

Implications of limb bone scaling, curvature and eccentricity in mammals and non-avian dinosaurs

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(Accepted 4 May 2000)

Abstract

Current theories of locomotor biomechanics are based largely on observations of extant terrestrial mammals. However, extant mammals are limited with respect to certain aspects of terrestrial locomotion, and this constraint has confounded interpretations of limb design in this group. Dinosaurs include a wide array of large and small bipeds, record several transitions between bipedalism and quadrupedalism, and show a unique covariation of cursoriality and body size. Thus, the wider applications of biomechanical theories may be tested by applying them to the limb bones of dinosaurs. A broad examination of hindlimb and forelimb bone scaling patterns in dinosaurs and mammals reveals several general similarities that provide insight into the general constraints acting on terrestrial locomotion, particularly in animals with parasagittally oriented limbs. Most limb bones scale with negative allometry in these two groups, and larger taxa tend to scale more negatively than smaller forms. However, the strongly negative scaling of large mammals is mostly restricted to ungulates, whose unusually short femora may be the result of constraints of cursoriality at large body sizes. Bipedal and quadrupedal dinosaurs scale very similarly, with most differences apparently resulting from size rather than posture. Bone curvature tends to decrease with increasing body size, while femoral midshaft eccentricity tends to increase. Femoral midshaft eccentricity is explained as a general adaptation to mediolateral bending on parasagittal limb bones. These trends are more pronounced in dinosaurs than mammals; additional morphological constraints present in the dinosaurian hindlimb may contribute to this distinction.

Key words: terrestrial locomotion, regressions, biomechanics, limb posture

INTRODUCTION

The universality of gravity and the conservative material properties of vertebrate bone (e.g. Currey, 1987) permit the application of theories of locomotor mechanics and dimensional scaling to all terrestrial vertebrates. Additionally, recent studies on extant mammalian and avian terrestrial locomotion have revealed correlations between limb morphology and body size (McMahon, 1975*a,b*; Alexander *et al.*, 1979; Scott, 1985; Bertram & Biewener, 1990; Christiansen, 1999*a,b*), kinematics (Biewener, 1983, 1989, 1990; Gatesy & Biewener, 1991), and bone loading (Lanyon, 1981, 1987; Rubin & Lanyon, 1982; Biewener, Thomason & Lanyon, 1983; Biewener & Taylor, 1986; Biewener & Bertram, 1993; Carrano & Biewener, 1999) that provide a framework within which the locomotor morphology of extinct vertebrates can be explained more precisely. These

correlations imply (among other things) that increases in body size create safety risks that require allometric, behavioural, and/or postural changes in organisms in order to maintain structural safety limits (Alexander, 1981; Biewener, 1989, 1990, 1993).

This biomechanical framework is derived primarily from studies of extant mammals (e.g. Jenkins, 1971; Jenkins & Camazine, 1977; Rubin & Lanyon, 1982; Biewener, 1983, 1989). Because the modern terrestrial mammalian fauna is morphologically depauperate (especially relative to most other late Cenozoic faunas), these studies necessarily omit several mammalian morphotypes known to have existed in the past. Therefore one may question whether these biomechanical tenets are truly universally applicable, or whether they accurately describe even the mammalian system. In addition, considerably less attention has been drawn to scaling patterns in non-mammalian terrestrial vertebrates. In particular, non-avian dinosaurs evolved an erect-limbed posture independently from mammals, and

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therefore present an under-used opportunity to test the general predictions of biomechanical theories based on locomotor data from extant mammals (e.g. Gregory, 1912; Maynard Smith & Savage, 1955; Biewener, 1983; Hildebrand, 1985; Bertram & Biewener, 1988, 1990). In other words, how broadly applicable are hypotheses of mechanical constraint on terrestrial locomotion?

Recent studies have been promising in this regard, demonstrating consistent patterns in the locomotor morphologies of non-avian dinosaurs. Comparisons of dinosaurs with mammals and birds have supported hypotheses of 'hip-driven' limb kinematics (Gatesy, 1990; Chiappe, 1995; Carrano, 1998a) and vertical limb postures (Charig, 1972; Gatesy, 1990) in dinosaurs that were similar to those of mammals. Multivariate statistical analyses have demonstrated that dinosaurs and mammals show similar patterns of variation in locomotor morphology (Coombs, 1978; Carrano, 1999). Large and small theropods, at least, seem to scale similarly to large and small mammals (Christiansen, 1999c).

In addition, non-avian dinosaurs represent the most diverse radiation of fully terrestrial bipeds. Extant bipedal mammals are highly specialized and low in diversity, while birds are primarily volant and not likely to have faced the same constraints on hindlimb morphology as obligatorily terrestrial taxa (Gatesy & Dial, 1996; Gatesy & Middleton, 1997). These factors frustrate both qualitative and quantitative attempts at comparing scaling patterns between bipeds and quadrupeds. In contrast, robust statistical comparisons are possible between bipedal and quadrupedal non-avian dinosaurs. Furthermore, transitions between bipedalism and quadrupedalism are documented in several non-avian dinosaur clades, in addition to the presence of 'semi-bipeds' (prosauropods and hadrosaurids) that are intermediate in locomotor morphology between bipeds and quadrupeds (e.g. Galton, 1990a; Weishampel & Horner, 1990; Bultynck, 1992).

Quantification of scaling patterns within all non-avian dinosaurs must be the first step in addressing these issues. In this paper, I examine scaling patterns of limb bone dimensions, femoral curvature, and femoral midshaft eccentricity in dinosaurs and compare them to those of terrestrial mammals (McMahon, 1975a,b; Alexander *et al.*, 1979; Economos, 1983; Scott, 1985; Bertram & Biewener, 1990; Christiansen, 1999a,b). I analyse different postural and size groups and compare scaling patterns to theoretical predictions. Finally, I evaluate the implications of these results for currently accepted theories of locomotor biomechanics and the evolution of dinosaur locomotion.

SCALING PATTERNS IN MAMMALS

Numerous previous studies have examined the correlations between limb bone dimensions and body mass, often generating (and testing) theoretically based expectations of these relationships (e.g. McMahon, 1975a,b;

Alexander *et al.*, 1979; Economos, 1983; Scott, 1985). Most of these studies have attempted to determine whether limb scaling conforms to the expectations of geometric or elastic similarity, based on the different predictions made by these two theories. The underlying principle is that the dimensions of most animals change with body size in accordance with regular, fundamental mathematical laws that are in turn related to the interactions between the material properties of bone and the effects of gravity. An excellent review of recent work is presented in Christiansen (1999c: 666–667), and the topic is only briefly summarized here.

Geometric similarity posits strict linear amplification of organismal structure as body size increases; scaling trends should be isometric. However, because doubling a linear dimension increases the mass eight-fold, larger animals will be forced to support masses that are proportionally greater to bone cross-sectional areas. Safety factors will accordingly be lower, increasing the risk of structural failure. Specifically, as a given length (L) doubles ($2L$) the associated area ($A = L^2$) quadruples ($[2L]^2 = 4L^2$) and the volume ($V = L^3$) increases eight times ($[2L]^3 = 8L^3$). As a result, L and D are proportional (\propto) to mass^{1/3} (because mass $\propto V$), and therefore $L \propto D$. *Elastic similarity*, by contrast, dictates that organismal structural dimensions will change as size increases so as to keep bone deformations constant, specifically to prevent Euler buckling (McMahon, 1973, 1975a). As a result, the mass increase associated with doubling a linear dimension has no impact on safety factor, but results in allometric scaling of linear elements with respect to body mass. Under this theory, $L \propto V^{1/4}$ and thus $L \propto M^{1/4}$, but $D \propto M^{3/8}$. Therefore $L \propto D^{2/3}$.

Empirical studies have tended to support patterns of geometric similarity in mammalian limb bones, with certain taxonomic groups (generally ungulates) deviating towards elastic similarity (McMahon, 1975a,b; Alexander *et al.*, 1979; Economos, 1983; Scott, 1985). However, these studies have generally employed least-squares regression in order to describe scaling patterns, a method not favoured here (see below). Reduced major axis regression indicates that most mammalian limb bones scale intermediately, with larger mammals scaling closer to elastic similarity and smaller mammals closer to geometric similarity (Biewener, 1990; Christiansen, 1999a,b).

The complexity of these scaling patterns is not adequately described by any single linear equation. The larger implication is that there is no single linear relationship between size and limb bone dimensions (Biewener, 1989, 1990; Christiansen, 1999a,b). Rather, scaling is the response of limb bones to several varying factors, including (but not excluded to) body size, posture, behaviour, and phylogeny. Biewener (1989, 1990) summarized the effects of several of these factors, explaining the tendency for the limb bones of larger animals to scale more negatively in terms of safety factor maintenance. Larger animals, faced with increasingly risky safety factors, cannot scale purely geometrically and respond by limiting their behavioural

repertoires, restricting limb abduction angles, and increasing relative limb dimensions (Biewener, 1989, 1990). This is often manifest as distinct scaling patterns for large vs small taxa (Bertram & Biewener, 1990; Christiansen, 1999b,c), but may also be viewed as a tendency towards curvilinear scaling throughout the taxonomic size range.

MATERIALS AND METHODS

Data were collected from 1486 dinosaur and 493 mammal specimens distributed across all major clades within both groups. Only terrestrial mammals were measured, but these included a large number of extinct taxa (Carrano, 1998b: appendix 1, supplemented with data from McMahon, 1975b, Biewener, 1983; Bertram & Biewener, 1988, 1990; and Holtz, 1994). Length, anteroposterior diameter, and mediolateral diameter of the femur, tibia, and humerus, as well as femoral and humeral circumferences were measured. Data were taken with Mitutoyo dial callipers (<200 mm) or measuring tape (>200 mm), and supplemented with measurements taken from photographs in the literature when direct access to specimens was not possible. The reliability of measurements from literature photographs were checked by comparing them with direct measurements for several specimens, and all deviations were <1%. Data from specimens that seemed to have suffered significant post-mortem damage were omitted, and measurements averaged from multiple specimens of the same taxon. The resulting sample included 316 dinosaur and 416 mammalian taxa.

Linear data were log-transformed before analysis, and proportional data (curvature, eccentricity) were arcsin-transformed (Sokal & Rohlf, 1995). Reduced major axis (RMA) regressions were performed to examine correlations between different limb bone dimensions. RMA was chosen instead of least-squares regression because both variables include a component of error and dependence of one variable on the other is uncertain (LaBarbera, 1989; Sokal & Rohlf, 1995). Where comparisons are made to previously published results of least-squares regressions, the RMA slope was calculated by dividing the least-squares slope by the *r*-value (Sokal & Rohlf, 1995). Lengths were regressed separately against anteroposterior and mediolateral diameters for each of the 4 measured limb bones. Femoral and humeral circumferences were regressed against one another in dinosaurs and mammals because these measures have been used to generate body mass estimates for dinosaurs (Anderson, Hall-Martin & Russell, 1985).

Many other variables scale predictably with body mass, but body mass obviously cannot be measured directly in dinosaurs. Unfortunately, existing equations derive body mass estimates entirely from limb bone measurements (Anderson *et al.*, 1985), precluding any independent comparison of these variables. Alternatively, volumetric measurements can be made from scale

(Colbert, 1962; Paul, 1988) or computer-generated (Henderson, 1999) models, but this drastically limits the dataset to a few well-known taxa. Instead, I have chosen to use several measures and calculations as proxies for body mass. These proxies are known to be positively correlated with body mass in extant taxa, but no effort is made to define this relationship further because none of these measures can be directly tested against body mass in dinosaurs. As a result, general scaling trends (relative isometry vs positive or negative allometry) can be examined, but scaling exponents cannot be compared explicitly to predicted values.

First, a principal components analysis was performed using femoral length, femoral anteroposterior diameter, tibial length, metatarsal III length, metatarsal III diameter, and distance from the proximal end of the femur to the fourth trochanter as variables. This analysis (described in detail in Carrano, 1999) generated a first principal component (PC1) that was highly positively correlated with all variables (all variable coefficients > 0.97). It is interpreted here as an indication of size-related variation in these data and used as a proxy for body mass, with the caveat that it necessarily includes a 'shape' component in addition to size variation (e.g. Jungers, Falsetti & Wall, 1995).

Second, the geometric mean (GM) was used as a proxy for mass (Jungers *et al.*, 1995). GM was calculated as the seventh root of 7 variables: femoral length, femoral anteroposterior diameter, tibial length, tibial anteroposterior diameter, metatarsal III length, humeral length, and humeral anteroposterior diameter. Finally, several additional measurements were used that are probably positively correlated with body mass: femoral circumference (FC; Anderson *et al.*, 1985), femoral anterior diameter (FAP), and tibial anteroposterior diameter (TAP). Regressions against these proxies serve only to determine whether scaling is absolutely positive or negative; without a further correlation between the proxy and body size, no more specific interpretations are possible.

Femoral curvature (CURV1) was examined in dinosaurs and mammals, calculated as:

$$\text{CURV1} = (\text{MA} / \text{FL}) \cdot 100 \quad (1)$$

where MA is the moment arm of the femur at midshaft (the deviation of midshaft from a straight line drawn between the ends of the bone) and FL is femur length (Biewener, 1983). Because diameter (or radius), as well as length, should be proportional to bending, Bertram & Biewener (1988) used a modified version of this formula:

$$\text{CURV2} = (\text{MA} / \text{FAP}) \cdot 100 \quad (2)$$

where FAP is femoral anteroposterior diameter. I calculated CURV2 and compared it to the results for CURV1. Both measures were regressed against body weight in mammals as well as several size proxies (FAP, FC, TAP, and GM) in both groups to test the hypothesis that limb bone curvature is inversely size-dependent (Biewener, 1983). For this analysis, mammalian taxa

Table 1. RMA log-log regressions of femoral length and diameter in dinosaurs. FL, femoral length; FAP, femoral anteroposterior diameter; FML, femoral mediolateral diameter; CI, 95% confidence intervals for the slope; *n*, sample size. *, slope significantly different from zero for at least $P < 0.05$ level

Group	Slope \pm CI	Intercept	r^2	<i>n</i>
FL vs FAP	0.947 \pm 0.031*	1.122	0.937	221
Saurischia	0.913 \pm 0.039*	1.193	0.938	129
Ornithischia	1.003 \pm 0.050*	1.006	0.944	92
Bipeds	0.953 \pm 0.046*	1.111	0.948	94
Semi-bipeds	0.971 \pm 0.073*	1.050	0.941	45
Bipeds + semi-bipeds	0.936 \pm 0.033*	1.121	0.952	139
Quadrupeds	0.910 \pm 0.100*	1.361	0.777	75
Small	0.920 \pm 0.049*	1.152	0.918	114
Large	0.751 \pm 0.089*	1.807	0.612	111
FL vs FML	0.817 \pm 0.027*	1.282	0.944	197
Saurischia	0.796 \pm 0.033*	1.336	0.950	111
Ornithischia	0.845 \pm 0.046*	1.121	0.938	85
Bipeds	0.839 \pm 0.042*	1.273	0.948	85
Semi-bipeds	1.021 \pm 0.111*	0.945	0.897	38
Bipeds + semi-bipeds	0.833 \pm 0.035*	1.272	0.944	123
Quadrupeds	0.901 \pm 0.058*	1.194	0.932	66
Small	0.751 \pm 0.042*	1.364	0.919	103
Large	0.699 \pm 0.072*	1.708	0.751	97

were segregated into those taxa smaller than the smallest known dinosaur (*c.* 10 kg), and those this size or larger.

I regressed FAP and femoral mediolateral diameter (FML) against one another to examine patterns of femoral eccentricity. A ratio (ECC) was also calculated to reflect this eccentricity and was regressed against body size proxies:

$$\text{ECC} = \text{FML} / \text{FAP} \quad (3)$$

ECC was also regressed against 3 size proxies (PC1, GM, TAP); FC was not used because it was redundant with ECC.

For any log-log regression, the slope represents the rate of correlated change between the 2 variables analysed, and the *y*-intercept is a measure of the absolute difference between the 2 (a *y*-intercept of 0 indicates pure symmetry between the 2 axes). Examining these 2 measures in different groups allows comparison of their scaling trends as well as the underlying relationships between the variables. Standard statistics were calculated that reflect the explanatory power (r^2) and significance from a slope of 0 (P -value), and I used the standard error of the least-squares slope to estimate the confidence intervals around the RMA slope (Sokal & Rohlf, 1995). All regressions and statistical measures were calculated and compared for dinosaurs and mammals, several internal clades, and different postural groups. Differential scaling with body size was tested by comparing bivariate and polynomial regressions for dinosaurs and mammals. In addition, both groups were separated into 'small' and 'large' categories at the median value for the *x*-variable being analysed, and calculated independent regressions for these 2 categories.

Table 2. RMA log-log regressions of tibial length and diameter in dinosaurs. TL, tibial length; TAP, tibial anteroposterior diameter; TML, tibial mediolateral diameter; other abbreviations as in Table 2

Group	Slope \pm CI	Intercept	r^2	<i>n</i>
TL vs TAP	0.743 \pm 0.040*	1.491	0.859	197
Saurischia	0.704 \pm 0.051*	1.577	0.839	119
Ornithischia	0.816 \pm 0.054*	1.324	0.914	78
Bipeds	0.836 \pm 0.048*	1.368	0.927	93
Semi-bipeds	0.986 \pm 0.067*	1.009	0.956	42
Bipeds + semi-bipeds	0.827 \pm 0.039*	1.359	0.922	135
Quadrupeds	0.836 \pm 0.112*	1.352	0.748	59
Small	0.756 \pm 0.059*	1.468	0.833	108
Large	0.634 \pm 0.111*	2.187	0.301	93
TL vs TML	0.771 \pm 0.039*	1.432	0.896	155
Saurischia	0.751 \pm 0.052*	1.496	0.896	88
Ornithischia	0.789 \pm 0.058*	1.349	0.911	66
Bipeds	0.775 \pm 0.046*	1.431	0.934	74
Semi-bipeds	0.913 \pm 0.082*	1.152	0.945	31
Bipeds + semi-bipeds	0.776 \pm 0.037*	1.417	0.937	105
Quadrupeds	0.908 \pm 0.139*	1.282	0.749	46
Small	0.752 \pm 0.064*	1.464	0.856	81
Large	0.785 \pm 0.138*	1.794	0.489	76

Table 3. RMA log-log regressions of humeral length and diameter in dinosaurs. HL, humeral length; HAP, humeral anteroposterior diameter; HML, humeral mediolateral diameter; other abbreviations as in Table 2

Group	Slope \pm CI	Intercept	r^2	<i>n</i>
HL vs HAP	0.853 \pm 0.043*	1.254	0.909	139
Saurischia	0.865 \pm 0.060*	1.257	0.912	74
Ornithischia	0.820 \pm 0.060*	1.274	0.915	65
Bipeds	0.861 \pm 0.098*	1.287	0.839	51
Semi-bipeds	0.871 \pm 0.129*	1.241	0.843	32
Bipeds + semi-bipeds	0.828 \pm 0.066*	1.297	0.875	83
Quadrupeds	1.010 \pm 0.135*	1.112	0.782	51
Small	0.870 \pm 0.086*	1.257	0.853	61
Large	0.920 \pm 0.103*	1.290	0.749	80
HL vs HML	0.840 \pm 0.037*	1.186	0.934	136
Saurischia	0.864 \pm 0.060*	1.173	0.912	74
Ornithischia	0.821 \pm 0.044*	1.183	0.957	61
Bipeds	0.895 \pm 0.082*	1.155	0.898	52
Semi-bipeds	0.979 \pm 0.144*	1.006	0.868	28
Bipeds + semi-bipeds	0.865 \pm 0.058*	1.171	0.915	80
quadrupeds	0.893 \pm 0.105*	1.165	0.836	50
Small	0.837 \pm 0.072*	1.209	0.887	64
Large	0.852 \pm 0.086*	1.275	0.816	73

RESULTS

Limb bone dimensions

In general, length and diameter of nearly all long bones show negatively allometric correlations with one another in both dinosaurs and mammals (Figs 1 & 2, Tables 1–6). Most slopes fall between the values predicted by elastic and geometric similarity, sometimes including both within their confidence intervals (see

Table 4. RMA log–log regressions of femoral length and diameter in mammals. Abbreviations as in Table 2

Group	Slope \pm CI	Intercept	r^2	n
FL vs FAP	$0.868 \pm 0.022^*$	1.238	0.936	370
Ungulata	$0.804 \pm 0.039^*$	1.329	0.908	148
Mammalia excluding ungulates	$0.942 \pm 0.037^*$	1.189	0.918	213
Bipeds	$0.941 \pm 0.145^*$	1.181	0.933	15
Quadrupeds	$0.859 \pm 0.024^*$	1.241	0.936	355
Small	$0.930 \pm 0.059^*$	1.181	0.889	111
Large	$0.772 \pm 0.035^*$	1.416	0.857	259
FL vs FML	$0.900 \pm 0.039^*$	1.196	0.885	244
Ungulata	$0.803 \pm 0.056^*$	1.312	0.923	65
Mammalia excluding ungulates	$0.925 \pm 0.053^*$	1.187	0.846	179
Bipeds	$1.079 \pm 0.174^*$	1.017	0.934	14
Quadrupeds	$0.888 \pm 0.039^*$	1.208	0.883	230
Small	$0.803 \pm 0.159^*$	1.297	0.678	91
Large	$0.784 \pm 0.051^*$	1.392	0.831	153

Table 5. RMA log–log regressions of tibial length and diameter in mammals. Abbreviations as in Table 3

Group	Slope \pm CI	Intercept	r^2	n
TL vs TAP	$0.850 \pm 0.029^*$	1.306	0.885	363
Ungulata	$0.766 \pm 0.055^*$	1.487	0.809	145
Mammalia excluding ungulates	$0.823 \pm 0.045^*$	1.321	0.844	209
Bipeds	$1.170 \pm 0.145^*$	1.085	0.957	15
Quadrupeds	$0.839 \pm 0.029^*$	1.309	0.892	348
Small	$0.775 \pm 0.076^*$	1.354	0.742	110
Large	$0.786 \pm 0.049^*$	1.481	0.742	253
TL vs TML	$0.800 \pm 0.033^*$	1.368	0.888	240
Ungulata	$0.721 \pm 0.072^*$	1.484	0.846	63
Mammalia excluding ungulates	$0.856 \pm 0.049^*$	1.336	0.856	177
Bipeds	$1.102 \pm 0.109^*$	1.208	0.975	14
Quadrupeds	$0.776 \pm 0.031^*$	1.374	0.907	226
Small	$0.776 \pm 0.086^*$	1.395	0.736	89
Large	$0.724 \pm 0.055^*$	1.526	0.778	151

Table 13). Exceptions include large dinosaurs (which tend towards geometric similarity) and ungulate mammals (which tend towards elastic similarity). Regressions from hindlimb bones (Tables 1 & 2) showed significantly higher slopes than those from the humerus (Table 3), indicating that hindlimb elements of larger dinosaurs are relatively more slender than forelimb elements. This trend was also apparent in mammals, but with much less marked differences between fore- and hindlimbs (Tables 4–6). In general, limb bone length scaled similarly against both anteroposterior and medio-lateral diameters, with the exception of dinosaur femora. Mammals and dinosaurs scale with similar slopes in femoral circumference (FC) vs humeral circumference (HC), but dinosaurs have an absolutely larger FC for a given HC (i.e. the y -intercept is greater) (Table 6).

Among dinosaurs, most postural groups scale

Table 6. RMA log–log regressions of humeral length and diameter in mammals. Abbreviations as in Table 4

Group	Slope \pm CI	Intercept	r^2	n
HL vs HAP	$0.821 \pm 0.033^*$	1.213	0.906	213
Ungulata	$0.732 \pm 0.048^*$	1.335	0.889	104
Mammalia excluding ungulates	$0.963 \pm 0.070^*$	1.118	0.862	109
Bipeds	$1.204 \pm 0.291^*$	0.968	0.926	9
Quadrupeds	$0.805 \pm 0.033^*$	1.230	0.909	204
Small	$0.823 \pm 0.120^*$	1.234	0.701	58
Large	$0.723 \pm 0.041^*$	1.378	0.865	155
HL vs HML	$0.868 \pm 0.045^*$	1.230	0.908	128
Ungulata	$0.709 \pm 0.042^*$	1.336	0.986	19
Mammalia excluding ungulates	$0.947 \pm 0.058^*$	1.177	0.899	109
Bipeds	$1.134 \pm 0.232^*$	1.035	0.947	9
Quadrupeds	$0.835 \pm 0.090^*$	1.260	0.909	120
Small	$0.875 \pm 0.121^*$	1.246	0.747	56
Large	$0.760 \pm 0.062^*$	1.364	0.890	72

similarly for hindlimb regressions, generally between elastic and geometric similarity but tending towards the latter. Quadrupeds have a significantly higher HL vs HAP slope than other postural groups (Fig. 2, Tables 1 & 2); semi-bipeds are generally more similar to bipeds than to quadrupeds. Among mammals, bipeds scale with steeper slopes than quadrupeds for all limb regressions scaling between isometry and positive allometry (Tables 3–5). Size variation in scaling was similar for both dinosaurs and mammals. Both groups showed more strongly negatively allometric scaling at larger sizes. Unlike mammals, none of the dinosaur regressions were significantly increased in explanatory power by the application of a second-order polynomial equation.

Femoral curvature

Femoral curvature in dinosaurs shows a slight decrease when regressed against any of the body mass proxies (Fig. 3a, Table 8). Regressions using CURV1 and CURV2 were similar for dinosaurs, although the latter produced larger absolute values for slope and intercept. Femoral curvature in mammals also shows a decrease with increasing body mass (Biewener, 1983), and a stronger decrease when regressed against FAP (Fig. 3b, Table 8), although neither slope can be significantly distinguished from zero. However, decreases are significant when mammals greater than 10 kg are examined separately (representing the body mass overlap with dinosaurs) (Table 8).

Among dinosaurs, most variation in femoral curvature seems to result from size, with some postural influence. Mean values of femoral curvature are small (curvature moment arm usually <2% of bone length) for very large quadrupeds but can exceed 5% in smaller taxa. Mean curvature of bipedal dinosaurs is nearly four times that of quadrupeds, with semi-bipeds intermediate

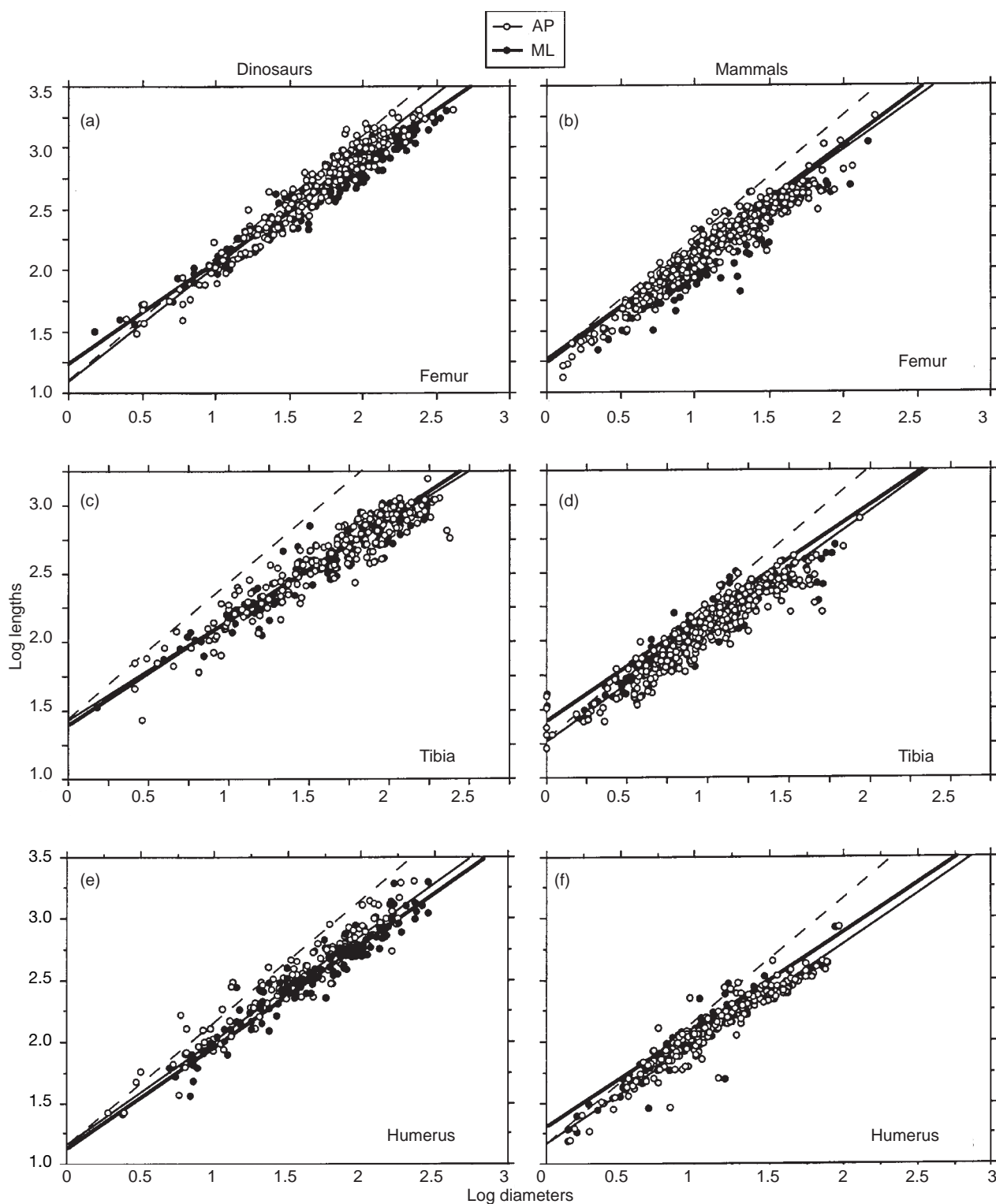


Fig. 1. Overall patterns of limb bone scaling. RMA log-log regressions of length against anteroposterior (AP) and mediolateral (ML) diameters for the femur, tibia and humerus. For each element, dinosaur and mammal data are plotted to the same scale for visual comparisons. Dashed lines, isometric scaling from the lowest point of each regression. All slopes are significantly different from zero and show negative allometry. Note that both diameters scale similarly with length for all limb bones, although femoral anteroposterior diameter scales more positively than mediolateral diameter.

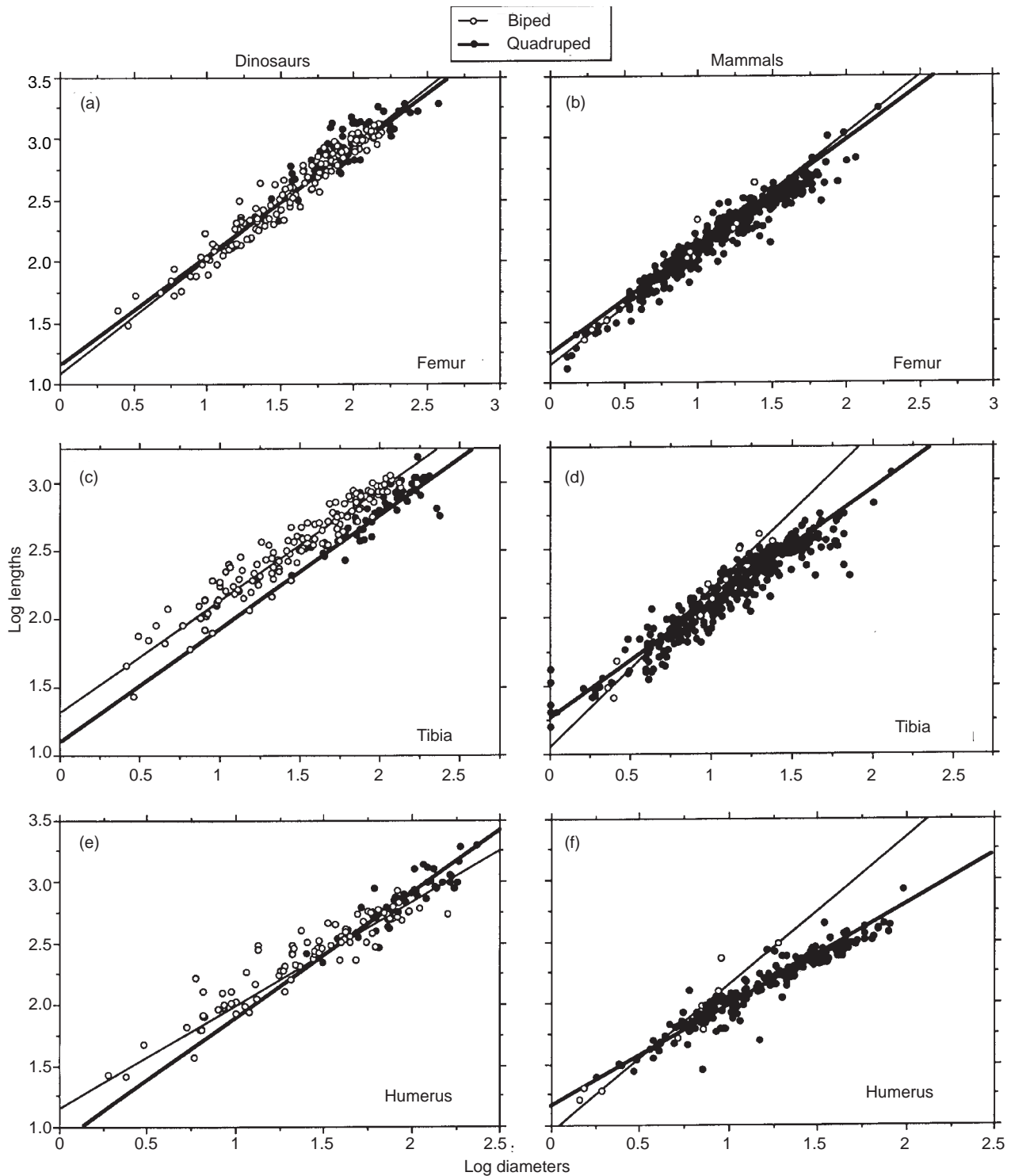


Fig. 2. Postural patterns of limb bone scaling. RMA log–log regressions of length against diameter for the femur, tibia and humerus, showing differences between bipeds and quadruped. For each element, dinosaur and mammal data are plotted to the same scale for visual comparisons.

between the two. Large bipeds have mean curvature values similar to those of large quadrupeds. Among mammals, mean femoral curvature values are always $< 2\%$, and are generally lower than all but the lowest values among dinosaurs. Mean values were comparably distributed for small vs large taxa.

Femoral eccentricity

Regressions reveal that femoral mediolateral diameter scales with slight positive allometry relative to antero-posterior diameter in dinosaurs (Fig. 3c), although confidence intervals include a slope of 1 for several

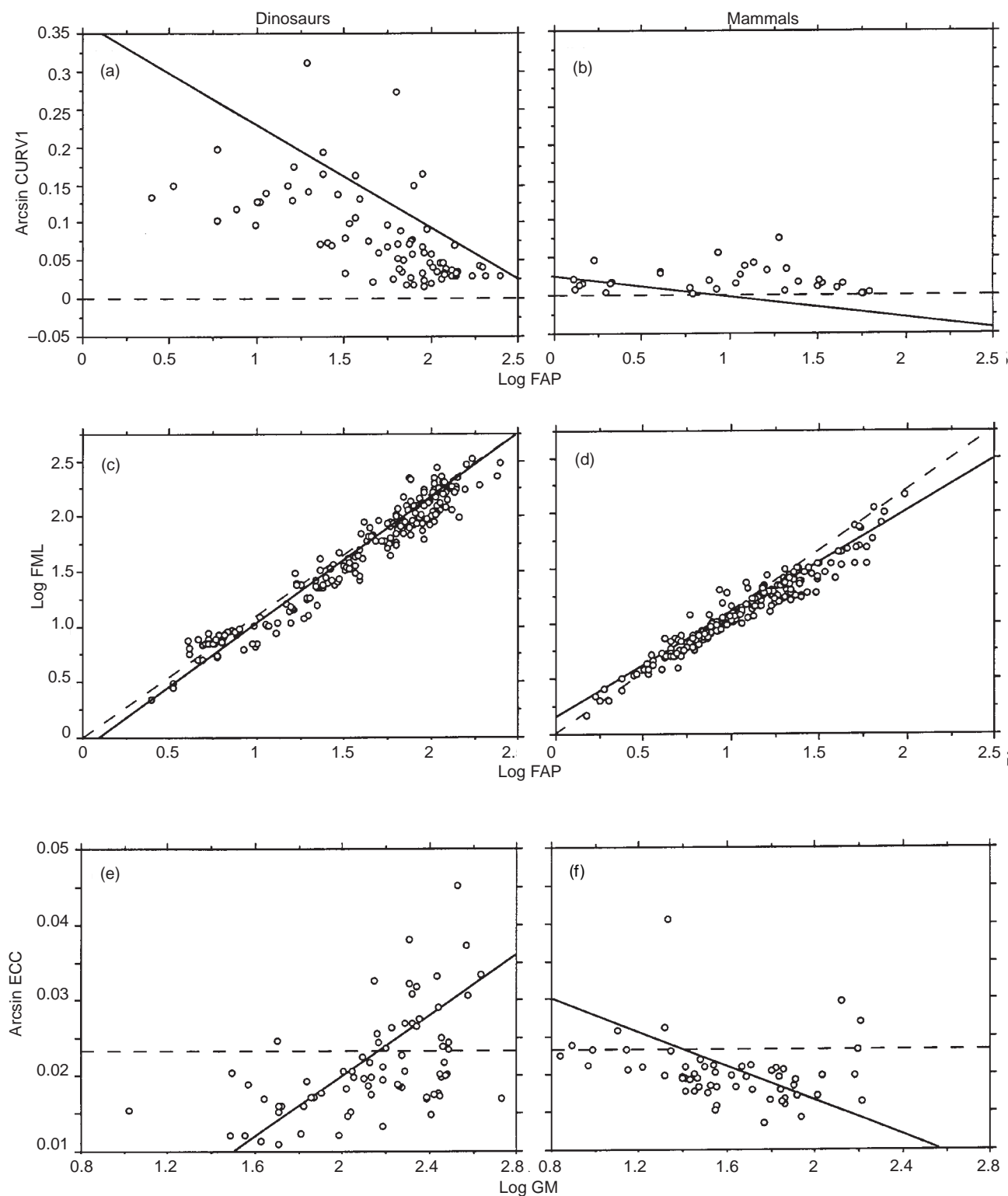


Fig. 3. RMA regressions of femoral eccentricity and curvature. RMA regressions of femoral curvature against femoral anteroposterior diameter (a, b), femoral mediolateral diameter against anteroposterior diameter (c, d), and femoral eccentricity against the geometric mean (e, f). For each regression, dinosaur and mammal data are plotted to the same scale for visual comparisons. Dashed lines, symmetrical scaling ($FML = FAP$) for FML vs FAP , and zero slope for the remaining regressions. CURV1, femoral curvature; FAP, femoral anteroposterior diameter; FML, femoral mediolateral diameter; ECC, eccentricity; GM, geometric mean.

Table 7. RMA log–log regressions of femoral and humeral circumferences in mammals and dinosaurs. FC, femoral circumference; HC, humeral circumference; other abbreviations as in Table 2

Group	Slope \pm CI	Intercept	r^2	n
FC vs HC				
Dinosauria	$0.935 \pm 0.100^*$	0.585	0.781	80
Mammalia	$0.966 \pm 0.064^*$	0.122	0.946	51

Table 8. Arcsin-log RMA regressions of femoral curvature in mammals (data from Biewener, 1983) and dinosaurs. BW, body weight; CURV1, CURV2, femoral curvature (calculated according to methods described in the text); other abbreviations as in Table 2

Group	Slope \pm CI	Intercept	r^2	n
Dinosauria				
CURV1 vs FC	$-0.170 \pm 0.017^*$	0.472	0.431	60
CURV1 vs FAP	$-0.136 \pm 0.012^*$	0.366	0.390	80
CURV1 vs TAP	$-0.116 \pm 0.010^*$	0.265	0.515	67
CURV1 vs PC1	$-0.041 \pm 0.005^*$	0.075	0.609	25
CURV1 vs GM	$-0.150 \pm 0.019^*$	0.396	0.436	38
CURV2 vs TAP	$-0.877 \pm 0.120^*$	1.896	0.192	45
CURV2 vs PC1	$-0.261 \pm 0.059^*$	0.460	0.343	15
CURV2 vs GM	$-1.179 \pm 0.220^*$	2.977	0.200	25
Mammalia				
CURV1 vs BW	-0.270 ± 0.196	-0.035	0.029	32
< 10 kg	0.512 ± 0.294	-0.058	0.007	16
≥ 10 kg	$-0.589 \pm 0.212^*$	0.099	0.607	16
CURV1 vs FAP	-0.027 ± 0.006	0.023	0.006	32
< 10 kg	-1.176 ± 0.674	-0.038	0.005	16
≥ 10 kg	$-1.881 \pm 0.639^*$	2.101	0.649	16

groups (Table 10a). As a result, mediolateral diameter increases more rapidly with size than anteroposterior diameter. The few instances of negative allometry all include isometry within the confidence intervals. Most y -intercepts are close to zero, as small dinosaur femora tend have nearly circular cross-sections. In mammals, femoral diameters scale closer to isometry than in dinosaurs (Fig. 3d, Table 11a), indicating little change in femoral eccentricity with body size. The y -intercepts are even closer to zero than for the dinosaur regressions.

Dinosaurian bipeds and quadrupeds show very similar slopes of FML vs FAP, as do mammalian bipeds and quadrupeds. However, whereas larger dinosaurs tend to show greater positive allometry than smaller taxa, the opposite is true of larger mammals. When regressed against body weight proxies (Fig. 3e, Table 10b), eccentricity exhibits a weak positive correlation in dinosaurs, indicating that larger taxa tend to have somewhat more eccentric femora than smaller taxa. Among mammals (Fig. 3f, Table 11b), eccentricity decreases slightly as size increases, with bipeds showing the most significantly negative slopes.

Most dinosaur groups have mean ECC values greater than, but within 1 SD of, 1 (Table 12). Mean mammalian eccentricity is comparable to that seen in dinosaurs (Table 12). There are no significant differences between

Table 9. Mean values of femoral curvature (CURV1) in dinosaurs (A) and mammals (B); data from Biewener (1983). SD, one standard deviation; other abbreviations as in Table 2

	mean \pm SD	n
(a) Dinosauria	3.261 ± 1.911	92
Saurischia	5.020 ± 3.689	46
Ornithischia	3.498 ± 2.611	34
Bipeds	7.097 ± 2.913	29
Semi-bipeds	2.481 ± 1.590	36
Bipeds + semi-bipeds	5.976 ± 3.126	40
Quadrupeds	2.481 ± 1.590	36
Small	6.510 ± 3.192	36
Large	2.920 ± 2.501	47
(b) Mammalia	1.212 ± 0.972	32
Ungulata	1.414 ± 1.277	13
Carnivora	1.352 ± 0.840	9
Rodentia	0.825 ± 0.460	10

large and small mammals, or between bipeds and quadrupeds.

DISCUSSION

Limb bone dimensions

The very similar scaling patterns of dinosaurs and mammals are consistent with the results from previous analyses of these groups (McMahon, 1975a,b; Alexander *et al.*, 1979; Economos, 1983; Scott, 1985; Bertram & Biewener, 1988, 1990; Christiansen, 1999b,c). Many of these studies attempted to detect either geometric or elastic similarity in mammalian limb bones, generally supporting the former but noting a trend towards the latter in larger taxa. However, RMA regressions of these data produced slopes that are intermediate between geometric and elastic similarity (Table 13). This suggests that neither geometric nor elastic similarity alone adequately explains the patterns prevalent in these limb bones (Biewener, 1989, 1990; Christiansen, 1999b,c).

In the current analyses, both mammals and dinosaurs scale predominately with negative allometry in all limb dimensions (Carrano, 1998a), and both show a decrease in slope as body size increases (Table 13). In general these results confirm previous conclusions regarding the significant similarities between dinosaurs and mammals in patterns of hindlimb bone allometry (Carrano, 1998a). There seem to be few significant differences between bipedal and quadrupedal dinosaurs in hindlimb regressions, suggesting that transitions between these two postures do not require radical alterations in hindlimb scaling. In fact, large bipeds and quadrupeds scale similarly, implying that the greater negative allometry of quadrupedal dinosaur limb bones is more directly related to their larger size.

Differences in forelimb scaling are small but significant, with dinosaur humeri scaling less negatively than mammalian humeri. However, quadrupedal dinosaur

Table 10. Log-log (a) and arcsin-log (b) RMA regressions of femoral eccentricity in dinosaurs. Abbreviations as in Tables 2 & 3

Group	Slope \pm CI	Intercept	r^2	n
Dinosauromorpha				
(a) FML vs FAP	$1.178 \pm 0.045^*$	-0.158	0.931	179
Dinosauria	$1.186 \pm 0.049^*$	-0.162	0.923	176
Saurischia	$1.183 \pm 0.068^*$	-0.158	0.922	99
Ornithischia	$1.194 \pm 0.076^*$	-0.171	0.923	77
Bipeds	1.110 ± 0.054	-0.126	0.958	76
Semi-bipeds	0.971 ± 0.120	0.234	0.876	36
Bipeds + semi-bipeds	1.110 ± 0.046	-0.111	0.954	112
Quadrupeds	1.114 ± 0.139	0.205	0.787	58
Small	1.181 ± 0.080	-0.165	0.925	93
Large	1.249 ± 0.195	0.387	0.483	86
(b) ECC vs PCI				
Dinosauria	$0.005 \pm 0.001^*$	0.021	0.153	40
Quadrupeds	0.010 ± 0.004	0.005	0.262	7
Small	$0.006 \pm 0.001^*$	0.023	0.261	26
Large	0.006 ± 0.001	0.016	0.126	22
ECC vs GM				
Dinosauria	$0.021 \pm 0.002^*$	-0.022	0.279	74
Bipeds	$0.011 \pm 0.001^*$	-0.001	0.217	52
Quadrupeds	1.000 ± 0.010	-1.713	0.001	19
Small	$0.017 \pm 0.003^*$	-0.011	0.221	36
Large	0.053 ± 0.009	-0.081	0.024	38
ECC vs TAP				
Dinosauria	$0.019 \pm 0.001^*$	-0.009	0.291	138
Bipeds	$0.012 \pm 0.001^*$	0.005	0.188	91
Quadrupeds	$0.039 \pm 0.006^*$	-0.020	0.193	40
Small	$0.044 \pm 0.005^*$	-0.028	0.238	74
Large	$0.014 \pm 0.002^*$	0.004	0.152	64

and bipedal mammal humeri scale nearly isometrically, whereas those of bipedal dinosaurs and quadrupedal mammals scale with negative allometry, i.e. humeral lengths increase faster than diameters in quadrupedal dinosaurs and bipedal mammals. This is somewhat puzzling – quadrupedal dinosaur humeri would be expected to scale more negatively because they would have been subjected to greater (and more frequent) supportive loads. Two factors may contribute to this discrepancy. First, longer humeri contribute more to stride length, an important benefit accompanying the transition from bipedalism to quadrupedalism. Second, bipedal dinosaur humeri may have encountered greater functionally imposed loading variability (many were used in prehension and predation) and accommodated by more positive scaling.

Previous analyses have reported that mammalian scaling relationships are more accurately explained by second-order polynomials, implying that larger and smaller mammals may have distinct scaling requirements (Scott, 1985; Bertram & Biewener, 1990; Christiansen, 1999b). It has been suggested that this may reflect general postural differences between small and large mammals: larger, more straight-limbed mammals must rely primarily on changes in bone dimension, rather than limb posture, to accommodate limb bone stresses (Bertram & Biewener, 1990; Biewener, 1990). Indeed,

Table 11. Log-log (a) and arcsin-log (b) regressions of femoral eccentricity in mammals. Regressions against body size proxies are least-squares due to the small sample sizes; the remainder are RMA. Abbreviations as in Tables 2 & 3

Group	Slope \pm CI	Intercept	r^2	n
(a) FML vs FAP	$0.961 \pm 0.029^*$	0.116	0.940	240
Ungulata	$0.961 \pm 0.084^*$	0.115	0.886	61
Mammalia excluding ungulates	$1.023 \pm 0.033^*$	0.068	0.949	179
Bipeds	$0.872 \pm 0.046^*$	0.157	0.993	14
Quadrupeds	$0.967 \pm 0.031^*$	0.112	0.937	226
Small	$1.081 \pm 0.080^*$	0.061	0.881	91
Large	$0.985 \pm 0.052^*$	0.116	0.890	149
(b) ECC vs GM				
Bipeds	-0.012 ± 0.002	0.041	0.063	58
Quadrupeds	$-0.007 \pm 0.001^*$	0.028	0.965	7
Small	-0.011 ± 0.002	0.040	0.033	51
Large	-0.023 ± 0.005	0.050	0.049	22
ECC vs TAP				
Bipeds	$-0.016 \pm 0.001^*$	0.038	0.016	239
Quadrupeds	$-0.008 \pm 0.001^*$	0.027	0.743	14
Small	-0.010 ± 0.001	0.031	0.009	225
Large	0.016 ± 0.002	0.010	0.033	90
Large	0.000 ± 0.001	0.019	0.000	149

Table 12. Mean values of femoral eccentricity (ECC) in dinosaurs and mammals. Abbreviations as in Table 2

	mean \pm SD	n
Dinosauria	1.248 ± 0.395	176
Saurischia	1.255 ± 0.429	99
Ornithischia	1.238 ± 0.349	77
Bipeds	1.027 ± 0.233	76
Semi-bipeds	1.191 ± 0.230	36
bipeds + semi-bipeds	1.080 ± 0.243	112
Quadrupeds	1.576 ± 0.437	58
Small	1.105 ± 0.303	93
Large	1.389 ± 0.429	86
Mammalia	1.129 ± 0.228	240
Ungulata	0.996 ± 0.241	61
Mammalia excluding ungulates	1.175 ± 0.205	179
Bipeds	1.082 ± 0.158	14
Quadrupeds	1.132 ± 0.232	226
Small	1.195 ± 0.220	91
Large	1.089 ± 0.225	149

phylogenetic groups that consist mostly of smaller taxa tend to scale more positively than those consisting mostly of larger taxa. However, ungulates seem to scale more negatively than other mammals of comparable size, and it has also been suggested that ungulates exhibit a uniquely derived limb bone allometry that more closely fits expectations of elastic similarity than geometric similarity (McMahon, 1975a,b; Alexander *et al.*, 1979; Scott, 1985). The recovery here of a linear regression of higher significance and steeper slope when ungulates (but not other large mammals) are excluded supports this interpretation.

Second-order polynomials were not required to explain patterns of scaling in dinosaur limbs, although a curvilinear equation would be significant (e.g. Christiansen, 1999b,c). This is similar to, but less

Table 13. Summary of regression results by category for each pair of variables (y/x). Symbols indicate whether the confidence intervals of the RMA slope include any predicted slopes. E, elastic similarity; G, geometric similarity; 0, between elastic and geometric similarity but including neither

Group	FL/FAP	FL/FML	TL/TAP	TL/TML	HL/HAP	HL/HML
Dinosauria	0	0	0	0	0	0
Saurischia	0	0	E	0	0	0
Ornithischia	G	0	0	0	0	0
Bipeds	0	0	0	0	0	0
Semi-bipeds	G	G	G	0	G	G
Bipeds + semi-bipeds	0	0	0	0	0	0
Quadrupeds	G	0	0	G	G	G
Small	0	0	0	0	0	0
Large	E	E	E	E	G	0
Mammalia	0	0	0	0	0	0
Ungulata	0	0	0	E	0	0
Mammalia excluding ungulates	0	0	0	0	G	G
Bipeds	G	G	0	G	G	G
Quadrupeds	0	0	0	0	0	0
Small	0	0	0	0	0	0
Large	0	0	0	0	0	0

pronounced than, the situation in mammals. However, dinosaurs do not display any morphological indicators of a flexed-limb posture, even at small body sizes (and the minimum adult size for dinosaurs is also projected to have been significantly greater than that for mammals; Peczkis, 1994). Therefore, dinosaurs may not have altered limb posture with size increases to the extent that mammals do (Biewener, 1989, 1990), for the simple reason that most (if not all) dinosaurs appear to have been fairly straight-limbed. Only the largest dinosaurs (sauropods, stegosaurs, and ankylosaurs) show size-related postural effects in the development of a fully columnar posture. In general, dinosaurs probably relied primarily on changes in limb bone dimensions for adequate support of locomotor stresses, and therefore no disjunction is apparent between the scaling relationships of large and small taxa.

Christiansen (1999a) suggested that large mammals preferentially shorten their limb bones relative to body mass, rather than thicken them. This is consistent with the results obtained here, but is less robust to removal of ungulates. Although large non-ungulates still scale more negatively than smaller mammals, the differences are much less pronounced, suggesting that all large mammals do not scale identically. This is clear only when scaling relationships are examined using a dataset that includes extinct large mammals, which permits examination of a sufficient diversity of large *non-cursorial* mammals. In this light, limb bone shortening appears to be used preferentially by ungulates. As such, it may reflect a constraint imposed on cursoriality at large body sizes: above 200 kg, body weight more strongly constrains distal limb length than it does at smaller sizes (Scott, 1985), and in order to benefit from relative distal limb lengthening (Carrano, 1999), large cursors such as ungulates must shorten the proximal limb segment. This results in limb bone scaling properties that are unique relative to those of most other mammals.

Femoral curvature

Bone curvature has been studied in extant mammals and shown to decrease significantly with increasing body size in the humerus, radius and tibia; femoral curvature tended to decrease non-significantly (Biewener, 1983; Bertram & Biewener, 1988, 1990). Additional regressions of femoral curvature against a proxy for body mass (FAP) produced very similar results, although a slightly steeper slope. Dinosaurian femora show a much stronger decrease in curvature with increasing body size (represented by any of the proxies) than mammalian femora. Interestingly, when the mammalian femoral data are divided into two groups at about 10 kg, larger mammals (equivalent in size range to dinosaurs) scale significantly negatively.

Bone curvature may be involved in creating a specific direction of weakness for bending, thereby generating more predictable forces on the limb during locomotion (Bertram & Biewener, 1988, 1990). However, as body weight increases, curvature incurs an increasing risk of failure in bending that outweighs the benefits of load predictability. A decrease in locomotor repertoire is necessary to restrict locomotor stresses, and in addition bone curvature becomes reduced. The competing demands of different locomotor styles and life habits, as well as changes in acetabular orientation and limb posture, might explain the low significance and low explanatory power of these equations ($0.1 < r^2 < 0.5$ for all regressions and $P > 0.1$; Biewener, 1983).

Femoral torsion is also a probable factor. Although a few studies have begun to identify torsion in vertebrate limbs by *in vivo* strain measurements (Lanyon & Bourn, 1979; Biewener, Swartz & Bertram, 1986; Keller & Spengler, 1989; Biewener & Dial, 1995; Demes *et al.*, 1998; Blob & Biewener, 1999; Carrano & Biewener, 1999), it seems likely that torsion is a significant component of strain in many vertebrate limb bones (Carrano, 1998a). Although torsion is independent of bone length,

it is strongly influenced by the radius of torque (Wainwright *et al.*, 1976; Cowin, 1987), which will be increased along with increasing bone curvature. As with other components of loading, torsion increases with body size, resulting in increasingly dangerous torsional loads unless behavioural and morphological mechanisms operated to minimize the potential for failure in this loading regime.

Large extant mammals seem to exhibit a reduced repertoire of locomotor habits (Gambaryan, 1974; Biewener, 1989, 1990) in association with lower bone curvature (Biewener, 1983) and straighter limb postures (Biewener, 1989, 1990; Heinrich & Biknevicius, 1998). Similarly, large dinosaurs – which were nearly 10 times heavier than the largest mammals – probably had correspondingly restricted locomotor repertoires. But, unlike mammals, all dinosaurs seem to have been restricted to a vertical limb posture. Consequently, dinosaurs had fewer options available to help minimize bone stresses as body size increased. The more significant negative scaling of femoral curvature in dinosaurs compared with mammals is consistent with this interpretation.

Femoral eccentricity

Several authors (e.g. Coombs, 1978; Galton, 1990b; McIntosh, 1990a) have noted that many dinosaur femora display a marked midshaft eccentricity, i.e. mediolateral diameter tends to exceed anteroposterior diameter by as much as a factor of two. Sauropod femora have a particularly pronounced eccentricity (Wilson & Sereno, 1998), but it is also present in large members of numerous other dinosaur clades. For example, exceptionally large specimens of the Asian hadrosaurid *Saurolophus angustirostris* are as large as many sauropods and show comparable femoral eccentricity (D. Fastovsky, pers. comm.).

The possible biomechanical implications of this morphology have been previously discussed (Wilson & Carrano, 1999) and are only summarized here. In brief, the centre of mass of any vertebrate is located between, not directly above, its limbs. As a result, a mediolateral couple is generated, equal to the product of the force from its centre of mass and the lateral distance between it and the limbs. This is equivalent to a mediolateral bending moment applied to the limb (in addition to axial compression and anteroposterior bending). Medi lateral bending thus has a direct relationship to both body mass (generating the original force by gravity) and the lateral displacement of the limbs, and will increase whenever either (or both) of these factors increases.

Why might larger animals have more eccentric femora? Limb bones of small animals experience only low absolute levels of mediolateral bending, and therefore a nearly circular femoral midshaft may be sufficient to resist these eccentric loads. But because strain levels

increase disproportionately with size, femoral design would be expected to increasingly accommodate to mediolateral bending, with the femur ultimately resembling an ellipse with its major axis oriented mediolaterally. In addition, mediolateral expansion of the femur may be a partial by-product of expanding the insertion areas for the muscles responsible for anteroposterior action of the bone.

Bertram & Biewener (1988, 1992) noted that an eccentric cross-sectional geometry would create eccentric loads in a preferential bending plane, similar to bone curvature. The curvature observed in dinosaur femora would have resulted primarily in anteroposterior bending. This is in addition to the mediolateral bending imposed by trunk support (see below), and is consistent with the generally circular cross-section of most femora. At large sizes, femoral eccentricity is pronounced, with a smaller anteroposterior diameter relative to mediolateral diameter. Therefore, in spite of reduced femoral curvature, anteroposterior bending is still encouraged by the eccentric cross-sectional geometry. In effect, this would *decrease* loading eccentricity by reducing the disparity between mediolateral and anteroposterior bending loads. Thus, curvature is most pronounced in smaller animals, which also show near-circular femoral cross-sectional geometry, and lowest in larger animals, which exhibit eccentric femoral cross-sections.

Mammalian femora scale closer to isometry than those of dinosaurs, indicating little change in eccentricity as body size increases. Absolute values of eccentricity are comparable in both groups, but the rate of change is not. In fact, a general trend towards decreased eccentricity is evident. In contrast to dinosaurs, mammalian femora seem to be designed in concert with many more variations in pelvic morphology, and therefore show less predictable changes in eccentricity with body size.

IMPLICATIONS

Scaling in terrestrial limb bones

Theories of biomechanics that seek to explain form–function relationships in vertebrate limbs are grounded on several physical tenets that are applicable to any terrestrial vertebrate, at least in principle (e.g. Gregory, 1912; Maynard Smith & Savage, 1955; Hildebrand, 1985; Biewener, 1989, 1990). These theories have been tested on extant animals with reasonable success (e.g. Lanyon, 1981; Swartz, Bertram & Biewener, 1989; Biewener & Bertram, 1993), but living taxa represent only a subset of the total diversity of terrestrial vertebrate design. Extinct mammalian taxa should therefore be included in any analysis of mammalian scaling patterns. Dinosaurs provide a means to test the broader applications of theories of terrestrial locomotor mechanics, as they include a diversity of both bipeds and quadrupeds and exhibit variations of locomotor

morphology and body size that differ from those seen in extant mammals (Carrano, 1999). If biomechanical theories truly explain the underlying mechanics of limb function and its relationship to bone morphology, then they should have predictive power when applied to the bones of extinct non-mammalian taxa as well as to extant mammals.

Scaling relationships between limb bones and body mass in terrestrial mammals have been examined in some detail, chiefly as a means of identifying the scaling 'principles' underlying the changes associated with body size. Although it seems that most mammalian limb bones scale close to geometric similarity (Alexander *et al.*, 1979; Biewener, 1983; Economos, 1983), those of ungulates (particularly bovids) are unusual in following elastic similarity (McMahon, 1975a,b; Scott, 1985). This scaling disjunction also characterizes a fundamental scaling difference between small and large mammals (Biewener, 1989, 1990; Bertram & Biewener, 1990; Christiansen, 1999a,b), as the latter are forced to alter limb bone dimensions more dramatically once shifts in posture and reductions in locomotor variation are exhausted (Biewener, 1989, 1990; Bertram & Biewener, 1990). This disjunction is also evident in dinosaurs, although the differences between small and large taxa are less marked, underscoring the widespread nature of the underlying physical interactions.

Dinosaurs show few scaling patterns that are not explicable in the light of currently accepted explanations for these trends in terrestrial mammals. Although dinosaurs and mammals are not identical in limb bone scaling, the strong overall similarities point to similar underlying mechanical (and perhaps biological) influences on bone shape. The differences detected in this study provide insight into unique features of dinosaur biology and evolution and do not require major renovations of existing biomechanical theories. In fact, the patterns of eccentricity observed in dinosaur femora point to underlying design constraints that should apply to the limb bones of other terrestrial vertebrates with parasagittal limbs.

Body mass estimates in dinosaurs

Although it is not possible to examine the relationship between bone dimensions and body weight in dinosaurs directly, comparisons of lengths to diameters reveal patterns that are very similar to those seen in mammals. This similarity has been used to infer underlying similarities in limb kinematics between these two groups (Carrano, 1998a), and may justify the use of mammalian scaling equations to predict body mass in dinosaurs (Anderson *et al.*, 1985; Peczis, 1994). However, the large proportion of ungulates in the sample used to generate the equations of Anderson *et al.* (1985) is problematic because the unusually negative allometry of ungulate limbs reduces the general scaling exponent for mammals. When the allometric equation is used to estimate dinosaurian masses from limb bone measure-

ments, the result is a series of predicted masses that are lower than those that would have been obtained had a non-ungulate sample been used. Indeed, the mass estimates of Anderson *et al.* (1985) have been criticized as too low (Alexander, 1985) and are substantially lower than those produced by other methods (Colbert, 1962; Bakker, 1972, 1984; Alexander, 1985). Notably, these discrepancies are greatest at large body sizes, where the regression must be extended beyond its original bounds and where small differences in slope have the greatest effect.

A more serious challenge to the results of Anderson *et al.* (1985) is highlighted by the different scaling relationships of the circumferences of the femur (FC) and humerus (HC) in mammals and dinosaurs. Although the two variables scale similarly in both groups, dinosaur femora are more robust relative to their humeri when compared to those of mammals. It has previously been suggested that the large tails of dinosaurs would have brought the centre of mass closer to the hips than in mammals, forcing the hindlimbs to support a greater percentage of body mass (Alexander, 1985; Henderson, 1999). Therefore, the use of predictive body-mass equations that are based on (HC + FC) in mammals will result in much lower estimated masses for dinosaurs than would have been obtained using only FC. Currently, it is impossible to determine whether it is more appropriate to use one, both, or neither of these variables for predictions of body mass in dinosaurs. Additional, independent methods of mass estimation (e.g. Henderson, 1999) should greatly enlighten this problem.

Postural effects on limb scaling

Bipedal and quadrupedal dinosaurs are similar in hindlimb scaling properties, and most differences (e.g. lower curvature and greater eccentricity in quadrupeds) are more probably related to the larger overall size of quadrupedal dinosaurs rather than inherent posture-related differences. This is supported by the fact that both trends are evident at large sizes in dinosaurs, mammals, and bipeds. The general similarities in scaling between bipedal and quadrupedal dinosaur hindlimb bones are probably tied to the circumstances surrounding the evolution of dinosaurian quadrupedalism. Unlike mammals, which originated as small, quadrupedal animals with obliquely oriented limbs, dinosaurs originated as medium-sized, upright bipeds. Thus, dinosaurs 'dropped down' to become quadrupeds, whereas mammals 'reared up' to become bipeds. Additionally, quadrupedalism in dinosaurs largely overlaps bipedalism because a series of intermediate 'semi-bipedal' taxa are also known that were presumably capable of using both postures (e.g. hadrosaurs and prosauropods). Thus a natural gradation exists between these two postures in dinosaurs that is reflected in overlapping patterns of limb bone scaling.

CONCLUSIONS

Although based primarily on examinations of locomotor behaviour in extant mammals, theoretical mechanics are essentially physical in nature and should be equally applicable to other vertebrate groups if they represent underlying principals that influence changes in the locomotor apparatus. Using dinosaur morphology as a test of this expectation, theories of mechanics are found suitable to explain patterns of limb bone scaling and changes in femoral curvature. Size seems to have a stronger influence than posture on dinosaurian scaling patterns. Bipedal and quadrupedal dinosaurs are similar in most aspects of hindlimb morphology, implying little change in scaling behaviour with this postural shift. The eccentric design of large dinosaur femora is interpreted as a means to increase resistance to mediolateral bending.

These morphological patterns, and their associated interpretations, lend support to existing theories of limb biomechanics and their continued application towards the interpretation of locomotor morphology in extinct terrestrial vertebrates. Thus, by applying concepts of terrestrial vertebrate biomechanics to dinosaur locomotor morphology, this study both confirms and extends these theoretical constructs.

Acknowledgements

This work was completed as part of a doctoral dissertation in the Department of Organismal Biology and Anatomy at the University of Chicago. I thank Andrew Biewener, Jim Hopson, Mike LaBarbera, Christine Janis, Steve Gatesy and Paul Sereno for their advice, criticisms and encouragements; they are hereby absolved of responsibility for any errors that remain. Chris Brochu kindly provided limb measurements for kangaroos. Comments from Chris Sidor, Jeff Wilson, Rick Blob, Bill Jungers, and two anonymous reviewers greatly improved earlier drafts of the manuscript. This research was supported by a grant from The Dinosaur Society.

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