

What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs

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Abstract

Traditional categories of locomotor habit in mammals are largely based on variables that are continuous in nature, making intermediate forms difficult to evaluate quantitatively. Interpretations of these categories have varied greatly among authors, mainly owing to the inconsistent meanings ascribed to these essentially morphological variables. As a result, it is not clear whether these categories reflect any true locomotor influence, or if they can be applied in any form to non-mammalian taxa. In order to rectify these two difficulties, locomotor categories are rejected here in favour of a multivariate continuum. By basing this continuum on morphological variables that fulfil predictions of limb design under biomechanical theory, it can be tied to limb mechanics and applied to both extant and extinct animals alike. A series of such measurements were taken from a large sample of mammal and dinosaur hindlimb bones, and subjected to statistical testing. Patterns of variation in dinosaurs are similar to those seen in mammals, ranging between extremes traditionally designated as ‘cursorial’ and ‘graviportal’. An evaluation of dinosaur locomotor evolution in light of this continuum suggests that dinosaurs originated as small cursors, but that most lineages acquired a more mid-grade locomotor habit. Large taxa (sauropods, armoured ornithischians) were essentially graviportal, while smaller forms tended towards cursoriality; only coelurosaur theropods developed cursoriality at large body sizes. The discrepancy between large, graviportal herbivores and large, mid-grade to cursorial carnivores in Mesozoic communities argues against pursuit predation as a major influence in dinosaur locomotor evolution.

Key words: graviportal, biomechanics, evolution, multivariate statistics

INTRODUCTION

Historically the concept of different locomotor categories among terrestrial reptiles, birds, and mammals (amniotes) has been both tacitly understood and yet difficult to define. Several factors have contributed to this problem. First, research into areas as varied as metabolic energetics (Taylor & Rowntree, 1973; Taylor *et al.*, 1974; Steudel, 1990*a, b*), kinematics (Jenkins, 1971; Jenkins & Camazine, 1977), and functional morphology (Gregory, 1912; Maynard Smith & Savage, 1955; Janis & Ehrhardt, 1988; Janis, 1990; Stein & Casinos, 1997) have addressed this topic, generating distinct concepts of locomotor types which are often incongruous if not contradictory. Second, attempts to investigate this topic have often (at least implicitly) treated cursoriality and other such locomotor types as distinct categories with their own morphological hall-

marks (Gregory, 1912; Maynard Smith & Savage, 1955). However, as investigations into amniote limb posture (Gatesy, 1991) and archosaur ankle morphology (Serenó & Arcucci, 1990; Sereno, 1991) have shown, the use of categorical types as such exemplars (e.g., Charig, 1972; Chatterjee, 1982), although occasionally illustrative, can obscure the genuine, more complex patterns present in biological data.

Classically, terrestrial locomotor habit has been described in terms of four categories: cursorial, subcursorial, mediportal, and graviportal (Gregory, 1912; Maynard Smith & Savage, 1955; Coombs, 1975). Each category was distinguished by a combination of morphological features; no single feature was used reliably to diagnose any one category. Gregory himself admitted that ‘the limb ratios have a certain degree of diagnostic value *when taken in groups* and that pure convergent evolution rarely brings about a close agreement in all four ratios at once’ (Gregory, 1912: 294; emphasis added). The continuous nature of the variables used in Gregory’s study strongly suggests that discrete categorization, particularly when based on complex

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combinations of multiple variables, may not be appropriate. Instead, I argue here that locomotor habit should be evaluated in the light of a multivariate continuum between extremes that reflect the range of interactions between mechanical requirements in biological systems.

In this study, I use previous investigations into mammalian terrestrial locomotion to analyse dinosaur locomotor morphology. Patterns revealed through statistical analyses are then interpreted in the light of dinosaur phylogeny in order to draw conclusions about dinosaur locomotor evolution and its potential similarities (and differences) from that of mammals. First, however, it is necessary to redefine traditional categories of terrestrial locomotor variation as ranges along a morphological continuum. This highlights two important questions: (1) can a suite of continuous morphological characteristics be applied to modern and extinct taxa alike (e.g. mammals and dinosaurs) to produce significant patterns that reflect locomotor habit? and (2) do these patterns represent morphologies that can be explained by biomechanical theory?

Such an analysis has several applications. First, it allows evaluation of fossil taxa relative to extant forms as well as to other extinct taxa (Coombs, 1975; Van Valkenburgh, 1985, 1987; Carrano, 1997). It also permits comparisons between different extinct taxa without specific reference to any modern analogue; this can be particularly important in recognizing that many extinct morphotypes may have no analogue among extant taxa. Finally, since some researchers have questioned whether so-called cursorial specializations even exist apart from the effects of allometric scaling (Biewener, 1989, 1990; Steudel & Beattie, 1993), the ability to develop a multivariate set of morphologic features in both extant and extinct forms of all body sizes can help to identify whether cursoriality is distinct from such scaling issues.

PERSPECTIVES ON TERRESTRIAL LOCOMOTION

What is a cursor?

Attempts to identify cursorial animals on the basis of morphology, behaviour, or performance have resulted in a series of differing and sometimes contradictory definitions. Most of these definitions are based on modern mammals, perhaps fittingly since it was this group upon which locomotor categories were originally founded (Gregory, 1912). Mammals additionally include the only diverse assemblage of large, extant terrestrial vertebrates; although certain birds (e.g. ratites) are occasionally considered in comparisons of locomotor performance (and usually as cursors: Coombs, 1975), the number of terrestrial bird taxa is comparatively small.

Among this variety of definitions, 'cursors' may include animals that can run, run often or for long distances (Gregory, 1912; Stein & Casinos, 1997), have

parasagittally oriented limbs (Jenkins, 1971; Jenkins & Camazine, 1977; Biewener, 1989, 1990), or are merely larger animals, which appear specialized as a result of limb scaling at large body sizes (Steudel & Beattie, 1993). Some of these definitions have found a role in evaluations of fossil taxa (Coombs, 1975), while others are restricted in application to living forms. Some are morphology-based, while others are performance-based. It is no surprise, therefore, that a consensus has not been reached and that little correspondence has been found between the predictions generated by differing definitions.

A resolution to this problem can only be found by choosing a definition that appeals simultaneously to both mechanical relevance and maximal utility. *Mechanical relevance* requires that a definition should have, as its basis, a consideration of the biomechanical requirements of locomotion and the manner in which these requirements affect the structure of an organism. *Maximal utility* addresses the ultimate goals of any definition of locomotor performance, which should be towards usefulness in biological study. The first issue can be addressed directly through the choice of variables selected for analysis, but these choices must be mitigated by the concerns raised by the second issue.

This second issue – utility – lies at the root of much of the discordance between various locomotor definitions. Many studies note more general similarities between traditional locomotor types, or describe additional aspects of biology that may overlap (or be related to) them, but are not designed to *distinguish* such types. For example, the distinction between mammals with parasagittally and more obliquely oriented limbs may be relevant to locomotor performance (Jenkins, 1971; Jenkins & Camazine, 1977), but it does not address the issues at the heart of Gregory's (1912) study. Although most 'cursors' do have parasagittally oriented limbs (a factor also related to the effects of scaling at large body sizes; see Biewener, 1989, 1990; Steudel & Beattie, 1993), this represents a correlation between mechanically related influences, and can obscure attempts to distinguish 'cursors' by essentially synonymizing posture and locomotor habit. In this sense, such observations add to, but do not obviate, more traditional descriptions.

Originally, attempts to categorize mammalian locomotor performance rested squarely on morphology (Gregory, 1912), and although explicit categorization is not supported here, I argue that *morphology should remain the fundamental basis for making distinctions between locomotor performance*. Such a link to morphology belies the original purpose of distinguishing between different locomotor types: applications for the interpretation of evolutionary patterns over time. Owing to the nature of the fossil record, it is impossible to assess aspects of locomotion in extinct animals without a direct and primary reliance on morphology. Since evolution provides the context for most (non-medical) studies of locomotion in animals, morphology logically becomes the most useful choice on which to

base definitions, and therefore analyses, of locomotor types. The continuum of locomotor variation should therefore be correlated with a continuum of morphological variation.

Certainly such a choice creates its own difficulties: among modern mammals, for example, it is difficult to distinguish between 'long-distance runners' and 'sprinters' on the basis of skeletal morphology alone. However, morphological variations can be predictably correlated with habit in a more general sense when morphological variables are chosen based on principles of biomechanical design. Since such principles argue for an inverse relationship between speed and power in limb design (Maynard Smith & Savage, 1955) while under constant selection for energetic efficiency, it is not surprising that skeletal morphology does not reliably distinguish between different 'subtypes' of cursors. This 'failure' on the part of morphology does not hamper its otherwise considerable utility; rather, we should consider other techniques (or a more detailed examination of morphology *vs* performance in modern animals) when attempting to address such finer distinctions.

Limb biomechanics

Two models of limb mechanics generate a series of predictions for limb morphology depending on primary limb use. Lever mechanics rely on the relationships between joints (fulcra) and the placement of muscles along limb bones (lever arms) to make predictions about limb design in which force, velocity, and lever arm lengths are interrelated (e.g. Maynard Smith & Savage, 1955; Hildebrand, 1985). For example, muscles will insert closer to a joint that is designed to work at high velocities than one designed to work slowly but with more force. This can be achieved by locating muscle insertion points proximally relative to the bone length and/or by lengthening the entire limb distal to the insertion point(s).

Pendulum theory models the walking limb as an inverted pendulum that oscillates around the foot during the support phase (Gregory, 1912; Cavagna, Saibene & Margaria, 1964; Cavagna, Heglund & Taylor, 1977). Since the period of oscillation decreases as mass is increased further from the point of rotation, this model predicts lengthening of the distal limb in order to facilitate movement of muscle masses farther from the point of rotation. In other words, since the limb rotates over the foot during the support phase, it will operate as a more efficient inverted pendulum if muscles are concentrated at the hip joint, rather than more distally along the limb. Lightening of individual limb elements would also increase the relative proportion of total mass represented by the proximal musculature, thereby accomplishing the same goal. Additionally, more slender limb elements would create less inertia to be overcome by muscular exertion during the swing phase of each stride (Fedak, Heglund & Taylor, 1982).

As a result, the following features have been predicted in the limbs of animals designed to move with greater speed at less energetic cost (*cursorial* in the traditional sense): more slender individual limb elements, longer distal limb segments, and hip muscle insertions more proximally placed along the limb. A complementary set of features (more robust individual limb elements, shorter distal limb segments, and more distally placed muscle insertions) have been predicted to occur in the limbs of animals designed to move with lower speeds, but using more limb power per stride (*graviportal* in the traditional sense). 'Cursorial' and 'graviportal' are therefore endpoints, and not categories, that bound morphological-mechanical variation in limbs (Carrano, 1997).

MATERIALS AND METHODS

Measurements

In this study, I first selected a subset of biomechanically relevant morphological features that have been used to distinguish extant mammals according to general locomotor performance. These features were measured and examined using principal components analysis in an attempt to corroborate the bivariate results of previous authors by using a multivariate technique. These same features were measured in dinosaurs and analysed using both bivariate and multivariate statistical techniques. Results from the dinosaurian data were combined with hypotheses of phylogeny in order to detect patterns in dinosaur locomotor evolution over time, and to make inferences about similar patterns in mammalian evolution.

Measurements were made on limb bones from a large, taxonomically diverse sample of mammal and dinosaur specimens housed in the following museum collections: the Field Museum of Natural History, Chicago (FMNH); American Museum of Natural History, New York (AMNH); Yale University Peabody Museum, New Haven (YPM); Harvard University Museum of Comparative Zoology, Cambridge (MCZ); Carnegie Museum of Natural History, Pittsburgh (CMNH); United States National Museum of Natural History, Washington (USNM); Museum of the Rockies, Bozeman (MOR); Black Hills Institute for Geological Research, Hill City (BHI); Royal Tyrrell Museum of Palaeontology, Drumheller (RTMP); Royal Ontario Museum, Toronto (ROM); Canadian Museum of Nature, Ottawa (CMN); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Fundación Miguel Lillo, San Miguel de Tucumán (PVL); Museo Provincial de San Juan, San Juan (PVSJ); Museo Provincial de La Rioja, La Rioja (MPLR); The Natural History Museum, London (BMNH); Oxford University Museum, Oxford (OUM); Muséum National de l'Histoire Naturelle, Paris (MNHN); Institute Royale des Sciences Naturelles de Belgique, Brussels (IRSNB); Staatliches Museum für Naturkunde, Stuttgart

Table 1. Sampling of taxa within major dinosaur and dinosauriform clades. The distribution of these samples reflects the overall record of dinosaur taxa. For example, the generally poor records of stegosaurs, pachycephalosaurs, and ankylosaurs are indicated by the low sample sizes for each of these three groups. Also note that the majority of dinosaurian genera are monospecific (Dodson, 1990)

Clade	Specimens	Genera	Species
Theropoda	350	107	116
Prosauropoda	101	17	20
Sauropoda	209	36	54
Saurischia total	660	160	190
Stegosauria	78	7	10
Ankylosauria	68	18	20
Ornithopoda	394	53	73
Pachycephalosauria	7	7	7
Ceratopsia	114	19	28
Ornithischia total	661	104	138
Dinosauria total	1321	264	328
Dinosauriformes	7	4	4
Total	1328	268	332

(SMNS); Humboldt Museum für Naturkunde, Berlin (HMN).

Linear morphological measurements under 200 mm were made with Mitutoyo dial callipers; linear measurements over 200 mm and circumferences were made with a measuring tape. When direct access to specimens was not possible or available, measurements were made from photographs in the literature. The sample included: 1328 dinosaur specimens, representing 268 genera and 332 species from all major dinosaur clades, as well as 4 genera of Dinosauriformes (Table 1; Carrano, 1998); and 216 mammal specimens, representing 168 genera and 150 species from all major terrestrial mammalian groups. Measurements included: maximal articular length, anteroposterior diameter, and midshaft circumference for the femur (FL, FD, and FC, respectively), tibia (TL, TD, TC) and metatarsal 3 (MTL, MTD, MTC). Additionally, 2 femoral muscle insertion points were identified and measured as a distance from the proximal end of the bone: that of the iliopsoas in mammals (on the lesser trochanter; F3L), and that of the caudofemoralis in dinosaurs (usually on or near the fourth trochanter; F4L). These data were taken entirely from individual specimens, which ranged from fully complete and articulated to single-element specimens. No composite samples were created from less complete specimens; this resulted in lower sample sizes for statistics that used all the measured variables.

Statistical analyses

Linear measurements were log-transformed before statistical analyses. These analyses included bivariate reduced major axis (Model II) regression (RMA) on dinosaurian data (LaBarbera, 1989) and principal component analysis (PCA) on both mammalian and

dinosaurian data. Since the purpose of this analysis was to examine a non-categorical continuum of morphological variation, discriminant analyses were not performed as they require *a priori* categorization of data. All of these analyses were designed to test whether variables that have been traditionally and theoretically associated with locomotor habit in mammals are statistically correlated with one another in dinosaurs. Since locomotor habit cannot be directly observed in extinct taxa, such a correlation would be one of the best means of supporting inferences about locomotion in dinosaurs.

In order to assess the relative cumulative placement of taxa in all RMA regressions, the variables must be accounted for in combination with one another. Therefore, residuals were produced for each taxon in each regression, and summed for each taxon over all regressions. Regressions were performed so that in all cases the positive residuals represented a trend towards a graviportal morphology, and the negative residuals represented a trend towards cursoriality. (This 'switching' of *y* and *x* variables creates less of a problem in RMA regressions.) PCA was performed using the Systat 5.1 package for Macintosh (Wilkinson, 1989). Since PCA does not permit missing data, composite entries were made for incomplete taxa. These entries were created by averaging values for multiple (similar-sized) specimens of a given species to produce a single entry which included all the relevant variables.

Additionally, a set of ratios was created from the dinosaurian data, reflecting the aforementioned mechanical relationships. The use of ratios in biological data analysis has been the subject of considerable controversy (Albrecht, 1978; Atchley, 1978; Atchley & Anderson, 1978; Sokal & Rohlf, 1995), much of which has centred on problems of distribution skewness and variable intercorrelation. The majority of ratios, however, are generated as a means to eliminate size as the major component of variation in data. Such ratios often involve uniform division of all variables by a common, size-related factor. As a result, these ratios can show spurious correlations with each other, and in addition can still include a considerable size component (Atchley, 1978).

However, ratios serve a different purpose in this study. Each ratio reflects a particular mechanical relationship that can only be expressed as such. Mechanical advantage, for example, is expressly and exclusively the ratio between 2 lever arms (which are distances from a single fulcrum); independent linear measurements do not reflect this relationship. Since the ratios used here do not share a uniform denominator, spurious intercorrelation should not be an issue. Furthermore, although ratio distributions are non-normal, ratios can be arcsin-transformed to accommodate this concern (Sokal & Rohlf, 1995). In this study, transformed ratios were subjected to the same bivariate and multivariate analyses as the linear data. These included length/diameter for each limb bone, reflecting individual element slenderness (FL/FD, TL/TD, MTL/MTD); metatarsal III length/femur length, representing relative

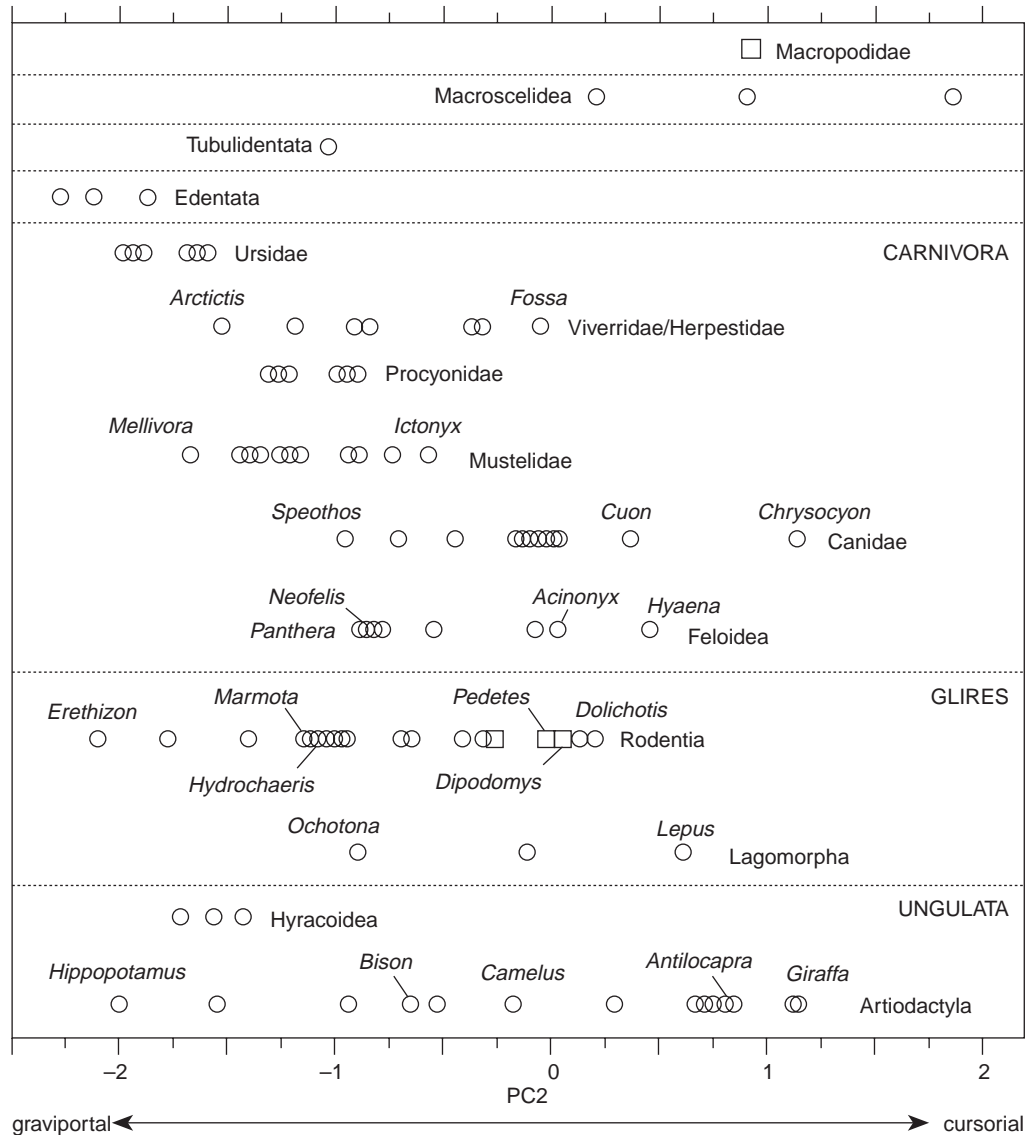


Fig. 1. PCA on mammalian data. PC2 (representing locomotor variation) is plotted on the x -axis, with taxa separated according to major taxonomic group for graphical purposes. The gradation of taxa along PC2 is consistent with that predicted by mechanical theory and the results of previous bivariate analyses: taxa low on PC2 ('graviportal') have more robust limb elements, shorter metatarsals, and more distal muscle insertion points, while the opposite characteristics are true of taxa high on PC2 ('cursorial'). □ = bipeds; ○ = quadrupeds.

distal limb length (MTL/FL); and caudofemoralis insertion/femur length, representing muscle lever arm length (F4L/FL).

RESULTS

Statistical analyses

Mammalian data

A PCA on linear data was successful in recovering a pattern similar to those described by more traditional bivariate studies on extant mammals (i.e. Scott, 1985;

Janis & Wilhlem, 1993). PC1 accounted for 92.2% of the variance in the data, and essentially arranged the taxa according to body size. Coefficients for all variables were high on PC1 (>0.950) as would be expected of size-related correlations, with the exception of MTL (which has been shown to vary less predictably with size than other limb measurements) (Garland, 1983; Scott, 1985; Garland & Janis, 1992). PC2 accounted for 5.6% of the variance, and arrayed the taxa according to general locomotor habit (Table 2, Fig. 1). Variable coefficients on PC2 confirm the biomechanical explanations of such a pattern: taxa placed high on this axis tended to have longer metatarsals, more slender limb elements, shorter femora, and a muscle insertion

Table 2. Coefficients for linear variables on each of the first four principal components as generated by PCA on mammalian data, with percentage variances and percentage of total variance for each PC. Measurement abbreviations as in the text

Variable	PC1	PC2	PC3	PC4
FL	0.983	-0.045	0.161	0.022
FD	0.980	-0.116	-0.076	-0.083
TL	0.977	0.155	0.120	-0.034
TD	0.974	-0.162	-0.069	-0.066
MTL	0.884	0.456	-0.096	0.039
F3L	0.958	-0.249	-0.051	0.128
Variance (%)	5.530	0.335	0.063	0.031
Total variance (%)	92.200	5.600	1.000	0.500

point located closer to the hip joint. PC2 thus combines mechanically relevant variables in a manner consistent with previously proposed mechanical models of limb function, producing a pattern which reflects basic locomotor performance in extant mammals. These results demonstrate a consistency between previous bivariate and current multivariate analyses towards detecting patterns of locomotor habit, and can thus serve as a departure point for analyses of the dinosaurian data.

Dinosaurian data I: linear

RMA regressions between the log-transformed variables revealed significant correlations in dinosaurs that are consistent with observed patterns in living mammals (Table 3). For example, MTL is strongly correlated with FL, but increases with negative allometry – in other words, FL increases at a faster rate than MTL (Scott, 1985). However, although regressions may suggest that two linear measurements are strongly correlated, such

correlation may be due to the influence of body size on each variable. Variation about the regression indicates the degree to which the taxa are deviating from expectation, which might be a signal of locomotor habit. For example, taxa that fall below a regression of FL on MTL tend to have relatively longer metatarsals than expected, and those above the line have shorter metatarsals; the former taxa would be described as having ‘cursorial’ features. The summed residual values were plotted univariately, and revealed a spread that reflects correlations among locomotor variables (Fig. 2). ‘Cursorial’ taxa are shown to have predominately longer metatarsals, more slender limb elements, and a more proximally placed muscle insertion point, as predicted by mechanical theory. ‘Graviportal’ taxa oppose ‘cursorial’ forms in these features. Most taxa are spread out away from zero in one direction or the other, indicating a high level of correlation between multiple positive or multiple negative residuals. Some taxa are located near zero, suggesting the possibility of conflicting correlations, but these merely represent taxa that fall near the regression line in one or more analyses; examination of the data does not reveal any instance in which an individual taxon exhibits strongly graviportal and strongly cursorial features.

PCA analysis confirmed these correlations by clustering taxa with the same associations of variables. Since the data are linear, and PC1 accounted for 95.7% of the total variance, it is assumed to reflect overall size. PC2, which accounted for 2.7% of the total variance, distributed taxa along a continuum between two extremes: shorter limb elements/longer lever arms/shorter distal limbs and longer limb elements/shorter lever arms/longer distal limbs. Coefficients for all variables were moderate, and agreed in sign with the patterns revealed by regression analyses (Table 4). When taxa are labelled according to traditional locomotor categories (i.e. Coombs, 1978), PC2 values show general agreement

Table 3. RMA regression statistics of linear and ratio data. Measurement abbreviations as in the text

Variables (<i>y</i> vs <i>x</i>)	Equation	r^2	<i>n</i>
Linear data:			
Log FD vs log FL	$y = 1.173 x - 1.283$	0.942	409
Log TD vs log TL	$y = 1.275 x - 1.472$	0.870	409
Log MTD vs log MTL	$y = 1.253 x - 1.050$	0.742	238
Log F4L vs log FL	$y = 1.078 x - 0.517$	0.950	318
Log FL vs log MTL	$y = 1.206 x + 0.234$	0.767	280
Ratio data:			
FL/FD vs TL/TD	$y = 0.789 x + 3.602$	0.423	177
FL/FD vs MTL/MTD	$y = 0.746 x + 4.926$	0.362	101
TL/TD vs MTL/MTD	$y = 0.870 x + 5.329$	0.397	135
FL/FD vs MTL/FL	$y = 17.438 x + 4.509$	0.321	143
TL/TD vs MTL/FL	$y = 21.385 x + 3.04$	0.597	170
MTL/MTD vs MTL/FL	$y = 21.198 x + 1.551$	0.584	147
FL/FD vs F4L/FL	$y = -23.182 x + 12.682$	0.203	277
TL/TD vs F4L/FL	$y = -35.754 x + 16.358$	0.186	150
MTL/MtD vs F4L/FL	$y = -40.591 x + 20.72$	0.469	85
MTL/FL vs F4L/FL	$y = -1.744 x + 0.895$	0.370	122
Residuals vs linear PC2	$y = 10.405 x + 0.143$	0.815	70
Residuals vs ratio PC1	$y = -0.976 x - 0.110$	0.330	69

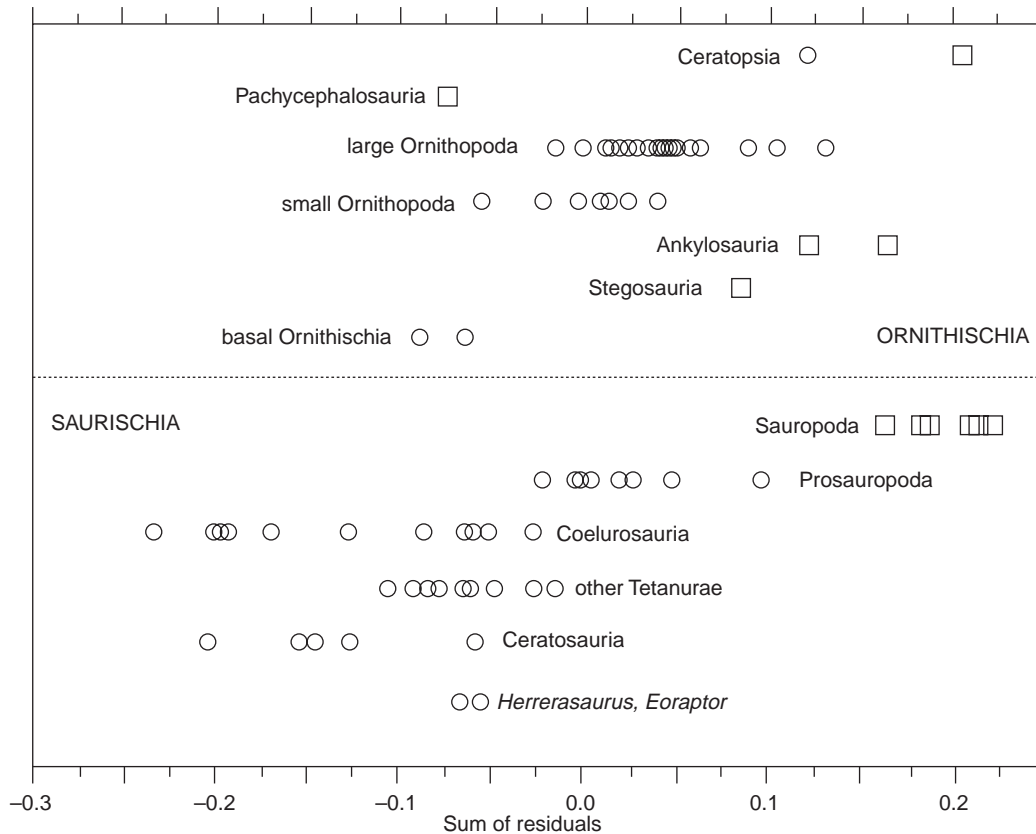


Fig. 2. Summed residuals results with dinosaur taxa separated according to major clade. Each point represents a single species. The x-axis (representing summed residual value) reveals a gradation between two extremes: slender limb bones/long distal limbs/short muscle lever arms ('cursorial') and robust limb bones/short distal limbs/long muscle lever arms ('graviportal'). The taxa are spread in both directions away from zero, indicating significant correlations of both positive (graviportal) and negative (cursorial) residuals. ○ = bipeds; □ = quadrupeds.

with these assignments but significant overlap between these 'categories' (Fig. 3a). Several discrepancies are apparent, however, mostly involving smaller-bodied 'cursors' that overlap the intermediate forms on PC2. This is likely due to the effects of body size on limb morphology, making it difficult to distinguish cursorial features at small body sizes (see Discussion).

As with the residual values from the regression analyses, the value for each taxon on PC2 can be used as a proxy for locomotor performance (Fig. 4). Note that, here again, many taxa are spread out towards the extremes, while those taxa close to zero on PC2 tend to exhibit few locomotor specializations rather than conflicting morphologies. Relative taxon placement on PC2 is similar to that generated with summed residuals; when PC2 is plotted against the summed residual values for each taxon, the resulting regression reveals a significant correlation representing the similar locomotor variations detected by each analysis (Table 3; Fig. 5).

Dinosaurian data II: ratios

Regressions of ratio data produce the same basic correlations revealed in linear data regressions (Table 3). In

these analyses, because the individual ratios already reflect biomechanically meaningful features, the r^2 of the regression indicates the degree and direction of correlation between the two (presumably related) variables. For example, dinosaurs with shorter muscle lever arms (F4L/FL) also have more slender femora (FL/FD) and relatively longer metatarsals (MTL/FL): the first ratio is negatively correlated with the latter two. Correspondingly, taxa with longer muscle lever arms therefore have more robust femora and relatively shorter metatarsals. Each of these associations is revealed through RMA regression of one ratio on another, and most are supported by moderate significance levels (0.20–0.60).

However, these correlations are generally lower than those produced with linear data analyses, indicating less explanatory power for each of these equations. This is to be expected: the high r^2 of certain linear data regressions generally comes about through the strong correlations between each variable and size, creating a strong intercorrelation between the two variables. In these cases, the slope describes the nature of this correlation for all the data. But because of this, the residuals about the regression must be examined in order to interpret the variation for each data point, since it is this

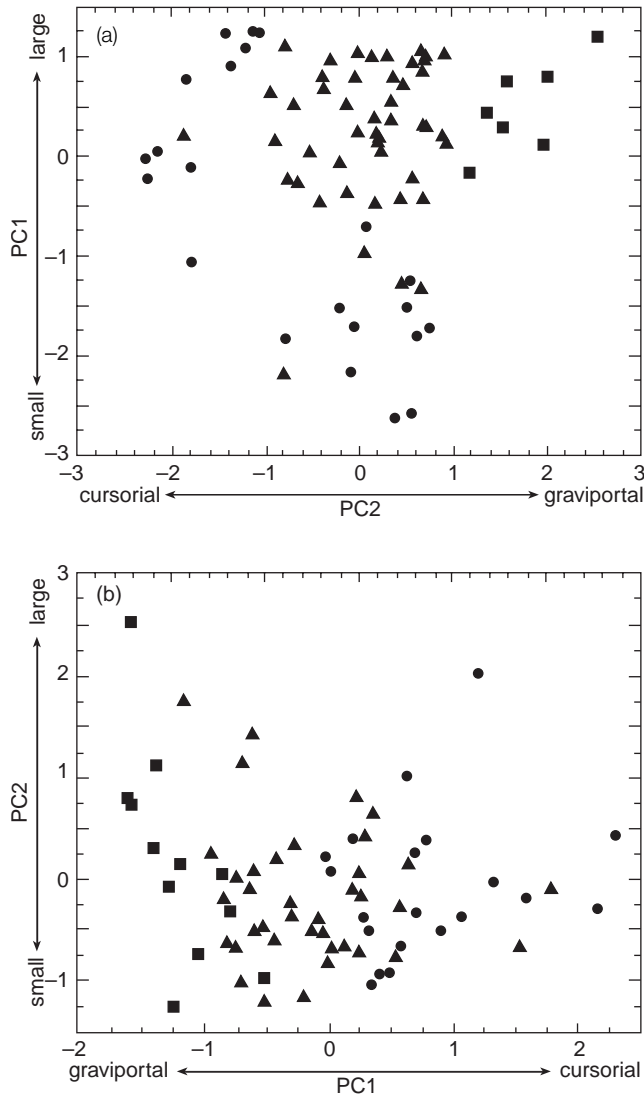


Fig. 3. PCA on dinosaurian data I. (a) PC1 (representing size) is plotted against PC2 (representing locomotor variation), based on linear data. (b) PC1 (representing locomotor variation) plotted against PC2 (not interpreted here, and given for graphical purposes only), based on ratio data. Note that when taxa are labelled according to traditional locomotor categories (Gregory, 1912; Coombs, 1978), these assignments are consistent with position on PC2, but that there is significant overlap between these ‘categories’. Additionally, small cursorial taxa appear very similar to larger intermediate forms on linear PC2 (see text for discussion). ● = cursorial; ▲ = intermediate (sub-cursorial/mediportal); ■ = graviportal.

deviation from the rule (i.e. the slope) which is of interest. Since ratio data confound the simple size correlations of most measurements, the interdependence of each variable on size is reduced and therefore so is the r^2 . Therefore, any degree of linearity to the ratio data regressions (here, an r^2 above 0.3) is interpreted as demonstrating some correlation between the two ratios.

PCA on ratio data also confirms these patterns. Unlike linear data, however, ratio data do not produce

Table 4. Coefficients for linear and ratio variables on each of the first four principal components as generated from PCA, with percentage variances and percentage of total variance for each PC. Measurement abbreviations as in the text

Variable	PC1	PC2	PC3	PC4
Linear data:				
FL	0.996	-0.034	0.024	-0.031
FD	0.982	-0.128	0.096	0.070
TL	0.989	0.105	0.013	-0.064
TD	0.984	-0.133	0.048	0.042
MTL	0.938	0.339	0.043	0.004
MTD	0.982	0.036	-0.168	0.075
F4L	0.977	-0.171	-0.055	-0.094
Variance (%)	6.702	0.192	0.045	0.026
Total variance (%)	95.742	2.738	0.648	0.373
Ratio data:				
FL/FD	0.265	0.959	-0.007	0.102
TL/TD	0.884	0.099	0.347	-0.294
MTL/MTD	0.925	-0.179	0.070	0.248
F4L/FL	-0.836	0.001	0.530	0.142
MTL/FL	0.932	-0.189	0.078	0.130
Variance (%)	3.273	0.996	0.412	0.195
Total variance (%)	65.470	19.925	8.243	3.906

a distinctly size-related PC1. PC1 from this analysis does not show the characteristically high variance of size-related PCs generated from linear data. Instead, each of the first three PCs account for large proportions of the total variance, supporting the assertion that no one axis is predominately influenced by size. In fact, PC1 (65.5% of total variance) shows the same basic distribution of taxa as PC2 from the linear data analysis, suggesting that this PC1 can be examined as reflecting a continuum of locomotor variation (Fig. 3b). Variable coefficients support this interpretation, with ‘cursorial’ taxa having more slender limb elements, longer distal limbs, and shorter muscle lever arms (Table 4). Taxon values on this PC1 showed significant correlations with summed residual values from RMA regressions (Table 3).

Phylogenetic patterns

Examination of locomotor variation in the context of hypotheses of dinosaur phylogeny (Serenó, 1997) reveals that several independent derivations of the statistical ‘extremes’ representing cursoriality (Heterodontosauridae, Hypsilophodontidae, basal Coelurosauria, Troodontidae, Elmsauridae, and Coelophysoidea) and graviportal (Neoceratopsia, Eurypoda, derived Ornithopoda, and Sauropoda) occurred within Dinosauria (Fig. 6). Furthermore, these results can be combined with body size estimates based on PC1 from the linear PCA results to reveal several general trends in dinosaur locomotor evolution.

Primitively (based on the morphology of *Lagosuchus*, *Marasuchus*, *Lagerpeton*, and *Pseudolagosuchus*) dinosaurs show a combination of small body size and highly cursorial limb morphology (Serenó, 1991). Basal

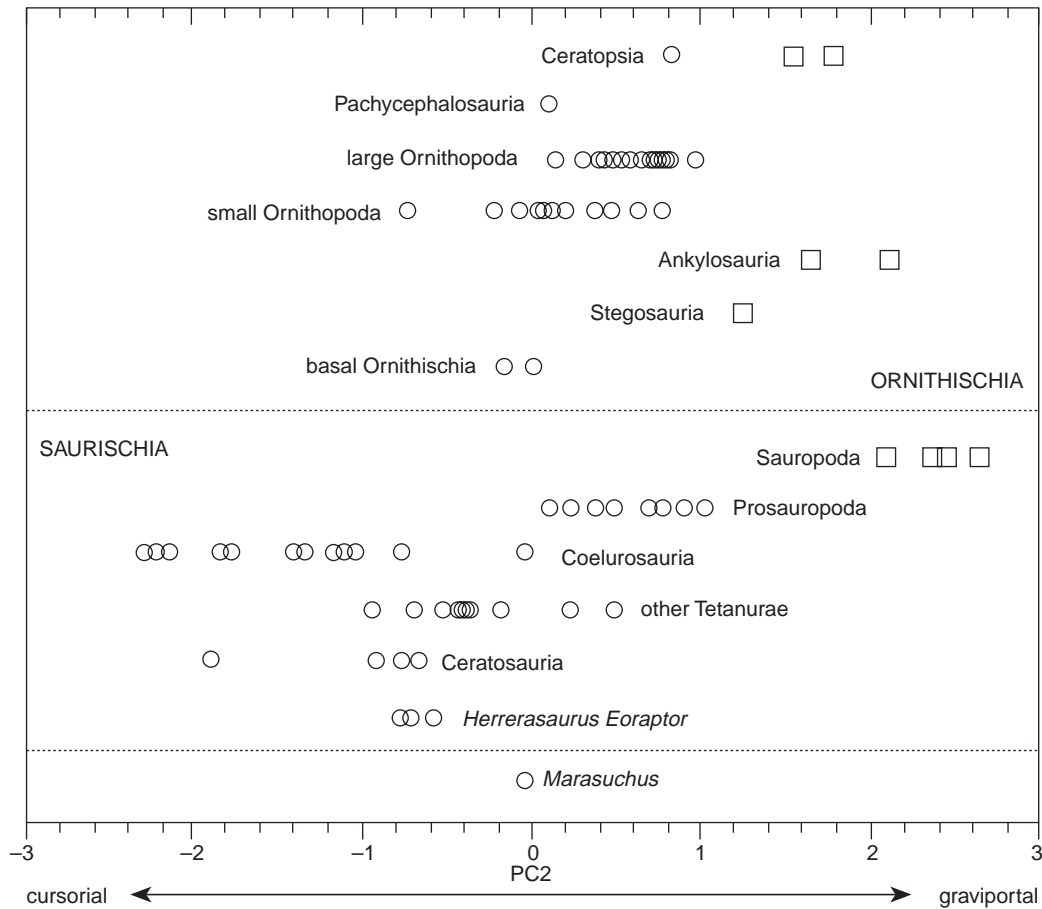


Fig. 4. PCA on dinosaurian data II. PC2 from linear data is plotted on the x-axis, while dinosaur taxa are separated according to major clade, with each point representing a single species. PC2 reveals a gradation similar to that shown by summed residuals in Fig. 1. ○ = bipeds; □ = quadrupeds.

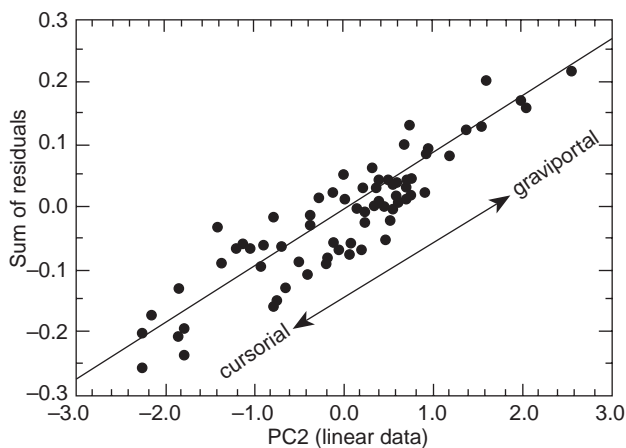
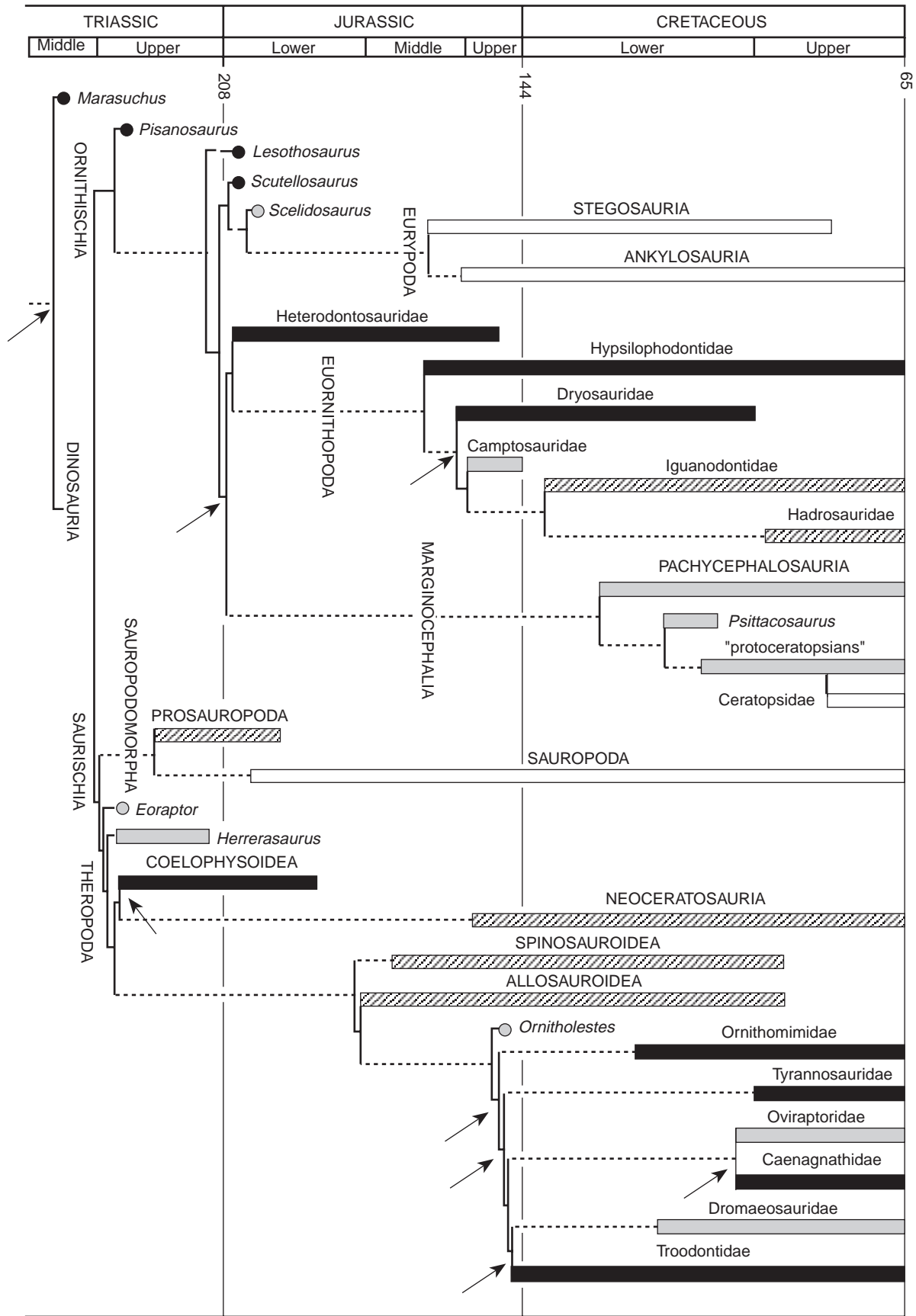


Fig. 5. Summed residuals regressed against PC2 from linear data. Note the high correlation between taxon placement in these two analyses; both reveal similar 'cursorial'-'graviportal' gradients. Statistical data are given in Table 2.

ornithischian (*Pisanosaurus*, *Lesothosaurus*) limb morphologies are very similar to this primitive condition, but invariably become more graviportal as body size increases in more derived lineages. This transition

occurs independently in derived ornithopods, ceratopsians, and thyreophorans, each of which originated from small, basal bipedal taxa (Serenó, 1986, 1997). Large ornithischian bipeds (derived Ornithopoda) do not show significant development or retention of cursorial features, and although some smaller bipeds (*Scutelosaurus*, Heterodontosauridae and Hypsilophodontidae) retain cursorial morphologies (Serenó, 1986), other smaller forms (*Psittacosaurus* and *Pachycephalosaurus* with known postcrania) do not. All quadrupedal ornithischians (Eurypoda and Neoceratopsia) show graviportal limb morphologies.

Basal saurischians possessed a mid-grade locomotor system, as evident in the very similar limb morphologies shared by prosauropods and basal theropods (*Eoraptor* and Herrerasauridae). All known sauropods are almost uniformly graviportal, with basal forms (*Vulcanodon*, *Shunosaurus* and *Barapasaurus*; Serenó, 1997) showing slightly less extreme graviportal morphologies. Most theropods retain a mid-grade locomotor apparatus, with a few small taxa (Coelophysoidea) developing cursorial features. Most larger theropods (Allosauridae, Spinosauridae and Neoceratopsia) are more cursorial than ornithischians of comparable size (i.e.,



Ornithopoda), but only slightly so. Only among coelurosaurians are there repeated, independent (Holtz, 1994; Sereno, 1997) acquisitions of cursorial features (Troodontidae, Elmsauridae, Tyrannosauridae and Ornithomimidae) and an association of cursoriality with large body size (Tyrannosauridae and Ornithomimidae). The independence of multiple derivations of cursoriality in theropods is emphasized by the sister-taxon relationships between several cursorial/non-cursorial groups (Coelophysoidea + Neoceratosauria, Caenagnathidae + Oviraptoridae, and Troodontidae + Dromaeosauridae; Sereno, 1997).

DISCUSSION

These results allow a preliminary look into dinosaur locomotor evolution. They largely confirm earlier results regarding inferences of locomotor habit for particular taxa (Coombs, 1975), but provide a statistical framework for more rigorous evaluation of these estimates. In addition, the similarity of these results to those from previous studies on mammals (Scott, 1985; Van Valkenburgh, 1987; Janis & Wilhelm, 1993), suggest that the predictions made by the two mechanical models of limb function (lever and pendulum mechanics) appropriately reflect limb use in dinosaurs as well. When combined with information on overall limb morphology and proportions (Carrano, in press), these results further support the hypothesis that dinosaurs and mammals shared similar general limb kinematic profiles.

Coombs (1975) attempted to determine morphological 'hallmarks' of cursoriality in modern taxa, and then identify dinosaurian taxa that possessed these features. In this study, various dinosaur genera were plotted onto locomotor categories as determined by living mammals and birds. In general, dinosaurs overlapped the categories outlined by modern mammalian quadrupeds, but none appeared to be as cursorial as modern birds. Most likely this distinction is an artefact due to the unusually short femora of birds (Coombs, 1975: 403, fig. 5, with moas located above modern mammalian cursors such as equids and bovids on the TL/FL axis). In fact, variables that do not involve a femoral length component show similar patterns for all three groups, patterns that are congruent with those presented here.

Furthermore, many of the smaller taxa labelled as 'cursors' by Coombs were determined here to have been similar to larger forms of intermediate size in the PCA. Several factors are likely to be responsible for this discrepancy, perhaps the most important being body size. Numerous authors have discussed the relationship between increased size and locomotor morphology (e.g. Scott, 1985; Garland & Janis, 1992; Janis & Wilhelm, 1993), noting that cursorial features become less pronounced as the effects of mass support become disproportionately large. Larger taxa therefore appear less cursorial than they might were they simply smaller in size, but the converse is also true: smaller taxa can also appear more cursorial than they might were they larger in size. However, PCA effectively segregates size-related variation on PC1, and so PC2 represents *non-size-related* variation in locomotor morphology. In a sense, this analysis has removed the 'muting' or 'enhancing' effects of size, and demonstrates that larger dinosaurian cursors are more derived in locomotor morphology than smaller ones. Small-bodied cursors (which in this analysis mostly share an *inherited* morphology, i.e. these were not independently derived morphologies; Fig. 5), appear disproportionately so due to their small – and essentially more permissive, biomechanically speaking – body masses.

Holtz (1994) demonstrated that arctometatarsus-bearing theropods have significantly longer distal limbs and more slender limb elements than most other theropods. Through bivariate analyses, Holtz demonstrated significant correlations between these variables in theropods. The current analysis shows that these theropods (as well as other forms possessing long metatarsals although lacking, technically, an arctometatarsus) also have more proximally placed muscle insertion points. Furthermore, most theropods are more 'cursorial' in these features than other dinosaurs, including bipedal ornithischians. This distinction (suggested in McGowan (1991) and Holtz (1994), but demonstrated here statistically) appears to be present at all body sizes, although it is most extreme in larger forms. In fact, no large herbivorous bipeds (including hadrosaurs and other ornithopods, pachycephalosaurs, and prosauropods) were revealed as cursorial by this analysis, and they appear to lack any other specializations typically associated with this locomotor habit (such as reduced digits, a cannon bone or its analogue, or increased mediolateral joint restriction; Coombs, 1975).

Fig. 6. Phylogenetic patterns of results. Linear-data PC2 values for various dinosaur lineages are plotted on a phylogeny of Dinosauria reveal multiple, independent derivations of cursorial morphology (phylogeny simplified from Sereno, 1997). Although this paper does not support the explicit use of categories, it is impossible to represent continuous variables on a phylogenetic diagram without resorting to a discrete labelling system. Therefore, data were partitioned into four groups for graphical purposes: cursorial ($PC2 < -1.0$; black); small-bodied intermediate ($-1.0 < PC2 < 1.0$; grey); large-bodied intermediate ($-1.0 < PC2 < 1.0$; hatching); and graviportal ($PC2 > 1.0$; white). Dashed lines, ghost lineages; heavy lines, potentially cursorial ancestral; arrows, estimated originations of cursorial morphologies. Cursoriality appeared independently multiple times, but few of these originations are matched between contemporary carnivores (Theropoda) and herbivores. Note the sister-taxon relationships between such cursorial and non-cursorial groups such as *Scutellosaur* + derived Thyreophora, Coelophysoidea + Neoceratosauria, Caenagnathidae + Oviraptoridae, Troodontidae + Dromaeosauridae, and Dryosauridae + derived Euornithopoda.

In a temporal context, it is clear that basal saurischians are less cursorial than either early ornithischians or their dinosauriform precursors. Only later (Lower Jurassic) do several small theropods reacquire cursorial features, and only among coelurosaurs (Upper Jurassic–Upper Cretaceous) does this occur at large body sizes. Sauropods and prosauropods appear to be fairly conservative throughout the duration of their lineage histories. Ornithischians initially retain primitively cursorial habits and small size, but several lineages then diverge and become both large and more graviportal. Within Dinosauria, all quadrupeds appear to have been graviportal, and most large bipedal herbivores (e.g. hadrosaurs and other large ornithopods, prosauropods, large pachycephalosaurs) were generally intermediate in locomotor habit.

It thus appears that no large dinosaurian herbivores show development of a cursorial morphology. It is surprisingly difficult to find exceptions to such a conclusion, even when other aspects of morphology are examined. This is in contrast to the situation presented by Cenozoic mammalian evolution, where large herbivores such as ungulates are the traditional exemplars of cursorial morphology (e.g. Gregory, 1912). Recent work has criticized the view of a supposed ‘arms race’ between mammalian carnivores and herbivores during the Tertiary (Janis & Wilhelm, 1993), citing lack of development of features that characterize modern cursors in archaic forms, and the disjunct timing of such developments between carnivores and herbivores when they eventually do occur. Herbivorous mammalian cursors appeared much earlier than their equivalently cursorial carnivorous pursuers, perhaps in association with substantial climatic and associated vegetational changes. As a result, cursorial features in mammals may well have evolved initially to take advantage of larger home range areas, and were only later co-opted for use in high-speed pursuit (and escape) among late Tertiary taxa (Janis & Wilhelm, 1993). Even among recent mammalian taxa, metatarsal/femur ratio is more strongly correlated with home range size than with maximal running speed (Garland, 1983; Garland & Janis, 1993).

Dinosaurs may illustrate a similar dissociation between limb morphology and speed. Unlike living mammals, in which cursorial morphologies are common among pursuit predators, it is difficult to defend widespread pursuit scenarios for Mesozoic ecosystems in which no large herbivores (and few small ones) exhibited cursorial morphologies. For example, Upper Cretaceous tyrannosaurids were similar in body mass to contemporary hadrosaurs, ceratopsians, and ankylosaurs (the remains of which often show tyrannosaurid tooth marks), but differed radically from them in locomotor morphology. Small herbivorous cursors may have been preyed on by large cursorial theropods, but the origination times of hypsilophodontids and dryosaurids (ornithopods) – apparently the only cursorial dinosaurian herbivores to survive the Upper Jurassic – do not coincide with those of cursorial theropod groups.

Upper Triassic–Lower Jurassic herbivores were also small (heterodontosaurids, *Scutellostaurus*, *Lesothosaurus*), and near in size to contemporary cursorial theropods (coelophysids), but originate significantly later in time than these carnivores. Additionally, several of these herbivores are likely to have inherited this condition from ancestral ornithischians (Fig. 6).

Juveniles of various species of dinosaurian herbivores also probably served as prey items for many theropods. However, specimens of young sauropods (*Patagosaurus*, *Apatosaurus*, *Diplodocus*), hadrosaurs (*Maiasaura*, *Hypacrosaurus*) and other ornithopods (*Valdosaurus*, *Dryosaurus*, *Camptosaurus*), ceratopsians (*Achelousaurus*, *Pachyrhinosaurus*, *Centrosaurus*, *Einiosaurus*), ankylosaurs (*Pinacosaurus*), and stegosaurs (*Stegosaurus*) do not show differences in locomotor morphology which might lead to the conclusion that juveniles were *more* cursorial than adults of these species. In fact, the only published study of biomechanical changes in limb morphology during ontogeny concluded that juveniles of the cursorial ornithopod *Dryosaurus* were possibly quadrupedal (Heinrich, Ruff & Weishampel, 1993), resulting in a rather awkward gait for these young animals. Actually, most juvenile dinosaurs are probably reasonable analogues of PC2 values from these analyses – in a sense, they represent the locomotor morphology of adults before changes inflicted by size during growth.

The possibility also exists that theropods were predators on other theropods instead of on contemporary herbivores – predation on (herbivorous?) ornithomimids by tyrannosaurids is one such possibility. Unfortunately, temporal and phylogenetic resolution does not permit detailed testing of these correlations. Tyrannosaurids and ornithomimids apparently originated at similar times, but this has been calculated from ghost lineages and is not yet supported by fossil evidence. Phylogenetic patterns suggest that their cursorial morphologies may not have been independently derived. (The nearly identical scaling properties of limb elements in these two groups suggests a non-independent derivation.) Other potential ‘prey’ theropods (troodontids, caenagnathids) are too poorly sampled in time and geography for effective comparisons to be made. Furthermore, specimens of these theropods do not show significant evidence of predation by other theropods.

Although predator–prey interactions may have involved pursuit in an individual sense, hypotheses of ‘arms-race’ driven development of pursuit predation analogous to that in modern ecosystems are not supported by these results. Instead, the independently acquired cursorial morphologies of dinosaurian predators may have been a response to a need for larger home range sizes, a need that may not have been paralleled in their herbivorous counterparts. Either active predation (Bakker, 1987; Paul, 1987, 1988) or scavenging (Horner & Lessem, 1993; Horner, 1994) in large theropods would be congruent with this pattern. It may be significant that most originations of cursoriality occurred in

coelurosaurs, but this pattern requires further examination. Finally, although resolution of Cretaceous environmental change is not yet sufficient to correlate the timing of major climatic events with morphologic changes in dinosaur evolution, the development of cursorial morphologies in dinosaurs may be more closely tied to a need for vagility rather than agility (Hotton, 1984; Farlow, Smith & Robinson, 1995).

CONCLUSIONS

These results demonstrate that a series of mechanically relevant morphological features underly a gradation in locomotor habit, from cursorial to graviportal, in both mammals and dinosaurs. Although dinosaurs do not overtly exhibit that extreme cursorial morphologies seen in some ungulate mammals (i.e. giraffids), both dinosaurs and mammals show similar overall morphological ranges. In contrast to modern mammals, however, where large herbivores and carnivores of several lineages independently acquire cursorial adaptations, large carnivores and small herbivores are the most cursorial among the dinosaurs. No large dinosaurian herbivores appear to have been cursorial; most, in fact, show graviportal specializations associated with the acquisition of quadrupedal posture and a substantial increase in body size. This suggests that large theropods with cursorial adaptations were likely adapted to covering large home range areas and did not evolve as pursuit predators on their large, herbivorous counterparts.

This study also has larger implications for general concepts of locomotor variation as applied to terrestrial vertebrates. Locomotor variation is best represented by a multivariate continuum, rather than a series of discrete categories, that should be predicated on underlying principles of skeletal biomechanics. Although this initially centers any discussion of locomotor evolution on skeletal morphology, it is impossible to discuss the evolution of locomotion without such a focus since other aspects of locomotor biology are unlikely to be recorded by the fossil record. The task ahead now involves elucidating more detailed correlations between hindlimb morphology and kinematics, bone strains, and muscle function in order to more effectively interpret patterns in vertebrate locomotor evolution.

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REFERENCES

- Albrecht, G. H. (1978). Some comments on the use of ratios. *Syst. Zool.* **27**: 67–71.
- Atchley, W. R. (1978). Ratios, regression intercepts, and the scaling of data. *Syst. Zool.* **27**: 78–83.
- Atchley, W. R. & Anderson, D. (1978). Ratios and the statistical analysis of biological data. *Syst. Zool.* **27**: 71–78.
- Bakker, R. T. (1987). *The dinosaur heresies*. New York: Zebra Books.
- Biewener, A. A. (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**: 45–48.
- Biewener, A. A. (1990). Biomechanics of mammalian terrestrial locomotion. *Science* **250**: 1097–1103.
- Carrano, M. T. (1997). Morphological indicators of foot posture in mammals: a statistical and biomechanical analysis. *Zool. J. Linn. Soc.* **121**: 77–104.
- Carrano, M. T. (1998). *Locomotor evolution in the Dinosauria: functional morphology, biomechanics, and modern analogs*. PhD thesis, University of Chicago.
- Carrano, M. T. (In press). Locomotion in non-avian dinosaurs: integrating data from *in vivo* bone strains, limb kinematics, and bone morphology. *Paleobiology* **24**.
- Cavagna, G. A., Saibene, F. P. & Margaria, R. (1964) Mechanical work in running. *J. App. Physiol.* **19**: 249–256.
- Cavagna, G. A., Heglund, N. C. & Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**: R243–R261.
- Charig, A. J. (1972). The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. In *Studies in vertebrate evolution*: 121–155. Joysey, K. A. & Kemp, T. S. (Eds). Edinburgh: Oliver & Boyd.
- Chatterjee, S. (1982). Phylogeny and classification of the thecodontian reptiles. *Nature* **295**: 317–320.
- Coombs, W. P., Jr. (1975). Theoretical aspects of cursorial adaptations in dinosaurs. *Q. Rev. Biol.* **53**: 393–418.
- Dodson, P. (1990). Counting dinosaurs: how many kinds were there? *Proc. Nat. Acad. Sci. USA* **87**: 7608–7612.
- Farlow, J. O., Smith, M. B. & Robinson, J. M. (1995). Body mass, bone 'strength indicator,' and cursorial potential of *Tyrannosaurus rex*. *J. Vert. Paleont.* **15**: 713–725.
- Fedak, M. A., Heglund, N. C. & Taylor, C. R. (1982) Energetics and mechanics of terrestrial locomotion. II. Kinetic energy changes of the limbs and body as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**: 23–40.
- Garland, T., Jr. (1983). The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool. (Lond.)* **199**: 157–170.

- Garland, T., Jr. & Janis, C. M. (1992). Does metatarsal/femur ratio predict running speed in cursorial mammals? *J. Zool. (Lond.)* **229**: 133–151.
- Gatesy, S. M. (1991). Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. *J. Zool. (Lond.)* **224**: 577–588.
- Gregory, W. K. (1912). Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. *Ann. N. Y. Acad. Sci.* **22**: 287–294.
- Heinrich, R. E., Ruff, C. B. & Weishampel, D. B. (1993). Femoral ontogeny and locomotor biomechanics of *Dryosaurus lettowvorbecki* (Dinosauria, Iguanodontia). *Zool. J. Linn. Soc.* **108**: 179–196.
- Hildebrand, M. (1985). Walking and running. In *Functional vertebrate morphology*: 38–57. Hildebrand, M., Bramble, D. M., Liem, K.F. & Wake, D. B. (Eds). Cambridge, MA: Belknap Press.
- Holtz, T. R., Jr. (1994). The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *J. Vert. Paleont.* **14**: 480–519.
- Horner, J. R. (1994). Steak knives, beady eyes, and tiny little arms (a portrait of *T. rex* as a scavenger). In *Dino fest: proceedings of a conference for the general public*: 157–164. Rosenberg, G. D. & Wolberg, D. L. (Eds). Knoxville, TN: The University of Tennessee Press.
- Horner, J. R. & Lessem, D. (1993). *The complete T. rex*. New York: Simon & Schuster.
- Hotton, N. (1984). An alternative to dinosaur endothermy: the happy wanderers. In *A cold look at the warm-blooded dinosaurs*: 311–350. Thomas, R. D. K. & Olson, E. C. (Eds). Boulder, CO: Westview Press.
- Janis, C. M. (1990). The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. In *Evolutionary paleobiology of behavior and coevolution*: 241–259. Boucot, A. J. (Ed.). New York: Elsevier.
- Janis, C. M. & Ehrhardt, D. (1988). Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zool. J. Linn. Soc.* **92**: 267–284.
- Janis, C. M. & Wilhelm, P. B. (1993). Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. *J. Mammal. Evol.* **1**: 103–125.
- Jenkins, F. A., Jr. (1971). Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *J. Zool. (Lond.)* **165**: 303–315.
- Jenkins, F. A., Jr. & Camazine, S. M. (1977). Hip structure and locomotion in ambulatory and cursorial carnivores. *J. Zool. (Lond.)* **181**: 351–370.
- LaBarbera, M. (1989). Analyzing body size as a factor in ecology and evolution. *Ann. Rev. Ecol. Syst.* **20**: 97–117.
- Maynard Smith, J. & Savage, R. J. G. (1955). Some locomotory adaptations in mammals. *J. Linn. Soc. (Lond.)* **42**: 603–622.
- McGowan, C. (1991). *Dinosaurs, spitfires, and sea dragons*. Cambridge, MA: Harvard University Press.
- Paul, G. S. (1987). Predation in the meat eating dinosaurs. In *Fourth Symposium on Mesozoic Terrestrial Ecosystems*: 173–178. Currie, P. J. & Koster, E. H. (Eds). Drumheller, Alberta.
- Paul, G. S. (1988). *Predatory dinosaurs of the world: a complete illustrated guide*. New York: Simon & Schuster.
- Scott, K. M. (1985). Allometric trends and locomotor adaptations in the Bovidae. *Bull. Am. Mus. Nat. Hist.* **179**: 197–288.
- Sereno, P. C. (1986). Phylogeny of the bird-hipped dinosaurs. *Nat. Geogr. Res.* **2**: 234–256.
- Sereno, P. C. (1991). Basal archosaurs: phylogenetic relationships and functional implications. *J. Vert. Paleont.* **11** (Memoir 2): 1–53.
- Sereno, P. C. (1997). The origin and evolution of dinosaurs. *Ann. Rev. Earth Planetary Sci.* **25**: 435–389.
- Sereno, P. C. & Arcucci, A. B. (1990). The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. *N. Jahrb. Geol. Paläont. Abh.* **180**: 21–52.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. 3rd edn. New York: W. H. Freeman.
- Stein, B. R. & Casinos, A. (1997). What is a cursorial mammal? *J. Zool. (Lond.)* **242**: 185–192.
- Steudel, K. (1990a). The work and energetic cost of locomotion. I. The effects of limb mass distribution in quadrupeds. *J. exp. Biol.* **154**: 273–285.
- Steudel, K. (1990b). The work and energetic cost of locomotion. II. Partitioning the cost of internal and external work within a species. *J. exp. Biol.* **154**: 287–303.
- Steudel, K. & Beattie, J. (1993). Scaling of cursoriality in mammals. *J. Morphol.* **217**: 55–63.
- Taylor, C. R. & Rowntree, V. J. (1973) Running on two or four legs: which consumes more energy? *Science* **179**: 186–187.
- Taylor, C. R., Shkolnik, A., Dmi'el, R., Baharav, D. & Borut, A. (1974) Running in cheetahs, gazelles, and goats: energy cost and limb configuration. *Am. J. Physiol.* **227**: 848–850.
- Van Valkenburgh, B. (1985). Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology*. **11**: 406–428.
- Van Valkenburgh, B. (1987). Skeletal indicators of locomotor behavior in living and extant carnivores. *J. Vert. Paleont.* **7**: 162–182.
- Wilkinson, L. (1989). *SYSTAT: the system for statistics*. Evanston IL: Systat.