

ESTIMATING THE BODY MASS OF THE LARGE PALEOGENE MAMMAL *CORYPHODON*

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INTRODUCTION

Coryphodon is an abundant large-bodied Paleogene mammal with a Holarctic distribution. It was among the first mammalian megaherbivores to evolve. Using body estimates based on tooth area, it has been inferred that *Coryphodon* underwent dwarfing during the Eocene (Uhen and Gingerich, 1995), similar to many other mammalian lineages (Gingerich 2003; Secord et al., 2012; D'Ambrosia et al., 2017). However, the original inference of dwarfing in *Coryphodon* was based on a small fraction of its available fossil record, prompting reanalysis herein with a larger dataset. Most *Coryphodon* specimens in museums are fragmentary, consisting of one or more partial limb elements and/or teeth that were opportunistically surface collected (Fig. 1). The first major goal of this research is to test whether various skeletal elements tightly scale with one another, such that missing skeletal data can be predicted, and more of the *Coryphodon* record be incorporated into study of its body mass evolution.

The second major goal of this research is to apply the robust universal scaling relationship between stylopodial diaphyseal circumference and body mass to *Coryphodon* data. This relationship was established much more recently than the 1995 study of tooth area (Campione and Evans, 2012) and has yet to be applied to *Coryphodon*. We aim to compare the stylopodial-derived and tooth-area-derived masses of *Coryphodon* to better characterize its body mass evolution.

METHODS

Limb bone diaphyseal least circumferences and



Figure 1. Typical preservation of *Coryphodon* fossils as they are found in museum collections (YPM 16131). Most specimens in museums were not quarried but were opportunistically surface collected over the past century and a half in various basins across the western United States. Note that despite the fragmentary nature of the collected material, several osteological measures that could scale tightly with body mass are preserved, such as limb bone circumferences and tooth areas.

lower first molar lengths and widths of *Coryphodon* specimens were measured in the collections of the American Museum of Natural History (AMNH), University of Michigan Museum of Paleontology (UM), specimens collected by Ken Rose from the southern Bighorn Basin (KR), and the Yale Peabody Museum (YPM), with digital calipers for smaller specimens, and flexible measuring tape for larger specimens. For this study, 11 specimens that preserve both a humerus and femur, ten specimens that preserve

both a tibia and femur, nine specimens that preserve both a radius and femur, and seven specimens that preserve both a lower first molar and femur were measured. Three linear regressions were created in PAST3 (Hammer et al., 2001) to predict femoral circumference from humeral, radial, and tibial circumference. To assess the strength of the linear relationships between variables, we examined R², p-value, and percent prediction error (i.e., ((observed value – predicted value)/ predicted value) * 100; Van Valkenburgh, 1990). We also compared *Coryphodon* body mass estimates based on lower first molar area (following Uhen and Gingerich, 1995 and Legendre, 1989) using the following equation:

$$\ln(\text{body mass}) = 1.5133 * (\ln(\text{length} * \text{width of lower first molar})) + 3.6515$$

versus stylopodial limb bone diaphyseal circumferences (following Campione and Evans, 2012) using the following equation:

$$\log(\text{body mass}) = 2.754 * (\log(\text{combined stylopodial circumferences})) - 1.097$$

RESULTS

The circumference of the femur is readily predicted by the circumference of the humerus, the radius, and the tibia (Fig. 2, Table 1), with regressions yielding low percent prediction errors and p-values and high R² values. These tight relationships were recovered despite the slight-to-severe diaphyseal crushing common to *Coryphodon* specimens, suggesting that perhaps absent this crushing, these relationships could be even stronger.

Body mass estimates based on tooth area in seven *Coryphodon* specimens of various size ranged from 344–772 kg; body mass estimates based on combined stylopodial least diaphyseal circumferences in these same 7 specimens ranged from 358–1172 kg (Table 2). Tooth area-derived body mass estimates are

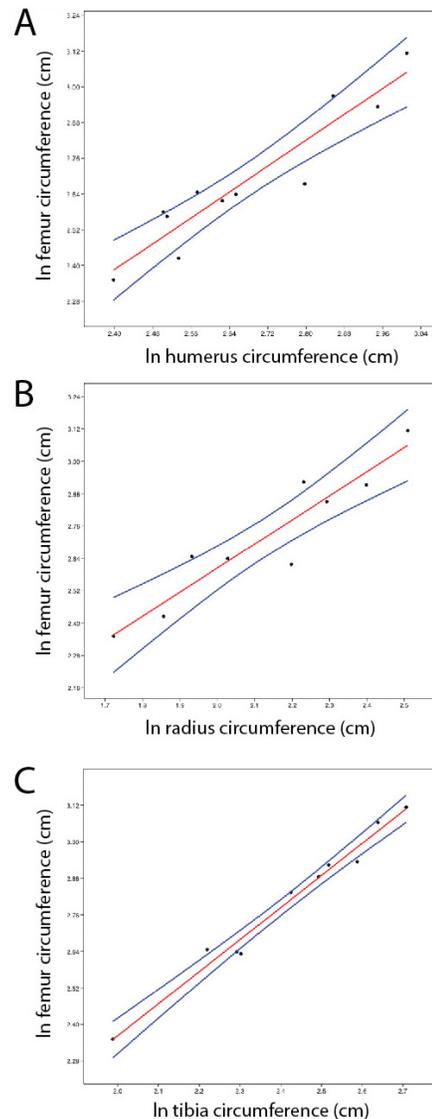


Figure 2. Linear regressions of skeletal dimensions of *Coryphodon* long bones. The circumference of the humerus, radius, and tibia can each predict femoral circumference with a great deal of confidence. See Table 1 for statistical values associated with each regression.

on average only 80% body mass estimates from limb bone circumferences (Table 2), with smaller specimens showing closer correspondence in estimates (~90%) than larger specimens (~70%).

DISCUSSION

This study examined two sets of relationships: first, the tightness of relationships among limb bone circumferences in *Coryphodon*, and second, the difference in body mass estimates using tooth area versus stylopodial limb circumferences. For the first aim, discovery of three tight scaling relationships means that isolated tibial, radial, and humeral limb

Table 1. Summary statistics for relationships among *Coryphodon* long bones.

independent variable (x)	dependent variable (y)	R ²	p	% prediction error
tibia circumference	femur circumference	0.98	5 x 10 ⁻⁸	4
radius circumference	femur circumference	0.88	0.0002	5
humerus circumference	femur circumference	0.88	2 x 10 ⁻⁵	9

Note: The circumference of the humerus, radius, and tibia can each predict femoral circumference with a great deal of confidence.

Table 2. Difference in body mass estimates based on tooth area versus those based on stylopodial limb circumference in *Coryphodon*.

specimen	body mass estimate from lower first molar area (kg)	body mass estimate from stylopodial limb circumferences (kg)	ratio of molar estimate / stylopodial estimate
AMNH 48153	344	358	0.96
AMNH 48152	366	430	0.85
YPM 35316	504	531	0.95
UM 98538	664	864	0.77
YPM 16131	642	932	0.68
YPM 35317	840	1140	0.74
UM 117640	772	1172	0.66
MEAN			0.80

Note: Specimens are listed in order of increasing stylopodial circumference-based mass estimate. Abbreviations: AMNH, American Museum of Natural History; UM, University of Michigan Museum of Paleontology; YPM, Yale Peabody Museum.

shafts can be used to estimate femoral circumference in *Coryphodon*. Humeral and femoral circumference is nearly equal in *Coryphodon*, indicating that body mass was roughly evenly distributed to the forelimbs and hindlimbs. Concerning the second part of the analysis, we found that tooth area substantially underestimates *Coryphodon* body mass, a problem already noted for several Paleogene taxa (Damuth, 1990), and that generally the larger the *Coryphodon* specimen, the worse tooth area is for predicting body mass. Future work will be able to utilize the scaling relationships discovered herein to estimate body mass in *Coryphodon* through time using both more accurate estimators and a much larger proportion of its considerable fossil record.

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