The scale of it all: postcanine tooth size, the taxon-level effect, and the universality of Gould's scaling law

Lynn E. Copes and Gary T. Schwartz

Abstract.—In a seminal paper in 1975, Gould proposed that postcanine occlusal area (PCOA) should scale metabolically (0.75) with body mass across mammals. By regressing PCOA against skull length in a small sample of large-bodied herbivorous mammals, Gould provided some marginal support for this hypothesis, which he then extrapolated as a universal scaling law for Mammalia. Since then, many studies have sought to confirm this scaling relationship within a single order and have found equivocal support for Gould's assertion. In part, this may be related to the use of proxies for both PCOA and body mass, small sample sizes, or the influence of a ''taxon-level effect,'' rendering Gould's scaling ''universal'' problematic.

Our goal was to test the universality of Gould's prediction and the impact of the taxon-level effect on regressions of tooth size on body mass in a large extant mammalian sample (683 species spanning 14 orders). We tested for the presence of two types of taxon-level effect that may influence the acceptance or rejection of hypothesized scaling coefficients. The hypotheses of both metabolic and isometric scaling can be rejected in Mammalia, but not in all sub-groups therein. The level of data aggregation also influences the interpretation of the scaling relationship. Because the scaling relationship of tooth size to body mass is highly dependent on both the taxonomic level of analysis and the mathematical methods used to organize the data, paleontologists attempting to retrodict body mass from fossilized dental remains must be aware of the effect that sample composition may have on their results.

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Introduction

One of the most important aspects of an organism's biology is its body mass, as this dictates, constrains, underlies, and is highly correlated with certain key adaptations such as diet, locomotion, energetics, ecology, life history, morphology and physiology (*diet*: Pirie 1978; Smith 1983; Janis 1986; Ross 1992; Fa and Purvis 1997; Iwaniuk et al. 2000; *locomotion*: Taylor et al. 1970, 1972, 1982; Rubin and Lanyon 1984; Anapol et al. 2005; Biewener 2005; *energetics*: Schmidt-Nielsen 1970; Taylor et al. 1970; Brown et al. 1993; Speakman 1996; West et al. 1997, 2002; Allen et al. 2002; Speakman et al. 2002; Enquist et al. 2003; *ecology*: Harestad and Bunnel 1979; Fleagle 1985; Eisenberg 1990; Churchfield 1996; Enquist et al. 2003; Agrawal 2004; Brown et al. 2004; Cottingham and Zens 2004; Kaspari 2004; Koehl and Wolcott 2004; Marquet et al. 2004; Tilman et al. 2004; *life history*: Sacher 1959; Fleagle 1985; Blondel 1987; Kappeler 1996; Speakman et al. 2002; Leigh et al. 2003; Palkovacs 2003; Webster et

al. 2004; *morphology*: Hill 1950; McMahon 1973; Anderson et al. 1979; Prange et al. 1979; Grand 1990; *physiology*: Stahl 1967; Umminger 1975; McNab 1990; Hastings 1996; West et al. 2003; Niven and Scharlemann 2005). Because teeth are the most frequently preserved skeletal element in the vertebrate fossil record, their size is often used to reconstruct the body mass of extinct organisms (Gingerich et al. 1982; Damuth 1990; van Valkenburgh 1990; Aiello and Wood 1994). Elucidating the precise relationship between tooth size and body mass has therefore been a goal of biologists and paleontologists for the past century (e.g., Matsumoto 1926; Schuman 1954; Garn et al. 1968; Gingerich 1974, 1977; Johanson 1974; Swindler and Sirianni 1975; Henderson and Corruccini 1976; Janis 1979, 1990a; Wood 1979; Gingerich et al. 1982; Leutenegger 1982; Gingerich and Smith 1985; Fortelius 1990; Kieser 1990; Roth 1990; Scott 1990; van Valkenburgh 1990; Plavcan and Gomez 1993; Strait 1993; Cuozzo 2001; Dayan et al. 2002; Vinyard and Hanna 2005).

In an influential paper, Gould (1975) proposed that one particular measure of tooth size in mammals, the postcanine occlusal area (PCOA), should scale in a predictable and universal manner to body mass in order to satisfy a mammal's metabolic needs. Gould reasoned that because basal metabolic rate has been shown to scale as body mass to the three-quarters power (Kleiber 1932, 1947; Heusner 1982; Feldman and McMahon 1983; McNab 1988, 2003; Ross 1992; West et al. 1999, 2002, 2003; Enquist et al. 2003; Agrawal 2004; Kozlowski and Konarzewski 2004), and that because the area of the postcanine dentition is directly related to the amount of food an organism can process, PCOA should also scale with body mass$^{3/4}$. This model of "functional equivalence" (hereafter, termed "metabolic scaling") yields a very different relationship than does a model of "geometric similarity," which predicts an isometric scaling coefficient of $2/3$ due to the regression of an area (measured in units squared) on a mass (measured in units cubed).

In his analysis, Gould (1975) analyzed the relationship of tooth size to body mass in large-bodied artiodactyls and hystricomorph rodents. By regressing PCOA against skull length (as a proxy for body mass) in samples ranging in size from 9 to 34 individuals from several different mammalian subfamilies, he provided marginal support for a hypothesis of metabolic scaling. For example, in the rodent analysis, the expected slope of isometry when regressing an area on a length is 2.0, but Gould discovered a scaling coefficient of 2.4. Gould found a similar positively allometric relationship in suines and cervids. Because he used a linear proxy for body mass, these results cannot be statistically compared with either hypothesis of a $2/3$ or $3/4$ scaling coefficient, but Gould concluded, "My data, perhaps, are only suggestive, but I believe that they do justify a general hypothesis of positive allometry for the scaling of postcanine tooth areas in interspecific plots for mammalian herbivores of fairly similar design" (Gould 1975: p. 358). Although Gould's is a landmark study, several important issues related to (1) the supposed universality of the scaling relationship; (2) the appropriateness of using surrogates of body mass, rather than body mass itself; and (3) the taxonomic level of analysis remain to be fully explored.

Universality.—Since Gould's (1975) analysis, several studies have sought to determine the scaling relationship between PCOA and body mass in a wide variety of mammalian groups, spanning such diverse clades as strepsirrhine primates (Vinyard and Hanna 2005), canids (Legendre and Roth 1988), and the (now defunct) Insectivora (Gingerich and Smith 1985). See Appendix 1 (all appendices online at http://dx.doi.org/10.1666/08089. s1) for a list of every study, of which we are aware, that has tested Gould's hypothesis. Although Gould specifically constrained his statement on the universality of his "law-like" scaling relationship to "mammalian herbivores of fairly similar design," many researchers testing his hypothesis have included a wider range of mammals in their studies.

Given the diversity of mammalian groups investigated, perhaps it is not surprising that some studies concluded that the scaling relationship of tooth size and body mass for certain orders is positively allometric, isometric, or negatively allometric (*positively allometric*: Pilbeam and Gould 1974; Gould 1975; Corruccini and Henderson 1978; Pirie 1978; Smith 1981; Prothero and Sereno 1982; Fortelius 1985; Gingerich and Smith 1985; Legendre and Roth 1988; Vinyard and Hanna 2005; *isometric*: Creighton 1980; Gingerich et al. 1982; Kanazawa and Rosenberger 1989; Yamashita 1998; *negatively allometric*: Kay 1975; Henderson and Corruccini 1976; Wood 1979; Perzigian 1981; Conroy 1987; Damuth 1990; Janis 1990a,b; Kieser 1990). A review of the literature revealed 55 reports of a positively allometric relationship, 64 cases in which the relationship was reported as isometric, and 45 reports of negative allometry; in fact, conflicting conclusions were often reported in the same paper. This lack of consensus may indicate that the underlying biology governing how body mass and tooth size relate may differ among diverse clades; thus, it is expected that no universal scaling relationship exists across mammals. It may be that other factors, perhaps mathematical in
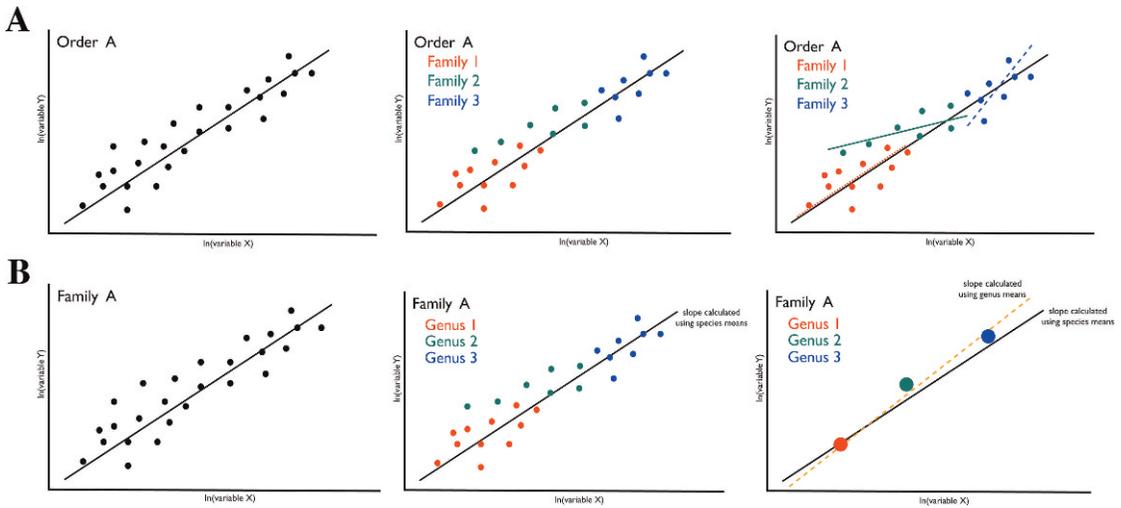
FIGURE 1. A, The Hierarchical TLE. Given a scatter of points from a single order (left) that is composed of members of three different families (middle), the scaling relationship for the entire order may be different from that of each family calculated separately (right). B, The Mathematical TLE. Given a similar scatter of points (left), the scaling relationship calculated from species means (middle) may be different from the scaling relationship calculated from genus means (right).

nature, are responsible for the diversity of scaling relationships reported in the literature. The two main mathematical issues that we address here related to the use of proxies for body mass in allometric analyses and to a phenomenon referred to as the ''taxon-level effect.''

Proxies.—Because only skeletal material was available for his analysis, Gould (1975) used skull length and femoral length as proxies for body mass in his allometric analyses. However, in some orders, neither skull length nor femoral length scales isometrically with body mass (Vinyard and Hanna 2005; Weiss 2006), rendering the use of such proxies problematic because they can bias the scaling relationship. The extent to which the choice of proxies for dependent and independent variables affects variation in the reported scaling relationships has not been investigated thoroughly.

Taxon-Level Effect.—For some time, it has been known that the taxonomic level at which allometric analyses are performed can influence the scaling coefficient, and this is referred to as the ''taxon-level effect,'' or TLE (Felsenstein 1985; Pagel and Harvey 1988, 1989; Harvey et al. 1991). Generally,

the TLE is reported to be a phenomenon wherein the slope of any particular scaling relationship may differ depending on the taxonomic level at which the investigation is performed. For instance, one single regression analysis of how tooth size scales with body mass across ten orders of Mammalia may differ, perhaps significantly so, from a series ten regression analyses performed on those orders separately. A thorough survey of the literature, however, reveals that two separate effects, one based on the hierarchical, nested nature of Linnean classification, and one based on the various mathematical ways data can be organized, have frequently been conflated under the umbrella term ''taxon-level effect.''

The first effect, which we term the ''Hierarchical TLE,'' depends on the taxonomic level at which the regression analysis is performed, and is simply a question of whether the allometric relationship is examined in a single genus, family, or order. In these analyses, the data points are always species means (Fig. 1A). The scaling coefficient (slope) can differ depending on the taxonomic level at which the analyses are performed. In the example shown in Fig-

ure 1A, analyzing all three families together as one order reveals a different scaling relationship than when each family is considered as a separate hierarchical taxonomic entity.

The second effect, the ''Mathematical TLE,'' refers to the practice of data aggregation. For example, a classwide regression might be generated by utilizing data points representing individuals, species means, genus means, or even family means (Fig. 1B). The scaling coefficient calculated by using any one of these taxonomic levels of data aggregation may differ significantly from a coefficient calculated from the same regression analysis using any other taxonomic level of data aggregation. This may lead different researchers to opposing conclusions if, for example, using individuals as points in a bivariate regression generates a scaling coefficient of ¾ whereas using species means results in a coefficient of ⅔.

Given the equivocal support for Gould's (1975) assertion regarding the universality of metabolic scaling, the potential mathematical error imparted by the use of proxies for body mass, and inconsistencies related to an understanding of how the TLE may bias regression analyses, we have critically reevaluated Gould's prediction as well as the impact of either type of TLE on regressions of tooth size on body mass in a large extant mammalian sample. In general, we investigated whether a universal scaling relationship between PCOA and body mass exists across mammals (at the level of class or within particular orders), whether that pattern best fits a model of geometric similarity or functional equivalence, and why previous studies have failed to reach a consensus as to the nature of the relationship.

To address these issues, we asked three specific questions regarding the relationship between maxillary and mandibular PCOA and body mass across a wide range of mammals at varying taxonomic levels:

1. Is the scaling coefficient (slope) of the relationship between PCOA and body mass for Mammalia significantly different from either functional equivalence (i.e.,

metabolic scaling, at 0.75) or isometry (i.e., geometric similarity, at 0.67)?

2. Does the relationship from (1) hold across (i.e., is it ''universal'' for) all mammalian groups regardless of taxonomic level? That is, do all taxonomic subgroups within Mammalia maintain the same category of scaling relationship (isometry or allometry) as that found in (1)? This constitutes a test of how a ''Hierarchical TLE,'' if present, may influence the interpretation of the relationship of body mass and tooth size.

3. Does the scaling relationship from (1) hold despite different taxonomic levels of data aggregation? That is, does the category of scaling relationship (isometry or allometry) change when generic means versus species means, or family means versus individuals, are used as data points in bivariate analyses? This constitutes a test of how a ''Mathematical TLE,'' if present, may influence the interpretation of the relationship of body mass and tooth size.

Materials and Methods

The total sample consists of 2370 specimens from 683 species representing 14 of the 20 extant orders of Mammalia: Afrosoricida, Artiodactyla, Carnivora, Chiroptera, Dermoptera, Erinacemorpha, Hyracoidea, Macroscelidea, Perissodactyla, Primates, Proboscidea, Rodentia, Scandentia, and Soricomorpha. Approximately one-quarter of the cases were culled from the literature (Schuman 1954; Zingeser 1967; Hershkovitz 1970; Boekschoten and Sondaar 1972; Pilbeam and Gould 1974; Gould 1975; Kay 1975; Henderson and Corruccini 1976; Gingerich 1977; Corruccini and Henderson 1978; Goldstein et al. 1978; Pirie 1978; Rosenberger 1979; Wood 1979; Creighton 1980; Perzigian 1981; Smith 1981; Thorington and Heaney 1981; Gingerich et al. 1982; Prothero and Sereno 1982; McHenry 1984; Fortelius 1985; Gingerich and Smith 1985; Herring 1985; Legendre and Roth 1988; Shea and Gomez 1988; Kanazawa and Rosenberger 1989; Rosenberger and Strier 1989; Fooden 1990; Kieser and Groeneveld 1990, 1991; Plavcan 1990; Plavcan and Gomez 1990;

Brown and Nicoletto 1991; Biknevicius and Ruff 1992; Rosenberger 1992; Pan et al. 1993; Anapol and Lee 1994; Kay 1994; Smith 1996; Polly 1998; Pan and Oxnard 2001; Swindler 2002; Popowics 2003; Wang et al. 2003; Vinyard and Hanna 2005; Tornow et al. 2006). Those data were supplemented with unpublished data provided by several researchers (see Acknowledgments), which provided an additional one-quarter of the total sample. Approximately half of the specimens included in the analysis were measured by one of us (L.E.C.) at the National Museum of Natural History (Washington, D.C.) and the American Museum of Natural History (New York).

Postcanine Occlusal Area and Body Mass.— Postcanine tooth area is measured by multiplying maximum mesiodistal length by maximum buccolingual breadth of each tooth (treated as a rectangle) and then summing the five or six individual tooth areas. Vinyard and Hanna (2005) reported that this simplification of area closely approximates the area calculated by tracing the occlusal outline digitally to calculate the area. This method of measuring ''occlusal'' area ignores any of the complex surface topography of teeth, including cuspal morphology, shearing crests, or relative degree of selenodonty. Because this method of determining PCOA has been used by all previous studies testing Gould's hypothesis, it was retained here.

The final sample consisted of 1260 males, 826 females, and 284 individuals of unknown sex. Body mass was noted from specimen tags when available. When masses were not available for a specimen, its sex-specific species mean was obtained from Silva and Downing (1995) if the sex was known. For monomorphic species where sex was not noted on the specimen tag and could not be assessed visually, we used the mean female body mass of that species, based on the assumption that this would not significantly bias the results. (To test this assumption, we performed regression analyses on four orders [Carnivora, Chiroptera, Primates, and Rodentia], first using all individuals and then again using only individuals of known sex. Within each order, the slopes for these two groupings

were nearly coincident and did not differ significantly from each other. In no case did assigning female body mass values to specimens of unknown sex alter our results.)

Only adults with relatively unworn teeth were included in the analysis. Wear of premolars and molars can potentially bias the mesiodistal and buccolingual dimensions of the tooth. Including extinct taxa would have also invited bias given that most body masses of fossilized animals are estimated from molar size (e.g., Gingerich 1974; Gingerich et al. 1982; McHenry 1984; Schwartz et al. 1995; McHenry and Berger 1998; Brown et al. 2004), so only extant taxa were included in these analyses.

Statistical Analysis.—All data were ln-transformed so that the slopes of any regression line become estimates of exponents, given the traditional allometric equation

$$y = bx^m \qquad (1)$$

which is logarithmically transformed into the equation for a straight line

$$\ln(y) = m * \ln(x) + \ln(b). \qquad (2)$$

Data were analyzed with reduced major axis (RMA) regressions, a model II regression technique, given that natural variation in the independent and dependent variables was expected to be partitioned symmetrically (Smith 1981, 1993, 2009; Warton et al. 2006). One possible reason that previous studies have failed to reach consensus regarding this particular relationship is the inconsistent use of both Model I and Model II regressions. To help evaluate the effect that regression model choice has on this particular scaling relationship, and because data such as these are frequently used by paleontologists interested in retrodicting body mass from tooth size, we provide both ordinary least squares (Model I) and RMA regression parameters in all tables and appendices.

To test for the influence of a Hierarchical TLE, we calculated regression slopes using species means (geometric, not arithmetic) at the taxonomic level of class, order, suborder, superfamily, family, subfamily, genus, and species for all of those categories containing six or more data points. (A geometric mean is

TABLE 1.   Regression parameters for classwide analysis of tooth size on body mass using species means. Compare with Appendices 2–4 (online) for an illustration of the Hierarchical TLE.

Class	Regression parameter	Maxillary PCOA	Mandibular PCOA
Mammalia	n	604	656
	RMA slope (95% CI)	0.56 (0.55–0.57)	0.58 (0.57–0.59)
	RMA intercept	0.52	0.13
	OLS slope (95% CI)	0.54 (0.53–0.55)	0.56 (0.55–0.57)
	OLS intercept	0.68	0.23
	SEE	0.01	0.01
	r^2	0.92	0.95

preferred because it is less susceptible to the effect of outliers [e.g., one large-bodied member of a family] and highly skewed distributions.) Testing for a Mathematical TLE requires the aggregation of the original data into increasingly broader taxonomic groups, in this case, species, then genus, and then family means. Species means were calculated as the geometric means of all individuals assigned to that species; genus means were calculated from all species means within that genus; and family means were calculated from the all genus means within that family. Using those species, genus, and family means, we then calculated regression parameters for the class or order.

We then used the RMA program SMATR (Warton et al. 2006) to statistically compare slopes generated from our analyses against 0.00, 0.67, 0.75, and one another.

Criteria for Determining Presence of TLEs.— The three questions introduced in the ''Introduction'' were tested in turn.

1. The scaling coefficient defining the relationship between PCOA and body mass was first determined by using species means calculated from all specimens included in the classwide analysis. Standard methods for comparing the slope to the two hypotheses (0.67 and 0.75) were used.
2. A Hierarchical TLE was declared to exist if the scaling coefficient generated at a lower taxonomic level changed our acceptance or rejection of a hypothesis of either metabolic scaling or isometry compared to the results from analyses at higher taxonomic level. For example, if the analysis rejected the metabolic scaling hypothesis when

class was used as the level of analysis, but not when order was used, then an HTLE was present.
3. A Mathematical TLE was declared to exist if the scaling coefficient generated using individual values or family or genus means changed our acceptance or rejection of a particular hypothesized scaling relationship compared to the results from analysis performed using species means. For example, if the result of an analysis using species means led us to reject a hypothesis of isometry, but was then altered (i.e., we were unable to reject the hypothesis of isometry) when using individuals or genus means, an MTLE was present.

Results

Classwide Analysis.—Regression statistics for the scaling of PCOA on body mass at the level of class are reported in Table 1. When analyzing all species, the RMA slope is 0.56 ± 0.01 (maxillary PCOA) and 0.58 ± 0.01 (mandibular PCOA). Both of these relationships are significantly different from isometry (0.67) and metabolic scaling (0.75) (Table 1, Fig. 2). The results for mandibular and maxillary PCOA do not differ significantly; thus only the results derived using mandibular PCOA are discussed in the text, although all data are reported in the tables and in the appendices.

Hierarchical Taxon-Level Effect.—Regression parameters for all orders with more than six species and statistically significant slopes are given in Appendix 2 and illustrated in Figure 3. The now-defunct order Insectivora
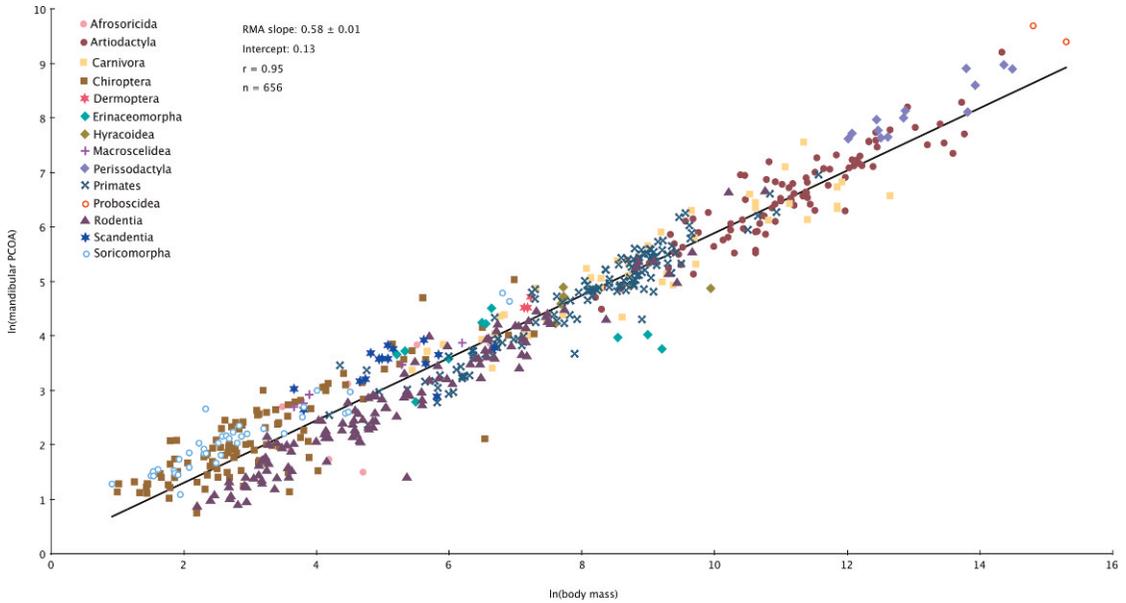
FIGURE 2. Bivariate scatterplot (with results of RMA regression) of ln(mandibular PCOA) on ln(body mass) for the entire class. Each data point is a species mean.

is included to facilitate comparisons with previous studies, but each of the three current orders formerly included within it, Afrosoricida, Erinaceomorpha, and Soricomorpha, are also listed. Although the entire classwide regression has a slope of 0.58 ± 0.01 and does not include either isometry or metabolic scaling, not all orders follow the same pattern (Fig. 3). For instance, the slopes for Artiodactyla, Insectivora, Primates, and Rodentia are significantly different from the classwide slope. While a hypothesis of isometry (0.67) is rejected at the level of class, it cannot be rejected for all orders in the analysis, as Carnivora, Insectivora, and Soricomorpha all have slopes significantly lower than isometry. The hypothesis of metabolic scaling is rejected at the level of class and by all orders within it, except for Afrosoricida, Perissodactyla, and Scandentia.

The influence of the Hierarchical TLE is illustrated within Primates in Figure 4. When the data are analyzed at the ordinal level, the hypothesis of metabolic scaling can be rejected, although the 95% confidence intervals do just overlap isometry. However, as analyses are performed at increasingly lower taxonomic levels (i.e., at the levels of family or subfamily), isometry is rejected in favor of

metabolic scaling. Interestingly, within the only genus in our data set to contain more than six data points (*Macaca*), metabolic scaling is rejected in favor of negative allometry (although isometry cannot be rejected by the 95% confidence intervals around the slope). Regression parameters for all families and genera across Mammalia with more than six species and statistically significant slopes are reported in Appendices 3 (family-level analyses) and 4 (genus-level analyses).

Mathematical Taxon-Level Effect.—All of the regression parameters listed in Table 1 and Appendices 2–4 are derived by using species means as the basis of the analysis. Another way to analyze these data is to lump larger taxonomic levels into a single datum for each of the dependent and independent variables and run, for example, a regression for the entire class using means of families or orders, rather than means of species. The results of this analysis are shown for the classwide data set in Table 2 and illustrated in Figure 5. The interpretation of the regression analysis does not change when the analysis is run using individuals or the means of species, genera, subfamilies, families or orders—both isometry and metabolic scaling hypotheses are
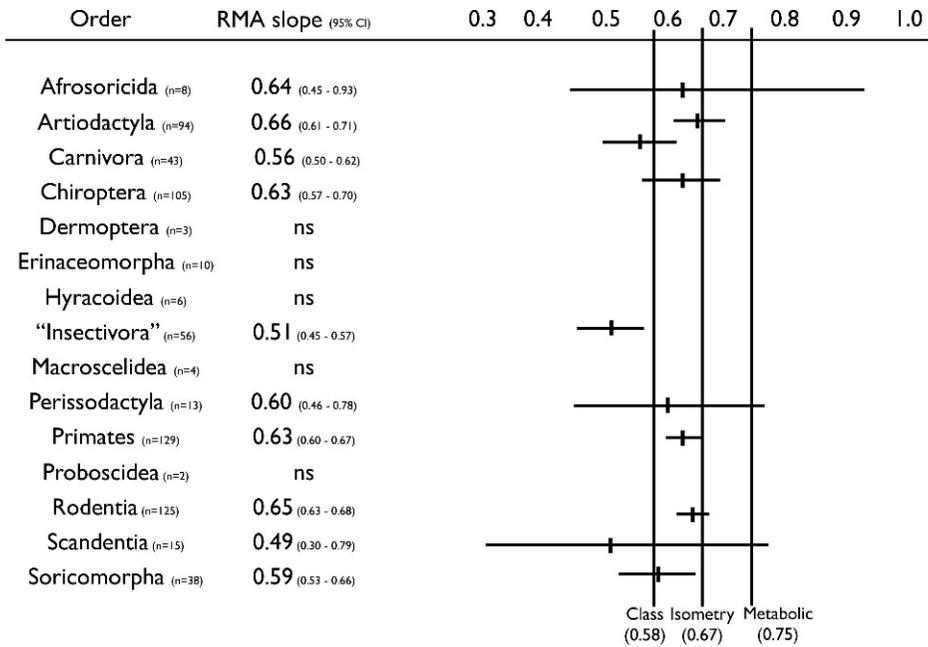
FIGURE 3. The Hierarchical TLE across Mammalia illustrating the scaling coefficients (RMA slopes) of ln(mandibular PCOA) regressed on ln(body mass) for all 14 orders included in the analysis (''Insectivora,'' though now defunct, is included for comparison to previous studies). The long vertical lines represent the slope of the classwide analysis as well as the two hypothesized coefficients for models of isometry and metabolic scaling. Each order's coefficient is represented by a short vertical line, with a horizontal line representing the 95% confidence intervals about the slope.
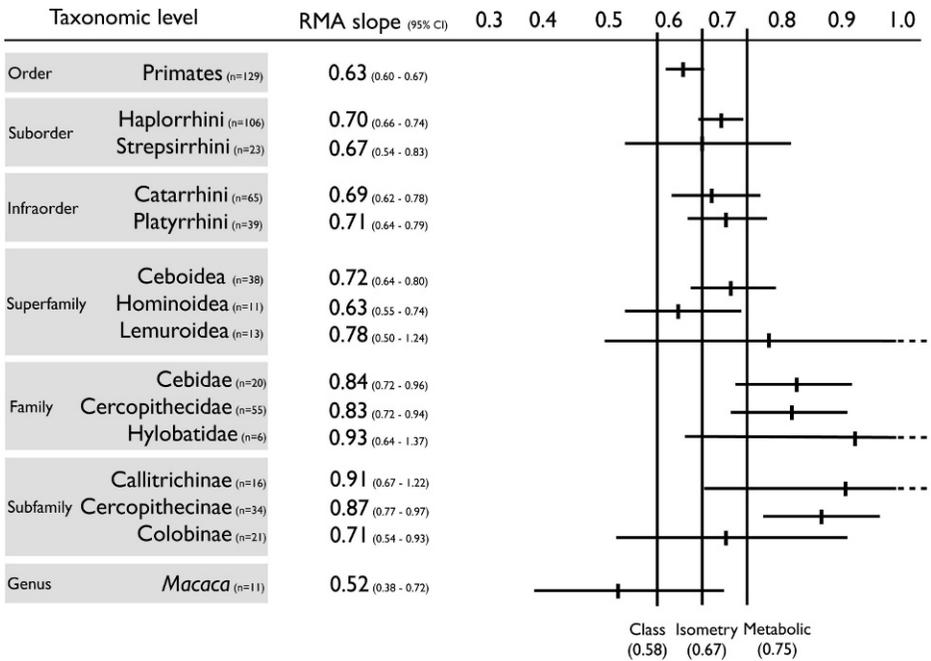

FIGURE 4. The Hierarchical TLE in Primates. All scaling coefficients are RMA slopes calculated using species means. The analysis is of ln(mandibular PCOA) regressed on ln(body mass).

TABLE 2. Mathematical TLE in Mammalia. Regression parameters are reported for four different mathematical levels of data aggregation for the entire class. See Appendix 5 (online) for additional examples of the Mathematical TLE.

Class	Taxonomic level of data aggregation	Regression parameter	Maxillary PCOA	Mandibular PCOA
Mammalia	Species means	n	604	656
		RMA slope	0.56 (0.55–0.57)	0.58 (0.57–0.59)
		RMA intercept	0.52	0.13
		OLS slope	0.54 (0.53–0.55)	0.56 (0.55–0.57)
		OLS intercept	0.68	0.23
		SEE	0.01	0.01
		r^2	0.92	0.95
	Genus means	n	370	370
		RMA slope	0.58 (0.57–0.59)	0.59 (0.58–0.60)
		RMA intercept	0.42	0.07
		OLS slope	0.56 (0.55–0.57)	0.58 (0.56–0.59)
		OLS intercept	0.54	0.15
		SEE	0.01	0.01
		r^2	0.94	0.96
	Family means	n	75	88
		RMA slope	0.56 (0.46–0.68)	0.59 (0.56–0.61)
		RMA intercept	0.57	0.09
		OLS slope	0.55 (0.52–0.59)	0.58 (0.55–0.60)
		OLS intercept	0.62	0.17
		SEE	0.02	0.01
		r^2	0.93	0.96
	Ordinal means	n	14	14
		RMA slope	0.59 (0.53–0.65)	0.60 (0.55–0.65)
		RMA intercept	0.54	0.13
		OLS slope	0.58 (0.52–0.64)	0.59 (0.54–0.65)
		OLS intercept	0.59	0.17
		SEE	0.03	0.02
		r^2	0.97	0.98

rejected in favor of negative allometry. Thus, a Mathematical TLE does not appear to be at play when the scaling relationship is analyzed across the entire class.

A similar investigation was done for the most speciose orders in the analysis; partial results are illustrated in Figure 6 (full regression parameters for six orders are reported in Appendix 5). In Artiodactyla, the hypothesis of metabolic scaling is rejected in favor of one of isometry when the regression analysis uses individuals or species or family means. Using genus means, both isometry and metabolic scaling are rejected in favor of negative allometry.

Similarly, in Carnivora, both hypotheses are rejected in favor of negative allometry using individuals or species or family means, but isometry cannot be rejected using genus means.

In Primates, interestingly, metabolic scaling can always be rejected, and isometry is similarly rejected except when using species or family means. Gould (1975) used individuals in his analyses, but most subsequent studies used species means, so our results may explain some of the disagreement in the conclusions reached by previous studies regarding this scaling relationship.

Finally, there is no Mathematical TLE present in Rodentia at all—analyses using each aggregation support a hypothesis of isometry and reject one of metabolic scaling.

The pattern of the MTLE is not consistent across these orders—the slope decreases consistently as the taxonomic level of data aggregation increases in Artiodactyla and Rodentia, but not in Primates or Carnivora. However, an MTLE is present in all but Rodentia, because choosing a particular level at which to aggregate the data may allow one to accept or reject a scaling hypothesis that
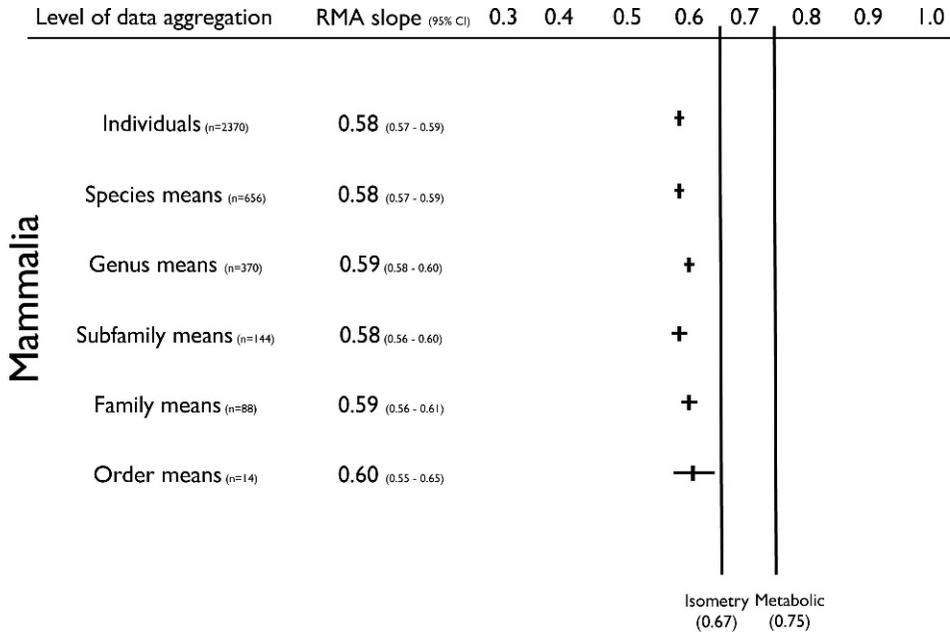
FIGURE 5.   The Mathematical TLE in Mammalia. Each scaling coefficient is calculated using a different mathematical aggregation of the data (from individuals up to and including the means of each order). The analysis is an RMA regression of ln(mandibular PCOA) on ln(body mass).

choosing a different level of data aggregation would not.

Discussion

The relationship between postcanine occlusal area and body mass has long been the subject of investigation for two main reasons: (1) the dentition is responsible for breaking down the food that fuels growth and (2) teeth are the most durable part of the skeleton and as such, they are the most frequently preserved elements in the fossil record. Previous studies have failed to reach a consensus on the nature of the relationship between these two variables across taxonomically and biologically diverse groups of mammals. Our results show that when the relationship is analyzed using species means across Mammalia, occlusal surface area scales with negative allometry to body mass (Mammalia$_m$ = 0.59 ± 0.01). This differs both from numerous previous studies (see Appendix 1) and from a sentiment present in the literature that the occlusal surface available for masticating food can be modeled sufficiently by resorting either to a simple geometric model of increasing body mass or to proportional

increases in metabolic demands that accompany increases in body mass.

Our results also suggest that previous studies have come to different conclusions regarding the scaling of PCOA to body mass for at least two reasons. First, the choice of taxonomic (i.e., hierarchical) level at which analyses are performed has an important effect on accepting or rejecting hypotheses of expected scaling coefficients. As stated above, the classwide analysis reveals a negatively allometric relationship, allowing us to reject both a model of geometric similarity and one of functional equivalence. However, it is clear that an analysis at the ordinal level fails to reject a hypothesis of isometry in several cases (see Fig. 3), suggesting that the presence of an HTLE may account for the varying interpretations present in the literature. None of the orders scale even close to a model of metabolic scaling, as Gould (1975) originally suggested; rather, slopes for all orders fall at or below the level of isometry. In only three cases (Afrosoricidae, $n = 8$; Perissodactyla, $n = 13$; and Scandentia, $n = 15$) can metabolic scaling be considered, as the 95% confidence intervals
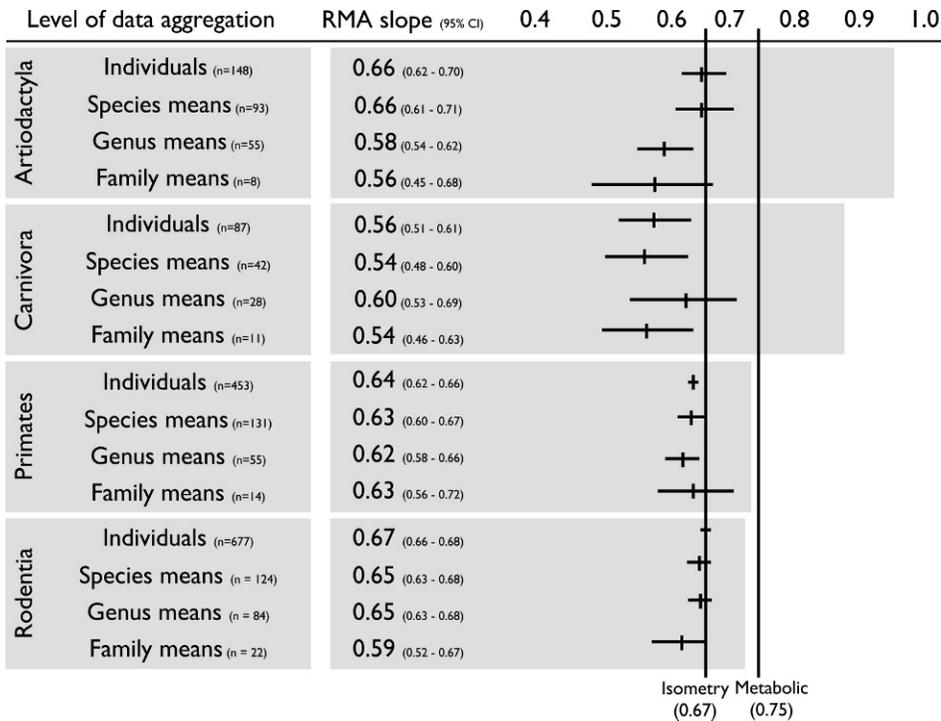
FIGURE 6.   The Mathematical TLE within four of the most speciose orders included in the study.

are wide enough to include a slope of 0.75. However, this may a statistical artifact of relatively small sample size (i.e., few species included in the regression analysis) rather than suggesting some underlying biological role of metabolic scaling for regulating post-canine occlusal area.

We also examined the effect an HTLE has within a single order, Primates. At the ordinal level we are unable to reject a hypothesis of isometry, but a hypothesis of metabolic scaling can be rejected outright (Primates$_m$ = 0.63 ± 0.03). As taxonomic level decreases, the slope values tend to increase, so that metabolic scaling cannot be rejected when only infraorders or families are examined. Within the subfamily Cercopithecinae, in fact, both hypotheses can again be rejected, but in this case it is because the scaling coefficient is greater than both hypothesized slopes (Cercopithecinae$_m$ = 0.87 ± 0.10).

Second, the choice of how to mathematically aggregate data also plays an important role in understanding the lack of consistency in the scaling literature. Although it is not common to use large aggregations of data such as family means when performing regression analyses, previous studies have used individuals, species means, or genus means as the basis of analysis. The purported scaling relationship between PCOA and body mass can change significantly depending on this choice—in some cases, isometry is rejected and in others it cannot be.

Although both hypotheses are rejected by all analyses using any mathematical aggregation when the entire class is analyzed, problems arise when looking just within Primates, for example. Using individuals or genus means as the basis of analysis, both hypotheses of geometric similarity and functional equivalence can be rejected (Primate Individuals$_m$ = 0.64 ± 0.02; Primate Genus$_m$ = 0.62 ± 0.04), but when using species or family means, isometry cannot be rejected (Primate Species$_m$ = 0.63 ± 0.04; Primate Family$_m$ = 0.63 ± 0.08). Because Gould (1975) used individuals as the basis of his analyses, and many later studies testing his hypothesis used species means, the presence of a Mathematical TLE may explain why conflicting conclusions of the universal scaling

nature of occlusal area and body mass were reached.

Given the caveats outlined above, it is evident that great care must be taken by paleontologists interested in retrodicting the body mass of fossil organisms from dental remains. Predictions from regression equations that are based on reference populations analyzed at different taxonomic (i.e., hierarchical) levels may differ given the fact that the Hierarchical TLE has potentially significant effects on this scaling relationship. Additionally, predictions can be biased if they are based on regression equations using different mathematical aggregates of data. Our results indicate that both the hierarchical level of analysis and the mathematical organization of data can have a measurable effect on the presumed relationship between any two biological variables.

Another source of disagreement between previous studies is the lack of phylogenetic control, that is, the possibility that phylogenetic effects may influence our interpretation of this one particular biological relationship (Cheverud et al. 1985; Smith and Cheverud 2002). Phylogenetically independent contrasts (Felsenstein 1985) is a method frequently used to control for phylogenetic relatedness, and has been used by at least one group investigating this particular scaling relationship (Vinyard and Hanna 2005). The method of phylogenetic independent contrasts attempts to control for the fact that related species are not independent data points in any interspecific allometric analysis, and treating them as such thus violates one of the fundamental assumptions of any statistical analysis (Garland 1992; Garland et al. 1999; Garland and Ives 2000). Other methods for controlling for the effect of phylogeny include phylogenetic autocorrelation, generalized least-squares, and Monte Carlo computer simulations (Garland et al. 2005).

Because this study is an interspecific allometric analysis, it may seem to beckon the application of some method that accounts for the phylogenetic non-independence of data. None of the available methods were used in this study, however, for the following reason. We focused explicitly on how two potentially confounding factors, known collectively as taxon-level effects, may have affected previous interpretations of the relationship between these two important biological parameters. Removing the effect of phylogeny (of which a taxonomy is a reflection) from a study designed to test for the bias of taxonomy is counterproductive.

Conclusion

In 1975 Gould proposed a metabolic scaling coefficient to define the relationship between PCOA and body mass, providing a statistic to paleontologists needing a method of determining body mass of fossil organisms from teeth. This study found that Gould's ''universal'' scaling relationship is not, in fact, universal and should be invoked only with great caution. Differences in how researchers organize (HTLE) and analyze (MTLE) their data when examining bivariate relationships, such as the one between PCOA and body mass, can result in radically different conclusions. In order to accurately compare results of different studies, or to apply lessons of extant animals to extinct organisms, biologists must pay careful attention to the scale at which scaling analyses are performed.

Acknowledgments

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