



Chewing efficiency and occlusal functional morphology in modern humans



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ABSTRACT

The reduction of occlusal dimensions in early *Homo* is often proposed to be a functional adaptation to diet. With their smaller occlusal surfaces, species of early *Homo* are suggested to have reduced food-processing abilities, particularly for foods with high material properties (e.g., increased toughness). Here, we employ chewing efficiency as a measure of masticatory performance to test the relationships between masticatory function and food properties. We predicted that humans are more efficient when processing foods of lower toughness and Young's modulus values, and that subjects with larger occlusal surfaces will be less efficient when processing foods with higher toughness and Young's modulus, as the greater area spreads out the overall bite force applied to food particles. Chewing efficiency was measured in 26 adults using high-speed motion capture and surface electromyography. The dentition of each subject was cast and the occlusal surface was quantified using dental topographic analysis. Toughness and displacement-limited index were negatively correlated with chewing efficiency, but Young's modulus was not. Increased occlusal two-dimensional area and surface area were positively correlated with chewing efficiency for all foods. Thus, larger occlusal surface areas were more efficient when processing foods of greater toughness. These results suggest that the reduction in occlusal area in early *Homo* was associated with a reduction in chewing efficiency, particularly for foods with greater toughness. Further, the larger occlusal surfaces of earlier hominins such as *Australopithecus* would have likely increased chewing efficiency and increased the probability of fracture when processing tough foods.

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1. Introduction

Differences in craniodental morphology between early *Homo* and *Australopithecus* are proposed to reflect adaptations to diet (Robinson, 1954, 1963; Jolly, 1970; Rak, 1983; Wood and Ellis, 1986; Wood and Collard, 1999; Teaford and Ungar, 2000; Strait et al., 2009). Although there is overlap in some specimens, species of early *Homo* have absolutely smaller measures of molar size, corpus thickness, and symphyseal dimensions compared to *Australopithecus* (e.g., Wood and Collard, 1999). These reductions in early *Homo*, particularly in the size of the occlusal surface, have been argued to indicate that masticatory processing function for foods of higher toughness was lost during selection for increased dietary

and behavioral flexibility in early *Homo* (Wood and Strait, 2004). Accordingly, species of *Australopithecus* are thought to have consumed food of higher toughness and/or Young's modulus (stress to strain ratio), fewer animal-based products, and unprocessed and uncooked plant foods (Wrangham et al., 1999; Aiello and Wells, 2002; Ungar et al., 2006b; Organ et al., 2011). Thus, the shift from a large to a small masticatory complex in early *Homo* reflects, to some extent, dietary change.

Reconstructing the functional and ecological implications of masticatory reduction in *Homo* requires a detailed understanding of the form-function relationships linking occlusal morphology and chewing performance. The 'Specialist Strategy' (Robinson, 1954) proposes that larger occlusal surfaces, such as those in *Australopithecus*, improve comminution of small, tough food objects by increasing the probability of fracture, in contrast to smaller dentition reflecting omnivory in *Homo* (Robinson, 1954, 1963; Jolly, 1970; Grine, 1981; Wood and Ellis, 1986). For example, Lucas et al. (1985)

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suggest that increased molar area increased fracture probability for small tough food objects. Alternatively, Walker (1981) proposed an 'Efficiency Strategy' positing that larger masticatory features, such as occlusal area, reflect adaptations to processing large quantities of food, regardless of their material properties. This hypothesis was supported by Demes and Creel (1988) who found that occlusal area scales linearly with osteologically modeled bite force, and as a consequence, the stress (defined as force/area) exerted during chewing is similar across hominoids, including robust and gracile fossil hominins. These evolutionary hypotheses are difficult to distinguish, in part because they could lead to similar morphologies: features that improve chewing performance for small, tough foods (Specialist Strategy) might also improve chewing efficiency for a broad range of foods (Efficiency Strategy), and vice versa. Few studies have empirically examined the effect of occlusal morphology on chewing performance, making it difficult to determine what performance variables would have been reduced (or improved) with the reduction of occlusal size in *Homo*.

The primary function of the masticatory system is to reduce food items to a size suitable for swallowing. Smaller food particles are digested at a faster rate in the gut, resulting in greater energy extraction (Pearce, 1964; McLeod and Minson, 1969; Latham, 1978; Milton, 1981; Clauss et al., 2009). However, net energy gained from increased particle size reduction is determined by the amount of energy spent during processing, which is influenced by food material properties and craniodental morphology. Previous researchers have defined masticatory 'efficiency' in several ways, including the number of chews necessary to process a given food volume (reviewed in Bates et al., 1976). In this study, we define efficiency as the reduction in food particle size divided by chewing work. This definition is consistent with many others, since, for example, the number of chewing cycles will generally correlate with the total mechanical work performed. However, defining chewing efficiency in terms of particle size reduction and chewing work enables us to compare a broad variety of foods with variable food material properties, and brings us closer to a measurement of net energy gained per unit of energy expended.

Chewing efficiency is influenced by changes in the size and shape of the dentition and masticatory morphology. Viewing the masticatory anatomy as a simplified third-class lever system, the force exerted by the adducting masticatory muscles, F_m , multiplied by the ratio of the muscles' anatomical moment arm, a , and the external moment arm of the food, A , determines the bite force, F_b , exerted on a food item (e.g., Hylander, 1975; Pruim et al., 1980; Weijs and Hillen, 1986; Ross et al., 2009; Fig. 1A). Mechanical work done on the food, or 'chewing work,' is equal to the product of F_b and adduction distance, or the change in masticatory gape, integrated over the time spent chewing, as work = force \times distance.

Variation in craniodental morphology may also affect efficiency by changing the ratio of a/A , thus also changing the bite force, F_b , produced per unit of muscle force. Similarly, variation in occlusal surface morphology may affect the amount of reduction in food particle size per unit of chewing work by changing the area over which bite forces may be applied to a food. Increased occlusal two-dimensional area has been related to an increase in chewing efficiency in experimental studies involving humans and select non-human primates (Dahlberg, 1942; Manly, 1951; Yurkstas, 1965; Walker and Murray, 1975; Helkimo et al., 1978; Sheine and Kay, 1982; Lucas et al., 1986; Agrawal et al., 1997; English et al., 2002; Lucas, 2004).

Chewing efficiency is also influenced by the food's material properties (FMPs)—fracture toughness (R); the energy required to propagate a crack; and Young's (elastic) modulus (E), the ratio of stress to corresponding strain along the linear portion of the stress–strain curve (Carlsson, 1973; Helkimo et al., 1978; Luke and

Lucas, 1985; Lucas et al., 1986; Ashby, 2002; Lucas, 2004; Williams et al., 2005). Foods with greater toughness, or to a lesser extent Young's modulus, require a greater amount of energy to reduce a food to a particular particle size (Agrawal et al., 1998; Peyron et al., 2002; Foster et al., 2006). For example, processing raw tubers with higher toughness and Young's modulus values requires greater masticatory effort than chewing roasted tubers with lower toughness and Young's modulus values (Dominy et al., 2008; Zink et al., 2014). Further, some occlusal morphologies may be better than others at reducing foods with particular FMPs. Bourdiol and Mioche (2000) found that larger occlusal wear facets were correlated with fewer chewing cycles for foods with higher elastic moduli in humans. Food material properties may influence masticatory mechanics through functional adaptations in craniodental morphology, the movement of the mandible, and/or the size of the masticatory musculature (Moller, 1973; Thexton, 1984; Van der Bilt et al., 1995; Agrawal et al., 1998; Bourdiol and Mioche, 2000; Peyron et al., 2002; Wall et al., 2006; Reed and Ross, 2010; Iriarte-Díaz et al., 2011). These changes occur either over evolutionary time through evolved changes in craniodental morphology or over the course of development through the growth or reduction of bone and muscle.

The relationships between qualitative measures of diet and occlusal morphology in primates are well established (e.g., Kay, 1975; Rosenberger and Kinzey, 1976; Anapol and Lee, 1994; Wright et al., 2009). Studies have also looked at quantitative measures of diet and masticatory morphology in primates and found trends linking occlusal morphology with FMPs and fragmentation indices (FIs; Kinzey, 1987; Peters, 1987; Kinzey and Norconk, 1990, 1993; Dumont, 1995; Yamashita, 1998, 2003; Lambert et al., 2004; Wright, 2005; Teaford et al., 2006; Dominy et al., 2008; Vogel et al., 2008, 2009, 2014; Norconk et al., 2009; Vinyard et al., 2009; Daegling et al., 2011; Venkataraman et al., 2014). However, these relationships have not been tested in a controlled lab setting, and the influences of food properties and masticatory morphology, particularly occlusal surface area, on chewing efficiency remain speculative.

In this study, we test whether variation in size and shape (topography) of the occlusal surface affects chewing efficiency for different FMPs in a sample of modern humans. We test the hypothesis (H1) that humans chew foods of lower FMPs and FIs more efficiently (i.e., with a greater reduction in food particle size per unit of chewing work). Foods with higher FMPs and FIs are expected to require greater amounts of work, either through increased time spent chewing or greater bite force, resulting in lower efficiency. We then test two competing hypotheses for occlusal surface area. The first (H2a) is that larger occlusal surfaces are less efficient for all foods, as larger surface areas may reduce the stresses (force/area) exerted on food particles. Alternatively, larger surfaces may improve chewing efficiency by providing greater surface area for grinding food particles (H2b). The results of these tests have implications for reconstructing the evolutionary pressures shaping changes in tooth shape and size in the hominin lineage (Robinson, 1954, 1963; Jolly, 1970; Grine, 1981; Walker, 1981; Lucas et al., 1986; Wood and Ellis, 1986; Demes and Creel, 1988). We conclude by discussing these results in the context of dietary reconstructions and craniodental evolution in Plio-Pleistocene hominins.

2. Materials and methods

2.1. Subjects

Twenty-six human subjects, 7 men and 19 women, were recruited for this study. Subjects were between ages 21 and 36, had

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