

Mass Allometry of the Appendicular Skeleton in Terrestrial Mammals

Per Christiansen*

Department of Vertebrates, Zoological Museum, DK-2100 Copenhagen Ø, Denmark

ABSTRACT Most analyses on allometry of long bones in terrestrial mammals have focused on dimensional allometry, relating external bone measurements either to each other or to body mass. In this article, an analysis of long bone mass to body mass in 64 different species of mammals, spanning three orders of magnitude in body mass, is presented. As previously reported from analyses on total skeletal mass to body mass in terrestrial vertebrates, the masses of most appendicular bones scale with significant positive allometry. These include the pectoral and pelvic girdles, humerus, radius+ulna, and forelimb. Total hindlimb mass and the masses of individual hindlimb bones (femur, tibia, and metatarsus) scale isometrically. Metapodial mass correlates more poorly with body mass than the girdles or any of the long bones. Metapodial mass

probably reflects locomotor behavior to a greater extent than do the long bones. Long bone mass in small mammals (<50 kg) scales with significantly greater positive allometry than bone mass in large (>50 kg) mammals, probably because of the proportionally shorter long bones of large mammals as a means of preserving resistance to bending forces at large body sizes. The positive allometric scaling of the skeleton in terrestrial animals has implications for the maximal size attainable, and it is possible that the largest sauropod dinosaurs approached this limit. *J. Morphol.* 251:195–209, 2002. © 2002 Wiley-Liss, Inc.

KEY WORDS: allometry; appendicular skeleton; mammals; long bone mass

If terrestrial animals scaled their structures of support in a geometric fashion, preserving their proportions as species size increased, this would present problems of support due to the well-known fact that bone cross sectional areas would then increase as the square of the increase in size, whereas body volume, and hence mass, would increase as the cube. Thus constructed, it might be expected that bone stresses in mammals would increase with size to $M^{0.33}$ (Biewener, 1982, 1989b), but this is not the case. Across most of their size range, bone stresses in terrestrial mammals have empirically been found to vary remarkably little, on the order of 50–100 MPa, which corresponds to 25–50% of the yield strength of bones (Alexander, 1977, 1981, 1985; Alexander et al., 1979b; Rubin and Lanyon, 1982; Biewener, 1983, 1989a,b, 1990; Biewener and Taylor, 1986; Alexander and Pond, 1992).

Studies on allometry of the appendicular skeleton in mammals have primarily focused on dimensional allometry, most often using only external measurements, as a means of coping with gravity and the demands of locomotion (e.g., McMahon, 1975a; Alexander, 1977; Alexander et al., 1979a; Biewener, 1983; Bou et al., 1987; Bertram and Biewener, 1990; Christiansen, 1999a,b). Results suggesting that the appendicular skeleton of mammals scales in accordance with geometric similarity (Alexander et al., 1979a), implying bone lengths and diameters or circumferences proportional to $M^{0.33}$, or elastic similarity, predicting bone lengths proportional to $M^{0.25}$

and diameters or least circumferences proportional to $M^{0.375}$ (McMahon, 1973, 1975a,b; Alexander, 1977) are now considered too simplistic (Biewener, 1983; Economos, 1983; Bertram and Biewener, 1990; Christiansen, 1999a,b). Many factors other than positive bone allometry contribute to maintaining bone stresses at comparable levels across a large size range of terrestrial mammals.

Long bone lengths to either sagittal diameters or least circumferences in smaller mammals tend to scale either isometrically or even with slopes indicating slightly negative allometry (Economos, 1983; Bertram and Biewener, 1990; Christiansen, 1999a,b), and a size-dependent change in limb postures to vertical maintains bone stresses at rather uniform levels (Biewener, 1989a,b, 1990). At a size of around 100–300 kg (Bertram and Biewener, 1990; Biewener, 1990), limb postures no longer change substantially with size and positive bone allometry increases (Prothero and Sereno, 1982; Economos, 1983; Bertram and Biewener, 1990; Christiansen, 1999a,b). Possibly an increase in duty factors with size during fast locomotion also contributes to reduc-

Contract grant sponsor: the Carlsberg Foundation; Contract grant number: 980192/20-1272.

*Correspondence to: Per Christiansen, Department of Vertebrates, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. E-mail: p2christiansen@zmuc.ku.dk

tion in bone stress among large species (Alexander et al., 1977), but the evidence is at present ambiguous (Biewener, 1983). Differential scaling is also found in other terrestrial tetrapods with parasagittal limb kinematics, such as the nonavian theropod dinosaurs (Christiansen, 1999c).

As differential scaling is present in analyses of bone measurements among a variety of terrestrial vertebrates, this implies that size-dependent differences in mass allometry of the appendicular bones could be expected as well. However, this has not previously been analyzed in a phylogenetically wide sample of mammals, probably because of the difficulty of obtaining suitable skeletal specimens from museum collections of animals with known body masses. Studies on skeletal mass allometry have most often focused on allometry of the entire skeleton.

Total skeletal mass in terrestrial mammals scales with positive allometry and has been found to scale to $M^{1.090}$ (Anderson et al., 1979; Prange et al., 1979) and $M^{1.123 \pm 0.042}$ (Reynolds, 1977; Reynolds and Karlotski, 1977), the latter study based on a considerably smaller sample than the former. The confidence limits for the slope in the latter study excluded one, implying that it was indeed positively allometric. More pronounced skeletal allometry has been found in rattlesnakes, in which skeletal mass scales to $M^{1.174}$ (Prange and Christman, 1976), but no confidence limits, were given for the slope. A correlation coefficient of 0.993 (Prange and Christman, 1976) certainly indicates that the confidence limits of the slope exclude 1.00, despite the small sample size ($n = 12$).

In birds the skeleton appears to scale with positive allometry as well, and previously reported slopes appear very similar to the ones reported from mammals. Total skeletal mass in birds has been found to scale to $M^{1.071}$ (Anderson et al., 1979; Prange et al., 1979). No confidence limits for the slope were given, but the very high correlation coefficient ($r = 0.993$) and large sample size ($n = 311$) strongly suggest that the confidence limits exclude 1.00. Reynolds (1977) and Reynolds and Karlotski (1977) computed a slightly steeper slope ($M^{1.1193 \pm 0.0652}$), based on 16 species of birds. Cubo and Casinos (1994) is among the few studies so far done that addresses the masses of individual skeletal parts and not just the entire skeleton. They found that although a number of skeletal elements in birds scaled isometrically (e.g., wing bones and most of the pectoral girdle), skull mass scaled with negative allometry, whereas the pelvic girdle and hindlimb long bones scaled with positive allometry.

Skeletal mass allometry in aquatic vertebrates could be expected to differ substantially from terrestrial animals because of the buoyancy of water. A crucial difference between terrestrial and aquatic or marine animals is the fact that a size increase in the latter results only in an overall body mass increase proportional to the cube of the increase in linear

dimensions, whereas no increase in weight occurs, due to the gravitational neutral medium in which the animals live.

Surprisingly, when relating skeletal mass to body mass in aquatic and marine animals the slopes differ only modestly from those of terrestrial animals. Reynolds and Karlotski (1977) found that skeletal mass in teleosts scaled to $M^{1.0297 \pm 0.0689}$, based on a rather small sample. Using a large sample Casadevall et al. (1990) found that skeletal mass in teleosts scaled to $M^{1.088}$, but the slope did not differ significantly from isometry. However, skeletal mass in marine fishes scaled to $M^{1.171}$, compared to $M^{0.928}$ in freshwater fishes. The two slopes, however, did not differ significantly from each other (Casadevall et al., 1990). Berrios-Lopez et al. (1996) found that coral reef fishes scaled isometrically, and also calculated a perfectly isometric slope for tilapia (*Oreochromis nilotica*). However, separate slopes calculated for juvenile and adult tilapia indicated positive allometry ($M^{1.16 \pm 0.07}$ and $M^{1.10 \pm 0.07}$, respectively).

Skeletal mass allometry in the largest of all animals, the baleen whales, has also been analyzed. Reynolds (1977) calculated an isometric slope ($M^{1.0174 \pm 0.05}$), whereas the large study of Smith and Pace (1971) found evidence of more pronounced skeletal allometry ($M^{1.107}$). Using a subset of Smith and Pace's (1971) data, Anderson et al. (1979) computed an even steeper slope, $M^{1.118}$. Although confidence limits were not computed, the high correlation coefficients computed for the two samples (0.975 for the total sample and 0.981 for the subsample), along with the large sample sizes ($n = 170$ and $n = 144$, respectively), indicate that the slopes are significantly positively allometric. Many of the above studies, however, have included multiple or even many specimens of each species, thus introducing intraspecific relationships when analyzing interspecific allometry. Skeletal mass in aquatic vertebrates, however, evidently scales with positive allometry in a fashion very similar to that of terrestrial vertebrates.

Bou and Casinos (1995) and Cubo and Casinos (1994) are among the only studies that have analyzed the scaling of the mass of individual skeletal elements to body mass, but are restricted to skeletal element mass in small mammals (insectivores and rodents) and birds, respectively. The present study analyzes the same factors in a phylogenetically much wider sample, which also includes some of the largest terrestrial animals (elephants, rhinos, and hippos). Furthermore, the present study also addresses the possibility of a size-dependent change in bone mass scaling, because studies of dimensional bone allometry have suggested that it may be present.

MATERIALS AND METHODS

The dataset used in this analysis is a subset of the dataset used in Christiansen (1999b), in which 98 specimens, representing 79 species, were used. In

this analysis only 79 specimens representing 64 different species were used (Appendix), as some of the specimens included in Christiansen (1999b) are skeletal mounts, which could not be disassembled in order to determine the mass of individual long bones. As in Christiansen (1999a,b), species with multiple specimens were averaged. In some cases, however, only one specimen was available. For instance, metacarpus mass in *Hippopotamus* (Appendix) was only available for the smaller animal (680 kg), so in this case only this specimen was used. In other cases bones were available from both individuals (e.g., humerus or femur) and so the average of their respective bone and body masses were used.

The giraffe used in the present study also differs from the one used in Christiansen (1999b), as an adult, 12-year-old female from the Copenhagen Zoo became available, thus replacing the large juvenile used in the previous study. Most animals had been obtained from zoos and safari parks, although some had been shot in the wild, and all had been weighed either shortly prior to or immediately after death. Even the huge *Loxodonta* bull had been weighed intact by suspending it from a mobile crane and fluid losses were thus not an issue (see Smith and Pace, 1971; Prosser, 1973; Anderson et al., 1979).

Masses of shoulder and pelvic girdles, individual long bones, and metapodials were determined by weighing them separately on one of three different scales, depending on their size. Bones up to 1,000 g were weighed on a digital scale with an accuracy of ± 0.05 g. Bones from 1–3 kilos were weighed on a balance scale, with an accuracy of ± 1.0 g, and the largest bones in the study (humerus, femur, and pelvis of the white rhinoceros bull, pelvis of the large hippopotamus bull, all bones from the African elephant bull save metacarpus and fibula, and humerus, ulna, femur, and tibia from the Asian elephant cow) were weighed on a large cargo scale (± 100 g).

In most cases fibula was not included for artiodactyls because of the extreme reduction of this bone in these taxa, and subsequently the fibula was often either missing or broken. Frequently, the radius and ulna in artiodactyls could not be weighed separately because the two bones are united by osteological fusion or extensive syndesmoses. Thus, instead of computing separate equations for radius and ulna they were pooled, as the data samples would otherwise be heavily biased towards carnivores. Pelvic mass as here defined is without the sacral vertebrae and in cases where they were co-ossified with the ilia, the pelvis was omitted from the study. However, in other cases the sacrum was fused to both ilia, but had been carefully removed from one half of the pelvis, probably during preparation. In such cases the half without the sacral vertebrae was weighed and multiplied by two. Metapodials that were still connected by ligaments and included carpals or tarsals and/or phalanges were also discarded. Total

limb mass is the combined mass of propodium, epimeral and metapodia, and excluding the carpals, tarsals, and sesamoids, since these small bones were not included in this study.

The skeletons of the included animals were prepared in the usual fashion for skeletal specimens in zoological museums by initial stripping of the skin and excess tissue and subsequent boiling of the skeleton in larger animals and cleaning by dermestid beetles in small taxa. The bones were then air-dried at room temperature. This would, of course, imply that the bones could be slightly lighter than bones of living animals, but the water content of bones is low (32% according to Mitchell et al. [1945]; 30–44% according to Spector [1956]). Furthermore, even dried bones contain a substantial amount of water (Anderson et al., 1979), so the difference should be modest. Since all specimens were subject to roughly the same preservational procedure, any difference from live animals should affect the intercepts, not the slopes of the equations. It cannot be ruled out, however, that larger bones, in part due to their lower surface area to volume ratio, could retain a slightly greater percentage of water, but this was not evaluated.

In addition to evaluating skeletal element mass to body mass in the total sample, two subsamples of large and small mammals were created. This was done because previous studies on allometry based on external measurements of the long bones of terrestrial mammals have demonstrated the presence of differential scaling between large and small forms (e.g., Economos, 1983; Bertram and Biewener, 1990; Christiansen, 1999a,b). Large forms are usually proportionally more massively built, and this would of course also reflect the bone masses, so the total sample was divided into two subsamples. Small mammals were species up to 50 kg and large mammals were taxa above 50 kg, following Christiansen (1999b). The division is rather arbitrary. Bertram and Biewener (1990) suggested that increases in bone allometry would be apparent in animals of around and above 100 kilos. Christiansen (1999b) decided to use a lower breakpoint in order to have a sample of small species which could be assumed to maintain stresses in long bones with increasing size at comparable levels to smaller species by postural changes (Biewener 1989a,b, 1990) and not bone allometry. Thus, differences in scaling patterns should be more readily detectable. Christiansen (1999c) found that scaling differences were not only apparent between small and large theropod dinosaurs, but also that scaling differences could be detected within the sample of large theropods. This suggests that a true breakpoint will always be arbitrary because bone allometry changes with size once postural changes are precluded from making a difference in stress reduction.

Logarithmic transformation of the standard power function can be used to describe allometric

trends in organisms (Gould, 1966). Thus, the raw data were logarithmically transformed and interspecific regression lines were fitted to the data by means of reduced major axis (RMA; model II) regression analysis. This procedure is appropriate, for although one may (arbitrarily) assign dependence to one variable in this kind of study (bone mass), error must be assumed on both variables (LaBarbera, 1989; Sokal and Rohlf, 1995). A model II regression makes no distinction between independent and dependent variables, but is merely a ratio of two standard deviations (Sokal and Rohlf, 1995). If the correlation between the variables is high, however, model I and model II regression equations will differ little from each other, the latter being $1/r$ times the former. Confidence intervals (95% CI) were computed for all intercepts and slopes. The standard error of the RMA regression slope may be approximated with the standard error of the least-squares regression slope (Sokal and Rohlf, 1995) and, thus, used to assign confidence limits to the RMA slope also. Correlation between the variables was evaluated by computing Pearson's product-moment correlations coefficient.

However, analyses of biological samples by means of traditional regression analyses violates some of the assumptions of a regression analysis. A standard regression equation is of the format:

$$y = \alpha + \beta x + \epsilon$$

where α is the intercept, β is the slope, and ϵ is the error term, which is assumed to be normally distributed with a mean of zero. However, in biological analyses the error terms are correlated as species are not independent of each other but, rather, can be arranged in a hierarchical sequence, thus producing a phylogenetic tree. Accordingly, a phylogenetic signal is introduced into the analysis and individual datapoints cannot be considered truly independent (e.g., Grafen, 1989; Harvey and Pagel, 1991; Garland and Janis, 1993; Garland and Ives, 2000). Thus, the method of independent contrasts (Felsenstein, 1985; Garland et al., 1992; Garland and Janis, 1993) may be employed, as it takes into account the phylogenetic signal. Character divergence between two taxa may well be influenced by the amount of time that has elapsed since they shared a common origin.

Accordingly, the data were subjected to analyses in the program PDTREE (Garland et al., 1992, 1993) using the method of phylogenetic independent contrasts. The tree structure was assembled from a variety of literature sources (Fig. 1) and the branch lengths used were divergence times, mainly assembled from the time of appearance in the fossil record of a given taxon. (Literature sources used in producing the tree were Kielan-Jaworowska et al., 1979; Janis, 1982; Savage and Russel, 1983; Lanave et al., 1985; Shoshani, 1986; Janis and Scott, 1987; Wayne

and O'Brien, 1987; Gentry and Hooker, 1988; Flynn et al., 1988; Novacek et al., 1988; Padmadisastra, 1988; Prothero et al., 1988; Tassy and Shoshani, 1988; Georgiadis et al., 1990; Marshall, 1990; Miyamoto et al., 1990; Nowak, 1991; Geffen et al., 1992; Novacek, 1992a,b; Bryant et al., 1993; Garland and Janis, 1993; Wyss and Flynn, 1993; Hunt, 1996; Flynn, 1996; Foote et al., 1999.)

The basal-most split between the carnivores and the ungulates was set at 85 million years, mainly because of the inferred age of the Proboscidea. The oldest proboscidean known from fossils is Late Paleocene in age (Gheerbrant et al., 1996). A number of authors, however, place the ordinal splits within Eutheria well into the Cretaceous (e.g., Novacek, 1992a; Archibald, 1996; Hedges et al., 1996), indicating that the fossil record around this time is incomplete, or that the ordinal diversification had not yet resulted in taxa with apomorphies pronounced enough to be recognized. Branch lengths and, thus, ultimately total tree height, are also sensitive to topology. The tree height would change if the Proboscidea were in fact the sister taxon of Artiodactyla+Perissodactyla, as suggested by Shoshani (1986), and not of the Perissodactyla (Fig. 1), as suggested by Novacek (1992a), among others.

The contrasts are computed for each trait by subtraction of the values of the traits in two sister taxa or from the value at the node, as appropriate (Garland and Janis, 1993). To standardize the independent contrasts, i.e., bring them to a common variance, each contrast is divided by the square root of the sum of all the branch lengths that make up the contrast in question.

In order to evaluate whether or not the contrasts have been properly standardized, so that their common variance is near independent of the branch lengths, one may generate a plot of the standard deviations of the contrasts vs. the absolute values of the standardized contrasts (Garland et al., 1992; Garland and Janis, 1993). Such a plot should show as little structure as possible, implying that the correlation between the two variables should be as low as possible. If a relationship can be detected in any of the plots, one may transform the branch lengths (Garland et al., 1992). The plots were evaluated by visual inspection and by the examination of the correlation coefficient between the two variables. In addition to raw branch lengths transformation of the branch lengths (square root, cube root, and log) were carried out. The procedure that resulted in the least correlation of the variables in each plot was used for further analysis. It turned out that this in no cases were the raw (i.e., unmodified) branch lengths (Table 1). For each data sample the same transformation mode was used for both the dependent and independent variables, as different modes of transformation for the dependent and independent variables would lead to problems of slope interpretation (Garland et al. 1992).

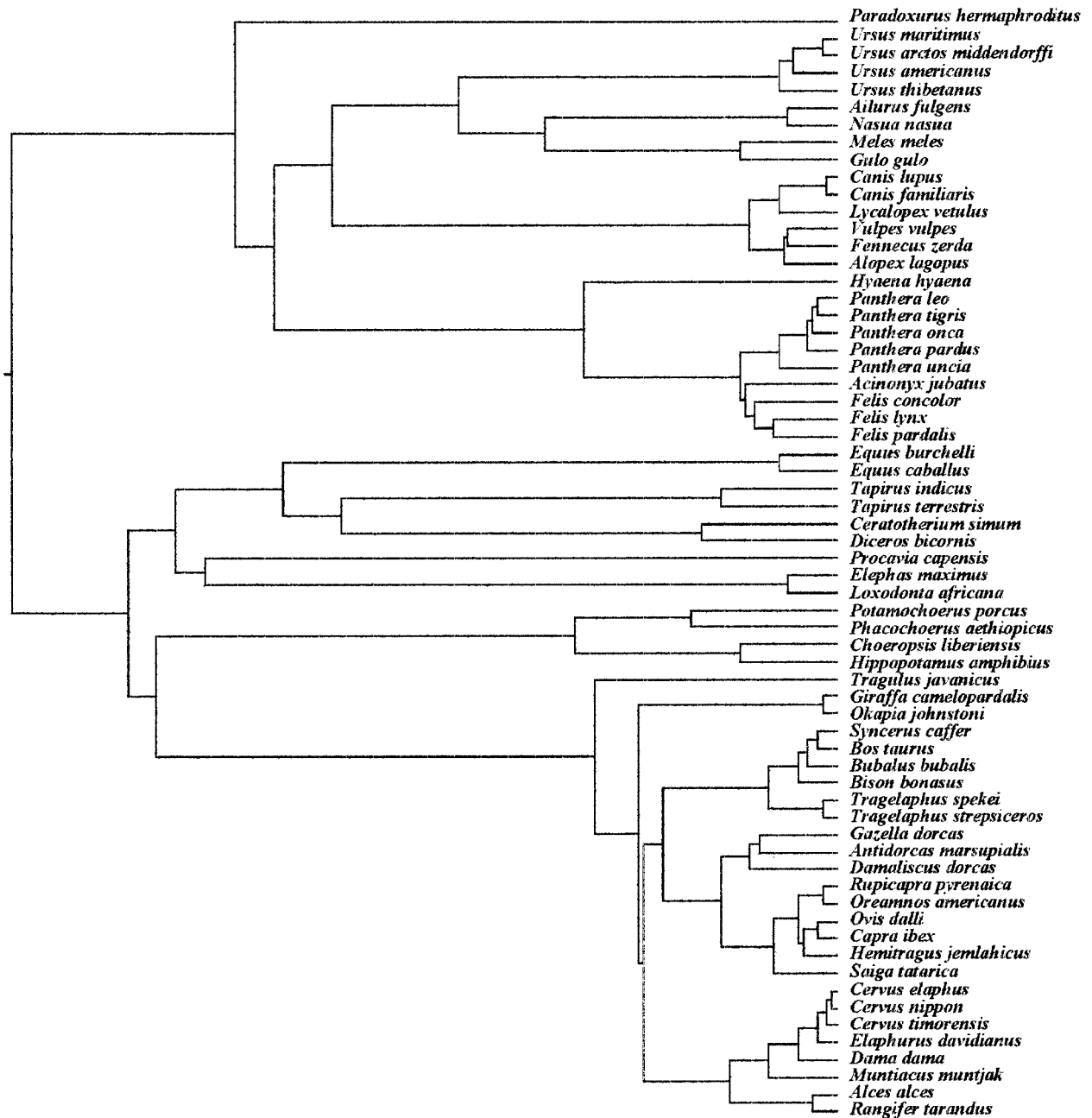


Fig. 1. Phylogenetic relationships among the 64 included species of mammals. For sources to the topology of the tree and branch lengths, see text.

The method of independent contrasts produces regressions through the origin, which can be used to test for linear relationships (Felsenstein, 1985; Garland et al., 1992; Garland and Janis, 1993). In order to construct scatterplots all contrasts for one trait (usually the “independent” variable) must be positivized, while the sign for the contrast for the corresponding “dependent” variable must be switched (Garland et al., 1992; Garland and Janis, 1993). The most recent version of PDTree also facilitates computation of confidence limits for the slope (Garland

and Ives, 2000). PDTree only computes confidence limits for the least-squares regression slope, but as with the traditional regression analyses the standard errors of the least-squares regression slopes were used to compute confidence limits for the RMA slopes.

The regression slopes produced by traditional RMA analyses and RMA analyses of independent contrasts were tested for significant departure from isometry ($M^{1.00}$). Additionally, the slopes of the subsamples (large vs. small mammals) computed by

TABLE 1. Transformation methods for the branch lengths of the various data samples prior to independent contrast analysis

Bone	All mammals	Large mammals	Small mammals
Scapula	Squareroot	Cube root	Squareroot
Humerus	Squareroot	Cube root	Squareroot
Radius + ulna	Squareroot	Squareroot	Squareroot
Metacarpus	Log	Squareroot	Log
Forelimb	Log	Squareroot	Log
Pelvis	Log	Squareroot	Squareroot
Femur	Squareroot	Cube root	Squareroot
Tibia	Squareroot	Squareroot	Squareroot
Metatarsus	Log	Squareroot	Squareroot
Hindlimb	Log	Squareroot	Squareroot

traditional RMA and independent contrast RMA analyses were tested against each other for significance. A two-sample *t*-test was employed to test whether all slopes from one sample showed significant departure from the slopes of any of the other samples. In all cases the significance level for rejection of the null hypothesis of slope equality was 0.05.

RESULTS

Taking the square root of the branch lengths of the total sample or log-transforming them (Table 1) always resulted in lower correlations and less structure in the plots (Fig. 2), implying better standardization of the contrasts than raw branch lengths (divergence times in millions of years). The slopes produced by both traditional RMA analysis and independent con-

trasts RMA analysis for all mammals were usually significantly higher than isometry for forelimb bone masses, whereas the hindlimb bones usually scaled according to geometric similarity (Table 2, Fig. 3). This parallels the conclusions of Christiansen (1999b) based on external bone measurements and shows that individual skeletal elements also grow progressively heavier with size in mammals, as has previously been found for total skeletal mass (e.g., Reynolds and Karlotski, 1977; Anderson et al., 1979; Prange et al., 1979). The slopes produced by traditional RMA analysis and independent contrasts RMA analysis are usually very similar (Table 2), with the exception of the metacarpus, although the difference between the two slopes falls well within their confidence limits.

The correlation coefficients of the samples are high (Table 2), although metatarsal mass evidently

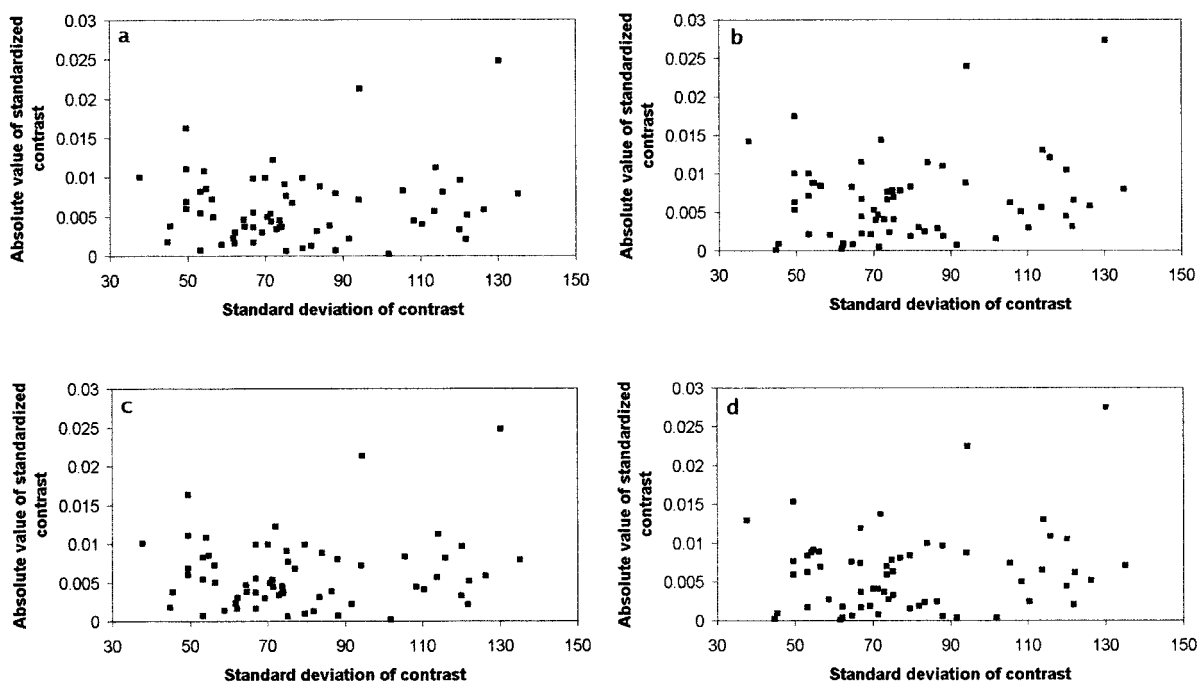


Fig. 2. The adequacy of the transformed branch lengths for the total sample of mammals for standardizing the independent contrasts, thus creating independence between the contrasts and their time of divergence. **a:** Log body mass (humerus sample). **b:** Log humerus mass. **c:** Log body mass (femoral sample). **d:** Log femur mass.

TABLE 2. Regression statistics for all mammals ($n = 64$) for both conventional RMA and independent contrasts RMA analyses, including confidence limits for the constants¹

	n	Conventional regression				Independent contrasts		
		a \pm 95% CI	b \pm 95% CI	r	SE	b \pm 95% CI	r	SE
Scapula	60	-3.630 ± 0.230	$1.145 \pm 0.047^{***}$	0.988	0.024	$1.156 \pm 0.083^{***}$	0.962	0.042
Humerus	64	-3.085 ± 0.214	$1.083 \pm 0.044^{***}$	0.987	0.022	$1.100 \pm 0.067^{***}$	0.971	0.034
Radius + ulna	63	-3.230 ± 0.074	$1.101 \pm 0.015^{***}$	0.985	0.001	$1.123 \pm 0.069^{***}$	0.971	0.035
Metacarpus	52	-3.487 ± 0.452	1.064 ± 0.091	0.955	0.045	$1.113 \pm 0.075^*$	0.971	0.037
Forelimb	52	-2.763 ± 0.232	$1.088 \pm 0.046^{***}$	0.989	0.023	$1.121 \pm 0.052^{***}$	0.987	0.026
Pelvis	54	-3.028 ± 0.213	$1.112 \pm 0.045^{***}$	0.990	0.022	$1.106 \pm 0.057^{***}$	0.983	0.028
Femur	64	-2.973 ± 0.189	$1.071 \pm 0.039^{***}$	0.990	0.019	1.045 ± 0.061	0.973	0.031
Tibia	63	-2.711 ± 0.248	0.998 ± 0.051	0.980	0.026	0.994 ± 0.062	0.970	0.031
Metatarsus	51	-3.139 ± 0.572	1.007 ± 0.116	0.932	0.058	0.987 ± 0.080	0.960	0.040
Hindlimb	51	-2.443 ± 0.253	1.036 ± 0.051	0.985	0.025	1.048 ± 0.049	0.986	0.025

¹Results for conventional RMA analyses are given as $\log Y = \log a + b(\log X)$, where X in all cases is body mass and Y is bone mass, both in grams. Slope for independent contrasts analyses is by regression through the origin, hence $Y = 0$. One, two, or three asterisks after the slopes indicates significance from isometry at the level of 5%, 1%, and 0.1%, respectively.

scales in a less constricted manner with body mass. This is not surprising, since metatarsal lengths have influence on locomotion (Garland and Janis, 1993), and the present sample spans the entire locomotor range from slow-moving species incapable of running with a suspended phase, such as elephants (usually termed “graviportal”), to very fleet species with an anatomy usually considered extensively adapted for fast locomotion (e.g., Gregory, 1912; Gambaryan, 1974; Coombs, 1978; Christiansen, 1998; Christiansen and Paul, 2001).

The raw branch lengths were also consistently inferior to transformed branch lengths in the two subsamples of small and large mammals (Figs. 4, 5), in terms of correlation between the variables. In the two subsamples the transformation that yielded the lowest correlations was usually the square root (Table 1). The slopes of skeletal element mass to body mass in large mammals are most often lower than corresponding slopes in the total sample, whereas the reverse is true for the slopes in the subsample of small mammals (Fig. 3, Fig. 6, Tables 2, 3). When comparing the traditional RMA slopes in the subsample of large mammals to isometry ($M^{1.00}$), only the slope for scapula (Fig. 6a, $t_{29} = 2.5462$; $0.05 > P > 0.01$) and pelvis ($t_{22} = 2.4536$; $0.05 > P > 0.01$) differ significantly from isometry. Of the slopes computed by independent contrasts analysis, only the forelimb is significantly different from isometry ($0.05 > P > 0.01$).

The slopes in the subsample of small mammals are, however, significantly different from isometry. The slopes computed by traditional RMA analysis are all significantly higher (humerus and forelimb: $0.05 > P > 0.01$; metacarpus, pelvis, femur, tibia, and hindlimb: $0.01 > P > 0.001$; and scapula, radius+ulna: $P < 0.001$) than isometry, with only one exception, metatarsal mass, which is close to being significant ($t_{21} = 1.9988$; $0.10 > P > 0.05$). This sample has the lowest correlation coefficient of all (Fig. 6d, Table 3) and subsequently a greater residual variance. The slopes computed by indepen-

dent contrasts analysis always display lower correlation coefficients than the corresponding slopes computed by traditional RMA analysis and the greater residual variance implies wider confidence limits (Table 3). Nonetheless, most of these are also significantly higher than isometry (humerus, forelimb, and pelvis: $0.05 > P > 0.01$; scapula and radius+ulna: $0.010 > P > 0.001$). The slopes for femoral mass and hindlimb mass are close to significance ($0.10 > P > 0.05$).

The corresponding slopes of the two subsamples appear to differ substantially from each other, but few can in fact be considered significantly different

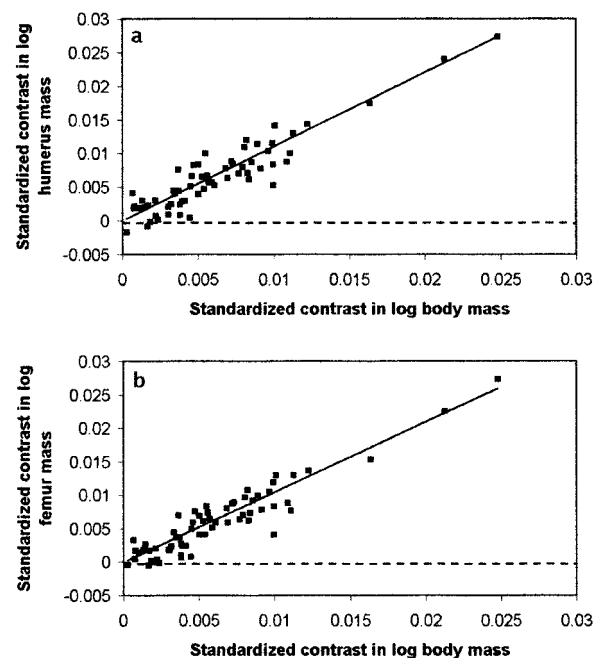


Fig. 3. The relationship between the standardized independent contrasts in log body mass and the standardized independent contrasts in log bone mass for the total sample of mammals. a: Humerus. b: Femur. Regression line was fitted to the data by means of a model II reduced major axis (RMA) analysis.

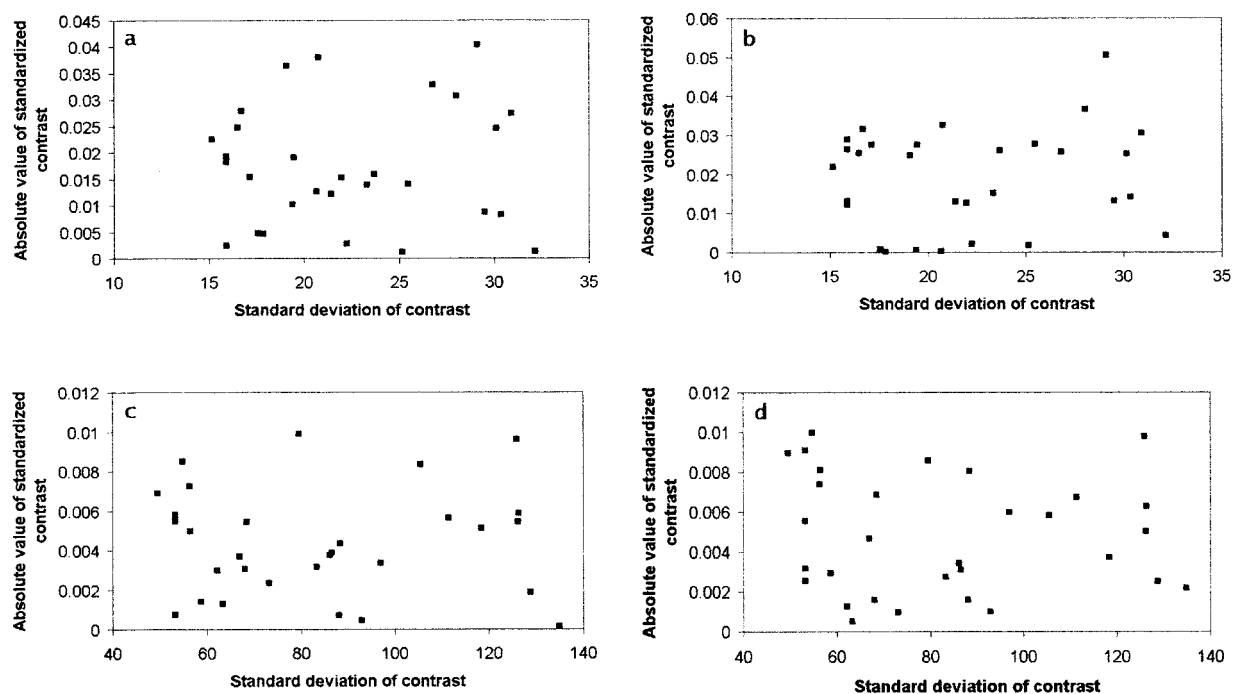


Fig. 4. The adequacy of the transformed branch lengths for the subsample of large mammals for standardizing the independent contrasts, thus creating independence between the contrasts and their time of divergence. **a:** Log body mass (scapula sample). **b:** Log scapula mass. **c:** Log body mass (radius+ulna sample). **d:** Log radius+ulna mass.

(Table 3), due to lower correlation coefficients than the total sample, greater residual variances and subsequent wider confidence limits, in addition to lower sample sizes. Despite the apparent differences

in the slopes, Fig. 6; Table 3, the wide confidence limits preclude assumptions of significance. However, when comparing the slope means of the subsamples they do differ significantly. The mean of the

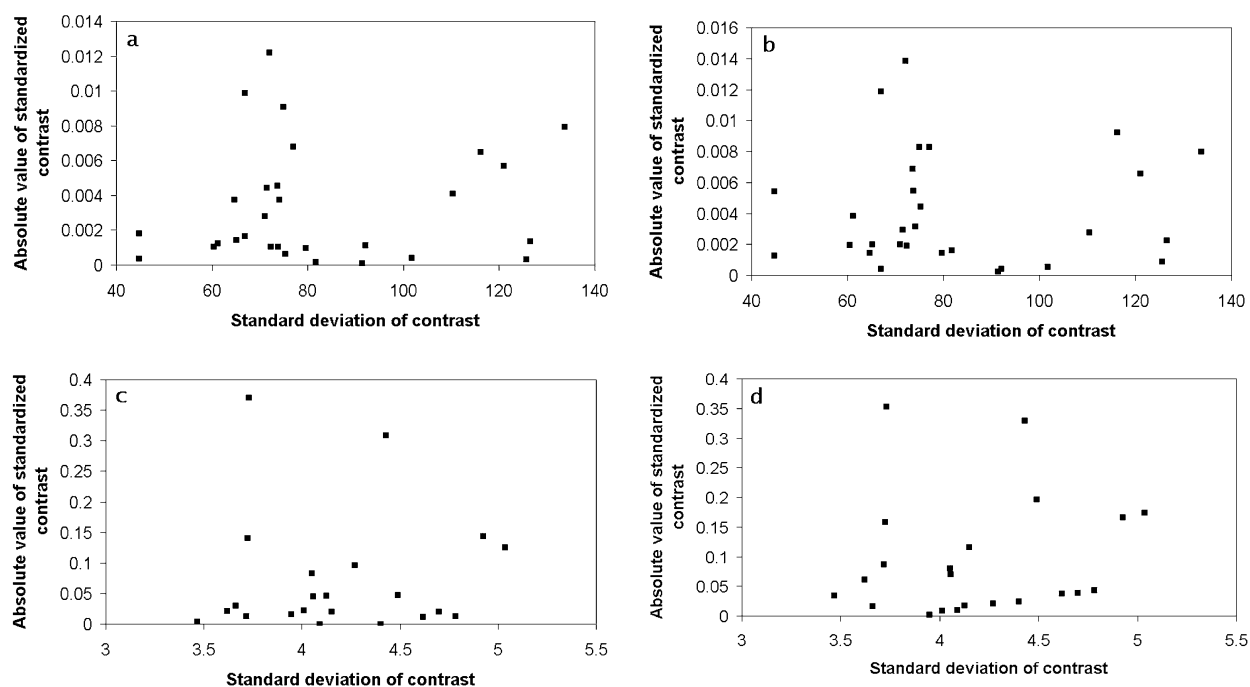


Fig. 5. The adequacy of the transformed branch lengths for the subsample of small mammals for standardizing the independent contrasts, thus creating independence between the contrasts and their time of divergence. **a:** Log body mass (pelvic sample). **b:** Log pelvic mass. **c:** Log body mass (metatarsus sample). **d:** Log metatarsus mass.

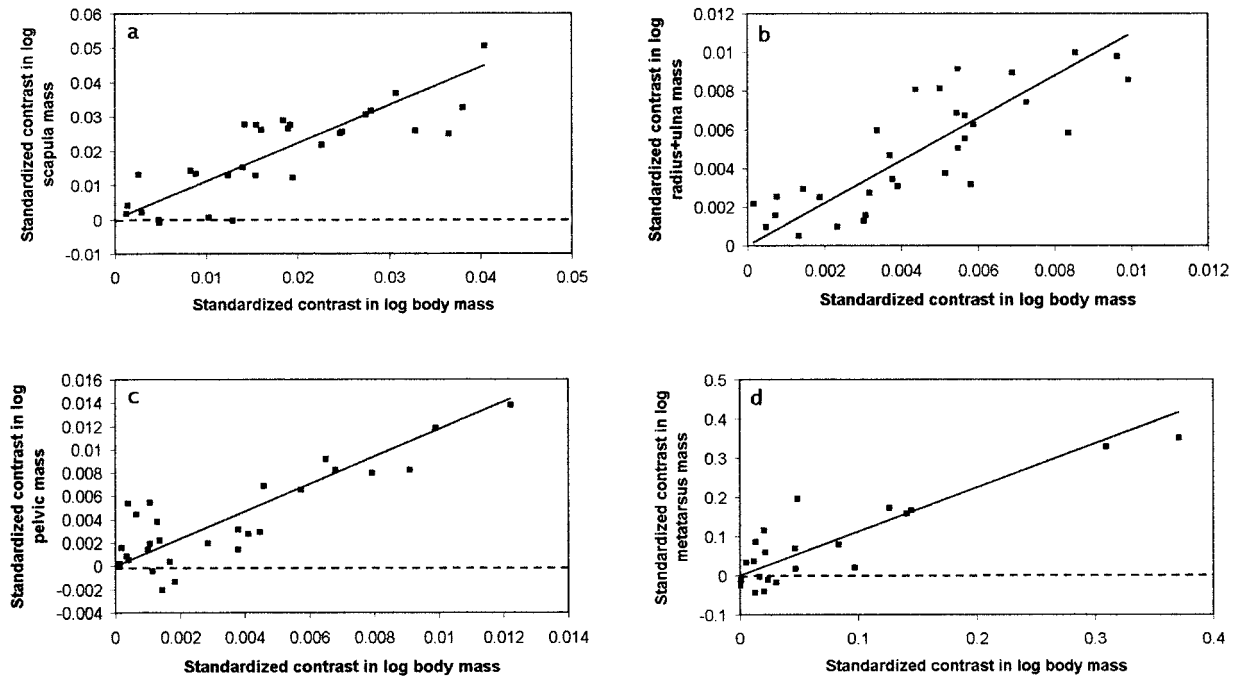


Fig. 6. The relationship between the standardized independent contrasts in log body mass and the standardized independent contrasts in log bone mass for the subsamples of large and small mammals. **a:** Large mammals (scapula). **b:** Large mammals (radius+ulna). **c:** Small mammals (pelvis). **d:** Small mammals (metatarsus). Regression line was fitted to the data by means of a model II reduced major axis (RMA) analysis.

slopes computed by traditional RMA analysis for large mammals (1.0478) is significantly lower ($P < 0.001$) than the mean of the slopes in small mam-

mals (1.1992). This is also the case with the means of the independent contrast slopes in large (1.0791) and small mammals (1.1621; $0.01 > P > 0.001$).

TABLE 3. Regression statistics for large ($n = 33$) and small ($n = 31$) mammals for both conventional RMA and independent contrasts RMA analyses, including confidence limits for the constants¹

		Conventional regression				Independent contrasts		
	n	a ± 95% CI	b ± 95% CI	r	SE	b ± 95% CI	r	SE
Large mammals								
Scapula	31	−3.589 ± 0.581	1.134 ± 0.107	0.968	0.053	1.107 ± 0.133	0.949	0.065
Humerus	33	−2.820 ± 0.502	1.034 ± 0.092	0.970	0.045	1.022 ± 0.117	0.950	0.057
Radius + ulna	32	−3.004 ± 0.604	1.054 ± 0.111	0.959	0.054	1.102 ± 0.123	0.954	0.099
Metacarpus	30	−3.485 ± 0.995	1.055 ± 0.183*	0.894	0.089	1.183 ± 0.203	0.896	0.061
Forelimb	30	−2.699 ± 0.503	1.075 ± 0.093	0.975	0.045	1.147 ± 0.125	0.960	0.061
Pelvis	24	−3.118 ± 0.575	1.126 ± 0.107	0.977	0.051	1.078 ± 0.136	0.958	0.066
Femur	33	−2.769 ± 0.462	1.032 ± 0.085*	0.975	0.042	0.993 ± 0.110*	0.953	0.054
Tibia	32	−2.401 ± 0.597	0.935 ± 0.110**	0.949	0.054	0.988 ± 0.119	0.946	0.058
Metatarsus	29	−3.224 ± 1.382	1.013 ± 0.256	0.780	0.124	1.102 ± 0.233	0.852	0.113
Hindlimb	29	−2.373 ± 0.603	1.020 ± 0.112*	0.961	0.055	1.069 ± 0.123	0.956	0.060
Small mammals								
Scapula	29	−3.979 ± 0.486	1.232 ± 0.116	0.971	0.057	1.226 ± 0.186	0.923	0.091
Humerus	31	−3.332 ± 0.479	1.143 ± 0.115	0.965	0.056	1.172 ± 0.168	0.926	0.082
Radius + ulna	31	−3.623 ± 0.473	1.202 ± 0.113	0.969	0.055	1.233 ± 0.167	0.934	0.082
Metacarpus	22	−4.564 ± 0.893	1.331 ± 0.208	0.942	0.099	1.183 ± 0.196	0.935	0.094
Forelimb	22	−3.071 ± 0.521	1.163 ± 0.121	0.975	0.058	1.163 ± 0.149	0.961	0.072
Pelvis	30	−3.183 ± 0.424	1.151 ± 0.101	0.974	0.049	1.174 ± 0.174	0.924	0.085
Femur	31	−3.317 ± 0.401	1.157 ± 0.096	0.976	0.047	1.126 ± 0.146	0.940	0.071
Tibia	31	−3.471 ± 0.457	1.188 ± 0.109	0.970	0.053	1.102 ± 0.150	0.934	0.073
Metatarsus	23	−4.175 ± 1.186	1.268 ± 0.279	0.942	0.134	1.123 ± 0.201	0.919	0.097
Hindlimb	22	−2.940 ± 0.503	1.158 ± 0.117	0.976	0.056	1.118 ± 0.151	0.957	0.072

¹Results for conventional RMA analyses are given as $\text{Log } Y = \text{Log } a + b(\text{Log } X)$, where X in all cases is body mass and Y is bone mass, both in grams. Slope for independent contrasts analyses is by regression through the origin, hence $Y = 0$.

One, two, or three asterisks after the slopes of large mammals indicates significance at the level of 5%, 1%, and 0.1%, respectively, from the corresponding slopes of small mammals.

DISCUSSION

Initially, it appears surprising that skeletal mass increases at a faster rate in small than in large mammals, despite the fact that the long bones are, of course, relatively heavier in large mammals, as indicated by the universally higher intercepts (Table 3). The general opinion of most analyses on limb bone proportions with size appear to favor the suggestion that large mammals evolve disproportionately thick long bone diaphyses with size (Prothero and Sereno, 1982; Alexander, 1997a,b). Bone stresses apparently are highly constrained among terrestrial mammals, largely due to postural changes and subsequent increases in effective mechanical advantage of the muscles among smaller species (Biewener, 1989a,b, 1990) and increases in dimensional bone allometry among larger species (Bertram and Biewener, 1990; Christiansen, 1999a,b), in addition to a reduction in locomotor intensity.

Economos (1983), however, suggested that a size-dependent decrease in bone length might be more important than simply evolving progressively thicker long bones with size, as also implied in McMahon's theory of elastic similarity (McMahon, 1973, 1975a,b), as this would reduce the length of the lever arm of the bending moments about the diaphyses. Bending-induced stresses are much more important in overall bone stress than simple axial compression (Alexander et al., 1979b; Alexander, 1984, 1989; Alexander and Pond, 1992; Carrano, 1997, 1998).

Christiansen (1999b) verified the suggestion of Economos (1983) that large mammals on average do not have disproportionately thick limb bones, but rather have considerably shorter limb bones than predicted for their body mass. Despite their massive appearance in rhinos and hippos compared to those of elephants, the long bones of all have circumferences that roughly correspond to the values predicted from their body masses (Christiansen, 1999b). In elephants, however, the limb bones are proportionally considerably longer than in other very large mammals (Alexander et al., 1979a; Alexander and Pond, 1992; Christiansen, 1999a), leading to lower bone strength indicator values (Alexander, 1985, 1989; Christiansen, 1997, 1998; Christiansen and Paul, 2001). The above is corroborated by the present study, in which bone mass in smaller mammals increase at a faster rate than in large animals.

However, whereas the above differences between large and small mammals in bone proportions compared to the expected values are relatively clear, there is greater fluctuation in actual limb bone mass compared to the predicted values. When using the equations from Table 2 to predict the masses of the long bones of a number of taxa, it is evident that most bones in large mammals on average are lower percentages of the predicted values than in morpho-

logically comparable smaller taxa. For instance, actual bone mass in *Tapirus indicus* varies from 101% (femur) to 58% (metacarpus) of the predicted values, whereas the variation in *Ceratotherium* is 76% (humerus) to 43% (metatarsus). Actual bone mass in *Felis concolor* (47 kg) ranges from 132% (humerus) to 105% (metatarsus), and in *Panthera tigris altaica* (221 kg) it ranges from 131% (femur) to 79% (metacarpus), with most values being around 10–20% lower in the latter species.

Despite their great size, both elephant species have actual bone masses rather close to the predicted values. Actual bone mass in *Loxodonta* ranges from 69% of the predicted value (tibia) to 108% (humerus), and the values in *Elephas* are 66% (tibia) to 100% (humerus) and 101% (femur). The metapodials of elephants are, however, much lighter than predicted (38% and 47% for metacarpus, and just 25% for metatarsus), which is to be expected from their metapodial morphology. In artiodactyls the smaller species also tend to have bone masses that are greater percentages of the predicted values than is the case among larger species.

However, the overall picture is less clear than is the case in analyses of allometry based on bone measurements. This becomes more evident when relating actual to predicted bone masses across the entire size spectrum, although the general trend of large mammals having actual bone masses that are lower percentages of predicted bone masses is still apparent. Much of this variation at any given size is due to the fact that artiodactyls usually have longer (Steudel and Beattie, 1993), and thus heavier, limb bones at any given body mass than carnivores. This is particularly the case for the metapodials.

Furthermore, several outliers (e.g., *Giraffa*, *Oka-pia*, large *Hippopotamus*) deviate considerably more from the predicted values than do other, similar-sized species. The above of course implies that the systematic deviation of actual bone mass from the predicted values with size gets less evident. It also implies that analyses using bivariate regression statistics will inevitably be somewhat simplified, as such analyses address the general trend of bone allometry with size, but not intraordinal differences in allometry, nor the other factors influencing bone mass besides body size. Differences in allometry between phylogenetically wide and narrow samples have also been reported in analyses of skeletal mass in fishes (Berrios-Lopez et al., 1996).

There are other differences between results obtained from analyses of dimensional allometry and mass allometry. One is that bone mass need not necessarily reflect external bone proportions across a large range of body sizes, as differences in the relative size of the medullary cavity will directly influence the results of mass allometry, whereas this may be less apparent in dimensional allometry. Furthermore, although the bone microstructure across most of the vertebrate spectrum is generally very

similar (e.g., Biewener, 1982) it remains to be proven that bone density is identical as well. In fact, Stein (1989) found that long bone density does in fact differ significantly between aquatic and terrestrial mammals, and that epipodial bones usually had higher densities than propodial bones. Additionally, Alexander and Pond (1992) suggested that bone density in rhinoceroses may differ slightly from that of other mammals, but did not elaborate on that.

Positive skeletal mass allometry has implications for the maximal terrestrial size attainable. The largest land animals of all time were the sauropod dinosaurs. Although earlier articles on skeletal mass allometry considered sauropods prime evidence that size constraints on land makes terrestrial animals of baleen whale proportions impossible, as the sauropods were considered aquatic (Smith and Pace, 1971; Reynolds, 1977; Reynolds and Karlotski, 1977), this argument has subsequently been invalidated. There is universal agreement among paleontologists that sauropods were terrestrial animals, as strongly suggested by studies of taphonomy (Dodson et al., 1980; Russell et al., 1980; Bakker, 1986), trackways (e.g., Pittman and Gillette, 1989; Barnes and Lockley, 1994; Pittman and Lockley, 1994), and especially morphology and functional anatomy (Riggs, 1901, 1903, 1904; Bakker, 1971, 1986; Coombs, 1975; Christiansen, 1997).

The largest well-known sauropod taxon is *Brachiosaurus brancai* from the Upper Jurassic of Tendaguru (Janensch, 1938, 1950). The single most complete specimen, the fine partial skeleton HMN SII, which is mounted at the Museum für Naturkunde in Berlin, is from a large animal with an estimated mass of 37,400 kg (Christiansen, 1997). Earlier figures of close to 80 tons are vastly exaggerated (Christiansen, 1997; Paul, 1997). Skeletal mass in *Brachiosaurus* HMN SII is predicted as 5,929 kg when using the equation from Anderson et al. (1979), and 9,964 kg when using the equation of Reynolds and Karlotski (1977).

Crile and Quiring (1941) gave the total skeletal mass of a 6,600 kg elephant as 1,782 kg, 27% of total body mass, considerably higher than the 12–15% suggested by Nowak (1991). The equation by Anderson et al. (1979) predicts the skeletal mass of *Brachiosaurus* and the elephant as 16% and 13.5% of total body mass, respectively, while the equation of Reynolds and Karlotski (1977) predicts skeletal mass as 27% and 21.5% of total body mass in *Brachiosaurus* and the elephant, respectively. The latter is clearly much more in accord with the actual skeletal mass of elephants and the great size and elephantine morphology of most sauropods (Christiansen, 1997) makes it likely that the skeleton of *Brachiosaurus* probably was around 10 tons in mass.

The reason for this discrepancy appears to be that the equation by Reynolds and Karlotski (1977) includes few species, some of which are large. This will skew the slope in the direction of increased positive allometry. It is evident, however, that when dealing

with very large animals the entire skeleton is considerably heavier than predicted from analyses spanning a wide size spectrum, and one evidently has to bear the presence of differential scaling between large and small forms in mind here as well.

There is fragmentary evidence of even larger sauropods than *Brachiosaurus*, such as *Supersaurus* (Jensen, 1985) and *Argentinosaurus* (Bonaparte and Coria, 1993; Bonaparte, 1996), both of which appear to have exceeded 50 tons in body mass (Christiansen, 1997; Paul, 1997), perhaps by a considerable extent for the latter taxon. A body mass of around 70 metric tons appears reasonable for *Argentinosaurus*, although Paul (1997) considers a mass of 90 tons more likely. At a body mass of 70 tons, total skeletal mass of *Argentinosaurus*, when predicted by the equation from Reynolds and Karlotski (1977), is a little in excess of 20 tons, 29% of total body mass, but the true value could well have been greater. Thus, it appears likely that for strictly biomechanical reasons the maximal terrestrial size attainable is not much greater than this, close to the theoretical lower estimate for the largest terrestrial animal given by Hokkanen (1986). He also suggested that a terrestrial animal with a mass of up to 10⁶ kilos was theoretically possible. Adult size is, however, not determined by mechanical factors alone, so this remains speculative.

The above indicates that the constraints of gravity makes the maximal size attainable on land substantially lower than the largest baleen whales (Smith and Pace, 1971), and especially when considering the heaviest blue whale (*Balaenoptera musculus*) ever recorded, which had a mass of 187 metric tons (McFarlan, 1992). However, the discrepancy is considerably less than originally suggested by Currey (1970), Smith and Pace (1971), Reynolds (1977), and Reynolds and Karlotski (1977). Furthermore, none of the above authors took into account the extinct giant mammals, some of which probably exceeded the mass of extant elephants by a factor of 2–4 (Fortelius and Kappelman, 1993; Garrutt and Nikolskaja, 1988). Thus, even within Mammalia the distinction between the largest size attainable on land and in the sea appears less than is usually assumed.

ACKNOWLEDGMENT

Dr. Erik Eriksen at Copenhagen Zoo kindly provided information on body masses and life stories of several of the specimens used in this article, as they were old zoo animals.

LITERATURE CITED

- Alexander R McN. 1977. Allometry of the limbs of antelopes (Bovidae). *J Zool Lond* 183:125–146.
- Alexander R McN. 1981. Factors of safety in the structure of animals. *Sci Progr* 67:109–130.
- Alexander R McN. 1984. Elastic energy stores in running vertebrates. *Am Zool* 24:85–94.

- Alexander R McN. 1985. The maximum forces exerted by animals. *J Exp Biol* 115:231–238.
- Alexander R McN. 1989. Dynamics of dinosaurs and other extinct giants. New York: Columbia University Press.
- Alexander R McN. 1997a. Biomechanics. In: Currie PJ, Padian K, editors. *Encyclopedia of dinosaurs*. San Diego: Academic Press. p 57–59.
- Alexander R McN. 1997b. Size and scaling. In: Currie PJ, Padian K, editors. *Encyclopedia of dinosaurs*. San Diego: Academic Press. p 665–667.
- Alexander R McN, Pond CM. 1992. Locomotion and bone strength of the white rhinoceros (*Ceratotherium simum*). *J Zool Lond* 227:63–69.
- Alexander R McN, Langman VA, Jayes AS. 1977. Fast locomotion of some African ungulates. *J Zool Lond* 183:291–300.
- Alexander R McN, Jayes AS, Maloij GMO, Wathuta EM. 1979a. Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *J Zool Lond* 189:305–314.
- Alexander R McN, Maloij GMO, Hunter B, Jayes AS, Nturi J. 1979b. Mechanical stresses in fast locomotion of buffalo (*Synceus caffer*) and elephant (*Loxodonta africana*). *J Zool Lond* 189:135–144.
- Anderson JF, Rahn H, Prange HD. 1979. Scaling of supportive tissue mass. *Q Rev Biol* 54:139–148.
- Archibald JD. 1996. Fossil evidence for a Late Cretaceous origin of “hoofed” mammals. *Science* 272:1150–1153.
- Bakker RT. 1971. Ecology of the brontosaurus. *Nature* 229:172–174.
- Bakker RT. 1986. The dinosaur heresies. New York: William Morrow.
- Barnes FA, Lockley MG. 1994. Trackway evidence for social sauropods from the Morrison Formation, eastern Utah (USA). *GAIA* 10:37–41.
- Berrios-Lopez M, Lewis AR, Hensley DA. 1996. Scaling of skeletal mass to body mass in fishes. *J Morphol* 227:87–92.
- Bertram JEA, Biewener AA. 1990. Differential scaling of the long bones in the terrestrial carnivora and other mammals. *J Morphol* 204:157–169.
- Biewener AA. 1982. Bone strength in small mammals and bipedal birds: Do safety factors change with body size? *J Exp Biol* 98:289–301.
- Biewener AA. 1983. Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size. *J Exp Biol* 105:147–171.
- Biewener AA. 1989a. Scaling body support in mammals: limb posture and muscle mechanics. *Science* 245:45–48.
- Biewener AA. 1989b. Mammalian terrestrial locomotion and size. Mechanical design principles define limits. *Bioscience* 39:776–783.
- Biewener AA. 1990. Biomechanics of mammalian terrestrial locomotion. *Science* 250:1097–1103.
- Biewener AA, Taylor CR. 1986. Bone strain: A determinant of gait and speed? *J Exp Biol* 123:383–400.
- Bonaparte JF. 1996. *Dinosaurios de America del Sur*. Museo Argentino de Ciencias Naturales.
- Bonaparte JF, Coria RA. 1993. Un nuevo y gigantesco sauropodo titanosaurio de la Formacion Rio Limay (Albiano-Cenomaniano) de la provincia Del Neuquen, Argentina. *Ameghiniana* 30:271–282.
- Bou J, Casinos A. 1985. Scaling of bone mass to body mass in insectivores and rodents. In: Duncker HR, Fleischer G, editors. *Functional morphology in vertebrates*. Stuttgart: Gustav Fischer Verlag. p 61–64.
- Bou J, Casinos A, Ocana J. 1987. Allometry of the limb long bones of insectivores and rodents. *J Morphol* 192:113–123.
- Bryant HN, Russell AP, Fitch WD. 1993. Phylogenetic relationships within the extant Mustelidae (Carnivora): appraisal of the cladistic status of the Simpsonian subfamilies. *Zool J Linn Soc* 108:301–334.
- Carrano MT. 1997. Mammals versus birds as models for dinosaur limb kinematics. *J Vert Paleontol* 17(Suppl 3):36A.
- Carrano MT. 1998. Locomotion in non-avian dinosaurs: integrating data from hindlimb kinematics, in vivo strains, and bone morphology. *Paleobiology* 24:450–469.
- Casadevall M, Casinos A, Viladiu C, Ontañón M. 1990. Scaling of skeletal mass and mineral content in teleosts. *Zool Anz* 225: 144–150.
- Christiansen P. 1997. Locomotion in sauropod dinosaurs. *GAIA* 14:45–75.
- Christiansen P. 1998. Strength indicator values of theropod long bones, with comments on limb proportions and cursorial potential. In: Perez-Moreno B, Holtz TR Jr, Sanz JL, Moratalla JJ, editors. *GAIA 15, theropod palaeobiology special volume*. p 241–255.
- Christiansen P. 1999a. Scaling of mammalian long bones: small and large mammals compared. *J Zool Lond* 247:333–348.
- Christiansen P. 1999b. Scaling of the limb long bones to body mass in terrestrial mammals. *J Morphol* 239:167–190.
- Christiansen P. 1999c. Long bone scaling and limb posture in non-avian theropods: evidence for differential allometry. *J Vert Paleontol* 19:666–680.
- Christiansen P, Paul GS. 2001. Limb bone scaling, limb proportions, and bone strength in neoceratopsian dinosaurs. *GAIA* Vol. 16.
- Coombs WP Jr. 1975. Sauropod habits and habitats. *Palaeogeogr Palaeoclimatol* 17:1–33.
- Coombs WP Jr. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Q Rev Biol* 53:393–418.
- Crile G, Quiring DP. 1941. A record of the body weight and certain organ and gland weights of 3734 animals (Appendix). In: Crile G, editor. *Intelligence, power and personality*. New York: Whittlesey House.
- Cubo J, Casinos A. 1994. Scaling of skeletal element mass in birds. *Belgian J Zool* 124:127–137.
- Currey JD. 1970. Animal skeletons. Institute of Biological Studies in Biology, no. 22. London: Arnold.
- Dodson P, Behrensmeyer AK, Bakker RT, McIntosh JS. 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology* 6:208–232.
- Economos AC. 1983. Elastic and/or geometric similarity in mammalian design? *J Theor Biol* 103:167–172.
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am Nat* 125:1–15.
- Flynn JJ. 1996. Carnivora phylogeny and rates of evolution: morphological, taxic, and molecular. In: Gittleman JL, editor. *Carnivore behavior, ecology, and evolution*. Ithaca, NY: Cornell University Press. p 542–581.
- Flynn JJ, Neff NA, Tedford RH. 1988. Phylogeny of the Carnivora. In: Benton MJ, editor. *The phylogeny and classification of the tetrapods*. Oxford: Clarendon Press. p 73–116.
- Footo M, Hunter JP, Janis CM, Sepkoski JJ Jr. 1999. Evolutionary and preservational constraints on origins of biologic groups: divergence times of eutherian mammals. *Science* 283:1310–1314.
- Fortelius M, Kappelman J. 1993. The largest land mammal ever imagined. *Zool J Linn Soc* 107:85–101.
- Gambaryan PP. 1974. How mammals run. New York: John Wiley & Sons.
- Garland T Jr, Ives AR. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am Nat* 155:346–364.
- Garland T Jr, Janis CM. 1993. Does metatarsal/femur ratio predict the maximal running speed in cursorial mammals? *J Zool Lond* 229:133–151.
- Garland T Jr, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst Biol* 41:18–32.
- Garland T Jr, Dickerman AW, Janis CM, Jones JA. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst Biol* 42:265–292.
- Garrutt VE, Nikolskaja VN. 1988. Über das Skelett vom Step-penelefanten aus Edersleben. *Beitr zur Heimatsforschung* 9:3–13.
- Geffen E, Mercure A, Gorman DJ, MacDonald DW, Wayne RK. 1992. Phylogenetic relationships of the fox-like canids: mitochondrial DNA restriction fragment site and cytochrome b sequence analyses. *J Zool Lond* 228:27–39.

- Gentry AW, Hooker JJ. 1988. The phylogeny of the Artiodactyla. In: Benton MJ, editor. The phylogeny and classification of the tetrapods. Oxford: Clarendon Press. p 235–272.
- Georgiadis NJ, Kat PW, Oketch H. 1990. Allozyme divergence within the Bovidae. *Evolution* 44:2135–2149.
- Gheerbrant E, Sudre J, Capetta H. 1996. Oldest proboscidean from the Late Paleocene of Morocco. *J Vert Paleontol* 3(Suppl 16):37A.
- Gould SJ. 1966. Allometry and size in ontogeny and phylogeny. *Biol Rev* 41:587–640.
- Grafen A. 1989. The phylogenetic regression. *Philos Trans R Soc (Ser B)* 326:119–157.
- Gregory WK. 1912. Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. *Ann NY Acad Sci* 22:267–294.
- Harvey PH, Pagel MD. 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press.
- Hedges SB, Parker PH, Sibley CG, Kuma S. 1996. Continental breakup and the ordinal diversification of birds and mammals. *Nature* 381:226–229.
- Hokkanen JEI. 1986. The size of the largest land animal. *J Theor Biol* 118:491–499.
- Hunt RM Jr. 1996. Biogeography of the order Carnivora. In: Gittleman JL, editor. Carnivore behavior, ecology, and evolution. Ithaca, NY: Cornell University Press. p 485–541.
- Janensch W. 1938. Gestalt und größe von *Brachiosaurus* und anderen riesenwüchsigen Sauropoden. *Der Biologe* 7:130–134.
- Janensch W. 1950. Die Skelettekonstruktion von *Brachiosaurus brancai*. *Palaeontographica* 3(Suppl 7):95–103.
- Janis CM. 1982. Evolution of horns in ungulates: ecology and paleoecology. *Biol Rev* 57:261–318.
- Janis CM, Scott KM. 1987. The interrelationship of higher ruminant families with special emphasis on the members of the Cervoidea. *Am Mus Novitates* 2893:1–85.
- Jensen JA. 1985. Three new sauropod dinosaurs from the Upper Jurassic of Colorado. *Great Basin Nat* 45:697–709.
- Kielan-Jaworowska Z, Brown TM, Lillegraven JA. 1979. Eutheria. In: Lillegraven JA, Kielan-Jaworowska Z, Clemens WA, editors. Mesozoic mammals. Berkeley: University of California Press. p 221–254.
- LaBarbera M. 1989. Analyzing body size as a factor in ecology and evolution. *Annu Rev Ecol Syst* 20:97–117.
- Lanave C, Preparata G, Saccone C. 1985. Mammalian genes as molecular clocks? *J Mol Evol* 21:346–350.
- Marshall CR. 1990. The fossil record and estimation of divergence times between lineages: maximum divergence times and the importance of reliable phylogenies. *J Mol Evol* 30:400–408.
- McFarlan D. 1992. The Guinness book of records. Enfield, UK: Guinness Publishing.
- McMahon TA. 1973. Size and shape in biology. *Science* 179:1201–1204.
- McMahon TA. 1975a. Allometry and biomechanics: limb bones of adult ungulates. *Am Nat* 107:547–563.
- McMahon TA. 1975b. Using body size to understand the structural design of animals: quadrupedal locomotion. *J Appl Physiol* 39:619–627.
- Mitchell HH, Hamilton TS, Steggerda FR, Bean HW. 1945. Chemical composition of the adult human body and its bearing on the biochemistry of growth. *J Biol Chem* 158:625–637.
- Miyamoto MM, Kraus F, Ryder OA. 1990. Phylogeny and evolution of antlered deer determined from mitochondrial DNA sequences. *Proc Natl Acad Sci USA* 87:6127–6131.
- Novacek MJ. 1992a. Mammalian phylogeny: shaking the tree. *Nature* 356:121–125.
- Novacek MJ. 1992b. Fossils, topologies, missing data, and the higher level phylogeny of eutherian mammals. *Syst Biol* 41:58–73.
- Novacek MJ, Wyss AR, McKenna MC. 1988. The major groups of eutherian mammals. In: Benton MJ, editor. The phylogeny and classification of the tetrapods. Oxford: Clarendon Press. p 31–71.
- Nowak RM. 1991. Walker's mammals of the world. Baltimore: Johns Hopkins University Press.
- Padmadisastra S. 1988. Estimating divergence times. *Theor Popul Biol* 34:297–319.
- Paul GS. 1997. Dinosaur models, the good, the bad, and using them to estimate the mass of dinosaurs. In: Wolberg DL, Stump E, Rosenberg GD, editors. *DinoFest international proceedings*. Acad Nat Sci Phila p 129–154.
- Penny D, Hasegawa M, Waddell PJ, Hendy MD. 1999. Mammalian evolution: timing and implications from using the LogDeterminant transform for proteins of differing amino acid composition. *Syst Biol* 48:76–93.
- Pittman JG, Gillette DD. 1989. The Briar Site: a new sauropod dinosaur tracksite in Lower Cretaceous beds of Arkansas. In: Gillette DD, Lockley MG, editors. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press. p 313–332.
- Pittman JG, Lockley MG. 1994. A review of sauropod dinosaur tracksites of the Gulf of Mexico. *GAIA* 10:95–108.
- Prange HD, Christman SP. 1976. The allometrics of rattlesnake skeletons. *Copeia* 1976:542–545.
- Prange HD, Anderson JF, Rahn H. 1979. Scaling of skeletal mass to body mass in birds and mammals. *Am Nat* 113:103–122.
- Prosser CL. 1973. Circulation of body fluids. In: Prosser CL, editor. *Comparative animal physiology*. Philadelphia: WB Saunders. p 822–856.
- Prothero DR, Sereno PC. 1982. Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. *Paleobiology* 8:16–30.
- Prothero DR, Manning EM, Fischer M. 1988. The phylogeny of the ungulates. In: Benton MJ, editor. The phylogeny and classification of the tetrapods. Oxford: Clarendon Press. p 201–234.
- Reynolds WW. 1977. Skeleton weight allometry in aquatic and terrestrial vertebrates. *Hydrobiology* 56:35–37.
- Reynolds WW, Karlotski WJ. 1977. The allometric relationship of skeleton weight to body weight in teleost fishes: a preliminary comparison with birds and mammals. *Copeia* 1977:160–163.
- Riggs ES. 1901. The largest known dinosaur. *Science* 13:549–550.
- Riggs ES. 1903. *Brachiosaurus altithorax*, the largest known dinosaur. *Am J Sci (Ser 4)* 5:299–306.
- Riggs ES. 1904. Structure and relationships of opisthocoelian dinosaurs. II. The Brachiosauridae. *Publ Field Columbian Mus Geol* 2:299–248.
- Rubin CT, Lanyon LE. 1982. Limb mechanics as a function of speed and gait: a study of functional strains in the radius and tibia of horse and dog. *J Exp Biol* 101:187–211.
- Russell DA, Beland P, McIntosh JS. 1980. Paleoecology of the dinosaurs of Tendaguru (Tanzania). *Mem Soc Geol France* 139: 169–175.
- Savage DE, Russel DE. 1983. Mammalian paleofaunas of the world. London: Addison-Wesley.
- Shoshani J. 1986. Mammalian phylogeny: comparison of morphological and molecular results. *Mol Biol Evol* 3:222–242.
- Smith AH, Pace N. 1971. Differential component and organ size among whales. *Environ Physiol* 1:122–136.
- Sokal RR, Rohlf FJ. 1995. Biometry. New York: WH Freeman & Co.
- Spector WS. 1956. Handbook of biological data. Philadelphia: WB Saunders.
- Stein BR. 1989. Bone density and adaptation in semiaquatic mammals. *J Mammal* 70:467–476.
- Steudel K, Beattie J. 1993. Scaling of cursoriality in mammals. *J Morphol* 217:55–63.
- Tassy P, Shoshani J. 1988. The Tethytheria: elephants and their relatives. In: Benton MJ, editor. The phylogeny and classification of the tetrapods. Oxford: Clarendon Press. p 283–315.
- Wayne RK, O'Brien SJ. 1987. Allozyme divergence within the Canidae. *Syst Zool* 36:339–355.
- Wyss AR, Flynn JJ. 1993. A phylogenetic analysis and definition of the Carnivora. In: Szalay FS, Novacek MJ, McKenna MC, editors. *Mammal phylogeny*. New York: Springer Verlag. p 32–52.

APPENDIX. Body masses and bone masses of the included animals. All values are in grams

Taxon	Body	Scapula	Humerus	Radius + ulna	Metacarpus	Pelvis	Femur	Tibia	Fibula	Metatarsus
ARTIODACTYLA										
Bovidae										
<i>Antilocapra americana</i>	21,200	26.57	36.46	40.16	38.42	67.08	52.48	60.08	—	46.06
<i>Bison bonasus</i>	225,000	—	621.79	504.43	221.73	882.21	719.27	586.04	—	270.97
<i>Bos taurus</i>	225,000	255.94	335.84	284.45	118.29	682.10	462.17	325.41	—	151.17
<i>Bubalus bubalis</i>	382,000	421.15	822.25	742.60	292.10	1510	1120	682.76	—	325.95
<i>Capra ibex</i>	36,000	44.03	76.23	61.39	28.94	106.29	85.87	86.05	—	27.55
<i>Damaliscus dorcas</i>	43,500	69.04	78.38	90.50	58.43	146.82	108.44	113.29	—	67.11
<i>Gazella dorcas</i>	19,000	9.66	17.85	18.17	16.08	30.97	29.67	33.46	—	21.79
<i>Hemitragus jemlahicus</i>	43,000	71.31	114.59	104.51	44.24	182.64	127.54	128.97	—	45.82
<i>Oreamnos americanus</i>	120,000	84.27	184.32	139.10	51.11	—	186.08	181.84	—	51.13
<i>Ovis dalli</i>	99,000	84.65	182.47	128.57	73.87	216.37	185.24	201.83	—	81.60
<i>Rupicapra pyrenaica</i>	34,000	—	58.69	49.92	30.88	105.86	77.15	82.67	—	36.29
<i>Saiga tatarica</i>	20,200	31.64	47.22	40.73	22.75	75.00	54.10	51.17	—	28.98
<i>Saiga tatarica</i>	26,200	35.89	55.23	52.34	26.87	101.89	71.51	62.20	—	31.94
<i>Syncerus caffer</i>	440,000	738.90	1153	870.15	365.52	—	1292	935.01	—	387.92
<i>Tragelaphus spekei</i>	29,000	26.30	73.37	60.52	37.64	93.66	113.09	116.38	—	55.15
<i>Tragelaphus strepsiceros</i>	190,000	434.12	537.83	469.23	293.37	951.93	651.18	568.14	—	319.30
Cervidae										
<i>Alces alces</i>	410,000	512.75	880.89	741.18	398.13	1027	949.87	873.92	—	559.91
<i>Cervus elaphus</i>	85,000	111.93	222.05	190.79	130.05	265.94	264.70	265.96	—	159.77
<i>Cervus nippon</i>	35,600	44.34	64.88	64.87	39.52	118.52	85.87	101.48	—	54.29
<i>Cervus timorensis</i>	37,000	77.76	109.15	101.83	58.13	207.66	135.68	137.75	—	71.85
<i>Dama dama</i>	45,000	42.24	58.44	62.84	43.10	116.13	81.68	97.98	—	57.31
<i>Elaphurus davidianus</i>	152,000	170.55	349.70	283.41	162.96	537.34	433.78	380.28	—	212.33
<i>Elaphurus davidianus</i>	194,000	179.49	334.07	280.21	170.95	492.97	427.09	371.09	—	210.27
<i>Muntiacus muntjak</i>	34,000	18.25	29.09	23.01	11.91	52.81	42.99	42.27	—	19.62
<i>Rangifer tarandus</i>	160,000	194.99	293.26	284.19	—	—	299.39	302.86	—	—
Giraffidae										
<i>Giraffa camelopardalis</i>	620,000	1205	1924	2493	1657	2776	1827	1967	—	1703
<i>Okapia johnstoni</i>	250,000	543.13	985.17	886.07	439.77	1703	949.05	749.54	—	428.37
<i>Okapia johnstoni</i>	260,000	536.34	814.76	866.31	416.69	1553	847.96	831.40	—	474.06
<i>Okapia johnstoni</i>	310,000	605.61	1001	932.93	450.07	1934	985.75	810.43	—	485.18
Hippopotamidae										
<i>Choeropsis liberiensis</i>	250,000	270.48	391.98	249.29	89.79	873.07	459.99	257.89	13.04	77.44
<i>Hippopotamus amphibius</i>	2,400,000	1763	2153	1373	—	5700	2484	1182	—	—
<i>Hippopotamus amphibius</i>	680,000	826.04	1474	1026.05	372.15	—	1812	929.00	—	383.24
Suidae										
<i>Phacochoerus aethiopicus</i>	88,000	127.21	226.28	156.01	—	255.97	173.49	113.95	—	—
<i>Potamochoerus porcus</i>	76,000	113.49	153.48	112.81	24.61	244.53	154.88	97.97	9.02	25.99
Tragulidae										
<i>Tragulus javanicus</i>	1400	0.88	1.73	1.35	0.82	—	2.78	3.22	—	1.32
CARNIVORA										
Canidae										
<i>Alopex lagopus</i>	4500	2.64	5.34	5.05	—	7.61	5.40	5.91	0.34	—
<i>Canis familiaris</i>	29,000	40.10	70.43	62.91	19.51	105.43	70.92	57.01	3.04	22.10
<i>Canis lupus</i>	35,000	35.45	69.80	77.14	—	92.40	72.62	72.31	5.05	—
<i>Fennecus zerda</i>	1200	0.94	1.93	1.66	0.64	2.46	1.95	2.07	0.22	1.07
<i>Lycalopex vetulus</i>	4200	2.94	6.46	5.39	—	9.94	7.35	7.70	0.45	—
<i>Vulpes vulpes</i>	5500	—	11.47	10.88	—	15.33	12.24	12.70	0.75	—
Felidae										
<i>Acinonyx jubatus</i>	39,000	33.60	73.37	71.39	17.20	110.42	89.03	81.33	5.30	31.84
<i>Felis concolor</i>	47,000	67.22	124.34	109.35	30.61	155.73	138.45	111.25	10.88	38.97
<i>Felis concolor</i>	45,700	35.15	72.27	64.70	18.68	114.72	86.72	73.91	5.01	26.35
<i>Felis lynx</i>	6700	9.36	24.61	21.35	—	25.38	27.07	28.03	2.30	—
<i>Felis pardalis</i>	13,000	13.47	26.73	25.63	6.31	41.31	31.05	24.73	3.52	8.40
<i>Panthera leo</i>	170,000	297.86	512.77	494.43	118.55	758.25	522.70	369.25	30.97	143.12
<i>Panthera onca</i>	67,400	78.36	166.55	132.78	32.56	—	167.80	115.61	12.60	39.18
<i>Panthera onca</i>	51,500	59.80	117.96	107.49	24.48	159.50	117.27	86.30	8.25	31.22
<i>Panthera onca</i>	47,300	69.31	158.46	119.82	—	176.30	156.24	106.42	10.93	—
<i>Panthera pardus</i>	51,000	42.27	88.50	80.97	22.75	133.53	110.25	90.95	10.13	30.84
<i>Panthera tigris altaica</i>	221,000	277.04	577.05	534.88	125.61	898.15	739.87	451.08	44.26	180.16
<i>Panthera tigris altaica</i>	230,000	354.64	658.26	602.73	—	913.60	642.08	477.03	47.78	—
<i>Panthera tigris sumatrae</i>	73,000	64.81	159.85	146.48	—	202.76	169.42	121.63	—	—
<i>Panthera tigris tigris</i>	115,000	142.04	320.02	290.36	—	417.42	333.77	246.81	22.65	—
<i>Panthera tigris tigris</i>	145,000	229.05	471.03	441.79	121.18	629.12	485.68	382.84	32.77	135.10
<i>Panthera tigris tigris</i>	145,000	187.27	393.41	372.12	96.98	546.75	434.10	328.82	30.95	114.72
<i>Panthera uncia</i>	30,000	43.96	85.58	82.50	19.83	113.77	91.74	80.93	12.78	27.84
<i>Panthera uncia</i>	34,800	31.57	82.80	80.98	19.97	111.15	91.86	79.60	7.02	25.29

APPENDIX. (Continued.)

Taxon	Body	Scapula	Humerus	Radius + ulna	Metacarpus	Pelvis	Femur	Tibia	Fibula	Metatarsus
Hyaenidae										
Hyaena hyaena	32,000	57.20	110.80	99.25	—	105.76	95.14	65.83	3.43	—
Mustelidae										
Gulo gulo	12,000	9.11	21.81	20.28	—	28.95	18.86	17.20	2.25	—
Meles meles	10,000	7.26	15.35	13.76	2.75	22.24	14.25	11.33	1.72	3.30
Procyonidae										
Ailurus fulgens	4400	5.25	10.18	7.52	1.97	12.96	9.93	6.80	1.07	2.49
Nasua nasua	3400	2.86	7.16	4.71	—	12.17	7.58	5.65	1.11	—
Ursidae										
Ursus americanus	105,000	113.57	278.70	204.40	35.02	253.85	247.02	127.52	31.22	28.77
Ursus arctos middendorffi	203,000	383.89	765.95	608.18	112.72	—	784.55	479.82	55.54	104.13
Ursus arctos middendorffi	496,000	885.15	1369	1090.64	190.32	—	1380	805.33	89.97	187.85
Ursus maritimus	173,000	241.02	580.45	430.00	96.22	770.24	551.09	364.11	29.81	95.95
Ursus thibetanus	98,000	192.39	322.37	266.88	35.55	—	314.12	159.50	18.67	27.03
Viverridae										
Paradoxurus hermaphroditus	2200	0.84	1.80	1.63	—	2.97	2.52	1.86	0.31	—
HYRACOIDEA										
Procaviidae										
Procavia capensis	2800	1.93	3.97	2.50	0.51	7.48	4.04	3.04	0.23	0.61
PERISSODACTYLA										
Equidae										
Equus burchelli	136,000	204.61	344.03	363.29	147.87	708.20	575.78	430.50	—	191.59
Equus caballus	675,000	611.21	815.81	—	—	—	1121	—	—	—
Rhinocerotidae										
Ceratotherium simum	1,900,000	2891	3964	3415	810.66	9800	3889	2058	214.25	652.63
Diceros bicornis	875,000	1518	2214	1840.15	486.83	—	2362	1241	—	369.38
Tapiridae										
Tapirus indicus	317,000	501.58	699.34	524.26	134.20	1560	842.68	469.42	—	202.15
Tapirus terrestris	173,000	264.03	432.36	309.00	87.73	—	536.49	304.36	37.90	110.83
PROBOSCIDEA										
Elephantidae										
Elephas maximus	3,524,000	—	10,200	7490	1130.38	—	11,100	4300	448.57	698.28
Loxodonta africana	6,250,000	17,000	20,300	15,450	2608.39	37,200	19,800	8200	1034	—