



Human Palaeontology and Prehistory

Functional morphology, biomechanics and the retrodiction of early hominin diets



Morphologie fonctionnelle, biomécanique et rétrodiction du régime alimentaire des premiers hominins

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ABSTRACT

A fundamental axiom that underlies evolutionary biomechanics maintains that natural selection has adapted skeletal and dental morphologies to facilitate function in intelligible ways. Because selection is held to result in the improvement of functional design, it is thought possible to predict the adaptive significance of a morphological feature from a design criterion. This rationale has been widely applied to the interpretation of morphological complexes in the paleontological record for which no strict extant analogues exist. In particular, biomechanical models have been used to infer the dietary habits of extinct hominin taxa from aspects of craniodental morphology. Many of these models are hampered by missing data and loosely justified assumptions. Craniodental morphologies may indicate more about what an extinct species was capable of processing intra-orally – and probably more about its phylogenetic history – than the constitution of its diet. Even a dedicated leaf-eating hominin cannot be expected to have possessed bilophodont molars. The dietary retrodictions based on comparative anatomical that have been proffered for Plio-Pleistocene hominin species are reviewed here. We argue that the application of finite element analysis to these fossils has not revealed convincing evidence of specific feeding behaviors. Indeed, the conclusions from these biomechanical models are often incongruent with data from stable light isotopes, microwear and phytolith analysis; nor do they conform with observations on the dietary repertoires and feeding behaviors of extant primates. For example, the sooty mangabey (*Cercocebus atys*) is a committed hard object feeder, but suffers no deleterious consequences from the “poor design” of its facial skeleton for processing hard foods. Because primates are adept at behaviorally circumventing mechanical problems, it is perhaps useful to consider the breadth of any fossil hominin's feeding

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repertoire in the context of behaviors that enable mechanical problems to be dealt with prior to ingestion.

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Un axiome fondamental sous-jacent à l'analyse évolutive de la biomécanique soutient que la sélection naturelle a permis les adaptations du squelette et des dents en facilitant leur fonction de manière intelligible. Puisque la sélection sous-tend à améliorer le patron fonctionnel, il est généralement estimé possible de prédire la valeur adaptative d'une caractéristique morphologique à partir d'un modèle. Ce raisonnement a été largement appliqué pour interpréter des complexes morphologiques dans le registre paléontologique pour lequel il n'existe pas d'équivalents actuels. En particulier, les modèles biomécaniques ont été utilisés pour déduire les habitudes alimentaires des taxons hominins éteints à partir de la morphologie cranio-dentaire. Nombre de ces modèles sont limités par des données manquantes et des suppositions vaguement justifiées. La morphologie cranio-dentaire peut vraisemblablement nous renseigner davantage sur les capacités d'un taxon éteint à traiter les aliments dans sa cavité buccale – et probablement plus encore sur son histoire phylogénétique – que sur la constitution de son régime alimentaire. Même un hominidé spécialisé dans une alimentation folivore n'a pas forcément des molaires bilophodontes. La rétrodiction du régime alimentaire basée sur l'anatomie comparée telle qu'elle a été appliquée aux taxons hominins plio-pléistocènes est examinée ici. Nous discutons le fait que l'application d'analyses par éléments finis à ces fossiles n'a pas révélé d'éléments convaincants concernant des habitudes alimentaires particulières. En effet, les conclusions basées sur ces modèles biomécaniques sont souvent contradictoires avec les données issues de l'analyse des isotopes stables légers, des micro-usures et des phytolithes, et ne sont pas non plus compatibles avec les observations sur les répertoires alimentaires et les habitudes de nutrition des primates actuels. Par exemple, le mangabey couronné (*Cercocebus atys*) est spécialisé dans la consommation d'aliments durs, mais ne souffre aucunement de la « faible constitution » de son squelette facial pour mastiquer de la nourriture dure. Parce que les primates sont des experts pour contourner de manière comportementale des problèmes biomécaniques, il serait peut-être utile de considérer l'ensemble des possibilités du répertoire alimentaire de chaque hominidé dans un contexte comportemental qui inclut la possibilité de faire face aux problèmes biomécaniques avant ingestion.

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1. Introduction

A fundamental axiom that underlies evolutionary biomechanical analyses holds that most osseous, muscular and dental features have been adapted by natural selection to facilitate function in intelligible ways (Kummer, 1972; Lauder, 1996). Accordingly, because selection is held to result in improvement of structural “design” in relation to function, it is deductively sound to conclude that one should be able to predict the function of a particular morphological attribute from its morphology. This design criterion is central to Rudwick's (1964) “paradigm method”, which has been widely applied to the interpretation of structures in the paleontological record for which there are no strict extant analogues. Despite the teleological underpinnings of the approach, it has been useful for generating hypotheses in paleontological contexts. However, the recognition of the pervasiveness of phylogenetic and developmental constraints on morphological variation (e.g., Alberch, 1982; Breuker et al., 2006; Klingenberg, 2008; Lauder, 1981; Narita and Kuratani, 2005; Plotnick and Baumiller, 2000; Reif et al., 1985; Richardson and Chipman, 2003; Rose and Lauder, 1996; Tseng and Flynn,

2015) has resulted in the paradigm being recognized by most (but seemingly not all) workers as merely a heuristic benchmark of design optimization rather than the inevitable outcome of selection. This understanding raises the possibility that detailed functional analyses of fossil forms may be intractable, particularly if the goal is to recreate elaborate biomechanical models based on missing data and loosely justified assumptions (Anderson et al., 2012).

Unfortunately, these difficulties, be they operational or theoretical in nature, are easily overlooked when analytical techniques promise unprecedented resolution, and perhaps insight, into function. For example, because finite element analyses purportedly provide a detailed and comprehensive depiction of the stress environment in fossil forms, they have become extremely popular tools for biomechanical analysis (Rayfield, 2007). This enthusiasm is understandable when it is claimed that such analyses can be used to retrodict the dietary habits of extinct hominin taxa (Ledogar et al., 2016; Smith et al., 2015; Strait et al., 2009, 2010, 2013; Wroe et al., 2010). Such inferences have been met with skepticism for a number of reasons, including concern over proximate methodological factors such as boundary conditions (i.e. the validity of model

assumptions) and more general theoretical issues over the causal linkage of ecology to morphology (e.g., Daegling et al., 2013; Grine et al., 2010; Gröning et al., 2011, 2012a, 2012b).

With constraint being recognized as ubiquitous in evolutionary processes (e.g., Galis et al., 2001; Gaunt, 1994; Gould, 1980; Hlusko, 2016; Klingenberg, 2008; Losos and Miles, 1994; Wagner, 2014), no rational biologist embraces the idea of optimality or perfection of design as the criterion of adaptation. However, across a gamut of methodological approaches, some specified optimal criterion (e.g., “sharp teeth are for slicing”) commonly serves as a benchmark for comparison. In theory, we may all appreciate the difficulties of recognizing adaptation, but in practice (i.e. within particular investigations) there is a tendency for researchers to become more susceptible to reductionist explanations.

For example, with respect to the australopith dentition, the statement that “the inferred poor performance of [...] teeth at processing compliant and tough foods is incompatible with a hypothesis that such teeth are adapted to feeding on those foods” (Strait et al., 2013: 341) is teleological at core. This does not invalidate the inference *per se*, but such a conclusion ignores the constraints of phylogeny and developmental genetics, and in so doing allows the dietary specification that excludes such foods (Ungar and Hlusko, 2016). Even when isotopic and microwear evidence both indicate that a species such as *Paranthropus boisei* consumed tough C₄ foods (such as grass blades and/or sedge pith), the biomechanical interpretation of its facial architecture and blunt occlusal topography is instead taken to indicate that it was “adapted to consume hard foods” (Smith et al., 2015). As such, the “Nutcracker Man” paradigm prevails.

There is ample evidence that the distribution and mechanical properties of food items may impact skeletal and dental morphologies related to their procurement, ingestion and mastication (Anthony and Kay, 1993; Bunn and Ungar, 2009; Daegling, 1992; Hylander, 1975; Kay, 1975, 1978; Kinzey, 1978; Lucas et al., 1986; McGraw, 1998; McGraw and Daegling, 2012; McGraw et al., 2012; Menegaz et al., 2010; Nash, 1986; Norconk et al., 2009; Ungar, 1996; Vinyard et al., 2003; Winchester et al., 2014; Wright, 2005; Yamashita, 1998, 2009). As a result, various anatomical attributes have been the subject of study in attempts to infer the dietary habits of extinct hominin species (e.g., Berthaume et al., 2010; Dumont et al., 2011; Lucas et al., 1985, 2008a; Macho, 2014; Macho and Shimizu, 2010; Macho et al., 2005; Rak, 1978, 1983, 1988; Rak and Hylander, 2008; Smith et al., 2015; Strait et al., 2009, 2010; Ungar, 2004, 2007; Wallace, 1975; Wroe et al., 2010). However, the success of these biomechanical inferences has been anything but uniform (Daegling, 2010; Daegling and Grine, 2007, 2017; Daegling et al., 2011, 2013; Grine et al., 2010; McGraw and Daegling, 2012; Ross et al., 2012). They have been limited by the challenge of successfully distinguishing among the many biomechanical and non-mechanical influences on cranial, mandibular and dental form.

The fact that a good number of morphological configurations appear to be explicable with reference to the

biological roles that they serve (Gans, 1988; Hildebrand, 1988) is testament to the potential of functional morphology to inform adaptive inferences. Even so, exactly how closely the structure of a trait can be related to its apparent biological function remains a topic of discovery.

Constructional morphology, the concept introduced by Weber (1955) under the name “Konstruktionsmorphologie” to characterize the operational interconnections between form and function, served to formalize the idea that “functional interpretation was a necessary but not sufficient explanation of organic form” (Reif et al., 1985: 129). This school of thought presaged the contribution of Gould and Lewontin (1979), which led most evolutionary biologists to acknowledge the folly of assuming that an organism can be viewed simply as a collection of adaptively optimized features that evolved by relentless and unfettered natural selection. Their articulation of the spandrels concept provided a repudiation of the paradigm method as a means for inferring adaptation, and since then it has become widely accepted that consideration must be paid to constraints, whether phylogenetic, genetic and/or developmental (Albertson and Kocher, 2006; Beldade et al., 2002; Bolker, 2000; Brakefield, 2006; Brakefield and Roskam, 2006; Brakefield et al., 2003; Cheverud, 1984; Salazar-Ciudad and Jernvall, 2002; Galis et al., 2001; Kangas et al., 2004; Maynard Smith et al., 1985; Ross et al., 2002; Ungar and Hlusko, 2016; Witmer, 1995). Consequently, Rudwick’s (1964) paradigm of structural optimality is ill-suited to be the ultimate arbiter of adaptation.

Moreover, diet is not the same thing as dietary adaptation. Presumably, selection acts to enable a species to process critical food resources with some degree of efficiency, but it does not necessarily dictate what can or cannot be eaten. Craniodental morphologies may tell us more about what an extinct species (or a particular individual) was capable of eating – or perhaps more about its phylogenetic history – than the constitution of its diet.

1.1. Adaptation and adaptationism

The adaptationist paradigm, which usually translates to a direct and predictive form–function relationship insofar as trophic phenotypes are concerned, has been famously criticized as Panglossian story-telling (Gould and Lewontin, 1979). The concept of adaptation is central to evolutionary theory because it relates to the causal mechanism of natural selection. As such, adaptation can be defined simply as the property of phenotypic (i.e. morphological and/or behavioral) features in relation to the selective demands of the environment (Bock, 1980). However, adaptation does not necessarily indicate a precise or even a close fit between the form and the function(s) (i.e. the biological role[s]) of a particular feature (Bock and von Wahlert, 1965; Godfrey-Smith, 2001; Lewens, 2009; Ross et al., 2002 and references therein). Unfortunately, the inductive fallacy that has ensnared generations of evolutionary morphologists is that if a trait is consistent with the hypothesis that it is an adaptation (which, by definition, has been shaped by natural selection), this is then taken as good evidence for the truth of the hypothesis (Pigliucci and Kaplan, 2000; Williams, 1966).

As aptly observed by [Bock \(1980\)](#), the state of *being* adapted is independent of the process of *becoming* adapted because an adaptation needs not evolve under the control of the same selective forces to which it is presently recruited. Thus, the observed state of any given trait is independent of whether it underwent the process of adaptive evolution in response to the same selective forces to which it is seemingly now adapted. [Bock \(1980: 224\)](#) notes that “adaptive features do not have to evolve by adaptive evolution, and features that have evolved adaptively may no longer be adaptive.” This notion also differs fundamentally from the perception of adaptation expressed by [Lauder \(1996\)](#) as “a trait that enhances fitness and that arose historically as a result of natural selection for its current biological role”. Notwithstanding his definition of adaptation, [Lauder \(1995\)](#) nevertheless recognized that the precise prediction of aspects of organismal function from morphology necessarily assumes a close match between structure and function, and that this assumption is unwarranted in many instances. Here too, the distinction between biological role and adaptation is critical.

1.2. Animals are products of their evolutionary heritage

Phylogenetic context provides a necessary source of information by which to gauge the strength of dietary inference from comparative functional studies because it may inform how constraints can limit form-function-behavior relationships (even if the precise nature of these constraints is currently undiscovered). Unfortunately, as noted by [Ross and Iriarte-Diaz \(2014\)](#), many biomechanical studies of primate feeding over the last few decades have neglected any consideration of phylogeny.

Genetically-determined ancestral patterns of morphology may simply be retained passively or through patterns of developmental constraint as plesiomorphies in descendant taxa, and thus what might be recognized as “robust” traits need not involve directional selection. Such “phylogenetic inertia” may be rooted in pleiotropy, genetic linkage, or developmental pathways that can impose constraints. Consideration of phylogenetic history is important in establishing the constraints under which morphology could have been adaptively modified by selection. As aptly observed by [Hildebrand \(1988: 728\)](#), “No amount of field observation or biomechanical analysis can fully explain form. We must know the history, the phylogeny.”

Thus, the high cusps and crests that adorn the cheek teeth of colobine monkeys are well-suited for shredding leaves, but this does not compel the conclusion that bilophodonty represents an obligate adaptation for folivory among primates. If a dedicated leaf-eating hominin had existed in the past, it would be rash to suggest that bilophodonty would be a decisive condition for inferring folivory in such a species. Because the low, bulbous and thickly enameled cusps of australopith cheek teeth are seemingly ill-equipped to process displacement-limited (i.e. tough) foods (e.g., sedges), some workers (e.g., [Strait et al., 2008, 2009, 2010](#); [Wood and Schroer, 2012](#)) have argued that any hypothesis that incorporates such foods can be discounted. While it should be acknowledged that *Paranthropus* molars are suboptimal for shredding fibrous

items, these teeth can also be viewed as representing a biological entity that is contingent upon not only a range of possible functions, but also the dentition of its predecessor ([Ungar and Hlusko, 2016](#)).

1.3. Constraints and adaptation

The predicted outcome of a morphological trait under a model of adaptive selection may fail if that trait is genetically and/or developmentally correlated with (i.e. constrained by) others that are under conflicting pressures ([Lande, 1979](#)). At the same time, however, developmental integration could be a major factor maintaining a relatively stable covariance structure of functionally related traits during the evolutionary diversification of a lineage ([Marroig and Cheverud, 2001](#)). Constraints, which may result in modularity of traits through integration, can affect the evolution of complex morphological systems by altering levels of evolutionary flexibility ([Cheverud, 1984](#)). Comparative studies have revealed differences in magnitudes of integration and modularity in the skulls of different mammalian (including primate) lineages, where enhanced “modularization” enables a broader spectrum of evolutionary response ([Porto et al., 2009](#); [Shirai and Marroig, 2010](#)). Modularity that affects morphological variation can be thought of in terms of the developmental and genetic components that may impact the ability to respond to functional selective pressures. Traits that perform one or more roles interact functionally through modularity ([Klingenberg, 2008](#)).

There is strong experimental evidence that inactivation of specific genes can disrupt development of the (mouse) mandible, and that these developmental disturbances can affect different parts of the mandible either separately or in concert. Some 37 quantitative trait loci have been identified as affecting aspects of mandibular size and shape ([Cheverud et al., 1997](#); [Klingenberg and Leamy, 2001](#); [Klingenberg et al., 2001](#); [Leamy et al., 1997, 1999](#)). Subsequent ontogenetic changes in form through modeling under mechanical load are similarly spatially structured ([Klingenberg et al., 2001](#)). Despite the expectation that ontogenetic growth trajectories should be under strong directional selective pressure, studies have found high levels of standing additive genetic (co)variance for growth trajectories. Additive genetic (co)variance is higher early on and decreases with age ([Irwin and Carter, 2013](#)). On top of this, plastic responses to altered loads during growth may induce changes in gene- and protein-expression patterns, which ultimately affect anatomical and functional variation ([Ravosa et al., 2007, 2008](#)). Interestingly, and perhaps unexpectedly, such epigenetic changes appear to influence the phenotypes of subsequent generations ([Agrawal, 2001](#); [Pigliucci et al., 2006](#); [West-Eberhard, 2005](#)).

Given the confusion that may surround adaptation and constraint, [Pigliucci and Kaplan \(2006: 128\)](#) have proposed a minimum of five essential questions that should be addressed when dealing with a trait of interest:

- how did it arise?
- how does it develop?

- how is it reproduced?
- how (and why) did it spread through the population?
- why (and how) is it being maintained in the population?

Obviously, some of these questions will be resistant to exploration in the fossil record. As noted by Brakefield (2006: 367), “Integrative research on generative constraints in which genetic variation and developmental mechanisms are explored together with natural selection and the performance of phenotypes is necessary to progress beyond the level of ‘just-so stories’”. The task before the paleontologist is formidable.

2. Liem's Paradox and the convenience of fallback foods

Karel Liem's (1980) studies of African cichlid fishes led him to observe that apparently specialized feeders frequently consume nonspecialized resources. Animals may actually avoid those foods to which their craniodental traits are seemingly adapted when more nutritious or more easily consumed and digested items are available to them. This seemingly contradictory phenomenon, which has been dubbed “Liem's Paradox”, highlights inconsistencies between trophic morphologies that are identified as adaptive and actual ecological observations (Binning et al., 2009; Lambert et al., 2004; Liem and Summers, 2000; Robinson and Wilson, 1998). Thus, for example, gorillas possess long molar shearing crests and are capable of processing very tough foods, but will choose fruits that are high in non-starch sugars over more highly fibrous items when they are able to do so (Remis, 2002). Still, it is the leaves and pith that are consumed when preferred fruits are unavailable to which gorilla teeth are seemingly adapted. Similarly, Norconk and Veres (2011) have presented a strong case that pitheciin monkeys (specifically *Pithecia* and *Chiropotes*) exemplify Liem's Paradox. These primates possess heavily decussated enamel (Martin et al., 2003) and molars with low cuspal shearing relief (Ledogar et al., 2013), traits that have been argued to represent specializations for seed predation. However, these monkeys open very hard pericarps only rarely; most of the fruit consumed falls into the hardness category of foods eaten by a wide variety of primates that lack such dental features.

As noted by Kinzey (1978: 378), “when a food item is critical for survival, even though not part of the primary specialization, it will influence the selection of dental features.” Fallback food items that are consumed only rarely are likely to have significant mechanical defenses and lower energy yields; as such, they are the very items that may require dental specializations. The question of whether a given trophic feature in an extinct species reflects phylogenetic inertia, an adaptation to preferred foods, or an adaptation to processing important albeit less commonly eaten fallback items is not a trivial one in the pursuit of dietary reconstruction.

The potentially important role of fallback foods as selective agents in the evolution of trophic morphologies has been the subject of a number of studies (Constantino and Wright, 2009; Lambert, 2007; Lambert et al., 2004; Marshall and Wrangham, 2007). Lambert et al. (2004)

presented evidence that suggested that thick tooth enamel in the grey-cheeked mangabey (*Lophocebus albigena*) to be an adaptation to the hard foods consumed during critical fallback episodes (but see McGraw et al., 2012).

On occasion, fallback foods feature in hypotheses that seek to explain trophic morphologies even in the face of decidedly contradictory evidence. For example, Ledogar et al. (2013) attempted to relate the differences in molar topography between *Pithecia* and *Chiropotes* to differences in fallback resources, despite the fact that Norconk and Veres (2011) had earlier specifically discounted the pertinence of a fallback strategy. Indeed, Norconk and Veres (2011) concluded that apparently specialized dentition of pitheciins affords them access to relatively abundant and high-quality resources with minimal seasonal variation in resource availability.

Fallback foods have understandably received considerable attention with respect to interpretations of the hominin fossil record (e.g., Dominy et al., 2008; Laden and Wrangham, 2005; Scott et al., 2005; Wrangham et al., 2009), and have been invoked as possible explanations for the discrepancy between diet related molar microwear and masticatory morphologies in species such as *Australopithecus afarensis* (Grine et al., 2006b) and *P. boisei* (Ungar et al., 2008). On the other hand, the notion that microwear traces of fallback foods should be especially visible in the fossil record because of the belief that “many individuals die during periods of food scarcity, and [...] it is during these periods that fallback foods are consumed” (Constantino and Wright, 2009: 601) has been shown to be erroneous (Gogarten and Grine, 2013). Data on primate mortality suggest that fallback episodes are no more likely to be visible paleontologically than any other period of time.

Since fallback food episodes are unlikely to be oversampled in the fossil record, they have the potential to remain as convenient and untestable explanations for perceived morphological adaptations. In the paleoanthropological context, hypotheses relating to fallback foods have proven to be malleable to a fault because they can survive any number of logical contortions once fallback episodes are deemed “invisible” in the fossil record. The reality of fallback foods as being of potential adaptive significance is not a matter of debate, but their invocation as such must be supported by something other than convenient, *ad hoc* rationalization. It is in this context that fallback food has become a favorite fallback hypothesis.

While fallback explanations can be valid, the issue concerns their resistance to testability in paleontological contexts (Kimbel and Deleuzene, 2009; McGraw and Daegling, 2012).

3. Mechanical loads and biomechanical inferences

3.1. Bones – crania and mandibles

Mechanical loads clearly influence the skeletal system, but it is not clear to what extent mechanical environments dictate particular morphologies. Bone material serves to equalize peak stress (or strain) levels within a narrow band of “optimal” magnitudes in long bone diaphyses (Rubin and Lanyon, 1984), but this relationship varies even among

different regions of the shaft (Judex et al., 1997; Rubin et al., 2013). The ubiquity of strain gradients in the skull (Hylander and Johnson, 1992; Ross and Metzger, 2004) establishes that bone does not adapt to a state of maximum strength with a minimum of material. While minimum levels and frequencies of strain seem to be required for bone to produce a physiological response (Beecher et al., 1983; Bouvier and Hylander, 1984; Lanyon and Rubin, 1985), defining these minimal values is far from straightforward (Gross and Srinivasan, 2006; Qin et al., 1998). Moreover, peak strain values may differ significantly across the skeleton (Ravosa et al., 2010), and the presence of such gradients implies the existence of local, site-specific controls on bone formation and maintenance (Goodship et al., 1979; Hylander and Johnson, 1997; Ravosa et al., 2010).

Adding to this complexity, patterns of bone material response to mechanical stimuli in long bone shafts do not translate easily to the skull (Daegling, 2010; Hylander and Johnson, 1992, 1997; Ravosa et al., 2010). Indeed, experimental evidence strongly suggests that mechanobiological influences are not uniform across the craniofacial region (Hylander et al., 1991; Ravosa et al., 2000; Ross and Hylander, 1996). Thus, across a range of species, significant strain disparities have been demonstrated between the lower facial and circumorbital regions of the skull (Hylander et al., 1991). The latter maintains considerably larger amounts of bone than is needed to resist masticatory loads (Hylander and Johnson, 1997; Hylander et al., 1991). This calls into question the value of biomechanical models that assume circumorbital – and especially supraorbital – features are adapted for resisting masticatory stresses (cf., Bookstein et al., 1999; Ravosa et al., 2000). It is unwise to assume that the entire primate facial skeleton is first and foremost an adaptation to accommodate masticatory forces (Daegling et al., 2013; Ross and Iriarte-Diaz, 2014). The robusticity of the mandibular corpus may be related more directly to allometric considerations than to dietary factors (Ravosa, 1990), and other aspects of jaw morphology (e.g., symphyseal depth) may be artifacts of somatic scaling that secondarily affect masticatory biomechanics (Smith, 1993).

Comparative anatomy and biomechanical analyses may serve to bracket a range of behavioral capabilities, but these approaches are inherently limited in their capability to identify specific adaptation in paleobiological contexts. The application of finite element analysis (FEA) to the hominin fossil record has demonstrated that under similar loading conditions, the form of the stress field in an australopithecine facial skeleton may differ from that in some extant primates (Dzialo et al., 2014; Ledogar et al., 2016; Smith et al., 2015; Strait et al., 2009, 2010, 2013; Wroe et al., 2010). Depending on one's perspective, connecting the different stress fields to different feeding adaptations is either eminently logical or a leap of faith (Daegling et al., 2013). Biomechanical studies may inform about the physical performance attributes of a morphological feature, but the biologically important question is whether these attributes have a tangible effect on fitness (which is implicit in the identification of adaptation). With regard to osseous traits involved in mastication, it is necessary to realize that both load magnitude and frequency have been implicated in bone metabolic activity

that results in changes in the mass and architectural properties of skeletal elements (Judex et al., 2006; Ozcivici et al., 2009; Qin et al., 1998; Ravosa et al., 2007; Rubin et al., 1990, 1991). Thus, a given jaw structure may be responsive to high chewing loads and/or low but frequent chewing loads.

The presence of strain gradients is evidence that primate crania are *not* optimized to dissipate or resist the stresses engendered by feeding forces that might be associated with different diets, but rather there appears to be a relationship between skull morphology and the ability to *generate* feeding forces (Ross and Iriarte-Diaz, 2014). Even in this regard, however, caution should be exercised when attempting to draw conclusions about the type of diet or food mechanical properties that may relate to force generation. The crania of colobine monkeys have larger areas of attachment of the masseter muscle than do cercopithecines monkeys, and colobines are more folivorous (Ravosa, 1990). Colobine crania also exhibit greater mechanical advantage to generate feeding forces than cercopithecines. This is an effect of their having shorter faces, and Hylander (2013) has argued that canine size is a prime driver of facial length because of gape requirements. Thus, the reduced mechanical advantage of long-faced cercopithecines does not have any necessary connection to relaxed dietary requirements (however these might be defined). On the other hand, colobines that consume more seeds have better mechanical advantage of the masticatory muscles than those that do not (Koyabu and Endo, 2010), and platyrrhine monkeys that harvest sclerocarps tend to present larger chewing muscles than their close relatives that do not prey upon seeds (Kay et al., 2013).

With reference to chewing, the processing of tough, fibrous foods entails increased cycle number in association with higher occlusal forces (Hylander, 1979). As such, mandibular morphology *per se* cannot distinguish between potential adaptations to feeding on either tough or hard items (Daegling and Grine, 2007, 2017; Hylander, 1988). There is a remarkable diversity of corpus shape associated with hard object feeding in primates (Daegling, 1992; Daegling and McGraw, 2001, 2007; Taylor, 2006), which means that similar feeding challenges do not necessarily have a singular morphological solution. As noted by Ross et al. (2012), because mandibular loading, stress, and strain regimes are determined by interactions among food mechanical properties, feeding behaviors, jaw kinematics and jaw morphology, it is difficult to discern whether similarities in chewing kinematics also translate to similarities in loading, stress and strain. It is not always clear what loading variables and specific morphological features of the mandible are of importance (Gröning et al., 2011; Shi et al., 2012). Data on food material properties do not effectively map mandibular form to diet (Ross et al., 2012). The relationship between food material properties and mandibular morphology does not necessarily hold across all comparisons, which suggests that one cannot necessarily predict one from the other (Daegling and Grine, 2007, 2017).

This presents additional problems for dietary inference from the cranium, since the mechanical loading environment of the mandible is much better understood than is the rest of the facial skeleton (Ross et al., 2012). Distinguishing the relevant factors that influence craniofacial

form in order to make informed and reliable inferences about trophic behaviors and habits is a daunting task (Shi et al., 2012; Walmsley et al., 2013), made even more so by genetic and developmental constraints that can affect interpretation (Ungar and Hlusko, 2016). Given this present uncertainty, an agnostic stance on what facial morphology reveals about specific diets and/or dietary adaptations would seem to be warranted (Daegling et al., 2013).

3.2. Teeth – crown morphology and enamel structure

Perhaps even more than for bones, the forms and structures of teeth have been tied to dietary function. This is to be expected given the incredible diversity of mammalian dentitions and diets (Ungar, 2010). No less in primates than in many other mammalian groups, there is clearly an operational relationship between tooth form and function (Kay, 1975; Lucas, 2004; Ungar, 2010). However, as with bone, it is not clear to what extent specific mechanical environments (i.e. diets) dictate particular morphologies. Most attention to dietary relationships among primates, and especially the retrodiction of diet for extinct taxa, has been based on the form of the tooth crowns, and upon the thickness and structure of the enamel cap.

Premolar and molar crown relief – cusp height and “sharpness” – is commonly related to masticatory function, and to the types and/or physical properties of the foods that are processed (Lambert, 2010; Lucas, 2004; Ungar, 2010). In particular, quantitative analyses of dental topography that employ measures of relief (Boyer, 2008; Ungar, 2004; Ungar and Bunn, 2008; Ungar and Williamson, 2000), complexity (Evans et al., 2007) and Dirichlet normal energy (Bunn et al., 2011; Godfrey et al., 2012) have differentiated among groups of primates that differ in the types of foods they consume. To date, dental topographic analysis has been applied to only a few fossil species (e.g., Godfrey et al., 2012; Ungar, 2004). While these methods are encouraging, it is not at all clear to what extent they can differentiate between anything but the broadest dietary categories.

Because many mammalian dental features are correlated with one another and represent iterative processes that are dependent upon relatively simple alterations in signaling proteins, they are not independent of one another (Jernvall et al., 2000; Kangas et al., 2004; Kassai et al., 2005). Because many aspects of the dentition have the developmental potential for correlated change, this may obscure functional (and certainly dietary) inference. Indeed, Gailer et al. (2016) have shown that supposedly “essential functional adaptations” in cheek tooth morphology may not be required to process food efficiently in extant bovids.

Tooth enamel thickness has long been regarded as being sensitive to diet, or at least to the mechanical properties of the foods consumed (e.g., Constantino et al., 2012; Lucas et al., 2008b; Martin et al., 2003; Schwartz, 2000; Teaford, 2007; Vogel et al., 2008). In particular, because enamel thickness is expected to be able to respond quickly in evolutionary time to dietary/ecological change (Hlusko et al., 2004), differences in enamel thickness have been related to corresponding differences in the hardness of food items (Lucas et al., 2008b; Vogel et al., 2008). However, while there seems to be some general correspondence

between these two variables, the reliability of tooth enamel thickness as a dietary indicator clearly breaks down in some cases where phylogenetically closely-related species that consume different amounts of hard items are considered. For example, the expected differences between Bornean and Sumatran orangutan molars are not apparent (Smith et al., 2012), nor is there a predictable relationship among mangabey species (McGraw et al., 2012). Of course, other factors can account for the evolution of a thicker coat of enamel. Rabenold and Pearson (2011) postulated an alternative hypothesis that relates enamel thickness to exogenous abrasives that may be found on or in dietary items. In the nine primate species sampled, they found a strong correlation between the amount of abrasive silica phytoliths in the diet and molar enamel thickness. In other words, it is not only resistance to fracture, but also resistance to prolonged wear to which enamel thickness can be related (Pampush et al., 2013).

Tooth enamel structure has been regarded as being sensitive to diet, or at least the mechanical properties of the foods consumed (e.g., Chai et al., 2009; Popowicz et al., 2004; Shimizu and Macho, 2008; Teaford, 2007; von Koenigswald and Pfretzschner, 1991). To date, however, there have been very few studies that have considered the degree of variation in structural features within teeth (e.g., prism decussation; Lynch et al., 2010). Indeed, most of the mechanical models for tooth enamel developed to date have been highly theoretical, being based on the behavior of glass, ceramics and polymer resins rather than actual dental tissues (Kim et al., 2007; Lucas et al., 2008b; Qasim et al., 2007; Rhee et al., 2001). Yet another theoretical study by Shimizu and Macho (2008) concluded that it is not possible to predict the absolute strength of a tooth unless its chemical composition is known, although they failed to determine the critical variables at the molecular level. It would seem that predicting tooth strength is problematic, especially since teeth are complex, composite structures.

It is perhaps noteworthy that the hyper-thick enamel and massive, low-cusped molars of *P. boisei*, a species envisioned by many as the quintessential hard object feeder (e.g., Constantino et al., 2011; Kay, 1985; Macho, 2014; Wood and Strait, 2004), exhibit little enamel decussation in comparison to the molars of *Homo* (Beynon and Wood, 1986). Nonetheless, the rounded, blunt cusps and the presence of well-developed Hunter-Schreger bands in the enamel of sea otters have led to their being proposed as a model from which to infer that species like *P. boisei* most likely consumed hard food objects with substantially higher biting forces than those exerted by modern humans (Constantino et al., 2010, 2011). The logic is that if sea otters, which possess thinner enamel than hominins, can process mollusk shells and the tests of sea urchins, then *P. boisei* must have been superbly well-adapted to crack hard objects with powerful bite forces (Constantino et al., 2010, 2011). Of course, this is not the first time that otters have been employed as analogies for *Paranthropus* feeding adaptations. Shabel (2005, 2007, 2008) envisioned *P. robustus* as a crab-eating durophage, with the Cape clawless otter (*Aonyx capensis*) as its trophic analogue. Here again, the critical consideration in the paleontological context is whether what *could* have been eaten constitutes evidence

for what was, in fact, consumed. If the latter is not true, then the adaptive inference is invalid.

4. Applications to extinct hominins

A variety of biomechanical studies have yielded statements concerning the dietary habits of extinct hominin species. Australopithec evolution, regardless of the details of specific phylogenetic hypotheses, is generally thought of as having been characterized by an increased buttressing of the facial skeleton and a concomitant increase in postcanine dental size and enamel thickness through time. The central question for dietary reconstruction is precisely what these features reflect in terms of feeding behavior.

Studies of morphological adaptation to diet in extinct hominin taxa all too often consider their results in isolation, where the nature of the structure under consideration (be it a tooth, the structural configuration of tooth enamel, or facial architecture) is seen as dictating the range of dietary options available to a species. But primates are behaviorally adept at circumventing mechanical problems (Boesch and Boesch, 1982; Ottoni and Izar, 2008). As such, it might be useful to consider the breadth of any fossil hominin's feeding adaptations in the context of a behavioral phylogenetic bracket between *Pan troglodytes* and *Homo sapiens*. Like cebid monkeys, both can deal with the problem of eating hard objects by mitigating it prior to ingestion, thereby bypassing the requisite performance capability of the masticatory apparatus.

It is both reasonable and parsimonious to assume that australopithec also had the behavioral capacity to alleviate at least some dietary challenges.

Notwithstanding this behavioral “black box”, what sorts of inferences about extinct hominin diets have been drawn from biomechanical considerations? Are these inferences, which are essentially based on measures of performance capabilities, congruent with paleontological data (e.g., stable isotope analysis and occlusal microwear) that more directly reflect ingested foods?

4.1. *Ardipithecus ramidus*

The postcanine dentition of *Ar. ramidus*, which is comparatively small and thinly-enameled, has been viewed as lacking the adaptations for heavy chewing and the consumption of abrasive foods, suggesting instead an omnivorous diet dominated by frugivory (Suwa et al., 2009). These inferences find consilience with the microwear signals and isotopic values obtained for *Ar. ramidus* tooth enamel (Suwa et al., 2009; White et al., 2009). The latter are consistent with a diet dominated (85–90%) by C₃ plant sources such as the flowers, fruits, seeds and leaves borne by trees.

4.2. *Australopithecus anamensis*

Australopithecus anamensis tooth morphology has been interpreted as indicating a shift in food resources to harder (Ward et al., 1999, 2001), tougher (White et al., 2006), harder and tougher (Macho et al., 2005), or perhaps more abrasive (Teaford and Ungar, 2000; White et al., 2006)

items. In particular, the thick enamel caps and pattern of enamel decussation have suggested adaptation for “habitually consuming a hard-tough diet” (Macho et al., 2005: 310) or a “tougher and probably harder and abrasive diet” (Macho and Shimizu, 2010: 30).

However, thickly enameled, low-cusped molars would have difficulty processing tough foods, whereas they would easily break down hard, brittle items (Lucas, 2004; Strait et al., 2009). As noted above, although enamel thickness and decussation have been claimed to carry an “unambiguous adaptive signal in relation to diet” (Lucas et al., 2008b: 383), neither appear to be perfectly correlated with food type. While the crack-stopping properties of decussated enamel prisms is reasonably well-established (e.g., Cuy et al., 2002; Hassan et al., 1981; He and Swain, 2007; Popowicz et al., 2001, 2004; Rasmussen et al., 1976; Xu et al., 1998), quantification of the form and degree of decussation has been difficult to achieve.

The occlusal microwear fabrics documented for *Au. anamensis*, although determined from a paltry sample of only three individuals, does not resemble those of extant hard object feeders (Grine et al., 2006a; Ungar et al., 2010). Rather, they appear to be reminiscent of the wear pattern described by Suwa et al. (2009) for *Ar. ramidus*. The *Au. anamensis* and *Ar. ramidus* specimens that have been sampled exhibit $\delta^{13}\text{C}$ values that differ very little (Cerling et al., 2013; White et al., 2009). Like the values for *Ar. ramidus*, those for *Au. anamensis* have a relatively narrow $\delta^{13}\text{C}$ range that is compatible with 90%–100% of the diet being comprised by C₃ resources (Cerling et al., 2013).

4.3. *Australopithecus afarensis*

White et al. (2000) argued that the postulated evolutionary trajectory from *Au. anamensis* to *Au. afarensis* involved an increase in postcanine tooth size and other adaptations to a “more heavily masticated” diet. In this context, such a diet may have involved larger forces alone (e.g., hard food items), or larger forces together with more chewing cycles (e.g., fibrous food items). Similarly, Ward et al. (2010) have conjectured that in the presumptive *Au. anamensis* – *Au. afarensis* lineage, “significant changes appear to occur particularly in the anterior dentition, but also in jaw structure and molar form, suggesting selection for altered diet and/or food processing.” Ungar (2004) observed that molar topographic relief in *Au. afarensis* implies that these teeth are well-suited to fracture brittle, less deformable foods but not as well-suited as the crowns of either gorillas or chimpanzees to fracture tough, more deformable foods. Because more bulbous cusps should allow transmission of higher stresses to a food item without engendering damage to themselves, Ungar (2004) suggested that the diet of *Au. afarensis* may have differed from that of *Pan* largely in hard, brittle fallback resources. In addition to the dental features enumerated above, *Au. afarensis* possesses very deep and robust mandibular corpora, tall mandibular rami, and robustly constructed zygomatic arches (Kimbel et al., 2004). As summarized by Kimbel and Delezene (2009: 40), *Au. afarensis* exhibits a number of craniodental attributes that are “conventionally

associated with ‘heavy mastication’ (however imprecisely defined) compared to extant great apes”.

In light of the morphology that has been described for *Au. afarensis*, the occlusal microwear data recorded for this species (Grine et al., 2006b; Ungar et al., 2010) suggest that the best modern analogs for the properties of the items that were consumed by the 19 individuals sampled are those extant primates (e.g., *Gorilla* and/or *Theropithecus*) which do not consume hard objects. Although *Au. afarensis* may have possessed the trophic apparatus to process a fairly wide range of foods, including hard, brittle items such as “nuts, seeds and hard fruit” (Wood and Richmond, 2000: 29), its molar microwear suggests that it did not always do so (at least those individuals that have been sampled do not appear to have done so during the periods in which their microwear fabrics were being formed). In the absence of any available isotopic data for *Au. afarensis*, Grine et al. (2006b) interpreted the constancy of its microwear across time and space as suggesting either that this species was able to track its preferred dietary resources in the face of changing habitats and environments, or that environmentally induced shifts in diet did not involve changes in mechanical properties of the foods typically consumed.

Subsequent isotopic analysis of some 20 specimens of *Au. afarensis* have shown that this species displays a significant range in the consumption of C₄-based resources (Wynn et al., 2013, 2016). The $\delta^{13}\text{C}$ values indicate more C₄ consumption on average than in earlier hominins such as *Ar. ramidus* and *Au. anamensis*. Wynn et al. (2013, 2016) also note a lack of any temporal pattern in the *Au. afarensis* isotope values, a finding consistent with the occlusal microwear data, which show little geochronological variation in this species. However, in contrast to the homogeneity exhibited by dental microwear, there is a wide range of variation in the carbon isotopic composition of *Au. afarensis* diet even within relatively brief temporal periods. Wynn et al. (2013, 2016) concluded that these opposing patterns suggest use of a mixture of C₃ and C₄ plant foods that may have varied little in terms of their mechanical properties.

It is unfortunate that none of the specimens of *Au. afarensis* from the Kada Hadar-2 submember of the Hadar Formation were found to preserve ante mortem microwear (Grine et al., 2006b), because it is in this sample that Lockwood et al. (2000) observed signs of an increase in jaw size. Fortunately, Wynn et al. (2013) were able to sample five specimens – including three associated with large jaws – from this temporal interval. With reference to the question of the relationship (or lack thereof) between isotope values and morphology, these five specimens show exactly the same spread of $\delta^{13}\text{C}$ values as the older Hadar Formation samples. In other words, there is no discernible change in diet (as deduced from stable isotopes) associated with an increase in mandibular (and presumably body) size in *Au. afarensis*.

4.4. *Australopithecus africanus*

The morphological attributes of *Au. africanus* have informed numerous speculations concerning its diet (e.g., Du Brul, 1977; Grine, 1981; Jolly, 1970; Kay, 1985;

Robinson, 1954; Strait et al., 2009; Wallace, 1975; Wolpoff, 1973). Most reconstructions have envisioned this species as having been primarily, if not exclusively, herbivorous.

Rak (1983) envisioned the “anterior pillars” of the *Au. africanus* maxilla as facial buttresses that linked this species with the enhanced masticatory apparatus of the South African australopith, *Paranthropus robustus*. Although Rak (1983) suggested that the pillars in *Au. africanus* were related to anterior tooth loading, this is difficult to reconcile with their presence in *P. robustus*, in which the incisors and canines are notably reduced. At the same time, McKee (1989) has noted that Rak’s scenario is also difficult to reconcile with their absence in a form such as *Au. afarensis*, which possessed an anterior dental battery as large as if not larger than that of *Au. africanus*. In fact, it has been argued that the anterior pillars of *Au. africanus* and *P. robustus* are not homologous (Villmoare and Kimbel, 2011).

Strait et al. (2008, 2009) have employed FEA modeling to argue that the anterior pillars of *Au. africanus* were part of an adaptation to the inclusion of hard seeds and nuts in its diet, with these items being processed by the premolars. Strait et al. (2010) have elaborated this hypothesis to the inclusion of “large, hard food items” in the diet. They postulated processing by the premolars rather than the molars because they found the cranium of *Au. africanus* to be relatively more rigid than that of the macaque monkey during premolar but not molar biting. Differences in the magnitude and distribution of strain energy and principal strains are implicitly argued in these models to be related directly to the modulation of morphology (Strait et al., 2008, 2009, 2010). However, the distributions of strains by themselves do not unambiguously define a state of adaptation (Daegling et al., 2011, 2013; Grine et al., 2010).¹ Indeed, the work of O’Higgins and colleagues, who have provided detailed investigation of aspects of craniofacial morphology pertinent to finite element analyses of fossil specimens (specifically Sts 5), suggests that a reliable model is probably unrealistic at present (e.g., Curtis et al., 2011; Fitton et al., 2015; Gröning et al., 2011, 2012a, 2012b; Shi et al., 2012; Toro-Ibacahe et al., 2016a, 2016b). Even so, there is little doubt that under comparable loading conditions, strain patterns in a macaque skull will not match that of Sts 5 (or any other australopith) in the finer details. What is important is how this observation informs hypotheses of skeletal adaptation, much less feeding ecology.

Occlusal microwear evidence for the premolars and molars represents a reasonable test of the model of premolar nutcracking presented by Strait et al. (2009, 2010). Because the premolars of *Au. africanus* display the same microwear fabrics as its molars (Grine et al., 2010), there is no evidence to support the argument for preferential premolar nutcracking in this species. In addition, a perhaps unlikely model for premolar “nutcracking” behavior exists

¹ More specifically, they failed to specify any basic process by which mechanical signals initiate bone response, and what the morphological outcome of that response would be. If it is simply a matter of normalizing peak strain (or modeling and remodeling toward a target strain magnitude), then bone activity ought to result in a uniform or nearly uniform strain field.

for at least one extant primate – the sooty mangabey, *Cercocebus atys* (Daegling et al., 2011). This committed hard object feeder employs the ingestive strategy hypothesized by Strait et al. (2009) to explain the unique facial skeleton of *Au. africanus*. Strait et al. (2009: 2126) concluded that “the facial skeleton of *Au. africanus* is better designed to withstand premolar loads than that of *Macaca fascicularis*”, but the facial morphologies of *M. fascicularis* and *C. atys* are very similar to one another in essential ways (i.e. both possess relatively long faces) when juxtaposed with *Au. africanus*. If sooty mangabeys suffer no obvious deleterious consequences for processing large, hard seeds given the design of their facial skeletons, it would seem unnecessary for *Au. africanus* to require such divergent facial morphology (Daegling et al., 2011).

4.5. *Australopithecus sediba*

Au. sediba is represented by two specimens from the site of Malapa, South African (Berger et al., 2010). With regard to the craniodental remains, the more complete specimen, designated MH1, is a juvenile whose M2s had reached occlusion just prior to death. The second specimen is represented by a fragmented adult mandible. The facial and dental morphologies of *Au. sediba* bear similarities with *Au. africanus*, which has led some workers to conclude that it is exclusively linked to that species (Irish et al., 2013; but see Carter et al., 2014), or that it is simply a somewhat unusual australopith closely-related to *Au. africanus* (Kimbel, 2013). Others have argued that it shares similarities with *Homo* with respect to a number of functionally consequential craniodental features (de Ruiter et al., 2013).

With reference to paleodietary reconstruction, comparative morphological studies do not present a consistent picture for *Au. sediba*. Ledogar et al. (2016) have argued that the overall architecture of its skull placed this taxon at risk of distractive temporomandibular joint forces under idealized muscle recruitment patterns. They suggest, on the basis of a finite element model, that *Au. sediba* would have been limited in its ability to produce large bite forces, with facial strains that were absolutely low in comparison to *Au. africanus*. The FEA model presented by Ledogar et al. (2016) is dependent on the correctness of their estimate of adductor muscle force. This is a significant problem with FEA studies because estimation of muscle force from morphological attributes is problematic even in neontological contexts other than through direct measurement of the cross-sectional area of the muscle itself (Hannam and Wood, 1989; Weijs and Hillen, 1985). However, muscle force has to be specified since the determination of high or low stress and strain is directly dependent on adductor force, and FEA depends on the correctness of the estimate.

On the other hand, the *Au. sediba* mandibles appear to retain the level of torsional strength and efficiency that sets australopiths apart from extant great apes and *Homo* (Daegling et al., 2016). At first glance, both studies would seem to suggest an “overdesigned” facial skeleton: i.e. needlessly strong given likely masticatory forces. As noted above, however, these forces are truly unknown in fossils.

Henry et al. (2012) evaluated isotopic, occlusal microwear and adherent phytolith data from the dental

specimens of *Au. sediba* in order to infer the types of foods that were consumed. Collectively, these data indicate a diet that contrasts with those inferred for *Au. africanus* (and *P. robustus*). Together they suggest almost exclusive consumption of C₃ resources that probably included some hard and tough foods. The microwear signature suggests the presence of hard objects in the diet in both individuals. The most common phytoliths recovered from the dental calculus are from wood and bark, which represent relatively tough materials. Thus, to some degree the two types of food that present mechanical challenges in terms of food breakdown – but are optimally performed by different processes – were part of this species’ diet. There is no reason to expect that *Au. sediba* was not capable of effective breakdown of hard and/or tough items, irrespective of the constraints on maximal adductor recruitment. Indeed, *Au. sediba* had the capacity to produce absolutely high bite forces by virtue of body size alone.

4.6. *Paranthropus robustus* and *P. boisei*

The morphological attributes of *P. robustus* have led a number of workers to surmise its dietary proclivities. In particular, its characteristically diminutive incisors and canines, large and thickly enameled postcanine teeth, molarized premolars, thick palate, robust mandible, and its orthognathic face with large, anteriorly positioned malars are part of a coherent and distinctive package that has been seen as reflecting the generation and distribution of powerful chewing forces associated with a herbivorous diet (Grine, 1981; Kay, 1985; Rak, 1983; Robinson, 1954). Most workers have interpreted the trophic morphology of *P. robustus* as being consistent with a diet that likely included at least some hard foods. Many of the craniodental features that characterize *P. robustus* are possessed also by *P. boisei* in even more exaggerated form. Thus, *P. boisei* exhibits greater molarization of the premolars, an even deeper maxilla, zygomatics that tend to be laterally bowed forming a “visor”-like configuration, and temporalis and especially masseter muscles that appear to have had more anterior attachments (Rak, 1983, 1988). The dimensions of *P. boisei* premolars and molars are the largest recorded for any hominin species.

Lucas et al. (1986: 269) have suggested that the M1–M3 size ratio of *P. boisei* indicates the consumption of “small mouthfuls of leaves and seeds”. The comparatively large masticatory muscles would have been able to generate powerful forces, but these could have been reduced to unexceptional levels if dissipated uniformly across the postcanine occlusal table. This would suggest bulk processing of soft, pliant foods (Demes and Creel, 1988; see also Walker, 1981). While postcanine megadontia is a defining characteristic of *P. boisei*, tooth size *per se* does not explain the size of the mandible (Plavcan and Daegling, 2006). Its large, thick corpora would have been able to withstand powerful bending and twisting moments (Daegling, 1989; Hylander, 1988). Rak and Hylander (2008) have concluded that the considerable height of the mandibular ramus in *Paranthropus*, the more rostrally positioned jaw muscles and resulting small gape, the topography of the glenoid fossa, the bulbous, low topographic relief of the unworn

premolar and molar cusps, and the small, non-projecting canines are all linked to a “rotatory” motion of the mandible during chewing. They further postulated that these derived masticatory movements are linked to the unusually broad mandibular corpora. The question, of course, is what the mandible of *P. boisei* was used to chew.

The problem with interpreting mandibular form vis-à-vis diet was highlighted by Hylander’s (1979) observation that the integrity of mandibular bone may be challenged both by intermittent high strains (e.g., those associated with fracturing hard objects) as well as by low, long-term cyclical strains (e.g., those producing fatigue from prolonged chewing of tough objects). The structural solution to both is the same for reducing (or maintaining) stress: increase the amount of bone. *Paranthropus* jaws are “robust”, being thick and exceptionally deep, but determination of diet is likely to be inaccessible from mandibular morphology (Daegling and Grine, 2017). Beyond the proposition that whatever was ingested required unusually large masticatory effort to process (numerous cycles, considerable force, or both), the diets of *P. robustus* and *P. boisei* remain uncertain on the basis of the morphology of their jaws.

Many workers have understandably viewed the craniodental features of *P. boisei* as specialized adaptations to a diet that likely consisted of small, hard objects. On the other hand, Cachel (1975) and Szalay (1975) independently argued that this species was adapted for meat-eating and especially bone-crushing. This view has not found much favor. Wood and Strait (2004) envisioned *P. boisei* as having been an ecological generalist, capable of consuming a broad array of foods with the sole exception of “tough, fibrous food items”. This is because the low, bulbous cusps of the cheek teeth would seem to be inconsistent with a diet consisting of leaves and grass blades (Lucas, 1982; Lucas et al., 2008a; Rak and Hylander, 2008). However, the combination of postcanine megadontia, mandibular corpus hypertrophy and thick enamel does not compel an interpretation that *P. boisei* was adapted for consumption of hard objects. It is neither necessary nor prudent to assume that the bunodonty possessed by *P. boisei* represents an optimal solution for the comminution of its food. Rather, phylogenetic considerations would suggest that other topographic solutions (e.g., high, pointed cusps and/or well-developed, sharp lophs) should not be expected in this species. It is equally plausible that the bulk processing of low quality fibrous foods drove selection in this lineage (Rabenold and Pearson, 2011).

Paranthropus boisei facial form has been generally interpreted as having been adapted to withstand the feeding stresses associated with high bite forces (e.g., Rak, 1978, 1983; Rak and Howell, 1978). The notion that the diet of this “hyper-robust” species included hard objects clearly gained indirect support from the microwear of its South African cousin, *P. robustus*, which indicates the consumption of hard food items, at least by some individuals (Grine, 1986; Grine and Kay, 1988; Scott et al., 2005). Most recently, FEA analyses of a *P. boisei* (OH 5) cranium concluded that it was structurally strong, allowing for high bite forces to be generated efficiently along the postcanine tooth row (Smith et al., 2015; Wroe et al., 2010).

This conclusion, which follows from the work of Ward and Molnar (1980) and Rak and Hylander (2008), was based on the observation that the *P. boisei* facial strain pattern differs substantially from that in chimpanzees (*P. troglodytes*). These FEA analyses substantiated what simpler models had predicted from basic mechanical principles.

The possible biomechanical significance of the large amount of overlap of the temporal and parietal along the squamosal suture in *P. boisei* has been a subject of interest since it was first recognized by Rak (1978). This has been most recently explored through FEA by Dzialo et al. (2014), whose models suggest that this sutural morphology was better suited to resist shear than tension. While this is yet one more line of evidence pointing to a uniquely derived morphology indicating “heavy” masticatory demands, the particulars of diet are not discernible.

An FEA analysis of a large, extinct lemur (*Hadropithecus*) with some superficial craniofacial resemblances to *P. boisei* has led to the conclusion that the hominin must have consumed hard objects because this sort of diet is inferred for *Hadropithecus*, a taxon that also exhibits moderately elevated $\delta^{13}\text{C}$ values (Dumont et al., 2011; Godfrey et al., 2011). However, as noted by Cerling et al. (2011b), despite the existence of certain morphological convergences between these taxa, it is far from certain that this implies similar diets. Rather, the moderately high $\delta^{13}\text{C}$ values of *Hadropithecus* probably reflect the consumption of plants that photosynthesize utilizing the Crassulacean acid metabolism (CAM) pathway rather than the eating of C_4 plants, which have been suggested to dominate *P. boisei* diets (Cerling et al., 2011a, 2013). This is pertinent because the former are highly abundant in the unique spiny forests of Madagascar but comprise virtually nothing of the possible dietary staples in Africa. As concluded by Cerling et al. (2011b), inferring diet for one extinct species from the inferred albeit unknown diet of another fossil taxon, especially one that is very distantly related and inhabited a very different environment, represents an inherently uncertain line of evidence that should be eschewed.

Thus, the form of the skull in *Paranthropus* has been taken to indicate the reliance on hard items such as nuts and seeds (Peters, 1987), a reliance on tough, fibrous foods (Du Brul, 1977), and the processing an unexceptional diet in greater quantity (Walker, 1981). These, in turn, translate respectively to higher bite forces, an increased number of masticatory cycles per day with the likelihood of high bite forces, and more daily chewing cycles but without appreciable change in occlusal forces. Unfortunately, and despite efforts to construct FEA models to answer this question, it is currently difficult to decide among these three possibilities. The outstanding issue is that both load magnitude and frequency are implicated in bone metabolic activity that results in increased bone mass and altered osseous architecture (Judex et al., 2006; Ozcivici et al., 2009; Qin et al., 1998; Ravosa et al., 2007; Rubin et al., 1990, 1991). Bone formation, composition and architecture are influenced by dynamic variation in the magnitude and frequency of mechanical loads (Biewener and Bertram, 1993; Biewener et al., 1986; Bouvier and Hylander, 1981, 1984, 1996; Lanyon and Rubin, 1985).

Finally, Scott et al. (2014) have provided at least some experimental evidence which argues that hard object feeding – whether habitual or on a “fallback” resource basis – does not explain the extreme dentognathic morphology of *P. boisei*. Their analysis, although based on a relatively small number of data points, suggests *P. boisei* morphology is better explained by reliance on tough foods that required prolonged postcanine processing and “concomitantly elevated masticatory stresses owing to higher repetitive loading and longer load durations resulting from extended bouts of milling and grinding” (Scott et al., 2014: 4). This is concordant with the argument presented by Rabenold and Pearson (2011) for extended bouts of processing of low quality, fibrous foods.

As detailed by Grine et al. (2012), molar microwear studies of *P. robustus* have provided some support for the notion that hard food objects comprised at least a portion of its diet, and texture analyses have revealed significant individual variation, which may reflect reliance upon less commonly eaten, but critical fracture-resistant foods by some individuals in the sample (Grine, 1986; Grine and Kay, 1988; Scott et al., 2005). Such potential seasonality in diet is also evidenced by the carbon isotope data (Sponheimer et al., 2005, 2006). Tooth enamel $\delta^{13}\text{C}$ values suggest a diet comprising some 35–40% C_4 vegetation, but with considerable interindividual variability. Importantly, this variability is also manifest within individual teeth, with changes of up to 5‰ in $\delta^{13}\text{C}$ values over intra-annual (seasonal) and inter-annual timescales (Sponheimer et al., 2006). In view of the fact that mineralization continues for months after initial enamel deposition, which results in isotopic overprinting that can dampen apparent dietary perturbations (Balasse, 2003; Passey and Cerling, 2002), changes of this magnitude are quite extraordinary, and almost certainly indicate that the individuals in question changed from a C_3 - to a C_4 -dominated diet during the period of enamel formation.

The first examination of molar microwear in *P. boisei* was a qualitative SEM study by Walker (1981), who reported that the teeth exhibited fine scratches and few, small pits. As such, he suggested that the diet of *P. boisei* may have entailed prolonged chewing of tough or fibrous vegetable foods, perhaps with relatively little nutritional value, rather than the consumption of hard food items. This inference, which appears to have been profoundly prophetic, was largely ignored. Subsequent study has confirmed that the occlusal wear fabrics of this species are dominated by fine striae, and that they appear to show remarkable uniformity over the geochronological record of the species (Ungar et al., 2008). The carbon isotope values obtained from *P. boisei* specimens from a variety of sites throughout East Africa are indistinguishable from those of C_4 grass consumers from the same regions (Cerling et al., 2011a; van der Merwe et al., 2008). Like the microwear signatures, the $\delta^{13}\text{C}$ values do not change over the half million years sampled, and they correspond to a diet where C_4 plants comprise, on average, some 77% of the biomass consumed, with individual values ranging between 61% and 91%. As such, the carbon isotope data for *P. boisei* are most consistent with its having been a reasonably devoted consumer of C_4 plants.

Paranthropus robustus provides an intriguing mixture of isotopic and microwear signatures that suggest a greater range of dietary variability than *P. boisei*, with the inclusion, perhaps seasonally, of hard food objects. By contrast, microwear and isotopic data for *P. boisei* point to a diet dominated by C_4 plants (likely grasses) that did not entail the processing of hard objects. Despite the popularity of *P. boisei*'s nickname, these data would appear to portend the demise of “Nutcracker Man” (Lee-Thorp, 2011).

4.7. Prospectus

Paleoanthropology does not lack for ideas, but, given the spotty nature of the fossil record, there are relatively few “facts” with which to work. Models are essential to the enterprise of functional morphology, and they will remain vital for testing and generating new hypotheses. Box and Draper (1987: 424) famously remarked that “all models are wrong, but some are useful.” Both parts of this statement demand that models be scrutinized. Vigilance as to their underlying assumptions will lead to more useful models and perhaps fewer “wrong” ones.

This review has been critical of FEA as an approach to paleoanthropological inference – specifically the retrodiction of diet and dietary adaptation. We do not advocate the abandonment of the approach, but propose that these models should first be utilized to investigate tractable questions of importance to skeletal biology and model design, such as sutural (Wang et al., 2012), periodontal ligament (Gröning et al., 2011; Wood et al., 2011), and muscular (Ross et al., 2005) influences on bone behavior and model accuracy. Iterative FEA models (e.g., Carter et al., 1989; Prendergast, 1997; Tseng, 2013) show great promise for resolving how bone modeling and remodeling algorithms alter morphology and performance. Although these will not resolve every operational problem in the application of FEA to fossils, they offer an incremental approach toward understanding skeletal adaptation. This can serve to improve our discrimination, while avoiding the potential pitfalls of trying to correlate simple mechanical variables (e.g., a strain gradient) with ecological adaptations.

In effect, we recommend a less ambitious role of FEA in hominin paleobiology. Even should an FEA model be judged accurate in all details, which is unlikely (Fitton et al., 2015; Godinho et al., 2017), it is perilous to assume that such models provide clear insight into dietary adaptation, much less paleoecology. In most applications of the method to hominin fossils, one or a handful of loadcases are sampled to infer performance. These stress fields represent a subset of the totality of loading situations that comprise the stress history of an individual skull (Curtis et al., 2008). Thus, a strain gradient from a single – even if critical – loading event provides a myopic description of performance in the context of understanding skeletal adaptation. Biting deforms the skull, but unlike a nutcracker in the kitchen drawer, the skull has to do a number of other things besides break food.

We should also be mindful that the morphology of a single individual (e.g., STS 5, OH 5) may not be an adequate guide for understanding morphological adaptation in a species. In the course of skeletal growth and modeling,

not every recognizable feature will have arisen strategically to provide structural reinforcement. Features that arise as a matter of physical necessity [Gould and Lewontin's (1979) "spandrels" or Seilacher's (1973) "fabricational noise"] need not qualify as adaptations if their appearance is an inevitable product of morphogenesis. In addition, while the use of single specimens to characterize a fossil species is perfectly understandable for preservational and perhaps computational reasons, it necessarily places interpretation in an essentialist framework. A sample of one means that variance is zero. The problem this poses is thrown into sharp relief when considering the reality of phenotypic plasticity. As Ravosa et al. (2016) have noted, ontogenetic perturbations of diet that alter masticatory load magnitude and frequency can produce intraspecific variations that may be on par with the differences attributed to "species-level" adaptations. This underscores the pitfall of using a monolithic "critical" loadcase as the determinant of an adaptive response. In this context, what appears as morphological "noise" within a species may, in fact, constitute a functional signal.

5. Conclusion: inferring diet from morphology

The reality of Liem's paradox means that perfect agreement between dietary inferences based on morphology and those related more directly to ingested foods should not be expected. The most challenging food resources, rather than the range of resources, may have an outsized influence on anatomical traits and variation. Biomechanical models (including FEA) measure performance under a precisely defined set of conditions. In many cases – especially in the paleontological context – these conditions are difficult to specify and are prone to error. In the best-case scenario, such models provide a snapshot of a state of stress in the skeleton, whereas bone tissue reflects an accumulated load history that is unlikely to be uniform (with or without compensatory metabolic activity). Consequently, relating a singular (or small set of) stress state(s) directly to feeding ecology is risky, but a more deliberate approach may prove to be rewarding. As Ross et al. (2012) have argued, only through an understanding of the myriad linkages of anatomy, behavior and competing functional demands can we expect to arrive at a realistic picture of the relationship of diet to morphology. In reviewing distinct lines of evidence for the diets of fossil taxa, what becomes clear is that a good biomechanical model tells us what was possible but not necessarily what was actually done. Understanding this difference will permit us to make more constructive inferences about dietary adaptation.

Meaningful dietary inferences that are predicated on the craniodental morphology of an extinct creature can be achieved only if they are founded on close and replicable associations between form and function in extant taxa. At the very least, even if a one-to-one correspondence between form and function could be realized for a single morphological attribute, almost all extinct species exhibit a *combination* of variably unique features in their skulls and teeth. It is this unique combination – one that almost certainly will not be manifest in any living species – that requires the function(s) of its components

to be deciphered in order to begin to appreciate the adaptive significance of such idiosyncratic anatomy. In order to do so, it is also necessary to consider other "nonmechanical" aspects of biology, such as phylogenetic history and the genetic/developmental constraints that underlie skeletal and dental structures. In the context of bone, such constraints force the admission that Wolff's Law, despite its immense heuristic appeal, is no longer a tenable algorithm of skeletal adaptation (Pearson and Lieberman, 2004).

A good number of morphological configurations (and behavioral attributes) appear to be explicable with reference to the function(s) that they serve, but exactly how closely the structure of a trait can be related to its biological function remains a topic of discovery. Even though an optimality criterion can usefully serve as a heuristic benchmark for initial investigation, it is folly to view an organism simply as a collection of adaptively optimized features that evolved by natural selection without consideration of history and constraint. Craniodental morphologies may tell us more about what an extinct species (or a particular individual) was capable of eating, and perhaps more about its phylogenetic history than the constitution of its diet. Developmental integration is likely a major factor maintaining a relatively stable covariance structure of functionally related traits during evolutionary diversification of a lineage.

Comparative anatomy and biomechanical analysis may serve to bracket the range of behavioral capabilities, but these approaches are inherently limited in their capability to identify specific adaptation in paleobiological contexts. The application of finite element analysis (FEA) to the hominin fossil record has not revealed convincing evidence of specific feeding adaptations, even as it provides a window into the mechanical consequences of even modest anatomical variation. Such biomechanical studies may inform about the physical performance attributes of a morphological feature (if it has been properly modelled), but not necessarily whether these attributes mean anything of biological relevance to the organism. With regard to osseous traits involved in mastication, load magnitude and frequency have both been implicated in bone metabolic activity that results in changes in bone mass and architectural properties. As such, mandibular or facial morphology *per se* does not distinguish between potential adaptations to feeding on either tough or hard items, given our current state of knowledge. The commonly weak relationship between food material properties and mandibular morphology suggests that one cannot predict the other.

Perhaps even more than for crania and mandibles, there is an operational relationship between tooth form and function. However, as with bone, it is not clear to what extent specific mechanical environments (i.e., diets) dictate particular morphologies. Retrodiction of the dietary habits of extinct taxa has been based in large measure on the form of tooth – particularly premolar and molar – crowns, and upon the thickness and structure of the enamel cap. Although cheek tooth crown relief is commonly related to the physical properties of the foods that are processed, it is not at all clear to what extent this can differentiate between anything but the broadest dietary categories. Tooth enamel thickness also has long been regarded as being sensitive to

diet, or at least to the mechanical properties of the foods consumed. However, although there seems to be some general correspondence between these two variables, the reliability of tooth enamel thickness as a dietary indicator clearly breaks down in instances where phylogenetically closely-related species that consume different amounts of hard items are considered.

Because primates are adept at behaviorally circumventing mechanical problems, it might be useful to consider the breadth of any fossil hominin's feeding adaptations in the context of a behavioral bracket between *Pan troglodytes* and *Homo sapiens*. Like bearded capuchin monkeys, both deal with the problem of eating various items by mitigating mechanical problems prior to ingestion, thereby adding to the total number of resources in their diets. The resourcefulness of primates in solving ecological problems is manifest. It is perhaps ironic that their cognitive flexibility hampers our own ability to discern adaptation from the details of their skeletons.

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