of the bone would affect the angle of the distal epiphysis compared to the femoral caput, the included species had been examined for this, and any distortion was judged to be minor. However, this is often difficult to assess without sectioning the bones or employing CAT scanning. Farlow et al. (1995) assumed that the femoral diaphysis of *Tyrannosaurus rex* MOR 555 was circular in cross section in the living animal. As it is now the femoral diaphysis is slightly ellipsoid, as is the femur of TMP 81.12.1, used in this analysis.

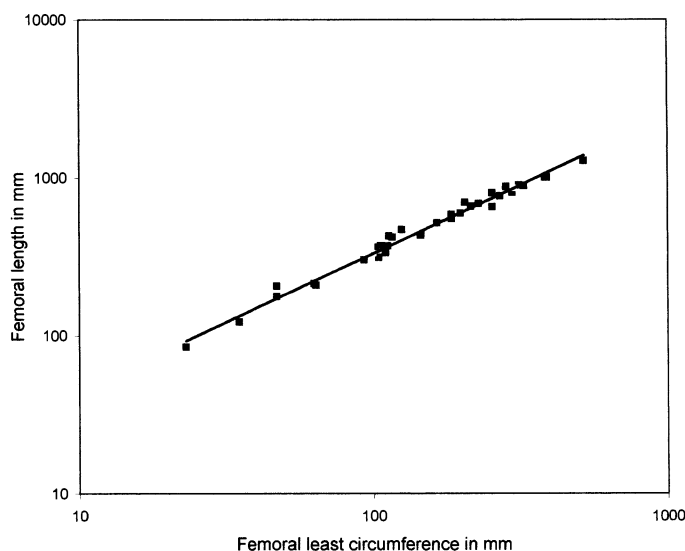


FIGURE 2. Femoral scaling in non-avian theropods ($n = 33$). Regression line fitted to the data by means of Reduced Major Axis analysis.

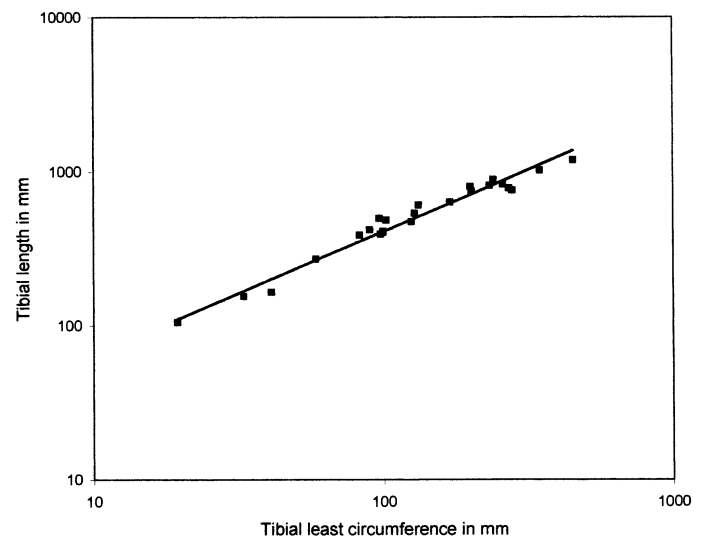


FIGURE 3. Tibial scaling in non-avian theropods ($n = 23$). Regression line fitted to the data by means of Reduced Major Axis analysis.

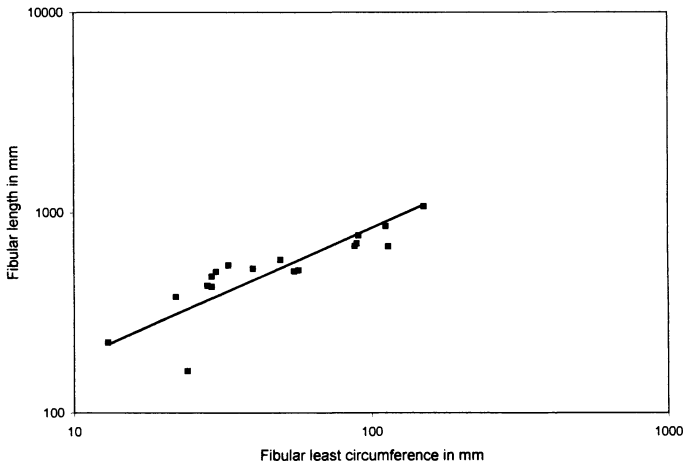


FIGURE 4. Fibular scaling in non-avian theropods (n = 18). Regression line fitted to the data by means of Reduced Major Axis analysis.

MOR 555 is seemingly well preserved but CAT scanning revealed slight crushing not readily detectable from surface examination (Farlow et al., 1995). Thus, the morphology of even well preserved bones could be slightly different from the original morphology.

The values calculated for theropod dinosaurs were compared to a data sample of 54 species of extant mammals (Table 2). Apart from one species of hyrax only species from the orders Carnivora, Artiodactyla and Perissodactyla were included, due to the parasagittal nature of their limb kinematics, making them comparable to dinosaurs, and the flexed nature of the limbs of even the largest bovinds and rhinos. Additionally, two adult elephants were included, a 3,534 kg female *Elephas maximus* and a 6,250 kg male *Loxodonta africana*. All mammal species are housed at the Zoological Museum in Copenhagen, and all had been weighed just after death.

It must be emphasized, however, that the calculated angle is not a measure of the true knee flexion in the living animal, as hip morphology and the angulation and morphology of the femorotibial, tibiotarsal and tarsometatarsal joints also contribute to limb posture. The exact anterior and posterior limits of the distal femoral condyles are also sometimes difficult to assess with accuracy, especially in theropods, which undoubtedly accounts for some of the variation observed in Table 2 in seemingly similar sized animals. Additionally, parasagittal animals usually support mass on the anterior part of the femoral distal

condylar surface when standing in a relaxed posture, and only during pronounced epipodial flexion does the proximal epipodial epiphysis move far posteriorly on the distal femoral epiphysis. This indicates that the true flexion at the knee joint in theropods was substantially less than the calculated values would suggest, as it is in the mammals. For example, the values calculated for the elephants are 50°, but the actual angle between the propodial and epipodial bones when standing upright is usually less than 10°.

The calculated angulation values were compared to both femoral length and body mass, respectively. The values were logarithmically transformed and regression lines were fitted to the transformed data using Least Squares and Reduced Major Axis analyses. Confidence limits (95% CI) were calculated for the regression coefficients. Additionally, polynomial regression lines were also fitted to the data to examine for signs of curvilinearity. The t distribution was again used to compare the regression coefficients to each other.

RESULTS

The regression figures for theropods are shown in Figures 2–4. The regression coefficients calculated for femora for all theropods (Table 3) are somewhat higher than the values calculated by Paul (1988) and Gatesy (1991). Only the regression coefficient calculated by RMA analysis for large theropods is comparable to the results obtained by the above two authors; the rest are either higher, i.e., closer to geometric similarity (all theropods, small theropods) or lower, i.e., closer to elastic similarity (large theropods, giant theropods). Unfortunately, neither Paul (1988) nor Gatesy (1991) calculated regression equations for the epipodial bones.

As in extant mammals femoral length is highly correlated with least circumference. However, even a correlation coefficient in excess of 0.99, as in this case (Table 3), should not a priori be taken as evidence that a linear regression model is able to extract all information from the data (Christiansen, 1999b). The residual scatter may not be random. It does, however, support the above claim about the uniformity of non-avian theropod appendicular anatomy. The tibial sample also has a very high correlation coefficient, which is actually higher than that of mammals (Christiansen, 1999b). The regression line is able to explain 96.6% of the variation in the tibial data in theropods, whereas the corresponding value for mammals is 90.2% (Christiansen, 1999b).

The fibula, however, shows substantially greater scatter about the regression line, as shown by the rather low correlation coefficient of 0.85 (Table 3). *Allosaurus* and particularly *Ornitholestes* constitute outliers (Fig. 4). When omitting these two spe-

TABLE 3. Regression equations for all theropods and subgroups. CI are 95% confidence limits for the regression coefficients. In all cases X is least circumference of diaphysis and Y is greatest length of bone. The sample consisting of fibulae from small theropods excludes *Ornitholestes*, as it constitutes a marked outlier.

Group	n	Least squares		Reduced major axis		Major axis		r
		a	b ± 95% CI	a	b ± 95% CI	a	b ± 95% CI	
All Theropods (Femur)	33	6.3832	0.8598 ± 0.0396	6.1727	0.8665 ± 0.0396	6.2025	0.8655 + 0.0406/−0.0390	0.9923
All Theropods (Tibia)	23	10.939	0.7879 ± 0.0671	10.238	0.8016 ± 0.0671	10.385	0.7987 + 0.0703/−0.0658	0.9829
All Theropods (Fibula)	18	59.421	0.5597 ± 0.1802	41.183	0.6548 ± 0.1802	48.489	0.6125 + 0.2185/−0.1829	0.8547
Small Theropods (Femur)	19	5.3203	0.9015 ± 0.0786	5.0184	0.9146 ± 0.0786	5.0449	0.9134 + 0.0830/−0.0767	0.9858
Small Theropods (Tibia)	14	6.8153	0.9007 ± 0.1029	6.3913	0.9155 ± 0.1029	6.4262	0.9141 + 0.1103/−0.0994	0.9839
Small Theropods (Fibula)	9	61.135	0.5754 ± 0.2564	48.625	0.6429 ± 0.2564	53.881	0.6126 + 0.3179/−0.2477	0.8950
Large Theropods (Femur)	15	13.401	0.7274 ± 0.1258	11.391	0.7562 ± 0.1258	11.920	0.7482 + 0.1358/−0.1201	0.9621
Large Theropods (Tibia)	10	53.331	0.4980 ± 0.2282	35.441	0.5714 ± 0.2282	44.352	0.5310 + 0.2762/−0.2248	0.8716
Large Theropods (Fibula)	9	119.35	0.4046 ± 0.2363	84.451	0.4833 ± 0.2363	106.66	0.4301 + 0.2835/−0.2351	0.8371
Giant Theropods (Femur)	8	22.381	0.6421 ± 0.1684	19.728	0.6638 ± 0.1684	20.747	0.6651 + 0.1880/−0.1604	0.9672
Giant Theropods (Tibia)	7	53.281	0.4986 ± 0.3813	30.291	0.5989 ± 0.3813	40.830	0.5458 + 0.5411/−0.3719	0.8325
Giant Theropods (Fibula)	8	109.30	0.4221 ± 0.2628	78.292	0.4974 ± 0.2628	97.368	0.4482 + 0.3214/−0.2592	0.8485

TABLE 4. Statistical comparison of the regression coefficients calculated by Reduced Major Axis analysis for mammals and theropods, including subgroups. Significance level for rejection of the null hypothesis is 0.05. Regression statistics for theropods and subgroups from Table 3. The t value has $n_1 + n_2 - 2$ degrees of freedom.

	All theropods	Small theropods	Large theropods	Giant theropods	<i>Struthio</i>	All mammals	Small mammals
Femur							
All theropods	0.30 > p > 0.20	0.05 > p > 0.01	0.40 > p > 0.30	0.70 > p > 0.60	0.01 > p > 0.001	—	—
Small theropods	0.10 > p > 0.05	0.01 > p > 0.001	0.20 > p > 0.10	0.01 > p > 0.001	0.05 > p > 0.01	—	—
Large theropods	0.01 > p > 0.001	0.01 > p > 0.10	0.10 > p > 0.05	0.10 > p > 0.05	—	—	—
<i>Struthio</i>	0.01 > p > 0.001	0.05 > p > 0.01	0.20 > p > 0.10	0.01 > p > 0.001	—	—	—
All mammals	p > 0.90	0.05 > p > 0.01	0.10 > p > 0.05	0.10 > p > 0.05	—	—	—
Small mammals	p < 0.001	0.05 > p > 0.01	0.10 > p > 0.05	0.10 > p > 0.05	—	—	—
Large mammals	0.30 > p > 0.20	0.10 > p > 0.05	0.50 > p > 0.40	0.10 > p > 0.05	—	0.30 > p > 0.20	p < 0.001
Tibia							
All theropods	0.10 > p > 0.05	0.01 > p > 0.001	0.90 > p > 0.80	0.50 > p > 0.40	0.40 > p > 0.30	—	—
Small theropods	0.05 > p > 0.01	0.05 > p > 0.01	0.30 > p > 0.20	0.20 > p > 0.10	0.01 > p > 0.001	—	—
Large theropods	0.20 > p > 0.10	0.05 > p > 0.01	0.05 > p > 0.01	0.01 > p > 0.001	—	—	—
<i>Struthio</i>	0.40 > p > 0.30	0.05 > p > 0.01	0.05 > p > 0.01	0.60 > p > 0.50	0.70 > p > 0.60	—	—
All mammals	p > 0.90	0.05 > p > 0.01	0.40 > p > 0.30	0.01 > p > 0.001	—	—	—
Small mammals	p < 0.001	0.05 > p > 0.01	0.40 > p > 0.30	0.01 > p > 0.001	—	—	—
Large mammals	0.10 > p > 0.05	0.01 > p > 0.001	0.40 > p > 0.30	0.60 > p > 0.50	—	—	p < 0.001
Fibula							
All theropods	p > 0.90	0.30 > p > 0.20	—	—	—	—	—
Small theropods	0.30 > p > 0.20	0.40 > p > 0.30	—	—	—	—	—
Large theropods	0.30 > p > 0.20	—	—	—	—	—	—
Giant theropods	—	—	—	—	—	—	—

cies the regression equation ($n = 16$) calculated by Reduced Major Axis analysis

$$Y = 68.329X^{0.5395 \pm 0.0979} \quad (3)$$

has a substantially higher correlation coefficient ($r = 0.9486$). None of the regression equations for all theropods calculated by Model I or Model II analyses appear to conform to either elastic or geometric similarity. The only possible exception is the regression coefficient calculated by RMA analysis for fibula, which appears rather similar to the coefficient of 0.67. The low correlation coefficient of this sample makes the regression equations calculated by Model I and Model II analyses quite different.

Examination of the residuals revealed a trend towards curvilinearity in the tibial sample (Fig. 5b), which also appears discernible in the femoral sample (Fig. 5a), although only weakly so. This is consistent with the pattern found in mammals (Bertram and Biewener, 1990; Christiansen, 1999b). The fibular sample (Fig. 5c) seems to show progressively slightly decreasing residuals, implying that the assumption of constant variance has not been met. The trend, however, is slight, and failure to meet the above assumption could not be verified analytically. The most obvious feature of Figure 5c is the great deviation of *Ornitholestes*.

Small theropods consistently scale their long bones with substantially higher regression coefficients than large theropods (Figs. 6–8, Table 3). Especially the regression coefficients for tibiae differ markedly. However, the correlation coefficient for tibia in large theropods is low and the residual variance rather high ($S^2 = 6.2736 \times 10^{-3}$), implying that there is substantial unexplained residual scatter about the regression line. The regression line for large theropods is able to explain only 76% of the observed variation in tibial proportions. The fibula again shows the poorest degree of correlation in both large and small theropods (Table 3). The largest theropods (above 1 ton in body mass) scale with even lower regression coefficients than large theropods (Table 3). Only the regression equation for the femur can be considered reliable in this respect, however, as both tibia and fibula show rather poor correlation coefficients. The overall trend is clear, however. Progressively larger theropods display progressively greater degrees of appendicular skeletal allometry, like mammals.

For comparison, intraspecific regression equations were also computed for 12 adult specimens of *Struthio camelus*. Due to the great reduction of the fibular diaphysis in avian theropods no regression equation was calculated for this bone. The regression equations calculated by RMA analysis are

Femur ($n = 12$; $r = 0.9235$)

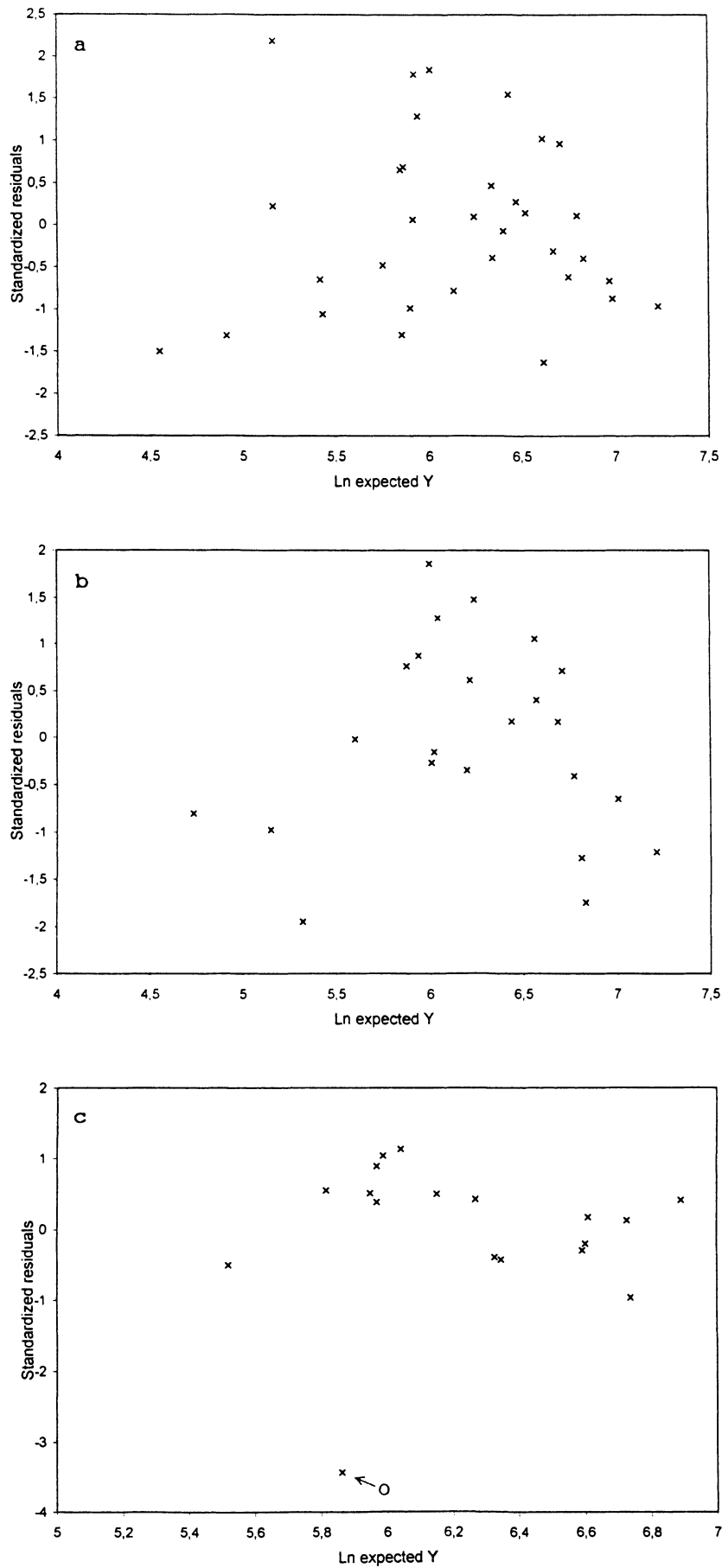
$$Y = 14.563X^{0.6180 \pm 0.1669} \quad (4)$$

Tibia ($n = 12$; $r = 0.9472$)

$$Y = 19.033X^{0.7323 \pm 0.1659} \quad (5)$$

As can be seen from the confidence limits (95% CI) the slope variances of the two samples are nearly identical (5.6091×10^{-3} , and 5.5418×10^{-3} for femur and tibia, respectively). The regression coefficients are rather similar to those of large theropods (Table 3), and especially the femoral coefficient is low, and actually lower than the coefficient calculated by Gatesy (1991) for a larger interspecific sample of birds.

In Table 4 the regression coefficients obtained from RMA analysis for theropods and subgroups (Table 3) and *Struthio* (equations [4] and [5]) are compared to extant mammals and subgroups (regression statistics from Christiansen, 1999b). Overall, non-avian theropods, including subgroups, follow much the same pattern as mammals. The regression coefficients for all mammals for femur ($L = C^{0.8636 \pm 0.0267}$) and tibia ($L =$



$C^{0.8044 \pm 0.0361}$) are very similar to the corresponding values for all theropods (Table 3) and significance cannot even be assumed at the 90% level (Table 4).

The femur in all theropods is significantly different from giant theropods, *Struthio* and small mammals ($L = C^{1.0132 \pm 0.0584}$). The last value is actually in accordance with geometric similarity (Christiansen, 1999b). Initially it may seem surprising that all theropods are not statistically different at the 5% level from large theropods (Table 4), as the regression coefficients calculated by RMA analysis appear rather different from each other (Table 3). This is due to the higher residual variance of the sample of large theropods. The regression coefficients obtained from Least Squares analysis are significantly different from each other, however. The femur in large mammals may appear to scale with a lower regression coefficient ($L = C^{0.8103 \pm 0.0805}$) than all theropods (Table 3), but the values do not differ enough to allow rejection at the 5% level. Both samples have low residual variances.

The femur in small theropods is significantly different from all other samples save large mammals, even small mammals. This may seem surprising, but the sample of small mammals consisted only of species less than 50 kilograms in body mass (Christiansen, 1999b), whereas larger theropods were allowed into the sample of small theropods. As noted above the femur in small mammals scales with an isometric regression coefficient, and the low residual variance of both samples makes a rejection of the null hypothesis easier, even in the case of regression coefficients not differing too much. However, the sample of large mammals has a higher residual variance ($S^2 = 0.0148951$).

The tibia follows much the same pattern, but the regression coefficients of giant theropods (Table 3) and large mammals ($L = C^{0.6844 \pm 0.1049}$) appear much lower than the corresponding value for all theropods. Unlike the tibial sample for all theropods, both of these samples, however, have low correlation coefficients and high residual variances ($S^2 = 9.9434 \times 10^{-3}$ and $S^2 = 0.0248409$ for theropods and mammals, respectively), making a rejection of the null hypothesis more difficult. This is also the case for the fibula in all theropod samples.

The tibia in small theropods differs from all other samples, having a higher regression coefficient than large theropods, giant theropods, *Struthio*, all mammals and large mammals, but lower than in small mammals ($L = C^{1.0413 \pm 0.0627}$). The last value is geometrically similar (Christiansen, 1999b). Large theropods scale with regression coefficients not significantly different from *Struthio* and large mammals (Table 4). The t value for the femur in large theropods and all mammals is not high enough and the difference between the two regression coefficients calculated by RMA analysis not great enough to allow rejection of the null hypothesis at the 5% level. The corresponding values calculated by Least Squares regression were significantly different, however ($t_{202} = 1.9685$; $0.05 > P > 0.02$).

Overall, the samples and subsamples of mammals and non-avian theropods follow each other rather closely. Skeletal allometry becomes progressively more pronounced as species size increases. In theropods the really large species appear to scale with the lowest regression coefficients, as is the case in the really large mammals capable of rapid locomotion with a suspended phase, in this case the ceratomorphs (Prothero and Sereno, 1982).

Like mammals (Christiansen, 1999b), all theropods scale with regression coefficients significantly different from either

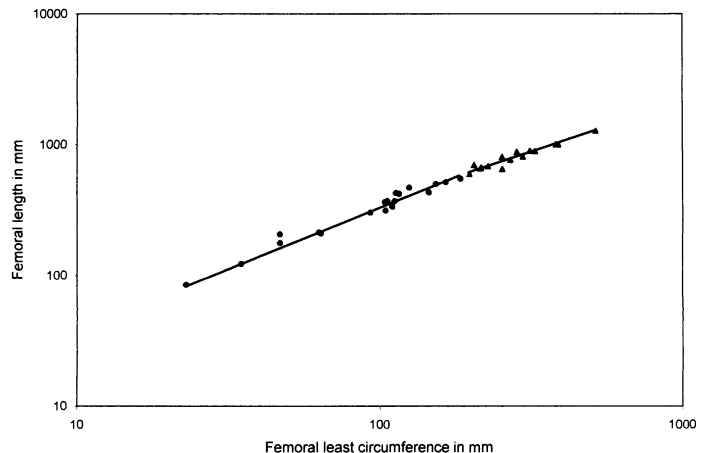


FIGURE 6. Femoral scaling in small (black circles, $n = 19$) and large (black triangles, $n = 15$) non-avian theropods. Regression lines fitted to the samples by means of Reduced Major Axis analysis. The regression line for small non-avian theropods is significantly steeper than for large species.

elastic or geometric similarity (Table 5). The fibula marks the exception, as the regression coefficient is in fact elastically similar. The low correlation coefficient (Table 3) and high residual variance of the sample ($S^2 = 0.0575934$) implies that not too much confidence should be placed in this conclusion, however. The regression equation calculated for the total sample excluding *Allosaurus* and *Ornitholestes* (eq. 3) is significantly lower than predicted from elastic similarity, and in fact conforms to the theory of static stress similarity ($L = C^{0.50}$, see McMahon, 1973).

Like small mammals (Christiansen, 1999b) small theropods approach geometric similarity to a far greater extent than large species, which are in fact elastically similar (Table 5). The fibula in small theropods also scales according to the theory of elastic similarity (Table 5), which could be interpreted as if the fibula grew progressively more important in support of mass as species size increased. The actual bone strength of the fibula, however, does not appear to follow any consistent pattern with size (Christiansen, in press), casting some doubt on this suggestion.

Limb postures of non-avian theropods appear in fact to have changed with size, as indicated by the change in femoral distal epiphysal angulation to femoral length and body mass (Figs. 9, 10). The slope calculated by RMA analysis for epiphysal angulation to femoral length is significantly steeper for mammals than theropod dinosaurs (Fig. 9), whereas this is not the case for the slope calculated by Least Squares analysis (Table 6).

The correlation coefficient of the mammal sample is low. In theropods the correlation is much better (Table 6) and therefore the regression coefficients calculated by Least Squares and RMA analyses do not differ greatly. The low correlation coefficient of the mammal sample results in the RMA regression coefficient being much higher than the coefficient calculated by Least Squares regression analysis. When analyzing the sample for curvilinearity the polynomial regression equation

$$\text{Ln}(Y) = 0.1939 \text{ Ln } X^2 - 1.8858 \text{ Ln } x + 7.6097 \quad (6)$$

←

FIGURE 5. Plots of standardized residuals against expected $\text{Ln } Y$ value in non-avian theropods. **Abbreviations:** a, femur; b, tibia; c, fibula. Notice the marked divergence of *Ornitholestes* (O) in the fibular sample.

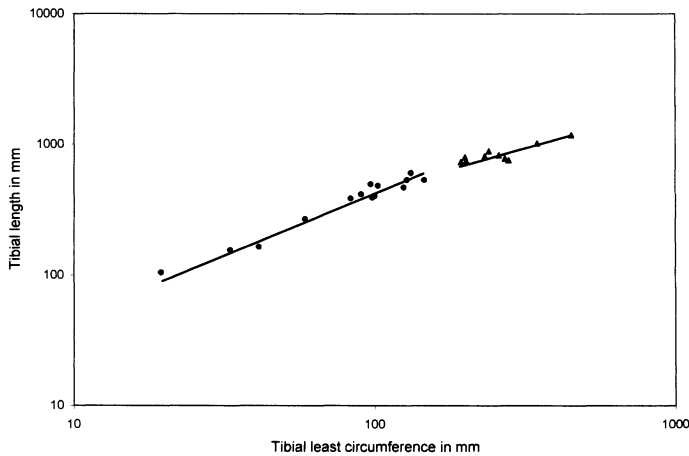


FIGURE 7. Tibial scaling in small (black circles, $n = 14$) and large (black triangles, $n = 10$) non-avian theropods. Regression lines fitted to the samples by means of Reduced Major Axis analysis. The regression line for small non-avian theropods is significantly steeper than for large species.

yields a significantly better fit to the data ($n = 56$; $r = 0.7667$), although only 59% of the variation in the data is explained by this regression line. The polynomial regression equation for theropods

$$\text{Ln}(Y) = -0.001 \text{Ln } X^2 + 0.2492 \text{Ln } X + 2.0007 \quad (7)$$

yielded a correlation coefficient exactly equivalent to the one obtained from linear regression models ($n = 11$; $r = 0.9396$), indicating that no curvilinearity was present in the data sample.

When comparing distal femoral epiphysal angulation to body mass (Fig. 10) the calculated correlation coefficients are almost identical to the values obtained when comparing epiphysal angulation to femoral length (Table 6). In theropods the correlation coefficient is virtually identical to the one obtained from comparing epiphysal angulation to femoral length, and the regression line explains 88% of the variation in the data. As with the previous analysis the regression coefficients calculated by Least Squares analysis for mammals and theropods are not significantly different, but the RMA values are (Table

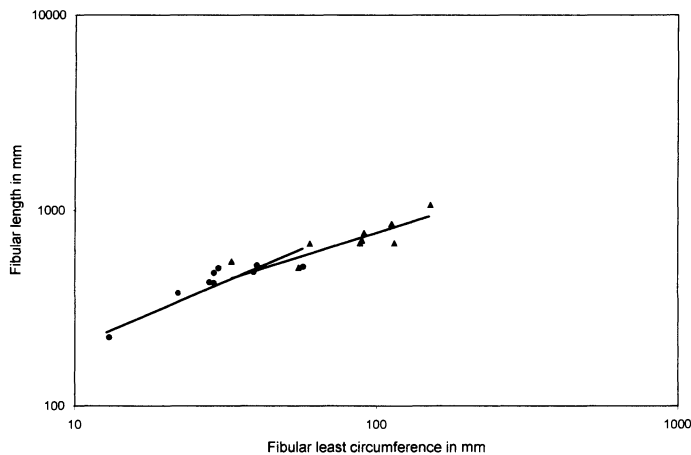


FIGURE 8. Fibular scaling in small (black circles, $n = 9$) and large (black triangles, $n = 9$) non-avian theropods. Regression lines fitted to the samples by means of Reduced Major Axis analysis. The regression line for small non-avian theropods is not significantly different from that of large species.

TABLE 5. Statistical comparison of the regression coefficients calculated by Reduced Major Axis analysis for theropods including subgroups, to the models of elastic similarity, predicting $L = C^{0.67}$ and geometric similarity predicting $L = C^{1.0}$, where L is bone length and C is circumference, both in mm. Significance level for rejection of the null hypothesis is 0.05. Regression statistics for theropods and subgroups from Table 3. The t value has $n - 2$ degrees of freedom.

Group	$L = C^{0.67}$	$L = C^{1.0}$
All theropods (femur)	$p \ll 0.001$	$p \ll 0.001$
All theropods (tibia)	$p < 0.001$	$p \ll 0.001$
All theropods (fibula)	$0.90 > p > 0.80$	$p < 0.001$
Small theropods (femur)	$p < 0.001$	$0.05 > p > 0.01$
Small theropods (tibia)	$p < 0.001$	$0.10 > p > 0.05$
Small theropods (fibula)	$0.90 > p > 0.80$	$0.05 > p > 0.01$
Large theropods (femur)	$0.20 > p > 0.10$	$p < 0.001$
Large theropods (tibia)	$0.40 > p > 0.30$	$0.01 > p > 0.001$
Large theropods (fibula)	$0.20 > p > 0.10$	$0.01 > p > 0.001$
Giant theropods (femur)	$p > 0.90$	$0.01 > p > 0.001$
Giant theropods (tibia)	$0.70 > p > 0.60$	$0.05 > p > 0.01$
Giant theropods (fibula)	$0.20 > p > 0.10$	$0.01 > p > 0.001$
<i>Struthio camelus</i> (femur)	$0.60 > p > 0.50$	$p < 0.001$
<i>Struthio camelus</i> (tibia)	$0.50 > p > 0.40$	$0.01 > p > 0.001$

6), due to the poor correlation of the mammal sample, making the Least Squares value much lower than the RMA value.

The mammal sample again showed signs of curvilinearity and a polynomial regression equation

$$\text{Ln}(Y) = 0.0212 \text{Ln } X^2 - 0.1061 \text{Ln } X + 3.1677 \quad (8)$$

yielded a considerably higher correlation coefficient than the linear analyses ($n = 56$; $r = 0.7574$). A polynomial regression model fitted to the theropod data, however,

$$\text{Ln}(Y) = 0.0003 \text{Ln } X^2 + 0.0716 \text{Ln } X + 3.1006 \quad (9)$$

again resulted in a correlation coefficient equivalent to the one obtained from linear regression models ($n = 10$; $r = 0.9378$).

One reviewer of this paper (Dr. James O. Farlow) suggested that part of the reason for the poor correlations of the mammal samples could be that mammals as a whole might be an anatomically more heterogeneous group compared to non-avian theropods. This might be circumvented by comparing theropods to

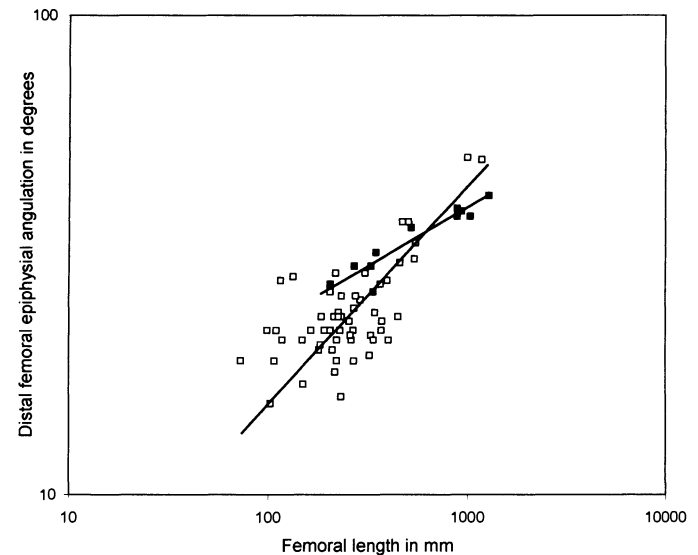


FIGURE 9. Distal femoral epiphysal angle to femoral length in mammals (open squares, $n = 56$) and non-avian theropods (black squares, $n = 11$). Regression lines fitted to the samples by means of Reduced Major Axis analysis. The regression line for mammals is significantly steeper than that of non-avian theropods.

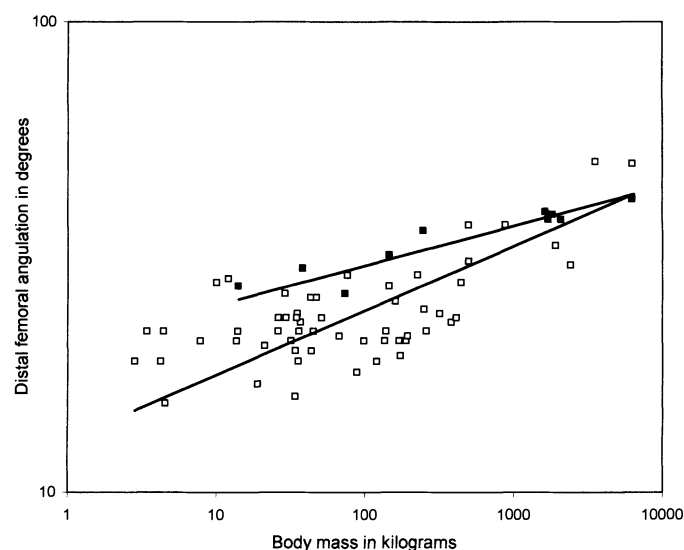


FIGURE 10. Distal femoral epiphysal angle to body mass in mammals (open squares, $n = 56$) and non-avian theropods (black squares, $n = 10$). Regression lines fitted to the samples by means of Reduced Major Axis analysis. The regression line for mammals is significantly steeper than that of non-avian theropods.

less inclusive samples, e.g., individual mammalian orders. Thus, regression equations were also computed for the subgroups Artiodactyla and Carnivora. Artiodactyls displayed markedly lower correlation coefficients than the total samples, both when comparing epiphysal angulation to body mass and femoral length ($r = 0.57$ and $r = 0.53$, respectively). The RMA slope for femoral length to epiphysal angle differed from the corresponding slope for theropods ($P < 0.05$), but body mass to epiphysal angle did not ($P > 0.05$). Removal of outliers only served to increase the correlation coefficients to the same level as the total samples ($r = 0.661$ and $r = 0.663$ for length and body mass, respectively).

Carnivores also displayed lower correlation coefficients than the total samples. However, when removing five outliers (*Ailurus*, *Gulo*, *Meles*, *Nasua* and *P. leo*; see Table 2), the correlation coefficients increased markedly ($r = 0.927$ [femoral length] and $r = 0.886$ [body mass]). After removal of the outliers the RMA slopes for the remaining 12 species (length^{0.469} and mass^{0.161}) were significantly higher than the corresponding values for theropods ($P < 0.05$, Table 6), as was the case for the sample of all mammals. Thus, it appears that mammals as a group may not be more heterogenous than individual orders. As noted above, the included mammals were chosen as they are anatomically and ecologically comparable. Rather, the low correlation coefficients of the samples are more likely due to the factors listed in the materials and methods section.

It is important to note, however, that although epiphysal angulation does increase in theropods, and at values roughly comparable to mammals, no theropod approaches the high values of the elephants (50° , Table 2). All theropods therefore displayed joint flexure, making fast locomotion possible. Columnar limbs imply that speed will increase only as the square root of effective limb length, but flexed limbs indicate the possibility for enhancing stride length during fast locomotion, as in all extant mammals capable of fast locomotion with a suspended phase. It would appear that theropods around the size of *Allosaurus* have become nearly as upright as they are going to get, and even gigantic *Tyrannosaurus rex* has an epiphysal angulation only slightly greater than *Allosaurus*.

DISCUSSION

Non-avian theropods scale their appendicular anatomy and apparently also their limb postures to size in a similar fashion to extant mammals. As in extant mammals the large theropod taxa are more sturdy than predicted by the comprehensive equations, although the deviation is markedly less than observed in extant large mammals (Christiansen, 1999a,b). When comparing the actual values (Table 1) to the values predicted by RMA analysis (Table 3) the femora of large theropods are shorter than predicted for their least circumferences. In the large specimen of *Tyrannosaurus bataar* the femur is 95% of the predicted value and in *T. torosus* AMNH 5438 it is 93%. The gracile specimen of *T. rex* TMP 81.12.1 has a femur 96% of the predicted value. In the robust specimen of *T. rex* CM 9780 femoral length is 88% of the predicted value, comparable to extant large bovids (Christiansen, 1999b).

Other large theropods had femora that were as long as or even longer than predicted for their least circumference (*Sinraptor* [TMP 90.300.1] 108%, *Allosaurus* [TMP cast] 103%, *Gorgosaurus* [TMP 81.10.1] 107%). This also is found in certain very long-limbed mammals capable of fast locomotion with a suspended phase, such as *Giraffa*, *Alces* and to a lesser extent, *Camelus* (Christiansen, 1999b), but among large mammals it is clearly the exception rather than the rule. Overall, femoral lengths in large non-avian theropods are considerably greater than is the case for very large mammals such as rhinos, which have markedly shorter long bones compared to the predicted values from the corresponding comprehensive equations for mammals (Christiansen, 1999b). As in small to medium-sized mammals smaller theropods had femora close to or longer than the predicted values (*Dilophosaurus* [UCMP 37302] 97% of the predicted value, *Elaphrosaurus* [HMN dd] 100%, *Oviraptor* 97%). Most ornithomimids were more gracile (*Dromiceiomimus* [AMNH 5201] 117%, large *Gallimimus* [G.I. DPS 100/11] 103%, small *Gallimimus* 104%, *Struthiomimus* [AMNH 5339] 118%).

The tibiae of large theropods appear more comparable to large mammals as they are considerably shorter than predicted for their least circumference. In *Tyrannosaurus torosus* tibial length is 92% of the predicted value, 88% in the gracile *T. rex*,

TABLE 6. Regression statistics for femoral distal epiphysal angulation compared to femoral length and body mass in mammals and non-avian theropod dinosaurs. In all cases Y is femoral distal epiphysal angulation in degrees, and X is either femoral length in mm or body mass in kg. Confidence limits (95% CI) are given for the regression coefficients. Two asterisks after the regression coefficients for theropods indicate significance from the corresponding value for mammals at the 1% level.

Group	n	X	Least squares		RMA		95% CI	r
			a	b	a	b		
Mammals	56	Length	4.8141	0.2886	2.1625	0.4335	0.0889	0.6659
	56	Mass	16.168	0.0892	13.312	0.1345	0.0277	0.6633
Theropods	11	Length	7.6861	0.2367	6.9852	0.2520**	0.0650	0.9396
	10	Mass	22.033	0.0748	21.390	0.0797**	0.0226	0.9378

85% in the robust *T. rex* and the large *T. bataar*, and just 83% in *Allosaurus*. In *Sinraptor* the tibia is more gracile, being 101% of the predicted length. *Gorgosaurus* TMP 81.10.1 has a markedly long tibia, 111% of the predicted value, comparable to much smaller ornithomimids. This supports the suggestions of Holtz (1994) that tyrannosaurids tend to have longer distal limb elements than other, less derived taxa of comparable size. Ornithomimids generally have tibiae 106–113% of the predicted values.

The fibula showed a interesting dichotomy with derived taxa having less sturdy (birdlike) fibulae, than comparably sized, less derived taxa. In *Allosaurus* fibular length is 75% of the predicted value, in *Sinraptor* 88%, and in otherwise gracile *Dilophosaurus* 89%. In contrast, even very large tyrannosaurids have more gracile fibulae (in *Tyrannosaurus rex* the fibula is 91% of the predicted value in gracile TMP 81.12.1 and curiously 104% in robust CM 9780, 89% in *T. bataar*, 99% in *Gorgosaurus* and 107–133% in the ornithomimids).

Animals capable of rapid locomotion are usually characterized by a number of appendicular adaptations, such as long limbs, well developed appendicular muscle scars and well developed ilia, long epi- and especially metapodia, pedes with reduced digital number and median symmetry and hinge-like joints, among others. Nearly all morphological characters indicative of fast-moving animals were present in non-avian theropods, including large forms (Coombs, 1978; Christiansen, in press). Another character is permanent joint flexure which was surely present in even elephant-sized taxa such as *Tyrannosaurus*, *Giganotosaurus* or *Carcharodontosaurus*.

Bending and torsionally induced skeletal stress is much more important than simple axial compression (e.g., Alexander, 1989, 1991; Alexander et al., 1979b; Alexander and Pond, 1992; Biewener, 1990; Carrano, 1998). In mammals another factor contributing to reduction in bending stress, besides a size dependent change in limb posture, is a size dependent change in diaphysal curvature (Biewener, 1983). At any given angle to vertical a bone with a curved diaphysis will be subjected to greater degrees of stress as it will cause axial compressive forces to induce bending moments about the diaphysis as well. These bending moments due to axial compression are sometimes even greater than ordinary secondary moments about the diaphysis (Biewener, 1983; Biewener et al., 1983a). Conversely, diaphysal curvature displays a slight but significant decrease with size among extant mammals (Biewener, 1983). The largest extant mammals, such as rhinoceroses, hippopotamuses and elephants have nearly straight long bone diaphyses.

In non-avian theropods the femora of even the largest taxa, such as *Tyrannosaurus rex*, have substantial diaphysal curvature. It appears, however, as if diaphysal curvature does in fact decrease with size among non-avian theropods. It would of course be interesting to compare this feature in non-avian theropods to mammals. However, as the decrease in diaphysal curvature among extant mammals is rather modest in absolute measure (Biewener, 1983), even a slight post mortem diaphysal distortion could seriously affect the values for theropods. As diaphysal distortion, unless severe, is often hard to verify in fossil long bones, a comparison between mammals and non-avian theropods for this character appears too uncertain.

One difference between mammals and non-avian theropods in appendicular scaling is apparent, however. As skeletal stress due to bending moments is much more important in overall bone stress during locomotion than stress due to axial compression, it is possible to evolve long bones more resistant to mechanical failure by either evolving disproportionately thick diaphyses, or alternatively by evolving progressively shorter long bones with size, thus decreasing the length of the lever arm of the secondary moments about the diaphysis. It is usually assumed that large extant mammals employ a combination of

the two, but that they rely primarily on the former (e.g., Alexander and Pond, 1992). However, this is not the case. Large bovids and even seemingly very stoutly built rhinoceroses have long bones approximately as thick as could be expected for their body mass, and no thicker than the seemingly thinner long bones of elephants (Christiansen, 1999a).

Rather, large mammals capable of rapid locomotion evolve markedly shorter long bones to body mass, and uniquely among megaherbivore mammals, elephants have long bones approximately as long as predicted for their mass (Alexander et al., 1979a; Christiansen, 1999a), making them appear thin. Even the largest non-avian theropods had very long limbs. In *Tyrannosaurus rex* hind limb length is in fact fully 50% greater than in a comparably sized African elephant (Christiansen, in press). This results in the seemingly sturdy long bones of large theropods being mechanically only slightly stronger than those of extant elephants and hippos (Christiansen, in press).

The combination of a markedly cursorial anatomy, long bone scaling apparently following the same adaptive trends as extant mammals, but very long and thus mechanically rather weak limbs among large taxa, is unknown among extant tetrapods. Based on analyses of bone strength and appendicular proportions Christiansen (in press) concurred with previous authors (e.g., Coombs, 1978; Bakker, 1986; Paul, 1988) that large theropods had morphological adaptations strongly suggestive of the capability of fast locomotion. The bone strength, however, casts serious doubt on the capability of large theropods to include a long suspended phase in the stride. Therefore, they probably could not have moved at such rapid speeds as suggested by Bakker and Paul.

On the other hand, if large theropods were capable of only slow locomotion, as maintained by some authors (e.g., Lambe, 1917; Colinvaux, 1978; Halstead and Halstead, 1981; Thulborn, 1982; Colbert, 1983), their osteoanatomy and the fact that their pattern of limb allometry is almost identical to that of extant mammals, seem hard to explain. However, it also seems hard to explain how large theropods would have been able to run with long suspended phases, when they failed to evolve the short, mechanically strong limbs of extant mammals.

Christiansen (in press) suggested that small theropods may well have run in a comparable fashion to extant medium-sized artiodactyls, perissodactyls and raites. Very large theropods, however, probably relied more on fast progression involving long strides with brief, if any, suspended phases as also suggested by Farlow et al. (1995). This could explain the great length of their limbs and also the pattern of allometry outlined in this paper. Such a form of locomotion would have allowed them to move at rather impressive speeds, due to their long limbs, and they could have been as fast as, or even faster, than extant large mammals (Christiansen, in press).

Mammals with parasagittal limb kinematics appear to be a superior extant analog than birds to non-avian theropods, due especially to the similarity in femoral limb kinematics (Gatesy, 1990, 1991; Carrano, 1997). Appendicular joint morphology is rather similar in ungulates and theropods, both avian and non-avian. As such, it is intriguing to note that limb allometry in non-avian theropods across the entire size range, but also when analyzing subsets within this range, also appears to follow the patterns observed in mammals more closely than in avian theropods. Appendicular allometry thus lends further support to the similarity in functional anatomy between non-avian theropods and mammals. Clearly, when theropods took to the skies, they changed more than just the functional morphology of their forelimbs.

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