

Problems of Body-Weight Estimation in Fossil Primates

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Body-weight estimates of fossil primates are commonly used to infer many important aspects of primate paleobiology, including diet, ecology, and relative encephalization. It is important to examine carefully the methodologies and problems associated with such estimates and the degree to which one can have confidence in them. New regression equations for predicting body weight in fossil primates are given which provide body-weight estimates for most nonhominid primate species in the fossil record. The consequences of using different subgroups (evolutionary "grades") of primate species to estimate fossil-primate body weights are explored and the implications of these results for interpreting the primate fossil record are discussed. All species (fossil and extant) were separated into the following "grades": prosimian grade, monkey grade, ape grade, anthropoid grade, and all-primates grade. Regression equations relating lower molar size to body weight for each of these grades were then calculated. In addition, a female-anthropoid grade regression was also calculated for predicting body weight in females of extinct, sexually dimorphic anthropoid species. These equations were then used to generate the fossil-primate body weights. In many instances, the predicted fossil-primate body weights differ substantially from previous estimates.

KEY WORDS: allometry; fossil primates; body weight; brain size; primate evolution; tooth size.

INTRODUCTION

While biologists have long recognized the importance of body size as one of the most significant parameters affecting behavioral and ecological adaptations in mammals (Schmidt-Nielsen, 1984), it has been only within

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the past decade or so that paleoprimatologists have attempted empirically rigorous analyses for predicting body weights of fossil (nonhominid) primates, particularly from dental dimensions (Gingerich, 1977, 1981; Gingerich *et al.*, 1982; Kay and Simons, 1980; Simons and Kay, 1983). Admittedly, tooth-size/body-weight correlations may be weak at an intraspecific level (Garn and Lewis, 1958; Garn *et al.*, 1968; Swindler and Sirianni, 1975; Henderson and Corruccini, 1976; Johnson, 1978), but higher correlations obtain across larger, interspecific samples of primates (Gingerich, 1977; Smith, 1981). Body-weight estimates derived from such correlations are increasingly used to make secondary inferences about many other characteristics of fossil primate species (e.g., Blumenburg, 1981, 1984; Cachel, 1983; Gingerich, 1981; Calder, 1984; Schmidt-Nielsen, 1984; Peters, 1983; Jungers, 1985).

There are now several published body-weight estimates for many fossil primates. Since these estimates are constantly being used to infer the diet, ecology, and social structure of these species, it is important to look carefully at the methodologies and problems underlying these estimates and the degree to which one can have confidence in them. Here, a different approach for calculating tooth-size/body-size regression equations in fossil primates is offered, together with new body-weight estimates for most nonhominid fossil-primate species.

Predictive equations relating dental size and body size in nonhuman fossil primates have been developed by Gingerich (1977, 1981; Gingerich *et al.*, 1982). These studies are particularly important in elucidating the functional adaptations of primate molars and in relating primate body size to various dietary regimes in the light of Kay's (1973, 1975, 1977) studies. In Gingerich's initial study (1977), regression equations were derived relating the logarithm of lower M2 length to log body weight in 7 species of living hominoids and in 38 species of noncercopithecoid primates. These equations were then used to predict the body weights of *Aegyptopithecus zeuxis* (7.5 kg using the hominoid equation and 5.6 kg using the noncercopithecoid equation) and *Proconsul africanus* (27.4 and 23.4 kg using the two equations). However, the body-weight estimates for the latter species were shown to be much too large by subsequent discoveries of *Proconsul africanus* remains from Rusinga Island (Walker and Pickford, 1983; see below). Gingerich's data set was later expanded to include body-weight predictions for numerous fossil primates (Gingerich, 1981; Gingerich *et al.*, 1982). In these later studies, the independent variable was lower M1 crown area (rather than just M2 length as in the 1977 study), and a "mouse-to-elephant" curve was generated using 43 primate species ranging in size from *Galago senegalensis* to *Gorilla gorilla*. Plesiadapiform primates were not included in these analyses, however, "because of their unusually specialized dentition." Plesiadapiforms deserve to be included in such a comparative study for three important reasons: (1) they represent the earliest adaptive radiation of the order Primates in the

fossil record and thus are critical to understanding the so-called "insectivore-primate" transition; (2) their dentition can hardly be considered more "specialized" than that of tooth-combed lemurs, which were included in Gingerich's original data set; and (3) even though the anterior dentition of plesiadapiforms is specialized, certainly the lower first molar, upon which all these analyses are based, is not.

Gingerich (1981) also investigated tooth-size/body-size relationships among the mainly Eocene omomyids in a separate contribution and provided a wealth of data on these fossil tarsiiform primates. He realized, however, that his "generalized primate" equation was not satisfactory for predicting body weight in modern tarsiers and somewhat arbitrarily adjusted his regression equation to predict body weight in omomyids (see below). The relationship of tooth size to body weight in other insectivorous mammals has been explored more recently by Gingerich and Smith (1985).

Kay and Simons (1980) and Simons and Kay (1983) have also contributed predictive equations relating tooth size to body size in Oligocene anthropoids from the Fayum of Egypt, and Fleagle (1978) has studied primate body-size distribution (based on molar size) through the Tertiary. The present study aims to build upon these contributions to primate paleobiology by adopting a slightly different approach to predicting body size in fossil primates.

There are at least three strategies that may be employed in correlating tooth size with body size: one can derive regression equations that are based on a mouse-to-elephant curve, or on extant forms within a more limited size range—i.e., "narrow allometry" (Smith, 1985)—or on forms of similar evolutionary "grade" or "level" of organization. The third approach has been adopted here by organizing the extant and fossil primates into six evolutionary grade categories: (1) prosimians; (2) anthropoids; (3) monkeys; (4) apes; (5) female anthropoids; and (6) all primates. This approach (which also approximates the narrow-allometry approach to some extent) has been taken because there is no compelling mathematical, logical, or intuitive rationale for trying to predict the body weight of a 30-g animal by using an equation derived from animals which may be hundreds, if not thousands, of times that size and/or of a totally different evolutionary grade (other than the philosophically comforting illusion that one has discovered some "higher" unifying principle of nature). In fact, there are compelling reasons *not* to do so. Extrapolation beyond the range of the data used to calculate a regression line is fraught with statistical dangers. A linear regression describes only the relationship among the points measured, and not the relationship of points beyond those actually measured.

One of the more important steps in estimating body weight for a fossil species is in the selection of the modern species to be used as a basis for comparison. In this study, the consequences of using different subgroups (grades)

Table I. M₁ Area, Body Weight, and Predicted Body Weight in Males of Extant Primate Species^a

Taxon (males)	log _e of M ₁ area	Log _e of body weight	95% confidence limits on log _e body weight, predicted from				
			Prosimian regression	Monkey regression	Ape regression	Anthropoid regression	All-primates regression
1. <i>Tupaia javanica</i>	1.60	4.65	4.88-5.62	-	-	-	5.14-5.64
2. <i>Tupaia minor</i>	1.35	3.81	4.41-5.28	-	-	-	4.66-5.23
3. <i>Tupaia glis</i>	2.06	5.18	5.67-6.31	-	-	-	6.01-6.41
4. <i>Tupaia tana</i>	2.07	5.53	5.69-6.33	-	-	-	6.03-6.43
5. <i>Tarsius sp.</i>	1.97	4.70	5.52-6.17	-	-	-	5.84-6.26
6. <i>Lepilemur mustelinus</i>	2.06	6.41	5.67-6.31	-	-	-	6.01-6.41
7. <i>Varecia variegata</i>	3.58	8.03	7.71-9.18	-	-	-	8.75-9.09
8. <i>Propithecus verreauxi</i>	3.41	8.22	7.50-8.84	-	-	-	8.46-8.78
9. <i>Nycticebus coucang</i>	2.22	7.17	5.92-6.58	-	-	-	6.31-6.68
10. <i>Avahi laniger</i>	2.54	6.90	6.38-7.15	-	-	-	6.91-7.23
11. <i>Indri indri</i>	3.76	8.74	7.93-9.54	-	-	-	9.06-9.43
12. <i>Perodicticus potto</i>	2.16	7.09	5.83-6.48	-	-	-	6.20-6.58
13. <i>Galago crassicaudatus</i>	2.50	7.03	6.32-7.08	-	-	-	6.83-7.16
14. <i>Galago senegalensis</i>	1.48	5.33	4.65-5.46	-	-	-	4.91-5.44
15. <i>Galago garnettii</i>	2.42	6.64	6.21-6.93	-	-	-	6.69-7.02
16. <i>Galago elegantulus</i>	1.46	5.68	4.62-5.43	-	-	-	4.87-5.41
17. <i>Galago alleni</i>	1.91	5.75	5.42-6.08	-	-	-	5.73-6.16
18. <i>Galago demidovii</i>	1.04	4.25	3.81-4.88	-	-	-	4.07-4.71
19. <i>Galago thomasi</i>	1.16	4.62	4.04-5.04	-	-	-	4.30-4.91
20. <i>Galago zanzibaricus</i>	1.39	4.98	4.48-5.34	-	-	-	4.74-5.29
21. <i>Galago moholi</i>	1.35	5.06	4.41-5.28	-	-	-	4.66-5.23
22. <i>Galago matchiei</i>	1.39	5.35	4.48-5.34	-	-	-	4.74-5.29
23. <i>Cercopithecus cephus</i>	3.13	8.32	-	8.13-8.46	-	8.16-8.44	7.97-8.27
24. <i>Cercopithecus nictitans</i>	3.13	8.79	-	8.13-8.46	-	8.16-8.44	7.97-8.27
25. <i>Cercopithecus mana</i>	3.03	8.47	-	7.97-8.31	-	7.99-8.29	7.80-8.09
26. <i>Cercopithecus mitis</i>	3.28	8.91	-	8.37-8.69	-	8.40-8.66	8.23-8.54
27. <i>Cercopithecus neglectus</i>	3.23	8.85	-	8.44-8.75	-	8.47-8.73	8.30-8.61
28. <i>Cercopithecus ascanius</i>	2.98	8.34	-	7.88-8.24	-	7.91-8.21	7.71-8.00
29. <i>Cercopithecus aethiops</i>	3.25	8.52	-	8.33-8.64	-	8.35-8.62	8.18-8.49
30. <i>Cercocebus albigena</i>	3.65	9.10	-	8.92-9.29	-	8.98-9.25	8.87-9.23
31. <i>Cercocebus torquatus</i>	3.80	8.99	-	9.13-9.55	-	9.21-9.49	9.12-9.51

32. <i>Cerocebus galeritus</i>	3.86	9.23	—	9.21-9.65	—	9.29-9.59	9.22-9.62
33. <i>Macaca nemestrina</i>	3.77	9.25	—	9.09-9.50	—	9.16-9.44	9.07-9.45
34. <i>Macaca mulatta</i>	3.70	9.01	—	8.99-9.38	—	9.06-9.33	8.95-9.32
35. <i>Macaca fascicularis</i>	3.50	8.68	—	8.71-9.04	—	8.75-9.01	8.61-8.95
36. <i>Macaca speciosa</i>	3.97	9.26	—	9.36-9.85	—	9.46-9.78	9.41-9.83
37. <i>Cynopithecus niger</i>	3.61	9.25	—	8.87-9.22	—	8.92-9.18	8.99-9.15
38. <i>Colobus polykomos</i>	3.68	9.25	—	8.96-9.34	—	9.03-9.30	8.92-9.28
39. <i>Colobus badius</i>	3.58	9.26	—	8.82-9.17	—	8.87-9.13	8.75-9.09
40. <i>Nasalis larvatus</i>	3.66	9.78	—	8.94-9.31	—	9.00-9.26	8.89-9.24
41. <i>Presbytis aygula</i>	3.21	8.75	—	8.26-8.58	—	8.29-8.56	8.11-8.41
42. <i>Presbytis cristatus</i>	3.37	9.06	—	8.51-8.83	—	8.55-8.80	8.39-8.71
43. <i>Papio cynocephalus</i>	4.52	9.88	—	10.10-10.83	—	10.25-10.71	10.33-10.87
44. <i>Presbytis johnii</i>	3.50	9.35	—	8.71-9.04	—	8.75-9.01	8.61-8.95
45. <i>Callitricus moloch</i>	2.38	6.52	—	6.83-7.42	—	6.89-7.35	6.61-6.95
46. <i>Saguinus geoffroyi</i>	1.86	6.21	—	5.89-6.73	—	5.99-6.62	5.63-6.07
47. <i>Aotus trivirgatus</i>	2.26	6.82	—	6.62-7.26	—	6.68-7.18	6.39-6.75
48. <i>Ateles geoffroyi</i>	3.26	8.73	—	8.34-8.65	—	8.37-8.63	8.20-8.50
49. <i>Cebus apella</i>	3.24	7.57	—	8.31-8.62	—	8.34-8.60	8.16-8.47
50. <i>Saimiri oerstedii</i>	2.13	6.81	—	6.38-7.09	—	6.46-7.00	6.14-6.53
51. <i>Saimiri sciureus</i>	2.09	6.62	—	6.31-7.03	—	6.39-6.94	6.07-6.46
52. <i>Alouatta seniculus</i>	3.71	9.00	—	9.01-9.39	—	9.07-9.34	8.97-9.34
53. <i>Alouatta villosa</i>	3.66	8.91	—	8.94-9.31	—	9.00-9.26	8.89-9.24
54. <i>Brachyteles arachnoides</i>	3.68	9.17	—	8.96-9.34	—	9.03-9.30	8.92-9.28
55. <i>Lagothrix lagoitricha</i>	3.30	8.83	—	8.40-8.72	—	8.43-8.69	8.27-8.58
56. <i>Ateles belzebuth</i>	3.38	8.67	—	8.53-8.84	—	8.56-8.82	8.41-8.72
57. <i>Pithecia monachus</i>	2.68	6.88	—	7.37-7.82	—	7.40-7.78	7.16-7.47
58. <i>Hylobates klossii</i>	3.34	8.68	—	—	8.35- 8.93	8.50-8.76	8.34-8.65
59. <i>Hylobates agilis</i>	3.38	8.70	—	—	8.42- 8.98	8.56-8.82	8.41-8.72
60. <i>Hylobates moloch</i>	3.50	8.70	—	—	8.63- 9.15	8.75-9.01	8.61-8.95
61. <i>Hylobates lar</i>	3.20	8.47	—	—	8.11- 8.73	8.27-8.54	8.09-8.39
62. <i>Pongo pygmaeus</i>	5.07	11.14	—	—	11.04-11.68	11.02-11.66	11.24-11.93
63. <i>Pan troglodytes</i>	4.70	10.69	—	—	10.52-11.03	10.50-11.02	10.62-11.22
64. <i>Gorilla gorilla</i>	5.40	11.98	—	—	11.49-12.26	11.48-12.24	11.78-12.56
65. <i>Pan paniscus</i>	4.39	10.60	—	—	10.07-10.51	10.06-10.49	10.11-10.62

*Body weight in grams; molar area in square millimeters. Data from Gingerich *et al.* (1974), Kay (1973), Orlosky (1973), Swindler (1976), W. Kinzey (personal communication, 1985), and T. Olson (personal communication, 1985).

of primate species to estimate fossil primate body weights are explored and the implications of these results for interpreting the primate fossil record are examined. The choice of the appropriate equation to predict body weight can accordingly be based upon one's assignment of a particular fossil primate to one of the grade categories listed above. This judgment can be left up to each individual investigator, although I, of course, have my own bias as to how various fossils should be classified.

MATERIALS AND METHODS

Body weights (grams) and lower first molar areas (square millimeters) for 65 extant primate species (including four tupaiid species) are listed in Table I (data from Gingerich *et al.*, 1982; Kay, 1973; Orlosky, 1973; Swindler, 1976; W. Kinzey, personal communication; T. Olson, personal communication). All data are for male animals. In addition, the same variables for a female sample of 23 sexually dimorphic anthropoid species are used to calculate the regression equation of female anthropoid body weight on first molar area.

The species were separated into five morphological and evolutionary "grades": (1) prosimians (species numbered 1–22 in Table I); (2) monkeys (species 23–57); (3) apes (species 58–65); (4) anthropoids (species 23–65); and (5) all primates (species 1–65). Data were converted to natural logarithms and least-squares regression equations were calculated using the FIT LINE function of the RS/1 statistical software package (BBN Research Systems, Cambridge, MA) for each grade. These regression lines and the 95% confidence envelopes around them are shown in Figs. 1 to 5; the corresponding equations and the regression equation for the female anthropoid grade are given in Table II, together with *R* values and relevant measures of central tendency. Statistics from the analysis of variance are summarized in Table III.

Table II. Regression Equations, \log_e of Body Weight (*B*) on \log_e of M_1 Area (*A*), for the Six Primate Grades

Grade	Regression equation	<i>R</i>	95% confidence limits on	
			Slope	Intercept
All primates	$\log_e B = 1.784 \log_e A + 2.54$	0.96	± 0.33	-0.38
Prosimians	$\log_e B = 1.614 \log_e A + 2.67$	0.91	± 0.22	± 0.75
Monkeys	$\log_e B = 1.561 \log_e A + 3.41$	0.93	± 0.19	± 0.73
Apes	$\log_e B = 1.572 \log_e A + 3.39$	0.99	± 0.14	± 0.33
Anthropoids	$\log_e B = 1.570 \log_e A + 3.38$	0.96	± 0.12	± 0.50
Female anthropoids	$\log_e B = 1.438 \log_e A + 3.55$	0.96	± 0.19	± 0.69

Table III. Analysis of Variance in the Regressions of \log_e of Body Weight on \log_e of M_1 Area in Extant Primate Groupings

Grade	Mean square	F value	Significance level	SD of regression
All primates	198.32	893.38	0.0001	0.471
Prosimians	32.05	97.08	0.0001	0.575
Monkeys	27.89	213.71	0.0001	0.361
Apes	13.18	389.98	0.0001	0.184
Anthropoids	52.52	477.14	0.0001	0.332

The next step in the analysis was to assign the fossil primates to one of three grades: prosimian, monkey, or ape. The predicted body weight for each fossil species was then calculated by substituting the natural log of its mean lower first molar area into the appropriate regression equation (see below). The predicted weight of female fossils in more sexually dimorphic higher-primate species was calculated by using the equation derived from the 23 extant female anthropoid species. Table IV gives the weights of 114 prosimian-grade fossils predicted by both the prosimian equation and the all-primate equation. Table V gives the weights of 16 monkey-grade fossils predicted by the monkey equation, the anthropoid equation, and the all-primate equation. Table VI gives the weights of 16 ape-grade fossils predicted by the ape equation, the anthropoid equation, the all-primate equation, and the female anthropoid equation.

RESULTS

Even though the correlation coefficients (R values) seem high (ranging from 0.91 to 0.99; Table II), perusal of the data in Figs. 1 to 5 reveals that a number of individuals actually fall outside of the 95% confidence intervals for these equations. This should be viewed as a cautionary note to those who uncritically use high correlation coefficients to justify their predictive equations. A partial assessment of the impact of using a taxonomically matched equation instead of an "all-primate" (i.e., mouse-to-elephant) equation to estimate fossil body weights can be made by simply scanning the data visually (Figs. 6–9). Traditionally, a "mouse-to-elephant" curve (or, for primates, a *Microcebus*-to-*Gorilla* curve) has been used to estimate body weights of fossils. Figures 6 to 9 indicate the differences between each "grade" curve and the overall primate curve. In the case of prosimians, the overall primate curve will overestimate body weight, particularly in the upper range of tooth size (Fig. 6). In monkeys, body weights estimated from an all-primate curve will tend to be underestimates for the lower range of tooth size and

Table IV. Predicted Body Weights (BW) in Prosimian-Grade Fossil Primates^a

Taxon	log _e m ₁ area	BW predicted from	
		Prosimian equation	All-primate equation
<i>Plesiadapis praecursor</i>	1.91	315	383
<i>P. simonsi</i>	2.75	1222	1713
<i>P. anceps</i>	2.10	428	537
<i>P. rex</i>	2.20	503	642
<i>P. churchilli</i>	2.43	729	968
<i>P. fodinatus</i>	2.24	537	690
<i>P. dubius</i>	2.02	376	466
<i>P. cookei</i>	3.32	3067	4736
<i>P. walbeckensis</i>	2.04	389	483
<i>P. remensis</i>	2.45	753	1003
<i>P. tricuspidens</i>	2.78	1283	1807
<i>Platychoerops daubrei</i>	3.02	1890	2773
<i>Phenacolemur pagei</i>	1.60	191	220
<i>P. jepseni</i>	1.32	122	134
<i>P. praecox</i>	1.57	182	209
<i>P. fremontensis</i>	0.71	45	45
<i>P. simonsi</i>	0.82	54	55
<i>Pronothodectes intermedius</i>	1.72	232	273
<i>P. matthewi</i>	1.46	152	172
<i>P. jepi</i>	1.65	207	241
<i>Palaechthon woodi</i>	0.85	57	58
<i>P. alticuspis</i>	1.15	92	99
<i>P. nacimienti</i>	1.39	136	151
<i>Paromomys depressidens</i>	1.10	85	90
<i>P. maturus</i>	1.89	305	369
<i>Torrejonia wilsoni</i>	2.28	572	741
<i>Ignacius frugivorus</i>	1.17	95	102
<i>I. graybullianus</i>	1.46	152	172
<i>Plesiolestes sirokyi</i>	2.49	803	1077
<i>Chiromyoides minor</i>	1.34	126	138
<i>Nannodectes intermedius</i>	1.69	221	259
<i>N. gazini</i>	1.59	188	216
<i>N. simpsoni</i>	1.94	331	404
<i>N. gidleyi</i>	2.05	395	491
<i>Elphidotarsius florencae</i>	0.74	48	47
<i>Carpodaptus hazelae</i>	0.67	43	42
<i>C. cygneus</i>	0.67	43	42
<i>Carpolestes dubius</i>	1.17	95	102
<i>Tinimomys graybulliensis</i>	1.07	81	86
<i>Niptomomys thelmae</i>	0.65	41	40
<i>N. doreenae</i>	0.30	23	22
<i>Elwynella oreas</i>	1.58	185	212
<i>Teilhardina americana</i>	1.07	81	86
<i>T. belgica</i>	0.91	63	64
<i>Tetonoides tenuiculus</i>	1.15	92	99
<i>T. pearcei</i>	0.99	71	74
<i>Tetonius steini</i>	1.66	210	245
<i>T. homunculus</i>	1.60	191	220
<i>Absarokius abbotti</i>	1.57	182	209
<i>A. noctivagus</i>	1.57	182	209
<i>Chlororhysis knightensis</i>	1.27	112	122

Table IV. Continued

Taxon	$\log_e m_1$ area	BW predicted from	
		Prosimian equation	All-primate equation
<i>Uintalacus nettingi</i>	0.98	70	73
<i>Uintanius rutherfordi</i>	1.16	94	100
<i>U. turricolorum</i>	1.21	112	110
<i>Anaptomorphus aemulus</i>	1.57	182	209
<i>A. wortmani</i>	1.24	107	116
<i>A. westi</i>	1.89	305	369
<i>Trogolemur myodes</i>	0.80	53	53
<i>Omomys vespertinus</i>	1.65	207	241
<i>O. minutus</i>	0.95	67	69
<i>O. lloydi</i>	1.32	122	134
<i>O. carteri</i>	1.64	204	236
<i>Arapahovius gazini</i>	1.60	191	220
<i>Shoshonius cooperi</i>	1.22	103	112
<i>Utahia kayi</i>	0.95	67	69
<i>Washakius insignis</i>	1.27	112	122
<i>Hemicodon gracilis</i>	2.35	641	839
<i>Stockia powayensis</i>	1.90	310	376
<i>Ourayia uintensis</i>	2.81	1347	1907
<i>O. hopsoni</i>	2.43	729	968
<i>Chumashius balchi</i>	1.62	197	228
<i>Dyseolemur pacificus</i>	1.27	112	122
<i>Macrotarsius seigerti</i>	2.64	1023	1408
<i>M. montanus</i>	2.90	1557	2239
<i>Ekgmowechashala philotau</i>	2.72	1165	1624
<i>Nannopithecus raabi</i>	1.29	116	127
<i>N. pollicarus</i>	1.11	87	92
<i>N. filholi</i>	1.22	103	112
<i>Pseudoloris isabena</i>	0.54	35	33
<i>P. crusafonti</i>	0.80	53	53
<i>P. parvulus</i>	0.52	33	32
<i>P. reguanti</i>	1.07	81	86
<i>Necrolemur zitteli</i>	1.61	194	224
<i>N. antiquus</i>	1.67	214	249
<i>Microchoerus erinaceus</i>	2.69	1109	1539
<i>M. edwardsi</i>	2.30	591	768
<i>Altanius orlovi</i>	0.28	23	21
<i>Kohatius coppensi</i>	1.36	130	143
<i>Aycrossia lovei</i>	1.48	157	178
<i>Steinius vespertinus</i>	1.54	173	198
<i>Loveina zephyri</i>	1.36	130	143
<i>L. minuta</i>	1.02	75	78
<i>Anemorhysis sublettensis</i>	0.76	49	49
<i>A. wortmani</i>	1.11	87	92
<i>A. pattersoni</i>	1.05	79	83
<i>A. pearcei</i>	0.91	63	64
<i>Cantius eppsi</i>	2.30	591	768
<i>C. ralstoni</i>	2.44	741	985
<i>C. abditus</i>	3.01	1860	2724
<i>Smilodectes gracilis</i>	2.74	1203	1683
<i>S. mcgrewi</i>	3.06	2016	2978
<i>Notharctus tenebrosus</i>	3.10	2150	3198

Table IV. Continued

Taxon	log _e m ₁ area	BW predicted from	
		Prosimian equation	All-primate equation
<i>N. robustior</i>	3.58	4666	7531
<i>Mahgarita stevensi</i>	2.25	545	702
<i>Periconodon huerzeleri</i>	1.85	286	344
<i>Protoadapis klatti</i>	2.57	914	1242
<i>Anchomomys gaillardi</i>	0.77	50	50
<i>Adapis sudrei</i>	2.62	991	1358
<i>A. magnus</i>	3.51	4168	6646
<i>Sivaladapis nagrii</i>	3.25	2739	4180
<i>Indraloris lulli</i>	3.19	2487	3755
<i>Copelemur feretutus</i>	2.69	1109	1539
<i>C. consortutus</i>	2.55	885	1199
<i>Agerina russelli</i>	2.02	376	466

^aBody weight in grams; molar area in square millimeters. Data from Gingerich (1975, 1976, 1979, 1981), Gingerich *et al.* (1982), Gingerich and Dorr (1979), Gingerich and Simons (1977), Gunnell and Gingerich (1981), Simpson (1955), Gazin (1968, 1971), Bown and Rose (1976, 1984), Szalay (1971, 1973), Wilson and Szalay (1972), Krause (1978), Rose (1975), Rose and Bown (1979).

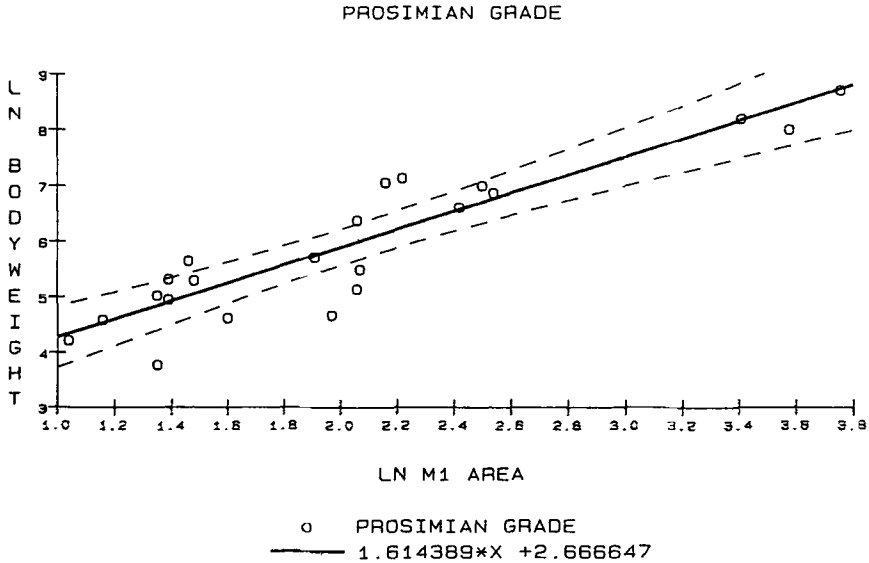


Fig. 1. Natural logarithms (LN) of body weight and M₁ area, modern prosimians; data from Table I. The least-squares regression equation is shown together with its plot (double line) and 95% confidence limits (dashed curves).

Table V. Predicted Body Weights (BW) in Monkey-Grade Fossil Primates^a

Taxon	log _e M ₁ area	BW predicted from		
		Monkey equation	Anthropoid equation	All-primate equation
<i>Homunculus patagonicus</i>	2.89	2755	2744	2199
<i>Neosaimiri fieldsi</i>	2.13	841	832	567
<i>Cebupithecia sarmientoi</i>	2.75	2214	2203	1713
<i>Stirtonia tatacoensis</i>	3.37	5829	5831	5178
<i>Apidium moustafai</i>	2.15	868	859	587
<i>A. phiomense</i>	2.58	1698	1687	1265
<i>Parapithecus grangeri</i>	2.98	3171	3161	2582
<i>Parapithecus fraasi</i>	2.61	1780	1768	1334
<i>Propitopithecus haeckeli</i>	3.14	4071	4064	3435
<i>Propitopithecus chirobates</i>	3.17	4266	4259	3624
<i>Aegyptopithecus zeuxis</i>	3.46	6708	6716	6079
<i>Qatrania wingi</i>	1.42	278	273	160
<i>Oligopithecus savagei</i>	2.50	1499	1488	1097
<i>Amphipithecus mogaungensis</i>	3.62	8611	8633	8088
<i>Vicroripithecus macinnesi</i>	3.33	5476	5476	4821
<i>Prohylobates tandyi</i>	3.55	7720	7735	7138

^aBody weight in grams; molar area in square millimeters. Data from Gingerich *et al.* (1982), Somons and Kay (1983), and Colbert (1937).

Table VI. Predicted Body Weights (BW) in Ape-Grade Fossil Primates^a

Taxon	log ₁₀ M ₁ area	Ape equation	Anthropoid equation	All-primate equation	Female anthropoid equation
<i>Oreopithecus bambolii</i>	4.06	17,541	17,226	17,730	11,888
<i>Micropithecus clarki</i>	3.03	3,474	3,419	2,823	2,703
<i>Limnopithecus logetei</i>	3.28	5,147	5,062	4,410	3,872
<i>Dendropithecus macinnesi</i>	3.64	9,064	8,909	8,381	6,498
<i>Proconsul gardoni</i>	3.95	14,756	14,494	14,571	10,149
<i>P. africanus</i>	4.10	18,680	18,343	19,042	12,595
<i>P. nyanzae</i>	4.37	28,557	28,026	30,825	18,565
<i>P. major</i>	4.75	51,896	50,894	60,718	32,064
<i>Pliopithecus antiquus</i>	3.46	6,830	6,716	6,079	5,016
<i>Dryopithecus laietanus</i>	4.14	19,892	19,532	20,450	13,337
<i>D. fontani</i>	4.51	35,586	34,916	39,571	22,706
<i>Ouranopithecus macedoniensis</i>	5.23	110,366	108,131	142,960	63,943
<i>Sivapithecus sivalensis</i>	4.60	40,995	40,215	46,462	25,843
<i>S. indicus</i>	4.83	58,851	57,705	70,033	35,974
<i>S. metzei</i>	5.04	81,869	80,242	101,861	48,655
<i>Gigantopithecus giganteus</i>	5.49	166,089	162,641	227,330	92,932

^aBody weight in grams; molar area in square millimeters. Gingerich *et al.* (1982).

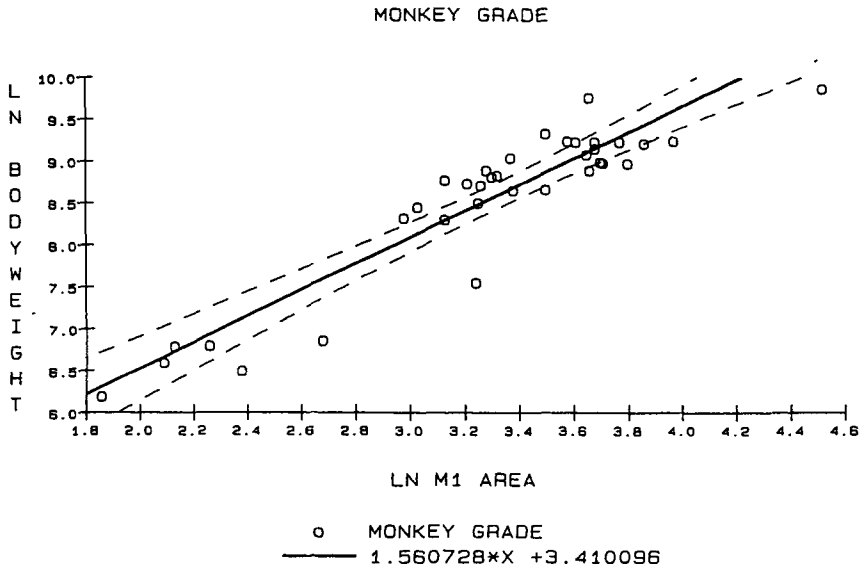


Fig. 2. Data points and least-squares regression of log body weight on log M₁ area in extant monkeys; data from Table I. Symbols and conventions as in Fig. 1.

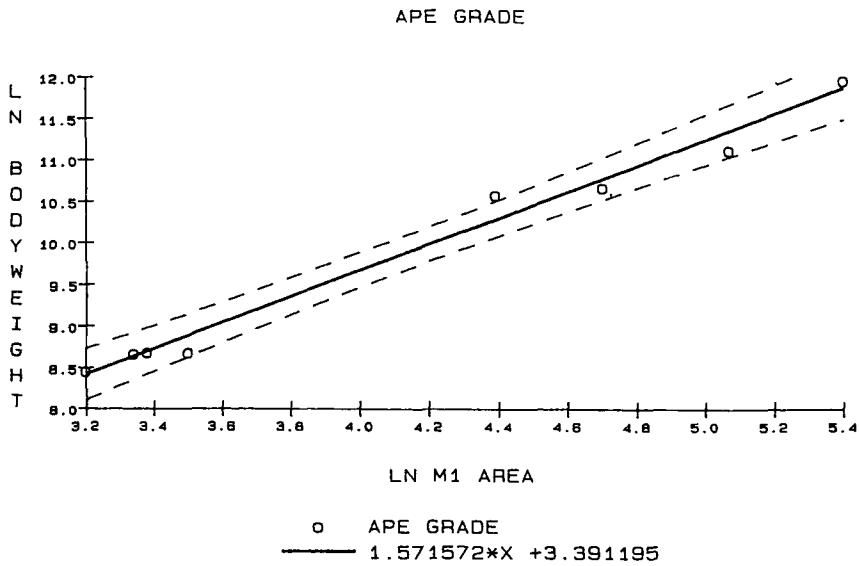


Fig. 3. Data points and least-squares regression of log body weight on log M₁ area in extant apes; data from Table I. Symbols and conventions as in Fig. 1.

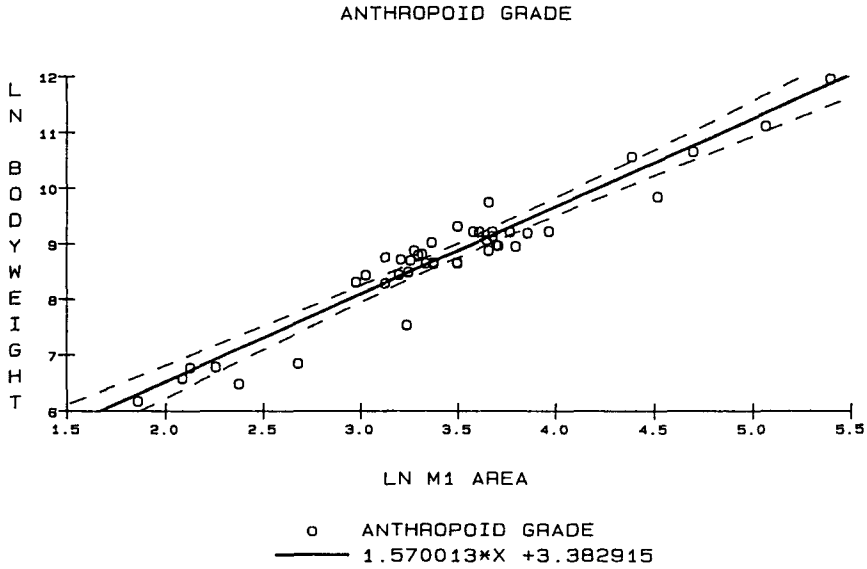


Fig. 4. Data points and least-squares regression of log body weight on log M_1 area in extant anthropoids; data from Table I. Symbols and conventions as in Fig. 1.

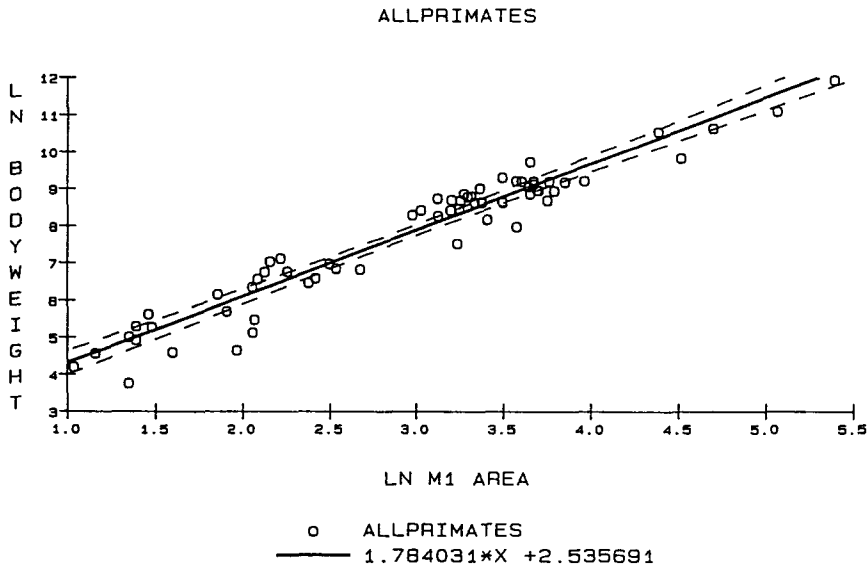


Fig. 5. Data points and least-squares regression of log body weight on log M_1 area in all extant primates; data from Table I. Symbols and conventions as in Fig. 1.

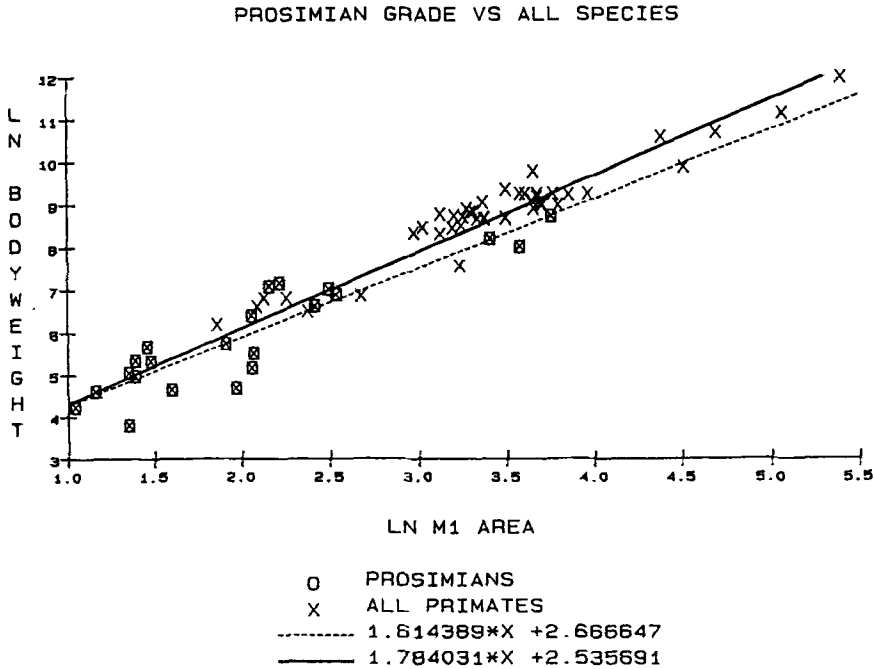


Fig. 6. Natural logarithms (LN) of M_1 area plotted against LN of body weight for all primate species; data from Table I. Lines indicate least-squares regressions calculated from all-primate data (X's, solid line) and from prosimian-grade data only (boxed X's, dashed line).

overestimates for the upper part of the range (Fig. 7). The difference between the ape curve and the all-primate curve in the range of tooth size relevant to apes (Fig. 8) indicates that body size will be underestimated for smaller apes and overestimated for larger apes using the all-primate curve. These trends are noteworthy in light of the fact that an analysis of covariance test for homogeneity of slopes indicates that the null hypothesis that all the slopes could have come from populations with the same slope cannot be rejected ($p = 0.17$) (R. German, personal communication).

Tables IV to VI list body-weight estimates for many nonhominid primate fossil species, derived from equations for the most applicable primate grade and for the all-primate equation. [It is unlikely that all of these are truly valid species: see Gingerich *et al.* (1982).] An inspection of the tables confirms that some body-weight estimates differ substantially depending upon which equation is used, while estimates of other body weights are little affected by the choice of equation. Nevertheless, some of these predicted fossil body weights differ significantly from those previously published by other workers (see below).

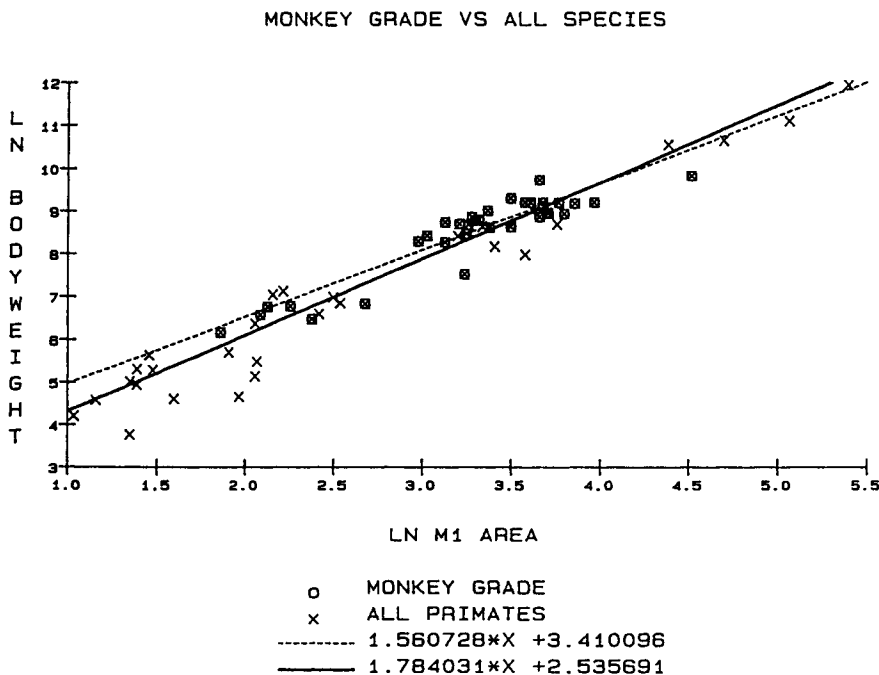


Fig. 7. Natural logarithms (LN) of M_1 area plotted against LN of body weight for all primate species; data from Table I. Lines indicate least-squares regressions calculated from all-primate data (X's, solid line) and from monkey-grade data only (boxed X's, dashed line).

DISCUSSION

In all published attempts to estimate body weights of extinct primates from the relationships of tooth size to body weight that obtain among modern species, some concept of taxonomic relevance has been used to select modern species for comparison. Nevertheless, the use of primate subgroups has been surprisingly uncommon. Gingerich (1977), in an attempt to estimate body weights of *Proconsul africanus*, first generated an equation using only modern hominoids but changed to a large range of primates for the reference equation after concluding that the hominoid equation had a large standard error. Later, in studies concerned with body weights of Omomyidae, Gingerich (1981) observed that modern tarsiers fell well below the overall primate equation. His method for predicting omomyid body weight was to take a line through the two tarsier values parallel to the overall primate line. Since this study has shown that the prosimian and all-primate slopes may give very different body-weight estimates, the decision to draw a tarsier-"grade" line parallel to an all-primate line becomes suspect. Despite widespread doubts

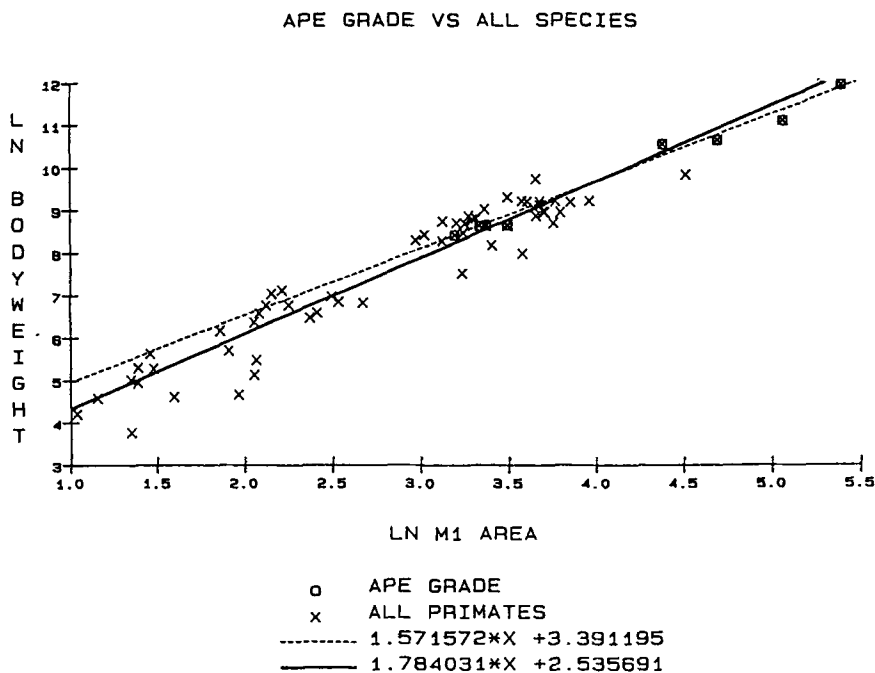


Fig. 8. Natural logarithms (LN) of M₁ area plotted against LN of body weight for all primate species; data from Table I. Lines indicate least-squares regressions calculated from all-primate data (X's, solid line) and from ape-grade data only (boxed X's, dashed line).

concerning the assumptions used to predict fossil body weights in the above-mentioned studies, only Gingerich (e.g., 1977, 1981) and Smith (1985) have attempted to use more specific equations to predict body weights of fossil primates. Most other recent studies have generally relied on an overall primate equation (e.g., Kay and Simons, 1980; Blumenburg, 1981, 1984; Cachel, 1983).

The results of this study on body weights of fossil primates have important implications for interpretations of the fossil-primate record. For example, it can be noted that approximately 70% of the Paleocene and Eocene primates in the data set have a body weight below "Kay's threshold" of 500 g (Kay and Cartmill, 1977; Gingerich, 1980) and were thus predominantly nonfolivorous. Of the 40 or so species of plesiadapiform primates in the data set, nearly three-quarters weighed less than 500 g (ranging in size from about 20 g in *Niptomomys* to 3–4 kg in *Plesiadapis cookei*). Consequently, these data militate against the notion that the Paleocene radiation of primates was due mainly to exploitation of new herbivorous and frugivorous ecological niches (Szalay, 1968) and supports, instead, the views of primate origins set

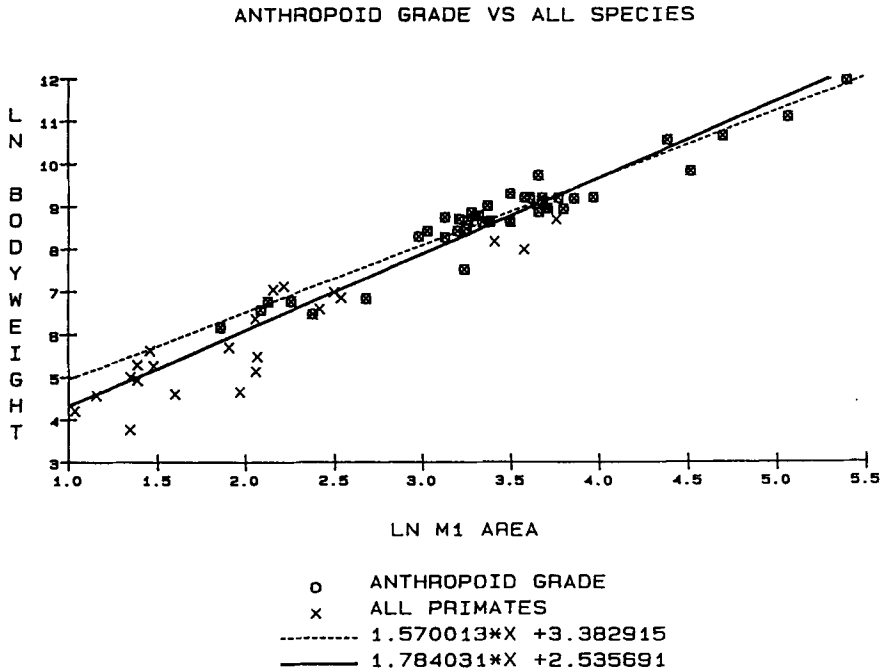


Fig. 9. Natural logarithms (LN) of M_1 area, plotted against LN of body weight for all primate species; data from Table I. Lines indicate least-squares regressions calculated from all-primate data (X's, solid line) and from anthropoid-grade data only (boxed X's, dashed line).

forth by Kay and Cartmill (1977). In addition, the first primates of "modern aspect," the Eocene Adapidae and Omomyidae, undoubtedly had (for the most part) nonoverlapping dietary regimes: while approximately 80% of all omomyids weighed below 500 g, nearly all the adapids were above 500 g in body weight.

It is clear from Table IV and Fig. 6 that an all-primate line overestimates body weight of prosimian-grade fossils, particularly at higher body weights. For example, the estimates of body weight in *Notharctus robustior* and *Adapis magnus* (based on a prosimian-grade regression) in this study are only about 65% of the weights calculated by Gingerich *et al.* (1982) for these same two species. The predicted weight of *Plesiadapis tricuspidens* (based on a prosimian-grade regression) is only about 30% of previously calculated values.

These differences in body-weight predictions have a profound influence on interpretations of primate paleobiology, particularly in calculations of encephalization quotients (EQ) (Table VII). To illustrate, according to Jerison's (1973) formula for EQ, *Plesiadapis tricuspidens* had an EQ of 0.62, inferred from a brain-volume estimate of 18 cm³ and a body-weight estimate

Table VII. Encephalization Quotients (EQ) for Tertiary Primates

Taxon	Brain size (cm ³)	EQ ^a					
		P	M	A	AN	All	F
<i>Plesiadapis tricuspidens</i>	18.0	1.24	—	—	0.98	—	—
<i>Adapis parisiensis</i>	8.8	0.72	—	—	—	0.98	—
<i>Smilodectes gracilis</i>	9.5	0.68	—	—	—	0.55	—
<i>Tetonius homunculus</i>	1.5	0.38	—	—	—	0.35	—
<i>Aegyptopithecus zeuxis</i>	32.0	—	0.73	—	0.73	0.78	—
<i>Proconsul africanus</i>	167.0	—	—	1.91	1.94	1.89	2.49
<i>Oreopithecus bambolii</i>	402.0	—	—	4.80	4.86	4.77	6.23

^aAbbreviations heading each EQ column indicate the source of the body-weight estimate used in calculating EQ. P, prosimian equation; M, monkey equation; A, ape equation; AN, anthropoid equation; All, all-primate equation; F, female anthropoid equation.

of 4 kg (Gingerich, 1976). However, the EQ of *Plesiadapis tricuspidens* may be as high as 1.24 if the body weight of 1283 g from Table IV is accepted as a more accurate estimate.

Previous EQ estimates for *Adapis parisiensis* range between 0.39 and 0.53 (Gurche, 1982; Gingerich and Martin, 1981). Using the body-weight estimates for *A. sudrei* (which is about the same size as *A. parisiensis*) presented here, the EQ for *A. parisiensis* may be as high as 0.72. In addition, the EQ of *Smilodectes gracilis* may be as high as 0.68, which is considerably above the 0.45–0.53 range previously reported by Gurche (1982). These new figures would suggest that the EQ of Eocene adapids was within the (low) range of modern prosimians, not below it as has been previously reported (e.g., by Gingerich and Martin, 1981). On the other hand, the EQ of the omomyid *Tetonius homunculus* could be as low as 0.38, which is lower than the 0.42–0.71 range reported by Gurche (1982).

The skulls of the Oligocene and Miocene “apes” *Aegyptopithecus zeuxis*, *Oreopithecus bambolii*, and *Proconsul africanus* are complete enough to give reasonable indications of cranial capacity. The EQ of Oligocene *Aegyptopithecus* ranges from 0.73 to 0.78, depending upon which body-weight estimate is used from Table V. The EQ of the early Miocene *Proconsul africanus* may be as high as 2.49, if we accept the body weight predicted in Table VI for female members of this species and the cranial capacity of approximately 167 cm³ reported by Walker *et al.* (1983). This EQ value is significantly greater than the 1.19–1.96 range predicted by Gingerich (1977) for this species. Interestingly, the EQ of middle Miocene *Oreopithecus* is much higher; outside limits of 4.7 to 6.2 can be inferred from a mean cranial-capacity estimate of 402 cm³ [the midpoint of the range of 276–529 cm³ estimated by Straus and Schön (1960)] and the predicted body sizes from Table VI. However, the EQ would be only half these values if the cranial capacity were closer to 200 cm³, as suggested by Szalay and Berzi (1973).

This type of analysis represents an improvement over previous attempts to derive body weights from dental dimensions in fossil primates because the investigator can choose among several alternative equations, depending upon which one seems most appropriate for the individual case under study. For example, the *Proconsul africanus* specimen mentioned previously can be analyzed in several ways. The predicted body weight for this species hovers around 18–19 kg no matter whether we adopt the ape equation, the anthropoid equation, or the all-primate equation (Table VI). However, when it is realized that the particular specimen in question from Rusinga Island is a female, it seems more appropriate to utilize the female anthropoid equation (last column, Table VI). This yields an estimate of about 12 kg, the same value predicted by Walker and Pickford (1983) from their study of the postcranial skeleton.

It seems to be both conservative and straightforward to use equations limited to a more closely related subgroup of primates rather than an overall "*Microcebus-to-Gorilla*" primate equation when attempting to estimate fossil body weights. It is not at all clear why this has not been common practice. There is, of course, no way to know if the body-weight estimates listed in Tables IV-VI are correct; but they are probably the best estimates available at present, given the "noise" inherent in the raw data.

Any inference about fossils that rests on an analogy with extant species must reflect to some degree the assumptions of the investigator as to which extant species are relevant and accurate analogies. The results of this study emphasize that taxonomic subgroups within the order Primates have different tooth-size/body-weight relationships and that those differences should be considered in primate paleobiological studies. It should be emphasized that these differences are biologically meaningful even though the null hypothesis of homogeneity of slopes cannot be formally rejected.

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