Correlation of Tooth Size and Body Size in Living Hominoid Primates, with a Note on Relative Brain Size in *Aegyptopithecus* and *Proconsul*

PHILIP D. GINGERICH
Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109

ABSTRACT   Second molar length and body weight are used to test the correlation between tooth size and body size in living Hominoidea. These variates are highly correlated ($r = 0.942, p < 0.001$), indicating that tooth size can be used in dentally unspecialized fossil hominoids as one method of predicting the average body weight of species. Based on tooth size, the average body weight of *Aegyptopithecus zeuxis* is estimated to have been between 4.5 and 7.5 kg, which is corroborated by known cranial and postcranial elements. Using Radinsky's estimates of brain size, the encephalization quotient (EQ) for *Aegyptopithecus* was between 0.65 and 1.04. A similar analysis for *Proconsul africanus* yields a body weight between 16 and 34 kg, and an EQ between 1.19 and 1.96.

Dental enamel is the hardest and densest tissue in the mammalian skeleton, and as a result teeth are the most commonly preserved remains of mammals in the fossil record. Most mammalian teeth do not continue to grow during life—once the teeth have formed and erupted, their size is effectively fixed. Tooth size has high heritability (Alvesalo and Tigerstedt, '74), and the variability of certain teeth within species is relatively low (especially M1 and M2: Gingerich, '74). These characteristics make mammalian teeth uniquely suited for detailed evolutionary study in the fossil record.

Body size is acknowledged to be one of the most important components of an animal's adaptation to its environment (McNab, '71; Van Valen, '73; Schmidt-Nielsen, '75). Tooth size is highly correlated with body size ($r = 0.93$-0.98: Gould, '75; Kay, '75), thus changes in tooth size during evolution usually reflect changes in overall body size. The study of fossil teeth offers a unique pathway to the study of this fundamental adaptation, body size, and its evolution through time.

In a recent paper, Henderson and Corruccini ('76) studied the relationship between tooth size and body size in American Blacks, found a very low correlation, and concluded that attempts to infer body size from tooth size in fossil *hominoid* primates are unjustified. However, the correlation of body size with tooth size across species of a superfamily like the Hominoidea is not the same as the correlation of these variables within a species. I have previously discussed this problem in connection with tooth size-body size correlation in squirrels of the family Sciuridae (Gingerich, '76), and here present a brief analysis of the correlation between body size and tooth size in hominoid primates.

DATA, CORRELATION, AND PREDICTIONS

Tooth size (length of M_2) and body size (weight) measurements for six species of hominoid primates were recently published by Kay ('75). In addition, average M_2 length and body weight for modern *Homo sapiens* (Australian aboriginals) are available in measurements published by Campbell ('25) and Pilbeam and Gould ('74). These data are summarized in table 1.

The relationship of body weight and tooth size in hominoid primates is illustrated in figure 1. Regressions of log body weight on log tooth size, and log tooth size on log body weight were calculated for the data in table 1 (fig. 1), and the correlation coefficient was

Means of second lower molar length, and body weight estimates for living Hominoidea

Species	N	M_2 length (mm)	Log M_2 length	Body weight (gm)	Log weight
(1) *Hylobates klossi*	7	5.6	0.748	5,300	3.724
(2) *Symphalangus syndactylus*	10	8.7	0.940	10,100	4.004
(3) *Pan paniscus*	3	9.0	0.954	35,000	4.544
(4) *Pan troglodytes* (females)	5	10.4	1.017	36,000	4.556
(5) *Pan troglodytes* (males)	5	11.3	1.053	45,000	4.653
(6) *Homo sapiens* (Austral. aboriginals)	152	12.5	1.097	57,000	4.756
(7) *Pongo pygmaeus* (females)	4	12.8	1.107	36,000	4.556
(8) *Pongo pygmaeus* (males)	4	15.2	1.182	78,000	4.892
(9) *Gorilla gorilla gorilla* (females)	5	14.5	1.161	123,000	5.090
(10) *Gorilla gorilla gorilla* (males)	6	17.6	1.246	167,000	5.223

Data from Kay ('75), Pilbeam and Gould ('74), and Campbell ('25). Numbers at left refer to points plotted in figure 1.
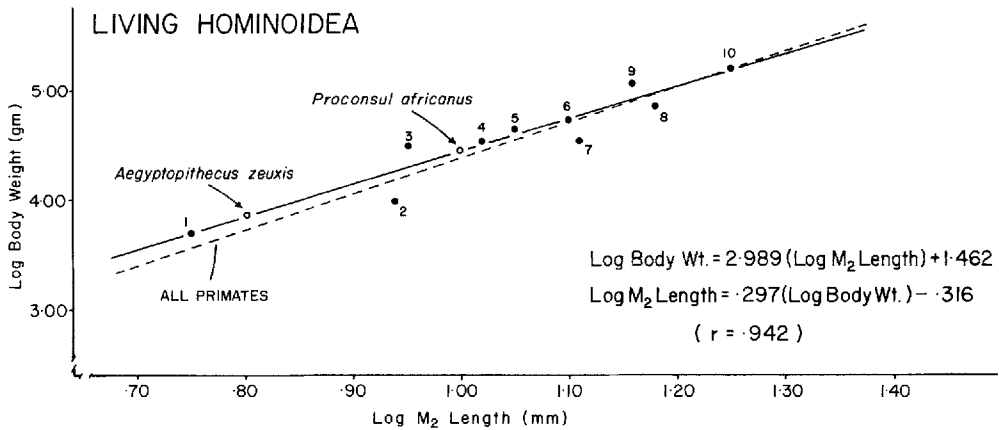

Fig. 1   Correlation of body weight and tooth size in living hominoid primates. Data and identifications of plotted points are given in table 1. Equations show regression of body weight on tooth size (solid line), and of tooth size on body weight (not plotted). Note high correlation of tooth size and body size within Hominoidea (r = 0.942), and allometric constant 2.989 insignificantly different from 3—indicating that body weight is proportional to the cube of tooth length. For comparison, dashed line shows regression of body weight on tooth size for a representative sample of 38 primate species (Cercopithecoidea excluded; see text for equation and discussion).

also calculated. The correlation coefficient r is 0.942 (p < 0.001) indicating that body weight is very strongly and significantly correlated with M_2 length in living Hominoidea. I do not know of any attempt to calculate in this way the correlation of body weight with the length or width of other teeth besides M_2, but the very high level of integration of all teeth in the middle of the cheek tooth series in mammals (Olson and Miller, '58; Gould and Garwood, '69) indicates that most of these tooth measures should also be highly correlated with body size.

One of the most important uses of regression and correlation is in making predictions when data are incomplete. Two examples can be given here of new body size predictions, based on tooth size in the fossil hominoids *Aegyptopithecus* and *Proconsul.*

Body size can be estimated from tooth size in Hominoidea using the relationship and regression equation shown in figure 1. The small number of samples available (10) is sufficient to demonstrate that a close correlation of tooth size and body size exists in Hominoidea, but due to the small number of samples the 95% confidence interval for predicted body weights using this regression is unreasonably large. Thus I have calculated regression equations and the correlation between tooth size and body size for *Homo sapiens* (table 1) and all of the other primate species listed by Kay ('75), making a total of 38 noncercopithecoid species. For all of these primates:

Log body weight = 3.289 log M_2 length + 1.095
Log M_2 length = 0.282 log body weight − 0.257

and the correlation coefficient r = 0.963.

The length of M_2 in the type specimen of *Aegyptopithecus zeuxis* measures 6.4 mm, and several other undescribed specimens are within about 0.1 mm of the type. Using the regression based on living Hominoidea (fig. 1), the average body weight of *Aegyptopithecus zeuxis* is estimated at about 7.5 kg. Using the regression given above for a range of primates, including hominoids, the body weight of *Aegyptopithecus* is estimated at 5.6 kg, with a 95% confidence interval ranging from 4.5-6.5 kg. The postcranial skeleton of *Aegyptopithecus* gives an independent confirmation of these body size estimates. Fleagle et al. ('75) indicated that the ulna of *Aegyptopithecus* was about the size of that of *Alouatta* or *Presbytis cristatus*. The average weights of these two living primates are, respectively, about 6.4 and 6.2 kg (Bauchot and Stephan, '69: pp. 233, 245), supporting the body weight estimate for *Aegyptopithecus* based on its molar size.

Two partial skulls of *Proconsul africanus* are known from Rusinga Island, Kenya, which have M_2 lengths of 10.0 and 9.8 mm respectively (LeGros Clark and Leakey, '51; Napier and Davis, '59). Using the average of these two values, 9.9 mm, the regression for living Hominoidea (fig. 1) predicts an average body weight of about 27.4 kg for *Proconsul africanus*. The regression given in the text above for a range of 38 primate species predicts an average body weight of 23.4 kg, with the 95% confidence interval ranging from 16.1-34.0 kg. Based on the cranial and postcranial skeleton, Napier and Davis ('59: p. 61) estimated the body size of *Proconsul africanus* to be that of a medium-sized baboon (16-26 kg: Bauchot and Stephan, '69: pp. 242-244), again indicating close agreement between body size estimates based on tooth size and other available evidence.

RELATIVE BRAIN SIZE OF *AEGYPTOPITHECUS* AND *PROCONSUL*

Jerison ('73: p. 61) has developed a simple but elegant method of quantifying and comparing relative brain size among living mammals, based on brain size and body weight. This encephalization quotient, EQ, is given by

$$EQ_i = \frac{E_i}{0.12\,P_i^{2/3}}$$

where E_i is the brain size (in cm^3 or gm) and P_i is the body weight in grams. An EQ = 1.00 means that a given species has a brain of average size for a living mammal of its weight. Jerison ('73) gives EQ values for a number of fossil primates. Using Jerison's method, Radinsky's ('73, '74) estimates of brain size in *Aegyptopithecus zeuxis* and *Proconsul africanus*, and the body weight estimates given above, a probable range of EQ values can be calculated for *Aegyptopithecus* and *Proconsul*.

Radinsky ('73) estimated the endocranial volume of *Aegyptopithecus zeuxis* to be between 30 and 34 cm^3. Combining the minimum brain size (30 cm^3) with the maximum weight calculated above (7.5 kg) yields a minimum estimate of encephalization in *Aegyptopithecus* of EQ = 0.65. Combining the maximum brain size (34 cm^3) with the minimum estimated weight (4.5 kg) yields a maximum estimate of encephalization in *Aegyptopithecus* of EQ = 1.04. The best estimate is probably in between, or about EQ = 0.85.

Radinsky ('74) estimated the endocranial volume of *Proconsul africanus* to be about 150 cm^3. Combining this with the maximum and minimum weights estimated above for *Proconsul africanus* (34.0 and 16.1 kg) yields a minimum EQ = 1.19 and maximum EQ = 1.96 for *Proconsul*. The best estimate is probably about EQ = 1.60.

Radinsky ('73: p. 245) first estimated the relative brain size of *Aegyptopithecus* (based on comparisons with foramen magnum area) to be near the middle of the anthropoid range, but comparison of the EQ values calculated above with the EQ of other higher primate species (Jerison, '73: p. 392) indicates a relative brain size significantly ($p = 0.05$) below that of living anthropoids. (EQ in modern anthropoids, *Homo* excluded, ranges from a low of 1.05 in *Presbytis* to a high of 4.79 in *Cebus*, with a mean of 2.07 and a standard deviation of 0.609.) Radinsky ('77) recently revised his estimates, and has independently reached a similar conclusion about relative brain size in *Aegyptopithecus*. Radinsky ('74: p. 21) estimated the relative brain size of *Proconsul* (again based on comparisons with foramen magnum area) to be near the mean value of modern anthropoids, but the EQ values calculated above suggest that encephalization in *Proconsul* was probably below average for living higher primates. It appears that there has been a significant increase in relative brain size in Hominoidea since the Oligocene (represented by *Aegyptopithecus*), and even since the early Miocene (represented by *Proconsul*).

It should be noted that Jerison's ('73: p. 381) published values for the encephalization quotient of two fossil prosimians, late Eocene

Necrolemur (EQ = 1.22) and early Oligocene *Rooneyia* (EQ = 1.75) appear remarkably high when compared to a value for *Aegyptopithecus* estimated to lie between 0.65 and 1.04. Radinsky ('77) suggests higher body weights and therefore a lower EQ for both *Necrolemur* and *Rooneyia. Smilodectes,* an Eocene prosimian for which there is a significant postcranial skeleton, has an encephalization quotient estimated by Jerison ('73) at EQ = 0.55, which is likely to be closer to the average for Eocene primates (see also Radinsky, '77).

CONCLUSIONS

Tooth size and body size are highly correlated in living Hominoidea and in primates in general. This correlation can be used to predict average body weight from dental dimensions for generalized fossil primate species (excluding some manifestly megadont fossil Hominidae). Estimates of average body size in *Aegyptopithecus zeuxis* and *Proconsul africanus* are corroborated by available cranial and postcranial evidence. These estimates of body size can in turn be used to estimate possible ranges of relative brain size in *Aegyptopithecus* and *Proconsul,* indicating that relative brain size has increased significantly in higher primates since the Oligocene and early Miocene.

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