

Chapter 10

Scaling of Reduced Physiologic Cross-Sectional Area in Primate Muscles of Mastication

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10.1 Introduction

In mammals, the functions of mastication (chewing) are to increase the surface area of food so as to increase the rate of digestion, to mechanically break down cell walls so that enzymes can digest intracellular contents, increasing the efficiency of digestion, and to break food into pieces that can be swallowed (Lucas, 2004). Food is broken down by the application of forces generated by the chewing muscles and transmitted by the bones of the skull to the teeth. The magnitude of the stress generated in the food (bite stress) is a function of a number of factors, including the size and arrangement (i.e., muscle and tooth lever arms) of the muscles and teeth, the location of the bite point, tooth size and shape, and the extent to which muscle force is recruited by the central nervous system (CNS). The relative importance of these various influences on bite stress in different primates is unknown. Primarily this is because, although the scaling of dental and skeletal dimensions is relatively well documented, the scaling of muscle physiological parameters and general principles of masticatory muscle force recruitment by the CNS are unknown.

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Here we present our data on the scaling of one reasonable estimator of muscle force potential: the physiologically related morphological variable, *reduced physiologic cross-sectional area* (RPCA). This variable combines muscle mass with the length and angle of pinnation of the constituent fibers to derive a representative estimate of the maximum force deliverable by a quantity of muscle. In this study we ask whether RPCA changes with body size according to the predictions of geometric similarity, metabolic demands, or fracture scaling.

Geometric similarity: If the primate feeding system scales with geometric similarity, then muscle RPCA will scale relative to body mass (M) to the power of 0.67; i.e., RPCA $\propto M^{0.67}$, lever arms will scale $\propto M^{0.33}$, tooth area will scale $\propto M^{0.67}$, and bite stress (force/area) will be independent of size (muscle force $\propto M^{0.67}$ /tooth area $\propto M^{0.67} = M^{0.0}$). Thus, if the feeding system scales with geometric similarity, relative muscle cross-sectional area and relative tooth area will increase at a lesser rate than increasing body mass, although bite stress will be invariant with respect to body mass.

Metabolic scaling: Resting metabolic rate scales $\propto M^{0.75}$ (Kleiber, 1961; Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Savage et al., 2004; West and Brown, 2005), and it has been suggested that dental dimensions of mammals should scale with metabolic rate, i.e., $\propto M^{0.75}$ in order for them to acquire the necessary amount of food per unit time (Pilbeam and Gould, 1974, 1975; Gould, 1975). This hypothesis assumes that the volume of food processed per chew increases isometrically with tooth surface area; i.e., $\propto M^{0.75}$, if that is indeed how tooth surface area scales. However, subsequent work has revealed that geometric similarity and not positive allometry of dental dimensions is the rule for mammals ($\propto M^{0.67}$) (Kay, 1975; Fortelius, 1985; Lucas, 2004; Vinyard and Hanna, 2005), demanding an explanation for how larger animals acquire enough energy. Larger animals might spend relatively more time feeding every day, take in more energetically rich foods, process more food per chew (e.g., food volume processed might scale $\propto M^{1.0}$), and/or extract energy more efficiently to meet their metabolic needs (Kay, 1985; Fortelius, 1985). One way to extract energy more quickly and efficiently would be to increase bite stress as body size increases, and this could be achieved by increasing muscle force faster than tooth area: e.g., RPCA \propto tooth area^{>1.0}, where tooth area $\propto M^{>0.67}$.

Fracture scaling: Lucas (2004) has suggested an alternative model of scaling of the feeding system based on the proposition that larger particles of food fracture at smaller stresses than smaller particles. Consequently, if larger animals eat larger food particles than smaller animals, the amount of stress needed to fracture the larger particles will decrease. Specifically, Lucas predicts that bite forces, and therefore RPCA, need only increase $\propto M^{0.5}$ in geometrically similar animals, an exponent substantially less than the geometric scaling prediction of $M^{0.67}$. In essence, according to the fracture scaling, larger animals require proportionally smaller masticatory muscles to eat larger particles of the same kind of foods as their smaller counterparts.

In this paper, we present an analysis of scaling patterns for RPCA of chewing muscles in a wide variety of primates. The geometric similarity, metabolic and fracture scaling hypotheses are tested using both published body weights and a directly measured size surrogate, craniobasal length, as independent variables. We

also evaluate the possibility that scaling patterns of RPCA differ between prosimians, platyrrhines, and catarrhines.

10.2 Materials and Methods

The sample consisted of 27 species of primates—prosimians, platyrrhines, cercopithecoid monkeys, and lesser apes. Three jaw elevator muscles—masseter, temporalis, and medial pterygoid—were examined. The muscle samples used in this study were dissected by CFR from preserved specimens in various museum and private collections between 1991 and 1993 and, although stored in 30% ethanol when received, were grossly titrated into buffered formalin (10%) at University of Wisconsin-Milwaukee (UWM) (see below). The skull, or craniobasal, length was measured on each specimen. Descriptions of the gross anatomy of the muscles in most of the species were published by Ross (1995), along with a preliminary account of the scaling of muscle mass.

The specimens were subsequently moved to UWM where RPCA was determined (Shahnoor, 2004). Muscle sampling and measurement protocols have been detailed previously in Anapol (1984), Anapol and Jungers (1986), Anapol and Barry (1996), Anapol and Gray (2003), and Anapol et al. (2004). Measurements of in situ sarcomere lengths, derived using histologic techniques, enabled restoration of in situ fiber lengths and pinnation angles to putative resting values (Anapol and Barry, 1996; Anapol and Gray, 2003; Anapol et al., 2004). These corrected variables were combined with muscle weights to calculate RPCA, using the formula of Schumacher (1961), after Weber (1851), and adjusted by Haxton (1944):

$$\text{RPCA (cm}^2\text{)} = [\text{mass (gm)} \times \cos \theta] / [l_f \text{ (cm)} \times \text{specific density}],$$

where l_f and θ represent resting fiber length and angle of pinnation of that fiber, respectively, and the specific density of muscle is 1.0564 gm/cm³ (Murphy and Beardsley, 1974).

Following (natural) log transformation of the data, Pearson's product—moment correlation coefficients r , and least squares linear regression (LSR) equations (Sokal and Rohlf, 1981a) were performed for RPCA on both the craniobasal length (CBL) measured on the specimens from which the muscles were dissected (Ross, 1995) and the cube root of body weight (M) taken from the literature (Smith and Jungers, 1997). M and RPCA were converted to $M^{1/3}$ and $\text{RPCA}^{1/2}$, so that isometry values would equal 1.0. Reduced major axis (RMA) slopes were calculated by dividing each LSR slope by its corresponding correlation coefficient. Confidence intervals were computed for LSR slopes and intercepts by multiplying each standard error by the table (Students' T-test; Sokal and Rohlf, 1981b) value for 0.025 at the error degrees of freedom. The standard error of the RMA slope approximates that of the LSR slope (Sokal and Rohlf, 1981), enabling use of the same confidence interval. After testing for homogeneity of slopes, ANCOVAs were performed on $\text{RPCA}^{1/2}$ s for each muscle separately and all muscles pooled with CBL or $M^{1/3}$ as the covariate. Groups

were prosimians, platyrrhines, and catarrhines, or prosimians and anthropoids. Most results were computed using Statistical Analysis Software (SAS, SAS Institute, Cary, NC) on the University of Wisconsin-Milwaukee IBM mainframe UWM-3270 computer. ANCOVAs were performed using SPSS.

10.3 Results

The mean variables used in the regressions in this study are presented in Table 10.1. This includes published body weights (Smith and Jungers, 1997) and means of cranio-basal lengths and RPCA of each muscle (masseter, temporalis, medial pterygoid) separated by species. In Table 10.2, Pearson's product-moment correlation coefficients (r), plus the probability that r is significantly different from 0, are shown for $M^{1/3} \times \text{CBL}$, $\text{RPCA}^{1/2} \times M^{1/3}$, and $\text{RPCA}^{1/2} \times \text{CBL}$. Published body weights are highly correlated with measured CBLs across all primates studied, and across prosimians and platyrrhines, but are not significantly correlated in catarrhines ($r = 0.63$; $P \leq 0.18$) (Table 10.2a). With the exception of catarrhines, correlation coefficients are similar for $\text{RPCA}^{1/2} \times$ either $M^{1/3}$ or CBL. In catarrhines, correlations between $M^{1/3}$ and $\text{RPCA}^{1/2}$ of muscles as a whole, masseter, and medial pterygoid are as strong or stronger than those between $\text{RPCA}^{1/2}$ and CBL (Table 10.2b and c), despite the fact that CBL was measured directly on the skulls upon which these muscles had been attached and M was taken from the literature. For $\text{RPCA}^{1/2} \times \text{CBL}$, the probability that r is greater than zero ($P \neq 0.00$) exceeds 0.05 in catarrhines only for muscles as a whole, masseter, and medial pterygoid.

Table 10.3 contains regression statistics (isometry = 1.0) for CBL vs $M^{1/3}$, and for $\text{RPCA}^{1/2}$ vs $M^{1/3}$, and $\text{RPCA}^{1/2}$ vs CBL. Results are presented for the three muscles separately and for the RPCA pooled within a species. The data were analyzed across all primates and subdivided into prosimians, platyrrhines, and catarrhines. The confidence intervals are broad, such that, even when differences between groups are dramatic, their statistical significance cannot be proven. Nevertheless, discussion of some general patterns is possible and provides hypotheses for future testing.

When CBL is regressed on $M^{1/3}$ (Table 10.3a), both LSR and RMA slopes indicate negative allometry (< 1.0) for primates as a whole, prosimians, platyrrhines, and catarrhines. Thus, in this primate sample, skull length increases at a slower rate than body weight.

When RPCA is regressed on published body mass, regression slopes across primates as a whole suggest negative allometry for the RPCA of each muscle individually and for the RPCA of all muscles pooled (Fig. 10.1, Table 10.3b). In contrast, within prosimians, platyrrhines, and catarrhines, pooled muscle RPCAs—and in most cases individual muscles—scale with positive allometry. The difference between intra-group and all-primate results is due to transposition of intra-group lines, with prosimians having the higher and platyrrhines the lower intercept values (Fig. 10.1). Slopes for all primates pooled suggest positive allometry for all muscles combined and for individual muscles. In prosimians, slope estimates are

Table 10.1 Mean variables of species used in the regressions. Each genus comprises >1 species, except *Callithrix* and *Colobus* where two separate species are listed

Genera	TYPE	<i>M</i> (g)	<i>N</i>	CBL (mm)	MXSEC (cm ²)	TXSEC (cm ²)	MPXSEC (cm ²)
<i>Eulemur</i>	PRO	2215	3	91.77	1.36	2.09	0.64
<i>Galago</i>	PRO	62	4	35.98	0.17	0.2	0.09
<i>Hapalemur</i>	PRO	945	2	66.4	1.22	1.15	0.63
<i>Otolemur</i>	PRO	1150	3	81.93	3.53	5.2	1.09
<i>Potto</i>	PRO	833	3	62.57	1.3	1.01	0.57
<i>Tarsier</i>	PRO	123	2	38.15	0.33	0.35	0.23
<i>Alouatta</i>	PLA	5950	2	108.2	1.94	2.18	1.44
<i>Aotus</i>	PLA	775	4	63.00	0.66	0.63	0.23
<i>Ateles</i>	PLA	8775	4	122.08	2.56	3.01	1.63
<i>Callicebus</i>	PLA	988	4	62.45	0.26	0.4	0.14
<i>Callimico</i>	PLA	484	3	53.9	0.45	0.7	0.2
<i>Callithrix</i>	PLA	345	4	45.45	0.19	0.27	0.09
<i>argentata</i>							
<i>Callithrix</i>	PLA	372	5	43.7	0.27	0.39	0.1
<i>jacchus</i>							
<i>Cebuella</i>	PLA	116	3	34.13	0.24	0.31	0.11
<i>Cebus</i>	PLA	3085	4	87.93	1.67	2.83	0.64
<i>Chiropotes</i>	PLA	2740	5	83.66	2.00	4.21	1.45
<i>Lagothrix</i>	PLA	7150	4	107.95	1.47	1.9	0.43
<i>Leontopithecus</i>	PLA	609	2	57.8	0.73	1.17	0.28
<i>Pithecia</i>	PLA	1760	2	77.65	1.33	1.63	0.84
<i>Saguinus</i>	PLA	411	3	47.7	0.31	0.25	0.25
<i>Saimiri</i>	PLA	721	5	62.6	0.11	0.24	0.09
<i>Colobus</i>	CAT	8285	4	103.78	4.36	5.18	1.74
<i>badius</i>							
<i>Colobus</i>	CAT	9100	3	113.93	3.43	2.82	1.53
<i>polykomos</i>							
<i>Hylobates</i>	CAT	5795	1	118.4	1.91	2.95	1.03
<i>Miopithecus</i>	CAT	1250	4	71.33	0.16	0.31	0.17
<i>Presbytis</i>	CAT	17000	3	89.57	2.35	2.12	1.16
<i>Symphalangus</i>	CAT	11300	1	128.5	1.29	3.52	1.1

Abbreviations= PRO, *prosimians*; PLA, *platyrrhines*; CAT, *catarrhines*; *M*, mass; CBL, craniobasal length; MXSEC, reduced physiologic cross-sectional area of masseter; TXSEC, reduced physiologic cross-sectional area of temporalis; MPXSEC, reduced physiologic cross-sectional area of medial pterygoid.

positively allometric for all muscles combined, masseter, and temporalis, while negatively allometric for the medial pterygoid. In platyrrhines, slopes for all muscles pooled, masseter, and temporalis are close to the values for prosimians, but that of medial pterygoid is much greater than in prosimians. In catarrhines, slopes of muscles pooled and taken individually are strongly positive with masseter exhibiting a steeper slope than temporalis, which in turn scales with a steeper slope than the medial pterygoid.

When $RPCA^{1/2}$ is regressed on CBL (Table 10.3c), all slopes are higher than when $RPCA^{1/2}$ is regressed on $M^{1/3}$ and all are positively allometric (Fig. 10.2, Table 10.2b). In prosimians, platyrrhines, and catarrhines, the absolute values of the slopes differ, but the slope values for masseter, temporalis, and medial pterygoid are more or less the same for both LS and RMA regressions, regardless of which independent variable is chosen. Slope estimates relative to both CBL and *M* are higher across catarrhines than for both prosimians and platyrrhines.

Table 10.2 Pearson's product-moment correlation coefficients between (a) body weight^{1/3} (M) \times craniobasal length (CBL), (b) RPCA^{1/2} \times body weight^{1/3}, and (c) RPCA^{1/2} \times craniobasal length

a.				
	Primates	PRO	PLA	CAT
$M \times \text{CBL}$	0.96	0.98	0.99	0.63
($Pr = 0.0$)	(0.00)	(0.00)	(0.00)	(0.18)
b.				
	Mm.	Masseter	Temporalis	Med Pterygoid
Primates	0.81	0.77	0.81	0.82
($Pr = 0.0$)	(0.00)	(0.00)	(0.00)	(0.00)
PRO	0.91	0.91	0.89	0.93
($Pr = 0.0$)	(0.01)	(0.01)	(0.02)	(0.01)
PLA	0.85	0.83	0.83	0.83
($Pr = 0.0$)	(0.00)	(0.00)	(0.00)	(0.00)
CAT	0.86	0.84	0.82	0.89
($Pr = 0.0$)	(0.03)	(0.04)	(0.04)	(0.02)
c.				
	Mm.	Masseter	Temporalis	Med Pterygoid
Primates	0.84	0.79	0.85	0.84
($Pr = 0.0$)	(0.00)	(0.00)	(0.00)	(0.00)
PRO	0.93	0.91	0.93	0.91
($Pr = 0.0$)	(0.01)	(0.01)	(0.01)	(0.01)
PLA	0.84	0.83	0.83	0.83
($Pr = 0.0$)	(0.00)	(0.00)	(0.00)	(0.00)
CAT	0.77	0.66	0.84	0.76
($Pr = 0.0$)	(0.07)	(0.15)	(0.04)	(0.08)

For abbreviations see Table 10.1.

The rank order of slope values among taxa is the same, regardless of the independent variable used: for muscles pooled, masseter, and temporalis: platyrrhines \leq prosimians $<$ catarrhines; while for medial pterygoid: prosimians $<$ platyrrhines $<$ catarrhines. However, when RPCA pooled across all muscles is regressed against M or CBL, tests of homogeneity of slopes reveal the slopes are not significantly different, allowing ANCOVA to test for differences in elevation of the regression lines. ANCOVA reveals that there is an effect of taxon membership on the mean RPCA when controlling for body mass, with prosimians having larger pooled RPCA than platyrrhines or catarrhines, but these effects are not significant for RPCA vs CBL. When platyrrhines and catarrhines are pooled together as anthropoids, homogeneity of slopes is confirmed for RPCA vs body mass, and ANCOVA again confirms that prosimians have larger pooled RPCA than anthropoids when controlling for body mass.

ANCOVAs were also performed on the data from individual muscles to ask whether prosimians have larger RPCAs than anthropoids when CBL and M are controlled. These analyses revealed that prosimians do not have larger RPCAs than anthropoids at similar CBLs, but that prosimians do have larger RPCAs for temporalis, masseter, and medial pterygoid than the anthropoids with similar M .

Table 10.3 Regression statistics for linear regressions of (a) craniobasal length on body weight^{1/3}, (b) RPCA^{1/2} on body weight^{1/3}, and (c) RPCA^{1/2} on craniobasal length

		PRO			PLA			CAT				
Primates		Intercept	r ²	Slope	Intercept	r ²	Slope	Intercept	r ²	Slope	Intercept	r ²
LSR	RMA	LSR		LSR	RMA	LSR	RMA	LSR		LSR	RMA	LSR
Estimate	0.75	0.78	0.92	0.81	0.83	2.40	0.87	0.87	0.99	0.45	0.71	0.40
Std. Err.	(0.04)	(0.11)		(0.08)	(0.17)	(0.17)	(0.03)	(0.07)		(0.28)	(0.82)	
95% CI	Slope ± 0.08	±0.23		Slope ± 0.22			Slope ± 0.06			Slope ± 0.78		
b.												
All muscles												
		Masseter			Temporalis			Med Pterygoid				
Slope		Intercept	r ²	Slope	Intercept	r ²	Slope	Intercept	r ²	Slope	Intercept	r ²
LSR	RMA	LSR		LSR	RMA	LSR	RMA	LSR		LSR	RMA	LSR
Primates (sid. err.)	0.86	1.06	0.66	0.84	1.08	-2.14	0.60	0.87	1.07	-2.06	0.66	0.85
CI	(0.12)	(0.30)		(0.14)	(0.34)	(0.34)		(0.13)	(0.31)	(0.31)		1.04
PRO	Slope ± 0.25			Slope ± 0.29				Slope ± 0.27				Slope ± 0.25
(sid. err.)	1.06	1.16	0.83	1.06	1.17	-2.27	0.82	1.12	1.26	-2.33	0.79	0.89
CI	(0.24)	(0.52)		(0.25)	(0.52)	(0.52)		(0.29)	(0.61)	(0.61)		0.96
PLA	Slope ± 0.67			Slope ± 0.69				Slope ± 0.81				Slope ± 0.50
(sid. err.)	1.00	1.18	0.72	0.99	1.19	-2.56	0.69	1.00	1.20	-2.41	0.70	1.03
CI	(0.17)	(0.42)		(0.18)	(0.44)	(0.44)		(0.18)	(0.43)	(0.43)		1.24
CAT	Slope ± 0.37			Slope ± 0.39				Slope ± 0.39				Slope ± 0.41
(sid. err.)	1.44	1.67	0.74	1.65	1.97	-4.65	0.70	1.36	1.65	-3.61	0.68	1.25
CI	(0.43)	(1.27)		(0.54)	(1.59)	(1.59)		(0.46)	(1.37)	(1.37)		1.41
	Slope ± 1.19			Slope ± 1.50				Slope ± 1.28				Slope ± 0.92

Table 10.3 (continued)

	All muscles			Masseter			Temporalis			Med Pterygoid		
	Slope	LSR	r^2	Slope	LSR	r^2	Slope	LSR	r^2	Slope	LSR	r^2
Primates (sid. err.)	1.13 (0.15)	1.35 (0.63)	0.70	1.10 (0.17)	1.40 (0.73)	0.62	1.16 (0.15)	1.37 (0.62)	0.72	1.11 (0.14)	1.33 (0.62)	0.70
CI	Slope \pm 0.31			Slope \pm 0.35			Slope \pm 0.31			Slope \pm 0.29		
PRO (sid. err.)	1.31 (0.26)	1.41 (1.08)	0.86	1.29 (0.29)	1.42 (1.18)	0.83	1.42 (0.28)	1.52 (0.88)	0.87	1.05 (0.25)	1.16 (1.01)	0.82
CI	Slope \pm 0.72			Slope \pm 0.81			Slope \pm 0.78			Slope \pm 0.69		
PLA (sid. err.)	1.14 (0.20)	1.35 (0.84)	0.71	1.12 (0.21)	1.36 (0.89)	0.68	1.13 (0.21)	1.36 (0.88)	0.69	1.18 (0.22)	1.41 (0.91)	0.70
CI	Slope \pm 0.43			Slope \pm 0.45			Slope \pm 0.45			Slope \pm 0.48		
CAT (sid. err.)	1.82 (0.74)	2.35 (3.44)	0.60	1.83 (1.03)	2.76 (4.79)	0.44	1.93 (0.63)	2.29 (4.79)	0.71	1.50 (0.64)	1.97 (2.95)	0.58
CI	Slope \pm 2.05			Slope \pm 2.86			Slope \pm 1.75			Slope \pm 1.78		

Abbreviations: LSR, least squares; RMA, reduced major axis; std. err., standard error; 95% CI, confidence interval. For additional abbreviations see Table 10.1.

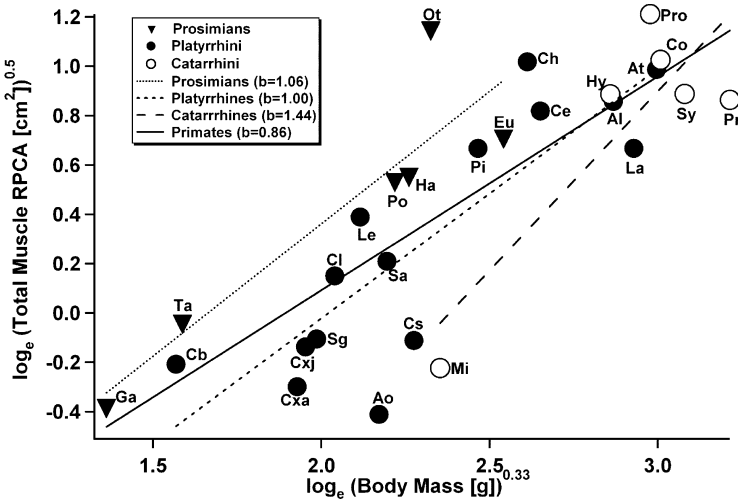


Fig. 10.1 Bivariate plot of \log_e of the square root of the sum of all muscle's RPCA cm^2 against \log_e cube root of body mass (g). Least squares regression lines for prosimians, platyrrhines, catarrhines, and all primates are shown. The slope values are given in the figure legend. ANCOVA reveals an effect of taxon group on relative RPCA: prosimians have larger RPCAs than the anthropoids at equivalent body masses

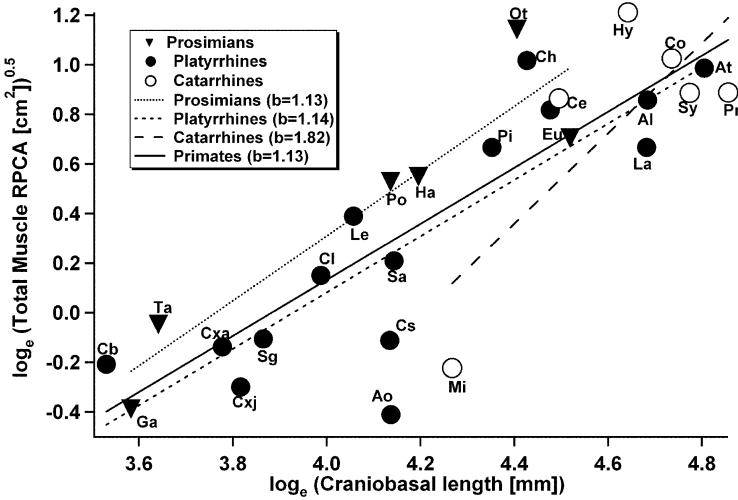


Fig. 10.2 Bivariate plot of \log_e of the square root of the sum of all muscle's RPCA cm^2 against \log_e of craniobasal length (CBL). Least squares regression lines for prosimians, platyrrhines, catarrhines, and all primates are shown. The slope values are given in the figure legend. ANCOVA reveals no effect of taxon group on relative RPCA: prosimians do not have larger RPCAs than the anthropoids at equivalent CBLs

10.4 Discussion

10.4.1 Data Issues

Certain limitations of the data set presented here must be acknowledged. Sample size and taxonomic sampling in studies of muscle anatomy are rarely as satisfactory as one would like. The current array is no exception, being skewed strongly toward platyrrhine species, and having low sample sizes within species. Cercopithecine primates in particular are poorly represented, and catarrhines are only represented by a cluster of similarly sized large animals and one small species, *Miopithecus talapoin* (Fig. 10.1). In addition, the specimens from which these muscles were collected come from diverse sources with diverse histories, including length of time since death of the animal. Moreover, some of the specimens lived in captivity and some lived in the wild. Whether these factors affect the results presented here cannot be determined at present. Finally, reduced physiologic cross-sectional area (RPCA) is a composite variable, derived from several measurements extracted from muscle tissue. Although great care is taken to standardize control measurement protocols, each of these raw variables—sarcomere length, muscle weight, fasciculus length, and angle of pinnation—is subject to measurement error. These limitations should be addressed in future work.

10.4.2 RPCA Scaling

RPCA is a physiologically relevant morphological variable in that it provides an estimate of maximum muscle force for a whole muscle, or a specific portion from in situ measurements (Gans and Bock, 1965; Gans, 1982). To estimate RPCA, muscle weight is converted to a volume by dividing it by the specific gravity of muscle. The cross-sectional area of the muscle volume is then estimated by dividing the muscle volume by the length of muscle fibers or fasciculi. Multiplying this value by cosine of the angle of pinnation isolates the proportion of the cross-sectional area contributing to whole muscle shortening (an angular adjustment that is not required for parallel-fibered muscles.)

In this study, in situ measurements of fasciculus (rather than fiber) length were used as the functional contractile length by which muscle weight was divided (Alexander, 1974). We argue that this is appropriate because, as other authors have demonstrated, what is ordinarily considered to be a muscle fiber extending between attachment sites (either tendon or bone) is often a series of shorter fibers with overlapping ends (Huxley, 1957; Fawcett, 1986; Gaunt and Gans, 1992). If the muscle is chemically treated so as to free-up individual cells from their fasciculi, the released individual fibers would often be shorter than the inter-attachment length, artificially inflating the calculation of cross-sectional area by reducing l_f in the equation. Moreover, chemical digestion of the muscle precludes measurement of the angle of pinnation. (We note that if, in an attempt to preserve pinnation angles, the muscle was

sectioned before maceration, fibers would likely be severed, reducing their lengths and also inflating the calculated RPCA.) Thus, by using fasciculus rather than fiber length, not only more accurate estimates of cross-sectional area are produced but also pinnation angles can be measured, allowing the calculation of a more physiologically relevant RPCA.

In general, our results suggest positive allometry of RPCA within primate subgroups: i.e., prosimians, platyrrhines, and catarrhines. When all LSR slopes are examined, only the slope of masseter $\text{RPCA}^{1/2}$ against $M^{1/3}$ in platyrrhines (slope = 0.99) and the slope of medial pterygoid $\text{RPCA}^{1/2}$ against $M^{1/3}$ in prosimians (slope = 0.89) are less than 1.0. Among RMA slopes, only the slope of medial pterygoid $\text{RPCA}^{1/2}$ against $M^{1/3}$ in prosimians (slope = 0.96) is less than 1.0. All regression slopes of $\text{RPCA}^{1/2}$ against $\text{CBL}^{1/3}$ are greater than 1.0.

The regression equations for catarrhines suggest stronger positive allometry than the other groups, but examination of Figs. 10.1 and 10.2 suggest that these equations should be viewed with skepticism. The RPCAs for the smallest catarrhine for which we have data, *Miopithecus talapoin*, fall well below the regression lines for the platyrrhines and prosimians, yet the larger catarrhines fall in amongst the larger platyrrhines in our sample. Although we cannot say for sure that the *Miopithecus* data are invalid for some reason, we suspect that they are. Because *Miopithecus* is so much smaller than the rest of the catarrhine sample, its low RPCA is driving the catarrhine regression values. We retained *Miopithecus* in the calculation of the primate regression equations because its body mass and CBL are close to the mean values of the sample, so its seemingly anomalous RPCAs have little effect on the slopes of these regression lines.

Different scaling relationships were documented depending on whether we examined scaling of the RPCA relative to body mass data from the literature (M) or skull length measured from the specimens (CBL). Regressions of RPCA on CBL were associated with steeper, more positive slopes than the regressions on body mass because CBL scales with negative allometry against body weight across primates as a whole, as well as within prosimians, platyrrhines, and catarrhines. The finding that skull length is increasing at a slower rate than body weight across groups and for primates as a whole is no surprise, since brain and related braincase size scale negatively allometric to body size (Martin, 1990). The vast departure in slope values by catarrhines may reflect different scaling coefficients at larger body sizes (catarrhines have, on average, larger body sizes than the other groups). Alternately, the slope value calculated for the catarrhines studied here may not be representative of the true scaling relationships within the group. Not only are CBL and M less tightly correlated in catarrhines ($r = 0.63$) than in prosimians ($r = 0.98$) and platyrrhines ($r = 0.99$), but catarrhines show higher correlation coefficients between RPCA and body mass than between RPCA and CBL, the reverse of the situation in prosimians and platyrrhines, and the confidence intervals of the slope values for all scaling analyses within catarrhines are much larger than those for the other groups.

The allometry of skull length against body mass begs the question: which independent variable should RPCA be regressed against to test the hypotheses presented in the Introduction? If body mass is seen as a logical choice for evaluating the

metabolic scaling hypothesis, then the observation that pooled RPCA^{1/2} scales at slopes higher than 1.00 within prosimians, platyrrhines, and catarrhines (Table 10.3b, Fig. 10.1) suggests that increasing relative bite force might indeed be one way that primates compensate for the fact that tooth area scales more slowly relative to body mass than the metabolic rate. However, RPCA is converted to bite stress via the masticatory system, which lies within the head, suggesting that scaling of RPCA against CBL might more accurately reflect the effect of RPCA scaling on bite stress. The observation that RPCA scales with strong positive allometry relative to CBL in all primate groups (Table 10.3c, Fig. 10.2) confirms the suspicion that positive allometry of RPCA relative to body size and size of the feeding system might be a strategy whereby primates increase food energy intake rate.

Whether the scaling relationships of the chewing muscles are computed relative to CBL or to *M* has little effect on the interpretation of the inter-specific scaling results: the relative values among taxonomic groups essentially are the same. The one exception would be in the scaling relationships of masseter between prosimians and platyrrhines. Relative to *M*^{1/3}, masseter RPCA^{1/2} scales with almost identical slopes (1.17 and 1.19) in the two clades; using CBL, platyrrhines have the lowest allometric slope of the three taxa, although slope ranges for prosimians and platyrrhines are slightly overlapping.

10.4.3 Geometric Similarity, Metabolic Scaling, or Fracture Scaling

Geometric similarity. The data currently available, e.g., that presented in Table 10.4, do not definitively exclude the possibility that jaw adductor RPCA scales with geometric similarity relative to body mass. Confidence intervals are very broad, so that whether LSR or RMA is used, slopes of 1.00 lie within the 95% CI. However, we believe that an argument for positive allometry of RPCA relative to both body mass and skull length is more likely to be correct in the long term. RMA slopes are most

Table 10.4 Review of previous published scaling studies relevant to the data presented in this paper

Variable	Taxon	Expectation of isometry in listed papers	Published slopes of variable vs. body mass	Published slopes converted to isometric slope value = 1.0	Reference
Chewing Frequency	Mammals	No expectation	-0.13 (RMA -0.13)	No expectation	Druzinsky, 1993
Jaw Length	Mammals	0.33	0.31	0.93	Druzinsky, 1993
Muscle PCA	Mammals	0.67	0.50 Theoretical	0.75	Lucas, 2005
Jaw-Muscle PCA	Humans	0.67	0.78	1.17	Weijjs and Hillen, 1985
Total jaw adductor RPCA	Prosimians	0.67	0.77 (RMA 0.83)	1.16 (RMA 1.25)	Perry and Wall, 2005
Metabolic Rate	Mammals	1.00	0.75 Empirical	0.75	Kleiber, 1961
Total Jaw Adductors	Rodents	0.67	0.78 (RMA 0.79)	1.17 (RMA 1.19)	Druzinsky, 1993

appropriate because the body masses upon which these analyses are based derive from the literature, and not from the specimens from which muscles were taken, introducing an error in the body mass estimates of unknown relative magnitude. If RMA is accepted to be the most appropriate regression model, then the only muscle that exhibits slope values less than one for $RPCA^{1/2}$ vs $M^{1/3}$ is the medial pterygoid of prosimians (slope = 0.96). However, even if LSR is regarded as the more appropriate regression model, only the masseter $RPCA^{1/2}$ of platyrrhines, and the regressions calculated across all primates, scales against $M^{1/3}$ with a slope < 1.0. Positive allometry is also consistent with other studies of physiologic cross-sectional area, reduced (Perry and Wall, 2005) or otherwise (Weijs and Hillen, 1985), which indicates positive allometry of muscle cross-sectional area to body mass. Thus, we argue that positive allometry of jaw-muscle RPCA is a reasonable hypothesis at present.

Metabolic scaling. Positive allometry of jaw-muscle RPCA is consistent with the metabolic scaling models summarized above, in which tooth area $\propto M^{0.67}$, metabolic rate $\propto M^{0.75}$, and positive allometry of RPCA compensates for this discrepancy by increasing bite stress with body size, allowing more food to be processed per chew. If positive allometry of RPCA did indeed compensate for decreases in tooth surface area relative to metabolic rate, then RPCA would scale $\propto M^{1.126}$ ($= \alpha M^{0.75/0.67}$), a figure close to the slope values found among prosimians and platyrrhines in this study, and for prosimians by Perry and Wall (2005). However, despite the similarities of these slope values, we hesitate to claim that this provides strong support for the idea that positive allometry of RPCA relative to body mass compensates for decreasing tooth surface area relative to metabolic rate. First, the confidence intervals of the slope values are very large, including a wide range of plausible slopes. Second, when scaling of RPCA relative to skull length is considered, the slope values are much higher than 1.12. The feeding system is largely housed in the head, suggesting that relative RPCA might be increasing faster than required by this metabolic model, generating even higher bite stresses than predicted. Two possible explanations for such strong positive allometry of RPCA (and estimated bite stress) are worth considering. First, it has been argued that larger primates eat “tougher” or “more obdurate” foods than smaller primates. Larger (>1000 g) primates obtain their protein from eating leaves (Kay and Simons, 1980), a behavior usually associated with increased molar occlusal surface area, e.g., as observed in *Alouatta* (Anapol and Lee, 1994). Since body size increases to length cubed, while surface area increases by length squared, the physiological cross-sectional area of masticatory muscle in animals on a comparatively tougher folivorous diet would have to increase faster than body size in order to provide enough chewing energy for the increasing diet of a larger animal. Second, size-related decreases in chewing speed also might be related to positive allometry of RPCA. Chewing cycle duration, the inverse of chewing frequency, scales positively with jaw length across mammals as a whole (Druzinsky, 1993) and within primates. Variation in chewing speed is influenced by many factors, including food type and, presumably, interspecific differences in fiber type composition of the masticatory muscles, but the primary determinant of chewing speed is body size: larger primates chew more

slowly than smaller primates (Ross et al., 2008). Larger animals must therefore meet increasing demands for energy in the face of decreasing chewing speed. One way to compensate for slowing chew speed would be to increase bite stress and use it to process more food per chew.

Fracture scaling. Our data definitively reject the fracture scaling model of Lucas (2004). Lucas hypothesizes that the cross-sectional area of the chewing muscles scales relative to $M^{0.50}$; i.e., with negative allometry. Using $RPCA^{1/2}$ and $M^{1/3}$, fracture scaling predicts a slope of $M^{0.75}$. In contrast, our data suggest that $RPCA$ increases more rapidly relative to body mass than predicted by fracture scaling, with RMA slopes ranging from 0.96 to 1.97, and LSR slopes ranging from 0.85 to 1.65, depending on the muscle and taxon. The 95% confidence intervals of the catarrhine and prosimian slopes include 0.75 (all muscles combined or separate), as do those of the LSR and platyrrhine and primate LSR equations. However, we have already given our reasons for being suspicious of the catarrhine slopes and for believing that the RMA slope calculations are more appropriate than LSR. Moreover, Perry and Wall (2005) also report higher slopes for the scaling of jaw adductor muscle mass relative to body mass than predicted for fracture scaling. We therefore think it unlikely that fracture scaling explains the scaling primate jaw-muscle $RPCAs$. There are various assumptions underlying the fracture scaling model, any of which might be undermining the applicability of the model: that food toughness remains constant at different body sizes, that foods are homogeneous, and that foods have linear stress–strain curves up to yielding. Violation of any of these assumptions could result in a deviation from the predictions of fracture scaling.

10.4.4 Intergroup Comparisons

Taken at face value, our regression results suggest clade-level differences in $RPCA$ scaling, with catarrhine slopes being steeper than platyrrhine and prosimian slopes, and prosimian slopes being steeper than those of platyrrhines. However, as discussed above, we are hesitant to attach biological significance to the steep catarrhine slopes at present; and, moreover, tests for homogeneity of slopes do not reveal that these slopes are significantly different. The ANCOVA results do reveal that prosimians have larger $RPCAs$ than anthropoid primates when controlling for body mass, but not when controlling for CBL. The reason for this is revealed by ANCOVA of CBL vs M , which reveals that prosimians have larger CBLs for their M than anthropoids. Prosimians do have larger masticatory muscle $RPCAs$ relative to body mass than anthropoids, but this effect is not separable from the effect of general increases in head length in prosimians vs anthropoids.

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