New Body Mass Estimates for *Omomys carteri,* a Middle Eocene Primate From North America

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ABSTRACT   We report new body mass estimates for the North American Eocene primate *Omomys carteri.* These estimates are based on postcranial measurements and a variety of analytical methods, including bivariate regression, multiple regression, and principal components analysis (PCA). All body mass estimation equations show high coefficients of determination (R^2), and some equations exhibit low prediction errors in accuracy tests involving extant species of body size similar to *O. carteri.* Equations derived from PCA-summarized data and multiple regression generally perform better than those based on single variables. The consensus of estimates and their statistics suggests a body mass range of 170–290 g. This range is similar to previous estimates for this species based on first molar area (Gingerich, J Hum Evol 10:345–374, 1981; Conroy, Int J Primatol 8:115–137, 1987). Am J Phys Anthropol 109:41–52, 1999.   © 1999 Wiley-Liss, Inc.

Evolutionary explanations for mammalian diversity in diet (Kay and Covert, 1984), locomotion (Fleagle, 1980), life history traits (Bonner, 1965; Calder, 1984), and other ecological, behavioral, and morphological characteristics (Fleagle, 1978; Schmidt-Nielsen, 1984; Jungers, 1985; Eisenberg, 1990) usually involve consideration of body size. As a result, body size is probably the most important single indicator of the adaptive profile of mammalian species (Damuth and MacFadden, 1990). One of the most widely employed measures of body size is body mass, primarily because its use facilitates straightforward comparison of species of various shapes (Schmidt-Nielsen, 1977). For paleontologists, body mass estimates can be derived from virtually any fossil remains, and the relative sizes of species represented by different anatomical regions can be inferred (Jungers, 1990).

Body mass estimation has become an integral part of paleoprimatology. The description of a new fossil primate specimen is often accompanied by a new body mass estimate for its taxon (e.g., Williams and Covert, 1994; Rafferty et al., 1995). Most predictions have been calculated based on tooth size; dental remains constitute the majority of the fossil record, and tooth size is strongly correlated with body mass across primate species (Kay and Simons, 1980; Gingerich,

1981; Gingerich et al., 1982; Conroy, 1987). Nevertheless, biomechanical considerations suggest that interspecific variation in body mass may be more accurately reflected by differences in postcranial dimensions (Hylander, 1985; Gingerich, 1990; Jungers, 1990; Ruff, 1990; Dagosto and Terranova, 1992). Differential scaling of dental and postcranial characters relative to body mass has resulted in the production of discordant body mass estimates for many fossil primates (Jungers, 1990; Dagosto and Terranova, 1992; MacLarnon, 1996). Therefore, as the primate fossil record continues to expand, body mass estimates based on teeth should be compared to predictions from postcranial remains.

The Eocene primate species *Omomys carteri* represents an excellent candidate for postcranial-based body mass estimation for three reasons. First, like other tarsiiform primates, most omomyids had relatively large teeth. For *O. carteri,* this observation raises the concern that previous body mass estimates based on molar dimensions (Gingerich, 1981; Conroy, 1987) may be too large. Second, a relatively complete collection of *O. carteri* postcranial material has recently become available (Covert and Murphey, 1994). This collection provides the opportunity to assess *O. carteri* body mass using multiple postcranial variables. Third, recent reviews of fossil evidence (Dagosto, 1993; Covert, 1995, 1997) highlight omomyid diversity, underscoring the need for improved understanding of body size variation among these species.

Omomys carteri is known from the middle Eocene of the western interior of North America. *Omomys* was the first fossil primate named from North American deposits (Leidy, 1869), and *O. carteri* is currently the type species for the subfamily Omomyinae and the family Omomyidae. Although *Omomys* has been known from abundant dental material for over 100 years, portions of its skeleton have been described only recently (Rosenberger and Dagosto, 1992; Dagosto, 1993[1]; Covert and Murphey, 1994). Recent

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[1] Based on comparison with the *O. carteri* material described here, the smaller calcaneal and talar remains described by Dagosto (1993) should probably no longer be attributed to *Omomys.*

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work suggests that *O. carteri* most closely resembled cheirogaleids in its quadrupedal running and leaping locomotor repertoire, frugivorous-insectivorous diet, and nocturnal activity pattern (Covert, 1986, 1995; Covert and Payseur, 1997).

The most popular method for estimating fossil primate body mass has been least-squares bivariate regression. However, those prediction equations which incorporate information from multiple variables should be statistically superior (i.e., explain more of the variation in body mass in a sample) to bivariate equations (Gingerich, 1990; Jungers, 1990; Sokal and Rohlf, 1995). Multiple regression is one technique which may offer improved body mass estimates, relative to bivariate methods.

Another multivariate method, principal components analysis (PCA), deserves consideration. In an interspecific dataset comprised of measurements for multiple linear variables, the first principal component represents a vector of size and size-correlated shape (Jolicoeur, 1963), suggesting that it may provide a useful summary of information relevant to body mass estimation. Specifically, body mass could be predicted using bivariate regression of body mass values on species scores for the first principal component of all predictor variables. To our knowledge, such a procedure has not been previously applied to body mass estimation, although the efficiency and appropriateness of PCA for separating the effects of size from orthogonal shape variation have been discussed (Jungers and German, 1981; Shea, 1985; Somers, 1986, 1989; Rohlf and Bookstein, 1987; LaBarbera, 1989; Sundberg, 1989).

MATERIALS AND METHODS

The *O. carteri* collection used in this study was amassed during 1993 and 1994 by Dr. Peter Robinson from the University of Colorado Museum (UCM) vertebrate locality 93026, in Uinta County, Southwestern Wyoming. The age of the site is middle Eocene. UCM 93026 is late Bridgerian (Bridger lithostratigraphic zone C), located in a laterally extensive bed which includes a number of other vertebrate localities. The sediment is a lignitic marl (limey and clayey soil, full of

TABLE 1. *Descriptions of measurements used in this study*

Abbreviation	Bone	Measurement
SGH	Scapula	Height of glenoid fossa
SGW	Scapula	Width of glenoid fossa
HHW	Humerus	AP[1] head diameter
HHH	Humerus	Height of head
HDA	Humerus	AP midshaft diameter
HDM	Humerus	ML[2] midshaft diameter
HAW	Humerus	Width of trochlea and capitulum (articular width)
HBW	Humerus	Biepicondylar width
RHM	Radius	Maximum diameter of head
RDM	Radius	Maximum diameter of distal articular surface
USNW	Ulna	Semilunar notch width
USNH	Ulna	Semilunar notch height
PAH	Os Coxae	Height of acetabulum
PAW	Os Coxae	Width of acetabulum
PILL	Os Coxae	Length of ilium
PISL	Os Coxae	Length of ischium
FHH	Femur	Height of head
FHA	Femur	AP head diameter
FCW	Femur	ML diameter of condyles
FCH	Femur	AP diameter of lateral condyle
FDA	Femur	AP midshaft diameter
FDM	Femur	ML midshaft diameter
TPW	Tibia	ML diameter of proximal articular surface
TPA	Tibia	AP diameter of proximal articular surface
TDA	Tibia	AP diameter of distal articular surface

[1] AP = antero-posterior.
[2] ML = medio-lateral.

plant debris). The site is rich with primate fossils: *O. carteri* specimens account for over 80% of the mammalian remains. Other fauna include mollusks, fish, amphibians, reptiles, birds, and mammals.

The UCM's *O. carteri* material comprises the largest collection for a single omomyid species. At least six individual animals are represented. The sample includes multiple fragments of the scapula, humerus, ulna, radius, pelvis, femur, tibia, fibula, calcaneus, talus, navicular, entocuneiform, and hallucial metatarsal.

Measurements were collected on *O. carteri* specimens and extant primate skeletal material, using sliding and digital calipers. Descriptions and abbreviations of the measurements are provided in Table 1. Linear postcranial dimensions were chosen to capture variation in joint articular surfaces and other weight-bearing areas.

Data were compiled for extant primate species listed in the Appendix. All animals were adults. Most individuals were wild-caught, although some zoo specimens were included. We intentionally focused on smaller primates because most experts agree that *O. carteri* weighed less than 400 g (Gingerich, 1981; Covert, 1986, 1997; Conroy, 1987). Species mean body masses were extracted from Smith and Jungers (1997). Body mass values calculated based on the largest sample sizes were used. Sex-specific mean weights were employed for species with weight dimorphism in excess of 100 g. For all other species, body mass values were computed as averages of the male and female weights reported by Smith and Jungers (1997).

Prior to all analyses, species mean body masses and measurement values were logarithmically transformed to base e (*ln*-transformed) to normalize the distribution of the data, and thus facilitate the application of parametric statistical techniques. Least-squares bivariate regressions were completed for each measurement, with *ln* body mass as the dependent variable, using SYSTAT 5.2.1 (Wilkinson, 1990). Least-squares regression was used because the goal was to predict species mean body mass (Sokal and Rohlf, 1995), and because it has been the most popular method among workers interested in estimating fossil primate body mass (Smith, 1994). Ninety-five percent confidence limits were calculated for each estimate. It should be noted that these confidence intervals were probably underestimated, because the species do not represent phylogenetically independent data points (Felsenstein, 1985; Smith, 1994). Therefore, the intervals were used as approximations only. Additionally, a correction factor (Sprugel, 1983) was employed to ameliorate statistical bias introduced by logarithmic transformation (Smith, 1993). This correction factor (CF) was calculated as

$$CF = \exp{(SEE^2/2)}$$

where SEE is the standard error of the estimate on a natural logarithmic scale.

Three bivariate regressions were performed for each independent variable, based on strepsirrhine ($n = 23$ species), haplorhine ($n = 29$), and all-primate (strepsirrhine + haplorhine; $n = 52$) subsets of the sample. As noted by Conroy (1987), regression sample grouping for body mass estimation should involve

consideration of size and phylogeny when possible. In terms of size, we took a "narrow allometric" approach (Smith, 1985). For example, the haplorhine subset was primarily comprised of smaller platyrrhine species, with only three catarrhine species being included. The phylogenetic affinities of *O. carteri* (and omomyids in general) with living primates are the subject of ongoing debate. Some researchers have argued that omomyids were closely related to haplorhines (Szalay and Delson, 1979; Covert and Williams, 1994; Kay et al., 1997), while others have claimed that these Eocene primates were linked with tarsiers, but not anthropoids (Gingerich, 1981; Rasmussen, 1986). This phylogenetic uncertainty led to the decision to group the animals at a broad taxonomic level for regression analyses (strepsirrhines and haplorhines).

Theoretically, body mass estimates based on multiple measurements should compare favorably with predictions derived from single characters (Gingerich, 1990; Jungers, 1990; Sokal and Rohlf, 1995). We incorporated information from multiple variables in the body mass estimates generated in three ways. First, means of the bivariate estimates were generated for each dataset. In addition to unweighted means, estimates weighted by reciprocal average percent prediction errors (APE, described below) were calculated, since, on average, better estimates were expected to derive from those equations with lower prediction errors. Second, first principal component species scores were treated as a new independent variable in a bivariate regression with body mass for prediction. These scores were calculated by applying principal components analysis (PCA) to the variance-covariance and correlation matrices (in separate analyses) of all variables in each regression group. Finally, multiple regression was employed to select the suites of variables with the highest R^2 values for each of the three datasets. The PROC RSQUARE procedure in the SAS computer program (SAS, 1986) was used to select the best multivariate linear model with *n* variables (where *n* = 2, 3, 4 or 5).[2]

Again, 95% confidence limits were calculated and Sprugel's (1983) correction factor for logarithmic bias was applied.

Variables inappropriate for body mass prediction might show high R^2 values (Smith, 1985). Consequently, we sought some measure of accuracy, independent of R^2. The ability of equations to estimate the body masses of living primates (with "known" values) provided such a measure. We used the percent prediction error statistic (Smith, 1985), calculated as

$$\frac{\text{actual} - \text{predicted}}{\text{predicted}} * 100 = \% \text{ difference}$$

Percent prediction errors were measured for three strepsirrhines (*Cheirogaleus major, Galago alleni,* and *Loris tardigradus*) and three haplorhines (*Callithrix jacchus, Saguinus fuscicollis,* and *Tarsius bancanus*). These species were chosen because they weigh between 100 g and 400 g, the probable size range of *O. carteri.* Average percent prediction errors (APE) were calculated for three species each in the strepsirrhine and haplorhine equations, and all six species in all-primate equations. Smith (1985) has argued that prediction equation accuracy should be measured using species not included in the regression database. Although we appreciate this point, its implementation results in new, more serious difficulty. Because the most relevant prediction errors were clearly those for species in the body size range of *O. carteri,* strictly adhering to Smith's suggestion would have entailed excluding these species from the regressions. We preferred to construct the equations by using all of the available species, rather than reserve them for measurements of prediction error. Additionally, Dagosto and Terranova (1992) reported that PE for species included in their regressions were generally similar to those that were not included.

RESULTS

Results of the bivariate regression analyses are presented in Table 2 and Figure 1.

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[2]Exploratory analysis using stepwise multiple regression failed to yield consistent results. Backward and forward selection models usually chose different numbers and different kinds of variables. Additionally, some models included all variables. Therefore, we did not employ these methods to estimate body mass in this study. We agree with James and McCulloch (1990) that stepwise regression procedures must be used cautiously, especially when variables are strongly intercorrelated.

TABLE 2. *O. Carteri body mass estimates and associated statistics from bivariate regression analyses*

Character	n[1]	Dataset	Body mass estimate (g)	Upper CL	Lower CL	R^2	Slope
SGH	1	AP	111.7	132.1	94.5	0.951	2.716
		S	113.0	150.8	84.7	0.917	2.726
		H	111.2	138.8	89.2	0.964	2.708
SGW	1	AP	251.9	286.5	221.5	0.948	2.503
		S	266.6	331.2	214.6	0.905	2.627
		H	230.6	267.8	198.6	0.973	2.514
HHW	3	AP	252.1	289.7	219.3	0.940	2.646
		S	269.6	348.0	208.9	0.872	2.751
		H	230.6	263.8	201.6	0.978	2.655
HHH	5	AP	277.3	316.6	242.9	0.942	2.852
		S	273.7	341.0	219.8	0.901	2.900
		H	285.4	339.1	240.2	0.959	2.803
HDA	1	AP	183.9	206.3	163.9	0.966	2.703
		S	175.8	215.1	143.6	0.940	2.693
		H	169.2	195.6	146.4	0.980	2.753
HDM	2	AP	356.9	393.3	323.9	0.962	2.589
		S	250.9	283.3	222.2	0.934	2.661
		H	345.0	392.2	303.5	0.974	2.593
HAW	6	AP	408.6	449.3	371.6	0.959	2.616
		S	373.0	418.5	332.5	0.963	2.670
		H	451.5	526.1	387.5	0.956	2.530
HBW	2	AP	334.7	374.1	299.4	0.952	2.781
		S	320.3	376.0	272.8	0.938	2.749
		H	122.8	144.9	104.0	0.956	2.282
RHM	2	AP	255.5	282.2	231.4	0.968	2.645
		S	274.2	322.4	233.2	0.943	2.646
		H	232.2	262.3	205.5	0.982	2.706
RDM	1	AP	262.6	295.5	233.3	0.955	2.599
		S	285.0	344.6	235.7	0.921	2.560
		H	235.5	274.3	202.2	0.972	2.680
USNW	2	AP	281.3	319.9	247.2	0.944	2.624
		S	277.6	340.0	226.7	0.913	2.608
		H	290.6	347.4	243.1	0.956	2.603
USNH[2]	1	AP	157.4	179.3	138.2	0.962	2.449
		S	166.1	203.6	135.4	0.941	2.517
		H	140.5	167.1	118.1	0.974	2.494
PAH[2]	2	AP	156.0	183.2	132.7	0.943	2.700
		S	137.5	175.3	107.9	0.930	2.654
		H	183.1	221.8	151.2	0.963	2.631
PAW	1	AP	202.6	229.6	178.7	0.958	2.577
		S	137.5	169.8	111.4	0.937	2.654
		H	218.7	259.4	184.5	0.967	2.502
PILL[3]	1	AP	221.5	252.0	194.7	0.953	2.618
		S	173.6	204.8	147.1	0.959	2.910
		H	271.6	322.5	228.8	0.961	2.424
PISL[2]	1	AP	389.2	457.7	331.0	0.894	2.318
		S	425.2	477.0	379.0	0.961	2.581
		H	311.2	425.4	227.6	0.874	2.454
FHH	8	AP	244.3	271.9	219.4	0.964	2.676
		S	247.2	289.1	211.3	0.951	2.548
		H	242.7	283.4	207.9	0.971	2.729
FHA	5	AP	257.9	297.4	223.7	0.937	2.695
		S	274.6	340.1	221.8	0.905	2.405
		H	235.0	280.7	196.7	0.962	2.886
FCW	4	AP	304.0	333.6	277.0	0.968	2.653
		S	303.9	348.1	265.4	0.956	2.816
		H	302.2	345.3	264.5	0.974	2.604
FCH[2]	4	AP	673.6	771.8	587.9	0.893	2.876
		S	524.4	628.4	437.6	0.896	2.622
		H	784.7	920.8	668.6	0.931	2.944
FDA	2	AP	331.2	369.4	296.8	0.954	2.671
		S	292.1	331.4	257.4	0.918	2.661
		H	324.6	370.8	284.2	0.973	2.736
FDM	2	AP	230.2	254.3	208.4	0.970	2.724
		S	271.4	333.7	220.7	0.960	2.526
		H	229.9	267.4	197.7	0.973	2.746
TPW	3	AP	339.1	370.6	310.2	0.968	2.664
		S	305.8	346.5	269.9	0.963	2.794
		H	378.7	428.2	334.9	0.974	2.544
TPA	3	AP	539.9	611.6	476.6	0.919	2.470
		S	555.9	694.4	445.0	0.842	2.280
		H	514.6	589.6	449.1	0.961	2.569
TDA[2]	3	AP	252.9	295.9	216.1	0.925	2.757
		S	186.8	229.0	152.4	0.936	2.862
		H	325.5	387.3	273.6	0.955	2.600
PCA-Corr.	—	AP	252.0	275.4	230.6	0.975	1.340
		S	247.7	283.6	216.3	0.962	1.207
		H	276.5	312.1	245.0	0.980	1.351
PCA-Cov.	—	AP	329.7	379.1	286.8	0.975	0.543
		S	245.0	280.5	213.9	0.961	0.549
		H	393.7	479.6	323.2	0.979	0.537

[1] n = number of *O. carteri* specimens from which the species mean was estimated; AP = all-primates; S = strepsirrhines; H = haplorhines; Upper CL = 95% upper confidence limit; Lower CL = 95% lower confidence limit; R^2 = coefficient of determination; PCA-Corr = species scores for first component in a principal components analysis on the correlation matrix of all variables; PCA-Cov = species scores for the first component in a principal components analysis on the variance-covariance matrix of all variables; Regression statistics are the results of analyses using *ln*-transformed values.

[2] Strepsirrhine and haplorhine slopes are significantly different ($P < 0.05$).

[3] Strepsirrhine and haplorhine intercepts are significantly different ($P < 0.05$).
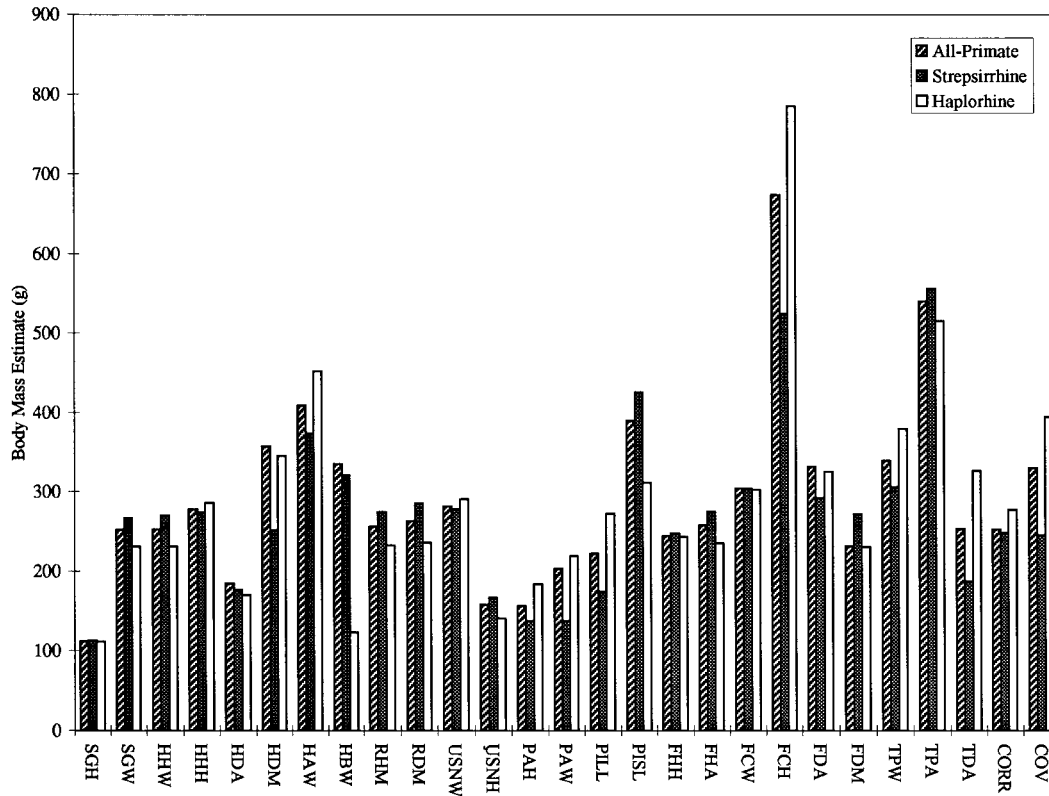
Fig. 1.   *O. carteri* body mass estimates derived from bivariate regression analyses (see Table 2 for confidence limits). Measurements are abbreviated as in Table 1. CORR and COV represent estimates based on species scores for the first component from principal components analyses on the correlation matrix and the variance-covariance matrix of all variables, respectively.

Most variables show regression slopes significantly less than 3.0 (one-sample *t*-tests; d.f. = 2, 27, or 50; $P < 0.05$). With body mass as the dependent variable, these differences indicate that most variables scale positively allometric with body mass. Those variables for which an isometric slope of 3.0 is not rejected are FCH (all-primates and haplorhines), FHA (haplorhines), and SGH, HHW, HHH, HBW, PILL, FCW, and TDA (strepsirrhines).

Most variables show similar relationships to body mass in strepsirrhines and haplorhines (analysis of covariance; $P > 0.05$). Only five characters display significantly different slopes for the two datasets, and one shows significantly different intercepts (see Table 2). This result suggests that body mass estimates based on the strepsirrhine and haplorhine datasets (and the all-primate group) will be similar, and this is generally observed (Fig. 1).

All variables are highly correlated with body mass. R-squared values are usually above 0.900, indicating that more than 90% of the variation in body mass can be explained by variation in single postcranial dimensions. R-squared values are not obviously ordered by anatomical region. Interestingly, strepsirrhine equations show the lowest R^2 values in 20 of 25 variables (Table 2). Also, haplorhine equations tend to have higher R^2 values than equations generated from the all-primate dataset. Standard errors of the estimate (SEE) are similarly distributed, with strepsirrhine equations tending to have larger values, and haplorhine equations frequently exhibiting smaller ones. These results might be explained by consideration of sample composition. First, the strepsirrhine group used in this study is more taxonomically diverse. The strepsirrhine dataset comprises seven

TABLE 3. *Descriptive statistics for* O. carteri *body mass estimates from bivariate analyses*

Statistic	All primates	Strep-sirrhines	Hap-lorhines
Unweighted mean	291.0	275.3	286.7
Weighted mean (APE)[1]	278.5	276.4	266.3
Median	257.9	273.7	242.7
Range	94.5–771.8	84.7–694.4	89.2–920.8
Standard deviation	120.5	108.5	140.1

[1] This mean is weighted by the reciprocal of APE.

TABLE 4. *Multiple regression equations for body mass estimation*

Equation	Variables	Slope	Intercept
All-primate equations			
AP 5	HHH	−1.330	0.907
	RDM	0.831	
	USNH	0.870	
	FDM	1.246	
	PILL	0.910	
AP 4	HHH	−1.534	1.659
	HDA	1.631	
	HAW	1.380	
	FCW	1.094	
AP 3	USNH	0.714	0.542
	PISL	0.387	
	TPW	1.512	
AP 2	USNH	0.989	2.163
	FDM	1.652	
Strepsirrhine equations			
S 5	HHH	−2.317	−1.208
	RDM	1.313	
	USNH	1.018	
	PILL	1.714	
	PISL	0.786	
S 4	HHH	−2.118	−2.648
	RDM	1.027	
	HAW	1.363	
	PILL	2.384	
S 3	HHH	−1.245	−2.780
	HAW	1.816	
	PILL	2.173	
S 2	PISL	1.325	0.833
	FDM	1.348	
Haplorhine equations			
H 5	HHW	1.001	3.252
	HDA	1.141	
	HBW	−1.144	
	RHM	1.896	
	PISL	−0.251	
H 4	HHW	0.869	2.594
	HDA	1.071	
	HBW	−0.712	
	RHM	1.466	
H 3	HDA	1.361	2.752
	HBW	−0.545	
	RHM	1.901	
H 2	HDA	1.091	2.201
	RHM	1.641	

Equations are designated by dataset (as abbreviated in Table 2) and the number of variables included.

primate families, while only four haplorhine families are included. Furthermore, strepsirrhine species often exhibit dramatic differences in locomotor behavior (Fleagle, 1988). For example, the strepsirrhines in this study include an acrobatic leaper (*Galago senegalensis*), a scurrying arboreal quadruped (*Microcebus murinus*), and a slow, cautious climber (*Loris tardigradus*). As alternative locomotor strategies entail differences in the functional and morphological relationships of postcranial variables and body mass, the greater strepsirrhine locomotor diversity may produce larger residuals, thereby inflating SEE and reducing R^2 values.

R-squared values from equations based on the first principal component (PCA-Cov and PCA-Corr, Table 2) are among the highest of the bivariate equations. Standard errors of the estimate for these equations are some of the lowest values, and 95% confidence intervals are relatively narrow. Additionally, correlation analyses of body mass and species scores in other principal components yield non-significant R^2 values (approximately 0.05; data not shown), indicating that most body mass related variation is included in the first principal component.

Descriptive statistics for the *O. carteri* body mass estimates generated from bivariate equations are presented in Table 3. Although the standard deviation and range attest to substantial variation in predictions, measures of central tendency are comparable among the three regression groups. Unweighted means and those weighted by reciprocal APE are similar. Combining results from the three databases, median and mean estimates all fall between 242 g and 291 g. The three estimates based on the first principal component from the correlation matrix are also in this range. PCA analyses

on the variance-covariance matrix produce higher estimates, ranging from 245.0 g to 393.7 g.

Results of multiple regression analyses are shown in Tables 4 and 5. There are no clear patterns in variable choice, although the five-variable equations for all-primates and strepsirrhines include four of the same measurements. In the haplorhine dataset, two variables were consistently chosen: RHM and HDA. Adjusted R^2 values (Bowerman and O'Connell, 1990) are quite high (>0.975) for all equations, a clear statistical improve-

TABLE 5. *O.* carteri *body mass estimates from multiple regression equations*

Equation	Estimate (g)	Upper CL	Lower CL	Adj R²	SEE
AP 5	183.9	213.2	158.6	0.981	0.187
AP 4	273.2	331.2	225.3	0.980	0.191
AP 3	263.5	320.0	217.0	0.978	0.201
AP 2	192.7	218.7	169.8	0.976	0.210
S 5	196.4	249.8	154.4	0.988	0.133
S 4	224.9	270.8	186.8	0.987	0.142
S 3	242.2	297.5	197.1	0.982	0.164
S 2	305.7	364.8	256.1	0.979	0.186
H 5	173.7	234.8	128.5	0.983	0.178
H 4	184.5	242.6	140.3	0.983	0.178
H 3	183.6	242.1	139.2	0.983	0.180
H 2	203.5	248.3	166.8	0.982	0.181

Abbreviations are as in Table 4; Adj R² = R² adjusted for multiple variables.

ment over the bivariate regressions. Standard errors of the estimate are decreased relative to bivariate equations. Surprisingly, however, confidence intervals show no obvious reduction in the multiple variable equations. In comparison to the bivariate predictions, body mass estimates from multiple regression are also somewhat surprising. Six of 12 estimates are below 200 g. These predictions are not independent as some equations include the same variables and are based on the same dataset. Nevertheless, this result differs from the majority of the predictions based on single characters.

Average percent prediction errors (APE) and range of errors are presented in Table 6. In the bivariate regression analyses, only five variables show APE consistently less than 20% across all regression and test species groups: HDA, RHM, RDM, FDM, and TPW. These variables also have among the highest R² values, and appear to represent the best individual predictors of body mass in this study. Average percent prediction errors can be strongly influenced by one errant (or highly accurate) prediction, so individual prediction errors (PE) should be inspected as well. In the haplorhine database, six variables (SGW, HHW, HDA, HDM, RHM, and PILL) predict each of the three haplorhine species' body masses with less than 20% error. Only one bivariate strepsirrhine equation (HBW) predicts the three strepsirrhine body masses within 20% of the actual values. Three bivariate all-primate equations show this level of accuracy in prediction of strepsirrhine (HBW, USNH, and PISL) and haplorhine (HDM, HDA, SGW) species. No bivariate equation estimates body mass for all six species with less than 20% error. The relative success of the haplorhine equations may be influenced by the species chosen for prediction. *Callithrix jacchus* and *Saguinus fuscicollis* are probably more similar in overall shape than any of the three strepsirrhine species are to each other. However, inspection of individual PE reveals that this shape similarity did not bias measurements of equation accuracy. Prediction errors for the two callitrichid species are usually no more similar to each other than either is to *Tarsius bancanus.*

With the exception of PCA-variance-covariance results, equations based on more than one variable exhibit APE below 20%, and most predict all relevant species within 20% of their actual body masses. Hence, these equations offer increases in both accuracy and precision (as measured by R² and SEE). On average, multiple regression equations perform better than bivariate equations based on the first principal component.

The differences in body mass estimates and APE between the two PCA methods are not easily explained. Species scores for analyses based on variance-covariance and correlation methods are perfectly correlated (R = 1.0). Comparing variable loadings on the first principal component yields nonsignificant correlations, however. Therefore, it appears that the two methods provide somewhat different information about body size. Nevertheless, it is unclear which technique performs best in body mass estimation. Interestingly, in this study, the correlation method shows smaller APE (mean and range).

DISCUSSION AND CONCLUSIONS

The measurements used here are generally better predictors of body mass than the tarsal variables utilized by Dagosto and Terranova (1992) in the only other published postcranial estimates of Eocene primate body mass. Nevertheless, choosing among the many *O. carteri* body mass estimates presented here is difficult because different equations produce discordant values. For example, HDA equations yield *O. carteri*

TABLE 6. Average percent prediction errors (APE) and ranges of prediction errors for body mass equations

Dataset Test group	All-Primates All-Primates		All-Primates Strepsirrhines		All-Primates Haplorhines		Strepsirrhines Strepsirrhines		Haplorhines Haplorhines	
Variable(s)	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range
SGH	19.8	3.0–42.4	24.7	12.5–42.4	9.8	3.0–22.1	24.8	13.9–43.3	9.5	3.4–21.4
SGW	17.1	1.2–47.4	24.3	1.2–47.4	9.9	4.6–17.2	24.0	4.7–51.3	5.0	0.6–9.8
HHW	25.1	8.5–44.3	29.6	21.0–44.3	15.1	8.5–20.7	30.0	11.9–48.6	7.3	0.1–13.5
HHH	30.9	8.1–50.1	33.7	20.4–50.1	25.7	8.1–45.2	33.8	21.5–49.8	25.8	10.2–47.0
HDA	15.3	0.4–28.7	17.0	0.4–28.7	13.4	6.3–19.5	17.9	6.1–32.8	7.0	0.5–12.2
HDM	17.9	1.8–37.2	21.0	7.6–37.2	9.5	1.8–16.9	36.9	10.4–68.2	7.4	1.6–13.9
HAW	19.6	1.3–65.8	18.8	1.3–35.0	35.8	13.7–65.8	18.1	12.7–28.8	42.2	21.9–68.2
HBW	26.2	8.3–352.4	14.4	8.3–19.5	146.8	41.5–352.4	10.5	3.9–15.9	377.9	34.9–833.1
RHM	14.0	0.3–24.9	16.2	6.3–21.8	15.5	0.3–24.9	13.4	0.9–25.7	13.3	9.5–18.4
RDM	14.6	0.3–30.2	12.5	0.3–20.1	16.5	5.6–30.2	13.9	7.5–26.5	14.2	4.7–21.1
USNW	20.9	4.6–40.2	21.8	12.0–40.2	25.1	4.6–36.1	22.6	13.7–39.4	27.4	7.5–37.9
USNH	14.1	5.7–29.1	10.6	5.7–14.3	22.6	16.1–29.1	13.2	2.2–20.3	14.3	7.6–22.1
PAH	24.5	1.2–46.6	29.6	11.6–46.6	25.9	1.2–43.9	29.0	19.6–38.6	26.0	12.0–42.5
PAW	20.0	0.4–45.7	26.3	0.4–45.7	15.2	0.8–24.6	22.6	1.9–43.8	16.1	5.2–26.9
PILL	28.5	15.5–52.8	30.5	18.8–52.8	23.9	15.5–35.4	30.3	2.6–44.7	2.2	0.1–3.6
PISL	23.0	12.8–46.2	16.4	12.8–18.3	37.4	16.4–49.7	18.9	14.6–27.1	43.7	34.3–57.6
FHH	27.4	14.1–33.6	28.4	14.1–42.0	23.8	18.1–33.6	27.9	12.6–29.1	23.9	18.4–32.7
FHA	30.2	5.7–52.3	30.1	18.5–52.3	22.1	5.7–34.8	29.9	14.6–53.0	21.1	14.8–26.6
FCW	18.8	1.3–39.8	21.3	1.3–39.8	11.0	2.8–20.2	21.5	2.0–40.0	11.1	3.5–20.8
FCH	29.4	0.9–64.9	25.6	0.9–48.6	31.1	5.3–64.9	19.2	8.2–35.4	28.5	8.1–69.3
FDA	24.2	0.1–36.0	29.0	15.3–36.0	11.4	0.1–29.3	28.4	4.1–54.1	10.6	2.0–26.7
FDM	17.1	1.3–31.5	13.8	1.3–29.1	18.6	11.8–31.5	17.3	11.9–24.8	18.6	11.7–31.2
TPW	14.1	7.8–29.8	15.4	7.8–29.8	17.2	3.0–27.1	14.8	2.9–21.4	17.4	7.7–32.2
TPA	46.7	3.5–76.3	56.3	40.8–76.3	22.7	3.5–48.7	46.6	30.2–55.6	22.0	10.8–44.3
TDA	28.3	5.2–84.2	31.2	5.2–51.3	44.0	5.8–84.2	30.6	16.6–40.2	26.7	10.2–40.0
CORR	14.9	1.3–18.6	18.1	7.1–29.2	9.7	1.3–18.6	18.1	6.7–28.8	12.4	0.2–27.7
COV	27.9	4.4–45.0	25.3	4.4–45.0	26.2	14.8–44.0	17.4	4.8–27.6	38.1	28.0–54.7
FIVE[1]	7.7	0.8–14.2	11.0	6.9–14.2	5.8	0.8–11.7	14.5	4.9–31.7	8.6	0.1–16.9
FOUR	4.0	0.6–10.0	1.4	0.6–2.1	6.7	4.5–10.0	6.3	3.2–9.9	8.0	2.5–14.3
THREE	9.1	0.6–17.7	8.7	0.6–17.7	7.0	1.5–10.1	8.5	5.8–9.9	6.9	0.5–17.8
TWO	14.8	4.6–26.0	11.8	4.6–21.6	14.5	4.9–26.0	7.0	0.9–10.2	10.7	6.5–14.1

[1] FIVE, FOUR, THREE, and TWO are multiple regression equations including that number of variables.

body mass estimates of 183.9 g, 175.8 g, and 169.2 g for the three regression databases. Comparable estimates from TPW are 339.1 g, 305.8 g, and 378.7 g. HDA and TPW each show APE below 20% for all regression and test species groups, as well as high R^2 values. Of course, this result may simply demonstrate that *O. carteri* had a narrow humeral diaphysis and/or a wide tibial plateau relative to living primates. But there is no obvious reason to prefer one of these estimates over the other.

Furthermore, there is little biological justification for choosing among estimates on the basis of regression dataset. Even if *O. carteri* was phylogenetically haplorhine (a point which is subject to argument), comparative work indicates that strepsirrhines, particularly cheirogaleids, constitute the most appropriate modern analogues for this species (Szalay, 1976; Gebo, 1988; Dagosto, 1993; Covert, 1997). Constructing regression datasets based entirely on tarsiers or

cheirogaleids might be the most logical approach (Dagosto and Terranova, 1992). Unfortunately, the small number of species (and paucity of intraspecific samples with known weights) in extant Tarsiidae and Cheirogaleidae makes this procedure problematic. Our study does show an overall similarity between all-primate, strepsirrhine, and haplorhine predictions derived from the same variable (see Fig. 1), indicating that reference population may be less important in the choice of estimates than the variables used.

Previous *O. carteri* body mass estimates, based on first molar area, include 310 g (Gingerich, 1981: all-primate regression), 85 g (Gingerich, 1981: tarsioid regression), 236 g (Conroy, 1987: all-primate regression), and 204 g (Conroy, 1987: prosimian regression). Given the postcranial estimates presented here, these weights are reasonable, with the exception of Gingerich's estimate derived from his tarsioid sample. Considering aver-

age prediction accuracy, confidence intervals, R^2 values, and the overall distribution of estimates produced here, we propose a body mass range for *O. carteri* of 170–290 g. In deriving this range, we have purposefully given more weight to estimates based on multiple variables, as the corresponding equations generally perform the best.

In addition to providing new body mass estimates for *O. carteri,* our investigation yields some general points regarding fossil body mass estimation. Estimates employing information from more than one variable apparently represent improvements over predictions based on one variable. In this study, multiple regression equations exhibit higher R^2 values and lower APE than bivariate equations. Both PCA-based methods produce equations with increased R^2 values. Additionally, equations derived from PCA on the correlation matrix feature increased prediction accuracy. Interestingly, the two PCA methods produce somewhat disparate results. As might be expected, species scores for the first principal component using the two methods are perfectly correlated. Therefore, the species are arranged in the same order along the axis of the first component, regardless of the method applied. Additionally, *ln*-transformation has standardized the variances of the variables, so it is not likely that differences in the results merely reflect a stronger impact of heterogeneity of variance on the variance-covariance matrix. Hence, it is not clear which method represents the best choice for body mass estimation. Given the overall improvement in R^2 values, the general consistency of body mass predictions with other estimates, and the apparent statistical and biological logic of its application, PCA warrants further examination as part of body mass estimation protocols. Additionally, the fact that PCA has not generally been used for this purpose suggests that the effectiveness of both the variance-covariance and correlation matrix methods should be evaluated. Furthermore, the application of PCA to body mass estimation can and should benefit from more general morphometric discussions on the best ways to "extract size information" from multivariate data (Jungers and German, 1981; Shea, 1985; Somers, 1986, 1989; Rohlf and Bookstein, 1987; LaBarbera, 1989; Sundberg, 1989). Whether these procedures will perform comparably with fewer variables and alternative regression groups remains to be seen.

We recognize that the fossil collection described here is relatively rare in its completeness. Nevertheless, researchers can now assess multiple measurements on many fossil species. Our results indicate that even two-variable multiple regression equations usually perform better than bivariate equations. Because stepwise multiple regression appears to have problems dealing with intercorrelated variables (data not shown; James and McCulloch, 1990), we recommend the use of R^2 selection procedures (such as PROC RSQUARE, SAS), which evaluate all possible combinations of variables before designating the one which explains the most variation in the dependent variable.

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APPENDIX. Species used in this study

Strepsirrhines	Family	n	Haplorhines	Family	n
Cheirogaleus major	Cheirogaleidae	5	*Callimico goeldii*	Callitrichidae	4
Microcebus murinus	Cheirogaleidae	4	*Callithrix jacchus*	Callitrichidae	4
Daubentonia madagascarensis	Daubentoniidae	3	*Cebuella pygmaeus*	Callitrichidae	4
Euoticus elegantulus	Galagonidae	3	*Leontopithecus rosalia*	Callitrichidae	4
Galago alleni	Galagonidae	3	*Saguinus fuscicollis*	Callitrichidae	4
Galago senegalensis	Galagonidae	10	*Saguinus leucopus*	Callitrichidae	3
Galagoides demidovii	Galagonidae	4	*Saguinus midas*	Callitrichidae	4
Galagoides zanzibaricus	Galagonidae	2	*Saguinus nigricollis*	Callitrichidae	2
Otolemur crassicaudatus	Galagonidae	4	*Saguinus oedipus*	Callitrichidae	4
Avahi laniger	Indridae	4	*Alouatta caraya*, f	Cebidae	2
Propithecus verrauxi	Indridae	4	*Alouatta caraya*, m	Cebidae	2
Hapalemur griseus	Lemuridae	4	*Alouatta seniculus*, m	Cebidae	4
Lemur catta	Lemuridae	4	*Aotus trivirgatus*	Cebidae	4
Eulemur fulvus	Lemuridae	4	*Ateles geoffroyi*, f	Cebidae	3
Eulemur macaco	Lemuridae	4	*Lagothrix lagotricha*, m	Cebidae	3
Eulemur mongoz	Lemuridae	4	*Cebus albifrons*, f	Cebidae	2
Varecia variegata	Lemuridae	6	*Cebus albifrons*, m	Cebidae	3
Arctocebus calabarensis	Loridae	4	*Cebus apella*, f	Cebidae	5
Loris tardigradus	Loridae	4	*Cebus apella*, m	Cebidae	5
Nycticebus coucang	Loridae	4	*Cebus capucinus*, m	Cebidae	3
Nycticebus pygmaeus	Loridae	3	*Chiropotes satanus*	Cebidae	4
Perodicticus potto	Loridae	4	*Saimiri sciureus*	Cebidae	5
Lepilemur mustelinus	Megaladapidae	4	*Pithecia pithecia*	Cebidae	4
			Macaca fascicularis, m	Cercopithecidae	4
			Macaca fascicularis, f	Cercopithecidae	3
			Trachypithecus frontatus	Cercopithecidae	4
			Trachypithecus obscurus, m	Cercopithecidae	3
			Tarsius bancanus	Tarsiidae	3
			Tarsius syrichta	Tarsiidae	5

When species are dimorphic, sex is indicated (m or f). Taxonomy follows Groves (1993).