THE ANATOMICAL RECORD 301:325–342 (2018)

# Jaw-Muscle Fiber Architecture and Leverage in the Hard-Object Feeding Sooty Mangabey are not Structured to Facilitate Relatively Large Bite Forces Compared to Other Papionins

ANDREA B. TAYLOR,[1]* CLAIRE E. TERHUNE,[2] MAXX TOLER,[3] MEGAN HOLMES,[4] CALLUM F. ROSS,[5] AND CHRISTOPHER J. VINYARD[6]

[1]Department of Basic Science, College of Osteopathic Medicine, Touro University, Vallejo, California
[2]Department of Anthropology, University of Arkansas, Fayetteville, Arkansas
[3]School of Osteopathic Medicine, Campbell University, Lillington, North Carolina
[4]Community and Family Medicine, Duke University School of Medicine, Durham, North Carolina
[5]Organismal Biology & Anatomy, University of Chicago, Chicago, Illinois
[6]Department of Anatomy & Neurobiology, NEOMED, Rootstown, Ohio

ABSTRACT

Numerous studies have sought to link craniofacial morphology with behavioral ecology in primates. Extant hard-object feeders have been of particular interest because of their potential to inform our understanding about the diets of early fossil hominins. Sooty mangabeys (*Cercocebus atys*) are hard-object feeders that frequently generate what have been described as audibly powerful bites at wide jaw gapes to process materially stiff and hard seeds. We address the hypothesis that sooty mangabeys have features of the masticatory apparatus that facilitate this feeding behavior by comparing fiber architecture and leverage of the masseter and temporalis muscles between sooty mangabeys and three papionin primates that do not specialize on hard objects. Contrary to predictions, sooty mangabeys do not have relatively larger muscle physiologic cross-sectional areas or weights compared to other papionins, nor do they consistently display improved leverage. In this regard, sooty mangabeys differ in their morphology from other hard-object feeders such as tufted capuchins. However, males of all four papionin species converge on a shared pattern of relatively longer anterior superficial masseter fibers compared with female conspecifics, suggesting that males are likely prioritizing muscle stretch to improve gape performance as part of a behavioral repertoire that includes agonistic social interactions and intense male–male competition. These findings strengthen support for the hypothesis that gape display behaviors can exert a strong selective influence throughout the musculoskeletal masticatory apparatus. Results also raise questions about the morphological suitability of extant cercopithecines as models for interpreting feeding

Additional Supporting Information may be found in the online version of this article.

Grant sponsor: National Science Foundation, Grant number: BCS 0962677, BCS 1723041, Grant sponsor: National Institutes of Health, Grant number: R24 HD050837-1, Grant sponsor: Yerkes National Primate Research Center, Grant number: ORIP/OD P51OD011132 and the Yerkes National Primate Research Center Comparative AIDS Core.

*Correspondence to: Andrea B. Taylor, Department of Basic Science, College of Osteopathic Medicine, Touro University, 1310 Club Dr., Vallejo, CA 94592-1159. E-mail: andrea.taylor3@tu.edu

Received 21 May 2017; Revised 25 July 2017; Accepted 29 August 2017.

DOI 10.1002/ar.23718

Published online in Wiley Online Library (wileyonlinelibrary.com).

behavior and diet in fossil hominins with limited jaw gape capacity. Anat Rec, 301:325–342, 2018. © 2018 Wiley Periodicals, Inc.

**Key words: jaw gape; bite force; sooty mangabeys; jaw-adductor PCSA; jaw-adductor fiber length**

Mangabeys (members of the genera *Cercocebus* and *Lophocebus*) are African primates of the Papionini tribe of Old World monkeys (Strasser and Delson, 1987). Though now recognized as members of two distinct clades (Harris and Disotell, 1998; Fleagle and McGraw, 2002), many mangabeys converge on a common feeding ecology that includes large quantities of mechanically resistant foods (Tappen, 1960; Chalmers, 1968; Jones and Sabater Pi, 1968; Fleagle and McGraw, 1999; Haddow, 1952). *Lophocebus*, for example, has features of the masticatory complex that have been adaptively linked to the frequent use of forceful incision of mechanically challenging fruits (Daegling and McGraw, 2007). Compared to *Lophocebus*, *Cercocebus* has molarized and heavily worn distal premolars that have been linked to the routine use of their postcanine dentition to powerfully crush obdurate nuts and seeds (Fleagle and McGraw, 1999, 2002; Daegling and McGraw, 2007; McGraw et al., 2011). Both mangabey genera have extremely thick molar enamel (Kay, 1981), which has also been adaptively linked to processing hard foods (McGraw et al., 2011).

Sooty mangabeys (*Cercocebus atys*) of the Tai Forest feed preferentially on *Saccoglottis gabonensis* seeds, which they recover from the forest floor (McGraw et al., 2011). The soft, oily nut is housed in a large, materially hard and stiff[1] outer seed (casing) with hard inner compartments. The seed casing is the stiffest tissue processed by these mangabeys (Daegling et al., 2010; McGraw et al., 2011). At Tai, feeding on *S. gabonensis* accounts for 48% and 62% of female and male feeding events, respectively, and these seeds comprise more than half their annual diet (McGraw et al., 2011, 2014).

Behavioral observations of oral processing reveal that Tai mangabeys frequently use forceful isometric bites (described as postcanine crushes by McGraw et al., 2011) delivered along the postcanine region to defeat the mechanical defense (e.g., Lucas et al., 2000) of the outer seed casing (McGraw et al., 2011). These bites involve relatively wide jaw gapes: "Several[2] foods were processed using conspicuous behaviors which we labeled postcanine crushes; in these situations, a monkey adopted a wide gape, inserted the food between upper and lower cheek tooth rows (the food was usually introduced distal to the canine), and performed one or a series of powerful, audible bites" (McGraw et al., 2011, p. 142). Preferential feeding on these relatively large, hard seeds has led to the hypothesis that sooty mangabeys spend a significant percentage of their feeding time generating forceful bites at relatively wide jaw gapes (McGraw et al., 2011). As such, researchers have addressed the utility of sooty mangabeys as a model for reconstructing the feeding behavior and diet of early hominins (Daegling et al., 2011; McGraw and Daegling, 2012), whose craniodental morphology has long been interpreted as favorable for processing hard objects (Jolly, 1970; Grine, 1981; Hylander, 1988; Daegling and Grine, 1991; Strait et al., 2009; Rak, 2014; but see Daegling et al., 2013).

It is of interest that, apart from the expansion of the upper and lower distal premolars, both mangabey genera display few of the craniofacial features that might be expected in hard-object feeders (Singleton, 2004; Daegling and McGraw, 2007; McGraw et al., 2012, 2014). For example, compared with closely related papionins, including other mangabeys such as *Lophocebus* that feed on less obdurate foods, *Cercocebus* have neither the expected size- nor shape-related features of the mandibular corpus and symphysis associated with the capacity to resist relatively large masticatory loads (Daegling and McGraw, 2007). Similarly, *C. atys* does not exhibit improved leverage for generating large postcanine occlusal forces (Singleton, 2004). However, compared with *Procolobus badius* and *Colobus polykomos*, two West African colobine species that feed on items requiring extensive incisal preparation, sooty mangabeys display significantly higher basal cortical (but not alveolar) bone mineral content at the $M_2$ (Ray et al., 2015). Their stiffer postcanine mandibular corpus has been functionally linked to resisting high magnitude bite forces on the premolars and molars during isometric biting of stiff nuts (Ray et al., 2015). Taken together, the craniodental evidence thus far indicates that sooty mangabeys have relatively few of the morphological features—and none of the mandibular shape differences—that would be expected for a hard-object feeding primate.

The need to generate forceful bites at relatively wide jaw gapes places competing demands on the masticatory apparatus. This competition is based on a theoretical trade-off between morphological features that maximize bite force (e.g., muscle leverage, muscle physiologic cross-sectional area) and features that maximize gape (e.g., fiber length and muscle stretch) (Herring and Herring, 1974). Empirically, bite forces are diminished at wide jaw gapes (Dumont and Herrel, 2003; Williams

[1]*Sacoglottis gabonensis* has an average elastic modulus (stiffness scaled to size; Lucas, 2004) of ~200 MPa and an average Shore D Hardness of 88.7, making these seeds the stiffest items in the sooty mangabey diet, and the hardest items second only to *Coula edulis* (McGraw et al., 2011, 2014). We thus use "hard" and "stiff" interchangeably to describe this item.

[2]Although several foods were observed, *S. gabonensis* seeds were reported as the food most frequently consumed by sooty mangabeys, representing 52% of both total actions and total focal periods, and the stiffest item in their diet (McGraw et al., 2011). The next stiffest item, *C. edulis*, represented <1% of both total actions and total focal periods.

et al., 2009; Santana, 2016). In anthropoid primates, the relationship between force and gape has been evaluated in only a handful of species. Marmosets, for example, routinely generate relatively wide jaw gapes while using their anterior teeth to gouge trees and maintain architectural features of the jaw adductors that facilitate muscle stretch but at some expense to muscle force (Vinyard et al., 2003; Taylor and Vinyard, 2004, 2008; Eng et al., 2009; Taylor et al., 2009). Tufted capuchins exhibit architectural features of the jaw adductors (Taylor and Vinyard, 2009) that have been linked to their feeding on relatively large and exceptionally mechanically challenging foods such as *Astrocaryum* palm nuts. This architectural relationship has also been explored in crab-eating macaques (Terhune et al., 2015) where males engage in wide-mouth display behaviors.

The general picture to emerge from these studies is one of species-specific solutions to the competing demands of generating bite forces at relatively wide gapes. Tree-gouging marmosets, for example, have an architectural configuration of the jaw adductors that facilitates muscle stretch (i.e., relatively long fibers), but at some expense to muscle force (i.e., relatively reduced physiologic cross-sectional area when compared to cotton-top tamarins) (Taylor and Vinyard, 2004; Taylor et al., 2009). Their architectural configuration also allows their jaw adductors to act on a more favorable portion of the length-tension curve at wide jaw gapes compared to closely related species that do not use wide jaw gapes during feeding. By reducing muscle stretch at wide jaw gapes, they are able to generate comparatively large muscle forces at the jaw gapes at which they gouge trees (Eng et al., 2009). In contrast, in tufted capuchins, forceful isometric premolar and molar biting at wide jaw gapes (Terborgh, 1983; Ross et al., 2016) is facilitated by adding muscle mass and increasing relative muscle PCSA, but with no trade-off in relative fiber length (Taylor and Vinyard, 2009). These species-specific patterns question the general predictability of performance from masticatory structure (van der Klaauw, 1946; Bock, 1959; Lauder, 1981, 1996; Wainwright et al., 2005), and in particular, whether we can consistently predict musculoskeletal features associated with hard-object feeding.

Here, we examine the sooty mangabey (*Cercocebus atys*) as a natural experiment to further address the morphological correlates of routinely feeding on large, hard/stiff items at relatively wide jaw gapes in primates. On the one hand, we might expect sooty mangabeys to exhibit a morphological configuration that favors relatively large muscle and bite forces without compromising jaw gape, similar to tufted capuchins that exploit mechanically challenging foods. Alternatively, sooty mangabeys have been empirically observed to generate relatively wide jaw gapes for feeding on large, hard objects (McGraw et al., 2011) and likely engage in wide-mouth gape display behaviors, similar to what has been documented for *Lophocebus albigena* and *Macaca fascicularis* (Deputte, 1994). These agonistic encounters may involve aggressive biting (Bernstein et al., 1983) and slashing with the canines (Bernstein and Gordon, 1974), biting behavior that requires the animals to adopt a sufficiently wide jaw gape to clear the canines. Thus, facilitating the production of relatively wide jaw gapes may come at some expense to muscle and bite force. Sooty mangabeys provide the opportunity to evaluate whether a primate species that feeds routinely on large, hard objects at relatively wide jaw gapes and engages in wide-mouth gape display has features of the jaw muscles and skull that facilitate meeting these competing functional demands.

Similar to macaques and other papionins, sooty mangabeys are sexually dimorphic in body size (Smith and Jungers, 1997), skull size, and likely bite force as well (e.g., Dechow and Carlson, 1990). They also exhibit significant dimorphism in maximum jaw gape (Hylander, 2013). Male and female *C. atys* gapes can reach 104% and 79% of jaw length, respectively, comparable to dimorphism levels reported for *Papio anubis* and *Macaca nemestrina* (Hylander, 2013). Sooty mangabeys are further characterized by sex-specific differences in oral processing behaviors, with adult males engaging in significantly greater average numbers of incisal and postcanine bites during feeding compared to adult females (McGraw et al., 2011). Thus, we begin by addressing variation in masticatory morphology between males and females. We then extend previous investigations of the relationship between feeding behavior and craniodental morphology in sooty mangabeys (e.g., Fleagle and McGraw, 1999, 2002; Daegling and McGraw, 2007) by comparing jaw-muscle fiber architecture and jaw-muscle mechanical advantage between *C. atys* and three closely related papionin species that do not specialize on hard objects—*Papio anubis*, *M. mulatta*, and *M. fascicularis*.

## HYPOTHESES AND PREDICTIONS

We test the hypothesis that *Cercocebus atys* exhibits features of the masticatory apparatus that facilitate the production of relatively large muscle and bite force without compromising relative maximum jaw gape. To address this hypothesis, we generate a series of predictions regarding jaw-muscle fiber architecture and leverage. All predictions are stated relative to the non-hard-object feeding condition and holding other competing factors constant.

### Predictions Related to Jaw-Muscle Fiber Architecture

*Prediction 1.* Cercocebus atys *have relatively larger superficial masseter and temporalis physiological cross-sectional areas*. Muscle physiological cross-sectional area (PCSA) is proportional to a muscle's maximum force-generating capacity (Powell et al., 1984). Thus, we predict that the hard-object feeding *C. atys* will have relatively larger jaw adductor PCSAs, which likely translate into larger maximum bite force.

*Prediction 2.* Cercocebus atys *have relatively larger superficial masseter and temporalis muscle mass*. Given two muscles of comparable volume, the only way to achieve a relatively larger PCSA without decreasing fiber length and pinnation angle is to increase muscle mass. We predict that *C. atys* will have relatively larger superficial masseter and temporalis masses.

*Prediction 3:* Cercocebus atys *do not differ in relative superficial masseter and temporalis fiber lengths or pinnation angles*. For two muscles of comparable volume, a muscle with a relatively larger PCSA typically comprises shorter, more pinnate fibers (i.e., fibers that have larger angles relative to the force-generating axis of the muscle).

This increased force production occurs because by angling fibers, more fibers can be packed adjacent to each other, which increases muscle PCSA. However, shorter, more pinnate-fibered muscles reduce fiber excursions, decrease muscle stretch and thus potentially limit jaw gape. Because *C. atys* feed on large objects at relatively wide jaw gapes, we predict that *C. atys* will maintain superficial masseter and temporalis fiber lengths and pinnation angles comparable to *Macaca* and *Papio* so as not to sacrifice jaw gape (Taylor and Vinyard, 2009).

### Predictions Related to Muscle Position and Leverage

*Prediction 4.* Cercocebus atys *have relatively longer jaw-muscle lever arms and improved mechanical advantage*. Jaw-adductor mechanical advantage is influenced by the lengths of both the muscle and bite-point moment arms. Jaw muscles positioned further anterior relative to the temporomandibular joint (TMJ) are at a greater mechanical advantage for generating bite force. Therefore, for two jaw muscles of similar internal architecture and bite point moment arms, the more rostrally-positioned muscle will have improved mechanical advantage for generating bite force. The disadvantage of this configuration, however, is that it increases muscle stretch per unit of jaw rotation and likely limits maximum gape. *Cercocebus atys* are predicted to have jaw muscles positioned further anterior relative to the TMJ to improve mechanical advantage for biting on mechanically resistant seeds.

*Prediction 5.* Cercocebus atys *have relatively shorter mandibles*. A shorter mandible tends to decrease the load arm (i.e., bite point moment arm) at the incisors and potentially the molars. Shorter load arms are favorable for converting muscle force into bite force. As a consequence of incisor and premolar/molar biting on hard objects, *C. atys* are predicted to have relatively shorter mandibles and relatively shorter load arms at the molars.

## MATERIALS AND METHODS

### Samples

We took architectural measurements of the superficial masseter and temporalis muscles, muscle lever arm lengths, and linear dimensions of the skull on a cadaveric sample of captive adult *C. atys* (six males and six females), *P. anubis* (three males and three females) and *M. mulatta* (five males and five females). We used previously published data on captive adult *M. fascicularis* (five males and five females; Terhune et al., 2015). All specimens lacked obvious craniodental pathology. No animals were euthanized for this study.

*Cercocebus*, *Macaca*, and *Papio* are all members of the Papionini tribe. *Papio anubis*, an African Old World monkey of the subtribe Papionina (Strasser and Delson, 1987), is most closely related to *Cercocebus*. While macaques and baboons feed on a variety of plant and animal matter, including fruits, leaves, flowers, insects, bark, and underground storage organs (De Vore and Washburn, 1963; Wheatley, 1980; Sussman and Tattersall, 1981; Lucas and Corlett, 1991; Nystrom, 1992; Barton, 1993; Yeager, 1996; Kunz and Linsenmair, 2006; Dominy et al., 2008), none specialize on hard objects. Comparing *C. atys* to multiple closely related species that do not specialize on hard objects allows us to minimize the influence of phylogeny and statistical issues associated with two-species comparisons (Garland and Adolph, 1994).

### Measurements

There are diverse methods for collecting and analyzing muscle fiber architecture (Loeb and Gans, 1986; Anapol and Barry, 1996; Wedeen et al., 2001; Ward et al., 2006; Jeffery et al., 2011; Kupczik et al., 2015). Our fiber architecture measurement protocol is based on previous work by Anapol and colleagues (Anapol and Barry, 1996; Anapol and Gray, 2003; Anapol et al., 2008). The details of our protocol are published elsewhere (Taylor et al., 2009; Taylor and Vinyard, 2009; Terhune et al., 2015) and thus briefly described here. Muscles were harvested from the skull and the deep and superficial masseter muscles were separated. Each muscle was weighed to the nearest 0.1 or 1.0 g, depending on muscle size. The superficial masseter muscles were sectioned along their lengths. We sectioned the anteriormost portion to ensure capture of the anterior fibers and then sectioned the remaining belly into ~0.5 cm segments (Fig. 1A). The temporalis muscles were sectioned into anterior, middle, and posterior portions (Fig. 1A). For each segment of the superficial masseter, we measured a maximum of 12 fibers from the superficial region and from intramuscular junction to intramuscular junction (Gaspard et al., 1973; Fig. 1B). For the temporalis, we measured a maximum of 12 fibers from the superficial and deep regions of each of the three temporalis portions (Fig. 1B). For each fiber, we measured the perpendicular distance ($a$) from the distal tendon of attachment of a fiber to intramuscular tendon and used this distance to estimate pinnation angle (Anapol and Barry, 1996) (Fig. 1B; see Table 1 for measurement definitions and abbreviations).[3]

We controlled for differences in muscle stretch due to varying jaw postures at the time of fixation by normalizing fiber length (Lf) to a standardized sarcomere length (Felder et al., 2005). We do this because when stretched to maximum jaw gape, the masseter fibers are significantly lengthened by as much as 74%, and the temporalis fibers by as much as 44%, relative to muscles from the ungaped side of the skull (Taylor et al., 2014). Likewise, masseter and temporalis PCSAs are significantly reduced by as much as 41% and 37%, respectively (Taylor et al., 2014). With normalization of the stretched fibers to a standard sarcomere length, fiber lengths and PCSAs between gaped and ungaped sides are not significantly different, indicating that we have effectively controlled for this error.[4]

[3]We measured fiber lengths, pinnation angles and muscle weights, and estimated PCSAs, for the deep masseter and medial pterygoid muscles for *C. atys* and these are provided in Supporting Information.

[4]We recognize that normalizing these muscles to the same standardized sarcomere length assumes the muscles are operating at the same sarcomere length when generating jaw movements and forces. While there is error associated with this assumption (e.g., Herring et al., 1984) we argue that while we cannot easily address this error, we can address the error associated with combining architectural estimates from muscles fixed in different jaw postures and our empirical data suggest to us that sarcomere-length normalization is the lesser of these two errors (Taylor et al., 2014).

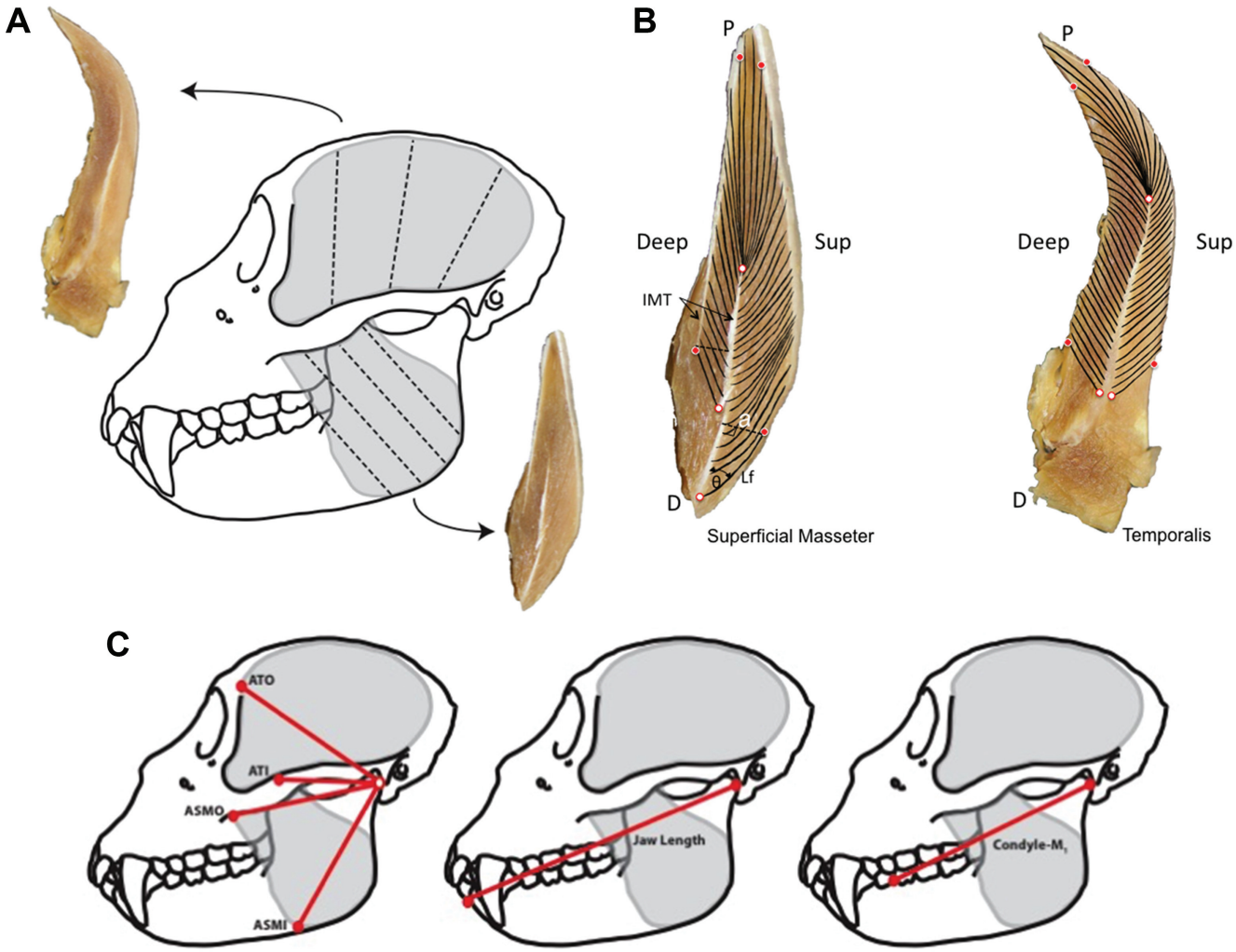


Fig. 1. Measurements collected in this study. (**A**) Schematic of a male *Cercocebus atys* skull referencing the temporalis (upper left) and superficial masseter (lower right) muscles. Dashed black lines on the skull indicate approximate locations at which muscles were sectioned for architecture measurements. (**B**) Cross sections show fiber length measurements (Lf, depicted as distances between white and red circles) taken at each section. Fibers were sampled from proximal-to-distal and from distal-to-proximal, from the superficial (superficial tendon to intramuscular tendon [IMT]), and intermediate (IMT to IMT) portions of the superficial masseter, and from the superficial and deep portions of the anterior, middle and posterior temporalis muscle. Superficial masseter cross section depicts a, the distance from the proximal myotendinous junction normal to the tendon of distal muscle attachment. Pinnation angle (θ) was computed as the arcsine of *a*/NLf (Anapol and Barry, 1996). P, proximal; D, distal; sup, superficial. (**C**) Illustration of the measurements describing muscle position (left), jaw length (middle), and condyle-$M_1$ length (right).

We measured *in situ* sarcomere lengths (Ls) (±0.01 μm) from the measured fibers (Supporting Information) using laser diffraction (Lieber et al., 1984) and normalized Lf of the measured fibers to a standardized Ls of 2.41 μm (the optimal Ls for macaque limb muscles (Walker and Schrodt, 1974). We believe this Ls provides a reasonable estimate given that sarcomere resting lengths generally have been observed in the range of 2.3–2.8 μm for mammalian muscles (Huxley, 1972; Burkholder and Lieber, 2001). Normalized Lf (NLf) was computed as:

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

We estimated whole-muscle fiber lengths by averaging NLf across all the measured segments for the superficial masseter, and averaging NLf for the anterior, middle, and posterior regions of the temporalis. We also estimated NLf for the anterior superficial masseter (ASM NLf). Based on theoretical models (Herring and Herring, 1974) and empirical data for baboons and macaques (Iriarte-Diaz et al., 2017), these muscles/muscle regions likely experience considerable stretching during jaw opening and thus provide important limits to jaw gape. We estimated pinnation angle (θ) for each fiber as the arcsine of *a*/NLf and computed an average θ for each muscle (Table 1). We estimated PCSA using NLf, θ and muscle mass for each muscle, using a muscle-specific density estimate of 1.0564 g/cm$^3$ (Murphy and Beardsley, 1974).

We employ conventional lever mechanics models to evaluate species differences in leverage (Dechow and

**TABLE 1. Measurements included in the study**

| Measurement | Abbreviation | Definition |
|---|---|---|
| Muscle weight (g) | MWt | Wet weights of the superficial masseter (SM) or temporalis (TM) muscle |
| Normalized fiber length (mm) | NLf | Average linear distance between proximal and distal myotendinous junctions of a fasciculus, normalized by a standard sarcomere length of 2.41 μm |
| Pinnation angle (°) | θ | Arcsine of the distance ($a$) from the proximal myotendinous junction normal to the tendon of distal muscle attachment, divided by NLf |
| Physiological cross sectional area ($cm^2$) | PCSA | Muscle mass × cos($\theta$)/NLf × 1.0564 ($gm/cm^3$) |
| Superficial masseter origin length (mm) | ASMO | Maximum linear distance from the posterior mandibular condyle to the anterior-most origin of superficial masseter on the zygoma |
| Superficial masseter insertion length (mm) | ASMI | Maximum linear distance from the posterior mandibular condyle to the anterior-most insertion of the superficial masseter on the mandible |
| Superficial masseter lever arm length (mm) | SMLever | Average of ASMO and ASMI |
| Temporalis origin length (mm) | ATO | Maximum linear distance from the posterior mandibular condyle to the anterior-most origin of the temporalis on the frontal bone |
| Temporalis insertion length (mm) | ATI | Maximum linear distance from the posterior mandibular condyle to the tip of the coronoid process |
| Temporalis lever arm length (mm) | TMLever | Average of ATO and ATI |
| Mandibular length (mm) | JawLg | Maximum linear distance from the posterior edge of the mandibular condyle to infradentale |
| Condyle-$M_1$ length (mm) | Cond$M_1$ | Maximum linear distance from the posterior mandibular condyle to the anterior edge of the first mandibular molar ($M_1$) |
| Nasion–inion length (mm) | NI | Maximum linear distance between nasion and inion |

Carlson, 1990; Spencer and Demes, 1993; Wright, 2005). To estimate lever arms, we measured distances from the posterior edge of the condyle to the anterior superficial masseter origin (ASMO) and insertion (ASMI; Table 1) and used their average as an estimate of the superficial masseter lever arm (Fig. 1C). Similarly, we averaged measurements from the posterior edge of the condyle to the temporalis origin (ATO) and insertion (ATI) to estimate temporalis lever arm (Fig. 1C; Terhune et al., 2015). We used mandibular length as a relevant and appropriate reference standard for this biomechanical study (Hylander, 1985; Bouvier, 1986) and as a load-arm estimate for incision (Fig. 1C; Vinyard et al., 2003). We used the distance between the mandibular condyle and $M_1$ as a load-arm estimate for molar biting (Fig. 1C; Daegling, 1990). The distance between nasion and inion (NI) was used to assess differences in jaw length and leverage relative to a skull size estimate independent of jaw length (Terhune et al., 2015)

### Statistical Analysis

We examined absolute and relative differences in muscle fiber architecture and muscle position between male and female *C. atys*, and between *C. atys* and *P. anubis*, *M. fascicularis* and *M. mulatta*. Sexes were treated separately in species comparisons.

To examine relative differences between groups, we scaled muscle mass$^{0.33}$, NLf, PCSA$^{0.5}$, and our lever arm estimates by mandibular length and condyle-$M_1$ distance. We also scaled moment arm estimates by nasion–inion (NI) length to evaluate leverage and jaw length differences relative to an estimate of skull size not directly related to jaw length.

We used two-tailed, non-parametric Mann–Whitney $U$-tests to evaluate absolute and relative differences in muscle architecture and muscle leverage between male and female sooty mangabeys. We initially tested for absolute and relative differences between species using two-way analyses of variance (ANOVA) with sex and species as independent variables. Finding significant sex and/or interaction effects between sex and species,[5] we tested our morphological predictions (1–5) separately for males and females using one-tailed Mann–Whitney $U$-tests. 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 protect 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 muscle and for males and females.

## RESULTS

### Sex Differences in *C. atys* Fiber Architecture and Muscle Leverage

***Absolute differences.*** Males have absolutely larger muscle weights, longer fibers, and a larger medial pterygoid PCSA compared with females, but only superficial masseter anterior fiber length and medial pterygoid weight are significantly different after sequential Bonferroni adjustment (Table 2 and Supporting Information). Superficial masseter lever arm is also significantly longer in males. Similar to other dimorphic catarrhines

[5]One-way ANOVAs by species with sex as a covariate yielded similar results.

**TABLE 2. Means, standard deviations (in parentheses), and maximum sample sizes for fiber architecture measurements of the superficial masseter and temporalis muscles, lever arm lengths, and bony measurements for male and female *Cercocebus atys*, *Papio anubis*, *Macaca mulatta*, and *M. fascicularis*[a]**

| | *Cercocebus atys* | | *Papio anubis* | | *Macaca mulatta* | | *Macaca fascicularis* | |
|---|---|---|---|---|---|---|---|---|
| Measurement | Male ($n = 6$) | Female ($n = 6$) | Male ($n = 3$) | Female ($n = 3$) | Male ($n = 5$) | Female ($n = 5$) | Male ($n = 5$) | Female ($n = 5$) |
| *Superficial masseter (SM)* | | | | | | | | |
| Muscle weight (g) | 11.68 (2.2) | 8.01 (2.2) | 52.76 (15.1) | 27.38 (3.2) | 12.42 (2.4) | 7.52 (1.0) | 11.00 (4.4) | 4.07 (0.9) |
| SM NLf (mm) | 15.51 (0.9) | 12.54 (2.2) | 22.65 (2.8) | 11.49 (3.9) | 15.98 (1.3) | 13.08 (2.5) | 17.60 (2.8) | 11.70 (2.2) |
| ASM NLf (mm) | 20.90 (1.2) | 14.66 (3.8) | 30.44 (0.7) | 19.80 (4.4) | 22.63 (4.1) | 15.70 (4.7) | 21.14 (3.0) | 12.53 (2.7) |
| PCSA ($cm^2$) | 7.06 (1.5) | 5.93 (0.8) | 21.18 (4.3) | 22.10 (5.3) | 6.69 (1.6) | 5.11 (1.0) | 5.51 (1.8) | 3.27 (0.6) |
| *Temporalis (TM)* | | | | | | | | |
| Muscle weight (g) | 33.89 (9.1) | 19.62 (4.1) | 126.41 (14.7) | 68.81 (15.7) | 52.12 (13.2) | 20.80 (3.1) | 53.40 (19.8) | 13.70 (3.2) |
| TM NLf (mm) | 23.95 (5.2) | 17.06 (3.0) | 44.37 (14.8) | 23.99 (8.4) | 28.48 (4.4) | 16.52 (2.6) | 26.86 (5.0) | 15.78 (3.9) |
| PCSA ($cm^2$) | 13.51 (4.0) | 10.95 (2.2) | 28.00 (6.2) | 29.11 (10.9) | 13.92 (1.9) | 11.76 (1.4) | 17.75 (4.9) | 8.11 (1.0) |
| *Bony measurements* | | | | | | | | |
| SM lever arm length (mm) | 54.32 (2.4) | 48.78 (1.5) | 72.30 (4.7) | 60.44 (10.3) | 50.67 (4.6) | 48.22 (5.0) | 51.37 (5.9) | 43.48 (5.1) |
| TM lever arm length (mm) | 42.25 (3.3) | 36.80 (3.5) | 50.78 (1.8) | 45.11 (0.8) | 47.90 (3.0) | 40.29 (4.2) | 46.12 (4.7) | 37.08 (4.5) |
| Jaw length (mm) | 105.17 (4.4) | 97.97 (4.8) | 154.85 (3.0) | 131.55 (10.4) | 103.56 (5.2) | 83.59 (7.2) | 101.14 (8.6) | 80.29 (7.9) |
| Condyle-$M_1$ length (mm) | 71.45 (4.4) | 64.49 (4.4) | 106.19 (6.8) | 90.17 (1.0) | 72.00 (5.0) | 59.84 (6.6) | 70.28 (6.6) | 57.08 (7.1) |
| Nasion–inion length (mm) | 99.30 (5.1) | 92.52 (3.9) | 108.31 (5.5) | 110.28 (1.7) | 95.23 (3.8) | 97.99 (4.7) | 87.91 (8.6) | 77.76 (2.1) |

[a]Not all measurements were available for each specimen.

**TABLE 3. Results of significance tests for relative differences in fiber architecture and leverage between male and female *Cercocebus atys***

| Measurement | Direction of observed difference | *P*-value |
|---|---|---|
| *Muscle measurements* | | |
| Superficial masseter | | |
| $PCSA^{0.5}$/JawLg | NS | 0.3367 |
| $PCSA^{0.5}$/Cond$M_1$ | NS | 0.8728 |
| SM NLf/JawLg | NS | 0.2002 |
| SM NLf/Cond$M_1$ | M>F | 0.0782 |
| ASM NLf/JawLg | M>F | 0.0250 |
| ASM NLf/Cond$M_1$ | M>F | 0.0163 |
| Pinnation angle (°) | M>F | 0.6310 |
| $Weight^{0.33}$/JawLg | NS | 1.000 |
| $Weight^{0.33}$/Cond$M_1$ | NS | 0.3367 |
| Temporalis | | |
| $PCSA^{0.5}$/JawLg | NS | 0.6310 |
| $PCSA^{0.5}$/Cond$M_1$ | NS | 0.8728 |
| TM NLf/JawLg | M>F | 0.0782 |
| TM NLf/Cond$M_1$ | NS | 0.1093 |
| Pinnation angle (°) | NS | 0.1495 |
| $Weight^{0.33}$/JawLg | NS | 0.3367 |
| $Weight^{0.33}$/Cond$M_1$ | NS | 0.2623 |
| *Leverage measurements* | | |
| SMLever/JawLg | NS | 0.5218 |
| SMLever/Cond$M_1$ | NS | 1.000 |
| SMLever/NI | NS | 0.5218 |
| TMLever/JawLg | NS | 0.7540 |
| TMLever/Cond$M_1$ | NS | 0.4647 |
| TMLever/NI | NS | 0.2506 |
| JawLg/NI | M>F | 0.0547 |

*P*-values based on two-tailed, non-parametric Mann–Whitney *U*-tests. Underlined values are significant or trend toward significance ($0.05 < P < 1.0$) prior to the sequential Bonferroni adjustment, which was applied separately for each muscle and for leverage. There were no significant differences between the sexes for any variable following the sequential Bonferroni adjustment.

(Hylander, 2013; Terhune et al., 2015), males have significantly longer jaws, greater condyle-$M_1$ lengths and longer crania (NI) (Table 2 and Supporting Information).

***Relative differences.*** Compared with females, male sooty mangabeys trend toward relatively longer fibers, most notably for the anterior superficial masseter (Tables 2 and 3; Fig. 2). There were no significant sex differences following the sequential Bonferroni adjustment and no other relative differences in architectural variables between the sexes. Males trend toward longer jaws relative to NI (Tables 2 and 3) but there are no sex differences in relative jaw-muscle position or leverage. Thus, sooty mangabeys do not exhibit the dimorphism in jaw-muscle fiber architecture or leverage observed for *M. fascicularis* (Terhune et al., 2015).

## Relative Differences Between Sooty Mangabeys, Baboons, and Macaques

***Jaw-muscle fiber architecture.*** *Prediction 1.* Contrary to our predictions, sooty mangabeys do not have relatively larger superficial masseter or temporalis PCSAs compared to other papionins (Tables 4 and 5; Fig. 3). This finding is observed for both males and females. Thus, sooty mangabeys do not have architectural features of the superficial masseter or temporalis muscles that indicate improved bite force abilities in comparison with other papionins.

*Prediction 2.* Contrary to our predictions, sooty mangabeys do not have relatively larger jaw-muscle weights compared with other papionin primates (Tables 4 and 5). Male *C. atys* maintain superficial masseter weights comparable to other papionins relative to both load-arm estimates and trend toward smaller temporalis muscle weights relative to jaw length compared to both

macaque species. Females display a roughly similar pattern as that observed for males.

*Prediction 3*. Our prediction that sooty mangabeys have relative jaw-muscle fiber lengths similar to other papionins is supported only for the anterior superficial masseter (ASM NLf) (Tables 4 and 5; Fig. 4). However, *C. atys* males have shorter superficial masseter fibers compared with *M. fascicularis*, significantly so relative to jaw length (Table 5), and trend toward relatively shorter temporalis muscle fibers compared to male *M. mulatta*. Female *C. atys* trend toward relatively longer superficial masseter fibers compared to *Papio*. Contrary to our prediction, both *C. atys* males and females have significantly smaller jaw muscle pinnation angles compared to other papionins (Tables 4 and 5; Fig. 5).

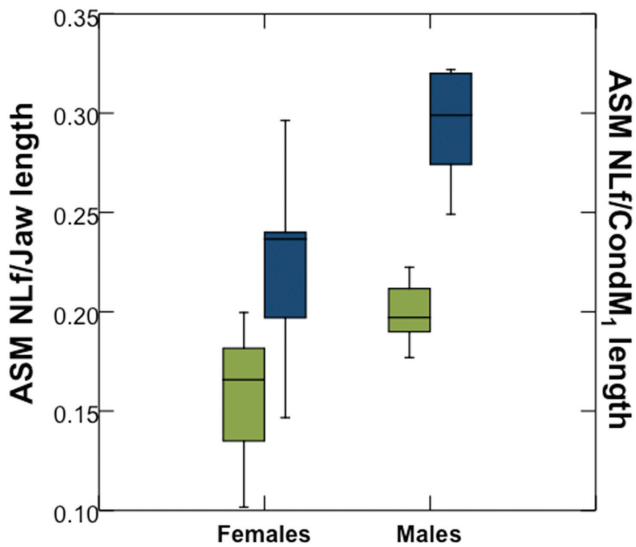


Fig. 2. Box plot of normalized fiber length differences in the anterior superficial masseter (ASM NLf) relative to jaw length (green) and condyle-$M_1$ (Cond$M_1$) length (blue) in *Cercocebus atys*. Males have relatively longer ASM fibers compared to females, significantly so prior to the Bonferroni adjustment. In this and all subsequent box plots, the center horizontal line marks the median of the sample. The length of each box shows the range within which the central 50% of the values fall. Whiskers indicate 10th and 90th percentiles. Outliers are plotted with asterisks; extreme values are plotted with empty circles (see also Table 3).

***Jaw-muscle leverage.*** *Prediction 4*. Based on conventional models of lever mechanics, sooty mangabeys do not consistently demonstrate improved muscle leverage compared to other papionins. *Cercocebus atys* males (but not females) trend toward longer superficial masseter lever arms relative to Cond$M_1$ compared with *Papio* and both macaques (Tables 6 and 7; Fig. 6). In addition, both male and female sooty mangabeys have significantly longer temporalis muscle lever arms relative to jaw length compared to *Papio* (Tables 6 and 7). Relative to Cond$M_1$, temporalis muscle lever arm is only significantly longer in male *C. atys*. The improved leverage in comparison with *Papio* is due to sooty mangabeys having significantly shorter jaws and Cond$M_1$ distances. However, both macaques have relatively longer temporalis muscle lever arms compared with sooty mangabeys (Tables 6 and 7). Some lever arm differences observed relative to jaw length are not observed relative to NI (Table 7; e.g., temporalis muscle lever arm in *C. atys* compared with *P. anubis*). Thus, not surprisingly, leverage in papionins is influenced to some degree by jaw length and facial prognathism.

*Prediction 5*. Our prediction that sooty mangabyes have relatively shorter jaws is supported only in comparison with *Papio* (Tables 6 and 7; Fig. 7). Male sooty mangabeys maintain relative jaw lengths comparable to macaques, and female sooty mangabeys have relatively longer jaws than *M. mulatta*. We observe the same pattern for relative condyle-$M_1$ length (Tables 6 and 7).

## DISCUSSION

### Sex-Specific Variation in Sooty Mangabey Jaw-Muscle Fiber Architecture and Leverage

Despite being sexually dimorphic in body and skull size (Smith and Jungers, 1997; Hylander, 2013; Tables 2 and 3 and Supporting Information), *C. atys* show few sex

**TABLE 4. Means and standard deviations (in parentheses) for ratios of fiber architectural variables for the superficial masseter and temporalis muscles for male and female *Cercocebus atys*, *Papio anubis*, *Macaca mulatta*, and *M. fascicularis***

| | *Cercocebus atys* | | *Papio anubis* | | *Macaca mulatta* | | *Macaca fascicularis* | |
|---|---|---|---|---|---|---|---|---|
| Measurement | Male | Female | Male | Female | Male | Female | Male | Female |
| *Superficial masseter (SM)* | | | | | | | | |
| PCSA$^{0.5}$/JawLg | 0.025 (<0.01) | 0.026 (<0.01) | 0.030 (<0.01) | 0.040 (0.01) | 0.025 (<0.01) | 0.029 (<0.01) | 0.023 (<0.01) | 0.023 (<0.01) |
| PCSA$^{0.5}$/Cond$M_1$ | 0.037 (<0.01) | 0.038 (<0.01) | 0.043 (<0.01) | 0.052 (0.01) | 0.036 (<0.01) | 0.042 (<0.01) | 0.033 (<0.01) | 0.032 (<0.01) |
| Weight$^{0.33}$/JawLg | 0.021 (<0.01) | 0.021 (<0.01) | 0.024 (<0.01) | 0.023 (<0.01) | 0.022 (<0.01) | 0.024 (<0.01) | 0.021 (<0.01) | 0.020 (<0.01) |
| Weight$^{0.33}$/Cond$M_1$ | 0.032 (<0.01) | 0.031 (<0.01) | 0.035 (<0.01) | 0.033 (<0.01) | 0.031 (<0.01) | 0.033 (<0.01) | 0.031 (<0.01) | 0.028 (<0.01) |
| SM NLf/JawLg | 0.148 (0.01) | 0.136 (0.02) | 0.146 (0.02) | 0.086 (0.02) | 0.154 (0.01) | 0.148 (<0.01) | 0.173 (0.02) | 0.145 (0.01) |
| SM NLf/Cond$M_1$ | 0.218 (0.02) | 0.194 (0.03) | 0.213 (0.02) | 0.128 (0.04) | 0.223 (0.02) | 0.209 (0.01) | 0.250 (0.03) | 0.204 (0.01) |
| ASM NLf/JawLg | 0.199 (0.02) | 0.158 (0.04) | 0.197 (<0.01) | 0.150 (0.03) | 0.218 (0.03) | 0.168 (0.03) | 0.205 (0.03) | 0.153 (0.02) |
| ASM NLf/Cond$M_1$ | 0.294 (0.03) | 0.226 (0.05) | 0.287 (0.01) | 0.220 (0.05) | 0.314 (0.05) | 0.238 (0.05) | 0.294 (0.04) | 0.215 (0.02) |
| Pinnation (°) | 8.22 (2.8) | 7.45 (2.6) | 13.36 (2.8) | 20.79 (5.8) | 12.19 (1.2) | 15.42 (2.9) | 15.52 (2.8) | 12.63 (2.9) |
| *Temporalis (TM)* | | | | | | | | |
| PCSA$^{0.5}$/JawLg | 0.035 (0.01) | 0.036 (<0.01) | 0.034 (<0.01) | 0.041 (0.01) | 0.029 (0.02) | 0.044 (<0.01) | 0.041 (<0.01) | 0.036 (<0.01) |
| PCSA$^{0.5}$/Cond$M_1$ | 0.051 (0.01) | 0.051 (0.01) | 0.050 (0.01) | 0.059 (0.01) | 0.041 (0.02) | 0.062 (0.01) | 0.059 (<0.01) | 0.050 (0.01) |
| Weight$^{0.33}$/JawLg | 0.030 (<0.01) | 0.029 (<0.01) | 0.032 (0.01) | 0.031 (<0.01) | 0.035 (<0.01) | 0.033 (<0.01) | 0.036 (<0.01) | 0.030 (<0.01) |
| Weight$^{0.33}$/Cond$M_1$ | 0.045 (0.01) | 0.041 (<0.01) | 0.047 (0.01) | 0.045 (<0.01) | 0.050 (<0.01) | 0.047 (0.01) | 0.053 (<0.01) | 0.042 (<0.01) |
| TM NLf/JawLg | 0.228 (0.05) | 0.185 (0.03) | 0.285 (0.09) | 0.181 (0.05) | 0.276 (0.03) | 0.210 (0.03) | 0.264 (0.03) | 0.195 (0.03) |
| TM NLf/Cond$M_1$ | 0.338 (0.09) | 0.264 (0.04) | 0.413 (0.11) | 0.266 (0.09) | 0.393 (0.04) | 0.296 (0.04) | 0.380 (0.05) | 0.274 (0.04) |
| Pinnation (°) | 5.75 (1.3) | 6.77 (2.3) | 8.69 (2.9) | 8.91 (5.5) | 6.23 (1.6) | 13.02 (4.5) | 9.59 (1.9) | 9.93 (1.7) |

**TABLE 5. Results of significance tests for relative differences in superficial masseter and temporalis fiber architecture between species (Predictions 1–3)[a]**

| | Prediction | *Papio anubis* | *Macaca mulatta* | *Macaca fascicularis* |
|---|---|---|---|---|
| *A. Males* | | | | |
| Muscle measurements | | | | |
| Superficial masseter (SM) | | | | |
| PCSA$^{0.5}$/JawLg | *C. atys* > | NS/0.0707 | NS/NS | NS/NS |
| PCSA$^{0.5}$/Cond$M_1$ | *C. atys* > | NS/0.0707 | NS/NS | NS/NS |
| Weight$^{0.33}$/JawLg | *C. atys* > | NS/NS | NS/NS | NS/NS |
| Weight$^{0.33}$/Cond$M_1$ | *C. atys* > | NS/NS | NS/NS | NS/NS |
| SM NLf/JawLg | *C. atys* = | NS/– | NS/– | –/**0.0176**[b] |
| ASM NLf/JawLg | *C. atys* = | NS/– | NS/– | NS/– |
| SM NLf/Cond$M_1$ | *C. atys* = | NS/– | NS/– | –/0.0679[b] |
| ASM NLf/Cond$M_1$ | *C. atys* = | NS/– | NS/– | NS/– |
| Pinnation angle (°) | *C. atys* = | –/**0.0389**[b] | –/**0.0285**[b] | –/**0.0106**[b] |
| Temporalis (TM) | | | | |
| PCSA$^{0.5}$/JawLg | *C. atys* > | NS/NS | NS/NS | NS/**0.0285** |
| PCSA$^{0.5}$/Cond$M_1$ | *C. atys* > | NS/NS | NS/NS | NS/NS |
| Weight$^{0.33}$/JawLg | *C. atys* > | NS/NS | NS/**0.0330** | NS/**0.0176** |
| Weight$^{0.33}$/Cond$M_1$ | *C. atys* > | NS/NS | NS/NS | NS/0.0679 |
| TM NLf/JawLg | *C. atys* = | NS/– | –/0.0881[b] | NS/– |
| TM NLf/Cond$M_1$ | *C. atys* = | NS/– | –/0.0881[b] | NS/– |
| Pinnation angle (°) | *C. atys* = | –/0.0707[b] | NS/– | –/**0.0176**[b] |
| *B. Females*. | | | | |
| Superficial masseter (SM) | | | | |
| PCSA$^{0.5}$/JawLg | *C. atys* > | NS/0.0201 | NS/0.0707 | 0.0446/– |
| PCSA$^{0.5}$/Cond$M_1$ | *C. atys* > | NS/0.0201 | NS/NS | 0.0446/– |
| Weight$^{0.33}$/JawLg | *C. atys* > | NS/NS | NS/**0.0330** | NS/NS |
| Weight$^{0.33}$/Cond$M_1$ | *C. atys* > | NS/NS | NS/NS | NS/NS |
| SM NLf/JawLg | *C. atys* = | –/0.0389[c] | NS/– | NS/– |
| ASM NLf/JawLg | *C. atys* = | NS/– | NS/– | NS/– |
| SM NLf/Cond$M_1$ | *C. atys* = | –/0.0707[c] | NS/– | NS/– |
| ASM NLf/Cond$M_1$ | *C. atys* = | NS/– | NS/– | NS/– |
| Pinnation angle (°) | *C. atys* = | –/0.0201[b] | NS/**0.0105**[b] | –/**0.0285**[b] |
| Temporalis (TM) | | | | |
| PCSA$^{0.5}$/JawLg | *C. atys* > | NS/NS | NS/0.0707 | NS/NS |
| PCSA$^{0.5}$/Cond$M_1$ | *C. atys* > | NS/NS | NS/0.0707 | NS/NS |
| Weight$^{0.33}$/JawLg | *C. atys* > | NS/NS | NS/0.0881 | NS/NS |
| Weight$^{0.33}$/Cond$M_1$ | *C. atys* > | NS/NS | NS/0.0881 | NS/NS |
| TM NLf/JawLg | *C. atys* = | NS/– | NS/– | NS/– |
| TM NLf/Cond$M_1$ | *C. atys* = | NS/– | NS/– | NS/– |
| Pinnation angle (°) | *C. atys* = | NS/– | –/**0.0105**[b] | –/0.0446[b] |

[a]We indicate a predicted difference relative to the hard-object feeder, *C. atys*. The first entry is the *P*-value from a one-tailed Mann–Whitney *U*-test of an architectural prediction between *C. atys* and the non-hard-object feeding species for that pairwise comparison. The second entry is the result of a two-tailed Mann–Whitney *U*-test for an architectural difference between the two species. We only performed two-tailed tests if the one-tailed test resulted in no statistical difference between the two species for the prediction. A significant result for the two-tailed test indicates a difference between the two species. Bold *P*-values signify a significant difference ($\alpha = 0.05$) following the sequential Bonferroni correction (Rice, 1989). *P*-values that are not bold indicate a *P*-value <0.05 but not significant following the Bonferroni adjustment. *P*-values that are underlined indicate a trend toward significance ($0.05 < P < 1.0$). NS signifies no statistical difference between the two species.
[b]For these two-tailed Mann–Whitney *U*-tests, *C. atys* is relatively smaller in comparison with other species.
[c]For these two-tailed Mann–Whitney *U*-tests, *C. atys* is relatively larger in comparison with other species.

differences in absolute or relative jaw-adductor fiber architecture or leverage. McGraw et al. (2011) note that male *C. atys* engage in more incisal and postcanine bites of stiff objects for a given ingestive event compared to females. They hypothesize that the relatively greater time investment of males compared with females[6] may be accounted for by their relatively poor leverage linked to functional tradeoffs for relatively larger gapes and canine displays. The possibility that females, compared with males, ingest and crush seeds that are less mechanically challenging may also play a role in this differential investment (Geissler et al., 2017). While we find that males trend toward having relatively longer anterior superficial masseter fibers compared with females, they do not exhibit clear differences in relative PCSA, muscle mass or muscle leverage that might underlie these sex differences in biting frequency. Future behavioral data are needed to determine if males and females differ in terms of ingested seed size and/or where the sexes tend to place objects along the postcanine toothrow. These data will be informative as to whether males are stretching their jaw adductors further during feeding and thereby diminishing their force-generating capacity because their muscles are operating on a less advantageous portion of the length-tension curve.

[6]Average number of postcanine crushes per 5-min focal period (McGraw et al., 2011).

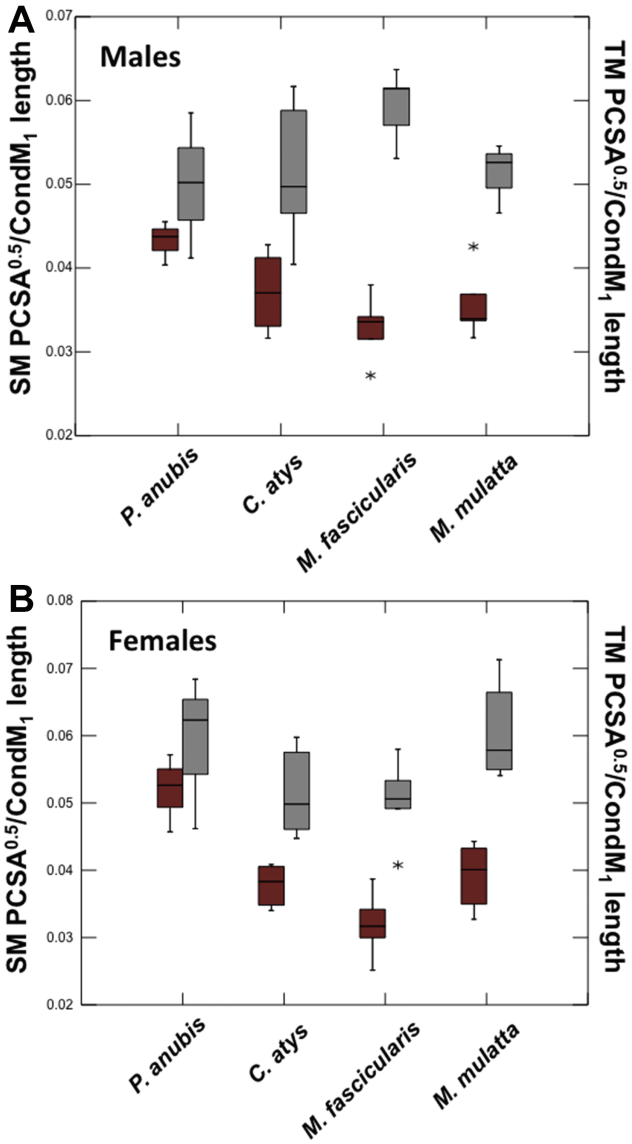


Fig. 3. Box plot of differences in superficial masseter (SM; burgundy) and temporalis muscle (TM; grey) PCSAs relative to condyle-$M_1$ length (Cond$M_1$) for (**A**) males and (**B**) females. Contrary to predictions, *C. atys* do not have the relatively largest jaw-adductor PCSAs compared to other papionin species. Results in Table 5 show a similar pattern relative to jaw length.

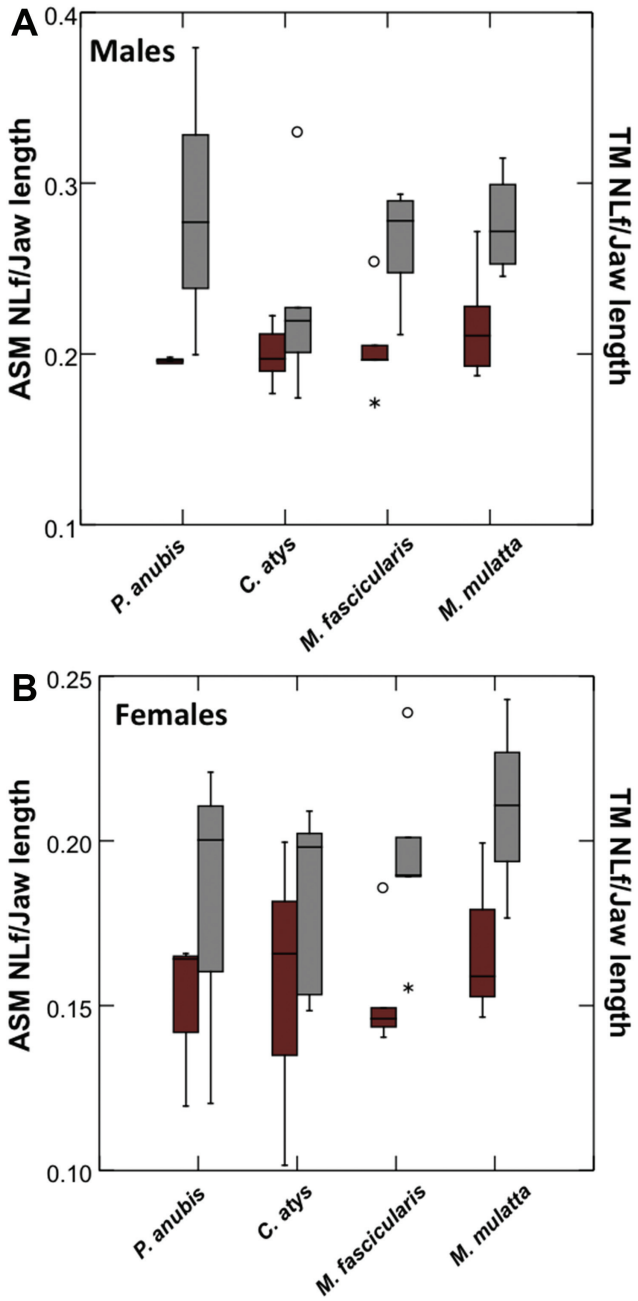


Fig. 4. Box plot of differences in normalized fiber length for the anterior superficial masseter (ASM NLf; burgundy) and temporalis muscle (TM; grey) relative to jaw length in (**A**) males and (**B**) females. Our prediction that *C. atys* have relative jaw-muscle fiber lengths similar to other papionins is supported only for ASM NLf. *Cercocebus atys* males trend toward relatively shorter TM fibers compared with *M. mulatta*. Results in Table 5 further show that male *C. atys* have significantly shorter superficial masseter (SM) fibers relative to jaw length, and trend toward shorter SM fibers relative to condyle-$M_1$ length, compared with male *M. fascicularis*, and female *C. atys* trend toward relatively longer SM fibers compared with female *Papio*.

## Sooty Mangabey Fiber Architecture and Leverage Are Not Consistently Structured to Maximize Bite Force Relative to Other Papionins

Contrary to our predictions, sooty mangabeys generally have the relatively smallest jaw-adductor PCSAs in our sample[7] (Tables 4 and 5; Fig. 3). In fact, *Papio* stand out morphologically as having a markedly relatively enlarged superficial masseter PCSA (Fig. 3). Sooty mangabeys do not mirror hard-object feeding tufted capuchins, which demonstrate a relative increase in jaw-adductor PCSA compared to untufted capuchins (Taylor and Vinyard, 2009). Sooty mangabeys do have enlarged postcanine tooth areas, which have been adaptively

[7]Estimates of total jaw-adductor PCSA (the sum of the superficial and deep masseter, temporalis and medial pterygoid muscles) faithfully track our results based on the superficial masseter and temporalis muscles (Supporting Information). Our limited sample sizes for *Papio* and macaques preclude statistical testing of total jaw-adductor PCSAs between species.

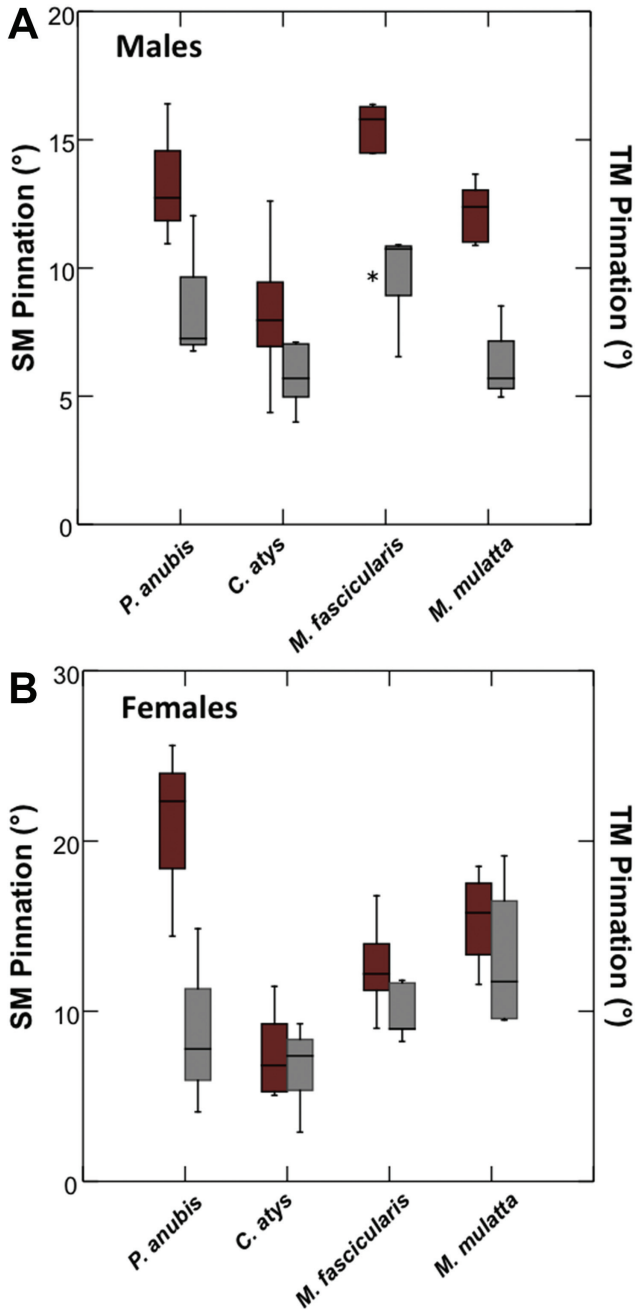


Fig. 5. Box plot of differences in pinnation angles (degrees) for the superficial masseter (SM; burgundy) and temporalis (TM; grey) in (**A**) males and (**B**) females. Contrary to predictions, both *C. atys* males and females have significantly smaller jaw muscle pinnation angles compared to other papionins (see also Table 5).

linked to facilitating crushing of hard objects (Fleagle and McGraw, 1999, 2002). However, the absence of relatively enlarged jaw adductor PCSAs suggests that evolutionary expansion of cheek tooth surface areas has occurred without concomitant increases in muscle and bite force. The behavioral implication of this disconnect supports the hypothesis that tooth expansion and thick enamel are related to repetitive loading and tooth longevity, rather than the evolution of relatively larger bite forces in sooty mangabeys.

We further predicted that sooty mangabeys would show increased bite force through improved muscle leverage. Our prediction is potentially supported only in comparison to *Papio*, where sooty mangabeys trend toward relatively longer lever arms for the masseter at the incisors and molars (males only), and have significantly relatively longer lever arms for the temporalis at the incisors and molars (females only; Tables 6 and 7). These findings show some support for Singleton's (2005) observation that, relative to cranial size, mangabeys (*Cercocebus* and *Lophocebus*) have shorter palates, longer masseter lever arms, and more posteriorly located molar bite points, compared with baboons. This configuration results in improved masseter mechanical advantage and the potential for increased molar and incisal bite forces. By contrast, Singleton (2005) also found that mangabeys (both *Cercocebus and Lophocebus*) have improved masseter leverage compared to *M. fascicularis*. In contrast with Singleton, and with our own predictions, we found that sooty mangabeys have either similar leverage to other papionins (e.g., superficial masseter lever relative to Cond$M_1$ in females) or relatively shorter superficial masseter and temporalis lever arms compared to both macaque species.

Multiple factors likely contribute to differences between our findings and those of Singleton (2005). First, we compare different species of *Cercocebus* (*C. atys* in our study vs. *C. galeritus* and *C. torquatus* in Singleton's study). Second, Singleton (2005) employed largely wild-shot specimens while our measurements are from captive samples. Third, we employ different estimates of masseter lever arms, bite-point load arms and skull size. Singleton (2005) used palate length and the position of the $M^2$-$M^3$ as bite-point load arm estimates and a Procrustes-based multivariate estimate of skull size incorporating not only facial length and breadth, but many other aspects of cranial size (Singleton, 2002). It seems likely that we converge on similar findings when comparing *Cercocebus* with *P. anubis*, despite differences in samples and measurements, because the strong positive allometry of facial length relative to facial breadth in *P. anubis* exerts a powerful influence on leverage differences. Where facial length is more similar between *Cercocebus* and macaques (Hylander, 2013), we speculate that differences in our moment arm measurements have a larger effect on leverage estimates in our two studies.

Bite force is an important performance variable related to ingestion and mastication and increasing bite force is frequently invoked as an agent for selection acting on masticatory musculoskeletal form (Huber et al., 2005; Herrel et al., 2008, 2016). Indeed, it has been argued that selection favored expanded postcanine tooth surface areas in *Cercocebus* (and *Mandrillus*) to facilitate crushing of hard objects and compensate for the high incidence of tooth wear/loss resulting from large postcanine occlusal forces (Fleagle and McGraw, 1999, 2002; McGraw et al., 2011). As noted above, the relatively enlarged mangabey cheek teeth are contrasted with the absence of musculoskeletal features in *C. atys* that would facilitate relatively large muscle and bite forces in comparison to other papionins that do not specialize on hard foods. We believe that multiple factors may account for the differential evolutionary trajectories of dental versus these musculoskeletal morphologies in sooty mangabeys. First, we acknowledge the potential impact of captivity on musculoskeletal growth and

**TABLE 6. Means and standard deviations (in parentheses) for data on relative leverage/relative muscle position for *Cercocebus atys*, *Papio anubis*, *Macaca mulatta*, and *M. fascicularis***

| | *Cercocebus atys* | | *Papio anubis* | | *Macaca mulatta* | | *Macaca fascicularis* | |
|---|---|---|---|---|---|---|---|---|
| Measurement | Male | Female | Male | Female | Male | Female | Male | Female |
| SMLever/JawLg | 0.52 (0.01) | 0.53 (0.03) | 0.47 (0.03) | 0.46 (0.04) | 0.49 (0.05) | 0.58 (0.02) | 0.48 (0.07) | 0.54 (0.02) |
| SMLever/Cond$M_1$ | 0.76 (0.03) | 0.76 (0.05) | 0.68 (0.05) | 0.67 (0.12) | 0.70 (0.06) | 0.81 (0.02) | 0.69 (0.10) | 0.76 (0.01) |
| SMLever/NI | 0.55 (0.04) | 0.53 (0.02) | 0.64 (0.02) | 0.55 (0.09) | 0.54 (0.07) | 0.49 (0.05) | 0.56 (0.09) | 0.56 (0.05) |
| TMLever/JawLg | 0.40 (0.03) | 0.40 (0.03) | 0.33 (0.02) | 0.34 (0.02) | 0.46 (0.02) | 0.48 (0.01) | 0.46 (0.02) | 0.46 (0.04) |
| TMLever/Cond$M_1$ | 0.58 (0.05) | 0.56 (0.02) | 0.48 (0.05) | 0.50 (0.01) | 0.67 (0.04) | 0.67 (0.01) | 0.66 (0.03) | 0.65 (0.04) |
| TMLever/NI | 0.42 (0.04) | 0.39 (0.04) | 0.47 (0.05) | 0.41 (0.01) | 0.51 (0.03) | 0.41 (0.04) | 0.53 (0.02) | 0.48 (0.05) |
| JawLg/NI | 1.06 (0.07) | 1.01 (0.05) | 1.43 (0.03) | 1.19 (0.10) | 1.11 (0.05) | 0.85 (0.07) | 1.15 (0.05) | 1.03 (0.07) |
| Cond$M_1$/NI | 0.72 (0.06) | 0.70 (0.04) | 0.98 (0.04) | 0.82 (0.01) | 0.78 (0.05) | 0.61 (0.07) | 0.80 (0.05) | 0.73 (0.07) |

**TABLE 7. Results of significance tests for relative differences in muscle position/leverage between species[a]**

| | Prediction | *Papio anubis* | *Macaca mulatta* | *Macaca fascicularis* |
|---|---|---|---|---|
| Muscle position/leverage | | | | |
| *Males* | | | | |
| SMLever/JawLg | *C. atys* > | 0.0194/– | NS/NS | NS/NS |
| SMLever/Cond$M_1$ | *C. atys* > | 0.0194/– | 0.0339/– | 0.0721/– |
| SMLever/NI | *C. atys* > | 0.0228/– | NS/NS | NS/NS |
| TMLever/JawLg | *C. atys* > | **0.0127**/– | NS/**0.0090** | NS/**0.0163** |
| TMLever/Cond$M_1$ | *C. atys* > | 0.0263/– | NS/0.0472 | NS/**0.0283** |
| TMLever/NI | *C. atys* > | NS/NS | NS/**0.0143** | NS/**0.0090** |
| JawLg/NI | *C. atys* > | NS/0.0455 | NS/NS | NS/0.0679 |
| Cond$M_1$/NI | *C. atys* > | NS/0.0455 | NS/NS | NS/0.0446 |
| JawLg | *C. atys* < | **0.0100**/– | NS/NS | NS/NS |
| *Females* | | | | |
| SMLever/JawLg | *C. atys* > | 0.0194/– | NS/**0.0143** | NS/NS |
| SMLever/Cond$M_1$ | *C. atys* > | NS/NS | NS/**0.0143** | NS/NS |
| SMLever/NI | *C. atys* > | NS/NS | NS/NS | NS/NS |
| TMLever/JawLg | *C. atys* > | **0.0127**/– | NS/0.0209 | NS/**0.0163** |
| TMLever/Cond$M_1$ | *C. atys* > | **0.0127**/– | NS/0.0209 | NS/**0.0090** |
| TMLever/NI | *C. atys* > | NS/NS | NS/NS | NS/**0.0163** |
| JawLg/NI | *C. atys* > | NS/**0.0201** | **0.0053**/– | NS/NS |
| Cond$M_1$/NI | *C. atys* > | NS/**0.0201** | **0.0330**/– | NS/NS |
| JawLg | *C. atys* < | **0.0125**/– | NS/**0.0280** | NS/0.0470 |

[a]We indicate a predicted difference relative to the hard-object feeder, *C. atys*. The first entry is the *P*-value from a one-tailed Mann–Whitney *U*-test of a prediction between *C. atys* and the non-hard-object feeding species for that pairwise comparison. The second entry is the result of a two-tailed Mann–Whitney *U*-test for an architectural difference between the two species. We only performed two-tailed tests if the one-tailed test resulted in no statistical difference between the two species for the prediction. A significant result for the two-tailed test indicates a difference between the two species opposite the predicted pattern. Bold *P*-values signify a significant difference ($\alpha = 0.05$) following the sequential Bonferroni correction (Rice, 1989), performed separately for each muscle and for males and females. *P*-values that are not bold indicate a *P*-value $<0.05$ but not significant following the Bonferroni adjustment. *P*-values that are underlined indicate a trend toward significance ($0.05 < P < 1.0$). NS signifies no statistical difference between the two species. Tests for differences in JawLg/NI, Cond$M_1$/NI and JawLg were treated separately.

plasticity in our mangabey sample. Moving beyond this logistical consideration, there are several possible (and non-mutually exclusive) explanations for why *C. atys* do not appear to have the ability to generate relatively large bite forces as expected for hard-object feeders: (1) sooty mangabeys may employ behavioral strategies to minimize the amount of oral processing needed to crush seeds; (2) the bite force needed to crush these seeds may be relatively low (or less than anticipated); and/or (3) feeding on these seeds is not a size-limited behavior.

Primates do employ behaviors that reduce oral processing activities (van Schaik and Knott, 2001; Fragaszy et al., 2004). Behavioral strategies employed by *C. atys* may relate to behavioral selection emphasizing specific seed properties (e.g., Geissler et al., 2017). The use of specific bite locations that minimize required forces could also be a behavioral strategy employed by *C. atys* (McGraw et al., 2011).

The seed casings of *S. gabonensis* are relatively tough (2,000–7,000 J $M^{-2}$) and stiff (>200 MPa). They do fall within the range of, or slightly exceed, the most mechanically challenging items, such as un-popped popcorn kernels or prune pits (Williams et al., 2005), that macaques and baboons have ingested and masticated in laboratory settings (Hylander et al., 1998, 2000, 2005). While these are not natural food items or feeding behaviors, it is clear that captive macaques and baboons are capable of feeding on items of approximately similar material properties as *S. gabonensis*. This comparison is challenged, however, by the obvious geometric (i.e., size and shape)

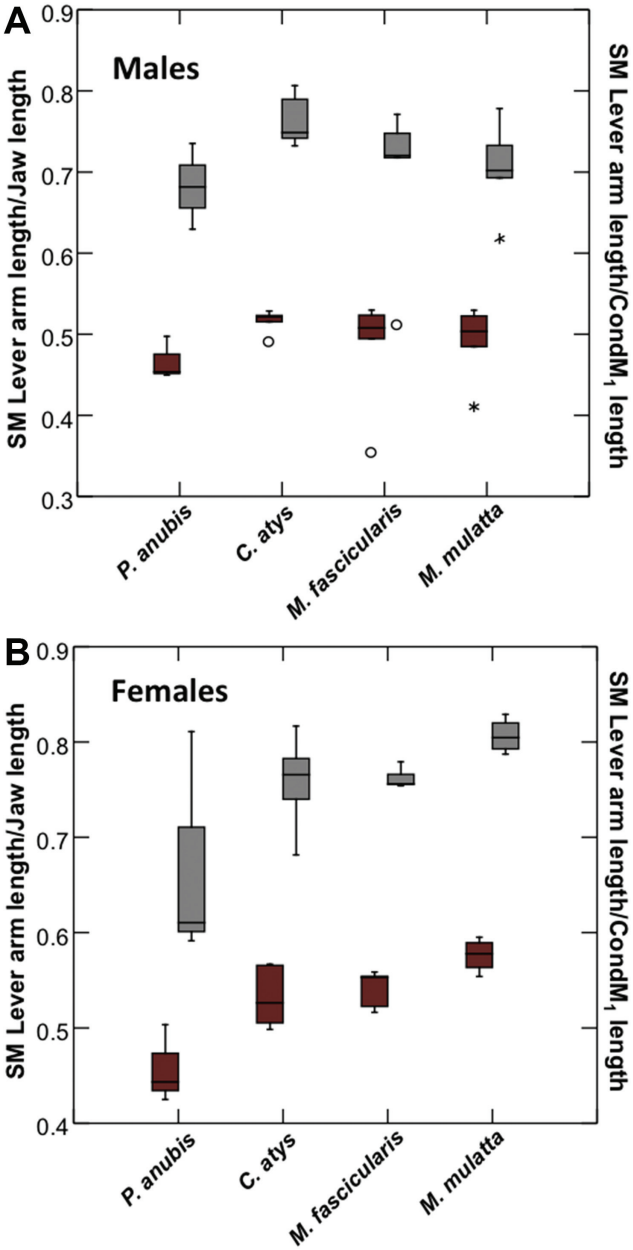


Fig. 6. Box plot of differences in superficial masseter (SM) lever arm length relative to jaw length (burgundy) and relative to condyle-$M_1$ (Cond$M_1$) length (grey) in (**A**) males and (**B**) females. *Cercocebus atys* do not show a consistent pattern of improved leverage for the SM muscle. Results in Table 7 show a similar pattern for the temporalis lever arm.

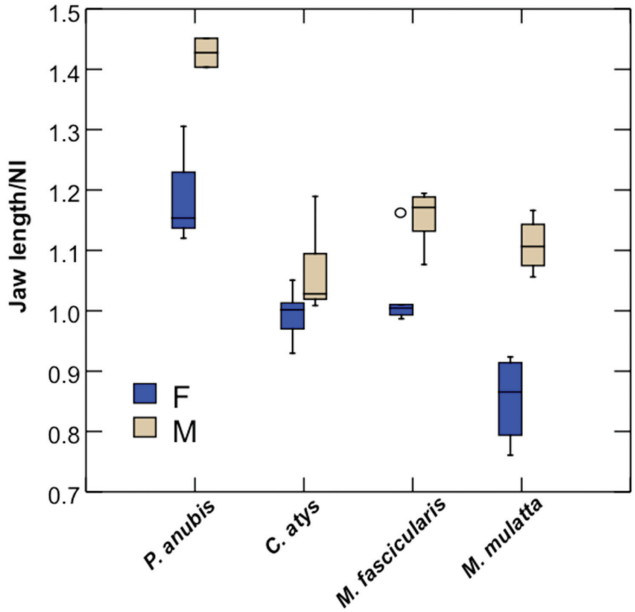


Fig. 7. Box plot of differences in jaw length relative to nasion–inion (NI). Our prediction that *C. atys* have relatively shorter jaws is supported only in comparison with *Papio* (see also Table 7).

differences between *S. gabonensis* and laboratory foods, raising the need for further lab testing to validate this comparison.

The fact that all four species examined here may have the biomechanical abilities to access these foods speaks to the advantages of being a moderately large-bodied primate (Smith and Jungers, 1997). It is possible that above a certain threshold for body size, feeding on mechanically challenging items is made possible without the need for morphological specializations (e.g., Taylor and Vinyard, 2013). We may expect to observe a higher incidence of feeding specializations in smaller-bodied primates such as tree-gouging marmosets (Coimbra-Filho and Mittermeier, 1977; Rosenberger, 1978; Vinyard et al., 2003; Taylor et al., 2009) or potentially tufted capuchins (Kay, 1981; Cole, 1992; Daegling, 1992; Wright, 2005; Taylor and Vinyard, 2009). In other words, larger animals benefit from being big because they can generate absolutely larger bite forces, thereby enabling them to more easily breach mechanically resistant food items that would be more challenging for smaller primates. These benefits of being relatively large may also extend to juveniles through larger sizes at weaning, though we lack the comparative data to address this question. Regardless, the fact that non-adult papionins often feed on the most mechanically challenging food items for a species (McGraw et al., 2011) raises the question of whether papionin diets are actually taxing their performance abilities.

Specific to *C. atys*, it is noteworthy that sooty mangabeys prefer hard seeds throughout ontogeny, beginning after weaning in the youngest and smallest individuals (McGraw et al., 2011). In fact, subadult *C. atys* eat a significantly higher percentage of *S. gabonensis* seeds compared with adults (McGraw et al., 2011). Employing neonatal body weight estimates for *C. atys* (650 and 530 g for males and females, respectively; Smith and Leigh, 1998), and assuming a growth in mass to weaning for *C. atys* of 3.5× (similar to that documented for mandrills; Setchell et al., 2001), we can estimate a mass at weaning for *C. atys* of roughly 2,275 g for males and 1,855 g for females.[8] If adult *C. atys* males weigh

[8]If growth in body mass is accelerated in mandrills compared with mangabeys, as it is in baboons (Leigh and Bernstein, 2006), then 20%–30% would likely overestimate *C. atys* mass at weaning.

11,000 g and adult females 6,200 g (Smith and Jungers, 1997), then this would suggest that juvenile sooty mangabeys process the same mechanically challenging food items as adults at 20%–30% of adult body mass.

We now have 30+ years of ontogenetic data on foraging and feeding behavior for a variety of primates (e.g., Watts, 1984; Pokempner et al., 1995; Tarnaud, 2004; Krakauer, 2005; Stone, 2006; Nowell and Fletcher, 2008; Chalk et al., 2016). Collectively, this body of work is establishing that ontogenetic variation in feeding behavior and diet is minimal, even for species that feed on mechanically challenging foods. Assuming that non-adult sooty mangabeys feed on hard objects of similar material and geometric properties as adults, size does not appear to be the limiting factor for feeding on these mechanically resistant items. Ontogenetic studies of jaw-muscle fiber architecture and mechanical advantage will help us understand how subadults with relatively smaller masticatory apparatuses achieve similar access to these challenging foods. We can speculate that mangabey PCSA scales with negative allometry during growth, which would confer a relative advantage to younger, smaller mangabeys by enabling them to generate relatively larger bite forces compared to adults (e.g., Taylor et al., 2015). Additional insights may also be gleaned from wear patterns of the teeth (e.g., Swan, 2016; Fitton et al., 2016).

One additional consideration is that jaw-muscle fiber type may play a role in facilitating the feeding behavior of *C. atys*. In primates and non-primate mammals, the expression of Type IIM or masticatory myosin has been functionally linked to dietary specializations that require the rapid production of high bite force (Rowlerson et al., 1983; Hoh, 2002). By contrast, Type I fibers are the predominant fiber type observed in the jaw adductors of grazers and ruminants that engage in repetitive chewing (Mascarello et al., 1979; Kang et al., 1994; Hoh et al., 2000). Fatigue of the jaw adductors can occur during submaximal activation (Ström et al., 1994, 1998) and frequent activation at either low or high force can fatigue a motor unit and impair its force-generating capacity (Burke et al., 1973; Nassar-Gentina et al., 1978; Kwa et al., 1995). Type I fibers are highly resistant to fatigue (i.e., they have high endurance) and thus are well suited for repetitive behaviors that involve frequent recruitment (Ström et al., 1994, 1998).

In a preliminary analysis of jaw-adductor fiber types, *C. atys* muscles expressed an abundance of Type I fibers (Taylor et al., 2016), notably more than has been previously observed for macaques (Maxwell et al., 1979; Miller and Farias, 1988) or baboons (Wall et al., 2013). These preliminary findings of a fatigue-resistant fiber phenotype suggest that Type I fibers may be advantageous to sooty mangabeys whose feeding behavior involves frequent crushing of relatively large, hard seeds. Additional data are needed comparing jaw-adductor fiber phenotype of the hard-object feeding sooty mangabey with closely related species that do not specialize on hard objects, and in other hard-object feeders.

## Sooty Mangabey Jaw-Muscle Fiber Architecture and Leverage Maintain Jaw Gape

Jaw-adductor muscle stretch, particularly the anterior superficial masseter fibers, likely constrains maximum jaw gape in mammals (Herring and Herring, 1974). Rather than decrease fiber length and increase pinnation to increase PCSA, we predicted that sooty mangabeys would maintain fiber lengths and pinnation angles comparable to other papionin species so as not to compromise jaw gape. The absence of relative differences in fiber lengths of the anterior superficial masseter and temporalis muscles supports our prediction, and combined with the presence of *less* pinnate fibered muscles in sooty mangabeys, suggests an architectural arrangement of the jaw adductors that favors muscle excursion/stretch. Likewise, the absence of a strong and consistent signal of improved muscle leverage for generating bite force further suggests a configuration that functions to maintain jaw gape in this species.

In primates and other mammals, maximum jaw gape is a performance measure that has been functionally and adaptively linked to feeding and non-feeding oral behaviors in diverse biological roles (Bock and von Wahlert, 1965). Given the importance of feeding on large, hard items, it is certainly possible that sooty mangabeys have musculoskeletal features that preserve gape to facilitate access to preferred nutritional resources (McGraw et al., 2011). For example, increased capacity for gape in cercopithecines compared with colobines has been functionally linked to more vertically directed forces during anterior biting (Ravosa, 1990; Singleton, 2005). This would be advantageous for primates that feed on large-diameter foods or engage in feeding behaviors that involve incisal biting, such as tree gouging (Vinyard et al., 2003). Maintaining features of the masticatory apparatus that facilitate muscle stretch and the generation of relatively wide jaw gapes is thus potentially beneficial to sooty mangabeys. Specifically, increased muscle stretch may improve biting leverage in this species by allowing more posterior bites on the toothrow and by improving muscle position on the length-tension curve during biting of large, hard seeds requiring wide gapes.

The ability to generate relatively wide maximum jaw gapes has also been functionally and adaptively linked to intraspecific sexual selection and to competitive social behaviors that involve canine gape display, particularly in sexually dimorphic taxa (Herring and Herring, 1974; Lucas, 1981; Smith, 1984; Deputte, 1994; Hylander, 2013; Terhune et al., 2015). Relative maximum jaw gape and relative canine height are significantly correlated in catarrhine primates and cercopithecines maintain marked levels of gape dimorphism (Hylander, 2013). Quantitative data on display behavior in primates are surprisingly lacking, but aggressive "yawning" or canine gape displays have been documented to occur more frequently in the wild in males compared with females in both grey-cheeked mangabeys and crab-eating macaques (Deputte, 1994) and aggressive biting by captive sooty mangabeys has been reported (Busse and Gordon, 1983). Terhune et al. (2015) showed that compared to females, male *M. fascicularis* have relatively longer superficial masseter and temporalis fibers, as well as bony features of the skull that reduce muscle stretch and favor gape over muscle and bite force. In the absence of evidence for sex-specific feeding behaviors in *M. fascicularis*, the authors interpreted these results as supporting a functional link between relatively long fibers in males and

improved gape performance as part of a behavioral repertoire that includes agonistic social interactions and intense male–male competition.

This study allows us to expand on our previous findings for *M. fascicularis*. Male sooty mangabeys[9] and *P. anubis* (one-tailed Mann–Whitney *U*-test, $\chi^2 = 3.86$, $P = 0.025$)[10] have relatively longer anterior superficial masseter fibers compared to females. Male *M. mulatta* similarly trend toward relatively longer anterior superficial masseter fibers compared with females (one-tailed Mann–Whitney *U*-test, $\chi^2 = 2.16$, $P = 0.071$). Moreover, despite the potential competing demand to generate relatively large occlusal forces during feeding, sooty mangabeys maintain levels of gape dimorphism (Hylander, 2013) and relative jaw-adductor fiber lengths comparable to *P. anubis* (Table 5). Male *M. fascicularis*, which generate relatively larger maximum jaw gapes in comparison to both male sooty mangabeys and *P. anubis* (Hylander, 2013), also display relatively longer superficial masseter fibers in comparison to males of both species (Table 5 for male sooty mangabeys vs. *M. fascicularis* and *P. anubis*; two-tailed Mann–Whitney *U*-test, $\chi^2 = 5.00$, $P = 0.0253$ for male *M. fascicularis* vs. *P. anubis*). Based on this shared pattern of relatively long fibers across males of four papionin species, we hypothesize that within *C. atys*, and within papionins more broadly, males are prioritizing muscle stretch over bite force to facilitate relatively wide maximum jaw gapes and canine display as a means of communicating social rank and fitness. That males of these four sexually dimorphic Old World monkeys (OWMs) have both relatively longer fibers and relatively wider maximum jaw gapes (Hylander, 2013) compared with female conspecifics strengthens the hypothesis that improved gape performance linked to gape display behavior has been a strong selective influence throughout the masticatory apparatus in this clade (e.g., Leigh et al., 2008).

We acknowledge that our data do not enable us to determine if the exploitation of large, hard objects and/or wide-mouth threat display have been the selective factor(s) favoring relatively long jaw-adductor fibers and muscle stretch in male sooty mangabeys. Likewise, we are currently unable to address the extent to which sex and species differences in relative fiber lengths may be attributed to developmental plasticity, functional adaptation, and/or selection. Ontogenetic and interspecific analyses of sex-specific scaling relationships between jaw-adductor fiber length and correlates of jaw gape in OWMs should shed additional light on the mechanisms underlying this male phenotype. For example, if the ability to generate relatively wide jaw gapes is a selection pressure exerted on males to facilitate canine gape display behavior, we would predict that maximum jaw gape and jaw-adductor fiber length are more strongly and significantly correlated in male compared with female OWMs.

## CONCLUSIONS

Despite evidence that sooty mangabeys are adept at routinely breaching large, hard food items at relatively wide jaw gapes, they appear strikingly unremarkable in jaw-muscle fiber architecture and leverage relative to expectations for a hard-object feeder. In this regard, sooty mangabeys differ from tufted capuchins, which are renowned for their musculoskeletal specializations of the masticatory apparatus (Cole, 1992; Daegling, 1992; Wright, 2005; Taylor and Vinyard, 2009), despite feeding only occasionally on exceptionally challenging items. That both tufted capuchins and sooty mangabeys feed on hard objects and incorporate large gapes and powerful isometric biting along the posterior dentition, yet follow different morphological pathways to achieve similar performances, suggests we are likely to observe multiple solutions to similar functional problems (Alfaro et al., 2005; Wainwright et al., 2005). While this many-to-one mapping of phenotypes to function and performance may promote the evolution of phenotypic diversity (Alfaro et al., 2005), it also complicates functional interpretations of fossil morphologies.

Importantly, macaques, baboons, and mangabeys have served as model species for understanding the evolution of human feeding behavior and diet (De Vore and Washburn, 1963; Jolly, 1970, 2001; Strait et al., 2009; Daegling et al., 2011). Whether ancestral hominins had a masticatory apparatus that facilitated generating and dissipating relatively large occlusal forces, repetitive forces, or both (Daegling et al., 2013; Strait et al., 2013), their relatively high TMJs and relatively short jaws reflect a bony configuration that is clearly not favorable for generating relatively wide maximum jaw gapes (Vinyard et al., 2003). If papionins are indeed prioritizing muscle stretch and gape over bite force, this raises the question of whether Old World monkeys are morphologically suitable extant models for interpreting the feeding behavior and diet of fossil hominins.

## ACKNOWLEDGEMENTS

We gratefully acknowledge the following for providing access to cadaveric specimens: *Cercocebus atys*, Yerkes National Primate Research Center and Kay Lee Summerville; *Macaca mulatta*, New England Regional Primate Research Center, Dr. Michael A. Nader, Department of Physiology and Pharmacology, Wake Forest University School of Medicine, Dr. William L. Hylander, Department of Evolutionary Anthropology, Duke University, and the University of Chicago; *M. fascicularis*, Dr. Michael A. Nader and Dr. William L. Hylander; and *Papio anubis*, Duke University Medical Center and University of Chicago. We thank Guest Editors Adam Hartstone-Rose (AHR), Damiano Marchi, and Sharlene Santana (SS), for inviting us to contribute to this special issue and for the helpful comments provided by AHR and SS. We thank two anonymous reviewers for their comments, which improved the accuracy and clarity of the manuscript.

[9]Based on two-tailed Mann–Whitney *U*-tests, these differences are significant ($P < 0.05$) for the anterior superficial masseter prior to the Bonferroni adjustment, and trend toward significance ($0.05 < P < 1.0$) for the temporalis muscle (Table 3).

[10]These comparisons are all relative to jaw length, which is significantly correlated with maximum jaw gape in catarrhines (Hylander, 2013).

## LITERATURE CITED


Alfaro ME, Bolnick DI, Wainwright PC. 2005. Evolutionary consequence of many-to-one mapping of jaw morphology to mechanics in labrid fishes. Am Nat 165:E140–E154.

Anapol F, Barry K. 1996. Fiber architecture of the extensors of the hindlimb in semiterrestrial and arboreal guenons. Am J Phys Anthropol 99:429–447.

Anapol F, Gray JP. 2003. Fiber architecture of the intrinsic muscles of the shoulder and arm in semiterrestrial and arboreal guenons. Am J Phys Anthropol 122:51–65.

Anapol F, Shahnoor N, Ross CF. 2008. Scaling of reduced physiologic cross-sectional area in primate muscles of mastication. In: Vinyard CJ, Ravosa MJ, Wall C, editors. Primate craniofacial function and biology. New York: Springer. p 201–216.

Barton RA. 1993. Sociospatial mechanisms of feeding competition in female olive baboons, *Papio anubis*. Anim Behav 46:791–802.

Bernstein IS, Gordon TP. 1974. The function of aggression in primate societies: uncontrolled aggression may threaten human survival, but aggression may be vital to the establishment and regulation of primate societies and sociality. Am Sci 62:304–311.

Bernstein I, Williams L, Ramsay M. 1983. The expression of aggression in Old World monkeys. Int J Primatol 4:113–125.

Bock WJ. 1959. Preadaptation and multiple evolutionary pathways. Evolution 13:194–211.

Bock WJ, von Wahlert G. 1965. Adaptation and the form-function complex. Evolution 19:269–299.

Bouvier M. 1986. A biomechanical analysis of mandibular scaling in Old World monkeys. Am J Phys Anthropol 69:473–482.

Burke RE, Levine DN, Tsairis P, Zajac FE. 1973. Physiological types and histochemical profiles in motor units of the cat gastrocnemius. J Physiol 234:723–748.

Burkholder TJ, Lieber RL. 2001. Sarcomere length operating range of vertebrate muscles during movement. J Exp Biol 204:1529–1536.

Busse CD, Gordon TP. 1983. Attacks on neonates by a male mangabey (*Cercocebus atys*). Am J Primatol 5:345–356.

Chalk J, Wright BW, Lucas PW, Schuhmacher KD, Vogel ER, Fragaszy D, Visalberghi E, Izar P, Richmond BG. 2016. Age-related variation in the mechanical properties of foods processed by *Sapajus libidinosus*. Am J Phys Anthropol 159:199–209.

Chalmers NR. 1968. Group composition, ecology and daily activities of free living mangabeys in Uganda. Folia Primatol 8:247–262.

Coimbra-Filho AF, Mittermeier RA, editors. 1977. Tree-gouging, exudate-eating and the "short-tusked" condition in *Callithrix* and *Cebuella*. Washington, DC: Smithsonian Institution press. p 105–115.

Cole TM. 1992. Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. Int J Primatol 23:253–282.

Daegling DJ. 1990. Geometry and biomechanics of hominoid mandibles. PhD dissertation. Stony Brook: State University of New York.

Daegling DJ. 1992. Mandibular morphology and diet in the genus *Cebus*. Int J Primatol 13:545–570.

Daegling DJ, Grine FE. 1991. Compact bone distribution and biomechanics of early hominid mandibles. Am J Phys Anthropol 86: 321–339.

Daegling DJ, Judex S, Ozcivici E, Ravosa MJ, Taylor AB, Grine FE, Teaford MF, Ungar PS. 2013. Viewpoints: feeding mechanics, diet, and dietary adaptations in early hominins. Am J Phys Anthropol 151:356–371.

Daegling DJ, McGraw WS. 2007. Functional morphology of the mangabey mandibular corpus: relationship to dental specializations and feeding behavior. Am J Phys Anthropol 134:50–62.

Daegling DJ, McGraw WS, Ungar PS, Pampush JD, Vick AE, Bitty EA. 2011. Hard object feeding in sooty mangabeys (*Cercocebus atys*) and the interpretation of early hominin feeding ecology. PLOS ONE 6:e23095.

Daegling DJ, McGraw WS, Vick AE, Rapoff AJ, Bitty EA, Paacho R. 2010. Masticatory effort and dietary hardness in sooty mangabeys (*Cercocebus atys*) from Tai Forest, Ivory Coast. Am J Phys Anthropol Suppl 50:90.

De Vore I, Washburn SL. 1963. Baboon ecology and human evolution. In: Howell FC, Bourliere F, editors. African ecology and human evolution. Chicago: Aldine Publishing Co. p 335–367.

Dechow PC, Carlson DS. 1990. Occlusal force and craniofacial biomechanics during growth in rhesus monkeys. Am J Phys Anthropol 83:219–237.

Deputte BL. 1994. Ethological study of yawning in primates. I. Quantitative analysis and study of causation in two species of Old World monkeys (*Cercocebus albigena* and *Macaca fascicularis*). Ethology 98:221–245.

Dominy NJ, Vogel ER, Yeakel JD, Constantino P, Lucas PW. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. Evol Biol 35: 159–175.

Dumont ER, Herrel A. 2003. The effects of gape angle and bite point on bite force in bats. J Exp Biol 206:2117–2123.

Eng CM, Ward SR, Vinyard CJ, Taylor AB. 2009. The morphology of the masticatory apparatus facilitates muscle force production at wide jaw gapes in tree-gouging common marmosets (*Callithrix jacchus*). J Exp Biol 212:4040–4055.

Felder A, Ward SR, Lieber RL. 2005. Sarcomere length measurement permits high resolution normalization of muscle fiber length in architectural studies. J Exp Biol 208:3275–3279.

Fitton LC, Swan KR, Cobb SN. 2016. The effects of dental wear on hard object food breakdown. Anat Rec 299: 150.

Fleagle JG, McGraw WS. 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. Proc Natl Acad Sci USA 96:1157–1161.

Fleagle JG, McGraw WS. 2002. Skeletal and dental morphology of African papionins: unmasking a cryptic clade. J Hum Evol 42: 267–292.

Fragaszy D, Izar P, Visalberghi E, Ottoni EB, de Oliveira MG. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. Am J Primatol 64:359–366.

Garland T, Adolph SC. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiol Zool 67:797–828.

Gaspard M, Laison F, Mailland M. 1973. Organisation architecturale et texture du muscle masséter chez les Primates et l'homme. J Biol Buccale 1:7–20.

Geissler E, Daegling DJ, Plovadore TA, McGraw WS. 2017. Female sooty mangabeys (*Cercocebus atys*) select softer seeds than males. Am J Phys Anthropol Suppl 162:192.

Grine FE. 1981. Trophic differences between 'gracile' and 'robust' australopithecines: a scanning electron microscope analysis of occlusal events. S Afr J Sci 77:203–230.

Haddow A. 1952. Field and laboratory studies on an African monkey, *Cercopithecus ascanius schmidti* Matschie. Proc Zool Soc Lond 122:297–394.

Harris EE, Disotell R. 1998. Nuclear gene trees and the phylogenetic relationships of mangabeys (Primates: Papionini). Mol Biol Evol 15:892–900.

Herrel A, De Smet A, Aguirre LF, Aerts P. 2008. Morphological and mechanical determinants of bite force in bats: do muscles matter?. J Exp Biol 211:86–91.

Herrell A, Lopez-Darias M, Vanhooydonck B, Cornette R, Kohlsdorf T, Brandt R. 2016. Do adult phenotypes reflect selection on juvenile performance? A comparative study on performance and morphology in lizards. Integr Comp Biol 56:469–478.

Herring SW, Grimm AF, Grimm BR. 1984. Regulation of sarcomere number in skeletal muscle: a comparison of hypotheses. Muscle Nerve 7:161–173.

Herring SW, Herring SE. 1974. The superficial masseter and gape in mammals. Am Nat 108:561–576.

Hoh JFY. 2002. 'Superfast' or masticatory myosin and the evolution of jaw-closing muscles of vertebrates. J Exp Biol 205:2203–2210.

Hoh JFY, Kim Y, Sieber LG, Zhong W, Lucas A. 2000. Jaw-closing muscles of kangaroos express alpha cardiac myosin heavy chain. J Muscle Res Cell Motil 21:673–680.

Huber DR, Eason TR, Hueter RE, Motta PJ. 2005. Analysis of the bite force and mechanical design of the feeding mechanism of the

durophagous horn shark *Heterodontus francisci*. J Exp Biol 208: 3553–3571.

Huxley HE. 1972. Molecular basis of contraction in cross-striated muscles. In: Bourne GH, editor. The structure and function of muscle. 2nd ed. New York: Academic Press. p 301–387.

Hylander WL. 1985. Mandibular function and biomechanical stress and scaling. Am Zool 25:315–330.

Hylander WL. 1988. Implications of in vivo experiments for interpreting the functional significance of "robust" australopithecine jaws. In: Grine FE, editor. Evolutionary history of the "robust" australopithecines. New York: Aldine de Gruyter. p 55–83.

Hylander WL. 2013. Functional links between canine height and jaw gape in catarrhines with special reference to early hominins. Am J Phys Anthropol 150:247–259.

Hylander WL, Ravosa MJ, Ross CF, Johnson KR. 1998. Mandibular corpus strain in primates: further evidence for a functional link between symphyseal fusion and jaw-adductor muscle force. Am J Phys Anthropol 107:257–271.

Hylander WL, Ravosa MJ, Ross CF, Wall CE, Johnson KR. 2000. Symphyseal fusion and jaw-adductor muscle force: an EMG study. Am J Phys Anthropol 112:469–492.

Hylander WL, Wall CE, Vinyard CJ, Ross CF, Ravosa MJ, Williams SH, Johnson KR. 2005. Temporalis function in anthropoids and strepsirrhines: an EMG study. Am J Phys Anthropol 128:35–56.

Iriarte-Diaz J, Terhune EC, Taylor AB, Ross CF. 2017. Functional correlates of the position of the axis of rotation of the mandible during chewing in non-human primates. Zoology 124:106–118.

Jeffery NS, Stephenson RS, Gallagher JA, Jarvis JC, Cox PG. 2011. Micro-computed tomography with iodine staining resolves the arrangement of muscle fibres. J Biomech 44:189–192.

Jolly CJ. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5:5–26.

Jolly CJ. 2001. A proper study for mankind: anaologies from the papionin monkeys and their implications for human evolution. Yrbk Phys Anthropol 44:177–204.

Jones C, Sabater Pi J. 1968. Comparative ecology of *Cercocebus agibena* (Gray) and *Cercocebus torquatus* (Kerr) in Rio Muni, West Africa. Folia Primatol 9:99–113.

Kang LHD, Hughes S, Pettigrew JD, Hoh JFY. 1994. Jaw-specific myosin heavy chain gene expression in sheep, dog, monkey, flying fox and microbat jaw-closing muscles. Basic Appl Myol 4: 381–392.

Kay RF. 1981. The nut-crackers—a new theory of the adaptations of the ramapithecinae. Am J Phys Anthropol 55:141–151.

Krakauer, EB. 2005. Development of aye-aye (*Daubentonia madagascariensis*) foraging skills: independent exploration and social learning. PhD dissertation. Duke University, Durham, NC.

Kunz BK, Linsenmair KE. 2006. The disregarded West: diet and behavioural ecology of Olive baboons in the Ivory Coast. Folia Primatol 79:31–51.

Kupczik K, Stark H, Mundry R, Neininger FT, Heidlauf T, Röhrle O. 2015. Reconstruction of muscle fascicle archigtecture from iodine-enhanced microCT images: a combined texture mapping and streamline approach. J Theor Biol 382:34–43.

Kwa SH, Weijs WA, Jüch PJ. 1995. Contraction characteristics and myosin heavy chain composition of rabbit masseter motor units. J Neurophysiol 73:538–549.

Lauder GV. 1981. Form and function: structural analysis in evolutionary morphology. Paleobiology 7:430–442.

Lauder GV. 1996. The argument from design. In: Rose MR, Lauder GV, editors. Adaptation. San Diego: Academic Press. p 55–91.

Leigh SR, Bernstein RM. 2006. Ontogeny, life history, and maternal investment in baboons. In: Swedell L, Leigh SR, editors. Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives. New York: Springer. p. 225–255.

Leigh SR, Setchell JM, Charpentier M, Knapp LA, Wickings EJ. 2008. Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). J Hum Evol 55:75–85.

Lieber RL, Yeh Y, Baskin RJ. 1984. Sarcomere length determination using laser diffraction. Effect of beam and fiber diameter. Biophys J 45:1007–1016.

Loeb GE, Gans C. 1986. Electromyography for experimentalists. Chicago: University of Chicago Press.

Lucas PW. 1981. An analysis of canine size and jaw shape in some Old and New World non-human primates. J Zool Lond 195:437–448.

Lucas PW, Corlett RT. 1991. Relationship between the diet of *Macaca fascicularis* and forest phenology. Folia Primatol 57:201–215.

Lucas PW, Turner IM, Dominy NJ, Yamashita N. 2000. Mechanical defenses to herbivory. Ann Bot 86:913–920.

Mascarello F, Aureli G, Veggetti A. 1979. Muscoli masticatori: determinazione istochimica dei tipi di fibre muscolari. Quaad Anat Prat 35:193–213.

Maxwell LC, Carlson DS, McNamara Jr JA, Faulkner JA. 1979. Histochemical characteristics of the masseter and temporalis muscles of the Rhesus monkey (*Macaca mulatta*). Anat Rec 193: 389–402.

McGraw WS, Daegling DJ. 2012. Primate feeding and foraging: integrating studies of behavior and morphology. Annu Rev Anthropol 41:203–219.

McGraw WS, Pampush JD, Daegling DJ. 2012. Enamel thickness and durophagy in mangabeys revisited. Am J Phys Anthrop 147: 326–333.

McGraw WS, Vick AE, Daegling DJ. 2011. Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. Am J Phys Anthrop 144: 140–153.

McGraw WS, Vick AE, Daegling DJ. 2014. Dietary variation and food hardness in sooty mangabeys (*Cercocebus atys*): implications for fall back foods and dental adaptation. Am J Phys Anthrop 154:413–423.

Miller AJ, Farias M. 1988. Histochemical and electromyographic analysis of craniomandibular muscles in the Rhesus monkey, *Macaca mulatta*. J Oral Maxillofac Surg 46:767–776.

Murphy RA, Beardsley AC. 1974. Mechanical properties of the cat soleus muscle in situ. Am J Physiol 227:1008–1013.

Nassar-Gentina V, Passonneau JV, Vergara JL, Rapoport SI. 1978. Metabolic correlates of fatigue and of recovery from fatigue in single frog muscle fibers. J Gen Physiol 72:593–606.

Nowell A, Fletcher A. 2008. The development of feeding behavior in wild western lowland gorillas (*Gorilla gorilla gorilla*). Behaviour 145:171–193.

Nystrom P. 1992. Mating success of hamadryas, anubis and hybrid male baboons in a "mixed" social group in the Awash National Park, Ethiopia. PhD dissertation. Washington University, St. Louis.

Pokempner A, Teaford MF, Pastor RF, Noble VE, Burnell CL, Glander KE. 1995. Deciduous dental microwear in *Alouatta palliata*. Am J Phys Anthropol Suppl 20:173.

Powell PL, Roy RR, Kanim P, Bello MA, Edgerton VR. 1984. Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs. J Appl Physiol 57:1715–1721.

Rak Y. 2014. The australopithecine face. New York: Academic Press.

Ravosa MJ. 1990. Functional assessment of subfamily variation in maxillomandibular morphology among Old World monkeys. Am J Phys Anthropol 82:199–212.

Ray TJ, McGraw WS, Sun Z, Jeon M, Johnson T, Cheffins K, Daegling DJ, Kim D-G. 2015. Mandibular bone mineral density variation in three West African cercopithecoid monkey species: associations with diet and feeding behavior. Arch Oral Biol 60: 1714–1720.

Rice WR. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Rosenberger AL. 1978. Loss of incisor enamel in marmosets. J Mammal 59:207–208.

Ross CF, Iriarte-Diaz J, Reed DA, Stewart TA, Taylor AB. 2016. In vivo bone strain in the mandibular corpus of *Sapajus* during a range of oral food processing behaviors. J Hum Evol 98:36–65.

Rowlerson A, Mascarello F, Veggetti A, Carpene E. 1983. The fibre-type composition of the first branchial arch muscles in Carnivora and Primates. J Muscle Res Cell Motil 4:443–472.

Santana SE. 2016. Quantifying the effect of gape and morphology on bite force: biomechanical modeling and in vivo measurements in bats. Funct Ecol 30:557–565.

Setchell JM, Lee PC, Wickings EJ, Dixson AF. 2001. Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). Am J Phys Anthropol 115:349–360.

Singleton M. 2002. Patterns of cranial shape variation in the Papionini (Primates: Cercopithecinae). J Hum Evol 42:547–578.

Singleton M. 2004. Geometric morphometric analysis of functional divergence in mangabey facial form. J Anthropol Sci 82:29–46.

Singleton M. 2005. Functional shape variation in the cercopithecine masticatory complex. In: Slice DE, editor. Modern morphometrics in physical anthropology. New York: Kluwer Academic/Plenum Publishers. p 319–348.

Smith RJ. 1984. Comparative functional morphology of maximum mandibular opening (gape) in primates. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum Press. p. 231–255.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. J Hum Evol 32:523–559.

Smith RJ, Leigh SR. 1998. Sexual dimorphism in primate neonatal body mass. J Hum Evol 34:173–201.

Spencer MA, Demes B. 1993. Biomechanical analysis of masticatory system configuration in Neandertal and Inuits. Am J Phys Anthropol 91:1–20.

Stone AI. 2006. Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (*Saimiri sciureus*). Ethology 113:782–792.

Strait DS, Constantino P, Lucas P, Richmond BG, Spencer MA, Dechow PC, Ross CF, Grosse IR, Wright BW, Wood BA, et al. 2013. Viewpoints: diet and dietary adaptations in early hominins: the hard food perspective. Am J Phys Anthropol 151:339–355.

Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, Lucas PW, Spencer MA, Schrein C, Dechow PC, Ross CF, et al. 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. Proc Natl Acad Sci USA 106:2124–2129.

Strasser E, Delson E. 1987. Cladistic analysis of cercopithecid relationships. J Hum Evol 16:81–99.

Ström D, Holm S, Möller Å. 1994. Fatigue development during electrical stimulation in the masseter muscle of rhesus monkeys (*Macaca mulatta*). Arch Oral Biol 39:417–423.

Ström D, Holm S, Möller Å. 1998. Frequency-dependent fatigue development during electrical stimulation in the masseter muscle of pigtail monkeys. J Orofac Pain 12:279–286.

Sussman RW, Tattersall I. 1981. Behavior and ecology of *Macaca fascicularis* in Mauritius: a preliminary study. Primates 22:192–205.

Swan KR. 2016. Dental morphology and mechanical efficiency during development in a hard object feeding primate (*Cercocebus atys*). PhD dissertation. The University of Hull and The University of York.

Tappen NC. 1960. Problems of distribution and adaptation of the African monkeys. Curr Anthropol 1:91–120.

Tarnaud L. 2004. Ontogeny of feeding behavior of *Eulemur fulvus* in the dry forest of Mayotte. Int J Primatol 25:803–824.

Taylor AB, Eng CM, Anapol FC, Vinyard CJ. 2009. The functional correlates of jaw-muscle fiber architecture in tree-gouging and nongouging callitrichid monkeys. Am J Phys Anthropol 139:353–367.

Taylor AB, Terhune CE, Hylander WL, Vinyard CJ. 2014. In vitro sarcomere-length operation range of the masseter and temporalis muscles in *Macaca fascicularis*. Am J Phys Anthropol Suppl 58: 252.

Taylor AB, Toler M, Wall CE. 2016. Fiber phenotype of the jaw adductors in the hard-object feeding sooty mangabey (*Cercocebus atys*). Am J Phys Anthropol Suppl 62:311.

Taylor AB, Vinyard CJ. 2004. Comparative analysis of masseter fiber architecture in tree-gouging (*Callithrix jacchus*) and nongouging (*Saguinus oedipus*) callitrichids. J Morphol 261:276–285.

Taylor AB, Vinyard CJ. 2008. The relationship between jaw-muscle architecture and feeding behavior in primates: tree-gouging and nongouging gummivorous callitrichids as a natural experiment. In: Vinyard CJ, Ravosa MJ, Wall CE, editors. Primate craniofacial function and biology. New York: Springer. p 241–262.

Taylor AB, Vinyard CJ. 2009. Jaw-muscle fiber architecture in tufted capuchins favors generating relatively large muscle forces without compromising jaw gape. J Hum Evol 57:710–720.

Taylor AB, Vinyard CJ. 2013. The relationships among jaw-muscle fiber architecture, jaw morphology and feeding behavior in extant apes and modern humans. Am J Phys Anthropol 151:120–134.

Taylor AB, Yuan T, Ross CF, Vinyard CJ. 2015. Jaw-muscle force and excursion scale with negative allometry in platyrrhine primates. Am J Phys Anthropol 158:242–256.

Terborgh J. 1983. Five new world primates. A study in comparative ecology. New Jersey: Princeton University Press. 260 p.

Terhune CE, Hylander WL, Vinyard CJ, Taylor AB. 2015. Jaw-muscle architecture and mandibular morphology influence relative maximum jaw gapes in the sexually dimorphic *Macaca fascicularis*. J Hum Evol 82:145–158.

van Schaik CP, Knott C. 2001. Geographic variation in tool use on *Neesia* fruits in orangutans. Am J Phys Anthropol 114:331–342.

van der Klaauw CJ. 1946. Cerebral skull and facial skull: a contribution to the knowledge of skull-structure. Arch Neerl Zool 7:16–37.

Vinyard CJ, Wall CE, Williams SH, Hylander WL. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. Am J Phys Anthropol 120:153–170.

Wainwright PC, Alfaro ME, Bolnick DI, Hulsey CD. 2005. Many-to-one mapping of form to function: a general principle in organismal design?. Integr Comp Biol 45:256–262.

Walker SM, Schrodt GR. 1974. I segment lengths and thin filament periods in skeletal muscle fibers of the Rhesus monkey and the human. Anat Rec A Discov Mol Cell Evol Biol 178:63–81.

Wall CE, Briggs MM, Huq E, Hylander WL, Schachat F. 2013. Regional variation in IIM myosin heavy chain expression in the temporalis muscle of female and male baboons (*Papio anubis*). Arch Oral Biol 58:435–443.

Ward SR, Hentzen ER, Smallwood LH, Eastlack RK, Burns KA, Fithian DC, Fridén J, Lieber RL. 2006. Rotator cuff muscle architecture. Clin Orthop Rel Res 448:157–163.

Watts DP. 1984. Composition and variability of mountain gorilla diets in the central Virungas. Am J Primatol 7:323–356.

Wedeen VJ, Reese TG, Napadow VJ, Gilbert RJ. 2001. Demonstration of primary and secondary muscle fiber architecture of the bovine tongue by diffusion tensor magnetic resonance imaging. Biophys J 80:1024–1028.

Wheatley BP. 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In: Lindburg D, editor. The macaques: studies in ecology, behavior and evolution. New York: Van Nostrand Reinhold. p 215–246.

Williams SH, Peiffer E, Ford S. 2009. Gape and bite force in the rodents *Onychomys leucogaster* and *Peromyscus maniculatus*: does jaw-muscle anatomy predict performance?. J Morphol 270:1338–1347.

Williams SH, Wright BW, Truong VD, Daubert CR, Vinyard CJ. 2005. Mechanical properties of foods used in experimental studies of primate masticatory function. Am J Primatol 67:329–346.

Wright BW. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. J Hum Evol 48:473–492.

Yeager CP. 1996. Feeding ecology of the long-tailed macaque (*Macaca fascicularis*) in Kalimantan Tengah, Indonesia. Int J Primatol 17:51–62.

Zar JH. 1999. Biostatistical analysis. Upper Saddle River: Prentice Hall.