# Estimating body mass from the astragalus in mammals

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Astragalar fossils have been intensively studied as an indicator of the functional morphology and phylogenetic relationships of mammals. However, relatively few studies have investigated the relationship between astragalar size and body mass, usually with a focus on a particular taxonomic group. Here, univariate and multiple regression models are used to analyze the relationship between astragalar size and body mass based on an extensive sample of extant land mammals (11 orders, 48 species, 80 individuals; body mass ranging from 18 g to 3.4 t). The analyses revealed the size of the tibial trochlea to be a better predictor of body mass than the total size of the astragalus. Based on these results, estimates of the body mass of several Paleogene land mammals were calculated and compared to those of previous studies. Thus, for example, the body mass of "*Baluchitherium*", the largest terrestrial mammal known to date, was estimated at about 10–15 t.

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## Introduction

The astragalus (= talus, anklebone) is a moderately compact bone forming part of the mammalian skeleton (Gray 1858). Owing to their robust morphology, astragali are frequently preserved in the fossil record, and more often found undamaged than long bones, vertebrae, or fragile skulls. The morphology of this element is highly diagnostic, easy to identify, and correlates well with the behavior of the animal (e.g., DeGusta and Vrba 2003). As a result, astragalar fossils have been widely used as an indicator of mammalian functional morphology, phylogenetic relationships, and taxonomy (e.g., Martinez and Sudre 1995; Nakatsukasa et al. 1997; Gebo et al. 2000; Plummer et al. 2008; Polly 2008; Dagosto et al. 2010; Parr et al. 2011).

In general, the body mass of an animal strongly correlates with its ecology, physiology, functional anatomy, diet, energetics, and life history (Peters 1983; Calder 1984; Legendre 1986, 1989; LaBarbera 1989; Damuth and MacFadden 1990; McNab 1990; Eisenberg 1990; Mendoza et al. 2004, 2005; Copes and Schwartz 2010), and estimates of the body mass of extinct species consequently form an important part of paleoecological analyses (e.g., Legendre 1986, 1989; Morlo 1999; Burness et al. 2001; Egi 2001; Smith et al. 2010). Several methodologies estimating the body mass of fossil taxa have

been suggested (Dagosto and Terranova 1992; Smith 2002; Mendoza et al. 2006), focusing mostly on either craniodental (Gingerich et al. 1982; Legendre 1986, 1989; Conroy 1987; Damuth 1990; Janis 1990; Van Valkenburgh 1990; Fortelius 1990; Egi et al. 2002, 2004; Mendoza et al. 2006; Figueirido et al. 2011) or long bone measurements (Alexander et al. 1979; Anyonge 1993; Ruff 1990; Scott 1990; Gingerich 1990; Egi 2001; Andersson 2004; De Esteban-Triviqno et al. 2008; Figueirido et al. 2011). The cross-sectional diaphyseal and articular dimensions of long bones in particular seem to be good predictors of body mass for a variety of mammals (Gingerich 1990; Ruff 1990, 2003; Scott 1990; Anyonge 1993; Egi 2001; Andersson 2004), and are likely to perform better than either craniodental dimensions or long bone length measurements in the case of extinct mammals with no close phylogenetic links or phenetic similarity to any living species.

The astragalus has broad articular facets for both the tibia and fibula, and thus, like long bones, appears to be well correlated with body mass. However, only a few studies have investigated this relationship, usually with a focus on specific taxonomic groups, such as prosimian primates, artiodactyls, catarrhine primates, pinnipeds, and hominoid primates (Dagosto and Terranova 1992; Martinez and Sudre 1995; Rafferty et al. 1995; Polly 2008; Parr et al. 2011). Because
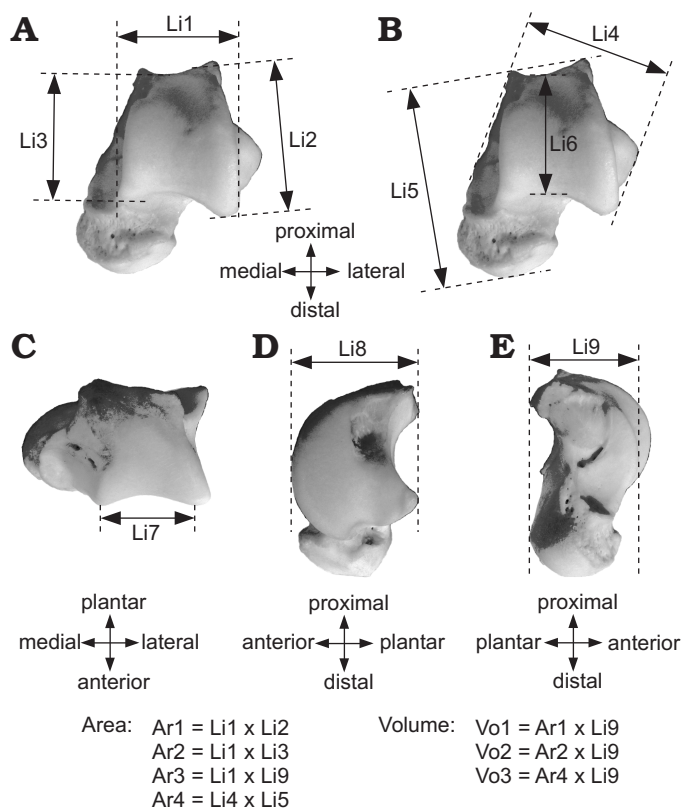
Fig. 1. Linear measurement positions on the astragalus (Li1–9) and their products (area, Ar1–4; volume, Vo1–3). The illustrations are based on a left astragalus of *Macaca fuscata* (Blyth, 1875) (Primates; Cercopithecidae). Dorsal (= anterior) (**A**, **B**), proximal (**C**), lateral (**D**), and medial (**E**) views. Abbreviations: Ar1–3, cross-sectional areas of the tibial trochlea; Ar4, cross-sectional area of the astragalus; Li1, transverse width of the tibial trochlea; Li2, proximodistal length of the lateral trochlear ridge of the tibial trochlea; Li3, proximodistal length of the medial trochlear ridge of the tibial trochlea; Li4, transverse width of the astragalus; Li5, proximodistal length of the astragalus; Li6, proximodistal length of the central part of the tibial trochlea; Li7, transverse width between the medial and lateral trochlear ridges of the tibial trochlea; Li8, dorsoventral thickness of the lateral part of the astragalus; Li9, dorsoventral thickness of the medial part of the astragalus; Vo1–2, volume of the tibial trochlea; Vo3, volume of the astragalus.

of this taxonomic restriction, the results of these studies are difficult to apply to other mammalian groups.

This article examines the allometric relationship between body mass and astragalar size based on an extensive sample of extant terrestrial mammals, with the ultimate aim of providing formulae capable of estimating the body mass of a variety of extinct taxa. As an example, the present results are applied to four groups of Paleogene land mammals, and their body mass estimates compared with those of previous studies.

*Institutional abbreviations*.—AMNH and AM, American Museum of Natural History, New York, USA; FAM, Frick Collection, American Museum of Natural History, New York, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

*Other abbreviations*.—Ar, areas; BM, body mass; CF, correction factor; d.f., degree of freedom; JMP, SAS Institute

software; Li, linear measurements; MPE, mean percentage prediction error; n, sample size; P, probability; PE, prediction error; PI, prediction interval; QMLE, quasi-maximum likelihood estimator; RE, ratio estimator; SE, the smearing estimate; SEE, standard error of estimate; R, correlation co-efficient; Vo, volumes.

# Material and methods

The core data of this study consist of the body mass (in g) and nine linear measurements (in mm) of the astragalus of 80 adult individuals, representing 48 species belonging to 11 orders of extant land mammals, and ranging from 18 g to 3.4 t (see SOM: Supplementary Online Material at http://app.pan. pl/SOM/app59-Tsubamoto_SOM.pdf). Body masses represent the actual weight of each specimen, and were recorded either while the animals were still alive, or just after their death. Owing to the limited availability of specimens for which such data could be obtained, the dataset is somewhat biased towards primates and carnivores (SOM). Nine linear measurements of the astragalus (Li1–9; Fig. 1) were taken to the nearest 0.01 mm using digital calipers. In addition, four areal (mm²) and three volumetric (mm³) variables were calculated based on these measurements (Fig. 1). For the Paleogene taxa, data were derived from tables and direct measurements of figures in the literature (Osborn 1923; Granger and Gregory 1936; Mellett 1977; Martinez and Sudre 1995; Gebo et al. 2000), on the assumption that the fossil astragali used represented adult individuals. Prior to analysis, all data were transformed to a natural logarithm. Analyses were carried out using Excel (Microsoft), JMP (SAS Institute), and KaleidaGraph (Synergy Software).

To estimate body mass (BM), least squares regression was used instead of major axis or reduced major axis regression, as it can provide prediction intervals for each value (Sokal and Rohlf 1995; Simpson et al. 2003; Zar 2010). However, major axis and reduced major axis regression helped to determine the slope (Gingerich et al. 1982; Natori 2002; Warton et al. 2006). Linear measurements (Li1–9), areas (Ar1–4), and volumes (Vo1–3) were analyzed both together and separately using stepwise multiple regression analyses (Mendoza et al. 2006), with the P values to enter and leave set to 5% in JMP. Accurate 95 % prediction intervals (PIs) for each body mass estimate can be calculated following the formula of Simpson et al. (2003: 238). However, in the case of large sample sizes, approximate PIs can be calculated more easily as ± SEE x $t_{(0.05)(2), d.f.}$, where SEE is the standard error of estimate and the degrees of freedom (d.f.) = sample size (n) – 2 (Ruff 2003). In the case of the present analysis, the 95 % PI for 80 specimens (d.f. = 78) was thus calculated as ± 1.991 × SEE.

When regression is performed using log-transformed data, a systematic detransformation bias is introduced (Smith 1993a, b). To correct for this bias, I calculated three correction factors (CFs): the quasi-maximum likelihood estimator (QMLE), the smearing estimate (SE), and the ratio estimator

(RE). The QMLE was calculated following Sprugel (1983), the SE following Duan (1983) and Smith (1993a, b), and the RE following Snowdon (1991) and Smith (1993a, b). The SE value is often similar to the QMLE value, while the RE is an unrelated measure (Smith 1993a). For the purpose of this analysis, I calculated an adjusted CF, consisting of the arithmetic mean of the minimum and maximum values from among the former three CFs. When estimating body mass, the log value determined by the regression analysis was first de-transformed to the actual value (in g), and then multiplied by this adjusted CF.

The degree of correlation (accuracy) between body mass and astragalar size was evaluated using the coefficient of determination adjusted for the number of variables (adjusted $R^2$), the percent standard error of estimate (%SEE), and the mean percentage prediction error (%MPE). %SEE for natural log-transformed data was calculated as $\%SEE = (e^{SEE} - 1) \times 100$ (Smith 1984a; Egi et al. 2002; Ruff 2003), while the percentage of prediction error of the de-transformed value (%PE) was calculated as %PE = (original value – estimated value) / estimated value × 100 (Smith 1981, 1984a, b). %MPE is the arithmetic mean of the absolute values of %PE for each variable calculated for each individual (Smith 1981, 1984a, b; Dagosto and Terranova 1992). Finally, %MPE for the values corrected using the adjusted CF was also calculated (%MPE$_{ad-CF}$).

# Results and discussion

The three stepwise multiple regression analyses retained only a single predictor per analysis: $\log_e(Li1)$ for the linear, $\log_e(Ar3)$ for the areal, and $\log_e(Vo1)$ for the volumetric
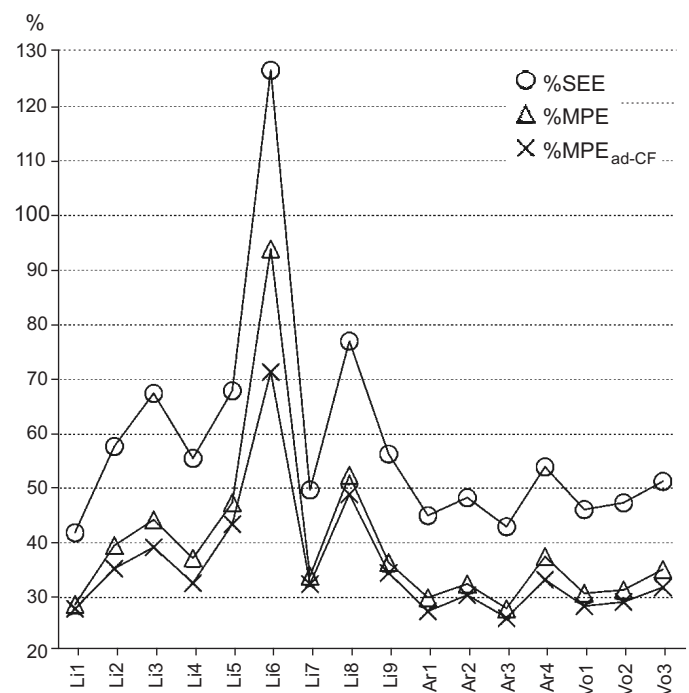


Fig. 2. Comparison of %SEE, %MPE, and %MPE$_{ad-CF}$ arising from the bivariate regression analyses of the 16 astragalar measurements (Li1–9, Ar1–4, and Vo1–3). Abbreviations: ad-CF, adjusted correction factor; MPE, mean percentage prediction error; SEE, standard error of estimate.

measurements, with Li1 and Ar3 being more accurate than Vo1 (Table 1; Fig. 2). When all predictors were included in a single multiple regression analysis, only $\log_e(Li1)$ was retained in the final model. These results were corroborated by individual bivariate regressions carried out for all 16 variables, which showed Li1, Ar3, and Vo1 to be the best predictors, respectively (Table 1; Figs. 2, 3). Additionally,

Table 1. Results of the bivariate regression analyses of the linear, areal, and volumetric measurements. Abbreviations: N, sample size; SEE, standard error of estimate; adjusted $R^2$, coefficient of determination adjusted by the number of variables; adjusted CF, adjusted correction factor (see text for details); %SEE, percent standard error of estimate; %MPE, mean percentage prediction error; %MPE$_{ad-CF}$, %MPE for the values corrected using the adjusted CF.

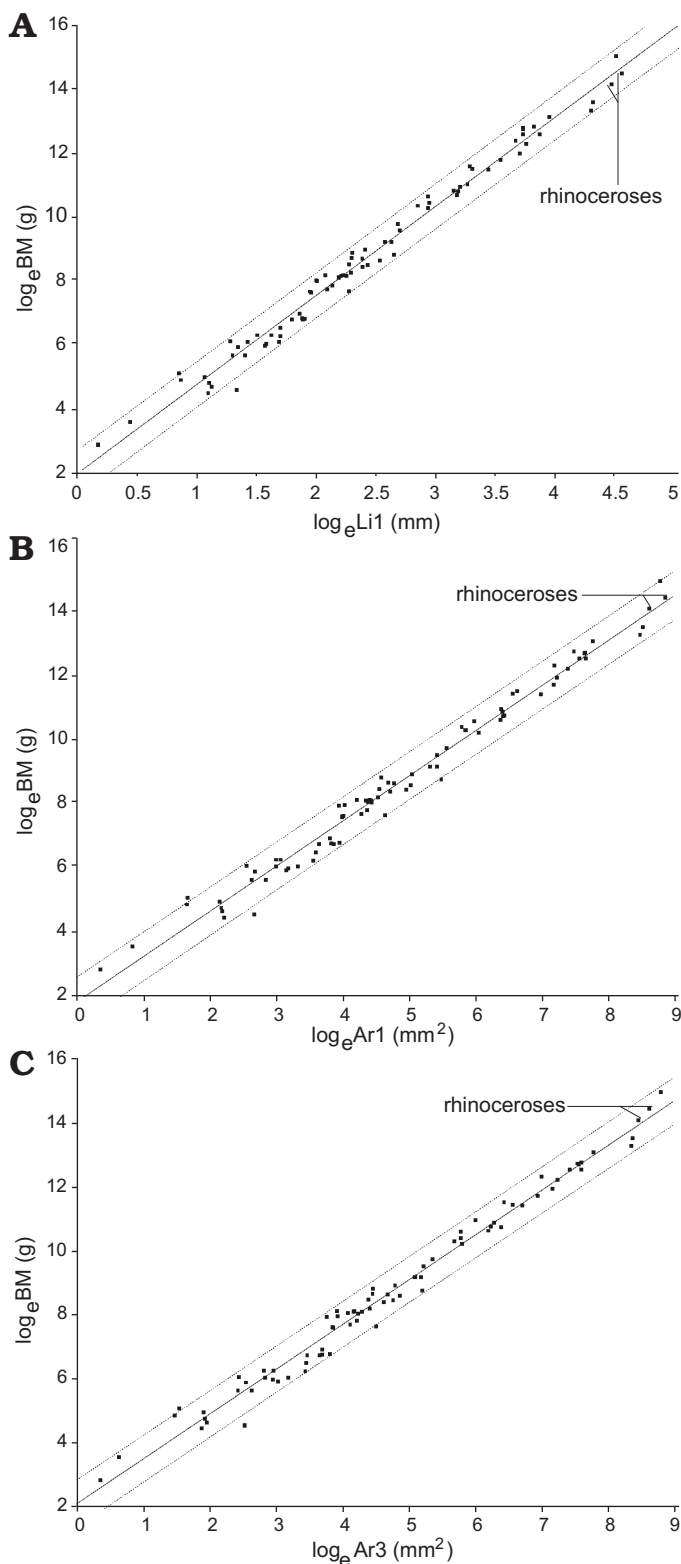| $\log_e$ measurement | N | slope | intercept | SEE | adjusted $R^2$ | adjusted CF | %SEE | %MPE | %MPE$_{ad-CF}$ |
|---|---|---|---|---|---|---|---|---|---|
| $\log_e$ Li1 | 80 | 2.789 | 2.078 | 0.3505 | 0.9846 | 1.030 | 41.98 | 28.83 | 28.00 |
| $\log_e$ Li2 | 80 | 2.838 | 1.639 | 0.4560 | 0.9739 | 1.256 | 57.77 | 39.55 | 35.37 |
| $\log_e$ Li3 | 80 | 2.782 | 1.924 | 0.5151 | 0.9667 | 1.249 | 67.39 | 44.35 | 39.24 |
| $\log_e$ Li4 | 80 | 2.722 | 1.670 | 0.4417 | 0.9756 | 1.194 | 55.53 | 37.17 | 32.66 |
| $\log_e$ Li5 | 80 | 3.125 | -0.463 | 0.5180 | 0.9664 | 1.345 | 67.86 | 47.48 | 43.49 |
| $\log_e$ Li6 | 80 | 2.868 | 2.333 | 0.8180 | 0.9161 | 1.506 | 126.60 | 93.86 | 71.31 |
| $\log_e$ Li7 | 80 | 2.715 | 3.132 | 0.4033 | 0.9796 | 1.045 | 49.68 | 34.01 | 32.57 |
| $\log_e$ Li8 | 80 | 2.802 | 2.562 | 0.5713 | 0.9591 | 1.354 | 77.06 | 52.38 | 48.96 |
| $\log_e$ Li9 | 80 | 2.789 | 2.209 | 0.4469 | 0.9750 | 1.207 | 56.35 | 36.49 | 34.59 |
| $\log_e$ Ar1 | 80 | 1.411 | 1.837 | 0.3716 | 0.9827 | 1.128 | 45.00 | 30.01 | 27.52 |
| $\log_e$ Ar2 | 80 | 1.399 | 1.968 | 0.3949 | 0.9805 | 1.128 | 48.42 | 32.50 | 30.46 |
| $\log_e$ Ar3 | 80 | 1.400 | 2.116 | 0.3580 | 0.9839 | 1.110 | 43.05 | 28.05 | 26.34 |
| $\log_e$ Ar4 | 80 | 1.463 | 0.633 | 0.4318 | 0.9766 | 1.250 | 54.00 | 37.57 | 33.36 |
| $\log_e$ Vo1 | 80 | 0.939 | 1.949 | 0.3793 | 0.9820 | 1.153 | 46.13 | 30.78 | 28.52 |
| $\log_e$ Vo2 | 80 | 0.934 | 2.032 | 0.3880 | 0.9811 | 1.148 | 47.41 | 31.37 | 29.29 |
| $\log_e$ Vo3 | 80 | 0.962 | 1.156 | 0.4142 | 0.9785 | 1.230 | 51.32 | 35.16 | 31.92 |

Fig. 3. Scatter plots of the best-performing body mass (BM [g]) regressions, based on **A**, Li1 (mm); **B**, Ar1 (mm²); **C**, Ar3 (mm²). The black line indicates the line of best fit, while the dashed lines represent the upper and lower 95% prediction limits.

Ar1 was also found to be a powerful predictor, as its adjusted $R^2$, %SEE, and %MPEs were better than those of Vo1 (Table 1; Figs. 2, 3).

All of the slopes of the major axis and reduced major axis analyses were identical to or slightly lower than the values inferred from the isometric hypothesis (Table 1; SOM). The adjusted $R^2$, %SEE, and %MPE of the regressions for Li1, Ar1 and Ar3 (Table 1; Fig. 2) were comparable to those of previous studies focusing on craniodental or limb bone measurements (Damuth 1990; Janis 1990; Scott 1990; Van Valkenburgh 1990; Dagosto and Terranova 1992; Egi et al. 2002; Figueirido et al. 2011). Some of the measurements illustrated in Fig. 1 were difficult to define for some taxa, owing to a high degree of morphological variation. However, Li1, Li2, and Li9 were more easily determined and more stable than other measurements, thus making them and their products (Ar1, Ar3, and Vo1) most suitable for this study in terms of practical measurement procedures.

In conclusion, the width (Li1) and cross-sectional areas of the tibial trochlea (Ar1 and Ar3) are better predictors of body mass than indicators of the overall size of the astragalus (Li4, Li5, Ar4, and Vo3) (Table 1; Fig. 2). Judging from the adjusted $R^2$, %SEE, %MPE, and %MPE$_{ad-CF}$, Li1 is as powerful a predictor as Ar1 and Ar3 (Table 1; Fig. 2), suggesting that the width of the tibial trochlea in terrestrial mammals is well constrained by body mass.

# Application to Paleogene mammals

The body mass of four groups of Paleogene land mammals with no close extant relatives were estimated using Li1 and Ar1 with adjusted CFs (Table 2; Fig. 4). The preferred areal measure, Ar3 (=Li1 × Li9), was not used here, as Li9 is often difficult to obtain from the literature. However, among the individual bivariate regression analyses, Ar1 performed almost as well as Ar3 (Table 1; Fig. 2).

**Largest terrestrial mammal**.—Several previous studies have provided estimates for the body mass of the largest terrestrial mammal known to date, the rhinocerotoid perissodactyl "*Baluchitherium*" (= *Paraceratherium* or "*Indricotherium*"). The present study slightly overestimates the body mass of rhinoceroses using Li1 and slightly underestimates them using Ar1 (Fig. 3, SOM). Therefore, the mean of these two estimates likely provides a better prediction for rhinocerotoids. In the case of "*Baluchitherium*", this (geometric) mean was 12.7 t, with the 95% prediction interval ranging from 10.9–13.7 t (Table 2). It should be noted that, owing to its large size, the body mass of "*Baluchitherium*" could only be estimated by extrapolation, which may be subject to large errors (Draper and Smith 1998; Reynolds 2002; Zar 2010). Nevertheless, the estimate of the present study is consistent with those of Fortelius and Kappelman (1993) (11 t) and Gingerich (1990) (9–15 t), who used several measurements of body length, as well as limb bone diameters and lengths.

Table 2. Body mass predictions for several Paleogene mammals based on Li1 and Ar1 (= Li1 × Li2), corrected using the adjusted CF (Fig. 1; Table 1). Abbreviations: BM, body mass; LPL and UPL, lower and upper 95% prediction limits.

| Species | Li1 (mm) | Li2 (mm) | predicted BM using Li1 | LPL using Li1 | UPL using Li1 | predicted BM using Ar1 | LPL using Ar1 | UPL using Ar1 | Specimen and reference |
|---|---|---|---|---|---|---|---|---|---|
| "*Baluchitherium grangeri*" | 177.50 | 95.00 | 15.4 t | 7.7 t | 31.0 t | 6.5 t | 3.1 t | 13.7 t | AMNH 26387 (Granger and Gregory 1936) |
| "*Baluchitherium grangeri*" | 201.50 | 123.50 | 22.0 t | 10.9 t | 44.2 t | 11.3 t | 5.4 t | 23.7 t | AMNH 26973 (Granger and Gregory 1936) |
| "*Baluchitherium grangeri*" | 190.00 | 99.00 | 18.7 t | 9.3 t | 37.5 t | 7.6 t | 3.6 t | 15.9 t | AMNH 5209 (Granger and Gregory 1936) |
| "*Baluchitherium osborni*" | 185.00 | 132.00 | 17.3 t | 8.6 t | 34.8 t | 11.0 t | 5.2 t | 23 t | Osborn (1923: fig. 8-B1) |
| *Hyaenodon crucians* | 13.04 | 14.02 | 10.6 kg | 5.3 kg | 21.3 kg | 11.0 kg | 5.3 kg | 23.1 kg | FAM 75565 (Mellett 1977) |
| *Hyaenodon horridus* | 17.93 | 20.33 | 25.8 kg | 12.8 kg | 51.8 kg | 29.2 kg | 13.9 kg | 61.1 kg | AM 9809 (Mellett 1977) |
| *Eosimias* sp. | 2.81 | 3.48 | 147 g | 73 g | 295 g | 177 g | 84 g | 370 g | IVPP V11846 (Gebo et al. 2000) |

Although the present estimate for "*Baluchitherium*" was lower than that of Economos (1981) (<20 t, based on "gravitational tolerance"), the latter still lies within its maximum upper prediction limits (Li1: 44.2 t; Ar1: 23.7 t; Table 2). By contrast, the estimate of Alexander (1989) (34 t), which was based on the head-body length as measured from the restoration drawings of "*Baluchitherium*" by Granger and Gregory (1935: figs. 1, 2), lies well beyond the maximum upper prediction limit of Ar1, and hence might be considered unlikely.

**Hyaenodontids**.—Hyaenodontids are archaic carnivorous mammals with a unique molar morphology. Here, the body mass of *Hyaenodon crucians* and *Hyaenodon horridus* was estimated at 11 kg and 26–29 kg, respectively (Table 2). These values are similar to previous estimates based on head-body length (9 kg and 32 kg, respectively; Van Valkenburgh 1987) and limb bone dimensions (10–25 kg and 25–60 kg; Egi 2001), but much lower than reconstructions based on the length of the skull (23 kg and 150 kg; Van Valkenburgh 1987). Because head-body length is considered to be a reliable predictor of body mass (Creighton 1980; Damuth 1990; Van Valkenburgh 1990), these comparisons may indicate that the astragalus performs well in estimating the body mass of hyaenodontids.

**Asian Eocene primate**.—The body mass of fossil primates has been used extensively in their identification, taxonomy, phylogeny, and functional morphology (e.g., Gingerich et al. 1982; Dagosto and Terranova 1992; Fleagle 1998; Gebo et al. 2000). Gebo et al. (2000) described an astragalus (IVPP V11846) of the anthropoid primate *Eosimias* sp. from the Middle Eocene of Central China, and estimated the body mass of the animal to be 90–147 g based on the equations of Dagosto and Terranova (1992). However, the latter were exclusively derived from data on prosimian, rather than anthropoid, primates. Using the present equations, I estimate the body mass of IVPP V11846 to be 147–177 g, with a 95% PI of 84–295 g (Table 2). This estimate is slightly higher, but overall consistent, with than that of Gebo et al. (2000).

**European Paleogene artiodactyls**.—Martinez and Sudre (1995) estimated the body mass of several European Paleogene artiodactyls based on the astragalus and m1, with their astragalar estimate consisting of the product of the tibial

trochlear width (~ Li1) and the astragalar length (~Li5). A recalculation of the body mass of these artiodactyls using Li1 (~"l" in Martinez and Sudre 1995: fig. 2) resulted in somewhat lower estimates, with the exception of *Diplobune minor*, which has a proximodistally much shorter proportion of the astragalus than other artiodactyls (Martinez and Sudre 1995) (Fig. 4). However, the prediction intervals of the present analysis included the estimates of the earlier study, except for *Doliochoerus quercyi* from Pech Desse (Fig. 4),
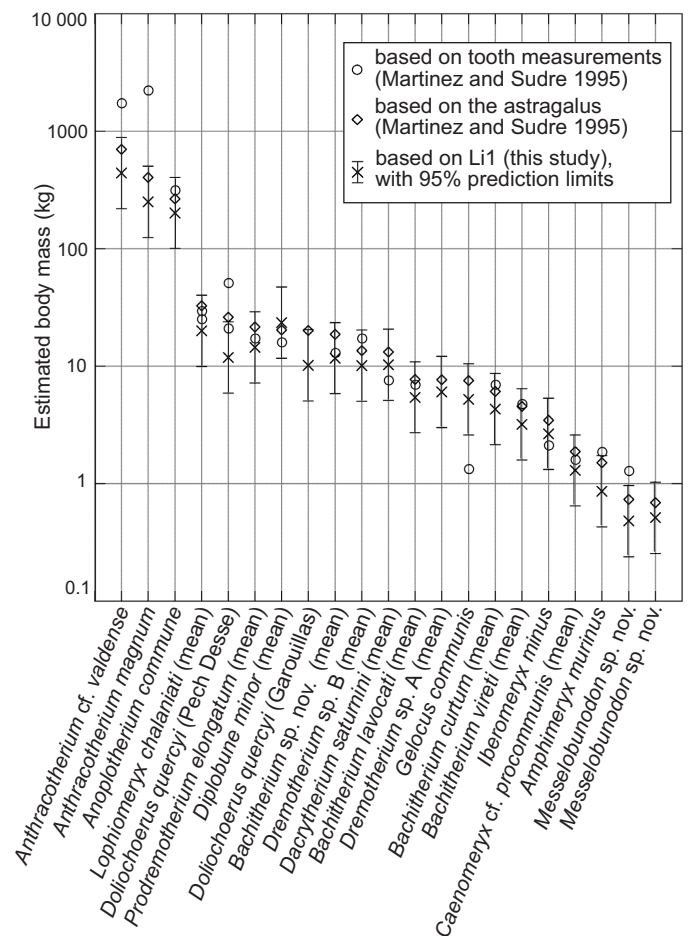


Fig. 4. Comparison of body mass estimates for European Paleogene artiodactyls based on Li1 (this study) with those of Martinez and Sudre (1995). Where shown, mean estimates refer to the results of the latter study.

which has a proximodistally long and mediolaterally narrow astragalus (Martinez and Sudre 1995).

# Concluding remarks

Tibial trochlear size is the best astragalar predictor of body mass, based on data from a wide variety of extant mammals, and yields estimates comparable in their accuracy to those based on long bone data. When applied to a range of Paleogene mammals, the equations derived here yield estimates similar to those of previous studies, thus further supporting the use of tibial trochlear size as a reliable indicator of body mass. The present results thus have the potential to contribute significantly to quantitative taxonomic, ecological, and physiological studies of fossil land mammals, particularly those with no close phylogenetic links and/or similar morphological proportions to any extant species.

# Acknowledgements

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