

Viewpoints: Diet and Dietary Adaptations in Early Hominins: The Hard Food Perspective

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ABSTRACT Recent biomechanical analyses examining the feeding adaptations of early hominins have yielded results consistent with the hypothesis that hard foods exerted a selection pressure that influenced the evolution of australopith morphology. However, this hypothesis appears inconsistent with recent reconstructions of early hominin diet based on dental microwear and stable isotopes. Thus, it is likely that either the diets of some australopiths included a high proportion of foods these taxa were poorly adapted to consume (i.e., foods that they would not have processed efficiently), or that aspects of what we thought we knew about the functional morphology of teeth must be wrong. Evaluation of these possibilities requires a recognition that analyses based on microwear, isotopes, finite element modeling, and enamel chips and cracks each test different types of hypotheses and allow different types of inferences.

Microwear and isotopic analyses are best suited to reconstructing broad dietary patterns, but are limited in their ability to falsify specific hypotheses about morphological adaptation. Conversely, finite element analysis is a tool for evaluating the mechanical basis of form-function relationships, but says little about the frequency with which specific behaviors were performed or the particular types of food that were consumed. Enamel chip and crack analyses are means of both reconstructing diet and examining biomechanics. We suggest that current evidence is consistent with the hypothesis that certain derived australopith traits are adaptations for consuming hard foods, but that australopiths had generalized diets that could include high proportions of foods that were both compliant and tough. *Am J Phys Anthropol* 151:339–355, 2013. © 2013 Wiley Periodicals, Inc.

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Recent years have seen much activity directed at improving our understanding of early hominin diets and dietary adaptations (Ungar, 2004; Scott et al., 2005; Grine et al., 2006a,b; Sponheimer et al., 2006; Van der Merwe et al., 2008; Berthaume et al., 2010; Constantino et al., 2010; Grine et al., 2010; Lee-Thorp et al., 2010; Strait et al. 2009, 2010; Ungar et al., 2008, 2010; Cerling et al., 2011; Ungar and Sponheimer, 2011). Much of this research has been driven by methodological innovations and/or access to previously unavailable specimens. Within the realm of biomechanics, recent analyses of teeth and crania (Lucas et al., 2008; Strait et al., 2009, 2010; Lawn and Lee, 2009; Constantino et al., 2010; Berthaume et al., 2010) have corroborated the hypothesis (e.g., Jolly, 1970; Lucas et al., 1985; Peters, 1987) that certain craniodental traits in australopiths are adaptations for consuming hard foods (like nuts and seeds), and that the *ingestion* of large, hard items using the premolars may have been a behavior that was important in *Australopithecus africanus* and possibly other early hominin species (Rak, 1983; Peters, 1987). In contrast, dental microwear texture analyses (Scott et al., 2005; Ungar et al., 2008, 2010) have not detected strong evidence of hard object feeding in most australopiths. These microwear analyses have also found that certain species that appear to be morphologically and functionally similar (*Paranthropus boisei* and *Pa. robustus*) have fundamentally different microwear signals, with evidence of hard object feeding being absent in the former. These species also differ in their stable carbon isotope signals whereby *Pa. boisei* consumed a high proportion of C4 foods while *Pa. robustus* and most other australopiths had isotopically mixed diets in which C3 foods predominate (although isotopic signals may fluctuate seasonally in at least some species) (Sponheimer et al., 2006; Lee-Thorp et al., 2010). Most nuts are produced by C3 plants, and the seeds of C4 plants are seasonally available resources that seem unlikely on their own to fully explain the strong C4 signal in *Pa. boisei* (Cerling et al., 2011). Thus, it has been hypothesized that the diet of *Pa. boisei* included a high proportion of tissues derived from C4 sedges or grasses that are both compliant and tough (Van der Merwe et al., 2008; Cerling et al., 2011). It has further been hypothesized (Ungar et al., 2010; Cerling et al., 2011) that the highly derived craniodental anatomy of *Pa. boisei* was adapted to eat compliant and tough foods, whereas the similarly derived anatomy of *Pa. robustus* was associated with the consumption of hard foods (Scott et al., 2005). These hypotheses represent a profound change in thought regarding australopith feeding adaptations. It was once proposed (Walker et al., 1986) that *Pa. boisei* and *Pa. robustus* converged on a common derived craniodental anatomy because they ate the same kinds of foods. In contrast, it has now been proposed that these species share a similar morphology despite the fact that they ate *different* foods [see Tobias (1967) for an earlier expression of this idea].

A theme emerging from recent dental microwear and isotopic studies is that dietary reconstruction is a key to understanding dietary adaptations. This may seem obvious but problems of interpretation arise when isotopic and microwear data point to adaptive scenarios that seem at odds with evidence from functional morphology. In such cases, it has been claimed that functional/biomechanical studies are either incomplete or mistaken (e.g., Grine et al., 2010; Cerling et al., 2011). However, we suggest the following: 1) reconstructing diet is *not* equivalent to understanding why and how

dietary adaptations evolved; 2) all the methods brought to bear on questions regarding diet and dietary adaptations have strengths and weaknesses; and 3) the various methods provide different types of information on profoundly different temporal scales and these differences need to be considered when setting out to test specific hypotheses. With these points in mind, we suggest that seemingly inconsistent results may instead be compatible, and that a focus on hypothesis testing can lead to a better understanding of early hominin diets and dietary adaptations. The four questions posed by the editors of the *AJPA* (paraphrased below for brevity) provide an excellent opportunity to explore these issues.

QUESTION 1: WHAT IS OUR HYPOTHESIS OF AUSTRALOPITH DIETARY ADAPTATION?

Before answering this question, we first define our understanding of adaptation. Adaptation is the end product of natural selection (Darwin, 1859). Thus, an adaptation is a heritable variant that spreads throughout a population because it enhances the reproductive fitness of its possessors relative to conspecifics lacking the trait. One can rarely measure fitness directly in the fossil record, so we employ a proxy definition, namely that an adaptation is a trait that provides an advantage during the performance of a behavior in a particular ecological setting relative to other, plesiomorphic expressions of the trait (e.g., Rudwick, 1964; Bock and van Wahlhert, 1965; Lauder, 1990). Thus, a comprehensive assessment of hominin feeding adaptations requires an understanding of functional morphology, diet, paleoecology, and phylogeny, yet any one of these fields of study could potentially produce data that might independently falsify an adaptive hypothesis.

Given this definition, we favor an adaptive hypothesis that is consistent with the current microwear, isotopic, functional, phylogenetic, and ecological data. This is a critical point. Despite evident disagreements in the literature (Strait et al., 2009, 2012; Grine et al., 2010), we do not believe that these data are necessarily contradictory. Rather, we believe that some *interpretations* of these data are contradictory, so one could go a long way toward resolving disagreements by evaluating the bases of these differing interpretations.

In our preferred hypothesis, australopiths are dietary generalists capable of shifting their diets according to the resources available in particular habitats. Several of the derived craniodental traits exhibited by australopiths can be interpreted as adaptations for feeding on hard

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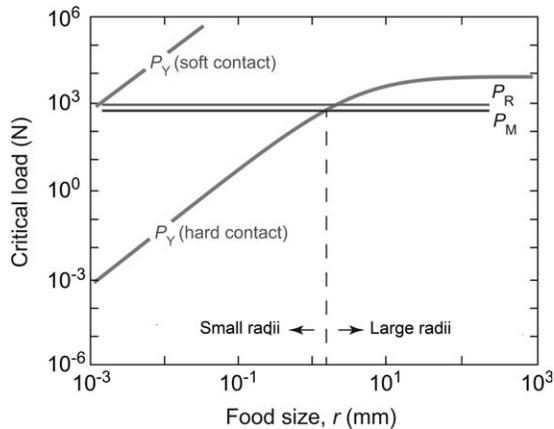


Fig. 1. “Damage map” illustrating the force in newtons (N), as a function of food particle size (measured as the radius r of the particle), needed to induce either yield/wear (P_Y) on a tooth’s occlusal surface or radial (P_R) or margin (P_M) fractures within a human tooth crown. P_Y is illustrated for bites on both hard foods (when the elastic modulus E of the food = 10 GPa) and soft foods ($E = 10$ MPa). The vertical dashed line indicates the food particle size at which the functions P_Y and P_M cross, denoting the boundary between foods with large radii versus small radii. Adapted from Lawn et al. (2010) with permission of the author.

objects (i.e., foods that are stiff with varying degrees of toughness and that fracture under the application of high loads) insofar as they either reinforce the teeth and facial skeleton against feeding loads (e.g., Jolly, 1970; Rak, 1983; Lucas et al., 1985), increase the mechanical advantage of the masticatory muscles (e.g., Rak, 1983; Demes and Creel, 1988), or both. If microwear accurately records the frequency with which hard objects were consumed, then it is possible that in many australopiths these items were fallback foods (Marshall and Wrangham, 2007) that were eaten infrequently but nonetheless exerted a selection pressure that induced morphological adaptation. If, on the other hand, microwear does not preserve such information (see below) then the possibility that hard foods were eaten more frequently cannot be ruled out. Regardless, adaptations for eating hard foods allowed australopiths to expand their dietary niche but did not preclude them from eating other foods (e.g., Wood and Strait, 2004). Isotopic evidence (Cerling et al., 2011) has been interpreted to mean that some australopiths (e.g., *Pa. boisei*) may have consumed large quantities of compliant and tough foods that their teeth were poorly designed to process. Isotopic analyses do not directly provide direct information about food material properties, so the logic underlying this interpretation is inductive (i.e., it uses a specific case to formulate a general principle that might be true, but that is not certainly true: *P. boisei* ate C4 foods and many C4 foods are tough, therefore *P. boisei* probably ate tough foods). Nonetheless, if this interpretation is true, it suggests that such foods were abundant and, perhaps, preferred, but they did not produce a sufficiently important selection pressure as to bring about adaptation in hominin postcanine dental morphology. In other words, an inability to efficiently process these foods did not have an adverse impact on fitness. Thus, referring back to our definition of adaptation given above, the inferred poor performance of australopith teeth at processing compliant and tough foods is

incompatible with a hypothesis that such teeth are adapted to feeding on those foods.

Differences with respect to microwear and isotopes among populations of East and southern African australopiths may reflect regional habitat differences or differences in niche partitioning. Although some southern and East African habitats may have been broadly similar (Cerling et al., 2011), it is possible that australopiths occupied different niches in those habitats, perhaps because of subtle differences in either resource availability or patterns of competition with other mammals. It has been noted that African bovids who are dietary generalists do not shift the isotopic composition of their diets in the manner described above (Cerling et al., 2011), but at least two southern African australopith species have been shown to isotopically shift their diet seasonally (Sponheimer et al., 2006; Lee-Thorp et al., 2010). We hypothesize that australopiths in both regions consumed similar C4 foods, but that some populations in Rift Valley habitats consumed these foods for longer stretches of time.

Our hypothesis implies that there may not always have been an especially close correspondence between diet and dietary adaptations in some populations of hominins. Although this might seem counter-intuitive, there is an excellent paleontological example of precisely this phenomenon. Hypsodonty in equids is generally considered an adaptation for eating an abrasive diet including grass, and Muhlbachler et al. (2011) found a relationship between crown height and mesowear that is consistent with such an adaptive hypothesis. However, these authors also found a statistically significant relationship between crown height and mesowear variability, suggesting that high crowned horses employed a wider range of diets than low crowned horses. They interpreted these results to mean that selection for hypsodont teeth was episodic, that most horse paleopopulations had low abrasion diets and thus experienced relatively weak selection for high crowned teeth, and that hypsodonty had the effect of allowing horses to expand their dietary breadth (Muhlbachler et al., 2011). Thus, hypsodonty is a derived trait that may be an adaptation to consume a specific type of food (grass), but its evolution also allowed taxa with the trait to fill a generalist dietary niche. Generalist species may have populations distributed across diverse habitats, and in some of those habitats grass eating may not have been necessary. Thus not all populations of a species, nor all species within a clade, need necessarily exhibit the behavior for which one of their morphological traits evolved. It is possible that an analogous phenomenon occurred in hominins, in which the most morphologically derived taxa (*Pa. robustus* and *Pa. boisei*) evidently differed in the composition of their diets despite being ecomorphologically similar. Indeed, robust australopiths provide a compelling argument that the alternative to our hypothesis (i.e., that there is always a close correspondence between diet and dietary adaptations in hominins) is false.

Evidence consistent with our preferred hypothesis derives from biomechanics and dental functional anatomy. The presence of enlarged premolars in some australopiths suggests that in at least those species premolar biting may have been a selectively important behavior (e.g., Rak, 1983; Strait et al., 2008, 2009). Reduced occlusal relief in many australopiths (e.g., Kay, 1981; Teaford and Ungar, 2000; Ungar, 2004) suggests that compliant and tough foods were not selectively

important. In contrast, large cheek teeth with blunt cusps and thick enamel are advantageous for resisting damage imposed by biting with high force on hard foods with large radii (e.g., Lucas et al., 2008; Lawn and Lee, 2009), where hard “large radius” foods are defined as those items predicted to induce cracks in tooth crowns before inducing microwear on tooth surfaces (Fig. 1). In contrast, hard “small radius” foods induce microwear before inducing cracks. We define size here specifically in terms of an object’s radius because the radius is a key variable governing whether or not contact between that object and a tooth creates surface yielding or crown fracture. There is direct evidence from enamel chip analysis that some australopiths generated high forces on their cheek teeth while biting on hard objects with large radii (Constantino et al., 2010), and at least one species (*Au. africanus*) evidently did so frequently (e.g., Grine et al., 2010; Strait et al., 2012).

When hard food items can be placed directly on the molars without ingestive processing (i.e., they are “ingestively small”), then presumably they would be fractured using the molar teeth because, as a simplification, molar bites have short load arms that maximize bite force (but see also Greaves, 1978; Taylor and Vinyard, 2009). In contrast, when hard foods require ingestive processing before mastication because they are too large to be placed directly on the molars (i.e., the foods are “ingestively large”), they may be fractured on the premolars, a behavior that is observed in living primates under both laboratory and natural (e.g., Wright, 2005) conditions. Note that the size terms described above are artificial constructs that vary on a sliding scale depending on the organism, food item, and tooth geometry in question. Their heuristic value is that they contextualize size in terms of behavior and mechanics; an object that is small enough to be placed directly on the molars may, when bitten, nonetheless fracture an enamel cap. Thus, an object may be ingestively small yet have a large radius in relation to how it might damage a tooth.

The concepts described above potentially provide insights into australopith feeding adaptations. Premolar biting shears, bends, and twists the rostrum relative to the rest of the face, and certain australopith facial features (e.g., the anterior pillar) seem well suited to reinforce the face against such loading regimes (Rak, 1983; Strait et al., 2009). It follows, therefore, that the ingestion of large, hard foods using the premolars may have been a selectively important behavior in at least some australopiths. It is unclear from biomechanical analysis whether or not these items were preferred or fallback foods. We had previously (Strait et al., 2009) accepted dental microwear evidence suggesting that many australopith species did not routinely consume ingestively small, hard foods on their molar teeth, but the prevalence of enamel chips on *Au. africanus* molar teeth (Grine et al., 2010; Strait et al., 2012) in the absence of a hard-object microwear signal suggests that microwear is not, in fact, recovering this aspect of australopith dietary behavior. Enlarged molar teeth with thick enamel may therefore be adaptations for masticating ingestively small hard objects (Jolly, 1970; Lucas et al., 1985). We argue below that isotopic and microwear data cannot exclude hard object feeding from the australopith behavioral repertoire, and thus cannot falsify our preferred adaptive hypothesis.

Hard foods that may have been consumed by australopiths include (but are not necessarily limited to) nut-oil

seeds, legumes, grass seeds, corms, and bulbs; the latter three could have contributed to the C4 component of australopith isotopic signals. The size, distribution, and fracture strength of modern African nut-oil seeds, legumes, and grass seeds have been described by Peters (1987, 1993). The edible parts of many of these foods are surrounded by a protective shell that must be fractured to allow the extraction (if necessary) and mastication of the inner kernel/tissue. Although modern plant species were not necessarily consumed by australopiths, they provide a coarse analogy for the Plio-Pleistocene flora. Among the tissues of the living plants, the largest and hardest (as judged by the forces needed to initiate fracture) are palm nuts (genus *Hyphaene*). Ingestive processing of palm nuts would almost certainly have required high bite forces on the premolars [average force to fracture = 1,804 N (Peters, 1993)], although these items may ultimately have been too resistant to have been a food source for australopiths. Medium-sized drupe endocarps that require high forces to fracture [hundreds of newtons (Peters, 1993)] and may also have required premolar processing include the genera *Sclerocarya*, *Balanites*, *Parinari*, *Schinziophyton*, and *Ziziphus*. There are many genera that produce smaller, less resistant seeds and drupe pyrenes (i.e., pits) (Peters, 1993) that could have been fractured using the molars in order to extract the softer kernels within. Moreover, monocot grasses (genera *Olyra*, *Panicum* = *Cynodon*, *Setaria*) and sedges (e.g., *Cyperus*), and various legumes produce very small, less resistant seeds, caryopses (i.e., grains), or fruits that could have been masticated on the molars (or on the entire postcanine row if many were eaten at once) without extensive ingestive processing. With respect to underground storage organs, Dominy et al. (2008) have recently summarized the mechanical properties of a wide range of African bulbs, corms, tubers, and rhizomes. Tubers and rhizomes tend to exhibit high fracture toughness, but corms and, to a lesser extent, bulbs exhibit low toughness and are roughly as stiff as many seed kernels. Thus, Dominy et al. (2008) describe bulb and corms as being hard foods, although they can be hundreds of times less stiff than seed shells, where stiffness is measured as the elastic modulus (Lucas, 2004). African corms include those in the families Iridaceae, Anthericaceae, Cyperaceae, Hypoxidaceae, and Haemodoraceae. African bulbs include the families Hyacinthaceae, Amaryllidaceae, Oxalidaceae, and Alliaceae. Corms and bulbs are generally ingestively small, and thus would be masticated directly on the molars without much ingestive processing (e.g., Altmann, 1998).

Alternatively, it has been hypothesized that East African australopiths comprise an anagenetic lineage that is morphologically adapted to consume compliant and tough food tissues that fracture when subjected to high displacements, including those derived from C4 plants such as sedges and/or grasses (Ungar et al., 2010; see also Van der Merwe et al., 2009). *Paranthropus boisei* potentially represents the extreme expression of such an adaptive trend (Cerling et al., 2011). In this scenario, derived australopith craniodental features reinforce the face against mechanical fatigue that results from repetitive rather than high magnitude loads. Certain types of mechanical data are consistent with this hypothesis, but at least one aspect of functional data is strongly inconsistent with it. Namely, this hypothesis posits that the facial skeleton is evolving adaptations for feeding on compliant and tough foods while occlusal morphology is

becoming maladapted to consume such items. We are not aware of any functional or comparative data suggesting that primate teeth lacking occlusal relief are advantageous for consuming compliant and tough foods, so the simultaneous evolution in robust australopiths of extraordinary facial morphology and very blunt teeth is difficult to reconcile with this hypothesis.

Another potential weak point of the hypothesis is that *Pa. robustus* ate hard foods but has either inherited its morphology from a compliant and tough food eating ancestor, or it has converged on a common morphology with *Pa. boisei* despite the fact that the two species had different diets. The latter scenario seems highly improbable but would be required if *Paranthropus* was paraphyletic, meaning that robust morphology evolved independently in two lineages (e.g., Walker et al., 1986). The former scenario would be the case if *Paranthropus* was monophyletic (e.g., Strait et al., 1997; Strait and Grine, 2004) and, while not impossible, it seems odd given that a diet of compliant and tough foods would have led to the evolution of a dental morphology especially well-suited for consuming hard foods. Again, we are not aware of a comparable example of such a phenomenon among primates.

Finally, the presence of large enamel chips on the teeth of both East and southern African australopiths suggests that hard foods with large radii were part of the australopith diet despite the lack of microwear evidence to this effect. One can infer that hard foods were eaten at least occasionally (possibly as fallback foods), and because chip frequency may be higher in *Au. africanus* than might be predicted from microwear (Strait et al., 2012), it appears that microwear may not faithfully record the consumption of such foods (e.g., Lucas et al., 2008; Lawn and Lee, 2009; Strait et al., 2009).

Question 2: What are the strengths and limitations of the methods used to examine diet and dietary adaptation in australopiths?

Finite element analysis, dental microwear analysis, enamel chip analysis, enamel crack analysis, and stable carbon isotope analysis are considered separately, below.

Finite element analysis (FEA). Finite element analysis is an engineering technique that can be used to examine how objects of complex geometry and material properties respond to complex loads. In FEA the structure of interest (e.g., a skull) is modeled as a mesh of simple bricks and tetrahedra (i.e., finite elements) joined at nodes, the elements are assigned material properties, certain nodes are constrained against motion, forces are applied, and displacements, stresses, and strains at each node and within each element are calculated (e.g., Cook et al., 2001; Zienkiewicz et al., 2005; see also Richmond et al., 2005; Strait et al., 2005; Ross et al., 2005; Rayfield, 2007; Panagiotopoulou, 2009 for reviews of FEA in the anthropology and vertebrate paleontology literature). Like analytical mechanics models, FEA provides an approximate solution to the governing differential equations of equilibrium that are the foundations of continuum mechanics (i.e., the mechanics of objects whose matter is assumed to be organized continuously rather than as a conglomerate of discrete particles). However, unlike analytical mechanics models, the accuracy of FEA (i.e. its ability to obtain the exact solution

admitted by the theory of elasticity) is only limited by the ability to accurately represent material properties, geometry, and loading conditions of the physical structure, and by the availability of computational resources. FEA can be used to test biomechanical hypotheses that make falsifiable mechanical predictions. Insofar as some hypotheses about evolutionary adaptation may depend directly on biomechanical hypotheses, the falsification of a biomechanical hypothesis can lead directly to falsification of an adaptive hypothesis. Thus, when applied to appropriate research questions, FEA based on realistic assumptions can test hypotheses of evolutionary adaptation.

Finite element analysis has several evident strengths as a tool in evolutionary biomechanics. First, it is able to incorporate geometrical, material, and loading complexity to a far greater extent than free-body biomechanical models reliant on simple shapes (i.e., the mandible as a bent beam, the rostrum as a cylinder, the supraorbital torus as a beam). Simple models have an intuitive appeal because they are easy to visualize and comprehend, and they have a long, distinguished history in evolutionary biomechanics (e.g., Endo, 1966, 1970, 1973; Smith, 1978; Greaves, 1978; Rak, 1983; Hylander, 1988; see also Hylander et al., 1991), but they should be viewed as a starting, rather than end point of biomechanical analysis. Although simple models are useful for illustrating broad, basic principles and making coarse predictions, FEA (given realistic assumptions) is a more powerful exploratory tool that can be used both to test and to formulate hypotheses (i.e., the model as hypothesis; Ross et al., 2011; Chalk et al., 2011).

Finite element analysis is also able to model the biomechanics of whole structures. In contrast, biomechanical assessments based on measurements in particular axes or planes may not capture mechanically important information beyond those axes or planes. It can also complement *in vivo* bone strain experiments: such experiments gather surface strain data from gages that may be distributed widely across a mandible or cranium, but it may be challenging to extrapolate between the gages to understand broad-scale deformation patterns and to understand strains deep within structures. Moreover, FEA fills in the gaps between strain gage locations, making it easier to understand global patterns of deformation in three dimensions.

Finite element analysis can also be a powerful experimental tool. To be sure, the nature of these experiments is qualitatively different from *in vivo* or *ex vivo* experiments based on actual primate tissues, but FEA provides an almost unparalleled opportunity to alter only one mechanical variable at a time, thereby isolating the effect of that variable on stress and strain. A strength of FEA is that direct control over each of the input variables means that FEA makes its assumptions explicit. For example, the material properties of the craniofacial skeleton in primates are impressively complex (e.g., Wang et al., 2006), but FEA provides a means of modeling material properties with varying levels of precision appropriate to the research question being posed (Strait et al., 2005). Lastly, FEA is the best tool available for understanding the biomechanics of fossil taxa to which *in vivo* and *ex vivo* experiments cannot be applied.

A limitation of FEA is that it will only be as accurate as the assumptions made by researchers regarding geometry, material properties, loads, and constraints, and it may be difficult to discern a priori which of these

variables has the strongest effect on stress and strain patterns. Thus, finite element models (FEMs) should be validated before interpretation (e.g., Richmond et al., 2005). Validation entails comparing FEA-generated strain data with strain data derived from *in vivo* or *in vitro* experiments. Generally speaking, there is no firm threshold that can be used to determine whether or not a model is “valid” or “invalid.” Rather, the comparison of strains allows a framework for assessing model validity along a scale, and final judgments about validity depend critically on the nature of the research questions being addressed. Moreover, there is a difference between the accuracy of a model and its utility as a comparative tool. For example, the strain magnitudes present in two models might not be strictly accurate (i.e., they might be too high or low in absolute terms), but the comparison between them might nonetheless be informative. Our research team places a premium on model validation, and we have characterized our macaque models as being “broadly realistic” insofar as they produce strains that mostly fall within the envelope of values recovered from *in vivo* feeding experiments. However, we do not claim that our models provide exact representations of an individual cranium or mandible during a single bite or chewing event, and we expect that all our models incorporate error. Based on our validation data (Strait et al., 2005, 2007, 2008, 2009; Ross et al., 2011; Nakashige et al., 2011), we believe it is justifiable to interpret the broad-scale deformation patterns preserved in our FEMs. Caution must be exercised when interpreting either finer-scale strain patterns or FEMs that are presented without validation. Obviously, FEMs of fossil specimens cannot be experimentally validated, so the best one can do is to validate an FEM of an extant organism that has been built with similar modeling assumptions.

Another limitation of FEA concerns sample size. The time required to construct FEMs has, to this point, limited the ability of researchers to consider the biomechanical consequences of intraspecific shape variation (Weber et al., 2011). Without such a consideration, it is difficult (or impossible) to assess the mechanical importance of the variation between species that underlies hypotheses of evolutionary adaptation. However, we predict that advances in computing power and software, coupled with the invention of new algorithms (e.g., see contrasting discussions in Bookstein, 2012; O’Higgins et al., 2011; Parr et al., 2012), will soon make it possible for researchers to more fully incorporate variation into their FEA-based studies.

More generally, FEA is a tool of biomechanics, which is in turn a subset of functional morphology. Functional morphology is best suited for testing hypotheses concerning the performance of a given anatomical system to perform particular behavioral roles (e.g., Bock and von Wahlert, 1965; Lauder, 1990); its ability to reconstruct diet is secondary. Moreover, although functional morphology can evaluate the likelihood that a given type of food may have been responsible for driving the evolution of a particular anatomical trait, it rarely can speak to whether or not that food item was frequently or infrequently consumed.

Our application of FEA to primate and hominin cranial biomechanics has recently been criticized (Grine et al., 2010), so it is necessary to consider whether or not those criticisms represent limitations of FEA. In a response to Grine et al. (2010), we demonstrated (Strait et al., 2012) that our *Macaca* FEM produces realistic

strains and that our modeling assumptions do not threaten the integrity of our results. We suggest that new data on enamel chips (Constantino et al., 2010) are consistent with our hypothesis of dietary adaptation (Strait et al., 2009) and that dental microwear data do not provide a compelling basis for rejecting that hypothesis. We highlight two additional points here.

First, Grine et al. (2010) imply that our FEA is unrealistic because bites on the molar and premolar teeth together do not produce strain energy density patterns that are “a combination” of patterns obtained when the molars and premolars are each loaded in isolation; rather, joint premolar and molar biting produces a pattern that resembles molar biting (Fig. 2). We suggest that Grine et al. (2010) are mistaken in assuming that a combination is expected. Rostral strains strongly reflect the degree to which the bite force displaces the rostrum *relative* to the zygomatic root (i.e., the rostrum shears superiorly). The displacement of the rostrum relative to the midface is minor during combined premolar and molar biting because the zygomatic root resists displacement of the entire face. The rostrum displaces relative to the rest of the face only when the face is unsupported beneath the root (as is the case during premolar-only biting). As illustrated using simple shapes, loads and constraints (Fig. 3), our results conform to mechanical predictions.

Second, Grine et al. (2010) criticized our methods for not distinguishing between evolutionary adaptation and “functional” adaptation (i.e., the modeling and remodeling of bone during life). However, we suggest this criticism rests on a false dichotomy. Most bony morphology is the product of interactions between both natural selection and ontogenetic mechanisms of skeletal adaptation: mechanisms of ontogenetic bone adaptation were produced by natural selection and are recruited by it to produce functionally sufficient skeletal structures. Moreover, biomechanical methods, including FEA, can test any hypothesis about a trait that makes specific, testable mechanical predictions, regardless of whether the trait is a product of an interaction between natural selection and ontogenetic mechanisms of skeletal adaptation (e.g., plasticity in bone cross-sectional geometry), or not (e.g., unworn enamel crown morphology).

Grine et al. (2010) hypothesize that the anterior pillar is functionally adapted to withstand molar rather than premolar loads because this structure experiences relatively low strains during molar bites and relatively high strains during premolar bites. The high strains indicate to them that premolar loading could not have been an important behavior, because if it had been, bone in the pillar would have functionally adapted to reduce the strains. Relatively low strain areas, therefore, are the key to understanding behavior. However, this interpretation assumes implicitly that strains in the pillar during premolar loading exceed the Customary Strain Stimulus (CSS, the range of strain magnitudes and frequencies above which modeling and remodeling strengthens bone, and below which they weaken bone; Skerry, 2006; see also Frost, 2003; Hughes and Petit, 2010). This hypothesis would be testable if the CSS of the pillar were known, but it is not. Moreover, it is not clear why relatively high strains in the pillar indicate a lack of premolar loading while strains in the zygomatic arch that are equally high or higher do not by the same logic indicate a lack of masseter contraction. Thus, as stated, Grine et al.’s (2010) hypothesis is not easily testable.

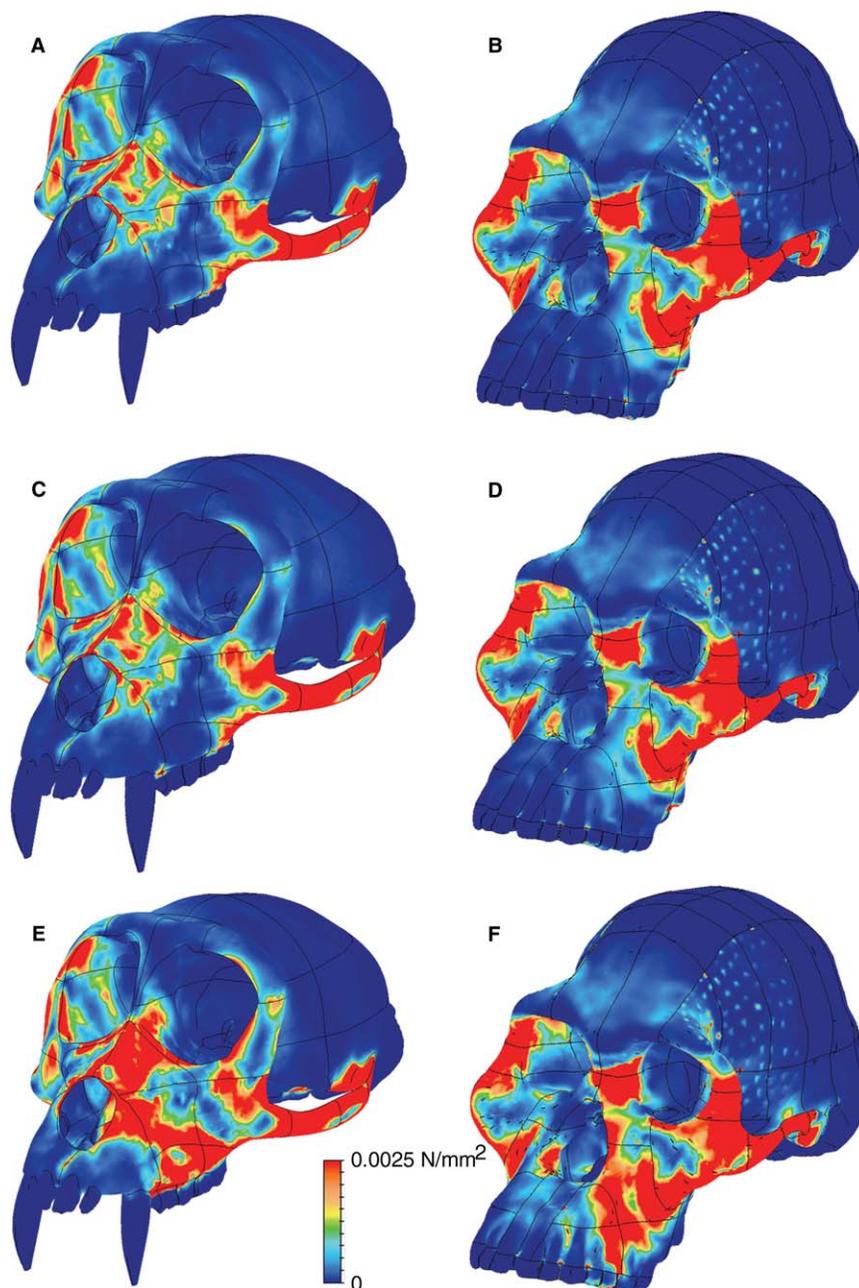


Fig. 2. Distributions of strain energy density (SED) observed in finite element analyses of *M. fascicularis* (A, C, E) and *Australopithecus africanus* (B, D, F) during simulated “maximal” bites on the molars alone (A, B), all of the postcanine teeth (i.e., the molars and the premolars) (C, D), and the premolars alone (E, F). SED distributions on the working (biting) side of the finite element models during “maximal” biting (muscles acting at peak levels on both sides) are nearly identical to those observed during “normal” biting (muscles acting at levels determined by electromyography during bites on apple with skin), although magnitudes are lower in the latter. SED distributions are also nearly identical to those of Von Mises’ strain in both crania under all loading conditions, indicating that the strain energy stored in both crania is primarily distortional. With respect to size, the models are not drawn to scale. Adapted from Strait et al. (2009). Note that Strait et al. (2009) mislabeled the scale to read N/m^2 rather than N/mm^2 .

Our hypothesis—that the shape and size of the anterior pillar are evolutionary adaptations to resist forces associated with premolar biting on large hard objects—has testable predictions. Namely, it predicts that 1) the pillar acts as a strut during premolar loading, 2) the pillar reduces strains relative to a morphology in which a pillar is absent, and 3) strain magnitudes in the pillar

will be relatively high, because if strains are high in a structure when it performs a function regularly, then the shape and size of the structure are likely to be optimized for the performance of that function. Note that predictions 2 and 3 are not contradictory; pillar strains should be relatively high but lower than they would be otherwise if the pillar were absent.

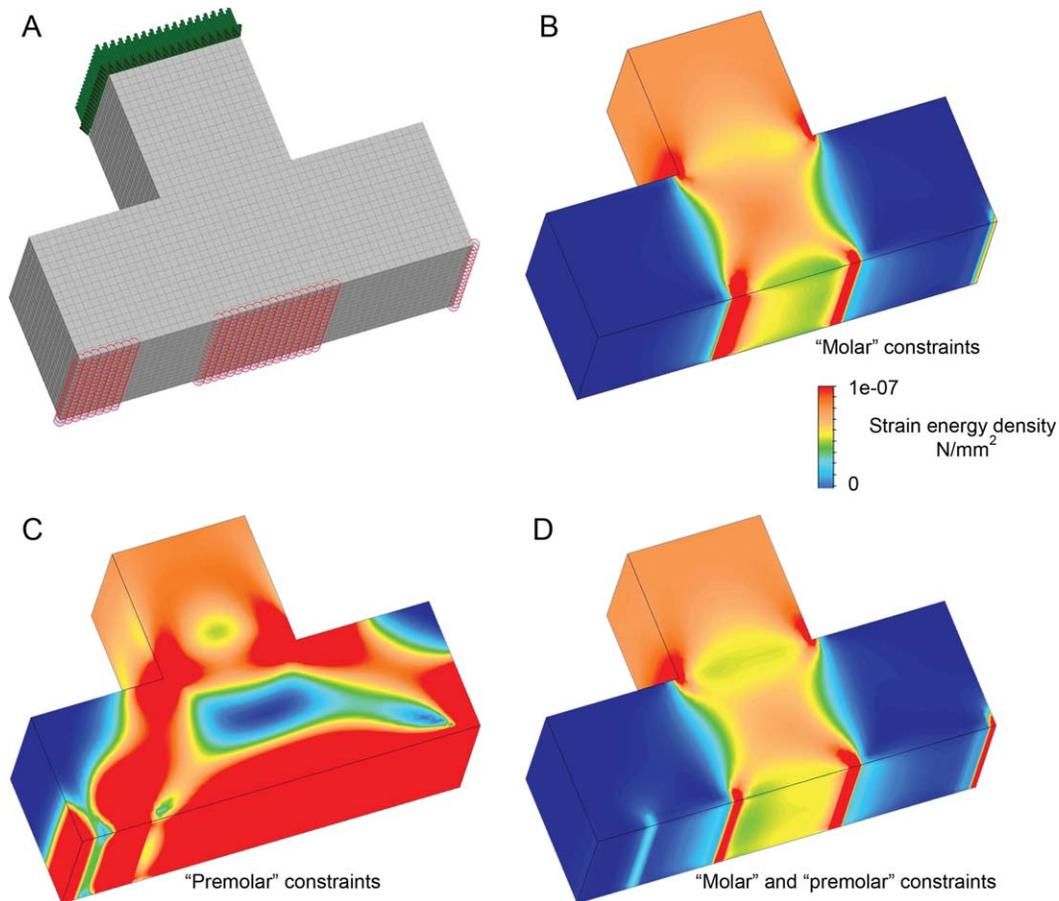


Fig. 3. Finite element analyses of a simple shape illustrating how the spatial positioning of model constraints can affect results. A simple shape (A) is subjected to a vertical load (green arrows) and is constrained (red circles) at potentially three different locations: anteriorly (the left patch of constraints that are analogous to the premolars), centrally (the center patch that is analogous to the molars), and posteriorly (the line of constraints to the right that is analogous to the axis between the two temporomandibular joints). The posterior constraints were enforced in all analyses, but enforcement of the central and anterior constraints varied: in the first analysis (B) the central constraints were enforced, in the second analysis (C) the anterior constraints were enforced, and in the third analysis (D) the anterior and central constraints were both enforced. Color mapping illustrates strain energy density. The similarity between (B) and (D) results from the fact that in neither case does the anterior (left) portion of the block shear against the central portion of the block. The comparison between (B) and (D) is analogous to comparisons between molar biting and biting on all of the cheek teeth.

Thus, our interpretation of strain magnitudes differs fundamentally from that of Grine et al. (2010). A logical extension of their line of reasoning is the argument (made to us by some of our colleagues) that the relatively low strain magnitudes in catarrhine browridges during feeding must mean that they are well designed for resisting feeding forces. However, this cannot be true if the relevant design criterion is to provide maximum strength during feeding with minimum material (Hylander et al., 1991). While it is not certain that this is a relevant design criterion in the primate cranial skeleton, we do know that it is not the *only* criterion, because there are areas of the cranium where *in vivo* strain magnitudes during feeding are never large (routinely $<100\ \mu\epsilon$). The catarrhine browridge is an excellent example of this argument (Hylander et al., 1991) and even though some evidence suggests that low strains associated with feeding play a role in maintaining browridge bone structure (Dechow et al., 2010), the relatively low strain levels suggest that other design criteria govern the evolution of browridge form. Comparable

arguments can be made regarding the postorbital septum, calvaria, medial orbital wall, orbital roof, and orbital floor (Ross, 2001; Ross and Metzger, 2004). Similarly, the anterior pillar of *Au. africanus* experiences relatively low strain magnitudes during molar loading (as might occur during mastication or molar biting), suggesting that its size and shape are not optimized for resisting forces generated during molar-loading behaviors. Thus, “[m]inimization of strain is neither a universal or ubiquitous criterion of optimization for bone tissue” (Grine et al., 2010:295). But we are confident that, in areas of the skull in which strain magnitudes are relatively high during the performance of a specific function, the shape and amount of bone in that area are important, and likely to be under selection (Hylander and Johnson, 1997) because those are the regions at the greatest risk of failure. Thus, the absence of data on functional adaptation in fossil hominins does not preclude the ability to test adaptive hypotheses regarding the evolutionary and functional significance of bone shape. Biomechanical data derived from FEA and *in*

vivo and *ex vivo* experiments can be used to assess hypotheses about functional and evolutionary adaptation as long as those hypotheses make discernibly different, testable mechanical predictions: certainly the question of whether derived skull characteristics in australopithecids represent functional or evolutionary adaptations will only be answered if testable hypotheses are addressed.

Dental microwear analysis. Dental microwear refers to the microscopic damage done to the surfaces of teeth by objects being processed in the oral cavity (e.g., Walker, 1981; Grine, 1981, 1986; Scott et al., 2005, 2006; Grine et al., 2006a,b; Teaford, 2007; Ungar et al., 2008, 2010). It has been suggested that occlusal topography and the mechanical properties of the foods interact to influence the movements of the teeth, and this, in turn, may influence the type of microwear that is produced by abrasive particles (e.g., Teaford, 2007; Ungar et al., 2010; Daegling et al., 2011). However, the relationship between occlusal morphology, jaw kinematics, and microwear has yet to be fully investigated. Regardless, microwear is a method of dietary reconstruction that is best suited for testing hypotheses about dietary behavior. As discussed below, microwear analysis is limited in its ability to test hypotheses about dietary adaptation if the object of natural selection is a food item that is only rarely consumed, or if the sampled individuals are not representative of the ecological setting, place, and time when selection acted on an extinct population.

The utility of microwear analysis depends on the strength of the correlation between microwear patterns and diet type (Scott et al., 2012; Ungar and Sponheimer, 2011). As a simplification, folivorous primates tend to exhibit fine scratches that are often aligned in the same direction, while hard object feeders tend to exhibit complex and/or pitted microwear textures (e.g., Scott et al., 2005, 2012; Ungar and Sponheimer, 2011). However, the relationship between microwear and diet in primates is not entirely straightforward. Although some primates exhibit differences in microwear textures that conform to dietary differences (e.g., Scott et al., 2012), others do not. We examined all *post hoc* pairwise comparisons between all the species in the Scott et al. (2012) data set following ANOVA. Within each pair of species, data were rank standardized in order to minimize the effect of extreme outliers in the long tails of non-normally distributed data. We used a simple procedure in which all pairwise comparisons were equivalent to a Student's *t*-test performed on the rank-ordered data. For our purposes, this is a conservative test procedure because it does not attempt to control for the likelihood of observing Type 1 error when making many comparisons (in our case, over 200 pairwise comparisons). This means that a finding of non-significance is fairly robust. Separate tests were performed for complexity and for anisotropy (i.e., the comparisons were univariate).

Scott et al. (2012) identify *Cercocebus atys*, *Cebus nigritus robustus*, *Cebus xanthosternos*, *Lophocebus albigena*, and *Pongo pygmaeus* as being species that consume hard foods either routinely or as fallbacks. One might therefore expect them to exhibit more complex microwear textures than soft-fruit frugivores or folivores. Yet, with respect to complexity (Table S1 in Supporting Information), *post hoc* comparisons revealed that:

1. None of the five hard object feeders differs significantly from the soft fruit eating *Ateles belzebuth*, *Ateles hybridus*, and *Pan troglodytes* (although some of the comparisons are nearly significant).
2. Four out of five hard object feeders (all except *Lophocebus albigena*) do not differ significantly from the soft fruit eating *Macaca fascicularis* (although the comparison with *P. pygmaeus* is nearly significant).
3. Four out of five hard object feeders (all except *C. nigritus robustus*) do not differ significantly from the folivorous *G. beringei*, and four out of five (all except *C. atys*) do not differ significantly from *G. gorilla* (although some of the comparisons are nearly significant).
4. Neither *C. xanthosternos*, *P. pygmaeus*, nor *L. albigena* differs significantly from the highly folivorous *T. cristatus* (although the comparison with the capuchin is nearly significant). Moreover, *P. pygmaeus* does not differ significantly from the folivorous *C. guereza*, and *L. albigena* does not differ significantly from the grass eating *T. gelada*.

Moreover, Scott et al. (2012) identify *A. palliata*, *T. gelada*, *C. guereza*, *G. beringei*, and *T. cristatus* as being the most folivorous primates in their sample, and thus might be expected to exhibit more anisotropic microwear textures than soft fruit or hard object feeders. However, with respect to anisotropy (Supporting Information Table S2):

1. Neither *C. guereza*, *G. beringei* nor *T. cristatus* are significantly different from *A. belzebuth*, *A. hybridus*, *C. nigritus robustus*, *C. xanthosternos*, *L. albigena*, *M. fascicularis* or *P. pygmaeus*.
2. Neither *G. beringei* nor *T. cristatus* are significantly different from *C. atys* and *P. troglodytes* (although most of these comparisons are nearly significant).
3. *Theropithecus gelada* is not significantly different from *A. belzebuth*, *A. hybridus*, *L. albigena* and *M. fascicularis* (although some of these comparisons are nearly significant).
4. *Alouatta palliata* is not significantly different from *C. xanthosternos*.

One might choose to analyze these data in a different way [i.e., by contrasting genera rather than species (Scott et al., 2012)], and increasing the samples sizes of some species would certainly increase statistical power. Nonetheless, these data represent the comparative sample upon which all inferences about early hominin microwear must currently be based, and the inability of these data to recognize the contrasting diets within these the pairs of species listed above raises the possibility that diet may not be the most important factor driving variation in microwear textures, and that alternative explanations ought to be considered (like the geometry and material properties of particles; see below).

The principal weakness of microwear is that it is ephemeral; any given microwear feature may be replaced by another in a matter of days or weeks (e.g., Teaford and Oyen, 1989). In fossils, therefore, a conservative interpretation is that microwear records information about the diet of an individual shortly before its death when "shortly" may be a matter of days (Grine, 1986). This limitation influences the types of hypotheses that can be tested with this approach. Microwear is best suited to testing the hypothesis that a given type of food item was *absent* from the diet because any evidence of

microwear features that are *only* produced by that food type provides positive evidence falsifying the hypothesis. However, the short time scale of microwear analysis renders it incapable of falsifying the hypothesis that a given food item was *present* in the diet because such an item could have been consumed before the time period in which the preserved microwear features were being deposited. In other words, microwear can potentially indicate what an animal *did* eat, but it is limited in its ability to determine what an animal *did not* eat. The former inference relies on positive evidence, while the latter depends on negative evidence.

Studies of early hominin microwear exemplify this principle. Scott et al. (2005) interpreted variation in microwear complexity in *Pa. robustus* as being indicative of the consumption of hard objects as fallback foods, but Grine et al. (2006b) interpreted a different microwear signal in *Pr. afarensis* [a pattern of fine scratches considered by them to be *Gorilla*-like and now known to lack complexity (Ungar et al., 2010)] as also being consistent with the consumption of hard fallback foods. These interpretations highlight a limitation of microwear analysis. If a given dietary hypothesis (e.g., the consumption of hard fallback foods) is consistent with different results (complex vs. non-complex microwear), then the data in question (i.e., microwear signals) are simply unable to falsify (i.e., test) the hypothesis (e.g., Ross et al., 2012). Put another way, if *Pr. afarensis*-like microwear is compatible with hard object feeding, then it is difficult to imagine a microwear signal that would not be compatible with such a behavior, and Ungar et al. (2010:3352) concede that “The microwear texture analysis data presented here cannot be used to falsify the notion of rare hard-object feeding, but it also provides no evidence for it.” This suggests that the microwear signal cannot exclude hard foods as a selectively important component of the early hominin diet.

Another potential limitation of microwear analysis is that there may be classes of foods that might not be expected to produce microwear features. In particular, it has been hypothesized (Lucas et al., 2008; Lawn and Lee, 2009; Strait et al., 2009) that microwear analysis might be unlikely to detect the consumption of hard objects with large radii (Fig. 1) because such objects would fracture the tooth crown before inducing yielding on the occlusal surface. In contrast, hard particles with small radii can induce microscopic yielding under very low forces because the point of contact between the particle and the tooth is so small that even very low forces (e.g., fractions of a Newton) can produce extraordinarily high stress (e.g., Lucas et al., 2008; Lawn and Lee, 2009). In contrast, compliant, soft particles are unlikely to induce microwear regardless of their toughness. It is these challenges to the premises of microwear analysis that have resulted in disagreements about its applicability (Strait et al., 2009, 2012; Grine et al., 2010; Daegling et al., 2011; Lucas et al., 2013).

Recent nanowear experiments (Lucas et al., 2013) expand our understanding of the mechanical basis of microwear formation. The geometry of microwear features depends critically on the hardness (i.e., resistance to indentation) of microscopic particles in relation to that of enamel. In such circumstances, quartz dust can be abrasive, i.e. capable of fracturing and removing enamel pieces, if dust particles possess sufficiently sharp asperities. In contrast, phytoliths deform during contact with enamel, forming U-shaped grooves, with prows forming

at the front of the features as enamel is rearranged in front of the path of the particle. Chips of enamel, as released for example by quartz, mutually deform with the parent surface producing flat troughs (Lucas et al., 2013). Other plant tissues seem too soft to mark enamel, appearing instead to act as particle transporters, although more research is needed on the role played by microscopic seed shell particles. Regardless, no plant tissues are hard enough to create steep, sharp angled pits or scratches on enamel surfaces. Thus, heavy pitting on enamel may not be evidence of a hard food diet, but rather of the presence of quartz dust, or its physical equivalent. Microgrooves with remnants of a prow, which may document the presence of phytoliths, do not necessarily reveal any information about the material properties of the food that contained the phytoliths.

We suggest that hypotheses about hominin diets need to be reconsidered in the light of this experimental evidence. The absence of pitting on early hominin teeth should not be interpreted to indicate an absence of hard foods in the diet, nor scratches/grooves to indicate leaves or other structural plant parts. We hypothesize that microwear textures reflect the relative abundance of different types of microscopic particles of varying geometry and hardness (e.g., phytoliths, quartz dust, etc.) that are introduced into the oral cavity during feeding. The dietary signal preserved in these textures is likely to be one that is indirect and may say little about the nature of the foods themselves. Studies are needed to document the frequency and distribution of these particles in various habitats occupied by primates.

Stable carbon isotope analysis. Dietary isotopic analysis examines the chemical signal left behind in mineralized tissues by the food items being consumed. The method most widely applied to early hominins has been stable carbon isotope analysis (e.g., Lee-Thorp et al., 1994; Schoeninger, 1995; Sponheimer and Lee-Thorp, 1999), which records whether or not the individual in question consumed one or the other, or both, of two broad categories of foods. These are 1) plants that employ the C3 photosynthetic pathway or the animals that eat those plants, and 2) plants that employ the C4 photosynthetic pathway or the animals that consume them. Typically, C3 plants consist of browse (e.g., leaves, fruits, stems, and roots of bushes and trees) and C4 plants consist of graze (e.g., tropical grasses), although a recent study suggests that the role of C3 grasses in African hominin paleoenvironments during the Miocene and, to a lesser extent, Plio-Pleistocene may be important (Feakins et al., 2013).

The main strengths of carbon isotope analysis are that it provides direct information about the chemical properties of what was eaten and it is not replaced over time, although it may be impacted by diagenesis. Carbon isotope analyses of early hominins have typically been performed on dental enamel, meaning that isotopes preserve dietary information about the time when the enamel was forming. Thus, the temporal scale of an analysis depends critically on the method used to sample the enamel. Data obtained from large full-thickness enamel fragments from the occlusal surface of a tooth contain dietary information averaged over months or even years, while it has been suggested that data obtained using laser ablation methods may provide information on the scale of days (e.g., Sponheimer et al.,

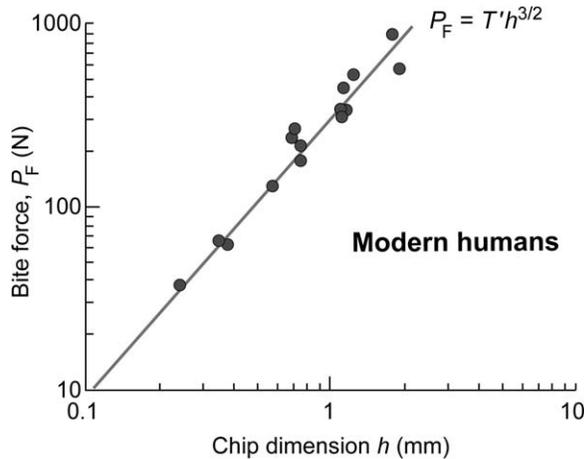


Fig. 4. Relationship between bite force (P_F) in Newtons (N) and resulting enamel chip size h in human teeth. T' is a coefficient proportional to material toughness (resistance to crack propagation). Adapted from Constantino et al. (2010). The strength of the relationship indicates that chip size is a good predictor of bite force.

2006). In this approach, sequential sampling of the tooth surface in the region of imbricational enamel might provide information allowing the assessment of seasonal fluctuations in diet (Sponheimer et al., 2006; Lee-Thorp et al., 2010). A complication, however, is that the mineralization of enamel may take weeks or months to complete, thereby lessening the precision of the seasonal isotopic signal (e.g., Hoppe et al., 2004). Regardless, carbon isotope analysis provides information about diet during short intervals of the individual's juvenile period and this may be significant if the foods eaten by weaned juveniles differ isotopically from those eaten by adults. A limitation of carbon isotope analysis is that the isotopic signal for an individual represents an agglomeration of the signals of all the foods that were eaten, and thus different combinations of foods can produce the same signal. Another limitation of the method is that if there is any mixture in the isotopic signal (i.e., a δC^{13} signature indicating the presence of both C3 and C4 foods), then it is difficult to exclude the possibility that any given food item was eaten, particularly if it has been hypothesized that the item in question might have been infrequently consumed (as would be the case with a fallback food). For example, *Pa. boisei* specimens exhibit δC^{13} values consistent with a diet composed of approximately 80% C4 foods (Van der Merwe et al., 2008; Cerling et al., 2011), but this does not exclude the possibility that its fallback foods were among the 20% of its diet derived from C3 foods. Thus, stable carbon isotope analysis is best suited for testing hypotheses pertaining to the relative abundance of broad categories of food. It generally cannot falsify a hypothesis suggesting that any given food item was a component of the diet, unless the species in question exhibits an isotopic signal that is either purely C3 or purely C4. Its utility for evaluating dietary adaptations lies primarily in its ability to contextualize adaptive hypotheses by providing a broad framework of dietary patterns. However, there are exceptional cases when isotopic signals seem to indicate a clear dietary preference independent of prevailing environmental conditions, and thus may provide information about adaptation. *Australopithecus sediba* has a strong C3 signal

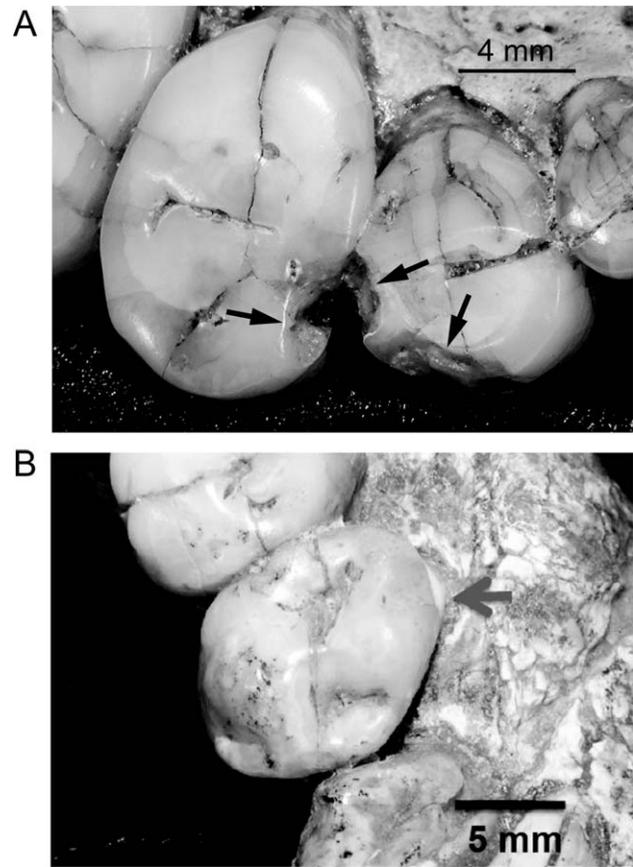


Fig. 5. Examples of ante-mortem enamel chips (arrows) in (A) *Paranthropus robustus* and (B) *Australopithecus africanus*. Adapted from Constantino et al. (2010).

despite the fact that it lived in a heavily C4 environment (Henry et al., 2012). This suggests that C4 plants were not among the preferred foods of this species, and that perhaps those foods were not selectively important to it.

Enamel chip analysis. It has long been recognized that some australopith species exhibit chipping on their teeth (e.g., Robinson, 1954, Tobias, 1967; Wallace, 1973). Recently, experimental analysis (Constantino et al., 2010; Chai et al., 2010) has validated the prediction, derived from principles of fracture mechanics (e.g., Lucas et al., 2009), that the size of a chip along the edge of the tooth crown is related to the force needed to create the chip (Fig. 4). More precisely, the feature being measured is the size of the scar left behind when a chip is "flaked" off of the enamel cap. Thus, teeth preserving large chip scars must have been exposed to large bite forces at some point in the past. Antemortem and postmortem chips can be easily distinguished in most cases because chip scars possessing margins that have been smoothed by wear were obviously created before death (Fig. 5; Wallace, 1973). Chip analysis investigates a narrow aspect of diet because only foods that are hard and have large radii can create chips; such foods are processed using high forces yet may have very localized contacts with teeth, and these conditions favor chip formation. Chips are unlike microwear insofar as they have the desirable

property of longevity; it may take months or years to wear away a chip scar. Indeed, given that antemortem chips are identified by having worn margins, it is almost certain that the time at which the chip was produced substantially predates the time at which the microwear preserved on the tooth's occlusal surface was created. Thus, chip analysis can falsify the hypothesis that hard foods with large radii were *absent* from the diet and its longer temporal scale makes it better equipped than microwear analysis to assess the hypothesis that such foods were *present* in the diet (because foods that are consumed rarely might leave traces that can be detected long after the feeding bout). Chip analysis also records information about the magnitudes of the bite forces that have been applied to the teeth in the past, and the mechanical relationships underlying chip analysis allow an estimate of maximum tooth strength (i.e., the force at which the tooth is expected to fail).

Constantino et al. (2010, 2012) have shown that large edge chips corresponding to high bite forces can be found in primates with diverse diets, but that primate and other mammalian seed predators exhibit higher frequencies of enamel chipping. Large, antemortem enamel chips corresponding to high bite forces (e.g., 500 to nearly 1,900 N) have been found in *Au. anamensis*, *Pr. afarensis*, *Au. africanus*, *Pa. robustus*, and *Pa. boisei* (Constantino et al., 2010). There is not yet definitive evidence as to chip frequency in early hominins. Grine et al. (2010) recently found chips in 10.8% of 158 *Au. africanus* postcanine teeth that preserve complete crowns, but this number may include chips in the center of the crown whose biomechanics have yet to be investigated. However, Wallace (1972) found that about two thirds of the 50 antemortem chips that he observed on 40 teeth from Sterkfontein, Makapansgat, and Swartkrans were edge chips, and so it is likely that edge chip frequency in *Au. africanus* exceeds that of living primate seed predators, which exhibit chips in less than 1% of all teeth within each species (chips in the seed eating primates were present in 7.1–16.0% of individuals, but typically each individual exhibited only one chip). Thus, despite sampling limitations, we predict that chip frequency is high in *Au. africanus* and, if so, this species must have consumed a diet that included large “hard” foods.

The strength of enamel chip analysis is that, unlike microwear, the mechanical basis of enamel chip formation is well established. A weakness of chip analysis is that, also unlike microwear, the distribution and size of chips have been examined systematically in only a few extant primates. Thus, the comparative context for interpreting chips has not yet been comprehensively documented. A second weakness is that it is not currently possible to differentiate chips caused by biting on hard foods from those caused by biting on hard non-food objects like pebbles or gravel. Data on modern human populations (Scott and Winn, 2011) reveal that hard particles derived from the use of grindstones or other methods of food preparation are likely to induce chipping, but at frequencies that generally are much higher than those seen in extant primates. Moreover, chips produced in this manner probably occur when pebbles are hidden within a softer food item, but grit on the outside of a food item might be more easily detectable. Regardless, we cannot at present rule out the possibility that some chips in australopiths are caused by biting on grit adhering to foods like underground storage organs. Ultimately,

more study is needed on chip size and frequency in primates that exploit grit-laden foods. However, such foods are likely to introduce grit particles with both large and small radii into the mouth. The former might chip teeth, while the latter might be expected to act as true abrasive particles that remove enamel from the occlusal surface (Lucas et al., 2013). An examination of the geometry of individual microwear features in fossil hominins should be able to reveal whether those features were created by crystalline quartz (or a comparable material) of an appropriate particle geometry, or softer objects. Such findings could provide clues as to the frequency with which grit was consumed.

Enamel crack analysis. Enamel crack analysis examines “ribbon-like” fractures that can traverse the depth of the enamel. These fractures (e.g., Lee et al., 2009) originate either 1) a short distance beneath the point of contact with the food item (*median fractures* that propagate from superficial to deep away from the point of tooth-food contact), 2) close to the enamel-dentin junction under the contact zone (*radial fractures* that propagate from deep to superficial toward the point of tooth-food contact), or 3) near the cervical margin of the enamel cap (*margin fractures* that occur as the base of the tooth expands under the occlusal load). All these fractures run vertically around the side walls of the tooth and usually remain confined to the enamel, although in principle a sufficiently high force would propagate the fracture through the underlying dentin. Bites on hard food tissues may produce either margin or radial/median fractures and given sufficient force, bites on soft/tough foods may produce margin fractures. When fractures run entirely between a cusp and the crown margin, it can be impossible to discriminate radial/median fractures from margin fractures. However, cracks that propagate only partially through the crown can easily be distinguished (Lee et al., 2011). Thus, the presence of partial radial/median fractures is evidence of hard object feeding, while the presence of partial margin fractures and the absence of partial radial/median fractures are suggestive of soft object feeding. Moreover, as was the case with enamel chip analysis, the mechanics of tooth crown geometry underlying enamel crack analysis (e.g., Lawn and Lee, 2009) allow one to estimate both the force needed to produce a given crack, and the maximum strength of the tooth crown. All other things being equal, thick cuspal enamel strengthens the tooth against radial and median fractures, while thick lateral enamel strengthens the tooth against margin fractures (Constantino and Wright, 2009). *Au. africanus* exhibits enamel that is on average absolutely and relatively thicker than that of extant hominoids, and enamel thickness in *Pa. robustus* is greater than that of *Au. africanus*. Compared with modern humans, enamel in both of these australopiths is thicker near the cusp tips than it is laterally (Olejniczak et al., 2008). On average, cuspal enamel is also absolutely thicker than lateral enamel in *P. boisei*, but this is not the case in East African early *Homo*, in which average cuspal and lateral enamel thickness are equal (Beynon and Wood, 1986).

There are practical impediments to enamel crack analysis in relation to fossils whose teeth may have been fractured postmortem (Grine et al., 2010), but it may be possible to discriminate between ante- and postmortem fractures because, during life, enamel fractures may be

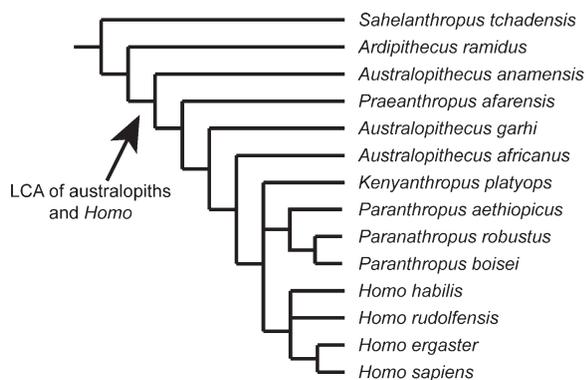


Fig. 6. Phylogeny of early hominins. Cladogram obtained by Strait and Grine (2004) in their analysis of “traditional” characters applied to all ingroup taxa. Last common ancestor of australopithecines and *Homo* indicated by arrow.

rendered more visible by rapid filling with a protein matrix or staining chemicals (Chai et al., 2009; Myoung et al., 2009; Lee et al., 2011). In contrast, postmortem fractures would either not be filled, or would be filled with mineral matrix. This is an area that warrants further study, and that may require methodological advances that improve our ability to analyze deep cracks non-destructively.

QUESTION 3: WHAT WERE THE DIET AND DIETARY ADAPTATIONS OF THE LAST COMMON ANCESTOR OF AUSTRALOPITHECINES, AND HOW MIGHT THIS AFFECT OUR PREFERRED HYPOTHESIS?

The last common ancestor (LCA) of the australopithecines is best considered the LCA of australopithecines and *Homo* (Fig. 6; note that we informally classify *Sahelanthropus*, *Orrorin* [not shown] and *Ardipithecus* as pre-australopithecines). It is possible to reconstruct the craniodental and mandibular morphology of this taxon using parsimony (Supporting Information Table S3) with the caveat that this reconstruction is merely a hypothesis that is dependent on the topology of the most parsimonious cladogram (Fig. 6). We use the most parsimonious cladogram from Strait and Grine (2004), an analysis based on skull characters, yet it is evident from recent fossil discoveries (e.g., Lordkipanidze et al., 2007; Tocheri et al., 2007; Jungers et al., 2009; Lovejoy, 2009; Lovejoy et al., 2009a,b; Berger et al. 2010; Zipfel et al., 2011) that postcranial traits evolved in a complex fashion in hominins, and that future reconstructions of hominin phylogeny must take postcranial traits into account. For example, the question has been raised as to whether or not *Ardipithecus ramidus* is, in fact, a hominin (see also Harrison, 2010; Wood and Harrison, 2011). Moreover, recent fossil discoveries might affect how characters are defined, and the data set upon which the cladogram was based does not include all early hominin species.

Nonetheless, as a working hypothesis, parsimony suggests that the australopithecine and *Homo* clade shares five synapomorphies that evolved in its LCA (Supporting Information Table S3). All these are dental, and pertain to the size, enamel thickness, and occlusal topography of the postcanine teeth (including the deciduous teeth). These traits are all consistent with the hypothesis that they are adaptations for consuming hard foods, although

they do not obviously contradict the hypothesis that this LCA was adapted to consume compliant and tough foods. Moreover, the skull morphology of the LCA of australopithecines and *Homo* resembles that of *Praeanthropus afarensis* in most (but not all) traits (Supporting Information Table S3). We have not yet examined the feeding biomechanics of *Pr. afarensis*, although we intend to do so and at that time may have additional insights as to the feeding adaptations of the LCA. However, as a generalization, a *Pr. afarensis*-like LCA is broadly compatible with our preferred “hard food hypothesis.” As is the case with other australopithecines, we would argue that the low relief occlusal morphology in *Pr. afarensis* is not especially adapted to the consumption of compliant and tough foods, although occlusal relief in this species is evidently greater than that in robust australopithecines (Ungar, 2004), and it would not be surprising if such foods were a regular component of its diet. The fact that occlusal relief in this species is greater than that in robust australopithecines (Ungar, 2004) suggests that, over time, compliant and tough foods became less, not more, important to the natural selection of feeding anatomy in the australopithecines. Moreover, there is no evidence that the degree of occlusal relief in the LCA is greater than that of its ancestor. Thus, we hypothesize that the diet of the LCA of australopithecines and *Homo* included hard foods as part of a generalized diet, and that this taxon possessed at least a few morphological characters that are adaptations for processing such foods. We are not suggesting that the LCA was a hard food specialist, or that hard foods were necessarily the predominant component of its diet. It would not surprise us if it had either an isotopically mixed diet, or a fully C3 diet, but we make no prediction in this regard.

It has been suggested (Grine et al., 2010) that the evolution of postcanine tooth size in australopithecines is incompatible with our adaptive hypothesis, but we disagree. Grine et al. (2010) note that if the ancestor of *Au. africanus* had extremely large premolars, like those of *Au. garhi*, then our interpretation of the selective forces influencing the face of *Au. africanus* might be falsified, because it would imply that premolar size had decreased rather than increased in the lineage leading to *Au. africanus*. However, parsimony suggests that the very large premolars seen in *Au. garhi* evolved in parallel with those of *Paranthropus*, and that the LCA of australopithecines and *Homo* gave rise to descendants with somewhat enlarged premolars. *Au. africanus* inherited premolars that were somewhat larger still, but unlike those of *Au. garhi*.

Grine et al. (2010) also argue that dental dimensions are inconsistent with our hypothesis because the premolars in *Au. africanus* are, on average, only approximately 11 to 12% larger than those of *Pr. afarensis*, while its molars are approximately 13% larger, but we never predicted that the percentage increase in premolar size should exceed that of molar size in *Au. africanus* relative to other hominins. Rather, we were careful to note that our FEA of *Au. africanus* did not explain the evolution of every aspect of australopithecine morphology (Strait et al., 2009:2127). However, in light of recently collected enamel chip data (Constantino et al., 2010; Grine et al., 2010), it would not surprise us if megadont molars evolved wholly, or in part, as an adaptation for fracturing hard food tissues that were ingestively small yet had large radii.

QUESTION 4: WHAT FURTHER STUDIES ARE NEEDED, AND WHAT RESULTS MIGHT FALSIFY OUR HYPOTHESIS OF AUSTRALOPITH DIETARY ADAPTATION?

In addition to continuing to document microwear patterns and isotopic signals in additional hominin species, there is a need for additional experimental studies that would further clarify the mechanical basis of microwear. Our work to date (Lucas et al., 2008, 2013) leads us to hypothesize that variation in microwear features is related most directly to variation in the size, shape, and material/mechanical properties of abrasive particles, rather than to diet or food material properties, *per se*. If true, this would imply that microwear conveys only indirect evidence about diet. Moreover, almost nothing is known about the nature of abrasive particles in the African habitats occupied by hominins, so field studies are needed to document this variation. There is also an urgent need for a systematic, comprehensive assessment of enamel chips in non-human primates and fossil hominins. Other research priorities include understanding the mechanical consequences of intraspecific morphological variation (in order to better frame interspecific comparisons) and devoting as much effort to investigating the biomechanics of ingestion as has already been devoted to investigating mastication. More work should be done using FEA to investigate strain and bite force production and efficiency in hominins and other primates. We further recommend conducting additional physical tests and modeling experiments designed to evaluate hypotheses pertaining to tooth crown fracture, performing modeling experiments in which morphologies are altered in order to examine their mechanical consequences (e.g., Strait et al., 2007; O'Higgins et al., 2010), and attempting to better understand the mechanical consequences of variation in the orientation and position of loads experienced during feeding (Benazzi et al., 2011). And, of course, researchers should continue recent efforts to document microwear patterns and isotopic signals in additional hominin species.

Beyond the experimental, mechanical, and comparative analyses described above, it is becoming increasingly clear that we will not be able to fully elucidate the nature of dietary adaptations unless we more fully understand the hierarchical relationships between strains, loads, the mechanical nature of feeding behavior, feeding ecology, food material properties and, ultimately, dietary categories such as folivory and frugivory (e.g., Ross et al., 2012). Thus, it will be important to gather additional information about the ecology and material properties of African plant foods. More generally, and perhaps more importantly, we need to observe how primates process their foods in the wild so that we can replicate those behaviors under laboratory conditions and model those behaviors using FEA. We predict that variation in these processing behaviors will better explain the evolution of dietary adaptations than will a consideration of food material properties alone (Kinzey, 1974, 1992; Kinzey and Norconk, 1990; Vinyard et al., 2003; Vinyard et al., 2009; Vinyard et al., 2001; Vinyard et al., 2008; Wright et al., 2008, 2009; Ross et al., 2012). In an ideal study, biomechanical, microwear, and isotopic data would all be collected from the same primate populations that are the subject of behavioral observations (Wood and Schroer, 2012).

There are several circumstances under which our preferred hypothesis would be either falsified or severely compromised. First, our hypothesis relies heavily on a functional interpretation of occlusal morphology, and if a combination of comparative, experimental, and mechanical data were to show that teeth with low occlusal relief were, contrary to conventional wisdom, highly efficient at fracturing compliant and tough foods, then a key premise of our hypothesis would be removed and the hypothesis that australopiths were adapted to consume those foods would be plausible. Our hypothesis would also be weakened if it were to be shown that our findings regarding the biomechanics of the anterior pillar in Sts 5 are anecdotal and that this feature does not behave like a strut in other specimens possessing a pillar. Moreover, our interpretation of the pillar would be compromised if it could be shown that *Au. africanus* was descended from an ancestor that possessed a pillar but lacked enlarged premolars and thick enamel (thereby removing the premise that high magnitude premolar loading might have been an important behavior leading to pillar evolution). Similarly, our hypothesis regarding the importance of premolar loading in *Au. africanus* would be compromised if virtual experiments revealed that the removal of the anterior pillar from the FEM of this species had neither local nor global effects on strain. Lastly, our hypothesis would be difficult to defend if FEA studies documenting the mechanical consequences of *intraspecific* variation reveal that there are no meaningful *interspecific* differences among extant hominoids and early hominins.

CONCLUSION

In summary, two views have emerged regarding the evolution of australopith feeding adaptations. In one view, based largely but not exclusively on paleodietary evidence reflecting the frequency with which foods were consumed, australopith craniodental traits are adaptations for feeding on compliant and tough foods. In the other view, based largely but not exclusively on assessments of biomechanical performance, those same traits are adaptations for feeding on hard foods. We favor the latter because key aspects of dental functional morphology seem to be incompatible with the former, and because we have questions regarding the efficacy of dental microwear analysis. Moreover, although isotopic and microwear analyses may reveal important aspects of early hominin dietary ecology, we are concerned that these approaches are, even under the best of circumstances, unable to falsify the hard food adaptive hypothesis. However, there is no doubt that recent studies using these methods have produced unexpected results and challenged conventional wisdom regarding early hominin feeding behavior. In order to test these competing hypotheses, it will be critical to collect comprehensive data on enamel chip size and frequency in early hominins and a wider range of extant primates so as to better assess the frequency of hard food consumption in australopiths. Concurrently, more work needs to be done to investigate the mechanical basis of microwear, as well as the stress-resistance capabilities of crania, mandibles, and teeth in additional early hominins. It is essential that these studies be complemented with observations of primate dietary ecology and food processing behaviors. We are optimistic that a consensus regarding early hominin diets and dietary

adaptations will emerge through recognition of the strengths and limitations of the various methods used to analyze these two related but different components of hominin feeding.

Indeed, we do not believe that the mechanical, micro-wear, and isotopic data are contradictory. Rather, insofar as they are all related to a common behavior (feeding), they must be congruent. Moreover, we believe that the quality of these data is high. Thus, the contradiction between methodological approaches is more apparent than real, and is based primarily on discordant *interpretations* of the data. We are optimistic that the normal “back and forth” of academic discourse will stimulate productive research and lead eventually to a consensus as to how best to formulate these interpretations. When that is achieved, then studies integrating all approaches will be possible. We hope that these paired viewpoints have contributed constructively to this discourse.

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LITERATURE CITED

- Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press.
- Benazzi S, Kullmer O, Grosse IR, Weber GW. 2011. Using occlusal wear information and finite element analysis to investigate stress distributions in human molars. *J Anat* 219: 259–272.
- Berger LR, De Ruiter DJ, Churchill SE, Schmid P, Carlson KJ, Dirks PHGM, Kibii JM. 2010. *Australopithecus sediba*: a new species of *Homo*-like australopithecine from South Africa. *Science* 328:195–204.
- Berthaume M, Grosse IR, Patel ND, Strait DS, Wood S, Richmond BG. 2010. The effect of early hominin occlusal morphology on the fracturing of hard food items. *Anat Rec* 293: 594–606.
- Beynon AD, Wood BA. 1986. Variations in enamel thickness and structure in East African hominids. *Am J Phys Anthropol* 70:177–193.
- Bock WJ, von Wahlert G. 1965. Adaptation and the form-function complex. *Evolution* 3:269–299.
- Bookstein FL. 2012. Allometry for the twenty-first century. *Biol Theory* 6: DOI 10.1007/s13752-012-0064-0.
- Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, Sponheimer M, Uno KT. 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc Natl Acad Sci USA* 108:9337–9341.
- Chai H, Lee JJ-W, Constantino PJ, Lucas PW, Lawn BR. 2009. Remarkable resilience of teeth. *Proc Natl Acad Sci USA* 106: 7289–7293.
- Chai H, Lee JJ-W, Lawn BR. 2010. Fracture of tooth enamel from incipient microstructural defects. *J Mech Behav Biomed Mater* 3:116–120.
- Chalk J, Richmond BG, Ross CF, Strait DS, Wright BW, Spencer MA, Wang Q, Dechow PC. 2011. A finite element analysis of masticatory stress hypotheses. *Am J Phys Anthropol* 145:1–10.
- Constantino PJ, Lee JJ-W, Chai H, Zipfel B, Ziscovici C, Lawn BR, Lucas PW. 2010. Tooth chipping can reveal the diet and bite forces of fossil hominins. *Biol Lett* 6:826–829.
- Constantino PJ, Markham K, Lucas PW. 2012. Tooth chipping as a tool to reconstruct diets of great apes (*Pongo*, *Gorilla*, *Pan*). *Int J Primatol* 33:661–672.
- Constantino PJ, Wright BW. 2009. The importance of fallback foods in primate ecology and evolution. *Am J Phys Anthropol* 140:599–602.
- Cook RD, Malkus DS, Plesha ME, Witt RJ. 2001. Concepts and applications of finite-element analysis, 4th ed. New York: John Wiley & Sons.
- Daegling DJ, McGraw WS, Ungar PS, Pampush JD, Vick AE, Bitty EA. 2011. Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. *PLoS One* 6:e23095.
- Darwin CR. 1859. On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life. London: John Murray.
- Dechow PC, Wang Q, Peterson J. 2010. Edentulation alters material properties of cortical bone in the human craniofacial skeleton: functional implications for craniofacial structure in primate evolution. *Anat Rec* 293:618–629.
- Demes B, Creel N. 1988. Bite force, diet, and cranial morphology of fossil hominids. *J Hum Evol* 17:657–670.
- Dominy NJ, Vogel ER, Yeakel JD, Constantino P, Lucas PW. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol Biol* 35:159–175.
- Endo B. 1966. Experimental studies on the mechanical significance of the form of the human facial skeleton. Tokyo: University of Tokyo.
- Feakins SJ, Levin NE, Liddy HM, Sieracki A, Eglinton TI, Bonnefille R. 2013. Northeast African vegetation change over 12 m.y. *Geology* 41:295–298.
- Frost HM. 2003. Bone’s mechanostat: a 2003 update. *Anat Rec* 275:1081–1101.
- Greaves WS. 1978. The jaw lever system in ungulates: a new model. *J Zool (Lond)* 184:271–285.
- Grine FE. 1981. Trophic differences between gracile and robust australopithecines: a scanning electron-microscope analysis of occlusal events. *S Afr J Sci* 77:203–230.
- Grine FE. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J Hum Evol* 15:783–822.
- Grine FE, Ungar PS, Teaford MF. 2006a. Was the Early Pliocene hominin ‘*Australopithecus anamensis*’ a hard object feeder? *S Afr J Sci* 102:301–310.
- Grine FE, Ungar PS, Teaford MF, El-Zaatari S. 2006b. Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *J Hum Evol* 51:297–319.
- Grine FE, Judex S, Daegling DJ, Ozcivici E, Ungar PS, Teaford MF, Sponheimer M, Scott J, Scott RS, Walker A. 2010. Craniofacial biomechanics and functional and dietary inferences in hominin paleontology. *J Hum Evol* 58:293–308.
- Harrison T. 2010. Apes among the tangled branches of human origins. *Science* 327:532–534.
- Henry AG, Ungar PS, Passey BH, Sponheimer M, Rossouw L, Bamford M, Sandberg P, de Ruiter DJ, Berger L. 2012. The diet of *Australopithecus sediba*. *Nature* 487:90–93.
- Hoppe KA, Stover SM, Pascoe JR, Amundson R. 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. *Palaeogeogr Palaeoclimatol Palaeoecol* 206:355–365.
- Hughes JM, Petit MA. 2010. Biological underpinnings of Frost’s mechanostat thresholds: the important role of osteocytes. *J Musculoskelet Neuronal Interact* 10:128–135.
- Hylander WL. 1988. Implications of *in vivo* experiments for interpreting the functional significance of “robust” australopithecine jaws. In: Grine FE, editor. *Evolutionary history of the “robust” australopithecines*. New York: Aldine de Gruyter. p 55–83.

- Hylander WL, Johnson KR. 1997. *In vivo* bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. *Am J Phys Anthropol* 120:203–232.
- Hylander WL, Picq PG, Johnson KR. 1991. Masticatory-stress hypotheses and the supraorbital region of primates. *Am J Phys Anthropol* 86:1–36.
- Jolly CJ. 1970. Seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5:5–26.
- Jungers WL, Harcourt-Smith WEH, Wunderlich RE, Tocheri MW, Larson SG, Sutikna T, Due RA, Morwood MJ. 2009. The foot of *Homo floresiensis*. *Nature* 459:81–84.
- Kay RF. 1981. The nut-crackers: a new theory of the adaptations of the Ramapithecinae. *Am J Phys Anthropol* 55:141–151.
- Kinzey WG. 1974. Ceboid models for the evolution of the hominid dentition. *J Hum Evol* 3:193–203.
- Kinzey WG. 1992. Dietary and dental adaptations in the Pitheciinae. *Am J Phys Anthropol* 88:499–514.
- Kinzey WG, Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. *Am J Phys Anthropol* 81:5–15.
- Lauder GV. 1990. Functional morphology and systematics: studying functional patterns in an historical context. *Ann Rev Ecol Syst* 21:317–40.
- Lawn B, Lee JJ-W. 2009. Analysis of fracture and deformation modes in teeth subjected to occlusal loading. *Acta Biomater* 5:2213–2221.
- Lawn BR, Lee JJ-W, Chai H. 2010. Teeth: among nature's most durable biocomposites. *Ann Rev Mater Res* 40:55–75.
- Lee JJ-W, Kwon JY, Chai H, Lucas PW, Thompson VP, Lawn BR. 2009. Fracture modes in human teeth. *J Dent Res* 88:224–228.
- Lee J-W, Constantino P, Lucas P, Lawn B. 2011. Fracture in teeth: a diagnostic for inferring tooth function and diet. *Biol Rev* 86:959–974.
- Lee-Thorp JA, Van der Merwe NJ, Brian CK. 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *J Hum Evol* 27:361–372.
- Lee-Thorp JA, Sponheimer M, Passey BH, de Ruiter DJ, Cerling TE. 2010. Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. *Philos Trans R Soc B* 365:3389–3396.
- Lordkipanidze D, Jashashvili T, Vekua A, Ponce de León MS, Zollikofer CPE, Rightmire GP, Pontzer H, Ferring R, Oms O, Tappen M, Bukhshianidze M, Agusti J, Kahlke R, Kiladze G, Martinez-Navarro B, Mouskhelishvili A, Nioradze M, Rook L. 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449:305–310.
- Lovejoy CO. 2009. Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326:74e1–74e8.
- Lovejoy CO, Latimer B, Suwa G, Asfaw B, White TD. 2009a. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. *Science* 326:72e1–72e8.
- Lovejoy CO, Suwa G, Simpson SW, Matternes JH, White TD. 2009b. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science* 326:100–106.
- Lucas PW. 2004. Dental functional morphology: how teeth work. Cambridge: Cambridge University Press.
- Lucas PW, Constantino P, Wood B, Lawn B. 2008. Dental enamel as a dietary indicator in mammals. *BioEssays* 30:374–385.
- Lucas PW, Constantino PJ, Chalk J, Ziscovici C, Wright BW, Fragszky DM, Hill DA, Lee JJ-W, Chai H, Darvell BW, Lee PKD, Yuen TDB. 2009. Indentation as a technique to assess the mechanical properties of fallback foods. *Am J Phys Anthropol* 140:643–652.
- Lucas PW, Corlett RT, Luke DA. 1985. Plio-Pleistocene hominid diets: an approach combining masticatory and ecological analysis. *J Hum Evol* 14:187–202.
- Lucas PW, Omar R, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, Thai LA, Watzke J, Strait DS, Atkins AG. 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *J R Soc Interface* 10:20120923.
- Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. *Int J Primatol* 28:1218–1235.
- Mihlbachler MC, Rivals F, Solounias N, Semprebon GM. 2011. Dietary change and evolution of horses in North America. *Science* 331:1178–1181.
- Myoung S, Lee J, Constantino P, Lucas P, Chai H, Lawn B. 2009. Morphology and fracture of enamel. *J Biomech* 42:1947–1951.
- Nakashige M, Smith AL, Strait DS. 2011. Biomechanics of the anthropoid postorbital septum investigated using finite element analysis. *J Anat* 218:142–150.
- O'Higgins P, Cobb SN, Fitton LC, Gröning F, Phillips R, Liu J, Fagan MJ. 2011. Combining geometric morphometrics and functional simulation: an emerging toolkit for virtual functional analyses. *J Anat* 218:3–15.
- Olejniczak AJ, Smith TM, Skinner MM, Grine FE, Freeney RNM, Thackeray JF, Hublin J-J. 2008. Three-dimensional molar enamel distribution and thickness in *Australopithecus* and *Paranthropus*. *Biol Lett* 4:406–410.
- Panagiotopoulou O. 2009. Finite element analysis (FEA): applying an engineering method to functional morphology in anthropology and human biology. *Ann Hum Biol* 36:609–623.
- Parr WCH, Wroe S, Chamoli U, Richards HS, McCurry MR, Clausen PD, McHenry C. 2012. Toward integration of geometric morphometrics and computational biomechanics: new methods for 3D virtual reconstruction and quantitative analysis of Finite Element Models. *J Theoret Biol* 301:1–14.
- Peters CR. 1987. Nut-like oil seeds: food for monkeys, chimpanzees, humans, and probably ape-men. *Am J Phys Anthropol* 73:333–363.
- Peters CR. 1993. Shell strength and primate seed predation of nontoxic species in eastern and southern Africa. *Int J Primatol* 14:315–344.
- Rak Y. 1983. The australopithecine face. New York: Academic Press.
- Rayfield EJ. 2007. Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. *Annu Rev Earth Planet Sci* 35:541–576.
- Richmond BG, Wright BW, Grosse I, Dechow PC, Ross CF, Spencer MA, Strait DS. 2005. Finite element analysis in functional morphology. *Anat Rec* 283:259–274.
- Robinson JT. 1954. Prehominid dentition and hominid evolution. *Evolution* 8:324–334.
- Ross CF. 2001. *In vivo* function of the craniofacial haft: The interorbital “pillar”. *Am J Phys Anthropol* 116:108–139.
- Ross CF, Iriarte-Diaz J, Nunn CL. 2012. Innovative approaches to the relationship between diet and mandibular morphology in primates. *Int J Primatol* 33:632–660.
- Ross CF, Berthaume MA, Dechow PC, Iriarte-Diaz J, Porro LB, Richmond BG, Spencer MA, Strait DS. 2011. *In vivo* bone strain and finite-element modeling of the craniofacial haft in catarrhine primates. *J Anat* 218:112–141.
- Ross CF, Patel BA, Slice DE, Strait DS, Dechow PC, Richmond BG, Spencer MA. 2005. Modeling masticatory muscle force in finite-element analysis: sensitivity analysis using principal coordinates analysis. *Anat Rec* 283:288–299.
- Rudwick MJS. 1964. The inference of function from structure in fossils. *Br J Philos Sci* 57:27–40.
- Schoeninger MJ. 1995. Stable isotope studies in human evolution. *Evol Anthropol* 4:83–98.
- Scott GR, Winn JR. 2011. Dental chipping: contrasting patterns of microtrauma in Inuit and European populations. *Int J Osteoarchaeol* 21:723–731.
- Scott RS, Teaford MF, Ungar PS. 2012. Dental microwear texture and anthropoid diets. *Am J Phys Anthropol* 147:551–579.
- Scott RS, Ungar PS, Bergstrom TS, Brown CA. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436:693–695.
- Scott RS, Ungar PS, Bergstrom TS, Brown CA, Childs BE, Teaford MF, Walker A. 2006. Dental microwear texture analysis: technical considerations. *J Hum Evol* 56:405–416.

- Skerry TM. 2006. One mechanostat or many? Modifications of the stie-specific response of bone to mechanical loading by nature and nurture. *J Musculoskelet Neuronal Interact* 6: 122–127.
- Smith RJ. 1978. Mandibular biomechanics and temporomandibular joint function in primates. *Am J Phys Anthropol* 49: 341–350.
- Sponheimer M, Lee-Thorp JA. 1999. Isotopic evidence for the diet of an early hominid, *Australopithecus africanus*. *Science* 283:368–370.
- Sponheimer M, Passey BH, DeRuiter DJ, Guatelli-Steinberg D, Cerling TE, Lee-Thorp JA. 2006. Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. *Science* 314:980–982.
- Strait DS, Grine FE. 2004. Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. *J Hum Evol* 47:399–452.
- Strait DS, Grine FE, Moniz MA. 1997. A reappraisal of early hominid phylogeny. *J Hum Evol* 32:17–82.
- Strait DS, Grosse IR, Dechow PC, Smith AL, Wang Q, Weber GW, Neubauer S, Slice DE, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Wright BW, Byron C. 2010. The structural rigidity of the cranium of *Australopithecus africanus*: implications for the allometry of feeding biomechanics. *Anat Rec* 293:583–593.
- Strait DS, Richmond BG, Spencer MA, Ross CF, Wood BA. 2007. Masticatory biomechanics and its relevance to early hominid phylogeny: an examination of palate thickness using finite element analysis. *J Hum Evol* 52:589–599.
- Strait DS, Wang Q, Dechow PC, Ross CF, Richmond BG, Spencer MA, Patel BA. 2005. Modeling elastic properties in finite element analysis: how much precision is needed to produce an accurate model? *Anat Rec* 283:275–287.
- Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Wright BW, Ross CF, Dechow PC, Wang Q, Grosse I, Byron C, Wood BA, Lawn B, Constantino P, Slice DE, Smith AL. 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proc Natl Acad Sci USA* 106:2124–2129.
- Strait DS, Weber GW, Constantino P, Lucas PW, Richmond BG, Spencer MA, Dechow PC, Ross CF, Grosse I, Wright BW, Wood BA, Wang Q, Byron C, Slice DE. 2012. Microwear, mechanics and the feeding adaptations of *Australopithecus africanus*. *J Hum Evol* 62:165–168.
- Strait DS, Wright BW, Richmond BG, Ross CF, Dechow PC, Spencer MA, Wang Q. 2008. Craniofacial strain patterns during premolar loading: implications for human evolution. In: Vinyard CJ, Ravosa MJ, Wall CE, editors. *Primate craniofacial function and biology*. New York: Springer. p 173–198.
- Taylor AB, Vinyard CJ. 2009. Jaw-muscle fiber architecture in tufted capuchins favors generating relatively large muscle forces without compromising jaw gape. *J Hum Evol* 57: 710–720.
- Teaford MF. 2007. What do we know and not know about dental microwear and diet? In: Ungar PS, editor. *Evolution of the human diet: the known, the unknown, and the unknowable*. Oxford: Oxford University Press. p 106–131.
- Teaford MF, Oyen OJ. 1989. *In vivo* and *in vitro* turnover in dental microwear. *Am J Phys Anthropol* 80:447–460.
- Teaford MF, Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. *Proc Natl Acad Sci USA* 97:13506–13511.
- Tobias PV. 1967. The cranium and maxillary dentition of *Australopithecus (Zinjanthropus) boisei*. Olduvai Gorge, Vol. 2. Cambridge: Cambridge University Press.
- Tocheri MW, Orr CM, Larson SG, Sutikna T, Jatmiko, Saptomo EW, Due RA, Djubiantono T, Morwood MJ, Jungers WL. 2007. The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* 317:1743–1745.
- Ungar P. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. *J Hum Evol* 46:605–622.
- Ungar PS, Grine FE, Teaford MF. 2008. Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLOS One* 3:e2044.
- Ungar PS, Scott RS, Grine FE, Teaford MF. 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. *Philos Trans R Soc B* 365: 3345–3354.
- Ungar PS, Sponheimer M. 2011. The diets of early hominins. *Science* 334:190–193.
- Van der Merwe NJ, Masao FT, Bamford MK. 2008. Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *S Afr J Sci* 104:153–155.
- Villmoare BA, Kimbel WH. 2011. CT-based study of internal structure of the anterior pillar in extinct hominins and its implications for the phylogeny of robust *Australopithecus*. *Proc Nat Acad Sci USA* 108:16200–16205.
- Vinyard CJ, Wall CE, Williams SH, Hylander WL. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. *Am J Phys Anthropol* 120:153–170.
- Vinyard CJ, Wall CE, Williams SH, Mork AL, Armfield BA, Melo LCD, Valenca-Montenegro MM, Valle YBM, de Oliveira MAB, Lucas PW, Schmitt D, Taylor AB, Hylander WL. 2009. The evolutionary morphology of tree gouging in marmosets. In: Ford SM, Porter LM, Davis LC, editors. *The smallest anthropoids: the marmoset/callimico radiation*. New York: Springer. p 395–409.
- Vinyard CJ, Wall CE, Williams SH, Schmitt D, Hylander WL. 2001. A preliminary report on the jaw mechanics during tree gouging in common marmosets (*Callithrix jacchus*). In: Brooks A, editor. *Dental morphology 2001: Proceedings of the 12th International Symposium on dental morphology*. Sheffield: Sheffield Academic Press. p 283–297.
- Vinyard CJ, Yamashita N, Tan CL. 2008. Linking laboratory and field approaches in studying the evolutionary physiology of biting in bamboo lemurs. *Int J Primatol* 29:1421–1439.
- Wallace JA. 1972. The dentition of the South African early hominids: a study of form and function. Ph. D. Thesis. Witwatersrand: University of the Witwatersrand.
- Wallace JA. 1973. Tooth chipping in the australopithecines. *Nature* 244:117–118.
- Walker A. 1981. Diet and teeth: dietary hypotheses and human evolution. *Philos Trans R Soc Lond B Biol Sci* 292:57–64.
- Walker A, Leakey REF, Harris J, Brown F. 1986. 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature* 322:517–522.
- Wang Q, Strait DS, Dechow PC. 2006. A comparison of cortical elastic properties in the craniofacial skeletons of three primate species and its relevance to human evolution. *J Hum Evol* 51:375–382.
- Weber GW, Bookstein FL, Strait DS. 2011. Virtual anthropology meets biomechanics. *J Biomech* 44:1429–1432.
- Wood BA. 1988. Are “robust” australopithecines a monophyletic group? In: Grine FE, editor. *Evolutionary history of the “robust” australopithecines*. New York: Aldine de Gruyter. p 269–284.
- Wood BA, Harrison T. 2011. The evolutionary context of the first hominins. *Nature* 470:347–352.
- Wood BA, Schroer K. 2012. Reconstructing the diet of an extinct hominin taxon: the role of extant primate models. *Int J Primatol* 33:716–742.
- Wood BA, Strait DS. 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *J Hum Evol* 46:119–162.
- Wright BW. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. *J Hum Evol* 48:473–492.
- Wright BW, Sadler B, Prodhon R, Ulibarri L, O’Brien J, Covert HH, Nadler T. 2008. It’s tough out there: variation in the toughness of ingested leaves among four colobines in Vietnam. *Int J Primatol* 29:1455–1466.
- Wright BW, Wright KW, Chalk J, Verderane M, Fragaszy D, Visalberghi E, Izar P, Ottoni E, Constantino PJ, Vinyard C. 2009. Fallback foraging as a way of life: using dietary toughness to compare the fallback signal among capuchins and implications for interpreting morphological variation. *Am J Phys Anthropol* 140:687–699.
- Zienkiewicz OC, Taylor RL, Zhu JZ. 2005. *The finite element method: its basis and fundamentals*, 6th ed. Oxford: Elsevier.