

Allometric Scaling in the Dentition of Primates and Prediction of Body Weight From Tooth Size in Fossils

PHILIP D. GINGERICH, B. HOLLY SMITH, AND KAREN ROSENBERG
Museum of Paleontology (P.D.G.) and Department of Anthropology (B.H.S. and K.R.), The University of Michigan, Ann Arbor, Michigan 48109

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ABSTRACT Tooth size varies exponentially with body weight in primates. Logarithmic transformation of tooth crown area and body weight yields a linear model of slope 0.67 as an isometric (geometric) baseline for study of dental allometry. This model is compared with that predicted by metabolic scaling (slope = 0.75). *Tarsius* and other insectivores have larger teeth for their body size than generalized primates do, and they are not included in this analysis. Among generalized primates, tooth size is highly correlated with body size. Correlations of upper and lower cheek teeth with body size range from 0.90–0.97, depending on tooth position. Central cheek teeth (P_4^1 and M_1^1) have allometric coefficients ranging from 0.57–0.65, falling well below geometric scaling. Anterior and posterior cheek teeth scale at or above metabolic scaling. Considered individually or as a group, upper cheek teeth scale allometrically with lower coefficients than corresponding lower cheek teeth; the reverse is true for incisors. The sum of crown areas for all upper cheek teeth scales significantly below geometric scaling, while the sum of crown areas for all lower cheek teeth approximates geometric scaling. Tooth size can be used to predict the body weight of generalized fossil primates. This is illustrated for *Aegyptopithecus* and other Eocene, Oligocene, and Miocene primates. Regressions based on tooth size in generalized primates yield reasonable estimates of body weight, but much remains to be learned about tooth size and body size scaling in more restricted systematic groups and dietary guilds.

Body size is one of the most important parameters for understanding the life history and ecology of primates and other mammals (Western, 1979). Body size influences the relative abundance and systematic diversity of animals in structured faunas (Hutchinson and MacArthur, 1959; McNab, 1971; Van Valen, 1973), body architecture and function (Schmidt-Nielsen, 1975), locomotion and substrate preference (Fleagle and Mittermeier, 1980), sexual dimorphism and social organization (Clutton-Brock and Harvey, 1977; Clutton-Brock et al., 1977), home range size (Milton and May, 1976), neonatal weight (Leutenegger, 1976), and longevity (Sacher, 1959). Insectivorous, frugivorous, and folivorous living primates can be distinguished by the size, shape,

and position of molar cusps and crests, and they also have characteristic body size distributions (Kay, 1975b, 1978; Kay and Hylander, 1978; Fleagle, 1978). Because most fossil primates are represented by dental remains, it is important to understand how tooth size is related to body size in order to reconstruct the life history and ecology of fossil species. In this paper we examine the relationship between tooth size and body size in generalized primates.

Tooth crown area (crown length multiplied by crown width) increases in relation to the square of a linear dimension, whereas body

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weight, being proportional to volume, increases in relation to the cube of a linear dimension, assuming geometric similarity is maintained. Thus one might predict theoretically that tooth area should increase or decrease as the $\frac{2}{3}$ (or 0.67) power of body weight. This is the "geometric scaling" model—the model that describes how area and volume are related if geometric similarity is maintained. Alternatively, one might expect tooth crown area, being directly involved in feeding and hence metabolism, to conform to metabolic scaling, which is proportional to the $\frac{3}{4}$ (or 0.75) power of body weight (Schmidt-Nielsen, 1975; Gould, 1975). This is the "metabolic scaling" model—the model that describes how area and volume are related if area scales in proportion to metabolism. Other alternatives are also possible (e.g., McMahon, 1973; Alexander et al., 1979), but these are the two most widely discussed in the literature on allometric scaling of tooth size.

In an absolute sense, large mammals usually have larger teeth than small mammals, but large mammals may have relatively larger teeth, relatively smaller teeth, or teeth of the same relative size as those of small mammals when differences in body size are taken into account. Both the geometric scaling model and the metabolic scaling model are illustrated in Figure 1, where the region between the two is stippled for clarity. Both models involve exponents less than unity (i.e. they are nonlinear). Thus in testing how well a given set of data points conforms to one or the other model, it is appropriate to fit an exponential equation of the form: $Y = bX^a$, where X is body size, Y is tooth size, b is a constant, and a is the exponent or allometric scaling coefficient (Huxley, 1932; Gould, 1966). Analytically, the easiest way to determine the parameters a and b is to transform both sides of this equation to logarithms: $\log Y = \log b + a \log X$, making it a linear equation of slope a and Y -intercept $\log b$.

A number of authors have investigated the relationship of tooth size to body size in mammals using skull length, femur length, or head-and-body length as a measure of body size (Pilbeam and Gould, 1974; Corruccini and Henderson, 1978; Pirie, 1978; Wood, 1979a, b; Wood and Stack, 1980; Creighton, 1980; see also Smith, 1981). Others have examined this problem by relating a specific measure of tooth size (incisor size, M_2 length and/or width, or post-canine cheek tooth area) to body weight (Pilbeam and Gould, 1974; Gould, 1975; Hylander, 1975; Kay 1975a, b, 1978; Gingerich, 1976,

1977a; Goldstein et al., 1978). In this paper we analyze tooth size at all positions individually to see how tooth size scales in relation to body weight. We also analyze the summed area of the postcanine cheek teeth in relation to body weight for both the upper and lower dentition.

We use body weight (mass) as our measure of body size because, among the measures most commonly used, this quantity facilitates comparison among animals of different head-and-body shape. Other authors have defended cranial length, femur length, or head-and-body length because these can more often be measured directly on the same individual specimens as the teeth under study and because they generally exhibit less intraspecific variation than body weight (Yablokov, 1974). The latter observation is at least partially an artifact of comparison of quantities of different dimensionality (Lande, 1977). Measuring tooth size and body size on the same individuals is essential in studying the *intraspecific* relationship of these quantities, but we are interested here in *interspecific* patterns of scaling across the order Primates. The total range of body sizes involved in this study is so much greater than within-species variability that we feel justified in combining average tooth size measurements for a species with body weights taken from a different source. We emphasize that this study is concerned with interspecific allometric scaling across an order and not intraspecific scaling within individual species.

MATERIALS AND METHODS

The most extensive compilation of information on tooth size in primates is the recent book by Swindler (1976). Swindler lists means and standard deviations of tooth length and width for (in most cases) large samples of both males and females of 56 species of primates. Initially we used all of the species in Swindler's book for which body weights were also available. A preliminary analysis indicated that *Tarsius* and tree shrews do not fall on the same regressions as more typical primates (Fig. 2B). They have relatively larger cheek teeth than would be predicted for generalized primates of their body size. This is probably a consequence of their specialized insectivorous dietary adaptation. Primates used in the analysis presented here include species representing the superfamilies Lemuroidea (3 species), Lorioidea (4 species), Ceboidea (8 species), Cercopithecoidea (21 species), and Hominoidea (7 species). *Tarsius* and tree shrews were not included. Measure-

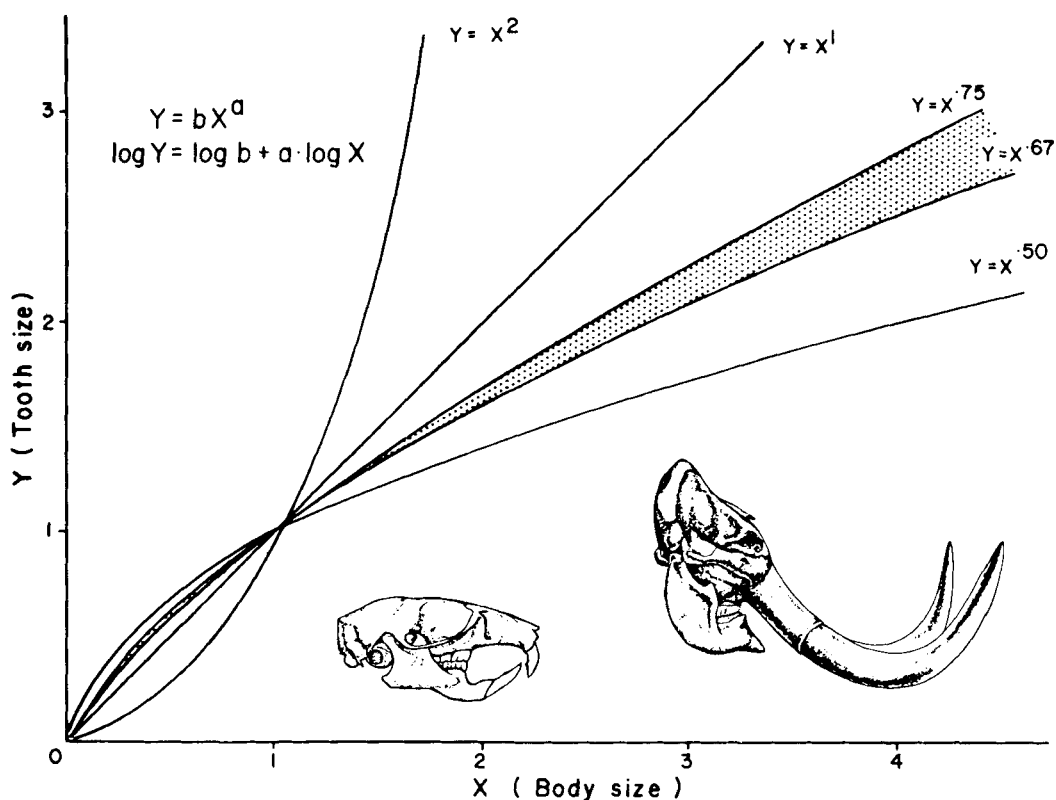


Fig. 1. Exponential models showing allometric change in tooth size (Y) as a function of body size (X), where exponent a is the allometric coefficient and b is a constant. $Y = X^1$ is an isometric baseline for comparison of measures of tooth size and body size where both have the same dimensionality (i.e. both are lengths, both are areas, or both are volumes). $Y = X^{0.7}$ is the isometric baseline for comparison of tooth crown area with body weight or volume (the "geometric model") in this paper. $Y = X^{0.75}$ represents metabolic scaling of tooth crown area and body weight. Logarithmic transformation, or conversion of linear scales shown here to logarithmic scales, makes each curve linear of slope a (1.00, 0.67, or 0.75 in the examples discussed here). Inset figures show that cheek tooth length in an elephant is equal to or less than that in a mouse when both are brought to the same skull length. This implies allometric scaling of tooth size equal to or less than isometric (geometric) scaling.

ments of lower incisors and canines are not included for those species having a specialized anterior tooth comb.

We used tooth crown area (mesial-distal crown length multiplied by buccal-lingual width, or $L \times W$) as our measure of tooth size. This compound measure has several advantages over the use of length or width alone. Crown area is based on two independent (orthogonal) measures of the same tooth, yielding a more accurate measure of tooth size than that given by any single measurement. Differences in crown shape have less influence on crown area than they do on individual length and width measurements. Kay (1975b) stated that frugivorous noncercopithecoid primates

have small teeth for their adult body size. However, analysis of tooth crown area for the same frugivorous and folivorous noncercopithecoid species in our study indicates only a slight tendency in this direction. We attribute Kay's result, in part, to the fact that he used the length of M_2 as a measure of tooth size, whereas we considered both length and width. Frugivorous species have short, broad lower molars and folivorous species have long, narrow lower molars: there is a shape difference but apparently little or no difference in crown area. Cercopithecoid frugivores and folivores cannot be differentiated by either relative tooth length (Kay and Hylander, 1978) or crown area (this study).

TABLE 1. Species included in this study, including sex, sample size for tooth measurements, measurements of upper and lower first molars, and body weights.

Genus and species	Sex	(N)	M ¹		M ₁		Body weight (gm)
			L (mm)	W (mm)	L (mm)	W (mm)	
<i>Lepilemur mustelinus</i>	M	(6)	3.50	3.27	3.50	2.25	610
	F	(11)	3.40	3.46	3.56	2.36	640
<i>Varecia variegata</i>	M	(6)	7.30	7.60	7.80	4.60	3,086
	F	(-)	-	-	-	-	-
<i>Propithecus verreauxi</i>	M	(22)	6.85	6.25	6.68	4.57	3,700
	F	(24)	6.94	6.30	6.65	4.54	3,500
<i>Nycticebus coucang</i>	M	(21)	3.50	4.30	3.40	2.70	1,300
	F	(9)	3.50	4.20	3.40	2.70	1,200
<i>Perodicticus potto</i>	M	(12)	3.50	4.00	3.20	2.70	1,200
	F	(10)	3.40	3.80	3.10	2.50	1,100
<i>Galago crassicaudatus</i>	M	(20)	4.20	5.00	3.90	3.30	1,200
	F	(11)	4.40	4.90	4.00	3.20	1,000
<i>Galago senegalensis</i>	M	(24)	2.50	3.00	2.30	1.90	300
	F	(20)	2.50	3.00	2.20	1.90	300
<i>Saguinus geoffroyi</i>	M	(11)	2.80	3.60	2.80	2.30	500
	F	(15)	2.90	3.90	2.90	2.30	510
<i>Aotus trivirgatus</i>	M	(9)	3.30	4.10	3.30	2.90	920
	F	(15)	3.30	3.90	3.30	2.90	1,000
<i>Ateles geoffroyi</i>	M	(14)	4.90	5.50	5.20	5.00	6,200
	F	(15)	5.30	5.70	5.30	5.10	5,800
<i>Cebus apella</i>	M	(35)	4.69	6.31	5.03	5.09	1,947
	F	(21)	4.56	6.04	4.86	4.80	1,521
<i>Saimiri oerstedii</i>	M	(11)	2.80	3.90	3.00	2.80	904
	F	(6)	2.70	3.70	2.70	2.60	637
<i>Saimiri sciureus</i>	M	(21)	2.80	4.10	2.90	2.80	750
	F	(6)	2.80	4.00	2.90	2.80	580
<i>Alouatta seniculus</i>	M	(20)	7.47	7.99	7.58	5.38	8,100
	F	(20)	7.10	7.30	7.20	5.10	6,400
<i>Alouatta villosa</i>	M	(15)	7.10	8.10	7.10	5.50	7,400
	F	(37)	6.90	7.30	6.80	5.20	5,700
<i>Cercopithecus cephus</i>	M	(9)	5.70	5.30	5.60	4.10	4,100
	F	(12)	5.40	5.10	5.40	3.80	2,900
<i>Cercopithecus nictitans</i>	M	(11)	5.60	5.10	5.70	4.00	6,600
	F	(7)	5.50	5.10	5.50	3.90	4,200
<i>Cercopithecus mona</i>	M	(27)	5.30	5.20	5.30	3.90	4,768
	F	(16)	5.30	5.00	5.20	3.70	3,700
<i>Cercopithecus mitis</i>	M	(31)	6.10	5.50	6.20	4.30	7,400
	F	(21)	5.90	5.40	6.00	4.30	5,300
<i>Cercopithecus neglectus</i>	M	(13)	6.30	5.50	6.30	4.40	7,000
	F	(7)	5.90	5.20	5.90	4.40	4,000
<i>Cercopithecus ascanius</i>	M	(19)	5.09	4.78	5.20	3.79	4,200
	F	(13)	4.91	4.76	5.01	3.62	2,900
<i>Cercopithecus aethiops</i>	M	(29)	5.74	5.59	5.88	4.40	5,000
	F	(20)	5.36	5.23	5.59	4.18	3,750
<i>Cercocebus albigena</i>	M	(31)	7.00	6.73	6.88	5.57	9,000
	F	(29)	6.56	6.22	6.49	5.18	6,400
<i>Cercocebus torquatus</i>	M	(14)	7.50	7.80	7.30	6.10	8,000
	F	(10)	7.20	7.60	7.30	6.00	5,500
<i>Cercocebus galeritus</i>	M	(10)	7.30	8.10	7.40	6.40	10,200
	F	(10)	7.10	7.40	7.00	5.90	5,500
<i>Macaca nemestrina</i>	M	(19)	7.40	7.20	7.50	5.80	10,400
	F	(11)	7.10	7.10	7.30	5.60	7,800
<i>Macaca mulatta</i>	M	(103)	7.20	7.00	7.20	5.60	8,200
	F	(87)	7.10	6.80	7.00	5.50	7,500
<i>Macaca fascicularis</i>	M	(66)	6.50	6.40	6.50	5.10	5,900
	F	(56)	6.30	6.20	6.40	5.10	4,100
<i>Macaca speciosa</i>	M	(7)	8.40	8.50	8.40	6.30	10,473
	F	(-)	-	-	-	-	-

(Table 1 continued on next page)

TABLE 1. Species included in this study, including sex, sample size for tooth measurements, measurements of upper and lower first molars, and body weights (continued)

Genus and species	Sex	(N)	M ₁		M ₂		Body weight (gm)
			L (mm)	W (mm)	L (mm)	W (mm)	
<i>Cynopithecus niger</i>	M	(10)	7.10	6.50	7.10	5.20	10,400
	F	(7)	6.40	6.00	6.60	4.90	6,600
<i>Theropithecus gelada</i>	M	(37)	-	9.30	-	7.50	20,500
	F	(24)	10.70	8.70	-	7.20	13,600
<i>Colobus polykomos</i>	M	(49)	7.00	6.50	7.20	5.50	10,400
	F	(31)	6.80	6.20	7.00	5.20	8,400
<i>Colobus badius</i>	M	(26)	7.00	6.00	7.20	5.00	10,500
	F	(27)	6.90	6.00	7.10	5.00	5,800
<i>Nasalis larvatus</i>	M	(21)	7.00	6.30	7.30	5.30	17,700
	F	(14)	6.80	6.00	6.90	5.00	10,000
<i>Presbytis aygula</i>	M	(20)	5.30	5.60	5.50	4.50	6,300
	F	(26)	5.30	5.30	5.40	4.30	6,200
<i>Presbytis cristatus</i>	M	(22)	5.95	5.88	6.12	4.74	8,600
	F	(33)	5.79	5.84	5.98	4.71	8,100
<i>Hylobates klossii</i>	M	(5)	5.50	5.90	6.00	4.70	5,900
	F	(4)	5.20	5.70	5.80	4.60	5,700
<i>Hylobates agilis</i>	M	(8)	5.70	6.00	6.00	4.90	6,000
	F	(9)	5.60	6.00	6.00	4.90	5,700
<i>Hylobates moloch</i>	M	(5)	5.90	6.50	6.40	5.20	6,000
	F	(5)	5.70	6.30	6.20	4.90	5,700
<i>Hylobates lar</i>	M	(5)	5.40	5.50	5.60	4.40	4,785
	F	(-)	-	-	-	-	-
<i>Pongo pygmaeus</i>	M	(8)	12.80	13.80	13.40	11.90	69,000
	F	(10)	11.90	12.20	11.40	11.10	37,000
<i>Pan troglodytes</i>	M	(19)	10.30	11.70	11.00	10.00	43,900
	F	(51)	10.10	10.90	10.80	9.40	31,500
<i>Gorilla gorilla</i>	M	(6)	15.70	15.40	16.20	13.70	160,000
	F	(11)	14.80	15.00	15.40	13.20	93,000

Tooth measurements used in this study are taken from Swindler (1976) or Gingerich and Ryan (1979). Body weights are from Harvey et al. (1978) or Bauchot and Stephan (1966, 1969).

Body weights were taken from Harvey et al. (1978) or Bauchot and Stephan (1966, 1969), compiled from various original sources. Body weights and other information used in our analyses are listed in Table 1, which includes length and width measurements of upper and lower first molars (M_i) as examples. The remaining tooth measurements used in our analyses can be found in Swindler (1976) or Gingerich and Ryan (1979).

There are several methods of fitting a linear equation to a given logarithmically transformed scatter of points. We have used a principal or major axis fit (Sokal and Rohlf, 1969; Jolicoeur, 1973) to estimate the structural relationship between tooth size and body size. This is the basis for the allometric coefficients or slopes discussed in the first part of the paper. Confidence intervals for allo-

metric coefficients, ranging from k_1 to k_2 , were calculated following Jolicoeur (1973), where:

$$k_1 = \frac{(S_{22} - S_{11}) + \sqrt{(S_{22} - S_{11})^2 + 4S_{12}^2 - 4Q}}{2S_{12} + 2\sqrt{Q}}$$

$$k_2 = \frac{(S_{22} - S_{11}) - \sqrt{(S_{22} - S_{11})^2 + 4S_{12}^2 - 4Q}}{2S_{12} + 2\sqrt{Q}}$$

and

$$Q = \frac{F_{(1-\alpha; 1, N-2)}(S_{11}S_{22} - S_{12}^2)}{N-2}$$

S_{11} , S_{22} , and S_{12} are elements of the sample covariance matrix,

$$\begin{aligned} S_{11} &= V(Y) & [Y &= \ln \text{tooth area}] \\ S_{22} &= V(X) & [X &= \ln \text{body weight}] \\ S_{12} &= \text{correlation}(Y, X) (\sqrt{S_{11}S_{22}}) \end{aligned}$$

and N is the sample size.

This method provides an actual confidence level of $(1 - \alpha)$ if the sample size is not small ($N > 10, 20$) and correlation of the two variates X and Y is at least moderate ($\rho > 0.6$). Both of these minimal conditions are met or exceeded in this study. We used a linear regression of body size on tooth size to derive equations estimating an unknown body size when tooth size is known. This has application in estimating body size in extinct primates and is discussed in the second part of the paper. In both cases, the correlation coefficient r is a measure of how well the scatter of logarithmically transformed points approximates a straight line. Natural logarithms to base e have been used throughout this paper.

STRUCTURAL RELATIONSHIP OF TOOTH SIZE AND BODY SIZE IN PRIMATES

R.J. Smith (1980) has questioned the appropriateness of fractional polynomial models (power functions) for studying the structural size relationship of various parts of organisms, but we feel that this can be justified (at least in the present study) on both theoretical and empirical grounds. In the introduction we showed how, theoretically, one might expect tooth crown area to increase as the square of a linear dimension while body weight increases in proportion to the cube of this linear dimension. Given geometric similarity, if tooth size Y is proportional to l^2 , and body size X is proportional to l^3 , then Y is proportional to X raised to the $2/3$ power. In other words, this "null hypothesis" of geometric similarity of tooth area and body weight is inherently a fractional polynomial (technically a monomial). McMahon (1973) gives a similar theoretical justification for the use of power functions in studying metabolic scaling.

Figure 2A illustrates graphically that a power function fits the scatter of untransformed body weights and tooth measurements in primates better than a straight line does. We can compare the goodness of fit of the linear and power function models by comparing the correlation coefficient of untransformed data (linear model, Fig. 2A) with that for logarithmically transformed measurements (Fig. 2B). The untransformed correlation coefficient is 0.937, while that for transformed measurements is 0.967. The latter is significantly greater than the former ($p < .02$), which further justifies using both logarithmically transformed data and power

functions in analyzing the relationship of tooth size to body size in primates.

SCALING OF TOOTH SIZE AND BODY SIZE

The distribution of points in Figure 2B shows graphically how lower first molar size ($L \times W$ of M_1) and body weight are correlated ($r = 0.967$) in generalized primates. The slope of the principal axis of this distribution is 0.638 (or 0.64), which is less than geometric scaling (0.67) but the difference between the two is not statistically significant. The difference between 0.64 and 0.75 is statistically significant ($p < .05$). Taken together, these results indicate that the first lower molar in primates conforms to the geometric model of allometric scaling outlined above, and not to the metabolic model.

We have calculated the correlation (r) and scaling coefficient (slope a) of tooth area and body weight at each tooth position in generalized primates. In addition, we have calculated the correlation and scaling of the sum of all upper and lower postcanine tooth areas with body weight. The results are listed in Table 2 along with the 95% confidence interval for each scaling coefficient. It should be noted that upper canines, upper molars, and lower cheek teeth (except P_3) all have correlation coefficients of about 0.95 or greater. Lower central cheek teeth (P_3 - M_2) are more highly correlated with body size than are upper cheek teeth. As a result, these teeth are probably the best teeth to use to predict the body weight of a primate from its tooth size (see below). Many of the species used in this analysis are sexually dimorphic and upper canine size is usually proportional to the degree of dimorphism, which probably accounts for the high correlation of canine size with body size in this analysis.

Figure 3 shows the pattern of change in allometric scaling coefficients (slopes) along the tooth row in both the upper and lower dentition. In the upper dentition there is a smooth decline in scaling coefficients from I^1 to M^1 , and then a steep increase from M^1 to M^3 . The general pattern of scaling in the lower dentition is more complicated. Lower incisors have lower slopes than the lower canine and anterior premolars, then there is a decrease from P_3 to M_1 and, again, a steep increase from M_1 to M_3 . The vertical bars associated with each point are the 95% confidence interval for the scaling coefficient at each tooth position. These show

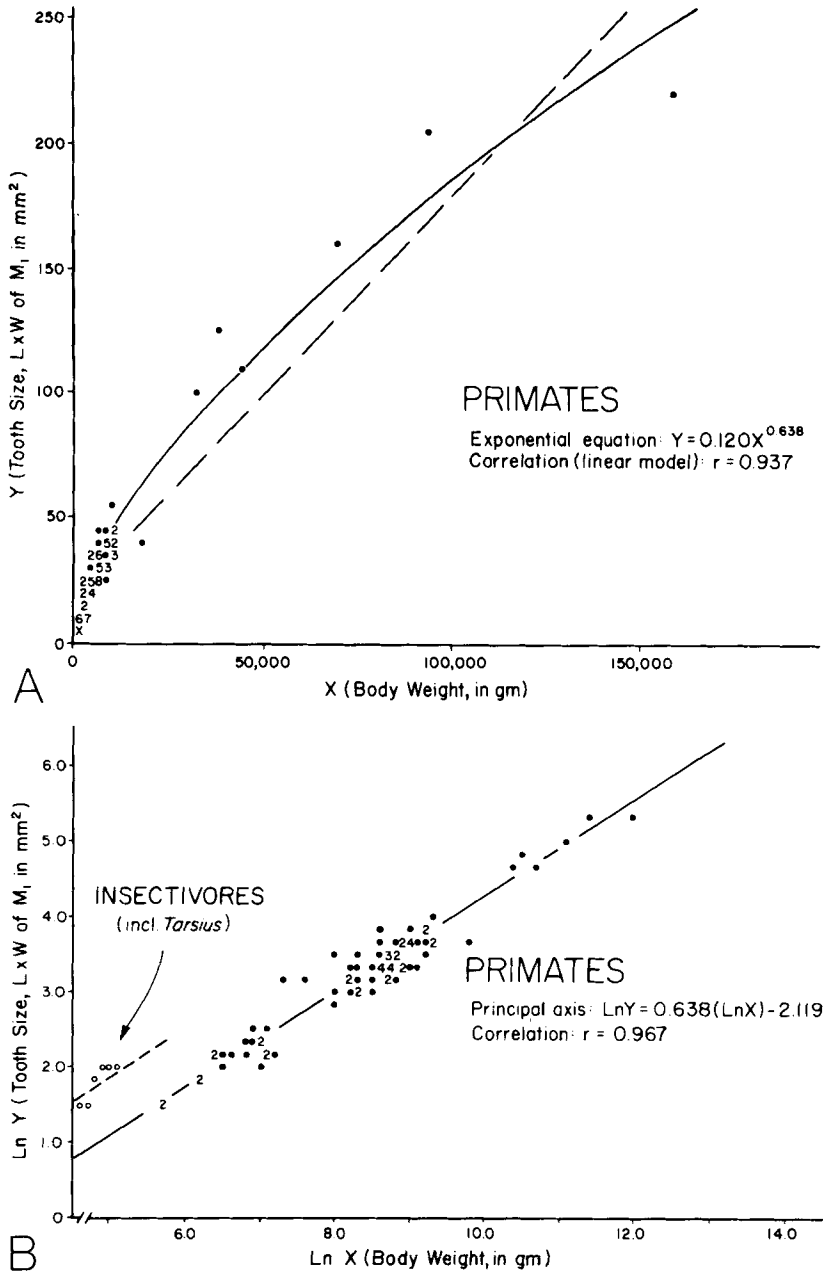


Fig. 2. Allometric scaling of tooth size and body size in primates. (A) Scatter plot of crown area of M_1 against body weight, showing both linear (dashed line) and exponential curves fit to the data (curves are principal axes of untransformed and log transformed data, respectively). (B) Scatter plot of natural logarithm of crown area of M_1 against natural logarithm of body weight, showing that tooth size in tree shrews and *Tarsius* (open circles) scales differently than that in generalized primates (solid circles). Note that the correlation of \ln tooth size with \ln body weight ($r = 0.967$) is significantly greater than the correlation of tooth size and body weight ($r = 0.937$) in generalized primates ($p < .02$). An exponent of 0.638 indicates tooth size/body weight allometry below geometric scaling (which would be 0.667). Each point represents an average for males or females of 43 species of generalized primates. Small numerals represent multiple points. Raw data and literature sources are listed in Table 1.

TABLE 2. Correlation and allometric scaling of tooth crown area and body weight in primates

Tooth Position	Correlation (r)	Slope (a)	95% Confidence interval of slope	N	s_{11}	s_{22}
UPPER DENTITION						
I ¹	0.835	0.79	0.68-0.93	73	0.82	1.20
I ²	0.858	0.75	0.65-0.86	73	0.73	1.20
C ¹	0.947	0.72	0.67-0.78	82	0.82	1.52
P ²	0.902	0.70	0.57-0.84	27	0.51	0.99
P ³	0.943	0.65	0.60-0.70	83	0.66	1.50
P ⁴	0.934	0.59	0.54-0.64	83	0.55	1.50
M ¹	0.946	0.57	0.53-0.61	82	0.51	1.49
M ²	0.945	0.68	0.63-0.73	83	0.71	1.50
M ³	0.947	0.78	0.72-0.84	81	0.87	1.41
Σ Cheek Teeth	0.949	0.62	0.57-0.67	78	0.58	1.44
LOWER DENTITION						
I ₁	0.854	0.72	0.62-0.83	70	0.68	1.18
I ₂	0.921	0.65	0.58-0.72	70	0.53	1.18
C ₁	0.882	0.79	0.69-0.89	75	0.83	1.27
P ₂	0.913	0.76	0.63-0.91	27	0.59	0.99
P ₃	0.954	0.78	0.72-0.83	83	0.92	1.50
P ₄	0.955	0.65	0.61-0.70	83	0.66	1.50
M ₁	0.967	0.64	0.60-0.68	83	0.63	1.50
M ₂	0.968	0.73	0.69-0.77	83	0.81	1.50
M ₃	0.947	0.80	0.74-0.86	81	0.92	1.41
Σ Cheek Teeth	0.964	0.69	0.65-0.73	77	0.70	1.44

Scaling coefficient (a) calculated as principal axis; confidence interval calculation including N , s_{11} , and s_{22} from Jolicoeur (1973).

clearly that the differences between, for example, allometric scaling in the central and peripheral cheek teeth are both real and significant.

The sums of upper and lower cheek teeth have scaling coefficients of 0.62 and 0.69, respectively, indicating that lower cheek teeth as a group scale significantly higher than upper cheek teeth do. Furthermore, lower cheek teeth as a group scale significantly higher than upper cheek teeth at some individual positions, and upper cheek teeth as a group scale significantly lower than lower cheek teeth at some individual positions. In other words, no single tooth or even group of contiguous cheek teeth is adequate to characterize allometric scaling in the primate dentition.

These results are interesting with respect to the question of whether primate teeth scale geometrically or metabolically. Both of these models, geometric and metabolic, are plotted as a horizontal line at the appropriate level (0.67 and 0.75, respectively) in Figure 3. Upper incisors and the upper canine clearly approximate metabolic scaling more closely than they do geometric scaling. P² has such a broad confidence interval that it does not really fit one model better than the other. P³ and M² both approximate geometric scaling and both

are significantly below metabolic scaling. P⁴ and M¹ scale significantly below even the geometric model, whereas scaling in M³ conforms closely to that predicted by the metabolic model. Scaling in M³ is significantly greater than that predicted by the geometric model.

In the lower dentition, scaling of I₁ is ambiguous, since the 95% confidence interval includes both the geometric and metabolic models. I₂ appears to scale approximately geometrically. The lower canine appears to scale metabolically. P₂ approximates metabolic scaling as well but, like P², it has such a broad confidence interval that neither model can be ruled out. P₃, M₂, and M₃ conform to the metabolic model, with scaling coefficients significantly higher than predicted by the geometric model, but P₄ and M₁ conform to the geometric rather than metabolic scaling model.

Upper cheek teeth as a group have an allometric coefficient much smaller than that predicted by the geometric scaling model. The upper limit of the 95% confidence interval for this coefficient is 0.67, which is the expected value given geometric scaling, indicating that the difference is statistically significant. Lower cheek teeth as a group approximate geometric scaling. Both summed upper and summed

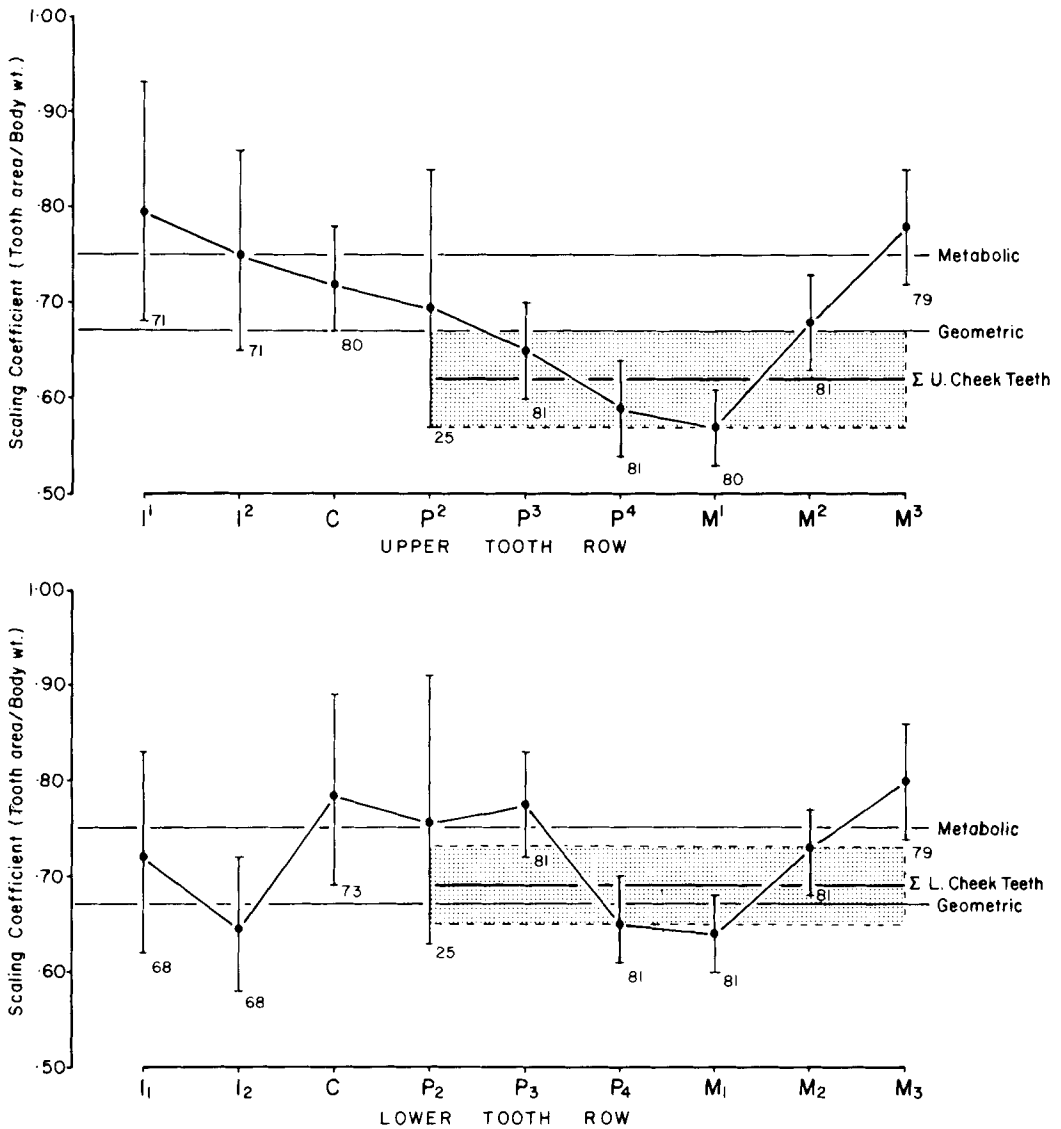


Fig. 3. Summary diagrams showing patterns of allometric scaling of tooth crown area and body weight in generalized primates. Upper and lower diagrams show scaling coefficients (solid circles) at each tooth position in the upper and lower dentition, respectively, with associated 95% confidence intervals (vertical bars). Heavy horizontal lines show scaling coefficients of summed crown areas of upper and lower cheek teeth, respectively, with stippled horizontal bars enclosing 95% confidence intervals of scaling coefficients of summed tooth areas. Note that in the upper dentition allometric scaling of anterior and posterior teeth exceeds metabolic scaling (0.75), while central cheek teeth (P^2 - M^2) are at or below geometric scaling. In the lower dentition incisors approximate geometric scaling while anterior and posterior cheek teeth exceed metabolic scaling and central cheek teeth (P_4 - M_1) are at or below geometric scaling. Note also that lower cheek teeth scale consistently higher than upper cheek teeth.

lower cheek teeth scale significantly below metabolic scaling in generalized primates.

The overall effect of the observed patterns of allometric scaling of tooth area and body

weight can be visualized by comparing the dentitions of small, medium, and large primates shown in Figure 4, which are drawn to approximately the same palatal length. Here

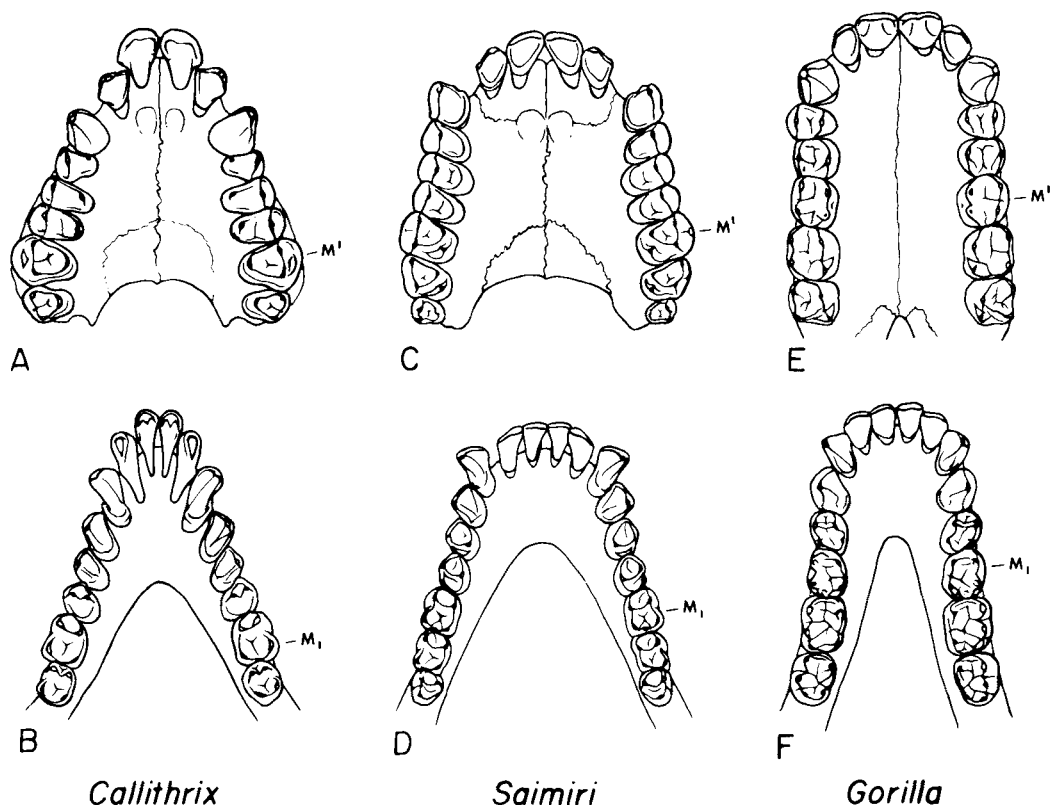


Fig. 4. Comparison of upper and lower dentitions of small (*Callithrix*, A and B), medium (*Saimiri*, C and D), and large (*Gorilla*, E and F) primates, all drawn at approximately the same palatal length to illustrate in a very general way how the dentition changes with changing body size. Note progressively more squared palatal shape in the sequence from *Callithrix* to *Gorilla*, corresponding to strong positive allometry of upper incisor size. Note small M_2 and absence of M_3 in *Callithrix*, small size of these teeth in *Saimiri*, and relative enlargement of these teeth in *Gorilla*, corresponding to strong positive allometry of posterior cheek teeth. In addition, note discrepancy in size of upper and lower cheek teeth in *Callithrix* and *Saimiri* compared with the more nearly equal size of these teeth in *Gorilla*, corresponding to the more positive allometry of lower cheek teeth compared with upper cheek teeth.

upper and lower dentitions of *Callithrix* (350–400 gm), *Saimiri* (600–700 gm), and *Gorilla* (100–150 kg) are compared to illustrate general trends of allometric change in incisors and cheek teeth.

The observation that teeth in three out of four incisor positions scale in excess of geometric scaling means that larger primates should have relatively larger incisors than smaller primates, and vice versa. Small primates like *Callithrix* tend to have V-shaped maxillary and mandibular tooth rows, whereas larger primates like *Gorilla* have a rectangular dental arcade with more nearly parallel tooth rows. If upper incisors scale at a higher rate than lower incisors, then larger primates should have a

disproportionately broader upper incisor row compared to the lower incisor row. In addition, as Hylander (1975) has shown, diet has an important influence on relative incisor size that is independent of body size differences.

The pattern of high allometric coefficients at the front and back of the cheek tooth row, grading into lower coefficients in the center of the cheek tooth row, indicates that larger primates have disproportionately larger premolars and last molars compared to the size of their central cheek teeth. Additional cheek tooth area in larger primates is added at the ends of the cheek tooth row. For example, *Gorilla* tends to have large second and third molars and, conversely, *Callithrix* has reduced second

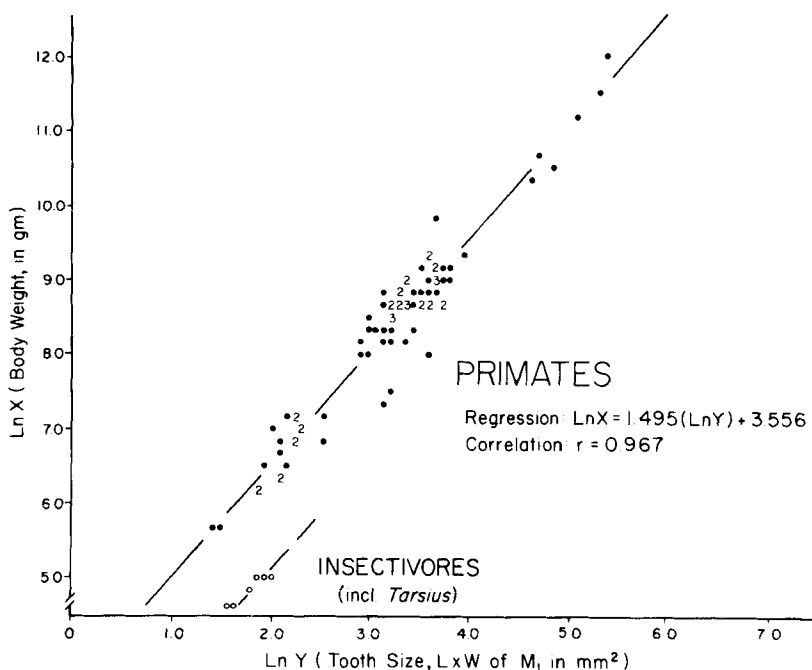


Fig. 5. Regression of ln body weight on ln crown area of M_1 in generalized primates. This regression can be used to estimate body weights of fossil primates known only from dental remains (Tables 3-5). Note that tree shrews and *Tarsius*, like other insectivores, have smaller body weights for their tooth size than generalized primates do, indicating that this regression will not predict body weights of specialized insectivorous primates with acceptable accuracy.

molars and no third molars. Tooth size reduction takes place at the ends of the cheek tooth series when primates become smaller.

Small primates tend to have narrower lower cheek teeth than upper cheek teeth, and the fact that lower cheek teeth scale at a higher rate than upper cheek teeth means that lower and upper premolars and molars should become more isometric with increasing body size; i.e., the differences in size between upper and lower cheek teeth should be diminished at larger body sizes. This trend is nicely illustrated by comparing the relative size of upper and lower molars in *Callithrix* or *Saimiri* with those in *Gorilla* (Fig. 4).

PREDICTING BODY SIZE FROM TOOTH SIZE IN GENERALIZED FOSSIL PRIMATES

The same measurements used to study allometric scaling of tooth size and body size in generalized primates can be used to construct a series of equations for predicting body weight from tooth size. The problem here is

slightly different than that discussed in the previous section. Instead of looking at the structural relationship of two variables, in this section we shall attempt to use one variable (tooth size) to predict the other (body weight). Whereas the principal axis (or major axis) is the best representation of the covariation of two variables, a linear regression of body size on tooth size is most appropriate for the prediction problem (Fig. 5).

Results of the regression of body weight on tooth size at each tooth position in the dentition of generalized primates are summarized in Table 3. Given the crown area (Y) of any tooth in the dentition, it is possible to substitute this value into Equation 1 of Table 3 and then solve for body weight (X) using values of a and $\ln b$ for the appropriate tooth.¹ The 95% confidence

¹Note that in our least squares regression equations the independent variable (tooth area) is termed Y and the dependent variable (body weight) is termed X . We have not followed standard practice in this instance in order to maintain consistency with the previous discussion of dental allometry.

TABLE 3. Equations and critical values for predicting body weight from tooth size in generalized primates.

Tooth Position	Correlation (r)	Slope (a)	Intercept (Ln b)	C ₁	C ₂	C ₃
UPPER DENTITION						
I ¹	0.835	1.01	5.42	0.00506	3.1402	0.00625
I ²	0.858	1.10	5.64	0.00440	2.6815	0.00611
C ¹	0.947	1.29	4.08	0.00193	3.3692	0.00239
P ²	0.902	1.25	4.38	0.00712	2.2620	0.01439
P ³	0.943	1.42	4.18	0.00203	3.0002	0.00309
P ⁴	0.934	1.53	3.64	0.00232	3.1163	0.00422
M ¹	0.946	1.62	2.72	0.00191	3.5074	0.00381
M ²	0.945	1.37	3.49	0.00194	3.6026	0.00275
M ³	0.947	1.20	4.40	0.00182	3.3944	0.00211
Σ cheek teeth	0.949	1.50	0.94	0.00184	5.0172	0.00322
LOWER DENTITION						
I ₁	0.854	1.13	5.60	0.00464	2.6981	0.00696
I ₂	0.921	1.38	4.86	0.00261	2.7464	0.00500
C ₁	0.882	1.09	5.07	0.00382	3.2353	0.00465
P ₂	0.913	1.18	4.49	0.00635	2.3081	0.01109
P ₃	0.954	1.21	4.65	0.00164	3.1154	0.00180
P ₄	0.955	1.44	4.20	0.00159	2.9375	0.00244
M ₁	0.967	1.49	3.55	0.00119	3.2151	0.00192
M ₂	0.968	1.31	3.92	0.00113	3.4244	0.00141
M ₃	0.947	1.17	4.43	0.00182	3.4601	0.00200
Σ cheek teeth	0.964	1.38	1.67	0.00135	4.9105	0.00195

X = body weight (gm); Y = tooth crown area (length × width, in mm); a = exponent, or slope of ln transformed data; b = constant, or X-intercept of ln transformed data; C₁, C₂, and C₃ are critical values for calculating the 95% confidence interval of ln transformed data (Draper and Smith, 1966).

Note: Slopes and intercepts are provided for computation of a predicted ln mean body weight (ln X) from a particular ln tooth crown area (ln Y) using Equation 1. Confidence limits are obtained by substituting both ln X and ln Y in Equation 2 with appropriate values for C₁, C₂, and C₃, where C₁ = mean square error [MSE]/N, C₂ = Y, and C₃ = MSE/Σ (Y_i - Y)². The value 1.96 (Z_{0.975}), taken from a normal table, is used throughout rather than t (0.975, N-2) because N is large in each case.

interval for this estimated body weight can be determined by substituting appropriate values of C₁, C₂, and C₃ into Equation 2 of Table 3.

The areas of M₁ and M₂ are most highly correlated with body size, and measurements of these teeth are consequently the best to use in predicting body weight from tooth size. It should be emphasized that the resulting predicted body weight, even if based on a single specimen, is a predicted average weight for the species represented. Obviously, the larger the number of teeth measured at a given position, the better the final prediction of body weight for the species under study. However, the low correlation of tooth size and body size within species (e.g., Garn and Lewis, 1958) precludes using tooth size to estimate and compare body weights of individuals in the same population or species. Measurement of as many different dental, cranial, and postcranial dimensions of a skeleton as available will contribute to the

accuracy of the final prediction, but for many fossil primates cranial and postcranial elements are unknown and any estimate of body size necessarily requires a prediction based on tooth size. Furthermore, the marginal contribution of each additional measurement in altering the final prediction diminishes rapidly after two or three variates are considered.

As an example, we have predicted the body weight of the Oligocene anthropoid *Aegyptopithecus zeuxis* based on the size of its teeth (Table 4). This particular example is useful because Gingerich (1977a) and Kay and Simons (1980) attempted to estimate the body weight of *Aegyptopithecus* previously, based on tooth size, cranial size, and the size of postcranial elements, furnishing some basis for comparison with our results. Depending on the measurements used and the procedure employed, lower cheek teeth yield estimates of

TABLE 4. Comparison of six methods of estimating the body weight of *Aegyptopithecus zeuxis*

- (1) *Body weight estimated from the size of M_1 in the holotype only.*
 M_1 measures 6.0 mm in length and 5.3 mm in width: $L \times W$ of $M_1 = 31.8$ and $\ln Y = 3.46$.
 Body weight $X = 6,030$ gm (95% confidence interval = 5,615 to 6,475 gm).
- (2) *Body weight estimated successively and cumulatively from the size of M_1 , M_2 , and P_4 in the holotype.*
 M_1 yields a body weight estimate of 6,030 gm (see above).
 M_2 measures 6.4 mm in length and 6.4 mm in width: $L \times W$ of $M_2 = 41.0$
 and $\ln Y = 3.71$.
 Body weight $X = 6,525$ gm (95% confidence interval = 6,085 to 6,995 gm).
 Average of estimates based on M_1 and $M_2 = 6,280$ gm.
 P_4 measures 4.9 mm in length and 4.1 mm in width: $L \times W$ of $P_4 = 20.1$ and $\ln Y = 3.00$.
 Body weight $X = 5,015$ gm (95% confidence interval = 4,635 to 5,425 gm).
 Average of estimates based on P_4 , M_1 , and $M_2 = 5,855$ gm.
- (3) *Body weight estimated from the means of length and width measurements of seven specimens preserving M_1 from Quarry I (Kay et al., 1981).*
 Average sample M_1 length is 5.86 mm and average M_1 width is 5.43 mm: average $L \times W$ of $M_1 = 31.8$ and $\ln Y = 3.46$.
 Body weight $X = 6,035$ gm (95% confidence interval = 5,620 to 6,480 gm).
- (4) *Body weight estimated from the means of length and width measurements of 3 specimens preserving M^1 from Quarry I (Kay et al., 1981).*
 Average sample M^1 length is 5.80 mm and average M^1 width is 7.30 mm:
 Average $L \times W$ of $M^1 = 42.3$ and $\ln Y = 3.74$.
 Body weight $X = 6,495$ gm (95% confidence interval = 5,935 to 7,110 gm).
 Average of weights based on M^1 and M_1 from Quarry I = 6,265 gm.
- (5) *Body weight estimated from ulna approximately the size of that of *Alouatta* or *Presbytis cristatus* (Fleagle et al., 1975).*
 The average body weight of *Alouatta* sp. and *Presbytis cristatus* ranges from about 6,350 to 8,350 gm (see Table 1).
- (6) *Body weights estimated from cranial dimensions of one known skull.*
 Regressions of cranial dimensions in 16 Old and New World monkey species give body weight estimates in *Aegyptopithecus* ranging from 2,560 gm to 10,040 gm. The average for all 7 dimensions used is 5,280 gm (Kay and Simons, 1980).

Methods 1-4 make use of Equations 1 and 2 in Table 3. Methods 5 and 6, based on postcranial and cranial dimensions, are included for comparison.

6,030 gm, 5,855 gm, or 6,035 gm for the average body weight of *Aegyptopithecus zeuxis*. Upper first molars yield an estimate of 6,495 gm as the average body weight of *Aegyptopithecus*. For comparison, the estimate from the size of one known ulna is about 7,350 gm, and the estimate based on cranial dimensions of the one known skull is 5,280 gm (Table 4). The estimates of body size in *Aegyptopithecus* based on tooth size are well within the range of estimates derived from the size of known cranial and postcranial elements, indicating that the estimates based on tooth size are reasonable.

For reference purposes we estimated the body weights of a number of representative species of generalized fossil primates based on their tooth size. These are listed in Table 5. Plesiadapiform primates are not included because of their unusually specialized dentitions. Tarsiiform Omomyidae are not included because they appear, like *Tarsius*, to have larger cheek teeth for their body weight than generalized primates (Fig. 5; see also

Gingerich, 1981). Fifteen species of lemuriform Adapidae are included in Table 5, and these range in size from an estimated body weight of about 110 gm in *Anchomomys gaillardi* to as much as 10,730 gm in *Adapis magnus*. It should be noted that upper molars (M^1) consistently give higher body weight estimates than lower molars (M_1) when both are preserved in the same species sample. In *Adapis* and *Sivaladapis* this discrepancy is as much as 50-60%. Both genera are of large body size, with broad upper molars and narrow lower molars, suggesting that perhaps tooth size in large Eocene folivorous primates did not scale exactly as it does in extant species (see discussion below).

South American Oligocene and Miocene Ceboidea and African Oligocene Parapithecidae and Miocene Cercopithecidae are presently known only from very small samples. This makes estimation of their body weights difficult since, in most cases, estimates based on upper teeth cannot be compared with those derived from lower teeth.

TABLE 5. Estimated body weights of some representative species of Eocene, Oligocene, and Miocene fossil primates, based on the regression coefficients given in Table 3. Tooth size in $\ln(\text{length} \times \text{width})$ for M^1 or M_1 , with sample size n , as indicated. Original measurements in mm.

Genus and species	Age	Locality (reference)	Tooth size $\ln(\text{length} \times \text{width})$	Estimated weight (gm)	95% Confidence interval
North American Adapidae					
<i>Cantius ralstoni</i>	Early Eocene	SC-4, Clarks Fork Basin, Wyoming (Gingerich and Simons, 1977)	$M^1 = 2.94$ ($n = 4$) $M_1 = 2.44$ ($n = 16$)	1,775 1,320	1,590-1,985 1,200-1,455
<i>Cantius abditus</i>	Early Eocene	YM-45, Bighorn Basin, Wyoming (Gingerich and Simons, 1977)	$M^1 = -$ $M_1 = 3.01$ ($n = 13$)	- 3,090	- 2,875-3,310
<i>Smilodectes gracilis</i>	Middle Eocene	Grizzly Buttes, Bridger Basin, Wyoming (Gingerich 1979)	$M^1 = -$ $M_1 = 2.74$ ($n = 5$)	- 2,065	- 1,905-2,235
<i>Notharctus tenebrosus</i>	Middle Eocene	Blacks Fork, Bridger Basin Wyoming (Gingerich, 1979)	$M^1 = -$ $M_1 = 3.10$ ($n = 20$)	- 3,530	- 3,295-3,780
<i>Notharctus robustior</i>	Middle Eocene	Henrys Fork, Bridger Basin Wyoming (Gingerich, 1979)	$M^1 = -$ $M_1 = 3.58$ ($n = 26$)	- 7,215	- 6,695-7,775
<i>Mahgarita stevensi</i>	Late Eocene	Typee Canyon, Brewster Co., Texas (Wilson and Szalay, 1976)	$M^1 = 2.79$ ($n = 1$) $M_1 = 2.25$ ($n = 1$)	1,395 995	1,230-1,575 890-1,110
European Adapidae					
<i>Cantius eppsi</i>	Early Eocene	Abbey Wood (Kent), England (Gingerich, unpublished)	$M^1 = 2.75$ ($n = 1$) $M_1 = 2.30$ ($n = 2$)	1,305 1,070	1,150-1,480 965-1,190
<i>Periconodon huerzeleri</i>	Middle Eocene	Buchsweller (Bas-Rhin), France (Gingerich, unpubl.)	$M^1 = 2.26$ ($n = 1$) $M_1 = 1.85$ ($n = 4$)	590 550	495-705 475-630
<i>Protoadapis klatti</i>	Middle Eocene	Geiseltal, East Germany (Gingerich, unpublished)	$M^1 = 2.95$ ($n = 2$) $M_1 = 2.57$ ($n = 3$)	1,805 1,600	1,620-2,015 1,465-1,750
<i>Anchomomys gaillardii</i>	Late Eocene	Lissieu (Rhône), France (Gingerich, unpublished)	$M^1 = 1.38$ ($n = 1$) $M_1 = 0.77$ ($n = 2$)	140 110	105-190 85-140
<i>Adapis sudrei</i>	Late Eocene	Robiac (Gard), France (Gingerich, 1977b)	$M^1 = 3.20$ ($n = 5$) $M_1 = 2.62$ ($n = 12$)	2,710 1,725	2,465-2,975 1,585-1,880
<i>Adapis magnus</i>	Late Eocene	Euzet (Gard), France (Gingerich, 1977c)	$M^1 = 4.05$ ($n = 7$) $M_1 = 3.51$ ($n = 23$)	10,730 6,500	9,630-11,955 6,050-6,990
African Adapidae					
<i>Oligopithecus savagei</i>	Oligocene	Quarry E (Fayum), Egypt (Gingerich, unpublished)	$M^1 = -$ $M_1 = 2.50$ ($n = 1$)	- 1,455	- 1,325-1,590
Asian Adapidae					
<i>Sivaladapis nagrii</i>	Late Miocene	Haritalyangar, India (Gingerich and Sahni, unpublished)	$M^1 = 3.76$ ($n = 3$) $M_1 = 3.25$ ($n = 5$)	6,710 4,415	6,125-7,350 4,125-4,725
<i>Indraloris lulli</i>	Late Miocene	Haritalyangar, India (Gingerich and Sahni, unpublished)	$M^1 = -$ $M_1 = 3.19$ ($n = 1$)	- 4,035	- 3,770-4,320
South American Ceboidea					
<i>Branisella boliviana</i>	Early Oligocene	Salla, Bolivia (Hoffstetter, 1969)	$M^1 = 2.67$ ($n = 1$) $M_1 = -$	1,150 -	1,005-1,310 -
<i>Homunculus patagonicus</i>	Early Miocene	Rio Gallegos, Argentina (Hershkovitz, 1970)	$M^1 = -$ $M_1 = 2.89$ ($n = 1$)	- 2,580	- 2,395-2,780
<i>Neosaimiri fieldsi</i>	Middle Miocene	La Venta (Huila), Colombia (Stirton, 1951)	$M^1 = -$ $M_1 = 2.13$ ($n = 1$)	- 830	- 740-935

(Table continued on next page)

TABLE 5. Estimated body weights of some representative species of Eocene, Oligocene, and Miocene fossil primates, based on the regression coefficients given in Table 3. Tooth size in $\ln(\text{length} \times \text{width})$ for M^1 or M_1 , with sample size n , as indicated. Original measurements in mm (continued)

Genus and species	Age	Locality (reference)	Tooth size $\ln(\text{length} \times \text{width})$	Estimated weight (gm)	95% Confidence interval
<i>Cebupithecia sarmiento</i>	Middle Miocene	La Venta (Huila), Colombia (Stirton, 1951)	$M^1 = 2.96$ ($n = 1$) $M_1 = 2.75$ ($n = 1$)	1,835 2,095	1,645-2,045 1,935-2,270
<i>Stirtonia tatacoensis</i>	Middle Miocene	La Venta (Huila), Colombia (Stirton, 1951)	$M^1 = -$ $M_1 = 3.37$ ($n = 1$)	- 5,280	- 4,925-5,655
African Parapithecidae					
<i>Apidium moustafai</i>	Oligocene	Quarry G (Fayum), Egypt (Simons, 1962)	$M^1 = -$ $M_1 = 2.32$ ($n = 3$)	- 1,105	- 995-1,225
<i>Apidium phiomense</i>	Oligocene	Fayum, Egypt (Gingerich, 1978)	$M^1 = -$ $M_1 = 2.60$ ($n = 2$)	- 1,675	- 1,535-1,830
<i>Simonsius grangeri</i>	Oligocene	Quarry I (Fayum), Egypt (Simons, 1974)	$M^1 = -$ $M_1 = 2.99$ ($n = 6$)	- 2,995	- 2,790-3,215
African Cercopithecidae					
<i>Victoriapithecus macinnesi</i>	Early Miocene	Rusinga Is., Kenya (von Koenigswald, 1969)	$M^1 = -$ $M_1 = 3.33$ ($n = 1$)	- 4,975	- 4,640-5,325
<i>Prohylobates tandyi</i>	Early Miocene	Wadi Moghara, Egypt (Simons, 1969)	$M^1 = -$ $M_1 = 3.55$ ($n = 3$)	- 6,900	- 6,410-7,430
European Oreopithecidae					
<i>Oreopithecus bambolii</i>	Late Miocene	Grosseto Lignite (Tuscany), Italy (Hürzeler, 1958)	$M^1 = 4.27$ ($n = 2$) $M_1 = 4.06$ ($n = 2$)	15,325 14,755	13,510-17,385 13,360-16,295
African Hominoidea					
<i>Propithecus chirobates</i> (?= <i>P. haeckeli</i>)	Oligocene	Quarry I (Fayum), Egypt (Kay et al., 1981)	$M^1 = 3.47$ ($n = 3$) $M_1 = 3.17$ ($n = 6$)	4,195 3,920	3,845-4,570 3,660-4,195
<i>Aegyptopithecus zeuxis</i>	Oligocene	Quarry I (Fayum), Egypt (Kay et al., 1981)	$M^1 = 3.74$ ($n = 3$) $M_1 = 3.46$ ($n = 7$)	6,495 6,035	5,935-7,110 5,620-6,480
<i>Micropithecus clarki</i>	Early Miocene	Napak, Uganda (Fleagle and Simons, 1978)	$M^1 = 3.11$ ($n = 2$) $M_1 = 3.03$ ($n = 2$)	2,340 3,180	2,120-2,585 2,965-3,410
<i>Limnopithecus legetet</i>	Early Miocene	Songhor, Kenya (Andrews, 1978)	$M^1 = 3.45$ ($n = 5$) $M_1 = 3.28$ ($n = 13$)	4,060 4,615	3,725-4,425 4,310-4,940
<i>Dendropithecus macinnesi</i>	Early Miocene	Rusinga Is., Kenya (Andrews, 1978)	$M^1 = 3.80$ ($n = 13$) $M_1 = 3.64$ ($n = 9$)	7,160 7,890	6,520-7,855 7,305-8,525
<i>Rangwapithecus gordon</i>	Early Miocene	Songhor, Kenya (Andrews, 1978)	$M^1 = 4.19$ ($n = 6$) $M_1 = 3.95$ ($n = 7$)	13,465 12,525	11,950-15,170 11,415-13,740
<i>Proconsul africanus</i>	Early Miocene	Rusinga Is., Kenya (Andrews, 1978)	$M^1 = 4.28$ ($n = 11$) $M_1 = 4.10$ ($n = 4$)	15,580 15,660	13,720-17,685 14,145-17,340
<i>Proconsul nyanzae</i>	Early Miocene	Rusinga Is., Kenya (Andrews, 1978)	$M^1 = 4.70$ ($n = 7$) $M_1 = 4.37$ ($n = 14$)	30,760 23,420	26,010-36,385 20,770-26,410
<i>Proconsul major</i>	Early Miocene	Songhor, Kenya (Andrews, 1978)	$M^1 = 4.78$ ($n = 5$) $M_1 = 4.75$ ($n = 7$)	35,015 41,255	29,360-41,765 35,570-47,845
European Hominoidea					
<i>Pliopithecus antiquus</i>	Late Miocene	Sansan (Gers), France (Hürzeler, 1954)	$M^1 = -$ $M_1 = 3.46$ ($n = 1$)	- 6,035	- 5,620-6,480
<i>Dryopithecus laietanus</i> (?= <i>D. brancoi</i>)	Late Miocene	La Trumba (Catalonia), Spain (Simons and Pilbeam, 1965)	$M^1 = -$ $M_1 = 4.14$ ($n = 1$)	- 16,624	- 14,975-18,455
<i>Dryopithecus fontani</i>	Late Miocene	St. Gaudens (Hte. Garonne), France (Simons and Pilbeam, 1965)	$M^1 = -$ $M_1 = 4.51$ ($n = 2$)	- 28,850	- 25,330-32,865

(Table continued on next page)

TABLE 5. Estimated body weights of some representative species of Eocene, Oligocene, and Miocene fossil primates, based on the regression coefficients given in Table 3. Tooth size in $\ln(\text{length} \times \text{width})$ for M^1 or M_2 , with sample size n , as indicated. Original measurements in mm (continued)

Genus and species	Age	Locality (reference)	Tooth size $\ln(\text{length} \times \text{width})$	Estimated weight (gm)	95% Confidence interval
<i>Ouranopithecus macedoniensis</i>	Late Miocene	Ravin de la Pluie (Macedonia).	$M^1 = 5.23$ ($n = 1$)	72,590	57,945-90,940
		Greece (de Bonis et al., 1974, 1975, 1977)	$M_2 = 5.23$ ($n = 3$)	84,345	70,045-101,570
Asian Hominoidea <i>Dionysopithecus shuangouensis</i>	Middle Miocene	Shihhung (Kiangsu), China (Li, 1978)	$M^1 = 3.33$ ($n = 1$) $M_2 = -$	3,345 -	3,060-3,655 -
<i>Sivapithecus sivalensis</i>	Late Miocene	Siwaliks, India and Pakistan (Simons and Pilbeam, 1965)	$M^1 = -$ $M_2 = 4.60$ ($n = 18$)	- 32,990	- 28,770-37,830
<i>Sivapithecus indicus</i>	Late Miocene	Siwaliks, India and Pakistan (Simons and Pilbeam, 1965)	$M^1 = -$ $M_2 = 4.83$ ($n = 8$)	- 46,475	- 39,830-54,230
<i>Sivapithecus meteai</i>	Late Miocene	Kazan (Anatolia), Turkey (Andrews and Tekkaya, 1980)	$M^1 = 5.09$ ($n = 1$) $M_2 = 5.04$ ($n = 1$)	57,860 63,550	46,910-71,365 53,575-75,380
<i>Gigantopithecus giganteus</i>	Late Miocene	Haritalyangar Siwaliks, India (Simons and Chopra, 1969)	$M^1 = -$ $M_2 = 5.49$ ($n = 1$)	- 124,260	- 101,050-152,790

However, body weights estimated from M^1 and M_2 in *Oreopithecus bambolii* are very consistent, yielding an average weight of about 15,000 gm.

Estimates of body weight in Oligocene and Miocene Hominoidea derived from upper and lower molars are, with few exceptions, reasonably consistent. In some cases discrepancies may be due to the small size of available samples. In one other case, *Proconsul nyanzae* from Rusinga Island, it is possible that lower teeth of a smaller species (*Proconsul africanus*) are included in the published sample. Estimated body weights for Miocene apes range from about 2,700 gm in *Micropithecus clarki* to 124,000 gm in *Gigantopithecus giganteus*.

DISCUSSION

Allometric scaling of tooth size and body size

Pilbeam and Gould (1974) and Gould (1975) reported that upper cheek teeth scale with positive allometry in a diverse range of rodents, artiodactyls, and primates (using cranial length as a measure of body size), implying that tooth size may scale metabolically rather than geometrically. They subsequently noted that positive allometry in the upper

cheek tooth row may be accomplished by a strong positive allometric increase in third molar size and in the size of the premolars, even though M^1 and M^2 scale geometrically (Pilbeam and Gould, 1975). Pirie (1978) duplicated Pilbeam and Gould's analysis of cheek tooth to skull length scaling for a wider range of primates and concluded that postcanine tooth area is in part related to the amount of food ingested, i.e., to metabolic rate. Similarly, Goldstein et al. (1978) found that postcanine tooth area scaled with positive allometry across a series of cercopithecoid primates representing three dietary classes.

In contrast, Kay (1975a) found that both M_2 area and postcanine tooth area scaled below geometric scaling when tooth area was compared with body weight in a broad range of primates and in bovid artiodactyls. Corruccini and Henderson (1978), Wood (1979a), and Wood and Stack (1980) supported Kay's conclusion using multivariate principal axes or linear regressions of tooth size and cranial size in primates.

Gould (1975) showed that major axis (or principal axis) slopes differ systematically from least squares regression slopes in yield-

ing a higher estimate of allometric scaling. This difference can be considerable when variates are not perfectly correlated. More recently, Smith (1981) has shown that regressions of tooth size on body size differ considerably depending on the measurement used to represent body size. Cranial length and body weight, for example, may yield very different results. In this study we have used principal axes to represent the structural relationship between tooth crown area and body weight. Our results confirm Pilbeam and Gould's (1975) inference that teeth at the front and back of the cheek tooth series scale with more positive allometry than teeth in the center of the cheek tooth series. However, stated in terms of crown area to body weight, it is clear that neither upper cheek teeth as a unit nor lower cheek teeth as a unit scale at a rate approaching metabolic scaling. Lower cheek teeth as a unit approximate geometric scaling, but the sum of crown areas of the upper cheek teeth scale significantly below even geometric scaling when the entire spectrum of generalized primates is considered.

Prediction of body weight from tooth size

There are two general problems associated with predicting the average body weight of a species from its tooth size: one concerns the *accuracy* of predictions based on one or more teeth, and the other concerns the *consistency* of predictions based on different teeth. One way to test the accuracy of body weight predictions is to compare weights predicted from tooth size with known weights in extant species. As new information about extant species used in our analysis becomes available, it will be possible to test how well weights predicted from tooth size in these new samples conform to actual body weights. A truly independent test would require predicting the body weights of additional extant species not included in the original analysis, and comparison of these predicted weights with actual weights. It is, in most cases, impossible to test the accuracy of body weights estimated for fossil primates (Table 5). The only way to test these is to compare body weights predicted from tooth size with those predicted from cranial and postcranial remains. This can be done to a limited extent for *Aegyptopithecus zeuxis* (Table 4), and our results based on tooth size agree reasonably well with body weights predicted from cranial size and from ulna size.

Since all available information on tooth size and body size in extant primates was used in

our analysis, we can at present only model the dispersion of body size predictions based on tooth size for each of the major groups of generalized primates (Fig. 6). The average weight predicted for each species from M_1 or M^1 size is plotted on the ordinate for comparison with the known average weight on the abscissa. Ideally, if predicted weights were equal to actual weights, all species would fall on the dashed diagonal line. Species in each of the four systematic groups shown in Figure 6 all show about the same amount of dispersion about the diagonal.

As a measure of consistency, body weight predictions based on M^1 (open circles) can be compared with those based on M_1 (solid circles) in Figure 6. In many cases these are equal (half-closed circles), but in others there is a substantial difference between body weights predicted from M^1 and those predicted from M_1 . Upper teeth give substantially greater predicted body weights than those based on lower teeth in five out of the six species of Lemuroidea and Lorisioidea shown. Predicted weights based on upper molars are equal to or, in most cases, greater than actual weights, indicating that upper molars of prosimian Lemuroidea and Lorisioidea usually overestimate body weight. On the other hand, predicted weights based on M_1 are about equally dispersed above and below the diagonal, indicating that M_1 provides a more accurate body weight prediction than M_1 does. This result suggests that the body weights of Adapidae in Table 5 based on lower molars are probably more reliable than those based on upper molars.

Prosimians have distinctly larger (broader) upper molars than higher primates do, and this distinction is reflected in our observation that upper molars of prosimians alone tend to overestimate body weight. Higher primates as a group have narrower upper molars than prosimians do, and since these contributed the majority of species used to construct our prediction equations, predictions should be more accurate for these primates. Apart from problems caused by the relatively broader upper molars of prosimians, it appears that body weight predictions based on upper and lower molars in generalized primates are reasonably consistent.

Our estimates of the body weights of Fayum primates differ from those of Kay and Simons (1980) by factors ranging from 1.07 in the case of *Aegyptopithecus* to 1.91 in *Oligopithecus*. These differences may be explained in part by

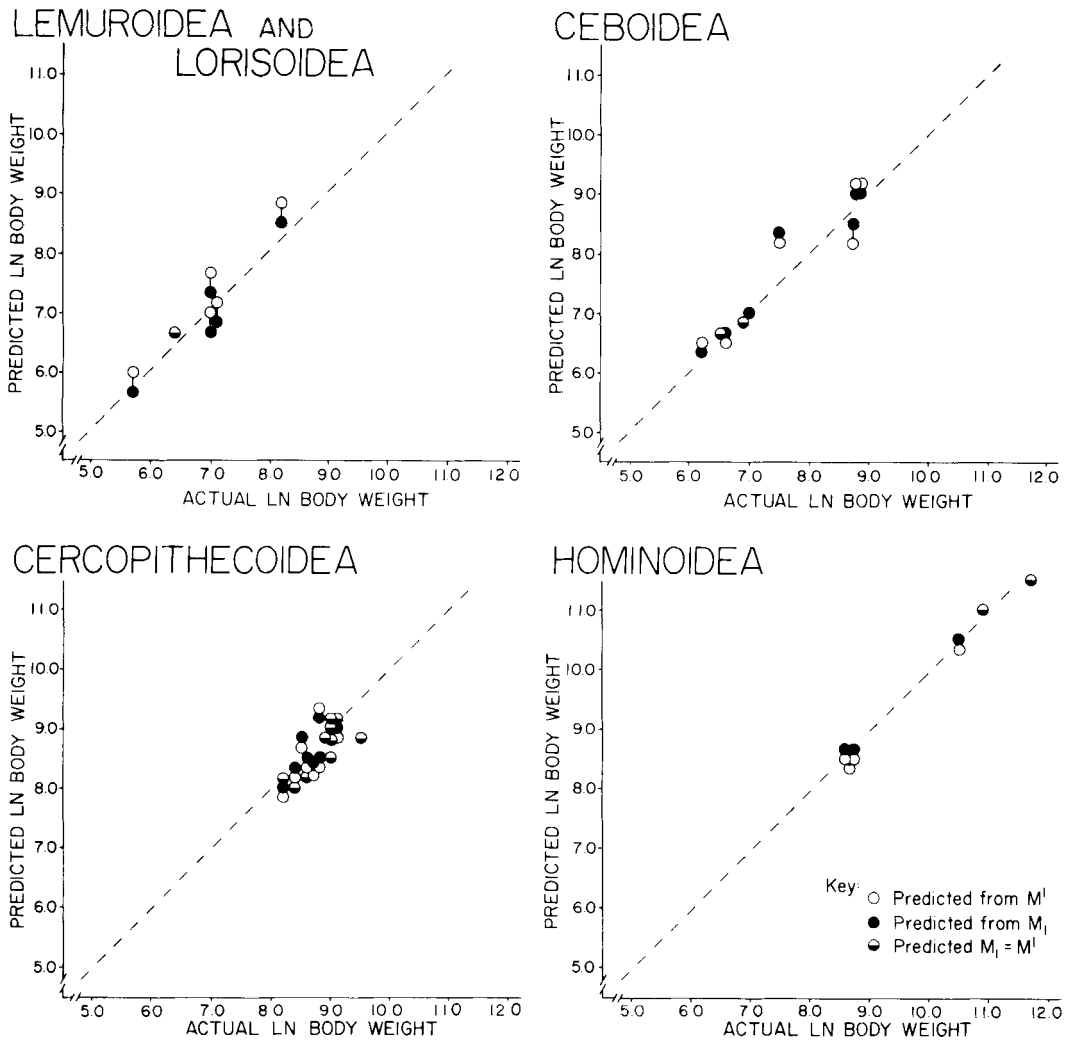


Fig. 6. Comparison of body weights predicted from tooth size (ordinate) with actual body weights (abscissa) for living Lemuroidea and Lorisoidea, Ceboidea, Cercopithecoidea, and Hominoidea based on data and equations in Tables 1 and 3. Dashed diagonal line represents a predicted body weight equal to the actual weight. Each circle is the average weight of a species predicted from M_1 (open circles) or M_2 (solid circles). Half shaded circles indicate species for which body size predictions based on M_1 and M_2 coincide. Note that M_1 yields body weight estimates substantially greater than those based on M_2 for Lemuroidea and Lorisoidea, and that estimates based on M_2 tend to approximate actual weights (dashed line) more closely than do estimates based on M_1 . Upper and lower molars both appear to yield reasonably accurate predicted body weights for Ceboidea, Cercopithecoidea, and Hominoidea.

the use of M_1 rather than M_2 measurements and in part by the fact that we included measurements of both length and width in calculating our estimates. Kay and Simons' estimates are based on the length of M_2 in each of the species studied. Among Miocene primates, our estimate of the average body weight of

Proconsul africanus based on the crown area of M_1 (15,620 gm) differs from that based on M_2 length (23,400 gm; Gingerich, 1977a) by a factor of 1.50. Andrews' (1978) measurements of M_2 in Rusings *P. africanus* and critical values from Table 3 yield a predicted body weight of 15,240 gm (95% confidence interval =

13,825–16,740 gm), which agrees with our estimate based on *M.* Since our new estimates are based on tooth length and width, not just length, we feel 15,000–16,000 gm is a better estimate for the body weight of *Proconsul africanus* than the 23,000–24,000 gm estimate given previously.

CONCLUSIONS

Much remains to be learned about allometric scaling of tooth size and body weight in the dentition of primates and other mammals. Our results demonstrate that there is a coherent pattern of differences in scaling at different tooth positions across the whole range of generalized primates. We have not investigated how this general pattern might change if primates were subdivided into smaller taxonomic groups or into dietary guilds. Some taxonomic groups of living primates (Lemuroidea, Ceboidea, Cercopithecoidea) are large enough to justify separate allometric treatment and separate body size prediction equations when adequate measurements of tooth size and body weight become available. Continued investigation of the relationship of tooth size and body size promises to clarify the functional relationship of these characteristics. This in turn should permit a much more perceptive understanding of dental, dietary, and body size adaptations in fossil primates.

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