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Jaw-Muscle Structure and Function in Primates: Insights Into Muscle Performance and Feeding-System Behaviors

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ABSTRACT

The jaw-adductor muscles drive the movements and forces associated with primate feeding behaviors such as biting and chewing as well as social signaling behaviors such as wide-mouth canine display. The past several decades have seen a rise in research aimed at the anatomy and physiology of primate chewing muscles to better understand the functional and evolutionary significance of the primate masticatory apparatus. This review summarizes variation in jaw-adductor fiber types and muscle architecture in primates, focusing on physiological, architectural, and behavioral performance variables such as specific tension, fatigue resistance, muscle and bite force, and muscle stretch and gape. *Paranthropus* and *Australopithecus* are used as one paleontological example to showcase the importance of these data for addressing paleobiological questions. The high degree of morphological variation related to sex, age, muscle, and species suggests future research should bracket ranges of performance variables rather than focus on single estimates of performance.

1 | Introduction

In primates and other animals, variation in feeding behavior and diet is believed to influence functional and evolutionary morphology of the feeding system and to play an important role in species diversification. The jaw-closing or jaw-adductor muscles—the masseter, medial pterygoid, and temporalis —are 'motors' of the masticatory system. These muscles are responsible for producing the movements and forces that enable animals to orally prepare, ingest, bite, and masticate their food. Our evolutionary history and that of our primate relatives is recorded in bones and teeth, while soft tissue anatomy is not preserved in thee primate fossil record. Yet, as aptly noted by Witmer [1: 19], "…the evolutionary interpretation of the paleobiology of extinct organisms often *requires* explicit reference to anatomical systems other than the skeleton, that is, to those portions of the organism not normally preserved in the fossil record" (italics in the original).

Since the 1970s, in vivo experimental research using electromyography has demonstrated that primates recruit their chewing muscles in specific patterns. We therefore have a fundamental understanding of the order in which primates recruit their chewing muscles during mastication and how strongly they are recruited. By contrast, before the 21st century, scant attention had been paid to the macro- and microscale anatomy that underpins primate chewing muscle activity patterns. Thus, while knowledge of soft tissues was already recognized as being profoundly important for reconstructing phylogeny and drawing meaningful paleobiological inferences

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about function and behavior (e.g., [1–3]), by the end of the 20th century only a small number of researchers had documented or compared fiber types and their contractile properties [4–18] or fiber architecture [19–29] in primate chewing muscles, with the majority of these studies focusing on just two primates—humans and macaques.

Since the beginning of the 21st century, evolutionary anthropologists have shown a renewed interest in the anatomy of the chewing muscles. Why this resurgence? The reasons are varied. From a neontological perspective, researchers recognize that understanding the full biology of the masticatory system is important. The primate masticatory apparatus has been well studied using in vivo and comparative approaches, and consequently much is known about jaw movements, patterns of jaw-muscle recruitment, and how the jaws are stressed, strained, and deformed under various loading conditions (e.g., [30–36]). Variation in primate craniomandibular and dental morphology has also been extensively studied (e.g., [37–43]). Yet, historically, our knowledge of muscle anatomy trailed behind these other areas of investigation, leaving gaps in our understanding of how muscle morphology changes in relation to size, diet, and other oral nonfeeding behaviors that may exert selective pressures on feeding-system morphology, such as social behaviors involving wide-mouth canine display and aggressive biting.

Another reason for renewed interest is the application of models, such as those in finite element analyses (FEA), to test form-function hypotheses about the masticatory apparatus. Building and validating these models requires a variety of input parameters, including estimates of muscle force (e.g., [44]). Given that craniometric estimates of muscle force fall short of the level of accuracy desirable for such models (e.g., [45, 46]), direct measures of muscle structure and form are critical for FEA modeling. Further, methodological advances have moved beyond classical methods for visualizing and analyzing muscle architecture to take advantage of nondestructive innovations in three-dimensional (3D) scanning methods such as diffusible iodine-based contrast-enhanced computed tomography (diceCT) and ultrasonography. Extant primates are the primary source of referential material for characterizing the anatomy of extinct primate taxa, and the bones and teeth of extant primate collections have been exhaustively documented and measured. It therefore is not surprising that anthropologists have shifted their attention to understanding how the anatomy of the chewing muscles relates to the bony and dental anatomy of the masticatory system, what important information is being missed in our functional and evolutionary interpretations, and how we might be able to marshal and apply that information to yield greater insights into the paleobiology of primates.

In this paper, we begin with a brief review of the fundamentals of chewing muscle anatomy, physiology, and mechanics. Although our focus is on nonhuman primates, this review necessarily draws on work more broadly as much of the foundational work has been conducted on humans and nonprimate mammals. We provide sufficient background to facilitate understanding of the functional and evolutionary relationships between fiber types, muscle fiber architecture, and feeding-system behavior and performance, and refer those interested in more detail to a number of excellent textbooks and comprehensive review papers (see, e.g., [47–52]). We then examine variation in fiber types and fiber architecture of the chewing muscles in extant primates, their functional significance, and their application to paleobiological studies of primates. We focus largely on physiological and architectural variables that have been closely linked to jaw-muscle function and performance, such as fatigue resistance, contractile velocity, specific tension, muscle force and stretch, and on behaviors that depend on jaw-muscle performance, such as bite force and gape, although we note these are not the only performance measures of the primate feeding system. We examine how these performance variables ultimately contribute to the wide variety of feeding and other oral nonfeeding behaviors observed in extant primates and their implications for reconstructing the paleobiology of primates. We conclude by considering directions for future research.

2 | Skeletal Muscle Anatomy and Physiology

2.1 | The Chewing Muscles

Muscles of mastication are branchiomeric (pharyngeal arch) muscles that derive from head (or cranial) mesoderm [53, 54]. Their genetic basis and embryological origins are thus distinct from all other skeletal muscles. In jawed vertebrates, the first pharyngeal arch gives rise to the four paired muscles of mastication—the masseter, temporalis, medial and lateral pterygoid muscles—the first three comprising the jaw adductors (also known as jaw-closing or jaw-elevator muscles). Though these are not the only mandibular muscles, these are the primary muscles involved in generating mandibular movements and occlusal forces (the forces between the upper and lower teeth in contact with each other or with food [32]) used in chewing, biting, and other feeding behaviors, and are thus the focus of much of the fiber type and muscle architecture work on the primate masticatory system. Far fewer studies have examined the lateral pterygoid, reflecting the distinct functional roles of this muscle (but see work in References [22, 55, 56]). Other muscles that act on the mandible, such as the anterior digastric, are comparatively less well studied in primates. Together, these two muscles can be referred to as the jaw-abductor muscles (e.g., [56]).

Each of the three jaw adductors originate on the cranium and insert on the mandible (Figure 1). While the general position of these muscles on the skull is similar across primates, variation in skull morphology can certainly result in differences in fiber orientation. The masseter can be divided into two portions: the superficial masseter is the larger of the two and runs from the inferior border of the zygomatic arch to insert onto the angle of the mandible; the smaller portion is the deep masseter [23], which is more vertically oriented and runs from the medial surface of the zygomatic arch to its insertion on the lateral aspect of the mandibular ramus, superior to the level of insertion of the superficial masseter (Figure 1). We do not differentiate here between the deep masseter and separate, deeper portions of the masseter (e.g., zygomatico-mandibularis; *sensu* [23, 57, 58]; see, e.g., [59]). The superficial and deep masseter muscles function to elevate the jaw. When acting unilaterally, the masseter produces side-to-side translation and thus can also laterally deviate the mandible.

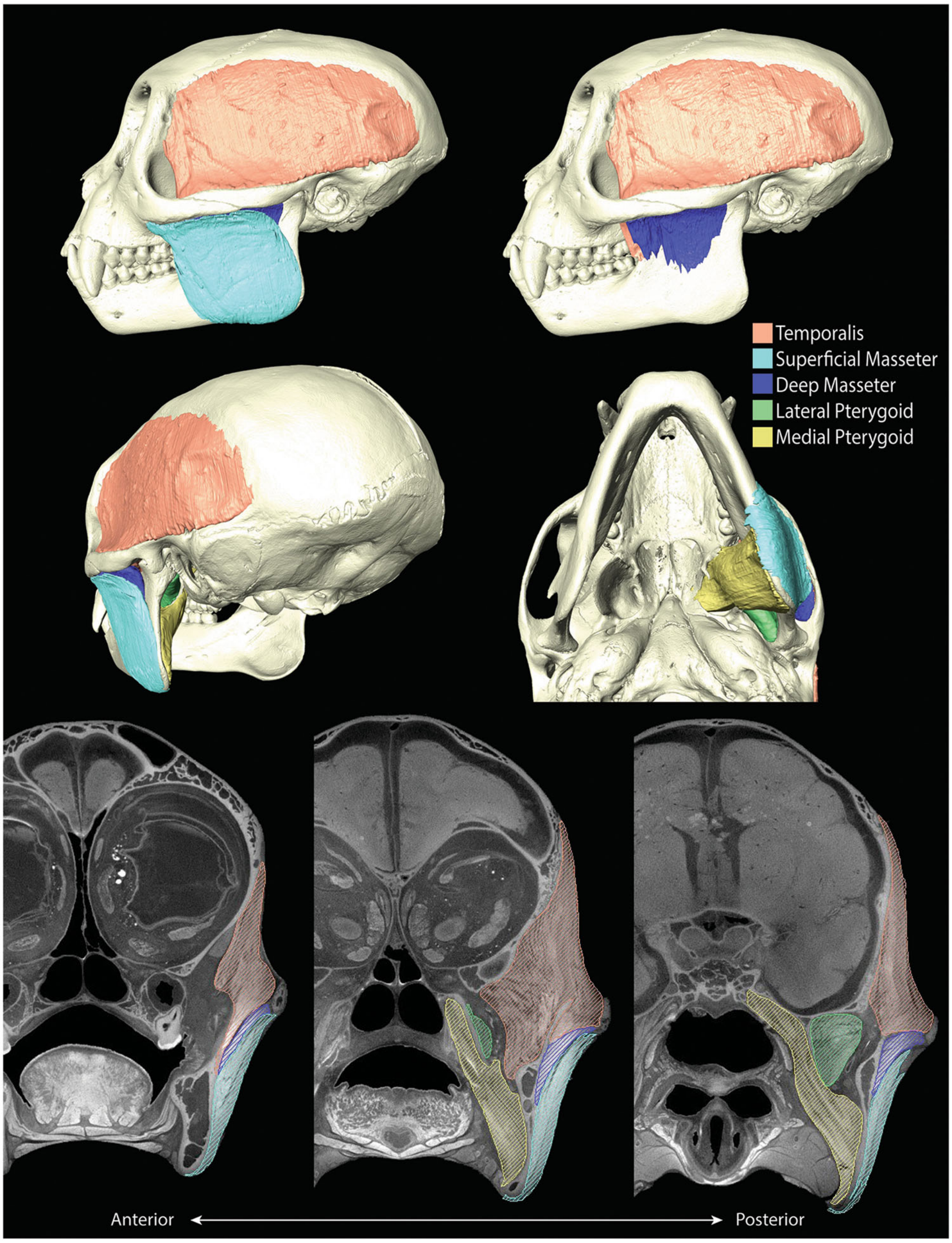


FIGURE 1 | False-color rendering of an adult male *Cebus* sp. skull showing positions of the masticatory muscles on a surface model of the skull (top) and in cross-section (microCT, bottom). Top left shows lateral view with all muscles in anatomical position, while top right shows lateral view with the superficial masseter (light blue) removed to make the deep masseter (dark blue) visible. Middle left is an oblique/posterior view showing the temporalis, masseter, and pterygoid muscles, and middle right is an inferior view showing the masseter and pterygoid muscles. This specimen was diceCT stained to make the soft tissues visible and then muscles were digitally segmented to assign voxels to particular muscles.

The medial pterygoid muscle also consists of two portions in some primate species. The larger deep portion originates from the pterygoid fossa and the medial aspect of the lateral pterygoid plate, whereas the smaller superficial portion originates from the area around the maxillary tuberosity. Both portions merge and attach to the medial surface of the angle of the mandible (Figure 1). Orientation of the medial pterygoid muscle is similar to that of the masseter, functioning bilaterally to elevate and protrude the jaw and acting unilaterally to produce side-to-side translation.

The temporalis muscle can be described as fan-shaped and originates from the temporal fossa of the cranium (Figure 1). This muscle can be somewhat arbitrarily subdivided into anterior, middle, and posterior portions based on the orientation of fibers on the skull, all of which pass inferiorly in the space formed between the zygomatic arch and the skull. The fibers further converge into a tendon that inserts into the coronoid process and a portion of the mandibular notch, as well as along the anterior and medial aspects of the mandibular ramus. Similar to the masseter, the temporalis can be divided into superficial and deep portions separated by a central myotendinous junction. As a result, the fibers in the superficial portion include a component of force that is directed laterally and the deep portion includes a medially directed force component [60]. The anterior temporalis fibers are oriented vertically and primarily elevate the jaw, whereas the posterior fibers are oriented more horizontally, thus playing an important role in retracting the mandible (in addition to some elevation) [61–63].

Like the masseter and medial pterygoid, the lateral pterygoid (Figure 1) consists of two heads. The superior head originates from the greater wing of the sphenoid medial to the infratemporal crest, while the larger inferior head originates from the lateral aspect of the lateral pterygoid plate. Both heads run horizontally and posteriorly to insert on the medial aspect of the neck of the mandibular condyle, with a small portion of the superior head also attached directly to the temporomandibular joint capsule and the articular disc (e.g., [64, 65]). Acting bilaterally, this muscle functions primarily to protrude the mandible, and unilaterally to produce side-to-side movements. It also has an important role in controlling condylar movements during jaw closing. Secondarily, the lateral pterygoid aids the digastric in depressing the mandible by pulling the mandibular condyle down onto the articular eminence during jaw opening.

The digastric muscle is a composite of contributions from the first (anterior belly) and second (posterior belly) pharyngeal arches. These two distinct muscle bellies are connected by an intermediate tendon that attaches to the hyoid via a tendinous pulley. The anterior belly attaches anteriorly to the digastric fossa of the mandible and the posterior belly attaches to the medial aspect of the mastoid process. In humans and other primates, the structure of this muscle varies considerably. For example, orangutans entirely lack the anterior belly and there is a wide range of anatomical variants documented for humans (e.g., [66–68]). The function of this muscle varies depending on whether the mandible or hyoid is fixed. If the hyoid is fixed by the infrahyoid muscles, contraction of the digastric acts to depress the mandible; conversely, if the mandible is fixed in place by the jaw adductors, the digastric functions to elevate the hyoid, as occurs during swallowing.

2.2 | Skeletal Muscle Structure and Function

The masticatory muscles, like other skeletal muscles, are a collection of fascicles contained within fibrous connective tissue (epimysium; Box 1). Most skeletal muscles attach to bone via tendons, which are formed by the continuation of the epimysium and do not have contractile properties. Within each fascicle is a group of muscle fibers that are held in place by surrounding connective tissue (perimysium). Each muscle fiber is an elongated, multinucleated cell, surrounded by loose connective tissue (endomysium) and containing hundreds of nuclei [48]. Muscle fibers typically do not run the full length of a muscle and generally do not run the full length of a fascicle.

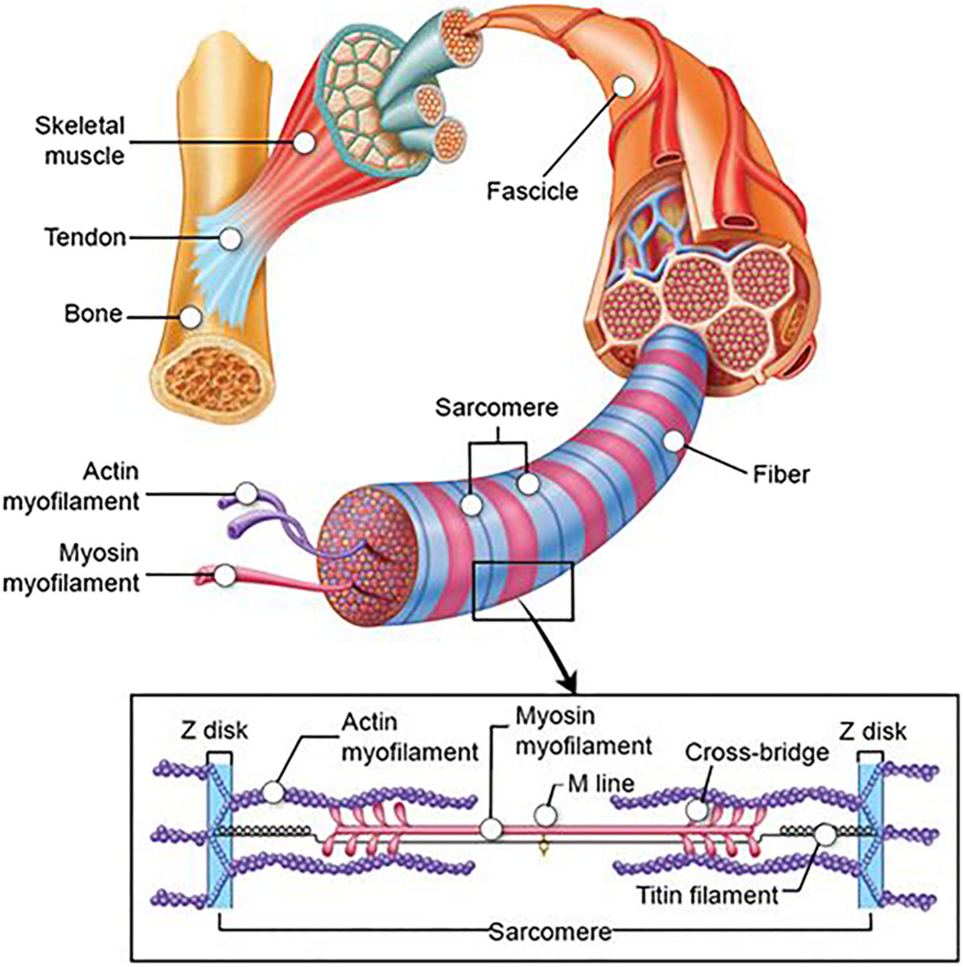
The initiation of contractile activity is through an action potential or electrical signal conveyed to a muscle fiber through a motor neuron. Motor neurons can extend to single fibers in small muscles, but for muscles like the jaw adductors, motor neurons typically extend to many muscle fibers forming a motor unit [73]. For a low-force contraction, only a small subset of the total muscle motor units will be activated, and if more force is needed, additional motor units will be recruited. Active motor units move the jaw and produce bite force by changing fiber lengths, fiber tension—defined as the force generated during muscle contraction—or both. An isotonic contraction maintains muscle tension while fibers either shorten (concentric contraction) or lengthen (eccentric contraction). As an example, the masseter muscle is active concentrically as the jaw closes and eccentrically when the jaw opens. An isometric contraction occurs when tension is generated but muscle length stays the same. Isometric contractions are important for mastication as most bite force production during the chewing cycle occurs when the teeth are near occlusion, thus involving little change in muscle length. In mammals, a chew cycle (also known as a 'gape' or 'masticatory' cycle), is commonly divided into a series of phases: the closing stroke, a power stroke, and an opening stroke [30, 32] (Box 2). When moving the jaw and producing bite forces, such as during chewing, the masticatory muscles are not all active at the same time. Instead, during rhythmic chewing, these muscles are active in specific motor patterns that facilitate both vertical and transverse jaw movements, precise occlusion of the teeth, and isometric bite force production.

Functional morphologists have extensively studied muscle activation patterns of the chewing muscles in mammals, including primates. Although there are clade- and species-level differences, mammals are thought to have a uniform activity pattern during mastication [32]. Weijs [76] proposed a series of five motor patterns for mastication by dividing the adductor muscles into pairs of three working- or balancing-side muscles active in a sequence (i.e., 'triplets'). Weijs [76] suggested that these patterns could be modified in specific taxa as seen in differences in the timing of the balancing-side deep masseter in anthropoids [77]. Subsequent work has examined how and when these patterns appeared during mammalian evolution and whether they are conserved across mammals [32, 36, 78–88]. More recent work explores whether mammalian patterns of jaw movements may have been present before the origins of mammals [89, 90]. Some studies have suggested the mammalian pattern is conserved within primates [32, 76, 78, 91, 92], although it is important to note that muscle activation patterns within primates have distinct evolutionary histories and vary with morphology [36, 62, 77, 85, 93]. One such example is muscle activation patterns during mastication in relation to symphyseal fusion. Anthropoids have a fused mandibular symphysis whereas strepsirrhines have an unfused or partially fused symphysis [94, 95]. Weijs [76] suggested these taxa should differ in their triplet patterns as the two halves of the mandible can move independently in strepsirrhines whereas the fused symphysis in anthropoids allows the mandible to move as a unit and effectively transfer muscle forces [96–100]. However, primates exhibit large amounts of variability in masticatory motor patterns, and strepsirrhines and anthropoids share jaw-adductor activation patterns at peak activity, but not at the start or end of muscle activity [101, 102].

2.3 | Muscle Mechanical Advantage

The positioning of the jaw adductors on the skull provides a mechanical constraint on the ability of the muscles to move the jaw and generate bite force (Box 3). The mandible

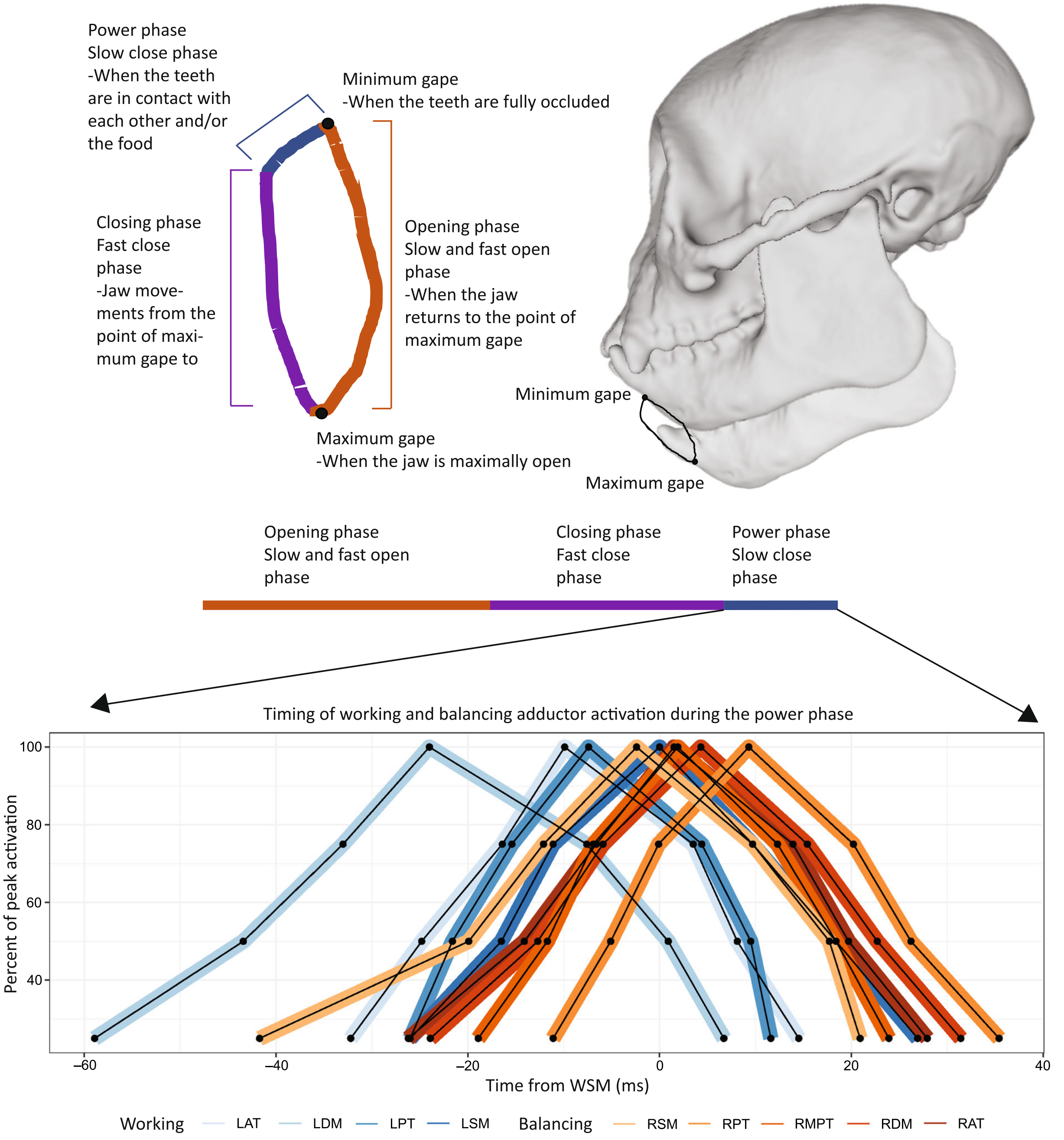
BOX 1 | Anatomy of a skeletal muscle



Each muscle fiber comprises several hundred to several thousand fibers, consisting of repeating filaments called sarcomeres, which give skeletal muscle its 'banded' or striated appearance. The sarcomere is the functional unit of contraction and is composed of two protein filaments—actin and myosin. Actin is a thin filament with a double helix shape whereas myosin is a thicker filament. The actin filament contains a polypeptide chain of tropomyosin, whereas molecules of troponin are attached to the myosin filament. Sliding filament theory of muscle contraction proposes that cross-bridges, connections between myosin and actin, initiate movement by the troponin proteins swiveling in their position on the myosin filament to propel the filaments past each other [69, 70]. Movement resulting from a single cross-bridge is limited, so after swiveling, the myosin troponin detaches from the actin tropomyosin and reattaches to a tropomyosin further along the polypeptide chain [71, 72]. This results in greater overlap between the actin and myosin filaments toward the center of the sarcomere [48]. Movement and detachment of cross-bridges within a sarcomere and across a muscle are not synchronized, and only a portion of the total possible cross-bridges is involved in any contraction [71]. Running through the overlapping actin and myosin in a sarcomere is a third filament, titin, an exceptionally large protein that maintains its position during contraction and relaxation and acts as a 'muscular spring' to aid in passive tension [48]. Image modified from: https://pressbooks.ccconline.org/bio106/chapter/muscular-levels-of-organization/.

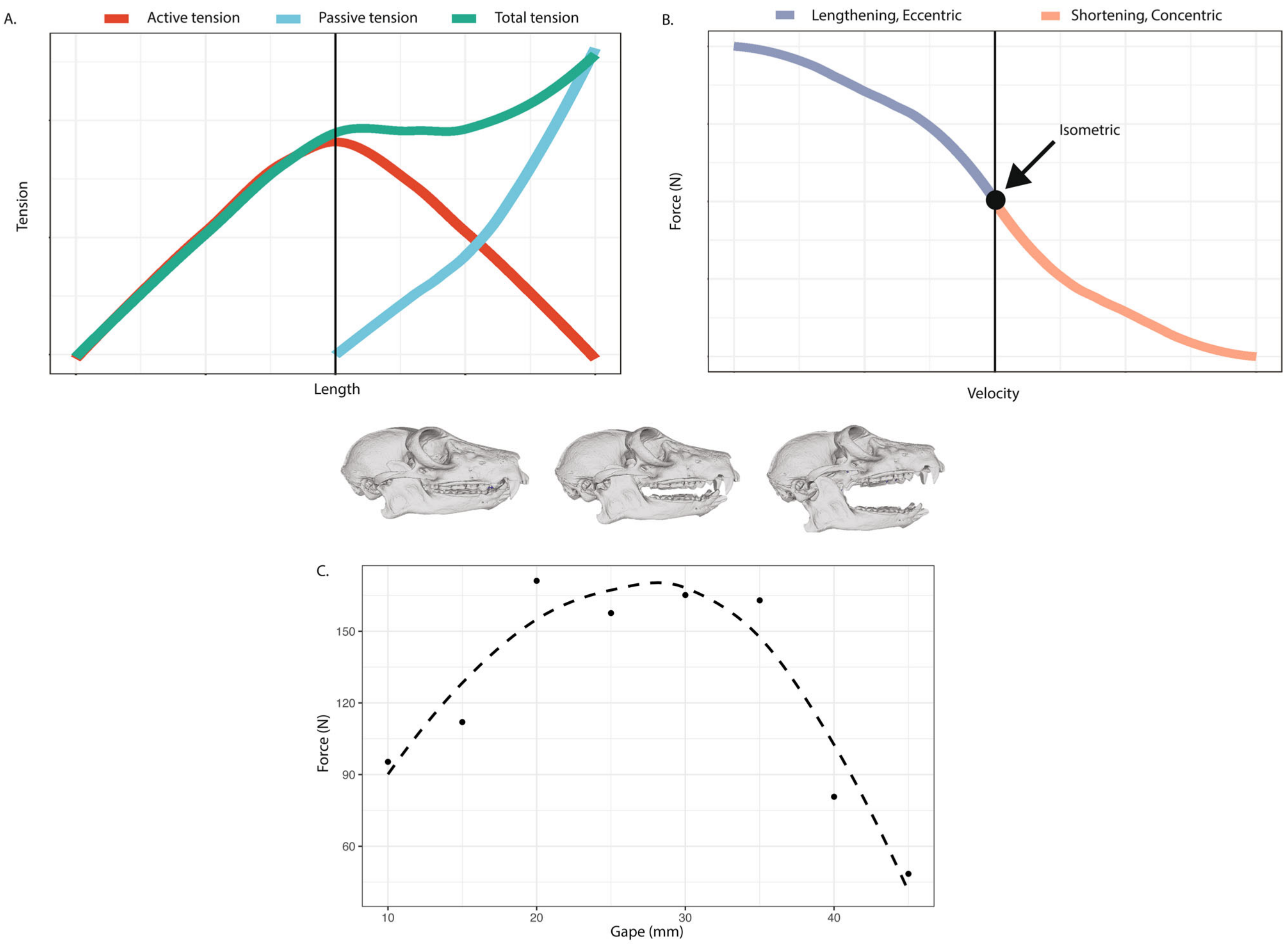
functions as a third-class lever [120], and like any lever system, placement of the fulcrum, effort, and load determines the mechanical advantage. Unilateral jaw mechanical advantage is the ratio of the in-lever (i.e., the distance from the axis of rotation below the mandibular condyle to the jaw adductor resultant) to the out-lever (i.e., the distance from the axis of rotation below the mandibular condyle to the bite point). Other things being equal, a primate with a relatively long face (prognathic), such as a baboon, would produce relatively less force at the incisors due to a longer out-lever, and therefore less favorable mechanical advantage, compared to a more orthognathic primate like a colobine. The jaw adductor resultant is further constrained as it must pass through a 'triangle of support,' drawn between the two mandibular condyles and the bite point, to avoid distractive forces at the temporomandibular joint (TMJ) that can result in dislocation and joint pathological conditions [121–123]. Loading occurring within the triangle of support avoids these forces. This triangle of support constraint on the jaw adductor resultant has been related to molar emergence across primates [124].

BOX 2 | The chewing cycle



This figure depicts the two-dimensional kinematics of a typical chewing cycle (top) and pattern of peak muscle activation (bottom) from tufted capuchins (*Sapajus* sp.). A chew cycle is defined from the point of maximum gape to minimum gape and the subsequent return to maximum gape [74], and can be subdivided into opening, closing, and power phases (for a recent discussion, see [75]). Primates typically chew on one side of the mouth at a time (i.e., unilaterally). Within a given chew cycle, the side of the mandible on which the food is chewed and the mandible is loaded is referred to as the 'working side' and the opposite side is the 'balancing side.' The timing of peak muscle activation differs by muscle and between the working (blue) and balancing (orange) sides. From the point of maximum gape, here, the working side posterior temporalis (blue, LPT) is activated first to initiate jaw retraction and guide the working side mandibular condyle around the articular eminence. This is followed by activation of the left middle and anterior temporalis (blue, LAT), left medial pterygoid, and left superficial masseter (blue, LSM) to elevate the lower jaw. Next the balancing side anterior temporalis (orange, RAT) is activated, followed by the middle temporalis, and then finally posterior temporalis (orange, RPT) on the balancing side. These jaw adductors guide the jaw closed and the teeth into precise occlusion during which bite forces are generated—'the power stroke.' Following the point of maximum occlusion, activation of the jaw adductors ends. The jaw begins to open through concentric activation of the jaw openers and the cycle begins again. Muscle abbreviations: LAT-left anterior temporalis, LDM-left deep masseter, LPT-left posterior temporalis, LSM-left superficial masseter, RSM-right superficial masseter, RPT-right posterior temporalis, RMPT-right medial pterygoid, RDM-right deep masseter, and RAT-right anterior temporalis.

BOX 3 | Muscle functional properties



For a single fiber, maximum active tension (or force) can be produced when the sarcomeres are at their resting length, which means the actin and myosin filaments maximally overlap and have the maximum number of cross-bridges (A). If the sarcomeres are shorter than their resting length, active tension decreases resulting in decreased force output. Similarly, lengths stretching the sarcomere beyond resting length have reduced filament overlap and fewer cross-bridges resulting in lower active tension and force. Muscles stretched beyond their resting point have an exponential increase in passive tension, that is, resistance from a sarcomere generated when a muscle is stretched. Titin, the large protein running through a sarcomere (Box 1), is proposed to play an essential role in generating passive tension during muscle stretching [103]. Passive tension increases as gape increases and contributes to reduced bite force production at larger gapes. While passive tension in primate muscles is not well studied, data from rabbits and miniature pigs suggest mandibular rotation can counteract passive tension to facilitate bite force production over a range of gapes [104, 105]. This is modeled as length-tension relationships (A) [106, 107]. In addition to length, the force a muscle can produce is also dependent on the speed of contraction—i.e., the force-velocity relationship (B). During concentric contraction, sarcomeres contracting at higher velocities have fewer myosin heads bound to actin filaments, which results in a decrease in force output [48, 108–110]. When velocity is zero, or during isometric contraction, force is larger than during concentric activation. In contrast, eccentric contraction results in higher force output as myosin and actin bind. This means that primates have a gape at which they can produce maximum muscle force, and presumably bite force, and gapes that are larger or smaller than this optimum result in lower forces. This theoretical tradeoff between muscle force and muscle stretch was modeled by Herring and Herring [111] and subsequently supported by experimental data in a range of animals [112–115] including primates [116–118]. (C) An in vivo bite force-gape curve for one adult, a female *Varecia variegata* recorded at the Duke Lemur Center [119]. Here, bite forces increase until approximately 28 mm of gape and decrease with larger gapes.

3 | Chewing Muscle Fiber Types in Mammals

Fiber types play an important role in regulating muscle function and 'fine tuning' muscles for specific motor tasks. Broadly speaking, fiber type diversity in mammalian jaw adductors has been linked to variation in feeding behavior and performance. Performance variables such as the forces associated with chewing and biting are influenced by the interaction between fiber type variation and whole muscle structure within the bony skull. In this regard, understanding variation in fiber type composition and distribution is important for research that aims to link primate feeding system morphology with feeding behavior and diet. Importantly, heterogeneity of fiber types in the chewing muscles, combined with the inherent plasticity of fiber types, affords a level of flexibility to the feeding system that is not reflected in either the bones or teeth, but that likely impacts feeding system performance. Below we review muscle fiber types and their physiological properties and consider the myosin heavy chain and fiber type diversification in primates. We then summarize fiber type data for primates and examine patterns of variation and their functional and evolutionary significance.

3.1 | Mammalian Fiber Types and Their Physiological Properties

Methods for identifying skeletal muscle fiber types and their physiological properties have changed substantially over the last 80 years. Early work based on metabolic, morphological, and functional profiles of animal and human limb muscles resulted in the well-known Type 1 (slow, fatigue-resistant) and Type 2 (fast, fatigable) fiber classifications [125–130]. Type 1 fibers are energy efficient—they contract at a slow rate, have high endurance, and a low tension cost. By contrast, Type 2 fibers have faster contraction times, fatigue more rapidly, and have a high tension cost [131–133]).

Later studies focused on identifying fiber types based on the myosin heavy chain (MHC) composition by utilizing immunohistochemical (IHC) staining or gel electrophoresis [134, 135]. Myosin is the protein expressed in greatest abundance in skeletal muscle and specific genes encode specific MHC protein isoforms. Myosin heavy chain proteins largely determine the contractile properties of mammalian muscle fibers, including maximum shortening velocity, adenosine triphosphate (ATP) consumption rate, specific tension, and tension cost [134, 136–141]. Specific tension is the maximum force a muscle can generate per unit cross-sectional area [142] and has largely been measured using single fibers from limb muscles, focusing on MHC-β (or MHC-1/slow) and MHC-2 (e.g., [143, 144], reviewed also in [145]). Importantly, far fewer studies have measured specific tension in mammalian jaw adductors [146–148], and no studies have documented specific tension in any primate jaw adductor. As we discuss below, the array of myosin expression found in mammalian jaw-adductor muscles produces a wide range of contractile properties. However, the lack of data on the contractile properties of primate chewing muscles hampers establishing clear relationships between primate fiber types and their functional characteristics.

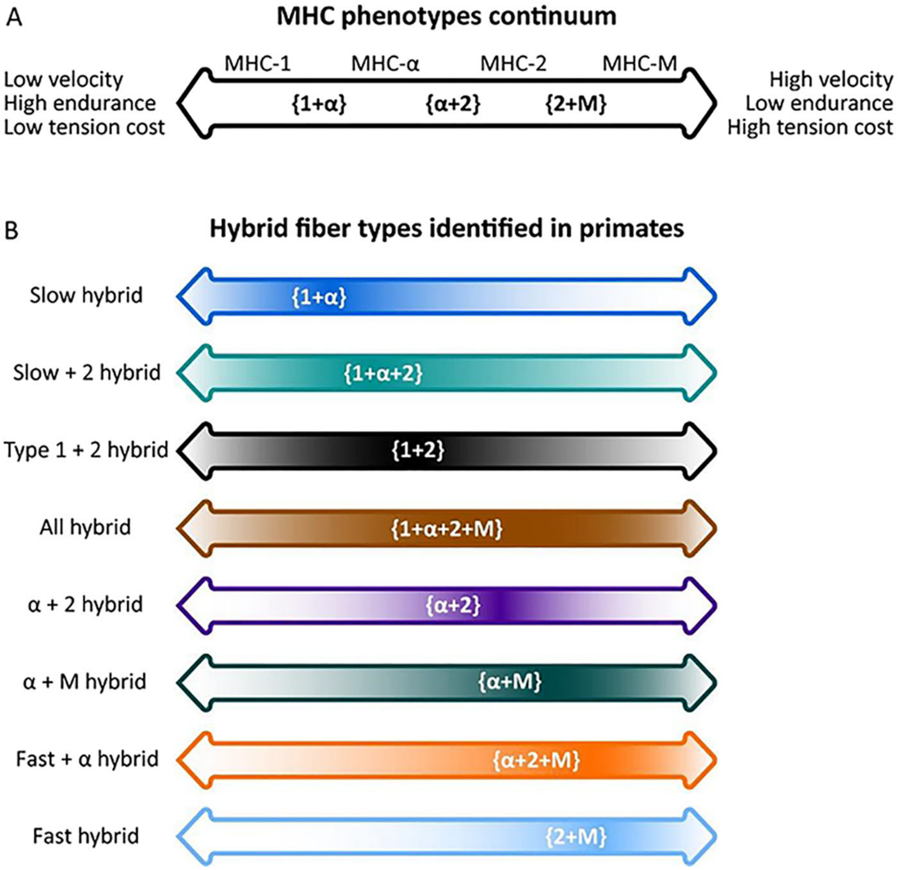
3.2 | The Myosin Heavy Chain in Mammalian Jaw-Adductor Muscles

The ability to identify and quantify MHC expression using IHC and gel electrophoresis led to a major advancement in characterizing the diversity of mammalian skeletal muscle fiber types. The expression of four major MHC isoforms has been identified in adult mammalian limb muscles: MHC-β, MHC-2A, MHC-2X, and MHC-2B. Later studies showed that the jaw adductors of adult mammals express a much greater diversity of MHC isoforms than the limb muscles (more on this below; see also [47, 149], for reviews). The initial discovery of additional myosins in mammalian jaw-closing muscles, including masticatory, α-cardiac (or MHC 1-alpha), and neonatal, was made in a variety of nonprimate mammals and/or humans (Box 4; Supporting information Table 1).

Masticatory myosin has now been reportedly expressed in the jaw-closing muscles of a wide variety of vertebrates including sharks [150] and crocodiles [151], indicating this is a phylogenetically ancient MHC isoform, as well as in some marsupial carnivores and possums (Hoh and Kang, unpublished observations, as reported in [149]), rodents such as the Eastern gray squirrel (*Sciurus carolinensis* [152]), and a variety of primate taxa [16, 145, 153, 154]. Masticatory myosin is not expressed in humans [16] though humans carry the MYH16 gene that encodes this protein [155]. Based on single fiber studies of domestic dog and cat masseter and temporalis, type 2M fibers have been shown to have shortening velocities and rates of tension redevelopment similar to Type 2A fibers, but significantly greater than Type 1 or Type 2A/2X/2B fibers [148]. In other words, masticatory myosin produces exceptionally high tension (force per unit cross-sectional area) but at moderately fast contraction velocity comparable to MHC-2A in the limb muscles. Myosin heavy chain α-cardiac was initially identified in the jaw-closing muscles of adult humans and rabbits [156] and subsequently reported to be expressed in kangaroos [157], marsupial possums (Hoh and Kang, unpublished observations as reported in [149]), and both anthropoid [145, 153, 154] and strepsirrhine primates (Taylor and Holmes, unpublished observations). Single fiber studies in rabbit masseter indicate that the α-cardiac isoform has a maximum shortening velocity intermediate between Type 1 and Type 2 fibers [140, 158] and a specific tension that might be even lower than Type 1 fibers, though more data are needed to confirm this [146]. Adult mammalian jaw-closing muscles are reported to express as many as eight MHC isoforms: MHC-β, MHC-α, MHC-2A, MHC-2X, MHC-2B, and MHC-M, as well as MHC-neo and MHC-embryo. In this paper we focus on the four major adult myosins expressed in mammalian jaw-adductor muscles: MHC-β, MHC-α, MHC-2, and MHC-M (Box 4).

In addition to the expression of a greater number of pure MHC isoforms in mammalian jaw-adductor muscles compared with limb muscles, these two regions can be further distinguished by the expression of hybrid fibers. Hybrid fibers (sometimes referred to as 'mixed fibers') co-express two or more isoforms along the length of the fiber [159] (Box 4; Figure 2). Both head and limb muscles express hybrid fibers. However, across eutherian mammals, jaw-closing muscles generally express both a greater abundance and greater variety of hybrid fibers compared with limb muscles (see [49] for a review). Moreover, while hybrid patterns in mammalian limb muscles tend to comprise a mix of 'nearest neighbor' pure isoforms (e.g., MHC-1/2A, MHC-2A/2X, MHC-2X/2B [49, 160]), hybrid patterns in mammalian jaw-closing muscles often co-express two or more isoforms from across the MHC continuum. Fiber type studies in humans [161–163], rabbits [131, 158, 164], and pigs [165] suggest that hybrid fibers display physiological properties (specific tension, velocity of shortening, stretch-activation kinetics, energy expenditure) that are intermediate to the constituent pure isoforms that contribute to the hybrid fiber type. It has been suggested that patterns of expression of hybrid fibers are tightly developmentally controlled [166]. This is based on observations that far fewer hybrid patterns are expressed compared with the maximum number of possible expression patterns in a given muscle. As discussed in Section 4.1, differences in specific tension across

BOX 4 | The myosin heavy chain continuum



(A) The four major MHC isoforms expressed in mammalian jaw-adductor muscles and (B) hybrid fiber types identified in primate jaw-adductor muscles. The contractile properties of MHC isoforms exist along a continuum, from isoforms that are slow-contracting, fatigue resistant, with low tension cost (A, left side) to faster, more fatigable isoforms, with higher tension cost (A, right side). Hybrid fiber types occur when multiple MHC isoforms are present within a single muscle cell and are most commonly formed between nearest-neighbor pure isoforms such as those bracketed within the top arrow (A). (B) Our work on primate jaw-closing muscles has revealed a greater array of hybrid fiber types with up to eight different hybrid patterns identified across our African ape, papionin, and platyrrhine tissue samples. Based on previous work demonstrating that hybrid fiber contractile properties are intermediate between their constituent pure fiber types, the hybrid fiber types in this figure have been placed along the continuum to approximate their intermediate operational range. However, this is only a schematic as the actual contractile properties of hybrid fibers in primate chewing muscles have not yet been determined. MHC-1 = MHC-β; MHC-α = MHC 1-alpha or alpha-cardiac.

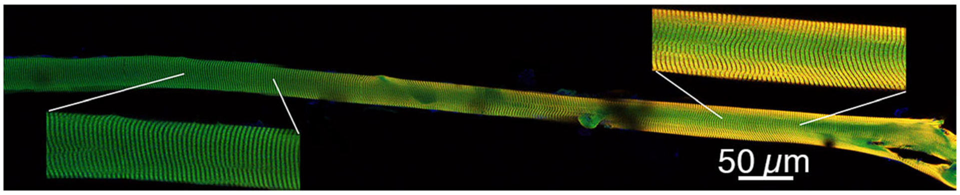


FIGURE 2 | Image of a single mouse muscle fiber dissected from the soleus used to demonstrate how multiple myosin heavy chain (MHC) isoforms can exist as a gradient in one cell. This hybrid fiber was stained using two monoclonal antibodies for MHC-1 (red—A4.74) and MHC-2A (green—A4.74). The yellow coloration represents regions of co-expression for MHC 1/2A. Note the gradual transition from green (MHC-2) on the left to yellow on the right of the fiber. Insets show the indicated regions at higher magnification (50 μm). Reproduced with permission from Medler [49]. https://doi.org/10.1242/jeb.200832.

pure and hybrid MHC isoforms have important implications for estimating muscle and bite force in both extant and fossil taxa.

3.3 | The Myosin Heavy Chain Continuum and Jaw-Adductor Fiber Types in Primates

Adult primate jaw-adductor muscles express the same four major MHC isoforms expressed in the jaw adductors of nonprimate mammals (Box 4). Studies quantifying MHC expression in primate masticatory muscles have focused on the superficial masseter and temporalis muscles, with fewer studies reporting on the deep masseter or medial pterygoid (e.g., but see [16, 167]). Collectively, these studies have been organized around two primary aims. One aim has been to document and describe within-species variation in masticatory muscle fiber types, such as intra- and intermuscular variation as well as variation related to sex and development (e.g., *Macaca mulatta* [8–10]; humans [4, 168]; tufted capuchins [*Sapajus apella*] [169]; olive baboons [*Papio anubis*] [170]; common chimpanzees [*Pan troglodytes*] [167, 171]). The second aim has been to document and compare fiber type composition broadly across mammals (e.g., [16, 172]), and more specifically across primates [145, 153], and to relate this variation to feeding behavior.

Variation in MHC expression within and between the chewing muscles is evident in multiple primate species. Adult rhesus macaques, for example, express a higher proportion of slow, Type I fibers in the anterior portions of the masseter and temporalis compared with the posterior portions of these muscles [8]. By contrast, common chimpanzees express roughly similar amounts of MHC-β in the anterior and posterior portions of both the masseter and the temporalis [167, 171]. Sexual dimorphism in both fiber type expression and fiber cross-sectional area has been reported in some species. For example, compared to male conspecifics, female rhesus macaques and olive baboons show a higher prevalence of Type 1 fibers in the temporalis and have significantly smaller cross-sectional areas in fibers that express fast fiber types [8, 170]. It has been argued that this fiber type dimorphism reflects greater fatigue resistance and/or energy savings, which would be advantageous if females need to recruit more deep anterior temporalis fibers, or to recruit deep anterior temporalis fibers more frequently than males to maintain adequate bite force during chewing.

3.4 | Fiber Type Development in Primate Chewing Muscles

Jaw-muscle fiber-type phenotype is not static. Rather, muscle is a highly plastic tissue that can respond to and be modified by intrinsic (e.g., genetics, hormones, neuromuscular activity, aging) and extrinsic factors (e.g., loading environment) [47, 51, 162, 173]. Fiber type diversification during development varies between individuals, jaw muscles, and jaw muscle region [162, 174–177]. The importance of the loading environment on development of adult masticatory muscle fiber phenotype is supported by experimental studies—rearing animals on soft foods or a liquid diet significantly impacts their developing fiber type expression and fiber size when compared to controls, and the impact is most pronounced in the jaw-closing (vs. jaw-opening) muscles [178–180] (see also [50], for a thorough review). Few studies have analyzed fiber type development in the jaw-closing muscles of primates. In humans, juveniles (aged 3–7 years) have been shown to express a significantly slower masseter fiber type (Type 1) than adults [181], while rhesus macaques show little difference between juvenile (age unspecified) and adult fiber type expression in either the masseter or temporalis [8]. However, fiber size (diameter) increases substantially from subadults to adults [8, 181]. A recent ontogenetic study of capuchin monkeys found that tufted capuchins develop a notably more heterogeneous fiber type expression in the masseter compared with untufted capuchins [182].

3.5 | Anthropoid Primate Jaw-Adductor Muscles Are Dominated by Hybrid Fiber Types

The average percentage of hybrid fibers in human jaw adductors has been reported as ranging from 30% for the temporalis to as much as 51.5% for the medial pterygoid [162]. Hybrid fiber percentages and combinations in the jaw adductors of nonhuman primates exceed these estimates for humans [145, 153, 170]. Across the anthropoid suborder, the jaw adductors have been shown to express as many as eight different hybrid combinations (Box 4). The two most commonly expressed patterns across species are the slow + 2 and fast + alpha hybrids, with additional combinations reported in respectable amounts. Even co-expression of all four MHC isoforms has been reported, though this pattern represents a very small fraction ($< 4\%$) of the total fiber type profile at the level of the clade; this is because it is exceedingly rare to find the co-expression of MHC-β with MHC-M (Figure 3).

Among the anthropoid primates sampled to date, hybrid fiber type proportions show within-species variation among individuals, between sexes, and between muscles/muscle regions, as well as between species and across clades. In a sample of tufted capuchins, for example, individuals ranged from co-expressing two to three hybrid patterns in the anterior superficial masseter to two to four hybrid patterns in the anterior temporalis, and within each muscle individuals varied in the hybrid combinations expressed [145]. Looking across muscle regions, in a sample of male *Pap. anubis*, 22.9%–100% of fibers in the deep anterior temporalis co-expressed both MHC-1 and MHC-2 compared with only 3.2%–10% in the superficial anterior temporalis and 1.8–2.2% in the superficial posterior temporalis [170]. However, in the study by Wall et al. [170], the antibodies used only allowed for quantifying the percentages of Type 1 and Type 2 fibers, masking the full extent of hybrid fibers and hybrid fiber combinations. In a sample of common chimpanzees (*Pan troglodytes*) the fast + alpha hybrid ranged from 57% in the deep anterior temporalis to 71% in the superficial anterior temporalis [153]. In a sample of gorillas (*Gorilla gorilla*), the co-expression of the slow + 2 hybrid ranged from 33% in the superficial anterior temporalis to 57% in the anterior superficial masseter to 91% in the deep anterior temporalis [153]. Again, fibers co-expressing MHC-1 and MHC-M were exceptionally rare (1%–3% at the clade level).

The take-home from these studies is that the MHC continuum in primate jaw adductors is represented by large amounts of hybrid fibers. It seems likely these hybrid patterns provide for a more finely partitioned continuum of contractile properties as well as greater flexibility in jaw-muscle function compared with nonprimate

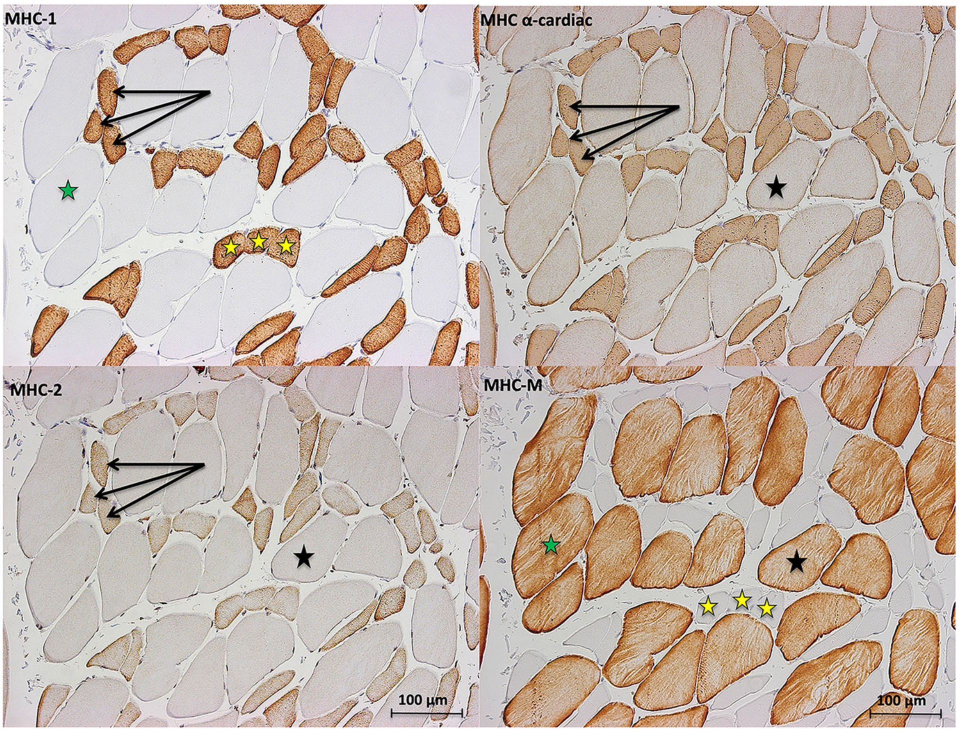


FIGURE 3 | Serial sections (5 μm) of an adult male *Cercocebus atys* (ABT6) temporalis muscle showing the expression of MHC-1 (NOQ7.5.4D, upper left), MHC-alpha (MYH6, upper right), MHC-2 (MY-32, lower left), and MHC-M (2F4, lower right). Black arrows point to small diameter fibers that co-express MHC-1, MHC-alpha, and MHC-2 (slow + 2 hybrid). Black stars indicate large diameter fibers that coexpress MHC-alpha, MHC-2, and MHC-M (fast + alpha hybrid). Note that fibers that express MHC-1 (upper left, yellow stars) do not express MHC-M (lower right, yellow stars) and fibers that express MHC-M (lower right, green star) do not express MHC-1 (upper left, green star). Modified from Figure 4 in Wall et al. [154]. Images taken at 20×.

mammals (and compared with mammalian limb muscles). While this abundance of hybrids in nonhuman primate jaw adductors is greater in comparison with other mammals, these results align fairly well with data for human jaw adductors which, even in the absence of MHC-M, reportedly express as much as 52% hybrids [162]. Positive and negative controls in fresh primate jaw adductor tissues [154] (Taylor and Holmes, unpublished data) also align with the patterning we observe in our fixed samples and proteomic analyses of the superficial masseter in seven primate species further confirm the presence of the four major MHC isoforms tested by our antibodies (Wall et al., unpublished data). It is important to emphasize that while IHC identifies the MHC isoforms expressed in these muscles, future work is needed to quantify the amount of each isoform as it is the proportion of MHC composition that is correlated with the contractile velocity of fibers [134].

3.6 | Primate Jaw-Adductor Fiber Types and Feeding Behavior

The relationship between jaw-adductor fiber type composition and ‘fine tuning’ muscles for specific feeding behaviors has been documented across multiple animal groups (e.g., [16, 157, 183]). For instance, in herbivorous mammals that chew thousands of times a day, their masseter muscles express a homogeneously slow, fatigue resistant fiber type—either 100% Type 1-β or nearly 100% Type 1-α along with a small fraction of hybrid Type 1-β/Type 1-α [157, 183–185]—presumably to conserve energy of muscle activation while maintaining chewing force [164, 186, 187]. By contrast, masticatory myosin along with additional Type 2 myosins have been found to dominate the jaw-closing muscles of predatory carnivores as well as the Eastern gray squirrel [152], providing faster contraction speeds and greater tension-generating capacity [16, 148]. These functional properties have been linked to the need for power during prey capture in the predatory carnivores, and to the feeding strategy of the Eastern gray squirrel, in which they “obliterate the shell” during nut cracking [152: 2517].

As with nonprimate mammals, fiber type composition in the jaw-closing muscles of some anthropoid primates has been functionally linked to feeding behavior, but hybrids complicate this relationship. For example, western lowland gorillas have a significantly greater proportion (per unit cross-sectional area) of the slow + 2 hybrid in their anterior superficial masseter compared with chimpanzees, while chimpanzees have a significantly higher fraction of the fast + alpha-cardiac hybrid (Figure 4 [153]). The higher fraction of slow + 2 in lowland gorilla masseter is consistent with the ‘Frequent Recruitment Hypothesis’ [183, 188] which posits that mammals that chew with unusually high frequency have chewing muscles that express a high proportion of slow-type, fatigue-resistant fibers. Lowland gorillas spend a much higher percentage of their daily activity budget on feeding, and their diet consists of a much higher percentage of fibrous foods, compared with chimpanzees [189–192]. Similar to herbivorous sheep and cattle, a fatigue-resistant fiber type is advantageous to lowland gorillas that generate a sizable number of daily chew cycles.

Sooty mangabeys (*Cercocebus atys*) are seed predators that habitually and preferentially feed on large, hard *Sacoglottis gabonensis* seeds, a behavior that involves the use of the postcanine dentition

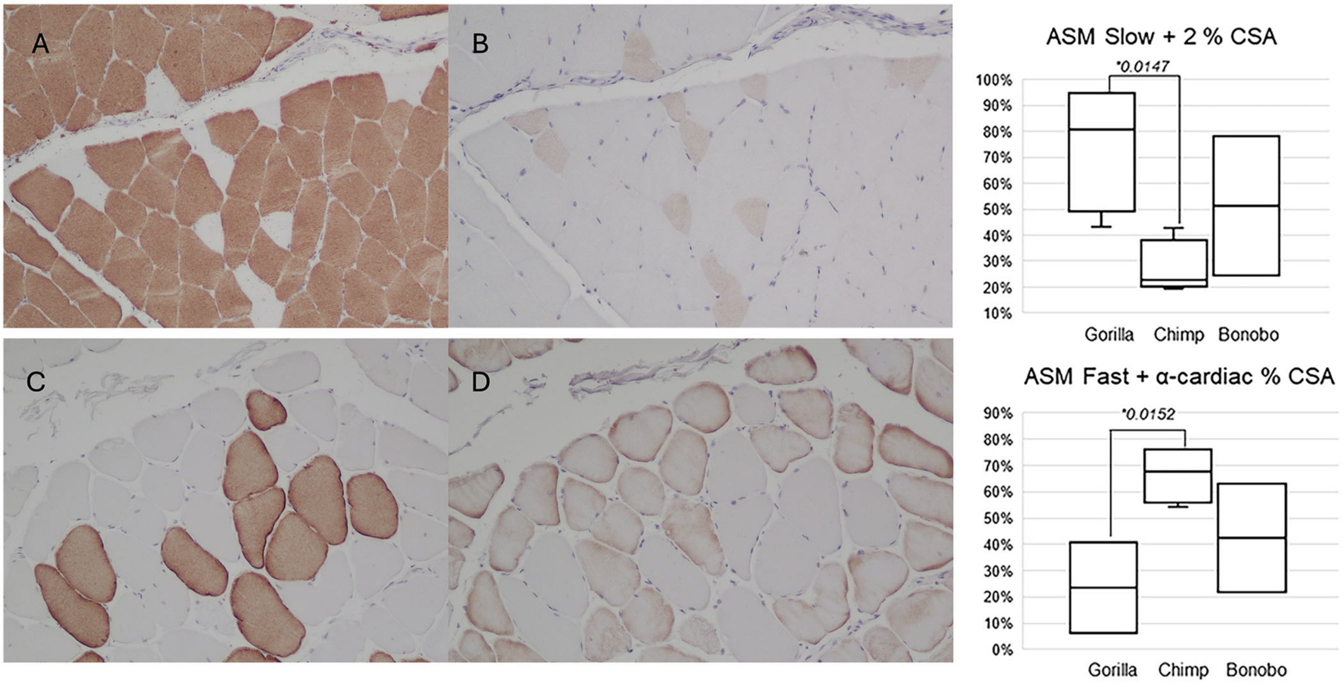


FIGURE 4 | The four panels on the left represent serial sections (5 μm) of anterior superficial masseter (ASM) for an adult female *Gorilla gorilla* (NCZ488; A, B) and adult female *Pan troglodytes* (CJV186; C,D). In *Gorilla*, a high fraction of ASM fibers express MHC-1 (A) whereas only a handful of fibers express MHC-M (B). By contrast, a small fraction of *P. troglodytes* ASM fibers express MHC-1 (C) while a large fraction express MHC-M (D). The box plots on the right confirm that *Gorilla* ASM comprises significantly more of the slower, more fatigue-resistant hybrid ($p = 0.0147$), and significantly less of the faster, higher-force hybrid fiber type ($p = 0.0152$). Images taken at 10×. Adapted from Taylor and Holmes [153].

to crush the hard seed casing [193]. This feeding behavior leads to the expectation that their chewing muscles should express greater amounts of fast-contracting, higher force fibers at the expense of slower, more fatigue-resistant fibers, as posited by the 'High Occlusal Force Hypothesis' [194]. Surprisingly, an initial assessment based strictly on fiber type frequencies for each MHC isoform reported greater amounts of MHC-β and MHC-α in sooty mangabey superficial masseter and temporalis compared to MHC-2 and MHC-M [154]. When we quantified hybrid patterns for sooty mangabeys and four additional papionin species, a degree of complexity was observed similar to that for the African apes. Sooty mangabey masseter maintains the slowest, most fatigue-resistant fiber type, similar to lowland gorillas, with 75% of masseter fiber type expression represented by the slow + 2 hybrid; the other species range between 39% and 62% for slow + 2 (Figures 5 and 6). Sooty mangabey temporalis has a faster, higher force fiber type than the masseter, but the proportion of faster, higher-force hybrid fibers is on the low end of the distribution compared with the other papionins. MHC-β and MHC-α have greater energy conservation during isometric contraction [137, 140, 195] than faster, higher force isoforms, suggesting that energy conservation rather than high force may be more advantageous to sooty mangabeys that generate isometric bite forces with high frequency.

Tufted capuchins (*S. apella*) are also seed predators that exploit both exceptionally tough [43] and hard [196] food items. Their superficial masseter expresses large amounts of MHC-2 and MHC-M (Figure 7) [145], consistent with earlier enzymatic work that found a preponderance of fast glycolytic fibers in tufted capuchin superficial masseter [169, 197]. Here we show that with only *S. apella* expressing MHC-M (masticatory myosin), tufted capuchins have a higher force fiber-type phenotype compared with untufted capuchins, especially that of *Cebus capucinus* (Figure 8). While this fiber-type phenotype provides some support for the High Occlusal Force Hypothesis, the fiber-type phenotype of *S. apella* superficial masseter is very different from that of the seed predator *Cer. atys*, suggesting there is not a one-to-one mapping of fiber-type phenotype to hard-object feeding in primates.

Importantly, none of these primate fiber-type phenotypes fit the phenotypes reported for nonprimate mammals with similar specialized diets. Gorillas, for example, do not exhibit the homogeneously slow, low-force (MHC-β or MHC-α) fiber-type phenotype reported for grazers like sheep and kangaroos. Neither do tufted capuchins exhibit the homogeneously fast, high-force (MHC-M) phenotype reported for carnivores. In this regard, anthropoid primate jaw-adductor muscles appear to be less specialized, which likely reflects the fact that their diets overall are more diverse. It must be kept in mind, however, that all these relationships between fiber type and feeding behavior in primates rely on the assumption that the kinetic properties (e.g., shortening velocity, rate of tension redevelopment) and specific tensions of the different MHC isoforms expressed in primate jaw adductors are similar to those empirically measured and reported from single fibers studies of nonprimate mammalian limb and chewing muscles; and, that hybrid fibers in primate jaw adductors are intermediate in their contractile properties when compared with their pure isoform constituents. While there is empirical evidence in vertebrate muscle to support the latter assumption, quantitation of the MHC isoform expression and fiber-specific contractile properties in these primate jaw-adductor muscles awaits further study.

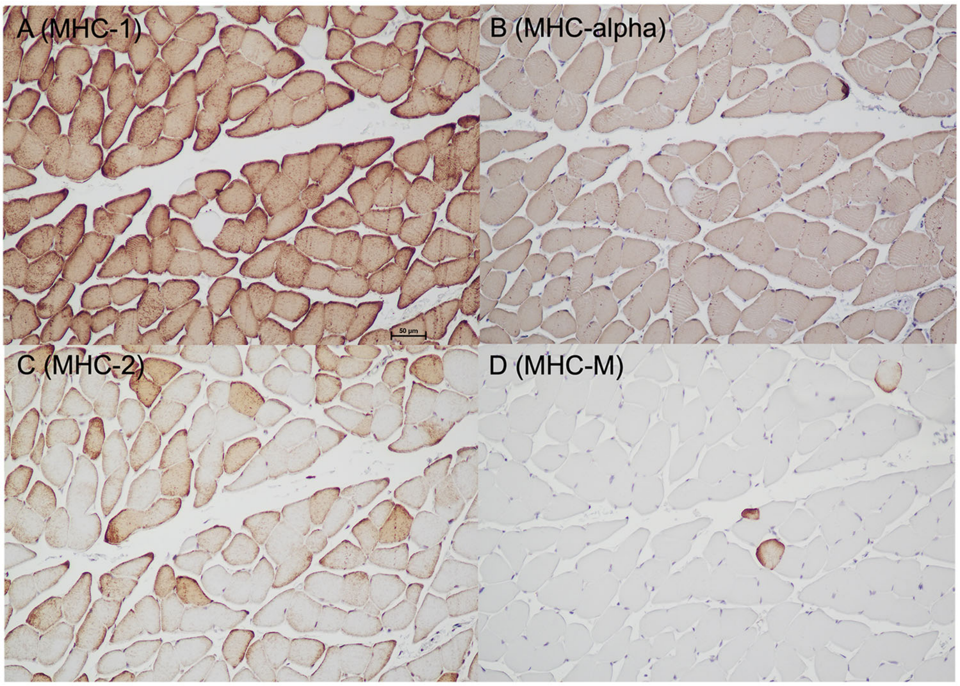


FIGURE 5 | Representative serial sections (5 microns) of an adult male sooty mangabey (*Cer. atys*) superficial masseter (ABT6) stained for (A) MHC-1, (B) MHC-alpha, (C) MHC-2, and (D) MHC-M. Note the abundance of fibers stained for MHC-1 and MHC-alpha, fewer fibers stained for MHC-2, and only a handful of fibers stained for MHC-M. Sooty mangabeys thus have the lowest-force fiber-type phenotype among the five papionin species studied to date. Images taken at 10×.

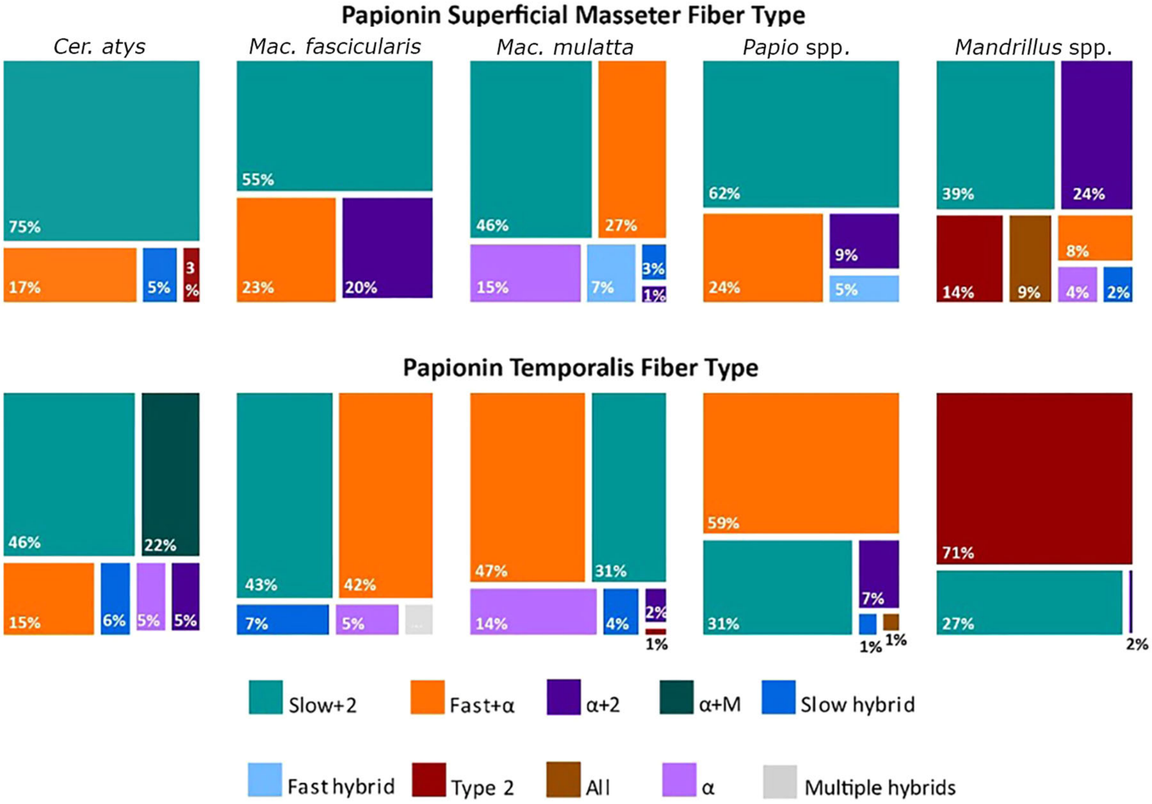


FIGURE 6 | Treemap of fiber type expression for five papionin species depicting the proportion of fiber types present within each group. Distribution of fiber types in either the masseter or temporalis is significantly different between species (log-linear analyses, $p < 0.0001$). See Box 4 for hybrid fiber type abbreviations.

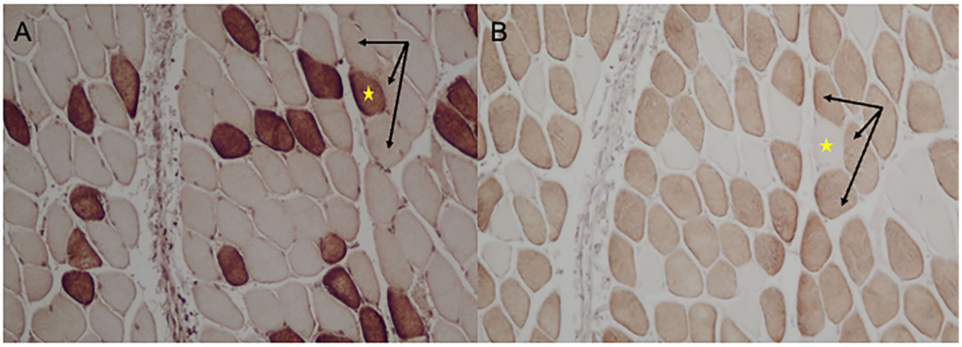


FIGURE 7 | Serial sections (5 microns) of an adult male (CJV222) tufted capuchin superficial masseter showing the expression of (A) MHC-2 and (B) MHC-M. Note the large fibers co-expressing MHC-2 and MHC-M (fibers indicated by black arrows in both panels). Smaller fibers stained darkly for MHC-2 (yellow star, A), but did not stain for MHC-M (yellow star, B). Images taken at 10×.

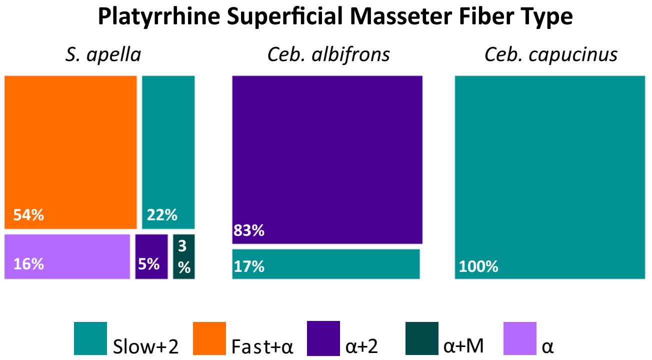


FIGURE 8 | Treemap of fiber type expression for three platyrrhine species depicting the proportion of fiber types present within each group. Distribution of fiber types in the masseter is significantly different between species (log-linear analyses, $p < 0.0001$). Note that only *S. apella* masseter expresses MHC-M (represented in both the Fast + alpha and alpha + M hybrids), but it is possible that MHC-M has been underrepresented in the untufted capuchin tissue samples. See Box 4 for hybrid fiber type abbreviations.

4 | Skeletal Muscle Fiber Architecture

Muscle fiber architecture refers to variation in how fibers are arranged internally within a muscle [108, 198]. The length and arrangement of fibers are important determinants of muscle performance, such as muscle excursion (the range through which a muscle can shorten or lengthen), whole-muscle contraction velocity, and force production. Muscle fibers can be arranged either in parallel (i.e., parallel-fibered) (Figure 9A), or at an angle (i.e., pinnate-fibered) (Figure 9B), relative to the force-generating axis of a muscle. In primates, all three jaw adductors are pinnate-fibered muscles (Figure 9C–E). The most common explanation for pinnation is that it allows more fibers to be packed into a given muscle volume, thereby increasing the muscle's force generating capacity (e.g., [198, 199]). Pinnate-fibered muscles are shorter and comprise fewer sarcomeres in series compared with parallel-fibered muscles of comparable volume. This means that pinnate-fibered muscles have smaller excursions and contraction velocities, but larger force-generating capacities. Variables that influence muscle stretch, contraction velocity, and muscle force are of particular interest to studies of primate jaw-muscle function and performance. These include fiber length—because of its relationship to muscle excursion and contraction velocity [200]—which translates into muscle stretch and the ability to open the mouth widely; and physiological cross-sectional area (PCSA)—because of its proportional relationship to the maximum force a muscle can generate [142]—making it a key variable for estimating bite force in static bite force models.

4.1 | Architecture Variables

Static architecture studies, or those carried out on cadaveric specimens, have traditionally measured variables such as muscle mass, fiber length, and pinnation angle. Because fibers are made up of sarcomeres, and the longer the fiber the more sarcomeres in series, serial sarcomere number and, by extension, fiber length, correlate well with excursion in normal muscle [201]. Physiological cross-sectional area can be estimated by combining muscle mass, fiber length, and the specific density of muscle, with or without pinnation angle. (While beyond the scope of this review, several recent studies have examined the impact of different variables on muscle-specific density, with hydration time, fixation method, and age having the greatest effect on density estimates [202, 203]. Likewise, whether to include pinnation angle in PCSA estimates has been recently discussed and debated, some suggesting it be excluded from static estimates of PCSA [204], and others suggesting that pinnation confers a mechanical advantage to muscle performance [205].) Physiological cross-sectional area theoretically measures the sum of the cross-sectional areas of all of the fibers in a given muscle, assuming all fibers are measured perpendicular to their orientation (whereas anatomical cross-sectional area [ACA] is taken perpendicular to the long axis of a muscle (i.e., perpendicular to intramuscular tendons) [52]. Thus, while PCSA and ACA will be very similar for parallel-fibered muscles, PCSA will be larger than ACA for pinnate-fibered muscles. Multiplying PCSA by a muscle's specific tension yields an estimate of, and has been shown to be proportional to, the maximum tetanic tension a muscle can produce [142]. Estimating muscle-specific tension (P_o) is relatively straightforward for a muscle comprising a homogeneous fiber type where the P_o of that fiber type has been empirically measured. However, the fact that mammalian jaw-adductor muscles, including and especially those of primates, comprise a mix of pure and hybrid fibers in varying proportions

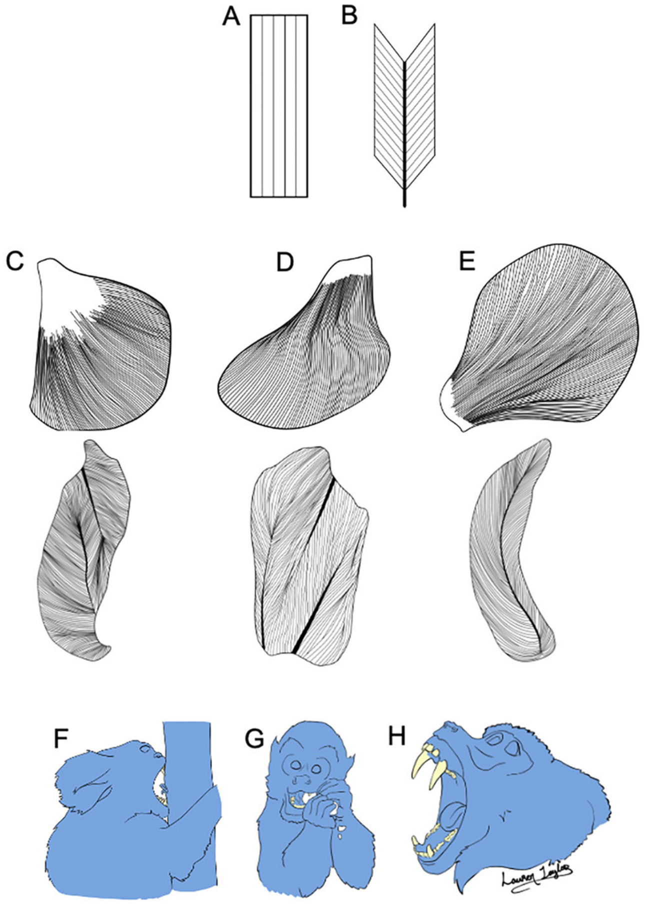


FIGURE 9 | Top: Muscle fibers may be oriented in parallel (A) or at an angle (B) relative to the axis of force generation. For muscles of comparable volume, parallel-fibered muscles pack in fewer, but longer fibers, making them well-suited for producing large excursions, whereas pinnate-fibered muscles pack in shorter, but more fibers, and thus are designed for producing large muscle forces. Middle: The masseter (C) and medial pterygoid (D) are multipinnate (i.e., fibers oriented in multiple directions), whereas the temporalis (E) is bipinnate (i.e., fibers oriented in two directions). Upper row represents whole muscles, lower row represents corresponding muscles in cross-section. All are left-sided muscles. (C) and (E) are from a common marmoset (*Ca. jacchus*); (D) is from a sooty mangabey (*Cer. atys*). Bottom: Fiber length and orientation have significant functional implications for muscle stretch/gape and muscle and bite force related to feeding (F, G) and for gape behaviors unrelated to feeding such as wide-mouth display (H). (C) and (E) modified from [211].

(see Section 3), characterized by different specific tensions, indicates these muscles are neither homogeneously ‘slow, low-force’ nor ‘fast, high-force.’ This heterogeneity of fiber types means that, at least for primates, multiplying PCSA by a single fiber-specific tension is likely to under- or overestimate a muscle's maximum tetanic tension [145].

Muscle architecture studies may involve normalizing fiber length estimates by in vitro measurements of sarcomere length. One reason for this approach is that static architecture studies frequently rely on opportunistic sampling and joints of interest may have been fixed in a variety of postures across individuals and species. For the masticatory apparatus, variation in TMJ angle at time of fixation equates to differences in jaw gape. Not standardizing by sarcomere length has the potential to introduce unwanted within- and between-species variation in fiber length measurements [206, 207], and in biomechanical variables that include fiber length, such as PCSA; the amount of error depends, at least in part, on the magnitude of the variation in jaw posture. It has been assumed that if joints are fixed in similar degrees of gape, variation in fiber length should be minimal, thereby circumventing the need to standardize fiber length by sarcomere length (e.g., [208–210]). Indeed, we found minimal variation in architectural estimates of fiber length when comparing between measurements standardized for sarcomere length and measurements taken with the jaws at or near occlusion [210, 211]. Apart from standardizing for joint posture, incorporation of sarcomere length improves the accuracy of musculoskeletal models of force generation [201, 212], as even small increases in fiber stretch (i.e., 10%) can result in sarcomere length changes of up to 8%–9% of presumed resting length [207].

Traditional methods employed in static architecture studies involve excising whole muscles from their skeletal attachments (often, though not always after fixation) to obtain muscle mass. Once this is done, fiber lengths and their orientations (i.e., pinnation angles) can be measured in a variety of ways. For example, surface pinnation can be measured (e.g., [213, 214]) or muscle bellies can be sectioned along their long axes to expose fibers, their internal orientations, and their intramuscular attachments [215–217]. If internal pinnation angle is not considered, muscles can be chemically digested, enabling fibers to be manually separated. Fiber length can be measured with either approach using a microscope or with calipers (e.g., [218, 219]). Because individual fibers are difficult to isolate, particularly in fixed muscle [220], architectural studies reporting on fiber length have typically measured fascicle length (i.e., length as measured from small fiber bundles surrounded by perimysium). Architectural studies of primate jaw adductors have largely been based either on chemical digestion [20, 55, 208, 209, 213, 221] or sectioning of muscle bellies [210, 211, 216, 217, 222–228].

The use of digital imaging techniques such as diceCT to quantify in situ 3D muscle architecture is becoming more common [229–233]. To date, only a handful of studies have used diceCT to quantify fiber architecture of the jaw adductors in primates (e.g., [216, 234–236]). Other imaging modalities, more frequently used in clinical settings, include ultrasound [237, 238] and diffusion tensor imaging [239, 240]. Digital imaging approaches offer the benefit of being nondestructive/noninvasive and the potential to efficiently measure large numbers of fibers (hundreds to thousands; e.g., [241]). However, these methods can be prohibitively expensive when used for nonclinical purposes and, at least for now, cannot resolve either in vitro or in vivo sarcomere length.

Fiber length estimates based on different dissection approaches (e.g., in situ sectioning of muscles vs. chemical digestion), as well as between dissection and digital approaches, have been found to be generally concordant, displaying overlapping ranges and/or no significant differences (e.g., [46, 216, 242]). By contrast, there seems to be greater variation between dissection-based and 3D reconstruction estimates of PCSA. For example, a comparison of jaw-adductor PCSAs estimated using diceCT on one side of a macaque and using dissection on the other reported identical values for the deep masseter while estimates for the superficial masseter and temporalis differed by 25% and 32%, respectively, with dissection estimates being larger for both muscles [216]. A study of nine bat jaw muscles/muscle regions reported significant differences in PCSAs estimated from dissection versus diceCT, but in contrast with the results of Dickinson et al. [216], dissection estimates were consistently lower than those obtained from diceCT [243]. Interestingly, despite significant differences between the two methods in the bat jaw muscles, the two PCSA estimates were strongly and significantly correlated and scaled isometrically [243]. On the other hand, a study of jaw-closing muscles in adult grasshoppers reported significant differences between PCSAs estimated from dissection versus several 3D methods, including diceCT [46]. Shrinkage of muscle volumes as part of the diceCT protocol likely accounts, at least in part, for the significantly smaller diceCT estimates compared with dissection-based estimates, but other 3D approaches that did not depend on muscle volume yielded significantly larger PCSAs by as much as 55%–60%. Collectively, these results advise caution when combining or comparing PCSA estimates based on these different methodological approaches.

4.2 | Architectural Features Associated With Feeding-System Performance

Primates face ecological challenges associated with gaining access to and processing available food resources. Gape and bite force are two key performance variables that can impact the ability of primates to overcome these challenges. The ability to generate a relatively wide jaw gape facilitates access to a larger range of foods, such as items that are relatively large and/or irregularly shaped, that require specialized ingestive behaviors (Figure 9F). Breaching mechanically challenging food items may require the ability to generate relatively large bite forces at potentially wide jaw gapes (Figure 9G). Muscle stretch/excursion, because of its relationship to fiber length and gape, and muscle force (PCSA), because of its relationship to bite force, are thus the two variables most often considered in architectural studies of chewing muscle function and performance. These two variables are potentially inversely related such that, without modifying other aspects of the masticatory system, they cannot simultaneously be optimized (Box 3). How animals meet these competing demands is at the heart of studies of muscle architecture and its relationship to masticatory apparatus function.

In primates, the question of how fiber architecture of the chewing muscles relates to feeding behavior and diet has been addressed through a variety of approaches. These include clade-based scaling relationships as well as narrower comparisons involving closely related species that differ in one or more key aspects of feeding behavior and/or diet while controlling for the effects of other variables such as body size or phylogeny. We briefly review this work and then offer an integrated analysis of data from across studies to update our understanding of these relationships.

4.3 | Clade-Based Architectural Scaling Patterns in Primates

Analyses of scaling relationships in the chewing muscles are central to understanding the biomechanical and evolutionary ways in which primates meet their energy demands. These relationships, in conjunction with other parts of the masticatory apparatus such as the teeth and jaws, directly impact the rate of food intake, the amount of food ingested and masticated, and how that food is processed. Architectural scaling patterns for the chewing muscles have been explored broadly across primates [56, 208, 209, 213, 217, 224, 225]. These studies have examined scaling of the chewing muscles as a synergistic muscle group and/or drilled down into the details of how each of the jaw adductors or abductors scales relative to a variety of independent variables (e.g., body mass, skull length/cranial geometric mean, load-arm estimates for incision and chewing/molar biting). Most studies have tended to prioritize analysis of PCSA over fiber length because of the relationship of PCSA to muscle and bite force. The majority of these analyses have examined interspecific scaling relationships in adults, though some have focused on ontogenetic patterns [22, 244–247].

Anapol et al. [217] report interspecific isometry of jaw-adductor PCSA relative to body weight for prosimians. In strepsirrhines, total jaw-adductor PCSA and fiber length were found to scale isometrically regardless of the independent variable [213]. Studies focusing on anthropoids have identified a mixture of clade-based scaling patterns. Platyrrhines reportedly range from negative allometry and/or isometry of superficial masseter and temporalis PCSAs and fiber lengths [225], to slight positive allometry for masseter, temporalis, and medial pterygoid PCSAs [217], to strong positive allometry of muscle PCSAs and no significant scaling relationships for fiber lengths [208]. Depending on the study and the muscle, slight to moderate positive allometry for the jaw adductors has also been reported for PCSAs in catarrhines [208, 217] and hominoids [224]. A few studies (e.g., [213, 217]; see also [41]) have tested scaling patterns against hypotheses of geometric similarity, fracture scaling, and metabolic scaling, all of which relate to the amount of force needed to fracture foods and are contingent upon scaling relationships of other parts of the masticatory apparatus and masticatory physiology (e.g., tooth areas, lever arms, metabolic rates, bite stress, etc.). To date, one study has evaluated scaling relationships of the lateral pterygoid and anterior digastric muscles [56], with results suggesting a significant positive relationship between lateral pterygoid fiber length and food item size. However, all of these studies are plagued by wide confidence intervals around the slopes, making it impossible to definitively rule out isometry for many of these scaling relationships.

Many factors have the potential to contribute to differences in slope estimates across studies evaluating the same taxonomic groups. For example, the opportunistic nature of sampling from primates likely means that studies differ in the composition of captive versus wild individuals as well as younger versus older adults. Given that aging is associated with progressive loss of skeletal muscle mass (i.e., sarcopenia; see [248] for a review), differences in specimen age between studies may lead to differences in muscle mass and variables that depend on muscle mass such as PCSA. Variation across studies in method of tissue preservation (e.g., freezing vs. fixation, type of fixative, length of fixation, fixation of intact muscles vs. muscles fixed in isolation) can also lead to differences in mass, fiber length, and PCSA [202, 249, 250]. Statistical treatment of the data—in this case, the use of regression models that differ in how they account for error—may also play a role.

Here we build on and extend previous scaling analyses of the primate jaw-adductor muscles by incorporating additional species and larger sample sizes within species. A recent study [242] showed that within-species sample size and representation of the full clade space are far more important for achieving reliable estimates of fiber length and PCSA when compared with differences in methodological approaches to quantifying muscle architecture. Based on this finding, we combine datasets from across studies that used different methods (e.g., [55, 213, 216, 221, 223–227]; Taylor, unpublished data). Our updated scaling analyses thus include a primate-wide sample ranging between 41 and 75 species depending on muscle (Figure 10; Supporting information Table 2). In these updated analyses fiber length and PCSA for each muscle are each regressed on body mass [252] and jaw length (typically collected on the same specimen), separately for strepsirrhines, platyrrhines, and catarrhines, using phylogenetic generalized least squares (PGLS) regression. Because the jaw-adductors fire at different times and experience different amounts of stretch throughout a gape cycle, it can be difficult to interpret the biomechanical

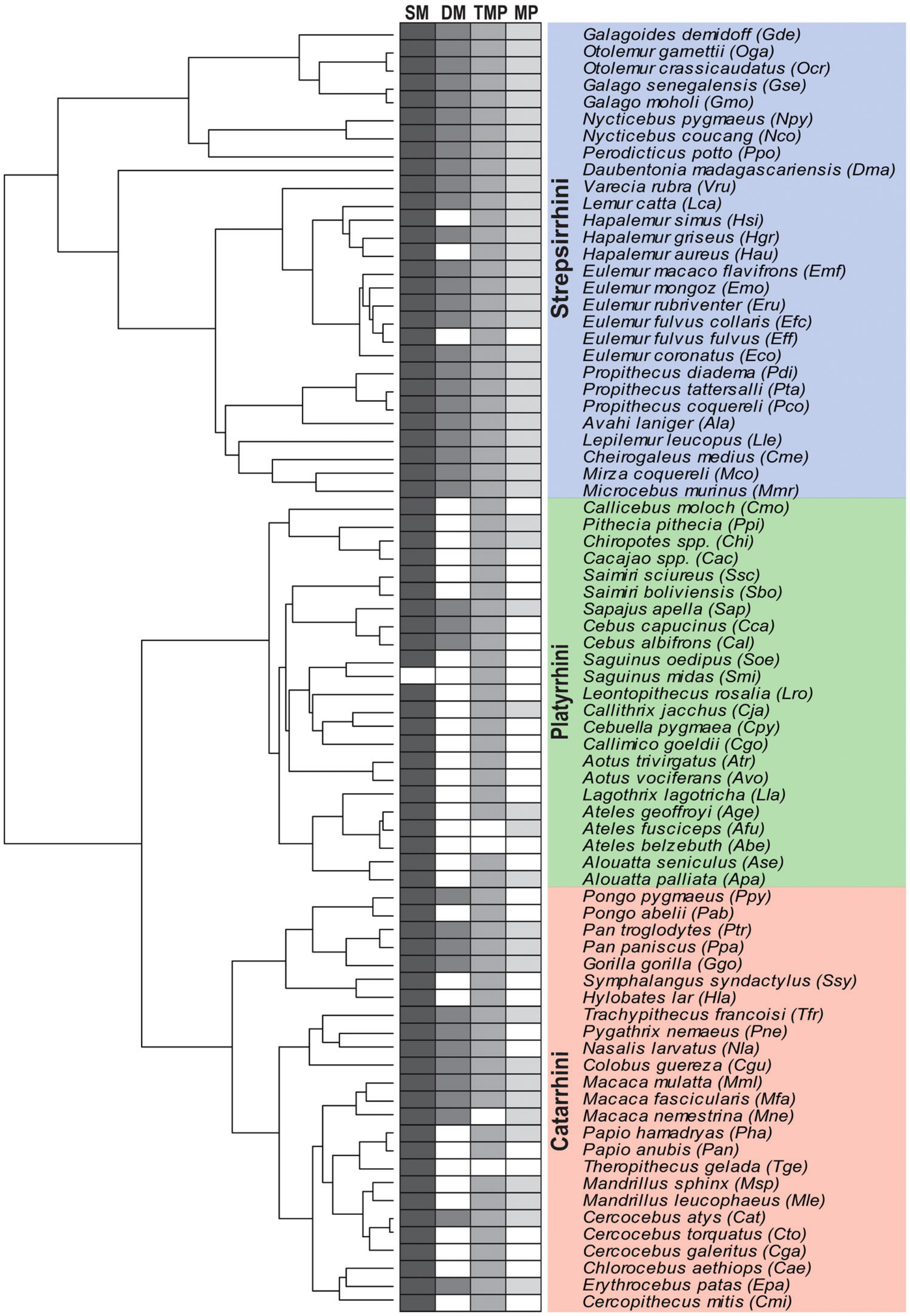


FIGURE 10 | Phylogenetic tree (generated from 10Ktrees.com [251]) showing species included in the muscle architecture analyses for the superficial masseter (SM), deep masseter (DM), temporalis (TMP), and medial pterygoid (MP). White squares indicate no data were available for that muscle. Species abbreviations are given in parentheses.

implications of scaling relationships of the combined jaw adductors (e.g., [208, 213, 217]). We therefore present scaling relationships separately for the superficial masseter, deep masseter, temporalis, and medial pterygoid.

After accounting for significant phylogenetic signal in the data, a pervasive pattern of isometry is shown for strepsirrhines, platyrrhines, and catarrhines, with some notable exceptions (Table 1; Figures 11 and 12). Strepsirrhines and platyrrhines are distinctive from catarrhines in showing size-correlated decreases (negative allometry) in fiber lengths. Perry et al. [213] found that strepsirrhines scaled with negative allometry for total jaw-adductor fiber length and our updated results suggest the temporalis and medial pterygoid muscles may be largely driving this result. Perry et al. [213] also found that total jaw-adductor PCSA scaled with positive allometry, and our updated results suggest that if this is indeed the case, the deep masseter may be unduly influencing this scaling relationship. In theory, negative allometry of fiber length suggests that smaller-bodied strepsirrhines are at a relative advantage for producing wider jaw gapes than larger-bodied strepsirrhines, which could be advantageous if smaller-bodied species are eating food items that are comparatively large relative to their body size. Platyrrhines are also distinctive from catarrhines in showing size-correlated decreases in fiber length and PCSA for the masseter and temporalis, a result which is consistent with prior work on this data set (i.e., [225, 242, 255]). Like strepsirrhines, given the position of these muscles on the skull, this means that the smaller-bodied taxa are at a relative advantage for muscle stretch and gape as well as for muscle force compared with larger-bodied species. This pattern appears to be clade-specific for platyrrhines and is consistent with the fact that smaller-bodied platyrrhines such as tufted capuchins and pitheciines feed on some of the largest and most mechanically challenging food items across the clade, while larger-bodied platyrrhines such as atelids and howler monkeys feed on some of the least mechanically resistant foods [253, 254].

Previous interspecific scaling studies of catarrhine jaw adductors varied markedly in sample composition and regression model. Anapol et al., [217] included a total of six catarrhines: two species each of *Colobus*, cercopithecoid monkeys, and gibbons, and did not account for phylogenetic covariation. Taylor and Vinyard [224] emphasized small and large-bodied hominoids, but they included only one cercopithecoid species and used phylogenetic least squares regression. Hartstone-Rose et al. [208] included 14 species of catarrhines, six of which were from the genus *Cercopithecus*, two each from *Cercocebus* and *Macaca*, but included no small or large-bodied hominoids and did not account for phylogenetic covariation. All of these studies suggested slight to moderate to strong positive allometry of jaw-adductor PCSAs (depending on the muscle and the independent variable), though in nearly all cases isometry could not be excluded. The updated catarrhine scaling results presented here, particularly for the superficial masseter ($n = 25$) and temporalis ($n = 22$), include more species and capture more of the catarrhine clade space than any previous scaling analyses. They show that catarrhine slopes for relative fiber length tend to be higher, and slopes for relative PCSAs either similar to or lower, than those for strepsirrhines and platyrrhines (Table 1; Figures 11 and 12). However, only superficial masseter PCSA relative to jaw length is statistically positively allometric in our analyses. This adult interspecific scaling pattern is to some extent underpinned by the ontogenetic pattern of strong positive allometry demonstrated for *Macaca fascicularis* [244]. The only negatively allometric relationship we observe in catarrhines is for medial pterygoid PCSA relative to jaw length, similarly reported by Hartstone-Rose et al. [208]. In general, these updated scaling analyses indicate widespread isometric relationships between PCSA and fiber length relative to body mass and jaw length in primates. From a biological perspective, what this suggests is that primates experience a proportional (or nearly proportional) increase in both fiber length and PCSA as body size and jaw length increase, at least when viewed at these large clade-level scales.

4.4 | Are There Clade-Based Architectural Tradeoffs Between Fiber Length and PCSA?

The architectural scaling analyses reviewed above explicitly analyze fiber length and PCSA relative to a biomechanical standard such as jaw length or an estimate of body size. However, the relationship between fiber length and PCSA is

TABLE 1 | Results of the phylogenetic generalized least squares (PGLS) regression analyses for fiber length (Lf) and physiological cross-sectional area (PCSA) on body mass (BM) and jaw length (JawLg). For each analysis, λ was allowed to vary to reach maximum likelihood. All variables were natural log-transformed before analysis, and $\sqrt{\text{PCSA}}$ and $\sqrt[3]{\text{body mass}}$ (BM) taken to make all variables a single dimension.

Clade	Architectural variable	Superficial masseter		Deep masseter		Temporalis		Medial pterygoid	
		BM	JawLg	BM	JawLg	BM	JawLg	BM	JawLg
Strepsirrhines	LF	I	I	I	I	—	—	—	—
Platyrrhines	LF	—	—	NS	NS	—	I	I	NS
Catarrhines	LF	I	I	I	NS	I	I	I	I
Strepsirrhines	PCSA	I	I	+	+	I	I	I	I
Platyrrhines	PCSA	—	I	I	NS	—	I	NS	I
Catarrhines	PCSA	I	+	I	I	I	I	I	—

Note: NS = regression model was not significant ($p > 0.05$). I = slope was not significantly different from a slope of isometry. – = slope was significantly different from and less than isometry (negative allometry). + = slope was significantly different from and greater than isometry (positive allometry).

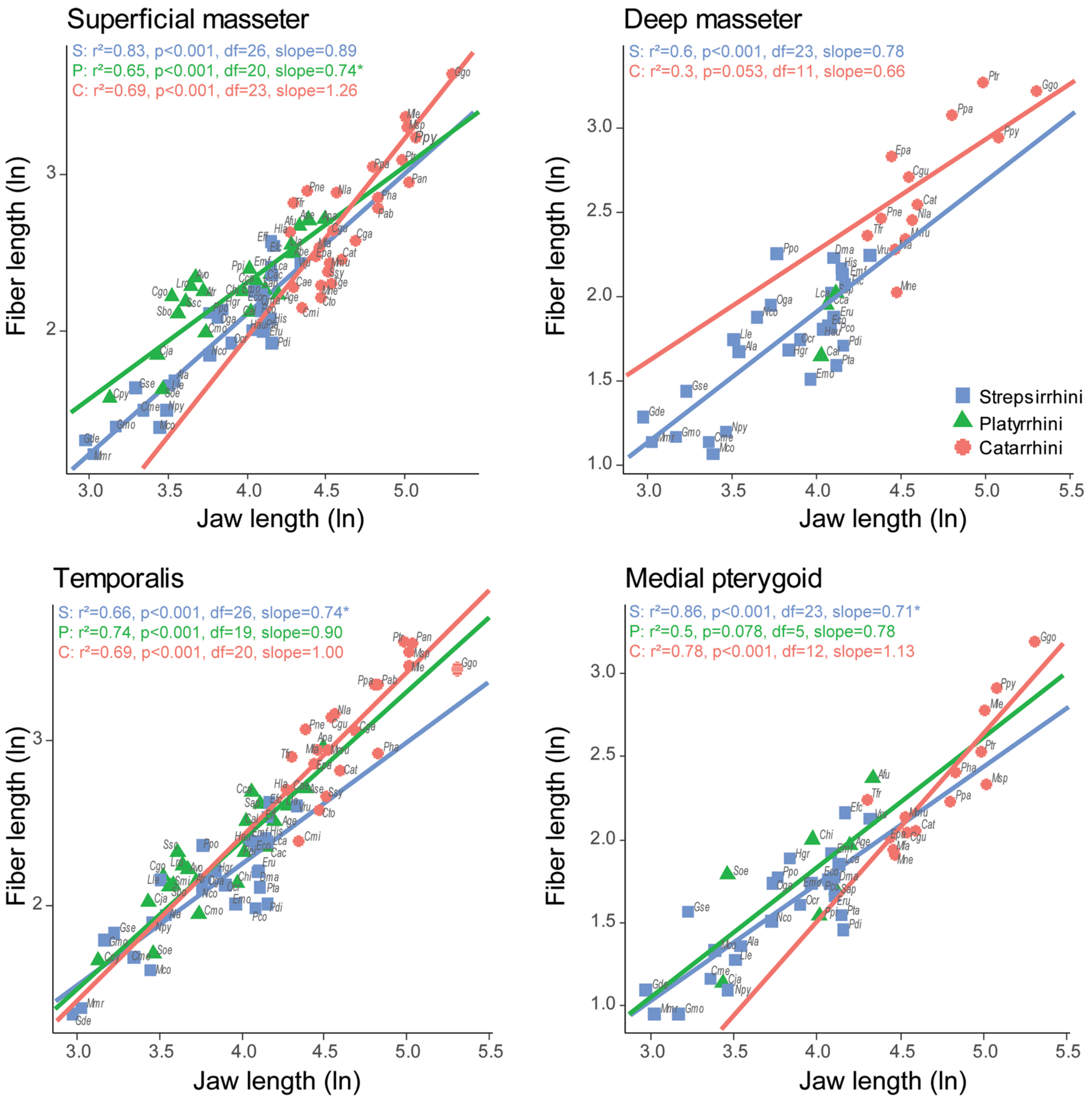


FIGURE 11 | Bivariate plots and PGLS lines of best fit showing the relationship between fiber length and jaw length for the superficial masseter, deep masseter, temporalis, and medial pterygoid. PGLS regression statistics are shown for each clade; slopes that depart significantly from 1 (isometry) are indicated with an asterisk. Slopes and regression statistics are not shown for platyrrhines for the deep masseter because of the small sample size ($n = 3$) for this muscle/clade. Species abbreviations are given in Figure 10. S, strepsirrhines; P, platyrrhines; C, catarrhines.

important because in theory, a muscle cannot simultaneously produce wide ranges of excursion/stretch (i.e., long fibers) and high force output (i.e., large PCSA). This theoretical architectural tradeoff is due to the fact that, for a muscle of similar volume, fibers oriented in parallel with the axis of force generation will be longer (i.e., have more sarcomeres in series and thus be geared for excursion and muscle stretch) compared with fibers oriented at an angle relative to the muscle's force-generating axis (i.e., have more fibers in parallel to each other and thus be geared for force output; Figure 9A,B).

There are structural ways in which primates have circumvented this tradeoff. Gouging trees at near-maximum capacity for gape is facilitated in common marmosets (*Callithrix jacchus*) by an architectural configuration of the superficial masseter and temporalis that allows these long-fibered muscles to act over a more favorable portion of the length-tension curve at wide gapes [117, 211]. *Sapajus apella* increases muscle force (PCSA) without compromising gape (fiber length) by adding muscle mass to the temporalis and to a lesser extent the superficial masseter [223]. Male cercopithecoids that engage in social signaling and aggressive behaviors involving canine gape display sacrifice some force-generating potential in the superficial masseter in favor of relatively long fibers to enhance fiber excursion and muscle stretch, but they also compensate for this tradeoff by adding muscle mass to the temporalis to improve vertical biting performance [226, 227, 255]. Diversifying functional roles of the superficial masseter and temporalis may thus be one strategy by which some primates avoid sacrificing force for excursion (or vice versa), that is, compensating for architectural tradeoffs between fiber length and PCSA in the superficial masseter by avoiding such tradeoffs in the temporalis through the addition of muscle mass to maintain or increase temporalis PCSA. This strategy is consistent with greater functional variation of the superficial masseter (i.e., generating

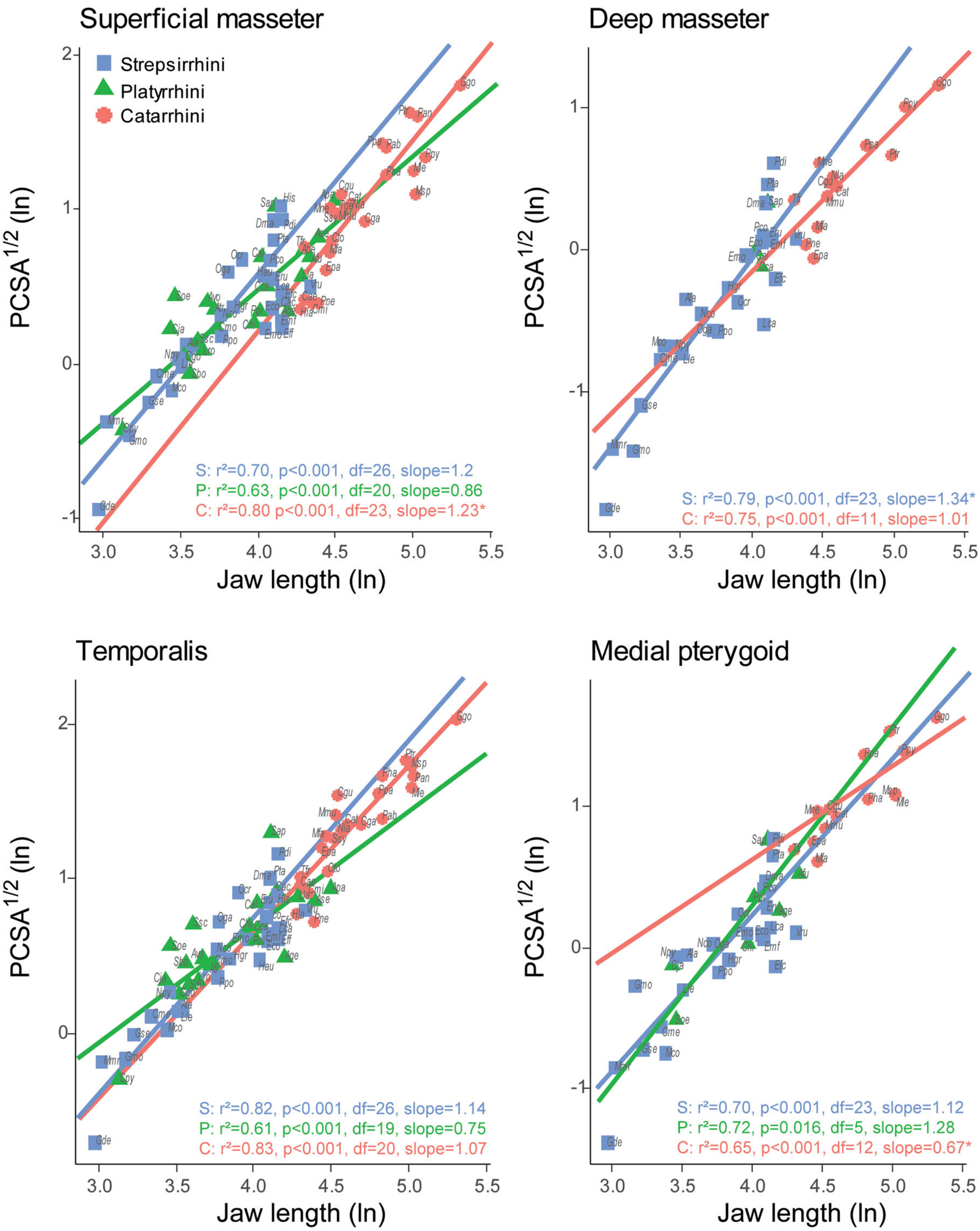


FIGURE 12 | Bivariate plots and PGLS lines of best fit showing relationships between physiological cross-sectional area (PCSA$^{1/2}$) and jaw length for the superficial masseter, deep masseter, temporalis, and medial pterygoid. PGLS regression statistics are shown for each clade; slopes that depart significantly from 1 (isometry) are indicated with an asterisk. Slopes and regression statistics are not shown for platyrrhines for the deep masseter because of the small sample size ($n = 3$) for this muscle/clade. Species abbreviations are given in Figure 10. S, strepsirrhines; P, platyrrhines; C, catarrhines.

transverse forces during the power stroke of mastication and transverse jaw movements during chewing, facilitating wide jaw gapes) as compared with the vertically-oriented anterior temporalis in primates and its more conserved role in generating vertically oriented occlusal forces during chewing, and suggests that fiber architecture of these two muscles may have evolved to support different functional roles in primates [36, 62, 85].

Our expanded data set reveals some interesting clade-based patterns of tradeoffs (Figure 13). Strepsirrhines are the most distinctive, with all four jaw adductors exhibiting a tradeoff such that taxa with the relatively largest PCSAs also tend to have the relatively shortest fibers. This tradeoff is strongest for the medial pterygoid and weakest for the temporalis. Catarrhines show a strong architectural tradeoff for the superficial

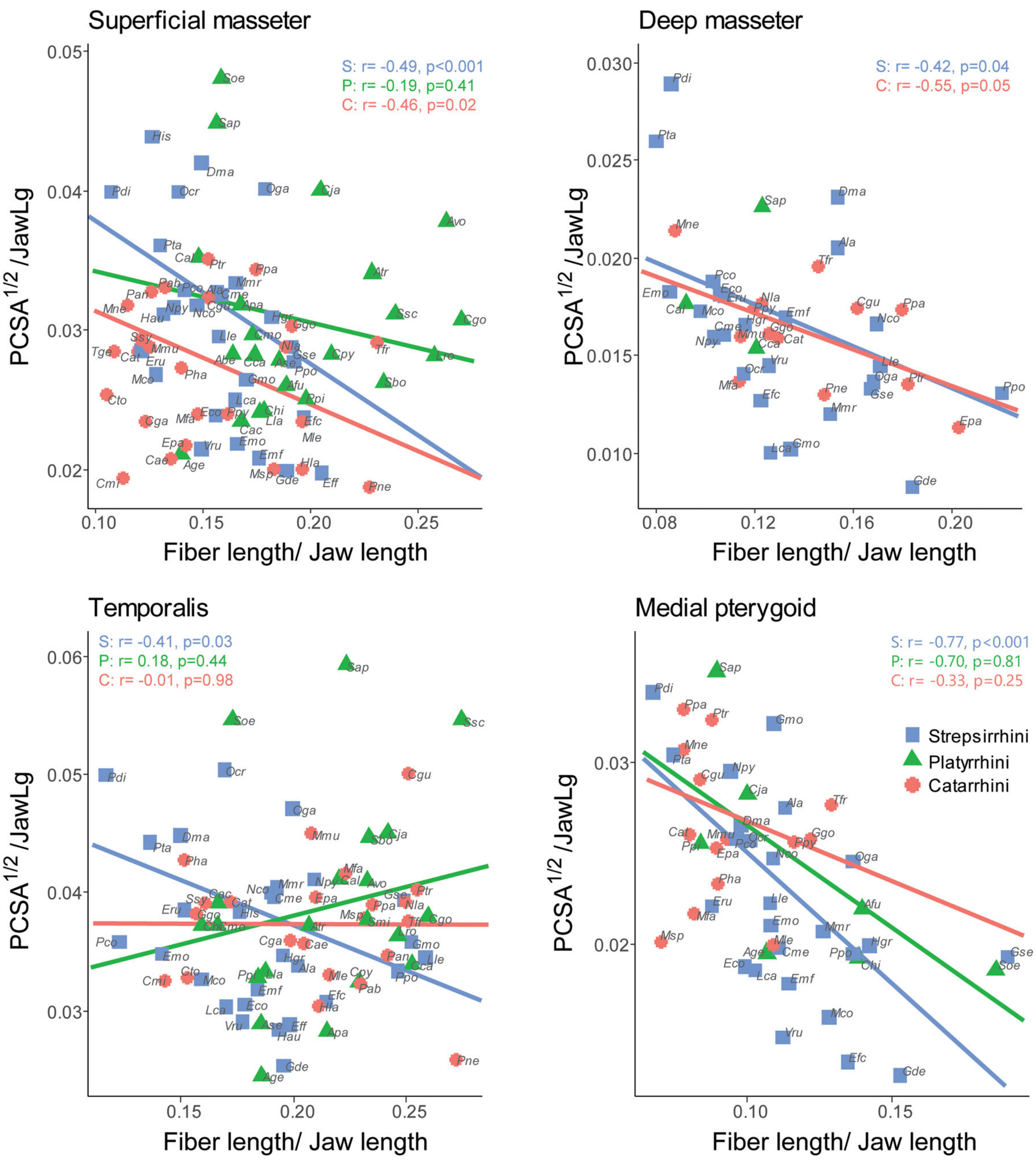


FIGURE 13 | Bivariate plots and PGLS lines of best fit showing relationships between physiological cross-sectional area (PCSA$^{1/2}$) and fiber length (both scaled by jaw length) for the superficial masseter, deep masseter, temporalis, and medial pterygoid. Correlations (*r*) and corresponding *p*-values are shown for each clade. Best fit line and correlations are not shown for platyrrhines for the deep masseter because of the small sample size ($n = 3$) for this muscle/clade. Species abbreviations are given in Figure 10. S, strepsirrhines; P, platyrrhines; C, catarrhines.

masseter and a weaker one for the medial pterygoid. However, there is appreciable scatter within each clade and consideration of these tradeoffs at both lower taxonomic levels and with respect to variation in both diet and social behavior will likely provide insights into which taxa are under pressure to circumvent this tradeoff and how they accomplish this.

4.5 | Diet-Based Analyses of Muscle Architecture

While much of the work examining clade-based architectural scaling patterns has focused on taxonomic variation, a few studies have explicitly analyzed scaling patterns related to diet within and across clades (e.g., [208, 213]). Here we took advantage of the enlarged data set and grouped our data on the basis of diet (following Scott et al. [256]). We used phylogenetic analysis of variance to test for architectural differences among dietary groups within strepsirrhines, platyrrhines, and catarrhines for the superficial masseter and temporalis muscles—the two muscles best represented in the data set. Whether scaled by jaw length or body mass, we observe no significant differences in fiber length or PCSA for either muscle between diet categories within any of the three clades (Figure 14).

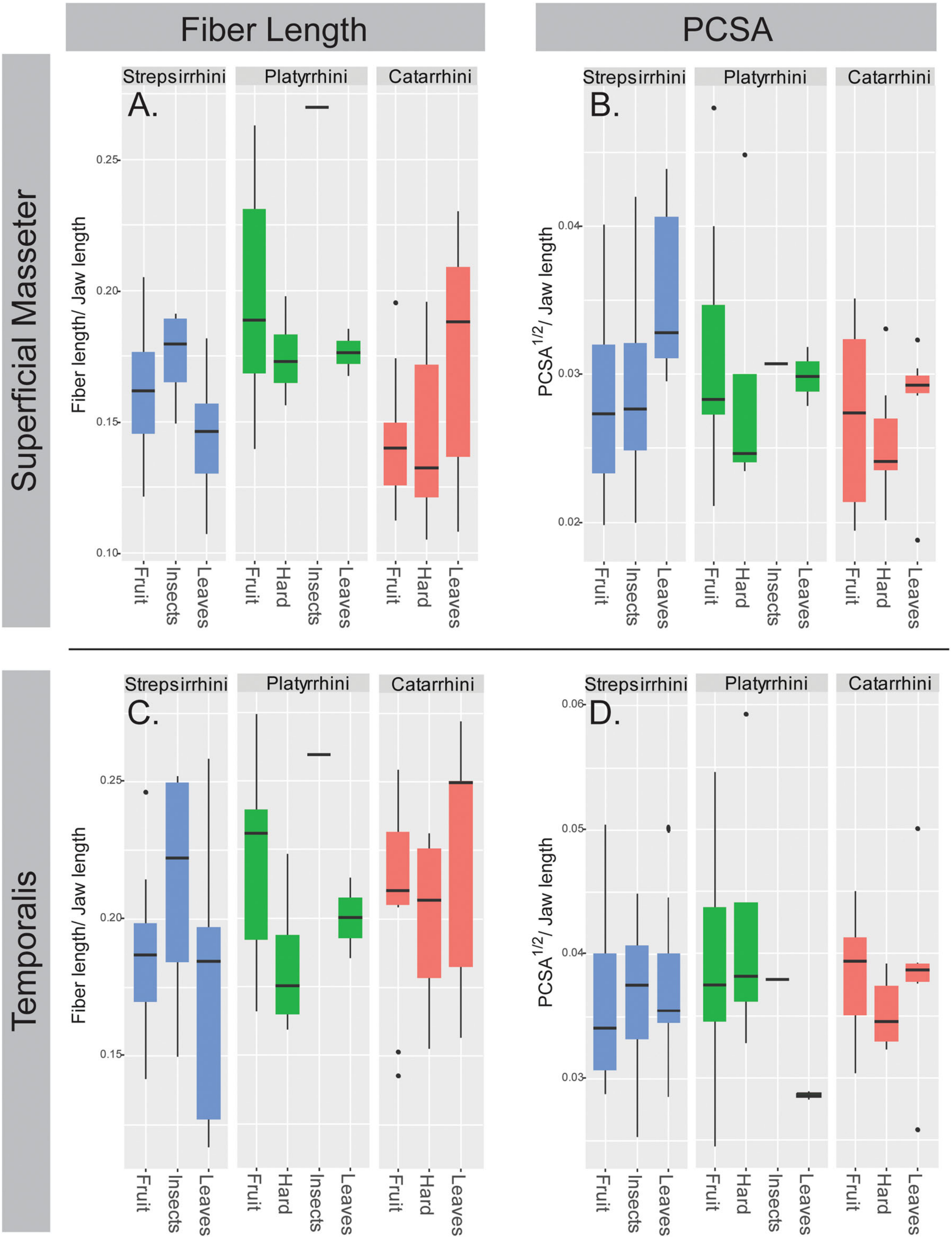


FIGURE 14 | Clustered box plots showing variation in fiber length (A, C) and physiological cross-sectional area (PCSA) (B, D) (both relative to jaw length) for the superficial masseter (A, B) and temporalis (C, D) in the three large clades examined here and dietary groups (following [256]) in each clade. Phylogenetic analysis of variances (ANOVAs) for each clade per variable are not significant ($p > 0.05$).

We do observe some trends previously reported by others. For example, Perry et al. [213] found that strepsirrhine frugivores and insectivores had higher slopes than folivores for total jaw-adductor fiber length regressed on jaw length. These results were consistent with their findings [213] that maximum ingested bite size and total jaw-adductor fiber length (both scaled by body mass) were significantly and positively correlated, but that frugivores fell above their line of best fit whereas folivores fell below, which the authors interpreted as indicating that folivores take smaller bites relative to fiber length than frugivores. In our updated analyses, we observe that, on average, strepsirrhine frugivores have relatively longer superficial masseter (but not temporalis) fibers, and that insectivores have relatively longer fibers than frugivores and folivores for both muscles

(Figure 14A,C); however, none of these differences are significant. Similarly, in an analysis of size-adjusted residuals of fiber length, Hartstone-Rose et al. [208] observed significantly longer temporalis (but not masseter or medial pterygoid) fibers in anthropoids with softer versus more obdurate diets, which the authors interpreted as indicating that taxa that consume softer and generally larger food items have relatively longer fibers compared with species that eat more obdurate and generally smaller foods. Our updated analyses show a similar trend for the temporalis for platyrrhines, but not for catarrhines, but these results are not significant (Figure 14C). Perry et al. [213] also found that total jaw-adductor PCSA scaled with positive allometry in folivorous strepsirrhines, whereas frugivores scaled with isometry. Our updated analyses also show that, on average, strepsirrhine folivores have relatively larger superficial masseter (but not temporalis) PCSAs compared with frugivores (Figure 14B,D), but again these differences are not significant. Data on in vivo jaw gapes and mechanical/geometric properties of foods ingested by these species in the wild are necessary to more fully understand these relationships.

As shown here, attempting to link dietary variation with fiber architecture requires unpacking higher-level taxonomic groups. Taking fiber length as one example, at high taxonomic levels platyrrhines stand out as having significantly longer superficial masseter fibers compared to catarrhines and strepsirrhines; this difference is not as pronounced for the temporalis (Figure 15A,B). We see a hint of dietary differences within each of these three clades as reflected in our four dietary classes (Figure 15C,D), but we already know based on our earlier analyses above that diet cannot explain the presence of relatively long superficial masseter fibers in platyrrhines compared to the other two clades. However, at lower taxonomic levels (i.e., superfamily/family/subfamily levels; Figure 15C,D) we see considerable variation in fiber length within each of the three clades and we begin to get a glimpse of the taxonomic groups that account for these differences. Focusing on platyrrhines specifically, cebids are distinct from atelids and pitheciids in their relatively longer superficial masseter fibers (Figure 15C), a pattern even more evident for the temporalis (Figure 15, compare C with D), driving home the importance of examining this variation at lower taxonomic levels. The cebids are notable because of their considerable variation in feeding behavior and diet [257] as well as body size, spanning an order of magnitude from pygmy marmosets (*Cebuella pygmaea*) to tufted capuchins [252]. When we drill down even further to the subfamily and genus levels (Figure 15E,F), we more clearly see important patterns that have been linked to well-documented behavioral differences among cebid species and genera that are otherwise obscured when viewed at higher taxonomic levels. This is almost certainly true for other architectural variables (e.g., PCSA) and across other primate families and subfamilies (e.g., Cercopithecinae vs. Colobinae, Lemuroidea vs. Lorisoidea).

4.6 | Comparative Approaches to Architectural Variation in Primate Jaw Adductors—It's Not All About Feeding Performance

In primates, there is a relationship between jaw-adductor fiber architecture, feeding behavior, and feeding performance, but the strength of this relationship depends, at least in part, on the distinctiveness of the behavior. For example, a preliminary assessment of superficial masseter and temporalis fiber architecture in African apes suggests little difference between western lowland gorillas (*Gorilla gorilla*) and common chimpanzees (*Pan troglodytes*) in either relative PCSA or fiber length [224]. Thus, the inclination of western lowland gorillas to fall back on fibrous vegetation during periods of fruit scarcity while chimpanzees continue to forage for fruit does not seem sufficiently distinct to be reflected in the architecture of these muscles. The relationship between jaw-adductor fiber architecture, feeding behavior, and feeding performance has been most clearly demonstrated when species characterized by specialized feeding behaviors and/or diets are compared with closely related taxa that do not engage in these same specialized behaviors. For example, in the relatively long masseter and temporalis fibers reported in habitual gum-feeding common and pygmy marmosets that actively gouge trees at relatively wide jaw gapes to stimulate the flow of exudates [117, 211]; a similar signal has been observed for the anterior digastric (a jaw abductor) in common marmosets [56]. Likewise, in the relatively large masseter and temporalis PCSAs reported in adult tufted capuchins that exploit mechanically challenging food items compared with untufted capuchins that feed on less mechanically resistant foods and have relatively smaller PCSAs [223]. It should be noted that these adult species differences are sometimes, but not always, present early in ontogeny. For example, infant tufted and untufted capuchins exhibit the adult pattern observed for relative PCSA for both the superficial masseter and temporalis muscles [247], but adult differences in relative fiber lengths between common marmosets and cotton-top tamarins (*Saguinus oedipus*) are not present in neonates [246].

It is also important to note that not all hard-object feeding primates have relatively large jaw-adductor PCSAs compared to closely related species that feed on less obdurate food items. Sooty mangabeys, which routinely process large, hard seed casings to gain access to the soft nut inside, do not have relatively large jaw-adductor PCSAs, nor do they exhibit features of the skull and mandible that would be expected for a species that generates and dissipates large occlusal loads [226]. The fact that two seed predators—tufted capuchins and sooty mangabeys—have very different muscle (and skeletal) morphologies may be related to different functional demands and/or selection pressures operating on the same morphologies. For example, the ability to generate a relatively wide jaw gape has been functionally and adaptively linked to social signaling and aggressive behaviors involving wide mouth opening [258, 259], especially in sexually dimorphic primates that engage in intense intermale competition for mates [260, 261] (Figure 9H). Consistent with this gape-related behavior, male sooty mangabeys and other sexually dimorphic cercopithecoids have relatively longer masseter and temporalis fibers compared to female conspecifics [226, 227]; (Figure 16). This pattern is reflected across the cercopithecoid clade with gape, canine height, and musculoskeletal morphologies favorable for gape significantly correlated in males, but not females [255]. Collectively, these studies indicate that male cercopithecoids have evolved a morphological package geared toward facilitating jaw-adductor muscle stretch and the capacity to generate wide jaw gapes as part of a biological role (*sensu* [262]) of male gape behavior and performance. Importantly, male and female cercopithecoids appear

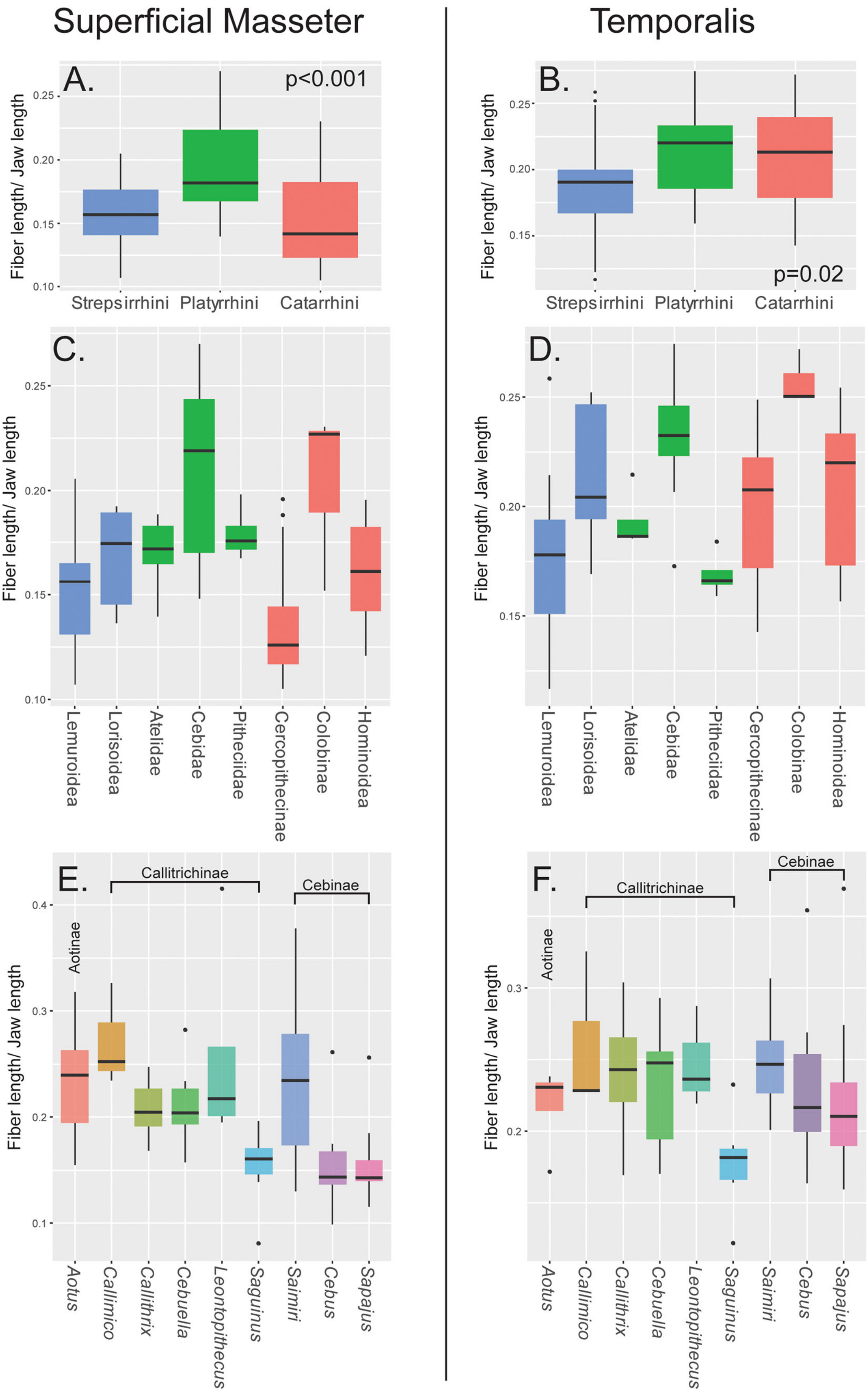


FIGURE 15 | Box plots showing variation in fiber length relative to jaw length in the superficial masseter (left column) and temporalis (right) for various different taxonomic levels. (A, B) Parvorder/infraorder level (species means); (C, D) superfamily/family/subfamily level (species means); and (E, F) subfamilies and genera within the family Cebidae (data based on individuals within each genus). *p*-values shown in (A) and (B) are for the overall analysis of variance (ANOVA) model for that variable; for the superficial masseter platyrrhines have significantly longer fibers than both strepsirrhines and catarrhines ($p < 0.001$) and for the temporalis platyrrhines have significantly longer fibers than strepsirrhines ($p = 0.035$) but not catarrhines.

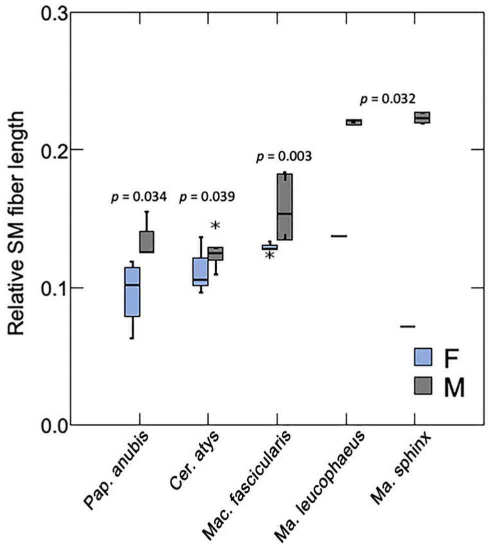


FIGURE 16 | Boxplot comparing relative superficial masseter (SM) fiber length between males and females of *Pap. anubis, Cer. atys, Mac. fascicularis, Ma. leucophaeus*, and *Ma. sphinx*. For statistical purposes, *Ma. leucophaeus* and *Ma. sphinx* were combined due to small sample sizes. Males of all four taxa have significantly relatively longer fibers compared with female conspecifics.

to be under different selection pressures, with canine gape display and canine clearance as part of social signaling and agonistic interactions, rather than feeding behavior, an important driver of feeding-system morphology in males.

The variety of ways in which primates approach similar behaviors (e.g., hard-object feeding) emphasizes the many-to-one mapping of masticatory apparatus form to function [263]. Further exploration of jaw-muscle fiber architecture in primates, especially in closely related taxa that differ in behavior, is likely to reveal additional relationships between muscle morphology, masticatory apparatus function, and behavior that expand our understanding of how primates respond to a wide range of selective pressures.

4.7 | Dynamic Muscle Architecture

While static estimates of PCSA and fiber length are considered proportional to muscle force output and fiber operating lengths, what static muscle architecture truly captures is maximum muscle force and excursion capacity. Yet muscles rarely, if ever, generate maximum contraction forces or undergo maximum excursion capacity [220, 264]. By contrast, studies of dynamic muscle architecture are aimed at capturing changes in fiber or fascicle length and rotation as well as whole muscle thickness and shape changes throughout a muscle's operating range. Muscle shape changes can be defined as a muscle's architectural gear ratio (AGR), which can circumvent length-tension or bite force-gape constraints. A lower AGR, defined as the ratio of whole muscle velocity to fiber velocity, favors force production, whereas a higher gear ratio favors increased velocity output [265]. Most analyses of AGR have focused on locomotor muscles in nonprimates (e.g., [265, 266]), but shape changes in the masseter and temporalis are well studied in humans. Ultrasound is commonly used in clinical settings to measure dynamic changes in thickness, elasticity, and pinnation angle in the masseter and temporalis and to examine functional heterogeneity, age-related changes, and other muscular changes associated with clinical conditions [267] (reviewed in [268, 269]).

Studies of architecture dynamics and the role of AGR specifically in the nonhuman primate feeding system are in their infancy. To date, architectural dynamics and AGR have been studied in one chewing muscle in a single primate species (*S. apella*). Work by Laird et al. [63, 270] showed that up to 80% of temporalis fascicle length can be explained by gape in tufted capuchins, and the muscle undergoes dynamic changes in architectural gearing in response to food material properties and gape cycle velocity. Specifically, as might be expected, the anterior temporalis is associated with lower AGRs (facilitating increased force production) when processing mechanically challenging foods compared to softer foods and during the power stroke (or slow-close phase) of the gape cycle. This illustrates the role of AGR in response to changing loading environments with food properties and the chewing cycle. Future studies of dynamic muscle architecture in the nonhuman primate feeding system would allow comparisons of dynamic operating ranges, tradeoffs in dynamic force and velocity production related to dietary adaptations, and the contributions of dynamic changes across multiple jaw adductors within the feeding system to force and excursion.

5 | What Can Jaw-Muscle Fiber-Type Phenotypes and Fiber Architecture Tell Us About the Paleobiology of Primates?

As is evident from this review, extant primates exhibit considerable variation in physiological and architectural aspects of their jaw-adductor muscles—variation that was almost certainly present in extinct primate taxa. This variation reflects a wide range of muscle performances, and, by extension, a wide range of physiological and behavioral performances related to feeding behavior, diet, and social signaling (among others). Returning to Witmer's [1] remark on the relevance of soft tissues, here we show how portions of primate anatomy not preserved in the fossil record (e.g., jaw-adductor muscle fiber types and architecture) can influence evolutionary interpretations of the paleobiology of fossil primates.

Among the many muscle performance variables (e.g., fiber-specific tension, contraction velocity, fiber length, PCSA) and behaviors that involve the jaw adductors (e.g., chewing, biting, social signaling), bite force has received the most attention in biological anthropology (e.g., [19, 45, 118, 213, 271–278]). We thus focus on this performance variable both because of historical interest and its importance to behavior writ large. We note here that even with this historical focus on bite force, published bite force estimates for extant primates range considerably. Tufted capuchins alone are characterized by a 10-fold difference in molar bite force estimates, 89 N [279] to 897.74 N [118], and this range can be attributed to the wide range of methods used to estimate bite force, including musculoskeletal measurements, dental chipping, and dental histological sectioning (e.g., [272, 279, 280]). Such wide variance emphasizes the need for improved understanding of the biological context for bite force, how this context relates to methods of force estimation, and how bite force varies in relation to other muscle performance variables, particularly gape.

In the absence of fossilized soft tissues and with (at the time) limited muscle architecture data and even more limited data on fiber types, initial estimates of maximum bite force potential in fossil primates relied on craniometric measures such as the cross-sectional area of the infratemporal fossa and the length of the masseter origin in extant and fossil primates [273] or in combination with muscular correction factors [276]. This approach has since been expanded to combine muscle and craniometric data to estimate bite force in fossil taxa [45, 277]. Another method of estimating bite force in fossil hominins is finite element modeling, an engineering tool that uses simple geometry to capture the stresses and strains of complex forms and function [281–283]. These models typically use muscle architecture data from extant primates to simulate the 3D external forces during biting or chewing in fossil hominins.

To estimate maximum bite force at the occlusal surface using both muscle architecture and fiber-type phenotype data, each jaw-adductor's PCSA value is multiplied by the muscle's fiber-type proportions and their specific tensions (P_o [145]). The resulting muscle force estimate for each muscle is then multiplied by the moment arm for that muscle (the in-lever) and divided by the bite point moment arm (the out-lever), yielding an estimate of the efficiency with which muscle force is converted to bite force at a given bite point (mechanical advantage). In-levers and out-levers can be readily estimated from skulls and mandibles, both of which tend to be relatively well-represented in the primate fossil record. (Mechanical advantage = (masseter in lever × [masseter PCSA*masseter P_o]) + (temporalis in lever × [temporalis PCSA*temporalis P_o]) + (medial pterygoid in lever) × [medial pterygoid PCSA*medial pterygoid P_o])/bite point out lever.)

To illustrate the importance of jaw-muscle fiber-type phenotypes and fiber architecture from extant primates for reconstructions of feeding behavior and diet in fossil taxa, we combine data on jaw-adductor fiber types, architecture, and jaw leverage to examine how these data and extant primate model selection might influence our paleobiological interpretations. We intentionally focus on two taxa that have been fundamental for understanding the evolution of the feeding system in fossil hominins, *Paranthropus robustus* and *Australopithecus africanus*, and we view these fossil species through the lens of three extant primate models: chimpanzees and gorillas, papionins, and tufted and untufted capuchins. As previously discussed (i.e., [284]), extant primates have their own evolutionary histories and some taxa, like *Paranthropus*, do not have good analogs among extant primates. It is therefore critical to consider which extant primates should be used to model muscle variables in fossil taxa. *Paranthropus robustus* is characterized by hypertrophied craniodental morphology including large jaw muscle attachment sites, in contrast to the relatively gracile morphology of *A. africanus* (e.g., [285]). *Paranthropus robustus* is believed to have been able to bite harder than *A. africanus* based on jaw leverage, although not necessarily when scaled to molar surface area [273]. Here, we assume *Par. robustus* had a relatively mechanically challenging diet and larger jaw muscles compared to *A. africanus* [272, 286, 287].

5.1 | The Gorilla and Chimpanzee Models

Comparing fossil hominins to chimpanzees and gorillas is a well-trodden path because of their relative phylogenetic proximity and similar craniodental morphologies. Gorillas have been used as a model for *Par. robustus* jaw-muscle fiber phenotype and architecture because of their robust craniodental morphology and chimpanzees have been used as a model for *A. africanus* [283]. In general, chimpanzees have increased mechanical advantage relative to gorillas and exhibit fiber phenotypes consistent with greater force output [153], but gorillas have, on average, larger superficial masseter and temporalis PCSAs relative to jaw length compared to chimpanzees [224]; (Taylor, unpublished data). Collectively, these data suggest gorilla jaw adductors are adapted for ‘frequent recruitment’ consistent with a higher chewing frequency and consumption of a greater proportion of fibrous plants during times of preferred food scarcity [191, 288], whereas chimpanzee jaw muscles can produce greater force compared to gorillas but have reduced performance over long durations. As a model for *Paranthropus*, the relatively larger PCSAs of gorillas infer that the large jaw musculature of *Par. robustus* could also be an adaptation for repetitive chewing in comparison to a more powerful but less fatigue-resistant morphology of *A. africanus*. Like herbivores, *Par. robustus* may have chewed many times per day rather than using high bite forces for particularly mechanically challenging foods. This characterization of robust morphology in *Paranthropus* as an adaptation for frequent use when consuming large volumes of food, rather than large bite forces, is consistent with these two influential hypotheses regarding fossil hominin diet regarding the consumption of large volumes of food and/or frequent grass seed consumption (i.e., [289, 290]). This model serves as a reminder that muscle performance metrics other than or in addition to bite force may play important roles in fossil hominin feeding behaviors.

5.2 | The Papionin Models

Papionins are another set of commonly used models for comparison with *Paranthropus* and *Australopithecus*. Here, *Par. robustus* is compared to *Cer. atys* because of their well-documented hard-object feeding behavior, where the mechanically challenging seed of *Sa. gabonensis* comprises more than 50% of their diet [291, 292]. In this comparison, *A. africanus* is modeled as *Mac. mulatta*, *Mac. fascicularis*, *Mandrillus sphinx*, and/or *Pap. anubis*; none of these extant species are obligate hard-object feeders. While jaw leverage and PCSA/jaw length are approximately equivalent between *Cer. atys* and macaques, *Ma. sphinx*, and *Pap. anubis* [227], *Cer. atys* exhibits a slower, more fatigue-resistant jaw-adductor fiber-type phenotype compared to these taxa [293]. This important difference in fiber types may reflect longer feeding times and a greater number of chews in *Cer. atys*, similar to gorillas. However, *Cer. atys* has lower chewing frequencies per ingestive event compared to other monkeys in the same habitat despite consuming mechanically challenging foods [42].

Collectively, neither muscle nor skeletal morphology distinguishes the hard-object feeding behavior of *Cer. atys* from other papionins, suggesting that muscle performance may not always be reflected in feeding behaviors (e.g., [39, 291, 294]). In the case of papionins, maximizing jaw-adductor muscle stretch to facilitate social signaling and aggressive interactions as part of male–male competition for females seems to outweigh the importance of maximizing jaw-adductor muscle force for hard-object feeding. Where diet is concerned, it has been proposed that *Cer. atys* makes use of behaviors not captured in skeletal or muscle morphology, such as food selection, to facilitate their hard-object dietary specialization [39, 42, 291]. As detailed in McGraw and Daegling [42], it must also be assumed that fossil hominin feeding behaviors are not fully captured in muscle models and skeletal morphology. This papionin example raises the consideration that the morphology of *Par. robustus* and *A. africanus* does not necessarily reflect adaptations for specific feeding behaviors.

5.3 | The Tufted and Untufted Capuchin Models

Our last example employs tufted capuchins (*Sapajus* sp.) as a model for *Par. robustus* because of their more robust morphology and propensity to consume mechanically challenging foods, and untufted capuchins (*Cebus* sp.) as a model for *A. africanus*. Tufted capuchins have improved leverage [43], relatively larger PCSAs [223], and a greater proportion of hybrid fiber types favoring muscle force [295]; (Figure 7) compared to untufted capuchins. Tufted capuchins are therefore consistent in displaying a pattern across their skeletal and muscle morphology that favors high force production for the consumption of mechanically challenging foods.

The capuchin model for jaw muscles suggests the robust craniodental morphology of *Par. robustus* could be an adaptation for producing higher bite forces compared to *A. africanus*. This model is consistent with original interpretations of the craniodental morphology of *Par. robustus* [285], but also suggestions of 'fallback' adaptations–morphologies that facilitate processing of less desirable foods when preferred foods are unavailable [296]. In both interpretations, the robust morphology of *Par. robustus* reflects high bite forces that are used to process foods that are more mechanically challenging than in *A. africanus*.

At first glance, tufted and untufted capuchins seem like an ideal model as there is consistency between skeletal and muscle phenotypes and diet. However, tufted capuchins exhibit greater overall cranial and postcranial robusticity compared to untufted capuchins, which is not necessarily the case for *Paranthropus* versus *Australopithecus*. Previous studies indicate the tail, forelimb, and hindlimb postcranial morphology of tufted capuchins exhibit elevated robusticity compared to *Cebus* [43, 297–300], but the extent to which robust cranial morphology in *Sapajus* reflects whole body robusticity compared to dietary adaptations is unknown. If whole body robusticity is driving cranial morphology in *Sapajus*, applying this model to the fossil record may imply that the cranial morphology in *Paranthropus* reflects whole-body robusticity. At present, postcranial remains attributed to *Par. robustus* are limited, but this taxon is proposed to exhibit a mix of locomotor characteristics, to have engaged in fewer arboreal activities, and had features more similar to extant apes compared to *A. africanus* [301, 302].

5.4 | Estimates of Feeding Performance in Fossils Require Multiple Models

We explored interpretations of bite force in *Par. robustus* and *A. africanus* using jaw-muscle fiber phenotype, architecture, and leverage based on three groups of nonhuman primates. Each of the models yields different interpretations of bite force in *Par. robustus*. We summarize these three model comparisons in Table 2. As we do not have an a priori preference for any of the models, bite force in *Par. robustus* could range from low but repetitive forces using the chimpanzee/gorilla model, high forces using the capuchin model, and average to low forces using the papionin model. Each of the models raises factors outside of bite force that may influence our interpretation, namely the roles of muscle fatigue, non-feeding behaviors that may be reflected in feeding-system morphology, and overall body size. It may also be the case that bite force in *Par. robustus* reflects more than one of these scenarios if, for example, routine feeding is contrasted with fallback scenarios.

Importantly, the three extant primate models used in this paper suggest there are multiple ways to achieve specific performances, such as increasing bite force—which can be increased by changing a variety of factors including fiber-type phenotype, muscle mass, or pinnation angle—none of which can be distinguished in fossils. As illustrated by fiber-type phenotype and muscle architecture data from extant primates and from these models, bite force should not be viewed in isolation, but instead should be considered in its biological context, which must include other factors such as muscle stretch or gape. Similarly, tradeoffs between two other performance variables, endurance and power (which differentiate masseter fiber-type phenotype in chimpanzees and gorillas [153]), can also be expected to play important roles in bite force interpretations for fossil hominins in some models. Thus, considerations of the feeding systems of fossil taxa should include a range of performance variables, not just bite force.

6 | Conclusions and Future Directions

Our review of fiber type and fiber architecture diversity in primate jaw adductors suggests important relationships between muscle structure, muscle function, and feeding behavior. Our review also emphasizes a high degree of variation related to sex, age, muscle, and species, and a diversity of muscle and muscle-related behavioral performances. This variation is not surprising given the highly plastic nature of muscle tissue.

Previous work has linked anthropoid jaw-closing muscle fiber-type phenotypes with feeding behaviors in ways that provide some support for the frequent recruitment and high occlusal force hypotheses. However, this relationship is complex, as demonstrated by the fact that two seed predators, tufted capuchins and sooty mangabeys, exhibit distinctive superficial masseter fiber-type phenotypes, the former expressing large amounts of MHC-M, the latter expressing large amounts of

TABLE 2 | Summary of bite force comparisons for muscle fiber-type phenotype, fiber architecture, and leverage between *Pan* versus *Gorilla*, *Cecocebus atys* versus other papionins (MMMP-*Macaca mulatta, Mac. fascicularis*, *Mandrillus sphinx*, and *Papio anubis*), and *Sapajus* versus *Cebus*.

Jaw leverage	$PCSA^2$/jaw length	Fiber phenotype for force output	Implications for bite force	References
Pan > *Gorilla*[a]	*Gorilla* > *Pan*	*Pan* > *Gorilla*	Gorillas are adapted for lower force, fatigue-resistant chewing. Chimpanzees are adapted for greater force but more fatigable chewing.	[45, 153, 224]; Taylor, unpublished data
Cer. atys = MMMP[b,c]	*Cer. atys* = MMMP	*Cer. atys* < MMMP	*Cercocebus atys* produces similar forces to other papionins but is more fatigue resistant. MMMP produces similar bite forces to *Cercocebus atys* but are less fatigue resistant.	[145, 154, 226, 293, 303]
Sapajus > *Cebus*[b]	*Sapajus* > *Cebus*	*Sapajus* > *Cebus*	*Sapajus* are adapted to produce high forces in all three measures. *Cebus* are adapted for lower forces in all three measures compared to *Sapajus*.	[43, 145, 223, 295]; see also Figure 8

[a] Leverage calculations based at the M_2 [45] and M^1 (Taylor, unpublished data; *Pan*: $n = 61$ and 47; *Gorilla*: $n = 35$ and 30, for the masseter and temporalis, respectively).
[b] Leverage calculated at the M_1.
[c] There was no consistent pattern of improved leverage for *Cer. atys* at the M_1 for the masseter or temporalis for males or females [226].

MHC-β. Architectural studies of the jaw adductors in these two hard-object feeders result in parallel findings, with relatively large masseter and temporalis PCSAs in tufted (compared with untufted) capuchins, consistent with their feeding behavior, but no differences in relative PCSAs between sooty mangabeys and closely related papionins that are not seed predators. Different evolutionary histories and different selection pressures on the masticatory apparatus—for example, specialized feeding behavior in the former versus social signaling and canine gape display behavior in the latter—likely account, at least in part, for this variation in muscle phenotypes. These results showcase both the many-to-one (i.e., multiple solutions for the same hard-object feeding behavior [263]) as well the one-to-many (i.e., the same features of the masticatory apparatus performing different behaviors) mapping of form to behavior.

Anthropoid primate jaw-closing muscles express MHC isoforms commonly expressed by other mammals, including MHC-β, MHC-α, MHC-2, and MHC-M, but with a greater abundance of hybrids and greater number of hybrid combinations. These hybrids likely contribute to a wide array of contractile properties. The prevalence of hybrid fiber types underscores the importance of future studies aimed at quantifying MHC content and measuring the contractile properties of these muscle fibers if we are to empirically translate fiber-type profiles into their actual fiber-type phenotypes, rather than infer them from other mammals. Additionally, given the high degree of heterogeneity of fiber types, each characterized by a different specific tension, we suggest that models of muscle and bite force would be improved by incorporating this heterogeneity to bracket ranges of variation rather than calculating simple bite force estimates based on a single specific tension value. Future work incorporating aspects of jaw-adductor muscle morphology, such as motor unit density [304], will improve our understanding of variation and performance range.

Studies of masticatory muscle architecture in nonhuman primates have varied substantially in methodological approach and sample composition. Our updated analyses show widespread isometry in scaling of both PCSA and fiber length relative to body mass and jaw length, though with some potentially interesting differences among clades. Primate clades show architectural tradeoffs between muscle force and jaw gape, but superimposed on these clade-based patterns are examples of primate species (e.g., tree-gouging marmosets, tufted capuchins, male papionins) that employ different morphological strategies to circumvent these tradeoffs. Our analyses further demonstrate the importance of drilling down to lower taxonomic levels (e.g., family/genus/species) to detect meaningful dietary signals in muscle architecture. Future use of imaging methods such as MRI, CT, and diffusion tensor imaging would allow for noninvasive methods of measuring architectural variables while at the same time enabling large numbers of fibers to be sampled within a given individual through automated imaging protocols [241], thereby more accurately characterizing the architecture of these muscles within species. We also emphasize the need for dynamic architecture studies of primates for all the chewing muscles. Study of dynamic architecture in nonhuman primate chewing muscles is in its infancy but holds the key to understanding how the masticatory muscles operate during feeding and how dynamic movements can shape performance variables. Muscle architecture dynamics have the capacity to bypass or alter muscle performance variables thereby resulting in modified estimates of performance ranges and output in vivo. Analyses of 3D architecture are also in their infancy, but they have potential to open new lines of investigation, and we suggest that more studies should be aimed at evaluating 2D and 3D architecture in the same specimens (e.g., [216]). Similarly, work aimed at developing predictive relationships between bony landmarks and muscle architecture (i.e., fiber length and PCSA) would further improve our understanding of masticatory apparatus function in fossil species.

Early in this review, we noted that modeling approaches like FEA have reinvigorated interest in jaw-muscle anatomy. Most finite element models of fossil hominins rely on a single primate taxon, macaques, as the extant model for comparison. This is because finite element models of macaques have been validated using in vivo measures of mandibular stress and strain, muscle activation, and muscle architecture [305–307]. Our comparisons of bite force models for *Par. robustus* and *A. africanus* highlight a range of possible performance outcomes depending on the extant primates used for comparison, while also illustrating the influence of performance variables other than bite force. Mandibular stress and strain and muscle activation patterns are unavailable for most nonhuman primates and are likely to remain so for the foreseeable future. However, by using empirically derived fiber-type phenotypes and architecture configurations in muscle force estimates, researchers can utilize modeling approaches such as FEA to (1) simulate a range of performance outcomes, for example bite force at wide and small gapes; and (2) reduce the number of assumptions in the model by, for example not assuming a single specific tension for all jaw adductors.

Moving forward, we recommend that future research on feeding system biomechanics consider multiple performance measures as well as a range of potential performance outcomes (such as increased gape, fatigue resistance, faster movements, or lower energy costs). Clarifying ontogenetic changes in physiological, architectural, and bony aspects of the masticatory apparatus and the mechanisms that underlie these changes is also crucial if we are to gain a better handle on the factors that account for variation in this system. Ultimately, comparative analyses will benefit from combining multiple lines of evidence, including muscle fiber phenotype, architecture, and leverage, validated by a range of performance variables in multiple extant primate taxa. Such integrated approaches to linking feeding system performance with masticatory apparatus form also require detailed in vivo experiments, data from wild primates on foraging strategies, as well as associations with feeding behavior, food geometric properties, and food material properties (e.g., [193]). We believe this multi-pronged approach to muscle structure, function, and feeding performance will provide a more robust basis for estimating performance metric ranges in fossil hominins.

Author Contributions

Andrea B. Taylor, Megan H. Holmes, Myra F. Laird, and Claire E. Terhune all contributed equally to the conception and design, data collection and analysis, and writing of this review paper.

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Ethics Statement

Capuchin data in Box Figure 2 were collected under IACUC 05-005 at NEOMED and IACUC 72430 at the University of Chicago. *Varecia* data in Box 3 were collected under IACUC 21241 at the University of Southern California, IACUC 807395 at the University of Pennsylvania, and A186-20-09 at Duke University.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this review paper are available in previously published papers and in supporting information files for publication in the online version of this manuscript.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.