

An alternative method for predicting body mass: the case of the Pleistocene marsupial lion

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Abstract.—Accurate estimates of body mass in fossil taxa are fundamental to paleobiological reconstruction. Predictive equations derived from correlation with craniodental and body mass data in extant taxa are the most commonly used, but they can be unreliable for species whose morphology departs widely from that of living relatives. Estimates based on proximal limb-bone circumference data are more accurate but are inapplicable where postcranial remains are unknown. In this study we assess the efficacy of predicting body mass in Australian fossil marsupials by using an alternative correlate, endocranial volume. Body mass estimates for a species with highly unusual craniodental anatomy, the Pleistocene marsupial lion (*Thylacoleo carnifex*), fall within the range determined on the basis of proximal limb-bone circumference data, whereas estimates based on dental data are highly dubious. For all marsupial taxa considered, allometric relationships have small confidence intervals, and percent prediction errors are comparable to those of the best predictors using craniodental data. Although application is limited in some respects, this method may provide a useful means of estimating body mass for species with atypical craniodental or postcranial morphologies and taxa unrepresented by postcranial remains. A trend toward increased encephalization may constrain the method's predictive power with respect to many, but not all, placental clades.

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Introduction

Body mass strongly influences animal ecology (Kozlowski and Weiner 1997; Kelt and Van Vuren 2001), energetics (Lundberg and Persson 1993), and physiology (Schmidt-Nielsen 1984; Seebacher 2003). Predicting body mass is, therefore, fundamental to understanding the biology of extinct species and to placing them within broader ecological contexts (Wroe et al. 1999; Egi 2001; Myers 2001; Wroe 2002; Reynolds 2002).

Various methodologies have been developed for estimating body mass in fossil species. Most have been based on the correlation of craniodental and body mass data in living taxa (Legendre 1989; Janis 1990; Van Valkenburgh 1990; Myers 2001). Because cranial and particularly dental remains are relatively abundant, these methods are applicable to a wide range of fossil species and can often draw on large sample sizes. However, the precision of

procedures based on these data diminishes where the morphology of fossil taxa departs widely from that of extant relatives (Van Valkenburgh 1990). Alternatively, predictions founded on circumference or cross-sectional area of limb elements are widely held to offer greater accuracy (Anderson et al. 1985; Anyonge 1993; Christiansen 1999; Wroe et al. 1999; Egi 2001). However, their use is limited by the availability of material. Another method, developed by Seebacher (2001), may also offer greater precision but similarly requires near-complete skeletons and is to some degree dependent on the efficacy of reconstructions. Either way, in some instances each of these methodologies is either inapplicable or unlikely to produce reliable results. Consequently, predicting body mass in fossil taxa that are morphologically atypical and/or not represented by postcranial material remains especially problematic.

With respect to Australia's fossil marsupials, few are represented by quantitatively derived body mass estimates (Wroe 2001, 2002). However, one taxon has received special attention, the Pleistocene marsupial lion (*Thylacoleo carnifex*). Historically, an extraordinary range of subjectively determined body mass estimates have been offered for this, Australia's largest mammalian carnivore. Predictions span a full order of magnitude from 200 kg (Martin 1984) to 20 kg (Webb 1998). But most subjective estimates for *T. carnifex* have converged on comparison with the leopard, *Panthera pardus* (see Wells et al. 1982; Finch and Freedman 1988; Flannery 1994). These lower figures and general comparisons with *P. pardus* have heavily influenced reconstructions of the animal's behavior, as well as broader interpretations of Australian ecology (Wells et al. 1982; Flannery 1994; Webb 1998). Mean body mass for the leopard is around 51 kg (Gittleman 1986).

Thylacoleo are highly specialized brachycephalic predators with greatly hypotrophied molar rows and hypertrophied sectorial third premolars. Consequently, quantitatively derived predictions based on dental data sets produce highly dubious results. The best dental predictor for body mass in non-dasyuromorphian taxa is upper molar row occlusal length (Myers 2001). Inputting a mean for this dimension of 14.2 mm in *T. carnifex* (Archer and Dawson 1982) into the equation of Myers (2001) gives an impossibly low body mass estimate of 5 g.

On the other hand, quantitatively derived estimates for *Thylacoleo carnifex* based on proximal limb-bone circumference data suggest that *T. carnifex* was much larger than the leopard. Wroe et al. (1999) gave mean body mass estimates of 101 kg and 130 kg. These authors used the methodologies of Anderson et al. (1985) and Anyonge (1993) to generate estimates for a single *T. carnifex* represented by postcranial material. The averages they then provided assumed geometric similtude for this specimen with others known from complete crania. But the assumption of geometric similtude can be problematic, even within species (Reynolds 2002). Still more recently, Burness et al. (2001) gave a mean estimate of 73 kg. This figure was derived by using

the method of Anderson et al. (1985). However, data were taken from a geographically restricted sample (South Australia) and the result was not corrected for logarithmic transformation bias (B. Kear unpublished data).

The presence of an allometric relationship between brain and body mass is widely recognized in the literature, although the nature of this relationship may vary considerably between taxa (Jerison 1983; Pagel and Harvey 1989). We hypothesize that estimates founded on this relationship may offer a viable alternative method for determining body mass. In the following study we evaluate the efficacy of equations derived from the correlation of brain and body mass among Australian marsupials as predictors of body mass. We suggest that this method is most likely to be of value in the prediction of body mass for taxa with morphologies that differ significantly from those of living relatives. Because its unusual anatomy compromises realistic estimations of body mass based on craniodental data, but the presence of postcranial remains allows more accurate predictions with which to compare our results, we will concentrate on the Pleistocene marsupial lion as a test case.

Methods

Brain mass, endocranial volume (ECV) and body mass data were drawn largely from the work of Haight and Nelson (1987). These authors calculated encephalization quotients for 32 species of extant Australian marsupials constituting eight families and three orders. Miguel and Henneberg (1997) offered limited criticism of Haight and Nelson (1987) with respect to data supplied for *Phascolarctos cinereus* and *Vombatus ursinus*. Consequently, we incorporated the data of Miguel and Henneberg (1997) for these two taxa. Data for two further species, *Thylacinus cynocephalus* and *Macropus rufus*, were also added. Paddle (2000) gave an average body mass of 29,500 g for *T. cynocephalus*, based on the four specimens from which body mass was recorded. Moeller (1997) provided a mean ECV of 53.4 ml taken from 52 specimens. For *M. rufus* body mass and ECV were averaged from three specimens held in the Australian Museum to give 63.2 ml

TABLE 1. Results from linear regressions of log-transformed brain and body mass data, and allometric equations from nonlinear regressions for four Australian marsupial taxa. Correction for logarithmic transformation bias (SME) and percent errors (PE) are shown for transformed data. 95% confidence intervals for the exponent, and coefficients of determination are shown for allometric equations. Where comparable, the range of percent errors for 29 regressions using craniodental data of Myers (2001) is also provided [R PE M (%)].

Taxon	Regression	SME (%) 95% CI	PE (%) +95% CI	R PE M (%) R ²
All marsupials (1)	log y = 1.5635(log x) + 1.7252 y = 45.78x ^{1.608}	7 1.596	32 1.620	27-95 0.98
Dasyuromorphia (2)	log y = 1.6005(log x) + 1.8033 y = 129.97x ^{1.382}	3.5 1.378	21 1.385	13-46 0.99
Diprotodontia (3)	log y = 1.6722(log x) + 1.5426 y = 33.16x ^{1.680}	6.2 1.667	28 1.693	20-107 0.98
Phalangerida (4)	log y = 1.8379(log x) + 1.4985 y = 57.60x ^{1.544}	3.9 1.501	29 1.607	0.95
Macropodoidea (5)	log y = 1.8726(log x) + 1.187 y = 16.79x ^{1.845}	0.3 1.829	7 1.860	0.99

and 37,670 g respectively. These latter figures did not differ greatly from averages for ECV of 60 ml provided by Moeller (1997) and 46,000 g in body mass by Wroe et al. (2002).

Haight and Nelson (1987) demonstrated that brain mass calculated on the basis of ECV significantly exceeds actual brain mass in all marsupials. On average, brain mass = 0.96 x ECV. Estimated brain masses based on ECV in fossil taxa were corrected accordingly. Determination of percent prediction error (PE%) and correction for logarithmic transformation bias follow the methods of Smith (1984, 1993, respectively). Allometric body mass equations were calculated by Model 1 nonlinear regression for the following taxa: all taxa combined; Dasyuromorphia; Diprotodontia, Phalangerida, and Macropodoidea. Model 1 regressions were chosen because the predictor (cranial volume) was assumed to be fixed for the purpose of this study (Sokal and Rohlf, 1981). Nonlinear regressions were used to avoid potential problems associated with transformation bias (Smith 1984). However, many previous studies present results based on log-transformed data, and to allow comparisons with a broader range of values given in the literature we also performed regressions on log-transformed data; results using both methods are presented for comparison. Body mass estimates were determined for a number of fossil species. Where consensus was clear on the relationships of these taxa to extant clades, we used equations derived from analysis of the closest extant taxa. Thylacoleonids are diprotodontian, but

whether they are more closely related to vombatiforms or phalangeridans remains contentious (Aplin and Archer 1987; Gillespie 1999; Murray et al. 1987). We therefore used correlation of brain and body mass data based on the diprotodontian data set to predict body mass for this species. Previous estimates based on proximal limb-bone data (Wroe et al. 1999) provide a basis for comparison, but to further test our result for *Thylacoleo carnifex* using ECV we used the equation presented Anderson et al. (1985) to reanalyze proximal limb-bone data from South Australian material. Data were also added from a New South Wales specimen and the result was corrected for logarithmic transformation bias.

Systematic nomenclature follows that of Aplin and Archer (1987). Institutional abbreviations: AM, Australian Museum; QM, Queensland Museum; and SAM, South Australian Museum.

Results

Predictive equations derived from brain and body mass data, together with their percent prediction errors and smearing estimates, are given in Table 1. All percent prediction errors are low and compare favorably with the best of 29 regressions calculated with craniodental variables (Myers 2001). Confidence intervals for allometric relationships likewise attest to strong predictive power (Table 2, Fig. 1).

Inputting the average brain mass for *Thylacoleo carnifex* of 111 ml (Table 2) into the diprotodontian equation derived from brain

TABLE 2. Endocranial volume (ECV) and estimated brain (BrM) and body masses (BoM) for nine specimens of *Thylacoleo carnifex*. Body masses predicted from the equation for diprotodontians (3) and corrected for transformation bias by using the smearing estimate given in Table I. Specimens are from widely separated localities in New South Wales (NSW), Queensland (Qld) and South Australia (SA).

Specimen number	ECV (ml)	BrM (g)	BoM (g)
AM F9 (NSW)	110	106	90,248
AM F18666 (NSW)	118	113	100,434
AM F52398-1 (NSW)	124	119	109,510
QM F744* (Qld)	131	126	120,493
SAM P16730 (SA)	104	100	81,870
SAM P16732 (SA)	102	98	79,150
SAM P20805 (SA)	120	115	103,425
SAM P16717 (SA)	130	125	118,899
SAM P13950 (SA)	104	100	81,870
Mean	116	111	97,480

and body mass data gave a predicted mean body mass of 97.5 kg. Using the equation derived from minimum measurements of midshaft proximal limb-bone circumference (see Anderson et al. 1985) gave a mean body mass estimate of 87.3 kg (Table 3). Christiansen's (1999) equations for predicting body mass among carnivorans used minimum femoral and humeral circumferences. Using these gives body mass estimates of 109 and 83 kg respectively. Correction for transformation bias would likely increase these latter two figures, but the data needed to compute a smearing estimate were not available in these instances. Estimated body masses for a selection of fossil species based on predicted brain mass data are provided in Table 4.

Discussion

Low percent prediction errors and tight confidence intervals support the hypothesis that endocranial volumes can be used to estimate body mass in fossil marsupials with reasonable accuracy. Note, however, that there were differences in slope between the allometric regressions and the linear regressions performed on log-transformed data (see Table 1). These differences are probably due to transformation bias in the linear regressions, highlighting the need to correct for this phenomenon where linear regression is applied (Smith 1993).

Thylacoleo carnifex falls outside our initial data range and such results must be treated with some circumspection (Nagy 2001). However, our figure of 98 kg is well within the range of estimates based on proximal limb bone circumference data (87 kg to 130 kg) and is closest to predictions calculated by using the method of Anderson et al. (1985), i.e., 87 kg to 101 kg. We emphasize that specimens from eastern states remain underrepresented in the data set used to calculate the lower estimate of 87 kg (Table 3). Archer and Dawson (1982) concluded that *T. carnifex* from the eastern states were larger than their conspecifics elsewhere. Consequently we suggest that the lesser figure of 87 kg is likely an underestimate for the species as a whole.

Direct comparisons of brain mass with carnivoran taxa further support the argument that most subjectively determined estimates of body mass in *Thylacoleo carnifex* have been too low. Our mean ECV of 116 ml in *T. carnifex* is close to the average of 125 ml for *P. pardus* (Gittleman 1986). Encephalization in marsupials is typically far less pronounced than in placentals (Jerison 1973). Certainly this holds true where extant or recent marsupials are contrasted with their closest ecomorphological equivalents. For example, Haight and Nelson (1987) give average brain and body mass in the native cat, *Dasyurus maculatus*, as 8.85 g and 2.77 kg respectively. Among living felids, the closest in body mass for which we have data is 2.20 kg for *Felis nigripes*. At 20.09 g (Gittleman 1986), brain mass in the felid is 2.49 times larger than that of the marsupial. Likewise, although the Tasmanian wolf (*Thylacinus cynocephalus*) and the gray wolf (*Canis lupus*) are comparable in body mass, at 29.5 kg and 33.1 kg grams respectively, brain mass in *C. lupus* exceeds that of *T. cynocephalus* by a factor of 2.45 (i.e., 53.4 g vs 132 g; see Moeller 1973 and Gittleman 1986).

We conclude that evidence tendered in the present study further buttresses the hypothesis that *Thylacoleo carnifex* was around twice the body mass of *Panthera pardus*, if not larger still (Wroe et al. 1999). This clearly affects interpretations of the animal's biology. Wells et al. (1982) posited that *T. carnifex* may have been semi-arboreal, caching prey in trees to avoid competition from scavenging Tasmanian devils (*Sarcophilus*) and hence filling a

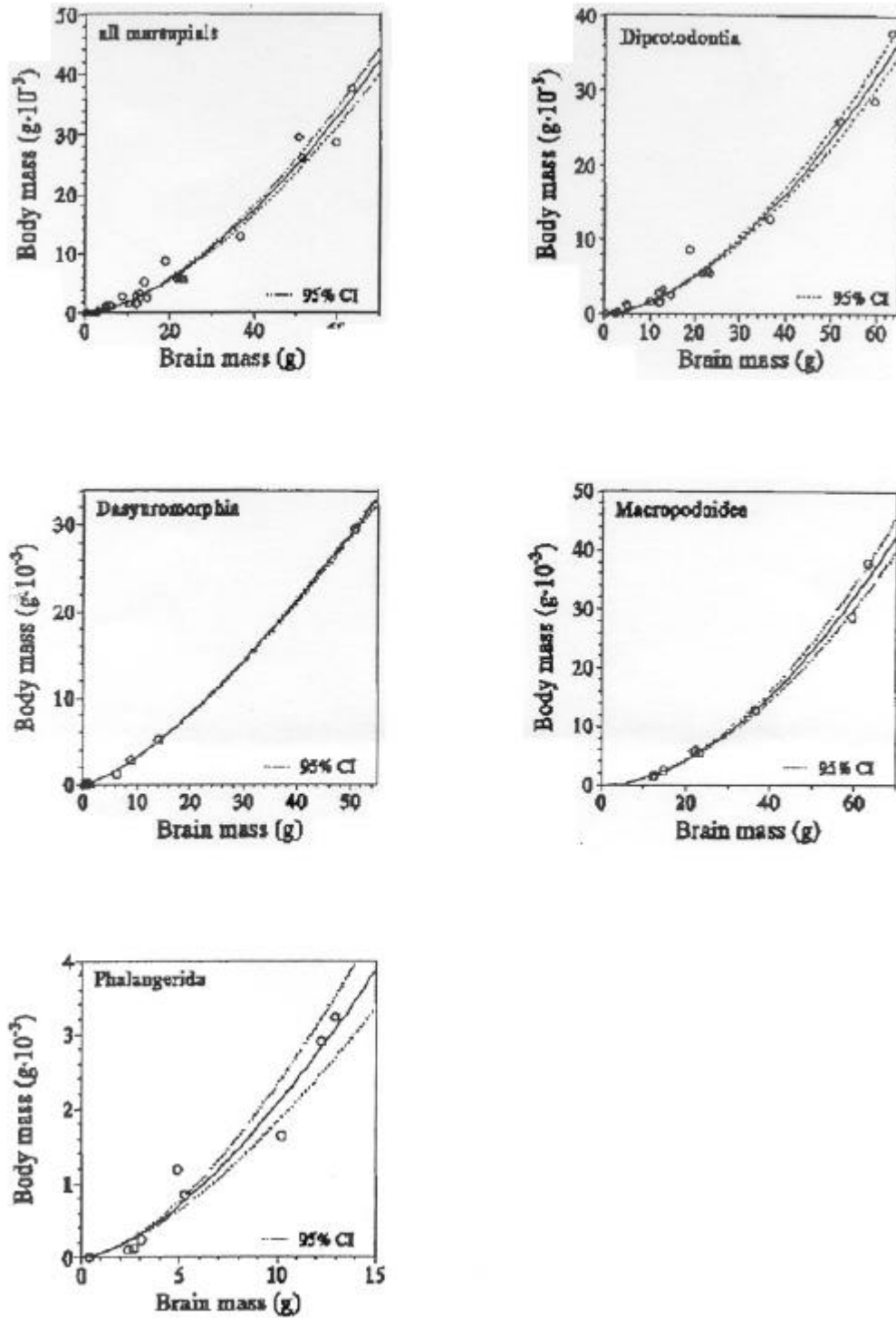


FIGURE 1. Body mass plotted against brain mass for five marsupial taxa. Data largely from Haight and Nelson 1987. Solid lines shows fitted allometric relationships and broken lines give 95% confidence intervals.

TABLE 3. Minimum mid-shaft circumference data for proximal limb bones of *Thylacoleo carnifex*. *f* = minimum mid-shaft circumference of femur. *h* = minimum mid-shaft circumference of humerus. MBoM = Mean body mass calculated with the following formula: $\log_{10} \text{BoM} = -1.11 + 2.73 \log_{10} C_{f+h}$ (Anderson et al. 1985). Correction for logarithmic transformation bias (SmE) (from Wroe et al. 1999 = 13.2).

Specimen number	<i>f</i> (mm)	<i>h</i> (mm)	MBoM (g)
SAM P40008	76.6	75.3	
SAM P12384	71.1	62.2	
SAM P13950		80.5	
SAM P40009	82.9		
SAM F18495	75.8		
SAM P40010		80.2	
SAM P19075		67.4	
SAM P44570		83.5	
SAM P19321	85.4		
SAM P40014	80.5		
AM F52398-1	84	88	
Total	557.3	542.1	
Mean	79.6	77.4	87,300

leopard-like niche. Finch and Freedman (1988) disagreed, arguing that the animal's limb morphology was inconsistent with this scenario. In our view, the evidence for significantly greater size in *T. carnifex* renders the semi-arboreal hypothesis unlikely for two additional reasons. The most obvious of these is that greater body mass constrains arboreal movement. But perhaps more importantly, at an average mass of 87 to 130 kg, *T. carnifex* was much larger than any contemporaneous mammalian competitor, whereas

leopards must contend with lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). Both are significantly heavier than the leopard and their social habits confer additional advantage (Palomares and Caro 1999). Conspecifics aside, the only conceivable threat to *T. carnifex* was the giant monitor lizard, *Megalania prisca*. Body mass in *M. prisca* has been the subject of considerable hyperbole, with figures of 1000 kg or more common in the literature (Flannery 1994; Webb 1998). It is likely that maximum dimensions have been based on extrapolations from material that was misidentified (R. Molnar personal communication 2001), and Wroe (2002) calculated mean body mass for the giant monitor at 97 to 158 kg depending on methodology. Although the largest *M. prisca* may have been able to displace marsupial lions from kills, on average the two taxa were of roughly comparable body mass and *M. prisca* was rare throughout its more limited range (Wroe 2002, 2003).

These results also eat into the proposition that low productivity has constrained the maximum body mass of Australia's mammalian carnivores (Flannery 1994; Burness et al. 2001). Averaging the four means based on nominated methodology presented here and by Wroe et al. (1999) gives a mean body mass of 104 kg. Burness et al. (2001) predicted that, given a landmass area of 7.7 million km², the expected maximal mean body mass for an

TABLE 4. Body mass predictions (BoM) for a selection of fossil marsupial taxa based on estimated brain masses (BrW). Individual regressions and smearing estimates used to calculate BoM are given in Table 1.

Taxon	Eqn	N	ECV (ml)	BrM (g)	BoM (g)
<i>Thylacoleo carnifex</i>	3	9	116	111	97,480
<i>Priscileo roskellyae</i>	3	1	12	11.5	2,701
* <i>Wynyardia bassiana</i>	3	1	18	17	4,654
<i>Barinya wangala</i>	1	1	2.7	2.7	317
<i>Macropus titan</i>	5	1	88	85	63,289
<i>Ekaltadeta ima</i>	5	1	25	24	5,928
<i>Simosthenurus maddoki</i>	5	1	86	82.6	59,848
<i>Sthenurus gilli</i>	5	6	70	67.2	40,759
<i>Simosthenurus occidentalis</i>	5	4	99.25	95.3	78,375
<i>Sthenurus brownei</i>	5	4	107.8	103.4	91,413
<i>Procoptodon rapha</i>	5	1	134	128.6	137,505
<i>Nambaroo gillespieae</i>	5	1	14.7	14.1	2,192
<i>Balbaroo fangaroo</i>	5	1	26.6	25.4	6,592
<i>Macropus thor</i>	5	1	71.6	68.7	42,526
⁺ <i>Thylacosmilus atrox</i>	1	2	45	43.2	26,357

*From Haight and Murray 1981.

⁺ From Quiroga and Dozo 1988.

Australian endothermic carnivore was 86 kg. Accepting a lower mean figure for *T. carnifex* of 73 kg and allowing for lower consumption in marsupials than placentals, Burness et al. (2001) proposed lower productivity as a cause for the unexpectedly low body mass of Australia's largest mammalian carnivore. Although landmass area undoubtedly constrains maximal body mass to some degree, Wroe (2002, 2003) offered reason to doubt the relationship described by Burness et al. (2001). However, accepting this relationship for the sake of argument, our results suggest that *T. carnifex* approached or exceeded the body mass that would be predicted on the basis of landmass area alone. Moreover, the only empirically determined estimate of body mass for Australia's largest mammalian herbivore of 2.7 tons (Wroe et al. 2002) greatly exceeds the 1789 kg expected for a continent of 7.7 million km².

Although our results suggest that ECV provides a good basis for predicting body mass in Australian marsupials, as with other procedures, this method has its pros and cons. Small sample size is the most obvious limitation. Many fossil taxa are represented by few, if any, endocrania. However, this latter restriction may be mitigated in part by the fact that adult or near-adult brain mass is achieved early in the development of most mammals (Grand 1983). We therefore posit that body mass estimates using ECV from juvenile and subadult individuals will provide figures that closely approximate adult body mass.

Clearly, as with predictions founded on craniodental data, estimates based on the relationship between brain and body masses are constrained by phylogeny. Moreover, a trend toward increased encephalization within many mammalian taxa is widely recognized (Jerison 1973, 1983; Pagel and Harvey 1989). Consequently, predictions may tend to underestimate the former in fossil taxa. However, this will be less problematic for conservative vertebrate clades and more recent fossil species. The relationship between brain size and intelligence is uncertain (Wynne and McLean 1999), but it is clear that, among mammals, marsupials and insectivores show relatively

little expansion in brain size (Jerison 1973). Hence, body mass predictions for these taxa derived by using the method described here are less likely to be affected by differences in brain mass between fossil and extant species. This is likely to be still less problematic for nonmammalian vertebrates.

In summary, although application is restricted in some respects, we suggest that predictive equations based on the correlation of brain and body mass may provide a useful test for estimates of body mass in a variety of fossil species. Estimates using this method for a highly specialized marsupial taxon produce results concordant with estimates based on proximal limb-bone circumference data, whereas prediction based on dentition is clearly inappropriate. Consequently, we posit that this method may be especially useful for determining body mass in extinct species whose anatomy departs widely from that of their closest living relatives. Its predictive power will be greatest in lineages that have not shown a marked trend towards increased encephalization; this includes marsupials, at least some placentals, and many nonmammalian clades. Within any taxon, the efficacy of this method is likely to be greatest for more recent fossil species.

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