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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

FUNCTIONAL MORPHOLOGY AND DIET OF LATE CRETACEOUS MAMMALS OF NORTH AMERICA

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

By

CYNTHIA LEIGH GORDON
Norman, Oklahoma
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FUNCTIONAL MORPHOLOGY AND DIET OF LATE CRETACEOUS MAMMALS OF NORTH AMERICA

A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY

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For mom

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

CHAPTER 1

CHAPTER 2

ABSTRACT

At the beginning of the Tertiary, there was an explosive mammalian radiation, with mammals hypothetically filling the ecological voids left by the demise of the dinosaurs at the end of the Cretaceous. Traditionally, Cretaceous mammals were considered ecological generalists, small insectivores living in the shadow of the dinosaurs, but there has not yet been a comprehensive study of the ecology of Cretaceous mammals before this extinction event. Body size and diet in Late Cretaceous (Lancian) therian mammals, marsupials and placentals, were examined in an attempt to understand better the roles Cretaceous mammals played in their environment.

It is impossible to directly measure body mass in extinct mammals. Least squares regression analysis was used to examine the relationship between various dental and cranial measurements in modern, dentally conservative primates, marsupials and insectivores in order to generate equations to predict body size (as measured by body mass) in Cretaceous mammals. Lower and upper first molars are the most highly correlated with body size. Skull length and area of the foramen magnum also are highly correlated with body size. Because Cretaceous mammals are known mainly by isolated teeth, regression equations generated from the first molars were used to predict body size in Cretaceous mammals. The range of body size in most Cretaceous mammals is well within that of modern mammals, with most species being less than 200 g in size. Latest Cretaceous marsupials had a larger range of body sizes, with five Lancian species over 200 g, compared to only two species of placentals.

Principal components analysis of tooth morphology and diet in modern mammals indicates that gross morphological differences in tooth shape can be detected within groups, as well as among groups. In general, tooth morphology separated species into groups along phylogenetic lines, with marsupials separated from primates and insectivores. However, some species did cluster outside of their own group. The insectivorous primate *Tarsius* clustered with insectivores, while the frugivorous marsupial *Caluromys* was placed close to primates. Differences between species were more difficult to distinguish in Late Cretaceous taxa. Nonetheless, the position of some species did indicate they had a more specialized tooth shape. The Cretaceous marsupial *Glasbius* grouped near modern *Caluromys*, indicating that teeth of *Glasbius* were becoming more specialized for a frugivorous diet. The large range of body size seen in some latest Cretaceous mammals, coupled with evidence that some were trending towards more specialized teeth, may indicate that Cretaceous mammals started radiating into different ecological niches before the extinction of the dinosaurs.

INTRODUCTION

At the beginning of the Tertiary Period, there was an incredible radiation of mammals not seen during the Cretaceous Period, when dinosaurs dominated the landscape. Cretaceous mammals were long considered to have been small, ecological generalists, not realizing their full ecological potential during the reign of the dinosaurs. At the end of the Cretaceous, mammals entered into the ecological niches left void by the extinction of the non-avian dinosaurs, and thereby were able to attain new and remarkable shapes and sizes.

Body size figures prominently in the biology of terrestrial vertebrates. Physiologically, body size is related to reproductive rate, temperature regulation and metabolic rates. For example, smaller mammals have higher surface area to volume ratios, resulting in higher basal metabolic rates. Thus, they have greater energy requirements relative to their body size than larger mammals. This means that smaller mammals must ingest foods that are relatively high in calories. Larger mammals have lower energy requirements relative to their body size. They have longer digestive tracts, which allows more time for food to be processed in the body. As such, they can eat large amounts of low calorie foods and still meet their energy requirements. Ecologically, body size is related to factors such as home range size, niche partitioning, habitat preference, and relative species abundance. For example, smaller mammals are generally more abundant, and tend to have smaller ranges.

Cretaceous marsupials and placentals, called therians, were small-bodied in comparison to most Tertiary forms, and did not vary so widely in size. This size

comparison is the result of general observations of tooth size in Cretaceous mammals, which are often known only by isolated teeth and jaws. Body size and tooth size are highly correlated. Least-squares regression can be used to generate equations using modern species to predict body size from tooth size in extinct forms. To date, predictive equations for body size have only been generated for primates and insectivores, and these equations were not based on dentally conservative taxa, the most appropriate modern analogs to predict body size in dentally conservative Cretaceous species. Moreover, no predictive equations have been generated for marsupials.

In addition to body size, tooth morphology can provide key insight into the paleobiological roles of early mammals. Teeth are tools an animal uses to procure and process food, designed to break down food as much as possible for digestion, and to do so in the most efficient way. Thus, mammals that feed mainly on insects and other invertebrate prey tend to have teeth with tall cusps and long shearing crests that allow them to puncture and cut their food efficiently. Mammals that are folivorous, eating leaves, bark, etc., do not need tall cusps for puncturing, but rather they need longer shearing crests to help slice and process leaves. Frugivorous mammals, those that feed on fruits and such, tend to have teeth that are low-crowned with bulbous cusps, allowing them to grind and pulp their food. Studying the functional relationship between teeth and diet in dentally conservative modern species allows for the inference of dietary preferences in Cretaceous species.

As yet, no one has attempted to thoroughly explore the ecology of Cretaceous mammals. In order to understand the ecological roles mammals may have played in their communities before the end of the Cretaceous, I examined body size and functional

morphology of teeth and diet in dentally conservative modern mammals. Regression equations were generated for modern marsupials, primates and insectivores. These equations were then used to estimate body size in Cretaceous mammals. Tooth morphology in these three groups was examined using landmark-based morphometrics. Based on this, and the results from body size studies, the relative body size diversity and dietary preferences of Cretaceous mammals are interpreted.

The following dissertation is divided into three chapters. Chapter 1, an examination of body size in Cretaceous marsupials of North America, is formatted for publication in the Journal of Mammalian Evolution. Chapter 2 is a collaborative effort with R. Cifelli, and is a comprehensive analysis of the body size of Late Cretaceous (Lancian) mammals of North America. Chapter 3 is a preliminary analysis of tooth morphology and diet in Late Cretaceous mammals. Chapters 2 and 3 are formatted for publication in the Journal of Vertebrate Paleontology.

A FIRST LOOK AT ESTIMATING BODY SIZE IN DENTALLY CONSERVATIVE MARSUPIALS

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Running Head: Estimating body size in dentally conservative marsupials

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ABSTRACT

The relationship between body size and tooth size has been documented for Recent primates and insectivores and resulting predictive equations used to estimate body size in fossil species. This relationship is an important one, as body size is related to a host of physiological and ecological factors. In this study, the relationship between body size and molar size in Recent, dentally conservative marsupials is examined and body size in Cretaceous marsupials is estimated. Body weight information and basic length, width and area measurements were taken from the molars of individuals from 22 species of Didelphidae and Dasyuridae. Least squares regression analysis shows that, as in previous studies on eutherians, the first upper and lower molars are generally the most highly correlated with body size. In fact, there is a strong relationship in these marsupials between body size and tooth size throughout the molar series, suggesting that a fairly accurate body size estimate could be obtained from molars other than the first molar. The inclusion of species that are morphologically divergent from the "average" morphotype may affect the analysis. Body mass estimated in Cretaceous marsupials indicates a range of sizes similar to that seen in Recent dentally conservative marsupials.

Key words: marsupials, Didelphidae, Dasyuridae, body size, tooth size

INTRODUCTION

The increasing number of studies in the past twenty years relating body size of an organism to its environment underscores the importance of this characteristic in ecological studies. Body size in mammals is an important determining factor for a number of ecological and physiological parameters, including, but not limited to, metabolic rates, temperature regulation, reproduction, home range, and locomotion (Western, 1979 and references cited therein; Peters, 1983; Schmidt-Nielsen, 1984; Temerin *et al.*, 1984; LaBarbera, 1986; Eisenberg, 1990; McNab, 1990).

One important outgrowth of such studies is the application of body-size analyses in vertebrate paleontology. The relationship between body size and environment in Recent mammals can serve as a template for the study of this relationship in extinct forms. Many of these studies have focused simply on the best predictors of body size (Janis, 1990; Van Valkenburgh, 1990) while others have focused on the practical uses of this predictive potential, for example, as part of an analysis of form-function relationships between extinct mammals and their environment (Kay, 1973; Gingerich, 1974; 1975; 1978; Kay and Hylander, 1978; Gingerich *et al.*, 1982; Gingerich and Smith, 1984; Strait, 1991).

The majority of early studies using body size estimates in mammals dealt mainly with primates (Gingerich, 1974; Kay, 1975; Wood, 1979; Gingerich *et al.*, 1982; Fleagle, 1985), with a few studies examining this relationship in insectivores (Gingerich and Smith, 1984; Legendre, 1989; Thewissen and Gingerich, 1989). Gingerich and Smith (1984) established equations to estimate body size in insectivores. Recently, Bloch *et al.* (1998) and Wood and Clemens (2001) used these equations to estimate body size of

extinct insectivorous mammals in the Eocene. To date, this relationship has not been examined for marsupials.

This study, part of a larger, more comprehensive study examining functional morphology and paleoecology of Cretaceous therian mammals, focuses on determining the best dental predictors of body size in Recent, dentally conservative marsupial taxa. As an example, the results are used to predict body size in some Cretaceous taxa. Although at least sixteen families of extant marsupials are recognized (Nowak, 1991, and references cited therein), two families, Didelphidae and Dasyuridae, are generally viewed as being dentally primitive. Although definition of the family Didelphidae is problematic, didelphids are consistently recognized as appearing in the Late Cretaceous (Clemens, 1979; Clemens *et al.*, 1979). Didelphidae are now exclusively New World in distribution (Nowak, 1991), reaching their greatest diversity in South America (Eisenberg, 1981; Lee and Cockburn, 1985). The dentition of didelphids often is considered to be the closest living analog to a morphotype for tribosphenic mammals (Crompton and Hiiemae, 1970; Crompton and Kielan-Jaworowska, 1978). For this reason, didelphids have figured prominently in studies treating the evolution of tooth occlusion in mammals (Crompton and Hiiemae, 1970; Hiiemae and Crompton, 1971; Crompton and Kielan-Jaworowska, 1978). Members of the family Dasyuridae are found only in Australasia and are principally nocturnal and terrestrial (Nowak, 1991). Whereas most didelphids appear to feed opportunistically on varied food resources, dasyurids are mainly carnivorous (Lee and Cockburn, 1985). Despite their different feeding strategies, the dentitions of the two families are remarkably similar.

MATERIALS AND METHODS

Basic tooth measurements and body weight data on Recent taxa were collected from individuals representing ten species of Didelphidae, comprising seven different genera; and twelve species of Dasyuridae, comprising seven different genera. Specimens are housed in the collections of the National Museum of Natural History (USNM; Table I). High-resolution molds (using 3M Express™ vinyl polysiloxane) were made of the upper and lower dentitions of individual adult specimens (male and female) that, where possible, had associated body weight and collection information. An attempt was made to include only those specimens with limited tooth wear. Nonetheless, it became necessary to include some worn specimens from a few of the rarer species. This is not unprecedented, because Johanson (1996) included worn teeth in her reevaluation of *Alphadon*, with the caveat that the wear did not severely alter basic length or width measurements. When body weight information was not associated with the individual specimens, mean body weights were taken from the literature (Silva and Downing, 1995; Strahan, 1995; see Table I). Specimens of only two species of Dasyuridae had original body weight information. To account for possible bias introduced by using original body weights for some dasyurid species, and mean body weights taken from the literature for others, an analysis of covariance was run on the slopes of regression lines generated for a sample that included all body weights from the literature and a sample using body weights from the literature plus some original body weights. No significant difference was found. Nonetheless, for consistency, mean body weights for all dasyurid species were taken from the literature. Mean tooth measurements for Cretaceous taxa were taken from Clemens (1966), Fox (1979a, b; 1981) and Cifelli (1994).

In their studies relating tooth size and body size in primates, Gingerich *et al.* (1982) and Gingerich and Smith (1984) used crown area (length x width) of upper and lower molars, arguing that tooth area is less influenced by differences in tooth shape than is length or width alone (see Kay, 1975), and thus is a more accurate depiction of tooth size. In this study, maximum length and width measurements were made on upper and lower molars, following the measuring techniques employed by Lillegraven (1969:16) for Didelphidae (Table II, III) and Dasyuridae (Table IV, V). Tooth area as well as separate length and width measurements were used in the analysis.

Two methods for fitting a straight line to a given set of points are reduced-major axis regression and least squares regression. The relative success of either method depends on a number of factors, one of which is the question being asked. Reynolds (2002) suggested that reduced-major axis is the best method for predictive purposes because, although there is error inherent in both *x*- and *y*- variables, the method yields more robust, less biased estimates of body size (Riggs *et al.*, 1978; Draper and Smith, 1998). Conversely, Gingerich and Smith (1984) suggested that reduced-major axis is best used for determining the *structural* relationship between two variables. For *predictive* purposes, their method of choice is least squares regression, where the *x*- variable is known (and therefore without measurement error), and there is assumed to be error only in the *y*- (dependent) variable (Gingerich and Smith, 1984). However, the difference in slopes calculated by either method is relatively low for variables that are highly correlated (Gingerich and Smith, 1984; Reynolds, 2002). For this study, in which the independent variable (tooth size) is known, least squares regression was used to generate predictive equations to estimate average body size of a species (as indicated by body

mass) for dentally conservative marsupials in general (a pooled sample of didelphids and dasyurids) as well as separately for Didelphidae and Dasyuridae, based on mean length, width and area of the molars for all species, as well as for males and females separately.

In allometric studies, the power function $Y = aX^b$ expresses the relationship between the independent (*x*-) and dependent (*y*-) variables. The data is usually logarithmically transformed into a linear equation, $\ln Y = b \ln X + \ln a$. In least squares regression analysis, this equation can then be used to estimate Y when only X is known. Smith (1993) cautions that a "detransformation bias" is introduced when a ln Y value is detransformed back into original arithmetic units. The detransformed estimated value of Y is the geometric mean, not the arithmetic mean. Since the geometric mean is always less than the arithmetic mean, the resulting estimated Y will be too low (Smith, 1993). Therefore, when using ln-transformed data in regression analysis the detransformed Y estimate should be multiplied by a correction factor. There are various correction factors that can be used (see Smith, 1993) for a discussion of correction factors and reasons for using each). In this study, all estimated values of mean body mass for a species were multiplied by a "smearing estimate", a correction factor used when the residuals are not normally distributed. It is calculated by using the mean of the detransformed residuals (Smith, 1993).

Gingerich *et al.* (1982), in their analysis of generalized primates and tree shrews, found that *Tarsius* and tree shrews fell well above the regression line. They noted that *Tarsius* and tree shrews have larger cheek teeth than what is expected for their body size (as compared to other primates) and attributed this to a more specialized insectivorous diet. Likewise, these analyses originally included two species of *Caluromys*, *C. derbianus*

and *C. philander*, but these two species also fell well above the regression line for marsupials used in this analysis, indicating that they have smaller teeth than expected for other didelphids of similar body size (see below). Therefore, they were removed from all subsequent analyses. All statistics were performed with Statview® and BIOMstat statistical packages at an alpha level of 0.05. All data were transformed using the natural (base *e*) logarithm.

RESULTS

Didelphidae

The ten species of didelphids used in this study span a wide range of body sizes, from the smallest, *Thylamys elegans* and *Gracilinanus* sp., with an average weight of approximately 27 g, to the largest, *Didelphis marsupialis*, at over 1300 g (Table I), resulting in a comparably wide range of tooth sizes. This spread of data along an axis is important in least squares regression, as this method is sensitive to extremes in data, particularly on the abscissa (independent variable) (Peters, 1983). Regression analysis of didelphids shows that lower molar size is strongly correlated with body size at all molar loci (correlation coefficients of 0.990–0.998), with those of m1 being the highest (Fig. 1). *Caluromys derbianus* and *C. philander* tend to fall above the regression line, particularly for the posterior molars, m3 and m4 (Fig. 2). This suggests that the posterior molars of these *Caluromys* species, especially m4, are comparatively smaller for a given body mass than in other didelphids. When *Caluromys* is removed from the analysis, correlation coefficients increase substantially for posterior molars (Fig. 1). In general, the correlation

between body size and tooth size decreases posteriorly in the molar series, with the exception of m4, which has a correlation coefficient similar to that of m1.

Upper molars show a pattern similar to the lowers, as M1 length and area are highly correlated with body size (Fig. 3). Unlike the lowers, the strength of the relationship between upper molar size and body size does not decrease posteriorly in the tooth row. In fact, the correlation coefficients are remarkably similar throughout the upper molar series. When *Caluromys derbianus* and *C. philander* are included in the analysis, there is a much weaker correlation between tooth area and body size in upper molars than in lower molars. Values for these species of *Caluromys* fall well above the regression line at all upper molar loci when tooth width is the independent variable (Fig. 2). This is particularly evident for M3 and M4, where tooth width in *Caluromys derbianus* and *C. philander* is much less than in other species with similar body mass. The removal of *Caluromys* from the analysis results in a better fit of the regression line for tooth size and body size at all upper molar loci (Fig. 3).

When tooth size is regressed on body size for males and females separately (excluding *Caluromys*), an analysis of covariance (ANCOVA) revealed no significant differences in the slopes between males and females at any position along the tooth row for upper or lower molars. This suggests that there is no statistical difference between males and females when predicting body size.

Dasyuridae

Body size data for Dasyuridae had to be obtained from the literature (Table I), because few of the important, but rare specimens of dasyurids at the USNM had associated body weight data. Nonetheless, as in Didelphidae, regression analyses showed

a strong correlation (r values range from 0.976–0.982) between lower molar size and body size in Dasyuridae. Interestingly, unlike didelphids (including *Caluromys*), the strength of the relationship between these variables does not decrease appreciably through the molar series from front to back (Fig. 4): correlation coefficients for m3 and m4 are nearly identical to those for m1 and m2.

Correlation patterns for the upper molars of dasyurids are similar to those for the lowers. The strength of the relationship between body size and tooth size is comparable throughout the molar row, with few exceptions (Fig. 5). The widths of the first two upper molars have the weakest correlation with body size, unlike the lowers, in which widths of all the molars are more strongly correlated with body size. Surprisingly, the highest correlation with body size was obtained for length and area of the M4.

As in Didelphidae, there are no differences in the regression slopes between males and females at any molar locus. Again, this suggests that there is no statistically significant difference in the relationship between body size and tooth size in males and females.

Pooled Didelphidae and Dasyuridae

Regression plots of molar size vs. body size for a pooled sample including all species of Didelphidae (except *Caluromys*) and Dasyuridae show that, despite a relatively strong correlation throughout the molar series, in general, the size of the first molar is most highly correlated with body size (Fig. 6). Tooth length or area of the lower first molar, with correlation coefficients of 0.985, would likely give the best prediction of body size when only tooth size is known. Either tooth length or area of the upper molars,

M1, M2, or particularly M3, could be used in predictive analyses, because both tooth characteristics are strongly correlated with body size in these three molars (Fig. 7).

Regression analyses performed separately on males and females (again, species of *Caluromys* excluded) show that, despite the larger body size of males, slopes of the regression line are not significantly different, indicating there is no difference in the relationship between body size and tooth size in males and females.

Actual vs. Predicted Body Mass

Table VI shows the average actual body mass for each modern species used in this analysis and the average body mass estimated from regression equations generated using Didelphidae, Dasyuridae, and a pooled sample. Overall, only the regression equations generated from tooth length and area of the lower and upper first molars were used because these consistently had some of the highest correlations between tooth size and body size.

Three questions were considered in the analysis. First, when comparing within a given group, Didelphidae, Dasyuridae, and the pooled sample, which tooth measurement of the lower and upper first molars is the best predictor of body size (of any species in the study, not just those within that group)? To answer this, the body mass for each species as predicted from equations generated from m1 length, m1 area, M1 length and M1 area within each group, was compared with the actual body mass of each species. For example, when examining the predicted body masses using all four equations generated from dasyurids, the frequency with which the predicted body mass was closest to the actual body mass was recorded for all four tooth measurements (lower and upper first molar length and area). A 1:1:1:1 success ratio (success = closest estimate to actual body

weight) between tooth characteristics was assumed. A Goodness of Fit G-test performed on the resulting frequencies showed that, statistically at least, within each group there was no significant difference between the success of one tooth parameter over another for predicting body size. In short, when using the predictive equations generated from either the pooled sample, Didelphidae or Dasyuridae, m1 length, m1 area, M1 length or M1 area all predict body size equally well for all three groups. A subsequent analysis examining the predictive success of M2 and M3 length, both of which are also highly correlated with body mass, showed that, when combined in the analysis with the first lower and upper molars, there is no significant difference between which tooth characteristics are the best predictors within any of the three groups.

Secondly, if one were to take each of the equations generated for m1 length, for example, from each group and compare them, which group's equation would be the best predictor? The estimated body mass, calculated from m1 length for dasyurids, m1 length for didelphids, and m1 length for the pooled sample could be compared with the actual body mass for all 22 species and the frequency of predictive success could be recorded. A G-test performed on each of the four tooth measurements showed that for m1 length and area, statistically at least, all three equations developed from didelphids, dasyurids, and a pooled sample, predicted body mass equally well. However, for M1 length and area there was a significant difference in the number of times the regression equation of one group best predicted body mass over another. Despite the fact that it was not statistically significant for m1 length or area, the overall trend is the same for the other two tooth measurements. That is, the regression equations generated for each tooth characteristic from Didelphidae and/or Dasyuridae more closely predict the actual body size than does

the equation from the pooled sample. Again, subsequent analysis with M2 and M3 length showed that, although not statistically significant, the regression equations from Didelphidae and Dasyuridae were better predictors than the equation generated from the pooled sample.

Finally, of the best predictive equations generated from Didelphidae and Dasyuridae for each tooth measurement, do they more successfully predict body size within their own group? For each tooth measurement, the accuracy of estimated body mass for species of Didelphidae as predicted from the didelphid equation was compared to that predicted using the dasyurid equation (and vice versa). That is, was there a difference in the number of times the didelphid equations more successfully predicted body mass for didelphids than for dasyurids? This was then tabulated also for the dasyurids. Intuitively, it seems likely that didelphid or dasyurid equations would predict better for the species from which the predictive equations were originally generated. This seems to be the case. Equations predicted body mass best for the group from which they were generated. However, it is interesting to note that an RxC test of independence showed that this was not significant for any tooth measurement. Therefore, statistically at least, either equation worked equally well for predicting body mass for either didelphid or dasyurid species using length or area of first molars.

Body Size in Cretaceous Marsupials

Cretaceous taxa chosen for this analysis represent relatively large samples of well-known species associated with widely available published data (Clemens, 1966; Fox, 1979a, b; 1981; Storer, 1991; Cifelli, 1994; see Johanson, 1996, for a recent taxonomic analysis of *Alphadon*). Average molar measurements for individual species

were used in the regression equations generated from didelphids and dasyurids to predict body weights for the Cretaceous marsupials (Table VII). Also included in the analysis are body sizes estimated using previously published equations for primates (Gingerich *et al.*, 1982) and insectivores (Bloch *et al.*, 1998). The resulting predicted body masses using marsupial equations vary considerably within each taxon, depending on the equation used. For example, body mass estimates for *Pediomys prokrejcii* range from 16.6 g using m1 area to nearly 39 g using M1 length, while those for *Alphadon halleyi* range from nearly 43 g using m1 length to over 90 g using M1 length. This is not unexpected, as similar results can be seen in the modern taxa (Table VI), and of course, body mass varies considerably in living members of a given species. Overall, estimated body sizes of Cretaceous marsupials (based on estimates using lower m1 size) range from the smallest species, *Pediomys prokrejcii*, with estimates ranging from 16.6–19.5 g, and *Alphadon perexiguus*, with an estimated body size between 25.0–32.7 g, to the largest, *Didelphodon vorax*, with an estimated body mass between 849.1–1579.7 g. The range of body sizes for Cretaceous marsupials is slightly less than that for modern dentally conservative marsupials, which range from the smallest species, *Planigale ingrami*, with a body mass around 4.2 g, to the largest, *Didelphis virginiana*, with a body size up to 3000 g (Silva and Downing, 1995).

Body mass estimates for primates and insectivores were not adjusted with a correction factor (Table VII). Since the detransformation bias is such that non-corrected body mass estimates are too low, any correction factor applied to estimated body mass generated from the primate equations would simply make estimates that are already too high even higher. Original data were not available in the literature to generate correction

factors for the insectivore regression equations used here. However, even if one assumes that the estimates are too low by 10% (the maximum correction factor for either didelphids or dasyurid lower molars only increases the estimate by 12%), then corrected body mass estimates using the insectivore regression equations are still far less than body mass estimates using marsupial equations.

DISCUSSION

There is a high correlation between body size and tooth size in the marsupials included in this study (generally, $r > 0.96$), consistent with the results of previous studies on dentally conservative eutherians such as primates, tree shrews and insectivores (Kay, 1975; Gingerich *et al.*, 1982; Gingerich and Smith, 1984). For the more dentally conservative marsupials in general, as well as for individual species of Didelphidae and Dasyuridae, the first upper or lower molar is consistently highly correlated with body size ($r > 0.97$). This relationship is not surprising because previous studies have shown the first molar to be a suitable predictor of body size (Gingerich *et al.*, 1982; Bloch *et al.*, 1998; Wood and Clemens, 2001). However, this study demonstrates that in marsupials often a tooth other than the first or second molar can be more highly correlated with body size.

It is interesting to note that the inclusion of some taxa in an analysis can significantly alter the strength of the relationship between tooth size and body size, suggesting that caution must be used when deciding which taxa should be used in the analysis. For instance, in the analysis of Didelphidae, the removal of *Caluromys* resulted in an increase in the strength of this relationship, particularly in the posterior molars.

Species of *Caluromys* differ from other didelphids in the sample in having a dietary regime that relies on fruits and nectar more heavily than in other didelphids (see Hume (1999) and references cited therein). Didelphids, though generally described as omnivorous, are generally opportunistic feeders, particularly members of *Didelphis*. Some species of mouse opossums (*Marmosa* sp., *Thylamys* sp.) include a greater concentration of animal material in their diets, while others may include a varied diet of fruit and insects (Hume, 1999). Kay (1975) found that insectivorous or folivorous primates had teeth with larger crushing surfaces and shearing blades than frugivores of similar body size. Morphologically the difference in diet between *Caluromys* and other didelphids is reflected in tooth morphology, as the upper and lower molars of *Caluromys* species have inflated, more rounded cusps than is typical of other didelphids.

Despite the sexual dimorphism exhibited in many marsupial taxa, these differences would not seem to have an effect on the predictive power of the relationship between body size and tooth size. Nonetheless, the resulting predicted body weight would, in general, probably be too low for males and too high for females. In spite of this, it is worth noting, as Gingerich *et al.* (1982) did, that the resulting predicted body weight is only an average for the species and so an over- or underestimate for males and females is expected.

It is clear that the choice of taxa used to generate regression equations can result in varying degrees of success in estimating body mass. The exclusion of the two species of *Caluromys* from the analysis clearly affected the strength of the correlation between tooth size and body mass, and thus affects the accuracy of the estimated body mass. *Caluromys* is morphologically divergent from the "average" didelphid morphotype in that

it has molars with more inflated, rounded cusps. Applying these equations to Cretaceous taxa may then be problematic, because one may not know if the fossil species is morphologically divergent. This suggests the need to further explore methods that can be used to recognize these morphological "outliers", possibly by quantifying the degree of morphological divergence through examination of residuals (Smith, 1984; Anthony and Kay, 1993) or thin plate spline techniques (see Rohlf and Marcus, 1993).

The choice of tooth measurement used in predicting body mass (whether using area or length of first upper or lower molars) seems to result in consistent estimates of body mass, at least within a narrow taxonomic group. In general, the equations generated using members of Dasyuridae and Didelphidae alone more accurately estimated body mass than when using the equations generated from the pooled sample. However, an equation generated from Dasyuridae or Didelphidae was no more accurate (statistically at least) in predicting body size of a species within its respective family than for a species in the other family, although in general, within-family accuracy of body size estimates was slightly better.

As a result of this study, estimating body size does not have to be limited by the regression equation or tooth characteristic available, at least not for modern, dentally conservative marsupials. Body size for many dentally conservative marsupials can be accurately predicted using the equations generated from members of either Didelphidae or Dasyuridae, using any molar available to the researcher. However, it is worth mentioning that caution must be employed when interpreting the results of body size predictions for fossil species, because the accuracy of the predictions depends on the choice of tooth measurement or regression equation.

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Table I. List of mean body masses for species of Didelphidae and Dasyuridae used in this study[a]

	N (male, female)	Body Mass (g) Mean (male/female)	Reference
Didelphidae			
Caluromys derbianus	8 (4, 4)	275.8 (288.8, 262.8)	This study
Caluromys philander	5 (3, 2)	226.0 (266.7, 165.0)	This study
Didelphis albiventris	2 (1, 1)	1332.6 (1265.2, 1400.0)	This study
Didelphis marsupialis	6 (3, 3)	1342.1 (1420.0, 1264.1)	This study
Gracilinamus agilis	2 (1, 1)	30.8 (29.0, 32.5)	This study
Gracilinamus sp.	2 (2, –)	27.4 (27.4, –)	This study
Marmosa xerophila	19 (9, 10)	51.6 (62.5, 41.7)	This study
Monodelphis domestica	6 (3, 3)	83.0 (95.3, 70.6)	This study
Philander opossum	13 (9, 4)	531.2 (574.8, 433.3)	This study
Thylamys elegans	7 (5, 2)	27.6 (30.6, 20.0)	This study
Dasyuridae			
Antechinus godmani	5 (4, 1)	95.0, 58.0	Strahan, 1995

Antechinus minimus	6 (2, 4)	65.0, 42.0	Strahan, 1995
Antechinus stuartii	5 (3, 2)	35.0, 20.0	Strahan, 1995
Dasyuroides byrnei	4 (2, 1)[b]	120.0, 100.0	Strahan, 1995
Dasyurus hallucatus	5 (2, 3)	500.0	Strahan, 1995
Dasyurus maculatus	2 (1, 2)	4000.0	Silva and Downing, 1995
Dasyurus viverrinus	3 (3, –)	1300.0, –	Strahan, 1995
Phascogale tapoatafa	2[b]	231.0	Strahan, 1995
Planigale maculata	3 (3, –)	12.0, –	Strahan, 1995
Sarcophilus harrisii	4 (3, 1)	9000.0, 7000.0	Strahan, 1995
Sminthopsis dolichura	1	14.8, –	Strahan, 1995
Sminthopsis macroura	5	20.0	Strahan, 1995

[a]Average values for males and females (if available) were pooled and included in the overall species average presented here.
[b]Includes specimens of unknown sex.

Table II. Length and width measurements (in mm) for lower molars of Didelphidae[a]

Species		m1				m2			
		N	Mean	CV	OR	N	Mean	CV	OR
Caluromys derbianus	L	8	3.01	3.74	2.89–3.25	8	2.86	3.80	2.75–3.08
	W	8	1.70	3.77	1.61–1.79	8	1.67	4.60	1.56–1.81
Caluromys philander	L	5	2.75	4.50	2.59–2.91	5	2.67	3.98	2.55–2.80
	W	5	1.64	3.32	1.56–1.69	5	1.66	5.00	1.56–1.74
Didelphis albiventris	L	2	5.06	1.17	5.02–5.11	2	5.14	1.37	5.09–5.20
	W	2	2.96	1.98	2.92–3.00	2	3.10	2.69	3.04–3.16
Didelphis marsupialis	L	6	5.33	4.25	5.04–5.64	6	5.62	4.27	5.32–5.93
	W	6	3.21	5.72	3.02–3.44	6	3.46	3.48	3.29–3.64
Gracilinanus agilis	L	2	1.56	2.08	1.54–1.59	2	1.65	5.60	1.59–1.72
	W	2	0.90	1.42	0.89–0.91	2	0.98	0.58	0.98–0.99
Gracilinanus sp.	L	2	1.48	0.05	–	2	1.69	3.84	1.65–1.74
	W	2	0.91	3.26	0.89–0.93	2	1.03	2.96	1.00–1.05
Marmosa xerophila	L	19	1.71	4.50	1.50–1.84	19	1.81	3.81	1.69–1.95
	W	19	1.01	5.34	0.94–1.18	19	1.1	5.71	0.99–1.28
Monodelphis domestica	L	6	2.05	4.88	1.96–2.24	6	2.23	4.61	2.07–2.36
	W	6	1.27	5.09	1.21–1.38	6	1.43	3.39	1.37–1.49
Philander opossum	L	13	3.75	5.25	3.41–4.04	13	4.06	4.88	3.82–4.50
	W	13	2.09	5.35	1.89–2.25	13	2.27	6.42	2.03–2.51
Thylamys elegans	L	7	1.50	4.20	1.41–1.57	7	1.71	5.04	1.59–1.80
	W	7	0.90	4.04	0.85–0.95	7	1.05	5.39	0.97–1.12

	m3				m4			
	N	Mean	CV	OR	N	Mean	CV	OR
Caluromys derbianus	8	2.70	4.01	2.55–2.89	8	2.34	4.82	2.08–2.45
	8	1.52	4.80	1.40–1.63	8	1.19	4.73	1.08–1.25
Caluromys philander	5	2.55	3.97	2.43–2.66	5	2.21	2.93	2.13–2.27
	5	1.50	7.10	1.41–1.62	5	1.18	3.16	1.12–1.22
Didelphis albiventris	2	5.43	2.53	5.33–5.53	2	5.71	1.63	5.64–5.78
	2	3.08	1.49	3.05–3.11	2	2.95	0.65	2.93–2.96
Didelphis marsupialis	6	6.05	4.45	5.75–6.41	6	6.28	7.91	5.45–6.94
	6	3.55	3.84	3.40–3.74	6	3.23	3.82	3.07–3.40
Gracilinanus agilis	2	1.61	6.01	1.54–1.68	2	1.63	12.87	1.48–1.77
	2	0.98	4.11	0.95–1.01	2	0.84	3.45	0.82–0.86
Gracilinanus sp.	2	1.70	1.71	1.68–1.72	2	1.66	0.17	–
	2	0.95	4.37	0.93–0.98	2	0.86	0.49	0.86–0.87
Marmosa xerophila	19	1.87	3.42	1.76–2.01	19	1.95	4.23	1.81–2.11
	19	1.08	4.80	1.00–1.18	19	0.98	3.71	0.92–1.05
Monodelphis domestica	6	2.36	2.74	2.28–2.44	6	2.48	5.06	2.32–2.62
	6	1.51	4.96	1.44–1.65	6	1.37	3.68	1.27–1.41
Philander opossum	13	4.32	5.19	4.08–4.84	13	4.53	4.38	4.31–4.88
	13	2.39	5.26	2.19–2.59	13	2.31	5.56	2.06–2.50
Thylamys elegans	7	1.80	4.74	1.67–1.87	7	1.72	3.35	1.66–1.81
	7	1.08	5.00	1.00–1.14	7	0.99	3.59	0.93–1.02

[a]Abbreviations: Length (L), Width (W), N (number of specimens), CV (coefficient of variation), and OR (observed range).

Table III. Length and width measurements (in mm) for upper molars of Didelphidae[a]

Species		M1				M2			
		N	Mean	CV	OR	N	Mean	CV	OR
Caluromys derbianus	L	8	2.95	4.41	2.79–3.18	8	2.81	3.09	2.71–3.01
	W	8	2.69	5.31	2.50–2.99	8	2.68	7.82	2.52–3.15
Caluromys philander	L	5	2.66	1.96	2.61–2.73	5	2.60	2.00	2.56–2.68
	W	5	2.69	5.57	2.53–2.88	5	2.65	5.57	2.49–2.83
Didelphis albiventris	L	1	–	–	5.25	2	5.28	0.13	5.27–5.28
	W	2	4.81	1.66	4.75–4.87	2	5.33	1.29	5.29–5.38
Didelphis marsupialis	L	6	5.21	2.52	4.99–5.36	6	5.63	5.29	5.36–6.04
	W	6	5.16	6.17	4.79–5.70	6	5.83	4.30	5.52–6.18
Gracilinanus agilis	L	2	1.72	0.25	1.72–1.73	2	1.72	6.22	1.64–1.79
	W	2	1.62	2.96	1.59–1.66	2	1.83	5.10	1.76–1.90
Gracilinanus sp.	L	2	1.69	6.36	1.62–1.77	2	1.74	1.26	1.72–1.75
	W	2	1.69	0.71	1.68–1.70	2	1.96	1.05	1.95–1.97
Marmosa xerophila	L	19	1.71	4.34	1.59–1.83	19	1.78	5.68	1.63–1.97
	W	19	1.98	4.96	1.82–2.19	19	2.17	4.08	1.97–2.31
Monodelphis domestica	L	6	2.10	9.56	1.89–2.38	6	2.18	5.94	1.98–2.32
	W	6	2.62	3.02	2.55–2.75	6	2.82	3.10	2.70–2.95
Philander opossum	L	13	3.71	4.61	3.46–4.01	13	3.99	5.84	3.67–4.46
	W	13	3.93	3.32	3.72–4.12	13	4.57	5.72	4.09–5.08
Thylamys elegans	L	7	1.62	6.92	1.41–1.73	7	1.70	6.91	1.49–1.82
	W	7	1.88	4.11	1.75–1.97	7	2.16	2.71	2.08–2.27

	M3				M4			
	N	Mean	CV	OR	N	Mean	CV	OR
Caluromys derbianus	8	2.61	4.17	2.52–2.83	7	1.92	6.22	1.76–2.06
	8	2.43	6.21	2.30–2.75	7	1.95	8.42	1.75–2.23
Caluromys philander	5	2.41	4.53	2.30–2.57	5	1.69	10.21	1.47–1.88
	5	2.52	6.79	2.27–2.68	5	1.92	6.95	1.71–2.05
Didelphis albiventris	2	5.30	7.18	5.03–5.57	2	4.00	13.05	3.63–4.37
	2	5.81	0.72	5.78–5.84	2	4.54	1.04	4.51–4.58
Didelphis marsupialis	6	5.92	5.40	5.54–6.37	6	4.43	10.98	3.79–5.26
	6	6.49	3.17	6.22–6.75	5	5.44	7.37	4.99–5.93
Gracilinanus agilis	2	1.60	10.62	1.48–1.73	2	1.18	11.13	1.08–1.27
	2	1.94	8.76	1.82–2.06	2	1.73	5.51	1.67–1.80
Gracilinanus sp.	2	1.60	0.53	1.60–1.61	2	1.13	1.37	1.12–1.15
	2	2.14	1.25	2.12–2.16	2	1.91	4.30	1.85–1.97
Marmosa xerophila	19	1.84	4.17	1.72–1.96	19	1.24	9.07	1.04–1.42
	19	2.34	4.79	2.11–2.53	19	2.11	6.19	1.87–2.41
Monodelphis domestica	6	2.33	5.50	2.13–2.53	6	1.45	9.03	1.29–1.62
	6	2.95	4.35	2.77–3.14	6	2.73	6.87	2.45–2.94
Philander opossum	13	4.13	4.25	3.87–4.51	13	2.96	8.84	2.59–3.53
	13	5.08	4.93	4.81–5.64	13	4.34	5.26	4.09–4.76
Thylamys elegans	7	1.73	5.37	1.64–1.86	7	1.10	6.53	1.02–1.19
	7	2.29	4.33	2.20–2.45	7	2.17	6.66	2.00–2.40

[a]Abbreviations as in Table II.

Table IV. Length and width measurements (in mm) for lower molars of Dasyuridae[a]

Species		m1				m2			
		N	Mean	CV	OR	N	Mean	CV	OR
Antechinus godmani	L	5	1.94	2.35	1.90–2.00	5	2.29	1.93	2.22–2.34
	W	5	1.08	2.46	1.04–1.10	5	1.28	1.95	1.26–1.32
Antechinus minimus	L	6	1.58	6.41	1.46–1.69	6	1.81	5.03	1.69–1.90
	W	6	0.85	5.70	0.78–0.90	6	1.06	3.84	0.99–1.11
Antechinus stuartii	L	5	1.68	4.27	1.61–1.80	5	2.00	3.68	1.90–2.10
	W	5	0.94	5.89	0.89–1.01	5	1.23	4.94	1.17–1.30
Dasyuroides byrnei	L	4	2.78	2.35	2.69–2.82	4	3.12	2.32	3.02–3.19
	W	4	1.40	5.53	1.29–1.45	4	1.81	4.80	1.68–1.87
Dasyurus hallucatus	L	5	3.75	0.98	3.72–3.81	5	4.32	1.71	4.24–4.43
	W	5	2.04	4.97	1.94–2.18	5	2.42	2.99	2.31–2.50
Dasyurus maculatus	L	3	5.11	3.85	4.89–5.26	3	5.75	3.20	5.64–5.96
	W	3	2.92	7.17	2.69–3.11	3	3.57	3.98	3.41–3.66
Dasyurus viverrinus	L	3	4.74	5.03	4.48–4.95	3	5.43	3.00	5.25–5.55
	W	3	2.77	3.26	2.71–2.88	3	3.23	3.06	3.12–3.31
Phascogale tapoatafa	L	2	2.78	7.80	2.63–2.93	2	3.24	5.45	3.13–3.37
	W	2	1.61	10.11	1.49–1.72	2	1.86	3.08	1.82–1.90
Planigale maculata	L	3	1.18	3.91	1.13–1.22	3	1.37	2.83	1.34–1.42
	W	3	0.63	6.32	0.59–0.67	3	0.84	4.45	0.80–0.87
Sarcophilus harrisii	L	4	9.06	4.11	8.60–9.43	4	10.05	1.96	9.77–10.22
	W	4	6.60	3.24	6.33–6.81	4	6.94	5.70	6.63–7.50
Sminthopsis dolichura	L	1	–	–	1.51	1	–	–	1.71
	W	1	–	–	0.78	1	–	–	0.99
Sminthopsis macroura	L	5	1.37	3.02	1.34–1.44	5	1.48	2.86	1.43 - 1.55
	W	5	0.75	2.24	0.72–0.77	5	0.91	3.29	0.88–0.96

	m3				m4			
	N	Mean	CV	OR	N	Mean	CV	OR
Antechinus godmani	5	2.25	0.98	2.23–2.27	5	1.99	2.68	1.90–2.04
	5	1.32	3.99	1.27–1.39	5	1.17	2.56	1.14–1.21
Antechinus minimus	6	1.85	5.21	1.70–1.93	6	1.74	3.24	1.64–1.81
	6	1.13	2.62	1.09–1.18	6	1.01	3.85	0.95–1.05
Antechinus stuartii	5	1.99	1.80	1.95–2.04	5	1.68	2.74	1.63–1.74
	5	1.25	4.66	1.20–1.33	5	1.05	2.65	1.02–1.10
Dasyuroides byrnei	4	3.09	3.89	2.96–3.21	4	2.69	1.96	2.64–2.76
	4	1.96	4.42	1.83–2.03	4	1.75	3.56	1.70–1.83
Dasyurus hallucatus	5	4.38	1.00	4.33–4.42	5	4.01	1.16	3.98–4.09
	5	2.56	3.20	2.46–2.67	5	2.38	4.34	2.28–2.51
Dasyurus maculatus	3	6.27	3.81	6.04–6.51	3	6.43	1.3	6.34–6.50
	3	3.71	6.47	3.43–3.86	3	3.69	6.59	3.42–3.89
Dasyurus viverrinus	3	5.6	0.89	5.56–5.66	3	5.49	1.02	5.44–5.55
	3	3.32	2.00	3.27–3.40	3	3.27	4.13	3.18–3.43
Phascogale tapoatafa	2	3.00	2.88	2.94–3.06	2	2.48	3.96	2.41–2.55
	2	1.88	1.99	1.86–1.91	2	1.67	3.8	1.63–1.72
Planigale maculata	3	1.33	2.11	1.30–1.36	3	1.24	6.06	1.17–1.32
	3	0.92	4.74	0.87–0.94	3	0.80	1.00	0.79–0.81
Sarcophilus harrisii	4	11.3	2.19	10.98–11.54	4	11.3	4.65	10.65–11.90
	4	7.05	2.16	6.92–7.20	4	6.71	3.45	6.45–6.91
Sminthopsis dolichura	1	–	–	1.73	1	–	–	1.62
	1	–	–	1.10	1	–	–	1.01
Sminthopsis macroura	5	1.55	3.80	1.48–1.65	5	1.41	3.76	1.33–1.47
	5	1.00	5.33	0.97–1.09	5	0.92	4.42	0.86–0.97

[a]Abbreviations as in Table II.

Table V. Length and width measurements (in mm) for upper molars of Dasyuridae[a]

Species		M1				M2			
		N	Mean	CV	OR	N	Mean	CV	OR
Antechinus godmani	L	5	2.09	4.47	1.93–2.15	5	2.15	2.85	2.06–2.23
	W	5	2.12	4.49	2.00–2.24	5	2.39	4.05	2.28–2.50
Antechinus minimus	L	6	1.66	6.63	1.51–1.85	6	1.73	6.16	1.60–1.88
	W	6	1.80	2.65	1.73–1.85	6	2.07	4.23	1.92–2.16
Antechinus stuartii	L	5	1.81	3.71	1.72–1.90	5	1.88	3.53	1.82–1.99
	W	4	1.97	3.67	1.88–2.05	4	2.28	3.43	2.21–2.35
Dasyuroides byrnei	L	4	2.58	5.86	2.44–2.73	4	3.01	3.17	2.91–3.14
	W	4	3.14	1.31	3.10–3.18	4	3.63	2.88	3.54–3.77
Dasyurus hallucatus	L	5	3.96	3.12	3.82–4.14	5	4.32	1.51	4.25–4.39
	W	5	4.14	5.28	3.84–4.36	5	4.61	3.65	4.41–4.87
Dasyurus maculatus	L	3	5.42	6.56	5.15–5.82	3	5.86	3.99	5.68–6.12
	W	3	5.27	5.68	5.09–5.61	3	6.41	5.44	6.14–6.80
Dasyurus viverrinus	L	3	5.06	5.64	4.73–5.23	3	5.20	2.31	5.08–5.32
	W	3	4.95	7.08	4.65–5.33	3	5.74	4.60	5.55–6.04
Phascogale tapoatafa	L	2	3.09	13.98	2.79–3.40	2	3.18	12.28	2.91–3.46
	W	2	3.20	2.80	3.12–3.25	2	3.54	4.67	3.43–3.66
Planigale maculata	L	3	1.39	9.73	1.24–1.50	3	1.25	4.44	1.21–1.31
	W	3	1.50	1.55	1.47–1.52	3	1.69	2.20	1.65–1.72
Sarcophilus harrisii	L	4	10.55	1.60	10.31–10.70	4	11.64	3.27	11.08–11.94
	W	4	10.38	4.10	10.02–10.97	4	11.14	4.64	10.41–11.59
Sminthopsis dolichura	L	1	–	–	1.47	1	–	–	1.62
	W	1	–	–	1.93	1	–	–	2.19
Sminthopsis macroura	L	5	1.31	5.51	1.19–1.37	5	1.36	2.74	1.32–1.41
	W	5	1.78	3.45	1.72–1.89	5	2.03	3.06	1.95–2.12

	M3				M4			
	N	Mean	CV	OR	N	Mean	CV	OR
Antechinus godmani	5	1.99	2.92	1.94–2.07	5	1.21	8.28	1.09–1.36
	5	2.30	5.26	2.18–2.44	5	2.03	5.83	1.86–2.13
Antechinus minimus	6	1.67	4.15	1.60–1.78	5	1.15	6.94	1.02–1.23
	6	2.07	4.70	1.93–2.17	5	1.75	4.74	1.65–1.82
Antechinus stuartii	5	1.77	3.96	1.66–1.83	5	1.05	5.79	0.96–1.11
	4	2.22	5.16	2.10–2.32	4	1.74	1.16	1.72–1.76
Dasyuroides byrnei	4	2.80	2.08	2.72–2.85	4	1.61	4.75	1.53–1.68
	3	3.45	3.80	3.31–3.57	3	2.60	6.04	2.42–2.73
Dasyurus hallucatus	5	4.19	2.18	4.09–4.32	5	2.21	3.38	2.12–2.29
	5	4.62	1.89	4.53–4.73	5	4.17	3.87	4.04–4.40
Dasyurus maculatus	3	6.33	5.25	5.98–6.65	3	3.35	1.90	3.29–3.42
	3	6.97	8.12	6.46–7.58	3	6.23	5.79	5.87–6.59
Dasyurus viverrinus	3	5.22	5.56	4.98–5.54	3	3.07	17.80	2.47–3.53
	2	6.58	3.37	6.42–6.73	2	5.07	0.88	5.04–5.10
Phascogale tapoatafa	2	2.77	2.45	2.72–2.82	2	1.53	9.81	1.42–1.63
	2	3.34	3.86	3.25–3.43	2	2.64	6.72	2.52–2.77
Planigale maculata	3	1.14	7.02	1.07–1.23	3	0.74	8.30	0.69–0.81
	3	1.69	2.01	1.66–1.73	3	1.27	5.37	1.20–1.31
Sarcophilus harrisii	4	11.81	3.15	11.27–12.13	3	4.26	6.66	3.98–4.55
	4	10.23	5.35	9.60–10.83	3	7.34	10.48	6.49–7.99
Sminthopsis dolichura	1	–	–	1.53	1	–	–	0.90
	1	–	–	2.13	1	–	–	1.81
Sminthopsis macroura	5	1.35	2.70	1.29–1.37	5	1.01	3.23	0.96–1.05
	5	2.04	3.04	1.98–2.13	5	1.65	2.08	1.63–1.71

[a]Abbreviations as in Table II.

Table VI. Mean body mass and estimated body mass of didelphids, dasyurids, and a pooled sample[a]

Species	Body Mass (g) Mean (male, female)	m1L Pooled	m1L Did	m1L Das	m1 LxW Pooled	m1 LxW Did	m1 LxW Das
Antechinus godmani	87.6 (95.0, 58.0)	66.7	67.2	66.9	65.2	60.7	69.5
Antechinus minimus	49.7 (65.0, 42.0)	33.8	35.7	33.1	32.4	30.8	34.2
Antechinus stuartii	29.0 (35.0,20.0)	41.8	43.5	41.2	42.1	39.7	44.6
Caluromys derbianus	275.8 (288.8, 262.8)	287.3	262.5	302.4	276.1	246.8	298.7
Caluromys philander	226.0 (266.7, 165)	212.4	198.0	221.3	225.4	202.7	243.4
Dasyuroides byrnei	115.0 (120.0,100.0)	219.6	204.3	229.1	177.9	161.0	191.5
Dasyurus hallucatus	500.0	593.2	516.0	639.4	525.0	461.0	572.2
Dasyurus maculatus	4000.0	1667.9	1353.2	1860.6	1538.4	1310.7	1697.2
Dasyurus viverrinus	1300.0	1295.4	1069.1	1433.1	1252.3	1073.1	1378.4

Species	Body Mass (g) Mean (male, female)	m1L Pooled	m1L Did	m1L Das	m1 LxW Pooled	m1 LxW Did	m1 LxW Das
Didelphis albiventris	1332.6 (1265.2, 1400)	1614.4	1312.6	1799.0	1546.1	1317.1	1705.8
Didelphis marsupialis	1342.1 (1420.0, 1264.1)	1914.5	1538.9	2145.5	1912.3	1619.4	2114.9
Gracilinanus agilis	30.8 (29, 32.5)	32.7	34.6	32.0	34.6	32.7	36.5
Gracilinanus sp.	27.4	27.3	29.2	26.5	32.3	30.7	34.2
Marmosa xerophila	51.6 (62.5, 41.7)	43.9	45.6	43.4	48.1	45.2	51.1
Monodelphis domestica	83.0 (95.3, 70.6)	80.3	80.0	81.1	93.8	86.4	100.2
Phascogale tapoatafa	231.0	219.9	204.6	229.4	222.9	200.4	240.6
Philander opossum	531.2 (574.8, 433.3)	596.3	518.6	642.9	547.1	479.8	596.6
Planigale maculata	12.0	12.7	14.3	12.0	12.3	12.0	12.9
Sarcophilus harrisii	8500.0 (9000, 7000)	11134.9	7947.5	13228.5	14239.6	11398.1	16106.3

Species	Body Mass (g) Mean (male, female)	m1L Pooled	m1L Did	m1L Das	m1 LxW Pooled	m1 LxW Did	m1 LxW Das
Sminthopsis dolichura	14.8 (14.8, 12.4)	29.3	31.3	28.6	26.0	24.8	27.4
Sminthopsis macroura	20.0	21.2	23.0	20.4	21.0	20.1	22.0
Thylamys elegans	27.6 (30.6, 20.0)	28.8	30.7	28.0	32.9	31.2	34.7

	Body Mass (g)	M1L			M1 LxW		
	Mean (male, female)	Pooled	Did	Das	Pooled	Did	Das
Antechinus godmani	87.6 (95.0, 58.0)	75.7	76.9	74.7	67.2	71.2	63.7
Antechinus minimus	49.7 (65.0, 42.0)	35.5	36.2	34.9	33.9	36.0	32.0
Antechinus stuartii	29.0 (35.0,20.0)	47.0	47.8	46.3	46.4	49.3	43.9
Caluromys derbianus	275.8 (288.8, 262.8)	235.2	237.6	232.7	185.3	195.6	176.3
Caluromys philander	226.0 (266.7, 165)	166.6	168.6	164.7	154.3	163.0	146.7
Dasyuroides byrnei	115.0 (120.0,100.0)	150.2	152.1	148.5	191.3	202.0	182.1
Dasyurus hallucatus	500.0	619.6	623.1	614.9	652.3	685.2	623.8
Dasyurus maculatus	4000.0	1738.4	1739.4	1729.9	1718.7	1798.3	1650.0
Dasyurus viverrinus	1300.0	1390.8	1393.1	1383.2	1369.1	1433.8	1313.2

	Body Mass (g)		M1L			M1 LxW	
	Mean (male, female)	Pooled	Did	Das	Pooled	Did	Das
Didelphis albiventris	1332.6 (1265.2, 1400)	1567.7	1569.4	1559.6	1356.0	1420.2	1300.6
Didelphis marsupialis	1342.1 (1420.0, 1264.1)	1526.7	1528.5	1518.7	1543.8	1616.0	1481.5
Gracilinanus agilis	30.8 (29, 32.5)	39.7	40.5	39.1	30.1	32.0	28.4
Gracilinanus sp.	27.4	37.3	38.0	36.7	31.3	33.3	29.6
Marmosa xerophila	51.6 (62.5, 41.7)	38.3	39.1	37.8	41.8	44.4	39.6
Monodelphis domestica	83.0 (95.3, 70.6)	76.0	77.2	75.0	97.9	103.6	92.9
Phascogale tapoatafa	231.0	274.3	276.9	271.6	270.5	285.1	257.7
Philander opossum	531.2 (574.8, 433.3)	500.6	503.9	496.5	533.9	561.2	510.1
Planigale maculata	12.0	19.6	20.0	19.3	18.0	19.2	17.0

	Body Mass (g)	M1L			M1 LxW		
	Mean (male, female)	Pooled	Did	Das	Pooled	Did	Das
Sarcophilus harrisii	8500.0 (9000, 7000)	15704.2	15546.0	15721.8	17792.8	18443.0	17243.5
Sminthopsis dolichura	14.8 (14.8, 12.4)	23.6	24.1	23.2	30.9	32.9	29.2
Sminthopsis macroura	20.0	15.9	16.2	15.6	21.9	23.4	20.7
Thylamys elegans	27.6 (30.6, 20.0)	32.1	32.7	31.6	34.8	37.0	32.9

[a]Body mass was estimated using regression equations generated for lower first molar length (m1L) and area (m1 LxW) and upper first molar length (M1L) and area (M1 LxW) from didelphids (Did), dasyurids (Das) and a pooled sample.

Table VII. Estimated body mass (in grams) for various Cretaceous marsupial taxa[a]

	Didelphidae		Dasyuridae		Primates	Insect.	Didelphidae		Dasyuridae		Primates	Insect.
Species	**m1 L**	**m1 LxW**	**m1 L**	**m1 LxW**	**m1 LxW**	**m1 LxW**	**M1 L**	**M1 LxW**	**M1 L**	**M1 LxW**	**M1 LxW**	**M1 LxW**
Pediomys prokrejcii	19.50	16.65	16.97	18.07	30.25	4.82	38.71	24.19	37.40	21.44	61.85	10.72
Pediomys krejcii	29.75	33.71	27.09	37.65	59.34	10.06	37.23	47.07	35.96	41.94	115.22	20.71
Pediomys elegans							51.10	61.79	49.47	55.18	148.60	27.10
Pediomys clemensi	73.99	75.57	74.35	87.21	128.31	23.37	66.00	64.74	64.03	57.83	155.22	28.38
Protalphadon lulli							52.93	60.99	51.26	54.46	146.80	26.76
Alphadon perexiguus	32.69	25.01	30.07	27.60	44.62	7.37						
Alphadon marshi							67.09	69.12	65.10	61.78	165.01	30.28
Alphadon halleyi	44.74	44.13	42.58	49.83	76.76	13.33	90.26	70.18	87.77	62.73	167.37	30.74
Turgidodon russelli	147.60	121.28	159.79	142.64	201.58	38.28	156.23	147.71	152.56	132.82	335.58	64.17
Turgidodon praesagus	209.62	200.09	235.68	240.16	325.20	64.55						
Turgidodon rhaister							355.61	398.78	349.43	361.48	849.19	171.36
Eodelphis sp.	456.28	452.62	557.94	561.45	709.16	151.30	414.68	591.26	407.95	537.65	1227.13	252.98
Eodelphis cutleri	496.66	544.41	612.90	680.37	845.94	183.45						

Species	Didelphidae		Dasyuridae		Primates	Insect.	Didelphidae		Dasyuridae		Primates	Insect.
	m1 L	m1 LxW	m1 L	m1 LxW	m1 LxW	m1 LxW	M1 L	M1 LxW	M1 L	M1 LxW	M1 LxW	M1 LxW
Didelphodon vorax	849.10	1223.38	1110.26	1579.72	1833.14	427.05	1091.84	1910.33	1082.08	1753.67	3672.92	806.92

[a]Body mass estimated using regression equations generated from didelphids, dasyurids, primates and insectivores (Insect.). See Table VI for abbreviations.

FIGURE LEGENDS

Figure 1. Regression plots showing the relationship between mean body size and mean tooth size (length and width [in mm], and area [LxW, in mm^2]) for lower molars of Didelphidae (*Caluromys* excluded), including regression equations and correlation coefficients for each tooth measurement.

Figure 2. Regression plots of mean body size vs. mean tooth size for upper and lower third and fourth molars of Didelphidae. Filled symbols represent two species of *Caluromys*, showing that they tend to have much smaller teeth relative to other didelphids of similar body size.

Figure 3. Regression plots showing the relationship between mean body size and mean tooth size (length and width [in mm], and area [LxW, in mm^2]) for upper molars of Didelphidae (*Caluromys* excluded), including regression equations and correlation coefficients for each tooth measurement.

Figure 4. Regression plots showing the relationship between mean body size and mean tooth size (length and width [in mm], and area [LxW, in mm^2]) for lower molars of Dasyuridae, including regression equations and correlation coefficients for each tooth measurement.

Figure 5. Regression plots showing the relationship between mean body size and mean tooth size (length and width [in mm], and area [LxW, in mm^2]) for upper molars of

Dasyuridae, including regression equations and correlation coefficients for each tooth measurement.

Figure 6. Regression plots showing the relationship between mean body size and mean tooth size (length and width [in mm], and area [LxW, in mm^2]) for lower molars of a pooled sample of marsupials (*Caluromys* excluded), including regression equations and correlation coefficients for each tooth measurement.

Figure 7. Regression plots showing the relationship between mean body size and mean tooth size (length and width [in mm], and area [LxW, in mm^2]) for upper molars of a pooled sample of marsupials (*Caluromys* excluded), including regression equations and correlation coefficients for each tooth measurement.

Figure 1

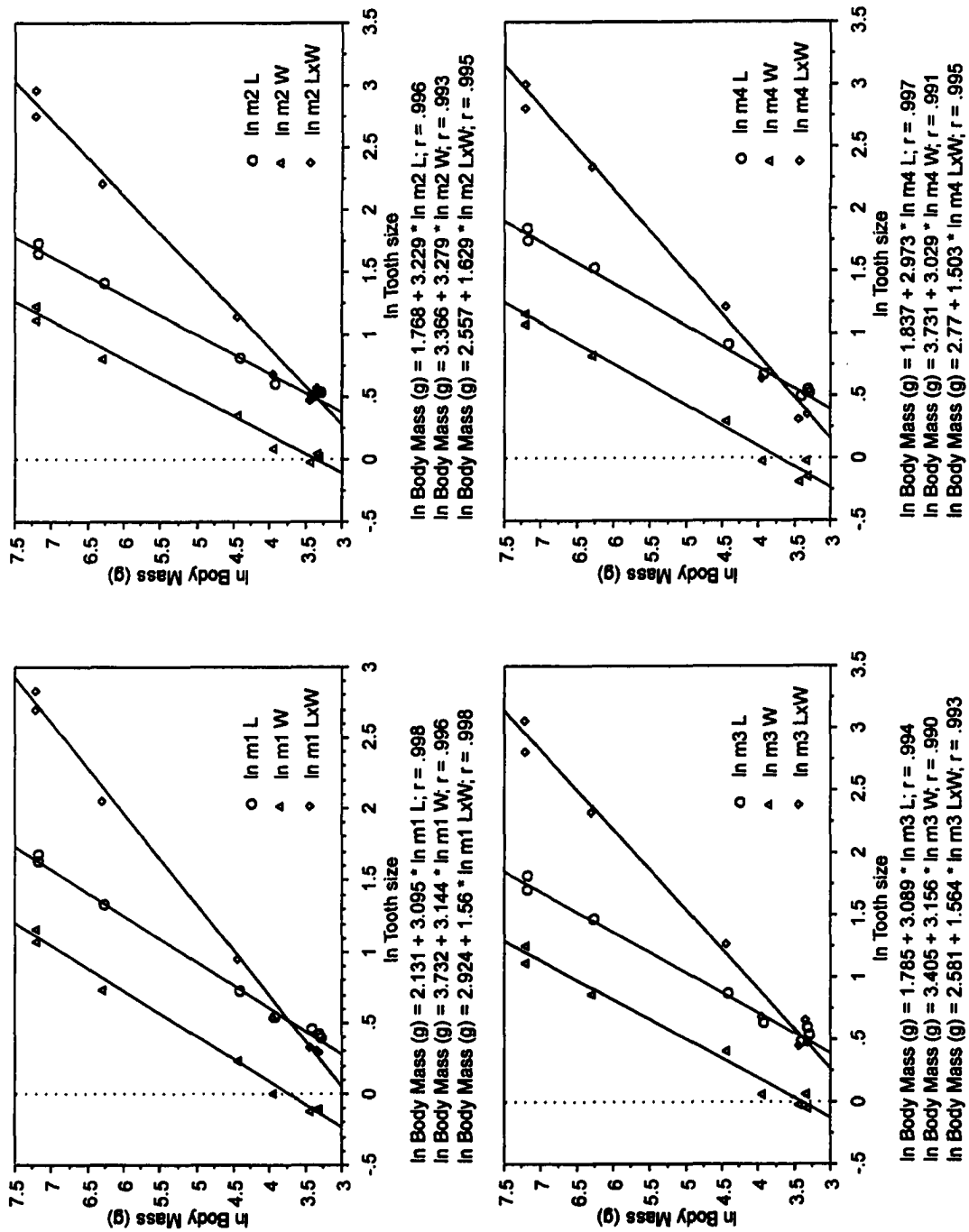

ln Body Mass (g)
ln Tooth size
ln m1 L
ln m1 W
ln m1 LxW
ln Body Mass (g) = 2.131 + 3.095 * ln m1 L; r = .998
ln Body Mass (g) = 3.732 + 3.144 * ln m1 W; r = .996
ln Body Mass (g) = 2.924 + 1.56 * ln m1 LxW; r = .998
ln m2 L
ln m2 W
ln m2 LxW
ln Body Mass (g) = 1.768 + 3.229 * ln m2 L; r = .996
ln Body Mass (g) = 3.366 + 3.279 * ln m2 W; r = .993
ln Body Mass (g) = 2.557 + 1.629 * ln m2 LxW; r = .995
ln m3 L
ln m3 W
ln m3 LxW
ln Body Mass (g) = 1.785 + 3.089 * ln m3 L; r = .994
ln Body Mass (g) = 3.405 + 3.156 * ln m3 W; r = .990
ln Body Mass (g) = 2.581 + 1.564 * ln m3 LxW; r = .993
ln m4 L
ln m4 W
ln m4 LxW
ln Body Mass (g) = 1.837 + 2.973 * ln m4 L; r = .997
ln Body Mass (g) = 3.731 + 3.029 * ln m4 W; r = .991
ln Body Mass (g) = 2.77 + 1.503 * ln m4 LxW; r = .995

Figure 2

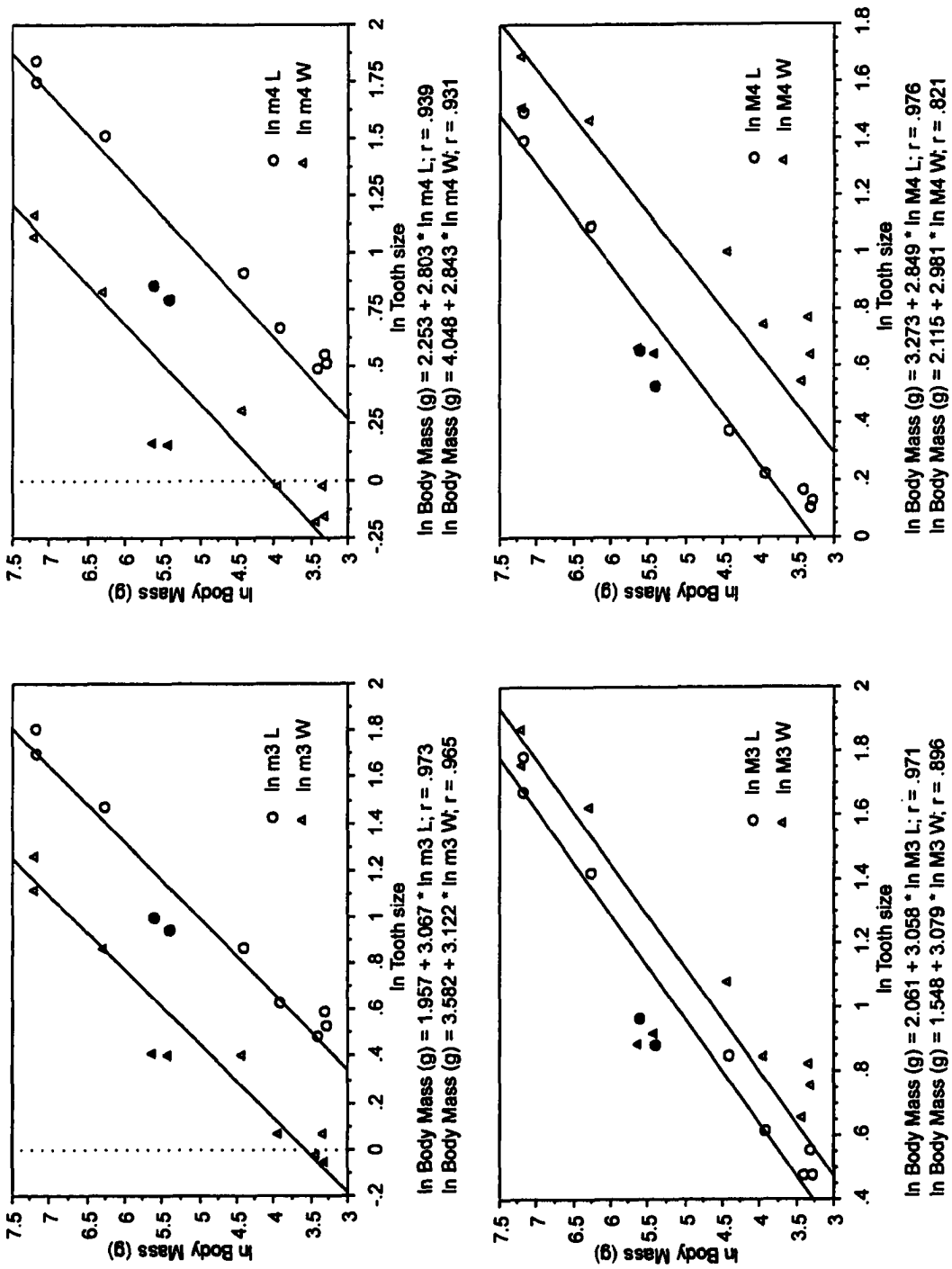

ln Body Mass (g)
ln Tooth size
ln m3 L
ln m3 W
ln Body Mass (g) = 1.957 + 3.067 * ln m3 L; r = .973
ln Body Mass (g) = 3.582 + 3.122 * ln m3 W; r = .965
ln m4 L
ln m4 W
ln Body Mass (g) = 2.253 + 2.803 * ln m4 L; r = .939
ln Body Mass (g) = 4.048 + 2.843 * ln m4 W; r = .931
ln M3 L
ln M3 W
ln Body Mass (g) = 2.061 + 3.058 * ln M3 L; r = .971
ln Body Mass (g) = 1.548 + 3.079 * ln M3 W; r = .896
ln M4 L
ln M4 W
ln Body Mass (g) = 3.273 + 2.849 * ln M4 L; r = .976
ln Body Mass (g) = 2.115 + 2.981 * ln M4 W; r = .821

Figure 3

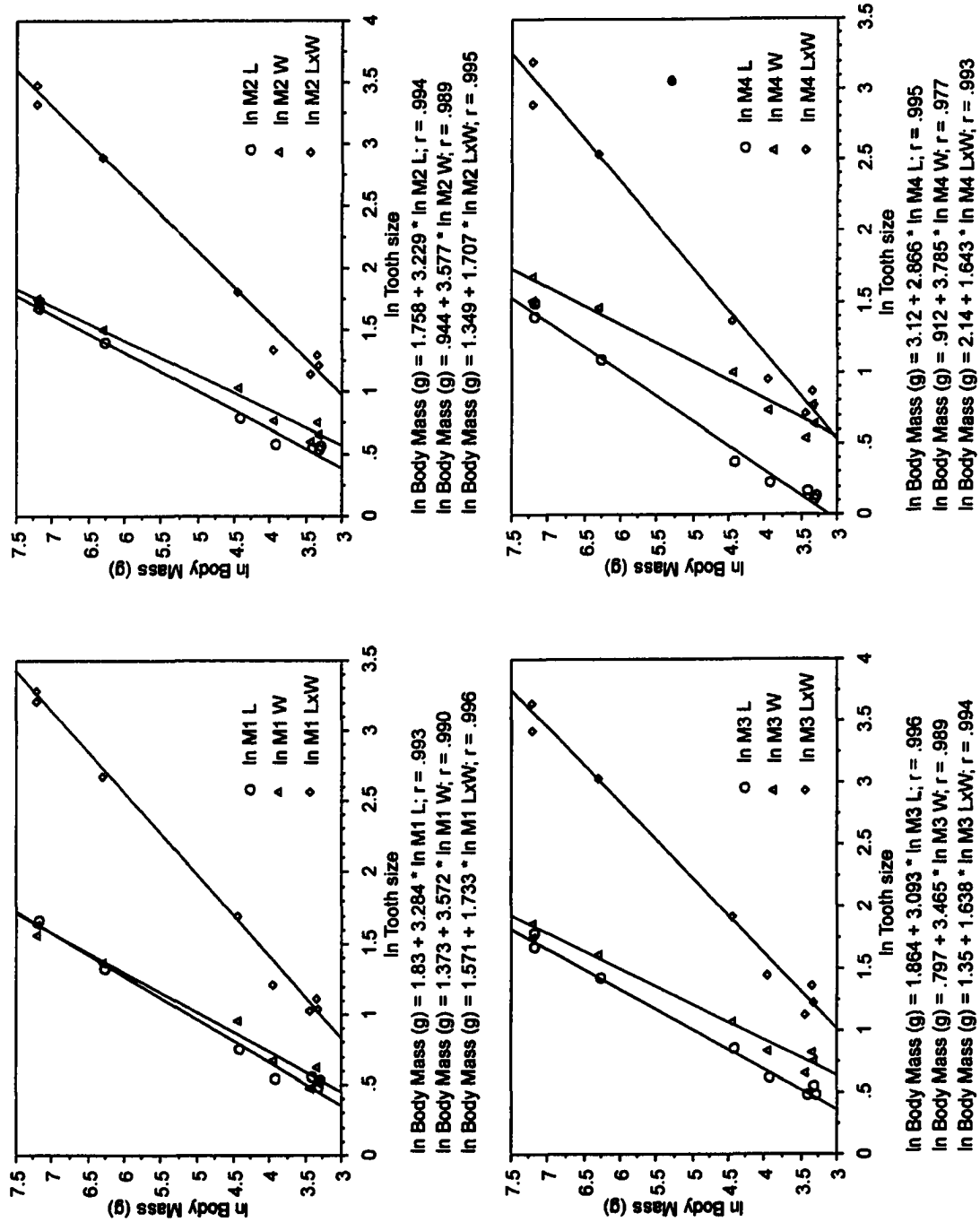
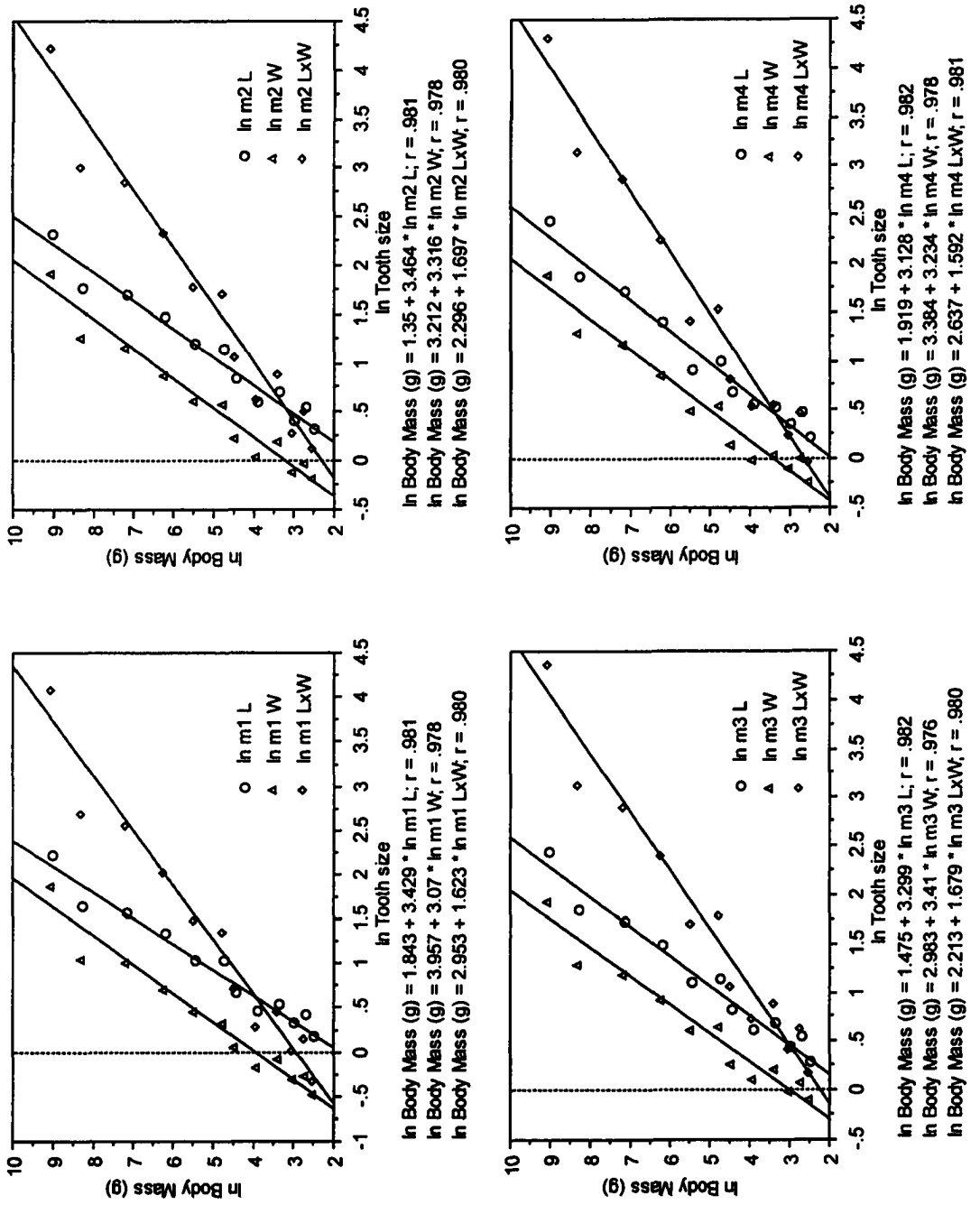
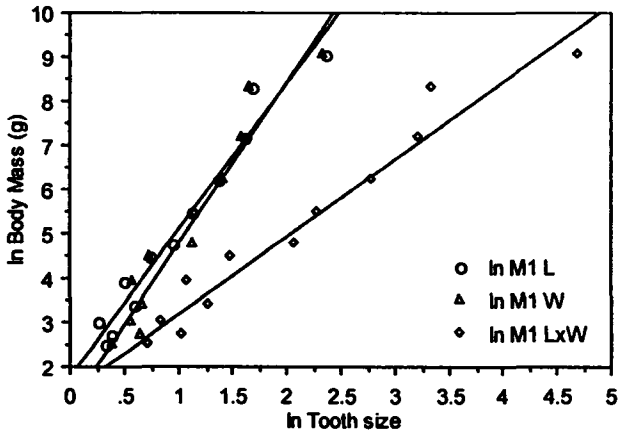
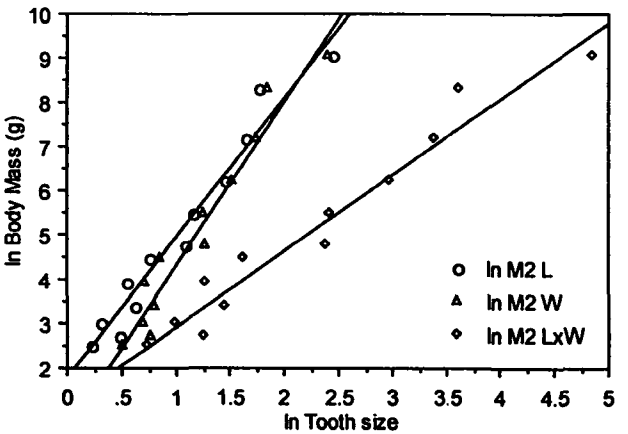

ln Body Mass (g)
ln Tooth size
ln M1 L
ln M1 W
ln M1 LxW
ln Body Mass (g) = 1.83 + 3.284 * ln M1 L; r = .993
ln Body Mass (g) = 1.373 + 3.572 * ln M1 W; r = .990
ln Body Mass (g) = 1.571 + 1.733 * ln M1 LxW; r = .996
ln M2 L
ln M2 W
ln M2 LxW
ln Body Mass (g) = 1.758 + 3.229 * ln M2 L; r = .994
ln Body Mass (g) = .944 + 3.577 * ln M2 W; r = .989
ln Body Mass (g) = 1.349 + 1.707 * ln M2 LxW; r = .995
ln M3 L
ln M3 W
ln M3 LxW
ln Body Mass (g) = 1.864 + 3.093 * ln M3 L; r = .996
ln Body Mass (g) = .797 + 3.465 * ln M3 W; r = .989
ln Body Mass (g) = 1.35 + 1.638 * ln M3 LxW; r = .994
ln M4 L
ln M4 W
ln M4 LxW
ln Body Mass (g) = 3.12 + 2.866 * ln M4 L; r = .995
ln Body Mass (g) = .912 + 3.785 * ln M4 W; r = .977
ln Body Mass (g) = 2.14 + 1.643 * ln M4 LxW; r = .993

Figure 4

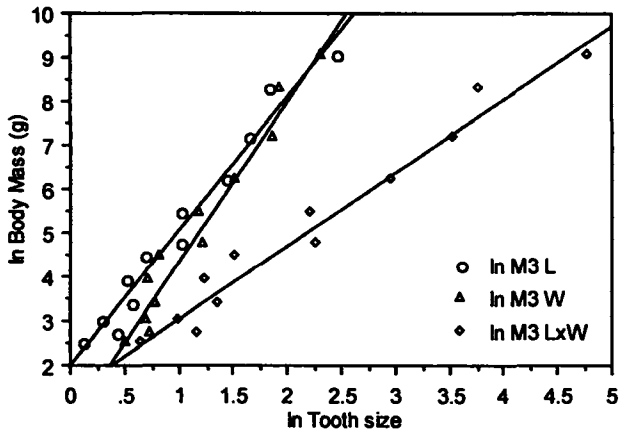

ln Body Mass (g)
ln Tooth size
ln m1 L
ln m1 W
ln m1 LxW
ln Body Mass (g) = 1.843 + 3.429 * ln m1 L; r = .981
ln Body Mass (g) = 3.957 + 3.07 * ln m1 W; r = .978
ln Body Mass (g) = 2.953 + 1.623 * ln m1 LxW; r = .980
ln m2 L
ln m2 W
ln m2 LxW
ln Body Mass (g) = 1.35 + 3.464 * ln m2 L; r = .981
ln Body Mass (g) = 3.212 + 3.316 * ln m2 W; r = .978
ln Body Mass (g) = 2.296 + 1.697 * ln m2 LxW; r = .980
ln m3 L
ln m3 W
ln m3 LxW
ln Body Mass (g) = 1.475 + 3.299 * ln m3 L; r = .982
ln Body Mass (g) = 2.983 + 3.41 * ln m3 W; r = .976
ln Body Mass (g) = 2.213 + 1.679 * ln m3 LxW; r = .980
ln m4 L
ln m4 W
ln m4 LxW
ln Body Mass (g) = 1.919 + 3.128 * ln m4 L; r = .982
ln Body Mass (g) = 3.384 + 3.234 * ln m4 W; r = .978
ln Body Mass (g) = 2.637 + 1.592 * ln m4 LxW; r = .981



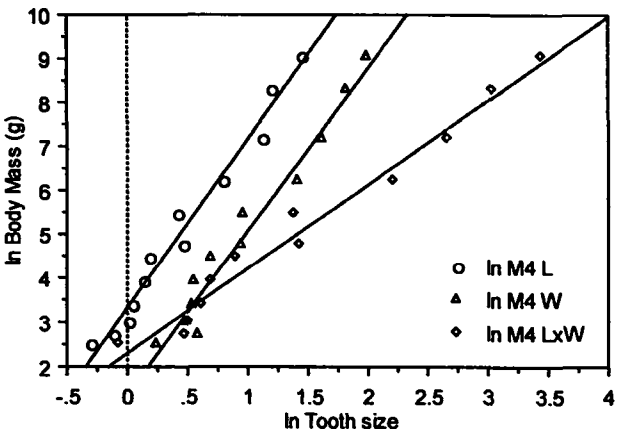
ln Body Mass (g) = 1.775 + 3.309 * ln M1 L; r = .981
ln Body Mass (g) = 1.108 + 3.662 * ln M1 W; r = .966
ln Body Mass (g) = 1.438 + 1.747 * ln M1 LxW; r = .977



ln Body Mass (g) = 1.756 + 3.168 * ln M2 L; r = .979
ln Body Mass (g) = .565 + 3.718 * ln M2 W; r = .973
ln Body Mass (g) = 1.196 + 1.715 * ln M2 LxW; r = .977



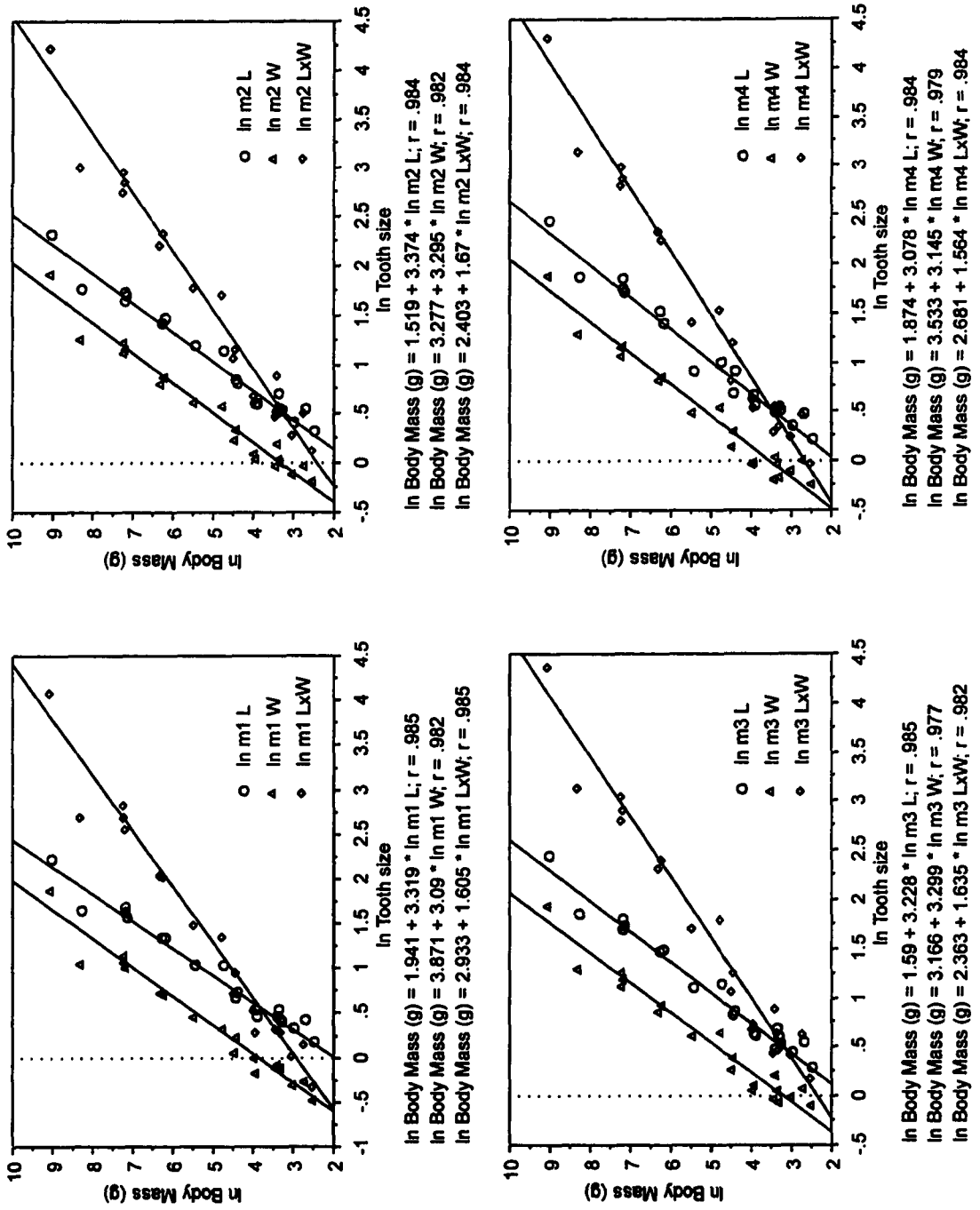
ln Body Mass (g) = 2.008 + 3.043 * ln M3 L; r = .983
ln Body Mass (g) = .647 + 3.666 * ln M3 W; r = .978
ln Body Mass (g) = 1.375 + 1.668 * ln M3 LxW; r = .983

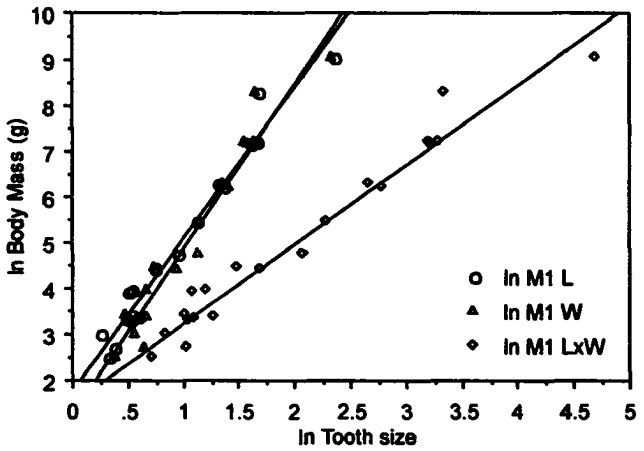


ln Body Mass (g) = 3.321 + 3.843 * ln M4 L; r = .988
ln Body Mass (g) = 1.358 + 3.723 * ln M4 W; r = .982
ln Body Mass (g) = 2.295 + 1.916 * ln M4 LxW; r = .988

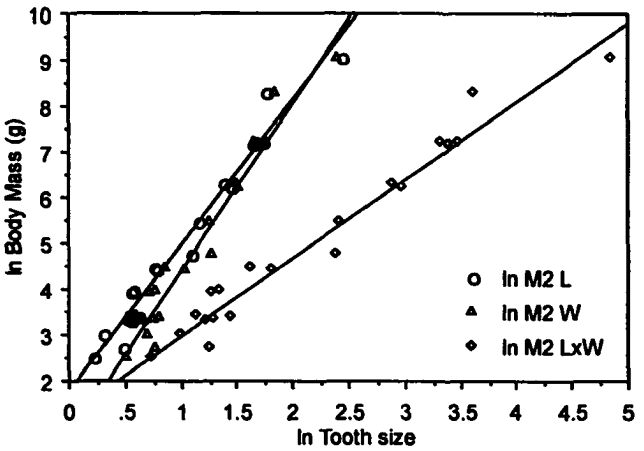
Figure 5

Figure 6

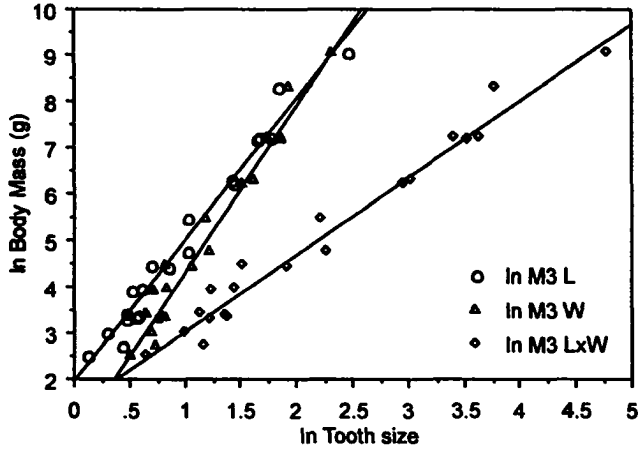

ln Body Mass (g)
ln Tooth size
ln m1 L
ln m1 W
ln m1 LxW
ln Body Mass (g) = 1.941 + 3.319 * ln m1 L; r = .985
ln Body Mass (g) = 3.871 + 3.09 * ln m1 W; r = .982
ln Body Mass (g) = 2.933 + 1.605 * ln m1 LxW; r = .985
ln m2 L
ln m2 W
ln m2 LxW
ln Body Mass (g) = 1.519 + 3.374 * ln m2 L; r = .984
ln Body Mass (g) = 3.277 + 3.295 * ln m2 W; r = .982
ln Body Mass (g) = 2.403 + 1.67 * ln m2 LxW; r = .984
ln m3 L
ln m3 W
ln m3 LxW
ln Body Mass (g) = 1.59 + 3.228 * ln m3 L; r = .985
ln Body Mass (g) = 3.166 + 3.299 * ln m3 W; r = .977
ln Body Mass (g) = 2.363 + 1.635 * ln m3 LxW; r = .982
ln m4 L
ln m4 W
ln m4 LxW
ln Body Mass (g) = 1.874 + 3.078 * ln m4 L; r = .984
ln Body Mass (g) = 3.533 + 3.145 * ln m4 W; r = .979
ln Body Mass (g) = 2.681 + 1.564 * ln m4 LxW; r = .984



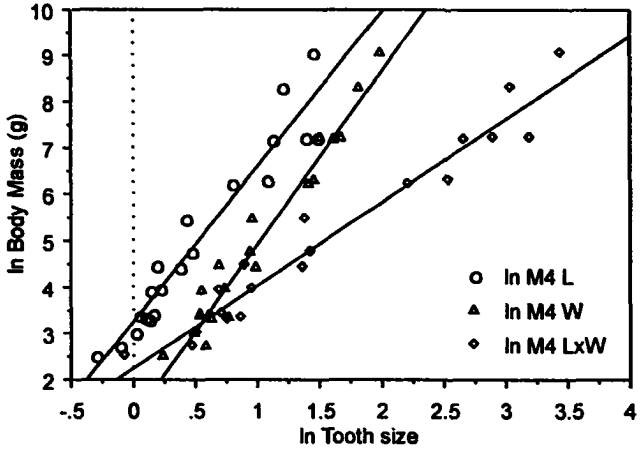
ln Body Mass (g) = 1.796 + 3.3 * ln M1 L; r = .985
ln Body Mass (g) = 1.223 + 3.62 * ln M1 W; r = .972
ln Body Mass (g) = 1.496 + 1.74 * ln M1 LxW; r = .982



ln Body Mass (g) = 1.767 + 3.182 * ln M2 L; r = .983
ln Body Mass (g) = .73 + 3.654 * ln M2 W; r = .976
ln Body Mass (g) = 1.267 + 1.708 * ln M2 LxW; r = .982



ln Body Mass (g) = 1.954 + 3.059 * ln M3 L; r = .987
ln Body Mass (g) = .684 + 3.606 * ln M3 W; r = .980
ln Body Mass (g) = 1.356 + 1.66 * ln M3 LxW; r = .985



ln Body Mass (g) = 3.259 + 3.345 * ln M4 L; r = .963
ln Body Mass (g) = 1.208 + 3.721 * ln M4 W; r = .976
ln Body Mass (g) = 2.241 + 1.792 * ln M4 LxW; r = .976

Figure 7

ESTIMATING BODY SIZE IN LATE CRETACEOUS THERIAN MAMMALS OF NORTH AMERICA

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Running Head: GORDON AND CIFELLI – ESTIMATING BODY SIZE IN LATE CRETACEOUS MAMMALS

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ABSTRACT

Body size in Late Cretaceous mammals of North America is poorly known, making it difficult to understand the nature and magnitude of the extensive mammalian radiation after the end-Cretaceous mass extinction event. In this study, the relationships of body size with various dental (length, width, and area of lower and upper molars) and cranial (skull length and area of foramen magnum) measurements are examined in dentally conservative, modern primates, insectivores and marsupials. Least-squares regression analysis indicates that size of the lower and upper first molar is most highly correlated with body size, as measured by either body mass or area of foramen magnum. Although body mass is generally used to represent body size, area of foramen magnum, less susceptible to the variation seen in body mass of a species, may be a useful tool to supplement the conclusions based on body mass. Regression equations generated using size of lower and upper first molars in modern species were used to estimate body mass in latest Cretaceous (Lancian) mammals. As expected, most Lancian mammals were quite small, less than 200 g in size. Marsupials exhibited a greater range of body size than placentals, with five species of marsupials greater than 200 g, and two species of placentals over 200 g.

INTRODUCTION

Archibald (1996a:159), in his book "Dinosaur Extinction and the End of an Era", stated, "All marsupials in the latest Cretaceous of eastern Montana were quite small, from the size of a mouse to that of a very well fed opossum or raccoon." General statements of this type are standard in the literature on Cretaceous mammals of North America, with only a handful of studies providing quantitative predictions (Cifelli and Madsen, 1998; Wood and Clemens, 2001; Clemens, in press). In contrast, an abundance of studies is available that include an examination of body size in Tertiary primates (Gingerich, 1974; Gingerich et al., 1982; Gingerich and Smith, 1984; Rose et al., 1993), insectivores (Bloch et al., 1998) and carnivores (Van Valkenburgh, 1990). Such studies are necessary for paleobiological inferences, as body size is related to a number of ecological and physiological processes such as diet, locomotion, metabolic rate and home range (Peters, 1983; McNab, 1990; Kelt and Brown, 1998).

After the end-Cretaceous extinction event, an explosive mammalian radiation occurred in which mammals are hypothesized to have expanded into the ecological voids created by the extinction of the dinosaurs (Van Valen, 1978; Archibald, 1983; Stucky, 1990). The ensuing changes in mammalian faunal composition (Archibald, 1982, 1983; Archibald and Clemens, 1984; Fox, 1989, 1990; Archibald and Bryant, 1990; Lofgren, 1995, 1997; Clemens, in press) and body-size evolution (on a larger scale) (Alroy, 1998, 1999) are well documented near the Cretaceous-Tertiary boundary. However, it is difficult to explore thoroughly the remarkable changes in mammalian body size at the beginning of the Tertiary when there is currently no baseline study of body size for Late Cretaceous mammals with which to compare.

Cretaceous mammals are often known only by isolated teeth or jaws. Since the teeth of Cretaceous mammals have a relatively conservative morphology, modern species of primates, insectivores and marsupials that possess a conservative dentition were used in this study. The relationship between body size and tooth size has been examined previously in modern primates (Kay, 1975; Gingerich et al., 1982), insectivores (Gingerich and Smith, 1984; Legendre, 1989; Bloch et al., 1998) and, most recently, marsupials (Gordon, submitted). Wood and Clemens (2001) used previously published regression equations to predict body size in a few Cretaceous mammal species. Unfortunately, resulting predictive equations often differ depending on the taxa upon which they are based (Rose et al., 1993). As Smith (1984) noted, "...relative size measurements from different studies are not generally comparable. Results are specific to the sample and line fitting technique used. Differences in results are often due to methodology rather than to differences in biologically-relevant parameters." This statement underscores the need to tailor the taxonomic sample included in regression analyses to the specific needs of the study.

No comprehensive study of body size in Late Cretaceous mammals has been undertaken to date. Moreover, as yet there has been no comprehensive study of dentally comparable modern species that might be used to generate predictive equations for Late Cretaceous mammals. In this study we predict body size in extinct Late Cretaceous (Lancian) therian mammals, eutherians (placentals) and metatherians (marsupials) of North America. Because of the limited fossil record we emphasized the relationship between body size and tooth size. Regression equations, examining the relationship of

body size with tooth size, as well as with other cranial and dental characteristics, are generated for modern species and used to predict the body size of Lancian mammals.

METHODS

Sixty-six modern species representing two families of marsupials (Didelphidae, Dasyuridae), three families of lipotyphlan insectivores (Erinaceidae, Soricidae, and Talpidae), six families of primates (Callitrichidae, Cebidae, Cheirogaleidae, Indriidae, Lemuridae, Lorisidae), and the single family of tree shrews (Tupaiidae) were studied. Selection of modern species concentrated on those species with a more conservative dentition because Cretaceous mammals of North America are known mainly by isolated teeth. For instance, some families of insectivores (e.g. Tenrecidae, Solenodontidae, Chrysochloridae) possess a specialized, zalambdodont dentition (Gingerich and Smith, 1984; Bloch et al., 1998) and so were not included in the analysis. Species within each group were selected to include a wide range of body sizes (Table 1).

Although marsupial and placental mammals from virtually the entire Late Cretaceous are known from North America, only mammals from the interval just before the Cretaceous/Tertiary boundary (the Lancian land-mammal age) were examined. The Lancian is the best known of North American, Late Cretaceous land-mammal ages (Lillegraven and McKenna, 1986; Cifelli et al., in press) and is most relevant to interpreting the initial radiations of mammals in the Cenozoic. Included were mammal species (and their associated tooth measurements) from the Hell Creek, Frenchman, Lance and Scollard formations of the Western Interior of North America, all late Maastrichtian in age (~70 to 65 million years) (Clemens, 1966, 1973; Lillegraven, 1969; Fox, 1977, 1989; Archibald, 1982; Storer, 1991; Johanson, 1996).

Data for all modern species were obtained from specimens housed at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Most specimens

used were unworn teeth. However, some slightly worn teeth from specimens of rare species had to be included. Also, many of the specimens did not have information on body mass. In these cases, average body mass was obtained from the literature (Silva and Downing, 1995; Strahan, 1995) (Table 1). Cranial and tooth row measurements were taken directly from the original specimens using digital calipers (accurate to 0.03 mm). Molds were made (using 3M Express™ vinyl polysiloxane) of the left upper and lower dentitions of individual adult specimens from both males and females. Measurements on individual teeth were taken with a Reflex® microscope (MacLarnon, 1989) on polyurethane casts made from these molds.

Least-squares regression analysis was used to generate equations for the prediction of mean body size from various mean tooth and cranial measurements. Reasons for using this method (instead of one based on the reduced major axis) in primates and insectivores has been explained previously in detail by Gingerich and Smith (1984) and Anthony and Kay (1993). The rationale has been reviewed by Gordon (submitted) for marsupials. Gordon (submitted) showed that regression equations generated from either Didelphidae or Dasyuridae predict body mass better than a regression equation from a pooled sample of both families. Moreover, the tooth morphotype of Cretaceous tribosphenic mammals is generally considered to be most similar to the dentition of modern Didelphidae (Crompton and Hiiemae, 1970; Crompton and Kielan-Jaworowska, 1978). Therefore, only the regression equations for Didelphidae are presented.

Allometric equations that describe the relationship between two variables (in this study, body size versus various dental and cranial measurements) take the form of

$$Y = aX^b.$$

This equation can be logarithmically transformed to the linear form,

$$\ln Y = \ln (a) + b (\ln X).$$

A least-squares regression line can then be fit to the data and the resulting equation used to estimate an unknown, dependent variable (body size) from a known, independent variable (e.g. tooth size). Most previous studies in paleontology using regression equations for predictive purposes have failed to take into account the inherent bias in transforming the predicted log value of *Y* back to its arithmetic mean. Smith (1993) argued that the detransformed value of *Y* is the geometric mean, which is always less than the arithmetic mean, resulting in underestimates for the predicted values of *Y*. The degree to which the resulting value of *Y* is underestimated is generally small, but Gordon (submitted), in a study predicting body size in marsupials, found that in some cases the detransformed values underestimated body mass by nearly 12%. Although the importance of using a "correction factor" in allometric studies has been known for many years (Finney, 1941; Sprugel, 1983), a more comprehensive study describing numerous correction factors that can be used to adjust predicted values for *Y* was done by Smith (1993). Body-mass estimates using equations generated in this study were adjusted using the "smearing factor" described by Smith, which is calculated by taking the mean of the detransformed residuals. Original data from previous studies were not available to calculate correction factors for body-mass estimates.

Figures 1 and 2 show the dental and cranial measurements included in the study. Besides skull length, two measurements were taken on the foramen magnum. The first is the horizontal diameter of the foramen, measured just above the occipital condyles. The

second is the midline vertical diameter of the foramen (Radinsky, 1981). Area of the foramen magnum was then determined by using the formula to calculate the area of an ellipse:

$$\text{Area} = \pi a b,$$

where $2a$ and $2b$ are the longest and shortest diameters, respectively (Fig. 2). Individual tooth measurements were taken following the method outlined by Lillegraven (1969). Mean data for dental and cranial measurements for all species are given in Appendices 1–4. Regression analyses were performed with Statview® 5.0 at an alpha level of 0.05. All data were transformed to natural logs (base e). Text abbreviations are as follows: greatest length (L); greatest width (W); skull length (SL); total length of lower tooth row (TLL); total length of upper tooth row (TLU); total length of lower molars (TLLM - obtained by simply adding individual molar lengths); total length of upper molars (TLUM); and area of foramen magnum (FA).

RESULTS

Modern Species

Area of the lower first molar is highly correlated with body size (as represented by body mass or area of the foramen magnum) for primates, insectivores and marsupials (Fig. 3). Area of the first molar scales with body size similarly in marsupials and insectivores. Marsupials have relatively smaller teeth size for a given body size than do insectivores. Compared to these two groups, smaller primates have relatively small teeth for a given body size, while teeth of larger primates are relatively large. The relationship between the area of the foramen magnum (FA) and m1 tooth size is similar in primates and insectivores. Figure 4 shows that relationships of skull length and body mass in marsupials and insectivores are very similar. When examining the relationship between FA and body mass, primates and insectivores are very similar. Compared to these two groups, marsupials tend to have a relatively larger foramen magnum at smaller body sizes than at larger.

Primates—Considerable research has been conducted on the primate dentition and its relationship to body size (Kay, 1975; Gingerich et al., 1982; Gingerich and Smith, 1984). Many of these studies, however, involve the use of taxa that are not necessarily appropriate in the present context. Gingerich (1984) and Kay (1975) included generalized primates in their studies, many of which are more advanced species in the subfamily Haplorhini, considered more derived than Strepsirhini (traditionally referred to as prosimians) (Nowak, 1991). We conducted analyses using only species of Strepsirhini, as well as analyses that included Strepsirhini and some smaller members of Haplorhini.

Tooth size, measured as length and area of the first lower and upper molars, is most strongly correlated with body mass ($r > 0.871$) (Table 2; Fig. 5). Length of m2 is the only measure that is more highly correlated with body mass than m3. All other measures using third molars are more strongly correlated with body size than second molars. The high correlation of m1 size with body size suggests it is probably a better predictor of body mass than other molars. As such, it is interesting that Kay (1975) chose to use length of the m2 to estimate body mass in primates. If the analysis is restricted to only Strepsirhini, the result is a strong correlation between tooth size and body size, particularly with length and area of the first two upper and lower molars (Table 2). Total lengths of the upper (TLU) and lower (TLL) tooth rows, as well as lengths of the upper (TLUM) and lower (TLLM) molar series, were highly correlated with body size ($r > 0.882$ and 0.880, respectively) (Fig. 6).

The area of the foramen magnum (FA) is more highly correlated with body mass ($r = 0.973$) than is skull length ($r = 0.949$) (Fig. 7). A separate analysis shows that when FA is regressed against tooth size, there is an even stronger correlation for lower and upper first molars ($r > 0.928$) than was seen between first molars and body mass. The results are similar when the analysis is restricted to Strepsirhini (Fig. 7). Skull length in primitive primates ($r = 0.943$) is not as strongly correlated with body mass as is FA ($r = 0.971$).

Insectivores--Three families of primitive lipotyphlan insectivores - Soricidae, Erinaceidae, and Talpidae - were included in this analysis. Legendre (1989) included Solenodontidae and Macroscelididae in his evaluation of body size and tooth size. Members of Solenodontidae possess a more specialized dentition and were not included

in our study. Bloch et al. (1998) also included Macroscelididae in their analyses. In an examination of scaling of tooth size in primates and insectivores, Gingerich and Smith (1984) found that teeth of Tupaiidae scale with those of insectivores, presumably because they are highly insectivorous. Based on their work, and the subsequent study of tooth size and body size in insectivores by Bloch et al. (1998), Tupaiidae were included with Insectivora in our analyses.

Previous studies have demonstrated that tooth size and body mass are highly correlated in insectivores (Gingerich and Smith, 1984; Legendre, 1989; Bloch et al., 1998), a finding supported by our studies. Length and area of M1/m1 and M2/m2 are more strongly correlated with body mass ($r > 0.964$) than is M3/m3 ($r > 0.888$) (Table 3; Fig. 8). This result is consistent with correlation coefficients obtained by Bloch et al. (1998:814) for m1 area ($r = 0.969$) and M1 area ($r = 0.966$). There is a much greater spread of data points about the regression line for third molars than for the first two molars. Most of this variation is due to Erinaceidae, with all but one genus (*Hylomys*), that falls well away from the regression line (Fig. 8). *Echinosorex gymnurus* is the only erinaceid species with teeth much larger than what would be expected for its body size. The other three genera have reduced third molars. One tree shrew species, *Ptilocercus lowii*, despite having first and second molars that fall within the average range of tooth size for insectivores, also has third molars that are much larger than expected given its body size (Fig. 8). Total lengths of the lower and upper tooth rows are not as highly correlated with body mass as are the molar series ($r > 0.974$) (Fig. 6). Again, most of the spread around the regression line for TLL and TLU occurs in Erinaceidae. This is not the case for length of the molar series. Only one species, *Echinosorex gymnurus*, has a

TLLM that is larger than expected for its body size, no doubt a byproduct of enlarged third molars.

Both FA and skull length are strongly correlated with body mass in insectivores (Fig. 7). Unlike primates, the correlation between body mass and skull length ($r = 0.971$) is slightly stronger than the association between body mass and FA ($r = 0.952$). A separate analysis shows that the regression of FA on tooth size results in a similar relationship as seen between body mass and tooth size. The highest correlation coefficients are for length and area of lower and upper first and second molars ($r > 0.917$). Second molars had a slightly stronger correlation with FA than first molars. Sizes of the lower and upper third molars had relatively high correlation coefficients as well ($r > 0.896$). Deviations from the regression line for FA and tooth size are not as great as the spread of data for body mass and tooth size, suggesting that the use of FA as a measure of body size may not be as sensitive to variation as body mass.

Marsupials--Results of the regression of body size on tooth size in modern, dentally conservative marsupials have been reported previously in detail (Gordon, submitted) and, thus, only a cursory explanation will be presented. Correlation between tooth size and body mass is high throughout the lower and upper molar series in didelphid marsupials (Table 4). This is also the case for a pooled sample of didelphids and dasyurids, although it is not presented here. Two species of *Caluromys*--*C. derbianus* and *C. philander*--have a tooth morphology that is considerably different than the standard tooth morphotype for marsupials (Figs. 9, 10). The more posterior third and fourth molars much smaller than what would be expected for their body size. Gordon (submitted) suggested that this may be due to the especially divergent tooth morphology

of *Caluromys*, probably reflecting the differences in diet between *Caluromys* and other didelphids. Thus, we removed the two species of *Caluromys* from the analysis of tooth size and body mass. Previous work has shown that M1/m1 length and area are the best predictors of body size and it is these equations that are used to estimate body size in Cretaceous mammals (see below). Figure 6 shows that there is a strong correlation for the regression of TLL and TLU with body mass (r = 0.977). This is similar to the correlation of body mass with TLLM and TLUM (r = 0.982).

The strength of the relationships of body mass with skull length (r = 0.981) and with FA (r = 0.984) are nearly equivalent (Fig. 7). When FA is regressed on tooth size (for all marsupials included in the study), results are similar to that of tooth size and body mass. The correlation is highest for M1/m1 and decreases slightly posteriorly in the tooth row.

Predicted Body Mass in Late Cretaceous Therian Mammals

It is often suggested that most Cretaceous mammals were no bigger than an opossum, or as Archibald (1996a) stated, "a well fed raccoon". Body masses of modern opossums and raccoons range from 2.0 – 5.5 kg and 2.0 – 12.0 kg, respectively (Nowak, 1991). This size estimate for Late Cretaceous therian mammals is certainly an overestimate. Table 5 shows the body masses of Late Cretaceous mammals estimated from equations generated using size of first molars from primates, insectivores and marsupials in our analyses, as well as those equations from earlier studies (Gingerich et al., 1982; Bloch et al., 1998). Only equations generated from first molars were used because these had the highest correlation with body mass in modern species and to facilitate comparison with earlier studies in which M1/m1 size were used.

Eutherians--Estimates of body mass for eight eutherian species vary according to different Late Cretaceous localities, equations from different studies, and whether the equation being used was based on size of lower or upper first molars (Table 5). Overall, the estimates using the equation from Bloch et al. (1998) were greater than those from our study, and would be greater still if a correction factor had been applied to their dataset. In this study, many of the same species as those of Bloch et al. (1998) were used to generate the insectivore equations. Perhaps the difference in estimates is due to their inclusion of the family Macroscelididae (elephant shrews). Estimated body mass based on upper M1 area for this study, as well as on equations from Bloch et al. (1998), is generally greater than estimates based on lower m1 area. Conversely, upper M1 L estimates for body mass are less than those based on lower m1 L.

Regardless, the range of estimates for each species is well within the range of body masses for modern species. North American Lancian eutherians range from the smallest, *Batodon tenuis*, at 5 – 6 g, to *Cimolestes magnus*, with a body mass that ranges from 458 g – 817 g. Wood and Clemens (2001) generated a similar estimate for *Batodon tenuis* (5.39 g). The range of body mass for *C. magnus* is close to that of a similarly sized modern insectivore, *Echinosorex gymnurus*, with a body mass that ranges from 445 g – 1400 g (Silva and Downing, 1995). Modern lipotyphlan body masses range from the smallest species, *Suncus etruscus*, with a minimum of 1.19 g, to *Erinaceus europaeus*, with a maximum of 1600 g (Silva and Downing, 1995). Most Lancian eutherians were less than 200 g in size (Fig. 11). Only two species of *Cimolestes* -- *C. magnus* and *C. stirtoni* -- were larger. Body mass of Lancian mammals estimated from marsupial or primate equations seem to be substantially overestimated. Nonetheless, body-mass

estimates using equations generated from Strepsirhini primates alone overestimate notably less than other primate equations from this or previous studies.

Metatherians--The smallest Lancian marsupial is *Pediomys krejcii*, with an estimated body mass ranging from 24 g – 47 g, while the largest is *Didelphodon vorax* with a range of 762 g – 1910 g (Table 5). For modern dasyurids and didelphids, the smallest known species is *Planigale ingrami*, at just around 4 g, and the largest is *Sarcophilus harrisii*, which can be as large as 8 kg (Silva and Downing, 1995). *Didelphis virginiana* has a body mass between 2 kg to over 5.5 kg (Nowak, 1991). Some Late Cretaceous marsupials attained a body size much greater than their eutherian contemporaries (Fig. 12). Only five of 13 species (*Didelphodon vorax*, *Turgidodon petiminis*, *T. rhaister*, *Pediomys hatcheri* and *P. florencae*) all attained a body size greater than 200 g.

Archaic ungulates--Based on the body mass estimates using the primate equations, archaic ungulates, which were first thought to have appeared in North America near the end of the Cretaceous (Archibald, 1996a, b), but are now believed to most likely be Paleocene (Lofgren, 1995), were mostly medium- to large-sized by Cretaceous standards (Table 5). *Alostera saskatchewanensis* was the smallest species, between 27 and 45 g, and the largest was *Ragnorak harbichti*, at nearly 600 g. Four of seven species were nearly 200 g or larger (Fig. 13).

DISCUSSION

Overall, body mass was most highly correlated with size of the upper and lower first molars in the primates, insectivores and marsupials we studied. Therefore, the most reliable estimates for body size in these groups will likely be generated from the first molar. Diet is highly related to body size (e.g. Kay, 1975; Robinson and Redford, 1986), a relationship that would be reflected in that between body mass and tooth size as well. Body mass and tooth size may scale similarly in marsupials and insectivores because of the similarities of their diets. Most species of marsupials are either omnivorous or insectivorous (with larger species, particularly dasyurids, relying more heavily on vertebrate prey) (Hume, 1999). If one were to remove the effect of diet in an analysis of body size, by regressing FA on m1 size instead, then the results are slightly different. Here, the relationship between m1 size and body size, as measured by area of the foramen magnum, is more similar in primates and insectivores. The similar relationship seen between marsupials and insectivores in body mass and tooth morphology, but not in FA and tooth morphology, supports the notion that diet affects tooth morphology, which in turn may distort the regression between body mass and tooth size.

Kay (1975) used m2 L to estimate body mass in primates even though tooth size of both m1 and m3 (length, width and area) are more highly correlated with body size than is m2 (with the exception of m2 L, which is more highly correlated than m3 L). When the analysis was restricted to Strepsirhini the correlation between tooth size and body size was generally much higher, perhaps a result of their more conservative dentition. There is also a wide spread of the data points about the regression lines in all analyses for primates, but this is not the case when the analysis is restricted to primitive

primates (e.g., Fig. 5). This finding may be due the primate species included in this study possessing more varied diets than those of insectivores or marsupials. For instance, diets of primate species included here range from those that consume mainly leaves (*Avahi laniger*, *Propithecus* sp.) to those that eat bamboo (*Hapalemur griseus*), mainly fruit (*Galago alleni*, *Cebus capucinus*), insects (*Arctocebus calabarensis*) or have plant exudates as a large part of their diet (*Cebuella pygmaea*, *Saguinus* sp.) (Kinzey, 1997; Garbutt, 1999). The spread of tooth size in relation to body size is likely partly the result of such varied diets and the subsequent associated differences in tooth shape and size. The extremely small size of the third molar in *Saimiri* (and to a lesser extent in *Cebus*) is indicative of a trend toward reduction of this tooth, thereby approaching the condition in Callitrichidae, a closely associated family (Nowak, 1991), which possesses only two upper and lower molars.

Lipotyphlan insectivores also had a very high correlation of tooth size with body size. Different results between ours and earlier studies (Legendre, 1989; Bloch et al., 1998) almost certainly are the result of differences in taxa included in the analyses. Diets of most insectivores are similar, which is reflected in the fact that there is little spread about the regression line.

One curious exception is the position of species of Erinaceidae. *Atelerix albiventris*, *Hemiechinus auritus*, *Erinaceus europaeus* all have reduced m3s, while *Echinosorex gymnurus* has third molars much larger than expected. Hedgehogs in general have relatively large body sizes for insectivores. Thus, many of them have an omnivorous diet. *Atelerix albiventris*, *H. auritus*, and *E. europaeus* are more omnivorous than other hedgehogs. Insects make up a major portion of their diet, but they also consume small

vertebrates, eggs, fruits, and seeds (Nowak, 1991). *Echinosorex gymnurus* has a diet that includes a large component of aquatic organisms, such as mollusks and crustaceans, as well as snails, earthworms and arthropods (Medway, 1969; Nowak, 1991). A diet rich in harder food items may explain the larger size of the third molar to provide greater crushing potential. Only *Hylomys suillus*, a species with a more restricted insectivorous diet, falls on the regression line. There is little deviation from the regression line in marsupials as well, with the exception of the two species of *Caluromys*. The deviations of *Caluromys derbianus* and *C. philander* from the average didelphid tooth morphotype may be the result of differences in tooth shape due to adaptations to a more frugivorous diet (Gordon, submitted).

Both skull length and size of the foramen magnum are highly correlated with body size in all of the groups we studied. One argument against using skull length as a measure of body size has been that skull shape varies considerably in mammals and, thus, is not indicative of overall size. This is probably not the case for the foramen magnum. Body mass is traditionally considered the best representative of body size, mainly because it is related to so many physiological and ecological aspects of a mammal (Western, 1979; Peters, 1983; Eisenberg, 1990; McNab, 1990). Nonetheless, size of the foramen magnum may prove to be a useful tool in evaluating the conclusions drawn about the relationship between body size (as indicated by body mass) and tooth size. Size of the foramen magnum does not fluctuate with the seasons as does body mass, for example, and therefore is less susceptible to collection biases. As such, when evaluating the relationship of body mass and tooth size, similar results for the relationship of

foramen magnum and tooth size may bolster the supposition that the association is biologically relevant and simply not the byproduct of the methods used.

Body-mass estimates indicate that most Lancian species were less than 200 g in size and not the racoon-sized animals envisioned by some. However, with the extinction of the non-avian dinosaurs, mammals had the opportunity to fill a variety of ecological niches left open (Archibald, 1983; Stucky, 1990). More species of marsupials than placentals attained larger body sizes. Newly arrived archaic ungulates were comparable in size to marsupials, with four of seven species over 200 g.

Our results support Smith's (1984) assertion that it is inaccurate to compare results of one allometric study with another. Clearly, the estimated body masses obtained for Lancian mammals vary among equations generated from different studies. A comparison of body masses estimated using insectivore equations from Bloch et al. (1998) and body masses estimated in this study indicates that, although they are different, these estimates are still well within the range of body masses for modern mammal species. Body masses of modern mammals can vary by sex, or seasonally, for example. Thus, when dealing with an unknown quantity, such as the body mass of a Cretaceous mammal for which there is no modern analog, it is not possible to predict one "best" mean body mass for a species. Rather, it is only possible to suggest that the predicted mean body mass for that species at least falls within the probable range of body sizes.

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TABLE 1. Mean body mass (grams) for each species included in this study. N = number of specimens.

Species	N (male, female)	Body mass (g)[a] Mean (male, female)	Reference
Insectivores			
Atelerix albiventris	9 (7, 2)	226.4 (210.6, 282.0)	This study
Crocidura cyanea	5 (3, 2)	7.4 (8.0, 6.5)	This study
Crocidura flavescens	13 (6, 7)	40.5 (42.4, 38.9)	This study
Echinosorex gymnurus	7 (4, 3)	633.6 (599.3, 679.3)	This study
Erinaceus europaeus	5 (1, 2)[b]	641.0 (653.0, 623.0)	Silva and Downing, 1995
Hemiechinus auritus	6 (3, 3)	296.0	Silva and Downing, 1995
Hylomys suillus	7 (4, 3)	50.0 (54.1, 44.6)	This study
Myosorex sp.	6 (3, 3)	13.3 (14.7, 12.0)	This study
Neurotrichus gibbsii	7 (5, 2)	9.7 (9.3, 10.8)	This study
Parascalops breweri	4 (2, 2)	57.4 (61.3, 53.5)	This study
Scapanus orarius	6 (3, 3)	60.8 (66.7, 54.9)	This study
Scapanus townsendii	5 (3, 2)	152.7 (161.2, 140.0)	This study
Sorex cinereus	5 (4, 1)	3.3 (3.4, 2.9)	This study
Sorex longirostris	5 (5, –)	3.1 (3.1, –)	This study
Suncus murinus	11 (7, 3)[b]	38.5 (35.8, 48.7)	This study
Talpa micrura	9 (4, 4)[b]	54.0 (52.8, 52.8)	This study
Urotrichus talpoides	6 (3, 3)	18.5 (18.0, 19.0)	This study
Primates			
Arctocebus calabarensis	2 (1, 1)	323.0 (300.0, 346.0)	This study

Species	N (male, female)	Body mass (g)[a] Mean (male, female)	Reference
Avahi laniger	2[b]	996.0	Kay, 1973
Callithrix argentata	1 (1, –)	420.0 (420.0, –)	This study
Callithrix humeralifer	3 (1, 2)	353.3 (300.0, 380.0)	This study
Callithrix jacchus	7 (3, 4)	338.9 (365.0, 319.3)	This study
Cebuella pygmaea	5 (–, 4)[b]	140.4 (158.0, 136.0)	Kay, 1973
Cebus capucinus	4 (2, 2)	2438.6 (2470.0, 2407.2)	This study
Eulemur fulvus	6 (1, –)[b]	1540.0	Silva and Downing, 1995
Galago alleni	4 (1, 2)[b]	260.0	Silva and Downing, 1995
Galago demidovii	9 (7, 2)	71.2 (70.9, 72.5)	This study
Hapalemur griseus	5 (2, 1)[b]	800.0	Silva and Downing, 1995
Leontopithecus rosalia	5 (3, 2)	564.0 (560.0, 570.0)	Silva and Downing, 1995
Loris tardigradus	3 (1, 2)	322.0	Silva and Downing, 1995
Microcebus murinus	6 (–, 2)[b]	60.0	Garbutt, 1999
Perodicticus potto	6 (2, 4)	828.3 (845.0, 820.0)	This study
Propithecus verreauxi	4 (1, –)[b]	3480.0	Silva and Downing, 1995
Saguinus fuscicollis	8 (2, 3)[b]	400.0	Silva and Downing, 1995
Saguinus midas	3 (2, 1)	376.7 (380.0, 370.0)	This study
Saguinus mystax	3 (3, –)	518.7 (518.7, –)	This study
Saimiri sciureus	7 (4, 3)	852.9 (992.5, 666.7)	This study
Varecia variegata	4 (–, 2)	3000.0	Silva and Downing, 1995

Species	N (male, female)	Body mass (g)[a] Mean (male, female)	Reference
Tree shrews			
Dendrogale melanura	3 (2, 1)	46.3 (47.5, 44.0)	This study
Ptilocercus lowii	7 (3, 4)	41.3 (43.8, 39.4)	This study
Tupaia berlangeri	4 (2, 2)	162.5 (157.5, 167.5)	This study
Tupaia minor	7 (2, 5)	48.8 (49.0, 48.7)	This study
Urogale everetti	2 (1, 1)	315.0 (355.0, 275.0)	This study
Marsupials			
Antechinus godmani	5 (4, 1)	95.0, 58.0	Strahan, 1995
Antechinus minimus	6 (2, 4)	65.0, 42.0	Strahan, 1995
Antechinus stuartii	5 (3, 2)	35.0, 20.0	Strahan, 1995
Caluromys derbianus	8 (4, 4)	275.8 (288.8, 262.8)	This study
Caluromys philander	5 (3, 2)	226.0 (266.7, 165.0)	This study
Dasyuroides byrnei	4 (2, 1)[b]	120.0, 100.0	Strahan, 1995
Dasyurus hallucatus	5 (2, 3)	500.0	Strahan, 1995
Dasyurus maculatus	2 (1, 2)	4000.0	Silva and Downing, 1995
Dasyurus viverrinus	3 (3, –)	1300.0, –	Strahan, 1995
Didelphis albiventris	2 (1, 1)	1332.6 (1265.2, 1400.0)	This study
Didelphis marsupialis	6 (3, 3)	1342.1 (1420.0, 1264.1)	This study
Gracilinanus agilis	2 (1, 1)	30.8 (29.0, 32.5)	This study
Gracilinanus sp.	2 (2, –)	27.4 (27.4, –)	This study
Marmosa xerophila	19 (9, 10)	51.6 (62.5, 41.7)	This study

Species	N (male, female)	Body mass (g)[a] Mean (male, female)	Reference
Monodelphis domestica	6 (3, 3)	83.0 (95.3, 70.6)	This study
Phascogale tapoatafa	2[b]	231.0	Strahan, 1995
Philander opossum	13 (9, 4)	531.2 (574.8, 433.3)	This study
Planigale maculata	3 (3, –)	12.0, –	Strahan, 1995
Sarcophilus harrisii	4 (3, 1)	9000.0, 7000.0	Strahan, 1995
Sminthopsis dolichura	1	14.8, –	Strahan, 1995
Sminthopsis macroura	5	20.0	Strahan, 1995
Thylamys elegans	7 (5, 2)	27.6 (30.6, 20.0)	This study

[a]Only one listed body mass indicates average for both male and female.

[b]Includes specimens of unknown sex.

TABLE 2. Regression equations generated from each mean tooth measurement for Primates (no. specimens = 21) and Strepsirhini (no. specimens = 11; italics). CI = confidence interval.

Tooth measurement	Y- intercept (ln b)	Slope (a)	95% CI for slope		Correlation (r)
			Lower	Upper	
m1 L	3.508	2.244	1.662	2.825	0.880
	2.298	*2.846*	*2.389*	*3.303*	*0.978*
m1 W	3.792	2.652	2.153	3.150	0.931
	3.167	*3.056*	*2.419*	*3.693*	*0.964*
m1 LxW	3.591	1.238	0.970	1.505	0.912
	2.702	*1.480*	*1.216*	*1.743*	*0.973*
m2 L	3.954	1.985	1.303	2.667	0.814
	2.091	*3.020*	*2.476*	*3.565*	*0.973*
m2 W	4.247	2.256	1.604	2.907	0.857
	2.741	*3.343*	*2.715*	*3.970*	*0.971*
m2 LxW	4.061	1.071	0.739	1.403	0.840
	2.381	*1.594*	*1.313*	*1.875*	*0.974*
m3 L	2.936	2.643	1.103	4.184	0.752
	1.535	*3.460*	*2.436*	*4.484*	*0.931*
m3 W	3.256	3.356	2.406	4.307	0.920
	2.883	*3.645*	*2.849*	*4.440*	*0.961*
m3 LxW	2.855	1.576	0.946	2.206	0.857
	2.151	*1.792*	*1.349*	*2.236*	*0.950*

Tooth measurement	Y- intercept (ln b)	Slope (a)	95% CI for slope		Correlation (r)
			Lower	Upper	
M1 L	3.559	2.274	1.676	2.872	0.877
	2.289	*2.933*	*2.493*	*3.372*	*0.981*
M1 W	2.866	2.515	1.775	3.255	0.853
	1.517	*3.197*	*2.242*	*4.152*	*0.930*
M1 LxW	3.191	1.210	0.883	1.537	0.871
	1.835	*1.559*	*1.244*	*1.874*	*0.966*
M2 L	4.615	1.544	0.883	2.206	0.746
	2.176	*3.023*	*2.449*	*3.597*	*0.970*
M2 W	3.923	1.841	1.025	2.657	0.735
	1.284	*3.307*	*2.253*	*4.362*	*0.921*
M2 LxW	4.284	0.847	0.482	1.212	0.744
	1.672	*1.607*	*1.230*	*1.983*	*0.955*
M3 L	3.267	2.791	1.331	4.250	0.785
	2.260	*3.449*	*2.336*	*4.561*	*0.919*
M3 W	2.310	3.324	1.551	5.097	0.780
	1.337	*3.924*	*2.355*	*5.494*	*0.883*
M3 LxW	2.757	1.548	0.752	2.343	0.791
	1.719	*1.880*	*1.250*	*2.511*	*0.914*

TABLE 3. Regression equations generated from each mean tooth measurement for insectivores (no. specimens = 22). CI = confidence interval.

Tooth measurement	Y- intercept (ln b)	Slope (a)	95% CI for slope		Correlation (r)
			Lower	Upper	
m1 L	0.984	3.176	2.767	3.586	0.964
m1 W	2.348	2.976	2.616	3.335	0.968
m1 LxW	1.662	1.554	1.377	1.730	0.972
m2 L	0.932	3.394	3.071	3.717	0.980
m2 W	2.413	3.164	2.864	3.464	0.980
m2 LxW	1.689	1.645	1.497	1.792	0.982
m3 L	1.817	3.419	2.591	4.246	0.888
m3 W	3.416	3.165	2.732	3.599	0.960
m3 LxW	2.621	1.677	1.380	1.974	0.935
M1 L	0.474	3.641	3.266	4.017	0.976
M1 W	0.361	3.348	2.895	3.801	0.960
M1 LxW	0.349	1.777	1.597	1.957	0.977
M2 L	0.933	3.519	3.192	3.846	0.981
M2 W	0.566	3.474	2.950	3.997	0.951
M2 LxW	0.694	1.778	1.586	1.969	0.974
M3 L	2.694	3.045	2.317	3.772	0.890
M3 W	1.692	3.551	2.848	4.254	0.920
M3 LxW	2.161	1.706	1.373	2.039	0.922

TABLE 4. Regression equations generated from each mean tooth measurement for Didelphidae (no. specimens = 8). CI = confidence interval.

Tooth measurement	Y- intercept (ln b)	Slope (a)	95% CI for slope		Correlation (r)
			Lower	Upper	
m1 L	2.131	3.095	2.930	3.259	0.998
m1 W	3.732	3.144	2.871	3.416	0.996
m1 LxW	2.924	1.560	1.459	1.661	0.998
m2 L	1.768	3.229	2.937	3.521	0.996
m2 W	3.366	3.279	2.901	3.657	0.993
m2 LxW	2.557	1.629	1.471	1.787	0.995
m3 L	1.785	3.089	2.769	3.409	0.994
m3 W	3.405	3.156	2.712	3.600	0.990
m3 LxW	2.581	1.564	1.382	1.746	0.993
m4 L	1.837	2.973	2.752	3.194	0.997
m4 W	3.731	3.029	2.623	3.435	0.991
m4 LxW	2.770	1.503	1.350	1.655	0.995
M1 L	1.830	3.284	2.897	3.671	0.993
M1 W	1.373	3.572	3.056	4.087	0.990
M1 LxW	1.571	1.733	1.592	1.873	0.996
M2 L	1.758	3.229	2.879	3.580	0.994
M2 W	0.944	3.577	3.057	1.097	0.989
M2 LxW	1.349	1.707	1.534	1.880	0.995

Tooth measurement	Y- intercept (ln b)	Slope (a)	95% CI for slope		Correlation (r)
			Lower	Upper	
M3 L	1.864	3.093	2.816	3.370	0.996
M3 W	0.797	3.465	2.958	3.972	0.989
M3 LxW	1.350	1.638	1.455	1.821	0.994
M4 L	3.120	2.866	2.579	3.153	0.995
M4 W	0.912	3.785	2.955	4.616	0.977
M4 LxW	2.140	1.643	1.454	1.833	0.993

TABLE 5. Body mass (grams) of Late Cretaceous taxa estimated from regression equations generated from size of lower and upper first molars in modern insectivores, marsupials and primates. Letter after name of species indicates formation in which species was found. L = Lancian, S = Scollard, F = Frenchman, HC = Hell Creek, HT = Hell Creek/Tullock, BCA = Bug Creek Anthills. A number indicates multiple specimens and/or localities for that species in that formation.

	Insectivores				Insectivores (Bloch et al., 1998)		Marsupials (Didelphidae)			
Late Cretaceous taxon	m1L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW
Eutherians										
Batodon tenuis L	6.65	5.40	–	–	5.39	–	19.50	18.54	–	–
Cimolestes cerberoides S	124.44	109.59	79.38	115.05	126.38	160.68	338.84	380.93	218.59	373.67
Cimolestes incisus F	176.45	132.95	–	–	154.73	–	476.18	462.46	–	–
Cimolestes incisus L	154.43	124.55	103.78	142.37	144.51	197.35	418.18	433.16	278.37	459.97
Cimolestes magnus S1	507.35	458.45	617.81	817.39	565.96	1064.94	1332.80	1602.36	1391.29	2528.95
Cimolestes magnus S2	–	–	509.85	672.78	–	882.60	–	–	1170.00	2091.59
Cimolestes magnus S3	559.75	517.32	–	–	642.32	–	1466.79	1808.97	–	–
Cimolestes magnus S4	510.52	472.75	–	–	584.47	–	1340.93	1652.55	–	–

Late Cretaceous taxon	Insectivores				Insectivores (Bloch et al., 1998)		Marsupials (Didelphidae)			
	m1L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW
Cimolestes propalaeoryctes S1	49.75	46.89	37.85	62.94	51.94	89.81	138.66	162.47	112.09	207.51
Cimolestes propalaeoryctes S2	53.04	53.17	–	–	59.24	–	147.60	184.30	–	–
Cimolestes stirtoni L	343.06	312.14	313.54	–	378.35	–	910.26	1089.36	754.64	–
Gypsonictops hypoconus L1	–	–	32.31	51.07	–	73.42	–	–	97.18	169.25
Gypsonictops hypoconus L2	26.11	27.80	21.04	33.84	30.03	49.35	73.99	96.12	66.00	113.27
Gypsonictops hypoconus L3	30.49	33.38	25.13	39.19	36.38	56.87	86.05	115.51	77.47	130.73
Gypsonictops illuminatus F	–	–	42.12	69.72	–	99.12	–	–	123.44	229.26
Gypsonictops illuminatus S1	46.59	56.43	49.52	81.51	63.05	115.24	130.09	195.65	142.84	267.00
Gypsonictops illuminatus S2	–	–	58.63	83.96	–	118.58	–	–	166.31	274.82
Metatherians										
Alphadon jasoni F	29.58	22.36	23.43	23.99	23.90	35.42	83.54	77.23	72.73	80.99
Alphadon jasoni S	40.70	42.51	62.75	57.67	46.86	82.55	114.03	147.22	176.84	190.54
Alphadon marshi L1	–	–	21.43	20.39	–	30.28	–	–	67.09	69.12

Late Cretaceous taxon	Insectivores				Insectivores (Bloch et al., 1998)		Marsupials (Didelphidae)			
	m1L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW
Alphadon marshi L2	–	–	26.47	25.65	–	37.78	–	–	81.17	86.46
Didelphodon vorax L1	319.43	350.38	472.23	613.06	427.05	806.92	849.10	1223.38	1091.84	1910.34
Didelphodon vorax L2	367.87	440.12	–	–	542.28	–	974.34	1538.05	–	–
Didelphodon vorax S	286.11	339.97	–	–	413.76	–	762.67	1186.88	–	–
Glasbius intricatus L	18.69	17.39	16.80	14.43	18.37	21.70	53.40	60.00	53.87	49.35
Glasbius twitchelli HT	26.95	27.61	23.02	21.29	29.81	31.57	76.30	95.45	71.58	72.10
Pediomys cooki L1	–	–	18.14	21.01	–	31.16	–	–	57.72	71.16
Pediomys cooki L2	–	–	23.43	24.54	–	36.21	–	–	72.73	82.81
Pediomys elegans F	18.03	17.78	30.77	33.09	18.81	48.30	51.59	61.38	92.99	110.83
Pediomys elegans L1	–	–	15.84	18.18	–	27.10	–	–	51.10	61.79
Pediomys elegans L2	–	–	12.67	16.17	–	24.21	–	–	41.78	55.13
Pediomys florencae L1	–	–	139.14	136.87	–	189.98	–	–	362.65	442.62
Pediomys florencae L2	–	–	140.65	145.43	–	201.43	–	–	366.21	469.60

Late Cretaceous taxon	Insectivores				Insectivores (Bloch et al., 1998)		Marsupials (Didelphidae)			
	m1 L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW
Pediomys hatcheri L1	–	–	59.44	69.15	–	98.33	–	–	168.38	227.42
Pediomys hatcheri L2	–	–	72.58	78.32	–	110.88	–	–	201.62	256.79
Pediomys krejcii F	8.41	8.04	8.13	7.89	8.19	12.12	24.53	27.66	27.98	27.39
Pediomys krejcii L1	–	–	7.38	8.10	–	12.43	–	–	25.66	28.11
Pediomys krejcii L2	–	–	9.34	11.24	–	17.05	–	–	31.72	38.68
Pediomys krejcii S1	10.25	9.79	11.15	13.75	10.06	20.71	29.75	33.71	37.23	47.07
Pediomys krejcii S2	8.41	8.04	–	–	8.19	–	24.53	27.66	–	–
Protalphadon lulli L	–	–	16.48	17.94	–	26.76	–	–	52.93	61.00
Turgidodon petiminis F	115.03	86.34	89.88	85.54	98.44	120.73	313.84	299.82	244.52	279.86
Turgidodon rhaister L	–	–	136.15	122.99	–	171.36	–	–	355.61	398.78
Archaic ungulates										
Alostera saskatchewanensis F1	–	–	35.00	38.20	–	55.48	–	–	104.45	127.51
Alostera saskatchewanensis F2	44.77	34.20	–	–	37.31	–	125.12	118.35	–	–

Late Cretaceous taxon	Insectivores				Insectivores (Bloch et al., 1998)		Marsupials (Didelphidae)			
	m1L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW
Alostera saskatchewanensis HC	–	–	27.38	32.78	–	47.87	–	–	83.70	109.83
Mimatuta morgoth HT	247.43	256.27	–	–	307.73	–	662.01	893.70	–	–
Oxyprimus erikseni HT	114.46	76.05	–	–	86.19	–	312.32	263.98	–	–
Procerberus formicarum HT	67.73	59.92	54.70	67.85	67.15	96.56	187.30	207.81	156.23	223.28
Protungulatum donnae BCA	181.09	189.90	224.12	304.04	224.80	410.25	488.40	661.47	557.46	963.98
Protungulatum mckeeveri HT	236.00	226.51	–	–	270.40	–	632.19	789.55	–	–
Ragnorak harbichti HT	510.52	596.79	–	–	746.07	–	1340.93	2088.04	–	–

Late Cretaceous taxon	Primates				Primates (Strepsirhini)				Primates (Gingerich et al., 1982)	
	m1 L	m1 LxW	M1 L	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW
Eutherians										
Batodon tenuis L	67.42	38.24	–	–	15.65	11.35	–	–	33.72	–
Cimolestes cerberoides S	534.26	421.08	437.99	528.97	216.06	199.65	162.45	218.45	610.91	799.08
Cimolestes incisus F	683.75	491.14	–	–	295.43	239.98	–	–	735.69	–
Cimolestes incisus L	622.30	466.28	517.80	611.56	262.17	225.53	201.60	263.35	690.96	970.40
Cimolestes magnus S1	1442.07	1316.73	1577.77	2010.30	761.17	780.15	848.41	1220.19	2420.45	4774.17
Cimolestes magnus S2	–	–	1399.42	1760.70	–	–	726.80	1028.59	–	3997.71
Cimolestes magnus S3	1545.78	1449.75	–	–	831.26	875.28	–	–	2718.76	–
Cimolestes magnus S4	1448.43	1349.35	–	–	765.44	803.31	–	–	2493.04	–
Cimolestes propalaeoryctes S1	279.51	214.13	275.81	350.81	95.00	88.95	89.47	128.69	269.97	461.11
Cimolestes propalaeoryctes S2	292.48	236.66	–	–	100.62	100.26	–	–	304.64	–
Cimolestes stirtoni L	1093.75	969.39	1032.94	–	536.05	540.98	491.27	–	1672.20	–
Gypsonictops hypoconus L1	–	–	249.84	304.28	–	–	78.76	107.14	–	381.13

Late Cretaceous taxon	Primates				Primates (Strepsirhini)				Primates (Gingerich et al., 1982)	
	m1 L	m1 LxW	M1 L	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW
Gypsonictops hypoconus L2	177.27	141.18	191.14	229.88	53.32	54.06	55.75	74.65	163.25	261.84
Gypsonictops hypoconus L3	197.78	163.34	213.57	254.07	61.26	64.36	64.33	84.92	194.68	299.37
Gypsonictops illuminatus F	–	–	294.85	376.10	–	–	97.51	140.77	–	506.14
Gypsonictops illuminatus S1	266.87	248.16	326.21	418.32	89.59	106.10	111.09	161.45	322.60	583.63
Gypsonictops illuminatus S2	–	–	362.47	426.83	–	–	127.27	165.70	–	599.59
Metatherians										
Alphadon jasoni F	193.57	118.67	204.43	181.88	59.62	43.93	60.80	55.20	132.37	191.35
Alphadon jasoni S	242.57	198.02	378.21	330.53	79.37	81.01	134.44	119.19	245.64	425.77
Alphadon marshi L1	–	–	193.32	162.83	–	–	56.57	47.87	–	165.02
Alphadon marshi L2	–	–	220.57	190.37	–	–	67.06	58.55	–	203.41
Didelphodon vorax L1	1039.96	1062.89	1334.00	1652.72	502.84	603.93	683.27	948.05	1868.87	3672.92
Didelphodon vorax L2	1149.05	1274.61	–	–	570.66	750.41	–	–	2327.27	–
Didelphodon vorax S	962.09	1037.64	–	–	455.58	586.82	–	–	1815.39	–

Late Cretaceous taxon	Primates				Primates (Strepsirhini)				Primates (Gingerich et al., 1982)	
	m1 L	m1 LxW	M1 L	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW
Glasbius intricatus L	139.94	97.13	166.05	128.69	39.51	34.57	46.50	35.35	103.93	120.42
Glasbius twitchelli HT	181.27	140.40	202.18	167.69	54.85	53.71	59.94	49.72	162.17	171.64
Pediomys cooki L1	–	–	174.19	166.16	–	–	49.46	49.14	–	169.54
Pediomys cooki L2	–	–	204.43	184.73	–	–	60.80	56.32	–	195.38
Pediomys elegans F	136.48	98.90	242.33	226.42	38.27	35.33	75.72	73.20	106.22	256.57
Pediomys elegans L1	–	–	160.09	150.57	–	–	44.36	43.28	–	148.60
Pediomys elegans L2	–	–	139.26	139.04	–	–	37.06	39.06	–	133.57
Pediomys florencae L1	–	–	621.87	595.36	–	–	255.32	254.40	–	936.15
Pediomys florencae L2	–	–	626.09	620.47	–	–	257.56	268.31	–	989.39
Pediomys hatcheri L1	–	–	365.58	373.99	–	–	128.68	139.75	–	502.35
Pediomys hatcheri L2	–	–	414.16	407.08	–	–	151.14	155.88	–	562.74
Pediomys krejcii F	79.62	52.53	105.49	85.31	19.32	16.58	25.90	20.81	49.48	69.45
Pediomys krejcii L1	–	–	99.37	86.87	–	–	23.98	21.31	–	71.15

Late Cretaceous taxon	Primates				Primates (Strepsirhini)				Primates (Gingerich et al., 1982)	
	m1 L	m1 LxW	M1 L	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW
Pediomys krejcii L2	–	–	115.07	108.56	–	–	28.97	28.40	–	95.90
Pediomys krejcii S1	91.57	61.47	128.58	124.52	23.07	20.01	33.43	33.88	59.81	115.22
Pediomys krejcii S2	79.62	52.53	–	–	19.32	16.58	–	–	49.48	–
Protalphadon lulli L	–	–	164.05	149.21	–	–	45.78	42.78	–	146.80
Turgidodon petiminis F	505.38	348.21	473.34	432.28	201.35	159.08	179.56	168.43	485.65	609.86
Turgidodon rhaister L	–	–	613.49	553.55	–	–	250.89	231.62	–	849.19
Archaic ungulates										
Alostera saskatchewanensis F1	–	–	262.65	249.69	–	–	84.00	83.04	–	292.48
Alostera saskatchewanensis F2	259.45	166.52	–	–	86.44	65.86	–	–	199.27	–
Alostera saskatchewanensis HC	–	–	225.31	224.98	–	–	68.93	72.61	–	254.38
Mimatuta morgoth HT	868.25	828.45	–	–	399.97	448.34	–	–	1383.21	–
Oxyprimus erikseni HT	503.60	314.75	–	–	200.45	140.98	–	–	429.87	–
Procerberus formicarum HT	347.61	260.32	347.10	369.21	125.26	112.35	120.35	137.46	341.79	493.78

Late Cretaceous taxon	Primates				Primates (Strepsirhini)				Primates (Gingerich et al., 1982)	
	m1 L	m1 LxW	M1 L	M1 LxW	m1 L	m1 LxW	M1 L	M1 LxW	m1 LxW	M1 LxW
Protungulatum donnae BCA	696.42	652.47	837.53	1025.18	302.39	337.00	374.85	512.41	1036.70	1937.94
Protungulatum mckeeveri HT	839.72	750.86	–	–	383.38	398.62	–	–	1228.34	–
Ragnorak harbichti HT	1448.43	1624.57	–	–	765.44	1002.90	–	–	3119.47	–

[a]Information for Cretaceous taxa and associated measurements was taken from Clemens (1966, 1973), Fox (1977, 1989), Lillegraven (1969), Storer (1991), Archibald (1982), and Johanson (1996).

APPENDIX 1. Mean lower molar measurements (mm) for all species studied. N = no. of specimens, CV = coefficient of variation, L = length, W = width.

		m1				m2				m3				m4			
Species	Measurement	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Insectivores																	
Atelerix albiventris	L	5	4.20	4.10	4.04–4.49	5	3.55	4.64	3.39–3.82	5	1.72	4.96	1.57–1.90				
	W	5	2.69	5.83	2.52–2.89	5	2.53	4.96	2.37–2.70	5	1.58	5.49	1.46–1.69				
Crocidura cyanea	L	5	1.54	5.13	1.50–1.68	5	1.59	5.22	1.52–1.71	5	1.21	6.43	1.12–1.31				
	W	5	1.15	9.20	1.00–1.25	5	1.01	6.43	0.92–1.09	5	0.71	3.87	0.67–0.75				
Crocidura flavescens	L	13	2.55	5.92	2.31–2.76	13	2.41	5.42	2.24–2.60	12	1.82	7.94	1.64–2.00				
	W	13	1.89	6.88	1.71–2.21	13	1.62	7.94	1.43–1.89	12	1.04	7.81	0.91–1.20				
Echinosorex gymnurus	L	7	7.06	4.41	6.58–7.46	7	6.03	4.06	5.61–6.30	7	4.80	4.53	4.46–5.25				
	W	7	4.52	4.72	4.29–4.91	7	4.17	4.53	3.83–4.42	7	3.11	5.81	2.85–3.40				
Erinaceus europaeus	L	5	5.46	5.60	5.10–5.90	5	5.00	3.12	4.81–5.19	5	2.67	5.62	2.21–3.42				
	W	5	4.04	5.59	3.83–4.32	5	3.50	5.62	3.23–3.76	5	2.08	5.22	1.98–2.21				
Hemiechinus auritus	L	5	4.66	6.54	4.16–4.98	5	4.06	6.62	3.74–4.44	5	2.03	7.03	1.75–2.22				
	W	5	3.30	9.72	2.98–3.79	5	2.86	7.03	2.52–3.03	5	1.73	9.8	1.48–1.89				

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Hylomys suillus	L	7	2.94	1.60	2.87–3.01	7	2.42	1.48	2.37–2.48	7	1.88	2.65	1.83–1.95				
	W	7	1.65	9.34	1.48–1.90	7	1.48	2.65	1.42–1.54	7	1.10	3.66	1.06–1.16				
Myosorex sp.	L	4	1.48	2.79	1.44–1.53	4	1.46	4.12	1.38–1.51	4	1.22	4.24	1.14–1.28				
	W	4	1.15	1.69	1.12–1.17	4	1.11	4.24	1.05–1.17	4	0.71	2.37	0.69–0.73				
Neurotrichus gibbsii	L	7	1.78	5.61	1.62–1.91	7	1.73	4.29	1.62–1.83	7	1.51	5.39	1.42–1.58				
	W	7	1.05	3.95	1.02–1.14	7	1.08	5.39	0.96–1.14	7	0.81	5.55	0.74–0.88				
Parascalops breweri	L	3	2.24	1.08	2.22–2.27	3	2.26	2.46	2.20–2.31	3	1.93	5.16	1.85–2.01				
	W	3	1.48	4.46	1.41–1.53	3	1.49	5.16	1.44–1.58	3	1.22	4.25	1.16–1.26				
Scapanus orarius	L	4	2.49	1.66	2.44–2.54	4	2.46	0.56	2.45–2.47	4	2.09	3.28	1.99–2.15				
	W	4	1.68	2.53	1.63–1.74	4	1.66	3.28	1.59–1.72	4	1.39	1.72	1.36–1.41				
Scapanus townsendii	L	3	3.01	3.03	2.94–3.12	3	3.07	5.13	2.89–3.19	3	2.63	3.47	2.53–2.73				
	W	3	2.15	4.19	2.07–2.25	3	2.13	3.47	2.05–2.19	3	1.75	6.84	1.62–1.86				

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Sorex cinereus	L	5	1.26	1.84	1.22–1.28	5	1.08	1.77	1.07–1.12	5	0.90	6.08	0.88–0.92				
	W	5	0.65	5.62	0.60–0.70	5	0.66	6.08	0.60–0.70	5	0.49	2.49	0.48–0.51				
Sorex longirostris	L	5	1.17	0.74	1.16–1.19	5	1.05	3.41	1.00–1.09	5	0.86	3.42	0.84–0.89				
	W	5	0.73	5.85	0.69–0.80	5	0.68	3.42	0.65–0.71	5	0.50	1.37	0.49–0.51				
Suncus murinus	L	9	2.16	6.82	2.02–2.46	9	2.06	7.41	1.91–2.32	8	1.56	7.34	1.39–1.81				
	W	9	1.65	5.54	1.50–1.81	9	1.40	7.34	1.29–1.57	9	0.92	8.12	0.81–1.02				
Talpa micrura	L	9	2.23	3.25	2.11–2.33	9	2.38	5.12	2.16–2.60	9	1.85	7.01	1.74–1.96				
	W	9	1.30	6.16	1.16–1.41	9	1.36	7.01	1.18–1.45	9	1.14	7.85	0.98–1.23				
Urotrichus talpoides	L	4	1.75	1.24	1.73–1.78	4	1.85	5.04	1.77–1.96	4	1.41	1.29	1.30–1.53				
	W	4	1.27	3.13	1.23–1.31	4	1.24	1.29	1.22–1.26	4	0.89	4.4	0.84–0.94				
Primates																	
Arctocebus calabarensis	L	1	–	–	3.9	1	–	–	4.16	1	–	–	4.29				
	W	1	–	–	2.82	1	–	–	2.85	1	–	–	2.72				

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Avahi laniger	L	2	4.86	–	4.81–4.90	2	4.50	–	4.36–4.65	2	4.21	–	4.13–4.29				
	W	2	2.91	–	2.85–2.97	2	3.11	–	2.97–3.25	2	2.89	–	2.79–3.00				
Callithrix argentata	L	1	–	–	2.36	1	–	–	2.23	–	–	–	–				
	W	1	–	–	1.93	1	–	–	1.73	–	–	–	–				
Callithrix humeralifer	L	3	2.51	8.37	2.28–2.70	3	2.31	3.22	2.23–2.38	–	–	–	–				
	W	3	1.97	7.52	1.80–2.08	3	1.80	1.88	1.76–1.82	–	–	–	–				
Callithrix jacchus	L	7	2.47	7.92	2.25–2.79	7	2.03	7.65	1.79–2.19	–	–	–	–				
	W	7	2.11	6.94	1.97–2.40	7	1.78	10.24	1.53–2.09	–	–	–	–				
Cebuella pygmaea	L	5	1.98	3.85	1.88–2.05	5	1.76	5.98	1.64–1.91	–	–	–	–				
	W	5	1.55	1.82	1.51–1.58	5	1.34	4.08	1.26–1.41	–	–	–	–				
Cebus capucinus	L	4	5.00	5.39	4.72–5.31	4	4.51	5.17	4.25–4.72	4	3.88	7.06	3.63–4.15				
	W	4	4.49	4.44	4.22–4.70	4	4.43	4.35	4.17–4.58	4	3.99	2.06	3.93–4.10				

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Eulemur fulvus	L	5	6.30	3.23	6.12–6.55	5	6.19	2.74	5.99–6.39	4	5.48	5.11	5.11–5.72				
	W	5	4.15	5.45	3.92–4.49	5	3.93	4.92	3.65–4.13	5	3.16	2.35	3.09–3.28				
Galago alleni	L	3	3.24	2.53	3.15–3.31	3	3.25	1.61	3.19–3.29	3	3.55	2.77	3.44–3.63				
	W	3	2.32	5.75	2.17–2.43	3	2.45	6.57	2.27–2.57	3	2.18	0.92	2.16–2.20				
Galago demidovii	L	9	2.02	7.51	1.82–2.25	9	2.04	7.01	1.86–2.24	9	2.24	7.62	2.01–2.52				
	W	9	1.53	9.33	1.40–1.81	9	1.65	7.17	1.52–1.86	9	1.51	7.96	1.39–1.70				
Hapalemur griseus	L	5	4.79	4.26	4.55–5.05	5	4.76	5.46	4.42–5.04	5	4.65	5.21	4.35–4.91				
	W	5	3.40	4.60	3.19–3.58	5	3.78	5.14	3.48–3.95	5	3.08	8.06	2.74–3.41				
Leontopithecus rosalia	L	5	3.32	2.98	3.20–3.47	5	2.96	3.3	2.82–3.09	–	–	–	–				
	W	5	2.70	4.08	2.55–2.85	5	2.30	3.66	2.23–2.43	–	–	–	–				
Loris tardigradus	L	2	3.02	–	2.99–3.05	2	3.13	–	3.10–3.16	2	3.61	–	3.56–3.67				
	W	2	2.16	–	2.15–2.17	2	2.30	–	2.29–2.31	2	2.29	–	2.29–2.29				

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Microcebus murinus	L	6	2.03	8.62	1.91–2.37	6	2.05	8.83	1.89–2.38	6	2.20	5.36	2.02–2.33				
	W	6	1.38	9.84	1.25–1.56	6	1.50	7.36	1.35–1.65	6	1.33	4.67	1.26–1.44				
Perodicticus potto	L	4	3.88	4.71	3.76–4.16	4	3.86	3.28	3.71–4.02	4	3.23	11.37	2.73–3.54				
	W	4	2.67	10.10	2.28–2.89	4	2.80	7.82	2.48–2.95	4	2.41	11.05	2.12–2.67				
Propithecus diadema	L	5	7.53	5.01	7.14–8.06	5	7.61	1.36	7.47–7.73	5	7.88	4.15	7.55–8.39				
	W	5	4.99	4.23	4.77–5.34	5	5.51	1.86	5.39–5.61	5	5.26	3.34	5.10–5.47				
Propithecus verreauxi	L	4	7.23	4.64	6.91–7.63	4	6.92	3.7	6.69–7.28	4	6.81	3.01	6.61–7.09				
	W	4	4.51	2.75	4.37–4.65	4	4.76	3.47	4.56–4.96	4	4.41	6.34	4.12–4.75				
Saguinus fuscicollis	L	7	2.32	6.64	2.07–2.54	7	2.07	7.08	1.89–2.32	–	–	–	–				
	W	7	1.94	7.59	1.71–2.16	7	1.64	7.29	1.52–1.86	–	–	–	–				
Saguinus midas	L	3	2.58	3.99	2.49–2.69	3	2.02	5.33	1.89–2.09	–	–	–	–				
	W	2	1.83	–	1.81–1.84	3	1.51	4.85	1.43–1.58	–	–	–	–				

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Saguinus mystax	L	3	2.71	1.86	2.67–2.77	3	2.42	5.6	2.32–2.58	–	–	–	–				
	W	3	2.25	3.19	2.17–2.32	3	1.94	7.75	1.76–2.04	–	–	–	–				
Saimiri sciureus	L	7	3.11	4.09	2.93–3.30	7	2.80	4.33	2.62–2.93	7	2.18	7.72	1.85–2.32				
	W	7	2.74	5.24	2.52–2.96	7	2.59	6.66	2.37–2.84	7	1.97	6.94	1.80–2.15				
Varecia variegata	L	4	8.00	1.50	7.90–8.15	4	7.21	1.99	7.03–7.33	3	5.87	3.36	5.73–6.09				
	W	4	5.35	3.84	5.14–5.55	4	4.94	3.62	4.71–5.12	4	3.65	6.4	3.48–3.99				
Tree shrews																	
Dendrogale melanura	L	2	2.23	–	2.18–2.28	2	2.26	–	2.23–2.30	2	1.90	–	1.85–1.95				
	W	2	1.47	–	1.36–1.58	2	1.48	–	1.35–1.61	2	1.17	–	1.15–1.19				
Dendrogale murina	L	1	–	–	2.29	1	–	–	2.32	1	–	–	2.02				
	W	1	–	–	1.62	1	–	–	1.56	1	–	–	1.28				
Ptilocercus lowii	L	6	2.58	2.78	2.50–2.69	6	2.62	2.79	2.52–2.74	6	2.47	3.2	2.34–2.59				
	W	6	1.82	0.04	1.73–1.93	6	1.83	0.0215	1.78–1.89	6	1.60	0.0168	1.58–1.65				

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Tupaia berlangeri	L	1	–	–	3.44	1	–	–	3.21	1	–	–	2.73				
	W	1	–	–	2.43	1	–	–	2.31	1	–	–	1.61				
Tupaia minor	L	7	2.42	2.39	2.33–2.47	7	2.44	2.33	2.38–2.53	7	1.98	2.36	1.92–2.04				
	W	7	1.56	0.04	1.46–1.63	7	1.48	0.0496	1.39–1.61	7	1.12	0.0579	1.03–1.23				
Urogale everetti	L	2	3.58	–	3.57–3.58	2	3.51	–	3.44–3.59	2	3.08	–	3.04–3.11				
	W	2	2.68	–	2.59–2.78	2	2.57	–	2.56–2.58	2	2.06	–	2.00–2.13				
Marsupials																	
Antechinus godmani	L	5	1.94	2.35	1.90–2.00	5	2.29	1.93	2.22–2.34	5	2.25	0.98	2.23–2.27	5	1.99	2.68	1.90–2.04
	W	5	1.08	2.46	1.04–1.10	5	1.28	1.95	1.26–1.32	5	1.32	3.99	1.27–1.39	5	1.17	2.56	1.14–1.21
Antechinus minimus	L	6	1.58	6.41	1.46–1.69	6	1.81	5.03	1.69–1.90	6	1.85	5.21	1.70–1.93	6	1.74	3.24	1.64–1.81
	W	6	0.85	5.70	0.78–0.90	6	1.06	3.84	0.99–1.11	6	1.13	2.62	1.09–1.18	6	1.01	3.85	0.95–1.05
Antechinus stuartii	L	5	1.68	4.27	1.61–1.80	5	2.00	3.68	1.90–2.10	5	1.99	1.80	1.95–2.04	5	1.68	2.74	1.63–1.74
	W	5	0.94	5.89	0.89–1.01	5	1.23	4.94	1.17–1.30	5	1.25	4.66	1.20–1.33	5	1.05	2.65	1.02–1.10

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Caluromys derbianus	L	8	3.01	3.74	2.89–3.25	8	2.86	3.8	2.75–3.08	8	2.70	4.01	2.55–2.89	8	2.34	4.82	2.08–2.45
	W	8	1.70	3.77	1.61–1.79	8	1.67	4.6	1.56–1.81	8	1.52	4.8	1.40–1.63	8	1.19	4.73	1.08–1.25
Caluromys philander	L	5	2.75	4.50	2.59–2.91	5	2.67	3.98	2.55–2.80	5	2.55	3.97	2.43–2.66	5	2.21	2.93	2.13–2.27
	W	5	1.64	3.32	1.56–1.69	5	1.66	5	1.56–1.74	5	1.50	7.1	1.41–1.62	5	1.18	3.16	1.12–1.22
Dasyuroides byrnei	L	4	2.78	2.35	2.69–2.82	4	3.12	2.32	3.02–3.19	4	3.09	3.89	2.96–3.21	4	2.69	1.96	2.64–2.76
	W	4	1.40	5.53	1.29–1.45	4	1.81	4.80	1.68–1.87	4	1.96	4.42	1.83–2.03	4	1.75	3.56	1.70–1.83
Dasyurus hallucatus	L	5	3.75	0.98	3.72–3.81	5	4.32	1.71	4.24–4.43	5	4.38	1.00	4.33–4.42	5	4.01	1.16	3.98–4.09
	W	5	2.04	4.97	1.94–2.18	5	2.42	2.99	2.31–2.50	5	2.56	3.20	2.46–2.67	5	2.38	4.34	2.28–2.51
Dasyurus maculatus	L	3	5.11	3.85	4.89–5.26	3	5.75	3.20	5.64–5.96	3	6.27	3.81	6.04–6.51	3	6.43	1.3	6.34–6.50
	W	3	2.92	7.17	2.69–3.11	3	3.57	3.98	3.41–3.66	3	3.71	6.47	3.43–3.86	3	3.69	6.59	3.42–3.89
Dasyurus viverrinus	L	3	4.74	5.03	4.48–4.95	3	5.43	3.00	5.25–5.55	3	5.60	0.89	5.56–5.66	3	5.49	1.02	5.44–5.55
	W	3	2.77	3.26	2.71–2.88	3	3.23	3.06	3.12–3.31	3	3.32	2.00	3.27–3.40	3	3.27	4.13	3.18–3.43

		m1				m2				m3				m4			
Species	Measurement	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Didelphis albiventris	L	2	5.06	1.17	5.02–5.11	2	5.14	1.37	5.09–5.20	2	5.43	2.53	5.33–5.53	2	5.71	1.63	5.64–5.78
	W	2	2.96	1.98	2.92–3.00	2	3.10	2.69	3.04–3.16	2	3.08	1.49	3.05–3.11	2	2.95	0.65	2.93–2.96
Didelphis marsupialis	L	6	5.33	4.25	5.04–5.64	6	5.62	4.27	5.32–5.93	6	6.05	4.45	5.75–6.41	6	6.28	7.91	5.45–6.94
	W	6	3.21	5.72	3.02–3.44	6	3.46	3.48	3.29–3.64	6	3.55	3.84	3.40–3.74	6	3.23	3.82	3.07–3.40
Gracilinanus agilis	L	2	1.56	2.08	1.54–1.59	2	1.65	5.6	1.59–1.72	2	1.61	6.01	1.54–1.68	2	1.63	12.87	1.48–1.77
	W	2	0.90	1.42	0.89–0.91	2	0.98	0.58	0.98–0.99	2	0.98	4.11	0.95–1.01	2	0.84	3.45	0.82–0.86
Gracilinanus sp.	L	2	1.48	0.05	–	2	1.69	3.84	1.65–1.74	2	1.70	1.71	1.68–1.72	2	1.66	0.17	–
	W	2	0.91	3.26	0.89–0.93	2	1.03	2.96	1.00–1.05	2	0.95	4.37	0.93–0.98	2	0.86	0.49	0.86–0.87
Marmosa xerophila	L	19	1.71	4.50	1.50–1.84	19	1.81	3.81	1.69–1.95	19	1.87	3.42	1.76–2.01	19	1.95	4.23	1.81–2.11
	W	19	1.01	5.34	0.94–1.18	19	1.10	5.71	0.99–1.28	19	1.08	4.8	1.00–1.18	19	0.98	3.71	0.92–1.05
Monodelphis domestica	L	6	2.05	4.88	1.96–2.24	6	2.23	4.61	2.07–2.36	6	2.36	2.74	2.28–2.44	6	2.48	5.06	2.32–2.62
	W	6	1.27	5.09	1.21–1.38	6	1.43	3.39	1.37–1.49	6	1.51	4.96	1.44–1.65	6	1.37	3.68	1.27–1.41

Species	Measurement	m1				m2				m3				m4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Phascogale tapoatafa	L	2	2.78	7.80	2.63–2.93	2	3.24	5.45	3.13–3.37	2	3.00	2.88	2.94–3.06	2	2.48	3.96	2.41–2.55
	W	2	1.61	10.11	1.49–1.72	2	1.86	3.08	1.82–1.90	2	1.88	1.99	1.86–1.91	2	1.67	3.8	1.63–1.72
Philander opossum	L	13	3.75	5.25	3.41–4.04	13	4.06	4.88	3.82–4.50	13	4.32	5.19	4.08–4.84	13	4.53	4.38	4.31–4.88
	W	13	2.09	5.35	1.89–2.25	13	2.27	6.42	2.03–2.51	13	2.39	5.26	2.19–2.59	13	2.31	5.56	2.06–2.50
Planigale maculata	L	3	1.18	3.91	1.13–1.22	3	1.37	2.83	1.34–1.42	3	1.33	2.11	1.30–1.36	3	1.24	6.06	1.17–1.32
	W	3	0.63	6.32	0.59–0.67	3	0.84	4.45	0.80–0.87	3	0.92	4.74	0.87–0.94	3	0.80	1.00	0.79–0.81
Sarcophilus harrisii	L	4	9.06	4.11	8.60–9.43	4	10.05	1.96	9.77–10.22	4	11.34	2.19	10.98–11.54	4	11.32	4.65	10.65–11.90
	W	4	6.60	3.24	6.33–6.81	4	6.94	5.70	6.63–7.50	4	7.05	2.16	6.92–7.20	4	6.71	3.45	6.45–6.91
Sminthopsis dolichura	L	1	–	–	1.51	1	–	–	1.71	1	–	–	1.73	1	–	–	1.62
	W	1	–	–	0.78	1	–	–	0.99	1	–	–	1.10	1	–	–	1.01
Sminthopsis macroura	L	5	1.37	3.02	1.34–1.44	5	1.48	2.86	1.43 - 1.55	5	1.55	3.80	1.48–1.65	5	1.41	3.76	1.33–1.47
	W	5	0.75	2.24	0.72–0.77	5	0.91	3.29	0.88–0.96	5	1.00	5.33	0.97–1.09	5	0.92	4.42	0.86–0.97

		m1				m2				m3				m4			
Species	Measurement	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Thylamys elegans	L	7	1.50	4.20	1.41–1.57	7	1.71	5.04	1.59–1.80	7	1.80	4.74	1.67–1.87	7	1.72	3.35	1.66–1.81
	W	7	0.90	4.04	0.85–0.95	7	1.05	5.39	0.97–1.12	7	1.08	5	1.00–1.14	7	0.99	3.59	0.93–1.02

APPENDIX 2. Mean upper molar measurements (mm) for all species studied. N = no. specimens, CV = coefficient of variation, L = length, W = width.

		M1				M2				M3				M4			
Species	Measurement	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Insectivores																	
Atelerix albiventris	L	5	3.73	2.22	3.63–3.84	5	3.47	3.10	3.33–3.61	5	1.70	12.16	1.48–1.95				
	W	5	4.38	5.78	3.97–4.58	5	3.34	5.50	3.20–3.66	5	1.91	7.46	1.69–2.06				
Crocidura cyanea	L	5	1.63	5.31	1.52–1.75	5	1.53	6.05	1.43–1.64	5	0.79	6.86	0.73–0.86				
	W	5	2.12	6.43	1.99–2.32	5	1.89	8.04	1.74–2.05	5	1.28	5.78	1.22–1.40				
Crocidura flavescens	L	13	2.65	7.39	2.24–2.98	13	2.39	8.80	2.02–2.75	11	1.09	7.03	0.95–1.20				
	W	13	3.39	5.83	3.04–3.80	13	2.90	6.99	2.57–3.30	9	1.72	9.89	1.44–1.89				
Echinosorex gymnurus	L	7	6.37	2.47	6.19–6.66	7	5.50	6.72	4.94–6.00	7	4.74	5.93	4.23–5.17				
	W	7	6.19	4.40	5.92–6.70	7	5.70	4.64	5.36–6.14	7	3.68	7.30	3.21–4.07				
Erinaceus europaeus	L	5	5.31	8.67	4.87–5.93	5	5.13	3.92	4.94–5.40	5	2.30	12.41	1.87–2.64				
	W	5	6.02	5.95	5.70–6.52	5	4.86	4.09	4.54–5.04	5	3.09	11.32	2.47–3.32				
Hemiechinus auritus	L	5	4.35	9.50	3.64–4.71	5	4.05	6.24	3.71–4.41	5	1.68	6.02	1.59–1.83				
	W	5	4.95	11.33	4.20–5.54	5	4.19	9.26	3.54–4.54	5	2.59	7.64	2.27–2.77				

Species	Measurement	M1				M2				M3				M4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Hylomys suillus	L	7	2.44	2.32	2.35–2.50	7	2.07	4.27	1.97–2.26	6	1.41	1.83	1.37–1.44				
	W	7	2.56	5.98	2.24–2.70	7	2.25	4.37	2.12–2.40	6	1.54	2.17	1.49–1.58				
Myosorex sp.	L	4	1.75	5.94	1.62–1.87	4	1.63	6.22	1.49–1.73	4	1.09	11.27	0.94–1.24				
	W	4	2.28	2.54	2.20–2.32	4	1.96	2.93	1.89–2.02	4	1.35	3.53	1.29–1.39				
Neurotrichus gibbsii	L	7	1.94	6.92	1.82–2.20	7	1.61	3.20	1.51–1.66	7	1.20	6.29	1.11–1.31				
	W	7	1.83	3.16	1.73–1.91	7	1.70	4.37	1.58–1.81	7	1.35	4.31	1.27–1.43				
Parascalops breweri	L	3	2.55	2.61	2.48–2.61	3	2.22	2.89	2.15–2.27	3	1.72	1.16	1.69–1.73				
	W	3	2.36	5.06	2.22–2.44	3	2.23	2.17	2.17–2.26	3	1.85	3.87	1.78–1.92				
Scapanus orarius	L	6	2.56	6.41	2.33–2.75	6	2.26	1.55	2.21–2.31	6	1.75	4.55	1.67–1.88				
	W	6	2.61	3.55	2.51–2.72	6	2.44	2.18	2.36–2.49	6	1.92	4.67	1.82–2.09				
Scapanus townsendii	L	4	3.13	5.38	2.94–3.31	4	2.97	4.91	2.77–3.11	4	2.18	1.03	2.16–2.21				
	W	4	3.78	3.67	3.65–3.92	4	3.27	3.61	3.11–3.39	4	2.68	2.39	2.60–2.75				

		M1				M2				M3				M4			
Species	Measurement	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Sorex cinereus	L	5	1.31	4.19	1.26–1.40	5	1.14	5.78	1.02–1.19	5	0.74	4.27	0.71–0.79				
	W	5	1.19	2.55	1.16–1.23	5	1.17	1.83	1.15–1.20	5	0.91	6.54	0.83–0.98				
Sorex longirostris	L	5	1.26	4.24	1.17–1.30	5	1.08	7.50	0.96–1.17	5	0.70	3.26	0.66–0.72				
	W	5	1.27	2.88	1.22–1.31	5	1.21	5.71	1.14–1.32	5	0.91	7.09	0.83–1.00				
Suncus murinus	L	7	2.24	7.46	1.96–2.42	7	2.11	6.01	1.91–2.27	6	1.11	9.24	1.00–1.30				
	W	8	2.98	3.22	2.87–3.16	8	2.54	6.58	2.28–2.80	6	1.72	9.32	1.59–2.03				
Talpa micrura	L	9	2.42	4.29	2.22–2.55	9	2.29	4.44	2.13–2.42	9	1.62	5.76	1.45–1.76				
	W	9	2.54	5.37	2.28–2.71	9	2.36	5.81	2.14–2.61	9	1.82	4.96	1.70–1.96				
Urotrichus talpoides	L	4	2.02	2.83	1.97–2.10	4	1.83	7.58	1.69–2.02	3	1.28	4.19	1.22–1.33				
	W	4	2.32	3.48	2.25–2.42	4	1.99	3.99	1.89–2.07	3	1.26	6.94	1.20–1.36				
Primates																	
Arctocebus calabarensis	L	2	3.73	–	3.64–3.82	2	4.00	–	3.96–4.05	2	4.78	–	4.64–4.92				
	W	2	4.43	–	4.37–4.50	2	4.78	–	4.64–4.92	2	4.09	–	4.06–4.12				

Species	Measurement	M1				M2				M3				M4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Avahi laniger	L	2	4.63	–	4.54–4.72	2	4.35	–	4.31–4.40	2	4.22	–	4.04–4.41				
	W	2	4.38	–	4.21–4.55	2	4.22	–	4.04–4.41	2	3.47	–	3.27–3.66				
Callithrix argentata	L	1	–	–	2.17	1	–	–	1.67	1	–	–	2.18				
	W	1	–	–	2.74	1	–	–	2.18	–	–	–	–				
Callithrix humeralifer	L	3	2.41	4.20	2.30–2.48	3	1.91	7.04	1.76–2.00	3	2.52	6.67	2.35–2.68				
	W	3	2.97	8.16	2.69–3.14	3	2.52	6.67	2.35–2.68	–	–	–	–				
Callithrix jacchus	L	6	2.44	5.96	2.27–2.64	6	1.77	3.85	1.67–1.86	6	2.35	8.50	2.23–2.75				
	W	6	3.06	6.73	2.83–3.35	6	2.35	8.50	2.23–2.75	–	–	–	–				
Cebuella pygmaea	L	5	1.85	2.56	1.79–1.89	5	1.46	2.03	1.43–1.51	5	1.92	5.92	1.78–2.06				
	W	5	2.26	3.48	2.13–2.34	5	1.92	5.92	1.78–2.06	–	–	–	–				
Cebus capucinus	L	4	4.66	6.69	4.39–4.94	4	4.90	4.17	4.64–5.13	4	4.99	6.12	4.72–5.43				
	W	4	5.46	2.90	5.32–5.62	4	4.99	6.12	4.72–5.43	4	4.19	7.92	3.88–4.64				

Species	Measurement	M1				M2				M3				M4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Eulemur fulvus	L	4	5.69	3.26	5.50–5.92	4	5.80	4.01	5.49–6.05	4	7.15	1.31	7.03–7.24				
	W	4	7.28	1.38	7.16–7.40	4	7.15	1.31	7.03–7.24	4	4.92	6.02	4.65–5.32				
Galago alleni	L	3	3.14	2.68	3.06–3.22	3	3.06	2.52	2.99–3.14	3	4.18	4.55	4.07–4.40				
	W	3	3.93	3.05	3.81–4.05	3	4.18	4.55	4.07–4.40	3	3.43	0.83	3.41–3.46				
Galago demidovii	L	9	2.12	10.29	1.87–2.50	9	2.15	12.12	1.88–2.51	9	2.91	7.02	2.57–3.22				
	W	9	2.77	5.97	2.54–3.04	9	2.91	7.02	2.57–3.22	9	2.26	8.19	1.97–2.61				
Propithecus diadema	L	5	7.63	2.64	7.40–7.90	5	7.54	3.66	7.17–7.87	5	7.43	2.32	7.16–7.58				
	W	5	7.14	3.29	6.99–7.55	5	7.43	2.32	7.16–7.58	5	5.70	3.80	5.39–5.96				
Hapalemur griseus	L	5	4.57	1.69	4.49–4.69	5	4.51	4.21	4.30–4.66	5	5.24	4.71	4.97–5.50				
	W	5	5.33	6.16	5.01–5.80	5	5.24	4.71	4.97–5.50	5	4.46	4.50	4.19–4.65				
Leontopithecus rosalia	L	5	3.18	2.95	3.09–3.34	5	2.57	5.12	2.46–2.79	5	3.21	4.14	2.99–3.36				
	W	5	4.10	3.85	3.98–4.37	5	3.21	4.14	2.99–3.36	–	–	–	–				
Loris tardigradus	L	3	3.15	3.82	3.01–3.23	3	3.42	5.88	3.19–3.55	3	3.92	3.40	3.82–4.07				
	W	3	3.78	4.47	3.68–3.98	3	3.92	3.40	3.82–4.07	3	3.12	6.49	2.93–3.33				

		M1				M2				M3				M4			
Species	Measurement	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Microcebus murinus	L	6	1.83	6.45	1.74–2.05	6	1.84	6.25	1.76–2.07	6	2.18	7.05	2.06–2.48				
	W	6	2.14	6.29	2.01–2.39	6	2.18	7.05	2.06–2.48	6	1.98	6.56	1.89–2.23				
Perodicticus potto	L	3	3.64	7.87	3.34–3.91	3	3.55	7.24	3.28–3.79	3	4.41	6.64	4.10–4.69				
	W	3	4.22	3.33	4.13–4.38	3	4.41	6.64	4.10–4.69	3	3.27	10.66	2.91–3.61				
Propithecus verreauxi	L	4	7.17	3.03	6.95–7.47	4	6.80	1.54	6.68–6.93	4	6.43	2.85	6.22–6.65				
	W	4	6.15	2.81	5.90–6.29	4	6.43	2.85	6.22–6.65	4	4.44	7.08	4.16–4.76				
Saguinus fuscicollis	L	7	2.31	7.39	2.09–2.58	7	1.66	14.35	1.17–1.92	7	2.24	7.33	1.91–2.38				
	W	7	2.70	5.96	2.47–2.90	7	2.24	7.33	1.91–2.38	–	–	–	–				
Saguinus midas	L	3	2.46	2.65	2.40–2.53	3	1.37	9.11	1.24–1.49	3	2.13	4.37	2.04–2.23				
	W	3	2.97	4.38	2.82–3.05	3	2.13	4.37	2.04–2.23	–	–	–	–				
Saguinus mystax	L	3	2.72	6.54	2.53–2.88	3	1.86	4.68	1.77–1.95	3	2.65	4.28	2.55–2.77				
	W	3	3.16	4.44	3.06–3.33	3	2.65	4.28	2.55–2.77	–	–	–	–				

Species	Measurement	M1 N	M1 Mean	M1 CV	M1 Range	M2 N	M2 Mean	M2 CV	M2 Range	M3 N	M3 Mean	M3 CV	M3 Range	M4 N	M4 Mean	M4 CV	M4 Range
Saimiri sciureus	L	7	3.02	3.92	2.85–3.22	7	2.67	8.86	2.35–3.01	7	3.37	6.50	3.14–3.74				
	W	7	3.85	6.59	3.57–4.29	7	3.37	6.50	3.14–3.74	7	2.33	10.28	2.07–2.73				
Varecia variegata	L	4	7.52	1.99	7.38–7.73	4	7.19	3.46	6.89–7.42	4	7.82	6.66	7.08–8.31				
	W	4	8.09	2.81	7.75–8.25	4	7.82	6.66	7.08–8.31	4	5.06	7.55	4.67–5.53				
Tree shrews																	
Dendrogale melanura	L	2	2.28	–	2.27–2.29	2	2.12	–	2.12–2.13	2	1.45	–	1.38–1.53				
	W	2	2.59	–	2.45–2.73	2	2.40	–	2.35–2.44	2	1.90	–	1.89–1.91				
Dendrogale murina	L	1	–	–	2.22	1	–	–	2.17	1	–	–	1.54				
	W	1	–	–	2.63	1	–	–	2.38	1	–	–	2.08				
Ptilocercus lowii	L	6	2.63	2.64	2.54–2.73	6	2.50	3.27	2.39–2.63	6	1.95	3.85	1.87–2.04				
	W	6	3.24	3.98	3.03–3.40	6	3.54	2.85	3.34–3.64	6	2.79	3.40	2.67–2.91				
Tupaia berlangeri	L	3	3.25	0.68	3.23–3.27	3	2.96	4.08	2.82–3.04	3	1.82	4.79	1.75–1.92				
	W	3	4.18	6.48	3.93–4.47	3	3.97	4.43	3.79–4.14	3	2.93	7.16	2.69–3.10				

Species	Measurement	M1				M2				M3				M4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Tupaia minor	L	6	2.42	3.20	2.30–2.51	6	2.21	2.05	2.15–2.28	6	1.53	3.82	1.42–1.59				
	W	6	2.82	4.62	2.60–2.94	6	2.68	5.14	2.46–2.84	6	1.98	2.62	1.90–2.06				
Urogale everetti	L	2	3.76	–	3.67–3.86	2	3.40	–	3.38–3.42	2	2.96	–	2.81–3.12				
	W	2	4.52	–	4.39–4.65	2	4.44	–	4.39–4.49	2	3.45	–	3.36–3.53				
Marsupials																	
Antechinus godmani	L	5	2.09	4.47	1.93–2.15	5	2.15	2.85	2.06–2.23	5	1.99	2.92	1.94–2.07	5	1.21	8.28	1.09–1.36
	W	5	2.12	4.49	2.00–2.24	5	2.39	4.05	2.28–2.50	5	2.30	5.26	2.18–2.44	5	2.03	5.83	1.86–2.13
Antechinus minimus	L	6	1.66	6.63	1.51–1.85	6	1.73	6.16	1.60–1.88	6	1.67	4.15	1.60–1.78	5	1.15	6.94	1.02–1.23
	W	6	1.80	2.65	1.73–1.85	6	2.07	4.23	1.92–2.16	6	2.07	4.70	1.93–2.17	5	1.75	4.74	1.65–1.82
Antechinus stuartii	L	5	1.81	3.71	1.72–1.90	5	1.88	3.53	1.82–1.99	5	1.77	3.96	1.66–1.83	5	1.05	5.79	0.96–1.11
	W	4	1.97	3.67	1.88–2.05	4	2.28	3.43	2.21–2.35	4	2.22	5.16	2.10–2.32	4	1.74	1.16	1.72–1.76
Caluromys derbianus	L	8	2.95	4.41	2.79–3.18	8	2.81	3.09	2.71–3.01	8	2.61	4.17	2.52–2.83	7	1.92	6.22	1.76–2.06
	W	8	2.69	5.31	2.50–2.99	8	2.68	7.82	2.52–3.15	8	2.43	6.21	2.30–2.75	7	1.95	8.42	1.75–2.23

Species	Measurement	M1				M2				M3				M4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Caluromys philander	L	5	2.66	1.96	2.61–2.73	5	2.60	2.00	2.56–2.68	5	2.41	4.53	2.30–2.57	5	1.69	10.21	1.47–1.88
	W	5	2.69	5.57	2.53–2.88	5	2.65	5.57	2.49–2.83	5	2.52	6.79	2.27–2.68	5	1.92	6.95	1.71–2.05
Dasyuroides byrnei	L	4	2.58	5.86	2.44–2.73	4	3.01	3.17	2.91–3.14	4	2.80	2.08	2.72–2.85	4	1.61	4.75	1.53–1.68
	W	4	3.14	1.31	3.10–3.18	4	3.63	2.88	3.54–3.77	3	3.45	3.80	3.31–3.57	3	2.60	6.04	2.42–2.73
Dasyurus hallucatus	L	5	3.96	3.12	3.82–4.14	5	4.32	1.51	4.25–4.39	5	4.19	2.18	4.09–4.32	5	2.21	3.38	2.12–2.29
	W	5	4.14	5.28	3.84–4.36	5	4.61	3.65	4.41–4.87	5	4.62	1.89	4.53–4.73	5	4.17	3.87	4.04–4.40
Dasyurus maculatus	L	3	5.42	6.56	5.15–5.82	3	5.86	3.99	5.68–6.12	3	6.33	5.25	5.98–6.65	3	3.35	1.9	3.29–3.42
	W	3	5.27	5.68	5.09–5.61	3	6.41	5.44	6.14–6.80	3	6.97	8.12	6.46–7.58	3	6.23	5.79	5.87–6.59
Dasyurus viverrinus	L	3	5.06	5.64	4.73–5.23	3	5.20	2.31	5.08–5.32	3	5.22	5.56	4.98–5.54	3	3.07	17.8	2.47–3.53
	W	3	4.95	7.08	4.65–5.33	3	5.74	4.60	5.55–6.04	2	6.58	3.37	6.42–6.73	2	5.07	0.88	5.04–5.10
Didelphis albiventris	L	1	–	–	5.25	2	5.28	0.13	5.27–5.28	2	5.30	7.18	5.03–5.57	2	4.00	13.05	3.63–4.37
	W	2	4.81	1.66	4.75–4.87	2	5.33	1.29	5.29–5.38	2	5.81	0.72	5.78–5.84	2	4.54	1.04	4.51–4.58

Species	Measurement	M1				M2				M3				M4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Didelphis marsupialis	L	6	5.21	2.52	4.99–5.36	6	5.63	5.29	5.36–6.04	6	5.92	5.40	5.54–6.37	6	4.43	10.98	3.79–5.26
	W	6	5.16	6.17	4.79–5.70	6	5.83	4.30	5.52–6.18	6	6.49	3.17	6.22–6.75	5	5.44	7.37	4.99–5.93
Gracilinanus agilis	L	2	1.72	0.25	1.72–1.73	2	1.72	6.22	1.64–1.79	2	1.60	10.62	1.48–1.73	2	1.18	11.13	1.08–1.27
	W	2	1.62	2.96	1.59–1.66	2	1.83	5.10	1.76–1.90	2	1.94	8.76	1.82–2.06	2	1.73	5.51	1.67–1.80
Gracilinanus sp.	L	2	1.69	6.36	1.62–1.77	2	1.74	1.26	1.72–1.75	2	1.60	0.53	1.60–1.61	2	1.13	1.37	1.12–1.15
	W	2	1.69	0.71	1.68–1.70	2	1.96	1.05	1.95–1.97	2	2.14	1.25	2.12–2.16	2	1.91	4.3	1.85–1.97
Marmosa xerophila	L	19	1.71	4.34	1.59–1.83	19	1.78	5.68	1.63–1.97	19	1.84	4.17	1.72–1.96	19	1.24	9.07	1.04–1.42
	W	19	1.98	4.96	1.82–2.19	19	2.17	4.08	1.97–2.31	19	2.34	4.79	2.11–2.53	19	2.11	6.19	1.87–2.41
Monodelphis domestica	L	6	2.10	9.56	1.89–2.38	6	2.18	5.94	1.98–2.32	6	2.33	5.50	2.13–2.53	6	1.45	9.03	1.29–1.62
	W	6	2.62	3.02	2.55–2.75	6	2.82	3.10	2.70–2.95	6	2.95	4.35	2.77–3.14	6	2.73	6.87	2.45–2.94
Phascogale tapoatafa	L	2	3.09	13.98	2.79–3.40	2	3.18	12.28	2.91–3.46	2	2.77	2.45	2.72–2.82	2	1.53	9.81	1.42–1.63
	W	2	3.20	2.80	3.12–3.25	2	3.54	4.67	3.43–3.66	2	3.34	3.86	3.25–3.43	2	2.64	6.72	2.52–2.77

Species	Measurement	M1				M2				M3				M4			
		N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range	N	Mean	CV	Range
Philander opossum	L	13	3.71	4.61	3.46–4.01	13	3.99	5.84	3.67–4.46	13	4.13	4.25	3.87–4.51	13	2.96	8.84	2.59–3.53
	W	13	3.93	3.32	3.72–4.12	13	4.57	5.72	4.09–5.08	13	5.08	4.93	4.81–5.64	13	4.34	5.26	4.09–4.76
Planigale maculata	L	3	1.39	9.73	1.24–1.50	3	1.25	4.44	1.21–1.31	3	1.14	7.02	1.07–1.23	3	0.74	8.3	0.69–0.81
	W	3	1.50	1.55	1.47–1.52	3	1.69	2.20	1.65–1.72	3	1.69	2.01	1.66–1.73	3	1.27	5.37	1.20–1.31
Sarcophilus harrisii	L	4	10.55	1.60	10.31–10.70	4	11.64	3.27	11.08–11.94	4	11.81	3.15	11.27–12.13	3	4.26	6.66	3.98–4.55
	W	4	10.38	4.10	10.02–10.97	4	11.14	4.64	10.41–11.59	4	10.23	5.35	9.60–10.83	3	7.34	10.48	6.49–7.99
Sminthopsis dolichura	L	1	–	–	1.47	1	–	–	1.62	1	–	–	1.53	1	–	–	0.9
	W	1	–	–	1.93	1	–	–	2.19	1	–	–	2.13	1	–	–	1.81
Sminthopsis macroura	L	5	1.31	5.51	1.19–1.37	5	1.36	2.74	1.32–1.41	5	1.35	2.70	1.29–1.37	5	1.01	3.23	0.96–1.05
	W	5	1.78	3.45	1.72–1.89	5	2.03	3.06	1.95–2.12	5	2.04	3.04	1.98–2.13	5	1.65	2.08	1.63–1.71
Thylamys elegans	L	7	1.62	6.92	1.41–1.73	7	1.70	6.91	1.49–1.82	7	1.73	5.37	1.64–1.86	7	1.10	6.53	1.02–1.19
	W	7	1.88	4.11	1.75–1.97	7	2.16	2.71	2.08–2.27	7	2.29	4.33	2.20–2.45	7	2.17	6.66	2.00–2.40

APPENDIX 3. Length of lower and upper tooth rows (mm) of species studied. N = no. specimens, CV = coefficient of variation.

	Total length lower tooth row				Total length upper tooth row			
Species	N	Mean	CV	Range	N	Mean	CV	Range
Insectivores								
Atelerix albiventris	9	16.72	7.48	14.57–18.10	9	20.41	5.90	18.55–21.80
Crocidura flavescens	13	10.30	6.30	9.27–11.42	13	13.24	6.15	11.99–14.59
Echinosorex gymnurus	7	36.38	2.12	35.53–37.85	5	40.87	2.60	39.33–41.88
Erinaceus europaeus	5	23.28	4.34	22.19–24.74	5	28.29	3.55	27.26–29.80
Hemiechinus auritus	6	19.33	6.97	17.20–21.24	6	23.42	6.39	20.45–24.54
Hylomys suillus	7	15.65	2.14	15.13–16.02	7	17.29	2.34	16.64–17.77
Myosorex sp.	6	6.48	4.73	6.07–6.92	6	8.65	1.41	8.42–8.77
Neurotrichus gibbsii	7	8.65	4.06	8.20–9.00	7	9.94	3.08	9.55–10.29
Parascalops breweri	4	11.83	2.32	11.47–12.07	4	13.61	1.58	13.40–13.90
Scapanus orarius	6	13.04	1.26	12.80–13.26	6	14.38	1.50	14.07–14.65
Scapanus townsendii	5	16.83	3.13	16.15–17.54	5	18.67	2.02	18.25–19.20
Suncus murinus	11	9.22	6.25	8.49–10.22	11	12.02	7.76	10.89–13.50
Talpa micrura	9	11.87	2.52	11.49–12.37	9	13.19	1.52	12.81–13.43
Urotrichus talpoides	6	8.60	2.05	8.44–8.92	6	10.20	2.04	9.97–10.47
Primates								
Arctocebus calabarensis	2	17.48	–	17.32–17.64	2	22.23	–	22.04–22.42
Avahi laniger	2	20.27	–	20.08–20.46	2	24.03	–	23.76–24.29
Callithrix argentata	1	–	–	14.69	1	–	–	14.69

Species	Total length lower tooth row				Total length upper tooth row			
	N	Mean	CV	Range	N	Mean	CV	Range
Callithrix humeralifer	3	15.50	5.24	14.72–16.34	3	15.22	5.03	14.51–16.03
Callithrix jacchus	7	14.60	4.58	13.49–15.49	7	15.16	4.81	13.90–15.92
Cebuella pygmaea	5	11.35	3.80	10.94–12.06	5	10.96	2.58	10.65–11.33
Cebus capucinus	4	33.94	5.64	32.28–36.00	4	33.43	4.23	31.50–34.64
Eulemur fulvus	6	34.83	3.49	33.61–36.61	6	40.31	2.43	39.25–41.69
Galago alleni	4	16.20	2.89	15.81–16.85	4	19.86	3.35	19.42–20.84
Galago demidovii	9	10.90	4.50	10.42–11.64	8	13.06	5.41	12.08–13.91
Hapalemur griseus	5	25.77	3.12	24.98–26.82	4	29.21	2.55	28.22–30.00
Leontopithecus rosalia	5	19.06	1.42	18.69–19.31	5	19.88	1.90	19.55–20.51
Loris tardigradus	2	15.41	–	15.23–15.59	3	17.66	1.31	17.52–17.93
Microcebus murinus	6	9.96	7.67	9.35–11.43	6	12.13	6.77	11.50–13.55
Perodicticus potto	6	19.80	3.38	18.83–20.88	6	23.32	1.69	22.78–23.92
Propithecus diadema	5	34.76	4.83	33.21–37.26	5	40.46	3.07	39.42–42.53
Propithecus verreauxi	4	33.38	1.79	32.57–34.01	4	37.82	1.47	37.35–38.58
Saguinus fuscicollis	8	14.67	4.60	13.75–15.94	8	14.91	3.95	14.26–15.83
Saguinus midas	3	15.64	3.54	15.17–16.25	3	15.74	1.34	15.60–15.98
Saguinus mystax	2	16.64	–	16.32–16.95	3	16.95	1.56	16.72–17.24
Saimiri sciureus	7	18.71	6.60	17.40–20.85	7	18.67	6.00	17.50–20.54
Varecia variegatus	4	42.04	2.16	41.09–43.27	4	50.21	2.14	48.71–51.27

Species	Total length lower tooth row				Total length upper tooth row			
	N	Mean	CV	Range	N	Mean	CV	Range
Tree shrews								
Dendrogale melanura	2	13.18	–	12.99–13.36	–	–	–	–
Dendrogale murina	3	14.47	2.39	14.11–14.8	3	17.81	3.83	17.29–18.58
Ptilocercus lowii	7	14.37	2.04	14.01–14.71	7	17.25	2.32	16.66–17.68
Tupaia berlangeri	4	20.41	1.39	20.13–20.73	4	25.02	2.27	24.33–25.70
Tupaia minor	7	13.97	1.42	13.63–14.17	7	16.90	2.40	16.38–17.42
Urogale everetti	2	28.46	–	28.00–28.92	2	33.30	–	32.65–33.95
Marsupials								
Antechinus godmani	5	14.766	3.38	13.96–15.30	5	16.578	2.33	15.95–16.86
Antechinus minimus	6	12.7517	2.50	12.4–13.17	6	14.44	2.54	14.00–14.93
Antechinus stuartii	5	12.768	5.99	11.86–13.70	5	14.324	4.19	13.56–14.98
Caluromys derbianus	8	24.4113	4.33	22.93–26.50	8	26.5725	4.24	25.53–29.13
Caluromys philander	5	22.666	5.01	21.48–24.08	5	24.84	5.50	23.46–26.76
Dasyuroides byrnei	3	18.5567	1.67	18.21–18.81	4	20.5275	2.93	19.75–21.04
Dasyurus hallucatus	5	28.636	2.04	27.99–29.15	5	31.794	2.30	30.95–32.43
Dasyurus maculatus	3	43.3	4.43	41.79–45.46	3	46.53	3.19	45.15–48.10
Dasyurus viverrinus	3	37.99	5.38	35.74–39.73	3	40.8233	4.38	38.82–42.25
Didelphis albiventris	2	47.51	–	46.51–48.51	2	51.975	–	50.42–53.53
Didelphis marsupialis	6	50.3617	5.35	46.44–53.35	6	55.1033	6.82	50.69–60.65
Gracilinanus agilis	2	12.45	–	12.19–12.71	2	13.995	–	13.97–14.02
Gracilinanus sp.	2	12.715	–	12.61–12.82	1	14.37	–	–

Species	Total length lower tooth row				Total length upper tooth row			
	N	Mean	CV	Range	N	Mean	CV	Range
Marmosa xerophila	19	14.4747	4.13	13.63–15.54	19	15.7353	4.00	14.82–16.81
Monodelphis domestica	6	18.1067	5.51	16.45–19.16	6	19.7083	5.31	18.10–20.98
Phascogale tapoatafa	2	20.25	–	19.23–21.27	2	22.54	–	21.04–24.04
Philander opossum	13	35.4415	4.08	32.32–37.77	13	38.4315	4.10	34.62–40.36
Planigale maculata	3	8.2367	1.95	8.07–8.39	3	9.2033	3.57	8.84–9.48
Sarcophilus harrisii	4	65.53	4.20	62.84–69.36	4	70.545	5.03	67.86–75.77
Sminthopsis dolichura	1	12.21	–	–	1	13.68	–	–
Sminthopsis macroura	5	10.758	2.36	10.48–11.12	5	12.414	2.13	12.13–12.75
Thylamys elegans	7	12.8843	3.94	12.37–13.60	7	14.6	4.73	13.64–15.48

APPENDIX 4. Skull length (mm) and area of foramen magnum (mm^2) for species studied.

N = no. specimens, CV = coefficient of variation.

	Skull length				Area of foramen magnum			
Species	N	Mean	CV	Range	N	Mean	CV	Range
Insectivores								
Atelerix albiventris	8	39.80	5.73	36.25–43.28	7	27.00	11.71	22.03–31.12
Crocidura cyanea	5	19.79	5.02	18.83–21.23	4	7.52	9.25	6.88–8.51
Crocidura flavescens	12	30.37	5.33	27.87–33.16	11	12.45	15.87	9.37–15.22
Echinosorex gymnurus	5	73.37	4.94	67.22–76.13	7	48.66	9.92	41.70–54.62
Erinaceus europaeus	4	56.01	5.05	53.63–59.35	4	44.04	14.99	37.91–50.11
Hemiechinus auritus	5	47.59	6.85	42.40–50.84	4	27.64	14.80	22.68–32.65
Hylomys suillus	7	33.16	3.37	31.00–34.36	7	21.65	5.98	20.33–24.18
Myosorex sp.	6	20.86	1.57	20.45–21.34	6	8.66	4.48	8.17–9.20
Neurotrichus gibbsii	6	22.30	2.84	21.56–22.96	5	9.92	6.52	8.83–10.52
Parascalops breweri	4	32.61	2.81	31.39–33.61	4	13.54	7.43	12.57–14.88
Scapanus orarius	5	33.93	1.53	33.21–34.39	5	14.92	4.51	13.94–15.63
Scapanus townsendii	5	42.40	1.76	41.57–43.47	4	20.75	5.93	19.26–22.09
Sorex cinereus	–	–	–	–	5	4.38	7.91	3.89–4.72
Sorex longirostris	–	–	–	–	5	4.71	9.47	3.95–5.08
Suncus murinus	11	28.14	6.14	26.24–31.06	11	10.86	8.55	9.62–12.28
Talpa micrura	8	31.57	1.75	30.32–32.04	8	15.68	7.98	14.20–17.64
Urotrichus talpoides	1	–	–	24.99	1	–	–	13.37

Species	Skull length				Area of foramen magnum			
	N	Mean	CV	Range	N	Mean	CV	Range
Primates								
Arctocebus calabarensis	2	54.88	–	54.82–54.93	2	33.72	5.30	32.45–34.99
Avahi laniger	2	50.22	–	49.35–51.09	–	–	–	–
Callithrix argentata	1	–	–	45.66	1	–	–	34.89
Callithrix humeralifer	3	45.98	4.10	44.65–48.14	3	33.32	9.20	29.81–35.40
Callithrix jacchus	7	41.48	12.10	35.71–47.88	7	33.05	8.40	30.22–37.72
Cebuella pygmaea	5	27.74	2.88	26.38–28.50	5	24.14	7.30	22.25–26.61
Cebus capucinus	4	93.95	3.46	89.95–97.90	4	119.10	11.80	104.20–131.19
Eulemur fulvus	4	80.65	2.19	79.13–83.20	3	95.33	17.50	78.54–111.92
Galago alleni	4	44.55	2.68	43.32–45.68	4	38.67	9.70	33.84–42.85
Galago demidovii	7	32.41	5.47	30.15–34.53	8	24.86	3.70	23.72–26.19
Hapalemur griseus	4	56.90	4.79	54.72–60.85	2	63.88	11.10	58.88–68.88
Leontopithecus rosalia	5	44.55	2.52	43.28–46.05	5	43.51	8.50	38.08–47.88
Loris tardigradus	2	48.11	–	47.98–48.24	2	30.91	11.00	28.51–33.32
Microcebus murinus	6	28.94	6.27	27.40–31.98	1	–	–	20.29
Perodicticus potto	6	59.23	3.04	56.33–61.21	6	55.39	8.20	50.36–63.08
Propithecus diadema	5	80.18	5.81	72.74–85.07	5	137.65	10.30	122.72–155.84
Propithecus verreauxi	3	73.90	2.56	72.04–75.82	3	99.38	5.50	93.60–104.47
Saguinus fuscicollis	7	37.86	9.63	34.37–45.55	8	33.33	11.90	28.02–40.50
Saguinus midas	3	48.44	0.74	48.08–48.80	3	31.59	5.90	30.13–33.70
Saguinus mystax	3	51.86	6.06	48.30–54.26	3	38.19	9.40	34.62–41.83

Species	Skull length				Area of foramen magnum			
	N	Mean	CV	Range	N	Mean	CV	Range
Saimiri sciureus	7	62.99	5.57	59.31–69.74	6	55.66	11.50	48.19–66.96
Varecia variegata	2	96.33	–	94.99–97.66	2	104.77	4.10	101.73–107.82
Tree shrews								
Dendrogale melanura	–	–	–	–	2	21.70	5.93	20.79–22.61
Dendrogale murina	2	33.14	–	32.41–33.86	2	22.96	2.93	22.48–23.43
Ptilocercus lowii	7	35.72	2.33	34.60–36.63	7	19.26	4.38	18.26–20.74
Tupaia berlangeri	3	45.27	2.78	43.95–46.45	4	25.36	5.08	23.60–26.69
Tupaia minor	7	32.99	0.96	32.43–33.41	7	22.72	6.57	20.99–25.15
Urogale everetti	2	56.69	–	56.50–56.88	2	34.67	6.42	33.09–36.24
Marsupials								
Antechinus godmani	5	33.87	4.79	31.30–35.19	5	19.14	5.20	17.53–19.93
Antechinus minimus	6	28.34	1.65	27.63–28.91	6	17.52	4.20	16.41–18.55
Antechinus stuartii	5	28.52	6.05	26.53–30.42	5	17.15	9.90	16.01–20.13
Caluromys derbianus	8	53.90	4.58	50.31–58.04	7	35.13	8.31	32.26–40.88
Caluromys philander	5	51.53	7.91	48.40–58.18	5	30.31	7.23	27.71–33.06
Dasyuroides byrnei	4	43.33	3.86	41.14–44.67	–	–	–	–
Dasyurus hallucatus	5	61.99	2.58	59.80–63.97	5	34.04	7.60	31.28–37.57
Dasyurus maculatus	2	93.72	–	93.48–93.96	–	–	–	–
Dasyurus viverrinus	3	81.31	6.42	75.90–86.32	3	43.49	8.20	41.09–47.61
Didelphis albiventris	2	98.23	–	95.02–101.43	2	51.41	1.69	50.80–52.03
Didelphis marsupialis	6	102.08	8.30	91.64–113.29	5	43.83	4.32	41.86–46.68

Species	Skull length				Area of foramen magnum			
	N	Mean	CV	Range	N	Mean	CV	Range
Gracilinanus agilis	2	29.09	–	29.08–29.09	2	16.32	6.08	15.62–17.02
Gracilinanus sp.	1	30.28	–	–	2	14.66	2.26	14.43–14.90
Marmosa xerophila	19	31.55	4.88	29.38–34.58	16	15.66	7.33	13.84–17.45
Monodelphis domestica	5	37.89	7.06	34.66–41.60	3	17.94	5.32	16.83–18.51
Phascogale tapoatafa	–	–	–	–	–	–	–	–
Philander opossum	13	73.57	6.69	63.25–78.98	13	39.60	7.96	34.16–42.94
Planigale maculata	3	19.68	4.55	18.69–20.43	3	9.73	5.70	9.16–10.26
Sarcophilus harrisii	4	131.95	8.05	119.16–145.12	4	109.75	13.50	93.62–126.18
Sminthopsis dolichura	1	28.52	–	–	–	–	–	–
Sminthopsis macroura	5	24.85	3.45	23.63–25.98	5	11.42	1.70	11.13–11.63
Thylamys elegans	7	28.47	4.96	25.77–29.81	6	15.26	6.90	13.74–16.75

FIGURE LEGENDS

FIGURE 1. **A**, Upper molar and **B**, lower molar, showing basic tooth measurements and terminology used in this study. Adapted from Crompton and Kielan-Jaworowska (1978).

FIGURE 2. Skull of *Didelphis* indicating jaw and cranial measurements. TLU = total length of upper tooth row, TLL = total length of lower tooth row, 2a and 2b = horizontal or vertical diameters of foramen magnum, respectively. Adapted from Hall and Kelson (1959) and Novacek and Wyss (1986).

FIGURE 3. Regression plots showing relationship of mean body mass (grams) with area of foramen magnum (mm^2) and with m1 area (mm^2) in insectivores (long-dashed line), marsupials (short-dashed line) and primates (solid line).

FIGURE 4. Regression plots showing relationship of mean body mass (grams) with skull length (mm) and with area of foramen magnum (mm^2) in insectivores (long-dashed line), marsupials (short-dashed line) and primates (solid line).

FIGURE 5. Regression plots showing relationship of mean body mass (grams) with tooth size (length [mm] and with area [LxW; mm^2]) for lower and upper molars of primates.

FIGURE 6. Regression plots showing relationship of mean body mass (grams) with mean tooth row length (mm) for each group. TLL = total length of lower tooth row (dashed line), TLU = total length of upper tooth row (solid line).

FIGURE 7. Regression plots showing relationship of mean body mass (grams) with mean skull length (mm; dashed line) and with area of foramen magnum (mm^2; solid line) for each group. SL = skull length, FA = area of foramen magnum.

FIGURE 8. Regression plots showing relationship of mean body mass (grams) with tooth size (length [mm] and with area [LxW; mm^2]) for lower and upper molars of insectivores.

Filled symbols represent species of Erinaceidae. Square symbol represents tooth area in *Ptilocercus lowii.*

FIGURE 9. Regression plots showing relationship of mean body mass (grams) with mean lower molar size (length [mm] and with area [LxW; mm^2]) in Didelphidae. Filled symbols represent two species of *Caluromys*, showing that their posterior lower molars are much smaller than would be expected for their body size.

FIGURE 10. Regression plots showing relationship of mean body mass (grams) with mean upper molar size (length [mm] and with area [LxW; mm^2]) in Didelphidae. Filled symbols represent two species of *Caluromys*, showing that their posterior upper molars are much smaller than would be expected for their body size.

FIGURE 11. Predicted body mass for Lancian eutherian species of North America based on size of lower and upper first molars. Multiple estimates for a single species using m1 area, for example, are result of different localities where that species is found.

FIGURE 12. Predicted body mass for Lancian metatherian species of North America based on size of lower and upper first molars. Multiple estimates for a single species using m1 area, for example, are the result of different localities where that species is found.

FIGURE 13. Predicted body mass for archaic ungulates (italics) of North America based on size of lower and upper first molars, showing their estimated body mass relative to other eutherians. Multiple estimates for a single species using m1 area, for example, are the result of different localities where that species is found.

Figure 1

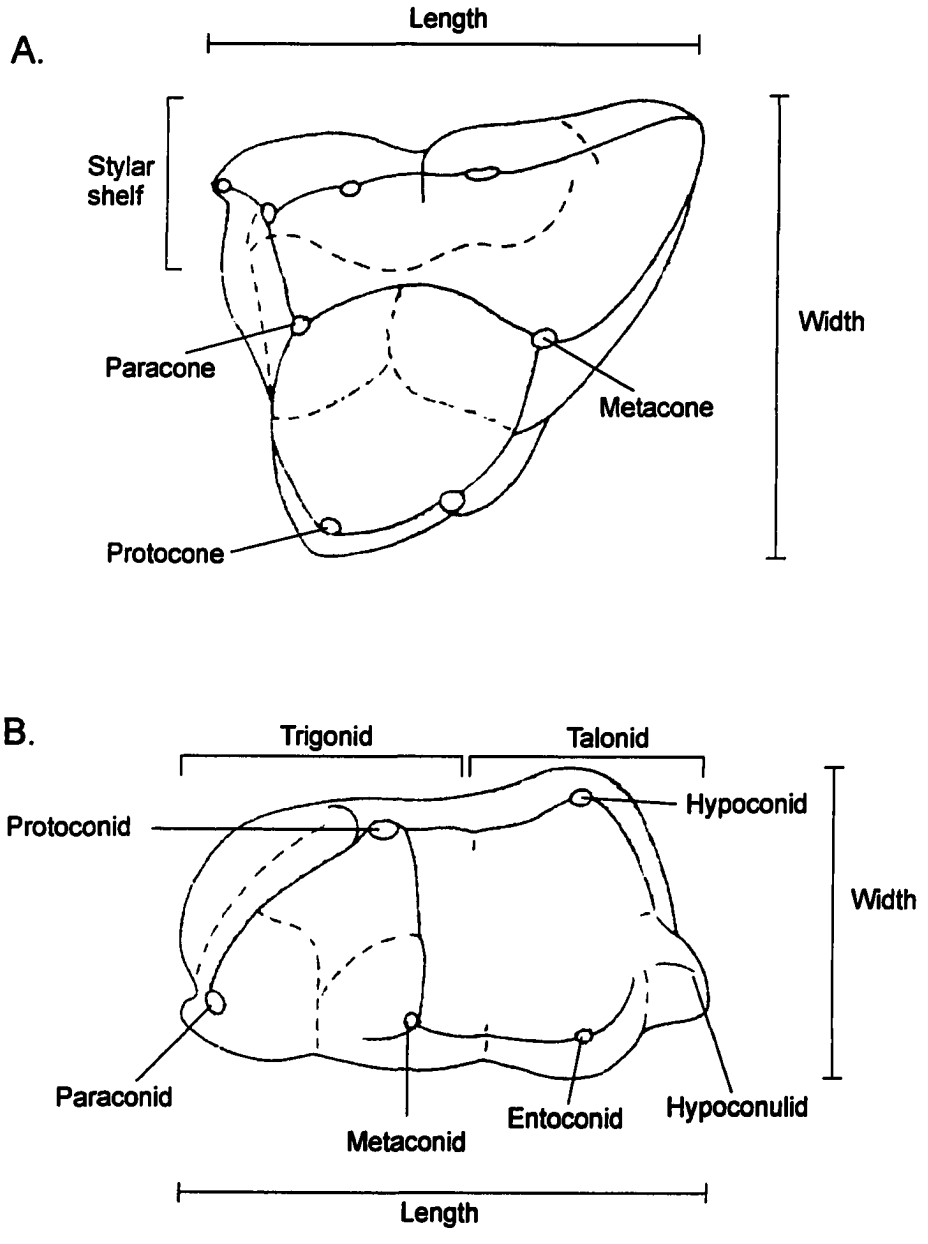

A.
Length
Stylar shelf
Width
Paracone
Metacone
Protocone
B.
Trigonid
Talonid
Protoconid
Hypoconid
Width
Paraconid
Metaconid
Entoconid
Hypoconulid
Length

Figure 2

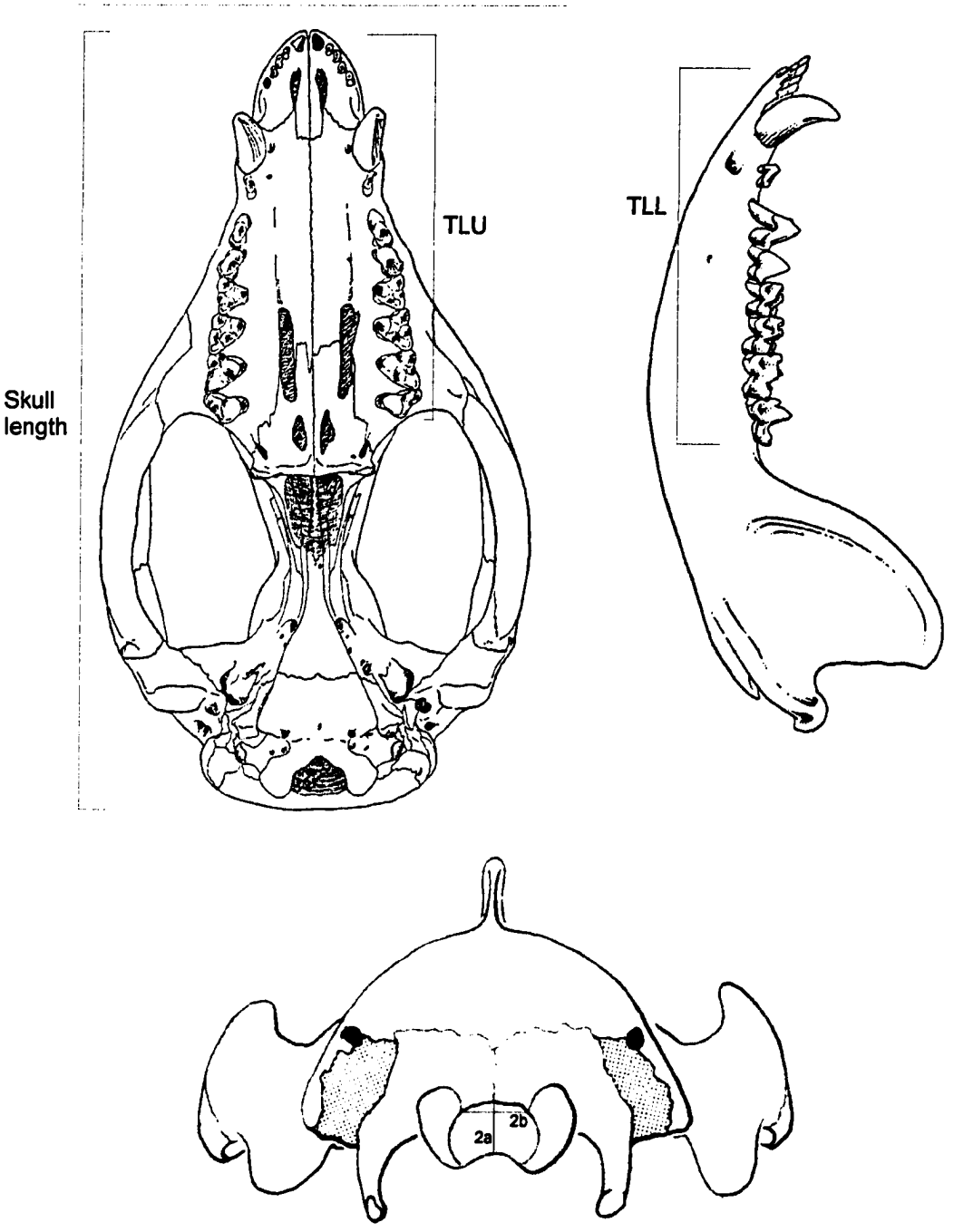


Figure 3

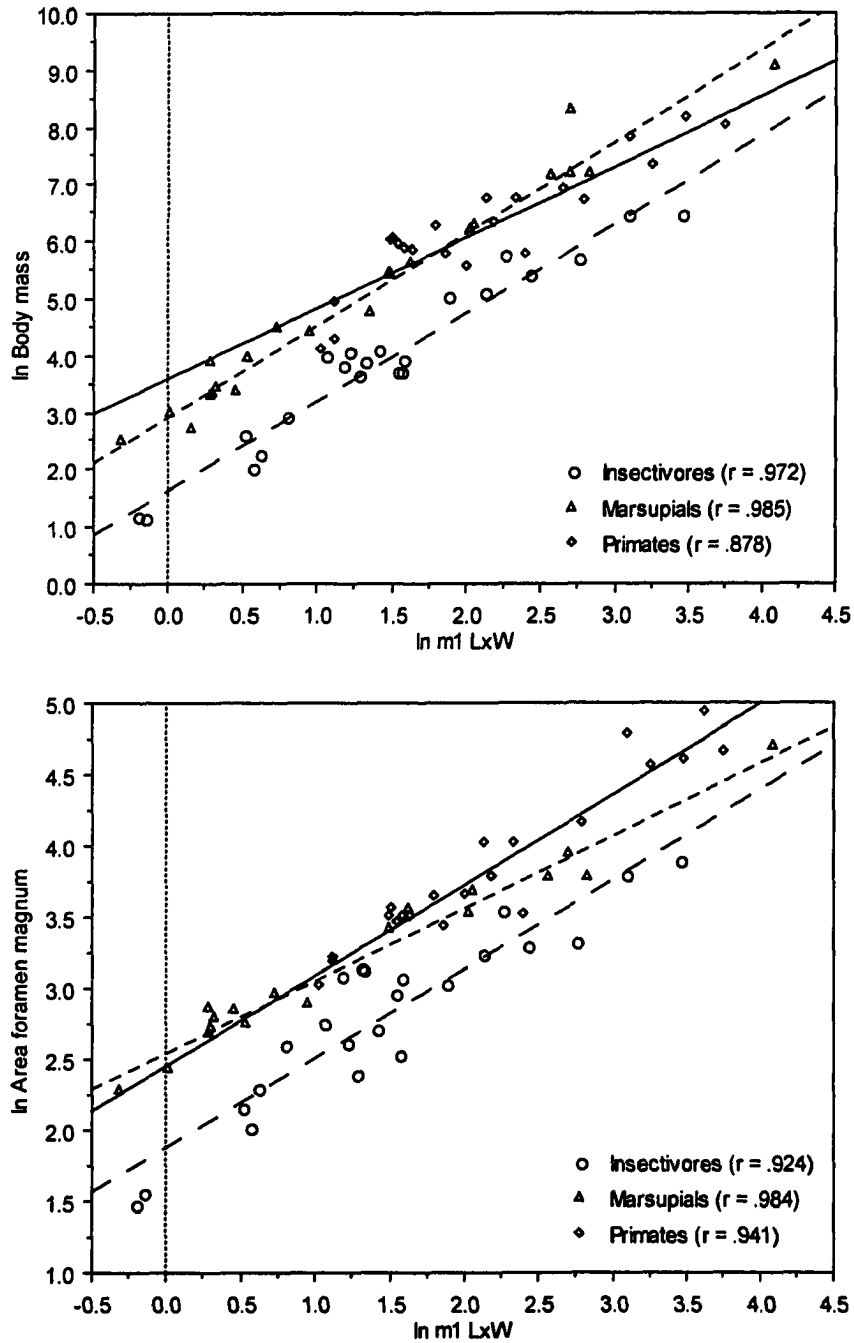
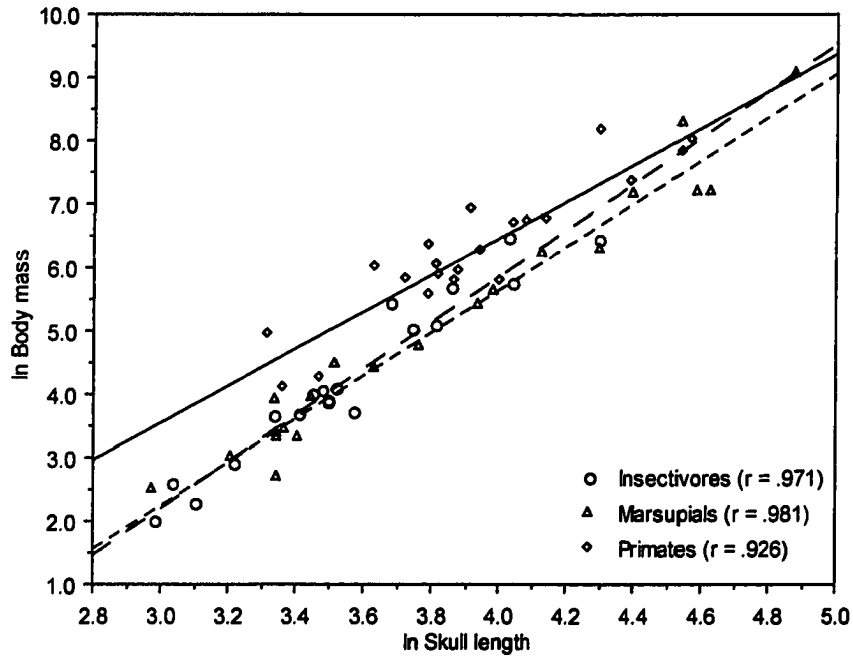

ln Body mass
ln m1 LxW
Insectivores (r = .972)
Marsupials (r = .985)
Primates (r = .878)
ln Area foramen magnum
ln m1 LxW
Insectivores (r = .924)
Marsupials (r = .984)
Primates (r = .941)

Figure 4


10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
ln Body mass
2.8
3.0
3.2
3.4
3.6
3.8
4.0
4.2
4.4
4.6
4.8
5.0
ln Skull length
Insectivores (r = .971)
Marsupials (r = .981)
Primates (r = .926)

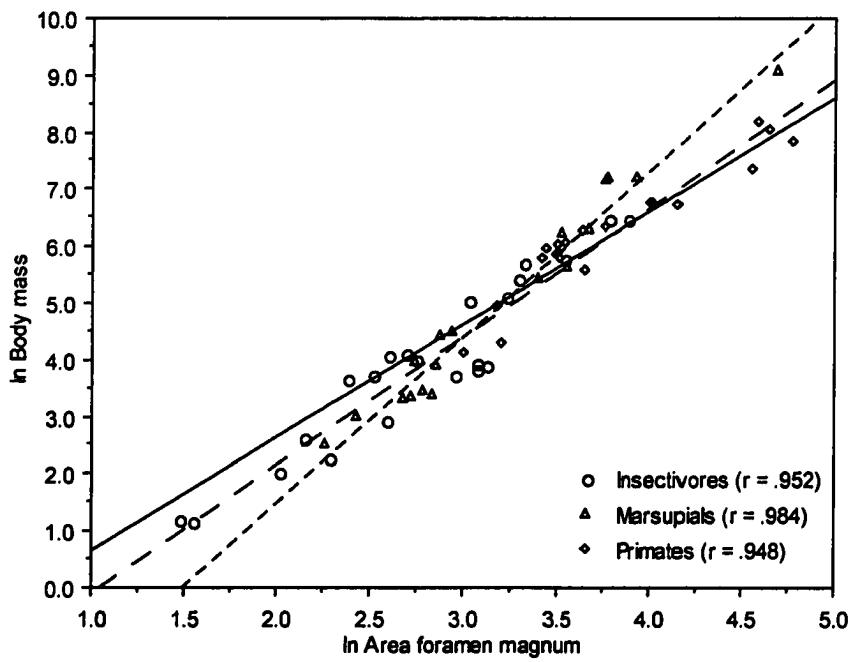

10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
ln Body mass
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
ln Area foramen magnum
Insectivores (r = .952)
Marsupials (r = .984)
Primates (r = .948)

Figure 5

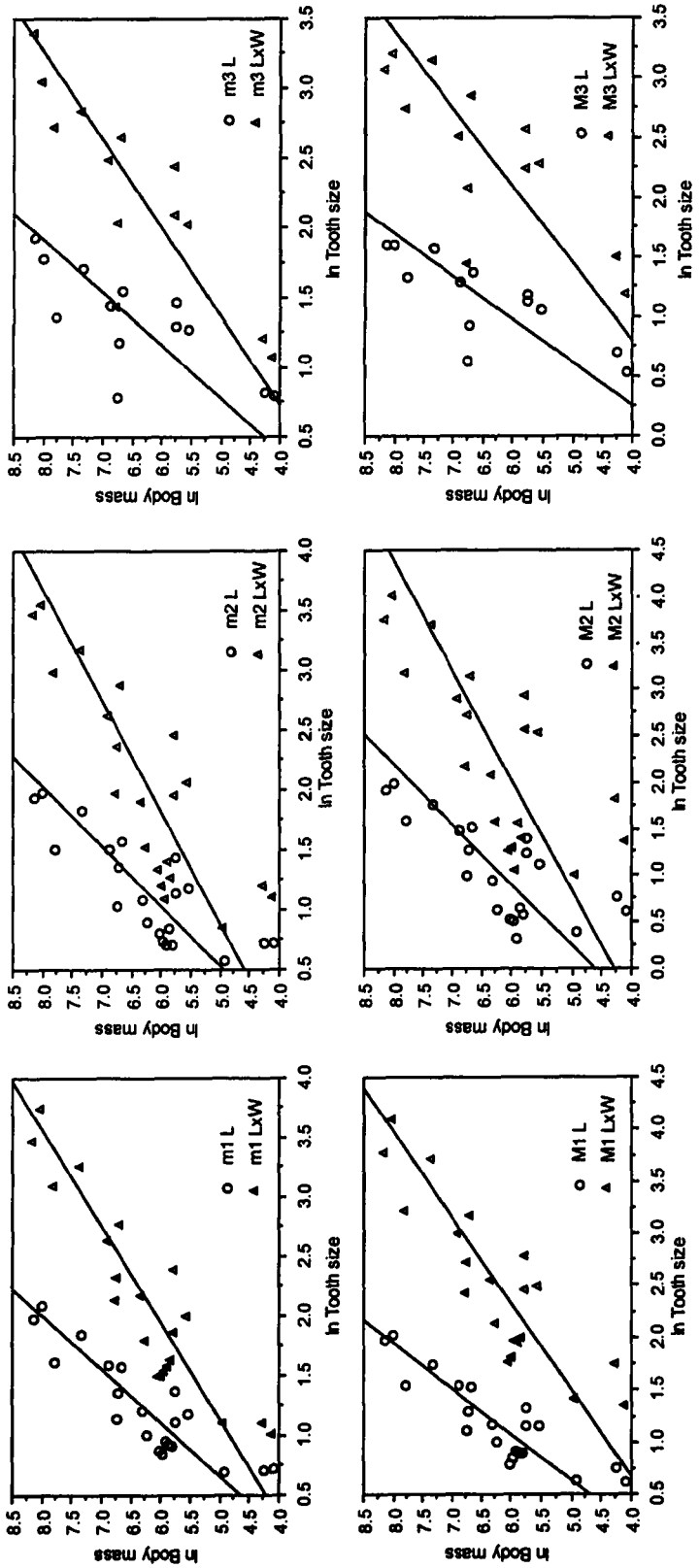

ln Body mass
ln Tooth size
m3 L
m3 LxW
M3 L
M3 LxW
m2 L
m2 LxW
M2 L
M2 LxW
m1 L
m1 LxW
M1 L
M1 LxW

Figure 6

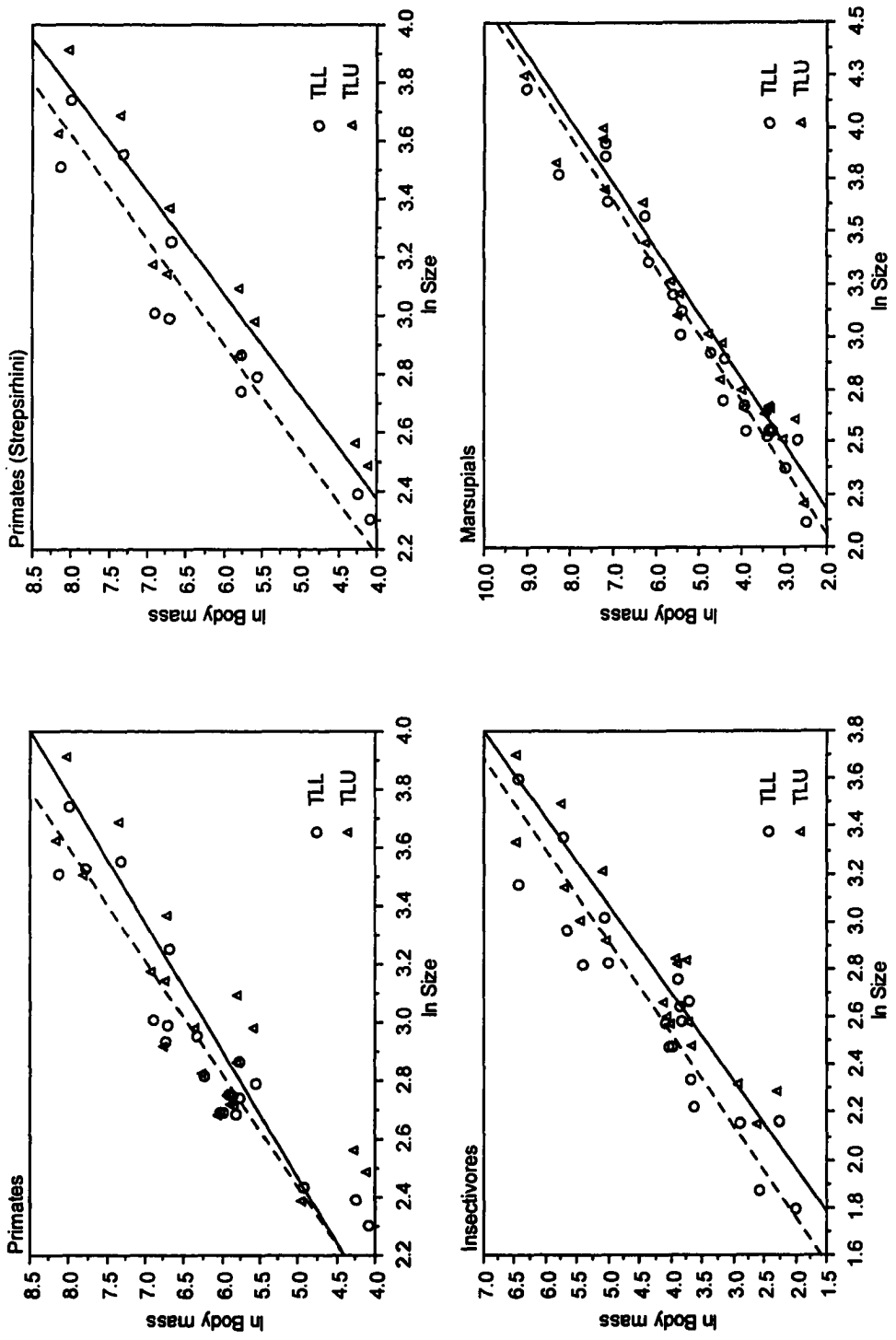

Primates (Strepsirhini)
Marsupials
Primates
Insectivores
ln Body mass
ln Size
TLL
TLU

Figure 7

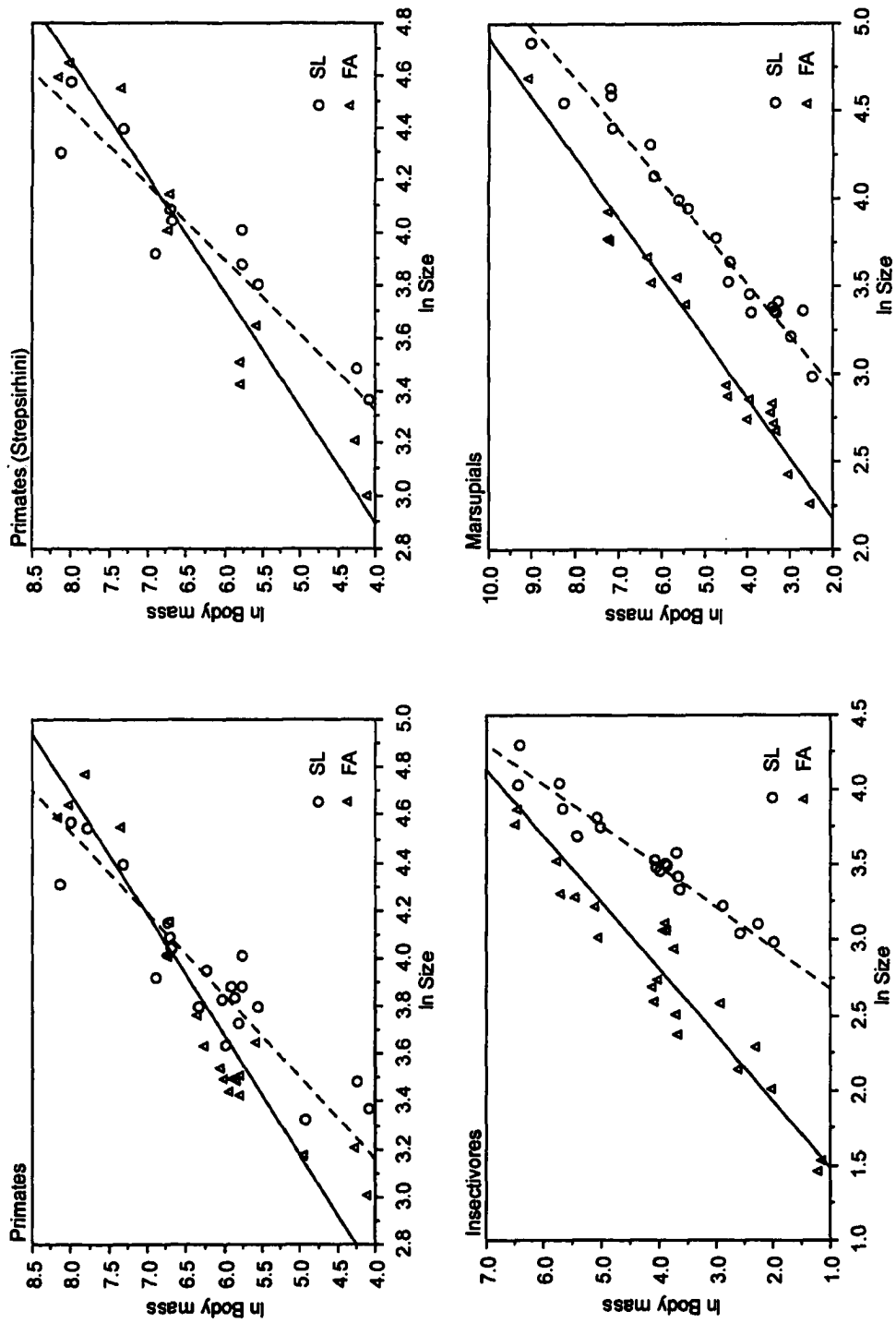

Primates (Strepsirhini)
Marsupials
Primates
Insectivores
ln Body mass
ln Size
SL
FA

Figure 8

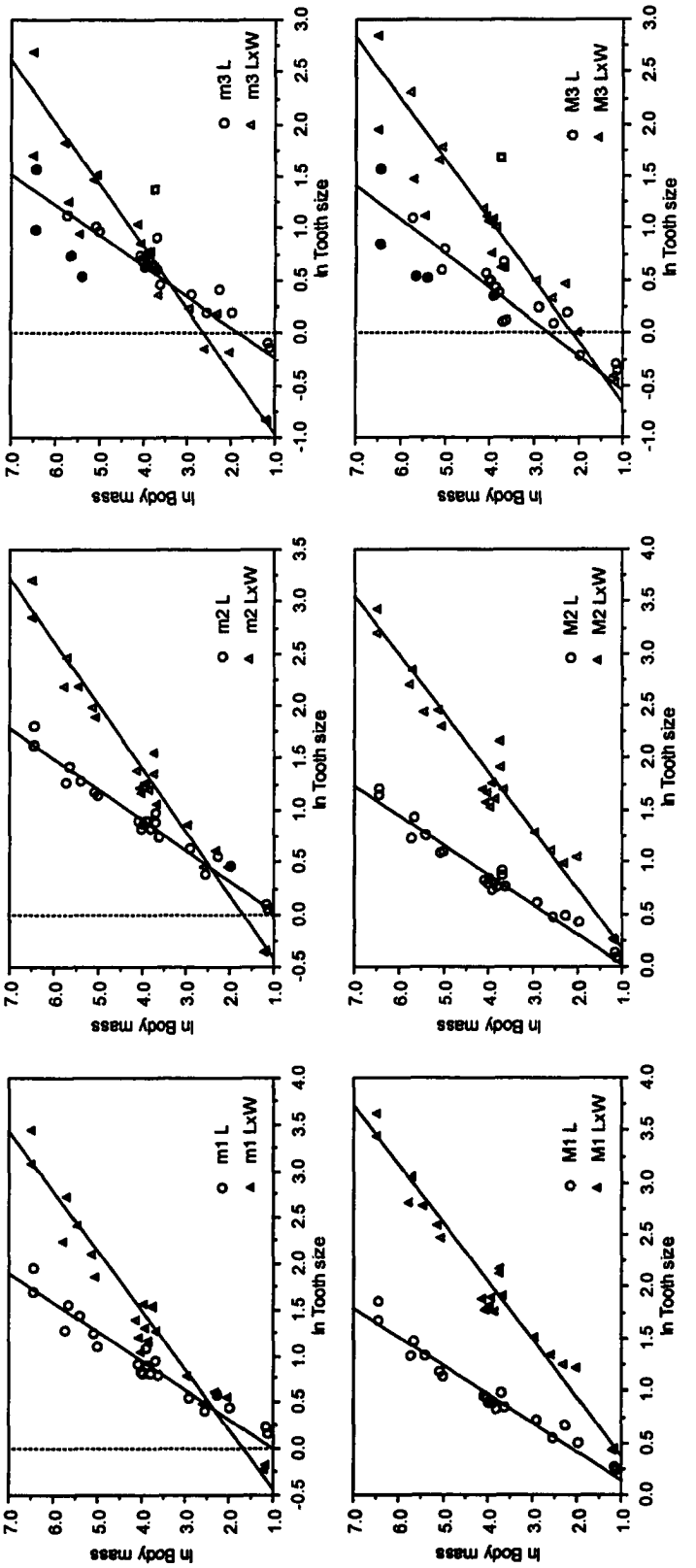

ln Body mass
ln Tooth size
m3 L
m3 LxW
M3 L
M3 LxW
m2 L
m2 LxW
M2 L
M2 LxW
m1 L
m1 LxW
M1 L
M1 LxW

Figure 9

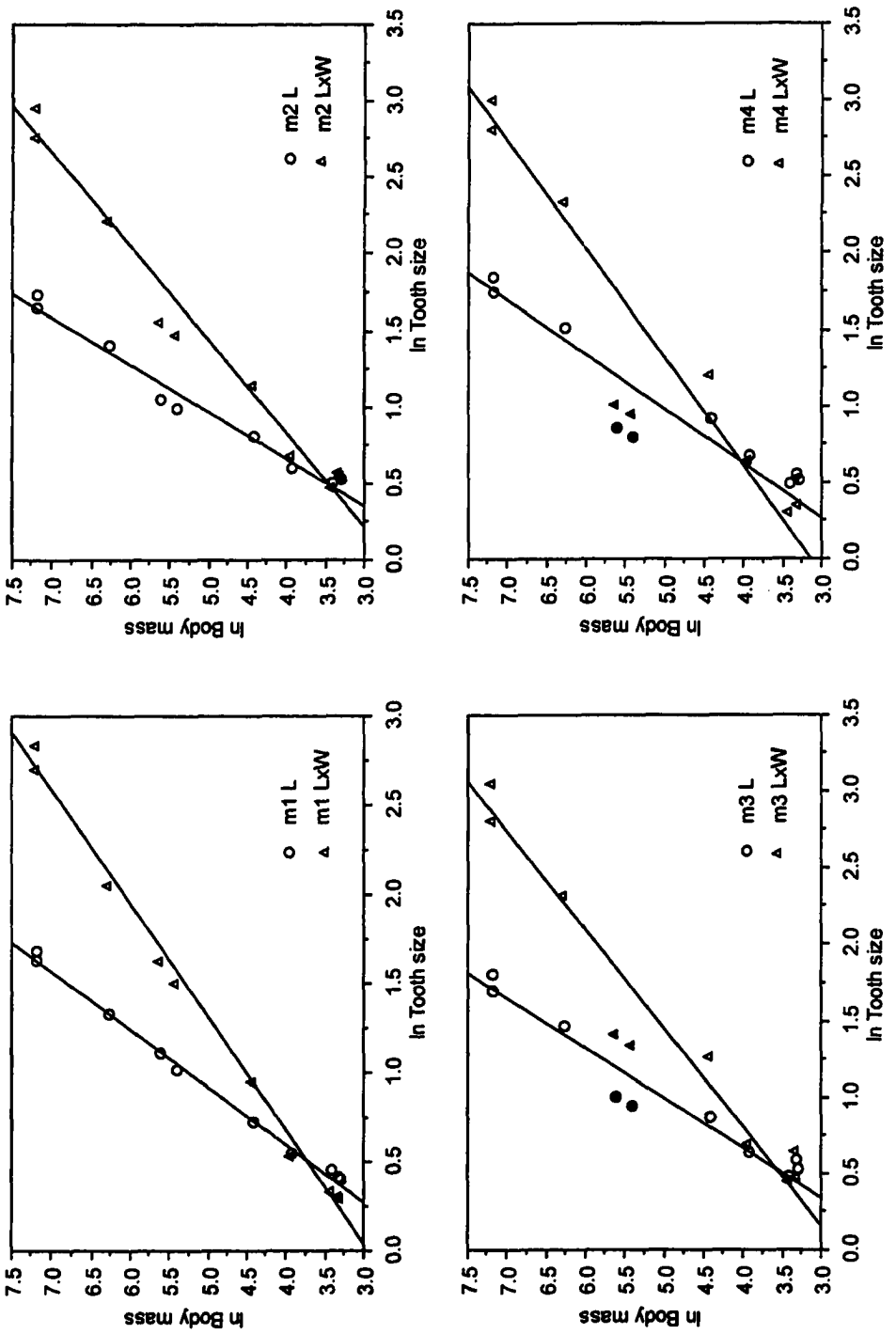

ln Body mass
ln Tooth size
m1 L
m1 LxW
m2 L
m2 LxW
m3 L
m3 LxW
m4 L
m4 LxW

Figure 10

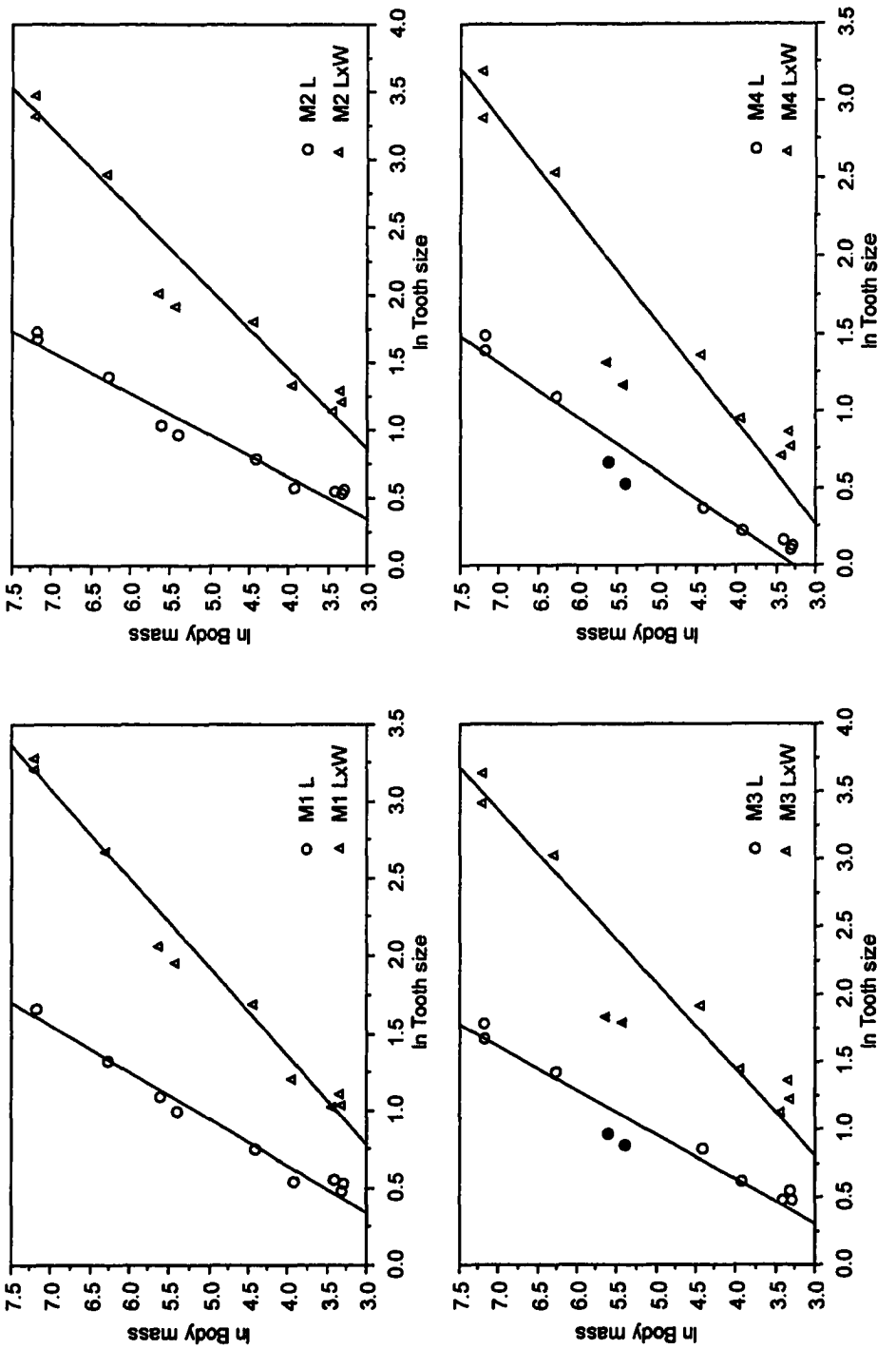

M2 L
M2 LxW
M1 L
M1 LxW
M4 L
M4 LxW
M3 L
M3 LxW
ln Body mass
ln Tooth size

Figure 11

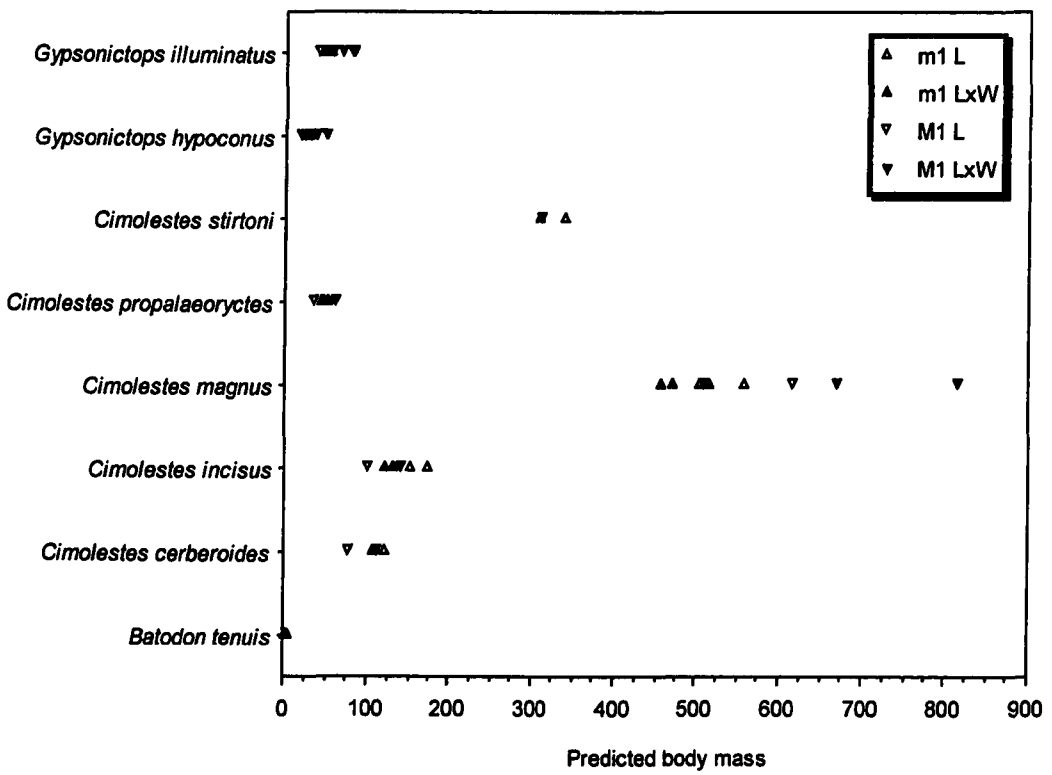

Gypsonictops illuminatus
Gypsonictops hypoconus
Cimolestes stirtoni
Cimolestes propalaeoryctes
Cimolestes magnus
Cimolestes incisus
Cimolestes cerberoides
Batodon tenuis
m1 L
m1 LxW
M1 L
M1 LxW
0
100
200
300
400
500
600
700
800
900
Predicted body mass

Figure 12

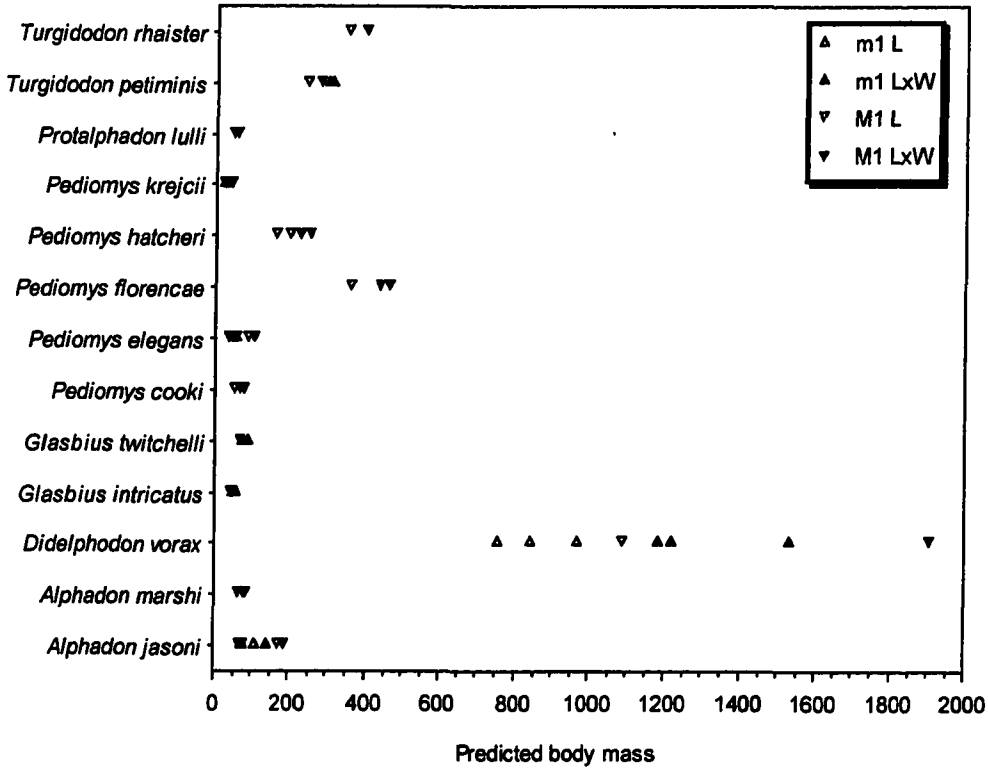
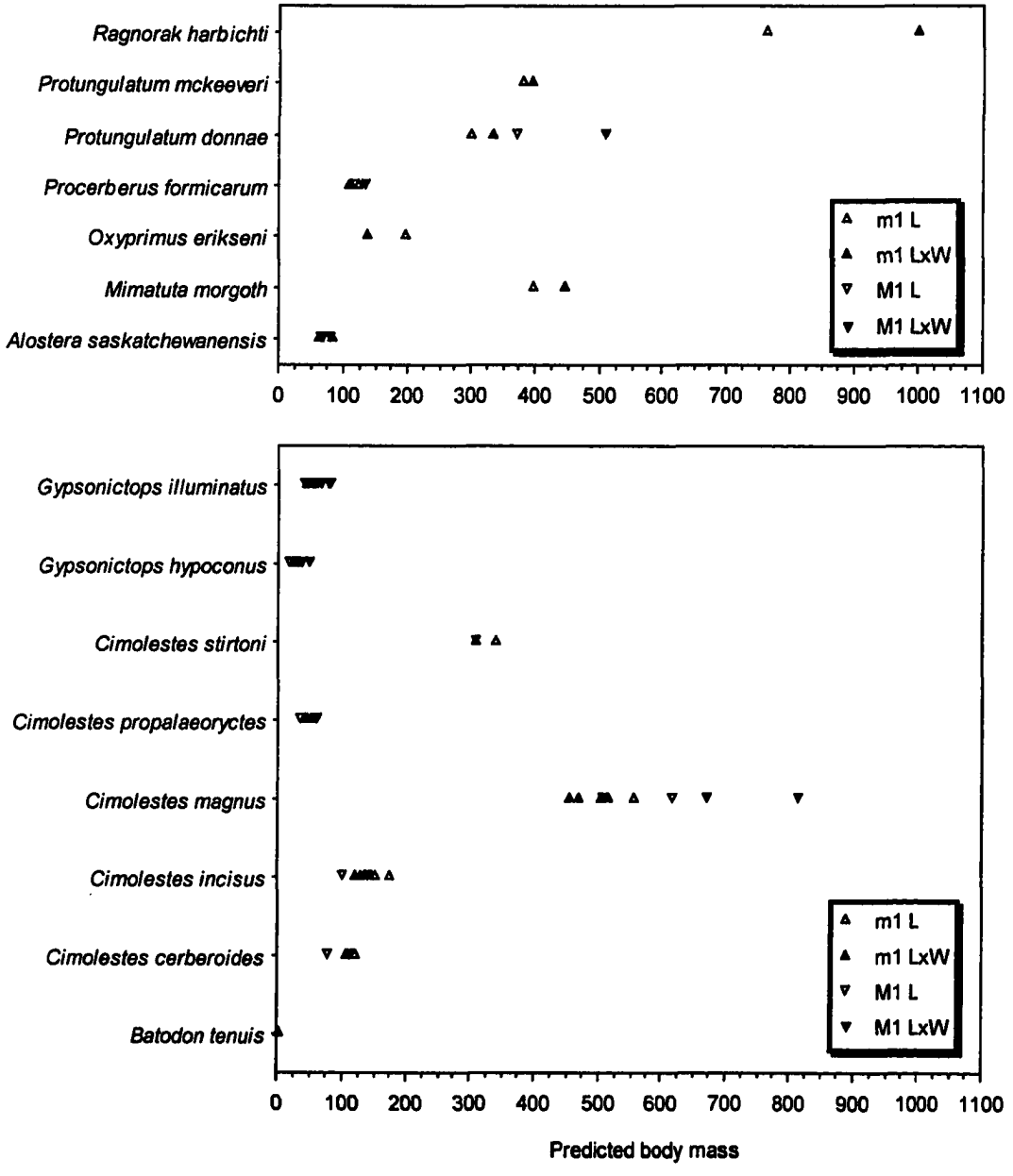

Turgidodon rhaister
Turgidodon petiminis
Protalphadon lulli
Pediomys krejcii
Pediomys hatcheri
Pediomys florencae
Pediomys elegans
Pediomys cooki
Glasbius twitchelli
Glasbius intricatus
Didelphodon vorax
Alphadon marshi
Alphadon jasoni
m1 L
m1 LxW
M1 L
M1 LxW
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Predicted body mass

Figure 13


Ragnorak harbichti
Protungulatum mckeeveri
Protungulatum donnae
Procerberus formicarum
Oxyprimus erikseni
Mimatuta morgoth
Alostera saskatchewanensis
m1 L
m1 LxW
M1 L
M1 LxW
0
100
200
300
400
500
600
700
800
900
1000
1100
Gypsonictops illuminatus
Gypsonictops hypoconus
Cimolestes stirtoni
Cimolestes propalaeoryctes
Cimolestes magnus
Cimolestes incisus
Cimolestes cerberoides
Batodon tenuis
m1 L
m1 LxW
M1 L
M1 LxW
0
100
200
300
400
500
600
700
800
900
1000
1100
Predicted body mass

MOLAR MORPHOLOGY AND DIET OF LATE CRETACEOUS THERIAN MAMMALS OF NORTH AMERICA: A PRELIMINARY ANALYSIS

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Running Head: MOLARS AND DIET OF LATE CRETACEOUS MAMMALS

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ABSTRACT

An analysis of the form/function relationship between tooth morphology and diet in modern species reveals that differences in tooth shape generally follow phylogenetic lines. Primates, marsupials and insectivores are easily distinguished from one another, with insectivores having taller principal cusps on their molars, as well as longer shearing crests. An exception to this is tree shrews, traditionally placed within primates, but clustering with insectivores in this analysis. Based on tooth morphology, other species of primates and marsupials, such as *Tarsius bancanus* and *Caluromys derbianus* and *C. philander*, respectively, either group close to, or within a group other than their own. Latest Cretaceous (Lancian) mammal taxa cluster intermediate between marsupials and placentals. The marsupial *Glasbius intricatus* falls close to the modern frugivorous marsupials *Caluromys derbianus and C. philander*, suggesting this species may have been frugivorous. Findings suggest that principal components analysis is able to detect gross form/function differences in tooth morphology, but techniques that can elucidate more subtle differences within groups must be explored.

INTRODUCTION

The relationship between tooth morphology and diet has been studied extensively in numerous modern species, particularly in primates (Kay, 1975, 1978; Sheine and Kay, 1982; Anthony and Kay, 1993), but also in insectivores (Freeman, 1979, 1981; Sanson, 1985; Strait, 1993) and carnivores (Van Valen, 1969; de Muizon and Lange-Badré, 1997). Differences in tooth shape between species often can be traced to different dietary regimes, and even to differences in soft- versus hard-object feeders (Strait, 1993; but see also Evans and Sanson, 1998), though phylogenetic constraints on a species can play a role in obscuring this relationship.

In the most basic sense, teeth are simply tools used to breakdown foodstuffs using the least amount of energy. The function of the molar dentition (as it relates to diet) is essentially defined by the size and shape of its cusps and shearing crests (see Kay and Hylander, 1978; Strait, 1993). The first thorough attempt to describe molar occlusion and the function of shearing crests was done by Crompton and Hiiemae (1970) and Crompton (1971). Since then, the functional relationship between principal shearing crests (crests 1-6 using the terminology employed by Crompton (1971) and diet has been examined in a variety of studies, most dealing with modern or extinct primates (Kay and Hiiemäe, 1974; Kay, 1975; Sheine and Kay, 1982; Anthony and Kay, 1993) with some studies on modern insectivores (Strait, 1993; Freeman, 1998). Insectivores tend to have teeth with tall, pointed cusps, and transversely oriented shearing crests, better suited to breakdown insect exoskeletons or more soft bodied food items, such as earthworms or larvae (Lucas, 1979; Lucas and Luke, 1984; Strait, 1997; Evans and Sanson, 1998). Carnivorous species emphasize postvallum-prevallid shear, as indicated by an enlargement of structures such

as the postmetacrista and paraconid with concomitant reduction in the paracone and protocone on upper molars and metaconid and talonid on lowers (Butler, 1990; de Muizon and Lange-Badré, 1997). Frugivorous species tend to have low-crowned molars with a more bulbous cusp morphology, better suited for grinding and pulping (Kay, 1975).

Although considerable research has been done on the form/function of the teeth in modern species, there are surprisingly few studies on fossil species, with the exception of fossil primates (eg. Rose, 1993; Gingerich, 1974), and particularly of Cretaceous mammal species. Traditionally, Cretaceous mammals have been considered ecological generalists, small omnivorous or insectivorous species (e.g. Clemens, 1970). However, a Late Cretaceous radiation of some mammal species into other dietary specializations has been suggested (Butler, 1990). For example, Butler (1972), in a study of wear facets on teeth, noted differences in the angle of jaw movement among Late Cretaceous mammals. Some species such as *Glasbius intricatus* exhibited a more transverse jaw movement, while species of *Cimolestes* had more vertical jaw movement, indicative of a trend toward omnivory/herbivory or carnivory, respectively. In this study, the form/function of teeth in modern, dentally conservative species representing a variety of dietary categories is examined by measuring basic tooth shape as indicated by cusp height and length of shearing crests. Because we do not have the benefit of examining Cretaceous mammals first hand, the results of this analysis on modern, dentally conservative species can then be applied to various Late Cretaceous mammals, most of which are known only by isolated teeth.

METHODS

General tooth morphology was examined by measuring height of cusps and length of the principal shearing crests on lower and upper second molars of modern species of marsupials, insectivores and primates. A set of 25 landmarks on upper second molars and of 13 landmarks on lower second molars was defined to capture the length and height of shearing crests and cusps, respectively (Figs. 1, 2). Landmarks were recorded on the Reflex microscope, a precision instrument (accurate to 0.001 mm) that allows the collection of x-, y- and z- coordinates from a set of previously defined points (MacLarnon, 1989). Distances from point to point can then be calculated from any of these coordinates using any standard spreadsheet program.

In order to assess possible differences in tooth morphology between dietary groups of species (Table 1), as well as differences between taxonomic groups, principal components analysis (performed with NT-SYS statistical program) was used to examine covariation among various tooth shape variables. Measurements were corrected for body size by dividing each by the cube root of body mass. Data was standardized, and the first three principal components were extracted from a correlation matrix of 19 tooth variables. Table 2 shows the resultant loadings of these variables with principal components. Species were then projected onto the first three principal components.

Variables used in the analysis include upper and lower cusp heights and shearing crests. Cusp height was measured on the principal cusps of upper molars (paracone, metacone and protocone) and lower molars (paraconid, metaconid, protoconid, entoconid and hypoconid). Cusp height was calculated by taking the distance from the microscope stage to the center of the talonid basin (lowest portion of lower molars) or trigon basin

(lowest portion of upper molars), and subtracting from it the distance between the microscope stage and the cusp apex.

Major shearing crests on upper molars include preparacrista, postparacrista, premetacrista, postmetacrista, preprotocrista and postprotocrista. Strait (1993) used the sum total length of the principal shearing crests on lower molars in her analysis of insectivores. She argued that different species emphasize different shearing crests (Kay, 1975) and so it is better to take the sum of all of the crests when dealing with broad taxonomic and dietary groups. She also suggested measurement error as further justification for using the sum total of all of the crests. Because of this, the sum of the principal shearing crests for m2s and for M2s was used in the present study. Nonetheless, despite possible measurement error and/or taxonomic differences that may affect the outcome, major shearing crests on lower molars (protocristid, paracristid and cristid obliqua) were also included in the analysis to allow for the fragmentary nature of Cretaceous specimens.

RESULTS

Based on a principal components analysis of molar shape, modern species largely group along phylogenetic lines (Fig. 3) with marsupials clustering separately from placentals. In addition, all four groups, marsupials, placentals, insectivores and tree shrews, form distinct clusters. Tree shrews, traditionally considered closely related to primates, cluster within the insectivores. The first three principal components account for 84 % of the total variation. Heavy loadings on the first axis (Table 2) indicate that relative to primates and marsupials, insectivores and tree shrews have a taller metacone, protoconid, and greater total length of shearing crests on both upper and lower molars. The second principal component indicates that marsupials have a relatively less developed postmetacrista. Axis three indicates that tree shrews, primates, and a few species of marsupials and insectivores have better developed pre-protocrista.

A separate analysis on modern species for which different dietary preferences are known (Table 1) indicates some distinct groupings (Fig. 4). For dietary groups, 84.4% of the total variation is explained by the first three principal components. There is a discrete cluster of highly insectivorous species (including the insectivores *Sorex longirostris, Talpa micrura, Scapanus orarius*, and the tree shrews *Tupaia minor* and *Ptilocercus lowii*), all possessing tall cusps (metacone, paracone, protoconid) and greater total shearing potential on upper and lower molars (Table 2). *Tarsius bancanus*, an almost exclusively insectivorous primate (Hladik, 1979), clusters closer to insectivores. Frugivorous marsupials, represented by two species of *Caluromys*, cluster closer to primates than with the rest of the marsupials. *Didelphis marsupialis*, an omnivorous marsupial, clusters between frugivorous marsupials and more insectivorous marsupials.

Two related species of bushbabies, *Galago alleni* and *G. demidovii*, have different dietary preferences (Table 1) and this is indicated by the analysis. *Galago demidovii* is the more insectivorous of the two, and tends to cluster closer to insectivores. *Hapalemur griseus*, a species whose main dietary preference is bamboo, clusters very closely with *G. alleni*.

Although there are some dietary tendencies that can be seen in Lancian taxa, they are not as obvious as those for modern taxa (Fig. 5). When Lancian mammals are included, 83.5% of the variation is explained by the first three principal components. Most Lancian taxa included in this study fall intermediate between marsupials and insectivores, with no clear distinction seen between placental or marsupial Lancian mammals. High loadings for the first principal component (Table 2) indicate that Lancian mammals had teeth similar to modern insectivores, with tall cusps and relatively longer shearing crests. *Glasbius intricatus*, a marsupial, falls closest to modern species of *Caluromys*. Marsupial species that have a conservative molar shape, such as species of *Pediomys* and *Alphadon marshi*, cluster close to each other. Placentals do not form such tight clusters. Different specimens of *Batodon tenuis*, *Gypsonictops* sp. and *Cimolestes magnus* do not fall near one another. One specimen of *C. magnus* has a relatively shorter length of the postmetacrista and greater cusp height. Similarly, one specimen of *Batodon tenuis*, a very small (5 – 6 g), rare species, groups with that of *C. magnus*, while the other does not.

DISCUSSION

On a larger scale, differences in tooth morphology largely separate species along phylogenetic lines, although groups of unrelated species with similar dietary preferences can be detected. For example, tree shrews have had enigmatic taxonomic affinities, traditionally placed within primates but now placed within a separate order, Scandentia (Nowak, 1991). They are highly insectivorous species and possess a tooth morphology, at least in terms of cusp height and shearing potential, that clusters them with Insectivora. Similarly, highly insectivorous primates such as *Tarsius bancanus* also cluster closer to insectivorans. Kay (1975) found that frugivorous primates were readily distinguished from folivorous or insectivorous primates, and that the latter two can readily be distinguished based on body mass (Kay, 1973). Curiously, folivorous primates, such as *Propithecus verreauxi*, do not group with either general insectivorans or insectivorous primate species, such as *Arctocebus calabarensis* or *Tarsius bancanus*, as would be predicted by Kay's analysis. This apparent inconsistency may be due to differences in methodology, or simply that subtle differences in the form/function of tooth morphology and diet in primates may not be detected when the overall analysis also includes marsupials and insectivorans. Most species of primates, while usually specializing in one type of food item, tend to consume many different types of foods on a seasonal basis (see Hladik, 1979; Kingdon, 1997; Garbutt, 1999). As such, differences in tooth morphology in relation to diet may simply be harder to detect. Frugivorous marsupials, such as *Caluromys philander* and *C. derbianus*, fall closer to primates. This is an indication of the overall cusp morphology of *Caluromys*, which has low-crowned molars with more

bulbous, rounded cusps, similar to that seen in frugivorous primate species such as *Cebus capucinus* and *Saimiri sciureus*.

Despite the overall impression that phylogeny may tend to swamp most detectable differences in tooth morphology as it relates to diet, there are indications that this is not always the case. For instance, the difference in diet between the closely related bushbabies – the frugivorous *Galago alleni* and the more insectivorous *G. demidovii* – are reflected in differences in their tooth morphology. *Galago demidovii* clusters closer to insectivorans, indicating that it has greater shearing potential and taller cusps than *G. alleni*. Within marsupials, there are clear distinctions among frugivorous, omnivorous and more insectivorous/carnivorous species. Further analyses that include only marsupials or primates may help tease apart subtle differences.

There is little discernable separation between Lancian marsupials and placentals from North America, based on gross tooth morphology. Nonetheless, most cluster intermediate between marsupials and insectivores, an obvious indication that they had not yet achieved the tooth specializations seen in modern primates. Instead, they possess tooth characteristics (tall cusps, greater total shear) that would have allowed them to better utilize invertebrate prey resources. However, there is some variation seen in the placement of specimens from the same species. The extreme variation seen in the position of two specimens of *Gypsonictops* sp. may indicate that these are two different species. One possibility for the disparate placement of specimens of *Batodon tenuis* and *Cimolestes magnus* is that these species, with a dentition more specialized than that of their Cretaceous counterparts, may be more sensitive to the fact that the two data points for each species are based on an upper and a lower molar, as opposed to two lowers, for

example. Thus, it may just be the result of the variation seen in using upper and a lower molars from two separate individuals.

The placement of a species such as *Glasbius intricatus*, which has molars that are strikingly similar to those of the modern marsupials *Caluromys philander* and *C. derbianus*, is a strong indication that this Lancian species probably had a very similar diet as *Caluromys*. By the Late Cretaceous, angiosperms had become the most diverse group of plants (Wing and Boucher, 1998), with the appearance of nuts and drupes in the Campanian and Maastrichtian (Friis and Crepet, 1987). With tooth morphology that is very similar to *Caluromys*, as well as the increased dominance of angiosperms as a newly available food source, *Glasbius* may represent the first early trend toward frugivory. Further analysis into the subtle differences exhibited in tooth morphology and diet in modern species, using more refined techniques such as thin plate spline, will allow us to explore in greater detail the diets of mammals in the latest Cretaceous of North America.

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Table 1. Generalized diets of species used in this study.

Species	Diet	Reference
Arctocebus calabarensis	Invertebrates, caterpillars, beetles, fruits, small lizards	Kingdon, 1997
Antechinus minimus	Mainly insects, invertebrates	Strahan, 1995
Caluromys derbianus	Mainly insects; also fruit, figs and small vertebrates; nectar in dry season	Reid, 1997; Eisenberg, 1989
Caluromys philander	Mainly fruit; also gums, invertebrates, small vertebrates	Eisenberg, 1989
Dasyuroides byrnei	Insects, small vertebrates	Strahan, 1995
Dasyurus hallucatus	Small mammals, lizards, invertebrates	Strahan, 1995
Didelphis marsupialis	Omnivorous, including invertebrates, small vertebrates, fruit	Reid, 1997
Echinosorex gymnurus	Earthworms, beetles, insect larvae, centipedes, spiders, snails, aquatic invertebrates	Medway, 1969
Galago alleni	Mostly fruit; also invertebrates such as beetles, moths, spiders	Kingdon, 1997
Galago demidovii	Mainly invertebrates such as beetles, moths, crickets; fruits and gums seasonally	Kingdon, 1997
Hapalemur griseus	Mainly bamboo; also leaves, grass; seasonally fruit	Garbutt, 1999
Hylomys suillus	Soil-dwelling arthropods, earthworms	Medway, 1969
Marmosa sp.	Mainly insects; also fruits, small rodents, lizards	Nowak, 1991

Species	Diet	Reference
Microcebus murinus	Mainly fruit; also insects, flowers and leaves, exudates, small vertebrates	Garbutt, 1999
Monodelphis sp.	Small vertebrates and insects, some seeds and fruits	Nowak, 1991
Philander opossum	Invertebrates, small vertebrates, some fruit	Reid, 1997
Planigale maculata	Insects, eggs	Strahan, 1995
Propithecus verreauxi	Leaves mainly, fruits and flowers seasonally	Garbutt, 1999
Ptilocercus lowii	Insects, small vertebrates, occasional fruits	Nowak, 1991
Scapanus orarius	Mostly earthworms; also snails, slugs, insects	Whitaker, 1980
Sorex longirostris	Invertebrates, spiders, larvae, snails, centipedes	Whitaker, 1980
Suncus murinus	Invertebrates, snails	Medway, 1969
Talpa micrura	Earthworms, insect larvae	Medway, 1969
Tarsius sp.	Primarily insects	Nowak, 1991
Tupaia sp.	Insects primarily; also fruit, seeds, leaves	Nowak, 1991

Table 2. Principal component loadings for three analyses: All modern species; Dietary groups of modern species; Dietary groups of modern species plus Lancian mammal species.[a]

	All modern species			Dietary groups of modern species			Modern + Lancian species		
Variable	I	II	III	I	II	III	I	II	III
Paracone	0.825	0.418	0.011	**0.866**	0.387	0.144	**0.866**	0.386	0.130
Metacone	**0.906**	-0.124	0.124	**0.890**	-0.156	0.283	**0.883**	-0.161	0.281
Protocone	0.766	0.495	-0.202	0.789	0.471	-0.158	0.792	0.473	-0.129
Preparacrista	0.830	0.132	0.298	**0.881**	0.048	0.286	**0.863**	0.088	0.159
Postparacrista	0.823	0.387	0.231	0.833	0.403	0.202	0.829	0.404	0.196
Premetacrista	**0.899**	-0.124	0.325	0.856	-0.240	0.340	0.832	-0.265	0.349
Postmetacrista	0.700	**-0.650**	0.195	0.554	**-0.793**	0.139	0.546	**-0.791**	0.136
Preprotocrista	0.430	-0.126	**-0.648**	0.526	0.039	**-0.541**	0.525	0.070	**-0.574**
Postprotocrista	0.654	-0.004	-0.483	0.736	0.278	-0.234	0.734	0.293	-0.305
SumUpperShear	**0.897**	-0.162	0.055	**0.893**	-0.190	0.066	**0.895**	-0.184	0.046
Paraconid	0.825	-0.395	-0.029	0.736	-0.451	-0.113	0.739	-0.450	-0.168
Protoconid	**0.921**	-0.266	0.050	**0.888**	-0.334	0.094	**0.866**	-0.375	0.121
Metaconid	0.851	-0.236	-0.219	0.830	-0.220	-0.337	0.829	-0.272	-0.308
Entoconid	0.818	0.272	-0.116	0.796	0.322	-0.276	0.781	0.317	-0.244
Hypoconid	0.777	0.510	0.001	0.825	0.444	0.100	0.802	0.452	0.194
Protocristid	0.819	-0.474	0.021	0.702	-0.566	-0.102	0.700	-0.523	-0.053
Paracristid	**0.862**	-0.049	-0.146	0.839	-0.057	-0.231	0.825	-0.059	-0.197
Cristid Obliqua	0.833	0.469	0.121	0.820	0.465	0.253	0.817	0.463	0.261
SumLowerShear	**0.946**	-0.084	-0.023	**0.930**	-0.113	-0.181	**0.932**	-0.112	-0.152
Percentage explained	66.80	11.30	5.80	65.00	13.60	5.90	63.90	13.70	5.80

[a]Relatively high loadings in bold: (component I) > |0.85|; (component II) > |0.60|; (component III) > |0.50|

FIGURE LEGENDS

FIGURE 1. Position of landmarks taken on the upper and lower second molars (modified from Crompton and Kielan-Jaworowska, 1978).

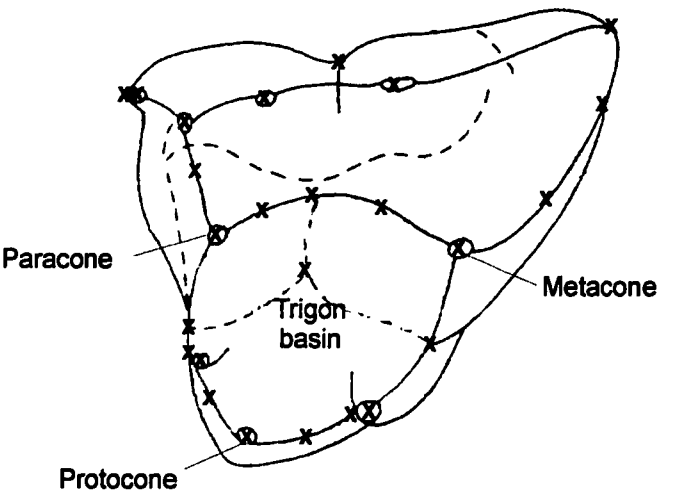
FIGURE 2. Location of principal shearing crests measured (modified from Crompton and Kielan-Jaworowska, 1978). **A.** Upper molar crests: 1, preparacrista; 2, postmetacrista; 3, postparacrista; 4, premetacrista; 5, preprotocrista; and 6, postprotocrista. **B.** Lower molar crests: 1, protocristid; 2, paracristid; 3, cristid obliqua; 4, postcristid; 5, postmetacristid; 6, pre- and postentocristid.

FIGURE 3. Projections onto first three principal components based on analysis of tooth morphology in 52 modern species of primates (diamonds), marsupials (crosses), insectivorans (circles) and tree shrews (triangles).

FIGURE 4. Projections onto first three principal components based on analysis of tooth morphology in insectivorans (circles – *Echinosorex gymnurus, Hylomys suillus, Scapanus orarius, Sorex longirostris, Talpa micrura*), insectivorous primates (squares – *Arctocebus calabarensis, Tarsius bancanus, Galago demidovii, Microcebus murinus*), frugivorous primates (diamonds – *G. alleni*), folivorous primates (upright triangles – *Hapalemur griseus, Propithecus verreauxi*), tree shrews (downward triangles – *Tupaia minor, Ptilocercus lowii*), insectivorous marsupials (crosses – *Antechinus minimus, Dasyuroides byrnei, Dasyurus hallucatus, Planigale maculata, Marmosa xerophila, Monodelphis domestica, Philander opossum*), frugivorous marsupials (plus signs – *Caluromys derbianus, Caluromys philander*), omnivorous marsupials (stars –*Didelphis marsupialis*).

FIGURE 5. Projections onto first two principal components based on analysis of tooth morphology in latest Cretaceous (Lancian) mammals of North America (filled squares = placentals; filled circles = marsupials). Lancian species: 1 = *Gypsonictops* sp., 2 = *Batodon tenuis*, 3 = *Cimolestes magnus*, 4 = *Cimolestes cerberoides*, 5 = *Cimolestes propaleoryctes*, 6 = *Pediomys cooki*, 7 = *Pediomys elegans*, 8 = *Pediomys krejcii*, 9 = *Alphadon marshi*, 10 = *Glasbius intricatus*. See Fig. 4 for explanation of symbols for dietary groups.

Figure 1


Paracone
Metacone
Trigon basin
Protocone

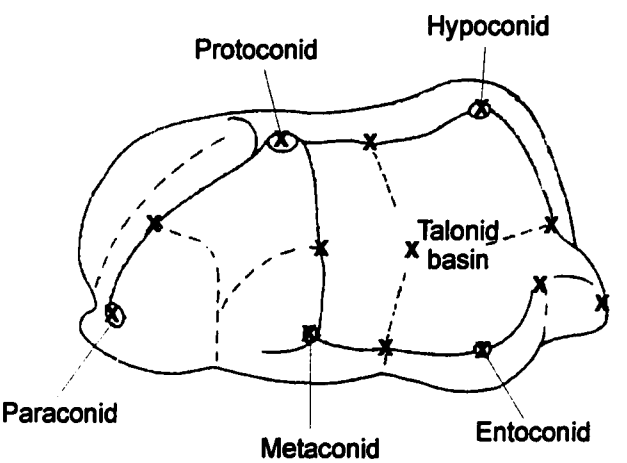
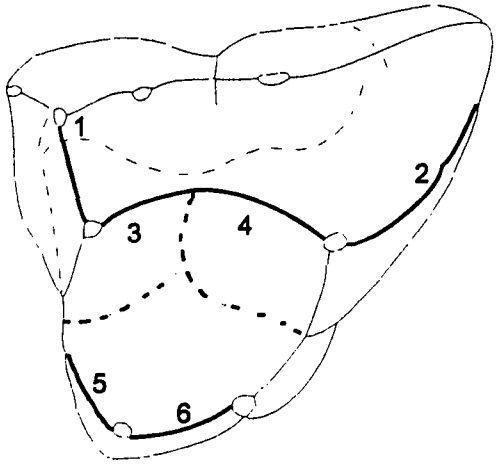

Protoconid
Hypoconid
Talonid basin
Paraconid
Metaconid
Entoconid

Figure 2

A.



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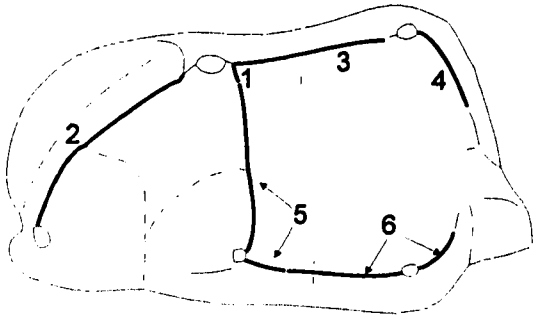
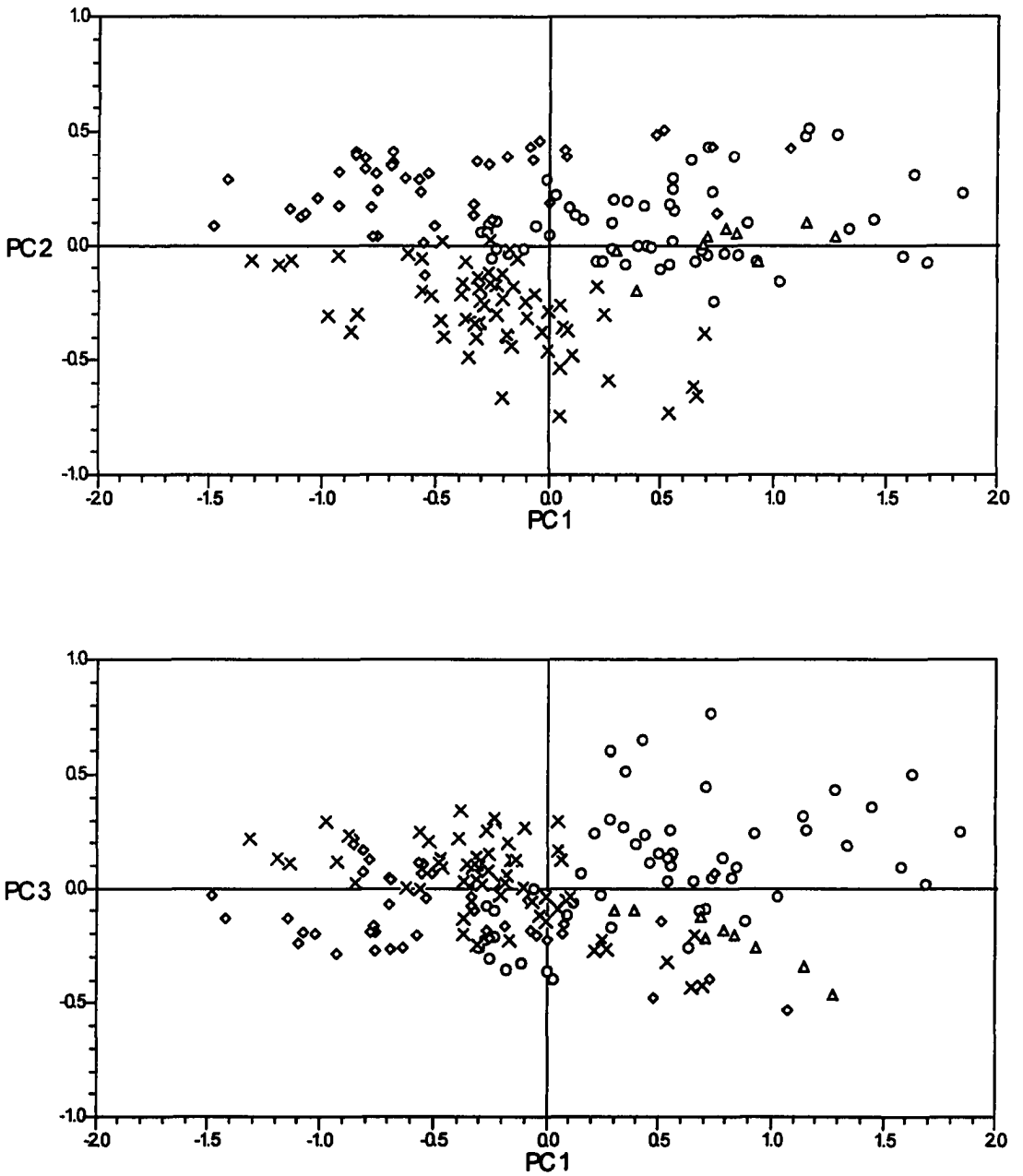


Figure 3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0.0
-0.5
-1.0
PC2
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-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
PC1
1.0
0.5
0.0
-0.5
-1.0
PC3
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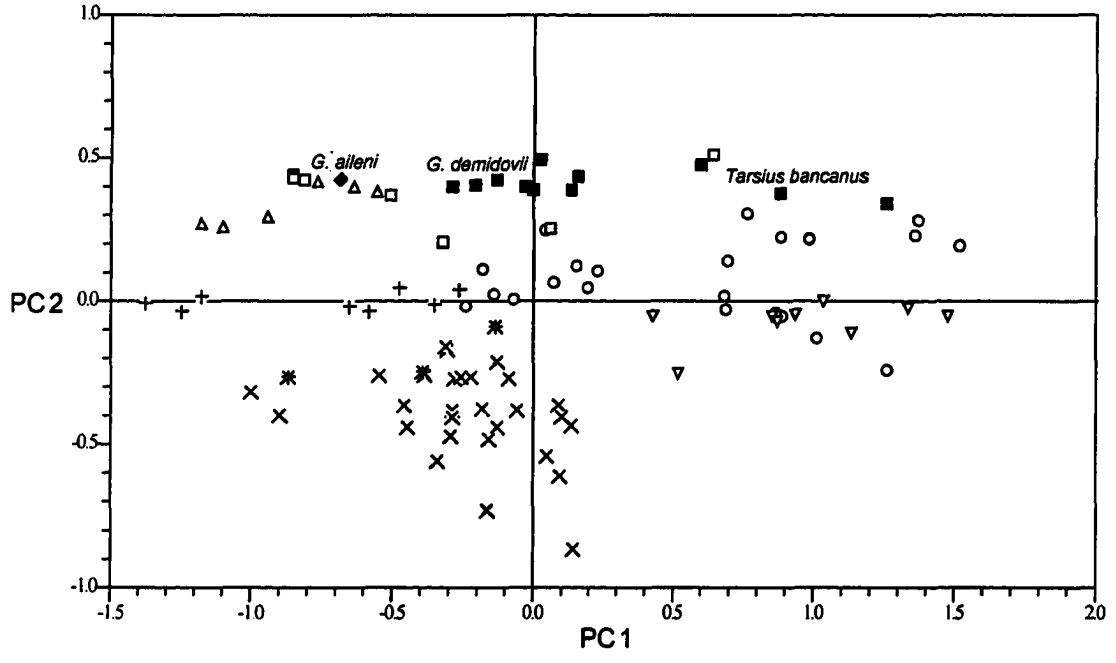
1.5
2.0
PC1

Figure 4


G. alleni
G. demidovii
Tarsius bancanus
PC 2
PC 1
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1.5
2.0

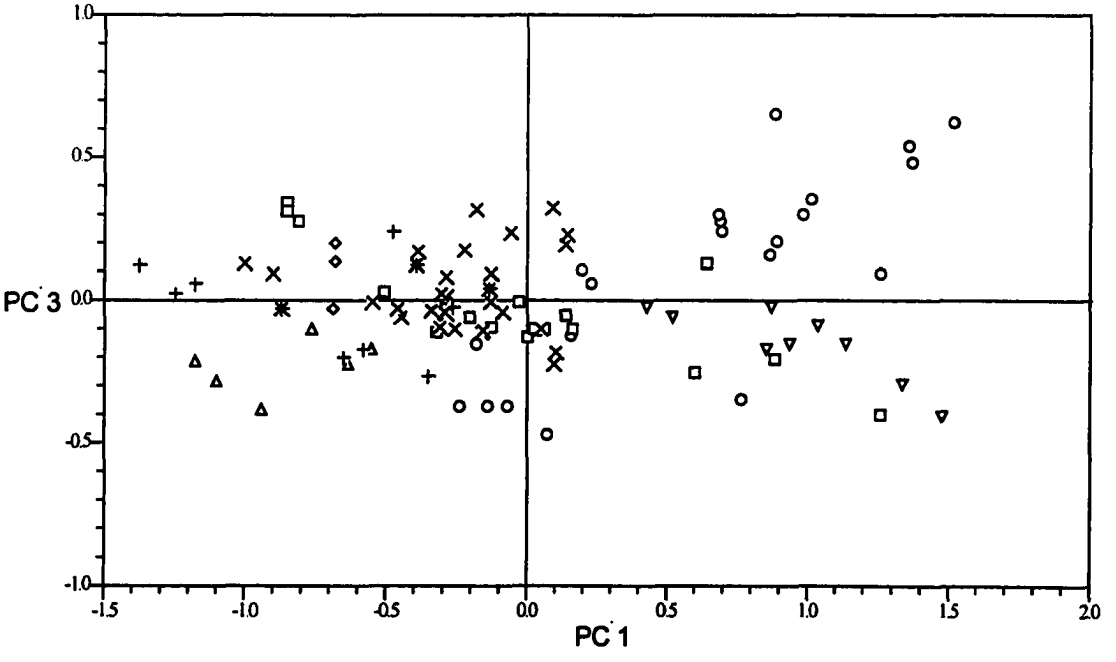
PC 3
PC 1
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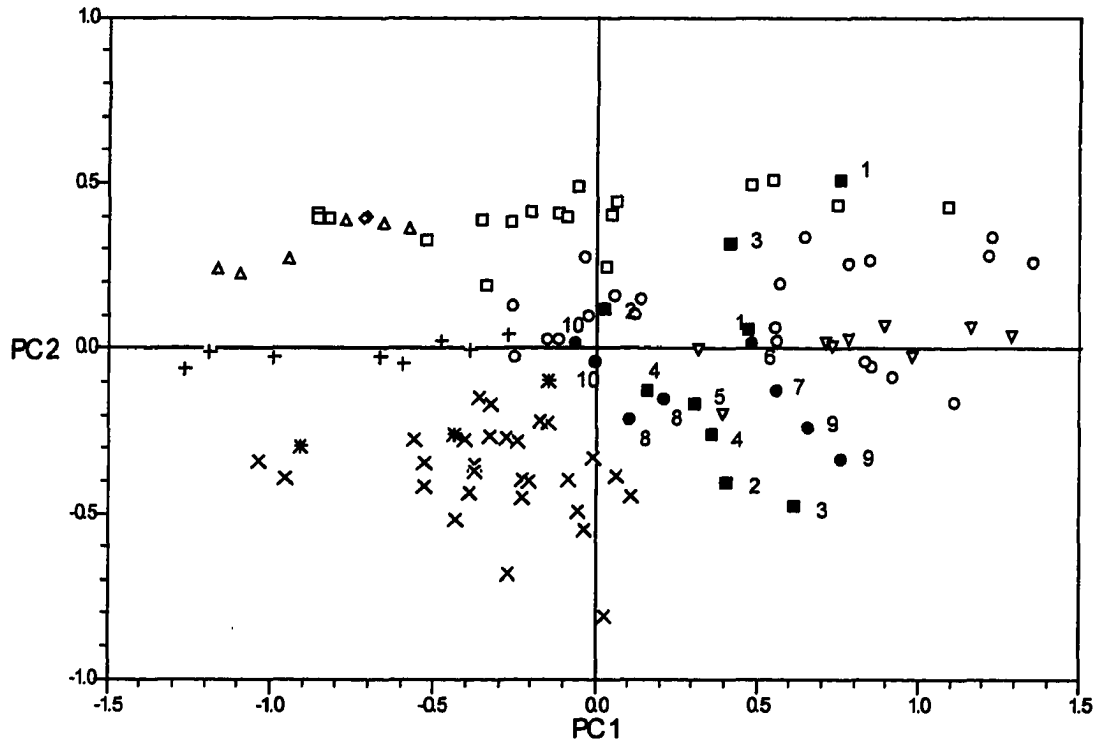
Figure 5



CONCLUSIONS

Body size (as measured by body mass) is most highly correlated with size of the first upper and lower molars in marsupials, primates and insectivores. The strength of this association is not equivalent within or between all three groups, however. For instance, although body mass is similarly correlated with tooth size in didelphid and dasyurid marsupials, it is not as strong when the analysis is performed on a pooled sample of the two families. Likewise, equations generated from didelphids and dasyurids predict body mass equally well for modern species of marsupials, and either predicts body mass better than equations generated from a pooled sample of the two families. The correlation of body mass with tooth size is higher in marsupials and insectivores than in primates. The inclusion in a regression analysis of taxa that may deviate from the "average" tooth morphotype for that group can affect the results. For example, two species of the marsupial *Caluromys* have teeth that are low-crowned and have bulbous cusps, a morphology quite unlike those of other didelphids. In the regression analysis, this distinctive tooth morphology resulted in a significant deviation of the data points from the regression line for molars of these two species. Removal of these species resulted in a much better fit of the regression line to the data, and consequently, presumably a more accurate regression equation.

In addition to tooth size, some cranial measurements are highly correlated with body mass. Skull length was more strongly correlated with body mass in marsupials and insectivores than in primates. The variation seen in the shape of skulls between different groups of mammals, and subsequent variation in skull length, suggests that skull length

may not be a very consistent indicator of body size. Body mass was highly correlated with the area of the foramen magnum in all three groups. Area of the foramen magnum was also highly correlated with tooth size, indicating that the size of the foramen magnum, like body mass, may be a good representative of body size of a species.

Estimated body masses indicate that Cretaceous mammals were indeed small, most less than 200 g in size. The smallest Lancian placental mammal was *Batodon tenuis*, at 5 – 6 g, while the smallest marsupial was *Pediomys krejcii*, at approximately 25 g. Marsupials achieved a greater diversity of body sizes, with five species larger than 200 g, and the largest species, *Didelphodon vorax*, at nearly 2000 g. In contrast, there were only two species of Cretaceous placentals over 200 g, with the largest, *Cimolestes magnus*, reaching over 800 g in size.

Preliminary analysis of tooth form and function in modern mammals indicates that tooth shape is intimately tied to phylogeny as well as function. In a principal components analysis, different tooth morphologies grouped along phylogenetic lines. Subsequent analysis of tooth morphology for different dietary categories indicates that some species do group along dietary lines, suggesting that it may eventually prove possible to separate morphological differences (or similarities) owing to genealogy from those related to function. When Cretaceous mammals were added to the analysis, species of Cretaceous marsupials and placentals grouped intermediate between modern marsupials and insectivores. One Cretaceous marsupial species, *Glasbius intricatus*, grouped close to the two modern species of frugivorous marsupials, *Caluromys*, a placement that is not surprising considering their very similar tooth morphologies. This suggests that *G. intricatus* might have been similarly frugivorous. Other Cretaceous

species such as *Cimolestes magnus* have high crowned, pointed cusps with relatively long shearing blades. This, coupled with its larger body size, suggest that this species may have been carnivorous.

It was during the Cretaceous that flowering plants first appeared. By the Late Cretaceous, angiosperms were the dominant land plants; coevolutionary interactions with animals had resulted in the appearance of pollinating insects and fruiting bodies. Body size estimates for Cretaceous mammals coupled with the preliminary results of tooth morphology and diet indicate that some Cretaceous species at least, such as *G. intricatus* or *C. magnus*, may represent early departures from insectivory to utilize these newly available food resources.