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News and Views

On the calculation of occlusal bite pressures for fossil hominins

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1. Introduction

Reconstructing the feeding behavior of fossil hominins, and especially of australopiths, is currently the focus of several lines of work (e.g., Grine et al., 2006; Sponheimer et al., 2006, 2013; Ungar et al., 2008; Strait et al., 2009; Constantino et al., 2010; Wroe et al., 2010; Cerling et al., 2011; Henry et al., 2012; Delezene et al., 2013; Zink et al., 2014; Smith et al., 2015). One of these lines of research consists of estimating bite forces from fossil skulls based on estimates of lever arm length and cross sectional area of the masticatory muscles (e.g., Demes and Creel, 1988; Eng et al., 2013). The results of such studies can be expressed as unitless values (Demes and Creel, 1988), or as estimates of the maximal vertical (i.e., perpendicular to the occlusal plane) adducting force that could be produced by a given jaw (Demes and Creel, 1988). Although this kind of analysis does not take into account other aspects, such as the differential activity of the muscles involved in mastication, or food processing modes, the results are still related to the bite force capabilities of fossil hominins.

Demes and Creel (1988) proposed the existence of a nearly linear correlation between bite force produced at the mesial margin of the second upper molar (M^2) and M^2 area for extant hominoids and fossil hominins, although early *Homo* (represented by the fossil specimens OH 24 and KNM-ER 1813) and *Australopithecus africanus* (represented by Sts 5) had somewhat lower bite forces by unit area than predicted. Recently, Eng et al. (2013) calculated absolute occlusal bite forces at the M^2 central point for extant great apes, *Homo sapiens* and fossil hominins, by taking into account muscle specific tension, skeletal morphology and muscle architecture. These authors found that maximum absolute bite forces at the M^2 central point were probably similar in extant great apes and australopiths, although values for *Australopithecus boisei* more than doubled those for *Au. africanus*, and values for *Homo* were lower than predicted by the regressions.

Eng et al. (2013) also estimated bite pressures on M^2 by dividing their absolute bite force values by M^2 area. The argument there is that bite pressures provide more realistic estimates of the masticatory capabilities of fossil hominins than absolute forces (see Walker, 1981; Demes and Creel, 1988). In this context, the term bite (or occlusal) pressure refers to the pressure that could be applied on a given flat area parallel to the occlusal plane. This bite pressure is not the actual pressure experienced by the masticated food, which depends, among other factors, on the nature of the food and on tooth relief. Hard pieces of food can be loaded at a specific point on the tooth surface, and for this reason they could experience very high pressures, whereas compliant foods can spread across the entire tooth surface and hence experience lower pressures. On the other hand, in prehistoric modern humans M^1 is usually worn flat by the time M^3 emerges, and M^2 reaches a similar wear stage six years later, so that it has lost most of its topography (if not the complete prominence of the four cusps) in prime adults (Brothwell, 1981). As a consequence, M^2 relief should not greatly affect pressure calculations. Still, the concept of bite pressure can be easily compared between species or individuals of different ages and should thus shed light on the biomechanical capabilities of modern and fossil hominins.

Eng et al. (2013) concluded that australopiths could produce bite pressures comparable to extant great apes. However, while bite pressures calculated for *Au. boisei* were twice those obtained for *Au. africanus*, it is worth mentioning that the fossil specimens analyzed correspond, respectively, to male (OH 5) and female (Sts 5) individuals. On the other hand, the calculated bite pressures for *H. sapiens* were higher than for fossil *Homo* taxa, which seems counterintuitive for a species practicing heavy food processing techniques.

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Alternatively, Smith et al. (2015) analyzed the masticatory biomechanics of OH 5, Sts 5 and several *Pan troglodytes* skulls, through a finite element analysis. These authors estimated bite forces on the M^2 central point that were very similar to those calculated by Eng et al. (2013), although slightly (~5–6%) higher; and they also calculated bite pressures by dividing bite forces by tooth area, again finding similar values to those of Eng et al. (2013). This mutually reinforces the usefulness of both methods for the calculation of masticatory forces.

The works by Demes and Creel (1988), Eng et al. (2013), Smith et al. (2015) and others (e.g., O'Connor et al., 2005; Wroe et al., 2010) are very interesting because they provide estimates of maximal bite forces that could have been produced by fossil hominins. However, the interpretation of so-obtained bite pressures (or bite force-molar area relations) is not straightforward. Indeed, as we show below, the M^2 area is not a reliable parameter for the calculations of bite pressures: M^2 area is a function of tooth width, but also of tooth length. This introduces a previously unnoticed mathematical problem in the methodology used by those works, making mathematically non-rigorous bite pressures derived from M^2 area.

Here we show that a mathematically self-consistent calculation (i.e., a calculation without contradictions or incompatibilities between its different parts or assumptions) of effective bite pressures at the M^2 central point can be calculated in a simple way from M^2 width. We also show that this new approach permits more reliable comparison between species.

2. Calculation of bite forces and pressures

The calculation of bite forces and pressures from traditional biomechanical arguments based on lever analysis depends on the condition that, with respect to the mandibular articulation, the moment of each masticatory muscle arm must be equal to the moment of the load arm, and therefore

$$F_m\, m = F_l\, l, \tag{1}$$

where F_m and F_l are, respectively, the muscle and load forces, and m and l, respectively, the muscle and load arm lengths. Eng et al. (2013) used a correction factor (denoted here as D) related to the differential recruitment of the working side and balancing side muscles, and with the maximum bite force that can be produced by a given muscle then being equal to

$$F_{bite} = \frac{DF_m m}{l}, \tag{2}$$

where the ratio m/l is known as mechanical advantage. In order to calculate bite forces and pressures, all muscles involved in mastication should be considered.

Lever properties imply that the calculated forces are perpendicular to the load plane, which should correspond to the occlusal plane. The load plane is usually taken to be parallel to the Frankfurt plane (e.g., Demes and Creel, 1988), because this plane and the occlusal plane are nearly parallel. As an exception to this assumption, the Ponginae are characterized by a marked airorhinchy (upward rotation of the premaxilla) that greatly affects the orientation of the occlusal plane. Also, the reconstruction of OH 5 exhibits an occlusal plane tilted upward posteriorly with respect to the Frankfurt plane (although this is not the case for other *Au. boisei* skulls). For both of these cases the actual maximum bite forces would be somewhat lower than those derived from equation (2).

Bite forces derived in this way can be converted to bite pressures by dividing by an appropriate crown area. In this sense, Eng et al. (2013) divided their bite force results at the M^2 central point by the M^2 area, in order to obtain bite pressures experienced on M^2. The procedure of Demes and Creel (1988), which compares their non-dimensional bite forces against M^2 area, is based on a similar rationale (although these authors used the M^2 mesial point). However, we believe the use of the M^2 area is not very reliable for calculating bite pressures.

As indicated by equation (2), the maximum bite force that can be produced by a given muscle is a function of load arm length, and therefore it is not the same if calculated for different points along M^2 (for example, for mesial, central and distal points on M^2), as the load arm length varies accordingly; in fact bite force produced by a given muscle varies greatly when calculated for different points on M^2 (see an example in Table 1). Thus, it is mathematically not self-consistent to calculate bite pressures from combining (i) forces obtained for a given point on the load arm derived from a mechanical advantage analysis, with (ii) an area (the molar area) extended along the load arm; indeed, (i) and (ii) are mutually incompatible. Thus, results obtained in that way cannot be reliably interpreted, and it is not possible to establish consistent error estimates for them.

Calculations of maximum masticatory forces from lever analyses yield, by their very nature, maximum forces that masticatory muscles would be capable of producing on a given point of the maxillary row. Therefore, to attempt to derive bite pressures on a mesio-distally extended area is a different issue. It could be that, in order to solve this problem, the mean F_{bite} derived from equation (2) along M^2 length should be divided by M^2 area. This "mean" bite force value, calculated for a given muscle and for a given length interval on the molar row, is

$$\overline{F_{bite}} = \frac{DF_m m}{l_2 - l_1}\int_{l_1}^{l_2}\frac{\mathrm{d}l}{l} = \frac{DF_m m}{l_2 - l_1}\ln\left(\frac{l_2}{l_1}\right), \tag{3}$$

where l_2 and l_1 are, respectively, the load arm lengths at the more mesial and distal points in the considered interval. The mean bite pressure that potentially could be produced by $\overline{F_{bite}}$ is $\overline{P_{bite}} = \overline{F_{bite}}/A_{2-1}$, where A_{2-1} is the molar area in the considered interval on the load arm.

The interval $l_2 - l_1$ can be taken as equivalent to the M^2 length if we decide to compute in that way. But as $l_2 - l_1$ can be taken as any arbitrary interval in the load arm, equation (3) describes $\overline{F_{bite}}$ and $\overline{P_{bite}}$ for any given interval on the molar row. For a complete analysis of $\overline{F_{bite}}$ and $\overline{P_{bite}}$, the sum of the values obtained for each muscle involved in mastication must be taken into account. However, the important point here is the mathematical argument, which is necessarily based on individual muscles.

To evaluate this alternative approach we have calculated, as an example, F_{bite} range, $\overline{F_{bite}}$ and $\overline{P_{bite}}$ generated by the temporalis muscle in the early *Homo* specimen KNM-ER 1813 for two different length intervals along the load arm, $l_2 - l_1 =$ (M^2 length) and $l_2 - l_1 =$ (total molar row length), and the results are shown in

Table 1
F_{bite} range, $\overline{F_{bite}}$ and $\overline{P_{bite}}$ generated by the temporal muscle in the early *Homo* specimen KNM-ER 1813 along a given interval, $l_2 - l_1$, on the molar row. Muscle and load arms used to calculate bite forces were measured on the cast (left side); molar areas (left side) used to calculate pressures were taken from Wood (1991).

	$l_2 - l_1 = M^2$ length	$l_2 - l_1 =$ total molar row length
F_{bite} range (n)	373–444	303–632
$\overline{F_{bite}}$ (n)	407	432
$\overline{P_{bite}}$ (n m^{-2})	248	93