RESEARCH ARTICLE

The evolution of micro-cursoriality in mammals

Barry G. Lovegrove* and Metobor O. Mowoe*

ABSTRACT

In this study we report on the evolution of micro-cursoriality, a unique case of cursoriality in mammals smaller than 1 kg. We obtained new running speed and limb morphology data for two species of elephant-shrews (*Elephantulus* spp., Macroscelidae) from Namaqualand, South Africa, which we compared with published data for other mammals. *Elephantulus* maximum running speeds were higher than those of most mammals smaller than 1 kg. *Elephantulus* also possess exceptionally high metatarsal:femur ratios (1.07) that are typically associated with fast unguligrade cursors. Cursoriality evolved in the Artiodactyla, Perissodactyla and Carnivora coincident with global cooling and the replacement of forests with open landscapes in the Oligocene and Miocene. The majority of mammal species, though, remained non-cursorial, plantigrade and small (<1 kg). The extraordinary running speed and digitigrady of elephant-shrews was established in the Early Eocene in the earliest macroscelid *Prodiacodon*, but was probably inherited from Paleocene, Holarctic stem macroscelids. Micro-cursoriality in macroscelids evolved from the plesiomorphic plantigrade foot of the possum-like ancestral mammal earlier than in other mammalian crown groups. Micro-cursoriality evolved first in forests, presumably in response to selection for rapid running speeds facilitated by local knowledge, in order to avoid predators. During the Miocene, micro-cursoriality was pre-adaptive to open, arid habitats, and became more derived in the newly evolved *Elephantulus* and *Macroscelides* elephant-shrews with trail running.

KEY WORDS: Elephant-shrews, Macroscelidae, Running speed, Cursors, Mammals

INTRODUCTION

The extraordinary diversity of modern placental mammals evolved from a single lineage that survived the asteroid impact event that drove the non-neornithean dinosaurs to extinction at the Cretaceous–Paleogene (K–Pg) boundary 65.5 million years ago (MYA) (O'Leary et al., 2013). The ancestral placental mammal was a small (6–245 g), insectivorous, tree-climbing (scansorial) forest-dweller that looked somewhat like an opossum with a bushy tail (O'Leary et al., 2013). The reconstruction of this virtual placental mammalian ancestor shows the ancestral condition of a plantigrade foot, in which the heel makes contact with the ground (O'Leary et al., 2013). From this ancestor, and given the freedom to radiate into niches evacuated by the non-neornithean dinosaurs, the first members of the modern placental mammals emerged within hundreds of thousands of years of the extinction event (O'Leary et al., 2013). During the Oligocene and Miocene, a high degree of cursoriality evolved in several modern placental orders (Carnivora, Artiodactyla and

Perissodactyla) in response to the emergence of open landscapes and grasslands following the Eocene Thermal Maximum (Janis, 1993; Janis and Wilhelm, 1993; Yuanqing et al., 2007; Jardine et al., 2012; Lovegrove, 2012b; Lovegrove and Mowoe, 2013).

Loosely defined, cursorial mammals are those that run fast. However, more explicit definitions of cursoriality remain obscure because locomotor performance is influenced by multiple variables, including behaviour, biomechanics, physiology and morphology (Taylor et al., 1970; Garland, 1983a; Garland, 1983b; Garland and Janis, 1993; Stein and Casinos, 1997; Carrano, 1999). In an evaluation of these definition problems, Carrano (Carrano, 1999) argued that '…morphology should remain the fundamental basis for making distinctions between locomotor performance…'. Carrano (Carrano, 1999) showed that a morphological continuum between 'cursorial' and 'graviportal' (weight-bearing) locomotion based upon measures of multiple morphological traits in a principal components analysis provided biologically realistic indices of mammalian locomotor performance. In short, cursorial taxa have longer metatarsals, more slender limb elements, shorter femora, and a muscle insertion point located closer to the hip joint, whereas graviportal mammals have more robust limb elements, shorter metatarsals, and more distal muscle insertion points (Carrano, 1999).

Variations in the dimensions of these traits are borne in limbs commonly associated with cursoriality, namely the derived digitigrade and unguligrade limbs, in which the metatarsals, in particular, are elongated relative to other hindlimb bones, resulting in the heel being raised off the ground (Hildebrand, 1974; Garland and Janis, 1993). The length ratio between the metatarsals (MT) and the femur (F), the MT:F ratio, is often used as a proxy for cursoriality in mammals (Garland and Janis, 1993; Carrano, 1999). Although higher MT:F ratios are often associated with increased hindlimb length, stride length and running speed (Hildebrand, 1974), they are also indicative of more specialized limb adaptations for fast running speeds (Steudel and Beattie, 1993) and cost-effective long-distance locomotion (Garland and Janis, 1993). Nevertheless, there is no direct relationship between MT:F ratio and maximum running speed; two mammals with similar body sizes can have similar maximum running speeds but very different MT:F ratios (Garland and Janis, 1993). MT:F ratios range from <0.1 in some plantigrade rodents to 1.4 in the giraffe (Carrano, 1999).

Several published observations on the morphology and physiology of elephant-shrews or sengis (Macroscelidea) prompted us to test the hypothesis that elephant-shrews are exceptional micro-cursorial animals relative to typical cursorial taxa. Elephant-shrews are placed in the superorder Afrotheria (Springer et al., 1997) as a sister family to Afrosoricida (tenrecs, golden moles and otter shrews) (Stanhope et al., 1998). The etymology of Macroscelidea confirms the early recognition of unusual hind limb morphology because the word is derived from *Macroscelides*, which comprises the Latin prefix '*macro*', meaning large, and the Greek word '*skelis*', meaning hip or thigh. Indeed, elephant-shrews that have been studied morphologically to date display extremely elongated metatarsals and distal muscle reductions (Evans, 1942; Carrano,

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List of symbols and abbreviations

AIC	Akaike's information criterion
CI	confidence interval
F	femur
K–Pg	Cretaceous–Paleogene boundary
M_b	body mass
ML	maximum likelihood
MRS	maximum running speed (km h^{-1})
MT	metatarsal
MT:F	metatarsal:femur ratio
OLS	ordinary least squares
PGLS	phylogenetic generalized least squares
RRS	relative running speed (body lengths s^{-1})
T_b	body temperature (°C)

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1999). Moreover, whereas their closest relatives, tenrecs (Tenrecidae) and golden moles (Chrysochloridae), display a mean body temperature (T_b) of 32.8°C (n=8 species), the mean T_b of elephant-shrews is 37.2°C (n=8 species), indicating a profound apomorphy (derived characteristic) of 4.4°C between sister Afrotherians (Lovegrove, 2012a; Lovegrove, 2012b) (see supplementary material Fig. S1). High body temperatures are correlated with the MT:F ratio in other cursors (Lovegrove, 2012b), and are thought to enhance muscle performance (Clarke and Pörtner, 2010). Elephant-shrews also display an exceptionally high MT:F ratio for their body size, comparable to those of the fastest unguligrade cursors (Lovegrove, 2012b). Last, elephant-shrews (*Elephantulus*) displayed the highest index of cursoriality in a principal components analysis of mammal limb dimensions (Carrano, 1999).

The extraordinary large hind limbs/quarters and speed of elephant-shrews were also recognized in the very first written description of these African small mammals in an annotation that accompanied a drawing now thought to have been that of *Macroscelides proboscideus* (Rookmaker, 1989). It was recorded during the fourth journey into the northwestern Cape of South Africa by Robert Jacob Gordon on 2 August 1779: 'Door mij, oliphantsmuis genaamt, om sign lange snuit dewelke hij op allerley manieren bewegen kan, sijn voorpoten veel korter als de agterpoten. Is egter seer geswind in het lopen….' The English translation reads: 'By me, called *oliphantsmuis* (elephant mouse), for the long snout which can be moved in many ways. Its front legs much shorter than the hind ones. It is very fast….'

The limbs and other unique characteristics of elephant-shrews (exposed shelter sites, mixed herbivory and insectivory, social monogamy, small precocial litters and small body size <1 kg), have been described as 'the micro-cursorial adaptive syndrome' (Rathbun, 1979; Rathbun, 2009).

Two ecologically relevant measures of running speed, maximum running speed (MRS; km h^{-1}) and relative running speed (RRS; body lengths s^{-1}), have been used in the literature (Van Damme and Van Dooren, 1999; Iriarte-Díaz, 2002). On average, large mammals display higher MRSs than small mammals (Garland, 1983a), whereas small mammals display higher RRSs than large mammals (Steudel and Beattie, 1993; Iriarte-Díaz, 2002). The regression of RRS as a function of body mass (M_b) has a negative slope, and displays an inflection at a M_b of ~500 g, i.e. the negative slope of the regression for mammals larger than 500 g is steeper, which the authors suggest confirms that RRS decreases more rapidly with increasing body size (Iriarte-Díaz, 2002). However, although we accept the concept of relative running speed as a notable ecological consideration, the allometric scaling patterns that have been reported and which quantify RRS are questionable because two body-size related variables (log

Table 1. Bone dimensions and maximum running speeds of *Elephantulus rupestris* and *E. edwardii*

	E. rupestris	*E. edwardii*
Body mass (g)	60.10±5.02 (n=10)	49.90±4.22 (n=4)
Femur length (mm)	26.54±0.69 (n=5)	26.13±0.38 (n=5)
Metatarsal length (mm)	26.68±1.15 (n=5)	24.54±1.26 (n=5)
MT:F ratio	1.067±0.041 (n=5)	1.075±0.042 (n=5)
MRS (km h^{-1})	23.6±4.8 (n=10)	19.4±2.2 (n=4)
MRS range (km h^{-1})	14.4–28.8	10.8–21.6

MRS, maximum absolute running speed; MT:F, metatarsal:femur.

body lengths s^{-1} and M_b) were regressed against each other (Iriarte-Díaz, 2002). Consequently, we resorted here to analyses of MRS only, using a phylogenetically informed approach.

In this study we measured the running speeds and limb morphology of two species of rock elephant-shrew, *Elephantulus edwardii* (Smith 1839) and *E. rupestris* (Smith 1831), from Namaqualand, South Africa. We recorded the MT:F ratio and maximal running speed (km h^{-1}) and compared these data with appropriate mammal models for which running speed and MT:F data were available. We tested the hypothesis that elephant-shrews display a micro-cursorial capacity which evolved in forest environments with some surety during the Early Eocene, but possibly as early as the Paleocene.

RESULTS
Metatarsal:femur ratios
The average MT:F ratio of the two species of *Elephantulus* was 1.07 (Table 1). Excluding the giraffe, only five mammals in the combined dataset of 135 mammals had MT:F ratios higher than those of *E. edwardii* and *E. rupestris* (three *Gazella* spp., the dik dik *Madoqua kirkii*, and the springbok *Antidorcas marsupialis*) (Fig. 1). No
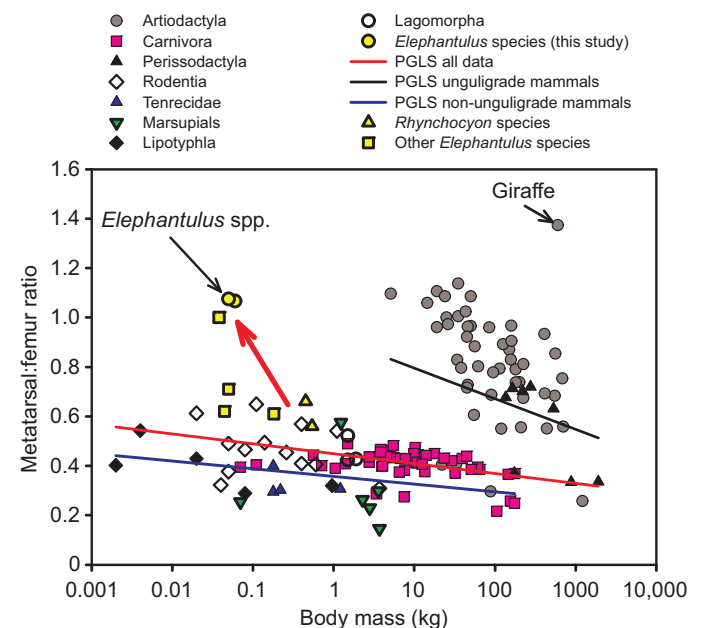

Fig. 1. The metatarsal:femur ratios (MT:F) of 135 mammal species plotted as function of log$_{10}$ body mass. The red line is the PGLS regression line for the combined dataset, whereas the black and the blue lines are the PGLS regression lines for the separate unguligrade and non-unguligrade datasets, respectively. The red arrow indicates the evolutionary trend of decreased body size and increased MT:F ratios that occurred in open-habitat *Elephantulus* species during Miocene aridification.

Table 2. Results of various regression models fitted to data sets of metatarsal:femur ratio as a function of $\log_{10}$ body mass (kg)

Statistics	OLS	PGLS Brownian	PGLS ML
All mammals (n=135)			
Slope	0.073	−0.042	−0.040
P	<0.001	<0.01	<0.01
Intercept	0.479	0.448	0.449
R^2	0.138	0.064	0.057
Pagel's lambda	0	1	0.964
AIC	−16.2	−216.6	−221.6
Unguligrade mammals (n=56)			
Slope	−0.237	−0.124	−0.124
P	<0.001	<0.001	<0.001
Intercept	1.252	0.919	0.919
R^2	0.327	0.193	0.193
Pagel's lambda	0	1	1
AIC	−26.2	−81.1	−81.1
Non-unguligrade mammals (n=79)			
Slope	−0.020	−0.033	−0.031
P	0.029	0.024	<0.01
Intercept	0.410	0.338	0.357
R^2	0.061	0.064	0.089
Pagel's lambda	0	1	0.589
AIC	−157.8	−146.7	−177.5

mammal smaller than 1 kg, apart from *E. edwardii* and *E. rupestris*, showed an MT:F ratio of >0.7 (Fig. 1). A statistical comparison of the MT:F ratios of *E. edwardii* and *E. rupestris* with those of other mammals is quite unnecessary because the data for these two species are so markedly higher than those of other similar-sized mammals (Fig. 1). Nevertheless, we report the results of the ordinary least squares (OLS) and the phylogenetic generalized least squares (PGLS) models fitted to the data because they bear relevance to previous studies that found no significant allometric relationships.

The OLS and PGLS regressions of MT:F ratio as a function of $\log_{10}M_b$ of the complete dataset (n=135) were significant (Table 2). However, whereas the slope of the OLS regression was positive, i.e. indicating an increase in MT:F ratio with body size (not shown in Fig. 1), those of the phylogenetic regressions were negative, consistent with the negative slopes for the separate unguligrade and non-unguligrade regressions (see below). Thus the positive slope of the OLS regression plus the large values of delta AIC (ΔAIC; a measure of each model relative to the best model, where AIC is Akaike's information criterion) of >200 between the OLS and the PGLS regressions render the OLS regression meaningless. The PGLS with maximum likelihood (ML) estimation showed the best fit to the data (Fig. 1, red line) and also showed a significant phylogenetic signal [λ=0.964, significantly different to both λ=0, lower 95% confidence interval (CI)=0.901, and λ=1, upper 95% CI=0.997] close to, but not quite equal to, a Brownian motion evolutionary model (Table 2).

There was a significant phylogenetic signal for both M_b and residual MT:F ratio in the unguligrade and non-unguligrade datasets (Table 3). The best fitting regression models for the 56 species of unguligrade mammal were the two PGLS regressions (ΔAIC=54.9 compared with the OLS regression), which both indicated a Brownian motion model of evolution (λ=1; Table 2, Fig. 1). For the 79 non-unguligrade mammals, the PGLS with ML estimation provided the best fit to the data (Fig. 1) and confirmed a significant phylogenetic signal (λ=0.589, lower 95% CI=0.279, upper 95% CI=0.819; Table 2). The slope of the unguligrade PGLS regression (−0.124) was steeper than that of the non-unguligrade PGLS regression (−0.031; Table 2, Fig. 1).

Maximum running speed model

The mean MRSs of *E. rupestris* and *E. edwardii* were 23.6 and 19.4 km h^{-1}, respectively (Table 1). The fastest individual run recorded was 28.8 km h^{-1} by a female *E. ruprestris*.

Piecewise regression identified a significant inflection in the regression of $\log_{10}$MRS as a function of $\log_{10}M_b$ of 143 species of mammals (excluding *Elephantulus* spp.) ranging in M_b from 9 g (*Perognathus longimembris*) to 6000 kg (*Loxodonta africana*) (Fig. 2). The inflection occurred at a body mass of 20 kg. The largest mammal in the small mammal data set was the Cape hunting dog (*Lycaon pictus*). The 80 species <20 kg comprised 49 rodents, eight lagomorphs, 12 marsupials, 10 carnivores and one artiodactyal (*Madoqua kirkii*). Both $\log_{10}M_b$ and residual $\log_{10}$ MRS showed significant phylogenetic signals as detected by Blomberg et al.'s (Blomberg et al., 2003) K estimate (Table 3).

In the significant OLS regression of the small mammal data there were no outliers, that is, no studentized residuals >3 (Jones and Purvis, 1997) or Cook's distance D-values >0.5. Four of the five species with the highest studentized residuals were lagomorphs, whereas those with the lowest residuals were the groundhog,
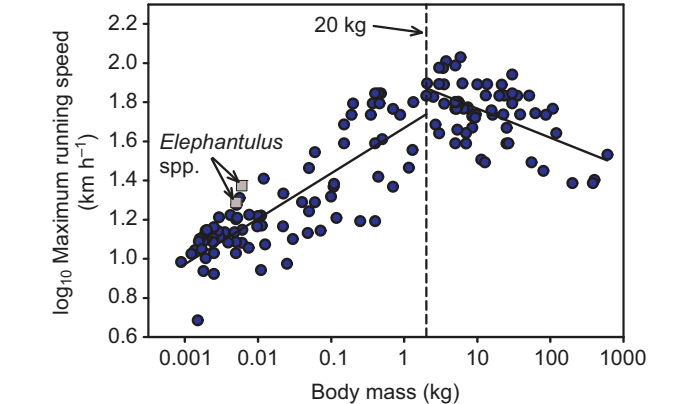

Fig. 2. Maximum running speed (MRS) as a function of body mass of 143 mammal species. The vertical dashed line indicates a significant inflection at 20 kg separating the allometries of the MRS of small and large mammals.

Table 3. Results of randomization tests used to detect phylogenetic signal (K) (Blomberg et al., 2003) in the data for body mass (M_b), maximum running speed (MRS) and metatarsal:femur (MT:F) ratio

Trait	N	K	Variance of K	Mean random K	Z	Randomization test probability (P)
$\log_{10}M_b$ for MRS[a]	80	1.328	0.008	0.041	8.036	<0.001
$\log_{10}$ residual MRS[a]	80	0.360	<0.001	0.001	4.041	<0.001
$\log_{10}M_b$ for MT:F ratio[b]	56	0.482	0.044	0.133	4.055	<0.001
$\log_{10}$ residual MT:F ratio[b]	56	0.772	0.003	0.015	4.589	<0.001
$\log_{10}M_b$ for MT:F ratio[c]	79	0.580	0.142	0.571	5.688	<0.001
$\log_{10}$ residual MT:F ratio[c]	79	0.397	0.002	0.004	2.875	<0.01

[a]80 mammal species <20 kg.
[b]56 unguligrade species.
[c]76 non-unguligrade species.

Marmota monax, the striped skunk, *Mephitis mephitis*, and the western pygmy possum, *Cercatetus concinnus*.

The presence of so many lagomorphs with high MRS residuals suggested that there may be differences in MRS between the four locomotor modes. A non-PGLS MANOVA confirmed a significant effect of locomotor mode on MRS (Table 4). We omitted the solitary unguligrade datum (*M. kirkii*) from the MANOVAs of the small mammal dataset because of sample size. Once corrected for phylogenetic effects, the PGLS MANOVA showed no significant influence of locomotor mode on MRS (Table 4). Thus the model against which the elephant-shrew MRSs were initially compared comprised 80 mammals smaller than 20 kg and included all locomotor modes (plantigrade, digitigrade, lagomorph-like and saltatorial), but excluded the solitary unguligrade datum for *M. kirkii*. Both body mass and residual MT:F ratio in this dataset showed a significant phylogenetic signal (Table 3).

The phylogenetic PGLS Brownian motion regression model of the small mammal data was significant and its AIC value was lower than that of the OLS regression (ΔAIC=18.88; Table 5). Thus a Brownian motion evolutionary model provided a considerably better fit to the data than a model that assumed no phylogenetic structure (star phylogeny). However, the evolutionary model with the lowest AIC, and hence the best fit of the models, was the PGLS model in which the branch length transformations were estimated with Pagel's lambda (λ=0.905, significantly >0, lower 95% CI=0.699, and <1, upper 95% CI=0.988; Table 5), confirming a significant phylogenetic signal. To our knowledge, there is no way of fitting 95% confidence and prediction intervals to a PGLS regression with ML estimated branch length transformations that would allow a comparison of the MRS of elephant-shrews with those of mammals smaller than 20 kg.

We resorted instead to fitting the 95% confidence and prediction intervals to a Brownian motion PGLS, which is equivalent to fitting an OLS to the phylogenetically independent linear contrasts (Blomberg et al., 2012) (Fig. 3). In this graphical representation, the most obvious observations were that (1) the MRS of seven of the

eight lagomorphs lay above the upper 95% confidence interval, and (2) the digitigrade mammals and lagomorphs showed a marginal body size overlap with the plantigrade mammals (non-sciurid rodents, sciurids and marsupials); three squirrels and a primate did overlap. Thus, as stated earlier, a lack of body-size overlap obviates a comparison of the MRSs of elephant-shrews with digitigrade mammals and Carnivora. The data for *E. edwardii* and *E. rupestris* lay above the regression line, but not above the 95% confidence intervals (Fig. 3).

There were 52 species in the plantigrade database that were smaller than 0.5 kg (44 rodents and eight marsupials). Interestingly, there was no significant phylogenetic signal for residual $\log_{10}$MRS using Blomberg et al.'s (Blomberg et al., 2003) K estimate as well as Pagel's ML lambda, which was not significantly different to 0 (P=1), but significantly different to 1 (P<0.001). Not surprisingly, the OLS of the MRS of these mammals was significant, but none of the PGLS models showed significance. When the data for *E. edwardii* and *E. rupestris* were mapped back onto the OLS regression, the datum for *E. rupestris* lay above both the 95% confidence and prediction intervals, indicating a significantly higher MRS than other plantigrade small mammals (Fig. 4). The two larger species with absolute MRSs slightly higher than that of *E. rupestris* were the marsupial *Dasyuroides byrnei* and the squirrel *Sciurus carolinensis*.

DISCUSSION
MT:F ratios
Although it was not a specific objective of this study to evaluate the allometry of MT:F ratios, the results of our analyses are noteworthy. Garland and Janis (Garland and Janis, 1993) analyzed the MT:F ratio allometry in 49 mammal species, 30 ungulates and 19 carnivores, and found no significant phylogenetically corrected relationship between MT:F ratio and $\log_{10}M_b$ in any of their regressions (complete dataset, ungulates, carnivores). In our expanded, more taxonomically diverse dataset (n=135 species), all of our phylogenetically corrected regressions showed significant

Table 4. Results of MANOVA analyses testing the influence of body mass and locomotor mode on the maximum running speeds of mammals smaller than 20 kg

Variable	d.f.	SS	MS	F	P
Non-PGLS MANOVA					
$\log_{10}M_b$	1	4.002	4.002	234.74	<0.001
Locomotor mode	3	0.613	0.204	11.99	<0.001
Residuals	75	1.289	0.017		
PGLS MANOVA					
$\log_{10}M_b$	1	0.144	0.144	28.17	<0.001
Locomotor mode	2	0.007	0.003	0.66	0.521
Residuals	76	0.388	0.005		

Table 5. Results of various regression models fitted to the small mammal dataset of $\log_{10}$MRS (km h^{-1}) as a function of $\log_{10}$ body mass (kg)

Statistics	OLS	PGLS Brownian	PGLS ML
Mammals <20 kg (n=80), including all locomotor modes except unguligrade			
Slope	0.232	0.150	0.167
Intercept	1.436	1.384	1.393
R^2	0.685	0.255	0.328
Pagel's lambda	0	1	0.905
AIC	−68.44	−87.32	−93.46
Plantigrade mammals <500 g (n=52)			
Slope	0.138	0.052	0.138
Intercept	1.305	1.172	1.304
R^2	0.254	0.033	0.254
Pagel's lambda	0	1	0
AIC	−77.10	−65.18	−79.10

allometries of the MT:F ratio and $\log_{10}M_b$. With the exception of the *E. edwardii* and *E. rupestris* data, the data fall neatly into either the unguligrade or non-unguligrade distributions. Although we did not test for interordinal differences within the non-unguligrade mammals, it would seem that carnivores and lagomorphs, for example, both considered to be cursorial, do not display MT:F ratios obviously different from other non-unguligrade mammals, such as primates and non-macropod marsupials, that are considered to be non-cursorial.

These data emphasize that the MT:F ratio of mammals smaller than 1 kg never exceeds 0.7, whereas it does in larger unguligrade mammals. Thus cursoriality never evolved in the majority of mammals, that is, those smaller than 1 kg (see Lovegrove and Mowoe, 2013). However, the rates of evolution of cursoriality as measured by the MT:F ratio accelerated during the Oligocene and Miocene in typical large-bodied herbivorous cursors (Garland and Janis, 1993; Janis and Wilhelm, 1993).

The negative slope of the allometry for unguligrade mammals that we report here can probably be attributed to the continuum of morphological traits along the cursorial–graviportal continuum (Carrano, 1999). In terms of fitness, longer metatarsals, more slender limb elements, shorter femora, and muscle insertion points located closer to the hip joint evolved in the smallest unguligrade mammals

because weight bearing was less important than maximum running speed. Consequently, small ungulates also have a higher maximum running speed than large ungulates (Garland, 1983a; Lovegrove, 2004).

The allometry of the non-unguligrade mammals is hardly worthy of mention because the slope of the best-fit regression is so low despite being significantly different from zero. Moreover, there seems to be no consistent taxonomic trend in MT:F ratios in these data. For example, the species with the top 10 highest ratios (0.490–0.649) include six rodents, one of which is saltatorial (*Dipodomys*), the saltatorial marsupial *Bettongia penicullta*, one lagomorph, *Lepus americanus*, one lipotyphlan, *Sorex cinereus*, and one carnivore, *Felis nigripes*.

We offer one explanation for the difference in the MT:F ratios of similar-sized unguligrade and non-unguligrade mammals: the evolutionary trade-off between locomotor performance and digit functionality (Lovegrove and Mowoe, 2013). The trade-off posits that the fitness benefits of unguligrady in herbivores far outweighed the fitness costs of the loss of digit numbers and functionality, which was not the case in carnivores (Lovegrove and Mowoe, 2013). The divergence in MT:F ratios occurred in the Oligocene and Miocene when there was a dramatic acceleration in the rate of evolution of the MT:F ratio in herbivores, but not in carnivores (Garland and
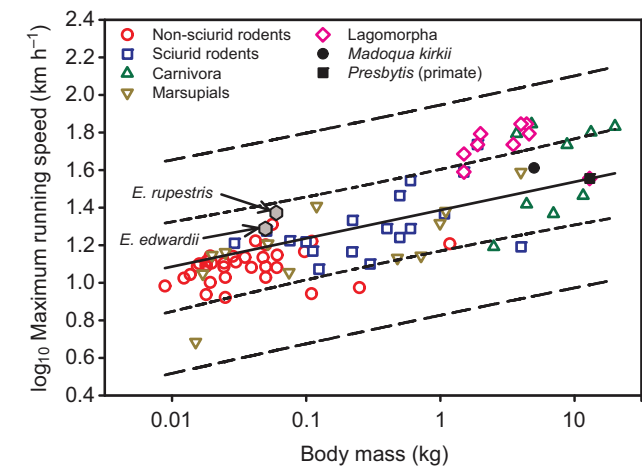

Fig. 3. Maximum running speed as a function of body mass for 80 mammals <20 kg. The regression line (solid line) and the 95% confidence (short dashed lines) and prediction (long dashed lines) intervals were obtained from a Brownian motion PGLS model, equivalent to an OLS regression of the phylogenetically independent linear contrasts (see Table 4 for regression statistics).
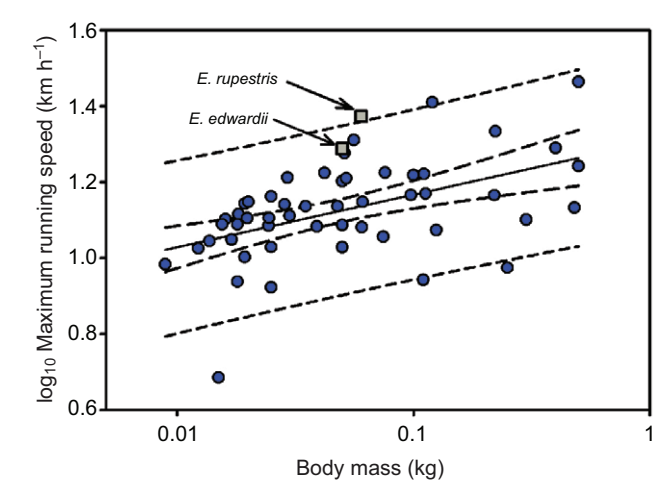

Fig. 4. Maximum running speed as a function of body mass of 52 plantigrade mammals <500 g. The regression line (solid line) and the 95% confidence (long dashed lines) and prediction (short dashed lines) intervals were obtained from an OLS regression model (see Table 4 for regression statistics).

Janis, 1993; Janis and Wilhelm, 1993), despite the fact that both herbivores and carnivores were also increasing in body size (Lovegrove and Mowoe, 2013).

Relative to other similar-sized mammals, elephant-shrews, such as *E. ruprestris*, display remarkable digitigrade-like adaptations of the limbs. The MT:F ratios of the elephant-shrews were more than double the average for 24 other species (0.42) of small mammals <1 kg, but were comparable to some of the highest of all mammalian ratios, namely those of the cursorial Artiodactyla >1 kg. *Elephantulus* elephant-shrews also displayed maximum running speeds faster than those of all mammals smaller than 1 kg, except for a larger squirrel and a marsupial. These fast running speeds can undoubtedly be attributed to the digitigrady of *Elephantulus* as quantified by their very high MT:F ratios for such small mammals. No other mammal smaller than 1 kg has an MT:F ratio that exceeds 0.7. Thus elephant-shrews are not only the smallest mammalian cursors, they can also run faster than the majority of mammals smaller than 1 kg.

Maximum running speeds
In absolute terms, the MRSs of elephant-shrews were comparable with those of larger digitigrade carnivores, but they were not as fast as those of lagomorphs, although these differences could not be quantified or tested statistically. Nevertheless, these observations, as well as the observation of comparatively slow MRSs in plantigrade mammals smaller than 1 kg (Lovegrove, 2004), support several hypotheses on the relationship between the evolution of limb morphology and body size in mammals during the Cenozoic (Lovegrove, 2000; Lovegrove, 2001; Lovegrove, 2004; Lovegrove and Haines, 2004; Lovegrove, 2012b; Lovegrove and Mowoe, 2013). For example, the Bowtie model argued that, following the evolution of larger, faster digitigrade carnivores following the Eocene Thermal Maximum, most plantigrade mammals were constrained from evolving to body sizes larger than ~0.5 kg (Lovegrove, 2000; Lovegrove, 2001; Lovegrove and Mowoe, 2013). Exceptions occurred with the evolution of body armour, arboriality, an aquatic lifestyle, or exceptionally fast running speeds, such as occurs in the Lagomorpha (Garland, 1983a; Lovegrove, 2001). But elephant-shrews are somewhat enigmatic in terms of these mammalian generalizations concerning body size and running speed because they are the only examples in which digitigrady and high running speeds, that is, micro-cursoriality, has evolved in small mammals.

The evolution of micro-cursoriality in elephant-shrews
The evolution of widespread cursoriality, especially unguligrady, was driven by Cenozoic cooling and the appearance of more open landscapes and C_4 grasslands following the Eocene Thermal Maximum (ca. 55 MYA), especially during the Miocene (Janis and Wilhelm, 1993; Edwards et al., 2010; Figueirido et al., 2012; Lovegrove, 2012b; Secord et al., 2012; Lovegrove and Mowoe, 2013). Moreover, during the Late Cenozoic, both unguligrade and digitigrade mammals showed body size increases (Alroy, 1998; Smith and Lyons, 2011; Lovegrove and Mowoe, 2013) and increased hypsodonty in unguligrade mammals (MacFadden, 2000; Jardine et al., 2012). Nevertheless, although unguligrady and digitigrady were synonymous with several crown orders (Carnivora, Artiodactyla, Perissodactyla), the most common condition remained plesiomorphic plantigrady (Lovegrove and Mowoe, 2013). During the dramatic radiation of the mammals within several 100,000 years of the K–Pg boundary (O'Leary et al., 2013), the evolution of digitigrady occurred surprisingly quickly in 'condoylarths' (e.g.

Phenacodontidae), ancestral lagomorphs (e.g. *Gomphos*) and perhaps the Macroscelidea.

Understanding the evolution of micro-cursoriality in elephant-shrews is complicated by uncertainty in the phylogenetic relationships between the Macroscelidea and North American 'condylarths' (Apheliscidae, Louisinidae, Amphilemuridae and Adapisoridae) (Zack et al., 2005b; Zack et al., 2005a; Hooker and Russell, 2012; O'Leary et al., 2013). Based upon cladistic analyses, Hooker and Russell (Hooker and Russell, 2012) argued that the Macroscelidea evolved from Paleocene, Holarctic 'condylarths', many of which, they argue, are basal macroscelideans (Fig. 5) (Zack et al., 2005b; Hooker and Russell, 2012). They suggested placing Apheliscidae within Macroscelidea, together with Louisinidae, Amphilemuridae and Adapisoridae. They dated the basal divergence of the Macroscelidea to the K–Pg boundary ~65 MYA (Fig. 5) (Hooker and Russell, 2012).

In contrast, both O'Leary et al.'s (O'Leary et al., 2013) combined phenomic/genomic phylogeny and Zack et al.'s (Zack et al., 2005b) phylogeny consider *Apheliscus* (Apheliscidae) to be a North American ungulate basal to Euungulata (=crown Perrisodactyla and Artiodactyla). Rare postcranial skeletons show cursorial specializations of the femur, tibiofibula (distal synostosis; Fig. 6), and the crus of the Paleocene apheliscines *Apheliscus* and *Haplomylus* (Zack et al., 2005b). Tibiofibular synostosis, in particular, is associated with enhanced parasagittal, cursorial capacity (Zack et al., 2005b). The *Apheliscus* fossil is dated at 55.8 MYA and the split of Aphelescidae with Hyopsodontidae at 63.3 MYA (O'Leary et al., 2013). Interestingly, *Hyopsodus* (Hyopsodontidae) had a long dachshund-like body with short legs and no morphological evidence of cursorial capacity (Zack et al., 2005b). However, other closely related families, such as Phenacodontidae and Didolodontidae, tended towards digitigrade cursoriality (Thewissen, 1990), so the possibility that the ancestral euungulate 'condylarth' may have been digitigrade cannot be ruled out. The point we wish to emphasize here is that the Early Eocene origin of *Apheliscus*, as well as the questionable phylogenetic placement of the Aphelescidae, does not detract from the development of our argument for an Early Eocene or perhaps even a Paleocene origin of micro-cursoriality in Macroscelidea.

There seems to be agreement that the Leptictidae, which were small, insectivorous saltatorial (jumping) and/or cursorial mammals, are the sister clade to Macroscelidea (Hooker and Russell, 2012; O'Leary et al., 2013) (Fig. 5). The hindlimbs of *Leptictis* and *Leptiptidium* show a degree of fibiotibular fusion (Rose, 1999; Rose, 2006) that is remarkably similar to the condition in modern elephant-shrews, for example *Rhynchocyon* (Zack et al., 2005b) and *Elephantulus* (present study) (Fig. 6). Thus we need to ask whether micro-cursoriality was derived independently in the Macroscelidea and Leptictidae, or whether it was inherited from a common Early Paleocene ancestor.

The date of the oldest leptictid, *Prodiacodon crustuluam*, cannot be separated from that of the Afrotherian origin or the Early Paleocene split between the Leptictidea and the Macroscelidea, ca. 65 MYA (Fig. 5) (O'Leary et al., 2013). Thus if micro-cursoriality was an inherited trait in the macroscelid and leptictid lineages, it would have evolved in the Early Paleocene, very soon after the K–Pg extinction event. However, the postcrania of *Prododiacodon* show fusion of the tibia and fibula at the distal end only, '…well below midshaft…', indicating an ancestral synostostic condition (i.e. non-cursorial hindlimb) compared with Eocene leptictids (Rose, 2006). Thus in the leptictid lineage, micro-cursoriality seems to have evolved for the first time in the Eocene.
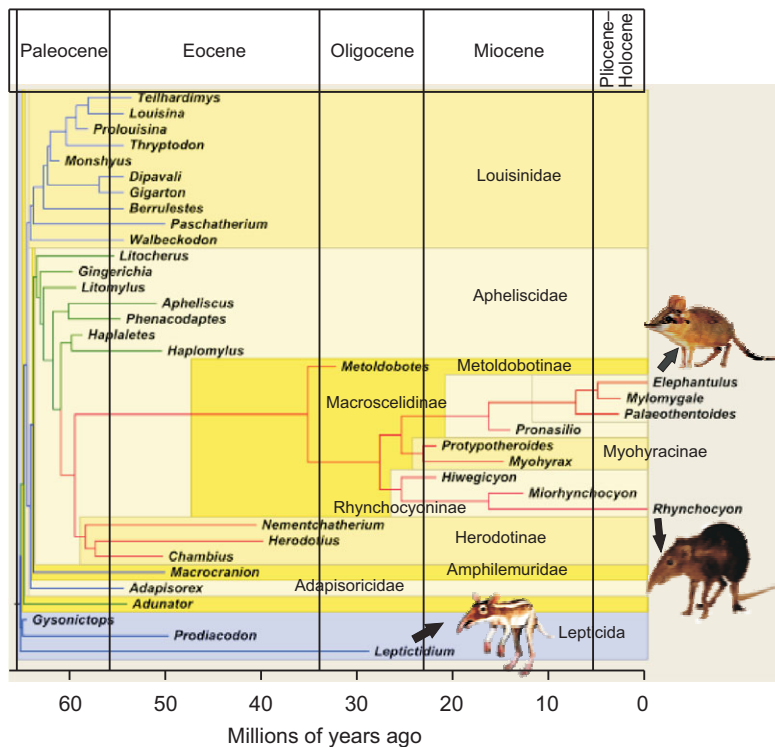
Fig. 5. A working model of the phylogeny of the Macroscelidae and their leptictid ancestors. The topology of the basal macroscelids follows Hooker and Russell (Hooker and Russell, 2012), Zack et al. (Zack et al., 2005b; Zack et al., 2005a), Butler (Butler, 1995) and Tabuce et al. (Tabuce et al., 2001), whereas that of the traditionally recognized macroscelid families follows Tabuce et al. (Tabuce et al., 2007) and Smit et al. (Smit et al., 2011). Note that the Aphelisidae have recently been recognized as North American ungulates basal to Euungulata (=crown Perrisodactyla and Artiodactyla) and not as macroscelids.

The oldest macroscelid is thought to be *Chambius kasserinensis* (late Early Eocene, Tunisia), estimated to have weighed ~13 g (Tabuce et al., 2007). Postcranial remains indicate micro-cursoriality (Tabuce et al., 2007). For example, the pulley-shape and the semicircular crests of the astragalar trochlea, and the calcaneus lengthened proximally and distally to subtarsal joints, are characteristics of fast running speeds and lateral stability (Tabuce et al., 2007). However, without postcranial data for stem macroscelids, the origin of micro-cursoriality in macroscelids cannot at present be reliably dated to earlier than the Early Eocene.

Prior to the flourishing of the Paleocene archaic mammals (Alroy, 1998; Yuanqing et al., 2007), some of which attained very large body sizes (Alroy, 1998; Alroy et al., 2000), the earliest Paleocene mammals were *de facto* small-bodied forest dwellers. Small body

sizes were retained by macroscelids into the Eocene, as discussed for *C. kasserinensis*. Thus the macroscelids show the first appearance of micro-cursoriality in a crown Eutherian order (Tabuce et al., 2007). It is estimated that the two subfamilies of elephant-shrews, Macroscelidinae (*Elephantulus*, *Petrodromus* and *Macroscelides*) and Rhynchocyoninae (*Rhynchocyon*), diverged 26–43 MYA from a forest-adapted ancestor (Douady et al., 2003; Smit et al., 2011)

The Rhynchocyoninae speciated ~8–10 MYA coincident with Miocene forest fragmentation induced by aridification (Smit et al., 2011) (Fig. 5). The four recognized species of *Rhynchocyon* are forest dwellers (Rathbun, 2009). Speciation within Macroscelidinae commenced ~11.5 MYA following dispersal from east Africa to southwestern Africa driven by the aridification of the Sahara and the creation of sub-Saharan arid corridors, and the emergence of savannas and C_4 grasslands (Fig. 5) (Douady et al., 2003; Rathbun, 2009; Smit et al., 2011). The Macroscelidinae display more derived cursorial specializations than *Rhychocyon*, such as a near twofold increase in the MT:F ratio (Table 6, Fig. 1) and smaller body sizes (<300 g). In the new open African landscapes, predatory pressures intensified with the influx of modern Carnivora ~30 MYA when Africa docked with Europe and Asia (Hedges, 2001). Micro-cursoriality was presumably pre-adaptive in newly emerging open landscapes with less canopy cover and shelter provided by trees, which undoubtedly also elevated avian predation. The presence of larger, faster carnivores and avian predators may have placed upper constraints on the body sizes of the macroscelilidids resulting in the evolution of their smaller sizes (Lovegrove, 2001; Lovegrove and Mowoe, 2013). Smaller body sizes require lower total energy demands and smaller home ranges, thus reducing daily movement distance requirements and the risk of predation (Garland, 1983a; Van Damme and Van Dooren, 1999; Blanckenhorn, 2000; Lovegrove, 2001). The establishment of a system of maintained trails along which the Macroscelidinae run at great speed also evolved with body size reduction and more open habitats (Rathbun, 2009).
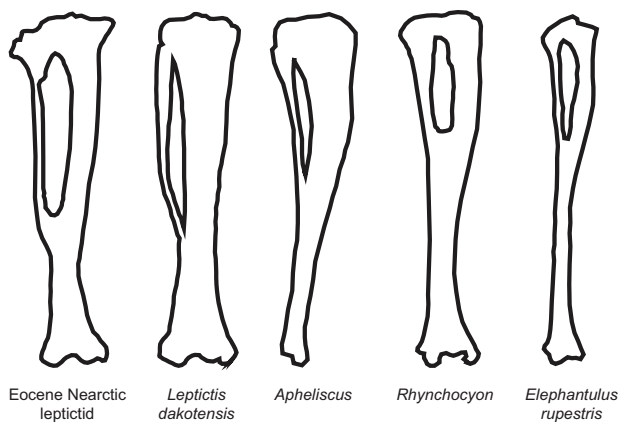

Fig. 6. Digitized outlines of the synostosed tibiofibula of an unnamed Nearctic leptictid (Rose, 1999), *Leptictis dakaotensis* (Rose, 2006), *Apheliscus* (Zack et al., 2005b), an extant *Rhynchocyon* (Rose, 1999) and *Elephantulus rupestris* (present study). The degree of distal synostosis (fusion) is indicative of increased cursorial capacity. Not to scale, but all limbs are scaled to the same length.

Table 6. Metatarsal:femur (MT:F) ratios and habitats of extant macroscelids and their putative condylarth leptictid ancestors

Species	MT:F	Habitat	Reference
Extant macroscelids			
Elephantulus edwardii	1.08	Open, rocky desert	Present study
Elephantulus rupestris	1.07	Open, rocky desert	Present study
Elephantulus proboscideus	1.00	Open, desert	Carrano, 1999; Rathbun, 2009
Elephantulus rozetti	0.71	Open, rocky desert	Evans, 1942; Rathbun, 2009
Elephantulus brachyrhyncus	0.62	Savanna, woodland	Carrano, 1999
Petrodromus tetradactylus	0.61	Closed forest	Evans, 1942; Rathbun, 2009
Rhynchocyon petersi	0.56	Closed forest	Carrano, 1999; Rathbun, 2009
Rhynchocyon cirnei	0.55	Closed forest	Evans, 1942; Rathbun, 2009
Leptictida			
Leptictis dakotensis	0.41	Oligocene forests	Rose, 2006
Leptictidium	0.47	Eocene forests	Rose, 2006
Prodiacodon tauricinerei	0.46	Early Eocene forests	Rose, 1999

Like other cursorial animals (Lovegrove, 2012b), the elevated body temperatures of elephant-shrews relative to their Afrotherian sister clades (Tenrecidae and Chrysochloridae) are thought to be linked with cursoriality and the proposed temperature dependence of muscle performance (Clarke and Pörtner, 2010). Selection for T_b tending towards supraendothermy ($T_b > 37.9°C$) (*sensu* Lovegrove, 2012a) presumably continued until the fitness benefits of enhanced locomotor capacity were balanced by the costs of the increased metabolic demands associated with micro-cursoriality. However, in small Macroscelilinae, that is, those with the highest mass-specific metabolic demands, this trade-off was optimized through the use of daily torpor (Lovegrove et al., 1999; Lovegrove et al., 2001a; Lovegrove et al., 2001b; Mzilikazi et al., 2002; Mzilikazi and Lovegrove, 2004), which profoundly decreases daily energy demands. Daily torpor is a plesiomorphic characteristic in mammals (Lovegrove, 2012a) and may have been retained throughout the Cenozoic in elephant-shrews to offset the costs of micro-cursoriality.

In conclusion, elephant-shrews are unique mammals in terms of their dramatic morphological specializations for fast running speeds relative to similar-sized mammals, and also because they are the only cursorial animals capable of offsetting high locomotor costs through daily heterothermy. Uniquely too, both of these characteristics are plesiomorphic, indicating a long history of micro-cursoriality within the Macroscelidea. We propose that micro-cursoriality evolved in small, ground-dwelling forest macroscelids perhaps as early as the Paleocene, but long before the proliferation of cursoriality in larger mammals during the Miocene.

MATERIALS AND METHODS
Animals were trapped on the farm NoHeep (30°02′S, 17°59′E, altitude; 600–1000 m), 22 km northeast of Kamieskroon, Namaqualand, South Africa, using Elliot traps baited with a mixture of peanut butter and rolled oats during July 2011. These two species of *Elephantulus* (*E. edwardii* and *E. rupestris*) are synoptic in this arid, rugged and highly heterogeneous environment in the Kamiesberg Mountains (Boyles et al., 2012). The two species were identified on the basis of morphological characters that had been verified with genetic analyses at the same study site (Boyles et al., 2012). Two of the authors of this latter study, Smit and McKechnie, assisted us in the field with species identifications. After measuring body weights and running speeds on the same morning of capture and on the following morning, the animals were released after 48 h in the evening at their exact place of capture. The elephant shrews were housed at room temperature in a farm building during captivity in rodent cages provided with paper toweling and a refuge tube. They were provided with water and tinned dog food.

Maximum running speeds were obtained by timing animals as they ran down a 30 m tunnel runway erected on a flat section of compacted fine gravel. The tunnel (1.2 m wide, 1.4 m high) was formed by U-shaped iron rods (10 mm diameter mild steel) placed every 3 m and covered with 30% green shade cloth. Along the length of the last 20 m of the tunnel, we placed three pairs of colour CCD cameras 3 m apart, each pair facing each other, linked to an eight-channel JPEG2000 digital video recorder. We placed a pile of rocks at the end of the tunnel and released the animals ~20 m from the rocks at the opposite end of the tunnel. Typically, the animals froze on release, but once they had orientated themselves and had visually located the rock pile, they ran down the tunnel towards the rock cover. Some animals were induced to start running with hand-clapping. Each animal was tested during two running sessions on two consecutive mornings, and on each occasion the individual completed three runs. Running speeds were calculated from playbacks of video recordings. The success of the runs was varied. In some cases the animals ran well, but stopped running in the middle of the tunnel. In other cases the animals 'bounced' off the side of the shade cloth tunnel or tried to climb the sides of the tunnel. For each individual, the 'best' run, or the MRS, was taken as the fastest, uninterrupted run down the full length of the tunnel.

We term our data 'maximum running speed' only in the sense that these were the fastest speeds that we measured using our method. Our estimates do not preclude the very real possibility that higher maximum speeds may be measured in elephant-shrews under more natural, free-ranging conditions. We suspect that the local knowledge exploited by elephant-shrews in the employment of their trail systems that they create within their territories (Rathbun, 2009) probably allows them to attain faster MRSs than those that we measured.

Maximum running speed
Our running speed and body mass data were compared with those of other mammals obtained from the literature (Garland, 1983a; Hayssen and Lacy, 1985; Robinson and Redford, 1986; Steudel and Beattie, 1993; Iriarte-Díaz, 2002; Lovegrove, 2003; Rojas et al., 2010) (supplementary material Table S1). There has been much discussion about the questionable methods used to measure running speed and hence the quality of the running speed data that have been used in past analyses (see Garland and Janis, 1993). However, Garland and Janis (Garland and Janis, 1993) make the point that it is unlikely that the data are biased in any systemic way and that, given the 'noise' in the data, it is '…perhaps surprising that we are able to show *any* significant correlations…' of MRS with morphological variables. The only species which we discarded from the dataset was that of the saltatorial Merriam's kangaroo rat, *Dipodomys merriami*. We have cause to question the unusually high value of the datum, although not necessarily the potentially high MRSs of kangaroo rats per se. First, the MRSs of this kangaroo rat were measured when they were released from traps, using a stopwatch (Kenagy, 1973). Thus the estimate is not comparable with MRS obtained more precisely when animals were timed as they ran over a carefully measured, uniform distance. Second, the MRS of *D. merriami* (31.2 km h^{-1}) was double that of the average MRS (16.0 km h^{-1}) for three other species of *Dipodomys* in the data set.

It became obvious during the preliminary data analysis that elephant-shrews display the most highly derived, digitigrade cursorial limbs of all mammals smaller than 1 kg. Thus the mammalian running speed model with

which to compare elephant-shrews was not intuitively obvious. We argue here that there is only one hypothesis that is reasonably testable, which is simply that the MRS of elephant-shrews exceeds those of mammals of equivalent body size irrespective of limb morphology. The MRSs of *Elephantulus* (40–60 g) cannot be compared with those of digitigrade mammals, such as carnivores and lagomorphs (rabbits and hares), which are mostly larger than 1 kg, because their smaller body sizes would require extrapolation of the digitigrade regression models way beyond the lower bounds of the regression data. Indeed, the same argument applies to a comparison with unguligrade mammals, although, as we show in the present study, unguligrade mammals do not show the same scaling pattern of MRS with mass compared with other locomotor modes (Iriarte-Díaz, 2002; Lovegrove, 2004). To select the best model with which to test the hypothesis we employed step-wise analyses of the allometric relationship of M_b and MRS in a phylogenetic context.

A phylogeny of all of the species used in the comparisons was compiled using Mesquite version 2.74 (Maddison and Maddison, 2009) from a variety of sources (DeWalt et al., 1993; Kruckenhauser et al., 1999; Oshida and Masuda, 2000; DeBry and Sagel, 2001; Herron et al., 2004; Steppan et al., 2004; Bininda-Emonds et al., 2007; Bradley et al., 2007; Meredith et al., 2008; Montgelard et al., 2008; Lovegrove, 2012a) (see supplementary material Appendix S1).

All statistical analyses were conducted using R version 3.0.1 (R Development Core Team, 2012). Because strong inflections have been observed in the scaling of M_b with both MRS (Garland, 1983a) and RRS (Iriarte-Díaz, 2002), we used piecewise regression (Crawley, 2007) to establish whether an inflection existed in the relationship between $\log_{10}$MRS and $\log_{10}M_b$. Data for mammals smaller than and equal to the inflection M_b, termed hereafter the small mammal dataset, were used for further analyses because this body size range embraced the elephant-shrew body sizes. Outliers in the regression analysis of the conventional species data of the small mammal data were identified using Cook's distance (Cook, 1977) calculated from OLS regressions. Evidence of phylogenetic signal was estimated using Pagel's lambda (λ) calculated with the R package 'caper' (Nunn, 2011), and with Blomberg et al.'s (Blomberg et al., 2003) K statistic using the R packages 'picante' (Kembel et al., 2010) and 'ape' (Paradis et al., 2004). OLS and PGLS models were fitted to $\log_{10}$MRS as a function of $\log_{10}M_b$ using the R package 'caper' (Nunn, 2011).

To determine whether MRS is influenced by locomotor mode in the small mammal dataset, we used a multivariate phylogenetic generalized linear model (PGLS) in which the dependent and independent data were first phylogenetically transformed following the method of Garland and Ives (Garland and Ives, 2000) as implemented by Outomuro et al. (Outomuro et al., 2013). We created a factor variable ('foot') which coded the data as either plantigrade, lagomorph-like, saltatorial or digitigrade, and then used a standard MANCOVA.

For the small mammal dataset, two PGLS regressions were calculated: a pure Brownian motion PGLS with branch length transformation set to λ=1, and a PGLS with Pagel's ML estimation of branch lengths. The best fit model was determined as the model with the lowest AIC.

To compare the MRS of elephant-shrews with those of similar-sized mammals, we also computed similar PGLS models for the data for mammals smaller than 500 g (n=52), termed hereafter the plantigrade dataset. This upper body size limit approximates the 95th percentile of the plantigrade body mass frequency distribution and the intersection between the plantigrade and digitigrade distributions (Lovegrove, 2000; Lovegrove, 2001).

Metatarsal:femur ratios

MT:F ratios were measured from animals obtained from the same site that were euthanized for a genetic study (Boyles et al., 2012). The MT:F data for *E. edwardii* and *E. rupestris* were compared with those for 135 species of mammal obtained from the literature (Garland and Janis, 1993; Steudel and Beattie, 1993; Carrano, 1999) (supplementary material Table S2). The datum for the giraffe (MT:F ratio=1.4) was excluded because it was a very large outlier that had a large leverage influence on the unguligrade regressions (see Fig. 1). As described earlier for MRS, a phylogeny of the species used in the MT:F ratio analyses was constructed using Mesquite (supplementary material Appendix S2).

Initial plots of the relationship between MT:F ratio and $\log_{10}M_b$ revealed obviously dichotomous allometric relationships: one unique to unguligrade mammals (Artiodactyla and Perrisodactyla), and another to non-unguligrade mammals, which in this dataset included Carnivora, Rodentia, Lagomorpha, Lipotyphla, marsupials and a monotreme. OLS and PGLS regressions were fitted to the complete dataset, and to the unguligrade and non-unguligrade data separately, as described above for the MRS analyses.

Tibiofibula outlines

The outlines of the synostosed tibiofibula of an unnamed Nearctic leptictid (Rose, 1999), *Leptictis dakaotensis* (Rose, 2006), *Apheliscus* (Zack et al., 2005b) and an extant *Rhynchocyon* (Rose, 1999) were digitized from published graphics. The outlines for *E. rupestris* were digitized from a photograph taken during the measurement of the MT:F ratios.

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1

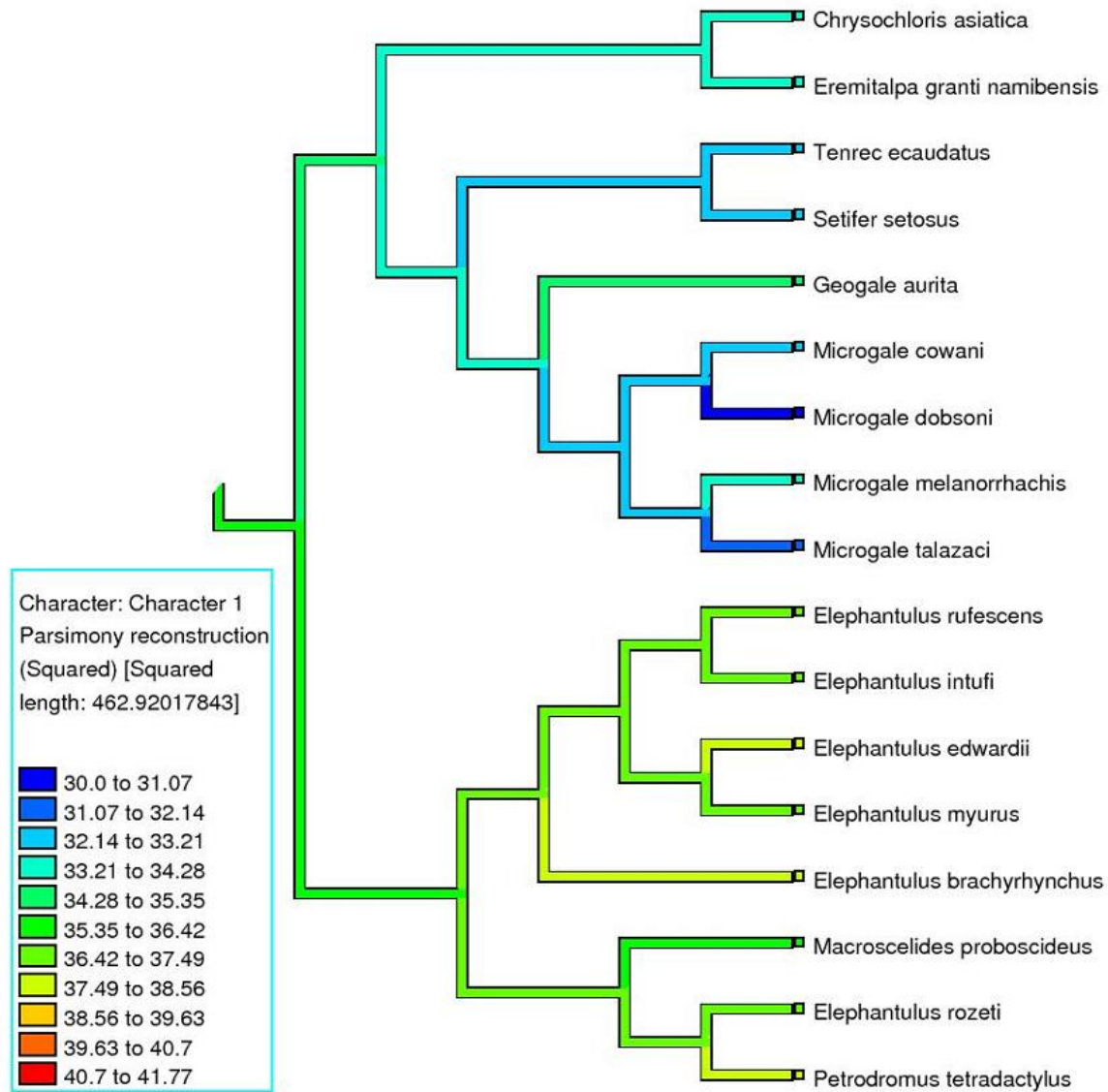2 **Supplementary information**

3 **The evolution of micro-cursoriality in mammals**

4

5 **Barry, G. Lovegrove and Metobor, O. Mowoe**

6

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9

10

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12 **Body temperature reconstruction**

16

Appendix S1. Phylogeny for maximum running speed (n = 80)

```
(((((((((Micropipodops_megacephalus:2.0,(Rattus_rattus:1.0,
Mus_musculus:1.0):1.0):7.0,(Lyomis_pictus:8.0,(Heteromys_da
smarestianus:7.0,((Chaetodipus_fallax:1.0,Chaetodipus_ordii
:1.0):5.0,((Perognathus_parvus:1.0,Perognathus_longimembris
:1.0):4.0,(((Dipodomys_microps:1.0,Dipodomys_ordii:1.0):1.0
,Dipodomys_deserti:2.0):2.0,(Zymomys_argurus:3.0,(Napeozapu
s_insignis:2.0,(Zapus_trinotatus:1.0,Zapus_hudsonicus:1.0):
1.0):1.0):1.0):1.0):1.0):1.0):1.0):1.0):1.0,(((Neotoma_lepi
da:3.0,(Mesocricetis_brandti:2.0,(Microtus_pennsylvanicus:1
.0,Pitymys_pinetorum:1.0):1.0):1.0):3.0,((Peromyscus_truei:
4.0,(((Peromuscus_maniculatus:1.0,Peromyscus_eremicus:1.0):
1.0,Permomyscus_leucopus:2.0):1.0,Peromyscus_crinitus:3.0):
1.0):1.0,Onychomys_torridus:5.0):1.0):1.0,(Leggadina_forres
ti:5.0,(Uromys_caudimaculatus:4.0,((Notomys_cervinus:1.0,No
tomys_alexis:1.0):2.0,(Pseudomys_hermannbergensis:2.0,(Pseu
domys_nanus:1.0,Pseudomys_australis:1.0):1.0):1.0):1.0):1.0
):2.0):3.0):1.0,(((((((((Spermophilus_tereticaudus:1.0,Sper
mophilus_tridecemlineatus:1.0):1.0,(Spermophilus_beldingi:1
.0,Spermophilus_undulatus:1.0):1.0):1.0,Spermophilus_citell
us:3.0):1.0,Marmota_monax:4.0):1.0,Spermophilus_saturatus:5
.0):1.0,Spermophilopis_leptodactylus:6.0):1.0,Ammospermophi
lus_leucurus:7.0):1.0,(Tamias_minimus:2.0,(Tamias_amoenus:1
.0,Tamias_striatus:1.0):1.0):6.0):1.0,(Tamiasciurus_hudsoni
cus:3.0,(Sciurus_vulgaris:2.0,(Sciurus_carolinensis:1.0,Sci
urus_niger:1.0):1.0):1.0):6.0):2.0):1.0,((Sylvilalagus_audu
bonii:1.0,Oryctolagus_cuniculus:1.0):4.0,(Lepus_americanus:
4.0,((Lepus_californicus:1.0,Lepus_alleni:1.0):2.0,(Lepus_t
ownsendii:2.0,(Lepus_europeus:1.0,Lepus_arcticus:1.0):1.0):
1.0):1.0):1.0):7.0):1.0,Presbytis:13.0):1.0,(((Urocyon_cine
reoargenteus:1.0,Vulpes_fulva:1.0):3.0,(Lycaon_pictus:3.0,(
Canis_mesomelas:2.0,(Canis_latrans:1.0,Canis_aureus:1.0):1.
0):1.0):1.0):1.0,((Mephitis_mephitis:1.0,Meles_meles:1.0):1
.0,(Nasua_narica:1.0,Procyon_lotor:1.0):1.0):3.0):9.0):1.0,
(Elephantulus_rupestris:1.0,Elephantulus_edwardii:1.0):14.0
):1.0,(Monodelphis_brevicauda:7.0,((Isoodon_obesulus:5.0,((
Dasyuroides_byrnei:3.0,((Sminthopsis_macroura:1.0,Sminthops
is_crassicaudata:1.0):1.0,(Antechinus_flavipes:1.0,Antechin
us_laniger:1.0):1.0):1.0):1.0,Myrmecobius_fasciatus:4.0):1.
0):1.0,(Cercatetus_concinnus:3.0,((Potorus_tridactylus:1.0,
Bettongia_penicilata:1.0):1.0,Macropus_eugenii:2.0):1.0):3.
0):1.0):9.0):5.0;
```

Appendix S2. Phylogeny for maximum MT:F ratio (n = 135)

```
(((((((((((((((((((Antilope_cervicapra:8.0,((Ourebia_ourebi:6
.0,((Gazella_thompsoni:4.0,((Antidorcas_marsupialis:2.0,(Ga
zella_dorcas:1.0,Gazella_subgutturosa:1.0):1.0):1.0,Gazella
_grantii:3.0):1.0):1.0,Saiga_tartarica:5.0):1.0):1.0,Madoqu
a_kirkii:7.0):1.0):1.0,(((Hippotragus_equinus:1.0,Hippotrag
us_niger:1.0):4.0,((((Damaliscus_dorcas:1.0,Damaliscus_luna
tus:1.0):1.0,Beatragus_hunteri:2.0):1.0,Alcephalus_buselaph
us:3.0):1.0,(Connoachaetes_gnou:1.0,Connoachaetes_taurinus:
1.0):3.0):1.0):1.0,(((Ovibos_moshatus:2.0,(Ovis_ammon:1.0,O
vis_canadensis:1.0):1.0):1.0,(Capra_causasica:1.0,Capra_aeg
aerus:1.0):2.0):1.0,(Oreamnos_americanus:2.0,(Rupricapra_py
renaica:1.0,Rupricapra_rupricapra:1.0):1.0):2.0):2.0):3.0):
1.0,Aepyceros_melampus:10.0):1.0,(((Boselaphus_tragocameleu
s:1.0,Syncerus_caffer:1.0):1.0,(Bison_bison:1.0,Bison_bonas
us:1.0):1.0):1.0,(Taurotragus_derbianus:1.0,Taurotragus_ory
x:1.0):2.0):8.0):1.0,(Cervus_elephas:1.0,Dama_dama:1.0):11.
0):1.0,(Alces_alces:1.0,Capreolus_capreolus:1.0):12.0):1.0,
((Odocoileus_virginianus:1.0,Odocoileus_hemionus:1.0):1.0,R
angifer_tarandus:2.0):12.0):1.0,Antilocapra_americana:15.0)
:1.0,(Phacochoerus_aethiopicus:2.0,(Tayassu_pecari:1.0,Taya
ssu_tajuca:1.0):1.0):14.0):1.0,Hippopotamus_amphibius:17.0)
:1.0,((Lama_guanicoe:1.0,Vicugna_vicugna:1.0):1.0,(Camelus_
dromedarius:1.0,Camelus_bactrianus:1.0):1.0):16.0):1.0,((Ce
ratotherium_simum:1.0,Diceros_bicornis:1.0):4.0,(Tapirus_sp
:4.0,(Equus_zebra:3.0,((Equus_asinus:1.0,Equus_burchelli:1.
0):1.0,(Equus_caballas:1.0,Equus_hemionus:1.0):1.0):1.0):1.
0):1.0):14.0):1.0,(((((Blarina_brevicauda:1.0,Sorex_cinereu
s:1.0):1.0,Suncus_murinus:2.0):1.0,Erinaceus_europaeus:3.0)
:1.0,Scalopus_aquaticus:4.0):10.0,((((((Canis_mesomelas:3.0
,((Canis_lupus:1.0,Canis_familiaris:1.0):1.0,(Canis_aureus:
1.0,Canis_latrans:1.0):1.0):1.0):1.0,Lycaon_pictus:4.0):1.0
,Vulpes_vulpes:5.0):1.0,Urocyon_cineroargenteus:6.0):1.0,((
(Ursus_americanus:1.0,Ursus_arctos_horribilis:1.0):1.0,Ursu
s_maritimus:2.0):3.0,((Mustela_erminea:3.0,((Mustela_nigrip
es:1.0,Mustela_putorius:1.0):1.0,Mustela_nivalis:2.0):1.0):
1.0,(Nasua_nasua:1.0,Procyon_lotor:1.0):3.0):1.0):2.0):6.0,
(((Mungos_mungo:1.0,Helogale_parvula:1.0):1.0,(Crocuta_croc
uta:1.0,Hyaena_hyaena:1.0):1.0):10.0,(((Panthero_pardus:1.0
```

```
100    ,Panthero_leo:1.0):1.0,Panthero_tigris:2.0):9.0,(((Profelis
101    _aurata:1.0,Caracal_caracal:1.0):1.0,Leptailurus_serval:2.0
102    ):8.0,(Pardofelis_marmorata:9.0,(((Leopardus_colocolo:2.0,(
103    Leopardus_geoffroyi:1.0,Leopardus_tigrinus:1.0):1.0):1.0,(L
104    eopardus_wiedii:1.0,Leopardus_pardalis:1.0):2.0):5.0,(Octoc
105    olobus_manul:7.0,(((Prionailurus_benagalensis:1.0,Prionailu
106    rus_viverrina:1.0):4.0,(Felis_nigripes:4.0,(Felis_chaus:3.0
107    ,((Felis_sylvestris_lybica:1.0,Felis_silvestris:1.0):1.0,Fe
108    lis_catus:2.0):1.0):1.0):1.0):1.0,((Gulo_gulo:1.0,Martes_pe
109    nnanti:1.0):3.0,(((Puma_concolor:1.0,Puma_yagouaroundi:1.0)
110    :1.0,Acinonyx_jubatus:2.0):1.0,(Lynx_rufus:1.0,Lynx_lynx:1.
111    0):2.0):1.0):2.0):1.0):1.0):1.0):1.0):1.0):1.0):1.0):1.0):6
112    .0):1.0,((Lepus_americanus:2.0,(Sylvilalagus_audobonii:1.0,
113    Oryctolagus_cuniculus:1.0):1.0):3.0,(((Microtus_pennsylvani
114    cus:2.0,(Ondatra_zibethicus:1.0,Rattus_norvegicus:1.0):1.0)
115    :1.0,((Dipodomys_spectabalis:1.0,Dipodomys_merriami:1.0):1.
116    0,(Liomys_salvini:1.0,Peromyscus_maniculatus:1.0):1.0):1.0)
117    :1.0,(((Sciurus_carolinensis:1.0,Tamiasciurus_hudsonicus:1.
118    0):1.0,Glaucomys_volans:2.0):1.0,(Tamias_striatus:2.0,(Marm
119    ota_monax:1.0,Spermophilus_tridecemlineatus:1.0):1.0):1.0):
120    1.0):1.0):16.0):1.0,(((Setifer_setosus:1.0,Echinops_telfair
121    i:1.0):1.0,Hemicentetes_semispinosus:2.0):1.0,Tenrec_ecauda
122    tus:3.0):19.0):1.0,((Didelphis_virginianicus:1.0,Monodelphi
123    s_domesticus:1.0):2.0,((Bettongia_penicullata:1.0,Dasypus_n
124    ovecinctus:1.0):1.0,Trichosurus_vulpecula:2.0):1.0):20.0):1
125    .0,Tachyglossus_aculeatus:24.0);
```

126   **Table S1. Maximum running speed and body mass data**

Species	Log_{10}mass(kg)	log_{10}MRS(km/h)	Foot
Micropipodops_megacephalus	-1.9101	1.0253	Plantigrade
Rattus_rattus	-0.6021	0.9743	Plantigrade
Mus_musculus	-1.7959	1.1017	Plantigrade
Lyomis_pictus	-1.3768	1.2231	Plantigrade
Heteromys_dasmarestianus	-1.301	1.0860	Plantigrade
Chaetodipus_fallax	-1.7447	1.0952	Plantigrade
Chaetodipus_ordii	-1.4078	1.0825	Plantigrade
Perognathus_parvus	-1.6126	1.0847	Plantigrade
Perognathus_longimembris	-2.0506	0.9834	Plantigrade
Dipodomys_microps	-1.2518	1.3104	Saltatorial
Dipodomys_ordii	-1.3206	1.1355	Saltatorial
Dipodomys_deserti	-1.0106	1.1651	Saltatorial
Zymomys_argurus	-1.2182	1.0811	Plantigrade
Napeozapus_insignis	-1.6021	0.9222	Saltatorial
Zapus_trinotatus	-1.5452	1.1411	Saltatorial
Zapus_hudsonicus	-1.7447	0.9373	Saltatorial
Neotoma_lepida	-0.9562	1.2207	Plantigrade
Mesocricetis_brandti	-0.9586	0.9420	Plantigrade
Microtus_pennsylvanicus	-1.301	1.0284	Plantigrade
Pitymys_pinetorum	-1.5229	1.1107	Plantigrade
Peromyscus_truei	-1.7144	1.1430	Plantigrade
Peromuscus_maniculatus	-1.7399	1.1149	Plantigrade
Peromyscus_eremicus	-1.7033	1.1048	Plantigrade
Permomyscus_leucopus	-1.6021	1.0288	Plantigrade
Peromyscus_crinitus	-1.8633	1.0443	Plantigrade
Onychomys_torridus	-1.7144	1.0024	Plantigrade
Leggadina_forresti	-1.8097	1.0883	Plantigrade
Uromys_caudimaculatus	0.0719	1.2086	Plantigrade
Notomys_cervinus	-1.4559	1.1355	Plantigrade
Notomys_alexis	-1.6108	1.1050	Plantigrade
Pseudomys_hermannbergensis	-1.7447	1.0883	Plantigrade
Pseudomys_nanus	-1.2147	1.1477	Plantigrade
Pseudomys_australis	-1.301	1.2019	Plantigrade
Spermophilus_tereticaudus	-0.9485	1.1697	Plantigrade
Spermophilus_tridecemlineatus	-0.9031	1.0726	Plantigrade
Spermophilus_beldingi	-0.5229	1.1007	Plantigrade
Spermophilus_undulatus	-0.2218	1.2888	Plantigrade
Spermophilus_citellus	-0.301	1.2422	Plantigrade
Marmota_monax	0.6021	1.1918	Plantigrade
Spermophilus_saturatus	-0.6536	1.3331	Plantigrade

Spermophilopis_leptodactylus	-0.2218	1.5442	Plantigrade
Ammospermophilus_leucurus	-1.1198	1.2246	Plantigrade
Tamias_minimus	-1.5331	1.2113	Plantigrade
Tamias_amoenus	-1.2924	1.2755	Plantigrade
Tamias_striatus	-1	1.2181	Plantigrade
Tamiasciurus_hudsonicus	-0.6576	1.1649	Plantigrade
Sciurus_vulgaris	-0.3979	1.2892	Plantigrade
Sciurus_carolinensis	-0.301	1.4640	Plantigrade
Sciurus_niger	0.0326	1.3678	Plantigrade
Sylvilalagus_audubonii	0.1761	1.5898	Lagomorpha
Oryctolagus_cuniculus	0.2788	1.7359	Lagomorpha
Lepus_americanus	0.1761	1.6862	Lagomorpha
Lepus_californicus	0.301	1.7933	Lagomorpha
Lepus_alleni	0.6435	1.8453	Lagomorpha
Lepus_townsendii	0.5441	1.7360	Lagomorpha
Lepus_europeus	0.6021	1.8452	Lagomorpha
Lepus_arcticus	0.6628	1.7940	Lagomorpha
Presbytis	1.1139	1.5559	Plantigrade
Urocyon_cinereoargenteus	0.5682	1.7939	Digitigrade
Vulpes_fulva	0.6812	1.8453	Digitigrade
Lycaon_pictus	1.301	1.8328	Digitigrade
Canis_mesomelas	0.8451	1.7656	Digitigrade
Canis_latrans	1.1239	1.8006	Digitigrade
Canis_aureus	0.9445	1.7359	Digitigrade
Mephitis_mephitis	0.3979	1.1918	Digitigrade
Meles_meles	1.0645	1.4650	Digitigrade
Nasua_narica	0.6435	1.4190	Digitigrade
Procyon_lotor	0.8451	1.3684	Digitigrade
Monodelphis_brevicauda	-1.1278	1.0557	Plantigrade
Isoodon_obesulus	-0.1439	1.1432	Saltatorial
Dasyuroides_byrnei	-0.9208	1.4093	Plantigrade
Sminthopsis_macroura	-1.699	1.1469	Plantigrade
Sminthopsis_crassicaudata	-1.7696	1.0485	Plantigrade
Antechinus_flavipes	-1.284	1.2095	Plantigrade
Antechinus_laniger	-1.6021	1.1617	Plantigrade
Myrmecobius_fasciatus	-0.3188	1.1317	Plantigrade
Cercatetus_concinnus	-1.8239	0.6851	Plantigrade
Potorus_tridactylus	-0.0009	1.3180	Saltatorial
Bettongia_penicilata	0.0414	1.3822	Saltatorial
Macropus_eugenii	0.6021	1.5897	Saltatorial

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Table S2. Body mass and metatarsal:femur ratio data

Species	Order	Log$_{10}$ body mass	MT:F ratio
Echinops_telfairi	Tenrecidae	-0.7447	0.2952
Hemicentetes_semispinosus	Tenrecidae	-0.7447	0.3994
Setifer_setosus	Tenrecidae	-0.6576	0.3024
Tenrec_ecaudatus	Tenrecidae	0.0839	0.3063
Dipodomys_merriami	Rodentia	-1.3979	0.3226
Dipodomys_spectabalis	Rodentia	-0.9586	0.6489
Glaucomys_volans	Rodentia	-1.3010	0.3767
Liomys_salvini	Rodentia	-0.3979	0.5684
Marmota_monax	Rodentia	0.5682	0.3084
Microtus_pennsylvanicus	Rodentia	-1.3010	0.4897
Ondatra_zibethicus	Rodentia	0.0414	0.5412
Peromyscus_maniculatus	Rodentia	-1.6990	0.6124
Rattus_norvegicus	Rodentia	-0.3979	0.4094
Sciurus_carolinensis	Rodentia	-0.2218	0.4055
Spermophilus_tridecemlineatus	Rodentia	-0.8539	0.4934
Tamias_striatus	Rodentia	-1.0969	0.4657
Tamiasciurus_hudsonicus	Rodentia	-0.5850	0.4536
Ceratotherium_simum	Perissodactyla	3.2790	0.3360
Diceros_bicornis	Perissodactyla	2.9420	0.3340
Equus_asinus	Perissodactyla	2.2180	0.7130
Equus_burchelli	Perissodactyla	2.1340	0.6770
Equus_caballas	Perissodactyla	2.7240	0.6310
Equus_hemionus	Perissodactyla	2.3440	0.7020
Equus_zebra	Perissodactyla	2.4410	0.7190
Tapirus_sp	Perissodactyla	2.2380	0.3700
Tachyglossus_aculeatus	Monotremata	0.5682	0.1453
Bettongia_penicullata	Marsupials	0.0899	0.5750
Dasypus_novecinctus	Marsupials	0.5539	0.2985
Didelphis_virginianicus	Marsupials	0.3598	0.2635
Monodelphis_domesticus	Marsupials	-1.1549	0.2535
Trichosurus_vulpecula	Marsupials	0.4472	0.2298
Blarina_brevicauda	Lipotyphla	-1.6990	0.4288
Erinaceus_europaeus	Lipotyphla	-0.0177	0.3200
Scalopus_aquaticus	Lipotyphla	-1.0969	0.2881
Sorex_cinereus	Lipotyphla	-2.3979	0.5428
Suncus_murinus	Lipotyphla	-2.6990	0.4021

Lepus_americanus	Lagomorpha	0.1761	0.5220
Oryctolagus_cuniculus	Lagomorpha	0.2788	0.4270
Sylvilalagus_audobonii	Lagomorpha	0.1761	0.4230
Acinonyx_jubatus	Carnivora	1.5910	0.4300
Canis_aureus	Carnivora	1.0414	0.4448
Canis_familiaris	Carnivora	1.4620	0.4200
Canis_latrans	Carnivora	1.0900	0.4090
Canis_lupus	Carnivora	1.6492	0.4394
Canis_mesomelas	Carnivora	0.8810	0.3830
Caracal_caracal	Carnivora	1.2463	0.4491
Crocuta_crocuta	Carnivora	1.8130	0.3860
Felis_catus	Carnivora	0.5786	0.4670
Felis_chaus	Carnivora	1.0107	0.4744
Felis_nigripes	Carnivora	0.1761	0.4899
Felis_silvestris	Carnivora	0.6532	0.4376
Felis_sylvestris_lybica	Carnivora	0.6972	0.4616
Gulo_gulo	Carnivora	1.0969	0.4072
Helogale_parvula	Carnivora	-0.2518	0.4437
Hyaena_hyaena	Carnivora	1.5050	0.3710
Leopardus_colocolo	Carnivora	1.0043	0.4132
Leopardus_geoffroyi	Carnivora	0.4393	0.4142
Leopardus_pardalis	Carnivora	1.1303	0.3765
Leopardus_tigrinus	Carnivora	0.4393	0.4366
Leopardus_wiedii	Carnivora	0.8129	0.3750
Leptailurus_serval	Carnivora	1.1446	0.4421
Lycaon_pictus	Carnivora	1.3711	0.4308
Lynx_lynx	Carnivora	0.9956	0.4502
Lynx_rufus	Carnivora	1.0354	0.4148
Martes_pennanti	Carnivora	0.6096	0.3990
Mungos_mungo	Carnivora	0.1461	0.4078
Mustela_erminea	Carnivora	-0.9586	0.4043
Mustela_nigripes	Carnivora	-0.1487	0.4002
Mustela_nivalis	Carnivora	-1.1549	0.3947
Mustela_putorius	Carnivora	0.0212	0.3896
Nasua_nasua	Carnivora	0.5310	0.2860
Octocolobus_manul	Carnivora	0.6021	0.3978
Panthero_leo	Carnivora	2.2452	0.3687
Panthero_pardus	Carnivora	1.7080	0.3860
Panthero_tigris	Carnivora	2.1610	0.3650
Pardofelis_marmorata	Carnivora	0.7404	0.4320
Prionailurus_benagalensis	Carnivora	0.6990	0.4472
Prionailurus_viverrina	Carnivora	0.8293	0.4306
Procyon_lotor	Carnivora	0.8750	0.2740

Profelis_aurata	Carnivora	1.0273	0.4115
Puma_concolor	Carnivora	1.7848	0.3952
Puma_yagouaroundi	Carnivora	0.8893	0.4277
Urocyon_cineroargenteus	Carnivora	0.5800	0.4560
Ursus_americanus	Carnivora	2.0210	0.2170
Ursus_arctos_horribilis	Carnivora	2.1900	0.2580
Ursus_maritimus	Carnivora	2.2430	0.2490
Vulpes_vulpes	Carnivora	0.7400	0.4810
Aepyceros_melampus	Artiodactyla	1.6990	0.9650
Alcephalus_buselaphus	Artiodactyla	2.1760	0.8700
Alces_alces	Artiodactyla	2.6130	0.9330
Antidorcas_marsupialis	Artiodactyla	1.5440	1.1370
Antilocapra_americana	Artiodactyla	1.6630	0.9630
Antilope_cervicapra	Artiodactyla	1.5440	1.0050
Beatragus_hunteri	Artiodactyla	2.2010	0.9670
Bison_bison	Artiodactyla	2.8450	0.5580
Bison_bonasus	Artiodactyla	2.3520	0.6740
Boselaphus_tragocameleus	Artiodactyla	2.3010	0.7380
Camelus_bactrianus	Artiodactyla	2.7400	0.6830
Camelus_dromedarius	Artiodactyla	2.6180	0.6930
Capra_aegaerus	Artiodactyla	1.6630	0.7270
Capra_causasica	Artiodactyla	1.7400	0.6060
Capreolus_capreolus	Artiodactyla	1.3980	1.0000
Cervus_elephas	Artiodactyla	1.9290	0.9600
Connoachaetes_gnou	Artiodactyla	2.1960	0.8300
Connoachaetes_taurinus	Artiodactyla	2.2550	0.7900
Dama_dama	Artiodactyla	1.6530	0.9220
Damaliscus_dorcas	Artiodactyla	1.6380	1.0240
Damaliscus_lunatus	Artiodactyla	2.1000	0.8920
Gazella_dorcas	Artiodactyla	1.2790	1.1060
Gazella_grantii	Artiodactyla	1.6990	1.0860
Gazella_subgutturosa	Artiodactyla	1.3800	1.0860
Gazella_thompsoni	Artiodactyla	1.2790	0.9610
Hippopotamus_amphibius	Artiodactyla	3.0830	0.2570
Hippotragus_equinus	Artiodactyla	2.3520	0.8110
Hippotragus_niger	Artiodactyla	2.2580	0.7370
Lama_guanicoe	Artiodactyla	1.9540	0.6870
Madoqua_kirkii	Artiodactyla	0.7080	1.0960
Odocoileus_hemionus	Artiodactyla	1.7480	0.8830
Odocoileus_virginianus	Artiodactyla	1.7920	0.8020
Oreamnos_americanus	Artiodactyla	2.0790	0.5500
Ourebia_ourebi	Artiodactyla	1.1610	1.0590
Ovibos_moshatus	Artiodactyla	2.3220	0.5550

Ovis_ammon	Artiodactyla	2.0570	0.7930
Ovis_canadensis	Artiodactyla	1.9780	0.7780
Phacochoerus_aethiopicus	Artiodactyla	1.9440	0.2960
Rangifer_tarandus	Artiodactyla	2.2040	0.9050
Rupricapra_pyrenaica	Artiodactyla	1.5310	0.8290
Rupricapra_rupricapra	Artiodactyla	1.5800	0.7960
Saiga_tartarica	Artiodactyla	1.4180	0.9730
Syncerus_caffer	Artiodactyla	2.6430	0.5510
Taurotragus_derbianus	Artiodactyla	2.8330	0.7530
Taurotragus_oryx	Artiodactyla	2.7480	0.8540
Tayassu_pecari	Artiodactyla	1.5190	0.4080
Tayassu_tajuca	Artiodactyla	1.3420	0.4050
Vicugna_vicugna	Artiodactyla	1.6530	0.7160

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