

Bite Force and Occlusal Stress Production in Hominin Evolution

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ABSTRACT Maximum bite force affects craniofacial morphology and an organism's ability to break down foods with different material properties. Humans are generally believed to produce low bite forces and spend less time chewing compared with other apes because advances in mechanical and thermal food processing techniques alter food material properties in such a way as to reduce overall masticatory effort. However, when hominins began regularly consuming mechanically processed or cooked diets is not known. Here, we apply a model for estimating maximum bite forces and stresses at the second molar in modern human, nonhuman primate, and hominin skulls that incorporates skeletal data along with species-specific estimates of jaw muscle architecture. The model, which reliably estimates bite forces, shows a significant relationship between second molar bite force and second molar area across species but does

not confirm our hypothesis of isometry. Specimens in the genus *Homo* fall below the regression line describing the relationship between bite force and molar area for non-human anthropoids and australopiths. These results suggest that *Homo* species generate maximum bite forces below those predicted based on scaling among australopiths and nonhuman primates. Because this decline occurred before evidence for cooking, we hypothesize that selection for lower bite force production was likely made possible by an increased reliance on nonthermal food processing. However, given substantial variability among in vivo bite force magnitudes measured in humans, environmental effects, especially variations in food mechanical properties, may also be a factor. The results also suggest that australopiths had ape-like bite force capabilities. *Am J Phys Anthropol* 151:544–557, 2013. © 2013 Wiley Periodicals, Inc.

Apes such as chimpanzees spend ~40% of the day feeding and chewing, whereas humans today, including hunter-gatherer populations, spend less than 5% of the day chewing foods with a higher energy density that have been cooked or mechanically processed (Organ et al., 2011). Because processed foods are usually softer and less tough, they usually require less time and force to comminute. Yet, despite much interest in how and when the transition from more to less mechanically demanding diets occurred, we lack reliable data on bite force and stress generation capabilities in nonhuman primates and fossil hominins. Here, we build on existing models to estimate bite forces and occlusal stresses in a large sample of nonhuman primate and hominin skulls. These estimates incorporate human and nonhuman primate masticatory muscle architecture data to account for variations in both skeletal geometry and muscle architecture. Additionally, we explore how different correction factors (CFs) for the relationship between the skeletal estimate of jaw adductor muscle cross-sectional area (CSA) and muscle physiological cross-sectional area (PCSA) influence estimates of bite force generation.

Archaeological and comparative data provide the most direct evidence for the transition from unprocessed to mechanically processed or cooked diets. Chimpanzees occasionally use rocks to break open hard foods like nuts and palm seeds (Goodall, 1986; Boesch and Boesch, 1990), and although such behaviors leave little archaeological trace, early hominins likely used rocks to pound open some foods, and perhaps to grind them before chewing. Evidence for the use of stone tools is at least 2.6 Ma old (de Heinzelin et al., 1999; Semaw et al., 2003), and possibly extends to 3.4 Ma (McPherron et al., 2010). Food processing may have become slightly more

intensive over the lower paleolithic (e.g., in the Acheulian), but it certainly became more elaborate during the middle paleolithic (Klein, 2009). Wrangham et al. (1999) posit that cooking began at least two million years ago, but the oldest evidence for controlled fire is dated to 1.0 Ma (Berna et al., 2012), and cooking hearths with burnt bones become common only in the middle paleolithic (James, 1989; Rowlett, 2000; Goldberg et al., 2001).

Interpretations of the fossil record have led to less consensus about changes in diet and the origin of cooking and mechanical processing. One line of evidence is postcanine tooth size, which increases in *Australopithecus*, becomes even larger in robust species such as *Au. boisei*, and then decreases in *Homo*. Postcanine crown size is similar in *H. habilis* and *Au. africanus* but is about 25% smaller in early African *H. erectus*, and then decreased roughly 10% over the Pleistocene (Wood, 1991; McHenry and Coffing, 2000; Lieberman, 2011). Several

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researchers suggest that these decreases were made possible by cooking (Wrangham et al., 1999; Lucas, 2004; Carmody and Wrangham, 2009), but mechanical food processing techniques such as grinding and pounding also alter food mechanical properties considerably and may explain these decreases. The hypothesis that the genus *Homo* consumed less tough food is supported by dental microwear analyses, which document a decrease in the prevalence of features such as scratches and pits between the genus *Australopithecus* and *Homo* (Ungar and Scott, 2009).

Another line of evidence used to make inferences about shifts in hominin diet and bite force production has been variations in skull morphology. Mastication generates bending and twisting strains within ranges known to stimulate bone growth and remodeling (Hylander, 1979; Hylander and Johnson, 1997; Hylander et al., 1998). Australopiths, especially *Au. boisei* and *Au. robustus*, have more robust mandibular corpora than humans or apes, a likely adaptation for resisting high and repeated bending forces in the transverse and sagittal planes as well as longitudinal twisting (Hylander, 1988; Daegling and Grine, 1991). Mandibular robusticity relative to body mass is similar in *H. habilis* and gracile australopiths such as *Au. africanus*, but declines considerably in *H. erectus* (Chamberlain and Wood, 1985; Wood and Aiello, 1998). Experiments examining facial strains (Hylander et al., 1991; Hylander and Johnson, 1994; Ross and Hylander, 1996; Ross, 2001) along with finite element models (Strait et al., 2009) indicate that the relatively taller, wider, and more buttressed face of australopiths, especially the more robust forms, would have effectively resisted vertical bending and shearing, as well as twisting in the coronal plane. Although reductions in face and jaw robusticity in *Homo* are often interpreted as evidence for a less mechanically demanding diet, facial flattening likely reduces in vivo stresses generated by masticatory forces (Lieberman et al., 2004; Wroe et al., 2010).

A final line of evidence, considered here, is to estimate maximum bite force capabilities from craniofacial morphology. The most frequently assessed parameter is effective mechanical advantage (EMA, the ratio of a muscle's in-lever and out-lever) of the jaw adductors, especially in the sagittal plane (e.g., Rak, 1983; Demes and Creel, 1988; Lieberman, 2011). These studies document that anterior advancement of the zygomatic arch, lowering the occlusal plane relative to the TMJ, and facial retraction augment the EMA of the masseter and temporalis muscles in *Australopithecus* relative to great apes, and in robust versus gracile australopiths. A common inference is that natural selection will favor more efficient torque production in species that chew more mechanically demanding diets. EMA estimates, however, quantify only efficiency rather than actual bite force. Additionally, most bite force analyses estimate maximum bite force, rather than chewing force, the forces used to break down foods. These caveats aside, maximum bite force estimates are useful for evaluating the maximum capabilities of the masticatory system, especially the ability to process mechanically demanding foods.

Inferences about the evolution of food processing must also consider that comminution is governed by the amount of stress (force per unit area) applied to a food item (Preuschoft, 1989; Lucas et al., 1994). In a landmark study, Demes and Creel (1988) showed that bite force equivalents (BFEs, relative measures of muscle

size and lever arms that are proportional to actual measures of force) increased isometrically with occlusal area, suggesting that molar stress was relatively constant across extant primates, humans, and hominins. If so, then the relatively larger jaw adductor muscles of robust australopiths increased bite force generation, but in proportion to increases in molar surface area, resulting in no change in bite stresses. Similarly, decreases in bite force in the genus *Homo* coupled with smaller molar surface areas, resulted in bite stresses similar to those of fossil hominins and nonhuman primates. Demes and Creel's seminal analysis, however, has several limitations. First, masseter CSAs were not measured directly, but instead were estimated as 80% of temporalis CSA based on relative sizes of the masseter and temporalis measured in orangutans and humans. This estimate may be problematic because of variation in the relative size of the masseter and temporalis across species. In addition, Demes and Creel did not include the medial pterygoid, and they estimated muscle moment arms only from their origin on the cranium without using their mandibular insertions. Finally, Demes and Creel did not account for variation in muscle architecture across species, particularly PCSA, a measure of the sum of the CSA of all muscle fibers, which is directly proportional to a muscle's maximum isometric force (Powell et al., 1984). Because pennation allows more fibers to be packed in a space and increases a muscle's PCSA, estimating muscle CSAs from skeletal dimensions ignores the effects of pennation and likely underestimates PCSAs, and hence maximum muscle force. Finally, estimating unitless BFEs rather than absolute values of force complicates interpretations of scaling relationships between force and tooth area and comparison with in vivo measures of bite force from other studies.

O'Connor et al. (2005) expanded on Demes and Creel (1988) to compare anterior bite force production capabilities in late *Homo*. O'Connor et al. estimated absolute bite forces by measuring masticatory lever arms and muscle CSAs from crania and mandibles. A muscle architecture CF was calculated for each muscle by dividing the average muscle CSAs of modern humans by PCSA values measured from computed tomography (CT) images. The muscle-specific CFs were applied to all taxa and were multiplied by muscle CSA to estimate muscle PCSA. Muscle PCSA estimates were then used to estimate muscle forces, which were combined with lever arms to estimate maximum bite forces. O'Connor et al. found that Neanderthals and modern humans have similar anterior bite force capabilities, and concluded that overall skull size and robusticity best predicts maximum bite force. O'Connor et al. (2005) is a substantial advance over Demes and Creel (1988), but they focused primarily on anterior bite forces in only the genus *Homo*. In addition, muscle architecture CFs were based on estimates of muscle architecture measured from CT images, but the accuracy of imaging-based methods of estimating PCSA is reduced across muscles (Weijs and Hillen, 1984; Goto et al., 2005; Eng et al., 2007).

Finally, Wroe et al. (2010) further elaborated the methods used by Demes and Creel (1988) and O'Connor et al. (2005) to estimate bite forces in a human, several nonhuman primates, and two fossil hominins, *Au. africanus* and *Au. boisei*, using a 3D finite element analysis (FEA). They found that the large EMA in humans allows them to produce relatively high bite forces while exerting relatively low muscle forces, especially in the

anterior dentition. Furthermore, scaled to produce the same bite force, peak transitory forces were relatively low in the human cranium and mandible relative to other taxa. Wroe et al. argue that these data provide evidence that the human jaw improves performance for hard object feeding. Although 3D FEA has advantages over models that use 2D data and approximate muscles as a single vector, Wroe et al. modeled only one female per group, and just two fossil hominins, neither from the genus *Homo*. Additionally, because Wroe et al. use the muscle CFs from O'Connor et al. (2005), their estimates of bite force do not account for the differences in muscle architecture across humans and nonhuman primates.

Here, we build upon the approaches used by Demes and Creel (1988), O'Connor et al. (2005), and Wroe et al. (2010) to estimate molar bite force and stress generation in a broad sample of extant apes and fossil hominins. We use physical measures of muscle mass, fiber length, and pennation angle to calculate muscle PCSA and estimate muscle architecture CFs for each extant primate. Species-specific CFs allow us to account for differences in muscle architecture related to the wide variation in feeding behaviors across primates. Our goal is to estimate molar bite force using both skeletal and muscular parameters known to influence comminution efficiency in vivo. We also test predictions for the scaling of maximum bite force and occlusal area (i.e., occlusal stress) among taxa.

BIOMECHANICAL MODEL AND HYPOTHESES

Torque (t), the rotational force about an axis, is the product of an exerted force (F) and its moment arm (r). In a biological system, muscle torque (t_{in}) must offset a resistant torque (t_{out}) to maintain equilibrium: $t_{in} = t_{out}$, or $F_{in} \times r_{in} = F_{out} \times r_{out}$. Applying this equation to mastication, the maximum magnitude of bite force produced at any location along the dental row (F_{Bite}) is equal to the muscle resultant force, F_{Muscle} , times the ratio of the muscle resultant in-lever arm (r_{Muscle}) divided by the out-lever arm (r_{Bite}), using the primary jaw adductors, the masseter (mass.), medial pterygoid (MP), and temporalis (temp.). Another factor to consider is differential recruitment of the working side (WS) and balancing side (BS) muscles. After Spencer (1998), we assume that BS muscle forces average 80% of WS forces for a typical molar. Therefore, overall bite force is estimated as:

$$F_{Bite} = \frac{1.8((F \times r)_{WSMass.} + (F \times r)_{WSTemp.} + (F \times r)_{WSMP})}{r_{Bite}} \quad (1)$$

The model and background information summarized above lead to three general hypotheses.

Hypothesis 1

We predict that muscle architecture CFs (the ratio of skeletally measured CSA to muscle PCSA) differ between humans and nonhuman primates. Because a muscle architecture CF indicates how a muscle's mass is arranged to modify its force-generating properties, species that comminute fracture resistant foods would benefit from packing more fibers in their jaw adductor muscles to increase muscle PCSA, hence, muscle force. These species would have relatively low CFs compared to species with smaller PCSAs. Conversely, species that regularly consume extremely soft and/or processed diets

do not need to generate high bite forces and would have lower PCSAs and thus, higher CFs. Therefore, we predict that humans will have relatively higher CFs compared with nonhuman primates. This hypothesis is important to test because if muscle architecture differs between humans and nonhuman primates, and only species in the genus *Homo* had human-like jaw muscle architecture, then bite force estimates that do not account for muscle architecture differences may under- or over-estimate differences between *Homo* and other primates.

Hypothesis 2

Following Demes and Creel (1988), molar bite force is predicted to correlate significantly and scale isometrically with molar occlusal area across anthropoids. The basis for this prediction is that bite force is proportional to PCSA and thus scales to the power of 0.67 against body mass. Using measures of M^2 area from this study along with body mass estimates from Smith and Jungers (1997), we found that in our sample of primates, M^2 area scales with body mass to the power of 0.46, so the predicted scaling coefficient of bite force relative to occlusal area should be close to 1.46 (0.67/0.46).

Hypothesis 3

Because of recent changes in food processing, we predict that *Homo* species generate relatively low maximum bite forces compared with other primates and fall below the regression line between molar bite force and molar occlusal area for nonhuman primates and australopiths.

MATERIALS AND METHODS

Skull Sample

We calculated bite forces for male and female skulls (crania plus mandibles) of six species of extant hominoids, one old world monkey (*Macaca fascicularis*), and eight fossil hominin species in *Australopithecus* and *Homo* (Table 1). Sample sizes in the extant species were chosen to be commensurate with the samples from fossil taxa. In extant species, adult individuals with a full dental row and no apparent pathology were chosen from the collections at the Museum of Comparative Zoology and Peabody Museum, Harvard University. The modern *Homo sapiens* sample consists of 12 late agricultural/early industrial individuals from the Campania and Lazio regions of Italy. Hominin measurements were obtained from casts. Presumptive males and females were not available for all hominin species. Additionally, no mandible was available for several fossil crania. In these instances, we measured mandibles of similar-sized individuals; for *H. habilis*, the OH 13 mandible was paired with the KNM-ER 1813 cranium. For *H. heidelbergensis*, the Mauer mandible was paired with the Kabwe and Petralona 1 crania and for *H. erectus*, the BK67 mandible was matched with the KNM-ER 3733 cranium.

Occlusal Area

Occlusal area of the second upper molar (M^2) was calculated as the product of buccolingual and mesiodistal

TABLE 1. Specimens used to estimate M^2 bite force in this study

Fossil specimens	Australopiths	
	<i>Au. afarensis</i> (n = 1)	Hadar composite (male) ^a
	<i>Au. africanus</i> (n = 1)	STS 5 (female) ^b
	<i>Au. boisei</i> (n = 1)	OH 5 (male) ^c
	<i>Homo</i> species	
	<i>H. habilis</i> (n = 1)	KNM-ER 1813 ^c with jaw from OH 13 (male)
	<i>H. heidelbergensis</i> (n = 3)	Kabwe ^d with Mauer jaw, Petralona 1 ^e with Mauer jaw, Atapuerca 5 ^f
	<i>H. erectus</i> (n = 4)	Zhoukoudian composite, ^b KNM-WT 15000, ^b KNM-ER 3733 ^b with the BK67 jaw, D2700 ^e
	<i>H. neanderthalensis</i> (n = 6)	La Ferrassie, ^d La Chapelle, ^g Amud I, ^h Le Moustier, ^h Shanidar-1, ^h Gibraltar-1 ^h
		Grotte des Enfants 6, ^h Skhul V, ^h Predmosti 3 ^h and 4, ^h Qafzeh 9, ^h Brno 3, ^h Dolni Vestonice 3 ^h
Extant specimens	Pleistocene	
	<i>H. sapiens</i> (n = 7)	
	<i>M. fascicularis</i> (n = 8)	4 males, 4 females
	<i>H. lar</i> (n = 8)	4 males, 4 females
	<i>P. pygmaeus</i> (n = 5)	3 males, 2 females
	<i>G. gorilla</i> (n = 8)	4 males, 4 females
	<i>P. paniscus</i> (n = 2)	1 male, 1 female
	<i>P. troglodytes</i> (n = 12)	6 males, 6 females
	<i>H. sapiens</i> (n = 12)	6 males, 6 females

^a Individual molar area measure from Kimbel et al. (2004).

^b Mean molar area from Wood (1991).

^c Individual molar area measure from Wood (1991).

^d Molar area measured from cast.

^e Individual molar area measure from Rightmire (1993).

^f Molar area measure from cast (Rubas, personal communications).

^g Mean molar area from Brace and Mahler (1971).

^h Individual molar area measure from Frayer (1976).

diameters. In non-fossil specimens, these measurements were taken using digital calipers (accuracy, 0.01 mm) following Wood (1991). Whenever possible, fossil measurements were taken from the literature (Brace and Mahler, 1971; Frayer, 1976; Wood, 1991; Rightmire, 1993; Kimbel et al., 2004). Because molar area could not be measured in the edentulous STS5 individual, second molar area values for *Au. africanus* were used.

Lever Arm Estimates

Bite force out-levers were measured using digital calipers on each skull from the glenoid fossa center to the center of the occlusal surface of M^2 . Using scaled photographs of the skulls, in-levers were measured with ImageJ software (NIH, Bethesda, MD) as the perpendicular distance between the approximate line of action of each major jaw adductor and the glenoid fossa center. Following Hiiemae (1971), the masseter's line of action was estimated in lateral view from the midpoint of the muscle origin on the zygomatic arch to the angle of the mandible; the line of action of the temporalis was estimated from the centroid of the muscle's origin (measured with ImageJ) to the coronoid process; and the line of action of the medial pterygoid was estimated in inferomedial view (perpendicular to the muscle's plane) between the lateral and medial pterygoid plates and the centroid of the muscle's insertion on the mandible.

Muscle Cross-Sectional and Physiological Cross-Sectional Areas

For the temporalis, modeling clay was used to fill the temporal fossa between the zygomatic arch and the lateral wall of the skull. The clay was then removed and scanned on a flatbed scanner and the area measured in ImageJ.

The height and width of the medial and lateral pterygoid plates were measured with calipers and modeled as an ellipse to estimate the medial pterygoid CSA. The CSA of the masseter was estimated as the maximum projected distance (in superior view) between the zygomatic arch and the mandibular ramus multiplied by the length of the muscle origin on the zygomatic arch. The reliability of muscle area and lever arm measures were tested using repeated measures made by a single observer. For all measurements, the intraclass correlation coefficient for measures made on a single skull was greater than 0.95 ($P < 0.05$).

Muscle PCSAs were estimated from skeletal estimates of CSA using species-specific muscle architecture CFs. For chimps, the masseter, temporalis, and medial pterygoid muscles were dissected from a formalin-fixed adult male (Harvard University MCZ 61063). Dissected muscles were weighed and fiber length (L_f') measured from three regions in each muscle using digital calipers. Pennation angle was measured with a goniometer as the angle between the fibers and the distal tendon. Under magnification, muscle fiber bundles were isolated from each fascicle and mounted on slides. Following Lieber et al. (1990), bundle sarcomere length (L_s') was determined by laser diffraction and normalized fiber length (L_f) calculated as:

$$L_f = L_f' \left(\frac{2.7 \mu\text{m}}{L_s'} \right) \quad (2)$$

where L_f' is measured fiber length and 2.7 μm is the optimal sarcomere length for human muscle (Lieber et al., 1994). PCSA was calculated as:

$$\text{PCSA} = \frac{M * \cos\theta}{\rho * L_f} \quad (3)$$

where M is muscle mass, θ is pennation angle, and ρ is muscle density (1.0564 g/cm^3 ; Mendez and Keys, 1960).

These data were combined with PCSA values from additional adult chimps for the masseter ($n = 1$; Spencer, personal communications), temporalis, and medial pterygoid ($n = 2$; Spencer, personal communications; Taylor, personal communications) to obtain an average PCSA for each muscle. For human CFs, PCSA was calculated using measures of muscle mass, fiber length, and pennation angle from the temporalis, masseter, and medial pterygoid measured by van Eijden et al. (1997) in 8 humans. Temporalis and masseter PCSA values reported in Taylor and Vinyard (2013) for *P. pygmaeus* ($n = 2$), *Hylobates* sp. ($n = 3$), *G. gorilla* ($n = 4$), *P. paniscus* ($n = 1$), and *Macaca* sp. ($n = 4$) were used to calculate CFs in the remaining anthropoid species. To compare masseter PCSA between primates and humans, we used the sum of the masses of the deep and superficial masseter along with the superficial masseter normalized fiber length and pennation angle reported in Taylor and Vinyard (2013) to calculate total masseter PCSA.

CSAs measured on the primate skulls were averaged and divided by the average PCSA for each species to calculate muscle architecture CFs for the temporalis, masseter, and medial pterygoid. Temporalis PCSA was not reported for *P. pygmaeus* and *P. paniscus*, so the chimp temporalis CF was used in these species. A medial pterygoid PCSA is available only for chimps, so the chimp medial pterygoid CF was used for all nonhuman primates. Species-specific CFs were used to calculate muscle PCSA for extant primates from skeletally measured CSA. Australopith muscle PCSAs were calculated using the chimp CF, whereas *Homo* PCSAs were calculated using the human CFs. We consider using the human CFs for *Homo* to be the most conservative choice for phylogenetic reasons as well as the general morphological similarities between *Homo* and later humans. Estimating *Homo* PCSAs using the chimp CFs allows us to test the effect of this assumption on bite force estimates. The normalized muscle CSAs were multiplied by muscle specific tension (35 N/cm^2) to calculate muscle force (Zajac, 1989).

Statistical Analyses

To test the hypothesis (H1) that muscle architecture CFs differ between humans and nonhuman primates, we examined whether the human masseter and temporalis CFs fell two standard deviations outside the mean CFs for nonhuman apes. Least squares regression of log-transformed M^2 bite force plotted against log-transformed M^2 occlusal area were used to test the hypothesis (H2) that bite force scales isometrically with molar area. Prediction intervals on the regression line of M^2 molar area and bite force for australopiths and nonhuman anthropoids were used to test the hypothesis (H3) that *Homo* species generate relatively low bite forces. Multiple stepwise regression was then used to examine the relative contributions of muscle force and EMA to bite force. ANOVA was used to compare total uncorrected muscle CSA, total muscle force, M^2 bite force, M^2 area, and average EMA in the masseter, temporalis, and medial pterygoid across species in *H. sapiens*, *P. troglodytes*, *P. pygmaeus*, *M. fascicularis*, *H. lar*, and *G. gorilla*. Pairwise comparisons were made using Dunnett's T3 post hoc test, which accounts for unequal variance across groups and is suitable for multiple comparisons (Dunnett, 1980). Significance was set to $\alpha = 0.05$. Although we can make general comparisons between *H. habilis* and other species, the single individual

representing *H. habilis* precludes making statistical comparisons with other species.

RESULTS

Differences in masticatory morphology among taxa vary in terms of the average EMA at M^2 as well as uncorrected total jaw adductor muscle CSA. Average EMA of the jaw adductor muscles at M^2 in australopiths is not significantly different from gorillas, orangutans, chimps, bonobos, gibbons, and macaques and most *Homo* species except *H. heidelbergensis* (Table 2 and Supporting Information Table S1). Additionally, the uncorrected total CSA of the masticatory muscles in australopiths is not significantly different from all species (Table 2 and Supporting Information Table S2). The pattern in *Homo* is different. While the uncorrected total jaw adductor muscle CSA in modern *H. sapiens* is similar to that of all *Homo* species (Table 2 and Supporting Information Table S2), modern humans have a significantly greater average masticatory muscle EMA at M^2 than *H. heidelbergensis* and *H. neanderthalensis* (Table 2 and Supporting Information Table S1). In addition, average jaw adductor muscle EMA at M^2 in modern humans ($0.58 \pm 0.01 \text{ cm}$) is significantly larger than that of most other extant apes (Gorillas: $0.49 \pm 0.01 \text{ cm}$; Chimps: 0.51 ± 0.01 ; Gibbons: 0.44 ± 0.01 ; Supporting Information Table S1). Modern humans, orangutans, and bonobos have similar average EMAs at M^2 (Table 2 and Supporting Information Table S1).

Dissections and muscle architecture data from Taylor and Vinyard (2013) were used to calculate muscle architecture CFs as the muscle CSA measured on the skull divided by the average PCSA for temporalis, masseter, and medial pterygoid muscles in each primate group (Table 3). With the exception of the human masseter, these CFs are considerably less than 1.0 (Fig. 1), indicating that the skeletally measured CSAs underestimate PCSAs, hence muscles' capability to generate force. Note also that the CFs vary across muscles and between species. As predicted (H1), the human CFs fall two standard deviations above the nonhuman ape CFs for the masseter (1.48 vs. 0.73 ± 0.20 ; mean ± 2 SDs) and temporalis (0.65 vs. 0.38 ± 0.12). As a consequence of the high CFs in humans, the uncorrected total muscle CSA estimates are similar between *P. troglodytes* and all *Homo* species (Table 2 and Supporting Information Table S2) but after correcting for muscle architecture differences, *P. troglodytes* generates significantly larger muscle forces than all *Homo* species (Table 4 and Supporting Information Table S3). If we assume that muscle size is proportional to skeletally measured CSA and that the accuracy of skeletal measures of CSA does not vary among taxa, these results suggest that the greater bite force capability of apes compared with humans is largely achieved through altered muscle architecture as opposed to a gross increase in muscle size.

Maximum estimated M^2 bite forces vary widely across species (Table 4). Gorillas, orangutans, and australopiths generate the highest estimated maximum M^2 bite forces, and gibbons and *H. heidelbergensis* generate the lowest M^2 bite forces. In terms of estimated molar occlusal stress, chimps, bonobos, orangs, and macaques generate the highest estimated M^2 bite stresses, whereas species in the genus *Homo* generate the lowest estimated M^2 stresses (Table 5). Note that gorillas and australopiths have large second molar areas compared with other

TABLE 2. *Masseter, temporalis, and medial pterygoid skeletally measured cross-sectional area and effective mechanical advantage at M² for the species used in this study*

	Skeletally measured cross-sectional area (cm ²)			Effective mechanical advantage		
	Masseter	Temporalis	Medial pterygoid	Masseter	Temporalis	Medial pterygoid
<i>H. sapiens</i>	11.14 ± 0.63	6.83 ± 0.37	1.95 ± 0.05	0.61 ± 0.01	0.49 ± 0.02	0.63 ± 0.01
Male	10.60 ± 0.75	6.65 ± 0.61	2.00 ± 0.08	0.60 ± 0.02	0.47 ± 0.03	0.62 ± 0.02
Female	11.79 ± 1.07	7.05 ± 0.40	1.90 ± 0.05	0.62 ± 0.02	0.51 ± 0.03	0.64 ± 0.02
Pleistocene <i>H. sapiens</i>	12.68 ± 0.29	7.21 ± 0.35	2.91 ± 0.15	0.53 ± 0.04	0.43 ± 0.04	0.35 ± 0.03
<i>H. habilis</i>	12.04	7.34	2.18	0.60	0.53	0.29
<i>H. heidelbergensis</i>	10.40 ± 0.17	6.17 ± 0.33	3.74 ± 0.15	0.47 ± 0.01	0.35 ± 0.02	0.26 ± 0.02
<i>H. erectus</i>	10.41 ± 0.68	6.68 ± 0.54	2.54 ± 0.16	0.54 ± 0.04	0.48 ± 0.02	0.45 ± 0.06
<i>H. neanderthalensis</i>	11.11 ± 0.33	7.93 ± 0.50	3.25 ± 0.18	0.48 ± 0.04	0.39 ± 0.02	0.38 ± 0.04
Australopith average	20.26 ± 4.87	14.45 ± 4.06	3.71 ± 0.74	0.62 ± 0.02	0.43 ± 0.02	0.48 ± 0.02
<i>Au. afarensis</i>	22.46	16.35	3.26	0.62	0.41	0.52
<i>Au. africanus</i>	10.95	6.67	2.70	0.65	0.48	0.47
<i>Au. boisei</i>	27.37	20.35	5.15	0.59	0.41	0.45
<i>P. troglodytes</i>	12.72 ± 0.76	9.95 ± 0.65	2.06 ± 0.03	0.52 ± 0.01	0.45 ± 0.01	0.57 ± 0.01
Male	13.89 ± 1.18	11.43 ± 0.84	2.13 ± 0.04	0.51 ± 0.01	0.45 ± 0.02	0.56 ± 0.01
Female	11.55 ± 0.78	8.48 ± 0.53	2.00 ± 0.05	0.54 ± 0.01	0.44 ± 0.01	0.58 ± 0.01
<i>P. paniscus</i>	10.18 ± 0.34	7.18 ± 1.14	1.01 ± 0.07	0.50 ± 0.00	0.45 ± 0.03	0.64 ± 0.02
Male	10.53	8.33	1.08	0.51	0.49	0.63
Female	9.84	6.04	0.94	0.50	0.42	0.66
<i>G. gorilla</i>	27.74 ± 2.31	20.70 ± 2.09	4.68 ± 0.44	0.48 ± 0.01	0.38 ± 0.01	0.61 ± 0.01
Male	33.40 ± 1.30	26.03 ± 1.19	5.74 ± 0.33	0.45 ± 0.01	0.37 ± 0.02	0.59 ± 0.02
Female	22.08 ± 1.39	15.37 ± 0.20	3.62 ± 0.18	0.51 ± 0.01	0.38 ± 0.01	0.64 ± 0.02
<i>P. pygmaeus</i>	17.68 ± 2.67	15.63 ± 2.18	3.79 ± 0.33	0.55 ± 0.01	0.44 ± 0.01	0.60 ± 0.02
Male	21.70 ± 1.70	18.99 ± 1.30	4.29 ± 0.16	0.53 ± 0.01	0.42 ± 0.01	0.59 ± 0.03
Female	11.66 ± 1.47	10.59 ± 0.47	3.04 ± 0.23	0.57 ± 0.00	0.46 ± 0.02	0.62 ± 0.01
<i>H. lar</i>	4.37 ± 0.19	2.80 ± 0.13	1.06 ± 0.04	0.42 ± 0.01	0.44 ± 0.01	0.46 ± 0.01
Male	4.75 ± 0.20	3.01 ± 0.18	1.17 ± 0.03	0.40 ± 0.02	0.44 ± 0.02	0.45 ± 0.02
Female	4.00 ± 0.17	2.60 ± 0.15	0.96 ± 0.02	0.43 ± 0.02	0.44 ± 0.02	0.47 ± 0.01
<i>M. fascicularis</i>	4.50 ± 0.23	4.00 ± 0.30	1.07 ± 0.07	0.46 ± 0.02	0.46 ± 0.01	0.57 ± 0.03
Male	5.07 ± 0.13	4.55 ± 0.35	1.21 ± 0.07	0.44 ± 0.01	0.47 ± 0.01	0.52 ± 0.01
Female	3.94 ± 0.14	3.46 ± 0.32	0.93 ± 0.06	0.47 ± 0.04	0.44 ± 0.00	0.62 ± 0.03

TABLE 3. *Muscle physiological cross-sectional area (PCSA), skeletally measured cross-sectional area (CSA), and muscle architecture correction factors (CFs; skeletally measured cross-sectional area/muscle physiological cross-sectional area) for the masseter, temporalis, and medial pterygoid muscles*

	Masseter			Temporalis			Medial pterygoid		
	CSA (cm ²)	PCSA (cm ²)	CF	CSA (cm ²)	PCSA (cm ²)	CF	CSA (cm ²)	PCSA (cm ²)	CF
Human ^a	11.14	7.53	1.48	6.83	10.47	0.65	1.95	5.28	0.37
Chimpanzee ^b	12.72	18.67	0.68	9.95	23.92	0.42	2.06	13.77	0.15
Bonobo ^c	10.18	16.77	0.61	7.18	NA	0.42^d	1.01	NA	0.15
Gorilla	27.74	37.74	0.74	20.70	47.24	0.44	4.68	NA	0.15
Orangutan	17.68	20.25	0.87	15.63	NA	0.42^d	3.79	NA	0.15
Gibbon	4.37	5.38	0.81	2.80	8.55	0.33	1.06	NA	0.15
Macaque	4.50	6.99	0.64	4.00	12.26	0.33	1.07	NA	0.15

^a PCSA values calculated from mass, fiber length, and pennation angle ($n = 8$) reported in Van Eijden et al. (1997).
^b PCSA values measured in this study and averaged with PCSAs for the masseter (Spencer, personal communications), temporalis, and medial pterygoid (Spencer and Taylor, personal communications).
^c PCSA values for masseter and temporalis in other nonhuman primates reported in Taylor and Vinyard (2013). See text for details.
^d In the absence of *P. paniscus* and *P. pygmaeus* temporalis PCSA data, the chimp temporalis CF was used for these species.

taxa, keeping their bite stresses comparatively low despite high bite forces. On the other hand, M^2 bite forces are concentrated on smaller molar areas in chimps, bonobos, and macaques, leading to relatively higher M^2 occlusal stresses (Table 5).

It is impossible to know when human-like muscle architecture evolved, but if we assume that the human CFs apply to the genus *Homo* and chimp CFs apply to australopiths, comparison of fossil hominins with extant primates suggests that the masticatory capabilities of australopiths are similar to, or greater than, extant non-human apes. However, australopith muscle forces and

bite forces are not significantly different from any of the taxa examined due to the small sample size and large variation among australopiths. Australopiths have the capacity to generate similar muscle forces compared with gorillas (3,113.97 ± 743.48 N vs. 4,051.98 ± 367.40 N) and orangutans (2,759.30 ± 342.76 N). Additionally, australopiths generate similar magnitudes of maximum M^2 bite forces (Table 4) and bite stresses (Table 5) compared with gorillas and orangutans. If we apply human CFs, australopith muscle forces (1,608.49 ± 395.84 N) are more similar to chimp muscle forces (1,966.84 ± 86.20 N) and they generate similar maximum M^2 bite

TABLE 4. Total masseter, temporalis, and medial pterygoid muscle force and molar bite force at M², both calculated using muscle cross-sectional areas measured on the skull and corrected using muscle architecture correction factors

	Muscle force (Newtons)	M ² bite force (Newtons)
<i>H. sapiens</i> ^a	816.49 ± 32.22	825.75 ± 45.17
Male	798.21 ± 46.30	789.22 ± 56.49
Female	838.41 ± 47.69	869.57 ± 74.53
Pleistocene <i>H. sapiens</i> ^a	963.95 ± 33.14	754.72 ± 51.18
<i>H. habilis</i> ^a	886.02	790.58
<i>H. heidelbergensis</i> ^a	932.56 ± 24.12	582.34 ± 17.88
<i>H. erectus</i> ^a	846.49 ± 53.39	753.45 ± 76.34
<i>H. neanderthalensis</i> ^a	997.99 ± 25.94	738.52 ± 61.90
Australopith average ^b	3,113.97 ± 743.48	2,796.01 ± 595.45
<i>Au. afarensis</i>	3,281.32	2,989.65
<i>Au. africanus</i>	1,750.73	1,681.57
<i>Au. boisei</i>	4,309.85	3,716.82
<i>P. troglodytes</i>	1,966.84 ± 86.20	1,780.18 ± 71.42
Male	2,164.28 ± 105.94	1,928.60 ± 98.65
Female	1,769.40 ± 76.68	1,631.76 ± 62.43
<i>P. paniscus</i>	1,354.46 ± 121.34	1,244.65 ± 135.01
Male	1,475.80	1,379.66
Female	1,233.12	1,109.65
<i>G. gorilla</i>	4,051.98 ± 367.40	3,420.10 ± 251.55
Male	4,991.04 ± 184.50	4,067.33 ± 97.59
Female	3,112.92 ± 89.41	2,772.86 ± 80.55
<i>P. pygmaeus</i>	2,759.30 ± 342.76	2,559.69 ± 295.84
Male	3,287.97 ± 187.37	2,978.83 ± 250.14
Female	1,966.28 ± 146.44	1,930.99 ± 169.41
<i>H. lar</i>	734.04 ± 26.33	578.19 ± 19.93
Male	796.81 ± 22.15	618.90 ± 25.81
Female	671.27 ± 10.83	537.48 ± 9.09
<i>M. fascicularis</i>	920.92 ± 56.67	806.93 ± 45.39
Male	1,042.14 ± 50.90	898.42 ± 40.88
Female	799.70 ± 51.01	715.45 ± 48.60

^a Bite forces in all *Homo* species were normalized using a correction factor calculated from human muscle architecture data.

^b Bite forces in australopith species were normalized using a chimpanzee-derived correction factor.

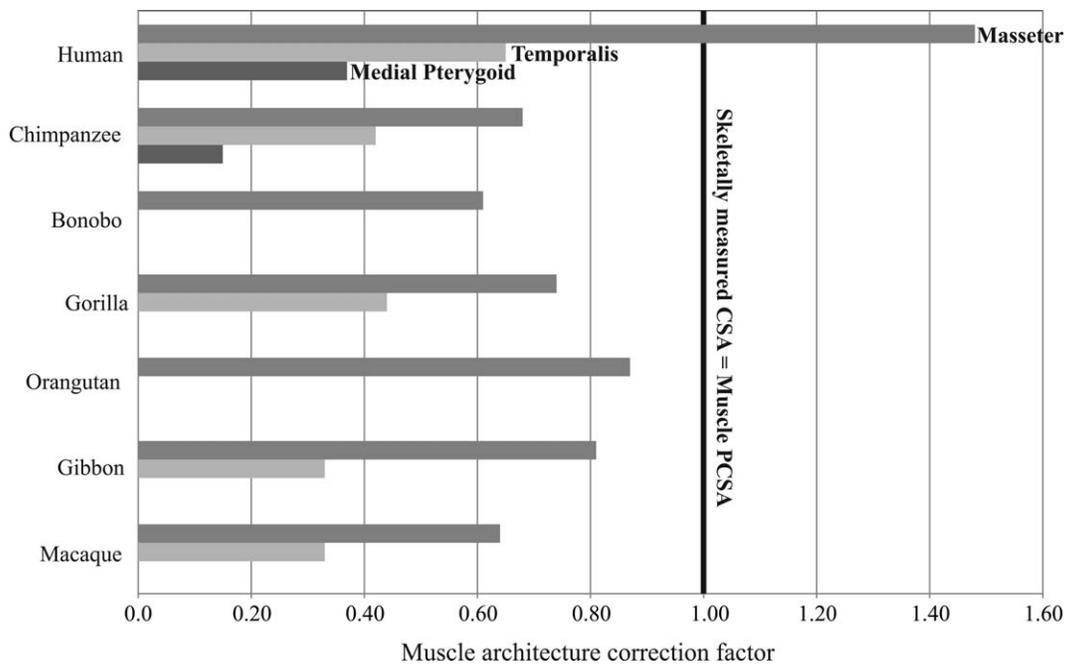


Fig. 1. Muscle architecture correction factors (skeletally measured cross-sectional area/muscle physiological cross-sectional area) for the human, chimpanzee, bonobo, gorilla, orangutan, gibbon, and macaque masseter, temporalis, and medial pterygoid muscles.

forces compared with chimps (1,413.75 ± 308.94 N vs. 1,780.18 ± 71.42 N). Australopiths are also more similar to chimps when using average chimp and human CFs.

Australopith bite stresses are significantly smaller than gorilla, chimp, and orangutan bite stresses when using the human CFs.

TABLE 5. M^2 molar area and M^2 bite stress for the species used in this study

	Molar area at M^2 (cm ²)	M^2 bite stress (N/cm ²)
<i>H. sapiens</i>	1.08 ± 0.02	768.42 ± 48.12
Male	1.08 ± 0.03	732.70 ± 52.41
Female	1.08 ± 0.04	811.28 ± 88.17
Pleistocene <i>H. sapiens</i>	1.27 ± 0.08	613.12 ± 61.02
<i>H. habilis</i>	1.64	482.06
<i>H. heidelbergensis</i>	1.30 ± 0.23	478.49 ± 83.47
<i>H. erectus</i>	1.56 ± 0.06	485.17 ± 48.47
<i>H. neanderthalensis</i>	1.31 ± 0.05	561.51 ± 32.84
Australopith average	2.61 ± 0.50	1,078.92 ± 178.74
<i>Au. afarensis</i>	2.12	1,410.21
<i>Au. africanus</i>	2.11	796.95
<i>Au. boisei</i>	3.61	1,029.59
<i>P. troglodytes</i>	1.18 ± 0.03	1,510.09 ± 59.52
Male	1.22 ± 0.04	1,591.25 ± 92.02
Female	1.15 ± 0.04	1,428.93 ± 66.96
<i>P. paniscus</i>	0.85 ± 0.08	1,462.32 ± 15.19
Male	0.93	1,477.50
Female	0.77	1,447.13
<i>G. gorilla</i>	2.60 ± 0.15	1,312.05 ± 41.05
Male	2.93 ± 0.10	1,389.02 ± 39.16
Female	2.26 ± 0.14	1,235.09 ± 48.81
<i>P. pygmaeus</i>	1.71 ± 0.09	1,478.38 ± 107.79
Male	1.84 ± 0.05	1,613.56 ± 109.73
Female	1.51 ± 0.01	1,275.62 ± 107.44
<i>H. lar</i>	0.43 ± 0.01	1,346.83 ± 43.95
Male	0.46 ± 0.02	1,355.06 ± 90.87
Female	0.40 ± 0.01	1,338.61 ± 26.63
<i>M. fascicularis</i>	0.45 ± 0.01	1,785.59 ± 99.84
Male	0.47 ± 0.01	1,921.62 ± 122.32
Female	0.44 ± 0.02	1,649.56 ± 138.65

When compared with most earlier *Homo*, modern humans have a greater average EMA at M^2 , but similar maximum jaw adductor muscle forces and M^2 bite forces. Modern *H. sapiens* generate similar total jaw adductor muscle force compared with Pleistocene *H. sapiens*, *H. erectus*, and *H. heidelbergensis*, and significantly lower muscle force compared with *H. neanderthalensis* (Table 4 and Supporting Information Table S3). Modern *H. sapiens* generate similar M^2 bite forces (Table 4 and Supporting Information Table S4) and bite stresses (Table 5 and Supporting Information Table S6) compared with Pleistocene *H. sapiens*, *H. neanderthalensis*, and *H. erectus*. Modern *H. sapiens* generate significantly higher bite forces (Table 4; $P < 0.05$) but not significantly different bite stresses compared with *H. heidelbergensis* (Table 5 and Supporting Information Table S6). It is worth noting that our modern human bite force estimates are slightly higher in females than males. However, this difference is not statistically significant and is likely due to our small modern human sample size.

Modern *H. sapiens* have absolutely lower maximum M^2 bite forces and occlusal stresses than most extant apes. Compared with modern *H. sapiens*, chimps and gorillas have significantly higher M^2 bite forces (Table 4 and Supporting Information Table S4) and M^2 occlusal stresses (Table 5 and Supporting Information Table S6) because of significantly higher muscle forces in chimps and gorillas compared with humans (Table 4 and Supporting Information Table S3). Although bite stresses are significantly higher in orangutans than humans (Supporting Information Table S6), higher muscle and bite forces in orangutans versus humans only approach

significance ($P < 0.10$; Supporting Information Tables S3 and S4).

If we apply the chimp CFs to fossil *Homo*, *Homo* bite force estimates are significantly greater than modern *H. sapiens* bite forces (except for *H. erectus*, whose are similar) and not significantly different from most nonhuman ape bite forces including chimps, bonobos, and orangutans ($P > 0.05$). However, *Homo* bite forces are significantly smaller than gorilla bite forces ($P < 0.05$). With chimp CFs, bite stresses are similar between fossil *Homo* and modern *H. sapiens*, except *H. neanderthalensis* who has significantly greater bite stresses than modern *H. sapiens* ($P < 0.05$). With chimp CFs, bite stresses are similar between fossil *Homo* specimens and nonhuman apes. Finally, applying average chimp-human CFs to fossil *Homo*, we find that fossil *Homo* bite forces and stresses are similar to modern *H. sapiens* bite forces and stresses and significantly smaller than chimp and gorilla bite forces and stresses ($P < 0.05$). Smaller bite forces and stresses in fossil *Homo* compared with orangutans only approaches significance ($P < 0.10$) with the average chimp-human CFs.

The regression between maximum M^2 bite force and M^2 molar area (Fig. 2) in all non-*Homo* species is highly significant with a slope of 0.90 (95% confidence interval: 0.83–0.97; R^2 : 0.93), but does not confirm H2 that bite force scales isometrically (predicted slope of 1.46) with molar area in nonhuman primates. When *Homo* is included in the analysis, the strength of the relationship and slope both decrease (95% CI: 0.55–0.92; $R^2 = 0.45$). As hypothesized (H3), species in the genus *Homo* fall below the regression line of M^2 area and bite force for australopiths and nonhuman primates, indicating a reduced ability to generate M^2 occlusal stress (Fig. 2). Species in the genus *Homo* fall below the regression line if we apply the average chimp-human CFs but do not fall below the line with chimp CFs.

DISCUSSION

Comparison With In Vivo Measures of Bite Force

Archaeological evidence suggests that advances in food processing techniques began with the Oldowan, and that the regular use of cooking probably began in the middle Pleistocene. Both changes may have decreased the selective advantage for having a large, robust masticatory complex to generate and resist high bite stresses during mastication. However, testing these and other hypotheses requires accurate and reliable estimates of maximum bite force from fossils.

Although we cannot test the accuracy of bite force estimates for fossil hominins, the predicted M^2 bite force values of extant hominoids including humans correspond well with published empirically measured maximum bite forces (Table 6). Of note, our estimates of maximum M^2 bite force for humans fall within the range of experimental measures of maximum bite force measured using a broad array of techniques on humans from western populations (Klatsky, 1942; Pruim et al., 1980; Gibbs et al., 1981; Van Sproonsen et al., 1989; Dean et al., 1992; Braun et al., 1995; Sinn et al., 1996). The only sample with significantly higher bite forces is a Yupik (formerly known as Alaskan Eskimo) population (Waugh, 1937), which is reported to have maximum bite forces nearly twice as high as those of other human populations. Yupik and Inuit skulls are reported to have enormous masticatory muscles, anteriorly positioned jaw adductor

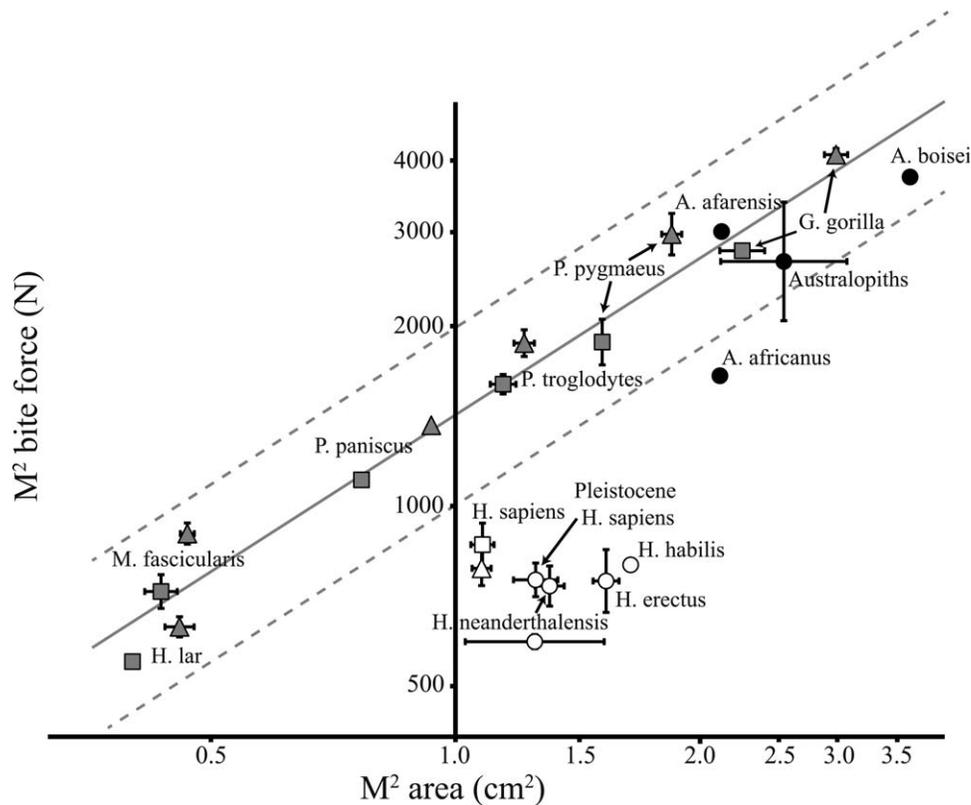


Fig. 2. Logarithmic plot of M^2 molar area and M^2 bite force. The black symbols represent australopith species, white symbols represent *Homo* species, and gray symbols represent extant nonhuman primates. Where identified, males are plotted as triangles and females as squares. Specimens with unidentified sex are plotted as circles. The regression line (fit on nonaveraged data) is represented by the gray solid line and the gray dashed lines show the 95% prediction intervals. The scaling equation of bite force at the second molar (BF) and second molar area (MA) is $BF = 3.02 \times MA^{0.74}$ when all specimens are included and $BF = 3.16 \times MA^{0.90}$ when *Homo* is excluded. The regression line shown here does not include *Homo*.

muscles, and low prognathism (Hylander, 1977). The latter two features indicate a high EMA, whereas the former would increase masticatory muscle force generation, together producing extremely high occlusal forces that may be adaptive for well-documented Yupik and Inuit feeding behaviors including chewing seal skin, eating frozen food and bone, and using the jaws as pliers (de Ponceins, 1941).

Although Yupik and Inuit populations may be adapted for generating large bite forces, individual bite force capabilities are also strongly affected by environmental factors during development. Modern humans that engage in vigorous masticatory activity associated with bruxism (i.e., teeth grinding) and have related severe dental attrition generate relatively high bite forces (911 N; Waltimo et al., 1994). However, our bite force estimates from a late agricultural/early industrial modern human sample are probably not lower than Yupik and Inuit bite forces solely from chewing a diet of processed foods because similar maximum bite forces have been measured in other indigenous populations include the Shipibo of Peru (601 N; $n = 24$), the Otomi of Mexico (738 N; $n = 43$), and army recruits from the Aymara of Peru (818 N; $n = 51$; Neumann and DiSalvo, 1958). While tortillas are a dietary staple for the Otomi, the Shipibo and Aymara eat both domesticated and wild foods, highlighting how bite force capabilities are influenced by a complex interplay of genetic, dietary, and extramasticatory factors. Another cautionary note to

consider is the remarkable range of published in vivo human bite forces. In vivo bite forces not only range across studies but also differ by as much 3-fold within the same population (Fig. 3). Although this large variability is hypothetically unique to humans, we lack enough in vivo bite force measures from other primates to make such a conclusion. Variation among in vivo bite forces across studies may also be due to methodological differences in transducer type and size and whether bite force is measured unilaterally or bilaterally.

In terms of nonhuman primates, there are few in vivo measurements available to test our results. Lucas et al. (1994) estimated maximum bite force in orangutans by measuring the amount of force required to break *Macadamia* seeds that they observed orangutans fracturing in a single bite. Lucas et al. found that orangutans would need $\sim 2,000$ N of force to break the seeds, which is below our maximum M^2 bite force estimate of $2,559.7 \pm 295.8$ N (Table 6). Our estimates of M^2 bite force for macaques, 806.9 ± 45.4 N, are higher than measures reported in the literature (Table 6). Hylander (1979) measured molar bite force in macaques (*Macaca fascicularis*) using a transducer-mounted plastic block. Hylander's average maximum bite force measure of 256.3 ± 39.3 N (range: 205.0–333.43 N) falls below the maximum M^2 bite force estimated here. Dechow and Carlson (1990) measured molar forces while maximally stimulating the masticatory muscles in anesthetized macaques (*Macaca mulatta*). Using unilateral measures

to estimate bilateral forces, they estimated maximum forces for males (369.3 ± 26.3 N) and females (286.2 ± 7.1 N), also below the values reported here.

TABLE 6. Comparison of empirical maximum bite force values with our M^2 bite force estimates

	Empirically measured bite force values (Newtons)	M^2 bite force estimate (N)
<i>H. sapiens</i>	721 (245–1,246) ^a	825.8 ± 45.2 (659.3–1,105.7)
Male	500 ± 22^b 517.0 (245–934) ^c 652 ± 426^d 756 ± 109 (403–1,206) ^e 814.0 ± 22.5 (417–1,280) ^f 911 ± 79 (660–1,150) ^g $1,277$ (890–1,548) ^h	789.2 ± 56.5 (659.3–986.6)
Female	368.1 ± 20.0^i 377.3 (111–734) ^c 412 ± 23^b 615.0 ± 18.4 (342–914) ^f $1,188$ (890–1,450) ^h	869.6 ± 74.5 (662.3–1,105.7)
<i>P. pygmaeus</i>	$2,000$ –3,000 ^j	$2,559.7 \pm 295.8$ (1,761.6–3,464.0)
<i>M. fascicularis</i>	256.3 ± 39.3 (205–333) ^k	806.9 ± 45.4 (617.7–988.0)
Male	369.3 ± 26.3^l	898.4 ± 40.9 (808.4–988.0)
Female	286.2 ± 7.1^l	715.5 ± 48.6 (617.7–850.0)

Bite force values are mean \pm s.e.m. (range).

- ^aGibbs et al. (1981).
- ^bDean et al. (1992).
- ^cKlatsky (1942).
- ^dVan Spronsen et al. (1989).
- ^ePruim et al. (1980).
- ^fBraun et al. (1995).
- ^gWaltimo et al. (1994).
- ^hWaugh (1937).
- ⁱSinn et al. (1996).
- ^jLucas et al. (1994).
- ^kHylander (1979).
- ^lDechow and Carlson (1990).

Tests of Study Hypotheses

Our first hypothesis (H1) is that CFs between skeletally measured muscle CSAs and PCSAs measured on jaw adductor muscles would be higher in humans than nonhuman primates. As hypothesized, nonhuman primate CFs were more than two standard deviations lower than human CFs, suggesting that nonhuman primates have ~55–147% larger PCSAs relative to skull size. Larger PCSAs indicate that nonhuman primate masticatory muscles pack more fibers in the same amount of space than human muscles, allowing them to achieve higher bite forces despite lower EMAs. Among primates, muscle architecture CFs varied between jaw adductor muscles most likely because these muscles (especially the masseter and temporalis) evolved different roles (Vinyard and Taylor; 2010). Conversely, variation in CFs among muscles may reflect differences in accuracy of the skeletal estimates of muscle size, particularly for the medial pterygoid whose complex attachments make it difficult to approximate muscle CSA on the skull. Similarly, differences in skull shape between chimps and humans may lead to variability in our ability to accurately measure CSA on the skull, ultimately causing differences in CFs between these species.

The human masseter has an exceptionally high CF, 1.48, indicating that the skeletally measured CSA overestimates the muscle’s PCSA. In contrast, the highly pennate arrangement of the medial pterygoid leads to a low CF in chimps and humans (0.15 and 0.37, respectively). As noted previously, the low medial pterygoid CF may also be due to the difficulty of estimating its CSA on the skull. Low CF values in the nonhuman primate jaw adductor muscles suggest that estimates of masticatory muscle force using skeletal CSAs underestimate muscle force capabilities by up to 85%. Therefore, care should be taken when estimating muscle force from skeletal measurements of muscle size. Muscle architecture CFs can be used to account for pennate muscle architecture, but CFs should be both species- and muscle-specific. Previous bite force estimates from fossils should be re-examined using human and nonhuman anthropoid specific muscle architecture CFs. Additionally, care

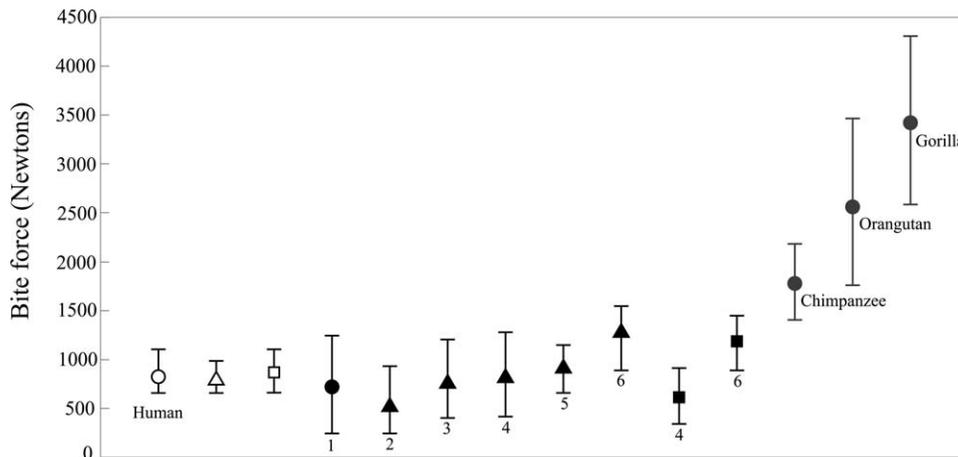


Fig. 3. Mean and ranges of maximum bite forces estimated in this study for humans (white markers) and nonhuman apes (gray markers), and in vivo bite force estimates (mean and range; black markers) from Gibbs et al. (1981) (1); Klatsky (1942) (2); Pruiim et al. (1980) (3); Braun et al. (1995) (4); Waltimo (1994) (5); and Waugh (1937) (6). Where identified, males are plotted as triangles and females as squares. Circles are the average of male and female bite forces. The ranges of in vivo bite forces demonstrate that bite force can vary up to 3-fold within populations.

should be taken when choosing CFs for fossil species as it influences bite force estimates. Using the human CFs or the chimp-human average CFs, fossil *Homo* species generate similar maximum M^2 bite forces compared with modern humans but significantly greater bite forces than modern humans when using the chimp CFs.

Our results do not confirm our hypothesis (H2) that M^2 bite force scales isometrically and with a high degree of correlation with molar occlusal area. As hypothesized (H3), species in the genus *Homo* fall below the regression line between bite force and molar area in nonhuman primates and australopiths, suggesting a reduced ability to generate occlusal stress.

If cooking did not begin regularly until one million years ago or more recently, then changes in the skull in early *Homo* such as smaller teeth, reduced facial buttressing and less robust mandibles, could be due to increases in nonthermal food processing (Wood and Collard, 1999; Klein, 2009; Lieberman, 2011). Cutting, slicing, mechanical pounding, and other methods of extra-oral mechanical processing decrease the size of food particles before ingestion and mastication. These processing techniques also break down cell walls of plants and fibrous connective tissue in meat, decreasing stiffness and toughness. Although later *Homo* was hypothesized to fall further from the regression line than early *Homo*, modern *H. sapiens* generate similar bite forces and stresses compared to early *Homo*. These results are not consistent with a two-stage shift in masticatory capabilities with the first related to first nonthermal food processing and then later to cooking. Reduced variation in bite forces across *Homo*, however, limits the ability to infer major dietary transitions from occlusal or craniofacial features. Larger sample sizes as well as additional sources of data such as enamel thickness and occlusal topography will be necessary to test for changes in masticatory abilities within *Homo*.

Comparison With Previous Studies

These results help refine previous estimates of bite force capabilities among hominins. Although Demes and Creel (1998) used unitless BFEs, there is good agreement between our data and Demes and Creel, which both estimate bite force values in australopiths to be similar to those of *G. gorilla* and *P. pygmaeus*. Similarly, both studies found bite force values in *Homo* to be less variable and slightly below what would be expected in species of similar molar size based on values from the other primates and hominins. In addition, O'Connor et al. (2005) calculated a maximum M1 bite force of 815 N for *H. sapiens*, 790 N for *H. neanderthalensis*, and 1,650 N for *P. pygmaeus*. The average maximum second molar bite force calculated in this study was 825.75 N in *H. sapiens*, 738.52 N for *H. neanderthalensis*, and 2,559.69 N for *P. pygmaeus*. These broadly comparable estimates differ primarily because of muscle architecture CFs. The human CFs used here are similar to O'Connor et al. in the temporalis (0.65 vs. 0.64) and medial pterygoid (0.37 vs. 0.26), but our masseter CF is 50% larger (1.48 vs. 0.99). Additionally, we used a masseter CF calculated from orangutan data and chimp muscle-derived temporalis and medial pterygoid CFs to estimate orangutan bite force. These were 12–42% lower than the muscle CFs used by O'Connor et al. (2005) and thus we estimated higher orangutan muscle forces and bite forces. Constantino et al. (2010) use molar tooth chip

size to estimate maximum molar bite forces for fossil and extant species. While our estimates of bite force from extant nonhuman primates are similar, we estimate lower bite forces for modern *H. sapiens* (825 vs. 1,470 N), *H. erectus* (753 vs. 2,075 N), and *Au. africanus* (1,711 vs. 2,598 N) and higher estimates for *Au. afarensis* (3,047 vs. 2,305 N) and *Au. boisei* (3,783 vs. 3,471 N).

When comparing our average bite force values with the estimates of Wroe et al. (2010), our estimates fall above their values for female *G. gorilla* (2,773 N vs. 1,723 N), *Au. boisei* (3,717 vs. 2,161 N), female *P. pygmaeus* (1,931 vs. 1,031 N), *Au. africanus* (1,682 vs. 831 N), and female *P. troglodytes* (1,632 vs. 1,511 N) but our bite force estimates fall below their average estimated bite force for female *H. sapiens* (870 vs. 1,317 N). There are several reasons why our results may differ. First, Wroe et al.'s estimates are based on only one female individual per species and thus may under represent average bite forces. Additionally, because Wroe et al. used human CFs to estimate muscle PCSA in anthropoids, they likely underestimate nonhuman anthropoid muscle PCSAs and subsequently, muscle forces (Taylor and Vinyard, 2013). On the other hand, Wroe et al. (2010) estimated *H. sapiens* bite force from a San hunter-gatherer, who may generate higher bite forces than our late agricultural/early industrial modern human sample that likely consumed a highly processed diet. Additionally, they estimate three-dimensional bite forces, whereas this study's moment arms are solely in the sagittal plane and 3D bite force estimates may be more accurate than 2D estimates. Finally, Wroe et al. represented muscles as multiple force vectors, which may more accurately represent muscles with complex attachments.

Nonetheless, the results presented here agree with Wroe et al. (2010) that human bite force estimates are influenced by their relatively greater EMAs compared with nonhuman apes. While Wroe et al. found the greatest relative difference in EMA at the anterior dentition and further discussed the implications for using teeth as tools in *Homo*, our study is limited to molar bite force estimates. Wroe et al. argued that the large EMAs allow humans to generate high bite forces with relatively low muscle forces that may have permitted gracilization of the mandible and cranium in later *Homo*. Wroe et al. did not include earlier *Homo* species in their analysis, but the results presented here indicate that modern humans generate similar or slightly higher bite forces than earlier *Homo*, suggesting that high bite force efficiency in modern humans may not apply to other *Homo* species. Furthermore, it should be evident that mechanical advantage is a poor proxy for bite force. Plotting second molar bite force against total jaw adductor muscle force and average EMA at M^2 demonstrates that muscle force covaries significantly with M^2 bite force across this sample (Fig. 4). Multiple stepwise regression confirms that muscle force is the best predictor of bite force. When EMA is added to the regression equation, the R^2 value changes from only 0.966 to 0.976, suggesting that M^2 bite force is increased by increasing muscle force rather than muscle mechanical advantage.

Limitations

Several limitations of this study merit consideration. One is that we used only a single static estimate of EMA, even though this ratio changes dynamically throughout the jaw joint's range of motion (Koolstra,

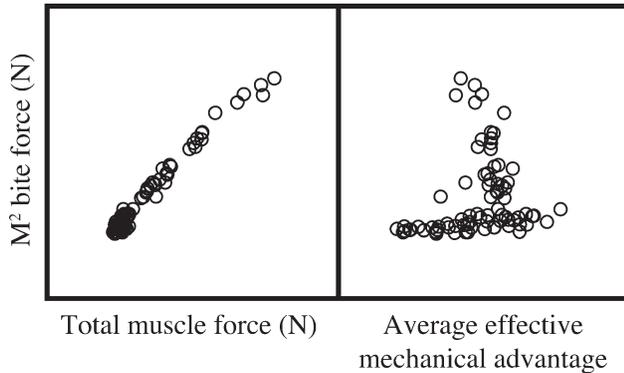


Fig. 4. Total jaw adductor muscle force and average jaw adductor muscle effective mechanical advantage plotted against bite force for all specimens used in this study. Muscle force is a better predictor of bite force than effective mechanical advantage.

2002). Using a single EMA for each muscle also does not account for muscles having distinct functional compartments with different fiber directions, attachment areas, and lines of action (van Eijden et al., 1997; Davis et al., 2010; Wroe et al., 2010). Furthermore, we used 2D rather than 3D estimates of lever arms, which may cause us to under- or over-estimate bite force (McHenry et al., 2007). Another limitation is that when estimating M^2 bite force, we assumed maximum activation of jaw adductor muscles, which is unlikely to occur commonly in normal mastication.

Another limitation is sample size. Larger sample sizes both across hominoids, and within fossil hominins are necessary not only for more accurate estimates of mean molar bite forces, but also to better understand ranges of variation. Furthermore, given the changes in diet that we assume occurred in *Homo*, using modern human muscle architecture to represent all *Homo* species may be erroneous. Muscle architecture data from hunter-gatherer populations who do not chew highly processed foods may be more representative of earlier *Homo*, but these data are not currently available. Additionally, reduced variation in our *Homo* sample does not reflect the large range of variation in vivo bite forces that have been measured in humans. This suggests that our bite force estimates may be representative of our specific study sample and care should be taken when using these data to predict bite forces in other human populations.

Another limiting factor to consider is muscle fiber types. Stedman et al. (2004) found that a gene encoding a muscle protein isoform was inactivated in masticatory muscles around 2.4 Ma in the genus *Homo*, and may have led to a shift in muscle fiber type, muscle fiber size, and even whole muscle size. However, because there is conflicting evidence for a difference in muscle stress in fast versus slow muscle fibers (Bodine et al., 1987; Lucas et al., 1987; Schiaffino and Reggiani, 2011), we would not expect a large influence on muscle force of fiber type alone. Nonetheless, more detailed analyses of the muscle fiber type and muscle fiber size profile in human and nonhuman primate masticatory muscles may reveal other factors influencing bite force variability among these species.

CONCLUSIONS

Efforts to model bite forces suggest that taxa in the genus *Homo* generate maximum bite forces below those

predicted based on scaling relationships among nonhuman primates and australopiths. We hypothesize that the advent of nonthermal food processing technologies in the lower paleolithic before cooking became common decreased the selective pressure acting on cranial form related to the generation of high bite stresses during mastication. Our data also support earlier interpretations that australopiths had ape-like bite force capabilities. Finally, M^2 bite force values are more highly correlated with muscle force than EMA across hominoids. Therefore, researchers should use caution when using EMA as a proxy for bite force in fossil hominins, and species-specific muscle architecture CFs should be used to account for differences in muscle architecture across primates.

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