

Dental allometry in mammals: a retrospective

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Kleiber suggested that mammalian metabolic rate scales with body mass at $M_b^{3/4}$. Bigger animals use relatively less energy. Gould reasoned that teeth should scale the same way given caloric need. In many cases though, cheek tooth occlusal area increases isometrically, one-to-one with body mass (i.e., $M_b^{2/3}$). Fortelius reconciled the discrepancy by noting that larger mammals also chew slower, so a given amount of food per bite but few bites per unit time could still mean metabolic scaling of energy consumed in a day. Here I revisit dental allometry, referencing new studies of tooth size, muscle mass, chewing rate, and food fracture scaling. Early predictions have held up reasonably well through the decades, though many more factors involved have emerged. These can be difficult to parse for interpreting deviations from expected tooth size in fossil mammals, including early hominins. Still, relative tooth size variation can help us generate dietary hypotheses.

Background

Early in the 20th century, Kleiber (1947) observed that while larger mammals need more energy to power bigger bodies, that need does not increase one-to-one with body size. He found that metabolic rate scales to the 3/4th power of an animal's mass ($M_b^{0.75}$). Put another way, larger mammals have lower mass-specific metabolic rates. For example, an elephant that weighs half a million times as much as a mouse burns only about nineteen thousand times the energy. The traditional explanation for this is that smaller mammals are less efficient endotherms than are bigger ones. The idea behind this is that because their surface areas are large relative to their volumes, they lose heat more quickly and need to burn more calories per gram of body weight.

Before we discuss scaling in any detail though, we need to define some terms. We call

things that scale one-to-one with body size *isometric*. If something is larger than expected given the size of an animal, it is *positively allometric*. And if it's smaller than expected, it is *negatively allometric*. But in considering these relationships, we need to remember that volume has three dimensions, area has two, and length has one. When considering teeth, for example, when crown volume increases one-to-one with body mass, it should scale at M_b^1 , whereas occlusal surface area and length should scale at 2/3rds power of mass, or $M_b^{0.67}$, and 1/3rds power of mass, or $M_b^{0.33}$, respectively. Dental researchers refer to each of these as isometry.

Kleiber's rule led Pilbeam and Gould (1974) to speculate that postcanine occlusal area would also scale with body mass at about $M_b^{0.75}$. The basic idea was that chewing surface should match the amount of food a mammal requires to meet its metabolic needs. Again, because area

and mass are measured in two and three dimensions respectively, simply enlarging an animal would lead to postcanine chewing surface scaling at $M_b^{0.67}$, not $M_b^{0.75}$. If Pilbeam and Gould were right then, a mouse enlarged to the size of an elephant should have tooth area larger than expected if they scaled one-to-one. It should be positively allometric.

Gould (1975) did find some support for this idea. Tooth area scales with positive allometry when compared with skull length in hystricomorph rodents, and slopes tend this way in some other taxa, such as pigs and deer (tooth area was compared to femur length for the cervids); though isometry could not be excluded in statistical analyses. Gould (1975) viewed $M_b^{0.75}$ metabolic scaling as “‘a criterion of subtraction’, or null hypothesis for tests of adaptive differences in lifestyle”.

Kay (1975), on the other hand, focused on the effects of those adaptive differences, especially for primates. He reasoned that we cannot consider the relationship between tooth size and body size without considering diet in the equation. Larger primates for example, tend to have different diets than smaller ones. They often eat lower quality leaves requiring more chewing and, for many taxa, this means larger occlusal area independent of body size. Further, when Kay grouped primates by diet, their postcanine tooth areas, and especially molar crushing surfaces, tended to scale isometrically (not significantly different from $M_b^{0.67}$). He viewed positive allometry in occlusal area as basically an effect of diet allometry; larger species need relatively larger teeth to process more low-quality food. And indeed, many studies that followed in the late 1970s and early 1980s found isometry of cheek tooth area (in whole or parts), both for primates (Corruccini & Henderson 1978, Goldstein 1978, Kay 1978, Lucas 1980) and other mammals (e.g., Creighton 1980, Gingerich *et al* 1982, Prothero & Sereno 1982, Fortelius 1985), to be a better rule-of-thumb, albeit with a few exceptions (*see below*).

So what about Kleiber’s rule? If larger mammals have lower mass-specific metabolic rates, they should require relatively fewer calories and relatively less food for a given body size. Why

would their cheek tooth surface area scale isometrically, even within a diet category, if their energy requirements are negatively allometric?

Fortelius (1985, 1988, 1990a, 1990b) proposed a simple yet elegant solution to this question and the apparent paradox between theory (metabolic scaling) and observation (dental isometry). He argued that there is no paradox if we consider chewing rate in the equation. Feeding is about accessing energy to fuel the body. The amount of food entering the gut in a fixed period of time is a function both of volume per bite (which should be roughly isometric to body mass, mouth volume, and tooth size) and chewing rate. If tooth size and chewing rate both scaled isometrically, larger animals would get more calories per unit time than they need. But as Fortelius noted, physiological rates (things like heartbeat, breathing, peristaltic gut beat) tend to scale with negative allometry, at about $M_b^{-0.25}$ (*see* Peters 1986). This has been termed physiological time allometry (Turvey *et al.* 1988). And indeed, Fortelius’ observations of ungulates at the Helsinki Zoo suggested to him a similar scaling exponent for chewing cycle duration — at least one that included $M_b^{0.25}$ within 95% confidence intervals. Note that rate and duration are inversely proportional, hence an exponent of -0.25 for the former and 0.25 for the latter. By simple arithmetic, if chewing rate also scales at -0.25 , and processed volume of food per chew scales with body mass at 1.00 , then volume processed per unit time should scale with the exponent $1.00 - 0.25 = 0.75$. In other words, the volume of food entering the gut each day should scale at $M_b^{0.75}$, the same rate at which metabolism scales. Problem solved.

The test of time

It has been four decades since Pilbeam and Gould first proposed metabolic scaling for cheek tooth area, and nearly three since Fortelius offered a solution to the apparent discrepancy between theory and observation. These ideas were originally developed with very limited data to back them up and lots of assumptions behind them. This led to qualifying statements like, “the

case is clearly not proved,” (Gould 1975) and, “certainly the hypothesis cannot at present be rejected” (Fortelius 1985).

More data have been collected, preferred methods of analysis have changed, and new theoretical approaches have emerged since Pilbeam and Gould, Kay, and Fortelius first formulated their seminal hypotheses on dental allometry. We still do not have all the answers, but can certainly look back and profit from contemplating how those formative ideas have stood the test of time.

Dental allometry

Postcanine occlusal areas, defined as the products of lengths and breadths of cheek tooth crowns, are quick and easy to measure. In most cases, all you need is a pair of calipers and a keen eye. It should come as no surprise then that the literature has become rife with such data. And this has led to a torrent of studies set on evaluating hypotheses about relationships between tooth size and body size in mammals. Unfortunately though, there has been no consensus on the results. By Copes and Schwartz’s (2010) reckoning, as of 2010, 55 studies reported positive allometry, 64 isometry, and 45 negative allometry. This at first glance suggests that there may be no consistent relationship between tooth size and body size in mammals. It may, however, be in part an artifact of inconsistent methods of analysis between studies.

Copes and Schwartz (2010) compiled dental allometry data for nearly 700 species of mammals spanning 14 orders and found that tooth area scaling relationships vary wildly depending on taxonomic level of the analysis and mathematical methods used to organize the data. For example, lumping species from different families together gives a different scaling coefficient than those obtained when families are considered separately. Slope tends to increase, at least within primates, at lower taxonomic levels. As Fortelius noted back in 1985, “the species of a genus, the genera of a family or the families of an order often give different lines, and it is not always obvious which one is the most relevant to the problem at hand”. Cope and Schwartz (2010) also found results to

vary depending upon whether data represent individuals, species means, genus means, or family means. When looking at primates for example, using individuals or genera as data points indicates that tooth area is negatively allometric, but isometry cannot be rejected when using species or family means.

Then there is the issue of how best to fit a curve to the data. Allometric studies typically begin with log-transformation to make the variance independent of the mean and the relationship between the two variables (in this case, tooth area and body mass) better approximate a straight line for ease of analysis. Some have used an ordinary least squares regression (OLS) to fit the line describing the relationship between $\log(\text{tooth area})$ and $\log(\text{body mass})$. Many do not consider this a great approach for dental allometry though, because it assumes, incorrectly, that body mass is measured without error (*see* Sokal & Rohlf 2012). Others use major axis (MA) and reduced-major axis (RMA) approaches, which work better when the variables show some random variation. Without getting into the math, the various approaches differ in how they minimize the offset between a data point in the scatter and the resultant regression line. Reduced major axis seems best in this case because variation in tooth area and body mass are not expected to be partitioned asymmetrically (*see* Smith 2009). The upshot of this though is that different methods can yield different outcomes. RMA often results in steeper slopes than OLS (*see*, for example, Copes and Schwartz’s (2010) results) depending on data symmetry and measurement error. So, different line-fitting algorithms can suggest different relationships between tooth area and body size.

In the end, Copes and Schwartz (2010) found little support for isometry and less for positive allometry when considering species means across the class Mammalia (their class-level scaling factor came out to 0.59). On the other hand, the relationship between occlusal area and body mass is more nearly isometric when species are considered order-by-order. In only a few cases are the confidence intervals of the slopes for individual orders so wide that positive allometry cannot be excluded. In sum, using RMA on

the ordinal level or below, isometry still seems to be the rule — or at least is closer to the rule than is positive allometry.

Chewing rate allometry

So, how about Fortelius' (1985, 1988, 1990a, 1990b) notion that tooth area (and volume of food consumed per chew) scales isometrically because slower chewing (less food processed per unit time) in larger mammals matches a metabolic requirement for relatively less energy? This hypothesis depends on chew cycle duration scaling at $M_b^{0.25}$. The data were very limited when Fortelius proposed this and, in fact, his MA regression slopes were uniformly below 0.25 (though 95% confidence limits included 0.25 in three of five cases). Druzinsky (1993) later analyzed chew rate data for a larger sample (including representatives of 26 mammalian species), and found that duration was actually proportional to body mass to the 0.13 power — significantly lower than 0.25. And Gerstner and Gerstein's (2008) even larger sample (132 species) yielded a scaling exponent of about 0.19 for the order and 0.14 when an independent contrasts method was used to remove clumping effects of closely-related species. In neither case did 95% confidence limits of the slope include 0.25. Regardless, it is clear that chewing rate does scale with negative allometry, and should slow down energy assimilation as body mass increases, even if not quite as much as Fortelius initially predicted.

Occlusal stress and fracture allometry

Early models of dental allometry also assumed that chewing stress, force per unit area, is more-or-less independent of body size. The idea was that stress acting on a given food item should not change with body size because larger animals have larger chewing muscles matched to their larger teeth. Fortelius (1988) reasoned that because muscle force is proportional to cross-sectional area at $M_b^{0.67}$, the same scaling coefficient as occlusal area, bite stress should be independent of body mass, at least if jaw muscles scale isometrically, as the limited data available

at the time (Cachel 1984) suggested (though *see* Clauss *et al.* 2008 for data on ruminants). As the theory went, bigger and smaller animals should be about equally able to fracture a mouthful of food with a given critical breaking stress.

But as Lucas (2004) points out, larger bits of a given food should be weaker than smaller ones to start with. And if food item size is matched to mouth size, we should not ignore fracture scaling. According to theory, it takes $\lambda^{1.5}$ times the force to fracture an item λ times longer in a given dimension than a smaller one, all else equal. For example, an 8 cm³ (2³) cube should require less than three times (2^{1.5}) the force to fracture as would a 1 cm³ cube of the same food type (Perry & Wall 2008). This means that larger animals should need relatively smaller adductors (jaw closing muscles), with force (and muscle cross-sectional area) scaling to the 0.5 power of mass rather than the 0.67 expected for isometry. But just as Cachel (1984) suggested earlier, Perry and Wall (2008) found that adductor physiological cross-sectional area, at least in prosimian primates, scales isometrically. So, not only is chewing rate a little faster than predicted for larger mammals by a physiological rate allometry model ($M_b^{-0.25}$), muscle cross-sectional area (and perhaps occlusal force) is a little greater.

Biology is a messy business

It is no surprise that the numbers are off a little. Relationships between teeth, food, and body size are really complex. There are so many variables that play a role in how food is processed and energy is assimilated and spent that parsing all the bits and pieces can be a formidable task. If the goal is to get an idea of how big an animal was in the past from a fossil tooth, "for many purposes this has been, and still is, enough" (Fortelius 1990a). If, on the other hand, the objective is an understanding how diet and food processing affect the relationship between tooth size and body mass, there remains a lot to be done. And many of us would like to take this even further if possible, and use deviation from expected tooth size given its predicted relationship with body size to retrodict the diet of a fossil species. Now *that* is a real challenge.

If the mass of a species with a mean molar tooth area of 100 mm² is doubled, enlarging all parts in equal measure, tooth area should grow to about 159 mm². If the new teeth were significantly larger or smaller, there should be a good reason. Diet is the usual suspect. Conventional wisdom matches occlusal area with volume of food; more requires a larger platform. Larger animals burn absolutely (though not relatively) more energy and therefore need absolutely more food. As the argument goes, bigger mammals should have teeth larger in proportion to their energy requirement, which in turn depends on body mass. If Gould (1975) had been right, tooth area in our hypothetical example should have scaled with positive allometry according to Kleiber's Law, and be 168 mm². This is not a huge difference. But, as we have seen, cheek tooth area has been suggested to scale with positive allometry, isometry, or even negative allometry depending on method of analysis and taxa considered. Why? Biology is a messy business.

Slop in the system

Slop in the system poses important limitations to determining relationships between occlusal area and body mass. It could be simple measurement error in either the dependent or independent variable (or both); but it is often a function of inherent variation among individuals within a species, or the proxy used to characterize those variables.

Researchers often consider tooth area or body mass values averaged over a sample, which may or may not be representative of a species. Body mass and tooth area can vary greatly among individuals, especially between males and females. Sometimes data for the sexes are considered separately, sometimes not. Tooth area can also vary with wear depending on approximal attrition and tapering of the crown. And body mass, if measured by weight, can fluctuate dramatically with food availability, reflecting season or location of sampling, age, social status, and other attributes (e.g., Gerstner & Gerstein 2008, Copes & Schwartz 2010). Assigning confidence limits to our estimates of species means would help, but the confidence intervals of species-mean-based regression lines are often already so wide

that it is impossible to choose between competing hypotheses.

Then there is the issue of the best proxies for tooth area and body mass. Tooth area is typically measured as the product of the maximum buccolingual and anteroposterior diameter of a crown. These are sometimes considered separately for a given tooth type, and other times summed for some or all of the cheek teeth. Yes, these values are convenient and easy to measure. But are they the best proxies for functional area? Kay (1975) for example, also considered M_2 crushing area in his study. Also, teeth are not rectangular — their projected or planimetric areas vary dramatically with shape of the occlusal plane. Some are more-or-less oval, but others have very uneven margins. Some have reentrant folds (think rodents), or infundibula (think ruminants). More importantly, teeth are three-dimensional. Functional surface area is often *much* greater than the product of buccolingual and anteroposterior diameters, depending on vertical relief of the occlusal surface and the complexity of features on the crown (*see* Ungar 2010 for examples). A crenulated surface, or one with very steep lophs, crests, or cusps, has a much larger functional area (think elephant or capybara) than does a flat one. And, as already mentioned, usable tooth area can change over time, both as features are obliterated by wear and as crown edges are truncated by approximal attrition.

Estimates of body size are even more problematic. Is weight the best proxy? Remember that this fluctuates with both Nature and Nurture. And most museum specimens are skeletonized, so it is impossible to measure anyway. Some have chosen live-weight species averages, but others use alternative proxies, such as skull length, orbit size, femur length or head diameter, and more. Each of these can add error to size estimates, and may or may not themselves scale isometrically. This can be a problem if the goal is to understand how teeth scale with body size. Fossil body size estimates are especially challenging. You cannot use teeth if the goal is to understand relationships between tooth size and body size; but that is often all there is in the fossil record. Skulls and postcranial elements can be limited to scraps, with small samples of fragmented specimens adding error to estimates.

How much can we make of residuals from a regression line when dependent variable (e.g., tooth area) values are measured much more reliably than independent (e.g., body mass) ones? Garbage in, garbage out.

Food varies in chemical and material properties

Food choice also throws a wrench in the works. As Kay (1975) noted, it's best to control for food type when considering relationships between tooth size and body mass. Some foods, such as colonial insects and fleshy fruits, are energy-rich with easily digestible proteins or simple carbohydrates requiring minimal processing with the teeth. These generally don't require large chewing platforms. Other foods, such as grass blades and dicot leaves, are tough and laden with difficult-to-digest cellulose. These may require a lot more chewing to burst cell walls and liberate their contents and to expose enough surface for digestive enzymes to act on. Food intake rates and digestibility can play an important role how food volume scales with body mass (Müller *et al.* 2012). Yet other foods have composite structures. They are neither homogenous nor linearly elastic — two assumptions often invoked to make fracture mechanics models simple enough for us to deal with (*see* Perry & Wall 2008).

External properties of foods, such as size, shape, and stickiness should be considered too when thinking about relationships between tooth size and diet (Lucas 2004). For example, Lucas (2004) argues that small food particles should select for large teeth to increase the probability of fracture during a given chew cycle. Thin sheets or rods (as opposed to thick blocks or spheres) might also select for larger teeth, as these too have low volumes. Also, sticky foods should not spread well along the tooth row, perhaps selecting for short, wide dental arches. Those that do not form a bolus should spread more evenly, making them better suited to fracture by a long, narrow row.

The physical properties of foods can be an impediment to assimilation, but animals are really concerned about energy yields of given food items, which can vary a lot. Since larger

mammals require less energy input per day per unit body mass, perhaps it's not surprising that many consume plentiful, lower quality foods with lower energy yields. This may contribute to the fact that mammalian tooth area often scales isometrically despite Kleiber's rule. Larger mammals may need bigger teeth to process greater quantities of mechanically challenging, low quality food. But this, of course, is an oversimplification. Remember that, for example, absolutely larger foods are also easier to break, all else equal (Lucas 2004).

Mammals vary in how they extract energy from food

Even if we could work out a scaling relationship between tooth size and body mass and control for food mechanical and chemical properties, different mammals take different approaches to extracting energy from food. This can complicate our interpretations of how diet affects relative tooth size. As Aristotle wrote nearly two and a half millennia ago in *De Partibus Animalium*, "teeth have one invariable office, namely the reduction of food". Mammals chew to fracture food. Teeth rupture protective casings, such as plant cell walls and insect exoskeletons, to release nutrients that would otherwise pass through the gut undigested. And fragmentation increases the exposed surface area for digestive enzymes to act on, which in turn can lead to more complete assimilation of energy stored in food.

So many factors affect the amount of energy a mammal squeezes from a given food item. It makes the head spin (*see* Lucas 1980). On a gross level, we must consider not only rate of chewing (Fortelius 1985, 1988, 1990a, 1990b), but also time spent, or total number of chews each day, which can range up into the tens of thousands (e.g., Kaske *et al.* 2002, Sanson 2006). We can also consider how muscle activity pattern and leverage modulate occlusal force during a given chewing cycle (e.g., Perry & Wall 2008). Cud chewing and cecotrophy affect digestive efficiency too, as do factors influencing chemical and mechanical breakdown of food after it leaves the mouth for the last time. Digestive enzymes and gut biota (types and densities)

play a role, as does gut size, shape, structure, and passage rate.

Then there is the shape of the tooth itself. Some teeth have internal structures evolved to resist wear and breakage, allowing them to tolerate more stress and abrasive conditions. Teeth also differ in the relative contributions of shearing, crushing, and grinding areas, the length and sharpness of crests, the height of cusps, extents of fissures and basins, and many other attributes that can be tied to function (*see* Ungar 2010 for review). All of these things can play an important role in efficiency of food fracture. Parsing the effects of each on energy assimilation so that we can dissect relationships between relative tooth size, diet, and metabolism in a broad spectrum of mammals is a very tall order.

Mammals vary in their energy requirements

Much of the discussion of relationships between teeth, diet, and body mass hinge on Kleiber's Law. But the relationship between metabolic rate and body size is also unclear. Recent studies have challenged both Kleiber's scaling exponent value (e.g., White & Seymour 2003) and the universality of its applicability (e.g., Agutter & Wheatley 2004, Bokma 2004). Is the "real" exponent 0.67, 0.75, or somewhere in between (e.g., Müller *et al.* 2012)? Some have even questioned whether a single exponent can sufficiently describe the relationship between metabolic rate and mass — the best-fit curve may actually be convex, even on a logarithmic scale (Kolokotronis *et al.* 2010). And even this seems to vary, depending on the taxa selected for study (Müller *et al.* 2012).

It turns out that metabolic rate varies considerably with phylogeny, environment, and behavior (e.g., *see* Lovegrove 2000, McNab 2008, Sieg *et al.* 2009). As Glazier (2006: 325) aptly wrote, metabolic scaling is "an evolutionarily malleable trait that responds to ecological circumstances". Without an understanding of how energy budget varies with circumstances and inheritance, it is very difficult to talk about caloric needs, let alone the role of occlusal area in meeting those needs.

Pushing the limits of knowability

With all these elements at play (e.g., variation in food properties and how animals extract energy from them, varying metabolic needs, etc.), is there any hope of uncovering a universal allometric relationship between tooth size and body mass in the mammals? With all the slop in the system and low confidence (or at least broad confidence limits) in our results, it is remarkable that any seemingly reasonable dental allometry hypothesis can be rejected at all. To go that extra step and retrodict diet of a fossil species using deviation of cheek tooth area from an inferred allometric line may be pushing the limits of knowability. Our ability to understand natural phenomena depends on the number of factors that affect those phenomena; and as we identify more variables involved in relationships between tooth size and body mass, we begin to realize how tenuous our inferences are. We seemed to know more four decades ago than we do today. Dental allometry was a much simpler prospect.

Yes, mammalian tooth area *does* tend toward isometry when considered order-by-order. And this may give us hope for untangling general patterns, albeit as "loose descriptions rather than powerful constraints" (Fortelius 1990b). This does not mean however, that we can draw conclusions about relative tooth size from a single data point, such as one fossil species, given our current grasp on everything involved. As Gomory (1995) wrote, "the level of detail is what separates the delusion of the gambler from the wealth of the casino owner. The gambler attempts to predict the individual and unpredictable spins of the roulette wheel; the owner concerns himself with the quite predictable average outcome".

I would argue that the most important thing we have learned about dental allometry over the past forty years is the more we discover, the more complicated the whole thing appears and the farther we appear to get from understanding relationships between tooth size, body size, and diet. As Rescher (1999) noted in more general terms, "in a complex world, the natural dynamics of rational inquiry will inevitably exhibit a tropism toward increasing complexity". This is certainly true for mammalian dental allometry.

We can understand the frustration that Sisyphus felt watching the boulder roll back down the hill again and again. Let's take another look at the primates.

The primates

Pilbeam and Gould's (1974) and Kay's (1975) original studies focused largely on higher primates and the implications of relative tooth size for inferring diets of early hominins. We can compare, for example, living folivores and frugivores. Leaves are tough, thin sheets requiring thorough chewing. So, all else equal, leaf-eating primates should have larger teeth than soft-fruit eaters. And many primate folivores do in fact have larger teeth relative to body mass than closely-related frugivores (Kay 1977, Vinyard & Hanna 2005). But not all. Old World monkeys show the opposite pattern — folivorous colobines have smaller molars than frugivorous cercopithecines (Kay 1977, Lucas 1980). And there are other outstanding issues. Why do insectivorous primates in many cases have larger molars than frugivores (Strait 1993)? And why *within* many primate species, especially sexually dimorphic ones, do females have relatively larger cheek teeth than males (Harvey *et al.* 1978)?

We cannot use a given form (e.g., relative occlusal area) to retrodict a given function (e.g., diet) for a fossil if the form-function relationship lacks consistency in analogous living species (Kay & Cartmill 1977). This has led me (Ungar 2011, 2012) to argue that we are better off looking at other lines of evidence to reconstruct the diets of early hominins. There has simply been too much we do not understand. That said, we may now have an answer, at least, for why Old World monkeys buck the trend seen in other higher primates. Colobines usually have shorter faces, perhaps related to leverage for the chewing muscles, than cercopithecines, whose longer jaws allow wider gapes for display and use of their long canines (*see* Scott 2011 for review). A longer face also means room in the jaw for bigger teeth. And when cheek tooth area is scaled against face length rather than body mass, folivorous colobines do indeed have larger post-

canines than cercopithecines (Scott 2011). Perhaps, as Vinyard and Hanna (2005) suggested, there is a modular developmental link between tooth size and jaw length. Indeed, Workman *et al.* (2002) found for mice that many quantitative trait loci affecting tooth size and jaw shape are the same. If nothing else, this example drives home the point that there are many variables to be accounted for if we are to use dental allometry to infer diets of fossil taxa. Early hominins provide a case in point.

Early hominins

Relative cheek tooth size has been considered a very important trait when comparing Plio-Pleistocene hominins. Marked differences between species and genera have often been invoked as evidence for distinct adaptive zones critical for understanding hominin evolution (Wood & Collard 1999, Leakey *et al.* 1964, Leakey *et al.* 2001). And researchers have been thinking about functional implications of relative tooth size ever since Robinson's (1954) benchmark comparison of the South African australopiths, *Australopithecus* and *Paranthropus*. Robinson suggested that the large, flat premolars and molars of *Paranthropus* were specialized for crushing and grinding tough vegetation whereas smaller back teeth and larger front ones in *Australopithecus* evinced a broader, "more clearly omnivorous diet, which may have included a fair proportion of flesh". Robinson also noted that "*Telanthropus*" (*Homo erectus*) has even smaller cheek teeth, and more human-like dental proportions.

Groves and Napier (1968) quantified Robinson's observations through incisor-to-molar row-length ratios, and compared results with those of living apes. For the extant species, the more folivorous gorilla had the lowest ratio, the frugivorous chimpanzee had the highest, and the orangutan, intermediate in diet, was also intermediate in incisor-to-molar size ratio. This made sense: big incisors for husking fruit, big molars for processing leaves. While early *Homo* fell in with the chimpanzees and orangutans, *Australopithecus* had a gorilla-like incisor-molar index, and *Paranthropus* had an even smaller incisor-to-molar size ratio. Groves and Napier (1968)

considered these results consistent with Robinson's interpretation of diet differences among the early hominins. Jolly (1970) took this one step further, and suggested that *Paranthropus* was specialized for small, tough seeds, whereas *Australopithecus* and especially early *Homo*, consumed more meat and a variety of plant parts. He wrote, "the trend to back-tooth dominance has been partially reversed".

It was in this backdrop that Pilbeam and Gould (1974) applied their model of metabolic scaling of cheek tooth area to these early hominins. They proposed that while early *Homo* showed a different pattern, *Australopithecus* and *Paranthropus* were actually "scaled variants of the 'same' animal". By their calculations, postcanine tooth area in *Australopithecus* and *Paranthropus* scaled with positive allometry, consistent with metabolic scaling; and tooth size variation afforded "no evidence for differences in diets or behavior". This challenge to Robinson's dietary hypothesis was countered by Kay (1975), who argued that because primates within diet categories tend to have occlusal areas that scale isometrically, positive allometry in early hominins *does* mean variation in diet. He suggested that, if Pilbeam and Gould's body mass estimates were right, relatively larger teeth in *Paranthropus* suggest it "probably had more fiber in its diet", consistent with Robinson's initial hypothesis (see also Goldstein *et al.* 1978, Wood & Stack 1980).

This didn't end the debate, though. Walker (1981) and Demes and Creel (1988) suggested that bite force per unit area may have been the same across the australopiths because *Paranthropus* had both larger cheek teeth and larger chewing muscles (judging from attachment sites) than *Australopithecus*. According to Walker and Demes and Creel, higher force spread over a larger area, suggested equivalent stress and perhaps a "more of the same" type diet. But as Kay (1985) reiterated with a regression of tooth area on body weight, based on a larger sample and newer weight estimates (McHenry 1984), *Paranthropus* (at least *P. boisei*) still had relatively larger cheek teeth than *Australopithecus*, and *Australopithecus* had larger ones than early *Homo*. And these differences, Kay argued, are still best explained by differences in diet. We can

add to this the fact the australopiths probably had overlapping if not similar average body weights (Jungers 1988, McHenry & Coffing 2000), and the whole allometry issue might become moot. If so, and we need to be cautious here given that the ranges of 95% confidence limits for weight estimates often exceed mean values (see Smith 1996), it is most likely that the early hominins really did differ in the sizes of their cheek teeth, and that these differences really do reflect differences in diet.

Final thoughts

So what can we take home from all of this? Kant could have been talking about dental allometry in *Prolegomena to Any Future Metaphysics* when he wrote, "every answer given on principle of experience begets a fresh question, which likewise begets a fresh question". It is a Sisyphean frustration. That said, we *have* made progress over the past four decades. General trends, "loose descriptions" as Fortelius (1990b) called them, like isometry within mammalian orders parsed by diet and negative allometry of chewing rate, *do* hold up reasonably well despite our uncovering more-and-more "noise" in the system.

What about using relative tooth size to infer diet in extinct species? This may be too much to ask, but dental allometry can still serve as a starting point. If a fossil tooth appears very large or small given the size of the skull that anchors it, or the skeleton that supports that skull, why not use this to generate an hypothesis about diet to be tested using other approaches? Both adaptive lines of evidence, like tooth shape and structure, and effects of diet in life, like stable isotope ratios and microwear, can be used to test such hypotheses (Ungar & Sponheimer 2011). According to Whewell's (1858) principle of consilience, our hypotheses are much more robust when we colligate disparate lines of evidence. And when those lines of evidence don't correspond, rather than eschewing the questions raised, we might embrace them and wonder why not. In this way, we might well push the limits of knowability.

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