Chapter 12

The Relationship Between Jaw-Muscle Architecture and Feeding Behavior in Primates: Tree-Gouging and Nongouging Gummivorous Callitrichids as a Natural Experiment

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Contents

12.1 Introduction

Feeding behavior and diet are among the most important factors underlying variation in primate craniofacial morphology. Thus, primate biologists interested in craniofacial evolution have directed a great deal of effort toward understanding the function and evolution of the primate masticatory apparatus. Teeth, because they are

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both in direct contact with foods and comprise a significant portion of the primate fossil record, have been well studied from functional perspectives (e.g., Mills, 1963; Kay, 1975, 1978; Hershkovitz, 1977; Szalay and Delson, 1979; Gingerich et al., 1982; Lucas, 1982, 2004; Oxnard, 1987; Plavcan, 1993; Kay and Williams, 1994; Ungar, 1998; Jernvall and Jung, 2000; Teaford et al., 2000; McCollum and Sharpe, 2001; Swindler, 2002). We therefore have a basic understanding of how primate tooth shapes relate to the ingestion and mechanical break down of foods. *In vivo* investigations, many of which were carried out by Hylander and colleagues (e.g., Hylander, 1979a,b, 1984, 1985; Hylander and Johnson, 1994, 1997; Hylander et al., 1987, 1992, 1998, 2000, 2005; Ross and Hylander, 2000; Vinyard et al., 2005; Wall et al., 2006), have significantly advanced our knowledge of how primates recruit their jaw muscles, and how these muscle activity patterns create internal loads in the masticatory apparatus during mastication and incision. Likewise, numerous comparative analyses have demonstrated associations between jaw form and diet within and among primate species (e.g., Bouvier, 1986; Cole, 1992; Daegling, 1992; Antón, 1996; Taylor, 2002, 2005, 2006a,b; Vinyard et al., 2003). Functional and adaptive hypotheses must draw on knowledge gained through these experimental investigations, biomechanical modeling, and comparative approaches if we are going to better understand the evolution of the masticatory apparatus in primates.

Recognition that jaw muscles are recruited in specific patterns, and knowledge of how these activity patterns generate the forces and movements necessary to facilitate specific feeding behaviors, is vital to understanding morphological adaptations of the primate masticatory apparatus. Even though it is well understood that jaw muscles are responsible for generating jaw forces and movements, we know surprisingly little about the architecture of these muscles in primates. This is because studies seeking to link primate feeding behavior and morphology have largely overlooked how jaw-muscle fiber architecture affects masticatory apparatus performance. Muscle fiber architecture plays a crucial role in modulating movements and forces during feeding. Yet despite this role of the jaw muscles in feeding performance (e.g., Taylor and Vinyard, 2004; Taylor et al., in press), studies have focused almost exclusively on bony form, without integrating information from jaw-muscle architecture. We suggest there are important insights to be gained from examining fiber architecture, which can be applied to comparative studies of masticatory function and adaptation in both living and fossil primates.

We begin this chapter with a brief description of muscle architecture and its importance for understanding muscle function. Subsequently, we illustrate the importance of integrating jaw-muscle fiber architecture and skull morphology in a study of feeding behavior using gummivorous callitrichids. Specifically, we compare fiber architecture of the jaw-closing muscles in tree-gouging common (*Callithrix jacchus*) and pygmy (*Cebuella pygmaea*) marmosets to that of nongouging cotton-top tamarins (*Saguinus oedipus*). Callitrichids provide a natural model for addressing morphological divergence as a function of feeding behavior both because these feeding behaviors are well documented from both field and laboratory research and because these taxa are closely related at the subfamily level (Callitrichinae:Primates), thereby limiting the influence of phylogenetic history. We demonstrate that tree-gouging marmosets exhibit architectural features of the masseter and temporalis muscles that can be functionally linked to tree-gouging based on the comparison to nongouging callitrichids. Thus, knowledge of jaw-muscle fiber architecture broadens and refines our understanding of the functional and/or adaptive correlates of this specialized feeding behavior. We end this chapter by exploring what this case study suggests for future research integrating jaw-muscle architecture with the existing data on primate masticatory apparatus form and function.

12.1.1 The Importance of Fiber Architecture for Understanding Muscle Function

At both macroscopic and microscopic levels, skeletal muscle is a highly organized tissue. Skeletal muscle is arranged hierarchically from whole muscle, to muscle fascicles, fibers, and myofibrils, down to the functional unit of contraction, the sarcomere. The sarcomere is comprised of smaller myofilaments, the thin actin and thicker myosin proteins that overlap each other and form cross-bridges, thereby providing the contractile properties of a muscle fiber (Lieber, 2002). The length–tension relationship describes the amount of isometric tension that a muscle can generate at varying amounts of overlap between the actin and the myosin filaments (Gordon et al., 1966). Maximum tetanic tension occurs at the plateau region of the length–tension curve, when the number of cross-bridges formed between the actin and the myosin filaments is maximized (Gordon et al., 1966).

Myofibrils are arranged in parallel, influencing the physiological cross-sectional area, while sarcomeres are arranged longitudinally in series (i.e., end-to-end), thereby modulating the distance through which a muscle fiber can move and, by extension, its contraction velocity. All other factors being equal, the thicker the muscle fiber, the greater its force-producing capability, while the longer the fiber, the greater the distance and speed through which a fiber can shorten (or lengthen). Thus, both fiber diameter and length influence how a muscle fiber functions.

If all fibers were arranged parallel to the force-generating axis of the muscle, then estimating the force-producing capability of a muscle would be a simple task of measuring a muscle's volume. This is because the maximum potential force a muscle can generate in a given direction is equal to the sum of the contractile forces produced by all of the individual fibers oriented in that direction. In reality, however, the directional arrangement of individual muscle fibers varies within a muscle. This variation can be extrapolated to differences in orientation both across species for a given muscle and across muscles within a given species.

Some muscles comprise parallel or nearly parallel fibers, such as the vastus medialis muscle in humans and guenons (Anapol and Barry, 1996; Lieber, 2002). Most muscle fibers, however, are angled relative to the force-generating axis of the muscle. Unipinnate muscles comprise fibers oriented at a single angle relative to the axis of force generation, while multipinnate muscles comprise fibers oriented at several angles. Pinnation angle for these muscles generally ranges from 0° to 30°; the force a muscle can generate drops precipitously beyond 60°; Gans, 1982. In rodents and other mammals, the jaw-closing muscles, and the masseter in particular, tend to be among the most complex and highly pinnate-fibered muscles (Herring, 1992; van Eijden et al., 1997). For example, angle of pinnation in pig masseter ranges from 0 to 25° (Herring et al., 1979). We note, however, that even in so-called parallel-fibered muscles, fibers rarely extend the entire length of the muscle (Lieber, 2002).

Because the directional arrangement of muscle fibers varies, muscle weight or volume is insufficient to inform us of a muscle's capacity to produce force or to move through a given range. We need additional information on fiber length (l_f), fiber pinnation angle, and physiological cross-sectional area (PCSA). Because the total shortening distance of a muscle fiber is equal to the sum of the shortening distances of the individual sarcomeres (Lieber, 2002), muscle fiber length (l_f) is proportional to a muscle's maximum potential range of motion (excursion) and contraction velocity. Physiological cross-sectional area is proportional to the maximum force that a muscle can generate, and is computed as:

$$\text{muscle mass (gm)} \times \cos\theta / l_f(\text{cm}) \times 1.0564\,\text{gm/cm}^3,$$

(Gans and Bock, 1965; Powell et al., 1984.) Here, θ represents the angle of pinnation, or the orientation of the fiber relative to the force-generating axis of the muscle. It has been both theoretically argued (e.g., Gans and Bock, 1965; Gans and de Vree, 1987) and empirically demonstrated for jaw muscles (e.g., Taylor and Vinyard, 2004; Perry and Wall, 2008; Shahnoor et al., 2008) that there is a trade-off between PCSA and fiber length. Thus, a muscle can be best suited to either force production or excursion, but not both.

Finally, muscle fibers will be shortened when a muscle is contracting concentrically. This shortening will increase angles of pinnation relative to their resting position. Stretching a muscle will produce the opposite effect. This means that the posture in which a muscle is measured will affect fiber length and, by extension, all variables involving fiber length. Ideally, fiber length and angle of pinnation should be measured with a muscle at its resting length (Lieber, 2002). In practice, however, this is not always possible. Comparative analyses of fiber architecture should minimally measure muscles from different individuals in similar functional positions if not at resting length (e.g., incisor tip-to-tip occlusion for the jaw muscles) (Taylor and Vinyard, 2004).

12.1.2 Feeding Behavior in Tree-Gouging and Nongouging Callitrichids: A Natural Model of Behavioral Divergence

Callitrichid monkeys have been described as representing an adaptive radiation of gum feeders (Sussman and Kinzey, 1984). Gums provide an important food source and some callitrichids, such as pygmy marmosets (*Cebuella pygmaea*), can spend up to 70% of their feeding time consuming tree exudates during certain times of the year (Garber, 1992 and references therein). While all callitrichids feed on gums, they vary in terms of how they gain access to these gums. Some callitrichids, such as the cotton-top tamarin (*Saguinus oedipus*), are opportunistic gum feeders, capitalizing on tree exudates that have been exuded through damage by insects or other means. By contrast, common (*Callithrix jacchus*) and pygmy (*C. pygmaea*) marmosets actively elicit exudate flow by mechanically injuring trees with their anterior dentition. We define this type of biting behavior as tree gouging. During tree gouging, marmosets anchor their upper jaw in the tree substrate while using their lower jaw to scrape holes in the tree bark to stimulate exudate flow (Coimbra-Filho and Mittermeier, 1977). They later return to eat these exudates.

This divergence in feeding behavior makes tree-gouging and nongouging callitrichids an exceptional natural model for evaluating the relationship between muscle fiber architecture, muscle function, and feeding behavior. This is because gouging marmosets differ from nongouging tamarins based on the presence or absence of this gouging behavior, rather than forming part of a continuum of feeding behaviors. Furthermore, apart from this distinction in gum-feeding behavior, tree-gouging marmosets (*C. jacchus* and *C. pygmaea*) and nongouging tamarins (*S. oedipus*) are closely related genera that have similar diets consisting of insects, fruits, and gums. Thus, gouging is likely to be a feeding behavior that uniquely differentiates marmosets from tamarins.

12.1.3 Are Tree Gougers Maximizing Jaw-Muscle Force or Muscle Stretch?

Numerous investigators (e.g., Szalay and Seligsohn, 1977; Szalay and Delson, 1979; Dumont, 1997; Spencer, 1999) have hypothesized that tree gouging requires the generation of large jaw forces. To the contrary, preliminary *in vivo* work (Vinyard et al., 2001, in press; Mork et al., 2004) suggests that common marmosets generate jaw forces during simulated tree gouging that are significantly less than their maximum biting ability. The *in vivo* work also reveals that maximum jaw gapes during gouging are significantly larger than those during chewing. Importantly, both laboratory and field studies indicate that common marmosets use jaw gapes during gouging which approach their maximum structural capacity for jaw opening (Vinyard et al., 2001, 2004; in press).[1] Increased gapes have been hypothesized to increase mandibular excursion and/or facilitate optimal incisor alignment for penetrating the tree substrate during a gouge (Vinyard et al., 2003). Collectively, these studies strongly suggest that the ability to generate wide jaw gapes is important for tree-gouging primates, and that any musculoskeletal features facilitating the production of wide gapes would be advantageous.

Comparative studies have shown that tree-gouging primates exhibit morphological features of the bony masticatory apparatus that distinguish them from closely related nongouging taxa. For example, the tree-gouging *Callithrix jacchus*

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[1] Maximum jaw-opening ability was measured on anesthetized animals by passively opening the jaws to their widest gape.

and *Cebuella pygmaea* have incisiform canines and long, chisel-like incisors with very thick labial and thin lingual enamel compared to nongouging callitrichids (Coimbra-Filho and Mittermeier, 1977; Rosenberger, 1978). This morphology has been referred to as the "short-tusked" condition (e.g., Hill, 1957; Napier and Napier, 1967; Coimbra-Filho and Mittermeier, 1977), and has been linked to the use of the canines and incisors as a functional unit for gouging trees.

Tree-gouging primates, including common marmosets, are characterized by skull shapes that are theoretically advantageous for achieving wide jaw gapes when compared to closely related, nongouging taxa. These features include relatively low condyles positioned closer to the height of the tooth row, anteroposteriorly elongated condyles (correlated with greater condylar curvature) and temporal articular surfaces, and higher superficial masseter origin–insertion ratios (Vinyard et al., 2003). Masseter muscle position, as reflected by a masseter origin–insertion ratio that deviates from 1.0 and a low condylar height, has been geometrically linked to the capacity to generate large gapes via reduction in masseter stretching (Herring and Herring, 1974). Carnivores, for example, which require wide jaw gapes for feeding, display, and/or fighting, show high superficial masseter origin–insertion ratios and relatively low condyles compared to other mammals where gape requirements are less important (Herring and Herring, 1974). A relatively low condyle, as exhibited by *C. jacchus*, is one way of reducing masseter stretch for a given gape. Individuals with lower condyles have an increased included angle from the masseter origin – condyle – masseter insertion (all other things being equal) (Fig. 12.1). An origin–insertion ratio that deviates from 1.0, and/or an increase in the aforementioned included angle, is theoretically predicted to reduce superficial masseter stretching and hence potentially increase maximum gape. The available evidence from the bony parts of the masticatory apparatus, therefore, strongly suggests that tree-gouging marmosets should be optimizing muscle excursion over muscle force production.

Here we present an analysis of the superficial masseter and anterior temporalis muscles in tree-gouging and nongouging callitrichids. Based on a geometric model, stretching of the masseter and temporalis muscles is thought to potentially limit maximum jaw opening in most mammals (Herring and Herring, 1974). Empirical evidence from pig masseter demonstrates that fiber elongation during gape, which may be as great as 50% of muscle resting length, is greatest at the anterior margin of the masseter relative to other regions along the muscle (Herring et al., 1979). Moreover, the longest masseter fibers are observed to lie in the anterior portion of the muscle in pigs (Herring et al., 1979), as well as the marmosets and tamarins examined here (Taylor and Vinyard, 2004).[2]

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[2] Fiber lengths change depending on the position of the jaws at the time of fixation. We observed longer fibers in the posterior region of the masseter muscle in common marmosets and cotton-top tamarins when the jaws were fixed with the incisors in tip-to-tip occlusion (Taylor and Vinyard, 2004). However, when adjusted for muscle resting length, the anterior fibers were observed to be the longest (unpublished data).

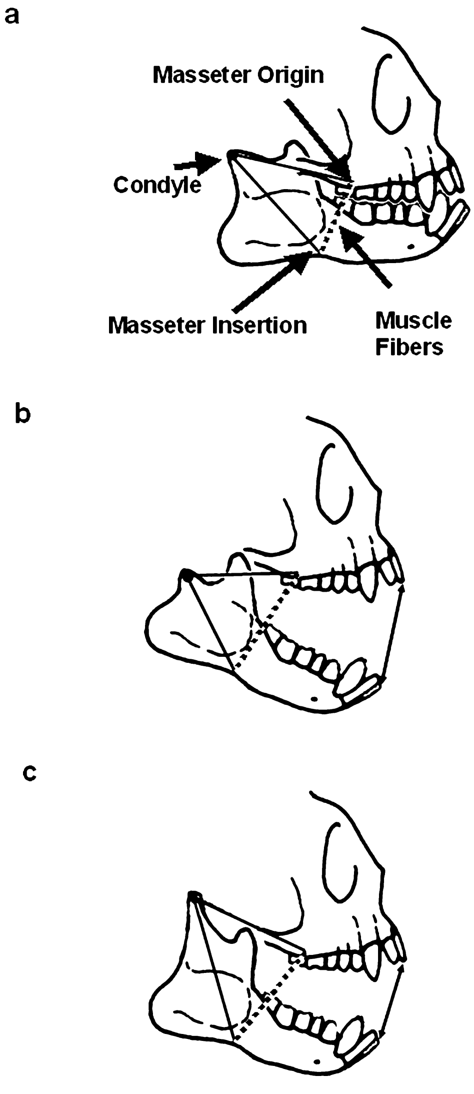

Fig. 12.1 Schematic representation of the upper and lower jaws in lateral view depicting (**a**) the distance from the condyle to both the masseter origin and insertion (*solid lines*). Idealized length of the most anterior masseter fibers is represented as the dark dotted line, while gape is shown between the upper and the lower incisors. Positioning the condyle closer to the tooth row (**b**) compared to a condyle positioned farther from the toothrow (**c**) results in a larger gape for the same amount of stretch in the anterior masseter fibers. (Note that the length of the dark dotted line is similar in (**b**) and (**c**).) Thus, with the condyle positioned closer to the tooth row, a wider gape can be achieved with less stretch of the masseter for a given degree of angular rotation of the mandible

12.2 Materials and Methods

12.2.1 Samples

We analyzed the superficial masseter and anterior temporalis muscles of 15 *Callithrix jacchus*, 5 *Cebuella pygmaea*, and 9 *Saguinus oedipus*. We determined adult status based on the patterns of tooth eruption and occlusion, as well as husbandry records documenting age in years. Cadavers were provided courtesy of the Wisconsin National Primate Research Center, New England Primate Research Center, and Southwest National Primate Research Center.

12.2.2 Data Collection

We removed the superficial fat and fascia overlying the jaw muscles and photographed the specimens in lateral view. We measured masseter and temporalis muscle lengths from intact muscles with calipers to the nearest 0.01 mm. We then dissected the masseter and temporalis muscles free from their bony attachments, trimmed them of excess tendon and fascia, blotted them dry, and weighed them to the nearest 0.0001 g. We measured jaw length (to the nearest 0.01 mm) from the posterior edge of the condyle to prosthion on each specimen.

We measured fasciculus length and angle of pinnation for both muscles, following Taylor and Vinyard (2004). Briefly, we bisected the masseter into a superior

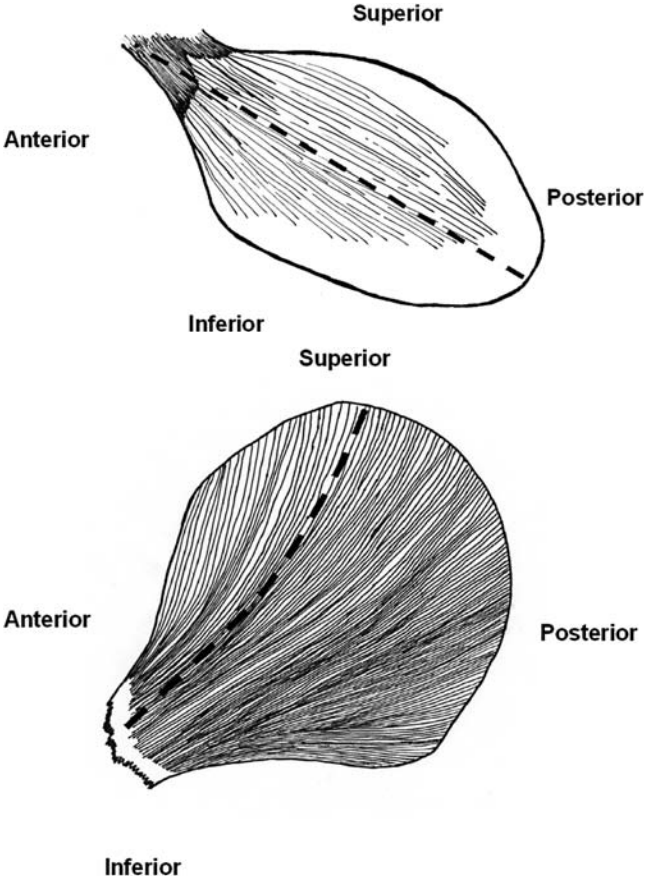

Fig. 12.2 Schematic of a left masseter muscle (**a**) and temporalis muscle (**b**) of *Callithrix jacchus*. The masseter muscle was bisected from superficial to deep, as depicted by the dotted line (**a**). The inferior portion was used for data analysis. The temporalis muscle was bisected into anterior and posterior portions, as illustrated by the dotted line, and the anterior portion used for data analysis (**b**) (Figure 12.2**a** reprinted with permission from John Wiley & Sons, Inc.)

and inferior portion along its length, roughly approximating the muscle's line of action (Fig. 12.2a). We analyzed the inferior portion in order to avoid the deep masseter, which has a different fiber orientation and muscle action than the superficial masseter. We bisected the temporalis muscle into anterior and posterior portions and analyzed the anterior portion (Fig. 12.2b). We oriented each segment so as to view the fibers in cross section, pinned the segment to a styrofoam block, and then visualized the proximal and distal attachments to tendon of individual fasciculi under a magnification light. Because of the exceptionally small size of the *Cebuella* muscles, we employed a pair of Zeiss (×2.3) binocular glasses in addition to the magnification light during data collection.

Depending on the position of the jaws at the time of fixation, muscle fibers may be either elongated or contracted relative to their resting lengths. To control for the effects of position at fixation on whole muscle and fiber lengths across individuals (and by extension, all variables involved), we only included specimens whose jaws were fixed in a standardized jaw posture. Following Taylor and Vinyard (2004), the incisors were in tip-to-tip occlusion in all specimens.

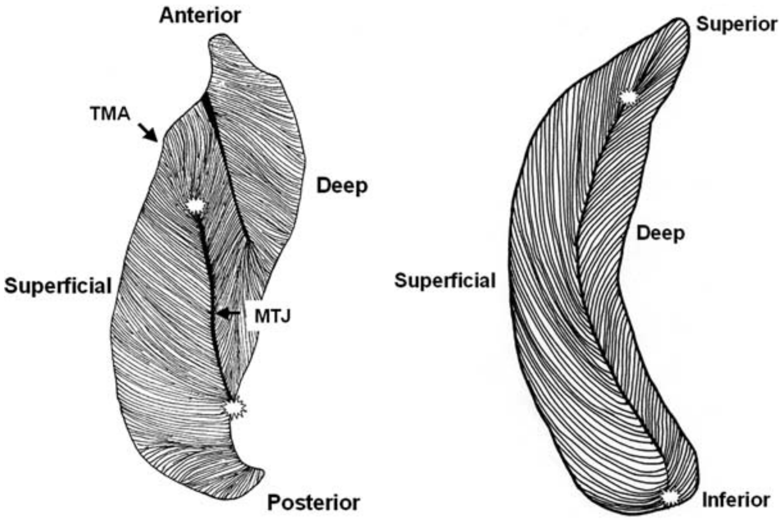

Fig. 12.3 Superior view of the internal architecture of marmoset masseter (**a**) and temporalis (**b**). The masseter is multipinnate in *Callithrix jacchus*, *Cebuella pygmaea*, and *Saguinus oedipus.* The fibers of the superficial portion of the masseter are bipinnate, and fasciculus measurements were taken from the myotendinous junction (MTJ) to the tendon of muscle attachment along the region of the zygomatic arch (TMA). The stars at the anterior and posterior ends of the MTJ mark the sampling sites for anterior and posterior fibers, respectively. The temporalis is bipinnate in all taxa. Fasciculus measurements were taken from the MTJ to the tendon of muscle attachment along the temporal bone. The stars at the superior and inferior ends of the MTJ mark the sampling sites for superior and inferior fibers, respectively (Figure 12.3a reprinted with permission from John Wiley & Sons, Inc.)

We selected anterior and posterior sampling sites for measurements along the length of the superficial masseter, whereas we chose proximal and distal sampling sites for the anterior temporalis muscle (Fig. 12.3). At each sampling site, we measured a maximum of six adjacent fasciculi. For each fasciculus, we measured the following: (1) fasciculus length, between the proximal and the distal myotendinous junctions (l_f); (2) the perpendicular distance from the tendon of insertion to the proximal attachment of the fasciculus (a); (3) the length of tendon from the proximal bony attachment to the proximal myotendinous junction (t_p); and (4) the length of tendon from the distal bony attachment to the distal myotendinous junction (t_d) (Table 12.1 and Fig. 12.4). We calculated the angle of pinnation (θ) as the arcsin of a/l_f (Anapol and Barry, 1996) (Table 12.1; Fig. 12.4).

12.2.3 Data Analysis

We used one-tailed Mann-Whitney U-tests to address the hypothesis that tree-gouging *Callithrix jacchus* and *Cebuella pygmaea* exhibit architectural properties of the masseter and temporalis muscles that are functionally linked to the production

Table 12.1 Muscle fiber architecture variables and predicted differences between tree-gouging marmosets (*Callithrix jacchus* and *Cebuella pygmaea*) and a nongouging tamarin (*Saguinus oedipus*)

Variable	Definition	Prediction
Fiber length for the superficial masseter and anterior temporalis muscles (l_f)	Calculated as the average fiber length of the six anterior and six posterior fasciculi for the superficial masseter, and the six proximal and six distal fasciculi for the anterior temporalis muscles.	l_f should be relatively greater in *C. jacchus* and *C. pygmaea* compared to *S. oedipus*.
Pinnation angle (θ) = arcsin a/l_f	Angle of fibers relative to the axis of force generation.	θ should be greater in *S. oedipus* compared to *C. jacchus* and *C. pygmaea*.
Maximum excursion of the anterior and distal tendons of attachment (h) for the masseter and temporalis muscles, respectively.	$l_f\,(\cos\theta - \sqrt{\cos\theta^2 + n^2 - 1})$, where θ represents the pinnation angle, and n is the coefficient of contraction: (fiber length after contraction/resting fiber length) = 0.767 (Anapol and Gray (2003) after Gans and Bock (1965) and Muhl (1982)).	h should be greater in *C. jacchus* and *C. pygmaea* compared to *S. oedipus*.
Physiological cross-sectional area (PCSA)	(muscle mass (g) × $\cos\theta$)/(l_f (cm) × 1.0564 g/cm^3), where θ represents the pinnation angle, and 1.0564 the specific density of muscle (Mendez and Keys, 1960; Powell et al., 1984).	PCSA should be relatively greater in *S. oedipus* compared to *C. jacchus* and *C. pygmaea*.
$[l_t/(l_f + l_t)]$	Ratio of total tendon length (l_t) to fasciculus + tendon length ($l_f + l_t$) (Anapol and Barry, 1996).	$[l_t/(l_f + l_t)]$ should be greater in *S. oedipus* compared to *C. jacchus* and *C. pygmaea*.

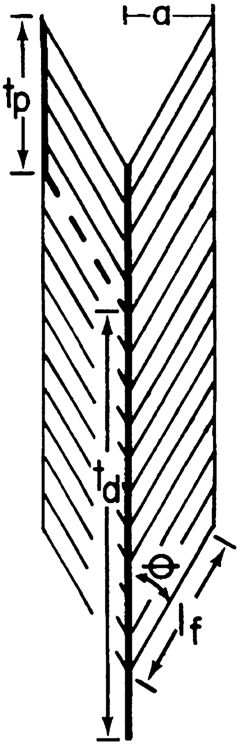

Fig. 12.4 Schematic of a bipinnate muscle depicting the measurements taken in this study (from Taylor and Vinyard, 2004). These measurements include: (1) fasciculus length (l_f); (2) the perpendicular distance from the proximal myotendinous junction to the tendon of anterior or distal muscle attachment (**a**); (3) length of tendon attaching to the most proximal end of the fasciculus (t_p); (4) length of tendon attaching to the anterior or distal-most end of the fasciculus (t_d); (5) angle of pinnation (θ)

of wide jaw gapes (Table 12.1). We evaluated differences in masseter and temporalis fiber lengths and associated architectural variables by holding other functional aspects of jaw gape constant. Specifically, we created shape ratios by dividing fiber length and the square root of PCSA against jaw length. The maximum excursion of the anterior masseter and distal temporalis tendons of attachment (h) were standardized relative to whole muscle length (Taylor and Vinyard, 2004).

12.3 Results

Tree-gouging common (*C. jacchus*) and pygmy (*C. pygmaea*) marmosets exhibit architectural features of the masseter and temporalis muscles that are functionally linked to facilitating muscle stretch and muscle excursion when compared to cotton-top tamarins (*S. oedipus*) (Table 12.2). For example, *C. jacchus* has both absolutely (Fig. 12.5) and relatively (Fig. 12.6) longer fibers for both muscles compared to *S. oedipus*. While *C. pygmaea* has relatively longer masseter fibers than *S. oedipus*, the difference in temporalis fiber length between these two taxa only approaches significance following Bonferroni adjustment (Fig. 12.6). Both marmosets have significantly greater maximum excursions of the anterior and distal tendon attachments of the masseter and temporalis muscles, respectively, compared to cotton-top

Table 12.2 Comparison of masseter and temporalis fiber architecture between tree-gouging marmosets (*Callithrix jacchus* and *Cebuella pygmaea*) and a non-gouging tamarin (*Saguinus oedipus*)

	C. jacchus vs. *S. oedipus*	Direction of difference	*C. pygmaea* vs. *S. oedipus*	Direction of difference
Masseter muscle				
Fiber length (mm)	**0.0035**	Cj > So	**0.0200**	So > Cp
Fiber length (mm)/jaw length (mm)	**0.0005**	Cj > So	**0.0285**	Cp > So
h/masseter muscle length (mm)	**0.0015**	Cj > So	**0.0040**	Cp > So
PCSA (cm^2)/jaw length (mm)	**0.0005**	So > Cj	**0.0015**	So > Cp
Total tendon length per muscle fasciculus	**0.0055**	So > Cj	**0.0040**	So > Cp
Pinnation angle	0.3500	So = Cj	0.0015	So > Cp
Temporalis muscle				
Fiber length (mm)	**0.0000**	Cj > So	0.1430	So = Cp
Fiber length (mm)/jaw length (mm)	**0.0000**	Cj > So	0.0480	Cp > So
h/temporalis muscle length (mm)	**0.0000**	Cj > So	**0.0045**	Cp > So
PCSA (cm^2)/jaw length (mm)	**0.0000**	So > Cj	**0.0015**	So > Cp
Total tendon length per muscle fasciculus	**0.0015**	So > Cj	**0.0100**	So > Cp
Pinnation angle	0.2105	So = Cj	**0.0140**	So > Cp

All boldface p-values significant based on one-tailed Mann-Whitney U-tests and significant at $p < 0.05$.

tamarins (*h*/muscle length) (Table 12.2). By contrast, cotton-top tamarins exhibit significantly greater PCSAs and higher proportions of muscle tendon to fiber (Figs. 12.7 and 12.8). Pinnation angles are significantly smaller in *C. pygmaea* compared to *S. oedipus*, but *C. jacchus* and *S. oedipus* do not differ in pinnation angles (Table 12.2).

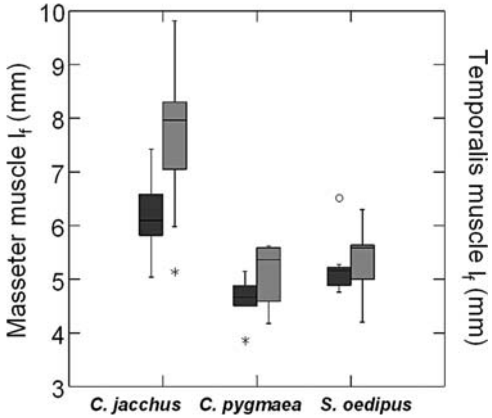

Fig. 12.5 Box plots comparing masseter and temporalis muscle fiber lengths (l_f). Masseter muscle fiber length depicted on the left (dark hatched box), temporalis fiber length on the right (light hatched box). *Callithrix jacchus* has significantly longer masseter and temporalis fibers. *Cebuella pygmaea* has fiber lengths that approach those of *Saguinus oedipus*, at roughly 25% of *S. oedipus*' body weight. Sample sizes for the masseter and temporalis muscles include *C. jacchus* (12, 15), *C. pygmaea* (5, 5) and *S. oedipus* (8, 9), respectively

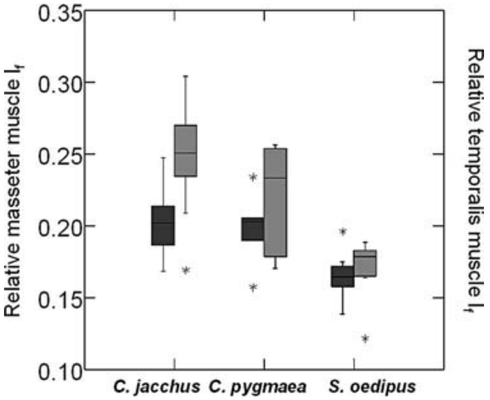

Fig. 12.6 Box plots comparing relative masseter and temporalis muscle fiber lengths (l_f/jaw length). Masseter muscle fiber length depicted on the left (dark hatched box), temporalis fiber length on the right (light hatched box). *Callithrix jacchus* and *Cebuella pygmaea* have relatively longer masseter and temporalis muscles compared to *Saguinus oedipus*, though the difference in relative temporalis fiber length only approaches significance between *C. pygmaea* and *S. oedipus* ($p = 0.048$) after Bonferroni adjustment. These data indicate that tree-gouging marmosets have jaw-closing muscles that facilitate increased muscle stretch during jaw opening, and thus the production of relatively wide jaw gapes. Sample sizes as in Fig. 12.2

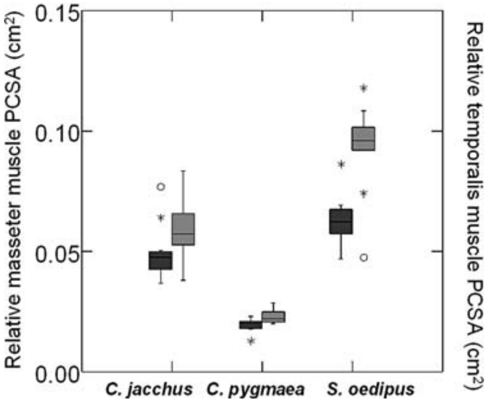

Fig. 12.7 Box plots comparing relative masseter and temporalis PCSAs (PCSA/jaw length). Masseter muscle PCSA depicted on the left (dark hatched box), temporalis PCSA on the right (light hatched box). *Saguinus oedipus* has significantly greater relative PCSAs for the masseter and temporalis muscles compared to *Callithrix jacchus* and *Cebuella pygmaea*. These data suggest that *S. oedipus* has the potential to generate relatively greater muscle and bite force compared to tree-gouging marmosets. Sample sizes as in Fig. 12.2

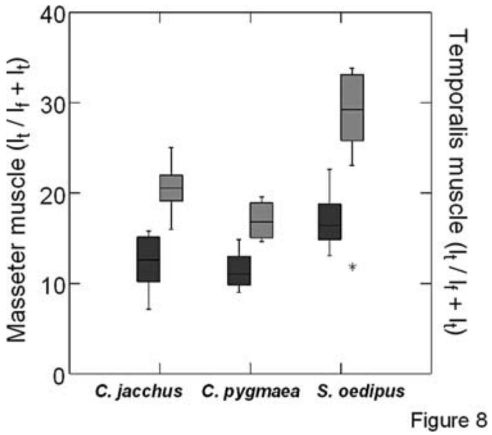

Fig. 12.8 Box plots comparing the ratio of total tendon length to fasciculus + tendon length $[l_t/(l_f + l_t)]$. Masseter muscle depicted on the left (dark hatched box), temporalis on the right (light hatched box). *Saguinus oedipus* has a significantly greater ratio of tendon to fiber for both the masseter and the temporalis muscles compared to *Callithrix jacchus* and *Cebuella pygmaea*. Lower ratios suggest the potential for greater neural control over jaw movement and jaw posture in marmosets. Sample sizes as in Fig. 12.2

12.4 Discussion

12.4.1 The Functional Significance of Jaw-Muscle Fiber Architecture in Tree-Gouging Marmosets

Results presented here demonstrate that tree-gouging marmosets have masseter and temporalis muscles that are well suited to facilitate muscle stretch. These features include relatively longer fibers and relatively greater maximum excursion capabilities. Elsewhere (e.g., Taylor and Vinyard, 2004; unpublished data), we have shown that common marmosets exhibit relatively longer fibers in both the anterior and the posterior portions of the masseter, and have higher ratios of muscle mass to effective maximal tetanic tension (M/P_0) for both the masseter and the temporalis. A higher ratio of M/P_0 (where the specific tension of muscle has been empirically determined to be 2.3 kg/cm^3; Spector et al., 1980; Sacks and Roy, 1982; Powell et al., 1984), reflects the dedication of a muscle to excursion and contraction velocity over its capacity to generate force (Sacks and Roy, 1982; Wottiez et al., 1986; Weijs et al., 1987; Anapol and Barry, 1996).

Marmosets also have lower ratios of tendon length to muscle fiber + tendon length $[l_t/(l_f + l_t)]$ for both the masseter and the temporalis muscles (Table 12.1; Fig. 12.8). This ratio contrasts the energy cost required for generating tension (Anapol and Gray, 2003) versus the relative amount of neural control in the muscle–tendon unit. Lower $l_t/(l_f + l_t)$ ratios indicate less noncontractile tendon relative to contractile fiber, suggesting higher energy cost because more of the muscle force is actively generated through hydrolysis of adenosine triphosphate (ATP) rather than by passive tension stored in the tendon (Lieber, 2002). However, because muscle fibers have increased neural control relative to tendon (Biewener and Roberts, 2000; Anapol and Gray, 2003), a greater proportion of contractile tissue indicates increased neural control of the masseter and temporalis muscles throughout their ranges of motion. We hypothesize that tree gouging is a highly modulated behavior that would benefit from greater, more deliberate neural control of muscle stretch as a means of minimizing the risk of injury to the masticatory apparatus.

For marmosets, the greater capacity for muscle excursion comes at the expense of a decrease in relative force production. Previous investigators have theoretically argued (Gans and Bock, 1965; Gans and de Vree, 1987) and empirically demonstrated (Anapol and Barry, 1996; Anapol and Gray, 2003; Taylor and Vinyard, 2004) that it is difficult for an individual muscle to simultaneously maximize excursion and force production. Our results demonstrate that there is an architectural trade-off in callitrichid jaw muscles between longer fibers, which facilitate muscle excursion, and shorter, sometimes more pinnate fibers, which improve force production

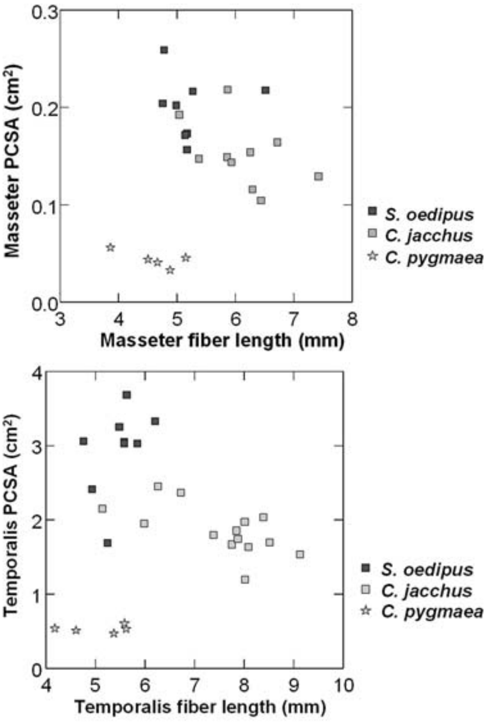

Fig. 12.9 Bivariate plot demonstrating the architectural trade-off between muscle force (PCSA) and muscle excursion (fiber length) for masseter (**a**) and temporalis (**b**) muscles. In general, marmoset masseter and temporalis, with their relatively low PCSAs and long fibers, are suited more for muscle excursion (i.e., production of wide gapes), while in *Saguinus oedipus* the larger PCSAs and shorter fibers make these muscles better suited for generating larger muscle forces with smaller excursions

(Fig. 12.9). Thus, *Saguinus oedipus*, with relatively higher PCSAs for the masseter and temporalis muscles, has the capacity to generate relatively greater maximal muscle force compared to marmosets. Furthermore, the higher ratios of tendon to fiber indicate that force production in *S. oedipus* is energetically more efficient compared to force production in marmosets. That said, we have no dietary or performance data to indicate that *S. oedipus* generates relatively greater maximum muscle or bite forces compared to marmosets. In lieu of such data, we conservatively interpret our finding of relatively greater PCSAs in *S. oedipus* as reflecting this structural trade-off between muscle excursion (fiber length) and muscle force (PCSA).

The combination of altered jaw-muscle fiber architecture shown here and muscle orientation (e.g., Vinyard et al., 2003) provide compelling evidence that tree-gouging common and pygmy marmosets are maximizing muscle stretch abilities. During the generation of wide jaw gapes, which involves active lengthening of the jaw-closing muscles, it is likely that marmosets are stretching their jaw-closing muscle well beyond their resting length. Bite forces in primates diminish as jaw-muscle fibers are stretched beyond their resting length (Dechow and Carlson, 1982, 1986, 1990), and decreases in bite force as gape increases are exacerbated by relatively inefficient jaw leverage for producing bite force at the anterior teeth. Alterations in both the bony and the soft tissue structures of the masticatory apparatus strongly suggest that tree-gouging marmosets are under pressure to reduce the amount of muscle stretch at a given gape in order to generate adequate bite forces at wide jaw gapes.

Collectively, relatively longer fibers of the masseter and temporalis muscles correspond with field and laboratory studies demonstrating that common marmosets gouge trees with relatively wide jaw gapes. The relatively lower muscle PCSAs support previous morphological and laboratory studies, which found no evidence that tree gouging requires generating relatively large bite forces (Vinyard et al., 2001, 2003, 2004, n.d.). The presence of relatively longer fibers, their capacity to enhance muscle stretch during jaw opening, and the performance data indicating that tree gouging involves the generation of wide jaw gapes, all suggest that longer masseter and temporalis fibers function to facilitate the production of wide jaw gapes during tree gouging in their natural environment (sensu Bock and von Wahlert, 1965).

12.4.2 Functional Partitioning of the Masseter and Temporalis Muscles

Most mammals have a basic masticatory muscle plan that includes four paired, recognizably distinct muscles: the masseter, temporalis, medial and lateral pterygoid muscles (e.g., Turnbull, 1970). Within this common organizational structure, the complexity of muscle architecture, the position of the muscles on the bony masticatory apparatus, and the proportional contribution to total muscle mass vary widely across taxa. Nevertheless, the primitive pattern for mammals, and one to which all three of these callitrichids conform, is characterized by a temporalis muscle that is relatively larger than the masseter and pterygoid muscles (Turnbull, 1970). Thus, while the force-generating capacity (PCSA) of the masseter and temporalis muscles are relatively lower in marmosets compared to tamarins, all three species have larger temporalis muscle weights (Eng et al., 2005) and maximum force-generating capacities relative to their masseters (Fig. 12.7).

If we consider the temporalis and masseter as part of a larger functional group involved in feeding, we can ask whether there are differences in the relative contributions of these two muscles to the overall force- and excursion-producing capabilities of the jaw-muscle group. If the PCSA of each muscle is expressed as a percentage of the combined PCSA for both muscles, it is apparent that there is less intermuscular diversity between the masseter and the temporalis muscles in marmosets compared to tamarins. That is, the force-generating capacities (PCSAs) of the two jaw-closing muscles are more similar within the marmosets than cotton-top tamarins (Fig. 12.10). Thus, while all taxa exhibit significant intermuscular diversity ($p < 0.05$), the disparity in % PCSA for the masseter and temporalis muscles is most pronounced in *S. oedipus*, suggesting a greater capacity for functional partitioning of these jaw-closing muscles in nongouging tamarins. We speculate that such partitioning may be more constrained in marmosets owing to their unique gape requirements for tree gouging. These observations on intersegmental differences in fiber architecture should be regarded as preliminary however, both because the masseter and temporalis muscles represent only two of the four muscles of mastication and because the masticatory muscles are architecturally complex and contain regionally differentiated, task-specific portions (e.g., Herring et al., 1979; Weijs and Dantuma, 1981; van Eijden et al., 1993; van Eijden and Turkawski, 2001), not all of which have been evaluated.

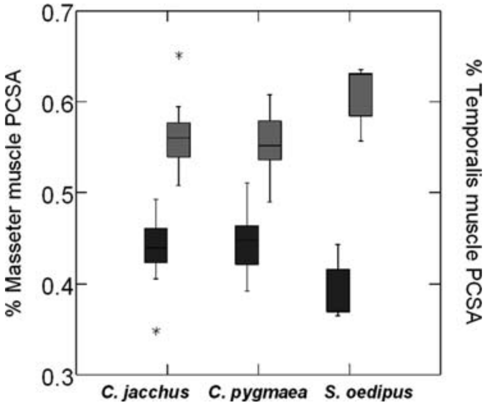

Fig. 12.10 The PCSA of the masseter depicted on the left (dark-hatched box) and temporalis on the right (light-hatched box), expressed as a percentage of the combined PCSA for both muscles. The disparity between the masseter and the temporalis muscles is greatest in *Saguinus oedipus*, suggesting a greater division of labor between these two jaw-closing muscles in terms of their dedication to generating force

12.4.3 Integrating Fiber Architecture with Bony Morphology in Studies of Feeding Behavior

Previous craniometric studies of the external morphology and internal geometry of tree-gouging marmosets suggest a masticatory apparatus that is well suited to facilitating the production of wide jaw gapes, but not necessarily the generation or dissipation of large jaw forces (Vinyard et al., 2003; Vinyard and Ryan, 2006). Based on the performance data collected during tree gouging in both laboratory and field settings, we argue that differences in skull form between tree-gouging and nongouging callitrichids are functionally linked to their divergent feeding behaviors. However, skull form alone is generally insufficient for determining skull function (Daegling, 1993; Daegling and Hylander, 2000; Vinyard and Ryan, 2006). Moreover, it is often impractical to obtain performance data on living primates in laboratory or natural environments, and impossible to obtain such data on extinct taxa.

We have shown a correspondence between variation in jaw-muscle fiber architecture and skull form in tree-gouging and nongouging callitrichids. Compared to nongouging tamarins, tree-gouging marmosets have relatively longer masseter and temporalis fibers that facilitate the production of wide jaw gapes. Common marmosets also have relatively longer mandibles, anteroposterior elongated glenoids and condyles, and lower condyles relative to the height of the mandibular toothrow, all of which assist in opening the jaw widely. Conversely, tree-gouging marmosets have relatively smaller PCSAs compared to tamarins, indicating less maximal force production capability. Likewise, common marmosets have no skull morphologies that can be functionally linked to generating or dissipating large jaw forces. To our knowledge, this is the first such study to demonstrate a relationship between jaw-muscle fiber architecture, skull form, and feeding behavior in a primate. Evaluation of fiber architecture, along with other anatomical and physiological parameters of muscle, provide an important means of corroborating functional hypotheses linking feeding behavior and diet to skull form.

Apart from providing data on muscle structure that is essential for building more robust interpretations of function and performance, an architectural analysis of muscle groups yields important information on how muscles may be functionally partitioned in various behavioral repertoires, information that cannot be readily gleaned from skeletal morphology (e.g., Anapol and Jungers, 1986, 1987; Anapol and Barry, 1996; Anapol and Gray, 2003). Knowledge of muscle structure aids our interpretation of jaw-muscle recruitment patterns, while muscle recruitment patterns inform our understanding of muscle fiber architecture and physiology. In this way, fiber architecture and jaw-muscle electromyography (EMG) are mutually informative. To date, we do not know whether jaw-muscle EMG and fiber architecture are correlated across primates. An improved understanding of this relationship will help us determine the extent to which muscle form reflects its function during various feeding and biting behaviors.

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References

Anapol, F.C., Jungers, W.L. (1986). Architectural and histochemical diversity within the quadriceps femoris of the brown lemur (*Lemur fulvus*). *Am. J. Phys. Anthropol*. 69:355–375.

Anapol, F.C., Jungers, W.L. (1987). Telemetered electromyography of the fast and slow extensors of the leg of the brown lemur (*Lemur fulvus*). *J. Exp. Biol*. 130:341–358.

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, J.P. (2003). Fiber architecture of the intrinsic muscles of the shoulder and arm in semiterrestrial and arboreal guenons. *Am. J. Phys. Anthropol*. 122:51–65.

Antón, S.C. (1996). Cranial adaptation to a high attrition diet in Japanese macaques. *Int. J. Primatol*. 17:401–427.

Biewener, A.A., Roberts, T.J. (2000). Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. *Exerc. Sport. Sci. Rev*. 28:99–107.

Bock, W.J., 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.

Coimbra-Filho, A.F., Mittermeier, R.A. (1977). Tree-gouging, exudate-eating and the "short-tusked" condition in *Callithrix* and *Cebuella*, in: Kleiman, D.G. (ed.), *The Biology and Conservation of the Callitrichidae*, Smithsonian Institution Press, Washington DC, pp. 105–115.

Cole, T.M. III. (1992). Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. *J. Hum. Evol*. 23:253–282.

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

Daegling, D.J. (1993). The relationship of *in vivo* bone strain to mandibular corpus morphology in *Macaca fascicularis*. *J. Hum. Evol*. 25:247–269.

Daegling, D.J., Hylander, W.L. (2000). Experimental observation, theoretical models, and biomechanical inference in the study of mandibular form. *Am. J. Phys. Anthropol*. 112:541–551.

Dechow, P.C., Carlson, D.S. (1982). Bite force and gape in rhesus macaques. *Am. J. Phys. Anthropol*. 57:179.

Dechow, P.C., Carlson, D.S. (1986). Occlusal force after mandibular advancement in adult rhesus monkeys. *J. Oral. Maxillofac. Surg*. 44:887–893.

Dechow, P.C., Carlson, D.S. (1990). Occlusal force and craniofacial biomechanics during growth in rhesus monkeys. *Am. J. Phys. Anthropol*. 83:219–237.

Dumont, E.R. (1997). Cranial shape in fruit, nectar, and exudate feeders: Implications for interpreting the fossil record. *Am. J. Phys. Anthropol*. 102:187–202.

Eng, C.M., Vinyard, C.J., Anapol, F., Taylor, A.B. (2005). Stretching the limits: Jaw-muscle fiber architecture in tree-gouging and nongouging callitrichid monkeys. *Am. J. Phys. Anthropol*. Supplement 40:103.

Gans, C. (1982). Fiber architecture and muscle function. *Exerc. Sport Sci. Rev*. 10:160–207.

Gans, C., Bock, W.J. (1965). The functional significance of muscle architecture: A theoretical analysis. *Ergeb. Anat. Entwicklungsgesch* 38:115–142.

Gans, C., de Vree, F. (1987). Functional bases of fiber length and angulation in muscle. *J. Morphol*. 192:63–85.

Garber, P.A. (1992). Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichinae. *Am. J. Phys. Anthropol*. 88:469–482.

Gingerich, P.D., Smith, B.H., Rosenberg, K. (1982). Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *Am. J. Phys. Anthropol.* 58:81–100.

Gordon, A.M., Huxley, A.F., Julian, F.J. (1966). The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *J. Physiol. Lond.* 184:170–192.

Herring, S.W. (1992). Muscles of mastication: Architecture and functional organization, in: Davidovitch, Z. (ed.), *The Biological Mechanisms of Tooth Movement and Craniofacial Adaptation*, Ohio State University College of Dentistry, Ohio, pp. 541–548.

Herring, S.W., Herring, S.E. (1974). The superficial masseter and gape in mammals. *Am. Nat.* 108:561–576.

Herring, S.W., Grimm, A.F., Grimm, B.R. (1979). Functional heterogeneity in a multipinnate muscle. *Am. J. Anat.* 154:563–576.

Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini)*. University of Chicago Press, Chicago.

Hill, W.C.O. (1957). *Primates: Comparative Anatomy and Taxonomy*. Edinburgh University Press, Edinburgh, and Wiley-Interscience, New York.

Hylander, W.L. (1979a). The functional significance of primate mandibular form. *J. Morphol.* 160:223–240.

Hylander, W.L. (1979b). Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: An *in vivo* approach to stress analysis in the mandible. *J. Morphol.* 159:253–296.

Hylander, W.L. (1984). Stress and strain in the mandibular symphysis of primates: A test of competing hypotheses. *Am. J. Phys. Anthropol.* 61:1–46.

Hylander, W.L. (1985). Mandibular function and biomechanical stress and scaling. *Am. Zool.* 25:315–330.

Hylander, W.L., Johnson, K.R. (1994). Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *Am. J. Phys. Anthropol.* 94:523–547.

Hylander, W.L., Johnson, K.R. (1997). In vivo bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional patterns of craniofacial form. *Am. J. Phys. Anthropol.* 102:203–232.

Hylander, W.L., Johnson, K.R., Crompton, A.W. (1987). Loading patterns and jaw movements during mastication in *Macaca fascicularis*: A bone-strain, electromyographic, and cineradiographic analysis. *Am. J. Phys. Anthropol.* 72:287–314.

Hylander, W.L., Johnson, K.R., Crompton, A.W. (1992). Muscle force recruitment and biomechanical modeling: An analysis of masseter muscle function during mastication in *Macaca fascicularis*. *Am. J. Phys. Anthropol.* 88:365–387.

Hylander, W.L., Ravosa, M.J., Ross, C.F., Johnson, K.R. (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, W.L., Ravosa, M.J., Ross, C.F., Wall, C.E., Johnson, K.R. (2000). Symphyseal fusion and jaw-adductor muscle force: An EMG study. *Am. J. Phys. Anthropol.* 112:469–492.

Hylander, W.L., Wall, C.E., Vinyard, C.J., Ross, C., Ravosa, M.J., Williams, S.H., Johnson, K. (2005). Temporalis function in anthropoids and strepsirrhines: An EMG study. *Am. J. Phys. Anthropol.* 128:35–56.

Jernvall, J., Jung, H.S. (2000). Genotype, phenotype, and developmental biology of molar tooth characters. *Yrbk. Phys. Anthropol.* 43:171–190.

Kay, R.F. (1975). The functional significance of primate molar teeth. *Am. J. Phys. Anthropol.* 43:195–215.

Kay, R.F. (1978). Molar structure and diet in extant Cercopithecidae, in: Butler, P.M., Joysey, K. (eds.), *Development, Function and Evolution of Teeth,* Academic Press, London, pp. 309–339.

Kay, R.F., Williams, B.A. (1994). Dental evidence for anthropoid origins, in: Fleagle, J.G., Kay, R.F. (eds.), *Anthropoid Origins*, Plenum Press, New York, pp. 361–445.

Lieber, R.L. (2002). *Skeletal Muscle Structure, Function, and Plasticity*, Second Edition. Lippincott, Williams and Wilkins, Baltimore, MD.

Lucas, P.W. (1982). Basic principles of tooth design, in: Kurten, B. (ed.), *Teeth: Form, Function and Evolution*, Columbia University Press, New York, pp. 154–162.

Lucas, P.W. (2004). *Dental Functional Morphology: How Teeth Work*. Cambridge University Press, Cambridge.

McCollum, M., Sharpe, P.T. (2001). Developmental genetics and early hominid craniodental evolution. *BioEssays* 23:481–493.

Mendez, J., Keys, A. (1960). Density and composition of mammalian muscle. *Metabolism* 9: 184–188.

Mills, J.R.E. (1963). Occlusion and malocclusion of the teeth of primates, in: Brothwell, D.R. (ed.), *Dental Anthropology*, Pergamon Press, New York, pp. 29–52.

Mork, A.L., Wall, C.E., Williams, S.H., Garner, B.A., Johnson, K.R., Schmitt, D., Hylander, W.L., Vinyard, C.J. (2004). The biomechanics of tree gouging in common marmosets (*Callithrix jacchus*). *Am. J. Phys. Anthropol.* Supplement 40:158.

Napier, J.R., Napier, P.H. (1967). *A Handbook of Living Primates*. Academic Press, New York.

Oxnard, C. (1987). *Fossils, Teeth and Sex*. Hong Kong University Press, Hong Kong.

Plavcan, J.M. (1993). Canine size and shape in male anthropoid primates. *Am. J. Phys. Anthropol.* 92:201–216.

Powell, P.L., Roy, R.R., Kanim, P., Bellow, M.A., Edgerton, V.R. (1984). Predictability of skeletal muscle tension from architectural determinations in guinea pig hindlimbs. *J. Appl. Physiol.: Respirat. Environ. Exerc. Physiol* 57:1715–1721.

Rosenberger, A.L. (1978). Loss of incisor enamel in marmosets. *J. Mamm.* 59:207–208.

Ross, C., Hylander, W.L. (2000). Electromyography of the anterior temporalis and masseter muscles of owl monkeys (*Aotus trivirgatus*) and the function of the postorbital septum. *Am. J. Phys. Anthropol.* 112:455–468.

Sacks, R.D., Roy, R.R. (1982). Architecture of the hind limb muscles of cats: Functional significance. *J. Morphol.* 173:185–195.

Spector, S.A., Gardiner, P.F., Zernicke, R.F., Roy, R.R., Edgerton, V.R. (1980). Muscle architecture and the force velocity characteristics of the cat soleus and medial gastrocnemius: Implications for motor control. *J. Neurophysiol.* 44:951–960.

Spencer, M.A. (1999). Constraints on masticatory system evolution in anthropoid primates. *Am. J. Phys. Anthropol.* 108:483–506.

Sussman, R.W., Kinzey, W.G. (1984). The ecological role of the Callitrichidae: A review. *Am. J. Phys. Anthropol.* 64:419–449.

Swindler. D.R. (2002). *Primate Dentition: An Introduction to the Teeth of Non-human Primates*. Cambridge University Press, Cambridge

Szalay, F.S., Delson, E. (1979). *Evolutionary History of the Primates*. Academic Press, New York.

Szalay, F.S., Seligsohn, D. (1977). Why did the strepsirhine tooth comb evolve? *Folia Primatol.* 27:75–82.

Taylor, A.B. (2002). Masticatory form and function in the African apes. *Am. J. Phys. Anthropol.* 117:133–156.

Taylor, A.B. (2005). A comparative analysis of temporomandibular joint morphology in the African apes. *J. Hum. Evol.* 48:555–574.

Taylor, A.B. (2006a). Diet and mandibular morphology in the African apes. *Int. J. Primatol.* 27:181–201.

Taylor, A.B. (2006b). Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. *J. Hum. Evol.* 50:377–393.

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

Taylor, A.B., Eng, C.M., Anapol, F.C., Vinyard, C.J. (n.d.). The functional significance of jaw-muscle fiber architecture in tree-gouging marmosets, in: Davis, L.C., Ford, S.M., Porter, L.M. (eds.), *The Smallest Anthropoids: The Marmoset/Callimico Radiation*, Springer-Verlag, in press.

Teaford, M.F., Smith, M.M., Ferguson, M.W.J. (2000). *Development, Function and Evolution of Teeth*. Cambridge University Press, Cambridge.

Turnbull, W.D. (1970) Mammalian masticatory apparatus. *Fieldiana Geol.* 18:1–356.

Ungar, P. (1998). Dental allometry, morphology, and wear as evidence for diet in fossil primates. *Evol. Anthropol*. 6:205–217.

van Eijden, T.M.G.J., Turkawski, S.J. (2001). Morphology and physiology of masticatory muscle motor units. *Crit. Rev. Oral. Biol. Med*. 12:76–91.

van Eijden, T.M.G.J., Blanksma, N.G., Brugman, P. (1993). Amplitude and timing of EMG activity in the human masseter muscle during selected motor tasks. *J. Dent. Res*. 72:599–606.

van Eijden, T.M.G.J., Korfage, J.A.M., Brugman, P. (1997). Architecture of the human jaw-closing and jaw-opening muscles. *Anat. Rec*. 248:464–474.

Vinyard, C.J., Ryan, T. (2006). Cross-sectional bone distribution in the mandibles of gouging and non-gouging platyrrhines. *Int. J. Primatol*. 27:1461–1490.

Vinyard, C.J., Wall, C.E., Williams, S.H., Hylander, W.L. (2003). A comparative functional analysis of the skull morphology of tree gouging primates. *Am. J. Phys. Anthropol*. 120:153–170.

Vinyard, C.J., Wall, C.E., Williams, S.H., Schmitt, D., Hylander, W.L. (2001). A preliminary report on the jaw mechanics during tree gouging in common marmosets (*Callithrix jacchus*), in: Brooks, A. (ed.), *Dental Morphology 2001: Proceedings of the 12th International Symposium on Dental Morphology*, Sheffield Academic Press Ltd., Sheffield, UK, pp. 283–297.

Vinyard, C.J., Wall, C.E., Williams, S.H., Mork, A.L., Garner, B.A., de Oliveira Melo, L.C., Valença-Montenegro, M.M., Valle, Y.B.M., Monteiro da Cruz, M.A.O., Lucas, P.W., Schmitt, D., Taylor, A.B., Hylander, W.L. The evolutionary morphology of tree gouging in marmosets, in: Davis, L.C., Ford, S.M., Porter, L.M. (eds.), The Smallest Anthropoids: The Marmoset/*Callimico* Radiation, Springer, New York, in press.

Vinyard, C.J., Williams, S.H., Wall, C.E., Johnson, K.R., Hylander, W.L. (2005). Jaw-muscle electromyography during chewing in Belanger's treeshrews (*Tupaia belangeri*). *Am. J. Phys. Anthropol*. 127:26–45.

Wall, C.E., Vinyard C.J., Johnson, K.R., Williams, S.H., Hylander, W.L. (2006). Phase II jaw movements and masseter muscle activity during chewing in *Papio anubis*. *Am. J. Phys. Anthropol*. 129:215–224.

Weijs, W.A., Dantuma, R. (1981). Functional anatomy of the masticatory apparatus in the rabbit (*Oryctolagus cuniculus* L.). *Neth. J. Zool*. 31:99–147.

Weijs, W.A., Brugman, P., Klok, E.M. (1987). The growth of the skull and jaw muscles and its functional consequences in the New Zealand rabbit (*Oryctolagus cuniculus*). *J. Morphol*. 194:143–161.

Wottiez, R.D., Heerkens, Y.F., Huijing, P.A., Rijnsburger, W.H., Rozendal, R.H. (1986). Functional morphology of the m. gastrocnemius medialis of the rat during growth. *J. Morphol*. 187:247–258.