Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals

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(With 2 figures in the text)

Functional least squares regression was used to fit the allometric equation, $y = bx^k$, to data on head–body lengths and body weights for 123 species of mammals. These measurements were found to be highly correlated and to scale isometrically. The scaling of M_1 area with head–body length was investigated for 288 species of terrestrial mammals. A method was described for estimating the body size of extinct mammals from M_1 area and the tooth size–body size relationships discovered among contemporary forms.

Contents

Introduction

Mammalian systematists and paleontologists have devoted considerable effort to comparison and description of the morphology of mammal teeth: the relative size, shape, and position of cusps and crests. In contrast, much less attention has been given to comparative study of tooth size among contemporary species of mammals or to quantitative investigation of allometric relationships between tooth size and body size among living members of most higher taxa of mammals. Recently, several investigators (Kay, 1973, 1975a, b, 1978; Gingerich, 1977; Gould, 1975; Pilbeam & Gould, 1974; Goldstein, Post & Melnick, 1978) have described relationships between tooth size and body size among species of several taxonomic groups of recent mammals (e.g. primates, rodents, artiodactyls). They employed a variety of measures of tooth size and body size and a nearly equal abundance of curve fitting techniques. Discussion has focussed on the nature of allometry between tooth size and body size: whether teeth (as food processing organs) increase in size in direct proportion to body size (isometric scaling) or whether they scale

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proportional to metabolic rate. The latter would lead to larger mammals having absolutely and relatively larger teeth in proportion to body size than smaller mammals. There has also been considerable discussion concerning the utility of tooth size-body size scaling for inferring the body size and/or dietary habits of extinct mammals known primarily from fossilized teeth (Wolpoff & Brace, 1975; Kay, 1975b; Pilbeam & Gould, 1975; Gingerich, 1977).

Several features necessarily influence the results of investigations of the quantitative relationship of tooth size to body size: (1) the dimensions chosen to represent tooth size and body size; (2) the precision with which these dimensions are measured (or estimated); (3) the magnitude of intraspecific variation in the relationship between tooth size and body size; (4) the group chosen for study; (5) the technique of curve fitting selected for the analysis. The same parameters were used to represent "tooth size" and "body size" for all mammals in the study. These are discussed in detail below. Included here are a larger and more diverse sample of recent mammals than has been previously analyzed. The goals of this study are two: (1) to discern and describe the quantitative relationship between tooth size and body size among species of recent mammals of varying degrees of morphological similarity and levels of taxonomic relatedness; and, (2) to determine the precision of body size estimates that can be made from regressions of body size on a measure of tooth size for several groups of contemporary mammals.

Materials and methods

The analyses reported here are based on 338 specimens representing nine terrestrial orders and 288 species of contemporary mammals. In most of the analyses each species was represented by a single specimen (exemplar). Edentata and Pholidota were excluded because of their highly specialized dentitions. Marine mammals and bats were likewise excluded because of their exceptionally specialized body forms. All specimens utilized were adults with teeth not worn beyond the maximal dimensions of the tooth crown. Individuals were judged adult on the basis of complete eruption of the permanent dentition and, for groups where this criterion was appropriate, (most placentals) on the basis of closure of the cranial sutures.

All specimens examined reside in the collections of the Mammal Division of the University of Michigan Museum of Zoology, Ann Arbor, and the Department of Mammalogy, Field Museum of Natural History, Chicago. The genus and species were recorded for each specimen with four measurements: (1) head and body length in millimeters (HBL); (2) weight in grams (when recorded by the collector); (3) maximum length of the crown of the lower first molar (M_1); and, (4) maximum width of the crown of M_1. The crown length was measured parallel, and width perpendicular, to the long axis of the tooth row. Head and body length was obtained by subtracting the length of the tail from the total length recorded by the original collector.

Measurements of M_1 were taken to 0·05 mm using an Anderson Craniometer (at UMMZ) or a vernier equipped Zeiss disecting scope and dial calipers (at FMNH). The crown area of M_1 was estimated as the minimum rectangle required to enclose the crown. It is realized that M_1 area as defined here does not represent the area of occlusal surfaces of the tooth but defend its use because it can be accurately and conveniently measured. Gingerich (1977) has found M_1 to be the least variable tooth within intraspecific samples of primates. M_1 area provides a relatively accurate, precise, and reproducible measure of tooth size for broad interspecific comparisons.

Prior to numerical analysis all measurements were converted to natural logorithms following the convention of Huxley (1932), Gould (1975), and others. The log transformed version of the allometric equation ($y = bx^k$; $\log(y) = k \log(x) + b$) was fitted to the data using the functional

regression by least squares technique described by Ricker (1973). This method was used to fit the allometric equation by calculating the line which minimizes the sum of the products of the vertical and horizontal distances of each point from the line (Tessier, 1948) and produces the least biased estimate of the true allometric slope of the major curve fitting techniques (Ricker, 1973). In choosing Model I regression for estimating body size from a measure of tooth size Sokal & Rohlf (1969) and Goldstein et al. (1978) are followed. Confidence limits on the slopes of the regressions and on predicted values of HBL were calculated using methods outlined in Sokal & Rohlf (1969) and advocated by Ricker (1973).

All computations were performed on the University of Michigan computer facility using standard Michigan Interactive Data Analysis Programs (MIDAS) programs.

Results

Relationship of head–body length to body weight

Previous workers have used a variety of measurements to estimate body size: weight, femoral length, basicranial length, or breadth of the foramen magnum. Most investigators have preferred body weight (Kay, 1973, 1975a, b, 1978; Gould, 1975; Gingerich, 1976; Goldstein et al., 1978). Since body weights are rarely recorded for museum specimens, these workers have relied on weight estimates collected from disparate sources in the literature. For animals such as many rodents, that vary seasonally in body weight or for those that display significant geographic variation in body size (many carnivores) mean body weights taken from the literature provide only crude estimates of body size for the particular specimens from which tooth measurements were taken. Extrapolation from skeletal measurements or use of mean weights for variable taxa inevitably introduce an inestimable and, possibly large, component of variance into the body size estimate.

HBL was chosen to represent body size in these analyses because intraspecific variation in HBL is consistently less than for body weight in most terrestrial mammals for which data are available (Long, 1968a, b; Yablokov, 1974) and because head and body lengths were available for all specimens in the study. Body weights were available for 123 of the specimens so the relationship between HBL and body weight was evaluated for these specimens. The isometric slope of log weight (proportional to length^3) plotted against log length (length^1) is 3·0. The slope of the functional regression of body weight on HBL is 2·991 (95% confidence interval = ±0·12). The correlation coefficient is 0·973. In all subsequent analyses HBL was used to represent body size.

Order of allometry

To quantify the relationship between tooth size and body size the functional regression of M_1 area on HBL was calculated for several groups of mammals (see Table I): (1) all species of mammals in the study ($N = 288$); (2) six orders of mammals treated separately ($12 \leq N \leq 136$); (3) South American caviomorph rodents ($N = 17$); (4) seven families of rodents and carnivores ($13 \leq N \leq 47$). The isometric slope of an area (proportional to l^2) plotted against a length (l) on a log–log scale is 2·0. The slope for all mammals falls significantly below this value (95% confidence interval) as do the slopes for Insectivora, Rodentia, and Felidae. For all other groups the isometric slope, (2·0), falls within the 95% confidence limit of the calculated slope. For several groups of mammals, then, larger animals have smaller teeth relative to their body size than smaller mammals.

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Correlation of head-body length with M_1 area

Gingerich (1976, 1977) has argued that tooth size, particularly M_1 area, is a good estimator of body size within a group of related mammals spanning a significant range of body sizes. This idea is supported by the high correlation coefficients for M_1 area vs. HBL reported in Table I. To assess the precision of the relationship between M_1 area and body size I computed confidence limits for the range of "predicted" body sizes (y_i) for any given M_1 area (x_i) following the procedure outlined by Sokal & Rohlf (1969) and based on the observed relationshjps for my samples of contemporary mammals. Figures 1

TABLE I

The relationship of M_1 area to HBL for selected mammalian taxa. Given slopes are those for the functional regression of M_1 area on HBL (Ricker, 1973). Confidence intervals are for the slopes

Taxon	N	R	Geometric mean slope	95% confidence interval
Mammalia	288	0·952	1·817	±0·064
Marsupialia	24	0·920	1·935	±0·337
Insectivora	20	0·897	1·594	±0·351
Primates	14	0·909	1·749	±0·458
Rodentia	136	0·927	1·726	±0·110
Carnivora	74	0·859	1·991	±0·238
Artiodactyla	12	0·852	2·007	±0·741
S. American hystricomorph rodents	17	0·921	2·009	±0·429
Sciuridae	47	0·905	1·878	±0·241
Muridae	13	0·884	1·753	±0·534
Cricetidae	40	0·845	1·964	±0·345
Mustelidae	17	0·883	2·254	±0·583
Canidae	18	0·707	2·447	±0·916
Felidae	15	0·960	1·594	±0·263
Viverridae	18	0·910	1·791	±0·372

TABLE II

*Observed and estimated range of variation in HBL for **Sciurus niger** (in mm). Estimates of HBL were made from the regressions shown in Figs 1 and 2 using mean M_1 area of the measured sample ($\overline{X}=9\cdot4$ mm²) as an estimator of body size*

Curve	Minimum HBL	Maximum HBL	Confidence limit
Mammalia	180	470	95%
Mammalia	245	342	50%
Rodentia	190	441	95%
Rodentia	250	335	50%
Measure sample ($N=50$)	251	334	Mean=293

and 2 illustrate the regression of HBL (dependent variable) on M_1 area for all mammals in the study, and for Rodentia, respectively. The dashed lines bracketing the fitted regression line in each of these Figures represent the 50 and 95% confidence limits for estimates of body size given tooth size.

What do these confidence limits mean with regard to estimating the body size of "real mammals"? To address this question a sample of 50 fox squirrels (*Sciurus niger*) was measured and the means of M_1 area and HBL for the sample was calculated. Mean M_1 area for the measured sample was then taken as the best estimate of tooth size for *S. niger* and used to estimate body size from the regressions in Figs 1 and 2. The estimates and confidence limits are given in Table II with the observed range of body sizes for the sample. The 50% confidence limits for estimated body size for both of the regressions fall remarkably close to the observed range while the 95% confidence limits grossly overestimate the range of body sizes for this species.
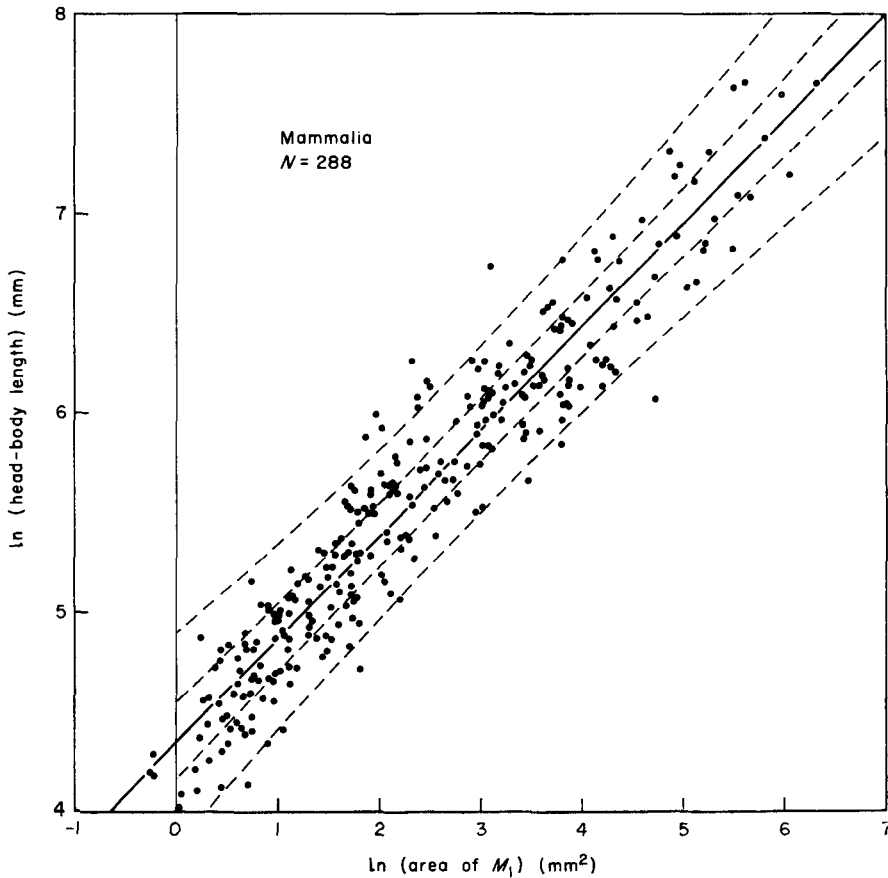

FIG. 1. The relationship of HBL to M_1 area for 288 species of mammals. Curve fitted by least squares regression. Dashed lines represent the 50 and 95% confidence limits on estimated values of HBL.
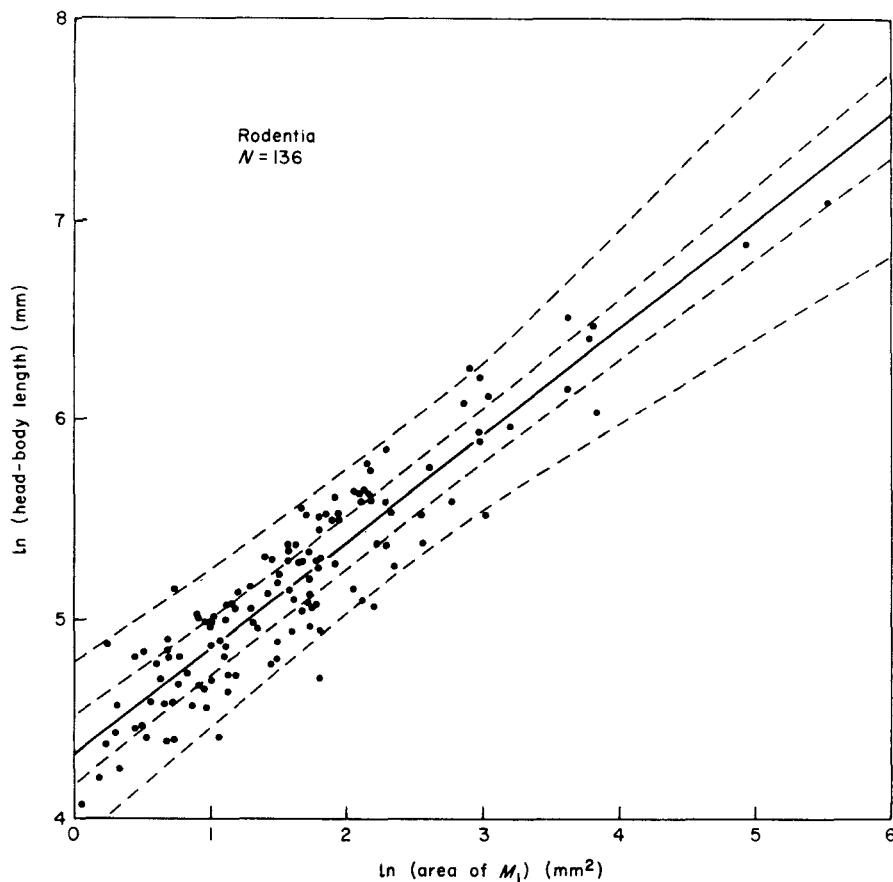
FIG. 2. The relationship of HBL to M_1 area for 136 species of rodents. Notation and confidence limits are the same as in Fig. 1.

Discussion

Scaling of tooth size with body size

Gould (1975) has advanced the hypothesis that poscanine tooth area of mammals scales in proportion to the basal metabolic rate which, in turn, scales with the 0·75 power of body mass (Kleiber, 1961). From this hypothesis it follows that postcanine tooth area should increase with positive allometry relative to body size. Simple geometric scaling (isometry) would result in an increase in tooth surface area proportional to the 0·67 power of body mass. The allometric exponent would be 0·75 if teeth scale with the basal metabolic rate. Recent studies of primate dentitions (Kay, 1975a, b; Goldstein et al., 1978) fail to sustain Gould's prediction of positive allometry for postcanine tooth area or for the area of individual teeth scaling with body size. The slopes of tooth size regressed on body size for many primates considered together and for smaller samples of primate species grouped by dietary habits (herbivores, frugivores, omnivores, insectivores) are all equal to or lower than the isometric slope of constant proportionality (Kay,

1975*a, b*; Goldstein *et al.*, 1978). In Gould's (1975) study, only one out of six samples of mammals surveyed (South American caviomorphs) showed a significant deviation from isometric scaling of tooth size with body size in the direction predicted by Gould's hypothesis. Gould used "basicranial length" to estimate body size. It is not known whether basicranial length itself scales allometrically with body mass—the parameter it is reputed to estimate—among caviomorph rodents. Gould states only that basicranial length was found to scale isometrically with femoral length. Another confounding factor is the expected high correlation of basicranial length with length of the tooth row—the major component in the estimate of poscanine tooth area.

The results of this study indicate that, for most groups of mammals surveyed, M_1 area scales isometrically with body size. For particular groups (insectivores, rodents, and felids) and for all mammals considered together the coefficient of tooth size allometry is less than isometric. In these groups larger forms have relatively smaller teeth.

The lowest slope calculated for log M_1 area vs. log HBL was that for 20 species of Insectivora (1·594). This result corresponds well with Kay's finding that "insectivorous" primates exhibit the smallest increase in tooth size with body size among the groups he examined. Kay (1975*a, b*) and Goldstein *et al.* (1978) have shown that, among contemporary primates, the scaling of tooth size with body size varies among groups with different dietary habits. Although the dietary habits of the mammals examined here were not surveyed there are clear differences in the scaling of teeth with body size between taxonomic groups (e.g. Carnivora and Insectivora). The reasons for differences in allometric coefficients between different higher taxa are unknown but, perhaps, reflect physical requirements for acquiring and processing different kinds of food. This point is underscored by the gross differences exhibited in tooth morphology and cranial musculature among the higher mammalian taxa. If the scaling of tooth size with body size in mammals were related to metabolic requirements as suggested by Gould, one would expect positive allometry and, more uniform scaling among major groups. The studies to date have shown neither phenomenon.

Estimating body size

Deriving estimates of the body size of extinct mammals represented only by fossil material is, at best, a speculative venture. The utility of such estimates depends to a large extent in the confidence that can be placed on their probable accuracy. The quantitative relationships between tooth size and body size described above for contemporary mammals suggest a potentially useful approach to estimating the body size of extinct mammals. For large and diverse taxa such as Rodentia, the observed range of variation in the tooth size–body size relationship among contemporary forms provides a reasonable estimate of the range of variation in extinct forms. The fitted regression line provides a best estimate of body size and the confidence limits provide an estimate of the precision of the technique.

The first consideration for estimating the body size of an extinct form from fossil teeth is the choice of an appropriate reference group. This requires an assessment of the taxonomic affinity or morphological similarity of the fossil form to a group of contemporary mammals and the group chosen will necessarily depend on the confidence of the investigator in his evaluation. For instance, a lower M_1 identifiable as a rodent would be

compared with the curve derived for modern rodents (Fig. 2) while a carnassial-like M_1 would dictate the choice of the curve for Carnivora. For forms of obscure taxonomic relationship a conservative estimate can be obtained from the curve for all mammals, encompassing the known range of variation in modern terrestrial mammals (with noted exceptions).

Independent and quantified estimates of body size are particularly valuable to workers concerned with the patterns of evolution of organs such as the brain within and among hypothesized phylogenetic lineages. Another group of workers for whom the technique has potential value is paleontologists concerned with the structure of paleocommunities. The confidence limits in Figs 1 and 2 clearly indicate that measurements of a single tooth are not nearly precise enough estimators of body size to detect small and subtle changes in size related to character displacement due to presence of sympatric competitors or slight body size changes related to minor climatic shifts (cf. Davis, 1977). The method may be productively employed, however, to estimate the probable *range* of body size for an animal with a given tooth size.

Summary

The allometric equation, $y = bx^k$, was computed for the relationship of head–body length to body weight among 123 species of contemporary mammals. Head–body length and weight were found to be highly correlated among species of mammals spanning a significant range of absolute size. Head–body length was found to scale isometrically with body weight among the species of mammals examined in this study.

The scaling of M_1 area with head–body length was investigated for 288 species of terrestrial mammals. M_1 area and head–body length were found to be highly correlated in interspecific comparisons of mammals. The scaling of M_1 area with head–body length differs among higher taxa of mammals. M_1 area increases most rapidly with increasing body size in some carnivores (e.g. Mustelidae) and most slowly in insectivores. For all groups studied, M_1 area increased in direct proportion to head–body length (isometric scaling) or with negative allometry such that larger species have relatively smaller M_1 area proportional to their body size.

Confidence limits were calculated for predicted values of head–body length from regressions of head–body length on M_1 area for interspecific comparisons within several higher taxa of mammals. The 50% confidence limits on estimates of head-body length from M_1 area coincide closely with the range of variation found in a large measured sample of squirrels. M_1 area was found to be a good "predictor" of body size among species of recent mammals spanning a significant range of absolute size. A method was described for estimating body size of extinct mammals from M_1 area and the tooth size–body size relationships among modern forms.

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