

Scaling of the Limb Long Bones to Body Mass in Terrestrial Mammals

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ABSTRACT Long-bone scaling has been analyzed in a large number of terrestrial mammals for which body masses were known. Earlier proposals that geometric or elastic similarity are suitable as explanations for long-bone scaling across a large size range are not supported. Differential scaling is present, and large mammals on average scale with lower regression slopes than small mammals. Large mammals tend to reduce bending stress during locomotion by having shorter limb bones than predicted rather than by having very thick diaphyses, as is usually assumed. The choice of regression model used to describe data samples in analyses of scaling becomes increasingly important as correlation coefficients decrease, and theoretical models supported by one analysis may not be supported when applying another statistical model to the same data. Differences in limb posture and locomotor performance have profound influence on the amount of stress set up in the appendicular bones during rigorous physical activity and make it unlikely that scaling of long bones across a large size range of terrestrial mammals can be satisfactorily explained by any one power function. *J. Morphol.* 239:167–190, 1999. © 1999 Wiley-Liss, Inc.

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Body size is a major factor in animal ecology and crucial with respect to the mechanical properties of the skeleton for support and locomotion in terrestrial animals. If animals scaled their structures of support in a geometric (isometric) fashion, all linear dimensions would be proportional to $M^{0.33}$. Therefore, skeletal stress could be expected to increase by the same amount (Biewener, '90), implying that, unless other anatomical adaptations were also present, small animals would either have to be mechanically highly overbuilt or large animals would operate closer to the limit of mechanical failure.

Initially recognized by Galileo (1638), this problem has received attention especially during the last two decades. It seems unlikely that terrestrial organisms would be highly overbuilt or operate close to the limit of mechanical failure, and indeed the safety factors (the ratio of yield stress of the structure to peak stress experienced) of most structures of support appear to be 2–4 (Alexander, '81; Rubin and Lanyon, '82; Biewener and Taylor, '86; Biewener, '89a,b, '90). McMahon ('73, '75a) proposed that terrestrial ani-

mals would optimize their skeleton so that they were similarly in danger of mechanical failure, or buckling, under gravity, regardless of size, and termed the model elastic similarity. Elastic similarity requires that limb-bone lengths scale to $M^{0.25}$ and diameters or least circumferences to $M^{0.375}$, implying bone lengths proportional to diameter or circumference $^{0.67}$.

McMahon ('75b) found reasonably good agreement with the theory from limb-bone data from artiodactyls, although only bovids appeared to conform well to the theory. Christiansen (in press), however, found that many of McMahon's results actually differed significantly from elastic similarity. Alexander ('77) also found support for elastic similarity in his studies of seven species of bovids. However, from analyses of data samples spanning a wider phylogenetic and size range, Alexander et al. ('79a) and Biewener

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('83) found that terrestrial mammals appeared to scale closer to isometry. Economos ('83) suggested that mechanical failure would be a much more important factor in terrestrial support for large mammals and that small and large mammals would show differential scaling. He did not pursue the issue further, except to note that the high regression slopes found by Alexander et al. ('79a) were the result of the small number of large species in the sample. Prothero and Sereno ('82) had previously suggested this also.

Larger, more recent analyses have largely failed to support either geometric or elastic similarity but have found regression slopes that were intermediate between the two (Bou et al., '87; Bertram and Biewener, '90; Christiansen, in press), and the latter two studies did indeed demonstrate differential scaling between large and small species. Animals not subjected to the forces of gravity, such as fishes and marine mammals, tend to be geometrically similar (Economos, '83; Berrios-Lopez et al., '96).

Additionally, static deformation under gravity seems a less likely explanation for optimization of the appendicular skeleton for terrestrial support, as peak forces occur during fast locomotion or strenuous jumping, and these are rather uniform across a large phylogenetic and size range, being approximately 50–100 MPa (Alexander, '77, '84, '85a; Alexander et al., '79b; Rubin and Lanyon, '82; Alexander and Jayes, '83; Biewener, '83, '90; Biewener et al., '83, '88; Biewener and Taylor, '86; Alexander and Pond, '92). During fast locomotion, the foot is on the ground for a shorter time than during walking or standing, implying that peak forces will be greater multiples of body mass in the former.

However, the duty factor (the duration of the time a foot is on the ground during a stride) during fast locomotion increases with body size in ungulates (Alexander et al., '77), implying that peak forces during fast locomotion in large animals will be lower multiples of body mass than in smaller forms. Biewener ('83) found no significant increase in duty factors across a phylogenetically wider sample, however, making the above suggestion tentative. In very large mammals, reduced locomotor performance also contributes to maintaining peak stresses in the limbs at comparable levels to much smaller mammals (Alexander et al., '79b; Biewener, '90; Alexander and Pond, '92).

A very important factor in maintaining peak stresses at rather uniform levels across a large size range, however, appears to be a size-dependent change in limb posture (Biewener, '83, '89a,b, '90), progressively aligning the long bones more steeply to vertical with size. This decreases the mass-specific amount of force necessary to counteract moments about the joints. Since muscle force is the single most important factor in determining the amount of force the bones must resist during locomotion (Biewener, '83, '90; Alexander, '85a), the change in limb posture accounts for most of the reduction in bone stress among small to rather large mammals (Biewener, '89a,b, '90; Bertram and Biewener, '90). As species size exceeds about 300 kg in mass, limb postures appear no longer to change significantly, as this would lead to essentially pillar-like limbs unfit for fast progression, and positive skeletal allometry increases, and, along with reduced locomotor performance among the largest species, this maintains peak forces at uniform levels to smaller mammals (Gambaryan, '74; Prothero and Sereno, '82; Biewener, '83, '89a,b, '90; Bertram and Biewener, '90).

The above indicates that limb-bone scaling should probably not be expected to follow any one model across a large size range, as many factors other than skeletal allometry contribute to maintaining skeletal stress at uniform levels across a large size range. Furthermore, elastic and geometric similarity also imply locomotory independence, which is hardly likely. Slow-moving animals would not be expected to be in need of limb bones as strong as comparably sized fast-moving forms, and many small mammals are highly adapted for a lifestyle imposing limits other than locomotion on the skeleton (e.g. fossoriality or arboreality).

Peak forces during locomotion can largely be separated into an axial component, acting along the long axis of the bone and exerting compressive stress, and a bending component, acting at right angles to the long axis of the bone and distorting it about its long axis (Alexander, '89, '91). Bending-induced stresses are clearly the most important (Alexander et al., '79b; Alexander, '84, '89, '91; Alexander and Pond, '92).

If limb bone allometry becomes increasingly important as size increases and as bending stress is the most important factor in determining the forces the bones must resist during fast locomotion, the implica-

tion is that animals could maintain resistance to bending forces by either evolving increasingly greater diaphysial least circumferences or by evolving increasingly shorter long bones, thus reducing the size of the lever arm of the bending forces. The general opinion seems to favor the former as the most important (Prothero and Sereno, '82; Biewener, '90; Alexander and Pond, '92; Alexander, '97a,b). Economos ('83), however, suggested that bending forces in large mammals were kept within comparable limits to small mammals by a progressively slower increase in length with mass.

Most previous analyses of long-bone scaling involve osteological measurements only, which cannot offer a solution to the problem of whether or not large mammals maintain bending resistance by evolving short or very thick long bones.

Mass is rarely recorded in museum specimens, which are what people usually have available for study, and in some cases body mass is simply taken as an average from literature (e.g., Biewener, '83; Steudel and Beattie, '93). This is unsatisfactory, though, as the skeletal specimen used may be a large or small one and thus not representative of the species mean, and mass can vary substantially at any given skeletal size. In the case of very large animals, this can amount to hundreds of kilograms (Laws et al., '75; Roth, '90).

In addition to analyzing long-bone scaling to body mass across a large size range of mammals using a much larger sample than previous analyses, the main purpose of this study is to determine whether mammals evolve progressively thicker or shorter limbs with size or alternatively a combination of the two.

MATERIALS AND METHODS

The six long bones (humerus, radius, ulna, femur, tibia, and fibula) from 98 specimens of extant terrestrial mammals, representing 79 species from seven orders, were measured using calipers and a measuring tape (Table 1). This is a considerably greater number than in previous analyses of this kind (e.g., see Alexander, '77; Alexander et al., '79a; Biewener, '83).

Lengths are given as the greatest length of the bone. For humerus and femur, it is the vertical distance from the caput to the trochlea and distal condyles, respectively. For radius, it includes the styloid process. For ulna, it includes both the olecranon process and

the styloid process, and for tibia it is the vertical distance from the intercondylar eminence to the medial malleolus. Least circumference is given as the minimum circumference of the diaphysis, usually located at midshaft in humerus and femur but often more proximally and distally situated in the radius and tibia, respectively.

Circumference was chosen over bone diameter, the parameter usually employed in analyses of scaling, to facilitate comparison among the various bones and also the various species, as the humerus and femur are usually more circular in cross-section than the radius or tibia, which tend to be more ellipsoidal or rectangular. Additionally, large animals often have more rectangular diaphysial cross-sections than do smaller species. Metacarpal and metatarsal lengths were also measured, and the parameter chosen was the longest metapodial bone in the case of species with unfused metapodia (e.g., carnivorans as opposed to the fused cannon bones of ungulates). Total forelimb length is given as the sum of the lengths of humerus, radius, and longest metacarpal, and hindlimb length as the sum of the lengths of femur, tibia, and the longest metatarsal. Limb lengths would have been slightly greater in the living animals, due to the carpals and tarsals, respectively, and the cartilage and menisci in the joints.

According to the data labels of the specimens, some were weighed in the field just after they had been shot (e.g., *Cervus elaphus*, *Dama*) but most were captive specimens, either from zoos or safari parks, and had been weighed just after death (e.g., *Panthera uncia*, *P. tigris*, *Ceratotherium*, *Elephas*, *Hippopotamus*). Occasionally juveniles were included (*Bos gaurus*, small specimen of *Tapirus terrestris*), but most specimens used were fully adult, as evidenced by epiphyseal closure in addition to overall size.

As differential scaling of the long bones might be expected between larger and smaller species as noted above, the sample was also divided into two subsets, one with species ranging in mass from 1–50 kg and the other with species above 50 kg. These were then treated as separate data samples and were analytically compared to each other and the overall sample. Finally, separate analyses were performed on the two largest of the included orders, Artiodactyla and Carnivora. It could be expected from a biome-

TABLE 1. List of mammals used in the analysis

Taxon	Body mass (kg)
Subclass Metatheria	
Order Marsupialia	
Family Phascolarctidae	
Koala (<i>Phascolarctos cinereus</i>)	5.9
Family Phalangeridae	
Oriental cuscus (<i>Phalanger orientalis</i>)	2.3
Brush-tailed possum (<i>Trichosurus vulpecula</i>)	4.3
Family Thylacinidae	
Tasmanian wolf (<i>Thylacinus cynocephalus</i>)	7.6
Subclass Eutheria	
Order Artiodactyla	
Family Bovidae	
Springbuck (<i>Antidorcas marsupialis</i>)	21.2
European bison (<i>Bison bonasus</i>)	225
Gaur (<i>Bos gaurus</i>)	54.5
Domestic cow (<i>Bos taurus</i>)	225
Asian water buffalo (<i>Bubalus bubalis</i>)	382
Ibex (<i>Capra ibex</i>)	36
Blesbok (<i>Damaliscus dorcas</i>)	43.5
Gazelle (<i>Gazella dorcas</i>)	19
Tahr (<i>Hemitragus jemlahicus</i>)	43
Mountain goat (<i>Oreamnos americanus</i>)	120
Dall's Sheep (<i>Ovis dalli</i>)	99
Chamois (<i>Rupicapra pyrenaica</i>)	34
Saiga (<i>Saiga tartarica</i>)	26.2
Saiga (<i>Saiga tartarica</i>)	20.2
African buffalo (<i>Synclerus caffer</i>)	440
Sitatunga (<i>Tragelaphus spekii</i>)	29.5
Greater kudu (<i>Tragelaphus strepsiceros</i>)	190
Family Cervidae	
Elk (<i>Alces alces</i>)	410
Red deer (<i>Cervus elaphus</i>)	85
Sika deer (<i>Cervus nippon</i>)	35.6
Sunda sambar (<i>Cervus timorensis</i>)	37
Fallow deer (<i>Dama dama</i>)	45
Muntjac (<i>Muntiacus muntjak</i>)	34
Pere David's deer (<i>Elaphurus davidianus</i>)	152
Pere David's deer (<i>Elaphurus davidianus</i>)	194
Reindeer (<i>Rangifer tarandus</i>)	160
Family Giraffidae	
Giraffe (<i>Giraffa camelopardalis</i>)	385
Okapi (<i>Okapia johnstoni</i>)	228
Okapi (<i>Okapia johnstoni</i>)	310
Okapi (<i>Okapia johnstoni</i>)	260
Okapi (<i>Okapia johnstoni</i>)	250
Family Hippopotamidae	
Pygmy hippopotamus (<i>Choeropsis liberiensis</i>)	250
Hippopotamus (<i>Hippopotamus amphibius</i>)	2,400
Hippopotamus (<i>Hippopotamus amphibius</i>)	680
Family Suidae	
Wart hog (<i>Phacochoerus aethiopicus</i>)	88
African bush pig (<i>Potamochoerus porcus</i>)	76
Family Tragulidae	
Asiatic mouse deer (<i>Tragulus javanicus</i>)	1.4
Order Carnivora	
Family Canidae	
Arctic fox (<i>Alopex lagopus</i>)	4.5
Golden jackal (<i>Canis aureus</i>)	9.2
Domestic dog (<i>Canis familiaris</i>)	29
Gray wolf (<i>Canis lupus</i>)	35
Fennec fox (<i>Fennecus zerda</i>)	1.2
Hoary fox (<i>Lycalopex vetulus</i>)	4.2
Red fox (<i>Vulpes vulpes</i>)	5.5
Family Felidae	
Cheetah (<i>Acinonyx jubatus</i>)	39

TABLE 1. (continued)

Taxon	Body mass (kg)
Family Felidae (continued)	
Cougar (<i>Felis concolor</i>)	47
Cougar (<i>Felis concolor</i>)	45.7
Lynx (<i>Felis lynx</i>)	6.7
Ocelot (<i>Felis pardalis</i>)	13.9
Lion (<i>Panthera leo</i>)	170
Jaguar (<i>Panthera onca</i>)	51.5
Jaguar (<i>Panthera onca</i>)	47.3
Jaguar (<i>Panthera onca</i>)	67.4
Leopard (<i>Panthera pardus</i>)	51
Indian tiger (<i>Panthera tigris tigris</i>)	145
Indian tiger (<i>Panthera tigris tigris</i>)	145
Indian tiger (<i>Panthera tigris tigris</i>)	145
Sumatran tiger (<i>Panthera tigris sumatrae</i>)	73
Siberian tiger (<i>Panthera tigris altaica</i>)	230
Siberian tiger (<i>Panthera tigris altaica</i>)	221
Snow leopard (<i>Panthera uncia</i>)	34.8
Snow leopard (<i>Panthera uncia</i>)	30
Snow leopard (<i>Panthera uncia</i>)	38
Family Hyaenidae	
Striped hyaena (<i>Hyaena hyaena</i>)	32
Family Mustelidae	
Wolverine (<i>Gulo gulo</i>)	12
European river otter (<i>Lutra lutra</i>)	6.2
Stone marten (<i>Martes foina</i>)	1.4
Old World badger (<i>Meles meles</i>)	10
Family Procyonidae	
Lesser panda (<i>Ailurus fulgens</i>)	4.4
Coatiundi (<i>Nasua nasua</i>)	3.4
Family Ursidae	
American black bear (<i>Ursus americanus</i>)	105
Kodiak bear (<i>Ursus arctos middendorffii</i>)	203
Kodiak bear (<i>Ursus arctos middendorffii</i>)	496
Polar bear (<i>Ursus maritimus</i>)	175
Asiatic black bear (<i>Ursus thibetanus</i>)	98
Family Viverridae	
Falanooc (<i>Eupleres goudotii</i>)	2.6
Palm civet (<i>Paradoxurus hermaphroditus</i>)	2.2
Slender-tailed meerkat (<i>Suricata suricatta</i>)	0.7
Order Hyracoidea	
Family Procaviidae	
Hyrax (<i>Procavia capensis</i>)	2.8
Order Perissodactyla	
Family Equidae	
Burchell's zebra (<i>Equus burchelli</i>)	136
Shire horse (<i>Equus caballus</i>)	675
Family Rhinocerotidae	
White rhinoceros (<i>Ceratotherium simum</i>)	1,900
Black rhinoceros (<i>Diceros bicornis</i>)	875
Javan rhinoceros (<i>Rhinoceros sondaicus</i>)	1,435
Family Tapiridae	
Malayan tapir (<i>Tapirus indicus</i>)	317
South American tapir (<i>Tapirus terrestris</i>)	57
South American tapir (<i>Tapirus terrestris</i>)	173
Order Proboscidea	
Family Elephantidae	
Asiatic elephant (<i>Elephas maximus</i>)	3,534
Asiatic elephant (<i>Elephas maximus</i>)	850
African elephant (<i>Loxodonta africana</i>)	6,250
Order Rodentia	
Family Castoridae	
European beaver (<i>Castor fiber</i>)	8.5
Family Chinchillidae	
Mountain viscacha (<i>Lagidium viscacia</i>)	2.4
Family Dasyprotidae	
Paca (<i>Agouti paca</i>)	6.5
Family Hydrochaeridae	
Capybara (<i>Hydrochaeris hydrochaeris</i>)	46

chanical perspective that the size difference between large and small species within the orders would make these two samples no more homogenous than a phylogenetically heterogeneous sample composed of species of comparable mass (e.g., small or large species).

Species with multiple specimens were averaged prior to analysis in order not to bias the samples. However, the Siberian tiger (*Panthera tigris altaica*) was kept separate from the Indian and Sumatran tiger (*P. tigris tigris* and *P. tigris sumatrae*) due to the great size of the former compared to the latter two subspecies. The values were transformed to logarithms, and regression lines were fitted to the data by means of least squares regression, the most commonly used method in analyses of scaling. The regression equation is thus

$$\ln Y = \ln a + b \ln X$$

which is mathematically similar to the standard power function

$$Y = aX^b$$

which describes an allometric relationship (Gould, '66; Labarbera, '89). However, Zar ('68) pointed out that the two were probably not statistically identical, as the least squares method requires that the residuals be normally distributed with a mean of zero, and this is often not the case with the log-transformed variables. Additionally, minimizing the sum of the squared residuals for calculating the regression slope is not equivalent in raw and log-transformed data. However, others have argued that this does not invalidate the model and usually creates no problems when analyzing broad allometry (Manaster and Manaster, '75; Labarbera, '89). In this data set, the residuals were normally distributed with a mean of zero.

However, the least squares method assumes that error is present on one variable (the dependent variable Y) only and that it is possible to assign dependence to one variable. In analyses of scaling, body mass is usually assumed to be the variable on which the osteological parameters depend (e.g., Alexander, '77; Alexander et al., '79a; Prange et al., '79; Biewener, '83; Economos, '83; Berrios-Lopez et al., '96), which seems reasonable. However, it is doubtful if error should be assumed for the osteological parameters only.

Thus, regression lines were also calculated using model II regression, in this case

the reduced major axis analysis (RMA). The RMA analysis is independent of any joint function of the variables but is just a ratio of two standard deviations (Sokal and Rohlf, '81). McArdle ('88) found that RMA usually generated a superior fit to simulated data samples compared to the major axis analysis and was also to be preferred over the least squares method when the samples indicated substantial variation between the variables.

Pearson's product moment correlation coefficient was calculated for all samples, and confidence limits (95% confidence interval [CI]) were calculated for the slopes. The standard error of the regression slope calculated by RMA analysis can be approximated by the standard error of the least squares regression slope (Sokal and Rohlf, '81), and the latter can thus be used to assign confidence limits to both slopes. The slopes of the various subsets were tested against each other for significance. Additionally, both the overall data set and the subsets were tested for significance against the regression slopes predicted by elastic and geometric similarity.

Since the slope for RMA is $1/r$ times the slope calculated from least squares regression analysis, the values will differ little if the correlation coefficient is high (>0.95), but an increasingly lower correlation coefficient (<0.90 or less) makes the choice of method increasingly important in evaluating whether or not the calculated slopes are in accord with either geometric or elastic similarity.

RESULTS AND DISCUSSION

The results for all mammals are shown in Figures 1a-d and 2a-d and Table 2. The correlation coefficients are generally high, making the regression equations calculated by model I and model II regression rather similar. The exceptions are the metapodials and ulnar least circumference. The metapodials could be expected to vary considerably, as metapodial length in ungulates, especially equids and artiodactyls with fused cannon bones, is considerably greater at any given body mass than in carnivorans or suids. Ulnar length correlates well with body mass (Table 2), but the least circumference does not. As can be seen from Figure 1d, there is substantial scatter about the regression line, and it appears as if two groups can be distinguished.

In equids and most artiodactyls, the ulnar diaphysis is greatly reduced and either fused

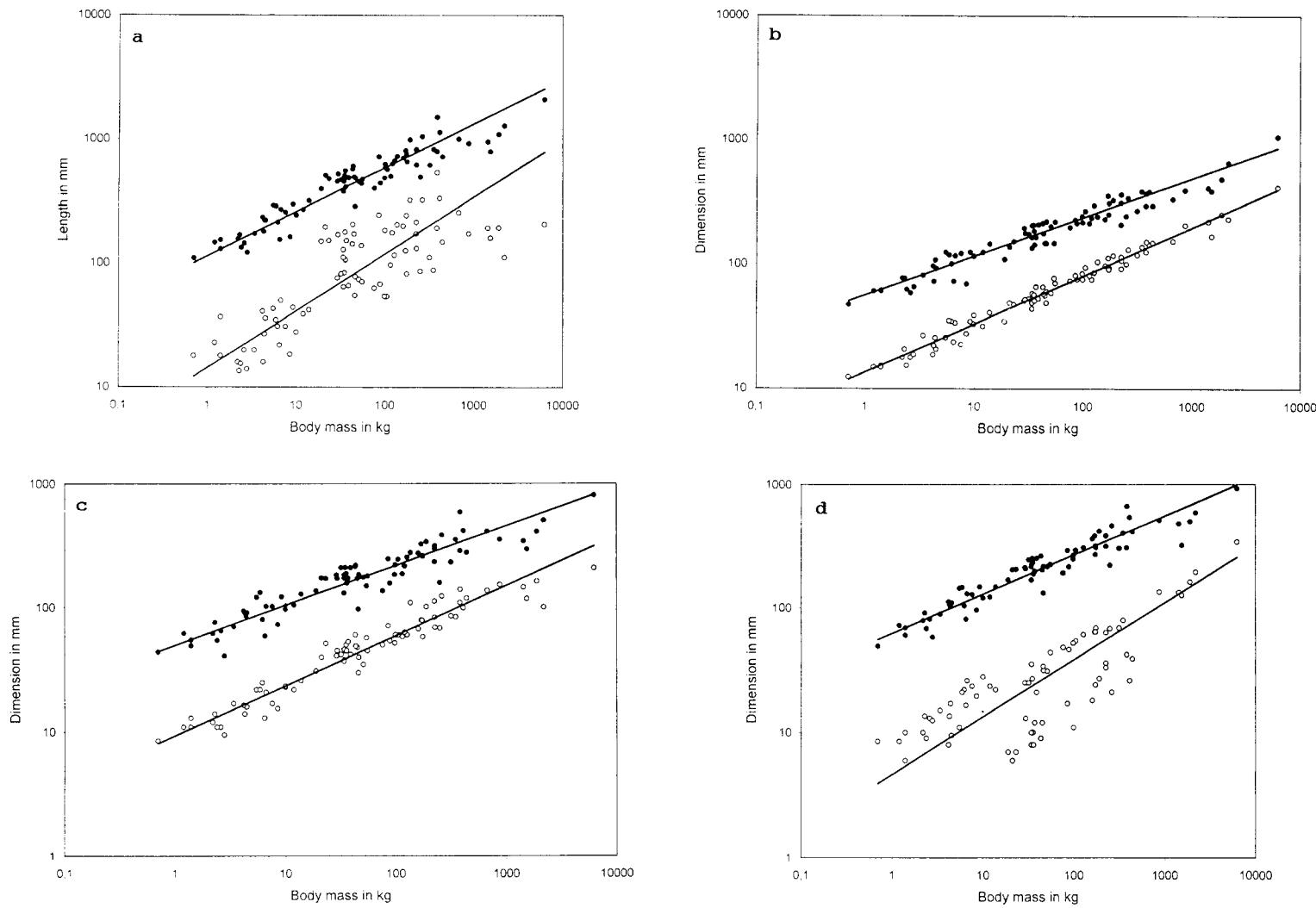


Figure 1

completely to the radial diaphysis or attached to it by means of extensive syndesmoses. The ulna is usually much too thin to be of any importance in support of body mass in these species. In contrast, the two epipodial bones are largely separate in carnivorans and the ulnar diaphysis usually subequal in circumference to the radial diaphysis, and it is reasonable to suppose that the ulna also provides a substantial part of the forelimb support in these species.

This is also the case in megaherbivores (except *Giraffa*). In elephants, the ulnar diaphysis is markedly thicker than the radial diaphysis, a quite unusual condition among terrestrial mammals. This also results in the circumference of the ulnar diaphysis of the two elephants falling markedly above the regression line (Fig. 1d), unlike their other bones, where the least circumference is either below (Figs. 1c, 2c) or close to (Figs. 1b, 2b,d) the regression lines.

Forelimb length correlates well with body mass (Table 2), although it is evident that large species have shorter forelimbs than predicted (Fig. 2a). When the values calculated by the comprehensive RMA equation (Table 2) are compared to the actual values of the individual specimens, the large *Hippopotamus* (2,400 kg) (Table 1) especially stands out among the large species, with the forelimb length merely 47% of the predicted value. This animal was a huge bull which had been kept in the Copenhagen Zoo for decades and was almost certainly somewhat overweight compared to a wild specimen of comparable size. However, *Choeropsis* also had a very short forelimb (61% of the predicted value), and this animal was not overweight. In rhinos, actual forelimb lengths were 65–73% of the predicted values.

The large bovids are more long-limbed, generally having forelimb lengths of 73–105% (of the predicted values). Among larger species, *Alces* and especially *Tragelaphus strepsiceros* and *Giraffa* are very long-limbed, having forelimb lengths 117%, 134%, and

159% of the predicted values, respectively. Equids also have quite long forelimbs (111% of predicted length in *Equus burchelli*), but the large shire horse proved more stocky-limbed (87%). The elephants are long-limbed compared to the other megaherbivores, as also found by Alexander et al. ('79a) and Alexander and Pond ('92), having a forelimb length 80% of the predicted value in the 3,534 kg *Elephas* and 82% in *Loxodonta*.

As expected, smaller species have proportionally longer forelimbs than large species. Smaller bovids have forelimb lengths 115–149% of the values predicted by the comprehensive RMA equation. Among smaller carnivorans, these values range from 112–138% of the predicted values, with canids on average having longer limbs to body mass than felids or mustelids. Carnivorans larger than about 100 kg have shorter forelimbs than smaller species and have forelimb lengths usually rather close to the predicted values. *Acinonyx* did not have an unusually long forelimb compared to other felids (actual forelimb length was 116% of the predicted value) despite its ability to exceed 100 kmh⁻¹ (Sharp, '97). Ursids and mustelids have shorter forelimbs than canids or felids.

Great differences are found in the limb proportions compared to the predicted values (Fig. 1a–d). Large species have actual bone lengths that are often considerably below the predicted values. In rhinos and hippos, the individual forelimb bones range from 73–84% of the predicted values in the rhinos and 42–65% in the 2,400 kg *Hippopotamus*. In *Diceros*, the massive olecranon process results in the ulna being very close to the predicted length (96%). Elephants are very long-limbed compared to rhinos and hippos, and actual bone lengths for humerus, radius, and ulna are 115%, 94% and 91%, respectively, of the values predicted by the comprehensive RMA equations in the 3,534 kg *Elephas* and 123%, 99%, and 94%, respectively, in *Loxodonta*.

The fast-moving ungulates have limb proportions that often differ substantially from the expected values. The humeri are usually quite short in smaller bovids and cervids, being 77–94% of the values predicted by the comprehensive RMA equation (Table 2). In contrast, the two epipodial bones are proportionally much longer, with the radii ranging from 106–133% of the values predicted by the comprehensive RMA equation (Table 2) and ulnae ranging from 104–129% of the

Fig. 1. Forelimb bones against body mass in all mammals. Regression lines fitted to the data by means of reduced major axis regression analysis. **a:** Forelimb length (filled circles) and metacarpal length (open circles). **b:** Humeral length (filled circles) and humeral least circumference (open circles). **c:** Radial length (filled circles) and radial least circumference (open circles). **d:** Ulnar length (filled circles) and ulnar least circumference (open circles).

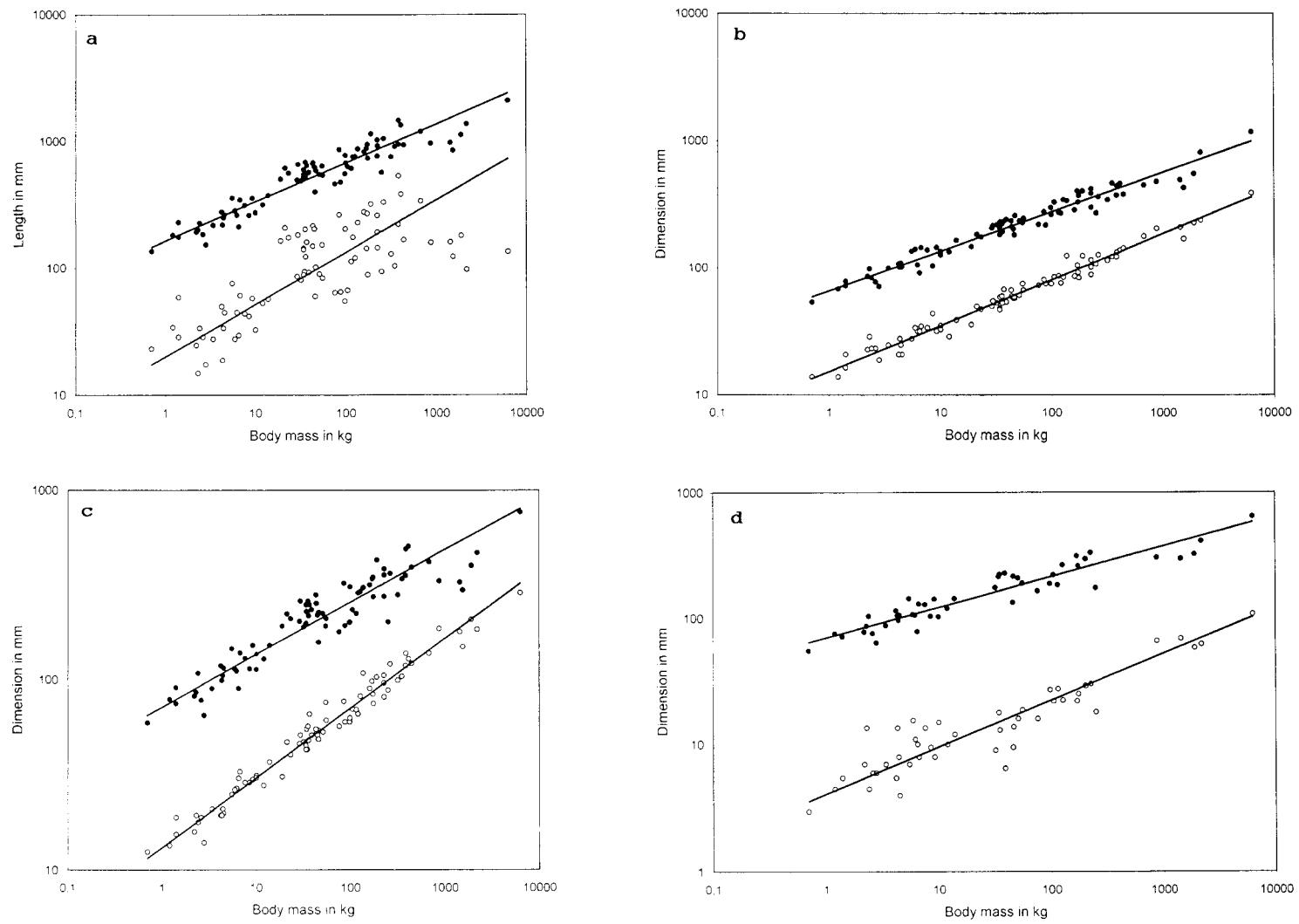


Figure 2

TABLE 2. Regression equations for all mammals in the form $Y = aX^b$, where X is body mass in kilograms and Y is an osteological parameter

Group	n	Least squares		RMA		95% CI	r
		a	b	a	b		
Length							
Forelimb	80	123.33	0.3344	114.30	0.3546	± 0.0380	0.9430
Humerus	80	57.541	0.2996	56.969	0.3109	± 0.0188	0.9636
Radius	80	53.953	0.2995	49.770	0.3210	± 0.0262	0.9330
Ulna	75	65.911	0.3016	62.087	0.3177	± 0.0234	0.9491
Metacarpal	80	20.107	0.3683	14.385	0.4574	± 0.0614	0.8053
Hind limb	80	176.62	0.2875	164.90	0.3058	± 0.0236	0.9403
Femur	80	68.338	0.3014	66.425	0.3089	± 0.0153	0.9757
Tibia	80	77.297	0.2571	71.804	0.2767	± 0.0231	0.9291
Fibula	47	75.407	0.2250	69.922	0.2430	± 0.0276	0.9260
Metatarsal	80	30.085	0.3047	20.320	0.4090	± 0.0618	0.7449
Least circumference							
Humerus	80	13.908	0.3816	13.680	0.3860	± 0.0132	0.9886
Radius	79	9.8743	0.3868	9.3455	0.4014	± 0.0244	0.9637
Ulna	73	6.8019	0.3551	4.6569	0.4579	± 0.0686	0.7756
Femur	80	15.732	0.3548	15.436	0.3599	± 0.0136	0.9860
Tibia	80	13.482	0.3600	13.207	0.3654	± 0.0143	0.9850
Fibula	47	4.5345	0.3379	4.1130	0.3681	± 0.0440	0.9180

predicted values. In large bovids (*Syncerus*, *Bison*, *Bubalus*) there is less difference, and both humeri and radii range from 78–105% of the predicted values, with ulnae being proportionally slightly longer than this. *Alces* and *Giraffa* display highly different fore-limb proportions from the other large ungulates, having humeri which are 103% and 102% of the predicted values, respectively, but radii which are 121% and fully 179%, respectively, of the predicted values. In carnivorans, the values differ less from each other, and both are around 120–130% in canids but only 105–115% in felids.

Metacarpal length differs greatly among the included species (Fig. 1a), and the rhinos (42–54% of predicted values), tapirs (56–72%), and especially hippos (34–48%) have a quite short and stocky metacarpus compared to fast-moving ungulates. In large bovids, the metacarpals are 63–124% of the predicted value. Smaller bovids and cervids have extremely long metacarpals (135–334%, the last value found in *Antidorcas*). In *Alces*, the value is 147% and in *Giraffa* a full 243%.

greatly contributing to the great overall fore-limb length. As expected, the unfused cannon bones of *Phacochoerus* were considerably shorter (61% of predicted value).

The equids also had quite long third metacarpals, although not to the extent seen in most artiodactyls (149% in *Equus burchelli* and 89% in *E. caballus*). The elephants had very short metacarpals (just 23% of the predicted value in the 3,534 kg *Elephas* and 26% in *Loxodonta*). The metacarpals of all carnivorans were considerably shorter than in comparably sized ungulates, ranging from 72% in the 230 kg *Panthera tigris altaica* to a full 147% in *Felis lynx*. The mustelids had rather short metacarpals (87% in *Gulo*, 68% in *Meles*), as did the ursids (45% in *Ursus americanus*, 46% in *U. thibetanus*, and 54% in *U. maritimus*).

The hind limb (Fig. 2a–d; Table 2) follows much the same pattern as the forelimb. Very large species tend to have shorter limbs and individual limb bones than predicted, with the elephants being more long-limbed. Most artiodactyls have proportionally slightly more elongated hind limbs than forelimbs, even among large species, ranging from 88% of the predicted length in *Syncerus* to 146% in *Antidorcas*. In contrast, felids and canids had hind limb lengths that, compared to predicted values, were either roughly comparable to or even slightly below the divergence from the predicted values of the forelimbs. Hind-limb lengths varied from 111–128% of the predicted values in canids and

Fig. 2. Hind-limb bones against body mass in all mammals. Regression lines fitted to the data by means of reduced major axis regression analysis. **a:** Hind-limb length (filled circles) and metatarsal length (open circles). **b:** Femoral length (filled circles) and femoral least circumference (open circles). **c:** Tibial length (filled circles) and tibial least circumference (open circles). **d:** Fibular length (filled circles) and fibular least circumference (open circles).

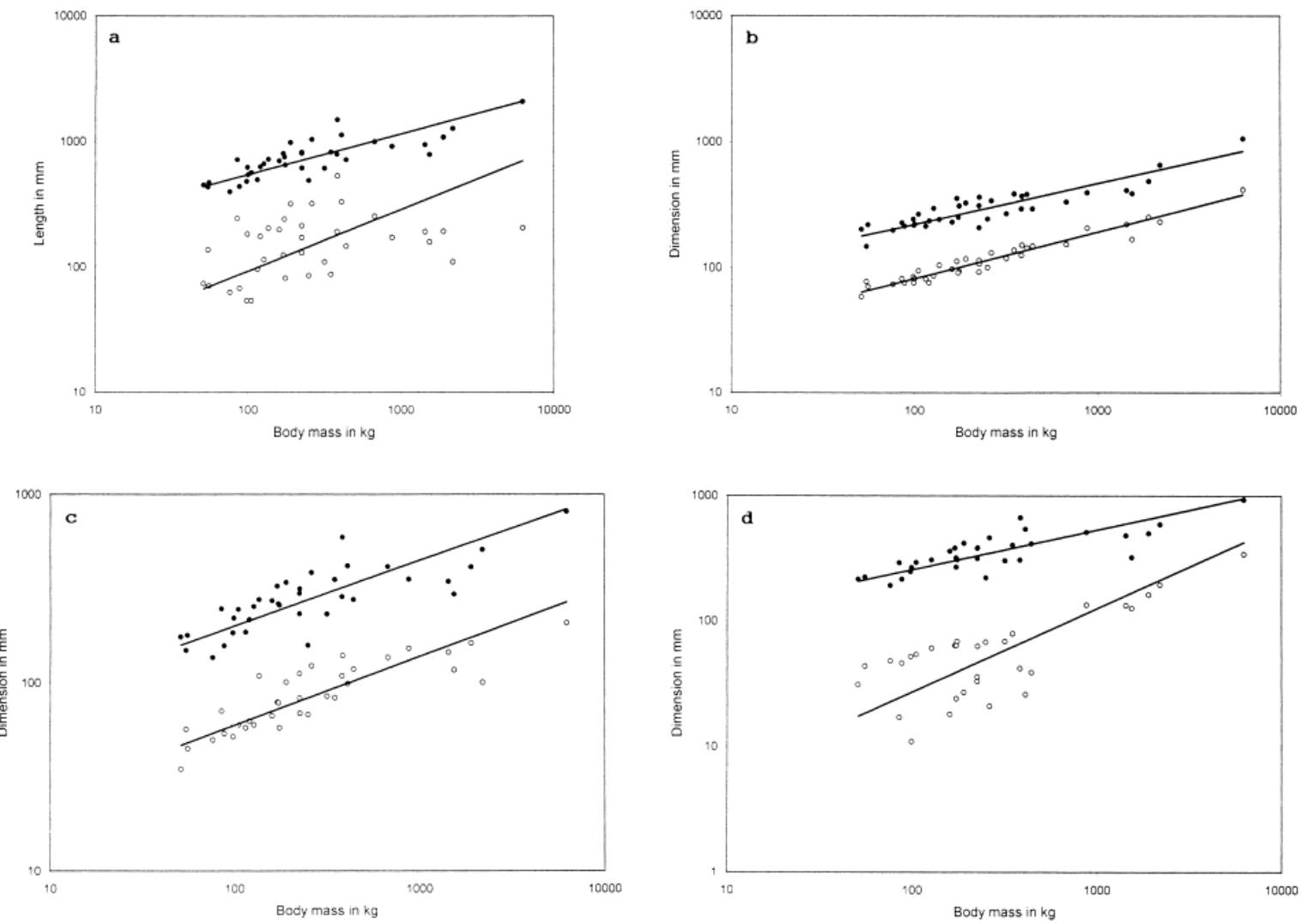


Figure 3

99–117% in felids. Ursids and mustelids also had proportionally shorter hind limbs than forelimbs, being 83–92% of the predicted values in ursids and 82% in *Meles* and 89% in *Gulo*.

Femoral length in most artiodactyls was usually slightly closer to the predicted values than was the case for the humeri. As with the radius, the tibia in the highly cursorial artiodactyls is usually more elongated than in comparably sized carnivorans, ranging from 119% in *Gazella* to 139% in *Tragelaphus strepsiceros*. In canids, the tibia ranged from 106% of the predicted value in *Alopex* to 118% in *Canis lupus*. Felids had tibial lengths ranging from 105% of the predicted value in *Panthera pardus* to 118% in *Acinonyx*. Ursids and mustelids had comparably shorter tibiae.

The metatarsals also show the heterogeneity noted above for the metacarpals (Fig. 2a) and usually are very long in ungulates with fused cannon bones, ranging from 170% of the length predicted by the comprehensive RMA equation (Table 2) in *Rangifer* to 293% in *Antidorcas*. Large bovids had metatarsal lengths closer to predicted values (139% in *Bison* and 96% in *Bubalus* but just 68% in *Syncerus*), as did equids (150% in *Equus burchelli* and 115% in *E. caballus*). Carnivorans had metatarsals that were subequal to or slightly more elongated compared to predicted values than was the case with the metacarpals. Curiously, *Vulpes* had a metatarsus fully 185% of the predicted value, by far the largest value of any carnivoran included. Suids, hippos, tapirs, and rhinos had short metatarsals, ranging from 40% of the predicted value in *Ceratotherium* to 61% in *Tapirus indicus* but just 27% in *Hippopotamus*, the latter value comparable to elephants (31% in the 3,534 kg *Elephas* and just 19% in *Loxodonta*).

The above results clearly show that large mammals, even fast-moving forms such as large bovids, have long bones that are considerably shorter than predicted compared to

smaller, anatomically very similar animals. This is also apparent in carnivorans and, to a lesser extent, perissodactyls, the only other groups with a large size range. Among mega-herbivore mammals, the trend towards increasingly shorter long bones to size is continued in forms capable of trotting and galloping with a suspended phase. Conversely, the rhinos and the hippo have proportionally much shorter limb bones than elephants.

Circumference is highly correlated with body mass in the bones primarily supporting body mass (Table 2), and, compared to length, the circumference values differed much less from the predicted values in all species (Figs. 1b–d, 2b–d), with the ulna and, in part, the fibula being the exceptions. The fibula is usually too thin to be of much importance in support of mass, and the ulna shows a marked dichotomy in this respect, as noted above. Elephants are quite unusual in this respect. The radii of the 3,534 kg *Elephas* and *Loxodonta* are 53% and 66%, respectively, of the predicted circumferences, but the ulnae are much sturdier, being 131% and 134% of the predicted values, respectively. This is also found to a lesser extent in felids and especially mustelids and ursids, whereas the two are more equal in girth among canids.

Humeral least circumferences in most artiodactyls were rather close to the predicted values, ranging from just 83% in *Gazella* to 110% in *Antidorcas*. This may seem rather surprising, as most of the artiodactyls are rather fast-moving forms, but the humeri were also rather short, as noted above, so parasagittal bending strength appears not to be reduced. Large forms such as *Tapirus*, *Syncerus*, *Bison*, or *Bubalus* also have long bones approximately as thick as predicted. Even in seemingly very sturdy-limbed rhinoceroses, the humeral least circumferences were close to the predicted values (111% in *Diceros* and 100% in *Ceratotherium*) and comparable to elephants (98% in the 3,534 kg *Elephas* and 104% in *Loxodonta*), but, unlike the rhinos, the elephants are long-limbed, and thus the strength of their bones is substantially less (Alexander, '85b, '89; Alexander and Pond, '92; Christiansen, '97). Femur and tibia in all species follow this pattern also.

The above matters little, as elephants are unable to run with a suspended phase (Gambaryan, '74; Alexander et al., '79b; Alexander

Fig. 3. Forelimb bones against body mass in large mammals. Regression lines fitted to the data by means of reduced major axis regression analysis. **a:** Forelimb length (filled circles) and metacarpal length (open circles). **b:** Humeral length (filled circles) and humeral least circumference (open circles). **c:** Radial length (filled circles) and radial least circumference (open circles). **d:** Ulnar length (filled circles) and ulnar least circumference (open circles).

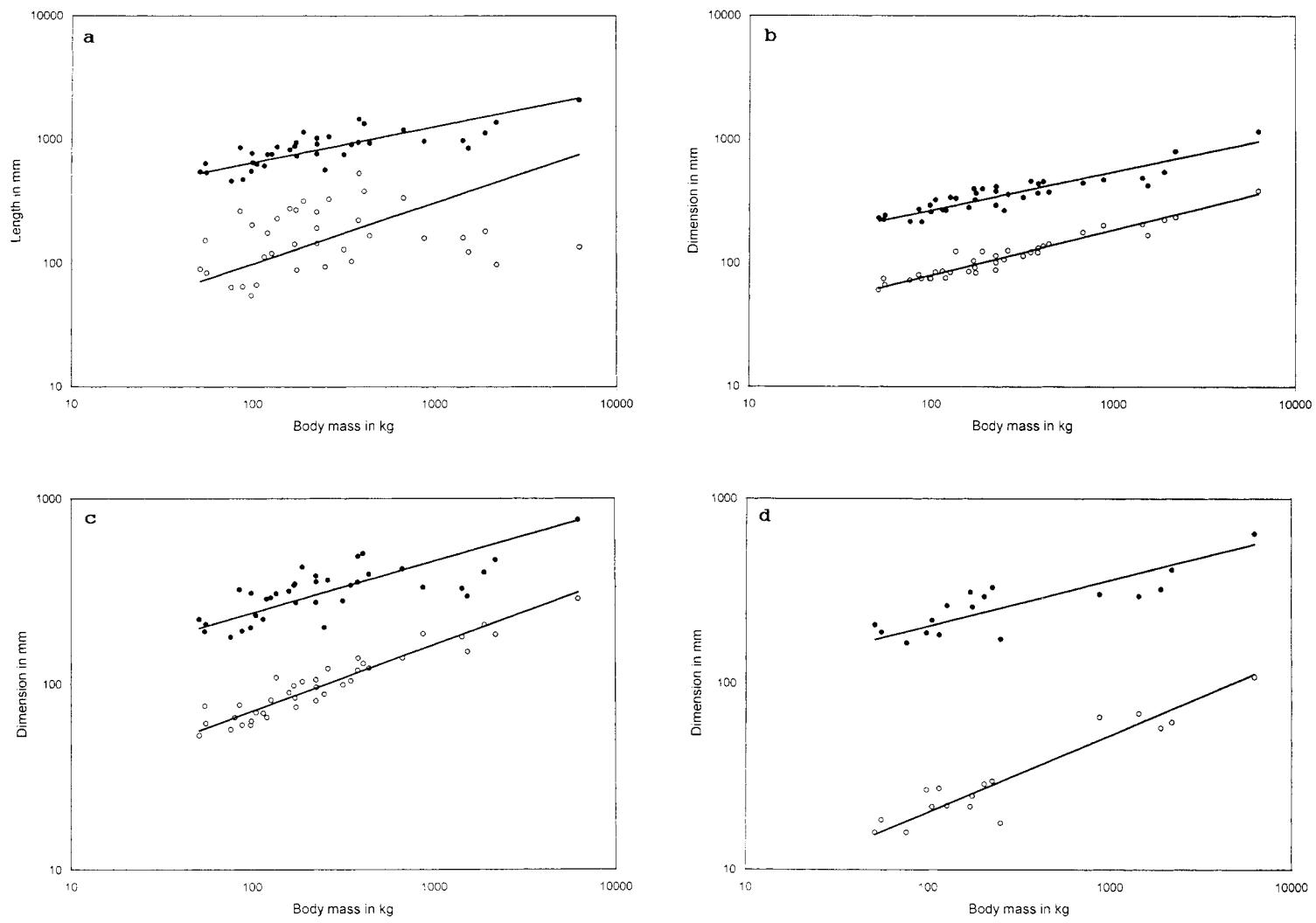


Figure 4

and Pond, '92), so the forces acting on their limbs are lower multiples of body mass (Alexander et al., '79b; Alexander and Pond, '92), in addition to being largely compressive. The lack of joint flexure in elephant limbs means that the limbs are kept rather straight during locomotion and the stresses set up in their limbs are comparable to those of other mammals, despite their massive size and long limbs (Gambaryan, '74; Alexander et al., '79b; Biewener, '90). Rhinoceroses and large bovids are capable of performing true running with a suspended phase (Gambaryan, '74; Alexander et al., '79b; Alexander and Pond, '92), and thus their limb bones are proportionally considerably shorter as a means of preserving bending strength. They are not, however, disproportionately thick, as suggested by Alexander ('97a, b), Alexander and Pond ('92), Biewener ('90), or Prothero and Sereno ('82).

In artiodactyls, the radius is much thicker than the ulna, except in suids, and one would expect very long-limbed species to have a radius markedly sturdier than predicted. This is also the case in some species (126% of the predicted value in *Antidorcas*, 136% in *Bison*, 133% in *Cervus timorensis*, 121% in *Dama*, and 136% in *Giraffa*) but not all (107% in *Bubalus*, 102% in *Gazella*, 109% in *Syncerus*, and just 94% in *Alces* and 93% in *Rangifer*).

When the RMA regression slopes for both length and least circumference calculated for all mammals (Table 2) are compared to the corresponding values calculated for large and small mammals (Figs. 3a-d, 4a-d, 5a-d, 6a-d; Table 3), a clear pattern emerges. No exponent for length in large mammals differs from the corresponding exponent for all mammals, and, in the case of ulna, femur, tibia, and fibula, the *t* values are so low (between 0.05 and 0.11) that significance cannot even be assumed at the level of 0.90. Among the exponents calculated for least circumference, only the ulna is significantly higher ($P < 0.05$) for large mammals, but

the low correlation coefficients and rather high residual variances of both samples indicate that this result is rather tentative.

For small mammals, the least circumference regression slopes are also not significantly different from the corresponding values calculated for all mammals, with the exception of the radius, which has a significantly higher slope in small mammals ($P < 0.01$). The correlation coefficients of both samples are high (Tables 2, 3), and conversely the residual variances are low, making this difference more reliable than the above. In marked contrast, the regression slopes for lengths in small mammals are all significantly higher than the corresponding values for all mammals ($P < 0.05$ for forelimb, humerus, and fibula, $P < 0.01$ for radius and ulna, and $P < 0.001$ for metacarpus, hind limb, tibia, and metatarsus). The only exception is femoral length, which proved nonsignificant at the 5% level, although the value ($t_{119} = 1.9208$) was very close to being significant (table value $t_{120} = 1.980$).

When compared to each other, the two subsets of large and small mammals (Figs. 3a-d, 4a-d, and 5a-d, 6a-d; Table 3) appear to differ slightly less than when small mammals are compared to all mammals. Initially this may seem surprising, but, in the case of the regression slopes for length, this is largely due to the considerably greater residual variances, as shown by the lower correlation coefficients, of especially large mammals (Table 3), making a rejection of the null hypothesis more difficult. The values calculated by least squares regression differ substantially, but the RMA is probably the more appropriate model to use on these kinds of data. The correlation coefficients for least circumference are usually considerably higher than for length (Table 3), but the regression slopes for large, and small mammals only differ for radius and ulna.

In accordance with the above conclusion that large mammals preserve bending strength by evolving progressively shorter but not particularly thicker long bones, one would expect the regression slopes for least circumference not to differ substantially between large and small mammals, and the two that do differ (radius and ulna) correlate rather poorly with body mass. This result seems reliable, as the other long bones that do not differ significantly display quite high correlation coefficients in both samples

Fig. 4. Hind-limb bones against body mass in large mammals. Regression lines fitted to the data by means of reduced major axis regression analysis. **a:** Hind-limb length (filled circles) and metatarsal length (open circles). **b:** Femoral length (filled circles) and femoral least circumference (open circles). **c:** Tibial length (filled circles) and tibial least circumference (open circles). **d:** Fibular length (filled circles) and fibular least circumference (open circles).

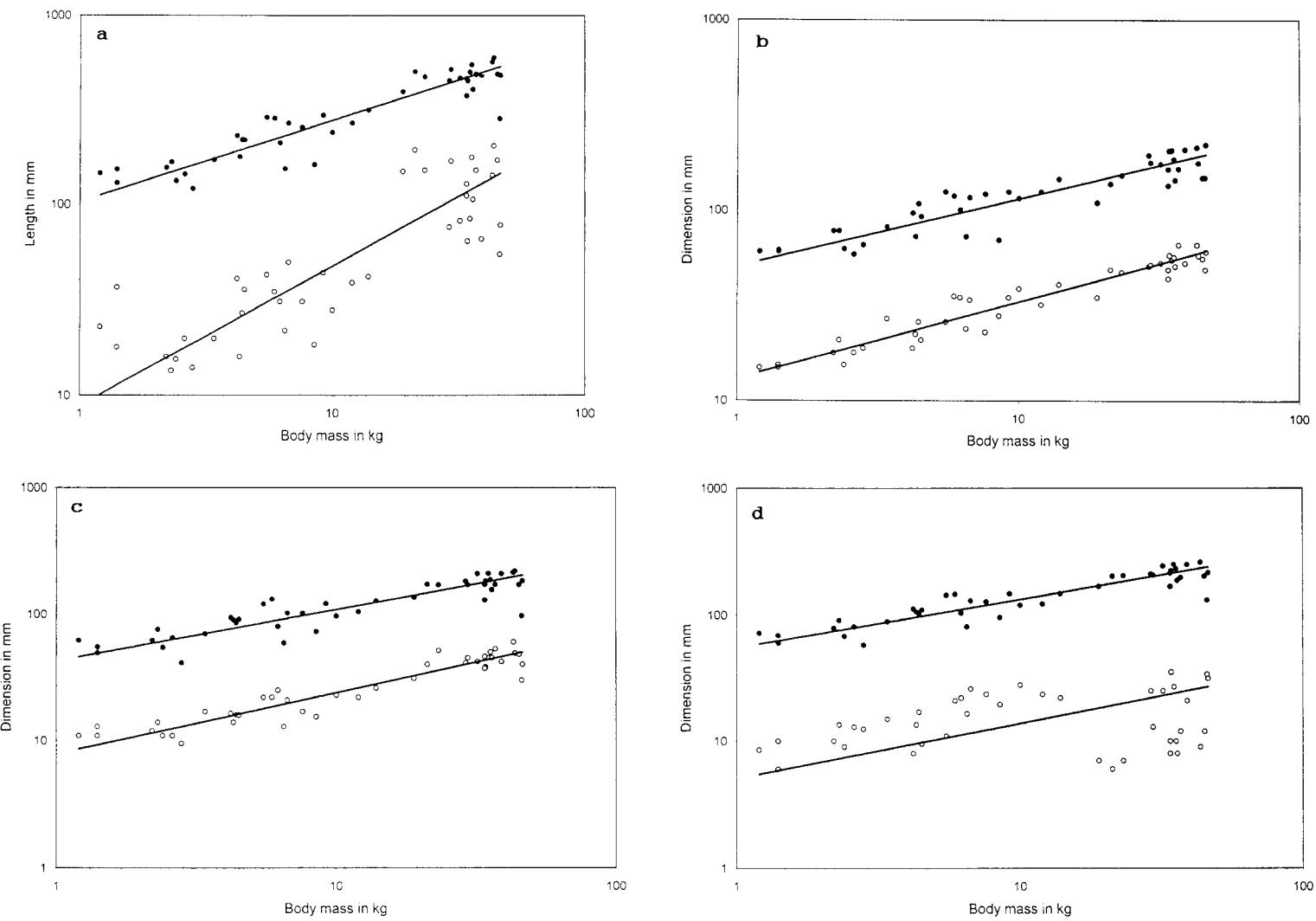


Figure 5

(Table 3). In contrast, the length exponents for large mammals are unanimously lower, often considerably so, as would be expected if length was the more important factor in preserving bending strength among large species. The high residual variances of the samples, however, do not allow significance to be assumed. If one compares the least squares regression slopes, however, the two samples do appear quite different (Table 3).

The Artiodactyla do not form a particularly more homogeneous group with respect to long-bone scaling than either all mammals taken together or large mammals, as shown by the often rather unimpressive correlation coefficients, especially for bone lengths (Table 4). The Carnivora, however, generally display much higher correlation coefficients than the Artiodactyla. Both are usually considered morphologically and biomechanically homogenous groups (McMahon, '75b; Bertram and Biewener, '90; Nowak, '91), so the markedly higher correlation coefficients observed among carnivorans could hardly be due to greater differences in locomotor style among the Artiodactyla. Rather, the carnivorans included in this study probably display slightly greater locomotory diversity than the included artiodactyls, with mustelids usually having a more bounding gait than larger species and *Gulo* and the ursids employing a type of locomotion usually described as rolling (Nowak, '91). This differs slightly from that of canids and felids, which tend to move in a similar fashion to artiodactyls.

It seems more likely that the Carnivora form a less divergent assemblage with respect to range of body mass and are thus largely subjected to similar anatomical modifications for coping with increases in body size. The included artiodactyls span a much wider range of body masses (1.4–2,400 kg), thus spanning the entire size range where differences in limb posture, locomotory potential, and possibly duty factors, as described in the introduction section, in addition to

differences in bone allometry, contribute markedly to maintaining peak stress in the bones during fast locomotion at fairly uniform levels. This of course is also the case in the sample for all mammals, which usually display considerably higher correlation coefficients, and thus it is possible that the artiodactyl sample just happened to include an assemblage of species pointing out these differences to a greater extent. McMahon ('75b) also generally calculated lower correlation coefficients for Artiodactyla compared to its subgroups.

Examination of the residuals of the above data sets failed to show significant departure from the applied power functions (Figs. 7–9), and it seems that no data set shows clear signs of nonlinearity. In the case of metacarpal length for all mammals, one may argue that a vague tendency towards curvilinearity is present in the plot of residuals (Fig. 7c), although rather indistinct. In all other cases, no structure is apparent in the plots of residuals, either for all mammals (Fig. 7a–c), small mammals (Fig. 8a–c), or large mammals (Fig. 9a,c).

When a polynomial regression model is applied to the samples comprising all mammals, the correlation coefficients were usually very similar to the ones obtained from linear regression. The exceptions were ulnar length and circumference, where the correlation coefficients were slightly higher ($r = 0.9546$ and $r = 0.8041$ for length and least circumference, respectively, compared to $r = 0.9491$ and $r = 0.7756$, as shown in Table 2).

The metapodials, however, displayed more distinct signs of curvilinearity, as noted above. Metacarpal length was better explained by the polynomial regression equation

$$\ln Y = -0.0488 \ln X^2 + 0.7430 \ln X + 2.4736,$$

$$r = 0.8451$$

compared to the r value of 0.8053 obtained from linear regression (Table 2). This was also the case for the metatarsus, with the equation

$$\ln Y = -0.0516 \ln X^2 + 0.7009 \ln X + 2.8462,$$

$$r = 0.8042$$

compared to $r = 0.7449$ obtained from linear regression (Table 2). This is probably largely due to the small end of the mass range included in this paper being dominated by carnivorans, which have rather short metapodials, as noted above (Figs. 1a, 2a), whereas the medium-large size range is

Fig. 5. Forelimb bones against body mass in small mammals. Regression lines fitted to the data by means of reduced major axis regression analysis. **a:** Forelimb length (filled circles) and metacarpal length (open circles). **b:** Humeral length (filled circles) and humeral least circumference (open circles). **c:** Radial length (filled circles) and radial least circumference (open circles). **d:** Ulnar length (filled circles) and ulnar least circumference (open circles).

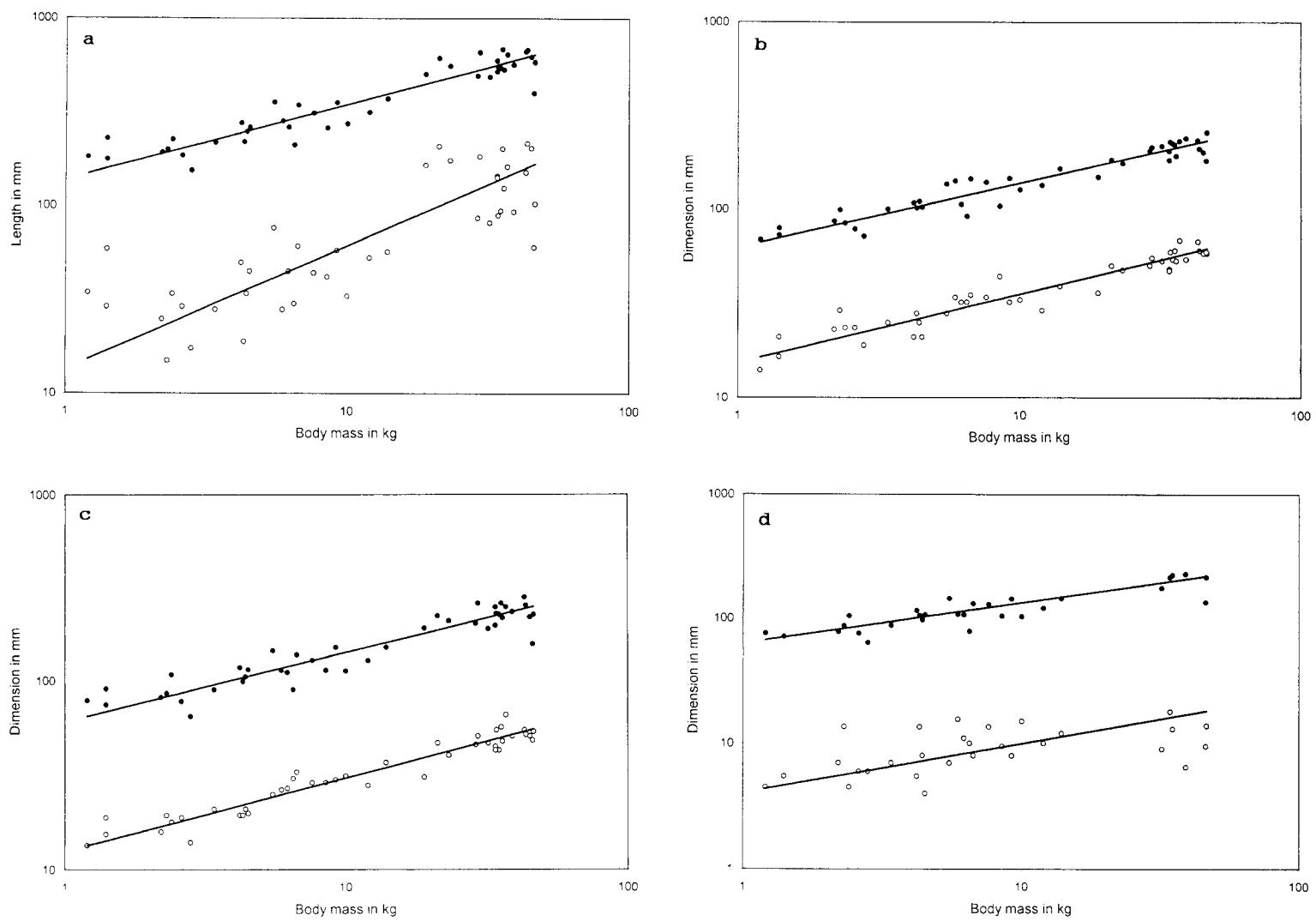


Figure 6

TABLE 3. Regression equations for small–medium and medium–very large mammals in the form $Y = aX^b$, where X is body mass in kilograms and Y is an osteological parameter¹

Group	n	Least squares		RMA		95% CI	r
		a	b	a	b		
1–50 kg							
Length							
Forelimb	43	112.24	0.3959	103.68	0.4292	±0.0524	0.9223
Humerus	43	55.068	0.3211	51.231	0.3514	±0.0451	0.9136
Radius	43	47.404	0.3637	42.803	0.4066	±0.0574	0.8944
Ulna	42	59.396	0.3522	55.229	0.3832	±0.0483	0.9191
Metacarpal	43	11.581	0.6179	8.8820	0.7294	±0.1224	0.8471
Hind limb	43	146.89	0.3739	138.19	0.3995	±0.0445	0.9357
Femur	43	64.846	0.3274	62.575	0.3424	±0.0317	0.9561
Tibia	43	64.618	0.3431	60.951	0.3636	±0.0417	0.9331
Fibula	29	71.265	0.2631	63.295	0.3236	±0.0744	0.8131
Metatarsal	43	18.010	0.5331	13.592	0.6534	±0.1184	0.8189
Least circumference							
Humerus	43	13.656	0.3864	13.188	0.4010	±0.0339	0.9638
Radius	42	8.4634	0.4528	7.9116	0.4811	±0.0520	0.9412
Ulna	41	10.852	0.1127	5.0618	0.4374	±0.1367	0.2581
Femur	43	16.044	0.3444	15.389	0.3619	±0.0351	0.9516
Tibia	43	13.005	0.3734	12.579	0.3874	±0.0326	0.9638
Fibula	29	5.8312	0.2059	4.0747	0.3887	±0.1302	0.5298
>50 kg							
Length							
Forelimb	36	173.83	0.2610 ³	122.26	0.3247 ²	±0.0676	0.8039
Humerus	36	60.830	0.2878	50.185	0.3226	±0.0511	0.8921
Radius	36	60.114	0.2754	40.670	0.3461	±0.0734	0.7957
Ulna	32	84.826	0.2542 ²	58.829	0.3195	±0.0722	0.7954
Metacarpal	36	3.9759	0.1829 ⁴	9.8864	0.4877 ²	±0.1583	0.3749
Hind limb	36	247.85	0.2224 ⁴	169.56	0.2911 ³	±0.0577	0.7640
Femur	36	76.147	0.2804	64.647	0.3101	±0.0463	0.9044
Tibia	36	101.67	0.2028 ⁴	66.813	0.2788 ²	±0.0670	0.7275
Fibula	17	82.910	0.2050	65.400	0.2472	±0.0760	0.8295
Metatarsal	36	89.011	0.1015 ⁴	10.454	0.4891	±0.1676	0.2076
Least circumference							
Humerus	36	15.911	0.3587	14.964	0.3698	±0.0315	0.9699
Radius	36	15.013	0.3106 ⁴	11.320	0.3617 ³	±0.0649	0.8587
Ulna	31	3.2481	0.4971 ⁴	1.2733	0.6647 ²	±0.1676	0.7479
Femur	36	15.946	0.3536	14.843	0.3666	±0.0339	0.9646
Tibia	36	15.323	0.3375	13.813	0.3564	±0.0400	0.9471
Fibula	17	3.5245	0.3877 ²	3.1031	0.4103	±0.0739	0.9449

¹Ninety-five percent confidence limits are given for the slopes.

²Significance at the 5% level from the corresponding regression coefficient from the 1–50 kg group.

³Significance at the 1% level from the corresponding regression coefficient from the 1–50 kg group.

⁴Significance at the 0.1% level from the corresponding regression coefficient from the 1–50 kg group.

dominated by the ungulates. For large species, the reduction in length as a means of preserving bending strength is also evident in the metapodials, forcing the regression curve downwards.

As noted above, there seems to be a tendency for large mammals to reduce the

length of their limbs to a greater extent than increasing the cross-sectional area of the bones as a means of coping with increased body mass. On average, the regression slopes for length for all mammals appear rather close to the value of $M^{0.33}$ predicted by geometric similarity, whereas the values for least circumference appear closer to the value of $M^{0.375}$ predicted by elastic similarity (Table 2), which at first glance is not what one might expect. This is also the case in the subset of large mammals (Table 3). In small mammals, the length coefficients on average appear to be considerably higher than predicted by even geometric similarity, whereas the least circumference values often appear elastically similar (Table 3).

Fig. 6. Hind-limb bones against body mass in small mammals. Regression lines fitted to the data by means of reduced major axis regression analysis. **a:** Hind-limb length (filled circles) and metatarsal length (open circles). **b:** Femoral length (filled circles) and femoral least circumference (open circles). **c:** Tibial length (filled circles) and tibial least circumference (open circles). **d:** Fibular length (filled circles) and fibular least circumference (open circles).

TABLE 4. Regression equations for the orders Carnivora and Artiodactyla in the form $Y = aX^b$, where X is body mass in kilograms and Y is an osteological parameter¹

Group	n	Least squares		RMA		95% CI	r
		a	b	a	b		
Carnivora							
Length							
Forelimb	31	128.15	0.3360	125.79	0.3426	±0.0254	0.9808
Humerus	31	56.807	0.3410	56.157	0.3451	±0.0201	0.9882
Radius	31	51.982	0.3339	50.688	0.3428	±0.0295	0.9740
Ulna	31	62.881	0.3338	61.643	0.3408	±0.0262	0.9794
Metacarpal	31	18.880	0.3260	17.170	0.3596	±0.0576	0.9066
Hind limb	31	162.24	0.3108	159.31	0.3173	±0.0242	0.9797
Femur	31	63.920	0.3461	63.461	0.3486	±0.0160	0.9927
Tibia	31	70.727	0.2855	69.031	0.2941	±0.0268	0.9709
Fibula	31	67.245	0.2826	65.410	0.2925	±0.0292	0.9661
Metatarsal	30	27.913	0.2727	24.991	0.3118	±0.0574	0.8746
Least circumference							
Humerus	31	13.924	0.3893	13.738	0.3941	±0.0232	0.9879
Radius	30	9.8697	0.3754	9.6970	0.3816	±0.0265	0.9838
Ulna	30	8.0623	0.4097	7.2234	0.4482	±0.0704	0.9139
Femur	31	14.928	0.3592	14.744	0.3636	±0.0215	0.9878
Tibia	31	13.222	0.3619	13.072	0.3659	±0.0206	0.9889
Fibula	30	4.1586	0.3437	3.7910	0.3772	±0.0598	0.9124
Artiodactyla							
Length							
Forelimb	31	184.85	0.2587	145.06	0.3134	±0.0672	0.8256
Humerus	31	57.796	0.2863	53.315	0.3045	±0.0394	0.9402
Radius	31	63.048	0.2693	48.801	0.3271	±0.0705	0.8233
Ulna	28	77.249	0.2730	62.433	0.3208	±0.0679	0.8511
Metacarpal	31	63.314	0.2116	28.740	0.3898	±0.1243	0.5429
Hind limb	31	269.14	0.2182	212.56	0.2714	±0.0613	0.8039
Femur	31	77.636	0.2660	72.877	0.2803	±0.0335	0.9490
Tibia	31	108.47	0.2027	84.223	0.2598	±0.0617	0.7803
Metatarsal	31	86.876	0.1631	34.248	0.3731	±0.1274	0.4370
Least circumference							
Humerus	31	14.312	0.3730	13.667	0.3834	±0.0337	0.9729
Radius	31	13.437	0.3452	12.167	0.3676	±0.0480	0.9390
Ulna	27	2.0937	0.4891	1.3595	0.5872	±0.1338	0.8330
Femur	31	17.182	0.3339	16.402	0.3444	±0.0320	0.9696
Tibia	31	15.371	0.3354	14.317	0.3514	±0.0399	0.9544

¹Ninety-five percent confidence limits are given for the slopes. No regression equation is given for fibula in artiodactyls, as it was usually broken in the specimens examined or very reduced.

When the regression slopes for the three data samples are compared statistically to the values predicted by geometric and elastic similarity (Table 5), no clear picture emerges. In all mammals, the regression slopes for length are in fact often significantly different from geometric similarity despite appearing quite similar, the exception being some of the forelimb bones. It is evident, however, that the values are usually highly significantly different from elastic similarity. For least circumference, the values are in fact closer to elastic similarity, although the frequently very high correlation coefficients make values that visually appear to differ little from the predicted value statistically different (e.g., femur). Clearly the slopes differ from geometric similarity to a much greater extent.

For small mammals, the regression slopes for length also frequently differ significantly from either elastic or geometric similarity (Table 5), although more so from the former, and the hind-limb bones are in fact rather close to being geometrically similar. A similar result was obtained by Christiansen (in press). The rather poor correlation of the metapodials (Table 3) makes the interpretation of the extent to which their regression slopes differ from geometric or elastic similarity tentative. As for all mammals, the regression slopes for least circumference also tend to conform to elastic similarity to a greater extent than geometric similarity (Table 5).

Large mammals are somewhat more equivocal due to the almost uniformly lower correlation coefficients (Table 3). If the length

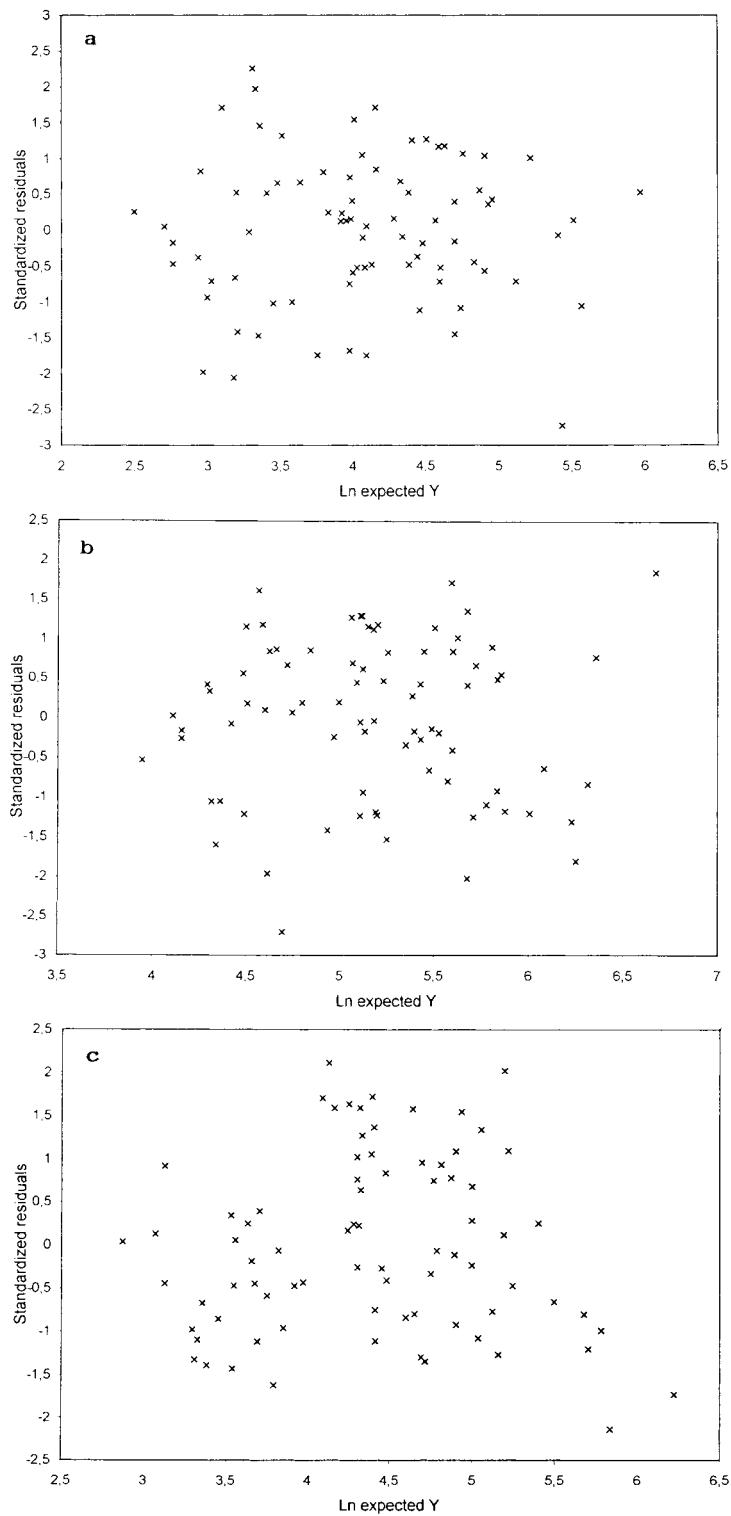


Fig. 7. Plots of residuals against expected value for the osteological parameter in question for all mammals. **a:** Humeral least circumference. **b:** Humeral length. **c:** Metacarpal length.

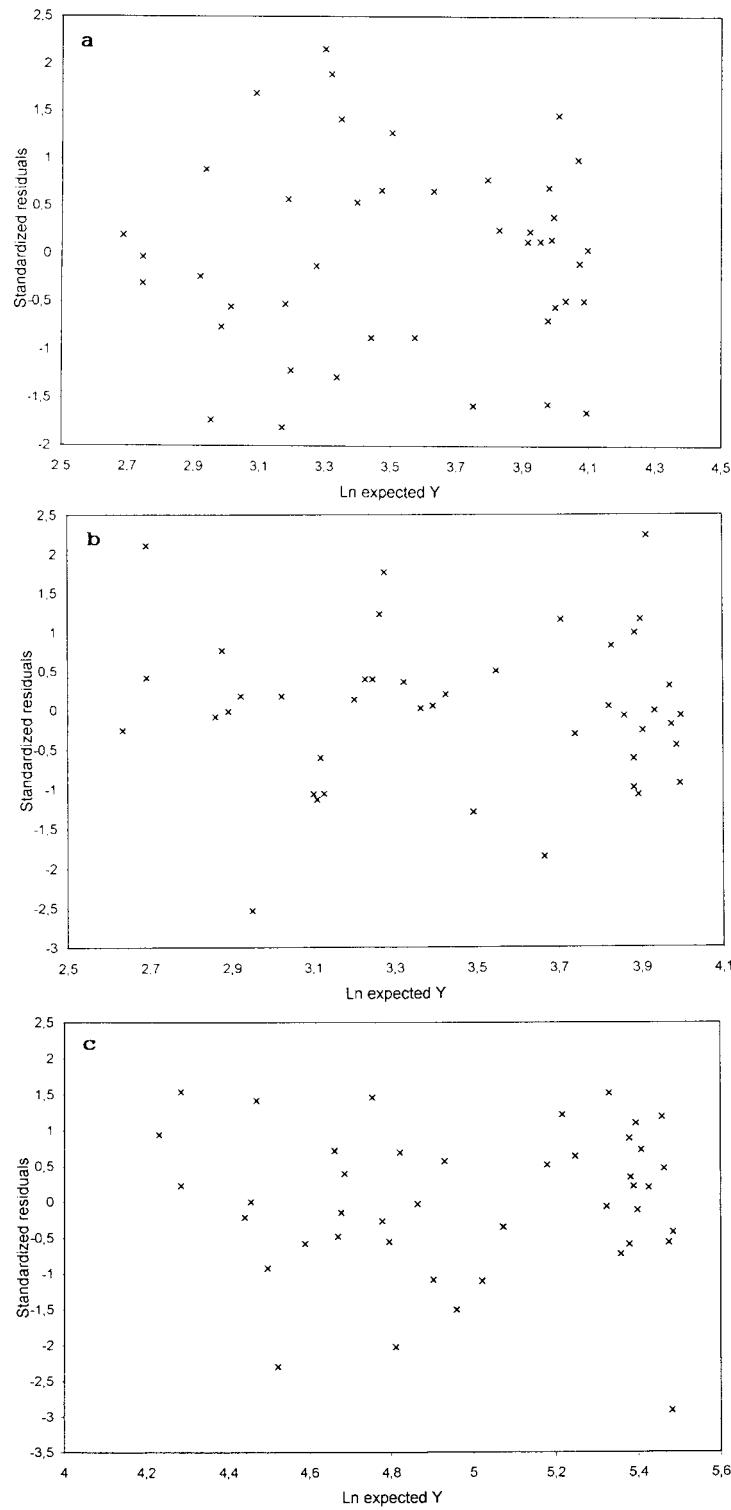


Fig. 8. Plots of residuals against expected value for the osteological parameter in question for small mammals. **a:** Humeral least circumference. **b:** Tibial least circumference. **c:** Tibial length.

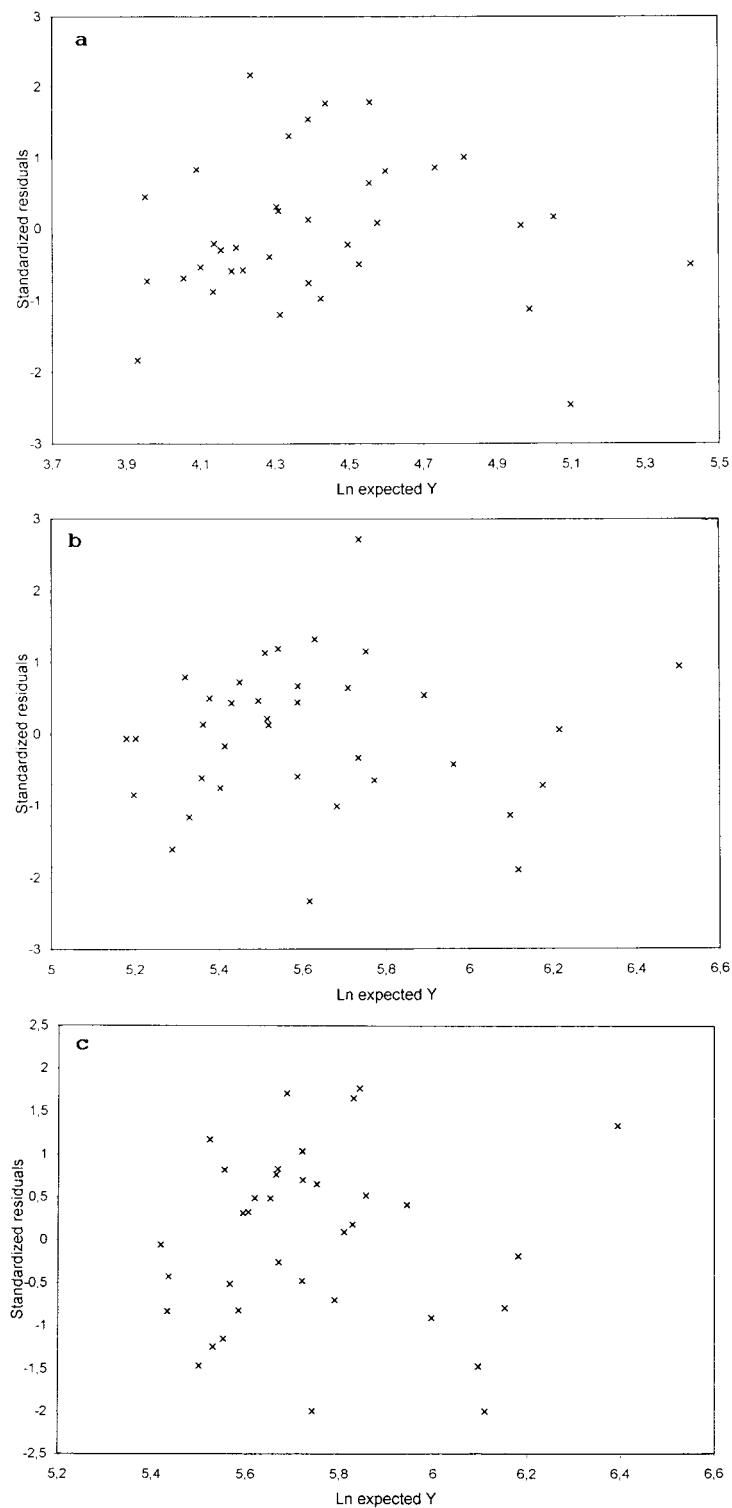


Fig. 9. Plots of residuals against expected value for the osteological parameter in question for large mammals. **a:** Radial least circumference. **b:** Radial length. **c:** Tibial length.

TABLE 5. Comparison of the calculated regression slopes with elastic similarity, predicting bone lengths proportional to $M^{0.25}$ and least circumferences to $M^{0.375}$, and geometric similarity, predicting lengths and least circumferences proportional to $M^{0.33}$

Group	n	Length						Least circumference					
		Least squares			RMA			Least squares			RMA		
		b	0.25 ¹	0.33 ¹	b	0.25 ¹	0.33 ¹	b	0.375 ¹	0.33 ¹	b	0.375 ¹	0.33 ¹
All mammals													
Forelimb	80	0.3344	0.1	NS	0.3546	0.1	NS	—	NS	0.1	0.3860	NS	0.1
Humerus	80	0.2996	0.1	1	0.3109	0.1	5	0.3816	NS	0.1	0.3860	5	0.1
Radius	80	0.2995	0.1	5	0.3210	0.1	NS	0.3868	NS	0.1	0.4014	5	0.1
Ulna	75	0.3016	0.1	5	0.3177	0.1	NS	0.3551	NS	NS	0.4579	5	0.1
Metacarpal	80	0.3683	0.1	NS	0.4574	0.1	0.1	—	—	—	—	—	—
Hind limb	80	0.2875	1	0.1	0.3058	0.1	5	—	—	—	—	—	—
Femur	80	0.3014	0.1	0.1	0.3089	0.1	1	0.3548	1	0.1	0.3599	5	0.1
Tibia	80	0.2571	NS	0.1	0.2767	5	0.1	0.3600	5	0.1	0.3654	NS	0.1
Fibula	47	0.2250	NS	0.1	0.2430	NS	0.1	0.3379	NS	NS	0.3681	NS	NS
Metatarsal	80	0.3047	NS	NS	0.4090	0.1	5	—	—	—	—	—	—
1–50 kg													
Forelimb	43	0.3959	0.1	5	0.4292	0.1	0.1	—	—	—	—	—	—
Humerus	43	0.3211	1	NS	0.3514	0.1	NS	0.3864	NS	1	0.4010	NS	0.1
Radius	43	0.3637	0.1	NS	0.4066	0.1	5	0.4528	1	0.1	0.4811	0.1	0.1
Ulna	42	0.3522	0.1	NS	0.3832	0.1	5	0.1127	0.1	1	0.4374	NS	NS
Metacarpal	43	0.6179	0.1	1	0.7294	0.1	0.1	—	—	—	—	—	—
Hind limb	43	0.3739	0.1	NS	0.3995	0.1	1	—	—	—	—	—	—
Femur	43	0.3274	0.1	NS	0.3424	0.1	NS	0.3444	NS	NS	0.3619	NS	NS
Tibia	43	0.3431	0.1	NS	0.3636	0.1	NS	0.3734	NS	5	0.3874	NS	0.1
Fibula	29	0.2631	NS	NS	0.3236	NS	NS	0.2059	5	NS	0.3887	NS	NS
Metatarsal	43	0.5331	0.1	1	0.6534	0.1	0.1	—	—	—	—	—	—
>50 kg													
Forelimb	36	0.2610	NS	5	0.3247	5	NS	—	—	—	—	—	—
Humerus	36	0.2878	NS	NS	0.3226	1	NS	0.3587	NS	NS	0.3698	NS	5
Radius	36	0.2754	NS	NS	0.3461	5	NS	0.3106	NS	NS	0.3617	NS	NS
Ulna	32	0.2542	NS	5	0.3195	NS	NS	0.4971	NS	NS	0.6647	1	0.1
Metacarpal	36	0.1829	NS	NS	0.4877	1	NS	—	—	—	—	—	—
Hind limb	36	0.2224	NS	5	0.2911	NS	NS	—	—	—	—	—	—
Femur	36	0.2804	NS	5	0.3101	5	NS	0.3536	NS	NS	0.3666	NS	5
Tibia	36	0.2028	NS	0.1	0.2788	NS	NS	0.3375	NS	NS	0.3564	NS	NS
Fibula	17	0.2050	NS	1	0.2472	NS	5	0.3877	NS	NS	0.4103	NS	5
Metatarsal	36	0.1015	NS	1	0.4891	1	NS	—	—	—	—	—	—

¹Percent level of significance. NS, no significant difference.

exponents had been found by least squares regression only, one might conclude that large mammals were elastically similar, whereas small mammals were geometrically similar, as is clearly the case in Table 5. The RMA regression slopes from Table 5 for length, however, show almost the opposite. The regression slopes for least circumference support neither geometric nor elastic similarity. The few least circumference regression slopes for large mammals showing a correlation coefficient that is sufficiently high (Table 3) to allow one to assume that the results of a *t*-test against a theoretical value might yield a reliable result (humerus and all three hind-limb bones) do not clearly support either geometric or elastic similarity, although most appear closer to elastic similarity.

No clear picture emerges from Artiodactyla and Carnivora either (Table 6). Carniv-

orans, however, are often geometrically similar with respect to length of the long bones, whereas the regression slopes for least circumference tend to be elastically similar. As the correlation coefficients for this data sample are generally rather impressive (Table 4), one may consider these conclusions more firm than much of the above. With the exception of the humerus and femur, the regression slopes for length in Artiodactyla are unimpressive to poor (Table 4). As with the subset of large mammals, this results in model I and model II regression slopes tending to support a different model for long bone scaling (Table 6). With the exception of the ulna, the correlation coefficients for least circumference are much higher (Table 4), but neither elastic nor geometric similarity appears to be supported.

Thus, when correlation coefficients are much below 0.95 and certainly when they

TABLE 6. Comparison of the calculated regression slopes for the orders Carnivora and Artiodactyla with elastic similarity, predicting bone lengths proportional to $M^{0.25}$ and least circumferences to $M^{0.375}$, and geometric similarity, predicting lengths and least circumferences proportional to $M^{0.33}$

Group	n	Length						Least circumference					
		Least squares			RMA			Least squares			RMA		
		b	0.25 ¹	0.33 ¹	b	0.25 ¹	0.33 ¹	b	0.375 ¹	0.33 ¹	b	0.375 ¹	0.33 ¹
Carnivora													
Forelimb	31	0.3360	0.1	NS	0.3426	0.1	NS	—			—		
Humerus	31	0.3410	0.1	NS	0.3451	0.1	NS	0.3893	NS	0.1	0.3941	NS	0.1
Radius	31	0.3339	0.1	NS	0.3428	0.1	NS	0.3754	NS	1	0.3816	NS	0.1
Ulna	31	0.3338	0.1	NS	0.3408	0.1	NS	0.4097	NS	5	0.4482	5	1
Metacarpal	31	0.3260	0.1	NS	0.3596	0.1	NS	—			—		
Hind limb	31	0.3108	0.1	NS	0.3173	0.1	NS	—			—		
Femur	31	0.3461	0.1	5	0.3486	0.1	5	0.3592	NS	1	0.3636	NS	1
Tibia	31	0.2855	5	1	0.2941	1	5	0.3619	NS	1	0.3659	NS	1
Fibula	30	0.2826	5	1	0.2925	1	5	0.3437	NS	NS	0.3772	NS	NS
Metatarsal	31	0.2727	NS	NS	0.3118	5	NS	—			—		
Artiodactyla													
Forelimb	31	0.2587	NS	5	0.3134	NS	NS	—			—		
Humerus	31	0.2863	NS	5	0.3045	1	NS	0.3730	NS	5	0.3834	NS	1
Radius	31	0.2693	NS	NS	0.3271	5	NS	0.3452	NS	NS	0.3676	NS	NS
Ulna	28	0.2730	NS	NS	0.3208	5	NS	0.4891	NS	5	0.5872	1	0.1
Metacarpal	31	0.2116	NS	0.1	0.3898	5	NS	—			—		
Hind limb	31	0.2182	NS	0.1	0.2714	NS	NS	—			—		
Femur	31	0.2660	NS	0.1	0.2803	NS	1	0.3339	5	NS	0.3444	NS	NS
Tibia	31	0.2027	NS	NS	0.2598	NS	5	0.3354	NS	NS	0.3514	NS	NS
Metatarsal	31	0.1631	NS	NS	0.3731	NS	NS	—			—		

¹Percent level of significance. NS, no significant difference.

are below 0.90, the choice of statistical model used to describe the data becomes increasingly important. One might very well find support for elastic similarity from one statistical model and geometric similarity from another, based on the same data. Regression slopes calculated from samples without sufficiently high correlation coefficients can probably yield little support to either geometric or elastic similarity, especially in the case of least circumference, where the regression slopes of the two differ less.

The results presented above indicate that rather than strong limb allometry in the sense of increasing the cross-sectional area of the bones, large mammals appear to rely more on developing proportionally shorter long bones as a means of reducing bending stress in their diaphyses, thus decreasing the size of the moment arm of the bending moments about the diaphyses. Some large species are very long-limbed, however (e.g., *Alces* and *Giraffa*), and their bones would appear rather undersized for fast locomotion, in contrast to the observed locomotory performance of the species (Alexander et al., '77; Nowak, '91). As noted by Alexander and Pond ('92), more work is needed to evaluate this apparent discrepancy, and their adaptations for coping with large size while main-

taining the capacity for fast locomotion are presently not fully understood. Unfortunately no study of the bone strength of these large, long-limbed species has been published. Other smaller species are also very long-limbed compared to phylogenetically similar forms (e.g., *Chrysocyon*) despite appearing not to have different limb kinematics or locomotory ability (Nowak, '91).

The above data samples tend to support neither geometric nor elastic similarity, making both questionable as a means of explaining long-bone scaling in terrestrial mammals. The apparently great importance of especially size-related differences in limb posture as a means of reducing skeletal stress, and to a lesser extent decreased locomotory performance among very large species, necessitates that these issues are also addressed when analyzing long-bone allometry. As pointed out by Economos ('83) a power function probably cannot satisfactorily explain skeletal allometry across a large size range of mammals, as it fails to address these issues.

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