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The evolution of mammalian body temperature: the Cenozoic supraendothermic pulses

Barry G. Lovegrove

Abstract In this study, I investigated the source(s) of variation in the body temperatures of mammals. I also attempted to reconstruct ancestral normothermic rest-phase body temperature states using a maximum parsimony approach. Body temperature at the familial level is not correlated with body mass. For small mammals, except the Macroscelidae, previously identified correlates, such as climate adaptation and zoogeography explained some, but not all, T_b apomorphies. At the species level in large cursorial mammals, there was a significant correlation between body temperature and the ratio between metatarsal length and femur length, the proxy for stride length and cursoriality. With the exception of two primate families, all supraendothermic ($T_b > 37.9°C$) mammals are cursorial, including Artiodactyla, Lagomorpha, some large Rodentia, and Carnivora. The ruminant supraendothermic cursorial pulse is putatively associated with global cooling and vegetation changes following the Paleocene–Eocene Thermal Maximum. Reconstructed ancestral body temperatures were highly unrealistic deep within the mammalian phylogeny because of the lack of fossil T_b data that effectively creates ghost lineages. However, it is anticipated that the method of estimating

body temperature from the abundance of ^{13}C–^{18}O bonds in the carbonate component of tooth bioapatite in both extant and extinct animals may be a very promising tool for estimating the T_b of extinct mammals. Fossil T_b data are essential for discerning derived T_b reversals from ancestral states, and verifying the dates of supraendothermic pulses.

Introduction

Unlike ectothermic vertebrates, birds and mammals maintain a high and fairly constant body temperature (T_b) through an endothermic process of heat production. The energetic cost of endothermy compared with ectothermy is large (Schmidt-Nielsen 1983). It is not often appreciated that there is a 10°C range in normothermic rest-phase T_b in those mammals that have been measured (Clarke et al. 2010). Given this high physiological diversity, there are important questions that remain unanswered about the evolution of elevated body temperatures. For example, are there any discernable patterns of change of T_b throughout the Cenozoic? Can the T_b diversity be explained by allometry, for example, the association with the evolution of large body sizes in some mammalian lineages during the Cenozoic (Alroy 1998)? Can apomorphic T_b pulses or reversals be identified, associated for example, with paleoclimates, phylogeny, biogeography, and ecology? What was the plesiomorphic T_b of Late Cretaceous mammals prior to their explosive radiation in the Cenozoic? This study provides some fresh insights into these questions.

B. G. Lovegrove (✉)
School of Biological and Conservation Sciences,
University of KwaZulu-Natal, Private Bag X01,
Scottsville 3209, South Africa
e-mail: lovegrove@ukzn.ac.za

When using T_b as a proxy for the degree of endothermy in modern mammals, three levels of endothermy have been described based upon subjectively chosen percentiles (20th and 80th) of the frequency distribution of normothermic mammalian T_bs; basoendothermy ($T_b < 35°C$), mesoendothermy ($35°C \leq T_b \leq 37.9°C$), and supraendothermy ($T_b > 37.9°C$) (Lovegrove 2012). Body temperature is correlated with basal metabolic rate (Clarke et al. 2010; Lovegrove 2003) and is a useful proxy for metabolic rate because it is thought to be independent of allometric effects (see results), is easy to measure, and displays less seasonal variation than BMR (Lovegrove 2005, 2012). I analyzed T_b at the level of family because hierarchical analysis of variance shows the greatest variance in metabolism between mammal families, and least between genera and species (Harvey and Pagel 1991). Species within genera and families are more similar to each other compared with species in other, even closely-related families. Thus, analysis at the family level is best for describing broad-scale T_b apomorphies.

I have proposed (Lovegrove 2012) that basoendothermy was the pleisiomorphic state of Maastrichtian mammals, and that meso- and supraendothermy are derived levels of endothermy associated with global cooling and vegetation changes following the Paleocene–Eocene Thermal Maximum (PETM) (see Zachos et al. 2001). In extant mammals, it has been shown that the BMR and T_b of small mammals (<500 g) is best explained by climate and zoogeography (Lovegrove 2000, 2003; Withers et al. 2006). However, explanations for the T_b variability in large mammals (>500 g) remain obscure (Lovegrove 2000). In this latter study, I argued that the energetics of locomotion may explain the tendency toward supraendothermy in cursorial large mammals. Entire orders of large mammals, such as Lagomorpha and Artiodactyla, and several carnivoran families, are supraendothermic (Lovegrove 2012). Other large mammals, such as monotremes, macropod kangaroos and other marsupials, xenarthrans, afrotherians, and Pholidota, are either meso- or basoendothermic (Lovegrove 2000, 2012).

There is no clear allometric association between body mass and T_b in large mammals. In this study, I examined the allometry of T_b and body mass at the family level where most physiological variation has been identified (Harvey and Pagel 1991). I also tested the hypothesis from Lovegrove (2000) that supraendothermy in large mammals is associated with cursorial, locomotor performance. I used the metatarsal:femur ratio (MT:F) as a proxy for locomotor performance (e.g., stride length) in typical cursors and cursor-like mammals (Garland and Janis 1993). Lastly, I employed a maximum parsimony approach to identify where and when the major apomorphies and reversals may have occurred in mammalian T_b during the Cenozoic.

Methods

The T_b data

I used the normothermic rest-phase T_b and body mass database from Clarke et al. (2010) for 596 species of mammals. I constructed a family-level phylogeny using Mesquite (Maddison and Maddison 2009) with all available divergences dates (supplementary material, Nexus file). For each family I calculated the mean T_b for all genera within the family. Some families are represented by a single species, but these data were not discarded. I did discard one family, Noctoryctidae, because the data for the single species of marsupial mole within the family were obtained from a single recording of an individual which may have been in an intermediate state of torpor. This datum had a very strong and unrealistic underestimating influence on the reconstructed T_b of the marsupials at the ordinal level.

The T_b of ancestral states, such as the root of ordinal and familial clades, and the root of all mammals, were calculated using maximum parsimony with the program Mesquite (Maddison and Maddison 2009).

The MT:F data

Metatarsal:femur ratio data were calculated from metatarsal and femur lengths for mammals >500 g from Carrano (1999). Where more than one set of observations were available for a species, I calculated the mean MT:F. The MT:F data were examined for allometric effects with body size using both OLS and phylogenetic regression models (Lavin et al. 2008). The MT:F for the giraffe (MT:F = 1.4) was a large outlier in the data. I discarded this datum on the argument that, although giraffes are indeed cursorial, the strongest selection for limb elongation was associated with achieving height rather than a fast running speed.

Comparative analyses

For all analyses of T_b and MT:F as a function of M_b, the detection of phylogenetic signal was performed using the method of Blomberg et al. (2003) using the MATLAB program physig.m. The phylogenetic variance–covariance matrix required for this analysis was obtained using the PDAP suite (Garland and Ives 2000) within MESQUITE (Maddison and Maddison) from the respective phylogenies.

Five different linear regression models of T_b as a function of body mass were calculated using the MATLAB program RegressionV2.m (Lavin et al. 2008): ordinary least squares (OLS, a nonphylogenetic regression), and four phylogenetic regressions; phylogenetic generalized

least squares (PGLS), and PGLS with Ornstein–Uhlenbeck transformation (RegOU), Pagel transformation (RegPagel), and Grafen transformation (RegGrafen). I ran 2,000 simulations for each model. Following the procedures outlined by Lavin et al. (2008), the Akaike Information Criterion (AIC) value was used as a heuristic indicator of the support for each regression model. The model with the lowest AIC value was considered the best fit of all regression models. The RegOU, RegGrafen and RegPagel models return measures of phylogenetic signal, the statistics d, ρ (rho) and λ (lambda), respectively (Lavin et al. 2008). Values approaching zero indicate little or no phylogenetic signal, whereas values approaching or exceeding one indicate strong phylogenetic signal. The 95% confidence and prediction intervals of the best-fit phylogenetic regressions were calculated using equations 17.26 and 17.29, respectively, from Zar (1984).

Results

T_b allometry

There was a strong phylogenetic signal in both T_b ($K = 1.483$, randomization test; $p \ll 0.001$) and body mass ($K = 0.819$, randomization test; $p \ll 0.001$). The OLS regression of T_b as a function of body mass was significant ($p < 0.05$) but explained only 4.8% of the variation in T_b (Table 1). All four phylogenetic regressions of T_b as a function of body mass were insignificant, i.e., regressions slopes were not significantly different from zero (Table 1). Regression slopes ranged from 0.103 to 0.118 (Table 1). The phylogenetic regression with the strongest fit to the data, i.e., with the lowest AIC value (390.3), was the Reg$_{Pagel}$ regression (Table 1). Although the maximum ΔAIC between the four phylogenetic models was small (4.7), that between the non-phylogenetic OLS regression and the four phylogenetic regressions was large (ΔAIC $\sim$ 39). Thus, there is no convincing allometry between T_b and body mass once the data are corrected for phylogenetic inheritance.

The T_b distribution

The lack of allometry of T_b and body mass allows a plot of T_b as a function of body mass to illustrate the distribution of familial T_bs with respect to the basoendothermic, mesoendothermic and supraendothermic ranges (Fig. 1). The supraendothermic families included both lagomorph families (Leporidae and Ochotonidae), two primate families (Cebidae and Aotidae), three rodent families (Caviidae, Aplodontiidae and Myocastoridae), four carnivoran families (Otariidae, Herpestidae, Mustelidae and Canidae), three artiodactyla families (Cervidae, Bovidae and Giraffidae), and one eulipotyphlan family (Soricidae). Basoendothermic families include seven marsupial families (Myrmecobiidae, Tarsiidae, Acrobatidae, Didelphidae, Burramyidae, Peramelidae and Notoryctidae), six chiropteran families (Natalidae, Molossidae, Noctilionidae, Rhinolophidae, Vespertilionidae and Emballonuridae), both monotreme families (Ornithorhynchidae and Tachyglossidae), four xenarthran families (Bradypodidae, Myrmecophagidae, Cyclopedidae and Dasypodidae), three Afrotherian families (Tenrecidae, Chrysochloridae and Orycteropodidae), one primate family (Tarsiidae), two rodent families (Mystromyinae and Bathyergidae), and Pholidota (Fig. 1). All other families are mesoendothermic.

Metatarsal:femur regression

Data for 44 species of cursorial or cursorial-like mammals were used to investigate T_b as a function of the MT:F. Both T_b and MT:F displayed a strong and significant phylogenetic signal (T_b; $K = 0.940$, randomization test; $p \ll 0.001$; MT:F; $K = 1.112$, randomization test; $p \ll 0.001$, Fig. 2). The regression of T_b as a function of body mass was not significant in the OLS regression and three of the four phylogenetic regressions (Table 4). There was ΔAIC ~ 5 between the OLS model and the phylogenetic models, confirming the phylogenetic signal. The Reg$_{Pagel}$ model was significant, but this regression did not display the lowest AIC value and hence was not the best fit to the data. For the regression of MT:F as a function of body mass, the

Table 1 Statistics of linear regressions of body temperature (°C) as a function of $\log_{10}$ body mass (g) for 113 families of mammals

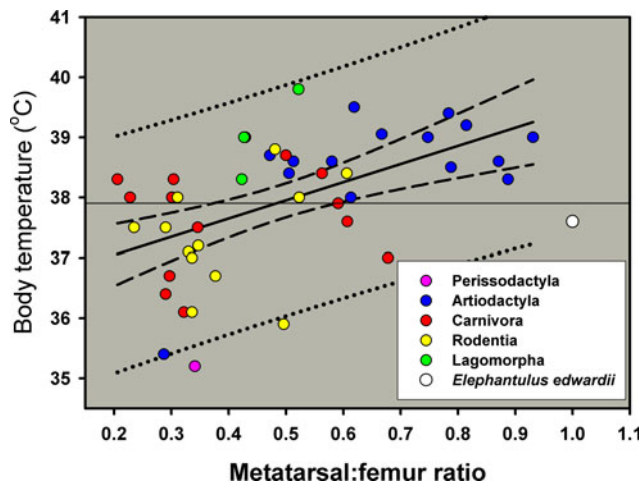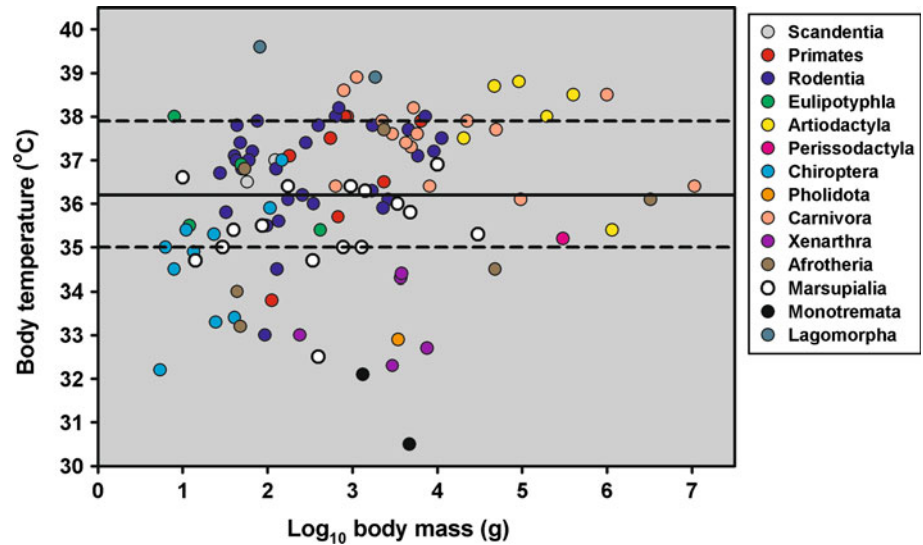| Statistic	OLS	PGLS	Reg$_{ou}$	Reg$_{Grafen}$	Reg$_{Pagel}$
Slope	0.299	0.103	0.109	0.118	0.114
Lower 95% CI	0.052	−0.193	−0.174	−0.562	−0.161
Upper 95% CI	0.541	0.365	0.380	0.377	0.379
Intercept	35.34	33.93	34.03	34.04	33.68
p	0.022	>0.5	>0.5	>0.5	>0.5
r^2	0.048	0.005	0.005	0.007	0.007
AIC	434.7	393.6	395.0	392.8	390.3
Signal strength	–	–	$d = 0.912$	$\rho = 0.772$	$\lambda = 0.918$

Fig. 2 Body mass as a function of the metatarsal:femur ratio of 44
species of large mammalian cursors from five mammal orders. The
dashed and dotted lines are the 95% upper and lower confidence and
prediction intervals, respectively. The *horizontal line* is the lower
limit of supraendothermy ($T_b = 37.9°C$) (color figure online)

OLS and all four phylogenetic regression were not significant (Table 2). Again, the $\Delta AIC \sim 20$ between the OLS
and the phylogenetic models confirmed a strong phylogenetic signal in the data. T_b and MT:F do not scale with
body mass; therefore, these two variables can be regressed
against each other without the need for multivariate analysis or residual–residual analysis.

With the exception of the Reg_{Grafen} model, all regressions of T_b as a function of MT:F were significant. The
lowest AIC value was for the Reg_{OU} model (120.30) but
this value cannot be considered statistically different from
that for the OLS (120.37, $\Delta AIC = 0.07$). In general, a
$\Delta AIC \geq 2$ is considered sufficient to render two AIC values
significantly different (Lavin et al. 2008). Thus, the OLS
model of these data can be considered to be the best fit to

the data. This regression explained 30.1% of the variation
in T_b as a function of MT:F.

Carrano (1999) has argued that cursorial and graviportal
limb morphometrics are endpoints that bound morphological-mechanical variation in limbs. Graviportal limbs have
more robust individual limb elements, shorter distal limb
segments, and more distally placed muscle insertions. They
are characteristic of very large mammals whose limbs are
designed to move with lower speeds, but using more limb
power per stride, and to support the weight of very large
mammals. The mammals with the lowest T_bs in Fig. 2 are
large graviportal species, the hippopotamus (Artiodactyla)
and the rhino (Perissodactyla). When these data were
excluded from the OLS regression, the percentage of T_b
variation explained by MT:F decreased to 26 percent.

Reconstructed body temperature

The reconstructed ordinal ancestral T_bs and body masses
estimated by maximum parsimony produced unreliable
results because of the lack of fossil T_b information within
ghost lineages (Fig. 3; Table 3, discussed later). The
reconstructed mean T_b of the ancestral mammal was
34.23°C (lower 95% CI = 32.02°C; upper 95%
CI = 36.45°C), and the mean body mass was 1,032 g
(lower 95% CI = 34.04 g; upper 95% CI = 31,332.9 g).

Reconstructed T_bs and body mass for Mid- to Late
Cenozoic divergences are more reliable and highlight
several apomorphies/reversals (Fig. 3). I identified ten
apomorphies/reversals in T_b arbitrarily as a change in the
mean reconstructed root T_b of more than 2°C between
sister families or clades of families (Table 4). These apomorphies/reversals are not necessarily 'significant' changes
in T_b; they merely identify the largest changes that have
occurred between sister taxa.

Table 2 Statistics of linear regressions of body temperature (°C) and metatarsal:femur ratio as a function of $\log_{10}$ body mass (g) for 44 species of cursorial mammals

Statistic	OLS	PGLS	Reg$_{ou}$	Reg$_{Grafen}$	Reg$_{Pagel}$
Body temperature as a function of $\log_{10}$ body mass (two-tailed test)					
Slope	−0.098	−0.475	−0.483	−0.438	−0.523
Lower 95% CI	−0.444	−0.872	−0.915	−0.870	−0.959
Upper 95% CI	0.255	−0.051	−0.056	−0.005	−0.109
Intercept	38.38	39.19	39.43	39.05	39.41
p	>0.50	>0.05	>0.05	>0.05	<0.05
r^2	0.006	0.102	0.105	0.086	0.125
AIC	136.1	121.1	122.5	123.1	122.6
Signal strength	–	–	$d = 0.859$	$\rho = 1.195$	$\lambda = 0.948$
Metatarsal:femur ratio as a function of $\log_{10}$ body mass (two-tailed test)					
Slope	0.063	−0.047	−0.047	−0.049	−0.049
Lower 95% CI	0.051	−0.117	−0.114	−0.118	−0.120
Upper 95% CI	0.124	0.014	0.018	0.018	0.019
Intercept	0.229	0.584	0.583	0.594	0.589
p	>0.05	>0.05	>0.05	>0.05	>0.05
r^2	0.078	0.041	0.042	0.043	0.044
AIC	−16.89	−39.20	−37.21	−37.22	−37.20
Signal strength	–	–	$d = 1.007$	$\rho = 1.275$	$\lambda = 1.040$
Body temperature as a function of metatarsal:femur ratio (one-tailed test)					
Slope	3.026	1.958	2.462	1.754	2.088
Lower 95% CI	1.636	0.125	0.733	0.023	0.302
Upper 95% CI	4.429	3.760	4.265	3.601	3.984
Intercept	36.48	36.49	36.62	36.58	36.45
p	<0.05	<0.05	<0.05	>0.05	<0.05
r^2	0.305	0.094	0.155	0.077	0.106
AIC	120.37	121.50	120.30	123.28	123.25
Signal strength	–	–	$d = 0.568$	$\rho = 1.288$	$\lambda = 0.965$

Discussion

Unlike many physiological variables, body temperature is not allometrically correlated with body mass at the level of family when the data are corrected for phylogenetic inheritance. Refinetti (2010) found a significant positive correlation ($r^2 = 0.28$, $p = 0.001$) between T_b and body mass in a sample of 55 species of mammals (Refinetti 2010). However, these data were not phylogenetically independent and were restricted to mammals less than 1 kg. Since body mass does not explain the large diversity of T_b in mammals, alternative factors need to be investigated.

MT:F ratios

One factor common to most supraendotherms is cursoriality; four artiodactyl families (Bovidae, Cervidae, Giraffidae, and Tayassuidae), three terrestrial carnivoran families (Canidae, Mustedilae and Herpestidae), and both lagomorph families (Leporidae and Ochotonidae). There are also four supraendothermic rodent families, of which two are represented by large-sized rodents, Myoproctidae and Caviidae, which can be considered to be more cursorial (elongated metatarsals) than smaller, plantigrade rodents. For example, the mara (*Dolichotis*) has lagomorph-like hindlimbs.

For all large (>500 g) cursorial mammals T_b was correlated with the MT:F. The OLS regression explained 30.1% of the variation in T_b as a function of the MT:F. Although this percentage may not seem high, it is, for the first time, a partial explanation for T_b diversity in large, cursorial mammals. These data support my prediction in the Bowtie model (Lovegrove 2000) that the high residual BMRs of large mammals are associated with cursoriality. The Bowtie model gets its name from the shape of residual BMRs plotted on a $\log_{10}$ body mass independent axis. Residual BMR variances are greatest at the smallest and largest body sizes, and decrease toward the middle of the log axis of body mass, and attain a minimum variance at

Fig. 3 The phylogeny of 113 mammal families. The ordinal divergence dates are from Bininda-Emonds et al. (2007). Within-order divergence dates are from Lovegrove (2012). *Branch length colors* represent body temperatures reconstructed using maximum parsimony analysis (color figure online)
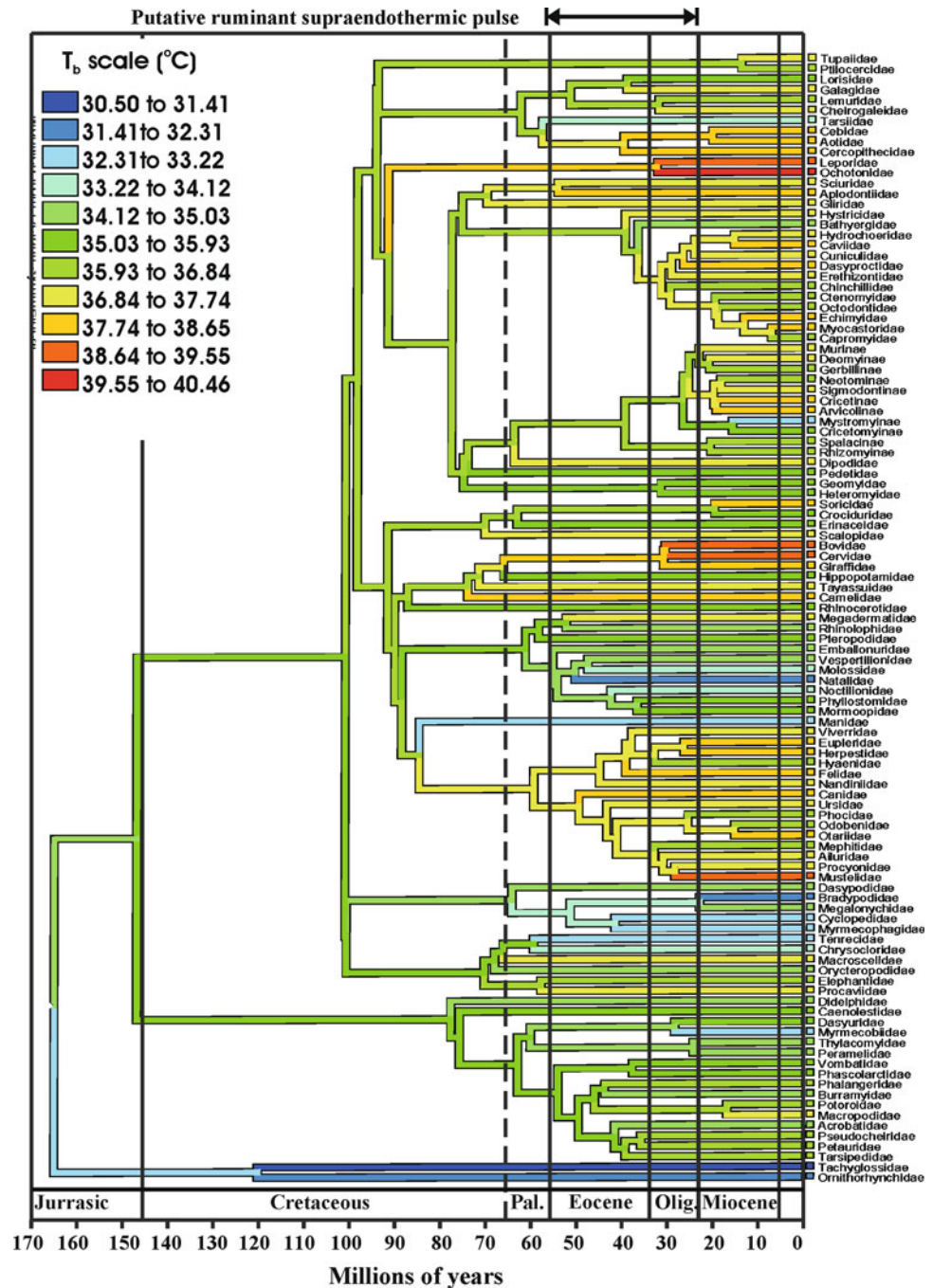
~385 g (Lovegrove 2000). Considering T_b as a proxy for BMR, the data also support the relationship between BMR residuals and maximum running speeds in non-plantigrade mammals (Lovegrove 2004).

There are two prevailing hypotheses which associate high T_b and metabolic rate with cursoriality, the Aerobic Capacity model (ACM) (Bennett and Ruben 1979), and the Muscle Power model (Clarke and Pörtner 2010). The Aerobic Capacity model, the oldest hypothesis, argues that endothermy evolved as a byproduct of selection for a high

metabolic aerobic capacity for sustained, endurance loco-motion. The model argues that there was no direct selection for warmth. The Muscle Power model argues that muscle temperature is positively correlated with muscle power. This new model on the evolution of endothermy argues that ATP generation by mitochondria and muscle power output are all strongly temperature-dependent (Clarke and Pörtner 2010). These authors argue that an increase in whole-organism locomotor ability followed strong selection for an increase in T_b. The difference between these two models is

Table 3 Body masses and body temperatures of mammalian orders reconstructed using square-change parsimony

Order	Mean body mass (g)	Mean reconstructed body temperature (°C)	Age of ordinal origin (mya)
Monotremata	1,500	32.9	166.2
Marsupials	378	35.1	147.7
Afrotheria	1,687	35.3	101.3
Xenarthra	1,811	34.3	101.3
Lagomorpha	432	38.6	91.8
Rodentia	389	36.6	91.8
Scandentia	99	36.7	94.3
Primates	676	36.4	91.3
Eulipotyphla	292	36.2	91.8
Pholidota	3,436	32.9	84.9
Carnivora	5,662	37.1	84.9
Chiroptera	68	35.1	88.7
Perissodactyla	299,916	35.2	87.3
Artiodactyla	14,256	36.7	87.3

Table 4 Changes by more than 2°C in the mean reconstructed root T_b (°C) between sister mammalian taxa

Sister taxa	T_b (°C) left taxon	T_b (°C) right taxon	ΔT_b (°C)
Tarsiidae/Haplorrhines	33.80	37.23	3.43
Rodentia/Lagomorpha	36.55	38.64	2.09
Bathyergidae/Caviidae	34.47	36.89	2.42
Mystromyinae/Cricetomyinae	33.00	35.50	2.50
Crociduridae/Soricidae	35.46	38.02	2.56
Hippopotamidae/(Bovidae, Cervidae, Giraffidae)	35.40	38.26	2.86
Natalidae/(Vespertilionidae, Mollosidae)	32.20	34.45	2.25
Manidae/Carnivora	32.94	37.07	4.13
Bradypodidae/Megalonychidae	32.25	34.40	2.15

that the ACM argues that selection for aerobic scope preceded the evolution of warmer body temperatures and therefore endothermy. The MPH argues that selection for warmer body temperatures preceded selection for aerobic capacity and was the physiological means of achieving a high aerobic scope.

Apart from the MT:F, can either the MPH or ACM provide an explanation for the unexplained variation of T_b in the T_b versus MT:R regression in cursorial mammals? Possibly. Consider the Lagomorpha. Although these mammals are considerably smaller than cursorial artiodactyls, they have similar supraendothermic body temperatures. However, rabbits and hares have a relative running speed (body lengths per unit time) considerably faster than any of the larger carnivoran or ungulate cursors (Garland 1983; Iriarte-Diaz 2002). These exceptional running speeds cannot be explained by the MT:F alone, because the MT:F of lagomorphs is smaller than those of artiodactyls. One explanation might involve variations in the dynamics of muscle power provided by the MPH. Clarke and Pörtner (2010) emphasized that muscle contraction frequency, relative to muscle stress and strain considerations, is the aspect of muscle power most influenced by muscle temperature. Hypothetically, lagomorphs may achieve faster relative running speeds than artiodactyls by increasing muscle contraction frequency rather than limb elongation. This hypothesis requires testing the contraction frequency of lagomorph muscles relative to unguligrade muscles.

Why lagomorphs never achieved the MT:F of the unguligrade limb, and hence the longest stride lengths, probably involves a trade-off between digit utility and running speed. The fitness benefits of a fast running speed through extreme limb modification, such a single unguligrade toe, must be measured against the fitness costs of the complete lack of digit functionality, for example the lack of the capacity for digging, climbing, catching prey with claws, holding and manipulating food items, and so on. In this regard, it may be noteworthy that the lagomorphs with the highest MT:F, the hares, do not burrow, whereas rabbits do. Moreover, the fastest cursors within other cursorial supraendothermic orders also display limited digit functionality. Cheetahs have retracted claws, elephant shrews (see below) cannot dig. Unlike most small rodents, large cursorial rodents cannot handle and manipulate food items.

In addition to the large cursorial mammals, there is one highly noteworthy cursor family that is <500 g, the Macroscleidea (elephant shrews). Using a principal components analysis of multiple limb dimensions, Carrano (1999) identified elephant shrews as having the highest value on a principal component axis describing the gradient from graviportal (weight-bearing) limbs to the most cursorial limbs. Indeed, the MT:F of the single macroscelid in this database (*Elephantulus edwardii*, MT:F = 1.07) is the highest of all cursorial ratios, with the exception of that of the giraffe (MT:F = 1.4). Moreover, the mean T_b of Macroscelidae (37.16°C) is 4.31°C higher than that ($T_b = 32.85$°C) of their closest relatives, the Tenrecidae (tenrecs) and Chrysochloridae (golden moles) (Lovegrove 2012). Thus, this large T_b apomorphy can probably be attributed to unusual cursoriality compared with other small mammals. The macroscelid datum falls within the 95% prediction intervals of the regression of T_b as a function of MT:F of large cursors (Fig. 2).

Reconstruction of ancestral states

Maximum parsimony analysis is the only method currently available to reconstruct ancestral conditions in an established chronogram using continuous data. However, the reliability of the method is only as good as the empirical data available for dated fossils (Finarelli and Flynn 2006). The latter study showed that the body size of the ancestral carnivore that was reconstructed when fossil data were included in the phylogeny was considerably smaller than the reconstruction lacking fossil data. Needless to say, physiological characters, such as T_b, are not preserved in fossils, although the body masses of fossils can be determined. These lack of data essentially render all long-fuse lineages as ghost lineages, and also render reconstruction by maximum parsimony very unreliable. As an extreme example, there are T_b and body mass data for only one perissodactyl family in my database, Rhinocerotidae ($T_b = 35.2$°C, body mass = 300 kg). The values for the reconstructed origin of Rhinocerotidae at 87.3 mya (Fig. 3) are exactly the same, because no additional empirical information has been added to this long ghost lineage. The body mass data, in particular, are completely unrealistic because all Maastrichtian (the last Cretaceous period before the K/T boundary at 65 mya) mammals, including the ancestor of Rhinocerotidae, were less than 1 kg (Luo 2007). In general, parsimony analyses that lack fossil data are likely to grossly overestimate body masses, especially in those lineages that underwent size increases during the Cenozoic (e.g., Artiodactyla, Perissodactyla, Carnivora) (Alroy 1998). If we assume that basoendothermy is the pleisiomorphic state (Lovegrove 2012), then ancestral body temperatures will also be overestimated with the lack of

fossil data. Nevertheless, despite these inherent limitations of parsimony analyses (character state overestimation), it is noteworthy that the reconstructed ancestral mammal T_b (34.23°C) still falls within the predicted basoendothermic range (Lovegrove 2012). Given the overestimates provided by parsimony analyses, this T_b can at best be considered to be the absolute maximum mean T_b that ancestral mammals were ever likely to have attained.

Obtaining T_b data for fossils is not, however, out of reach. A new geochemical measurement of bioapatite ("a clumped isotope paleothermometer") is based on temperature-dependent bonding preferences of ^{13}C and ^{18}O within carbonate ions in the bioapatite crystal lattice (Eagle et al. 2010, 2011). The abundance of ^{13}C–^{18}O bonds in the carbonate component of tooth bioapatite in both extant and extinct animals decreases with increasing body temperatures (Eagle et al. 2010). These authors have estimated the T_b of an extinct Miocene rhino to be similar to that of the extant white rhino (*Ceratotherium simum*; $T_b = 36.6$°C) (Eagle et al. 2010). If this procedure proves to be as reliable as its authors claim, then it will be possible to estimate the T_bs of fossil mammals within each ordinal lineage, eliminate ghost lineages, and produce more reliable ancestral state reconstructions using parsimony analyses. In this respect, the phylogeny that I have presented here should be valuable as a template to which fossil T_b data can be added.

The Late Cenozoic T_b pulses

Four of the T_b pulses listed in Table 4 are associated with the locomotor adaptations discussed above. These include the 2.09°C increase in T_b in the Lagomorpha relative to Rodentia (91.8 mya), a 2.42°C increase in the cavid rodents relative to the subterranean family Bathyergidae (36.1 mya), a 2.86°C increase in the clade including Bovidae, Cervidae and Giraffidae relative to Hippopotamidae (65.9 mya), and a 4.13°C increase in Carnivora relative to Pholidota (84.9 mya). Based on maximum parsimony reconstruction, three of these apomorphies occurred in the Cretaceous, and one in the Mid-Cenozoic.

I would argue that the Cretaceous apomorphies are unrealistic, and again suffer from the ghost lineage effect where fossil data are lacking. There is no fossil evidence to suggest that any mammal had attained the MT:F ratios of extant mammal between 65.9 and 91.8 mya. The condylarth ancestors of the Artiodactyla and the creodont ancestors of the Carnivora had MT:Fs <0.4 in the Early Eocene, more than 60% lower than the largest ratios attained by some ruminants in the Early Miocene (Janis and Wilhelm 1993). Indeed, the MT:F of ungulates started to increase only in the Early Eocene, with a "step-up" in six families occurring around the Oligocene/Miocene boundary (Janis and Wilhelm 1993). This pulse (step-up) was coincident

with global cooling following the PETM (Zachos et al. 2001) and the subsequent reduction of forests and the appearance, for the first time in the Cenozoic, of open woodlands, savannas and grasslands in the Miocene (Janis 1993). Following the pulse, ratios remained fairly constant throughout the Late Cenozoic (Janis and Wilhelm 1993).

If we assume that the MT:F ratio can be used as a proxy for T_b based upon the T_b versus MT:F correlation discussed earlier, I would argue that, at the earliest, supraendothermy in Artiodactyla was attained at the Oligocene/Miocene boundary. Based upon the MT:F pulse (Janis and Wilhelm 1993), I would also argue that the putative ruminant supraendothermic pulse occurred from the Early Eocene to the Oligocene/Miocene boundary (shown in Fig. 3). Extrapolation from the T_b versus MT:F regression also suggests that Eocene condylarths and creodonts, the putative ancestors of the artiodactyla and carnivores, would have displayed middle or upper mesoendothermic body temperatures.

Based upon molecular dating and maximum parsimony T_b reconstruction, the onset of the supraendothermic pulse occurred in lagomorphs about 91.8 mya. Again this represents an unrealistic estimate caused by ghost lineages. However, extinct stem lagomorphs, such as *Gomphos elkema*, show evidence of cursorial, lagomorph-like hindlimbs as early as 55 mya, during the Late Paleocene (Asher et al. 2005). These authors argue that, despite the estimated molecular Cretaceous origin of Glires (Rodentia and Lagomorpha), these two lineages probably diverged soon after the Cretaceous/Cenozoic boundary. The lagomorph lineage may therefore have tended toward supraendothermy long before the ruminants, and consequently would represent the earliest Cenozoic supraendothermic pulse of all mammal lineages.

Extant Carnivora do not display MT:Fs as large as those of the Artiodactyla. Ratios range from 0.21 for the American black bear (*Ursus americanus*) to 0.68 for the coyote (*Canis latrans*). The higher ratios overlap with the lower MT:F limits of ruminants, and are also greater than the upper carnivoran MT:F limits provided by Janis and Wilhelm (1993). These discrepancies are probably reflective of the larger sample size in the data from Carrano (1999). Nevertheless, like the Lagomorpha, the upper limit to carnivoran MT:Fs may be a consequence of the trade-off between maximum running speed and digit functionality. From an evolutionary perspective, the benefits of claw retention presumably outweighed those of a faster running speed. Consequently, carnivores do not, on average, attain the ubiquitous supraendothermy of the Artiodactyla.

The Carnivora do not show the Eocene/Oligocene pulse in MT:F like the Artiodactyla (Janis and Wilhelm 1993). In fact, the MT:F ratio seems to decline slightly from the condylarth and creodont condition (Janis and Wilhelm 1993). Although the data from the latter study do not identify the pulses that occurred in some felids and canids (MT:F = 0.56–0.68, Fig. 2), these pulses clearly occurred at some stage following the cat-like and dog-like carnivore diversification 59.1 mya (Fig. 3). I would argue that they were probably tied to the ruminant pulse, coincident with the appearance of open habitats (woodlands and savannas) and grasslands (Janis 1993).

The apomorphy between the Caviidae and the Bathyergidae is difficult to interpret because of the ghost lineage data limitation problem. The difference between the body temperatures of these two groups seems to involve an apoendothermy in the Caviidae and a reversal in the Bathyergidae. Establishing whether the low T_bs of the Bathyergidae is indeed a reversal, or whether it represents a retained pleisiomorphic state, cannot be resolved at this stage. The same interpretation problem applies to the Pholidota–Carnivora apoendothermy. Is the low T_b of the Pholidota a reversal from an ancestral state, or a pleisiomorphic state retained from the time of the divergence of these two groups 84.9 mya? These two examples illustrate the difficulty of identifying character state reversals in the absence of fossil T_b data. Nevertheless, it does seem clear that the highest T_bs observed in large rodents are associated with cursoriality. In particular, cavids such as the coypu *Myocastor* (MT:F = 0.52, T_b = 38.0°C) and the mara *Dolichotis* (MT:F = 0.61, T_b = 38.4°C), fall into the supraendothermic range and display characteristics of typical cursors (Fig. 2).

The remaining apomorphies occur within the non-cursorial shrews, primates, rodents, xenarthrans, and marsupials. I have previously provided one explanation for the shrew apomorphy as a consequence of climate adaptation (Lovegrove 2012). Soricid shrews colonized North America from Asia about 14 mya (Dubey et al. 2007). Among small mammals, those inhabiting high-latitude, cold environments display the highest BMRs and T_bs, presumably associated with the need for enhanced thermogenesis in response to cold (Lovegrove 2003). The crocidurid shrews that colonized Africa from Asia display a significantly lower T_b than the soricids (Lovegrove 2012; Sparti 1990, 1992).

The difference in the T_bs of tarsiers compared with Haplorrhines (and Strepsirrhines) suggests a T_b reversal in tarsiers. However, this interpretation is complicated by the uncertain phylogenetic position of tarsiers. The phylogeny shown in Fig. 3 places tarsiers basal to the Haplorrhines. This placement, although commonly depicted in primate phylogenies, is not certain. Matsui et al. (2009) state that "…the position of tarsiers among primates could not be resolved by the maximum likelihood (ML) and neighbor-joining (NJ) analyses with several data sets. As to the position of tarsiers, any of the three alternative topologies

(monophyly of haplorhini, monophyly of prosimians, and tarsiers being basal in primates) was not rejected at the significance level of 5%, neither at the nucleotide nor at the amino acid level". However, morphological evidence suggests that tarsiers are basal to all primates. Unlike all other primates, tarsiers display unusual retinogeniculate projections suggesting a basal position within primates (Rosa et al. 1996). Indeed a basal position of tarsiers would make sense of the T_b trends within primates because it would place tarsiers basal to other basoendothermic primates, such as the cheirogalid dwarf and mouse lemurs, and the slow lorises (Lovegrove 2012). This placement would negate the apparent T_b reversal and support the hypothesis that basoendothermy was basal within primates, and was retained from the Late Cretaceous in insular (island dwelling) primates that continued to inhabit Eocene-like tropical forests until the present (Lovegrove 2012).

I am reluctant to infer too much about the T_b differences that involve single species within families or subfamilies, such as the Mystromyinae (1 species)/Cricetomyinae (4 species) difference within rodent subfamilies, the Natalidae (1 species)/(Vespertilionidae, Mollosidae, 15 species) difference in chiropteran families, and the Bradypodidae (1 species)/Megalonychidae (1 species) difference in xenarthran sloth families. All three supposed apomorphies involve a single species in each grouping showing an apparent T_b reversal which may represent equivocal data. Until such time as T_b reversals can be differentiated from plesiomorphies, the physiological meaning of these latter pulses can not be resolved.

Conclusions

There is no allometric relationship between T_b and body mass in mammals at the familial level after the data are corrected for phylogenetic inheritance. Thus, T_b diversity needs to be explained by alternative factors. In small mammals, with the exception of the Macroscelidae, T_b variation can be explained, in part, by climate adaptation. In large mammals, the major pulses in body temperature leading to supraendothermy in ruminants are associated with cursoriality which was also arguably associated with post-PETM global cooling and subsequent vegetation changes. The lagomorph supraendothermic pulse probably occurred before the Eocene. The pulses were associated with an increase in length of the distal (e.g., metacarpal) components of the hindlimb. The five existing single-origin hypotheses on the evolution of endothermy, namely niche expansion (Crompton et al. 1978), optimal enzyme function (Heinrich 1977), aerobic capacity for sustained activity (Bennett and Ruben 1979), efficient parental care during gestation and lactation (Farmer 2003), and assimilation efficiency (Koteja 2004), cannot individually account for the supraendothermic pulses, and hence the most derived forms of endothermy. Although I have argued that explanations for the evolution of endothermy probably follow the Correlated Progression model (Kemp 2006), which argues that no one of the functions of endothermy was paramount over the others, the MPM may, however, singularly account for supraendothermy in large mammalian cursors. Irrespective of the predictions of the ACM and the MPM, it seems that the strongest selection for the capacity for sustained endurance locomotion occurred only in the Cenozoic, and not at the onset of mammalian endothermy possibly associated with the major mammalian encephalization pulses as early as the Early Jurassic (Rowe et al. 2011). The ACM therefore cannot be considered to be a realistic model for a single-origin of endothermy. Further interspecific comparisons of muscle contraction frequency are required to explain the variation in supraendothermy that was not explained by the MT:F. Other potential sources of the unexplained T_b variance may be similar to those in small mammals, for example climate adaptation and zoogeography (Lovegrove 2000, 2003).

Future reconstructions of ancestral T_b states require data from fossils to eliminate ghost lineages. In particular, it is not possible at present to distinguish derived T_b reversals from plesiomorphic basoendothermy. However, the method of determining abundance of ^{13}C–^{18}O bonds in the carbonate component of tooth bioapatite in both extant and extinct animals is a very promising tool for estimating the T_b of extinct mammals (Eagle et al. 2010).

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