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PHILIP D. GINGERICH

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Philip D. Gingerich, Director

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PREDICTION OF BODY MASS IN MAMMALIAN SPECIES FROM LONG BONE LENGTHS AND DIAMETERS

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Abstract.— The relationships of body mass to long bone length and parasagittal midshaft diameter are studied using measurements of mass and six different bones in 41 adult individuals representing 36 species of mammals ranging in size from shrew to elephant. Analysis of variance yields coefficients of determination ranging from 0.92 to 0.99, with the former representing lengths of distal segments (longest metacarpal and metatarsal), and the latter representing midshaft diameters of proximal segments (humerus and femur). A computer program is listed that automates body mass prediction and prediction interval estimation using coefficients derived from individual and multiple regressions. Body masses of the Eocene condylarth *Copecion*, the Eocene pantodont *Coryphodon*, and the Oligocene perissodactyl *Baluchitherium* [or *Indricotherium* or *Paraceratherium*] are investigated as examples.

INTRODUCTION

Adult body mass or weight is a physiological variable of interest in a broad range of ecological and functional studies of mammals. To place these in evolutionary context, it is important that body mass be quantified for extinct as well as living species. Prediction of body mass from tooth size, useful in paleontological investigations, has been quantified in a few broadly comparative empirical studies (e.g., Gingerich et al., 1982, and Conroy, 1987, for primates; Legendre and Roth, 1988, for carnivores; Legendre, 1989, for these and five additional orders of mammals), but teeth represent a single anatomical system and it is important that other systems be investigated as well.

Investigation of the postcranial skeleton is particularly important because body weight is routinely transmitted through skeletal elements to the substrate and we can expect, a priori, that skeletal dimensions will have a close relationship to body mass (Hylander, 1985; Jungers, 1987, 1988). Anderson et al. (1985) used midshaft circumference of the humerus and femur to predict body mass across a broad range of mammals. This general approach is extended in the analysis that follows.

PREDICTION OF BODY MASS

R. McNeill Alexander and colleagues studied the allometry of limb bone size in adult mammals ranging from shrews to elephant (Alexander et al., 1979; see Table 1). Their analysis involved regression of long bone length and midshaft diameter on body mass, which is

TABLE 1—Mammalian species and body masses measured by Alexander et al. (1979) and included in this analysis. All individuals were apparently healthy adults.

Order	Species	Mass (g)
Insectivora	*Sorex minutus* (Pygmy shrew)	2.9
	" "	3.1
	Sorex araneus (Common shrew)	6.2
	Rhynchocyon chrysopygus (Elephant shrew)	550.
	" "	631.
Primates	*Galago crassicaudatus* (Thick-tailed bushbaby)	644.
	Cercopithecus mitis (Sykes monkey)	3,580.
	Cercopithecus aethiops (Vervet monkey)	3,620.
	Colobus abyssinicus (Abyssinian colobus)	12,300.
	Papio anubis (Anubis baboon)	15,000.
	Homo sapiens (Human)	64,000.
Lagomorpha	*Oryctolagus cuniculus* (Rabbit)	1,010.
	" "	1,122.
	Lepus capensis (Brown hare)	2,440.
Rodentia	*Sylvaemus sylvaticus* (Wood mouse)	13.7
	Mus musculus (Laboratory mouse)	29.1
	Acomys cahirinus (Spiny mouse)	52.
	Rattus norvegicus (Laboratory rat)	204.
	" "	285.
	Pedetes capensis (Spring hare)	2,110.
Carnivora	*Putorius putorius* (Ferret)	580.
	Genetta genetta (Common genet)	1,850.
	Felis catus (Domestic cat)	2,540.
	Ichneumia albicauda (White-tailed mongoose)	4,100.
	Canis mesomelas (Black-backed jackal)	7,200.
	Vulpes vulpes (Red fox)	8,000.
	Canis familiaris (Domestic dog)	23,000.
	Crocuta crocuta (Spotted hyaena)	41,000.
	Panthera leo (Lion)	145,000.
Proboscidea	*Loxodonta africana* (African elephant)	2,500,000.
Artiodactyla	*Rhynchotragus kirki* (Kirk's dik-dik)	4,400.
	" "	4,890.
	Gazella thomsoni (Thomson's gazelle)	29,000.
	Litocranius walleri (Gerenuk)	37,000.
	Phacochoerus aethiopicus (Warthog)	65,000.
	Gazella granti (Grant's gazelle)	68,000.
	Alcelaphus buselaphus (Kongoni)	117,000.
	Connochaetes taurinus (Wildebeest)	161,000.
	Oryx beisa (Beisa oryx)	176,000.
	Camelus dromedarius (Arabian camel)	326,000.
	Syncerus caffer (Cape buffalo)	500,000.

appropriate for study of allometric scaling of limb size, but inappropriate for prediction of body mass from limb bones. Professor Alexander has generously made available original measurements used in the limb allometry study, and these have been analyzed further to develop equations predicting body mass from long bone lengths and diameters.

Alexander et al. (1979) showed that distributions of long bone length and diameter are linear when plotted against body mass using logarithmic scales, indicating that these relationships can be modeled using the standard allometric power function $Y = aX^b$, where X is the independent variable (body mass) and Y is the dependent variable (long bone length or

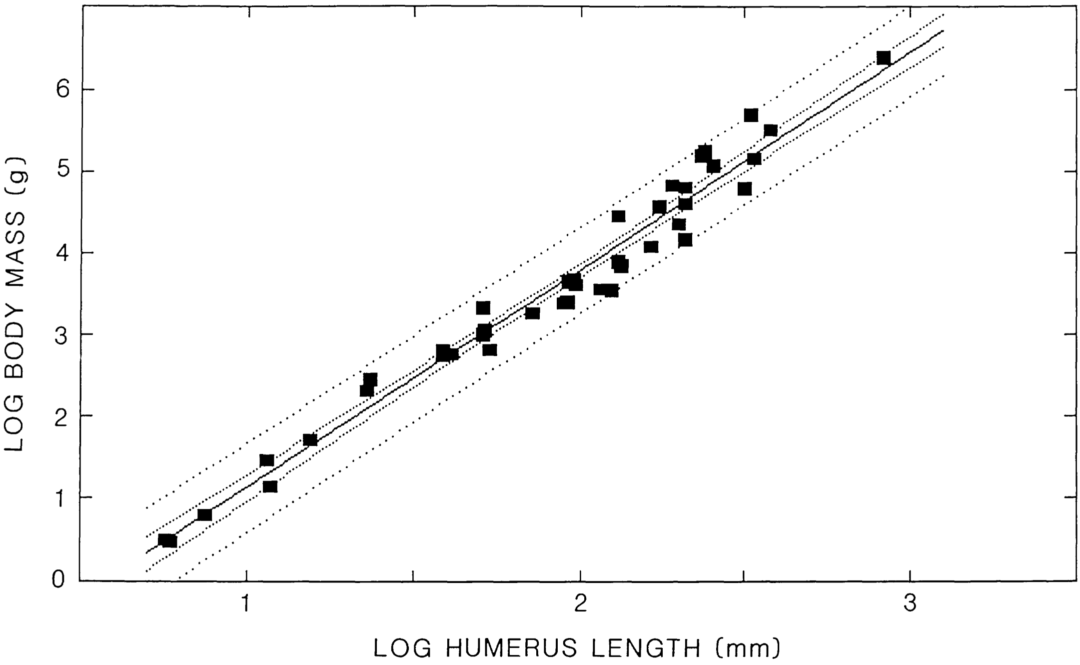

FIG. 1— Regression of $\log_{10}$ body mass (g) on $\log_{10}$ humerus length (mm) for 41 adults representing 36 mammalian species (solid squares; data of Alexander et al., 1979). Solid line is linear regression. Central pair of heavier dotted lines show 95% confidence limits for regression, and outer pair of lighter dotted lines show 95% prediction limits for individual samples (k = 1; limits computed as shown in Appendix following Sokal and Rohlf, 1969, p. 424-425). Coefficient of determination r^2 is 0.969 (Table 2).

diameter) of special interest. Reversing dependent and independent variables because body mass is the variable of interest here, the relationship of body mass to humerus length is illustrated in Figure 1.

Log body mass is highly correlated with log humerus length (r = 0.984) and the coefficient of determination r^2 = 0.969 indicates that 96.9% of observed variation in log body mass can be explained by variation in log limb length (and vice versa). Remaining variation, often significant, is due to independent factors. Comparison of coefficients of determination for all long bone lengths and diameters analyzed here shows that diameters of proximal segments (humerus and femur) have the highest r^2 values, indicating that diameters of these bones are most narrowly related to body mass and that body mass is best predicted by diameters of these bones. Lengths of distal segments (longest metacarpal and longest metatarsal) have the lowest r^2 values. These are 0.918 and 0.922, respectively, indicating that distal segment length is still closely related to body mass and that distal segments contribute importantly (though less so) to prediction of body mass.

A computer program BODYMASS predicting body mass from long bone lengths and diameters is provided in the Appendix. The program is based on data of Alexander et al. (1979) for species listed in Table 1. Ulna diameter was not measured by Alexander et al. (1979), and hence it is not used in any predictions calculated here. Also, because of metapodial specialization, measurements of Artiodactyla are excluded from individual regressions and predictions using metacarpal and metatarsal measurements.

TABLE 2—Coefficients of determination (r^2) for regression of body mass on long bone length and diameter, and prediction of body mass from long bone length and diameter.

	Maximum length		Midshaft diameter (parasagittal)	
Element	N	r^2	N	r^2
Humerus	41	0.969	41	0.992
Ulna	40	0.972	--	--
Longest metacarpal	29	0.918	26	0.985
Femur	40	0.965	40	0.991
Tibia	41	0.964	41	0.981
Longest metatarsal	30	0.922	27	0.966

Source code for BODYMASS is published in full both to encourage use of the program and to encourage modification as better data for body size prediction become available. Organization and calculations of the program are best illustrated by reference to several example predictions of body size in fossil mammals. Both the value and limitation of the Alexander et al. data for body size prediction are discussed in context of these examples.

EXAMPLE OF *COPECION BRACHYPTERNUS*

Copecion brachypternus is a phenacodontid mammal of the order Condylartha that is common in early Eocene faunas of North America. It is represented by one good associated partial skeleton, University of Michigan [UM] specimen 64179, described and illustrated by Thewissen (1990). The specimen preserves a nearly complete humerus, femur, tibia, and third metatarsal. Measurements of these long bones are listed in Table 3, together with body mass predictions and 95% prediction limits derived from them. The humerus is 80.6 mm long and, using the relationship shown in Figure 1, this yields a predicted body mass for the species of 3,483 g. The 95% confidence limits for this prediction (lighter dotted lines in Fig. 1) range from 1,033 g to 11,738 g. Broad prediction limits like these dictate caution in interpreting any body mass estimate derived from a single measurement or a single bone. The credibility of a prediction depends in large degree on the consistency of multiple estimates based on different measurements and different bones.

The four long bone lengths known for *Copecion brachypternus* yield estimates of 3,483, 3,414, 2,444, and 2,683 g, respectively, which are all reasonably consistent. The four long bone diameters known for this species yield estimates of 3,807, 2,900, 4,268, and 2,609 g, respectively, which are again reasonably consistent among themselves and also consistent with predictions based on lengths. The mean value of 3,152 g listed at the bottom of the column of individual body mass predictions is a weighted geometric mean of all 8 individual predictions. A geometric mean (exponentiated mean of log values) is appropriate here because we are interested in proportional relationships (and the analysis yielding each prediction was appropriately based on logged measurements). This geometric mean value is a weighted mean, with each logged prediction weighted by the appropriate coefficient of determination listed in Table 2. Weighting is included to emphasize more highly correlated measures over less highly correlated ones, although no great difference between these was found in this study.

TABLE 3—Body size determination for Eocene condylarth *Copecion brachypternus* based on associated partial skeleton UM 64179. Table shows screen copy generated by the computer program in the Appendix.

Copecion brachypternus UM 64179	Measurement (mm)	Predicted body mass(g)	95% Prediction limits Min(g)	 Max(g)
Humerus length	80.6	3,483	1,033	11,738
Ulna length		---		
Metacarpal length		---		
Femur length	97.9	3,414	937	12,439
Tibia length	97.2	2,444	665	8,986
Metatarsal length	36.6	2,683	408	17,657
Humerus diameter	8.2	3,807	2,101	6,898
Ulna diameter		---		
Metacarpal diameter		---		
Femur diameter	7.5	2,900	1,526	5,512
Tibia diameter	8.1	4,268	1,677	10,860
Metatarsal diameter	3.5	2,609	697	9,757
N, geom. mean, max, min	8	3,152	2,101	5,512
Multiple regression	All species: (Artio.rem.):	11 L&D-	6 L-	

The weighted geometric mean in Table 3 (3,152 g; or, rounded, 3,200 g) is the mass estimate of choice for *Copecion brachypternus*. If all 6 long bone length measurements and/or all 11 length and diameter measurements were available for *C. brachypternus*, body mass predictions based on multiple regression would automatically be printed at the bottom of Table 3. Multiple regressions were calculated with and without Artiodactyla, and body mass predictions at the base of the data table are calculated both ways. Predictions based on one or both multiple regressions should normally fall reasonably near the mean of individual predictions.

Comparison of individual body mass prediction values with the mean of prediction values (or one or more prediction values based on multiple regression) indicates how limb bone sizes in the fossil species under consideration differ from those of an average living mammal of the same body mass. For example, predictions of mass based on humerus length and femur length in *Copecion brachypternus* are both greater than the mean, while predictions of mass based on tibia length and metatarsal length are both less than the mean. This means that *C. brachypternus* had limbs with slightly longer proximal segments and shorter distal segments than is typical in mammals living today (as represented by the sample in Table 1).

Prediction limits for mean body mass estimated from several individual lengths and/or diameters can be calculated in several different ways. In proportional (log) space, prediction limits are equidistant from predicted body mass, and the mean prediction range centered on mean predicted body mass can be exponentiated to yield a new prediction range. Alternatively, and this is the method employed here, the maximum of individual minimum limits and the minimum of individual maximum limits can be used to constrain prediction values to a reasonable range. The rationale for this is that all values below the maximum of individual minima are, in some sense, ruled out by this maximum. Similarly, all values above the minimum of individual maxima are ruled out by this minimum. Thus it is unlikely that body mass will fall outside maximum minimum and minimum maximum limits.

Finally, we can ask how body mass estimated from long bone length and diameter compares with body mass estimated from tooth size in *Copecion brachypternus*. Thewissen (1990) found the mean crown area (length multiplied by width) for M^1 in 84 specimens of *C. brachypternus* to be 36.7 mm^2, which yielded a predicted body mass for the species of 7,500 g using the

TABLE 4—Body size determination for Eocene pantodont *Coryphodon marginatus* based on associated partial skeleton AMNH 15782. Table shows screen copy generated by the computer program in the Appendix.

Coryphodon marginatus AMNH 15782	Measurement (mm)	Predicted body mass(g)	95% Prediction limits	
			Min(g)	Max(g)
Humerus length	245.0	68,171	19,987	232,509
Ulna length	290.0	69,577	21,805	222,013
Metacarpal length	64.5	25,962	4,039	166,864
Femur length	372.0	118,073	31,841	437,833
Tibia length	235.0	36,355	9,812	134,699
Metatarsal length	52.2	7,954	1,198	52,822
Humerus diameter	46.5	345,788	188,246	635,175
Ulna diameter	48.0	---		
Metacarpal diameter	15.5	276,931	109,599	699,737
Femur diameter	34.0	182,898	95,214	351,331
Tibia diameter	40.9	328,724	126,466	854,454
Metatarsal diameter	11.9	101,678	26,116	395,872
N, geom. mean, max, min	11	90,227	188,246	52,822
Multiple regression	All species: (Artio.rem.):	11 L&D- 164,659 (153,170)	6 L- 57,534 (49,291)	

primate regression of Gingerich et al. (1982) or 6,500 g using the herbivore regression of Legendre (1989). In this example, crown area of M^1 yields an estimate twice the body mass predicted from long bone dimensions, and it appears that *Copecion* had relatively large teeth for its body mass.

EXAMPLE OF *CORYPHODON MARGINATUS* AND *CORYPHODON SUBQUADRATUS*

Coryphodon is interesting in being the largest late Paleocene and early Eocene land mammal known from North America. Body size change is best studied in the Bighorn and Clarks Fork basins of Wyoming where four species are known that appear to represent a single evolutionary lineage: Clarkforkian *Coryphodon proterus* Simons, early Wasatchian *C. eocaenus* Owen, late early to early middle Wasatchian *C. marginatus* Cope, and middle Wasatchian *C. subquadratus* Cope. Three of these species were large, the one exception being *C. marginatus* which was clearly smaller. Body size is closely related to metabolic physiology, and mass of the largest mammal in a fauna may be controlled by ambient environmental temperature. In a preliminary study of body size change in relation to environmental temperature, I estimated the body size of *C. marginatus* to have been about 400 kg and that of *C. subquadratus* to have been about 800 kg based on tooth size (Gingerich, 1989).

Body mass predictions from long bone lengths and diameters are listed in Tables 4 and 5, respectively, based on one associated partial skeleton of each species conserved in the American Museum of Natural History [AMNH]. Measurements are available for all elements used to predict body size, and computer calculations include body mass estimates based on multiple as well as individual regressions. Here, in contrast to *Copecion brachypternus* discussed above, there are substantial inconsistencies in body mass predictions. For example, in Table 4, predicted body masses for *Coryphodon marginatus* based on limb lengths range from 7,954 to 118,073 g, while predicted body masses based on limb diameters range from 101,678 to 345,788 g. There is little overlap between predictions calculated from lengths and those calculated from diameters. With the exception of femur length (and humerus length in *C. subquadratus*), lengths all yield predictions smaller than the geometric mean of individual

TABLE 5—Body size determination for Eocene pantodont *Coryphodon subquadratus* based on associated partial skeleton AMNH 15341. Table shows screen copy generated by the computer program in the Appendix.

Coryphodon subquadratus	Measurement	Predicted	95% Prediction limits	
AMNH 15341	(mm)	body mass(g)	Min(g)	Max(g)
Humerus length	395.0	244,634	70,831	844,914
Ulna length	370.0	134,850	42,010	432,859
Metacarpal length	79.5	43,556	6,698	283,244
Femur length	490.0	245,333	65,619	917,241
Tibia length	295.0	72,872	19,560	271,487
Metatarsal length	71.7	21,010	3,117	141,630
Humerus diameter	66.4	872,613	472,191	1,612,596
Ulna diameter	59.2	---		
Metacarpal diameter	19.9	548,871	214,866	1,402,080
Femur diameter	44.1	373,183	193,441	719,938
Tibia diameter	51.2	600,523	229,653	1,570,317
Metatarsal diameter	19.8	466,744	115,951	1,878,804
N, geom. mean, max, min	11	210,276	472,191	141,630
Multiple regression	All species:	11 L&D- 489,380	6 L- 161,722	
	(Artio.rem.):	(435,049)	(155,953)	

predictions. Diameters all yield predictions greater than the geometric mean of individual predictions. Predictions based on multiple regression are similarly inconsistent, depending on whether limb bone lengths are considered alone or with diameters. *Coryphodon* has limb bones that are relatively short and thick in comparison to all living species listed in Table 1 and forming the basis for prediction equations utilized here. Skeletal restorations of *Coryphodon* have been published by Marsh (1893), Osborn (1898), and Patterson (1939) with little discussion of their meaning for body form or life habits. More recently, Lucas (1986) described *Coryphodon* as weighing 150 to 300 kg and resembling the extant pygmy hippopotamus *Hexaprotodon* in locomotion. Hippopotami are not included in data used to predict body mass here, and prediction of mass for this body form appears to be poorly estimated by generalized equations. Prediction of body mass in *Coryphodon* will require separate analysis utilizing animals of similar form.

The predicted body mass of *Coryphodon* species is not well constrained by the analysis presented here, and this is evident in the inconsistency of individual body mass estimates based on different skeletal measurements. Nevertheless, whatever the absolute mass of *Coryphodon*, mean predicted masses of 90 kg and 210 kg for small and large species, respectively, are consistent with a doubling or halving of body size in comparing largest to smallest species (as in my estimates of 400 and 800 kg based on tooth size, or Lucas' estimates of 150 and 300 kg).

EXAMPLE OF *BALUCHITHERIUM GRANGERI*

Baluchitherium grangeri is a large rhinocerotoid from the Oligocene of Mongolia first described by Osborn (1923) and further illustrated by Granger and Gregory (1936). *Baluchitherium* is often synonymized with *Paraceratherium* and *Indricotherium*, and *B. grangeri* is sometimes synonymized with *P.* or *I. transouralicum* (Gromova, 1959; Lucas and Sobus, 1989). This species is regarded as the largest terrestrial mammal that ever lived, with a body mass estimated at 20 metric tons (Economos, 1981) or more (Alexander, 1989).

TABLE 6—Body size determination for Oligocene rhinoceratid *Baluchitherium grangeri* (size grade II) based on associated partial skeleton AMNH 26166. Table shows screen copy generated by the computer program in the Appendix.

Baluchitherium grangeri AMNH 26166 (grade II)	Measurement (mm)	Predicted body mass(g)	95% Prediction limits Min(g)	Max(g)
Humerus length	985	2,819,296	787,519	10,092,997
Ulna length	1350	4,536,416	1,344,224	15,309,263
Metacarpal length	535	4,875,088	620,803	38,283,436
Femur length	1390	3,905,880	999,177	15,268,465
Tibia length	920	2,361,346	603,996	9,231,773
Metatarsal length	500	8,011,758	958,136	66,992,872
Humerus diameter	200	15,314,280	8,081,477	29,020,338
Ulna diameter		---		
Metacarpal diameter	80	24,756,508	8,937,298	68,576,064
Femur diameter		---		
Tibia diameter		---		
Metatarsal diameter		---		
N, geom. mean, max, min	8	6,067,578	8,937,298	9,231,773
Multiple regression	All species: (Artio.rem.):	11 L&D-	6 L-	4,285,104 (1,633,440)

TABLE 7—Body size determination for Oligocene rhinoceratid *Baluchitherium grangeri* (size grade I) based on reconstructed third metacarpal AMNH 26175. Table shows screen copy generated by the computer program in the Appendix.

Baluchitherium grangeri AMNH 26175 (grade I)	Measurement (mm)	Predicted body mass(g)	95% Prediction limits Min(g)	Max(g)
Humerus length	1200	4,781,076	1,322,609	17,283,024
Ulna length	1620	7,443,634	2,185,016	25,358,022
Metacarpal length	635	7,449,756	926,728	59,886,908
Femur length	1660	6,256,844	1,585,279	24,694,772
Tibia length	1100	4,078,336	1,032,208	16,113,826
Metatarsal length	600	13,997,618	1,624,768	120,591,600
Humerus diameter		---		
Ulna diameter		---		
Metacarpal diameter		---		
Femur diameter		---		
Tibia diameter		---		
Metatarsal diameter		---		
N, geom. mean, max, min	6	6,708,826	2,185,016	16,113,826
Multiple regression	All species: (Artio.rem.):	11 L&D-	6 L-	6,889,515 (2,569,752)

An independent estimate can be attempted using the body mass prediction program in the Appendix, and screen copy generated using this program is shown in Tables 6 and 7. The best associated postcranial elements of larger *Baluchitherium grangeri* (size grade II) are parts of AMNH 26166 described by Granger and Gregory (1936, pp. 38 and 53). Unfortunately, these yield inconsistent estimates of body mass. Most of the long bone lengths in AMNH 26166 are based on measurements or good estimates reported by Granger and Gregory (1936; femur length and tibia length are scaled up from smaller specimens, and metatarsal length is taken from another specimen of similar size). These measurements and good estimates yield individual body mass predictions ranging from about 2 to 8 metric tons, and a multiple regression prediction of 4.3 tons. Long bone diameters of the humerus and third metacarpal can be scaled from figures in Granger and Gregory (1936). These yield estimates of 15 and 25 tons, respectively, suggesting the same problem of prediction encountered with *Coryphodon*. In this instance we not only have few (if any) mammals proportioned like *Baluchitherium* among the extant species used to derive prediction coefficients, but *Baluchitherium* lies well outside the range of body masses available for living mammals.

The maximum individual minimum prediction limit in Table 6 is about 9 metric tons, as is the minimum maximum limit. If 9 tons is a reasonable estimate for the mass of *Baluchitherium grangeri* of size grade II, and if size grade I is 60% heavier than size grade II (ratio of multiple regression results), then we might expect a *B. grangeri* of size grade I to weigh 14 to 15 tons or more, and the limit of 20 tons proposed by Economos (1981) may be reasonable. Better prediction will require better sampling of body mass and long bone lengths and diameters for large extant mammals of similar body form (especially rhinoceros, no Perissodactyla are included in data analyzed here).

DISCUSSION

Mammals exhibit a wide range of body forms and locomotor styles, and there is probably no single skeletal measure that adequately predicts body mass. Midshaft diameters of proximal limb bones have the highest coefficients of determination calculated here. Thus midshaft thicknesses of the humerus and femur are good limb measures to use for body mass prediction. Parasagittal diameter is easier to measure, especially on smaller bones, but midshaft circumference is surely as good (Anderson et al., 1985) and it would probably be slightly better if easier to measure over the full range of mammalian sizes. Mammals generally move parasagittally, which is the reason for measuring diameter in a parasagittal plane.

Middle and distal limb segments contribute significantly to body mass estimation. Measurement of distal as well as proximal segments, and long bone lengths as well as diameters, is important for body mass prediction because the consistency of predictions based on different measures provides an important indication of accuracy. It is clear from examples given here that better body mass predictions will result if extant species used to generate prediction coefficients are similar in body form to those of extinct species whose body masses are to be estimated. Accuracy is most important, while generality and precision can probably never achieved simultaneously in any case.

It goes without saying that prediction coefficients generated from a broad range of different species can only be used to predict the average body masses of species, not body masses of individual animals. These will be similar when an individual is truly representative of its species, but there is rarely any way to know how representative a particular individual might be. Species include individuals of different masses, and the contribution of individual variation to breadth of prediction limits is substantial.

Body mass is so important in ecology and functional morphology that we would do well to develop standard routines for interpreting body mass from tooth and bone size. Better understanding of body mass in extinct mammals will facilitate study of evolutionary ecology and the functional evolution of morphology.

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APPENDIX

Microsoft® **QuickBASIC** source code for computation of mammalian body mass predictions and prediction intervals based on long bone lengths and diameters. BODYMASS program ends with a routine for calculating encephalization quotients.

```
'PREDICTION OF BODY MASS FROM LONG BONE LENGTHS AND PARASAGITTAL MIDSHAFT DIAMETERS
'P. D. Gingerich              University of Michigan                   October 1990
'
'---------------------------------------------------------------------------Front matter
COLOR 15, 1
CLS 0
LOCATE 2, 1
PRINT "     *****    ****   *****  *     *    *     *     *     ****   ****            "
PRINT "     *    *  *    *  *    *  *   *     **   **    * *   *      *                "
PRINT "     *****   *    *  *    *    *       * * * *   *   *   ****   ****            "
PRINT "     *    *  *    *  *    *    *       *  *  *  * *** *      *      *           "
PRINT "     *****    ****   *****     *       *     *  *     *  ****   **** PDG        "
COLOR 7, 1
LOCATE 8, 1
PRINT "Program computes: (1) adult body mass predictions for mammal species, with 95%  "
PRINT "prediction intervals, using individual long bone lengths and parasagittal mid-  "
PRINT "shaft diameters; (2) geometric mean of predictions weighted by associated coef- "
PRINT "ficients of determination, with maxmin and minmax PI range; (3) predictions    "
PRINT "using all lengths together or all lengths and diameters together.  Predictions   "
PRINT "based on single or multiple regression of mass (g) on long bone length and/or   "
PRINT "diameter (mm) using mass and bone measurements for 41 individuals of 36 species "
PRINT "provided by R. McNeill Alexander (see Alexander et al. 1979. Allometry of the   "
PRINT "limb bones of mammals from shrews to elephant. J.Zool.Lond.,189:305-314; meta-  "
PRINT "carpals and metatarsals omitted for artiodactyls).  Prediction intervals for    "
PRINT "individual predictions calculated following Sokal & Rohlf (1969, Biometry,      "
PRINT "p. 424-425).  Program ends with optional routine to calculate encephalization  "
PRINT "quotients from brain and body mass using scaling of Jerison (1973).             "
LOCATE 22, 1: INPUT "Species to be analyzed:  ", Species$
LOCATE 23, 1: INPUT "Source ref. (if any):    ", Ref$
CLS 0
COLOR 15, 1
LOCATE 1, 1: PRINT Species$
COLOR 7, 1
LOCATE 2, 3: PRINT Ref$
'---------------------------------------------------------------------------Setup screen
LOCATE 1, 25: PRINT "Measurement"
LOCATE 2, 25: PRINT "   (mm)    "
LOCATE 3, 25: PRINT "-----------"
LOCATE 1, 39: PRINT " Predicted "
LOCATE 2, 39: PRINT "body mass(g) "
LOCATE 3, 39: PRINT "-------------"
LOCATE 1, 55: PRINT "  95% Prediction limits "
LOCATE 3, 55: PRINT "-----------------------"
LOCATE 2, 55: PRINT "  Min (g)  "
LOCATE 2, 68: PRINT "  Max (g)  "
LOCATE 17, 1: PRINT "N, geom. mean, max, min"
'-------------------------------------------------------------------------Initial values
LET V = 12
DIM Label$(1 TO V)
DIM Meas(1 TO V) AS DOUBLE
DIM Loga(1 TO V), B(1 TO V), R2(1 TO V) AS DOUBLE
DIM Massest(1 TO V) AS DOUBLE
DIM N(1 TO V), Xbar(1 TO V), S2yx(1 TO V), Sb(1 TO V) AS DOUBLE
DIM T05nm2(1 TO V)
R2loggmtot = 0: Count = 0: Halfitot = 0: R2tot = 0
Minci = 0: Maxci = 100000000
'---------------------------------------------------------------------------Coefficients
Label$(1) = "Humerus length        "
  N(1) = 41: Loga(1) = -1.5579: B(1) = 2.6752: R2(1) = .9685
  T05nm2(1) = 2.021: Xbar(1) = 1.9154: S2yx(1) = .06655: Sb(1) = .077259
```

```
Label$(2) = "Ulna length             "
  N(2) = 40: Loga(2) = -1.8459: B(2) = 2.7162: R2(2) = .97185
  T05nm2(2) = 2.022: Xbar(2) = 1.9787: S2yx(2) = .05931: Sb(2) = .074985
Label$(3) = "Metacarpal length       "
  N(3) = 29: Loga(3) = -.063602: B(3) = 2.4746: R2(3) = .91817
  T05nm2(3) = 2.052: Xbar(3) = 1.3217: S2yx(3) = .14524: Sb(3) = .14218
Label$(4) = "Femur length            "
  N(4) = 40: Loga(4) = -1.7511: B(4) = 2.6544: R2(4) = .96504
  T05nm2(4) = 2.022: Xbar(4) = 2.0104: S2yx(4) = .075244: Sb(4) = .081958
Label$(5) = "Tibia length            "
  N(5) = 41: Loga(5) = -2.6904: B(5) = 3.0581: R2(5) = .96384
  T05nm2(5) = 2.021: Xbar(5) = 2.0459: S2yx(5) = .076397: Sb(5) = .094856
Label$(6) = "Metatarsal length       "
  N(6) = 30: Loga(6) = -1.3562: B(6) = 3.0604: R2(6) = .92179
  T05nm2(6) = 2.048: Xbar(6) = 1.4612: S2yx(6) = .15419: Sb(6) = .16846
Label$(7) = "Humerus diameter        "
  N(7) = 41: Loga(7) = 1.2061: B(7) = 2.5984: R2(7) = .99246
  T05nm2(7) = 2.021: Xbar(7) = .90825: S2yx(7) = .015928: Sb(7) = .036267
Label$(8) = "Ulna diameter           "
  N(8) = 0: Loga(8) = 0: B(8) = 0: R2(8) = 0
  T05nm2(8) = 0: Xbar(8) = 0: S2yx(8) = 0: Sb(8) = 0
Label$(9) = "Metacarpal diameter     "
  N(9) = 26: Loga(9) = 2.1836: B(9) = 2.7377: R2(9) = .98534
  T05nm2(9) = 2.064: Xbar(9) = .35153: S2yx(9) = .033483: Sb(9) = .068174
Label$(10) = "Femur diameter          "
  N(10) = 40: Loga(10) = 1.0632: B(10) = 2.7418: R2(10) = .99138
  T05nm2(10) = 2.022: Xbar(10) = .91988: S2yx(10) = .018552: Sb(10) = .041474
Label$(11) = "Tibia diameter          "
  N(11) = 41: Loga(11) = 1.1929: B(11) = 2.6828: R2(11) = .98138
  T05nm2(11) = 2.021: Xbar(11) = .8846: S2yx(11) = .039327: Sb(11) = .059168
Label$(12) = "Metatarsal diameter     "
  N(12) = 27: Loga(12) = 1.7879: B(12) = 2.9932: R2(12) = .9661
  T05nm2(12) = 2.06: Xbar(12) = .45294: S2yx(12) = .074488: Sb(12) = .11213
'
'--------------------------------------------------------Individual regression estimates
FOR i = 1 TO V
  LOCATE 3 + i, 3: PRINT Label$(i), : INPUT "", Meas(i)
  IF B(i) > 0 THEN
    Massest(i) = (10 ^ Loga(i)) * (Meas(i) ^ B(i))
  END IF
  IF Massest(i) > 0 THEN
    LOCATE 3 + i, 40: PRINT USING "##,###,###"; Massest(i)
  ELSE
    LOCATE 3 + i, 47: PRINT "---"
  END IF
  IF Massest(i) > 0 AND B(i) > 0 THEN
    R2loggmtot = R2loggmtot + R2(i) * ((LOG(Massest(i)) / LOG(10)))
    R2tot = R2tot + R2(i)
    Count = Count + 1
    LOCATE 17, 28: PRINT USING "##"; Count
    LOCATE 17, 40: PRINT USING "##,###,###"; 10 ^ (R2loggmtot / R2tot)
    Syhat = SQR(S2yx(i) + (S2yx(i) / N(i)) + ((Sb(i) ^ 2) * ((LOG(Meas(i)) / _
        LOG(10)) - Xbar(i)) ^ 2))         'Prediction interval
    'Syhat = SQR((S2yx(i) / N(i)) + ((Sb(i) ^ 2) * ((LOG(Meas(i)) / LOG(10)) - _
        Xbar(i)) ^ 2))          'Confidence interval
    Halfci = ABS(T05nm2(i) * Syhat)
    Lowci = 10 ^ ((LOG(Massest(i)) / LOG(10)) - Halfci)
    Highci = 10 ^ ((LOG(Massest(i)) / LOG(10)) + Halfci)
    LOCATE 3 + i, 55: PRINT USING "##,###,###"; Lowci
    LOCATE 3 + i, 70: PRINT USING "##,###,###"; Highci
    IF Lowci > Minci THEN
      Minci = Lowci
    END IF
    IF Highci < Maxci THEN
      Maxci = Highci
    END IF
    LOCATE 17, 55: PRINT USING "##,###,###"; Minci
    LOCATE 17, 70: PRINT USING "##,###,###"; Maxci
  END IF
NEXT
LOCATE 18, 1
PRINT "--------------------------------------------------------------------------------"
```

```
'
'---------------------------------------------------------Multiple regression estimates
LOCATE 19, 1: PRINT "Mult.regr. All species: "
LOCATE 20, 1: PRINT "          (Artio.rem.):"
LOCATE 19, 33: PRINT "11 L&D-": LOCATE 19, 55: PRINT "   6 L-"
Plength = Meas(1) * Meas(2) * Meas(3) * Meas(4) * Meas(5) * Meas(6)
Pdiameter = Meas(7) * Meas(9) * Meas(10) * Meas(11) * Meas(12)
IF Plength > 0 AND Pdiameter > 0 THEN
  Lhumerl = 1.1263 * (LOG(Meas(1)) / LOG(10))
  Lulnal = -.34705 * (LOG(Meas(2)) / LOG(10))
  Lmetacl = -.42902 * (LOG(Meas(3)) / LOG(10))
  Lfemurl = .14743 * (LOG(Meas(4)) / LOG(10))
  Ltibial = -.51599 * (LOG(Meas(5)) / LOG(10))
  Lmetatl = .41567 * (LOG(Meas(6)) / LOG(10))
  Lhumerd = .67837 * (LOG(Meas(7)) / LOG(10))
  'Lulnad = (LOG(Meas8) / LOG(10))
  Lmetacd = .83146 * (LOG(Meas(9)) / LOG(10))
  Lfemurd = .97864 * (LOG(Meas(10)) / LOG(10))
  Ltibiad = -.27735 * (LOG(Meas(11)) / LOG(10))
  Lmetatd = .056296 * (LOG(Meas(12)) / LOG(10))
  Multloggm = 1.0539 + Lhumerl + Lulnal + Lmetacl + Lfemurl + Ltibial + Lmetatl + _
        Lhumerd + Lmetacd + Lfemurd + Ltibiad + Lmetatd
  Multgm = 10 ^ Multloggm
  LOCATE 19, 42: PRINT USING "##,###,###"; Multgm
END IF
IF Plength > 0 THEN
  Lhumerl = 1.1494 * (LOG(Meas(1)) / LOG(10))
  Lulnal = .54825 * (LOG(Meas(2)) / LOG(10))
  Lmetacl = -.015956 * (LOG(Meas(3)) / LOG(10))
  Lfemurl = 1.6607 * (LOG(Meas(4)) / LOG(10))
  Ltibial = -1.7635 * (LOG(Meas(5)) / LOG(10))
  Lmetatl = .93805 * (LOG(Meas(6)) / LOG(10))
  Mul6loggm = -1.0061 + Lhumerl + Lulnal + Lmetacl + Lfemurl + Ltibial + Lmetatl
  Mul6gm = 10 ^ Mul6loggm
  LOCATE 19, 64: PRINT USING "##,###,###"; Mul6gm
END IF
IF Plength > 0 AND Pdiameter > 0 THEN
  Lhumerl = 1.369 * (LOG(Meas(1)) / LOG(10))
  Lulnal = -.53119 * (LOG(Meas(2)) / LOG(10))
  Lmetacl = -.065223 * (LOG(Meas(3)) / LOG(10))
  Lfemurl = .87466 * (LOG(Meas(4)) / LOG(10))
  Ltibial = -1.0127 * (LOG(Meas(5)) / LOG(10))
  Lmetatl = .13456 * (LOG(Meas(6)) / LOG(10))
  Lhumerd = .6123 * (LOG(Meas(7)) / LOG(10))
  'Lulnad = (LOG(Meas8) / LOG(10))
  Lmetacd = .90372 * (LOG(Meas(9)) / LOG(10))
  Lfemurd = .73021 * (LOG(Meas(10)) / LOG(10))
  Ltibiad = -.46398 * (LOG(Meas(11)) / LOG(10))
  Lmetatd = -.098183 * (LOG(Meas(12)) / LOG(10))
  Multloggmp = .90053 + Lhumerl + Lulnal + Lmetacl + Lfemurl + Ltibial + _
        Lmetatl + Lhumerd + Lmetacd + Lfemurd + Ltibiad + Lmetatd
  Multgmp = 10 ^ Multloggmp
  LOCATE 20, 41: PRINT USING "(##,###,###)"; Multgmp
END IF
IF Plength > 0 THEN
  Lhumerl = 2.0805 * (LOG(Meas(1)) / LOG(10))
  Lulnal = -.82606 * (LOG(Meas(2)) / LOG(10))
  Lmetacl = .16526 * (LOG(Meas(3)) / LOG(10))
  Lfemurl = 1.6647 * (LOG(Meas(4)) / LOG(10))
  Ltibial = -1.1229 * (LOG(Meas(5)) / LOG(10))
  Lmetatl = .3828 * (LOG(Meas(6)) / LOG(10))
  Mul6loggmp = -.81709 + Lhumerl + Lulnal + Lmetacl + Lfemurl + Ltibial + Lmetatl
  Mul6gmp = 10 ^ Mul6loggmp
  LOCATE 20, 63: PRINT USING "(##,###,###)"; Mul6gmp
END IF
LOCATE 21, 1
PRINT "--------------------------------------------------------------------------------"
'
'-----------------------------------------------------------------------Encephalization
LOCATE 23, 60: PRINT "Ctrl-Break to exit"
LOCATE 22, 1: INPUT "Brain mass (g)      ", Brainw
  IF Brainw > 0 THEN
```

```
    Eq = Brainw / (.12 * ((10 ^ (R2loggmtot / R2tot)) ^ .667))
    Eq1 = Brainw / (.12 * (Maxci ^ .667))
    Eq2 = Brainw / (.12 * (Minci ^ .667))
    LOCATE 22, 30: PRINT "Jerison EQ = "
    LOCATE 22, 43: PRINT USING "###.###"; Eq
    LOCATE 22, 58: PRINT USING "###.###"; Eq2
    LOCATE 22, 73: PRINT USING "###.###"; Eq1
  END IF
Altcalc:
  IF Brainw > 0 THEN
    LOCATE 23, 1: INPUT "Alternative body mass (g)"; Altbodwt
    IF Altbodwt > 0 THEN
      Eqa = Brainw / (.12 * ((Altbodwt) ^ .667))
    END IF
    LOCATE 23, 43: PRINT USING "###.###"; Eqa
  END IF
GOTO Altcalc
'------------------------------------------------------------------------------------End
```