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Jaw-muscle architecture and mandibular morphology influence relative maximum jaw gapes in the sexually dimorphic *Macaca fascicularis*

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ABSTRACT

Maximum jaw gape is a performance variable related to feeding and non-feeding oral behaviors, such as canine gape displays, and is influenced by several factors including jaw-muscle fiber architecture, muscle position on the skull, and jaw morphology. Maximum gape, jaw length, and canine height are strongly correlated across catarrhine primates, but relationships between gape and other aspects of masticatory apparatus morphology are less clear. We examine the effects of jaw-adductor fiber architecture, jaw-muscle leverage, and jaw form on gape in an intraspecific sample of sexually dimorphic crab-eating macaques (*Macaca fascicularis*). As *M. fascicularis* males have relatively larger maximum gapes than females, we predict that males will have muscle and jaw morphologies that facilitate large gape, but these morphologies may come at some expense to bite force.

Male crab-eating macaques have relatively longer jaw-muscle fibers, masseters with decreased leverage, and temporomandibular joint morphologies that facilitate the production of wide gapes. Because relative canine height is correlated with maximum gape in catarrhines, and males have relatively longer canines than females, these results support the hypothesis that male *M. fascicularis* have experienced selection to increase maximum gape. The sexes do not differ in relative masseter physiologic cross-sectional area (PCSA), but males compensate for a potential trade-off between muscle excursion versus muscle force with increased temporalis weight and PCSA. This musculoskeletal configuration is likely functionally significant for behaviors involving aggressive canine biting and displays in male *M. fascicularis* and provides additional evidence supporting the multifactorial nature of the catarrhine masticatory apparatus. Our results have implications for the evolution of craniofacial morphology in catarrhine primates and reinforce the importance of evaluating additional factors other than feeding behavior and diet in analyses of masticatory apparatus form, function, and evolution.

Introduction

Maximum jaw gape is a performance measure (*sensu* Arnold, 1983) that has been functionally linked to ingestion, mastication, and display behaviors across mammals (Arendsen de Wolf-Exalto, 1951; Herring, 1972, 1975; Greaves, 1974, 1995; Herring and Herring, 1974; Hylander, 1979a; Lucas, 1981, 1982; Jablonski, 1993a; Dumont and Herrel, 2003; Vinyard et al., 2003; Williams et al., 2009; Santana et al., 2010; Hylander, 2013). A large gape facilitates the exploitation of food items that may otherwise remain inaccessible to individuals or taxa with smaller gapes (Hylander, 1979a; Bourke et al., 2008; Norconk et al., 2009). Maximum jaw opening ability is also a critical component of canine displays (or ‘yawning’) in some primates (Herring and Herring, 1974; Smith, 1984; Jablonski, 1993a). Canine displays occur in multiple contexts, but in Old World monkeys these behaviors are often interpreted as aggressive threats or other social displays. A wide jaw gape also facilitates canine biting and slashing during aggressive encounters with conspecifics or predators (Altmann, 1967; Kummer, 1968; Hadidan, 1980; Troisi et al., 1990; Plavcan and van Schaik, 1992;

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Plavcan, 2001; Hylander, 2013). Male primates engage in agonistic canine display behaviors with other males to compete for access to mates while females generally compete for access to resources (Plavcan, 2011). In crab-eating macaques and mangabeys these display behaviors occur more frequently in males than in females, and in older individuals compared to subadults (Deputte, 1994). Canine size, along with timing of canine eruption, wear, and breakage, are significantly correlated with male reproductive success in sexually dimorphic mandrills (Leigh et al., 2008). Collectively, these data suggest that maximum jaw gape, which facilitates maximum canine clearance beyond the occlusal plane (Herring and Herring, 1974; Lucas, 1981; Hylander, 2013) and arguably signals social rank, may also be correlated with male fitness in sexually dimorphic Old World monkeys.

Building on previous work for primates (e.g., Lucas, 1981) and other mammals (e.g., Herring and Herring, 1974), Hylander (2013) recently demonstrated that maximum jaw gape varies within and among catarrhine species as a function of canine height. Thus, in catarrhines exhibiting marked canine sexual dimorphism, males have both relatively more projecting canines and are capable of achieving relatively larger maximum gapes compared to conspecific females. The ability of primates and other mammals to produce relatively large gapes has been correlated with relative muscle fiber length, jaw-adductor position on the skull (i.e., leverage), and aspects of jaw form (Herring and Herring, 1974; Dechow and Carlson, 1990; Wall, 1999; Vinyard et al., 2003; Taylor et al., 2009; Hylander, 2013).

Some morphological features that facilitate a relatively wide jaw gape, however, do so at the expense of relative bite force production. For example, adult male catarrhines might be predicted to have relatively long jaw-adductor muscle fibers, more caudally positioned jaw muscles, and/or relatively long mandibles to increase relative maximum gape (e.g., Herring and Herring, 1974; Lucas, 1982; Smith, 1984; Vinyard et al., 2003; Taylor et al., 2009; Hylander, 2013). A potential trade-off in bite force follows (Gans and Bock, 1965; Gans, 1982; Van Eijden et al., 1997) because for two muscles of comparable volume, increasing jaw-muscle fiber length will improve muscle stretch and excursion, but at some expense to muscle physiologic cross-sectional area (PCSA), which determines the muscle's intrinsic force-generating capacity (Powell et al., 1984). Additionally, caudally positioned jaw muscles and longer jaws would be expected to decrease muscle leverage. Given these potential trade-offs, if selection has acted on behaviors emphasizing relatively wide maximum jaw gapes in male catarrhines, then selection for these behaviors may come at some expense to male masticatory features that facilitate muscle and bite forces (Hylander, 2013). In fact, Dechow and Carlson (1990) previously showed that in the highly dimorphic Rhesus macaque (*Macaca mulatta*), females have greater mechanical advantage of the masseter for both incisor and molar biting compared to males. This mechanical advantage in females was due to their shorter load arm (i.e., more posteriorly placed molars) relative to masseter moment arm lengths. With improved leverage, females could convert a greater percentage of masseter muscle force to bite force compared to males, particularly at the molars. Similarly, Hylander (2013) hypothesized that in early hominins, reduced canine size and maximum jaw gape facilitated increased mechanical efficiency of the masticatory apparatus.

The interplay among competing functional demands is a fundamental challenge for organisms when navigating their complex environments. These interactions are difficult to identify in fossils where we essentially lack a physiological and behavioral record. Thus, paleontological studies often turn to living species to better understand the functional and adaptive significance of the morphological configurations we observe across the evolutionary history of primates, including our own evolution. Here we look specifically at the non-masticatory use of the feeding apparatus in studying the morphological correlates of maximum jaw gapes to better understand the factors that influence intra- and interspecific variation in masticatory form. We extend previous work (e.g., Herring and Herring, 1974; Lucas, 1981, 1982; Dechow and Carlson, 1990; Hylander, 2013) to explore the musculoskeletal correlates of jaw gape in the sexually dimorphic crab-eating macaque (*Macaca fascicularis*), with the explicit intention of testing Hylander's (2013) hypothesis. Linear maximum gape is sexually dimorphic in *M. fascicularis*, with male gapes reaching 112% of jaw length while female maximum gapes are only ~80% of their jaw length (Hylander, 2013). Given that large gape likely contributes to canine display behaviors, we hypothesize that as selection acted to increase relative male canine length in Old World monkeys, a functional consequence of displaying elongated canines was an increase in relative maximum jaw gape (Hylander, 2013). Based on this hypothesis, we explore musculoskeletal mechanisms for achieving relatively wide maximum gapes and the concomitant costs to relative muscle and bite forces in crab-eating macaques.

We acknowledge that this analysis of one species may not fully characterize the evolutionary pattern observed for all Old World monkeys, as multiple morphological solutions to the challenges of increasing gape may readily exist across primates (Bock, 1959; Vinyard et al., 2003). That said, there are advantages to examining these potential tradeoffs in a single species. First, macaques, including *M. fascicularis*, have long served as model species for experimental and comparative approaches to understanding masticatory apparatus form, function, and evolution in primates (e.g., Hylander, 1979a,b; Bouvier and Hylander, 1981; Hylander and Crompton, 1986; Hylander et al., 1987, 1992; Hylander and Johnson, 1989, 1994; Dechow and Carlson, 1990; Hiiemae et al., 1995; Wall, 1999; Ross et al., 2005, 2010). Thus, by identifying which of the predicted musculoskeletal changes underlie the capacity for relatively wide mouth opening in male *M. fascicularis*, we extend this previous work to better understand how the macaque masticatory apparatus has evolved to meet multiple and often competing demands, including those linked to both feeding and non-feeding behaviors involving the masticatory apparatus. Moreover, addressing these relationships in a single species enables us to control for the interspecific variation in feeding and social behaviors that would be present in a broader comparative analysis. From this perspective, intraspecific variation serves as an important baseline for interpreting the functional and adaptive significance of interspecific patterns in both living and fossil primate species.

Predictions linked to facilitating increased jaw gape and diminished muscle and bite force

To determine potential musculoskeletal features that facilitate relatively wide jaw gapes in male *M. fascicularis*, we draw on biomechanical theory and previous studies to generate a series of predictions regarding internal muscle architecture, muscle position and leverage, and skull morphology. We frame these predictions in terms of the expected musculoskeletal attributes that maximize jaw gape in males and the attendant costs to males in terms of their capacity to generate muscle and bite forces. Most predictions are not mutually exclusive.

Prediction 1a. Males have relatively longer and less pinnate muscle fibers. Muscle architecture refers to the internal orientation of muscle fibers relative to the force-generating axis of the muscle (Lieber, 2010). Two architectural variables underlying muscle function are 1) fiber length (Lf), which is proportional to maximum muscle excursion and contraction velocity (Bodine et al., 1982), and 2) physiologic cross-sectional area (PCSA), which is proportional to a muscle's maximum force-generating capacity (Powell et al., 1984). For two muscles of comparable volume, a muscle comprising long fibers oriented parallel to the force-generating axis of the muscle (i.e., parallel-fibered muscle) tends to produce large excursions and high contraction velocities (Gordon et al., 1966; Bodine et al., 1982). By contrast, a shorter, more pinnate-fibered muscle (i.e., fibers oriented at an angle relative to the force-generating axis) is better suited for generating large forces as it has a larger PCSA (Woittiez et al., 1984). Theoretically (Gans and Bock, 1965; Gans, 1982) and empirically (Taylor et al., 2009), jaw muscles face an architectural trade-off between maximizing muscle excursion versus force when other variables are held constant.

While it is clear that the anterior fibers of the superficial masseter (and medial pterygoid) likely experience significant stretching during wide mouth opening based on their distance from the mandible's axis of rotation (e.g., Bennett, 1908; Grant, 1973; Sun et al., 2002), it is more difficult to predict how other jaw-muscle fibers are stretched at wide gapes. Given this uncertainty, we take a general exploratory approach in examining the correlates of muscle stretch across the jaw muscles as they relate to gape. Theoretical (Herring and Herring, 1974) and empirical (Taylor et al., 2009) data suggest that the temporalis should behave similarly to the superficial masseter. We therefore examine regional fiber architecture in both the superficial masseter and temporalis to determine if males have relatively longer and less pinnate fibers compared to females.

Prediction 1b. Males have relatively longer anterior compared to posterior masseter fibers. Because the anterior superficial masseter fibers are likely positioned farther from the mandibular axis of rotation during jaw opening compared to the posterior masseter, they will stretch more for a given degree of angular rotation (Herring and Herring, 1974). Both sexes should have relatively longer anterior compared to posterior masseter fibers when stretched (Herring et al., 1984). We predict that because of their relatively larger gapes, males should exhibit a significantly higher ratio of anterior to posterior masseter fiber lengths compared to females.

Prediction 1c. Males have relatively smaller jaw-muscle physiologic cross-sectional areas (PCSAs) or relatively larger muscle masses. If muscle volume is held constant, increasing fiber length comes at some expense to PCSA. Because of the potential trade-off between maximizing muscle excursion during the production of relatively wide gapes versus generating jaw-muscle forces, males are predicted to have relatively smaller jaw-muscle PCSAs compared to females.

While we have observed the predicted architectural trade-off between fiber length and PCSA in callitrichids (Taylor et al., 2009), other primates circumvent this trade-off. For example, *Cebus apella* increases muscle mass relative to non-apelloid capuchins, thereby improving muscle (and presumably bite) force with minimal compromise to jaw gape (Taylor and Vinyard, 2009). Similarly, male *M. mulatta* have relatively larger jaw muscles than females (Grant, 1973; Cochard, 1985), enabling males and females to maintain similar relative bite forces despite decreased jaw-muscle leverage in males (Dechow and Carlson, 1990). Given these observations, we also examine whether male *M. fascicularis* have relatively larger jaw-muscle masses than females.

Prediction 2. Males have relatively shorter jaw-muscle lever arms and reduced mechanical advantage. Jaw muscles positioned closer to the mandibular axis of rotation (AR) require less stretch for a given degree of angular gape compared to muscles positioned farther from the AR. Therefore, given two jaw muscles of similar internal architecture, the more caudally-positioned muscle will facilitate a wider jaw gape for a given amount of stretch (Herring and Herring, 1974; Dechow and Carlson, 1990). More caudally positioned jaw muscles, however, are at a mechanical disadvantage for generating bite force as the muscle exhibits a shorter lever arm. Male macaques are predicted to have jaw muscles positioned relatively closer to the temporomandibular joint (TMJ) with reduced mechanical advantage compared to females.

Prediction 3. Males have relatively longer mandibles. For a given degree of angular rotation, a longer mandible produces an absolutely larger linear gape (i.e., distance between upper and lower incisors). Increasing mandibular length, however, tends to increase the load arm during, for example, incisal biting. As a consequence of their increased gape, males are predicted to have relatively longer mandibles and concomitantly relatively longer load arms for incisal biting.

Prediction 4. Males have TMJs positioned relatively closer to the occlusal plane of the mandible. The extent to which the jaw adductors can be stretched during mouth opening is an important factor influencing maximum jaw gape. Herring and Herring (1974) argue that an increase in the included angle from adductor jaw-muscle origin to the TMJ to the muscle insertion reduces muscle stretch for a given degree of angular gape. Reduced stretching per unit of angular rotation facilitates a larger maximum gape. A decrease in condylar height relative to the mandibular occlusal plane increases this included angle for the masseter (and medial pterygoid) muscles. Thus, male macaques are predicted to have mandibular condyles positioned relatively closer to the occlusal plane compared to females.

Prediction 5a. Males have relatively anteroposteriorly elongated glenoid fossae. Cineradiographic studies (Hylander et al., 1987; Wall, 1999) demonstrate that sagittal sliding (i.e., anteroposterior translation of the mandibular condyle along the glenoid fossa) is strongly correlated with (submaximal) gape during chewing. Parasagittal sliding is limited by the anteroposterior (AP) length of the glenoid fossa (Kay and Hiiemae, 1974; Hylander et al., 1987; Wall, 1999). Male macaques are predicted to have relatively AP elongated glenoid fossae allowing for increased AP condylar translation when generating wide gapes.

Prediction 5b. Males exhibit greater anteroposterior curvature of the mandibular condyles. Angular rotation of the condyle also impacts jaw opening (Herring, 1972; Hiiemae and Kay, 1973; Wall, 1999). Similar to translation, condylar rotation is limited by the AP length of the articular surface, suggesting that increased curvature of the condylar articular surface facilitates larger gapes (cf. Ruff, 1988; Hamrick, 1996). Males are predicted to exhibit increased condylar articular curvature compared to females to facilitate increased condylar rotation and larger maximum gapes.

Materials and methods

Samples

We took architectural measurements of the superficial masseter and temporalis muscles and linear dimensions of the skull on five adult male and five adult female *M. fascicularis* (Table 1). All cadavers were captive specimens without obvious craniodental pathologies. Measurements of temporomandibular joint height and shape (Table 1) were taken from 12 adult female and 11 adult male osteological specimens (Terhune, 2010) housed at the National Museum of Natural History in Washington, DC. All were wild-caught and free of apparent pathological conditions. Because our cadaveric and osteological specimens differ in size, only within-sample comparisons are conducted.

Table 1
Measurements included in study.

Measurement	Abbreviation	Definition
Normalized fiber length (mm)	NLf	Average linear distance between the proximal and distal myotendinous junctions of a fasciculus (Fig. 2a), normalized by standard sarcomere length
Pinnation angle (°)	θ	Arcsine of the perpendicular distance from the tendon of insertion to the proximal attachment of the fasciculus (a) (Fig. 2a) divided by NLf
Physiologic cross sectional area (cm^2)	PCSA	Muscle mass × cos (pinnation angle)/NLf × 1.0564 (gm/cm^3)
Muscle weight (g)	MWt	Wet weights of superficial masseter or temporalis
Ratio of anterior to posterior masseter fiber lengths	Ant/Post NLf Ratio	Anterior NLf/Posterior NLf for the superficial masseter
Superficial masseter origin length (mm)	ASMO	Distance from posterior mandibular condyle to anterior-most origin of superficial masseter on zygoma (Fig. 2b)
Superficial masseter insertion length (mm)	ASMI	Distance from posterior mandibular condyle to anterior-most insertion of superficial masseter on mandible (Fig. 2b)
Superficial masseter lever arm length (mm)	SMLever	Average of ASMO and ASMI
Temporalis origin length (mm)	ATO	Distance from posterior mandibular condyle to anterior-most origin of temporalis on the frontal bone (Fig. 2b)
Temporalis insertion length (mm)	ATI	Distance from posterior mandibular condyle to anterior-most insertion of temporalis on coronoid process (Fig. 2b)
Temporalis lever arm length (mm)	TempLever	Average of ATO and ATI
TMJ height above the occlusal plane (mm)	TMJHt	Perpendicular distance from the center of the mandibular condyle to the mandibular occlusal plane (defined by occlusal surfaces of I_1 and M_1; Fig. 2b)
Glenoid fossa length (mm)	GlenArcLg	Sum of the distances between semilandmarks from the anteriormost attachment of the glenoid fossa joint capsule to the posterior edge of the articular eminence (Fig. 2c)
Condyle arc length (mm)	CondArcLg	Sum of the linear distances between semilandmarks from anterior to posterior on mandibular condyle articular surface at the midline (Fig. 2c)
Condyle chord length (mm)	CondChordLg	Distance between the endpoints of the articular surface of the mandibular condyle in an AP plane (Fig. 2c)
Condylar curvature ratio	CondCurve	CondArcLg/CondChordLg
Mandibular length (mm)	JawLg	Distance from the posterior mandibular condyle to infradentale (Fig. 2b)
Condyle-M_1 distance (mm)	CondM_1	Distance from the posterior mandibular condyle to the anterior edge of M_1
Nasion-inion (mm)	N–I	Linear distance between nasion and inion

Measurements

Muscle architecture We briefly describe our architectural measurement protocol (see Taylor et al., 2009 for details). For each specimen, skin and overlying fascia were removed and the *in situ* position of the muscles documented (Fig. 1). Muscles were harvested en masse from the skull, blotted dry, trimmed of fat and fascia, and weighed to the nearest 1.0 g or 0.1 g (depending on size). We separated the deep and superficial masseters and sectioned superficial masseters along their lengths into approximately 1.5 cm segments (Fig. 2a). We sectioned the temporalis into anterior, middle, and posterior segments. We measured up to ten adjacent fibers at each of the following muscle locations: the superior and inferior masseter and proximal and distal temporalis (Fig. 2a). We measured fiber length (Lf) as the distance between the proximal and distal myotendinous junctions (MTJ; Fig. 2a). For each fiber, we measured the perpendicular distance (a) from the distal MTJ to the central tendon (Fig. 2a), which we used in our estimate of pinnation angle (Anapol and Barry, 1996). For the purposes of this study, we did not measure the deep masseter, zygomaticomandibularis, or zygomatic temporalis as these muscle portions likely do not significantly impact maximum jaw gape.

To control for differences in gape at the time of fixation, we normalized fiber lengths (Lf) to a standardized sarcomere length (Ls), following Felder et al. (2005) and Taylor et al. (2009). We measured *in situ* sarcomere lengths (±0.01 μm) from the measured fibers using laser diffraction (Lieber et al., 1984) and normalized raw Lf to an optimal Ls estimate of 2.41 μm taken from macaque limb muscles (Walker and Schrodt, 1974). Normalized Lf (NLf) was computed as:

$$\mathrm{NLf} = \mathrm{Lf}\,(2.41\ \mu\mathrm{m}/\mathrm{Ls}).$$

Using these normalized fiber length data, we calculated average NLf for the anterior and posterior masseter regions, for the anterior, middle, and posterior regions of the temporalis, and for whole superficial masseter and temporalis muscles (Table 1). We calculated pinnation angle (θ) for each muscle region and muscle as the arcsine of a/NLf (Table 1). We estimated physiologic cross sectional area (PCSA) using NLf, θ and mass for each muscle, and employed a muscle-specific density of 1.0564 g/cm^3 (Murphy and Beardsley, 1974; Table 1).

Muscle position Superficial masseter position was measured as the distances from the posterior portion of the condyle to the anterior-most muscle attachment on the zygoma (anterior superficial masseter origin length: ASMO), and to the anterior-most attachment along the inferior edge of the mandible (anterior superficial masseter insertion length: ASMI; Table 1; Fig. 2b). These distances were averaged to estimate the superficial masseter lever arm (Table 1). Temporalis muscle position was measured as the distances from the posterior condyle to the most supero-anterior attachment on the frontal bone (temporalis origin length: ATO) and to the coronoid process (temporalis insertion length: ATI). These two measures were averaged to estimate the temporalis lever arm (Table 1).

Skull morphology Linear measures of TMJ height and shape were calculated from three-dimensional landmarks (Terhune, 2010, 2011; Table 1; Fig. 2b, c). To quantify maximum potential translation and rotation at the TMJ, we used semilandmarks describing the articular surfaces of the glenoid fossa and mandibular condyle (Table 1; Fig. 2c). For the condyle, we divided the articular surface length by a condylar chord to estimate condylar curvature (as a proxy for rotational ability; Table 1; Fig. 2c).

Figure 1. Photographs of female (left) and male (right) heads with masseter and temporalis muscles exposed *in situ*. Both individuals are shown at the same scale for comparison.

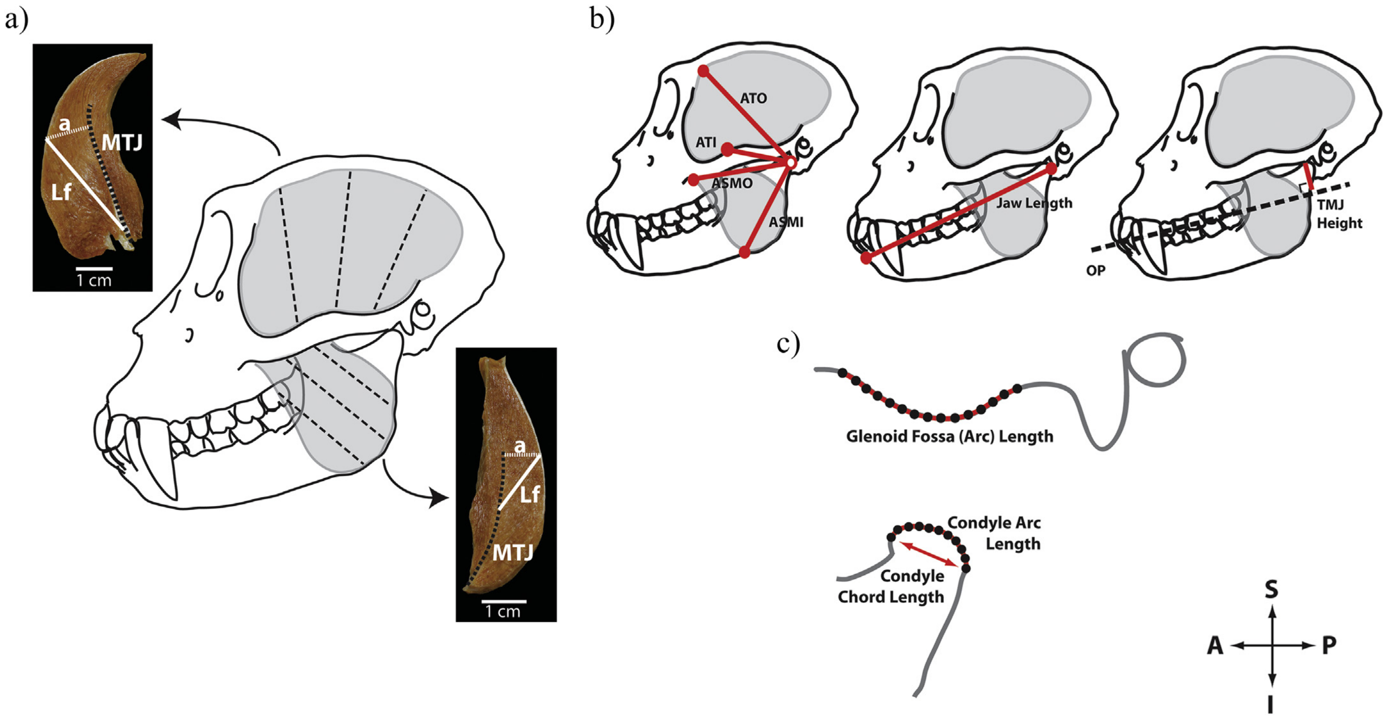

Figure 2. Measurements collected in this study. **a)** Schematic of an *M. fascicularis* skull referencing the temporalis (left) and superficial masseter (right) muscles. Dashed black lines on the skull indicate the approximate locations at which muscle architecture measurements were taken. Cross sections show the measurements taken at each section (Lf = fiber length, a = perpendicular distance from the myotendinous junction [MTJ, black dotted line] to the superficial tendon). Pinnation angle was computed as the arcsine of a/NLf. **b)** Illustration of the measurements describing muscle position (left), jaw length (middle), and height of the TMJ above the occlusal plane (OP; right). **c)** Schematic illustrating the cranial (top) and mandibular (bottom) components of the TMJ and measurements used in this analysis. Abbreviations: S = superior, A = anterior, P = posterior, I = inferior. See Table 1 for further descriptions.

Analytical methods

We examined absolute and relative differences between the sexes in muscle fiber architecture, muscle position (i.e., leverage), and skull dimensions. To examine relative differences and assess our predictions, we scaled muscle architectural variables (i.e., muscle mass, NLf, PCSA), muscle position variables, and linear skull dimensions by mandibular length and condyle-M_1 distance. Mandibular length is significantly correlated with maximum jaw gape in catarrhine primates (Hylander, 2013). Thus, we use mandibular length as an independent variable to assess whether males have architectural features of the jaw-closing muscles that facilitate muscle stretch and the generation of relatively wide maximum jaw gapes independent of their absolutely longer jaws. Mandibular length also serves as an estimate of the load-arm for incision (Hylander, 1985; Vinyard, 2008), while condyle-M_1 distance acts as a load-arm estimate for biting at M_1 (e.g., Daegling, 1990). We used muscle mass$^{0.33}$ and PCSA$^{0.5}$ to provide dimensionless ratios for comparison. Superficial masseter and temporalis lever arms as well as jaw length were scaled by nasion-inion length to assess leverage and jaw length differences between the sexes relative to an estimate of overall skull size not directly related to jaw length (Table 1). Because pinnation angles and other musculoskeletal ratios are already dimensionless, these variables were not size-adjusted for statistical analysis.

To assess differences between males and females, we used one-tailed Student's *t*-tests to address Predictions 1–5 and two-tailed *t*-tests when we had no directional prediction. We reverted to a two-tailed test of significance for any unsupported prediction (i.e., a non-significant result in the predicted direction; Zar, 1999). To guard against Type I error, we used the sequential Bonferroni adjustment (Rice, 1989) and an *a priori* $\alpha = 0.05$. We employed this adjustment separately for each prediction. Separate Bonferroni adjustments were also conducted for comparisons relative to jaw length and condyle-M$_1$ length, respectively.

Results

The gross morphology of the multipinnate superficial masseter and bipinnate temporalis muscles of *M. fascicularis* resemble those of other non-human primates (Turnbull, 1970; Taylor and Vinyard, 2004, 2009). A detailed description of the macaque masseter can be found in Antón (1999).

Differences in absolute muscle architectural and skull measures

As expected, males are significantly larger than females in most muscle architectural and skull measures (Table 2). On the other hand, there are no significant sex differences in posterior superficial masseter fiber lengths, superficial masseter lever arm length, or TMJ height above the occlusal plane (Table 2).

Relative differences in muscle architecture

As predicted, males have significantly longer anterior superficial masseter and temporalis fibers (NLf) relative to jaw length (Fig. 3a, b) and condyle-M$_1$ distance compared to females (Table 3). The ratio of anterior to posterior superficial masseter fiber lengths exceeds 1.0 in males and females, while males exhibit significantly larger ratios than females (Table 3). Middle temporalis fibers are significantly longer than anterior fibers relative to jaw length and condyle-M$_1$ distance ($p = 0.001$) in males. In females this comparison did not remain significant ($p < 0.025$) after Bonferroni adjustment. Contrary to prediction 1a, masseter and temporalis pinnation angles do not differ between males and females (Table 3).

Table 2
Means, standard deviations (SD), and tests of absolute differences in muscle architecture, leverage estimates, and bony measurements between male and female macaques.[a]

Measurement[b]	Females	Males	p-value[c]
	Mean (±SD)	Mean (±SD)	
A. Cadaver Sample			
Superficial Masseter			
Weight[d]	4.07 (0.93)	11.00 (4.36)	**0.022**
NLf	11.71 (2.21)	17.55 (2.58)	**0.005**
Anterior NLf	12.53 (2.70)	21.14 (3.00)	**0.001**
Posterior NLf	10.81 (1.53)	12.8 (1.92)	0.11
PCSA	3.22 (0.65)	5.61 (1.69)	**0.019**
Temporalis			
Weight[d]	13.7 (3.15)	53.4 (19.82)	**0.002**
NLf	15.78 (3.89)	26.83 (5.03)	**0.005**
Anterior NLf	14.15 (3.61)	24.4 (4.54)	**0.004**
Middle NLf	17.71 (3.84)	29.72 (6.41)	**0.008**
Posterior NLf	16.22 (4.62)	26.38 (3.97)	**0.006**
PCSA	8.16 (0.94)	18.19 (4.36)	**0.001**
SMLever	43.48 (5.08)	51.37 (5.91)	0.053
TempLever	37.08 (4.51)	46.12 (4.69)	**0.014**
Mandibular length	80.28 (7.84)	101.14 (8.58)	**0.004**
Condyle-M$_1$ distance	57.37 (6.91)	70.28 (6.56)	**0.016**
Nasion-inion	77.76 (2.14)	87.91 (8.64)	**0.034**
B. Osteological Sample			
TMJHt	12.00 (1.93)	11.39 (2.21)	0.49
GlenArcLg	9.86 (0.68)	11.31 (1.02)	**0.0005**
Mandibular length	69.37 (3.88)	78.27 (6.41)	**0.0005**
Condyle-M$_1$ distance	46.66 (2.66)	52.01 (4.73)	**0.003**
Nasion-inion	72.86 (2.04)	74.33 (3.10)	**0.003**

[a] Due to differences in absolute variation, values for cadaver (A) and osteological (B) samples are reported separately.
[b] See Table 1 for abbreviations.
[c] Results based on two-tailed Student's *t*-tests. Bold and underlined p-values signify a significant difference ($\alpha = 0.05$) after the sequential Bonferroni correction.
[d] Levene's test for equality of variance indicated unequal variance for masseter and temporalis muscle weights; p-values shown are for tests with equal variances not assumed.

Relative superficial masseter PCSA does not differ significantly between males and females, while males have significantly larger temporalis PCSAs relative to both mandibular length and condyle-M$_1$ distance (Table 3; Fig. 3c). Given the differences in relative NLf, these findings for relative PCSA suggest potential differences in muscle weights between sexes. Indeed, males have significantly larger relative temporalis masses than females (Table 3; Fig. 3d), accounting for their relatively larger PCSAs and relatively longer fibers. Males also have larger masseters relative to condyle-M$_1$ distance, but this difference is not significant after Bonferroni correction (Table 3; Fig. 3d). Thus, contrary to prediction 1c, macaques do not exhibit an architectural trade-off between increasing relative fiber lengths (muscle excursion) and increasing relative PCSA (muscle force).

Differences in muscle position and leverage

For most comparisons, males and females do not differ significantly in relative jaw-muscle position or leverage (Table 4; Fig. 4a–b). Males do exhibit significantly shorter superficial masseter lever arms relative to jaw length (Fig. 4a). Overall, male and female *M. fascicularis* show few differences in jaw-muscle leverage, suggesting that posterior migration of muscle position is not a major factor contributing to the relatively larger gapes of males.

Differences in mandibular and TMJ morphology

Males have relatively longer mandibles than females (Table 4). Males also have TMJ heights that are significantly closer to the mandibular occlusal plane relative to both mandibular length and condyle-M$_1$ length (Table 4; Fig. 4c). However, the differences in relative TMJ height and relative superficial masseter lever arm are primarily related to relatively longer jaws in males, as we observed no sex differences in absolute TMJ height or masseter lever arm (Table 2). While males also have significantly greater condylar curvature compared to females (Fig. 4d), we observed no significant sex difference in relative glenoid fossa lengths.

Discussion

Many studies of masticatory apparatus functional morphology in primates have emphasized force production and load resistance (e.g., Hylander, 1979a,b, 1985, 1988; Bouvier and Hylander, 1981; Demes and Creel, 1988; Daegling, 1990; Dechow and Carlson, 1990; Daegling and Grine, 1991; Spencer, 1995, 1999; Daegling and McGraw, 2001, 2007; Taylor, 2002, 2006; Taylor et al., 2008; Daegling et al., 2011; Eng et al., 2013). Less attention has been paid to how masticatory morphology relates to gape and jaw kinematics (e.g., Herring and Herring, 1974; Smith, 1984; Wall, 1999; Vinyard et al., 2003; Taylor et al., 2009; Hylander, 2013). Our results show that male crab-eating macaques exhibit masticatory apparatus features related to jaw-muscle fiber architecture, jaw length, and TMJ shape that collectively facilitate the generation of relatively wider maximum gapes compared to females. In the absence of sex differences in feeding behavior (e.g., Wheatley, 1980; Corlett and Lucas, 1990; Lucas and Corlett, 1991, 1998; Yeager, 1996), we hypothesize that the differences in craniofacial morphology between male and female crab-eating macaques are plausibly linked

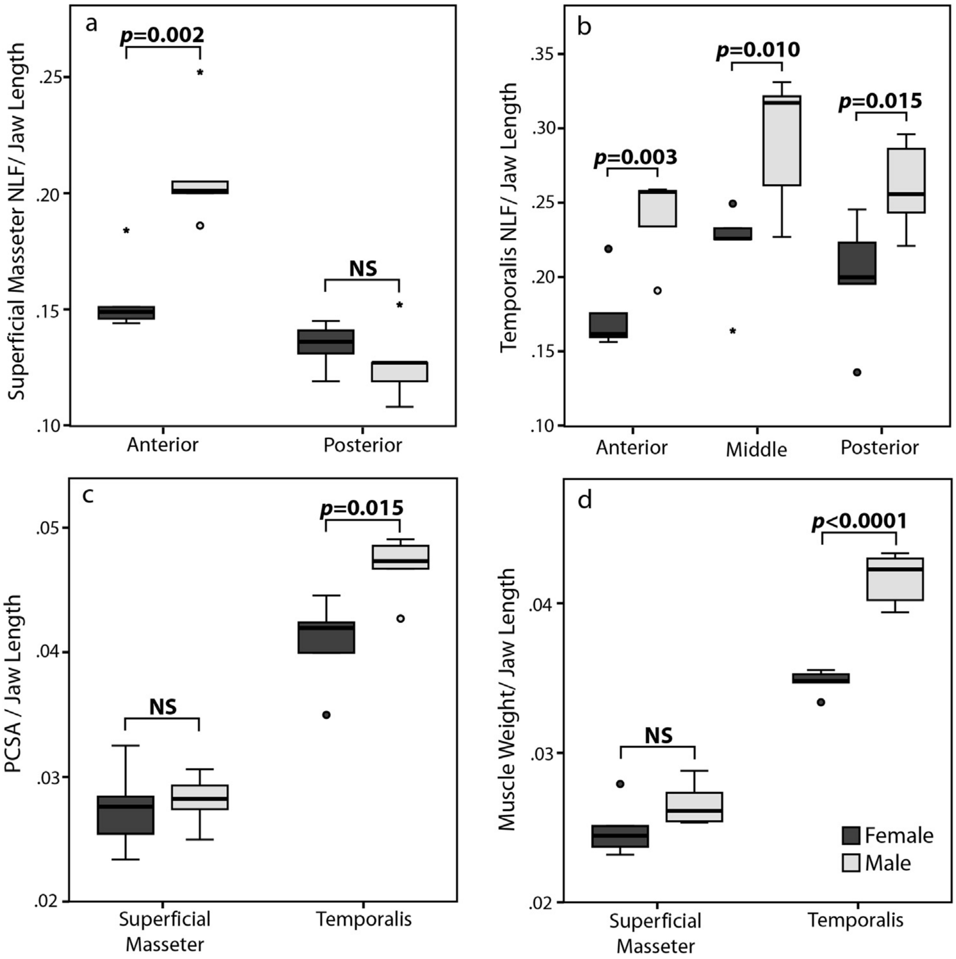

Figure 3. Box plots of differences in jaw-muscle fiber architecture relative to jaw length. As predicted, males have significantly relatively longer **a)** anterior masseter and **b)** temporalis fibers (anterior, middle, and posterior) compared to females. **c)** Males have significantly larger relative temporalis PCSAs compared to females, but males and females do not differ in relative masseter PCSAs. These results indicate that males do not increase relative fiber length at the expense of jaw-muscle force. **d)** Males have significantly larger temporalis muscle weights compared to females, which accounts for their relatively larger temporalis PCSA and relatively longer fibers. Average masseter muscle weight is also larger in males compared to females but this difference is not significant following Bonferroni correction. All significant differences relative to jaw length were also significant relative to condyle-M_1 length (not shown). Line within box denotes median. Boundaries of the box represent 25th and 75th percentiles. Whiskers indicate 10th and 90th percentiles. Solid circles denote 5th and 95th percentiles. Asterisks represent outliers. NS = not significant.

to the functional and adaptive consequences of male canine displays and increased canine sexual dimorphism (cf. Hylander, 2013).

The marked sexual dimorphism in gape in *M. fascicularis* is not unique among catarrhines. Hylander (2013) demonstrated that males have relative gapes (i.e., gape/jaw length) that are on average 121% larger than female relative gapes across 27 catarrhine species. Importantly, cercopithecines that routinely exploit resistant foods, such as *Cercocebus atys*, *Theropithecus gelada*, and *Macaca fuscata* (Dunbar, 1977; Iwamoto, 1979, 1993; Hill, 1997; Tsuji et al., 2006; McGraw et al., 2011; Daegling et al., 2011), preserve these levels of gape dimorphism despite the potential competing need to generate significant occlusal forces during feeding. Given that male cercopithecines maintain relatively large gapes while still needing to generate sufficient occlusal forces during feeding, we can speculate that display behaviors exert a strong selective influence on the evolution of their masticatory apparatus (Leigh et al., 2008; cf. Hylander, 2013).

We acknowledge that we cannot discount the roles of developmental plasticity and/or functional adaptation in shaping this morphology. Plasticity in TMJ form of both humans and other mammals is well documented (e.g., Moffett et al., 1964; Bouvier and Hylander, 1981, 1982, 1984; Hinton and McNamara, 1984; Ravosa et al., 2008), with the TMJ constantly undergoing modeling and remodeling during development and throughout adulthood, primarily due to altered dental function (e.g., Stegenga and de Bont, 2006; Endo et al., 2011). Similarly, skeletal muscle is highly plastic (Bottinelli and Reggiani, 2006), and experimental studies (e.g., Williams et al., 1986) have demonstrated that sarcomeres can be rapidly added to muscle fibers as a result of stretching. Future ontogenetic studies of jaw-muscle fiber length in male and female macaques should shed additional light on the functional and evolutionary bases of the relatively long-fibered muscles we observe in male crab-eating macaques.

Structure-performance relationships in the primate masticatory apparatus

We observed several morphological differences between male and female crab-eating macaques that facilitate increased gapes in males (Tables 3 and 4). The sexual dimorphism in these musculoskeletal traits was not consistently segregated to 1) regional anatomy, such as the TMJ versus muscle attachment sites, 2) specific tissues, such as muscle versus bone, or 3) functional role, such as reducing muscle stretch versus enhancing jaw movements. The lack of wholesale shifts in morphology or partitioning to these anatomical or functional categories suggests that the masticatory

Table 3
Means, standard deviations (SD), and tests of relative differences in muscle architectural variables between male and female macaques.[a,b]

Measurement	Prediction	Females	Males	Differs as predicted?	One-tailed p-value	Two-tailed p-value
		Mean (±SD)	Mean (±SD)			
Superficial masseter						
NLf/JawLg	1a: M > F	0.145 (0.013)	0.173 (0.019)	Yes	**0.012**	
/CondM$_1$		0.203 (0.015)	0.249 (0.027)	Yes	**0.005**	
Anterior NLf/JawLg	1a: M > F	0.155 (0.021)	0.209 (0.031)	Yes	**0.002**	
/CondM$_1$		0.217 (0.021)	0.301 (0.034)	Yes	**<0.001**	
Posterior NLf/JawLg	1a: M > F	0.134 (0.014)	0.127 (0.019)	No (ns)	0.20	0.39
/CondM$_1$		0.188 (0.012)	0.182 (0.022)	No (ns)	0.30	0.60
Pinnation Angle	1a: M < F	12.87 (2.68)	15.34 (3.05)	No (ns)	0.11	0.21
Anterior Pinnation	1a: M < F	10.46 (2.31)	12.78 (2.62)	No (ns)	0.09	0.18
Posterior Pinnation	1a: M < F	15.64 (4.21)	18.48 (3.89)	No (ns)	0.15	0.30
Ant/Post NLf Ratio	1b: M > F	1.16 (0.13)	1.66 (0.14)	Yes	**<0.001**	
PCSA$^{0.5}$/JawLg	1c: M < F	0.023 (0.003)	0.023 (0.002)	No (ns)	0.37	0.73
/CondM$_1$		0.032 (0.005)	0.033 (0.003)	No (ns)	0.27	0.53
Weight$^{0.33}$/JawLg[c]	1c: M > F	0.020 (0.002)	0.021 (0.002)	No (ns)	0.10	0.20
/CondM$_1$		0.028 (0.003)	0.031 (0.002)	No (ns)	0.04	
Temporalis						
NLf/JawLg	1a: M > F	0.195 (0.030)	0.264 (0.034)	Yes	**0.005**	
/CondM$_1$		0.273 (0.037)	0.380 (0.049)	Yes	**0.002**	
Anterior NLf/JawLg	1a: M > F	0.175 (0.026)	0.240 (0.029)	Yes	**0.003**	
/CondM$_1$		0.244 (0.033)	0.345 (0.041)	Yes	**0.001**	
Middle NLf/JawLg	1a: M > F	0.219 (0.033)	0.292 (0.045)	Yes	**0.010**	
/CondM$_1$		0.307 (0.043)	0.420 (0.064)	Yes	**0.006**	
Posterior NLf/JawLg	1a: M > F	0.200 (0.041)	0.260 (0.031)	Yes	**0.015**	
/CondM$_1$		0.280 (0.052)	0.375 (0.045)	Yes	**0.007**	
Pinnation Angle	1a: M < F	10.07 (1.52)	9.8 (1.99)	No (ns)	0.41	0.81
Anterior Pinnation	1a: M < F	13.36 (3.23)	12.77 (3.84)	No (ns)	0.40	0.80
Middle Pinnation	1a: M < F	7.46 (2.55)	8.13 (2.38)	No (ns)	0.34	0.68
Posterior Pinnation	1a: M > F	7.61 (2.91)	7.94 (0.90)	No (ns)	0.41	0.81
PCSA$^{0.5}$/JawLg	1c: M < F	0.036 (0.004)	0.042 (0.003)	No	**0.015**	
/CondM$_1$		0.050 (0.006)	0.060 (0.004)	No	**0.014**	
Weight$^{0.33}$/JawLg[c]	1c: M > F	0.030 (0.001)	0.036 (0.002)	Yes	**<0.0001**	
/CondM$_1$		0.042 (0.002)	0.053 (0.003)	Yes	**<0.0001**	

[a] See Table 1 for abbreviations.

[b] Initially, we used one-tailed Student's *t*-tests to test each prediction. If the p-value for the predicted difference was not statistically significant, we present this finding as ‘No (ns)’. In such instances, we performed two-tailed *t*-tests to determine a potential significant difference in the opposite direction. Bold and underlined p-values signify a significant difference ($\alpha = 0.05$) after the sequential Bonferroni adjustment.

[c] Levene's test for equality of variance indicated unequal variance for masseter and temporalis muscle weights. P-values shown are for tests with equal variances not assumed.

apparatus of *M. fascicularis* possesses multiple potential morphological pathways for impacting gape performance.

Evolutionary morphologists have long recognized that the organ systems of animals are complex, with multiple morphologies that can affect function and performance (e.g., van der Klaauw, 1945; Bock, 1959; Lauder, 1981, 1996; Dullemeijer, 1989; Wainwright et al., 2005). Thus, our observation that males exhibit only a subset of the potential morphological changes that could improve gape performance is not surprising. Similar complex relationships among masticatory apparatus morphologies, feeding

Table 4
Means, standard deviations (SD), and tests of relative differences in muscle position and skull dimensions between male and female macaques.[a,b]

Measurement	Prediction	Females	Males	Differs as predicted?	One-tailed p-value	Two-tailed p-value
		Mean (±SD)	Mean (±SD)			
SMLever/JawLg	2: M < F	0.54 (0.02)	0.51 (0.02)	Yes	**0.013**	
/CondM$_1$		0.76 (0.01)	0.73 (0.03)	No (ns)	0.04	0.09
/N-I		0.56 (0.05)	0.58 (0.03)	No (ns)	0.18	0.36
TempLever/JawLg	2: M < F	0.46 (0.04)	0.45 (0.02)	No (ns)	0.35	0.69
/CondM$_1$		0.65 (0.04)	0.66 (0.04)	No (ns)	0.31	0.63
/N-I		0.48 (0.05)	0.53 (0.02)	No (ns)	0.03	0.06
JawLg/N-I[c]	3: M > F	1.03 (0.07)	1.15 (0.05)	Yes	**<0.007**	
JawLg/N-I[d]	3: M > F	0.97 (0.05)	1.07 (0.05)	Yes	**<0.001**	
TMJHt/JawLg	4: M < F	0.17 (0.03)	0.15 (0.03)	Yes	**0.016**	
/CondM$_1$		0.26 (0.04)	0.22 (0.04)	Yes	**0.019**	
GlenArcLg/JawLg	5a: M > F	0.14 (0.02)	0.15 (0.02)	No (ns)	0.33	0.65
/CondM$_1$		0.21 (0.02)	0.22 (0.02)	No (ns)	0.23	0.45
CondCurve	5b: M > F	1.22 (0.06)	1.29 (0.06)	Yes	**0.005**	

[a] See Table 1 for abbreviations.

[b] Initially, we used one-tailed Student's *t*-tests to test each prediction. If the p-value for the predicted difference was not statistically significant, we present this finding as ‘No (ns)’. In such instances, we performed two-tailed *t*-tests to determine a potential significant difference in the opposite direction. Bold and underlined p-values signify a significant difference ($\alpha = 0.05$) after the sequential Bonferroni adjustment.

[c] JawLg/N-I is based on data from the cadaveric sample.

[d] JawLg/N-I is based on data from the osteological sample.

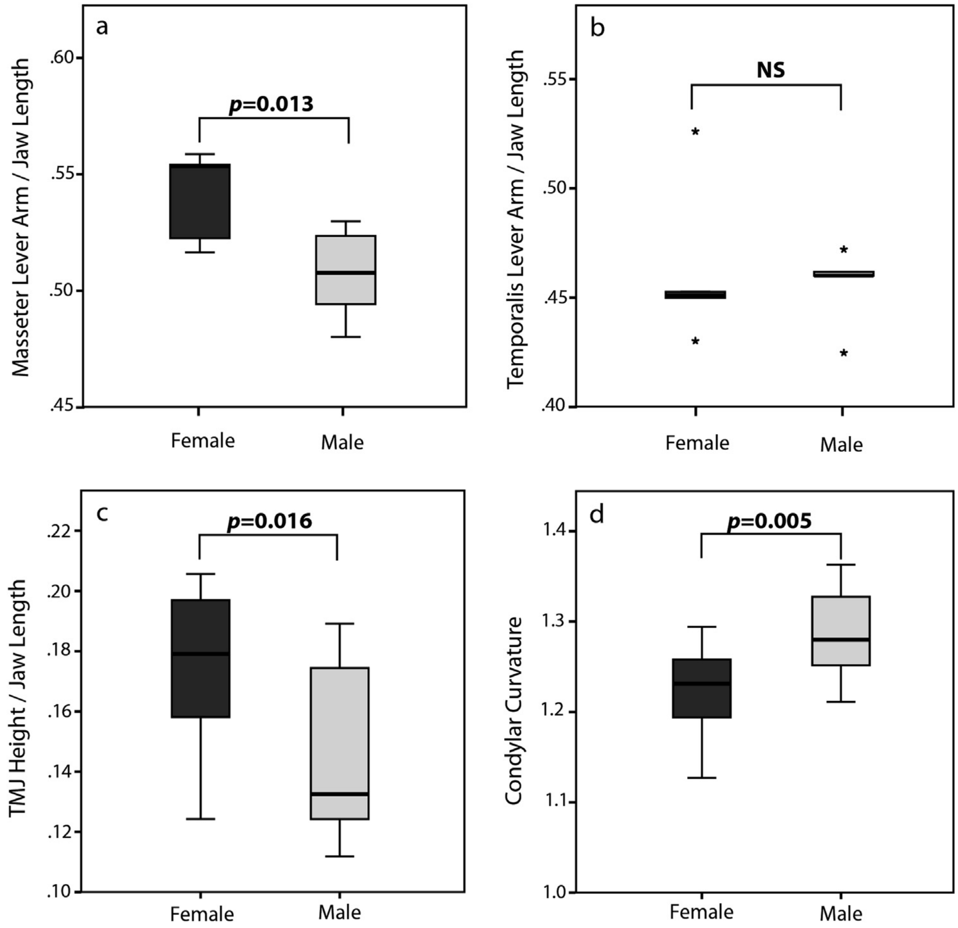

Figure 4. Box plot of muscle lever arms relative to jaw length for the **a**) superficial masseter and **b**) temporalis muscles, **c**) TMJ height relative to jaw length, and **d**) condylar curvature. P-values indicate that males have significantly shorter masseter lever arms, TMJ heights that are significantly closer to the occlusal plane of the mandible, and greater condylar curvature, compared to females. See Figure 3 for explanation of box plots.

behaviors, and performance have been observed in other primates (Daegling and McGraw, 2001; Vinyard et al., 2003; Ross et al., 2012). Our results add to previous observations of complex relationships in the primate masticatory apparatus in two ways. First, by examining both muscular and bony morphology, we show that morphological contributions to improving performance can be broadly distributed across muscle architecture, bony morphology, and positional relationships in the skull. Second, we show that these complex patterns of relationships between masticatory apparatus form and performance exist for non-feeding oral behaviors.

The intraspecific complexity of form-function relations has implications for interspecific comparisons of the primate masticatory apparatus. The multiple morphological contributions to performances in the masticatory apparatus suggest that primates possess different possible ways of altering form to improve a performance. This many-to-one mapping of form to function and performance (see Wainwright et al., 2005) implies that we will observe multiple different solutions to similar functional problems across primates (Daegling and McGraw, 2001, 2007; Ross et al., 2012). Indeed, Dechow and Carlson (1990) found slightly different relationships in jaw-muscle leverage between male and female Rhesus macaques compared to our observations in *M. fascicularis*. Similarly, pairwise comparisons of closely related species yielded several different morphological solutions for improving gapes in tree-gouging primates (Vinyard et al., 2003). Thus, while researchers have documented trends across higher primate clades (e.g., Hylander, 1979a, 1985; Ravosa, 1991), we are likely to discover significant details about primate evolutionary history by comparing closely related species. Finally, the morphological complexity of the masticatory apparatus warrants caution when inferring function or performance from form given that similar morphologies across taxa may yield different functions due to the complex relationships among parts of the organ system (Lauder, 1996).

An added complicating observation is that morphologies can participate in several functions and have performance implications for multiple behaviors. The potential for a given form to participate in multiple functions may be beneficial or competitive among performances. For example, in cercopithecoids, increased relative gapes in males may have been facilitated by evolutionary changes in the dentition. Comparative studies show that bilophodonty is a derived feature in Old World monkeys (Kay, 1977, 1978; Maier, 1977a), although not an autapomorphy of the clade (e.g., Maier, 1977b). Functional analysis of molar cusps and assessments of feeding behavior suggest this derived cusp pattern may be beneficial for fracturing tough seeds and leaves (Happel, 1988; Lucas and Teaford, 1994). If bilophodonty improves the efficiency of breaking down these foods, then the evolution of this cusp pattern may have relaxed constraints on generating relatively large bite forces during feeding. While highly speculative, the relaxation of force-related demands could have benefitted the evolution of features facilitating jaw-muscle stretch and relatively large jaw gapes in male cercopithecoids.

Similarly, increased body size of male cercopithecoids likely enables absolutely larger jaw-muscle and bite forces. Given that absolute forces are essential in food breakdown, larger size likely allows males to maintain a breadth of potential food items in their diet even if they are at a relative disadvantage in biting efficiency due to decreased leverage and changes in muscle architecture. However, increased body size by itself is unlikely to drive changes in gape dimorphism given that hominoids demonstrate decreased gape dimorphism at even larger body sizes (see Hylander, 2013).

Architectural trade-offs and functional divergence in macaque jaw muscles

Male crab-eating macaques have relatively longer jaw-muscle fibers than females, facilitating their relatively larger jaw gapes. Males also have relatively larger temporalis PCSAs and similar (rather than reduced) relative masseter PCSAs compared to females. Males accomplish this relative increase in jaw-muscle force generating ability by increasing relative temporalis weight and maintaining similar relative masseter weight (Table 3; Fig. 3d). Thus, male *M. fascicularis* appear to meet the competing demands for wide mouth opening and occlusal force production by augmenting muscle weight rather than optimizing jaw-muscle architecture for excursion at the expense of force production (Fig. 5).

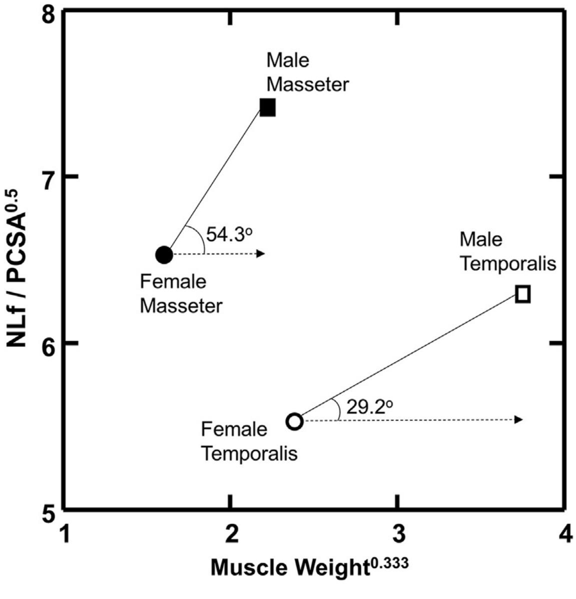

Figure 5. Graphic illustration of relative change in excursion versus force production (NLf/PCSA$^{0.5}$) plotted against change in muscle weight$^{0.333}$ for male and female *M. fascicularis*. For comparison, females are depicted as the initial condition and males as derived. In this graph, a theoretical 90° angle (either upward or downward), calculated from a horizontal ray emanating from the female architectural location, would represent an architectural shift solely toward increasing fiber length (upward) or scaled PCSA (downward). Increasing only scaled muscle weight while maintaining the architectural relationship (i.e., a similar NLf/PCSA$^{0.5}$) would result in a closed angle (i.e., 0°). While the figure demonstrates a clear shift toward increasing NLf, both the masseter and temporalis exhibit significant changes in scaled muscle weight. The masseter appears to have experienced relatively greater changes in fiber length (54.3°) compared to the temporalis (29.2°), which appears to have experienced considerable increases in weight. (Relatively equivalent changes in NLf/PCSA$^{0.5}$ versus weight$^{0.333}$ would yield an angle = 45°). As a theoretical comparison, if we model masseter and temporalis weight in males as changing isometrically with body size, changes in male masseter and temporalis both yield angles of approximately 89° (not shown).

By maintaining significantly larger jaw muscles, males circumvent the architectural trade-off between maximizing muscle stretch versus muscle force (Gans and Bock, 1965; Van Eijden et al., 1997; Taylor et al., 2009). The net effect is that male macaques have the capacity to generate both absolutely and relatively larger muscle forces than females (see Dechow and Carlson, 1990), despite having longer fibers that facilitate muscle stretch and relatively wide gapes. Architectural trade-offs in jaw muscles have been examined for only a handful of primates. Tree-gouging marmosets increase excursion by sacrificing maximum force production (Taylor et al., 2009). Alternatively, *C. apella* circumvent this architectural trade-off by increasing relative PCSA through enlarging jaw muscles without appreciably altering fiber length or pinnation angle compared to non-apelloid capuchins (Taylor and Vinyard, 2009). Even tree-gouging marmosets avoid certain aspects of the architectural trade-off as their sarcomere-length operating ranges allow them to act on more favorable portions of the length–tension curve at larger jaw gapes, resulting in relatively larger forces at these gapes compared to non-gouging tamarins (Eng et al., 2009). Collectively, these initial evaluations suggest that primates employ a range of strategies in jaw-muscle architecture, including metabolically non-optimal increases in muscle mass, to address competing needs for excursion and force production in feeding and non-feeding behaviors.

Dechow and Carlson (1990) hypothesized that architectural rearrangement of the masseter and temporalis, rather than increased muscle size, was needed to maintain relative levels of muscle force in male Rhesus macaques. Following Gans and Bock (1965), they emphasized the potential for spatial constraints on muscle attachment sites and position to limit packing of fibers. Our results for *M. fascicularis* indicate that males increase relative temporalis force by increasing temporalis muscle mass, while concurrently rearranging muscle architecture to improve excursion. The potential differences between these closely related macaque species further underscore the observation that primate species are likely to differ in morphological strategies for improving jaw movements and/or bite forces throughout their evolution. Furthermore, the different morphological solutions emphasize the need for research on other sexually dimorphic primates to better understand the range of morphological changes in muscle architecture underlying intra- and inter-specific differences in behaviors across primates.

In addition to fiber architecture, we also need to consider factors not examined here that influence jaw-muscle function and performance such as fiber size, fiber type, and their respective distributions across the jaw muscles. Maxwell et al. (1979) demonstrated that male *M. mulatta* possess relatively larger fibers and a higher proportion of type II (i.e., fast twitch, low oxidative capacity) fibers in the masseter and temporalis compared to females. Recently, Wall et al. (2013) reported that *Papio anubis* males have a significantly higher proportion of type II fibers in the deep anterior temporalis and larger fiber areas in the superficial anterior and posterior temporalis compared to females. These findings indicate that male jaw adductors comprise fibers that are well suited for generating rapid and forceful muscle and bite forces. Given that testosterone influences fiber phenotype of the jaw-closing muscles (e.g., Lyons et al., 1986; Reader et al., 2001; Korfage et al., 2005), we hypothesize that *M. fascicularis* likely exhibits sexual dimorphism in fiber phenotype as well. Larger fibers and a higher proportion of type II fibers in the jaw adductors of male *M. fascicularis* would provide additional means of reducing the force-related deficits of increased excursion beyond the observed changes in muscle architecture.

Finally, we observed architectural variation within and between the masseter and temporalis muscles supporting previous arguments of different functional roles for jaw-muscle regions (e.g., Wall et al., 2013) and muscles (Vinyard and Taylor, 2010). As predicted, anterior superficial masseter fibers were longer than posterior fibers and the ratio of anterior/posterior fiber lengths was significantly greater in males compared to females (Table 3). These empirical results support previous arguments that the anterior-most masseter fibers experience greater stretching than more posterior fibers during jaw opening (Herring and Herring, 1974; Herring et al., 1984; Taylor and Vinyard, 2004). The relatively longer middle versus anterior temporalis fibers in males was not anticipated, as we expected anterior fibers to stretch further during wide mouth opening. This observation deserves further consideration and assessment across other species. In particular, kinematic analyses tracking the location of the instantaneous center of rotation of the mandible during wide jaw gapes would be beneficial for interpreting this result. Male crab-eating macaques have relatively larger temporalis PCSAs and weights compared to similar masseter force-producing abilities between the sexes. This difference in sexual dimorphism between temporalis and masseter supports previous arguments suggesting these two muscles may have evolved distinct functional roles in primates, with the temporalis dedicated to generating vertically-oriented occlusal forces during chewing (Hylander et al., 2005; Vinyard et al., 2007, 2008; Vinyard and Taylor, 2010).

Implications for studies of fossil primates

Our results for *M. fascicularis* have implications for inferring jaw-muscle forces in fossil primates. Demes and Creel (1988) were among the first investigators to generate craniometric estimates of jaw-muscle forces in primates. They estimated muscle forces in a sample of female *M. fascicularis* using infratemporal fossa area as a proxy for temporalis cross-sectional area and taking 80% of the measured temporalis area as an estimate of the masseter cross-sectional area. When compared with our architectural estimates of muscle force,[1] masseter values based on cranial proxies underestimated muscle force by 13%. As we only report superficial masseter PCSA, we are likely minimizing the divergence between these two estimates. Cranial estimates of temporalis muscle force underestimated architecture-based estimates by 57%. Similarly, Eng et al. (2013) found that craniometric estimates of cross-sectional areas underestimated masseter PCSA by 36% and temporalis PCSA by 68% in crab-eating macaques.

In addition to errors associated with estimating muscle forces from craniometric data, these divergent muscle force estimates are likely due, in part, to measurement error (in both studies) and comparing different individuals. That said, our results are consistent with previous studies highlighting the difficulties of accurately estimating jaw-muscle forces from craniometric measures (e.g., Antón, 1999, 2000; Eng et al., 2013; Taylor and Vinyard, 2013). Collectively, these findings suggest that *in silico* models of primate feeding behavior will be improved by muscle (and bite force estimates) derived from architectural data. Given the errors associated with craniometric estimates of muscle force, we advise cautious interpretations of modeled muscle and bite forces in fossils where muscle architectural variables cannot be measured. Future studies aimed at comparing jaw-muscle forces estimated from craniometric and actual muscle architectural variables in extant primates may be useful for bracketing the errors associated with estimating jaw-muscle forces in fossil primates (Eng et al., 2013).

This work also has implications for the evolution of the masticatory apparatus in papionin primates. In previous analyses of *Theropithecus*, Jablonski (1993a,b) observed that the fossil *Theropithecus darti* and, to a greater extent, *Theropithecus oswaldi*, were characterized by dental and mandibular features that favored improved masticatory efficiency for molar chewing of grasses including a longer masseter moment arm in *Theropithecus oswaldi*. These features coincided with a decrease in incisor and canine size and with shortening of the lateral aspect of the glenoid fossa, the latter thought to have limited bilateral anteroposterior translation of the condyle. Collectively, these observations led to the suggestion that improved masticatory efficiency came at the expense of wide jaw gapes and canine gape displays in this genus. Our results for *M. fascicularis* indicate that relatively wide maximum jaw gapes can be achieved in the absence of evidence for extensive anteroposterior translation of the condyle by increasing relative masseter fiber length, and that muscle (and presumably bite) forces do not require a concomitant expense of wide jaw gape. Future comparative studies of the musculoskeletal correlates of gape and force in extant African papionin primates (e.g., *C. atys*; McGraw et al., 2011) are likely to further improve our interpretations of function and behavior in these fossils.

Our results also inform debates regarding evolutionary explanations for canine size reduction in early hominins (Greenfield, 1990; White et al., 1994, 2006; Ward et al., 1999, 2001; Haile-Selassie, 2001; Plavcan, 2001; Haile-Selassie et al., 2004; Kimbel et al., 2004, 2006; Semaw et al., 2005; Kimbel and Delezene, 2009). Multiple hypotheses have been advanced, including the adoption of hand-held weapons (initially proposed by Darwin, 1871), crowding of the molar tooth row (Jungers, 1978), "incisification" of the canines for use during feeding (Szalay, 1975; Wolpoff, 1980; Greenfield, 1992), and decreased male–male competition in early australopiths (Reno et al., 2003; Lovejoy, 2009; Suwa et al., 2009; White et al., 2009; but see, for example, Leutenneger and Shell, 1987; Plavcan and van Schaik, 1997; Plavcan et al., 2005; Scott and Stroik, 2006; Gordon et al., 2007). In a more recent study, Hylander (2013) proposed a non-mutually exclusive hypothesis that canine reduction in extant catarrhines is linked to decreased relative maximum jaw gape and increased mechanical efficiency of the masticatory apparatus. Hylander (2013) provides support for the functional and evolutionary link between canine size and relative maximum jaw gape by demonstrating that in sexually dimorphic catarrhines, males have significantly larger relative maximum jaw gapes compared to females, and that relative maximum jaw gape is significantly correlated with relative canine size across species.

Assuming that selection acted to increase jaw gape and canine crown height within and among sexually dimorphic catarrhine species, Hylander (2013) predicts an increase in relative jaw-muscle fiber length and/or a decrease in jaw-muscle leverage to facilitate relatively wide maximum gapes in males. Our findings that male *M. fascicularis* have both relatively longer masseter and temporalis fibers and decreased masseter leverage support these predictions. Our findings further show that males display a significant increase in relative temporalis PCSA, largely by increasing muscle mass. While developing and maintaining additional muscle mass is metabolically costly, the benefit is that male *M. fascicularis* may be capable of generating relatively large vertical muscle (and bite) forces at relatively wide jaw gapes. Other primates have similarly avoided this tradeoff between gape and force production by adding muscle mass (e.g., *C. apella*; Taylor and Vinyard, 2009). These data indicate that at least some primates have borne the costs of additional growth and maintenance of jaw-muscle mass to maintain or increase muscle and bite force without sacrificing fiber length and jaw gape. Given the robust features of the early hominin mandible (Hylander, 1988; Daegling and Grine, 1991), we can speculate that early hominins may likewise have borne the added

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[1] Muscle force estimates were generated by multiplying muscle PCSAs by the specific tension of muscle (22.5 N/cm^2; Powell et al., 1984).

costs of maintaining greater jaw-muscle mass while undergoing a relative reduction in canine height and jaw gape.

Conclusions

The primate masticatory apparatus is a multifaceted system with musculoskeletal morphologies that function in both feeding and non-feeding oral behaviors. Our evaluation of musculoskeletal features that contribute to sexual dimorphism in gapes of *M. fascicularis* yielded several morphologies that likely functionally contribute to the relatively larger jaw gapes of males. These features were distributed throughout the masticatory apparatus involving aspects of jaw-muscle architecture, bony morphology, and relative position of features on the skull. Thus, aspects of the masticatory apparatus related to specific performances, such as jaw opening ability, have multiple morphological contributors to performance. We also observed changes in muscle weight that likely help preserve biting ability in males given that several gape-related improvements negatively impact bite force production (Hylander, 2013).

These results have several important implications for future studies of the masticatory apparatus in extant and fossil primates. Given the complexity of the masticatory apparatus, functional and performance needs can be addressed by multiple morphologies yielding numerous potential pathways of morphological change within and across species. Because of this complexity, we should not expect to reliably predict how individual features will evolve in response to functional changes, nor expect similar responses across species. We also expect competing demands on masticatory apparatus morphology from feeding and non-feeding behaviors, but the multiple potential morphological pathways offer opportunities to avoid negative trade-offs in performance. The multiple morphological responses we observed suggest that we can expect to find significant, but not necessarily predictable, patterns of integration that incorporate multiple regions and tissues. In particular, we demonstrate that the jaw muscles are likely integrated with the rest of the masticatory apparatus for non-feeding display behaviors in addition to any patterns of covariation linked to feeding. When considering interspecific comparisons, primatologists should expect to see varying evolutionary changes in form and in patterns of morphological integration for the same putative functional need given the complexity and many-to-one mapping of masticatory apparatus forms to functions. In the end, we are left with an enumerative approach to unraveling the evolutionary history of form-function relationships tied to feeding and non-feeding oral behaviors involving the primate masticatory apparatus.

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