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Functional and ecological correlates of the primate jaw abductors

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Abstract

While the *adductor* musculature of the primate jaw has been extensively analyzed within the context of dietary and social ecology, little is known about the corresponding muscles of jaw *abduction*. Nonetheless, these muscles significantly contribute to a species' maximum gape potential, and thus might constrain dietary niche diversity and impact social display behaviors. In this study, we quantify the architectural properties of the digastric (a jaw abductor) and lateral pterygoid (a jaw abductor and anterior translator) across a broad sample of male and female anthropoid primates. We test the hypothesis that the abductor musculature reflects specialization to dietary and behavioral ecology. Our sample comprises 14 catarrhine and 13 platyrrhine species spanning a wide range of dietary and social categories. All specimens were sharp dissected and muscles subsequently chemically digested using a standardized protocol. Our findings demonstrate that relative fascicle lengths within the lateral pterygoid (but not the digastric) are significantly greater within species that habitually consume larger food items. Meanwhile, canine length is more strongly associated with fascicle lengths in the digastric than in the lateral pterygoid, particularly within males. Neither dietary mechanical resistance nor the intensity of social competition relates to the size or architectural properties of the jaw abductors. These findings suggest that dietary—and to a lesser extent, socioecological—aspects of a primate's life history may be reflected in the architecture of these muscles, albeit to varying degrees. This underlines the importance of considering the complete masticatory apparatus when interpreting the evolution of the primate jaw.

KEYWORDS
diet, digastric, lateral pterygoid, muscle architecture, social ecology

1 | INTRODUCTION

The primate masticatory apparatus performs a diverse array of tasks, encompassing both ingestive and social behaviors that range from the oral acquisition and processing of food items to communicative social displays (Hylander, 2013; McGraw & Daegling, 2012; Plavcan & van Schaik, 1992; Terhune, Hylander, Vinyard, & Taylor, 2015; Vinyard et al., 2007). As the morphology of masticatory structures relates to key parameters of functional performance (such as maximum bite force and gape potential), both dietary properties and socioecological factors have been considered in relation to the anatomy of the masticatory apparatus, particularly the skull and jaw adductor musculature (Hartstone-Rose, Deutsch, Leischner, & Pastor, 2018; Hylander, 2013; Perry, Hartstone-Rose, & Wall, 2011; Taylor, Eng, Anapol, & Vinyard, 2009; Taylor & Vinyard, 2009; Terhune et al., 2015). However, far less attention has been paid to the corresponding muscles associated with jaw abduction and protrusion. Nonetheless, these muscles functionally constrain maximum attainable gape, and therefore a species' dietary and social ecology. In this study, we analyze the architectural properties of the masticatory muscles associated with jaw abduction and protrusion—the digastric (which refers hereafter to the combined anterior and posterior bellies of the digastric complex) and lateral pterygoid (for which the superior and inferior heads were integrated and inseparable so as to form a single muscle belly), respectively (Figure 1)—across a broad range of primate taxa. In so doing, we test the hypothesis that dietary and socioecological factors have shaped the anatomy of these hitherto understudied components of the primate masticatory apparatus.

Both the overall volume and internal architectural configuration (e.g., fascicle organization) of a muscle dictate its contractile properties. Muscle fascicles consist of individual fibers that are themselves comprised of serially arranged sarcomeres—the functional contractile units of skeletal muscle that contract simultaneously to shorten the fibers and produce tension (Gans & Bock, 1965; Lieber, 1986). As resting sarcomere length is relatively conserved across vertebrates (Gokhin, Bang, Zhang, Chen, & Lieber, 2009; Walker & Schrodt, 1974), longer fascicles possess a greater number of sarcomeres such that an increase in fascicle length is functionally related to an increase in both contractile velocity (i.e., closing distance over time) and excursion potential (i.e., maximum linear stretch of all of the combined sarcomeres; Bodine et al., 1982; Gans, 1982; Bang et al., 2006; Gokhin et al., 2009). This contractile velocity, as well as fiber fatigability, is additionally influenced by the histochemical profile of constituent muscle fibers (Korfage, Koolstra, Langenbach, & Van Eijden, 2005; Schiaffino & Reggiani, 1994; Schiaffino & Reggiani, 2011). Within the primate masticatory complex, a higher proportion of type I fibers is associated with a slower, more fatigue-resistant contractile profile, while a higher proportion of type II-M fibers is associated with a faster, but more fatigable profile (Hoh, 2002; Korfage et al., 2005; Rowlerson, Mascarello, Veggetti, & Carpenè, 1983; Schiaffino & Reggiani, 1994; Schiaffino & Reggiani, 2011).

The contractile force potential of a muscle, meanwhile, is directly proportional to the sum cross-section of a muscle's fibers, known as the muscle's "physiological cross-sectional area" (PCSA)—calculated as a muscle's mass divided by its density times its fascicle length (Anapol & Barry, 1996; Gans, 1982; Gans & Bock, 1965). For a given volume of muscle, shorter, more densely packed fascicles enhance force generation potential, while fewer, longer fascicles equate to faster-contracting muscles with increased excursion potential (Gans, 1982; Lieber, 1986). Thus, within skeletal muscle, there exists a functional dichotomy or trade-off that precludes muscles of a given volume from being simultaneously wholly

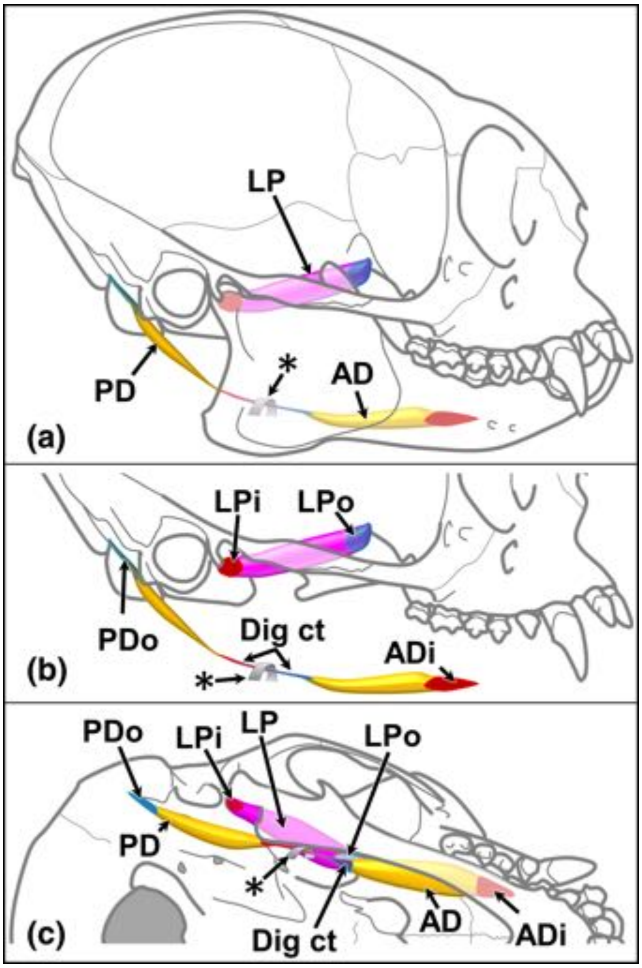

FIGURE 1 Schematic view of the Lateral Pterygoid (LP; magenta), Anterior and Posterior Digastrics (AD and PD, respectively; yellow) of *Callithrix jacchus*. The lateral pterygoid runs from the lateral pterygoid plate of the sphenoid bone to the medial aspect of the neck and head of the mandibular condyle; the posterior head of the digastric originates on the mastoid notch of the temporal bone, then blends into a central tendon that gives rise to the anterior digastric, which then inserts onto the ventromedial margin of the dentary. Lateral view with (a) and without the mandible (b) and inferior view (c) with origins (o; blue) and insertions (i; red). The posterior and anterior digastric insert and originate, respectively, on a central tendon (Dig ct) that loops through a ligamentous sling (asterisk) anchored on the mobile hyoid bone (not shown)

optimized for both force and excursion/velocity (Gans & Bock, 1965; Lieber & Fridén, 2000; Lieber & Ward, 2011).

The theoretical relationship between gape requirements and the fascicle lengths of the masticatory *adductors* is relatively clear (i.e., the fascicles stretch as the jaw is opened, and subsequently contract to produce the force necessary to close the jaw once more). Therefore, theoretically, animals that need to open their mouth to wide gapes require mandibular adductor muscles with long fascicles. The relationship between gape and fascicle lengths in the mandibular *abductors* is less obvious as these muscles are in contraction, rather than tension, as the jaw is opened. However, the same principle theoretically applies: if the adductors must stretch to accommodate a wide gape, then so too must the abductors even though they are in their stretched position not at maximum gape, but at occlusion. Thus, longer fascicles within the jaw abductor musculature maximize the excursion range (i.e., range of gapes) at which abductive forces can still be produced.

1.1 | Behavioral and ecological correlates of jaw muscle morphology

The primate order spans a remarkable diversity of dietary and socioecological niches. Subsistence strategies include specialized insectivores (e.g., *Tarsius*; Jablonski & Crompton, 1994), frugivores (e.g., *Varecia*; Britt, 2000), gummivores (e.g., *Callithrix*; Coimbra-Filho & Mittermeier, 1976), folivores (e.g., *Colobus*; Harris, 2006), and a number of omnivorous generalists that span the dietary specialties. Within these broad categories, however, significant variation can exist. For instance, folivory includes both young-leaf specialists and taxa which specialize on tougher, older foliage, yet these two foodstuffs differ significantly in their mechanical properties (Coiner-Collier et al., 2016). Similarly, frugivores include taxa which specialize in the exploitation of both soft, ripe and hard, unripe fruit (Coiner-Collier et al., 2016). Even within a species, some taxa exhibit remarkable dietary consistency (e.g., *Cercocebus atys*, wherein the most frequently consumed food across all ages and both sexes are the seeds of *Sacoglottis gabonensis*; McGraw, Vick, & Daegling, 2011), whereas the diets of other species can drastically vary either seasonally or between sexes (Chapman & Chapman, 1990). Further, the extent of socioecological competition is similarly variable, including solitary species, pair-bonds and, among gregarious taxa, a huge diversity of competition levels ranging from intensive inter-individual conflicts to highly cooperative and egalitarian groups (e.g., Altmann, 1967; Clutton-Brock, 1974; Kappeler & van Schaik, 2002; Plavcan & van Schaik, 1992).

In recent years, numerous studies have sought to explore the relationship between social/dietary behaviors and muscle architectural properties within the jaw *adductor* musculature of primates. Across anthropoids, species that habitually consume larger foods show an increase in fascicle lengths across the jaw adductors, particularly within the temporalis, as a means of satisfying their increased gape demands (Hartstone-Rose et al., 2018). Similar trends are also observed within strepsirrhines (Perry et al., 2011) and within the Callitrichidae, in which tree-gouging marmosets possess longer fascicles than nongouging tamarins, to facilitate their specialized feeding behavior that necessitates wide-gape jaw postures (Eng, Ward, Vinyard, & Taylor, 2009; Taylor et al., 2009; Taylor & Vinyard, 2004; Taylor & Vinyard, 2008). Similar trends have also been reported for myological force: for example, capuchin monkeys that frequently consume mechanically challenging foods (e.g., *Sapajus apella*) show an increase in muscle size and physiological cross-sectional area (PCSA) relative to non-obdurate feeding taxa (Taylor & Vinyard, 2009). Additionally, as social behaviors also place functional demands upon the anatomy of the masticatory apparatus, the architectural properties of the jaw adductors have also been suggested to reflect the socioecology of a species. In particular, an increase in canine length and the practice of wide-gape "yawning" display behaviors—both features more commonly observed in males of highly dimorphic anthropoid taxa—may necessitate longer fascicles within the jaw adductors to enable canine clearance, and to maximize the efficacy of such displays (Dickinson, Fitton, & Kupczik, 2018; Hylander, 2013; Taylor et al., 2018; Terhune et al., 2015).

A close relationship between the masticatory adductors and dietary ecology has also been observed outside of the primate order. Within felids (Hartstone-Rose, Perry, & Morrow, 2012), musteloids (Hartstone-Rose, Hertzig, & Dickinson, 2019) as well as canids, ursids and carnivorans in general (Hartstone-Rose et al., in press), species that predominantly consume relatively small prey possess significantly shorter fascicles than taxa that consume relatively larger prey. Dietary choices have also been shown to reflect muscle architectural properties in suids (Herring, 1985) and bats (Santana, Grosse, & Dumont, 2012).

1.2 | The mammalian jaw abductors

Within mammals, the two masticatory muscles associated with jaw abduction and protrusion are the digastric (which in most primates consists of two muscle bodies connected via a central tendon) and the lateral pterygoid, respectively (Figure 1). Though the anterior and posterior bellies of the digastric possess distinct fascicular orientations (with the anterior digastric running anteroposteriorly within the jaw, and the posterior digastric running obliquely in an anteroinferior direction), the pull of the posterior digastric is translated into the anteroposterior plane by virtue of its tendinous attachment to the anterior digastric around a ligamentous sling bound inferiorly to the hyoid (Gorniak, 1985). Because of that anchoring on the hyoid, the resultant pull of these combined muscle bellies is caudal (and dorsal at more extreme gapes) around the temporomandibular joint such that the posterior digastric contributes directly to jaw opening as well as to elevation of the hyoid (Gorniak, 1985). However, since the hyoid is itself mobile, the digastric also serves to pull the hyoid cranially if the infrahyoid muscles do not simultaneously counter this action. Although the complex movements of the hyoid have been documented (Nakamura et al., 2017; Orsbon, 2018), for the purposes of this article, we are considering the primary role of the digastric as a mandibular abductor (see discussion of limitations). Fascicles within the lateral pterygoid muscle are also largely described as anteroposteriorly aligned, though the precise orientation may vary between taxa (Dickinson, Basham, Rana, & Hartstone-Rose, 2019; Dickinson, Kolli, Schwenk, Davis, & Hartstone-Rose, 2020). While the primary action of the lateral pterygoid is anterior translation of the mandible, cineradiographic studies demonstrate that this action secondarily assists in abduction, as rotation around the temporomandibular joint is associated with an anterior shift of the mandibular condyle (Hylander, Johnson, & Crompton, 1987; Wall, 1999). Consequently, contraction of the lateral pterygoid muscle can be considered complementary to that of the digastric during mandibular abduction. While a functional distinction between superior and inferior portions of this muscle has been suggested via electromyographic studies in both humans and macaques—in which the superior belly acts predominantly as a stabilizer of the temporomandibular joint during jaw movements (McNamara Jr, 1973; Wang, Yan, & Yuan, 2001; Widmalm, Lillie, & Ash Jr, 1987)—fascicles from these heads are highly interdigitated, and thus may be considered a single anatomical unit which may perform several functional roles.

Variation in the morphology and architectural configuration of these muscles has been described in only a handful of mammalian taxa. Within *Macaca*, the lateral pterygoid is described by Antón (2000) as relatively simple in its architecture, and morphologically conserved across three taxa (*Macaca fascicularis*, *Macaca mulatta*, and *Macaca nemestrina*). Muscle masses are consistently greater within the two larger taxa (*M. nemestrina* and *M. mulatta*) relative to *M. fascicularis*; however, fiber lengths do not scale significantly with body mass (Antón, 2000). Additionally, dry-weight muscle masses of the anterior digastric, posterior digastric, and lateral pterygoid are all reported to scale isometrically against body mass in both anthropoid primates specifically and across the primate order as a whole (Cachel, 1984). It has further been suggested that gouging primate taxa such as *Callithrix jacchus* and *Daubentonia madagascariensis* display several adaptations within the lateral pterygoid towards this feeding strategy. These include an overall increase in muscle mass to increase fascicle length, which permits wider gapes, and protractive force (Dickinson et al., 2020). This increase in contractile potential may serve a dual purpose: both enhancing the ability to forcefully protrude the mandibular dentition into opposing substrates, and to resist loads during gouging and prevent posterior dislocation of the jaw (Dickinson et al., 2020).

Beyond the primate order, the morphology of the digastric is described as relatively conserved among nonaquatic mustelids (Scapino, 1976). However, this muscle is greatly enhanced in size and cross-sectional area within river otters, which pursue agile and fast-moving aquatic prey; this expansion is interpreted to reflect an adaptation for increased force to counter the resistance of water while hunting (Scapino, 1976). A similar adaptation is described within noctilionoid bats, wherein insectivorous species show a slight increase in digastric PCSA, potentially allowing them to open their jaws powerfully during predatory pursuit (Curtis & Santana, 2018). By comparison, frugivorous noctilionoid species show an increase in digastric fascicle lengths that is theorized to permit a wider abductive gape to accommodate large fruits (Curtis & Santana, 2018).

1.3 | Aims and predictions

Preliminary analyses of the jaw abductors within Carnivora, Chiroptera, and select gouging primate taxa suggest that the architecture of these muscles might relate to some aspects of an animal's feeding ecology. This study seeks to investigate the anatomy of the jaw abductor musculature within the context of several specific dietary and social pressures across a broad sample of catarrhine and platyrrhine taxa (including both male and female specimens of taxa that span a gradient of sexual dimorphism), to evaluate the hypothesis that diet and social ecology might impose similar selective pressures upon these muscles to those imposed upon the corresponding jaw adductor musculature. To investigate the potential impact of these external pressures (though see limitations below), our sample incorporates both large- and small-object feeding specialists, obdurate and nonobdurate feeding taxa, and species representing an array of socio-ecological niches.

- Prediction 1: Fascicle lengths within both the digastric and lateral pterygoid will relate to food item size. Species that habitually consume larger food items have been demonstrated to possess relatively elongated fascicles within the jaw adductor musculature, so as to facilitate the production of bite force at wider gapes. We predict that this same trend will be observed within the digastric and lateral pterygoid, such that large-item consumers can maximize the abductive potential of the jaw and accommodate food items of a larger size.
- Prediction 2: Fascicle lengths within the digastric and lateral pterygoid will relate to canine size and socioecology. In addition to dietary pressures, many primate taxa also experience socioecological pressures towards maximizing gape potential (e.g., for agonistic interactions). Two key variables that may influence socially driven gape potential are canine length, as species must be capable of producing sufficient jaw abduction to facilitate canine clearance, and the frequency/importance of wide-gape display behaviors. As both variables are likely to assert selective pressures upon the abductive potential of the jaw, we predict that fascicle lengths within the digastric and lateral pterygoid will relate both to (a) canine length and (b) intrasexual competitiveness, following criteria and classifications outlined in Plavcan and van Schaik (1992). However, as these relationships have previously been tested only in catarrhines, it is possible that the same relationship will not hold true among platyrrhines.
- Prediction 3: PCSA within the digastric and lateral pterygoid will not relate to dietary mechanical properties. An increase in the contractile force potential of the digastric is described within predatory noctilionoid bats as an adaptation towards facilitating powerful, rapid jaw motions during insect pursuits (Curtis & Santana, 2018). Though a heavy reliance upon insectivory is observed within certain primate lineages (e.g., *Tarsius*), this mode of capture relies more heavily upon rapid leaping and grasping motions than high-speed jaw capture. Moreover, both catarrhines and platyrrhines are largely characterized by frugivorous and folivorous diets, supplemented by gummivory and granivory in select taxa. While encompassing variation in the mechanical resistance of foods (which may be expected to impact the adductor musculature, but see Hartstone-Rose et al., 2018), these dietary modes are not predicated on abductive power. Subsequently, we predict that obdurate and nonobdurate feeding taxa will not be distinguished in the force producing capacity of their jaw abductor musculature. Two possible exceptions to this, however, may be in gouging taxa—for which the need to resist posterior loading of the jaw may necessitate an increase in the strength of the lateral pterygoid (Dickinson et al., 2020)—or gummivorous taxa for which the consumption of sticky foodstuffs requires an increase in abductive power to separate the jaws.
- Prediction 4: Architectural properties within the digastric and lateral pterygoid will scale with isometry relative to both body mass and cranial size. Within both anthropoid primates and across primates as a whole, the mass of the lateral pterygoid and the digastric complex are both reported to scale isometrically against body mass (Cachel, 1984). Similarly, within bats, the architectural properties of the digastric are reported to scale closely with body size such that muscle mass, PCSA, and fascicle lengths all scale isometrically (Herrel et al., 2008). Additionally, a recent, comprehensive effort to analyze the scaling of architectural properties within the jaw adductor musculature of catarrhines and platyrrhines (both independently and collectively) concluded that muscle masses similarly track both overall body size and cranial size, resulting in an isometric scaling relationship (Hartstone-Rose et al., 2018). Similar trends are further observed for PCSA and fascicle lengths, though these tend towards slight positive and slight negative allometry, respectively. We therefore predict that architectural properties in the digastric and lateral pterygoid will follow these previously established trends, resulting in an isometric relationship between architectural variables and two body size proxies (body mass and cranial geometric mean).

2 | MATERIALS AND METHODS

2.1 | Data collection

Our sample consisted of 27 anthropoid specimens—14 catarrhine and 13 platyrrhine taxa (Tables 1, S1, and S2, Supporting Information) from various captive facilities and curated at the Universidad de Valladolid and North Carolina State University. Access to the osteological remains of these specimens can be freely accessed by contacting authors FP and AHR. All individual animals died humanely of reasons unrelated to this research, were adult, and presented no apparent masticatory pathologies. Additionally, all specimens were freshly frozen (without fixation) and in a consistent posture of jaw occlusion. No freezing damage was observed in any specimen and, as in all of our previous masticatory dissection research (e.g., Dickinson et al., 2018; Hartstone-Rose et al., 2012, 2018, 2019) muscles were excised while the specimen was in occlusion without stretching them

TABLE 1 Sample, including body mass, cranial size, dietary and competition categories, and architectural properties of the jaw abductor musculature

Species	Parvorder	Sex	Body mass (g)	Cranial GM	Canine length	Dietary size	Comp. Level	Diet Mech. Resistance	LP mass (g)	LP FL (cm)	LP PCSA (cm^2)	Digastric mass (g)	Digastric FL (cm)	Digastric PCSA (cm^2)
Aotus nancymae	Plat.	M	791	3.21	5.93	Small	Low	Low	0.35	0.61 (0.13)	0.544	0.19	0.68 (0.06)	0.27
Callithrix jacchus	Plat.	M	317	2.26	5.10	Large	Low	High	0.11	0.39	0.26	0.12	0.62	0.19
Cercocebus atys	Cat.	M	11,000	6.10	23.45	Large	High	High	0.74	0.97 (0.25)	0.73	2.88	1.54 (0.41)	1.84
Cercocebus torquatus	Cat.	F	6,230	5.13	8.50	Large	High	High				1.68	1.07 (0.16)	1.50
Cercopithecus campbelli	Cat.	F	2,700	4.75	7.90	Small	High	Low	0.96	0.59 (0.09)	1.53	1.69	0.87 (0.28)	1.99
Cercopithecus cephus	Cat.	F	4,290	4.54	16.53	Small	High	Low	0.94	0.68 (0.15)	1.31	1.95	1.19 (0.43)	1.70
Cercopithecus hamlyni	Cat.	F	3,360	4.12	4.36	Large	High	High	0.62	0.48 (0.18)	1.21	0.59	0.98 (0.44)	0.57
Cercopithecus mona	Cat.	F	5,100	4.38	7.64	Small	High	Low	0.33	0.82 (0.33)	0.38	0.66	0.79 (0.18)	0.80
Cercopithecus neglectus	Cat.	M	7,350	5.21	27.00	Small	High	Low	0.65	0.53 (0.08)	1.15	2.49	1.00 (0.33)	2.43
Cercopithecus petaurista	Cat.	F	2,900	4.02	9.82	Large	High	High	0.44	0.53 (0.13)	0.79	0.89	0.88 (0.27)	1.05
Chiropotes sagulatus	Plat.	M	3,000	4.81	16.80	Large	Low	High	1.40	0.79 (0.20)	1.66	0.73	0.98 (0.35)	0.78
Chlorocebus aethiops	Cat.	M	3,563	4.65	7.28	Large	High	High	0.51	0.72 (0.27)	0.67	1.43	1.33 (0.41)	1.04
Colobus guereza	Cat.	F	9,200	5.35	12.52	Large	High	High	0.67	0.89 (0.16)	1.08	3.04	1.17 (0.25)	2.49
Macaca silenus	Cat.	M	8,900	6.05	27.46	Large	High	Low	1.11	0.70 (0.21)	1.49	2.46	1.28 (0.41)	1.90
Macaca sylvanus	Cat.	M	13,267	6.10	24.62	Small	High	High	0.40	0.59 (0.42)	0.65	2.32	1.27 (0.39)	1.82
Mandrillus sphinx	Cat.	F	12,900	6.82	N/A (canine tip broken)	Large	High	High	1.89	0.86 (0.22)	2.10	3.39	1.35 (0.38)	2.39
Miopithecus talapoin	Cat.	M	1,380	3.36	5.02	Small	High	Low	0.17	0.69 (0.42)	0.23	0.25	0.67 (0.24)	0.35
Saguinus labiatus	Plat.	F	539	2.44	7.17	Small	Low	Low	0.06	0.35 (0.06)	0.16	0.16	0.53 (0.09)	0.28
Saguinus midas	Plat.	F	515	2.54	5.89	Small	Low	Low	0.04	0.29 (0.06)	0.13	0.14	0.50 (0.08)	0.28
Saguinus oedipus	Plat.	F	404	2.32	3.97	Small	Low	Low	0.09	0.44	0.20	0.20	0.45	0.43
Saimiri sciureus	Plat.	F	721	2.77	6.30	Small	Low	Low	0.05	0.32 (0.12)	0.15	0.17	0.55 (0.1)	0.29
Sapajus apella	Plat.	F	2,696	4.24	7.71	Large	High	High	0.41	0.49	0.80	0.74	0.83	0.85
Callithrix pygmaea	Plat.	M	124	1.69	2.38	Large	Low	High	0.04	0.15 (0.04)	0.23	0.06	0.21 (0.05)	0.29
Mico argentatus	Plat.	M	360	2.09	3.92	Large	Low	High	0.11	0.25 (0.05)	0.42	0.07	0.37 (0.09)	0.21
Leontopithecus rosalia	Plat.	M	600	2.66	4.61	Small	Low	Low	0.19	0.28 (0.07)	0.65	0.29	0.59 (0.24)	0.58
Callimico goeldii	Plat.	M	630	2.69	5.83	Small	Low	Low	0.08	0.21 (0.05)	0.37	0.11	0.42 (0.12)	0.25
Saguinus bicolor	Plat.	F	496	2.52	4.12	Small	Low	Low	0.06	0.19 (0.03)	0.28	0.16	0.32 (0.07)	0.48

Note: Data on body mass were collected from the specimen directly or sourced from Mittermeier, Wilson, and Rylands (2013). Dietary classifications also follow Mittermeier et al. (2013); competition level was sourced from Plavcan and van Schaik (1992). Data were not collected on the lateral pterygoid *Cercocebus torquatus*.

beyond this length. Architectural data for the lateral pterygoid, anterior digastric, and posterior digastric were collected from thawed specimens following a standardized sharp and chemical dissection protocol. In brief, the skin and overlying musculature and fascia were removed before muscle bodies were separated from adjacent tissues and excised from their bony and tendinous attachments. It should be noted that the lateral pterygoid is one of the least accessible muscles in all of anatomy—spaced between the mandible and cranium and deep to many structures (Figure 1). To access it, especially in small specimens, usually requires careful excision of its insertion on the medial part of the mandibular condyle from a ventral approach, then dislocation of the temporomandibular joint (via severing all ligaments and other craniomandibular connections at least on one side), then removal from its origin once it can be fully visualized. This usually must be done simultaneously with the excision of the adducting medial pterygoid to avoid damaging either. It should also be noted that while the superior and inferior portions of the lateral pterygoid have been suggested to function independently, the fascicles of this muscle are interdigitated so as to preclude the anatomical separation of these compartments without comprising the fascicular integrity of one or both portions (as shown in *Callithrix* by Dickinson et al., 2019). Thus, the muscle is considered herein as a single anatomical unit which may perform several functional roles.

Immediately following excision, all muscles were blotted dry, trimmed of excess connective tissue, and weighed using an analytical balance to the nearest 0.01 g. Following weighing, muscle fascicle lengths were calculated following a chemical digestion protocol modified from Rayne and Crawford (1972) and employed in several recent anatomical investigations (e.g., Hartstone-Rose et al., 2018; Herrel et al., 2008). Each muscle was immersed in either a 10% sulfuric acid solution at 60°C (following Perry & Wall, 2008 and Perry et al., 2011) or a 35% nitric acid solution at room temperature (following Herrel et al., 2008) until connective tissues were dissolved. Muscles were then transferred into a 50% aqueous glycerol solution to prevent further digestion. Fascicles were carefully separated using fine-tip forceps, and either measured using digital calipers, or photographed alongside a scale bar and digitally measured in the software package ImageJ (v 1.51). For each muscle, a sample of approximately 40 fascicles were measured.

Muscle masses and fascicle lengths were subsequently combined to calculate physiological cross-sectional area (PCSA), using a formula modified from Schumacher (1961),

$$q = \frac{m}{lp},$$

in which q represents PCSA, m represents muscle mass (in g), l represents the average fascicle length of each muscle, and p represents a constant defining the specific density of skeletal muscle: 1.0564 g/cm^3, following Murphy and Beardsley (1974). As pennation angles within the masticatory apparatus have been shown to vary across single muscle portions and also as a product of functional gape angle (Hartstone-Rose et al., 2018), PCSA and not RPCSA was calculated and, thus, pennation angles were not considered. Furthermore, the muscles studied in this article are not particularly pennate. Orsbon, Gidmark, and Ross (2018)describes the anterior digastric as unipennate but the posterior digastric as relatively bipennate in *Macaca*; however, other in situ studies of 3D fascicle orientation in in three-dimensional space show the lateral pterygoid and both components of the digastric complex as generally cylindrical muscles without bipennation in the traditional feather-like sense (Dickinson et al., 2019, 2020). Furthermore, the impact of pennation angle of muscles that are substantially pennate has been shown to be negligible on total PCSA (Boettcher, Leonard, Dickinson, Herrel, & Hartstone-Rose, 2019) (Figure 2). We therefore consider any impact to be negligible in practical terms.

Data for the digastric were collected for all specimens; data for the lateral pterygoid were collected for all specimens bar one (*Cercocebus torquatus*) for which the muscle was damaged during the process of extraction. In the case of the digastric, the anterior and posterior bellies were individually dissected and the architectural data for these bellies were then combined in subsequent analyses. Mass and PCSA data were simply summed for each belly; fascicle length was determined using the following weighted formula from Hartstone-Rose et al., 2018):

$$\mathrm{FLdig} = \frac{\mathrm{FL}_{\mathrm{AD}} M_{\mathrm{AD}} + \mathrm{FL}_{\mathrm{PD}} M_{\mathrm{PD}}}{M_{\mathrm{AD}} + M_{\mathrm{PD}}},$$

in which FLdig represents the weighted fascicle length of the digastric complex; $\mathrm{FL}_{\mathrm{AD}}$ and $\mathrm{FL}_{\mathrm{PD}}$ represent the fascicle lengths of the anterior and posterior digastric bellies, respectively; and M_{AD} and M_{PD} represent the muscle masses of the anterior and posterior digastric bellies.

Data for the corresponding jaw adductor musculature were also collected simultaneously (see Table S1; also see Hartstone-Rose et al., 2018 and Deutsch et al., 2020 for analyses on subsets of these adductor data).

Following the removal of all soft tissues from the skull, a cranial geometric mean was calculated to serve as a proxy of overall cranial size within each specimen following the protocol outlined in Deutsch et al. (2020). From lateral and superior cranial photographs of each specimen, eight craniometric measurements were taken

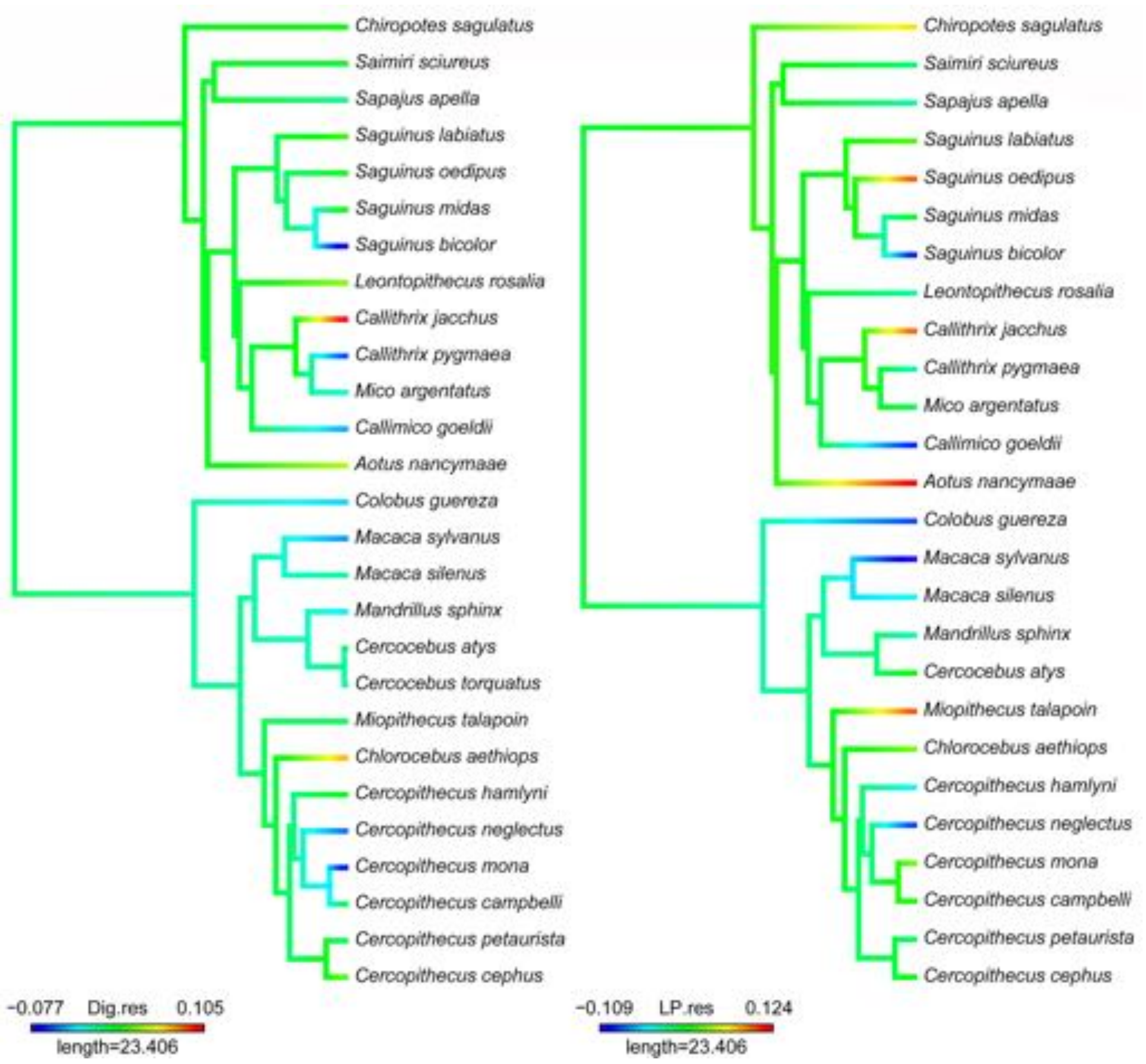

FIGURE 2 Fiber length residuals (res.) on body mass for the digastric (Dig., left) and the lateral pterygoid (LP, right) mapped onto a phylogeny of the species included in this study. Ancestral reconstructions were performed using a Maximum Likelihood approach

(Table 2). The product of these eight values was subsequently taken to the eighth root.

2.2 | Ecological classification

As discussed above, primate dietary and social ecology is both complex and highly diverse. Thus, to facilitate quantitative comparisons between broadly similar groups, simplifications of food size, food mechanical properties, and competition level were necessary (see limitations). Taxa were first classified by sex and parvorder, and subsequently subdivided into discrete groups determined by four ecological traits: food item size (small vs. large object feeders), food item compliancy (mechanically resistant vs. mechanically nonresistant food items), canine length (measured from lateral photographs that included scale bars), and social competitiveness (on the basis of the frequency and intensity of interindividual conflicts). Dietary characteristics (food item size and mechanical resistance) were determined following previously published accounts of dietary behaviors (primarily Mittermeier et al., 2013), and made by considering both the basis of food type (e.g., frugivory vs. folivory) and the specific mechanical properties of consumed foodstuffs, where available. Thus, despite their shared niche as frugivores, soft-fruit specialists

TABLE 2 Measurements used to calculate cranial geometric mean

Measurement	Description
Cranial length	Measured in the midsagittal plane from the inion to interdentale
Cranial height	Measured as the highest point on the frontal bone to the posterior edge of the palate
Jaw length	Measured from the posterior edge of the condyle to the infradentale)
Jaw height	Measured in the coronal plane from the occlusal plane to the inferior border of the mandible
Jaw width	Measured as the width of the mandibular corpus at a point directly inferior to the first molar
Bizygomatic breadth	Measured between the lateral surfaces of the zygomatic arches at their widest points
Orbital height	Measured from the most inferior to most superior point of the orbital socket
Orbital width	Measured from the most lateral to most medial point within the orbital socket, directly perpendicular to orbital height

such as *Saimiri* were distinguished from unripe fruit specialists such as *Chiropotes*, with the diet of the latter classified as large and mechanically challenging alongside large nut and seed-specialists (e.g., *Cercocebus*). This is clearly an oversimplification (see limitations), but, until universally compatible quantification of these dietary parameters are available across the primate order, these generalizations may provide some preliminary adaptive insight—as they have done in previous studies using similar methods (e.g., Curtis & Santana, 2018; Deutsch et al., 2020; Perry et al., 2011).

Food item size was estimated relative to the cranial size of each taxon. Canine length was measured on each specimen following dissection, following a modified protocol of the "canine overlap" method used in Hylander (2013) to represent the vertical distance between the upper and lower canine tips measured with the teeth in occlusion and the skull in lateral view—a proportional metric to the minimum distance of jaw abduction necessary to produce clearance between the upper and lower canines. While Hylander (2013) measured this distance using calipers, it was measured here from lateral photographs of each specimen. Thus, some discrepancy between data for individual taxa may be present that render these values to be not directly comparable between the previous study and the data presented here. Finally, social competitiveness was determined by assigning previously published metrics of social competition intensity by Plavcan and van Schaik (1992), which divided extant anthropoids between classes of high- and low-intensity competition on the basis of behavioral observations.

2.3 | Statistical analysis

To assess scaling relationships, reduced major-axis (RMA) regressions were conducted between each architectural variable and the two body size proxies (body mass and cranial geometric mean). Prior to analysis, all variables were linearized (i.e., areas and volumes were taken to the square- and cubic-root respectively, such that isometry for all slopes = 1) and log-transformed to standardize regression outputs. These regressions were conducted independently for the lateral pterygoid and the combined anterior and posterior digastric. Further, to assess the impact of canine length upon excursion potential within the jaw abductors, log-adjusted fascicle lengths for each muscle were also independently regressed against log-adjusted canine length for each sex and parvorder.

From each RMA regression, the residuals of muscle masses, fascicle lengths and PCSAs relative to each body size proxy were saved, and tested for the presence of phylogenetic signal (Pagel's lambda and Blomberg's K; Pagel, 1999; Blomberg, Garland Jr, & Ives, 2003). These tests were run using a consensus phylogeny for the taxa of interest, sourced from the 10kTrees website (https://10ktrees.nunn-lab.org), and the function *phylosig* from the package *phytools* (Revell, 2012) with 1,000 simulations. A significant phylogenetic signal was not detected in any of the variables ($p > .05$), therefore the rest of the analyses did not include phylogenetic corrections.

Residuals of mass, fascicle length, and PCSA were analyzed through pooled two-way t tests to compare the body-size adjusted characteristics of each muscle between each pair of ecological traits. Relative fascicle lengths (i.e., the above described residuals) were compared between small versus large-object feeders, and between low- versus high-intensity competition taxa. Additionally, relative PCSA was compared between taxa with mechanically challenging versus mechanically nonchallenging diets. Finally, to illustrate patterns of variation among species, fascicle length residuals on body mass were plotted on the 10kTrees consensus phylogeny using the *contmap* function in *phytools*, which estimates character states at internal nodes via Maximum Likelihood (Revell, 2012, 2013).

3 | RESULTS

None of the variables analyzed (muscle mass, PCSA, and fascicle length residuals on body mass or cranial

TABLE 3 Descriptive statistics of reduced major axis (RMA) regressions of muscle architectural variables from the lateral pterygoid and digastric muscles against two size proxies (body mass and cranial geometric mean)

Size proxy	Muscle	Architectural variable	Parvorder/ group	Slope	95% CIs	r^2	*p*	Result
Body mass	LP	MM	Anthropoids	0.88	0.68–1.14	0.86	**<.01**	Isometry
			Catarrhines	0.86		0.54	.055	Isometry
			Platyrrhines	1.26	0.70–2.27	0.78	<.01	Isometry
		PCSA	Anthropoids	0.92	0.62–1.36	0.75	**<.01**	Isometry
			Catarrhines	1.30		0.43	.14	Isometry
			Platyrrhines	1.34	0.52–3.46	0.67	.01	Isometry
		FL	Anthropoids	1.11	0.82–1.51	0.82	**<.01**	Isometry
			Catarrhines	0.88		0.32	.28	Isometry
			Platyrrhines	1.68	0.79–3.56	0.72	<.01	Isometry
	DIG	MM	Anthropoids	0.97	0.86–1.10	0.96	**<.01**	Isometry
			Catarrhines	1.12	0.71–1.75	0.83	**<.01**	Isometry
			Platyrrhines	0.90	0.66–1.22	0.91	**<.01**	Isometry
		PCSA	Anthropoids	0.97	0.79–1.19	0.90	**<.01**	Isometry
			Catarrhines	1.31	0.71–2.42	0.75	<.01	Isometry
			Platyrrhines	0.87	0.38–1.99	0.70	<.01	Isometry
		FL	Anthropoids	1.12	0.95–1.33	0.93	**<.01**	Isometry
			Catarrhines	1.04	0.57–1.88	0.76	<.01	Isometry
			Platyrrhines	1.46	0.94–2.28	0.85	**<.01**	Isometry
Cranial geometric xmean	LP	MM	Anthropoids	1.01	0.82–1.24	0.90	**<.01**	Isometry
			Catarrhines	1.00	0.44–2.23	0.70	<.01	Isometry
			Platyrrhines	1.26	0.78–2.04	0.83	**<.01**	Isometry
		PCSA	Anthropoids	1.06	0.76–1.48	0.79	**<.01**	Isometry
			Catarrhines	1.49	0.26–8.63	0.58	.04	Isometry
			Platyrrhines	1.34	0.61–2.98	0.71	.01	Isometry
		FL	Anthropoids	1.27	0.97–1.68	0.84	**<.01**	Isometry
			Catarrhines	1.01		0.38	.20	Isometry
			Platyrrhines	1.68	0.89–3.19	0.76	<.01	Isometry
	DIG	MM	Anthropoids	1.12	1.00–1.26	0.96	**<.01**	Positive allometry
			Catarrhines	1.29	0.94–1.77	0.90	**<.01**	Isometry
			Platyrrhines	0.90	0.67–1.22	0.92	**<.01**	Isometry
		PCSA	Anthropoids	1.11	0.91–1.36	0.90	**<.01**	Isometry
			Catarrhines	1.51	0.95–2.39	0.83	**<.01**	Isometry
			Platyrrhines	0.87	0.37–2.01	0.70	.01	Isometry
		FL	Anthropoids	1.29	1.10–1.51	0.94	**<.01**	Positive allometry
			Catarrhines	1.20	0.74–1.95	0.81	**<.01**	Isometry
			Platyrrhines	1.47	0.96–2.25	0.86	**<.01**	Isometry

Note: As described in text, all data were linearized such that $\beta = 1$ describes isometry for all variables. All data were also log-transformed prior to analysis. For each regression, three slopes are reported: data for the whole (pooled) sample, and independent regressions for catarrhines and platyrrhines analyzed separately. Statistically significant correlations following Holm–Bonferroni correction are shown in bold.

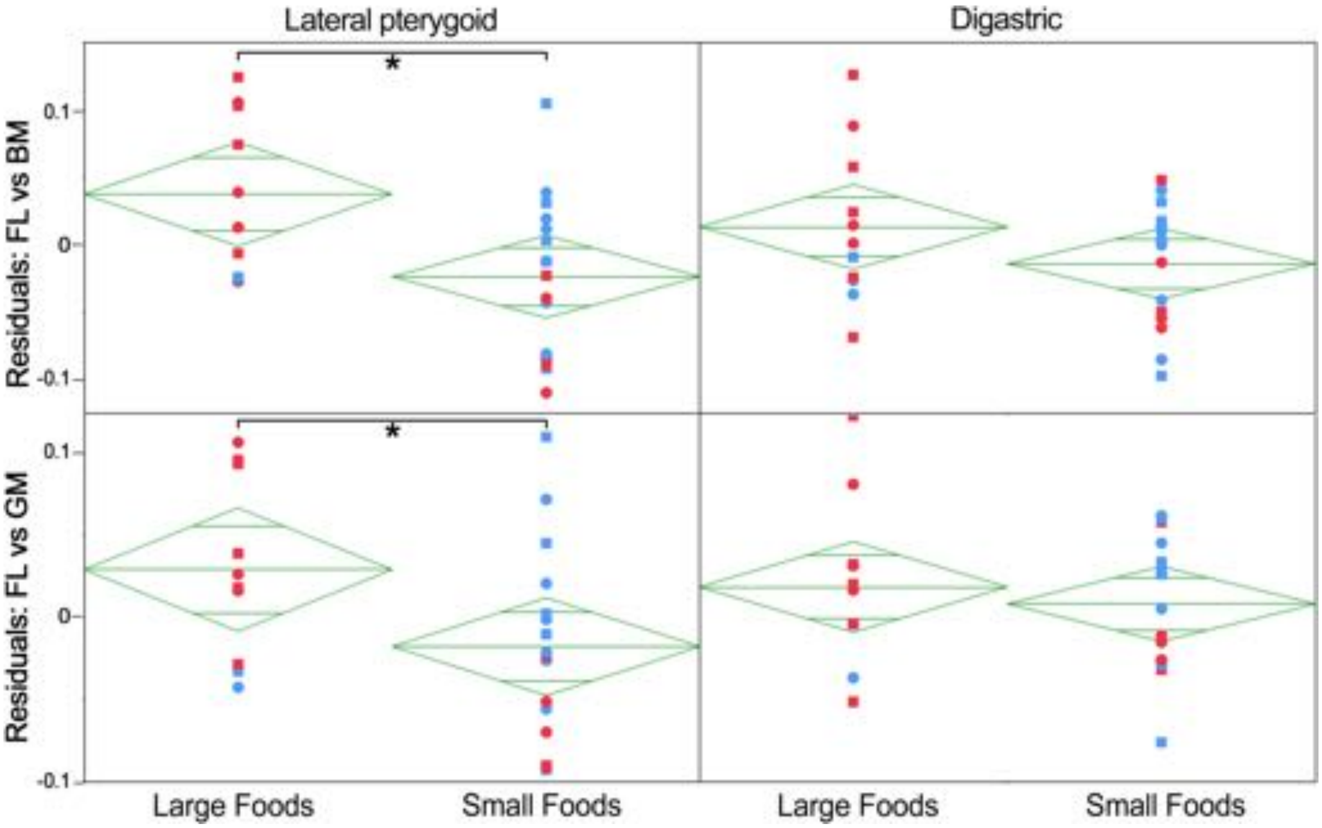

FIGURE 3 Residuals of lateral pterygoid and digastric fascicle lengths (following reduced major-axis regressions against body mass and cranial geometric mean), classified by dietary size (following Mittermeier et al., 2013). Red and blue coloring denotes male and female specimens; squares and circles denote platyrrhine and catarrhine taxa, respectively. Asterisk denotes significance to alpha of .05

TABLE 4 Descriptive statistics of reduced major axis (RMA) regressions of fascicle lengths of the digastric and lateral pterygoid against canine length

Muscle	Sample/subsample	r^2	Slope	p
Digastric fascicle lengths	Whole sample	.80	3.08	**<.01**
	Males	.85	3.34	**<.01**
	Females	.74	2.33	**<.01**
	Platyrrhines	.86	2.59	**<.01**
	Catarrhines	.63	6.34	.02
Lateral pterygoid fascicle lengths	Whole sample	.68	3.16	**<.01**
	Males	.71	3.40	**<.01**
	Females	.62	2.46	.03
	Platyrrhines	.76	2.26	**<.01**
	Catarrhines	.20	7.71	.54

Note: As described in text, all data were log-transformed prior to analysis. For each muscle, data are reported for the sample, divided by sex, and divided by parvorder. Statistically significant results following Holm–Bonferroni correction are shown in bold.

geometric mean) exhibited a significant phylogenetic signal; lambda values ranged from 6.61×10^{-6} to 0.05 (all $p > .05$) and K values from 0.13 to 0.37 (all $p > .05$). A lack of phylogenetic signal in these data is further illustrated by the pattern shown for fascicle length residuals on body mass in Figure 2.

3.1 | Scaling of architectural properties

When analyzing each parvorder independently, all architectural variables scale isometrically with both body mass and cranial geometric mean, supporting prediction 4 (Table 3). When analyzing the combined anthropoid

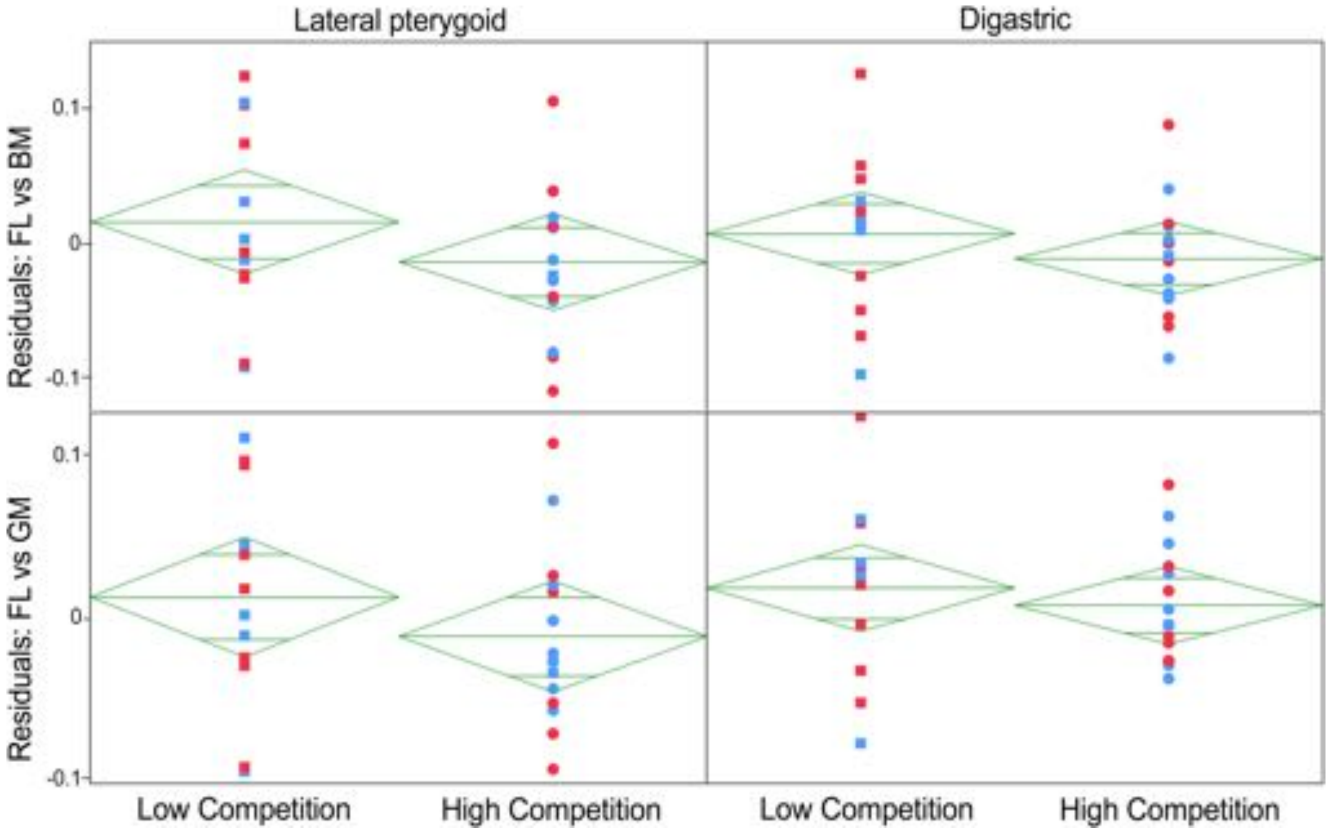

FIGURE 4 Residuals of lateral pterygoid and digastric fascicle lengths (following reduced major-axis regressions against body mass and cranial geometric mean), classified by competition level (following Plavcan & van Schaik, 1992). Red and blue coloring denotes male and female specimens; squares and circles denote platyrrhine and catarrhine taxa, respectively

sample, two of the digastric variables scale with positive allometry relative to cranial geometric mean, but isometrically relative to body mass: muscle mass (slope = 1.12, 95% CIs = 1.00–1.26) and fascicle length (slope = 1.29, 95% CIs = 1.10–1.51). Additionally, several variables approach positive allometry, but with 95% confidence intervals that cannot preclude the possibility for isometry: fascicle lengths in the digastric of anthropoids and platyrrhines relative to body mass, fascicle lengths in the lateral pterygoid of anthropoids relative to cranial geometric mean, muscle mass and PCSA of the digastric in catarrhines relative to cranial geometric mean, and fascicle lengths of the digastric in platyrrhines relative to cranial geometric mean (Table 3).

3.2 | Food item size

Across our whole-primate sample, relative fascicle lengths within the lateral pterygoid were greater in taxa that habitually consume larger food items ($p = .02$ and $p = .05$ when scaled relative to body mass and cranial geometric mean, respectively; Figure 3). However, these same trends were not statistically significant within the digastric ($p = .18$ and $p = .56$). Therefore, prediction 1 was only partially supported. To explore potential taxonomic trends within our sample, data were subsequently analyzed independently within each parvorder. These subanalyses demonstrate a more significant relationship between food item size and jaw abductor fascicle lengths within catarrhines (adjusted for body mass, $p = .03$ and .22 for the lateral pterygoid and digastric, respectively) than in platyrrhines ($p = .31$ and .66).

3.3 | Canine size and socioecology

Across our sample as a whole, fascicle lengths were positively and significantly correlated with canine length in both the digastric and the lateral pterygoid ($r^2 = .80$ and .68 for the digastric and lateral pterygoid, respectively; full summary statistics presented in Table 4). When divided by parvoder, the relationship between fascicle lengths and canine length was stronger within platyrrhines ($r^2 = .86$ and .76 for the digastric and lateral pterygoid, respectively) than among catarrhines ($r^2 = .63$ and .20). This low correlation among catarrhines appeared largely driven by taxa within the genus *Cercopithecus*,

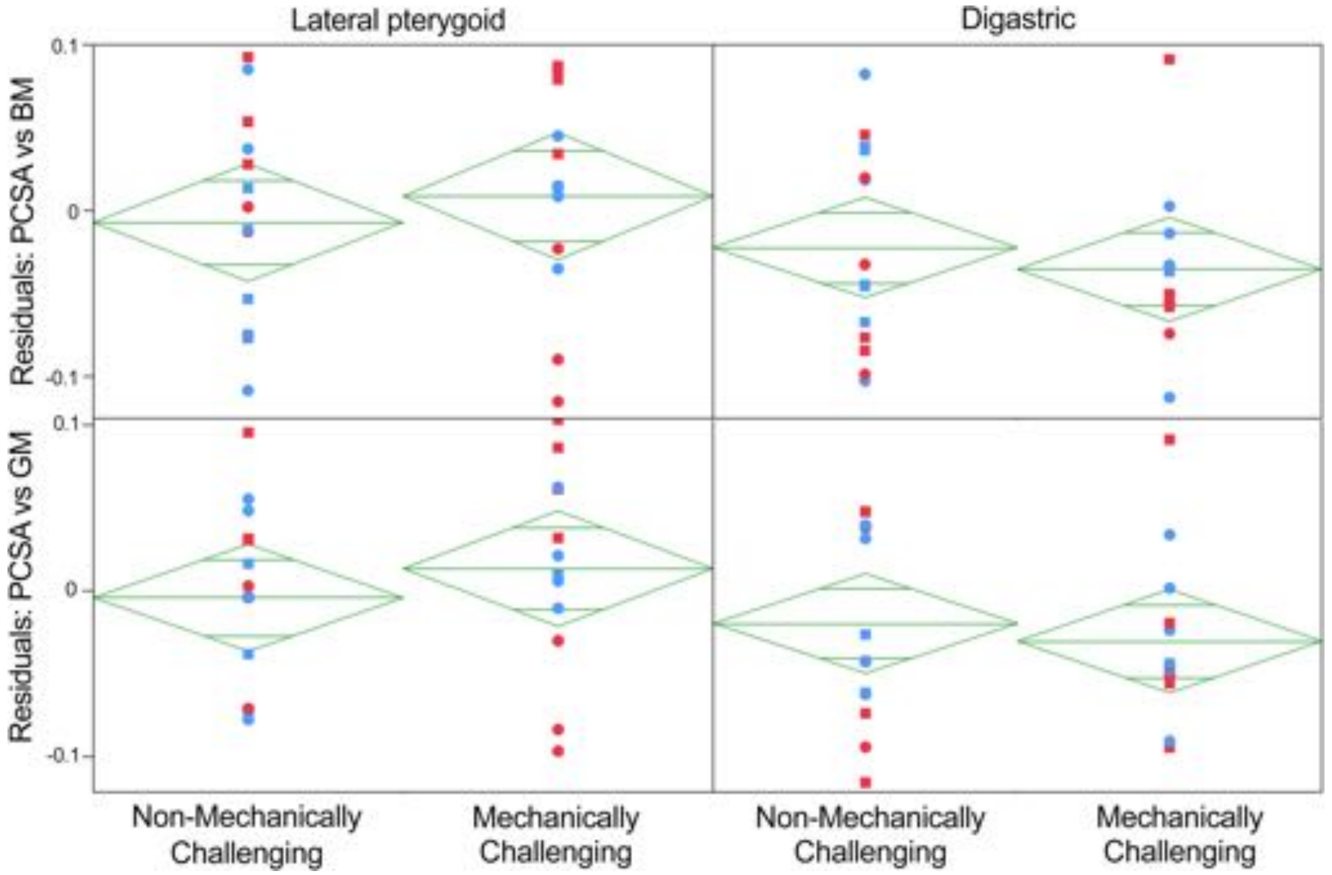

FIGURE 5 Residuals of lateral pterygoid and digastric physiologic cross-sectional areas (following reduced major-axis regressions against body mass and cranial geometric mean), classified by dietary mechanical resistance (following Mittermeier et al., 2013). Red and blue coloring denotes male and female specimens; squares and circles denote platyrrhine and catarrhine taxa, respectively

TABLE 5 Descriptive statistics of 2-tailed *t* tests, on residuals of digastric and lateral pterygoid PCSA versus two scaling proxies (body mass and cranial geometric mean) between high- and low-mechanical resistance dietary categories

Size proxy	Variable	Sample/subsample	*p*
Body mass	Digastric PCSA residuals	Anthropoids	.54
		Catarrhines	.46
		Platyrrhines	.92
	Lateral Pterygoid PCSA residuals	Anthropoids	.54
		Catarrhines	.67
		Platyrrhines	.05
Cranial geometric mean	Digastric PCSA residuals	Anthropoids	.62
		Catarrhines	.50
		Platyrrhines	.98
	Lateral Pterygoid PCSA residuals	Anthropoids	.45
		Catarrhines	.73
		Platyrrhines	.05

Note: Data are presented for the sample as a whole and for each parvorder independently.

which possessed relatively long canines in combination with relatively short abductor fascicles, particularly within the lateral pterygoid (Figure 2). When divided by sex, males showed a stronger correlation between relative fascicle lengths and canine length ($r^2 = .85$ and .71 for the digastric and lateral pterygoid, respectively) than females ($r^2 = .74$ and .62). When including both sex and parvorder as classifiers, the strongest correlations were observed in the digastric and lateral pterygoid of male platyrrhines ($r^2 = .87$ and .84 for the digastric and lateral pterygoid, respectively), and in the digastric of female platyrrhines ($r^2 = .83$). Conversely, this relationship was weaker within male catarrhines ($r^2 = .58$ and $-.11$ for the digastric and lateral pterygoid, respectively).

Finally, a comparison of relative abductor fascicle lengths between taxa of low- and high-intensity social competition (following Plavcan & van Schaik, 1992) yielded no significant differences when adjusted for either body mass or cranial geometric mean. This was true both for the sample as a whole ($p = .26–.56$; Figure 4), and within each sex individually (females, $p = .57–.82$; males, $p = .40–.66$). Thus, prediction 2 is only partially supported.

3.4 | Dietary mechanical resistance

No significant differences in the force production capacity of the jaw abductor musculature were observed between obdurate and nonobdurate feeding taxa, supporting prediction 3. This was true when analyzing the sample as a whole (Figure 5), and within each parvorder independently (Table 5). Similarly, gummivores did not demonstrate an increase in jaw abductor PCSA: of the seven gummivorous taxa analyzed here, four expressed positive residuals for relative lateral pterygoid and digastric PCSA, while three expressed negative residuals.

4 | DISCUSSION

Despite the widespread attention paid to the ecological contributors of jaw adductor architecture within primates, the corresponding muscles of jaw abduction are poorly understood. While this study has attempted to fill this gap, it does so with several key limitations, most importantly the oversimplification of the movements enacted by these muscles. That is, while the lateral pterygoid and digastric muscles are the mandibular abductors within the muscles of mastication (i.e., the counterparts to the masticatory adductors in the temporalis, masseter and medial pterygoid groups), they are neither the only mandibular abductors (indeed many of the muscles of the anterior neck can perform this function—especially those associated with the hyoid) nor are they pure mandibular abductors. This last point is particularly important: the lateral pterygoid aids in opening the mouth by anteriorly and inferiorly translating the mandibular condyle along the articular tubercle (Terhune, 2011a, 2011b). While this is done most often in association with mandibular abduction, it is also used in mandibular protrusion (discussed in detail in Dickinson et al., 2020) and, when performed unilaterally, produces mandibular yaw. Likewise, although the digastric muscles are most often associated with mandibular abduction, their central tendon anchors on the highly mobile hyoid (Orsbon et al., 2018) and as such, their activation, in combination with other hyoidal muscles, causes movement of this bone and the associated tissues (e.g., during swallowing). Although all specimens in the current study were decapitated prior to excision of these muscles (relieving the caudal tension on the hyoid, presumably normalizing the resting tension on the digastric muscles), it is beyond the scope of the current inquiry to assess the complex nonabductive adaptations of these muscles. One future direction that would aid in extirpating these competing functions would be to examine these muscles in carnivorans—a lineage that includes taxa with highly constrained temporomandibular joints and jaw movements limited almost exclusively to pure hinge-like abduction/adduction.

A second limitation is the potential interrelatedness of variables analyzed herein: for instance, sex (and in specific taxa, sexually dimorphic variables such as canine length) may inherently be functionally related to food size and/or body size. As the first study to evaluate functional trends in this muscle group, the impact of sample composition cannot be directly compared using other studies, but it is hoped that this research may generate future studies which evaluate the primate jaw abductors across other taxa in a more quantitative manner. Relatedly, the nature of a sample reliant on fresh, cadaveric primate material also precludes potentially interesting questions regarding, for example, the impact of sexual dimorphism upon the variables analyzed here. If possible, future studies may wish to target taxa that are more readily available and thus allow for intraspecific analyses that may consider this and other related effects. For instance, deep investigation of this anatomy in macaque species may elucidate intraspecific variation and sexual dimorphism in this anatomy.

Third, the use of broad categories to classify diet across the sample—while necessary to support quantitative comparisons between groups—obscures some level of detail with regards to the dietary ecology of individual species (for instance, variation in the relatively toughness of folivores between young-leaf and tougher, old-leaf consumers). Where possible, known specialists are classified using finer-level detail—e.g., the unripe fruit exploitation of *Chiropotes* assigns the species to the mechanically challenging category, which distinguishes it from less obdurate-feeding frugivores—but primate diets are inherently more complex and more variable than any classification system may comprehensively describe. Subsequently, until quantified dietary variables (e.g., like those argued for by Lucas, 2004) are available and directly comparable across the order, these types of oversimplifications are still informative and unavoidable. A final limitation, albeit another unavoidable one, is the use of captive animals in this study. Although most comparative studies that use specimens of captive specimens have couched their findings as documenting functional anatomy that has been primarily influenced by evolutionary adaptation (see Perry et al., 2011 for a discussion of this), it is undeniable that the diets fed to captive animals could influence their masticatory anatomy. For instance, diets that are more or less obdurate than those of wild conspecifics could make individual animals develop stronger or weaker masticatory adductors than would be found in their wild conspecifics. Although it is hard to conceptualize the effects of food obduracy the abductors examined in this study, if captive animals are fed larger or smaller foods than are their wild conspecifics, the influence of the different necessary gape angle may indeed change this anatomy relative to wild type. On the contrary, using only captive animals may actual standardize the influence of diatary variability on this anatomy (since captive primates have more homogenous diets across species)—helping focus solely on the evolutionary adaptation of interest in our study. While this limitation is the case for virtually all previously published anatomical studies of the primate masticatory system, it is nevertheless useful to exercise caution when interpreting ecological variables through the use of captive specimens.

Beyond these limitations, the data presented here provide the first insight into the variance that characterizes jaw abductors across anthropoids, and explores the relative contributions of potential ecological factors (e.g., food size, food mechanical resistance, and socioecology) in driving interspecific trends in the functional capabilities of these muscles.

To begin, we demonstrate that the overall scaling of these muscles—relative to both overall body mass, and to cranial size—is strongly conservative, with most architectural variables scaling isometrically relative to both size proxies. This trend mirrors previous findings of the scaling of jaw abductors in bats (Curtis & Santana, 2018; Herrel et al., 2008) and of jaw adductors in anthropoids and strepsirrhines (Hartstone-Rose et al., 2018; Perry et al., 2011) and suggests that, while ecological niche diversity does appear to impact some components of architecture within these muscles, body size alone serves as the main determinant of muscle size and organization. Interestingly, some discrepancies were observed between parvorders—with some correlations between myology and size proxies reaching significance in platyrrhines but not in catarrhines. While this variation is interesting in its own right and certainly suggestive of the need to more explicitly analyze variation in these muscles across a broader spectrum of catarrhines in future studies, some degree of caution is advised when analyzing residuals from the catarrhine-only regressions.

Of the ecological factors analyzed here, food item size appears to relate most strongly to muscle architecture. Within the lateral pterygoid, large-object feeding taxa possess significantly longer muscle fascicles (Figure 3), which would imply a relatively larger gape capacity. Within the digastric, this trend is not statistically significant; though of the 12 taxa that exhibit positive residuals for lateral pterygoid fascicle lengths, 10 also exhibit positive residuals for fascicle lengths in the digastric. A tendency towards increased gape potential, on the species level, can therefore be observed in both muscles. Conversely, greater jaw abductor PCSA values were not observed in obdurate-feeding taxa, nor in sticky-food specialist gummivores.

From a broader perspective, these observations further add to a growing volume of literature on the jaw *adductor* muscles of primates—suggesting that, among architectural variables, fascicle lengths associate more strongly with dietary ecology than do either muscle mass or PCSA. Across a sample of 24 strepsirrhine species, fiber length was shown to correlate strongly with maximum ingested food sizes—facilitating wider gapes in (largely frugivorous) taxa that frequently consume relatively large food items (Perry et al., 2011). Likewise, among callitrichids, fascicle lengths have been shown to vary as a consequence of masticatory function even among closely related species (Eng et al., 2009; Taylor et al., 2009; Taylor & Vinyard, 2004). Most pertinent to this study, meanwhile, is the recent study on the jaw adductors of anthropoids (Hartstone-Rose et al., 2018) that includes data from many specimens also used within this study—and which again suggests that taxa consuming softer, larger foods show an increase in jaw adductor fascicle lengths relative to species that consume smaller but more obdurate food items.

That this trend is observed more strongly in the lateral pterygoid than in the digastric within our own sample is surprising, though it is possible that anterior translation of the jaw facilitated by the lateral pterygoid may be particularly important among large-object feeding specialists. However, more explicit testing of this hypothesis remains necessary. Diet-associated differences in the digastric might also be instead manifested in other muscle properties, such as the material properties of the interconnecting tendon between the muscle's anterior and posterior portions, a possibility which future studies may wish to explore.

Interestingly, while a stronger relationship was observed between food item size and the architecture of the lateral pterygoid, the inverse was observed when considering canine size, with consistently stronger relationships between digastric fascicle lengths and canine length, particularly within males and most notably within male platyrrhines. This tentative observation could imply that the digastric is more strongly associated with pure rotational abduction (e.g., to facilitate canine clearance) as opposed to maximizing functional masticatory gape—though this relationship requires further analysis.

In addition to canine size, we also evaluated a second, more indirect proxy for socioecological competition (competitive intensity, following Plavcan & van Schaik, 1992) relative to the same myological variables. This would enable a more comprehensive assessment of competition levels (e.g., factoring in not only canine size but also body size dimorphism; though it should be noted that not all primate taxa analyzed herein utilize wide gape postures during indirect competition events, and thus this proxy is only a loose estimation of social pressures upon the masticatory apparatus). This comparison yielded no significant differences between high- and low-competition taxa in terms of myological gape potential.

When analyzing our data between parvorders, similarly interesting trends also emerge, with a stronger relationship between food item size and jaw abductor fascicle lengths observed within catarrhines than in platyrrhines, but a stronger relationship between canine length and fascicle lengths observed within platyrrhines. This trend may largely reflect the impact of a single genus (*Cercopithecus*), that comprises 6/27 (22%) of our total taxa and 6/14 (43%) of catarrhines. These taxa occupy an unusual niche within our sample, consuming foods that are relatively small but possessing relatively large canines for their body size. Relative fascicle lengths within the genus vary, but typically fall slightly below the anthropoid average, thus corresponding more strongly with dietary size than with canine length and contributing to the parvorder dichotomy outlined above.

On the specific level, it is interesting to note the exceptional myology of the taxon *C. jacchus*, possessing exceedingly elongated fascicles relative to its body size (Figure 3). Within *C. jacchus*, the positive residual for digastric FL within this species is ~50% greater than the next closest taxon, *Chlorocebus aethiops* (these two data points can be seen as the two positive outliers in digastric FL in Figure 4); similarly, relative fascicle lengths within the lateral pterygoid are the second-longest, behind only *Miopithecus talapoin*. This finding is further reinforced by earlier observations of the jaw adductor musculature within this taxon, which are reported to possess relatively elongated fascicles (Dickinson et al., 2019; Hartstone-Rose et al., 2018; Taylor et al., 2009; Taylor & Vinyard, 2004) as an adaptation towards their dietary niche of primary gouging to stimulate exudate flow from tree bark (Coimbra-Filho & Mittermeier, 1976, 1977). It would therefore appear that this taxon has evolved longer fascicle lengths across the masticatory apparatus as a means of maximizing gape potential. Interestingly, however, the two additional gouging taxa within our sample (*Mico argentatus* and *Callithrix pygmaea*, which are sister to *C. jacchus*, Figure 2) possess relatively unremarkable fascicle lengths in either the digastric or the lateral pterygoid. We therefore suggest that further work is needed to explore this relationship within other gouging primate lineages such as *D. madagascariensis* (Erickson, 1994; Sterling, 1994) or *Nycticebus pygmaeus* (Nekaris, 2014; Starr & Nekaris, 2013) and to look more deeply at patterns within the gouging and nongouging Callitrichidae, with a specific emphasis upon jaw loading during gouging behaviors and the mechanical properties of gouged materials.

It is similarly interesting to note that the three gouging marmoset taxa within our sample (*C. jacchus*, *C. pygmaea*, and *M. argentatus*) all possess relatively high PCSA values within the lateral pterygoid—indeed, all three species rank among the highest values when adjusted for either body mass or cranial size. From a functional perspective, an increase in lateral pterygoid PCSA may serve two roles: first in enabling the initial penetration of the jaw into tough tree bark during the onset of gouging events, but also in opposing posterior displacement of the jaw during gouging through continuous recruitment of this anterior jaw translator. This anatomy also corresponds with a recent analysis of the masticatory musculature of the gouging aye-aye relative to the generalist mongoose lemur (Dickinson et al., 2020). That study revealed a volumetric increase of the lateral pterygoid in the aye-aye, inferred to help resist posterior dislocation of the jaw; a potentially important role in this taxon, given experimental data have recorded notably high antero-posterior forces during gouging activities within this taxon (Toler & Wall, 2013). We therefore conclude that an increase in the size and strength of the lateral pterygoid may be interpreted as an adaptation towards primary gouging behaviors.

Collectively, this study underlines the importance of considering the complete masticatory apparatus (including both the abductor and adductor musculature) when interpreting the evolution of the primate jaw. Though the abductor musculature is rarely considered within studies of masticatory anatomy (in part due to the relative inaccessibility of the lateral pterygoid), it would appear that dietary—and to a lesser extent, socioecological—aspects of a primate's life history may be reflected in the architecture of these muscles, albeit to varying degrees. Thus, while further work is unquestionably needed to better contextualize these trends within an adaptive evolutionary framework, we suggest that such work promises much potential in advancing our understanding of the interplay between a species' masticatory repertoire and their associated anatomy.

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AUTHOR CONTRIBUTIONS

Edwin Dickinson: Conceptualization (equal); formal analysis (lead); investigation (lead); methodology (equal); project administration (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **J Pastor:** Data curation (equal); funding acquisition (equal); resources (lead); writing – review and editing (supporting). **Sharlene E. Santana:** Conceptualization (supporting); formal analysis (equal); funding acquisition (equal); investigation (supporting); methodology (supporting); visualization (equal); writing – review and editing (equal). **Adam Hartstone-Rose:** Conceptualization (equal); data curation (lead); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (equal); resources (equal); software (equal); supervision (lead); visualization (equal); writing – original draft (supporting); writing – review and editing (lead).

DATA AVAILABILITY STATEMENT

Architectural data used in this study, in addition to the corresponding raw data for the jaw adductor musculature, are presented in Table S1. Data on individual muscle portions of the abductor musculature are presented in Table S2. For further information about any specimen used within this study, please contact the corresponding author.

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