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Comparative analysis of encephalization in mammals reveals relaxed constraints on anthropoid primate and cetacean brain scaling

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Abstract

There is a well-established allometric relationship between brain and body mass in mammals. Deviation of relatively increased brain size from this pattern appears to coincide with enhanced cognitive abilities. To examine whether there is a phylogenetic structure to such episodes of changes in encephalization across mammals, we used phylogenetic techniques to analyse brain mass, body mass and encephalization quotient (EQ) among 630 extant mammalian species. Among all mammals, anthropoid primates and odontocete cetaceans have significantly greater variance in EQ, suggesting that evolutionary constraints that result in a strict correlation between brain and body mass have independently become relaxed. Moreover, ancestral state reconstructions of absolute brain mass, body mass and EQ revealed patterns of increase and decrease in EQ within anthropoid primates and cetaceans. We propose both neutral drift and selective factors may have played a role in the evolution of brain–body allometry.

Introduction

The scaling relationship between brain mass and body mass has generated great interest since the early years of evolutionary biology (Darwin, 1871; Snell, 1891). This interest is grounded in the quest to understand the biological basis of intelligence in relatively large-brained species such as humans. Snell proposed a model to explain phylogenetic variation in brain mass encompassing two factors, one dependent on body mass (slope of the line) and one independent of body mass (*y*-intercept). Snell (1891) suggested that brain mass scales with body surface area and therefore expected the brain–body mass relationship to scale at a 2/3 ratio. After the discovery of the large-brained hominin fossil, *Homo erectus*, Dubois extended the work of Snell by proposing the ''index of cephalization,'' a measure that specified the relative mass of the brain after body mass was taken into consideration (Dubois, 1897). Dubois reduced Snell's scaling exponent from 2/3 to 0.56; however, this relationship was calculated from brain and body measurements of species that he considered equally ''intelligent,'' and in retrospect, the small number of samples and subjective grouping were responsible for the reduced slope (Jerison, 1973).

Similar to the ''index of cephalization'' of Dubois, Jerison introduced the encephalization quotient (EQ) (Jerison, 1973), which provided a quantitative value to describe relative brain mass that could be compared across a wide range of species of varying body mass. Encephalization is defined as a higher-than-expected brain mass relative to total body mass, and it is often hypothesized that deviations from this brain–body allometric relationship may correlate with cognitive abilities (Jerison, 1985; Williams, 2002; Roth & Dicke, 2005). The

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EQ of a particular species is determined by calculating the ratio of its observed brain mass to its ''expected'' brain mass. The expected brain mass is calculated from a prediction equation based on either a theoretical scaling relationship (i.e. Jerison, 1973) or an empirically determined one (i.e. Martin, 1981; Holloway & Post, 1982). Thus, the EQ represents how many times larger (or smaller) a species' brain is in comparison with what would be expected for its body mass. Accordingly, a species with an EQ that is > 1 has a brain that is larger than expected for its body mass, and an EQ that is < 1 indicates that the species has a brain that is smaller than expected. Although the exact EQ depends on the composition of species in the reference sample used in the analysis, without exception modern humans have always been found to have the highest EQ in comparative studies of mammals and primates (Jerison, 1973; Marino, 1998).

The two most well-established slopes of the regression line are the 2/3 exponent (Snell, 1891; Jerison, 1973), which produces the equation $EQ = \text{brain mass}/0.12 \times \text{body mass}^{2/3}$ (Jerison, 1973), and the 3/4 exponent (Pilbeam & Gould, 1974; Martin, 1981), which produces the equation $EQ = \text{brain mass}/0.059 \times \text{body mass}^{0.76}$ (Martin, 1984). The 2/3 exponent is derived from the theoretical expectation that brain mass scales with body surface area (Snell, 1891; Jerison, 1973). The 3/4 exponent is based on an empirical fit to large cross-species data sets and seems to accord with the hypothesis that brain mass scales with basal metabolic rate (BMR), that is, a species brain mass is dependent on the maternal energy available during gestation (Martin, 1981; Marino, 1998). In either case, brain mass has a negative allometric relationship with body mass, indicating that brain mass does not usually increase in equal proportion to increases in body mass as a whole.

Although allometric studies have provided valuable insights into the brain–body relationship, most past studies have not explicitly taken phylogeny into consideration when calculating the brain–body regression lines. Felsenstein (1985) established that individual data points in comparative studies should not be considered independent due to the structured pattern of trait similarity among species due to common ancestry. Moreover, many succeeding reports have studied individual mammalian orders, such as Primates (Bronson, 1981; Armstrong, 1985; Isler *et al.*, 2008; Montgomery *et al.*, 2010), Carnivora (Radinsky, 1978; Finarelli & Flynn, 2006, 2007, 2009), Cetacea (Marino, 1998) and Chiroptera (Hutcheon *et al.*, 2002; Jones & MacLarnon, 2004). There are few studies of encephalization among all mammals (Jerison, 1973; Martin, 1996; Isler & van Schaik, 2009). Therefore, studying brain mass in the context of a phylogenetic tree of mammals can assist in refining our estimates of the brain–body relationship as well as determining the timing and tempo of major changes in mammalian brain–body allometry.

Humans are the most encephalized species, with a brain mass at least six times larger than expected for a mammalian species of its body mass (i.e. average EQ $\approx$ 6) (Jerison, 1973). Presumably, it is this high degree of encephalization that makes humans unique in cognitive performance, including the skills needed for complex language and culture (Sherwood *et al.*, 2008). However, recent studies point to additional factors beyond EQ that might also be involved in the evolution of cognition including the possible importance of total number of neurons (Herculano-Houzel, 2011). In addition, encephalization is not exclusive to humans, with evidence of varying degrees of relative brain mass enlargement among many other mammalian species. Primates in particular demonstrate numerous independent shifts to larger relative brain mass among different lineages (Harvey *et al.*, 1980; Armstrong, 1985; Williams, 2002; Isler *et al.*, 2008; Montgomery *et al.*, 2010), and other clades such as Carnivora (Radinsky, 1978; Cutler, 1979; Dunbar & Bever, 1998; Finarelli & Flynn, 2009), Cetacea (Marino, 1998; Tartarelli & Bisconti, 2007) and Proboscidea (Shoshani *et al.*, 2006) show independent increases in relative brain mass as well. Although most past research on encephalization has focused solely on evolutionary trends of increasing brain mass, there is also evidence that relative brain mass has been reduced within multiple lineages (Niven, 2005; Safi *et al.*, 2005; Montgomery *et al.*, 2010) including particular clades of bats (Safi *et al.*, 2005) and primates (Montgomery *et al.*, 2010). Safi *et al.* (2005) argued that a reduction in brain mass might have benefits as well, such as adaptation to habitat complexity and flying efficiency in bats.

Because previous publications on brain mass evolution have been limited by the size of data sets, number of replicate species and redundancy (i.e. extracting information from multiple papers that lead back to the same publication), in this study we curated data on brain and body mass from the largest number of extant mammalian species yet assembled, including 630 species from 21 mammalian orders. We calculated the allometric relationship between brain and body mass and tested whether specific clades deviated from brain–body allometric scaling regularities. In addition, we traced the phylogenetic history of encephalization and reconstructed the ancestral state of EQ, brain mass and body mass for all mammals in our data set. Comparisons between mammals using our large data set can lead to important insights concerning human evolution, including a more accurate inference of the ancestral brain mass at the stem of the hominin lineage. Tracing the evolution of brain and body mass in mammals allows us to estimate the ancestral EQ of multiple species and determine the timing of major changes in encephalization during mammalian descent. We propose that among anthropoid primates, several changes in brain mass may have been advantageous and thus selected, whereas others may

have been due to neutral drift, and we discuss these changes in the light of population size.

Materials and methods

Data collection

All data on body mass and brain mass of mammals were collected from published literature sources, except for brain masses measured directly from post-mortem specimens in our own collections (by CCS; $n = 94$ individuals), and have been entered into a MySQL database that is publicly available at (http://homopan.wayne.edu/brainbodydb/brainbody_list.php; see also Dryad repository: doi: 10.5061/dryad.5kh0b362). This publicly available database contains brain and body mass as well as other information from more than 2000 individuals in 930 species. We then parsed this data set into a smaller one (Table S1), where the data points used for this study had to satisfy two main criteria to be included: (i) all measurements were from adult individuals and (ii) published data were obtained from its original source. If authors noted emaciation, the data were not included in our analysis. Domesticated species were also removed from the analysis due to the process of artificial selection and its effects on reduced brain size in domesticated animals (Kruska, 1988). Both male and female data were collected if available, and if there were multiple measures (male and female) for a single species, the brain mass and body mass were averaged. For the data set from the study of Mace *et al.* (1981), we corrected for measurement error by subtracting 0.59 g from all rodent species from this data set as proposed by Isler & van Schaik (2006). In some instances, brain size was measured and reported as endocranial volume, which was converted to brain mass in grams by multiplying the volume by 1.036 (Stephan *et al.*, 1981). For cases that had only brain mass of an individual and no recorded body measurement, the body weight was averaged from *CRC Handbook of Mammalian Body Masses* (Silva & Downing, 1995). These procedures resulted in 630 adult mammalian species from 21 orders (Table S1) being included in our analysis. The female data set is a subset of this larger data set, including only measurements from adult female individuals ($n = 130$).

Phylogenetic comparative methods

Character states in related species should not be considered statistically independent, because they are inherited from a common ancestor (Felsenstein, 1985, 2008; Garland *et al.*, 1992). We corrected for nonindependence of character states using two methods: 1) independent contrasts (Felsenstein, 1985) and phylogenetic generalized least squares (PGLS). Both methods were calculated from log-base-10-transformed body and brain mass data and a time-calibrated supertree of mammals (Bininda-Emonds *et al.*, 2007). Taxa for which we did not have data were pruned from this tree. Independent contrasts were calculated using PDAP:PDTREE (Midford *et al.*, 2005) in MESQUITE version 2.74 (Maddison & Maddison, 2009). We took an approach similar to the generalized least squares (GLS) method by transforming the branch lengths and accounting for polytomies (Paradis, 2006). As suggested in Garland *et al.* (1992), the absolute values of the contrast were plotted against their standard deviations and were found to have no correlation ($r^2 = 0.001$, $P = 0.35$), suggesting an appropriate branch length transformation. The branch lengths were transformed using the method of Grafen (1989) with a rho of 0.5. Polytomies were counted using a Perl script that searched the tree from the tips to the root and counted the number of branches, indicated by commas in the tree file. Independent contrasts were standardized by dividing raw contrasts by their standard deviations.

Phylogenetic generalized least squares was performed in BayesTraits (Pagel,1997) using the random-walk model, as the directional model cannot be performed with ultrametric trees. We followed a method similar to that of Capellini *et al.* (2011a,b) and tested for phylogenetic signal (λ parameter) in our data. The λ parameter predicts the pattern of covariance among species on a given trait, whereas a λ set to 0 allows for no phylogenetic signal (the data are independent) and can be considered equivalent to ordinary least squares regression (OLS). A λ set to 1 suggests species are not independent and can be considered similar to independent contrasts. The λ parameter was estimated by maximum likelihood (ML) and likelihood ratios (LR) were computed, where LR equals the absolute value of $2 \times$ [(likelihood score of the best-fitting model) − (likelihood score of the worst-fitting model)], to determine the best-fitting model (see Table S2). The λ estimated with ML was found to be a significantly better predictor of phylogeny, and this model was used for PGLS analysis.

Encephalization quotient

Encephalization was quantified by the calculation of an EQ, derived by the allometric formula $E = kP^{\alpha}$, where E = brain mass, P = body mass, $k = y$-intercept (proportionality constant) and α = allometric exponent (Snell, 1891; Huxley, 1950; Gould, 1971; Jerison, 1973). After this equation is log-transformed, the slope of the line corresponds to the allometric exponent, whereas the y-intercept indicates the encephalization level, independent of body size (Kruska, 2005). When this allometric formula is applied, EQ is a ratio of observed brain mass to ''expected'' brain mass, where the expected brain mass is derived from the body mass of that species, using the following equation, $EQ = E/kP^{\alpha}$. If the EQ is > 1, the brain mass is larger than expected for a species of that body size. We used our new data set to derive the EQ equation from the log body mass vs. log brain mass linear LSR line plotted in this study (Fig. 1a). We have chosen

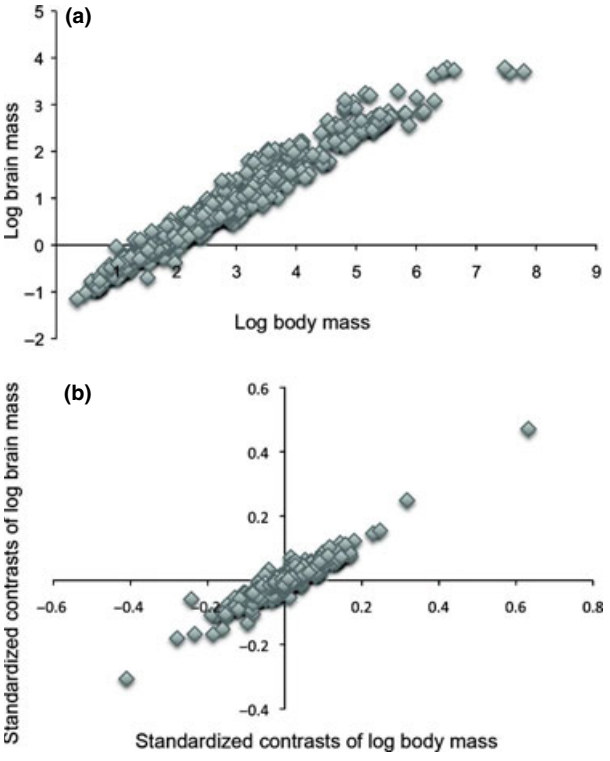

Fig. 1 (a) Relationship between log brain mass (g) and log body mass (g) in adult mammals (n = 630). (b) Relationship between standardized contrasts of log body mass and log brain mass.

to use this regression line to derive the EQ equation rather than the independent contrast or PGLS regression line because by taking phylogeny into consideration, the tip data have been transformed into values that are statistically independent and can no longer be used in the same biological context as the standard nonphylogenetic regression line. The 0.746 exponent is the slope of the log body mass vs. log brain mass regression line (Fig. 1a), and this regression line has a y-intercept of −1.253. Based on the allometric formula $E = kP^{\alpha}$, and after log transformation of the y-intercept (see Jerison, 1973), the formula is EQ = brain mass/0.056 × body mass$^{0.746}$. The independent contrast regression line has a slope of 0.631 and a y-intercept of −0.0008, and the formula is EQ = brain mass/0.998 × body mass$^{0.631}$ and the PGLS regression line has a slope 0.60 and a y-intercept of −0.89, with a formula of EQ = brain mass/0.128 × body mass$^{0.60}$. As one can see, the y-intercepts of the regression lines are very different because the phylogenetically controlled regression lines are based on residuals of body and brain measurements and not actual measurements. Because of this, the calculated EQs for the equations are distinctly different. For example, humans have an EQ of 5.72 when using the standard regression line (Fig. 1a) – derived equation, whereas the EQ decreases to 1.16 in the independent contrasts analysis and 12.6 for the PGLS-derived equation. There is a significant correlation between the standard and independent contrast EQ values (F = 2423, r^2 = 0.79, P < 0.0001), as well as the standard and PGLS-derived EQ values (F = 1557, r^2 = 0.71, P < 0.0001) (Fig. S3). However, to determine the effect of phylogenetic relationships, all statistical tests were performed using the independent contrasts and PGLS-derived EQ as well as the standard regression line – derived EQ. Results remained significant after accounting for phylogeny (Figs S3, S5 and S6). Therefore, to retain the same biological context as other encephalization studies, we chose to mainly report EQ values using the standard log brain mass vs. log body mass regression line in the main body of the text (Fig. 1a).

Statistical analyses

Linear LSR analysis and box plot statistics were performed using GRAPHPAD PRISM version 5.0 for Mac OS X (GraphPad Software, San Diego, CA, USA, http://www.graphpad.com). LSR was used to derive the EQ because EQ is calculated from a prediction equation, a ratio of observed to expected brain mass, and LSR allows for uncertainty regarding the y-variable. To estimate the scaling relationships in clades, we chose to use reduced major axis regression (RMA), which is appropriate for studies of scaling in comparative biological data because variation in both the x- and y-variables is taken into account. We tested whether Primates and Cetartiodactyla RMA slopes deviated significantly from other mammals using the software program, Standardised Major Axis Tests & Routines (SMATR) version 2.0 (Falster *et al.*, 2006). All regression analyses were performed with log body mass on the x-axis and log brain mass on the y-axis. To determine whether EQs were statistically different in sister clades, we performed a Mann–Whitney two-tailed test on the mean EQ of the clades using GRAPHPAD PRISM. Levene's test of equality of variance was performed in SPSS.

Ancestral state reconstruction

Ancestral reconstructions of EQ, body mass and brain mass were all completed using the time-calibrated revised supertree of Bininda-Emonds *et al.* (2007) with absent species pruned. Weighted squared parsimony model of Maddison (1991) was performed in MESQUITE version 2.74 (Maddison & Maddison, 2009). ML reconstructions were performed using the analysis of phylogenetics and evolution (APE) package (Paradis *et al.*, 2004) in R version 2.7.1 (R Development Core Team 2008), using the method of restricted maximum likelihood (REML). We used the standard regression line (Fig. 1a) to calculate the EQ for these reconstructions. All character-state reconstructions were performed using the full data set, n = 630, and the female-only data set, n = 130.

Results

Allometric relationship between body mass and brain mass in mammals

To calculate the relationship between body mass and brain mass among adult mammalian species in our data set (Table 1), we performed linear LSR analysis of log body mass vs. log brain mass (Fig. 1a). Similar to previous studies, our results demonstrate a significant negative allometric relationship ($F_{1,628}$ = 13 230, slope = 0.75, r^2 = 0.955, $P < 0.0001$) between these character states (Fig. 1a). Notably, two clades deviated from the general mammalian regression line, Primates and Cetartiodactyla (Fig. S1). Using the software SMATR, we tested whether these clade-specific RMA regression lines differed significantly from the brain–body allometric relationship of other mammals. Cetartiodactyla (slope = 0.64, r^2 = 0.762) had a significantly shallower slope when compared to all other mammals in the analysis (F = 4.62, P = 0.032, ANCOVA). Primates (slope = 0.82, r^2 = 0.908) had a significantly steeper slope as compared to other mammals (F = 7.81, P = 0.006, ANCOVA).

Our full data set includes measurements from both males and females; however, sexual dimorphism within species may affect the brain–body allometric scaling relationship, as comparative studies are highly dependent on these measurements and even small changes could affect the results. Taking this into consideration, we analysed a reduced data set of only adult females representing 130 species from 13 orders. LSR analysis of the log brain mass vs. log body mass data demonstrated a significant relationship ($F_{1,628}$ = 1283, slope = 0.68, r^2 = 0.91, $P < 0.0001$) between body size and brain size (Fig. S2). However, the female-only data set yielded a significantly lower slope than the combined male/female data set (P = 0.0001, ANCOVA). The female-only data set was comprised of mostly Primates (36%) and Carnivora (31%), whereas a large proportion of the male/female data set consisted of mostly Rodentia (41%) followed by Primates (12%). To take phylogeny into consideration, we performed both independent contrast and PGLS. LSR analysis of independent contrasts confirmed a significant negative allometric relationship ($F_{1,628}$ = 4707, slope = 0.63, r^2 = 0.88, $P < 0.0001$) to body mass and brain mass. Prior to running PGLS, we first tested for phylogenetic signal (λ) and found that the ML λ estimation (λ = 0.96) was a significantly better predictor of phylogeny than either $\lambda = 1$ or $\lambda = 0$ (LR = 734.6, $P < 0.0001$ and LR = 72.8, $P < 0.0001$, respectively) (Table S2). Similar to independent contrasts, PGLS confirmed a significant negative relationship between body mass and brain mass (slope = 0.60, r^2 = 0.85, $P \leq 0.0001$). We found the independent contrast and PGLS-derived EQs (Table S1) to be highly correlated ($F_{1,628}$ = 30 676, r^2 = 0.98, $P < 0.0001$) (Fig. S3).

Table 1 Summary of species included in analysis.

Order	Number of species	Mean EQ
Monotremata	3	0.80
Didelphimorphia	13	0.82
Paucituberculata	1	1.29
Dasyuromorphia	18	0.87
Peramelemorphia	9	0.52
Diprotodontia	33	0.78
Rodentia	258	0.98
Lagomorpha	15	0.77
Scandentia	3	1.44
Primates	76	2.38
Carnivora	60	1.07
Perissodactyla	3	1.00
Cetartiodactyla	35	1.42
Chiroptera	42	0.99
Eulipotyphla	33	0.89
Xenarthra	9	0.79
Afrosoricida	12	0.64
Macroscelidea	3	1.11
Hyracoidea	1	1.07
Sirenia	1	0.27
Proboscidea	2	1.27

EQ, encephalization quotient.

Ancestral reconstruction of relative brain size

In determining the EQ, we used the following equation, EQ = brain mass/(0.056 × body mass $^{0.746}$) derived from the log brain mass vs. log body mass LSR line of our complete adult mammalian data set described above (Fig. 1a). To trace the evolution of encephalization among mammals, we reconstructed the ancestral state of the EQ for all mammalian species using the phylogenetic relationships of the study of Bininda-Emonds *et al.* (2007) (Nexus File 1, Supporting information). Reconstructions were performed using both parsimony and ML methods. The inferred ancestral values were nearly identical, and therefore, we present only the parsimony results. Ancestral values for both methods can be found in the supplement. The inferred EQ for the last common ancestor (LCA) of all extant mammalian species was 0.94. Eutheria had an inferred EQ value of 1.03, Boreoeutheria had 1.06 (1.15 and 1.02 for Euarchontoglires and Laurasiatheria, respectively) and Metatheria had an inferred EQ of 0.88. EQ values extended from a minimum of 0.14 in the fin whale (*Balaenoptera physalus*) to a maximum of 5.72 in *Homo sapiens*.

As mammalian orders are monophyletic and originated at approximately the same time (Meredith *et al.*, 2011), we examined the range of EQs found in each order. This allowed us to examine broadly phylogenetic patterns while also exploring variations in EQ (Fig. 2). Primates (F_{593} = 176.7, $P < 0.001$, Levene's test) and Cetartiodactyla (F_{552} = 265.0, $P < 0.001$, Levene's test) had a significantly larger variance in EQ when compared to other mammals. When taking phylogeny into consideration,

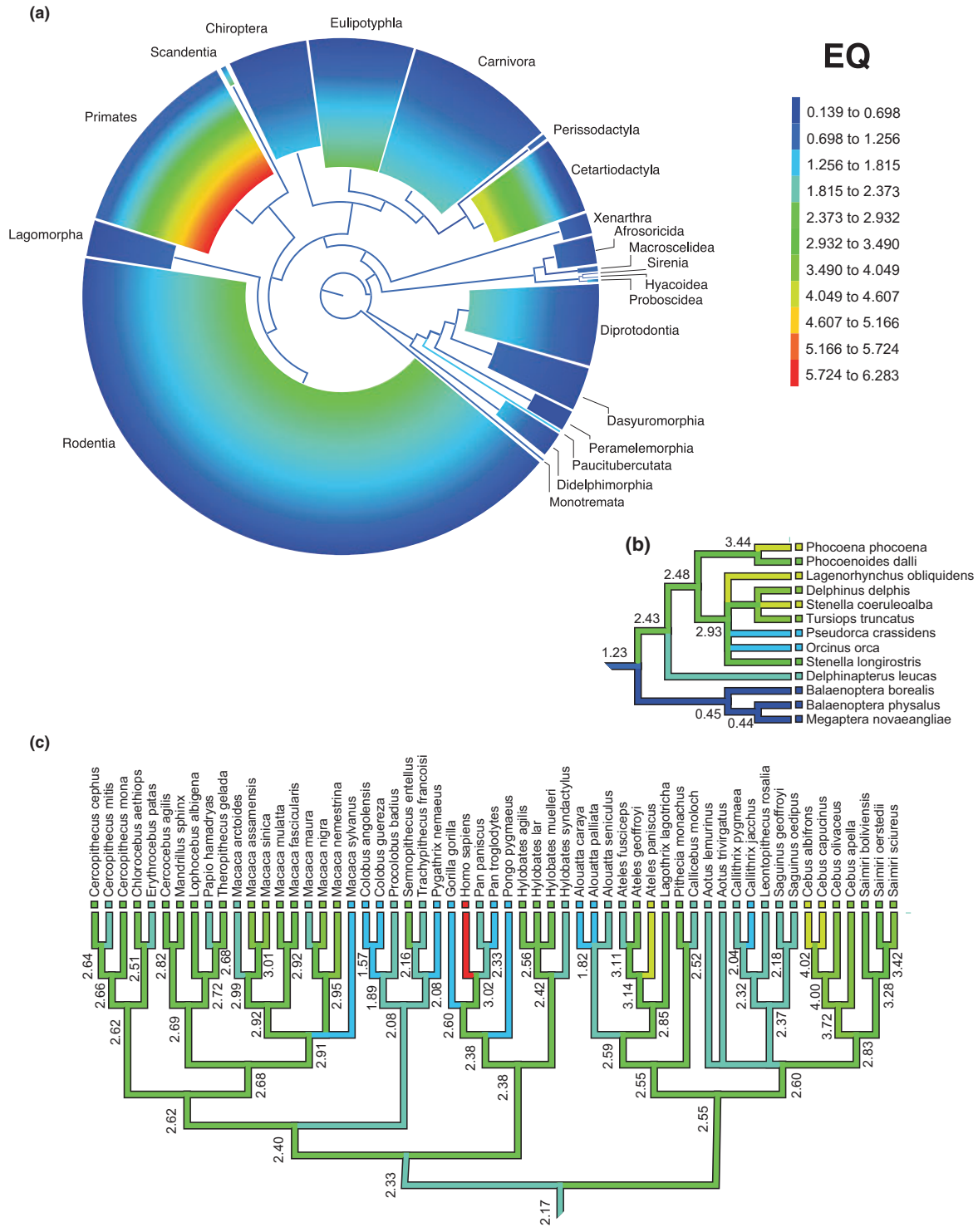

Fig. 2 Character history reconstruction of the EQ of 630 mammalian species using the weighted squared parsimony model in MESQUITE and the time-calibrated supertree of Bininda-Emonds *et al.*'s study (2007). EQ was divided into 11 bins (see key on top right), with each colour representing a specific range of EQ, the darkest blue indicating the lowest EQ range and red indicating the highest EQ range. If the EQ range is present in that order, the colour range is represented as a gradient on the tree. (a) Phylogeny of mammals is condensed so that each box indicates a specific mammalian order and the size of the box represents the number of species included from that order. (b, c) Detailed view of the evolutionary history of EQ in (b) Cetacea and (c) Anthropoidea. Numbers at each node indicate the inferred ancestral EQ.

Primates and Cetartiodactyla continued to have a significantly larger variance in EQ (Fig. S3). EQ values within these highly encephalized taxa ranged from 0.90 to 5.72 in Primates and 0.14–4.43 in Cetartiodactyla. Other clades had considerably less variation in EQ, and the next two most variable orders were Rodentia (0.25–2.26) and Eulipotyphla (0.39–2.92).

EQ within Primates and Cetartiodactyla

We calculated the mean and range of EQ for each mammalian order in this analysis (Fig. 3). As previously observed, the two orders that encompassed the largest variance in EQ were Primates and Cetartiodactyla; therefore, we investigated these orders in more detail by comparing the mean EQs of nested sister clades. Within Primates (Fig. 4), the Haplorrhini (mean EQ = 2.64) were significantly different ($U = 149.0$, $P < 0.0001$) in mean EQ when compared with the Strepsirrhini (mean EQ = 1.63). Within Haplorrhini, the anthropoid primates (mean EQ = 2.65) demonstrated the largest mean EQ; however, there was no significant difference between the anthropoid sister taxa of Catarrhini (mean EQ = 2.57) and Platyrrhini (mean EQ = 2.77) ($U = 337.0$, $P = 0.482$), suggesting neither group has a greater average relative brain size. Anthropoid primate EQ values ranged from 1.31 in *Gorilla gorilla* to 5.72 in *H. sapiens* (Table S1).

Upon further investigation into the Cetartiodactyla, comparisons between the clades Ruminantia (mean EQ = 0.86) and Cetancodonta (mean EQ = 2.28) demonstrated that the mean EQ of Cetancodonta significantly differed from that of Ruminantia ($U = 72$, $P = 0.042$). Within Cetancodonta, Cetacea (mean EQ = 2.43) was responsible for the large mean EQ in comparison with Hippopotamidae (mean EQ = 0.34). Comparisons of the sister taxa Mysticeti (mean EQ = 0.21) and Odontoceti (mean EQ = 3.10) revealed that the Odontoceti was solely responsible for the large peak in EQ within Cetartiodactyla ($U = 0$, $P = 0.007$) (Fig. 5).

In our study, Proboscidea had an average EQ of 1.27 (Table 1; *Loxodonta africana* [EQ = 1.09] and *Elephas maximus* [EQ = 1.46]). Interestingly, when taking phylogeny into consideration, Proboscidea was the only group to have a notable shift in relative brain size (Fig. S4). Although Carnivora had an average EQ of 1.07,

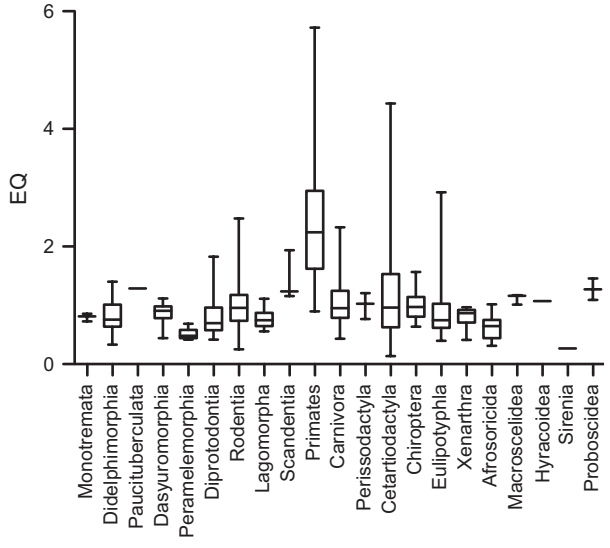

Fig. 3 Box plot representing the mean, interquartile, and range of EQs for 21 different mammalian orders included in this analysis.

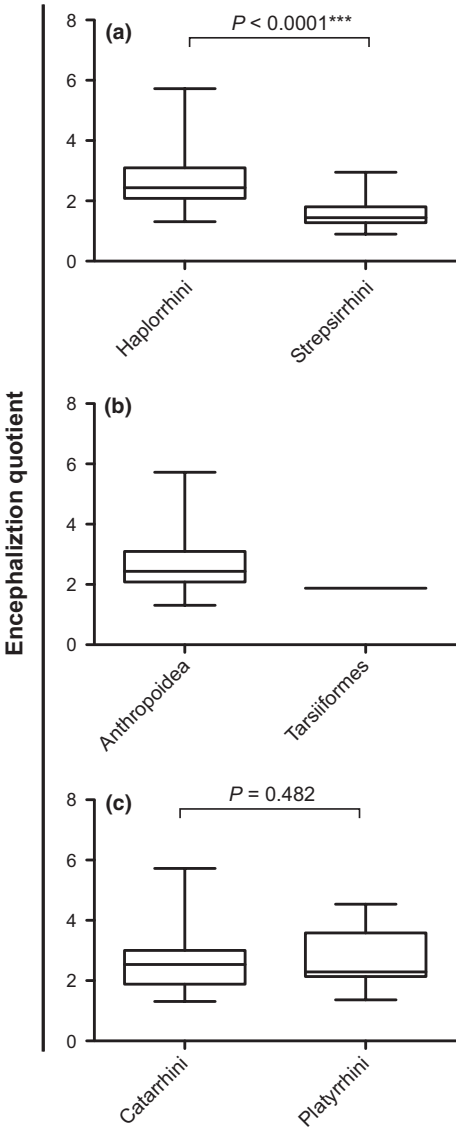

Fig. 4 Box plots representing comparison of mean, interquartiles, and range of EQ in primate sister clade pairs, including (a) Haplorrhini and Strepsirrhini, (b) Anthropoidea and Tarsiiformes, (c) Catarrhini and Platyrrhini. Tarsiiformes *P*-value was not obtainable in this analysis due to the limited number of species ($n = 1$).

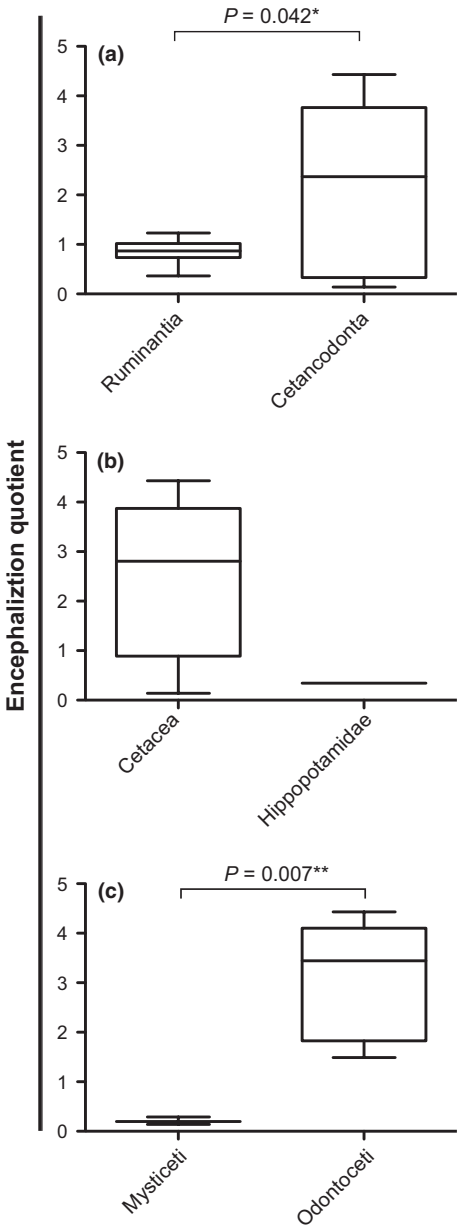

Fig. 5 Box plots representing comparison of mean, interquartiles, and range of encephalization quotient in cetartiodactyl clades, including (a) Ruminantia and Cetancodonta, (b) Cetacea and Hippopotamidae, (c) Mysticeti and Odontoceti. Hippopotamidae *P*-value was not obtainable in this analysis due to the limited number of species ($n = 1$).

certain groups within this order had higher-than-average EQ values for the clade, including Canidae (mean EQ = 1.41), where EQ values ranged from 1.10 in *Otocyon megalotis* to 1.92 in *Vulpes vulpes*, Ursidae (mean EQ = 1.38), where EQ values that ranged from 0.71 in *Melursus ursinus* to 2.33 in *Heloarctos malayanus*, and Musteloidae (mean EQ = 1.41), where EQ values ranged from 0.63 in *Mephitis mephitis* to 2.05 in *Bassariscus sumichrasti*. Rodentia, the largest order in the analysis ($n = 258$), had a mean EQ of 0.98, and although most species in this order had an EQ of close to 1, there were a few outliers including *Gerbillus dasyurus* (EQ = 2.48), *Tamiops macclellandi* (EQ = 2.26) and *Tscherskia triton* (EQ = 2.09). Unexpectedly, within Eulipothyphla, the Talpidae (mean EQ = 1.69) also had a higher-than-average EQ, with values ranging from 0.97 in *Talpa europaea* to 2.92 in *Neurotrichus gibbsii*. *Neurotrichus* is the smallest of the American moles, with a body mass ranging from 9 to 11 g (Nowak, 1991).

Increases and decreases in relative brain size in anthropoid primates and cetaceans

Within Primates (crown node EQ = 1.45), the LCA of extant Platyrrhini was estimated to have an EQ of 2.55, and reconstructions within the suborder ranged from 1.82 for crown *Alouatta* to 3.72 for crown *Cebus*. A similar pattern in the change in EQ can be found among Catarrhini as well (crown EQ = 2.33), in which the reconstructed EQ ranged from 1.57 for crown *Colobus*, to 3.02 for the most recent common ancestor of humans and chimpanzees. These results demonstrate that relative brain mass both increased and decreased within major primate clades during evolution. For cetaceans (crown EQ = 1.23), similar patterns of concomitant expansion and reduction emerged. The ancestral EQ for crown Mysticeti (EQ = 0.45) was much lower than the reconstructed LCA for crown Cetacea, whereas the ancestral EQ for crown Odontoceti (EQ = 2.43) was much higher. The ancestral state reconstruction on the exclusively female data set when compared to the full data set that included both sexes revealed very similar patterns (Nexus File 2, Supporting information).

One limitation to reconstructing the ancestral EQ is that this method cannot determine whether an encephalization event was due to a change in brain mass or body mass with respect to an ancestral species. To address this issue, we separately reconstructed the ancestral states in both brain and body mass (Nexus File 3, Supporting information). When using this approach, we traced the body and brain mass reconstructions and determined whether changes in EQ were due to alterations in brain mass, body mass, or both measures. For example, both *Homo* and *Cebus* demonstrated an increase in EQ when compared to the ancestral state (Fig. 2). After estimating brain and body mass separately, both genera show a larger increase in brain size than body size when compared to the ancestral state. For example, since the LCA of apes, body mass increased from 28.8 to 65.1 kg ($\sim$ 2-fold) in the last $\sim$ 18 Myr on the *Homo* lineage, whereas the brain mass increased nearly fivefold, from 254.6 to 1250.4 g. Since the LCA of *Cebus*, body mass increased slightly over the last $\sim$ 18 Myr from 1.3 to

2.2 kg, whereas the brain mass more than doubled in size, from 32.4 to 69.1 g. Both *Alouatta* and *Colobus* are inferred to have undergone a decrease in EQ compared to ancestral state (Fig. 2). According to the body and brain mass reconstructions, *Alouatta*'s body mass nearly doubled from 2.5 to 4.3 kg in the last ~ 19 Myr, whereas the brain mass stayed nearly constant (47.2–48.7 g). The brain size decreased in *Colobus* from 91.1 to 79.0 g, whereas the body mass increased from 6.6 to 8.9 kg in the last ~ 19 Myr, leading to a decrease in EQ.

Among cetaceans, Mysticeti demonstrated a decrease in relative brain size, whereas Odontoceti increased in relative brain size as compared to their ancestral EQ (Fig. 2). Ancestral reconstructions of body and brain mass data reveal that brain mass increased in crown Odontoceti from the crown Cetacea (471.76–1101.36 g), whereas the body mass decreased slightly from 267.9 to 242.9 kg. Although crown Mysticeti brain mass also increased by < 1 order of magnitude compared to crown Cetacea (471.76–2997.6 g), body size increased ~ 1.5 orders of magnitude, 267.9–12 380.2 kg.

Discussion

We curated data on brain and body mass for new and previously published measurements in 630 mammalian species. Using these data, we confirmed a scaling exponent value of 0.75 for the complete data set and calculated the EQ for each species based on the standard regression (Fig 1a). There was a reduction in the overall slope when accounting for phylogeny. It has been suggested that this disparity in slope could be due to a bias in contrasts within a specific group (Isler *et al.*, 2008). The integration of phylogenetic history did not eliminate the significant relationship between brain and body size, nor did it have any effect on statistical significance of this relationship. Additionally, the much smaller female data set that consisted of 130 species also displayed a reduction in slope compared to the overall data set. This reduction in slope is likely due to lack of small (i.e. *Suncus etruscus*) and large (i.e. *B. physalus*) species, which leads to a smaller range in brain and body mass among the female data set compared to the complete data set.

Evaluations of relative brain mass in mammals revealed highly encephalized species among primates and cetaceans; however, we were interested not only in the most encephalized species but in the variance in encephalization within mammalian orders. By taking a phylogenetic approach, we found primates and cetaceans encompassed the widest range in EQ among mammals (Fig. 3). Anthropoid primates and odontocete cetaceans were found to have a significantly larger EQ than their respective sister clades (Fig 4). Additionally, we used our data set to infer the ancestral states of EQ, brain mass and body mass and found evidence of both increasing and decreasing relative brain mass within primate and cetacean lineages. These results generally extend findings by Shultz & Dunbar (2010), who showed encephalization patterns vary across different mammalian groups during evolution. Together, these results suggest relaxed phylogenetic constraints on brain and body mass coevolution in anthropoid primates and cetaceans.

Lineages with evidence of encephalization

Along with primates and cetaceans (discussed in detail below), various studies have indicated a possible increase in EQ in other mammalian orders, including Proboscidea and Carnivora (Hart *et al.*, 2008; Mazur & Seher, 2008; Finarelli & Flynn, 2009). In the current study, the family Ursidae ranged widely in EQ, from EQ = 0.71 in *M. ursinus* to EQ = 2.33 in *H. malayanus*. Consistent with our results, Finarelli & Flynn (2009) reported that Canidae, Ursidae and Musteloidea have independent and significant increases in brain size. Social learning abilities are correlated with brain size in primates (Reader & Laland, 2002), and black bears have demonstrated social learning through food conditioning, teaching cubs to forage for human food or trash as opposed to wild foraging (Mazur & Seher, 2008).

Elephants, which possess the largest absolute brain size among terrestrial mammals, exhibit complex social and cognitive abilities and have demonstrated examples of tool use (Hart *et al.*, 2008). Prior to taking phylogeny into consideration, these large mammals were not identified as having high EQs relative to other mammals (*L. africana* [EQ = 1.09] and *E. maximus* [EQ = 1.46]). Our results are consistent with those of Shoshani *et al.*'s study (2006), which calculated the EQs of elephants to range from 1.13 to 2.36 (Shoshani *et al.*, 2006). When phylogeny was taken into account, elephants display an increase in relative brain size (Fig. S4), suggesting that brain enlargement is more pronounced in the narrow comparison to their close relatives.

Adaptive explanations for variation in brain size

Previous studies have proposed adaptationist explanations in which physiological and ecological factors have been hypothesized to support increases in brain size among mammals. The maternal energy hypothesis (Martin, 1996) proposes that the mother's investment in the offspring influences brain size and demonstrates a correlation between the maternal BMR and the brain size of offspring. An alternative explanation for the evolution of encephalization is the expensive tissue hypothesis (Aiello & Wheeler, 1995), which proposed that instead of increasing BMR to supply more energy for increased brain size, reductions in gut size or other energetically expensive organs allow for the reallocation of energy to the brain. In contrast to these two hypotheses concerning the evolution of encephalization, the social brain hypothesis does not take into consideration brain energetics

(Dunbar, 1998). Instead, this adaptationist perspective proposes that the evolution of a relatively large neocortex is a direct result of complex social demands within a species, as social relationships are hypothesized to be cognitively demanding.

In support of the expensive tissue hypothesis (Aiello & Wheeler, 1995), we found increases and decreases in EQ values of certain primate lineages over time. For example, the EQs of ancestral species that were phylogenetically reconstructed in the current study demonstrate that howler and colobus monkeys (*Alouatta* and *Colobus*), both folivores with large guts (Milton, 1998), independently underwent decreases in EQ during their evolution. These folivores have an enlarged large intestine to help digest the carbohydrates that are predominant in leaves, grasses and stems (Chivers & Hladik, 1980). As proposed by the expensive tissue hypothesis, freed energy from a reduced gut may have allowed for the increase in brain size among primates. The same hypothesis can be applied here in reverse; reducing the brain size might have freed up energy, allowing for a reallocation of energy to maintain a large gut size. This possibly allowed these folivorous primates (e.g. leaf-eating colobus monkeys) to exploit a new diet rich in leaves and grasses. Interestingly, similar patterns are demonstrated in gorillas, where brain size has not changed substantially from the reconstructed ancestral state, even though body size has increased dramatically. Eighty-five percentage of their diet consists of leaves, shoots and stems (Nowak, 1991), and gorillas have the lowest EQ (1.31) among anthropoid primates. However, there are conflicting views regarding correlation between diet quality or gut size and relative brain size (Allen & Kay, 2011; Hartwig *et al.*, 2011; Navarrete *et al.*, 2011).

Although it is possible to relate an individual's metabolic allocation among organs to the evolution of encephalization, other perspectives exist. Martin (1996) suggested that the primary link in the evolution of encephalization is that between the developing brain of offspring and the mother's metabolic capacity. Thus, leaf-eating monkey mothers whose diet is relatively poor will have less metabolic capacity from which they can provide nutrients to their developing offspring, resulting in relatively small brains. Moreover, the low metabolic capacity in mothers of these species may constrain the development of large social groups (Martin, 1996).

In addition to metabolic allocation (Aiello & Wheeler, 1995) and maternal metabolic capacity (Martin, 1996) as driving forces of adaptations associated with the evolution of encephalization, social complexity has been implicated (Dunbar, 1998; Shultz & Dunbar, 2010). In this view, increased sociality drives brain evolution (i.e. the social brain hypothesis). It has been proposed that the emergence of complex sociality requires enhanced cognitive abilities (Dunbar, 1998; Whiten & van Schaik, 2007). This viewpoint first assumes that a brain that is larger than expected by body mass enhances cognitive abilities, and it also assumes that social behaviour is the driving cause of cognitive enhancements. In other words, there is a selective advantage gained by social acumen, and a relatively large brain facilitates social advantages. It is thus not surprising that we observed deviations in brain–body scaling in cetaceans, specifically odontocetes, as this has been previously observed in other studies (Worthy & Hickie, 1986; Marino, 1998, 2002; Marino *et al.*, 2004), and in support of the social brain hypothesis, several odontocete cetacean species are characterized by complex social groups (i.e. cooperative actions and fission–fusion societies) (Marino, 2002). Similar to primates, cetaceans demonstrate encephalization and de-encephalization among lineages; for example, as compared to the reconstructed EQ of the stem Cetacea, there is a pronounced decrease in EQ of the Mysticeti clade and a distinct increase in the EQ of the Odontoceti. Ancestral reconstructions of body and brain mass revealed there was a rapid increase in mysticete body mass compared to the reconstructed EQ of the cetacean LCA; the brain mass also increased, although at a much slower rate. The size of baleen whales may be related to the massive biomechanical forces needed to open their mouths when feeding (Goldbogen *et al.*, 2007). With respect to odontocetes, high encephalization was acquired at least 10 Myr after the adoption of a fully aquatic lifestyle by Archaeoceti ancestors in the Eocene, indicating that the relatively large brains of odontoctes, and particularly delphinids, could have been related to the emergence of social complexity and/or the acquisition of the novel sense of echolocation (Marino *et al.*, 2007); however, this remains to be explicitly tested.

Neutral evolution and brain–body allometry

It has long been appreciated that primates and toothed whales have larger brains than would be predicted by body mass in other mammals (Jerison, 1973; Martin, 1981; Worthy & Hickie, 1986; Marino, 1998, 2002; Barton, 2006), and in the present study, we have demonstrated that increased *variance*, in addition to an increase in relative brain mass, characterizes the most encephalized mammalian lineages. Primates (0.90–5.72) and cetaceans (0.14–4.43) have a significantly greater range in EQ than other mammalian orders. That is, these two groups encompass the most encephalized species (i.e. humans and dolphins), as well as species with lower-than-expected relative brain size (i.e. lemurs), to the smallest relative brain size (i.e. baleen whales). Although adaptive explanations for the evolution of encephalization, such as those discussed above, are attractive, other possible explanations should also be considered.

As in neutral mutation at the molecular level, we suggest that small changes in phenotype may have little, if any, consequences on the fitness of an organism. Ohta (1973, 1974) proposed that mutations that are nearly neutral (slightly deleterious) are more likely to become

fixed in populations with small sizes. This is because the effects of random drift are stronger in small populations (Hartl & Clark, 2007; Hedrick, 2011). At the phenotypic level, the expectation of the nearly neutral theory would be that shifts in phenotypes would become fixed more rapidly in small populations, resulting in increased phenotypic diversity among related lineages with small population sizes and more homogenous phenotypes among related lineages with large populations. For example, primates are notable among mammals, in that they generally have small population sizes in comparison with other orders such as rodents (Ohta, 1998). It is thus reasonable to consider that some of the phenotypic diversity in primate brain–body allometry might not be strictly associated with selective pressures (i.e. social complexity), but rather a result of neutral, or at least nearly neutral, evolution in small populations. Indeed, some other studies have emphasized the importance of other features in the evolution of the brain irrespective of brain size such as subtle modifications of neocortical circuits (Hakeem *et al.*, 2009; Jacobs *et al.*, 2010), gyrification of the neocortex (Zilles *et al.*, 1989; Marino *et al.*, 2007; Rogers *et al.*, 2010) and neuronal density (Herculano-Houzel, 2011).

Study limitations

It should be noted that there are limitations in accurately measuring whole brain mass and body mass, with the resulting calculation of EQ depending on these measurements. Most studies in the primary literature containing empirical data from brain and body measurements across diverse species are more than 50–100 years old. Additionally, many studies do not describe details such as when (i.e. how long after time of death) the individuals were measured or whether the animal was ill prior to death. Due to the difficulties of obtaining well-controlled brain and body mass measurements without sacrificing the animal, it is probable that some of the animals in this study were weighed after signs of emaciation, as they may have been deceased for hours or days prior to being weighed.

We acknowledge that another limitation to this study is the lack of inclusion of data derived from extinct species; however, the uncertainties of body mass reconstruction as well as taxonomic uncertainty among fossil taxa pose a serious challenge to direct evaluation of the evolution of encephalization. Nonetheless, the careful addition of data from the fossil record could provide a secondary assessment of the accuracy of ancestral state reconstructions (Finarelli & Flynn, 2006). In this study, the reconstructed EQs for stem taxa may be overestimates if there is a trend towards increasing brain size within a lineage over time (Shultz & Dunbar, 2010). For example, fossil taxa in early anthropoid primates appear to be less encephalized than their modern descendants (Simons *et al.*, 2007). In our data set, the most recent common ancestor of humans and chimpanzees was estimated to weigh 52.8 kg and have a brain mass of 477.5 g. According to the fossil record, *Ardipithecus ramidus* from 4.4 Ma is estimated to have had a body mass of 51 kg and brain mass of 300–350 g (Lovejoy *et al.*, 2009; Suwa *et al.*, 2009). *Australopithecus afarensis* from $\sim$ 3.7 to 2.9 Ma is estimated to have had a body mass of 35 kg and brain mass of 430 g (McHenry, 1982). Although it is not entirely clear how closely these species represent the character states of the most recent common ancestor of humans and chimpanzees, they are usually considered to fall early on the lineage leading to humans, prior to a general trend of increasing brain size to *H. sapiens*. From these estimates, we can conclude that our ancestral reconstructions are reasonable with respect to both brain and body mass for the hominin stem, but the addition of fossil data would aid in generating more accurate estimates.

Conclusion

In this study, we examined brain mass and body mass data from adult mammalian species, calculated the EQ for each and traced encephalization, body mass and brain mass through time. We confirmed there was a significant relationship between body mass and brain mass among species in our data set, with an exponent of 0.75 that agrees with several previous studies (Pilbeam & Gould, 1974; Martin, 1981). The relationship remained significant after correcting for the nonindependence of the character traits, although the value of the exponent was decreased. This strong relationship between brain and body mass allows one to calculate an EQ for a given species in the data set based on the scaling law that generally characterizes mammals. Results demonstrated that anthropoid primates and cetaceans exhibit the greatest variance in EQ values among mammals, and we suggest that changes in relative brain mass may not always be due to natural selection. Ancestral reconstructions revealed evidence for both increases and decreases in brain size throughout evolutionary history, most distinctively in primates and cetaceans.

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Supporting information

Additional Supporting information may be found in the online version of this article:

Figure S1 A colored graphical representation of the log brain mass vs. log body mass plot (Fig. 1a)
Figure S2 A graphical representation of the relationship between log brain mass vs. log body mass in our adult female dataset ($n = 130$), linear regression analysis demonstrated a significant relationship ($F_{1,128} = 1283$, slope = 0.68, $r^2 = 0.909$, $P < 0.0001$) between body mass and brain mass.
Figure S3 To take phylogeny into consideration, we have calculated the EQ based on three regression lines, the log brain vs. log body regression line of Fig. 1a, the independent contrast regression line of Fig. 1b and the PGLS regression line.
Figure S4 A comparison of the mean and range of EQs for the 21 different mammalian orders for the log brain vs. log body regression line derived EQ (A), the independent contrast derived EQ (B), and the PGLS derived EQ (C)
Figure S5 A comparison of the mean and variance distributions of EQ in primate sister clade pairs, for the log brain vs. log body regression line derived EQ (A, B, C), the independent contrast derived EQ (D, E, F), and the PGLS derived EQ (G, H, I)
Figure S6 A comparison of the mean and variance distributions of EQ in cetartiodactyl clades, for the log brain vs. log body regression line derived EQ (A, B, C), the independent contrast derived EQ (D, E, F), and the PGLS derived EQ (G, H, I)
Table S1 Brain mass, body mass, and EQ dataset of 630 mammals
Table S2 PGLS phylogenetic signal (λ) values from BayesTraits
Table S3 Summary of parsimony and REML ancestor value reconstructions for key nodes
Table S4 Ancestral reconstruction of body mass, brain mass, and EQ for REML

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