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Estimating body mass in New World "monkeys" (Platyrrhini, Primates), with a consideration of the Miocene platyrrhine, *Chilecebus carrascoensis*

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ABSTRACT

Well-constrained estimates of adult body mass for species of fossil platyrrhines (New World "monkeys") are essential for resolving numerous paleobiological questions. However, no consensus exists as to which craniodental measures best correlate with body mass among extant taxa in this clade. In this analysis, we analyze 80 craniodental variables and generate predictive equations applicable to fossil taxa, including the early platyrrhine *Chilecebus carrascoensis*.

We find mandibular length to be the best craniodental predictor of body mass. There is no significant difference in predictive value between osteological and dental measures. Variables associated with the mandible and lower dentition do significantly outperform the cranium and upper dentition. Additionally, we demonstrate that modern platyrrhines differ, morphometrically, from early fossil forms. *Chilecebus* possesses unusual cranial proportions in several key features, as well as proportionally narrow upper incisors and wide upper cheek teeth. These variables yield widely divergent body mass estimates for *Chilecebus*, implying that the correlations observed in a crown group cannot be assumed a priori for early diverging fossils. Variables allometrically consistent with those in extant forms yield a body mass estimate of slightly less than 600 grams for *Chilecebus*, nearly a factor of two smaller than prior preliminary estimates.

Scaled to body mass, the brain of *Chilecebus* is markedly smaller than those of modern anthropoids, despite its lowered body mass estimate advocated here. This finding, in conjunction with a similar pattern exhibited by fossil catarrhines, suggests that increased encephalization arose independently in the two extant subgroups of anthropoids (platyrrhines and catarrhines).

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INTRODUCTION

Motivated by the discovery of the well-preserved cranium of the early, fossil platyrrhine (New World "monkey") *Chilecebus carrascoensis* (Flynn et al., 1995), we explore methods for estimating body mass in fossil platyrrhine species from cranial morphometrics. Adult body mass is highly correlated with a diverse suite of ecological, macroevolutionary, physiological, and life history variables among living mammals (Gittleman and Harvey, 1982; Schmidt-Nielsen, 1984; Gittleman, 1986; Damuth, 1987; McNab and Eisenberg, 1989; Gittleman, 1991, 1993; Gillooly et al., 2005). It follows that improved estimators of body mass for fossil taxa are essential to understanding the biology of extinct species (Gingerich and Smith, 1984; Martin, 1984; Damuth and MacFadden, 1990; Eisenberg, 1990; Jungers, 1990). However, it remains unclear which morphometric variables correlate best with body mass among living mammals, let alone among fossil taxa. Previous attempts to estimate body mass from various skeletal and dental proxies in anthropoids have emphasized the Catarrhini (Old World "monkeys" and hominoids) (e.g., Delson et al., 2000), rather than platyrrhines (Hills and Wood, 1984; Conroy, 1987; Martin, 1990). Since the most reliable morphometric correlates of body mass are identified in the context of comparisons to phylogenetically closely related taxa (Eaglen, 1984; Conroy, 1987; Damuth and MacFadden, 1990; Dagosto and Terranova, 1992), we investigate these associations in platyrrhine primates.

There has been considerable research into various cranial, postcranial, and dental variables as body mass estimators for extinct primates (e.g., Gingerich, 1974; Gingerich et al., 1982; Gingerich and Smith, 1984; Bouvier, 1986; Gingerich, 1990; Martin, 1990; Ruff, 1990; Dagosto and Terranova, 1992; Spocter and Manger, 2007). While a particular variable's reliability as an estimator of body mass for a fossil taxon depends on the strength of the correlation with body mass among extant taxa, those variables that tend to perform better in a statistical sense are not typically the most useful to paleobiologists. Limb bone measures generally correlate better with body mass than do cranial or dental variables. These elements are rare as fossils, however, and when found as isolated elements can be difficult to identify to low taxonomic levels (Damuth and MacFadden, 1990). The most common primate fossils by far are isolated teeth or jaws, elements that typically correlate with body mass more poorly (Gingerich et al., 1982; but also see Dagosto and Terranova, 1992).

Using morphometric proxies to estimate body mass in fossil taxa requires the potentially problematic assumption that the allometric relationship between a given variable and body mass observed among living forms also applies to fossil taxa. As an example, estimates of body mass from different morphometric variables for the early catarrhine *Aegyptopithecus* yield widely varying results (Radinsky, 1977; Martin, 1990; Dagosto and Terranova, 1992; Simons, 1993). Thus, fossil taxa might be characterized by fundamentally different allometries of the skull and dentition; the more unusual these morphometries are, the more uncertain body size estimates (and derived indices such as encephalization quotients) become. In practice, such deviations are difficult to identify because they require a robust and well-resolved phylogeny (of living and fossil forms) and well-preserved and relatively complete fossil material. To minimize these potential problems with a single estimator, body mass estimates from several proxies often are averaged (e.g., Radinsky, 1971; Martin, 1990). This approach makes the optimistic assumption that inaccuracies among variables offset one another, such that variables yielding overestimates counterbalance those underestimating mass.

To elucidate the pattern of increased encephalization (brain volume scaled to body mass) among platyrrhines, we apply a suite of craniodental body mass estimators to the 20.1 Ma fossil *Chilecebus carrascoensis* from the Abanico Formation of central Chile (Flynn et al., 1995). Represented by the best-preserved and -dated early primate skull from South America, *Chilecebus* provides an excellent test case for application of these methods. The completeness and exceptional preservation allow many of the proxy variables to be

applied. Moreover, the antiquity of this fossil allows methods of estimating body mass in extinct taxa to be judged against the backdrop of potentially significant evolutionary change in allometry.

METHODS

Variables, Specimens, and Body Mass Data

We assembled a suite of 80 morphometric variables from the literature (Gingerich and Schoeninger, 1979; Radinsky, 1981a, 1981b, 1982; Gingerich et al., 1982; Anthony and Kay, 1993; Hartwig, 1993; Kobayashi, 1995). Appendix 1 lists measurement variables and their descriptions. Of these potential body mass proxies, 32 were measurements of osteological features on the cranium and mandible, while 48 were measurements of the dentition. All teeth except the third molars (which do not occur in callitrichines) were measured. Specimens of extant taxa examined were from the collections of the Mammalogy Division, Zoology Department of the Field Museum of Natural History, and the Mammalogy Collections, Division of Vertebrate Zoology of the American Museum of Natural History. In total, 157 specimens representing 17 platyrrhine species were measured. Specimen numbers are given in appendix 2. Extant taxa were chosen to ensure a sample containing at least one species from each of the 15 platyrrhine genera and the full range of body sizes (from 13.5 kg for *Brachyteles arachnoides* to 125 grams for *Callithrix pygmaea*). Body mass data were obtained from the Masses of Mammals Database (v. 3.03: Smith et al., 2003). Average body masses used in the regression analysis are listed by species in table 1. In addition, we measured preserved morphometric variables for the fossil taxon *Chilecebus carrascoensis* (SGOPV 3213, Museo Nacional de Historia Nacional, Santiago, Chile). Mean measurement values for extant taxa are given by species in appendix 3.

TABLE 1
Body mass for measured extant platyrrhine species
Masses given in grams, from Smith et al. 2003.

Genus	Species	Mass [g]
Alouatta	*caraya*	5862.5
Aotus	*vociferans*	873.0
Ateles	*geoffroyi*	5284.9
Brachyteles	*arachnoides*	13499.9
Cacajao	*melanocephalus*	3800.0
Cacajao	*calvus*	5796.0
Callicebus	*moloch*	854.7
Callimico	*goeldii*	480.0
Callithrix	*pygmaea*	125.0
Callithrix	*jacchus*	292.0
Cebus	*apella*	2500.0
Chiropotes	*satanas*	3000.0
Lagothrix	*lagotricha*	6300.0
Leontopithecus	*rosalia*	535.5
Pithecia	*pithecia*	1375.5
Saguinus	*mystax*	618.0
Saimiri	*sciureus*	743.2

Allometric Regression Analyses

Morphometric variables and body masses for the living platyrrhines were log-transformed (base 10) to determine allometric relationships between the variables and body mass. Species average masses were fit to species-average log-variables using ordinary (Model 1) least-squares regression (Sokal and Rohlf, 1995). Because similarity in morphometry may arise from close phylogenetic relationship (Felsenstein, 1985), we performed phylogenetically corrected regressions (Garland and Ives, 2000), which were executed in the PDAP (Midford et al., 2003) module for the Mesquite software package (Maddison et al., 2002, 2004). Phylogenetic relationships among extant taxa were obtained from molecular phylogenies of the Platyrrhini (Canavez et al., 1999; von Dornum and Ruvolo, 1999) (figure 1). Slopes and intercepts describing the relationship between the morphologic predictor and body mass were calculated for each variable.

To assess a variable's efficacy in predicting body mass, we quantified the relative performance among estimators using the log-likelihood fit of each regression model to the data:

$$LnL \propto -\frac{1}{2} nLn\left(\frac{ESS}{n}\right)$$

(Burnham and Anderson, 2002).

In the equation, n is the sample size, and ESS is the error sum of squares of the regression; therefore, the regression likelihood is proportional to its ability to minimize residual variance. Model log-likelihoods were rescaled

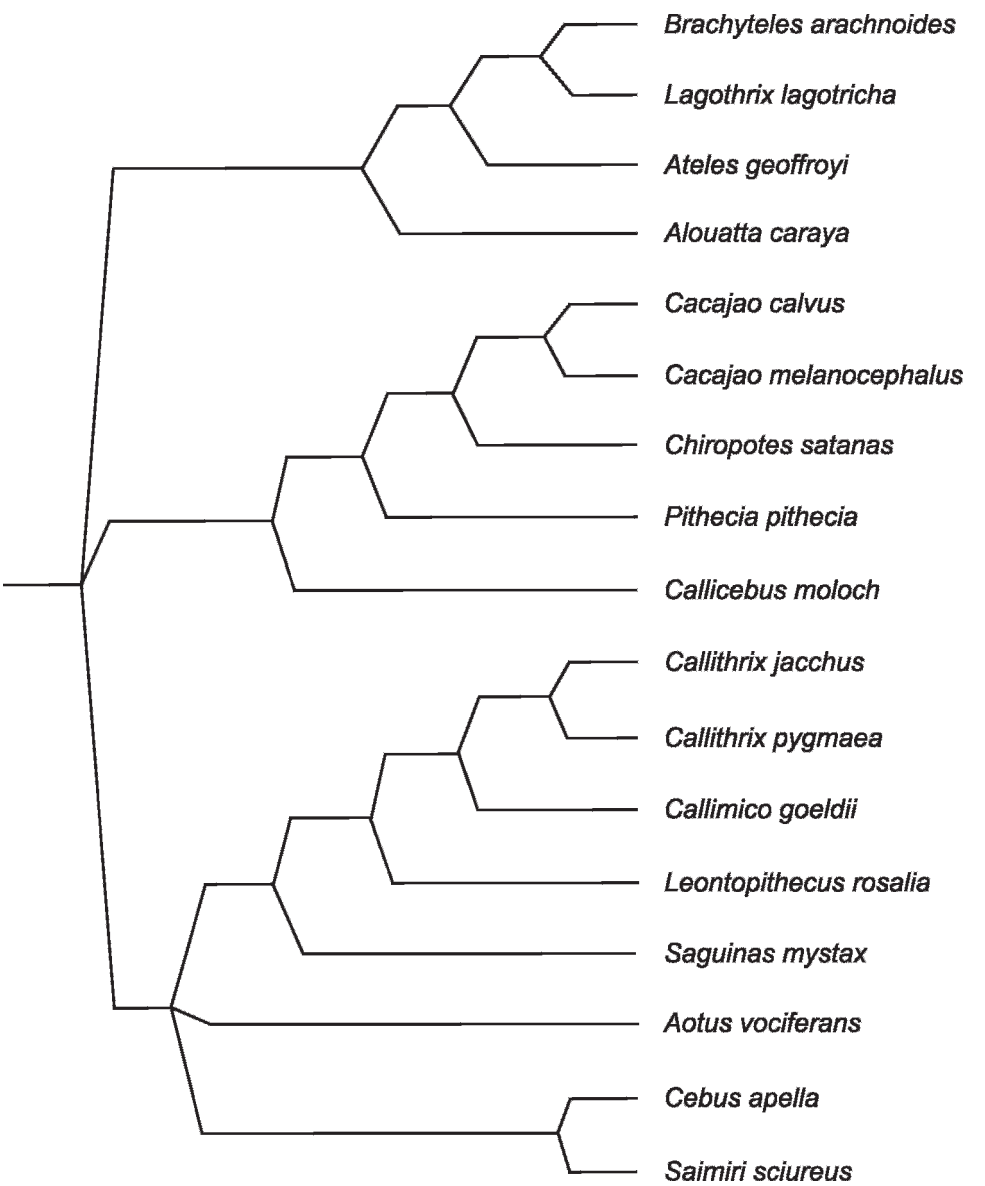

Fig. 1. Cladogram from molecular phylogenies (Canavez et al., 1999; von Dornum and Ruvolo, 1999) of platyrrhine primates used in the phylogenetically corrected regressions of body mass on morphometric variables. This cladogram is a synthetic topology of these two phylogenetic analyses. The topologies for the two analyses were congruent for overlapping taxa, with two exceptions. First the *Callicebus*/*Cacjao*/*Chiropotes*/*Pitehca* clade was basal to all other Platyrrhini in von Dornum and Ruvolo (1999), but was allied with the *Ateles*/*Bachyteles*/*Lagothrix*/*Allouata* clade in Canavez et al. (1999). Second, *Aotus* was allied with *Saimiri* and *Cebus* in Canvez et al. (1999), but left in an unresolved polytomy in von Dornum and Ruvolo (1999). Therefore both nodes are conservatively left in polytomies here.

such that the maximum value across all variables was 0, with poorer predictors having progressively more negative log-likelihoods (Edwards, 1992). We employed a log-likelihood difference of 2 (Edwards, 1992; Royall, 1997; Wagner, 2000a, 2000b) as the cutoff for identifying one variable as a significantly better predictor of body mass than another.

Body Mass Estimation in *Chilecebus*

The body mass of the fossil platyrrhine *Chilecebus carrascoensis* was estimated from 46 measurements preserved in SGOPV 3213, the holotype cranium, using the regression equations generated above from living taxa. We calculated a weighted average of these estimates using the proportional likelihoods for each regression model over the set of all models (Burnham and Anderson, 2002). Model averaging is appropriate when there is no clearly identifiable "correct" model. This method has been employed to a limited extent in previous work (e.g., Radinsky, 1971; Martin, 1990), where the mass estimates from several proxies were averaged to reduce errors associated with any single predictor. However, simply calculating the mean of the individual variable estimates implicitly assumes that all of the variables perform equally well in predicting body mass. Since regression model likelihoods quantify an individual variable's relative predictive ability, a more appropriate averaging technique takes advantage of this information. Using proportional likelihoods, poorly performing models influence the final body mass estimate less, whereas better fitting models more strongly influence the final estimate.

Estimating Relative Brain Size in *Chilecebus*

X-ray computed tomographic scans of the *Chilecebus carrascoensis* cranium were performed on the medical scanner at Children's Hospital of San Diego (CT HiSpeed Adv SYS#HSA1; 140 Kv, 170 mA) to estimate endocranial volume (Flynn et al., 1995). The skull and surrounding matrix were embedded in modeling clay to better mimic the density of the human body, and scanned at 1.0 mm resolution. The series of individual axial and transverse scan slices were composited into 3-D images using Cemax VIP software© (Freemont, CA). The resulting brain volume measure was used in conjunction with body mass estimates to determine the relative brain volume in *Chilecebus*.

To determine whether increased encephalization observed in extant anthropoids was inherited from their last common ancestor, or whether New and Old World anthropoid primates evolved this trait independently, log-encephalization quotients (logEQs) were calculated for the extant catarrhine and platyrrhine taxa considered in Martin (1990). The encephalization quotient (EQ) is the ratio of observed brain volume to expected brain volume for a given body mass (Jerison, 1970; Radinsky, 1971). The metric of interest, however, is not relative volume but deviation of observed volume from the allometric regression of brain volume on body mass, i.e., the natural logarithm of the EQ (logEQ) (Marino et al., 2004; Finarelli and Flynn, 2007; Finarelli, 2008). Positive logEQs imply larger than expected brain volumes for a given body mass, and negative values the opposite. To assess the relative brain volume for extant platyrrhines and the extinct taxon *Chilecebus*, we used the allometry relating body mass to brain volume for strepsirrhine primates (as an outgroup to anthropoids) given in Martin (1990) as a frame of reference.

RESULTS AND DISCUSSION

Body Mass Estimators

We performed phylogenetically corrected regression of body mass on each of the 80 morphometric variables for the extant taxa. Slopes and intercepts for the predictive equations and the corresponding log-likelihoods for the phylogenetically corrected regressions are given for each variable in table 2; scatterplots for the regressions are given in appendix 4. The relative ability of the morphometric variables surveyed in this analysis to accurately predict body mass, as measured by the log-likelihood fits for the regressions, is highly uneven. The maximum likelihood observed among the variables is for mandibular length, indicating that this variable is the single best predictor of body mass among the 80 variables surveyed. Only one variable (pterygoid-zygomatic length) had a log-likelihood fit within 2LnL units of mandibular length, and therefore, there is no significant difference in the ability of those two variables to predict body mass among extant platyrrhine species.

The two optimal predictors are both craniomandibular, osteological measurements, not dental variables. Teeth are frequently employed as body mass predictors for fossil mammals (Gingerich, 1974; Legendre, 1986; Legendre and Roth, 1988) because of their

TABLE 2

Regressions of body mass on morphometric variables for extant taxa

Slopes and intercepts of predictive equations for phylogenetically corrected regressions for each measurement variable (appendix 1) in living platyrrhines sampled (table 1). Also given are R^2, error sum of squares (ESS) and the log-likelihood (LnL), rescaled such that the maximum likelihood observed among models (mandibular length) is 0. Measurement regressions are ordered in decreasing LnL. Teeth are upper (U) or lower (L) lengths, widths (anterior or posterior for molars), and areas.

Measurement	Slope	Intercept	R^2	ESS	LnL
Mandibular length	2.689	−1.349	0.636	0.117	0.000
Pterygoid-zygomatic length	2.268	0.210	0.592	0.135	−1.136
Bizygomatic width	2.828	−1.616	0.626	0.166	−2.783
Moment arm of the masseter	1.672	0.916	0.510	0.175	−3.225
LM1L	2.205	1.822	0.449	0.195	−4.077
Skull length	3.123	−2.720	0.537	0.196	−4.105
Temporal fossa length	3.202	−2.233	0.374	0.198	−4.193
LM1A	1.136	1.856	0.431	0.202	−4.371
Moment arm of the temporalis	1.760	1.434	0.434	0.213	−4.786
Mandibular height	2.016	1.010	0.516	0.215	−4.841
LM2A	1.056	1.942	0.375	0.232	−5.470
Foramen magnum width	3.339	−0.253	0.387	0.232	−5.474
LP3L	1.767	2.419	0.374	0.234	−5.535
LM1WPos	2.187	1.955	0.350	0.239	−5.716
Bulla width	2.939	0.302	0.327	0.241	−5.781
Occipital width	2.488	−0.525	0.315	0.242	−5.803
LM1WAnt	2.269	1.968	0.353	0.244	−5.864
Condyle Width	2.614	2.008	0.447	0.244	−5.879
Cheek tooth row, upper	1.982	0.653	0.273	0.244	−5.880
Cheek tooth row, lower	2.054	0.471	0.359	0.245	−5.885
Facial height (length)	2.299	−0.075	0.532	0.248	−6.003
Foramen magnum area	1.483	0.199	0.277	0.249	−6.015
LP3A	0.893	2.340	0.323	0.249	−6.018
Braincase width	3.086	−1.814	0.551	0.250	−6.070
LP4L	1.935	2.265	0.325	0.251	−6.083
LP4A	0.980	2.192	0.303	0.251	−6.099
LP2L	1.760	2.395	0.506	0.252	−6.118
LM2WPos	1.952	2.109	0.356	0.252	−6.134
LM2WAnt	2.259	1.952	0.419	0.253	−6.169
Temporal chord	3.246	−1.778	0.183	0.255	−6.229
UP3L	1.866	2.326	0.306	0.261	−6.396
UP4L	2.028	2.220	0.313	0.262	−6.438
LM2L	1.957	1.960	0.496	0.263	−6.452
Braincase length	2.792	−1.345	0.288	0.270	−6.678
LP2A	0.844	2.355	0.456	0.272	−6.724
UP3A	0.932	2.138	0.275	0.273	−6.764
UP2W	1.752	2.117	0.384	0.274	−6.783
UP4A	1.015	2.009	0.267	0.277	−6.893
Palate length	2.025	0.388	0.394	0.281	−6.985
UP2A	0.877	2.254	0.422	0.287	−7.170
LP3W	1.704	2.316	0.412	0.296	−7.408
LP4W	1.830	2.205	0.209	0.297	−7.450
Foramen magnum height	2.476	0.754	0.264	0.303	−7.598
UM1A	1.080	1.747	0.399	0.309	−7.743
UP3W	1.782	2.006	0.383	0.309	−7.758
UM1L	2.078	1.875	0.393	0.310	−7.793
UM2WAnt	2.212	1.674	0.398	0.311	−7.813
UP4W	1.964	1.847	0.199	0.311	−7.813
UM2WPos	2.046	1.799	0.397	0.312	−7.826

TABLE 2
(*Continued*)

Measurement	Slope	Intercept	R^2	ESS	LnL
UM2A	0.955	1.965	0.395	0.313	−7.858
Palate width	1.830	1.034	0.400	0.315	−7.908
UM1WAnt	2.157	1.676	0.378	0.318	−7.998
Masseteric fossa length	1.778	0.544	0.291	0.320	−8.027
Maxillary incisor size	2.476	0.525	0.286	0.322	−8.086
LP2W	1.527	2.373	0.350	0.323	−8.102
UP2L	1.683	2.427	0.353	0.323	−8.118
UM2L	1.677	2.186	0.353	0.331	−8.315
UC1L	1.497	2.293	0.459	0.333	−8.355
UM1WPos	2.130	1.695	0.326	0.344	−8.624
LC1L	1.403	2.527	0.328	0.349	−8.728
UC1W	1.310	2.351	0.296	0.366	−9.116
UI2L	1.900	2.341	0.240	0.381	−9.432
Postorbital constriction	3.056	−1.526	0.234	0.395	−9.720
UI2W	1.584	2.394	0.293	0.418	−10.176
Bulla length	2.383	0.061	0.181	0.425	−10.308
Condyle length	2.493	0.950	0.094	0.430	−10.398
Frontal chord	2.163	−0.202	0.446	0.431	−10.409
LC1W	1.178	2.436	0.188	0.434	−10.469
Vertical face height	1.808	0.683	0.357	0.440	−10.585
Occipital chord	2.033	0.687	0.111	0.456	−10.877
LI2W	1.569	2.340	0.111	0.480	−11.284
UI1L	1.660	2.295	0.059	0.488	−11.407
Parietal chord	2.852	−1.035	0.089	0.499	−11.591
LI1L	1.670	2.692	0.230	0.500	−11.601
LI1W	1.427	2.489	0.141	0.515	−11.847
UI1W	1.417	2.391	0.243	0.535	−12.150
LI2L	1.511	2.663	0.025	0.540	−12.216
Skull vault height	1.723	0.573	0.006	0.558	−12.479
Orbit width	1.791	0.885	0.003	0.610	−13.192
Basal length of pterygoid fossa	0.928	2.093	0.092	0.646	−13.655

higher preservation potential. However, dental measurements are generally considered to be less reliable estimators than osteological variables (including measurements of the postcranium) (Gingerich et al., 1982; Dagosto and Terranova, 1992), potentially reflecting specialized adaptations to unusual diets/food items or unusual food-processing methods (Gingerich and Smith, 1984). To test this assumption, we partitioned the data into osteological (both cranium and mandible), and dental (both upper and lower) splits.

Eight of the 10 best predictors in this analysis are osteological (table 2): mandibular length, pterygoid-zygomatic length, bizygomatic width, moment arm of the masseter, skull length, temporal fossa length, moment arm of the temporalis, and mandibular height. Among these, both mandibular length and pterygoid-zygomatic length exceed the best dental variable by at least 2 LnL units. While osteological features include the best predictors of body mass, they also include the three worst predictors: vault height, orbital width, and pterygoid length. Further, a Mann-Whitney test (Sokal and Rohlf, 1995) recovers no significant difference in the median rank log-likelihood scores across osteological and dental partitions ($U = 656$, $p > 0.05$). Thus, while median log-likelihood for the osteological variables is slightly higher than that of dental variables (−6.45 versus −7.60), the variance of log-likelihoods for osteological variables also is higher. Thus, while the best predictors are osteological, among platyrrhine primates osteological characters do not universally outperform dental ones.

Among dental variables, the best predictor of body mass is lower M1 length (table 2), a commonly used proxy for body mass in

mammals (Van Valkenburgh, 1990; Janis et al., 1998a, 1998b). Lower M1 area, another commonly used proxy (Gingerich, 1974; Legendre, 1986; Legendre and Roth, 1988; Finarelli and Flynn, 2006), was the next best estimator and was not significantly different than lower M1 length (LnL difference = 0.298). As noted above, the distribution of log-likelihoods for dental variables was less dispersed than the distribution for osteological variables. Eight dental measures (as opposed to two osteological) were within 2 LnL units of the optimal dental score. However, among these, only upper cheek tooth row length was from the upper dentition. A Wilcoxon signed-rank test performed on 24 upper/lower pairs of dental measurements demonstrates that variables from the lower dentition significantly outperform their upper dentition counterparts as predictors of body mass ($W = 160$, $p < 0.05$).

Thus, regression model likelihoods demonstrate: 1) that the single best predictor is mandibular length, and 2) that the lower dentition significantly outperforms the upper dentition in predicting body mass. Thus, it appears that predictors associated with the mandible may outperform those of the cranium among extant platyrrhines. To test this, log-likelihoods were separated into mandibular and cranial partitions, rather than osteological (including the mandible) and dental (including both upper and lower) partitions. Median mandibular log-likelihoods were higher than cranial log-likelihoods (-6.12 versus -7.81), a significant difference (Mann-Whitney test, $U = 519$, $p < 0.05$).

Intraspecific variability must be a concern when evaluating evolutionary allometries through species mean values. Platyrrhines, and primates in general, are sexually dimorphic (Martin et al., 1994), a feature that leads to a range of variance that is discounted when averaging over species. When estimating body mass for fossil taxa allometries must use species averages. Sex identification for fossil mammals generally is not possible, except in rare instances (e.g., Coombs, 1975; Fleagle et al., 1980; Krishtalka et al., 1990; Van Valkenburgh and Sacco, 2002). This is due to the fact that fossil taxa are often known from a limited number of specimens and rarely represent a population sample for a species. It is therefore difficult to rigorously evaluate sexual dimorphism or other forms of intraspecific variation. However, large degrees of within-species variation can negatively impact the precision of prediction allometries.

More troublesome would be if there were a tendency for the range of variation to increase or decrease as a function of body mass (e.g., Rensch's rule: Rensch, 1950). To assess this potential impact of intraspecific variation on model estimates for extant Platyrrhini, we calculated the difference between log-transformed maximum and minimum values for the 17 species, yielding an observed proportional range (table 3). This range was not calculated for *Brachyteles* due to its low sample size. The observed intraspecific proportional ranges average approximately 14% of the total observed variation across all taxa. In addition, there is no association between the percentage of total range that the proportional range represents, and the major variable partitions. Mann-Whitney tests (Sokal and Rohlf, 1995) comparing osteological/dental splits ($U = 641$, $p > 0.05$) and mandibular/cranial splits ($U = 818.5$, $p > 0.05$) were not significant. We also regressed observed proportional range against the species average body mass for each taxon. For each measurement variable, a t-test for the slope of the regression (Sokal and Rohlf, 1995) was not significant; regression slopes ranged from -0.073 to 0.066 with a median value of 0.013. Therefore, proportional ranges do not vary as a function of species body size.

Body Mass Estimates for *Chilecebus*

One of the main objectives in deriving morphometric proxies for body mass among extant taxa is to apply the predictive equations to fossil taxa. Here we apply the body mass proxies derived above to the fossil platyrrhine *Chilecebus carrascoensis* (Flynn et al., 1995). The only known specimen of this taxon (a skull, SGOPV 3213) lacks the mandible, and pterygoid-zygomatic length (the second best predictor variable) could not be measured. There are, however, 46 measurements that can be evaluated on this nearly complete skull. Of these, 24 variables are osteological and 22 dental. Body mass estimates derived from these variables

TABLE 3

Range of variation observed among platyrrhine species

The range is calculated as Log[Max] – Log[Min] for each measurement. *Brachyteles* was not included here due to low sample sizes for this species. Species Abbreviations: Al_cara, *Alouatta caraya*; Ao_voci, *Aotus vociferans*; At_geof, *Ateles geoffroyi*; Ca_calv, *Cacajao calvus*; Ca_mela, *Cacajao melanocephalus*; Ci_molo, *Callicebus moloch*; Cl_goel, *Callimico goeldii*; Cx_jacc, *Callithrix jacchus*; Cx_pyg, *Callithrix pygmaea*; Ce_apel, *Cebus apella*; Ch_sata, *Chiropotes satanas*; La_lago, *Lagothrix lagotricha*; Le_rosa, *Leontopithecus rosalia*; Pi_pith, *Pithecia pithecia*; Sg_myst, *Saguinas mystax*; Sm_sciu, *Saimiri sciureus*.

Species	Al_cara	Ao_voci	At_geof	Ca_calv	Ca_mela	Ci_molo	Cl_goel	Cx_jacc	Cx_pyg	Ce_apel	Ch_sata	La_lago	Le_rosa	Pi_pith	Sg_myst	Sm_sciu
Skull L	0.180	0.036	0.078	0.045	0.051	0.054	0.087	0.048	0.043	0.050	0.037	0.037	0.042	0.099	0.024	0.051
Occ W	0.139	0.133	0.096	0.058	0.041	0.058	0.102	0.089	0.042	0.137	0.123	0.080	0.073	0.069	0.070	0.046
Cond L	0.178	0.111	0.249	0.109	0.088	0.121	0.146	0.114	0.144	0.086	0.204	0.140	0.105	0.086	0.070	0.096
Cond W	0.249	0.131	0.174	0.232	0.184	0.230	0.244	0.201	0.172	0.213	0.161	0.197	0.107	0.159	0.336	0.221
For H	0.181	0.104	0.085	0.180	0.070	0.092	0.159	0.121	0.140	0.141	0.058	0.160	0.115	0.109	0.074	0.151
For W	0.213	0.085	0.092	0.090	0.046	0.040	0.072	0.112	0.105	0.135	0.088	0.088	0.062	0.092	0.104	0.082
For P	0.369	0.162	0.132	0.191	0.070	0.109	0.209	0.186	0.223	0.248	0.108	0.224	0.135	0.134	0.165	0.159
Ptery L	0.328	0.344	0.339	0.126	0.034	0.342	0.112	0.089	0.164	0.268	0.087	0.098	0.095	0.172	0.116	0.121
Pter-zy	0.236	0.123	0.218	0.073	0.083	0.157	0.092	0.150	0.078	0.132	0.098	0.164	0.123	0.173	0.102	0.104
Bul L	0.174	0.080	0.115	0.113	0.101	0.096	0.189	0.065	0.126	0.079	0.128	0.209	0.067	0.071	0.087	0.069
Bul W	0.169	0.138	0.172	0.055	0.080	0.161	0.093	0.101	0.105	0.094	0.075	0.120	0.055	0.078	0.118	0.109
O Chord	0.178	0.186	0.161	0.124	0.106	0.152	0.126	0.217	0.140	0.125	0.126	0.102	0.198	0.124	0.041	0.108
Case W	0.196	0.025	0.065	0.024	0.024	0.042	0.059	0.059	0.031	0.054	0.040	0.044	0.022	0.052	0.030	0.027
Temp L	0.191	0.066	0.095	0.055	0.067	0.091	0.067	0.046	0.045	0.059	0.039	0.036	0.044	0.058	0.073	0.061
PO Con	0.217	0.051	0.074	0.046	0.027	0.062	0.074	0.055	0.034	0.074	0.052	0.061	0.038	0.029	0.040	0.033
Zygo W	0.228	0.032	0.079	0.056	0.057	0.046	0.072	0.040	0.070	0.112	0.026	0.064	0.068	0.145	0.053	0.091
Case L	0.236	0.082	0.067	0.044	0.038	0.069	0.083	0.052	0.060	0.046	0.031	0.043	0.034	0.069	0.059	0.068
F Chord	0.211	0.051	0.249	0.090	0.056	0.090	0.162	0.069	0.065	0.133	0.128	0.065	0.128	0.091	0.084	0.104
P Chord	0.281	0.133	0.194	0.102	0.087	0.099	0.209	0.040	0.067	0.214	0.117	0.098	0.072	0.111	0.090	0.030
Vault H	0.223	0.255	0.055	0.035	0.063	0.076	0.105	0.116	0.038	0.075	0.062	0.043	0.085	0.073	0.081	0.076
Orb W	0.505	0.027	0.066	0.067	0.049	0.063	0.088	0.028	0.069	0.072	0.058	0.051	0.043	0.069	0.064	0.074
Fac H	0.294	0.132	0.121	0.134	0.083	0.097	0.157	0.085	0.143	0.078	0.109	0.192	0.079	0.166	0.078	0.055
Vert H	0.219	0.140	0.088	0.219	0.062	0.087	0.146	0.089	0.105	0.111	0.098	0.128	0.074	0.173	0.100	0.075
T Chord	0.224	0.120	0.056	0.089	0.033	0.096	0.098	0.057	0.063	0.106	0.059	0.063	0.060	0.083	0.055	0.056
Jaw L	0.177	0.028	0.060	0.053	0.077	0.051	0.082	0.056	0.098	0.076	0.064	0.073	0.101	0.151	0.039	0.078
Jaw H	0.539	0.147	0.076	0.171	0.091	0.165	0.129	0.122	0.172	0.172	0.118	0.149	0.137	0.138	0.060	0.190
MArm M	0.286	0.173	0.230	0.126	0.155	0.087	0.111	0.219	0.107	0.084	0.112	0.120	0.086	0.171	0.051	0.221
MArm T	0.494	0.180	0.174	0.108	0.105	0.125	0.123	0.193	0.152	0.086	0.260	0.171	0.141	0.234	0.134	0.100
Mass L	0.236	0.146	0.144	0.114	0.062	0.131	0.127	0.082	0.111	0.128	0.061	0.104	0.127	0.166	0.073	0.120
U Row L	0.168	0.073	0.064	0.050	0.022	0.207	0.172	0.068	0.043	0.193	0.089	0.046	0.099	0.070	0.081	0.078
L Row L	0.098	0.061	0.066	0.055	0.010	0.156	0.161	0.057	0.036	0.041	0.072	0.064	0.075	0.057	0.041	0.108

TABLE 3
(*Continued*)

Species	Al_cara	Ao_voci	At_geof	Ca_calv	Ca_mela	Ci_molo	Cl_goel	Cx_jacc	Cx_pyg	Ce_apel	Ch_sata	La_lago	Le_rosa	Pi_pith	Sg_myst	Sm_sciu
Pal L	0.105	0.062	0.133	0.094	0.089	0.053	0.064	0.081	0.036	0.085	0.278	0.126	0.090	0.119	0.061	0.060
M1 Pal W	0.105	0.068	0.089	0.062	0.045	0.070	0.127	0.055	0.027	0.113	0.094	0.089	0.153	0.139	0.090	0.091
M Inc	0.015	0.075	0.080	0.094	0.059	0.090	0.093	0.086	0.061	0.047	0.105	0.085	0.068	0.074	0.069	0.084
UI1W	0.184	0.149	0.104	0.169	0.061	0.287	0.161	0.125	0.180	0.111	0.110	0.343	0.162	0.128	0.198	0.132
UI2W	0.251	0.060	0.109	0.109	0.104	0.173	0.213	0.149	0.152	0.135	0.166	0.421	0.135	0.219	0.068	0.107
UC1W	0.285	0.062	0.340	0.148	0.071	0.136	0.189	0.145	0.146	0.098	0.086	0.221	0.410	0.272	0.082	0.266
UP2W	0.117	0.075	0.272	0.085	0.143	0.056	0.200	0.093	0.105	0.071	0.091	0.112	0.171	0.258	0.070	0.063
UP3W	0.096	0.039	0.247	0.122	0.086	0.088	0.223	0.071	0.106	0.054	0.146	0.068	0.139	0.138	0.075	0.051
UP4W	0.145	0.055	0.230	0.050	0.119	0.094	0.229	0.084	0.055	0.055	0.166	0.071	0.135	0.116	0.044	0.062
UM1W1	0.085	0.087	0.179	0.045	0.052	0.082	0.188	0.092	0.076	0.065	0.066	0.112	0.095	0.111	0.040	0.131
UM1W2	0.319	0.085	0.190	0.038	0.032	0.090	0.181	0.101	0.057	0.065	0.088	0.085	0.099	0.140	0.053	0.075
UM2W1	0.331	0.113	0.159	0.047	0.026	0.073	0.209	0.066	0.072	0.036	0.088	0.080	0.094	0.075	0.125	0.060
UM2W2	0.345	0.137	0.166	0.066	0.054	0.076	0.149	0.099	0.064	0.050	0.081	0.109	0.171	0.066	0.175	0.099
UP2L	0.138	0.114	0.153	0.080	0.098	0.245	0.124	0.084	0.205	0.124	0.115	0.097	0.092	0.121	0.190	0.107
UP3L	0.236	0.071	0.134	0.087	0.043	0.137	0.180	0.071	0.114	0.072	0.101	0.096	0.086	0.120	0.110	0.066
UP4L	0.268	0.104	0.103	0.110	0.036	0.137	0.111	0.076	0.221	0.042	0.062	0.061	0.153	0.099	0.068	0.072
UM1L	0.191	0.079	0.116	0.097	0.047	0.104	0.073	0.036	0.106	0.064	0.057	0.066	0.049	0.069	0.053	0.035
UM2L	0.079	0.062	0.144	0.113	0.073	0.059	0.097	0.058	0.120	0.058	0.074	0.059	0.208	0.064	0.148	0.059
UI1L	0.102	0.175	0.126	0.079	0.081	0.089	0.161	0.126	0.157	0.065	0.094	0.241	0.060	0.122	0.094	0.058
UI2L	0.096	0.076	0.115	0.204	0.133	0.166	0.097	0.105	0.165	0.148	0.189	0.175	0.083	0.202	0.078	0.069
UC1L	0.222	0.174	0.268	0.154	0.097	0.156	0.165	0.124	0.174	0.079	0.169	0.156	0.190	0.211	0.122	0.108
LI1W	0.102	0.108	0.166	0.137	0.170	0.272	0.243	0.178	0.115	0.131	0.252	0.181	0.132	0.197	0.093	0.069
LI2W	0.228	0.118	0.175	0.063	0.084	0.265	0.151	0.185	0.096	0.064	0.246	0.221	0.116	0.218	0.090	0.129
LC1W	0.227	0.079	0.298	0.145	0.164	0.104	0.212	0.168	0.239	0.153	0.097	0.139	0.287	0.312	0.158	0.119
LP2W	0.202	0.055	0.292	0.160	0.113	0.119	0.088	0.076	0.137	0.089	0.151	0.092	0.144	0.228	0.097	0.120
LP3W	0.123	0.070	0.336	0.051	0.065	0.140	0.070	0.084	0.159	0.059	0.095	0.094	0.080	0.232	0.170	0.072
LP4W	0.131	0.064	0.352	0.048	0.072	0.053	0.156	0.063	0.159	0.064	0.085	0.084	0.076	0.214	0.127	0.065
LM1W1	0.218	0.071	0.299	0.065	0.037	0.073	0.124	0.089	0.087	0.063	0.066	0.085	0.049	0.106	0.099	0.074
LM1W2	0.119	0.081	0.179	0.054	0.027	0.173	0.096	0.071	0.085	0.072	0.062	0.101	0.064	0.081	0.092	0.073
LM2W1	0.129	0.059	0.126	0.078	0.038	0.144	0.150	0.070	0.057	0.050	0.076	0.042	0.063	0.108	0.092	0.060
LM2W2	0.102	0.129	0.137	0.058	0.017	0.124	0.087	0.092	0.064	0.073	0.063	0.058	0.058	0.110	0.126	0.095
LP2L	0.334	0.062	0.271	0.146	0.156	0.172	0.189	0.079	0.375	0.180	0.094	0.160	0.356	0.284	0.086	0.186
LP3L	0.109	0.068	0.211	0.146	0.127	0.161	0.135	0.104	0.362	0.040	0.075	0.038	0.206	0.200	0.104	0.144
LP4L	0.065	0.060	0.178	0.066	0.070	0.187	0.137	0.110	0.128	0.084	0.089	0.182	0.127	0.192	0.100	0.063
LM1L	0.114	0.053	0.120	0.077	0.023	0.067	0.054	0.039	0.219	0.067	0.110	0.047	0.073	0.170	0.037	0.065
LM2L	0.120	0.059	0.117	0.074	0.063	0.109	0.130	0.083	0.159	0.072	0.112	0.128	0.068	0.170	0.070	0.047
LI1L	0.243	0.109	0.163	0.095	0.100	0.355	0.157	0.188	0.381	0.130	0.186	0.234	0.081	0.449	0.106	0.058

TABLE 3
(*Continued*)

Species	Al_cara	Ao_voci	At_geof	Ca_calv	Ca_mela	Ci_molo	Cl_goel	Cx_jacc	Cx_pyg	Ce_apel	Ch_sata	La_lago	Le_rosa	Pi_pith	Sg_myst	Sm_sciu
LI2L	0.105	0.167	0.149	0.157	0.060	0.287	0.176	0.130	0.400	0.109	0.194	0.382	0.151	0.362	0.173	0.124
LC1L	0.228	0.075	0.345	0.167	0.118	0.194	0.116	0.125	0.156	0.116	0.200	0.256	0.329	0.399	0.060	0.361
UP2A	0.179	0.114	0.356	0.114	0.163	0.225	0.276	0.162	0.253	0.159	0.162	0.187	0.230	0.378	0.248	0.148
UP3A	0.274	0.105	0.361	0.179	0.115	0.225	0.365	0.136	0.141	0.079	0.216	0.154	0.197	0.247	0.167	0.097
UP4A	0.413	0.106	0.333	0.141	0.123	0.142	0.330	0.142	0.244	0.086	0.158	0.124	0.142	0.158	0.090	0.103
UM1A	0.384	0.115	0.242	0.121	0.072	0.130	0.215	0.110	0.146	0.102	0.111	0.139	0.118	0.188	0.071	0.127
UM2A	0.401	0.158	0.216	0.121	0.071	0.070	0.201	0.108	0.132	0.078	0.121	0.093	0.172	0.128	0.274	0.117
LP2A	0.519	0.098	0.541	0.304	0.181	0.182	0.261	0.124	0.407	0.148	0.235	0.251	0.462	0.425	0.170	0.281
LP3A	0.197	0.113	0.547	0.150	0.066	0.239	0.123	0.170	0.454	0.087	0.149	0.096	0.259	0.340	0.238	0.150
LP4A	0.192	0.091	0.530	0.068	0.043	0.201	0.233	0.149	0.219	0.106	0.145	0.145	0.160	0.348	0.188	0.109
LM1A	0.252	0.120	0.342	0.086	0.031	0.165	0.141	0.091	0.220	0.120	0.171	0.130	0.080	0.242	0.094	0.111
LM2A	0.222	0.114	0.245	0.123	0.070	0.135	0.218	0.129	0.167	0.092	0.152	0.166	0.127	0.199	0.172	0.110

range widely, from about 85 grams (temporalis length) to approximately 1.7 kg (upper P4 width), a greater than 20-fold difference in maximum and minimum estimates (table 4). The arithmetic mean of these estimates is 589 grams (table 4). Within the range of estimates, osteological variables generally produce lower estimates than do the dental variables; body mass estimates derived from osteological variables range from 85 to 1137 grams, with a mean of 494 grams, whereas dental variables yield a range from 374 to 1725 grams, with a mean of 997 grams. In contrast, the weighted average, which incorporates the proportional likelihoods of the regressions to weight individual measurement estimates, yields an estimated body mass of 319 grams (table 4), considerably lower than the simple mean. Notably the weighted average is also lower than the minimum mass estimate generated from the dental variables. Thus, while there is considerable overlap in body mass estimates between the osteological and dental partitions, the weighted-average model demonstrates that the lower estimates are derived from the variables known to be more reliable body mass indicators among extant taxa.

This broad range of body mass estimates for *Chilecebus* is worrisome with regard to estimating body mass for fossil platyrrhines in general. If these variables conform to the same allometries in *Chilecebus* as are observed among extant taxa, then all should yield similar mass estimates. To the contrary, our results prove that at least some of these variables must scale differently in *Chilecebus* than in modern platyrrhines. While this might be interpreted as hindering reliable body mass estimation for *Chilecebus*, the allometric scalings observed among extant taxa must be assumed to hold for the fossil members of the group in any analysis of this kind. The large range of estimated body masses for *Chilecebus* is by no means unique among extinct primates; for example, body mass estimates for the basal catarrhine *Aegyptopithecus* (Kay and Simons, 1980) also vary widely depending on the morphometric proxy employed.

Flynn et al. (1995) originally estimated the body mass of *Chilecebus* at 1.0–1.2 kg, based on upper cheek tooth regressions across all primates. They noted, however, an unusual

TABLE 4

Estimated body mass for *Chilecebus carrascoensis*

Estimates based on morphometric proxies preserved in the holotype cranium. The first set of estimates are based on all of the preserved measurements. The second set relates only the 20 measurements for which *Chilecebus* conforms to the extant allometry (see text). Individual measurement estimates are given, and their arithmetic mean is presented at the bottom. Weighted estimates refer to a weighted average model using proportional likelihoods as model weights (see text). The sum of these represents the weighted average model and this is also given at the bottom.

		All Measurements		Reduced Measurement Set	
Measurement	LogL Weights	Body Mass Estimate	Weighted Estimate	Body Mass Estimate	Weighted Estimate
Skull length	1.046E-02	429.949	53.699	429.949	218.554
Occipital width	1.916E-03	1136.862	26.012	1136.862	105.869
Condyle length	1.934E-05	206.305	0.048	.	.
Condyle width	1.775E-03	1007.406	21.355	.	.
Foramen magnum height	3.183E-04	336.396	1.278	.	.
Foramen magnum width	2.661E-03	865.273	27.492	.	.
Foramen magnum area	1.549E-03	476.250	8.811	.	.
Basal length of pterygoid fossa	7.447E-07	1040.611	0.009	1040.611	0.038
Bulla length	2.037E-01	317.039	0.080	.	.
Bulla width	2.116E-05	100.113	2.341	.	.
Occipital chord	1.959E-03	628.653	0.090	628.653	0.366
Braincase width	1.199E-05	444.242	7.782	444.242	31.672
Temporal fossa length	1.467E-03	84.945	9.721	.	.
Postorbital constriction	9.584E-03	326.561	0.149	.	.
Zygomatic arch width	3.812E-05	85.852	40.250	.	.
Braincase length	3.926E-02	546.801	5.212	546.801	21.212
Frontal chord	7.982E-04	424.186	0.097	.	.
Parietal chord	1.913E-05	729.496	0.051	729.496	0.208
Skull vault height	5.868E-06	882.893	0.025	882.893	0.104
Orbital width	2.415E-06	155.830	0.002	.	.
Facial height (length)	1.184E-06	194.083	3.635	.	.
Vertical face height	1.568E-03	455.752	0.087	455.752	0.356
Temporal chord	1.606E-05	564.098	8.423	564.098	34.281
Cheek tooth row, upper	1.250E-03	862.867	18.268	862.867	74.351
Palate width	6.346E-01	408.763	1.139	.	.
UI1W	5.013E-03	975.584	0.039	975.584	0.159
UI2W	2.523E-02	1205.903	0.348	1205.903	1.416
UC1W	5.299E-03	1039.983	0.224	1039.983	0.911
UP2W	2.072E-04	1295.374	11.123	.	.
UP3W	1.773E-03	1697.284	5.497	.	.
UP4W	1.764E-03	1725.191	5.286	.	.
UM1WAnt	5.876E-04	1566.878	3.991	.	.
UM2WAnt	2.334E-04	1516.114	4.647	.	.
UP2L	1.954E-04	650.189	1.469	650.189	5.977
UP3L	3.356E-06	681.960	8.620	681.960	35.084
UP4L	2.416E-05	665.608	8.069	665.608	32.840
UM1L	1.803E-05	554.851	1.736	554.851	7.064
UM2L	7.192E-04	866.640	1.607	866.640	6.540
UI1L	2.712E-04	374.210	0.032	.	.
UI2L	2.566E-04	430.239	0.261	.	.
UC1L	2.133E-04	774.311	1.380	774.311	5.617
UP2A	1.140E-04	897.992	5.234	.	.
UP3A	2.567E-04	1075.035	9.403	.	.
UP4A	2.532E-04	1070.204	8.231	.	.
UM1A	1.892E-04	910.563	2.993	.	.
UM2A	1.059E-03	1106.215	3.241	.	.
Averaged Estimates		**589.559**	**319.486**	**722.252**	**582.619**

combination of morphological features in *Chilecebus*, including a relatively small braincase and the proportions of the upper dentition. Cranial osteological measures tend to produce lower body mass estimates than do dental variables for *Chilecebus*. However, does this imply that dental variables generally overestimate mass, or that the cranial osteological metrics consistently underestimate it? To determine which measures scale uniquely in *Chilecebus* relative to extant platyrrhines, we regressed all other variables preserved in *Chilecebus* against skull length for the set of extant platyrrhine species. This offers a way to describe allometric differences between *Chilecebus* and the suite of extant platyrrhines. Regression residuals were calculated for *Chilecebus* and extant taxa relative to each variable's allometry; variables in which the *Chilecebus* residual was greater than two standard deviations of that observed among the extant taxa were considered variables in which *Chilecebus* deviates significantly from extant platyrrhine allometry for that variable.

The results of this analysis demonstrate that a unique morphometry relative to living platyrrhines explains the much heavier body mass proposed in the initial description of *Chilecebus*. Flynn et al. (1995) noted that *Chilecebus* has proportionally wider upper premolars and molars than extant primates of the same skull length. Here, residuals for all upper cheek tooth widths in *Chilecebus* do exceed those in extant platyrrhines by more than two standard deviations (table 5). Thus, upper cheek tooth widths (and areas derived from them) will lead to overestimates of body mass. Mesiodistal lengths of both upper incisors of *Chilecebus* are significantly less than in the extant regression, meaning that these variables produce underestimates of body mass (table 5). Several osteological characters in *Chilecebus* also deviate significantly from the modern allometries, including: foramen magnum height and width (and the area derived from them), occipital condyle length and width, length and width of the auditory bullae, temporalis length, postorbital constriction, bizygomatic width, length of the frontal chord, orbital width, facial height, and the palatal width at M1 (table 5). All of these are significantly shorter in *Chilecebus* than predicted by modern allometries, and therefore would yield underestimates of body mass. Thus, no simple pattern accounts for the discrepancy between dental and cranial osteological variable-derived estimates of body mass in *Chilecebus*, rather various individual variables deviate from the modern allometries, and point to a fundamentally different skull form in *Chilecebus* relative to extant platyrrhines (Flynn et al., 1995).

Even so, 20 variables from both the osteological and dental partitions *do* conform to modern allometries, and should, therefore, provide reliable estimates of body mass. Limiting estimates to those variables greatly narrows the range of estimates: 430 to 1206 grams, with an average value of 722 grams (table 4). Excluding those measures not conforming to extant allometries eliminates both the extreme high and low body mass estimates for *Chilecebus* (e.g., upper P3, upper P4 width, and anterior widths of the upper M1 and upper M2, all of which predict masses > 1.5 kg; temporalis length, bizygomatic width, and width of the auditory bullae predicting masses ≤ 100 grams). The reduced set of 20 measurements produces a weighted-average estimate of 583 grams (table 4). We consider this constrained weighted-average to be the most reliable estimate of the body mass for *Chilecebus,* as this estimate is based on those metrics that can be shown to conform to the extant allometries and utilizes the relative reliabilities of predicting body mass in the extant taxa in weighting the impact of each variable upon the final estimate.

Relative Brain Size in *Chilecebus*

Flynn et al. (1995) noted the small braincase of *Chilecebus* (7.46 cc, based on CT data), and suggested that a low level of encephalization may characterize platyrrhines ancestrally. However, the initial body mass estimate for *Chilecebus* based on upper cheek teeth (1.0–1.2 kg) is approximately double the 583 gram estimate from this analysis. We have shown that upper cheek tooth widths overestimate body mass in *Chilecebus*, and therefore the original hypothesis of a relatively small brain in *Chilecebus* might simply reflect an inflated body mass estimate.

TABLE 5

Measurements taken on the *Chilecebus carrascoensis* cranium, and their deviation from the extant allometries for each measurement

Two standard deviations of the residuals of extant taxa around each allometry are given. Values in bold indicate measurements where *Chilecebus* falls more than two standard deviations from the regression line. Sign indicates whether the measurement is anomalously large (+) or small (−) on *Chilecebus*, and therefore will over- or underestimate body mass, respectively.

Measurement	*Chilecebus* Residual	2 Standard Deviations	Sign
Occipital width	0.065	0.147	
Condyle length	**−0.231**	**0.080**	−
Condyle width	**0.100**	**0.090**	+
Foramen magnum height	**−0.125**	**0.112**	−
Foramen magnum width	**0.080**	**0.040**	+
Basal length of pterygoid fossa	0.026	0.171	
Bulla length	**−0.120**	**0.095**	−
Bulla width	**−0.233**	**0.079**	−
Occipital chord	−0.036	0.100	
Braincase width	−0.016	0.046	
Temporal fossa length	**−0.255**	**0.068**	−
Postorbital constriction	**−0.077**	**0.067**	−
Zygomatic arch width	**−0.263**	**0.039**	−
Braincase length	−0.047	0.110	
Frontal chord	**−0.117**	**0.088**	−
Parietal chord	−0.017	0.114	
Skull vault height	−0.038	0.139	
Orbital width	**−0.170**	**0.116**	−
Facial height (length)	**−0.172**	**0.044**	−
Vertical face height	−0.085	0.086	
Temporal chord	0.005	0.066	
Cheek tooth row, upper	0.104	0.141	
Palate width	**−0.217**	**0.216**	−
UI1W	0.023	0.145	
UI2W	0.112	0.125	
UC1W	0.077	0.175	
UP2W	**0.172**	**0.133**	+
UP3W	**0.226**	**0.116**	+
UP4W	**0.214**	**0.108**	+
UM1WAnt	**0.177**	**0.117**	+
UM2WAnt	**0.211**	**0.110**	+
UP2L	−0.032	0.126	
UP3L	0.010	0.109	
UP4L	0.008	0.097	
UM1L	−0.022	0.143	
UM2L	0.115	0.173	
UI1L	**−0.215**	**0.128**	−
UI2L	**−0.133**	**0.110**	−
UC1L	−0.006	0.148	

LogEQs for extant anthropoids, relative to a baseline allometry for strepsirrhine primates, show that extant catarrhines and platyrrhines have relatively large brains. Both clades have similar distributions of logEQs; catarrhine logEQs range from 1.39 to 2.25 (table 6: including hominoids, but not *Homo sapiens*), extant platyrrhines from 1.54 to 2.44 (table 6), and they are indistinguishable with a Mann-Whitney test ($U = 47$, $p > 0.05$). Although modern anthropoids possess large brains relative to body mass compared to other mammals (Radinsky, 1973, 1977; Martin, 1990), it is unclear whether this condition

typifies Anthropoidea ancestrally, or whether, as Kay et al. (1997) have suggested, Catarrhini and Platyrrhini each evolved relatively large brains in parallel. Martin (1990) analyzed 25 living haplorhines (Anthropoidea plus tarsiers), demonstrating that living anthropoids are large-brained compared to strepsirrhine primates relative to a ''basal insectivores'' reference frame.

Tejedor et al. (2006) noted that the ~16.4 Ma cebine platyrrhine *Killikaike blakei* possesses a strongly vaulted frontal and large anterior cranial fossa, suggesting an expanded forebrain early in cebine evolutionary history. Only the anterior portion of the skull is preserved, thus a total brain volume cannot be estimated, although enlarged forebrains do correlate with relatively larger brains in cebines, suggesting that the brain of *Killikaike* was likely quite large. Contemporaneous European hominoids, however, lacked significantly expanded brains (Begun, 2002). Martin (1990) noted that several fossil haplorhines also had much smaller brains than their extant relatives, including early ''tarsioids'' and the early catarrhine *Aegyptopithecus zeuxis* (logEQs: 0.90–1.06, table 6). These fossil haplorhines have larger brains than expected relative to the strepsirrhine allometry, yet are below the smallest calculated logEQ value for extant anthropoids. The constrained weighted-average body mass model for *Chilecebus* (583 grams) yields a logEQ of 1.11 (table 6), which is comparable to encephalization values observed among contemporaneous haplorhines, but is lower than observed values in all extant anthropoids. The largest and smallest body mass estimates for *Chilecebus* from the reduced set of measurements, 1206 grams and 430 grams, yield logEQs of 0.62 and 1.32, respectively. Thus, only if the sole smallest reliable morphometric proxy (of 20 estimators) is correct for *Chilecebus* would its estimated encephalization even begin to approach the lower bound of observed logEQs among extant anthropoid species (table 6).

The logEQ estimates for *Chilecebus* and Martin's (1990) data for *Aegyptopithecus*, imply that early taxa basal to Platyrrhini and Catarrhini (but postdating the divergence between these two clades) had smaller relative brain volumes than extant members of either clade, suggesting that the elevated encephalizations of crown-clade platyrrhines and crown-clade catarrhines have been achieved convergently, pointing to a complex transformation in relative brain size within Anthropoidea. Martin's (1990) suggestion that tarsiers and their fossil allies may exhibit an independent evolutionary trend of increasing encephalization emphasizes this pattern of multiple independent acquisitions of large relative brain volume in Primates. If confirmed, this evolutionary pattern in Primates would mirror independent increases in encephalization observed across mammalian lineages (Jerison, 1970; Radinsky, 1971; Martin, 1984), and within subclades of Carnivora (Finarelli and Flynn, 2007; Finarelli, 2008) and the Cetacea (Marino et al., 2004). The convergent acquisition of higher degrees of encephalization in platyrrhines and catarrhines may yield insights into the evolutionary history of these features in other clades.

CONCLUSIONS

Morphometric body mass estimation methods were evaluated using a suite of 80 cranial, mandibular, and dental variables for 17 species of extant platyrrhine primates, spanning the range of body masses within this group. The accuracy with which each morphological variable predicts body mass was quantified using the likelihood fit of the regression to the observed body mass data, with a log-likelihood difference of 2 indicating significantly better predictive power of one variable over another with respect to the observed data.

The best cranial morphometric predictor of body mass in platyrrhines is mandibular length. Only one variable, pterygoid-zygomatic length, fell within 2 LnL units of mandibular length, indicating no significant difference in the predictive power of these variables with respect to the body mass data. While the best predictors were osteological measurements, the distribution of rank fits between osteological and dental variables does not differ significantly, and, contrary to the conclusions of some previous studies, there was no consistent difference between the relative predictive ability of dental versus cranial osteological variables. Mandibular and lower

TABLE 6
Mass, brain volumes, and calculated logEQ values
Values relative to Martin's 1990 regression for strepsirrhine primates as a frame of reference. Fossil "tarsioids" and the fossil catarrhine *Aegyptopithecus* from Martin, 1990. Data for *Chilecebus* are from this study. Minimum, maximum, and median logEQs for the extant Platyrrhini and Catarrhini are given to the right.

Species	Body Mass [g]	Brain Volume [mL]	Ref	logEQ	Min	Median	Max
Aegyptopithecus zeuxis	6710.00	34.40	Martin 1990, p 388	0.98			
Necrolemur antiquus	233.00	3.80	Martin 1990, p 388	1.06			
Tetonius homonculus	74.00	1.50	Martin 1990, p 388	0.91			
Rooneyia viejaensis	782.00	7.40	Martin 1990, p 388	0.90			
Chilecebus carrascoensis	**582.62**	**7.46**		**1.11**			
Platyrrhini (extant)					**1.54**	**1.96**	**2.44**
Aotus trivigatus	535.50	16.90	Martin 1990, p 362	1.99			
Callicebus moloch	854.70	18.30	Martin 1990, p 362	1.75			
Saimiri sciureus	743.20	23.60	Martin 1990, p 362	2.10			
Cebus appella	2500.00	76.20	Martin 1990, p 362	2.44			
Lagothrix lagotricha	6300.00	97.20	Martin 1990, p 362	2.06			
Allouatta seniculus	6145.50	60.30	Martin 1990, p 362	1.60			
Callimico goeldii	480.00	11.10	Martin 1990, p 362	1.64			
Cebuella pygmaea	125.00	6.10	Martin 1990, p 362	1.96			
Callithrix jacchus	292.00	7.20	Martin 1990, p 362	1.54			
Catarrhini (extant)					**1.39**	**2.00**	**2.25**
Miopithecus talapoin	1250.00	39.00	Martin 1990, p 362	2.25			
Cercopithecus ascanius	3605.00	63.40	Martin 1990, p 362	2.01			
Cercocebus albigena	7758.00	96.90	Martin 1990, p 362	1.91			
Macaca mulatta	4600.00	83.00	Martin 1990, p 362	2.11			
Papio anubis	16650.00	177.00	Martin 1990, p 362	2.00			
Theropithecus gelada	21500.00	133.00	Martin 1990, p 362	1.54			
Colobus badius	8617.00	61.60	Martin 1990, p 362	1.39			
Hylobates lar	5422.00	99.90	Martin 1990, p 362	2.19			
Symphalanges syndactylus	10725.00	123.70	Martin 1990, p 362	1.94			
Pongo pygmaeus	55000.00	418.00	Martin 1990, p 362	2.04			
Pan troglodytes	45290.00	393.00	Martin 1990, p 362	2.11			
Gorilla gorilla	114450.00	465.00	Martin 1990, p 362	1.65			

dental measurements do correlate significantly better with body mass than those from the cranium and upper teeth.

Applying the 46 measurable body mass proxies to the cranium and upper dentition of the 20 Ma platyrrhine *Chilecebus* yields a wide range of body mass estimates (85 grams to ~1.7 kg). An initial weighted-average model, applying the likelihood fits of each variable, produced a body mass estimate of 319 grams, considerably less than a previous preliminary report (1.0–1.2 kg: Flynn et al., 1995). The wide range of body mass estimates for *Chilecebus* underscores the hazards of applying body mass proxies to early diverging fossil taxa with potentially novel morphometries. Compared to the extant platyrrhine regression, 26 proxies in *Chilecebus* differ significantly from the allometry observed among extant taxa. Importantly, variables that both significantly underestimate and overestimate body mass are among the proxies that are inconsistent with modern allometries. Applying the weighted-average model technique to a constrained set of only the 20 proxies that follow extant allometries yields the most reliable body mass estimate for *Chilecebus*: 583 grams.

Based on this 583 gram body mass estimate, the encephalization of *Chilecebus* (logEQ = 1.11) was found to be lower than that of all living anthropoid primates. This EQ is comparable to that of the early catarrhine *Aegyptopithecus*, indicating that the high

degree of encephalization observed among modern anthropoids likely was attained independently in both the platyrrhine and catarrhine clades.

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APPENDIX 1
Measurement Variables

Location	Measurement Name	Description
Cranial/ventral	Skull length	from the back of the occiput to the anterior tip of the premaxilla
	Occipital width	across the mastoids at the widest part of the occiput
	Condyle length	at the longest part of the condyle, from the most posterior to the most anterior point along the condyle plane
	Condyle width	at the widest part of the condyle, along the lateral axis, perpendicular to measurement condyle length
	Foramen magnum height	along the anterior-posterior axis of the skull
	Foramen magnum width	measured perpendicular to measurement foramen magnum height
	Foramen magnum area	product of length and width measurements
	Basal length of pterygoid fossa	distance between sphenobasin and the base, or upper part of contact, of the vomer
	Pterygoid-zygomatic length	from the posterior base of the pterygoid plate to the most posterior point of zygomatic skull attachment
	Bulla length	at longest part of bulla, at oblique angle to the midline of the skull
	Bulla width	at widest part of bulla
	Occipital chord	chord from the lambda to the opisthion
Cranial/dorsal	Braincase width	at widest part of braincase
	Temporal fossa length	from the most posterior point of the lamboidal crest to the back of the supraorbital process
	Postorbital constriction	at narrowest point posterior to orbits
	Bizygomatic	across the widest portion of the zygomatic arches
	Braincase length	from the postorbital constriction to the occipital condyles
	Width of infratemporal fossa	from parietal-sphenoid-temporal junction to anterosuperior zygomatic-temporal suture
	Frontal chord	from bregma to nasion
	Parietal chord	from bregma to lambda
Cranial/posterior	Skull vault height	from top of skull (highest point) to condyles
Cranial/anterior	Orbit width	at widest part of the orbit
	Facial height (length)	along bony midline from nasion to acanthion, or uppermost midline point of the premaxilla
	Vertical face height	from the line between nasion and intersection of the intermaxillary and interpalatine sutures on the hard palate
Cranial/lateral	Temporal chord	from the bregma on top of the skull to the asterion
Mandibular	Mandibular length	from the back of the condyle to the front of the median incisor alveolus
	Mandibular height	from ventral base of the ramus to the base of the tooth
	Moment arm of the masseter	from dorsal surface of the condyle to central border of the angular process
	Moment arm of the temporalis	from posterior point to most anterior point of masseteric fossa
	Masseteric fossa length	from back of the condyle to most anterior point of the masseteric fossa
Palate	Palate length	from most posterior point of tooth row to most anterior point of maxilla
	Palate width	chord across palate at M1
Dental	Cheek tooth row (upper and lower)	length of all premolars and molars
	Width of all teeth (upper and lower)	at the widest part of tooth: I1,I2,C1, P2,P3,P4 width of anterior and posterior lophs: M1,M2
	Length of all teeth (upper and lower)	mesiodistal length of: I1,I2,C1,P2,P3,P4,M1,M2
	Area of cheek teeth (upper and lower)	product of length and width: P2,P3,P4 average of width measurements for: M1,M2
	Maxillary incisor size	chord between the distal cemento-enamel junction of the left and right lateral incisors

APPENDIX 2
Platyrrhine Specimens Examined

Species	n	Specimen	Sex
Alouatta caraya	8	FMNH 96012	M
		FMNH 96013	M
		FMNH 26560	M
		FMNH 26568	M
		FMNH 96011	F
		FMNH 26555	F
		FMNH 26559	F
		FMNH 26569	F
Aotus vociferans	10	FMNH 70682	M
		FMNH 70685	M
		FMNH 70688	M
		FMNH 70690	M
		FMNH 54293	M
		FMNH 70681	F
		FMNH 70683	F
		FMNH 70684	F
		FMNH 70686	F
		FMNH 70687	F
Ateles geoffroyi	10	FMNH 41584	M
		FMNH 13896	M
		FMNH 13897	M
		FMNH 13898	M
		FMNH 13899	M
		FMNH 66940	F
		FMNH 66941	F
		FMNH 13902	F
		FMNH 13903	F
		FMNH 49336	F
Brachyteles arachnoides	2	AMNH 80405	F
		AMNH 128	?
Cacajao calvus	10	AMNH 70191	M
		AMNH 73717	M
		AMNH 73718	M
		AMNH 73716	M
		AMNH 98316	M
		AMNH 76392	M
		AMNH73719	F
		AMNH 98397	F
		AMMH 76390	F
		AMNH 76649	F
Cacajao melanocephalus	6	AMNH 78562	M
		AMNH 78566	M
		AMNH 78567	M
		AMNH 78569	F
		AMNH 78568	F
		AMNH 78571	F
Callithrix pygmaea	10	AMNH 76327	M
		AMNH 239605	M
		AMNH 182942	M
		AMNH 182943	M
		AMNH 75280	M
		AMNH 74056	F
		AMNH 74371	F
		AMNH 73751	F
		AMNH 74369	F
		AMNH 182944	F
Cebus apella	10	FMNH 92111	M
		FMNH 92114	M
		FMNH 92115	M
		FMNH 92116	M
		FMNH 92120	M
		FMNH 92112	F
		FMNH 92113	F
		FMNH 92117	F
		FMNH 92118	F
		FMNH 92119	F
Chiropotes satanas	10	FMNH 95518	M
		FMNH 95519	M
		FMNH 93255	M
		FMNH 95513	M
		FMNH 95512	M
		FMNH 93254	F
		FMNH 93522	F
		FMNH 95514	F
		FMNH 95515	F
		FMNH 95516	F
Lagothrix lagotricha	10	FMNH 70574	M
		FMNH 70575	M
		FMNH 70576	M
		FMNH 70577	M
		FMNH 70578	M
		FMNH 70581	F
		FMNH 70582	F
		FMNH 70583	F
		FMNH 70584	F
		FMNH 70589	F
Leontopithecus rosalia	10	FMNH 122012	M
		FMNH 57150	M
		FMNH 57586	M
		FMNH 57838	M
		FMNH 57839	M
		FMNH 63769	F
		FMNH 48356	F

APPENDIX 2
(*Continued*)

Species	n	Specimen	Sex	*Species*	n	Specimen	Sex
						FMNH 57152	F
Callimico goeldii	11	FMNH 148062	M			FMNH 57998	F
		FMNH 148065	M			FMNH 134505	F
		FMNH 145462	M				
		FMNH 153715	M	*Pithecia pithecia*	10	FMNH 93251	M
		AMNH 183290	F			FMNH 93252	M
		FMNH 153712	F			FMNH 95508	M
		FMNH 159976	F			FMNH 95509	M
		FMNH 159975	F			FMNH 95504	M
		FMNH 150674	F			FMNH 93250	F
		AMNH 239601	?			FMNH 93253	F
		AMNH 176602	?			FMNH 95510	F
						FMNH 95511	F
Callithrix jacchus	10	FMNH 20420	M			FMNH 95506	F
		FMNH 20228	M				
		FMNH 20229	M	*Saguinas mystax*	10	FMNH 86951	M
		FMNH 20420	M			FMNH 86952	M
		FMNH 20736	M			FMNH 86953	M
		FMNH 20419	F			FMNH 86954	M
		FMNH 20227	F			FMNH 86955	M
		FMNH 20419	F			FMNH 86959	F
		FMNH 20737	F			FMNH 86960	F
		FMNH 20739	F			FMNH 86961	F
						FMNH 87138	F
Callicebus moloch	10	FMNH 92100	M			FMNH 87139	F
		FMNH 92101	M				
		FMNH 92102	M	*Saimiri sciureus*	10	FMNH 70647	M
		FMNH 92109	M			FMNH 70650	M
		FMNH 60749	M			FMNH 70651	M
		FMNH 48934	F			FMNH 70652	M
		FMNH 50872	F			FMNH 70655	M
		FMNH 92103	F			FMNH 70643	F
		FMNH 92104	F			FMNH 70644	F
		FMNH 92105	F			FMNH 70645	F
						FMNH 70646	F
						FMNH 70648	F

Specimen numbers are for Field Museum of Natural History (FMNH) and American Museum of Natural History (AMNH) mammalogy collections.

APPENDIX 3
Species Means for Extant Platyrrhine Taxa

Species	Al_cara	Ao_voci	At_geof	Br_arac	Ca_calv	Ca_mela	Ci_molo	Cl_goel	Cx_jacc	Cx_pyg	Ce_apel	Ch_sata	La_lago	Le_rosa	Pi_pith	Sg_myst	Sm_sciu
Skull L	105.38	65.28	111.70	111.51	96.36	91.59	69.77	51.94	49.01	34.44	104.72	96.16	116.33	59.21	84.31	58.41	69.94
Occ W	43.48	24.20	52.23	59.19	51.11	49.78	25.91	30.56	21.67	21.01	44.50	44.92	49.43	21.37	32.33	21.78	28.77
Cond L	8.53	8.43	13.03	10.63	10.64	9.70	7.09	5.84	6.17	4.33	10.72	9.95	12.06	6.63	8.39	6.49	6.80
Cond W	3.66	2.44	5.47	4.83	3.61	3.44	2.50	2.00	1.95	1.36	3.77	3.44	4.96	2.16	2.72	2.10	2.24
For H	12.27	9.16	18.15	16.63	12.90	12.47	7.43	7.12	6.41	6.01	15.00	12.20	15.35	6.55	9.78	7.42	8.49
For W	13.47	9.43	16.29	14.94	13.28	12.29	9.67	7.68	6.95	5.62	14.54	13.04	14.65	7.82	11.99	7.92	9.47
For P	165.17	86.36	295.55	248.46	171.35	153.19	71.90	54.67	44.57	33.75	218.16	159.10	224.88	51.22	117.24	58.77	80.42
Ptery L	27.70	12.54	24.86	14.66	15.37	15.67	16.37	9.04	10.25	4.44	21.89	20.32	32.08	12.71	18.62	11.82	12.34
Pter-zy	35.16	15.89	29.80	37.38	27.55	24.56	17.24	15.84	12.65	9.22	32.51	25.31	32.93	14.73	21.34	13.72	15.18
Bul L	23.51	22.79	36.34	28.80	25.93	21.90	18.46	12.91	13.89	9.61	26.63	24.06	29.23	13.87	21.21	15.28	17.99
Bul W	12.18	9.93	12.03	14.42	12.07	10.80	9.30	6.16	6.33	4.55	11.61	11.50	12.82	6.84	10.48	6.64	7.08
O Chord	19.73	14.55	29.11	22.36	24.24	23.41	15.80	12.74	11.12	6.82	24.99	22.79	24.33	14.56	20.16	12.34	20.71
Case W	50.21	37.02	64.23	62.91	53.60	51.10	37.58	29.76	27.24	20.80	58.49	55.80	65.57	30.26	45.50	30.75	39.08
Temp L	59.97	40.38	79.35	81.32	67.54	60.96	43.86	40.26	32.35	27.03	70.26	58.21	75.38	39.08	52.19	38.51	47.99
PO Con	37.76	34.73	52.06	47.14	42.88	40.46	33.87	27.23	22.46	18.00	44.32	44.64	51.28	25.12	37.98	25.92	32.17
Zygo W	71.78	42.40	70.48	71.85	66.65	60.25	43.68	35.29	30.51	22.49	71.45	63.74	73.63	36.51	54.12	36.46	40.13
Case L	49.00	33.90	68.92	75.62	64.77	65.73	37.43	37.37	28.00	26.38	62.37	53.73	65.38	34.05	45.85	33.13	41.35
F Chord	44.34	33.11	65.99	53.00	44.09	44.59	32.49	28.38	26.13	19.62	61.50	40.94	60.51	28.69	43.68	26.22	36.15
P Chord	32.23	29.64	47.41	45.29	42.38	41.86	30.19	26.71	20.56	17.49	30.27	39.18	38.40	26.61	27.23	27.79	31.54
Vault H	28.85	29.56	60.74	56.34	50.36	44.55	34.13	27.35	21.83	19.39	58.15	49.67	54.51	28.21	40.11	28.58	37.57
Orb W	25.17	23.34	27.38	21.53	18.92	18.79	18.31	12.52	11.16	9.06	24.63	24.56	29.05	12.94	20.09	13.15	17.00
Fac H	39.03	22.52	40.98	37.32	32.62	28.89	23.17	15.24	15.45	9.58	38.60	34.40	38.35	18.86	28.99	17.71	21.04
Vert H	34.10	22.54	41.31	31.23	26.41	24.39	21.43	13.72	15.47	8.63	36.20	29.92	38.60	19.31	28.85	17.36	20.67
T Chord	37.78	30.93	51.36	53.32	46.92	43.74	29.90	25.17	22.44	17.50	46.45	46.33	52.68	27.40	35.91	26.63	35.23
Jaw L	79.00	37.48	69.91	78.54	65.34	58.88	43.38	33.83	28.28	20.29	62.95	60.01	74.46	36.92	51.17	34.90	34.84
Jaw H	21.50	8.40	16.34	18.44	18.54	16.60	12.60	6.99	5.24	3.83	15.65	18.63	18.72	7.55	13.85	7.15	7.22
MArm M	57.32	16.41	31.66	52.05	39.56	36.96	21.33	16.37	10.60	8.14	24.86	28.51	33.28	13.00	21.62	12.52	11.28
MArm T	20.44	6.49	16.42	24.82	20.93	16.51	6.40	9.81	8.49	7.19	15.88	11.98	19.40	7.94	10.77	8.58	8.09
Mass L	54.35	23.10	43.07	47.74	36.09	31.18	31.16	17.67	15.23	9.88	41.85	43.38	56.89	21.28	34.80	19.58	18.27
U Row L	37.89	15.70	26.90	31.96	21.30	19.23	16.27	16.22	9.29	6.88	25.46	19.76	28.31	12.97	19.22	10.46	14.73
L Row L	41.59	17.46	28.35	32.98	24.14	22.00	17.90	16.97	10.15	7.84	27.83	23.13	32.03	14.48	21.81	12.31	15.37
Pal L	42.04	18.76	34.83	36.65	24.54	22.33	21.00	15.20	15.49	8.70	35.16	28.44	33.84	19.22	27.29	18.12	18.38
M1 Pal W	24.52	13.24	21.24	36.30	26.93	24.73	12.65	18.73	9.12	10.95	20.39	16.48	21.76	12.03	13.18	11.70	11.70
M Inc	15.76	11.87	16.91	15.45	14.60	12.96	10.68	6.98	7.42	4.99	18.05	12.37	17.70	9.09	11.69	9.24	10.18
UI1W	5.67	3.10	5.49	4.17	4.08	3.67	3.31	1.97	2.79	1.57	5.72	6.20	4.55	3.50	4.93	2.75	3.13
UI2W	5.15	2.58	4.80	4.43	3.66	3.30	2.70	1.73	2.40	1.40	5.83	5.24	4.41	2.74	3.84	2.07	2.82

APPENDIX 3
(*Continued*)

Species	Al_cara	Ao_voci	At_geof	Br_arac	Ca_calv	Ca_mela	Ci_molo	Cl_goel	Cx_jacc	Cx_pyg	Ce_apel	Ch_sata	La_lago	Le_rosa	Pi_pith	Sg_myst	Sm_sciu
UC1W	8.95	3.32	6.39	4.79	6.76	5.55	3.21	2.40	2.77	1.27	8.63	8.90	7.28	3.83	5.60	3.29	3.85
UP2W	7.46	3.52	4.92	5.36	5.08	4.52	3.31	2.80	2.30	1.29	8.01	5.10	5.78	3.40	3.86	2.96	3.84
UP3W	8.47	3.69	5.80	6.12	5.42	4.88	3.75	3.11	2.65	1.69	8.55	6.12	6.68	4.05	4.91	3.13	4.18
UP4W	8.38	3.93	6.11	6.81	5.26	4.75	4.12	3.07	2.89	2.07	8.42	6.24	6.81	4.36	4.90	3.30	4.14
UM1W1	8.50	4.07	5.93	7.21	4.78	4.53	4.73	3.84	3.24	2.18	7.68	5.46	6.89	4.35	5.14	3.42	4.20
UM1W2	8.25	4.11	6.43	6.71	4.96	4.42	4.89	3.66	3.35	2.17	7.44	5.46	6.64	4.40	5.21	3.30	4.04
UM2W1	8.26	4.08	6.02	7.05	4.71	4.34	4.53	3.30	2.60	1.95	7.00	5.19	6.93	3.49	5.25	2.90	3.90
UM2W2	9.04	3.92	6.22	6.98	4.59	4.18	4.45	3.16	2.77	1.89	6.51	5.00	6.37	3.59	5.09	2.80	3.49
UP2L	5.38	2.24	3.65	3.86	3.44	3.09	2.31	1.80	1.97	0.97	4.63	3.51	3.99	2.88	3.08	2.16	2.36
UP3L	5.13	2.44	4.03	4.55	3.35	2.97	2.43	1.90	1.95	1.05	4.61	3.48	4.03	2.71	3.12	1.88	2.20
UP4L	5.08	2.57	4.17	4.66	3.42	3.27	2.49	2.00	1.96	1.23	4.52	3.78	4.32	2.83	3.35	2.03	2.16
UM1L	7.94	3.70	5.68	6.77	3.96	3.64	3.74	2.70	2.83	1.85	5.85	4.12	6.02	3.92	4.24	2.88	3.09
UM2L	9.02	3.40	5.73	6.73	3.83	3.64	3.47	2.29	2.00	1.43	5.11	4.09	5.95	2.89	4.14	1.83	2.51
UI1L	4.43	4.16	5.24	3.68	4.60	4.18	2.92	2.11	2.68	1.36	5.51	4.06	4.58	2.90	3.61	2.87	3.01
UI2L	4.06	2.61	3.95	3.53	3.48	3.04	2.38	1.67	2.13	1.15	4.66	2.91	3.95	2.74	2.85	2.48	2.40
UC1L	7.10	3.24	5.81	4.61	7.06	6.04	2.95	2.83	2.47	1.38	7.85	6.85	6.51	3.40	4.53	2.89	3.36
LI1W	4.36	3.24	4.08	4.26	3.72	3.74	2.49	1.77	2.41	1.47	4.62	6.50	3.92	3.10	4.64	2.44	2.35
LI2W	4.90	3.53	4.55	5.06	4.42	3.87	2.84	2.09	2.55	1.74	4.96	7.53	4.40	3.30	5.04	2.57	2.63
LC1W	9.14	3.39	5.58	5.35	7.19	6.03	2.93	2.58	2.71	1.42	8.57	9.09	6.42	4.24	5.50	3.76	3.76
LP2W	6.80	2.68	4.49	4.93	4.03	3.89	2.62	2.36	2.29	1.01	6.11	4.66	5.53	3.03	3.84	2.38	3.16
LP3W	5.69	2.67	4.33	4.84	4.15	3.76	2.70	2.21	2.11	1.04	5.53	4.51	5.01	3.01	3.69	1.99	2.90
LP4W	5.68	3.01	4.55	5.10	4.30	3.87	3.03	2.27	2.06	1.17	5.67	4.42	5.06	3.34	3.70	2.01	2.96
LM1W1	5.08	3.05	4.93	5.24	4.10	3.87	2.99	2.42	2.14	1.45	5.56	4.23	4.80	3.10	3.72	2.21	2.88
LM1W2	6.29	3.29	5.13	5.43	4.14	3.85	3.07	2.49	2.21	1.46	5.36	4.22	5.12	2.99	3.87	2.22	2.78
LM2W1	5.20	3.16	5.52	5.38	4.26	3.81	3.23	2.17	1.78	1.32	5.40	4.17	5.27	2.44	3.86	2.00	2.80
LM2W2	6.85	3.23	5.48	5.62	4.22	3.83	2.92	2.17	1.94	1.31	4.99	4.01	5.29	2.53	3.88	1.83	2.46
LP2L	5.89	2.14	3.95	3.91	4.27	3.70	1.97	2.19	1.63	1.06	4.54	3.66	4.33	2.69	3.15	2.23	2.24
LP3L	5.62	2.12	3.54	4.26	3.58	3.36	2.06	1.92	1.56	1.00	4.37	3.64	4.05	2.48	3.16	1.92	1.91
LP4L	5.84	2.49	3.77	5.04	3.67	3.29	2.26	2.03	1.86	1.33	4.48	3.65	4.42	2.83	3.56	2.09	2.10
LM1L	7.81	3.53	5.33	7.03	4.49	4.19	3.56	2.81	2.59	1.70	5.92	4.42	5.81	3.51	3.90	2.78	3.02
LM2L	8.74	3.69	5.41	6.98	4.16	4.09	3.73	2.67	2.28	1.48	5.38	4.31	5.80	3.14	4.34	2.53	2.75
LI1L	2.83	2.44	3.12	2.44	1.92	1.94	1.53	1.37	1.44	0.84	3.02	1.75	3.29	1.83	1.92	1.79	1.59
LI2L	3.41	2.08	3.68	2.32	2.64	2.44	1.95	1.38	1.48	1.00	3.71	2.25	3.84	1.93	2.35	1.88	1.84
LC1L	5.73	2.27	3.97	3.96	5.83	4.87	2.00	2.26	1.74	1.39	6.36	5.96	5.38	2.80	3.52	2.48	2.40
UP2A	40.16	7.89	17.97	20.72	17.51	13.94	7.65	5.04	4.53	1.25	37.06	17.92	23.06	9.80	11.89	6.39	9.07
UP3A	43.41	8.98	23.35	27.83	18.19	14.48	9.12	5.89	5.17	1.78	39.38	21.28	26.92	10.96	15.32	5.90	9.22
UP4A	42.58	10.08	25.51	31.74	18.02	15.52	10.27	6.14	5.65	2.54	38.08	23.59	29.39	12.34	16.39	6.69	8.95

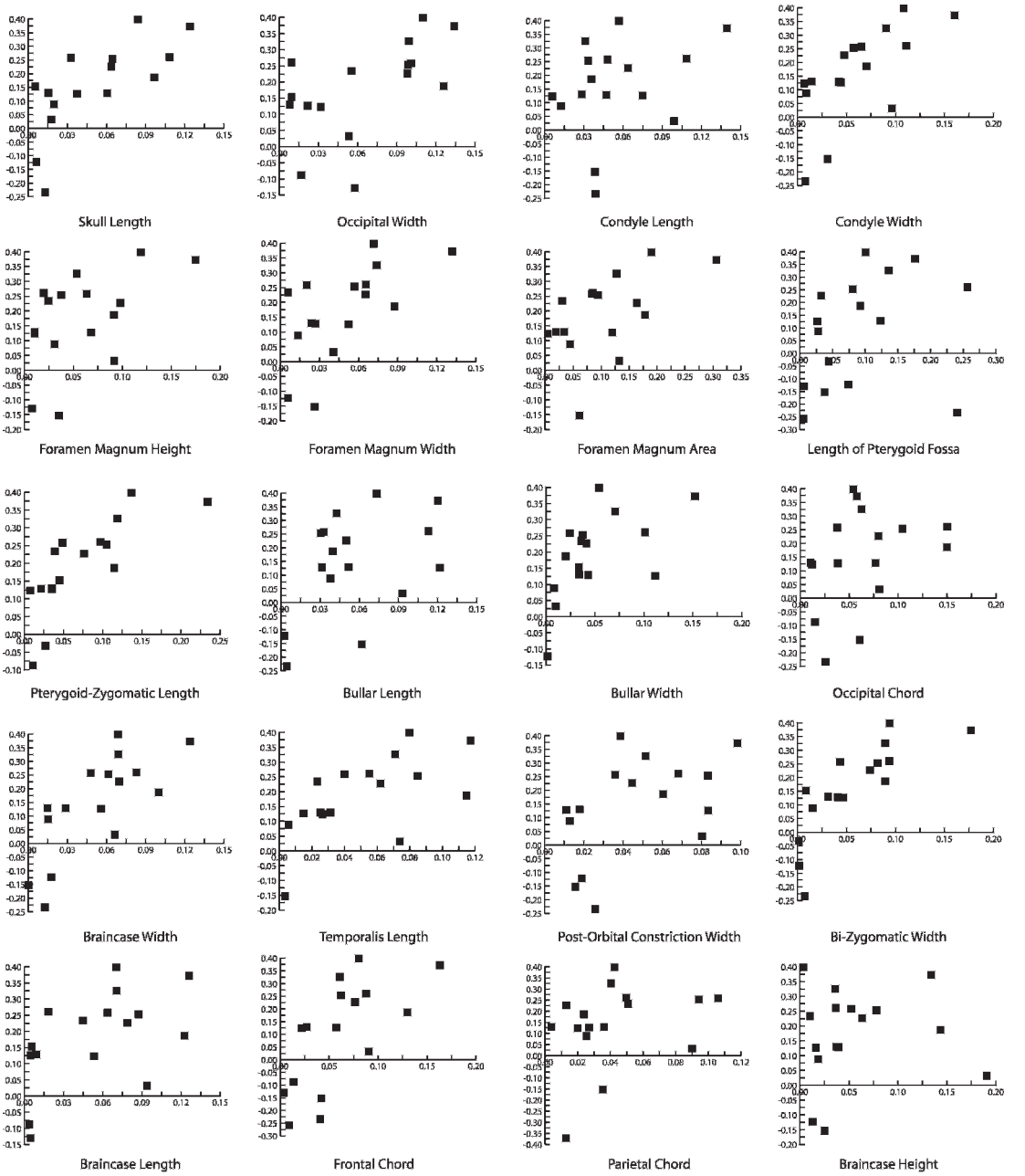
APPENDIX 3
(*Continued*)

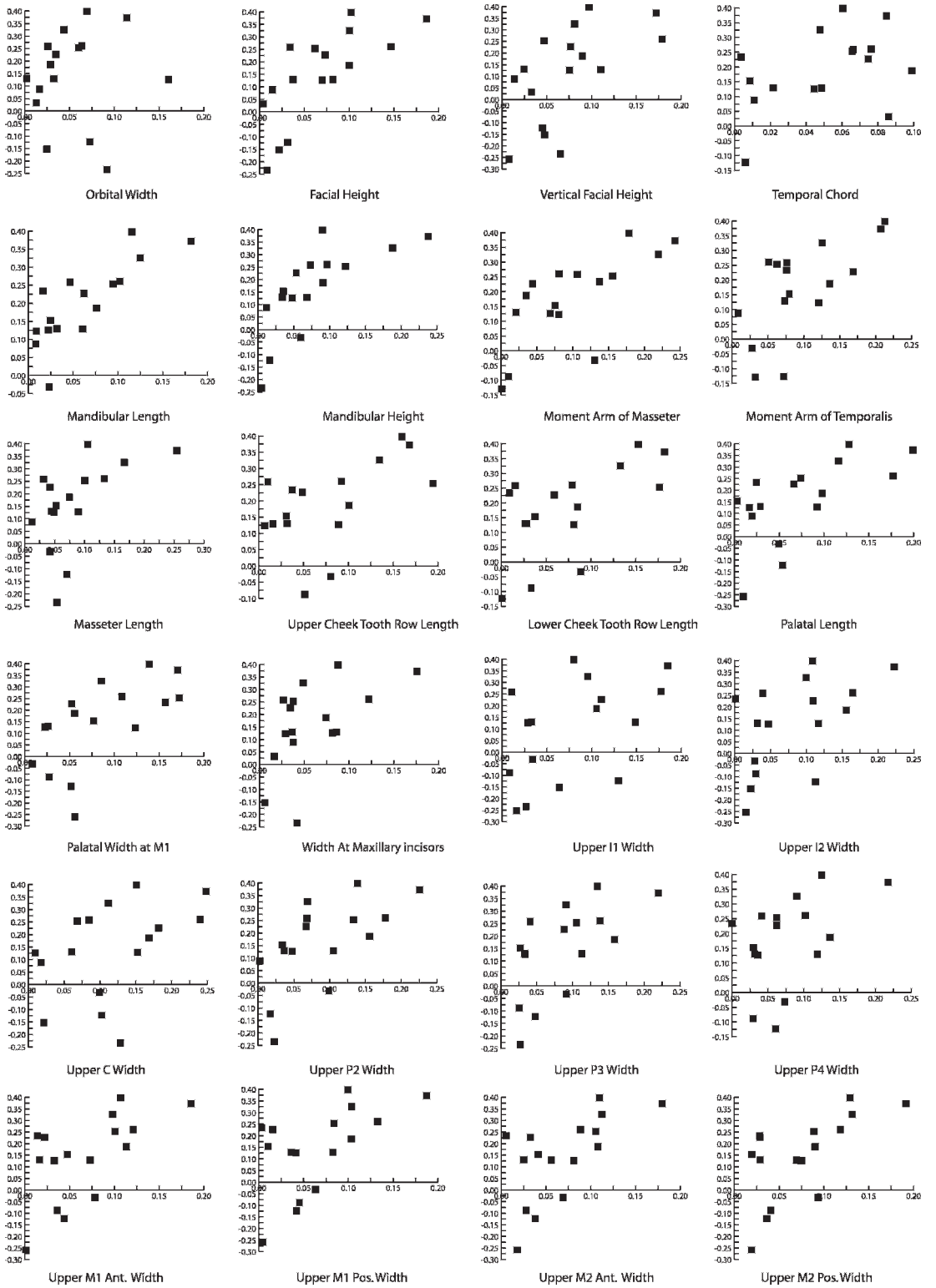
Species	Al_cara	Ao_voci	At_geof	Br_arac	Ca_calv	Ca_mela	Ci_molo	Cl_goel	Cx_jacc	Cx_pyg	Ce_apel	Ch_sata	La_lago	Le_rosa	Pi_pith	Sg_myst	Sm_sciu
UM1A	66.49	15.14	35.08	47.06	19.31	16.29	17.99	10.11	9.31	4.03	44.18	22.46	40.72	17.16	21.93	9.69	12.74
UM2A	77.98	13.58	35.05	47.22	17.79	15.50	15.61	7.40	5.37	2.74	34.47	20.83	39.56	10.25	21.39	5.22	9.24
LP2A	40.07	5.72	17.73	19.28	17.21	14.39	5.16	5.17	3.72	1.07	27.74	17.05	23.98	8.14	12.11	5.29	7.09
LP3A	32.00	5.66	15.33	20.62	14.83	12.64	5.55	4.26	3.29	1.04	24.17	16.45	20.28	7.48	11.65	3.82	5.54
LP4A	33.20	7.50	17.14	25.73	15.77	12.74	6.85	4.60	3.83	1.57	25.37	16.15	22.36	9.44	13.19	4.20	6.20
LM1A	44.14	11.17	26.82	37.51	18.49	16.17	10.79	6.90	5.64	2.48	32.33	18.70	28.80	10.68	14.80	6.17	8.55
LM2A	52.15	11.80	29.72	38.38	17.64	15.64	11.46	5.80	4.23	1.95	27.96	17.62	30.64	7.80	16.80	4.82	7.21

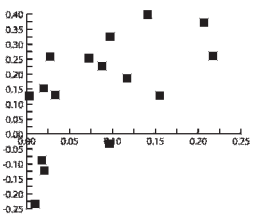
Species Abbreviations: Al_cara, *Alouatta caraya*; Ao_voci, *Aotus vociferans*; At_geof, *Ateles geoffroyi*; Br_arac, *Brachyteles arachnoids*; Ca_calv, *Cacajao calvus*; Ca_mela, *Cacajao melanocephalus*; Ci_molo, *Callicebus moloch*; Cl_goel, *Callimico goeldii*; Cx_jacc, *Callithrix jacchus*; Cx_pyg, *Callithrix pygmaea*; Ce_apel, *Cebus apella*; Ch_sata, *Chiropotes satanas*; La_lago, *Lagothrix lagotricha*; Le_rosa, *Leontopithecus rosalia*; Pi_pith, *Pithecia pithecia*; Sg_myst, *Saguinas mystax*; Sm_sciu, *Saimiri sciureus*.

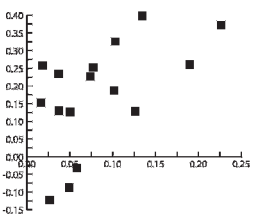
APPENDIX 4
Scatterplots of Regressions of Body Mass on Measurement Variables

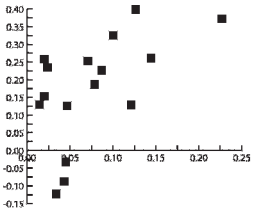
Y-axis is body mass in all plots, X-axis variable indicated in each plot. Plots are phylogenetically independent contrasts.

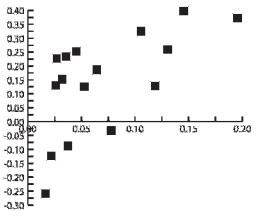


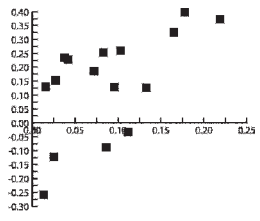

Orbital Width
Facial Height
Vertical Facial Height
Temporal Chord
Mandibular Length
Mandibular Height
Moment Arm of Masseter
Moment Arm of Temporalis
Masseter Length
Upper Cheek Tooth Row Length
Lower Cheek Tooth Row Length
Palatal Length
Palatal Width at M1
Width At Maxillary incisors
Upper I1 Width
Upper I2 Width
Upper C Width
Upper P2 Width
Upper P3 Width
Upper P4 Width
Upper M1 Ant. Width
Upper M1 Pos. Width
Upper M2 Ant. Width
Upper M2 Pos. Width


Upper P2 Length


Upper P3 Length


Upper P4 Length


Upper M1 Length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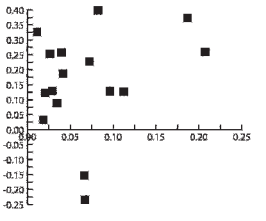
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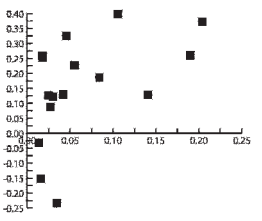
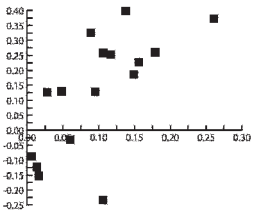
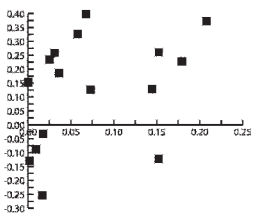
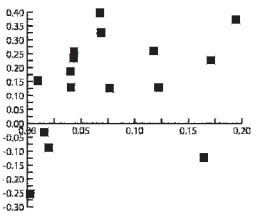

Upper I2 Length


Upper C Length


Lower I1 Width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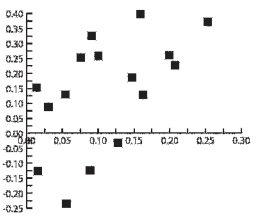
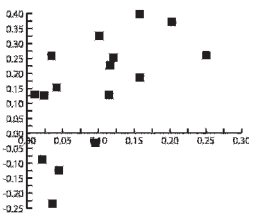

Lower C Width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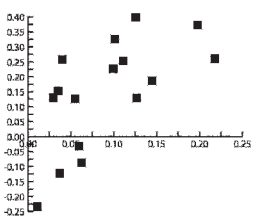
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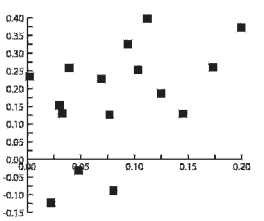
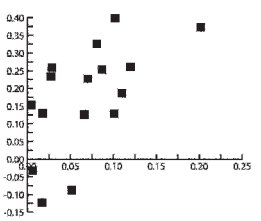

Lower P4 Width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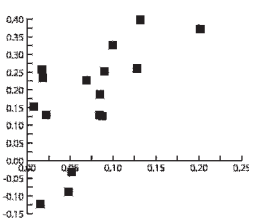
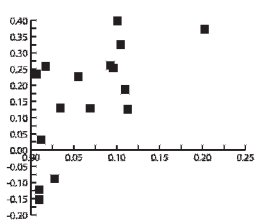

Lower M1 Pos. Width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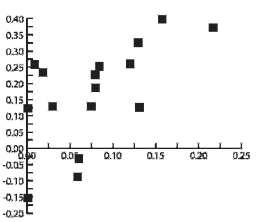
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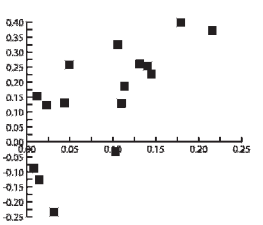
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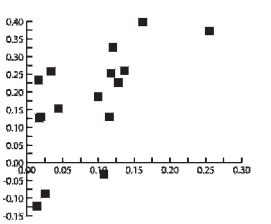
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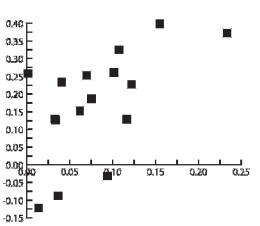
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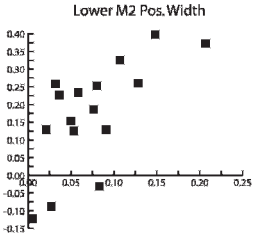
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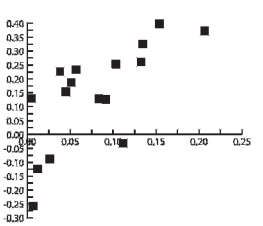
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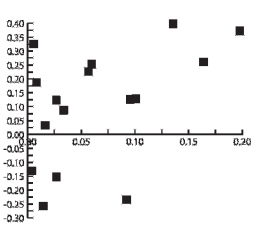
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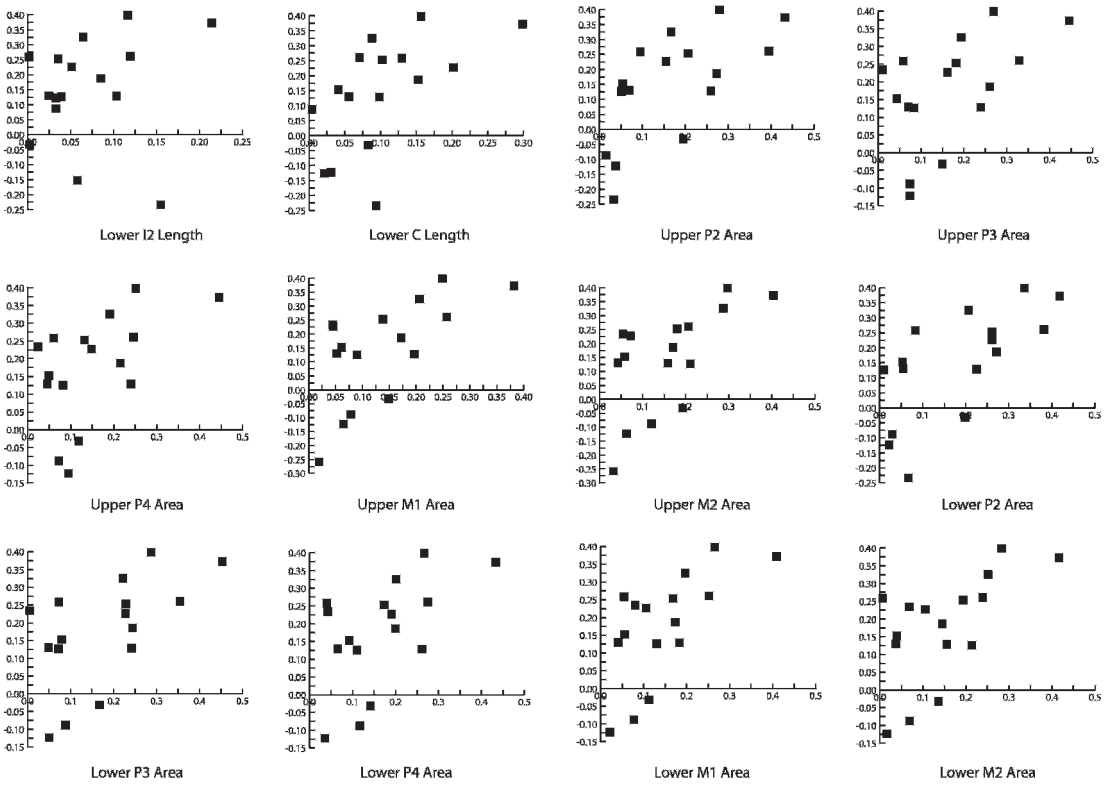
Lower I2 Length
Lower C Length
Upper P2 Area
Upper P3 Area
Upper P4 Area
Upper M1 Area
Upper M2 Area
Lower P2 Area
Lower P3 Area
Lower P4 Area
Lower M1 Area
Lower M2 Area

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