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## KEYWORDS

brain size, body size, cetaceans, dolphins, encephalization, evolution, macroevolution, whales

## ABSTRACT

*Cetaceans rival primates in brain size relative to body size and include species with the largest brains and biggest bodies to have ever evolved. Cetaceans are remarkably diverse, varying in both phenotypes by several orders of magnitude, with notable differences between the two extant suborders, Mysticeti and Odontoceti. We analyzed the evolutionary history of brain and body mass, and relative brain size measured by the encephalization quotient (EQ), using a data set of extinct and extant taxa to capture temporal variation in the mode and direction of evolution. Our results suggest that cetacean brain and body mass evolved under strong directional trends to increase through time, but decreases in EQ were widespread. Mysticetes have significantly lower EQs than odontocetes due to a shift in brain:body allometry following the divergence of the suborders, caused by rapid increases in body mass in Mysticeti and a period of body mass reduction in Odontoceti. The pattern in Cetacea contrasts with that in primates, which experienced strong trends to increase brain mass and relative brain size, but not body mass. We discuss what these analyses reveal about the convergent evolution of large brains, and highlight that until recently the most encephalized mammals were odontocetes, not primates.*

Cetaceans, together with primates, have reached the upper range of mammalian brain size. Cetacea include species with the largest brains to have ever evolved and species that rival anthropoid primates for brain size relative to body size, superseded only by our own species (Marino 1998). How and why their large brains evolved, what cognitive abilities they possess, and what the convergent evolution of large

brains reveals about the evolution of the human brain are questions of considerable interest (Jerison 1973; Marino 1996) and substantial debate (Manger 2006; Marino et al. 2007, 2008).

The encephalization quotient (EQ) quantifies variation in brain mass not explained by the allometric relationship between brain and body mass (Jerison 1973). Variation in mammalian EQ, or other measures of relative brain size, is associated with factors such as diet (Clutton-Brock and Harvey 1980), social behavior (Dunbar 1992; Sawaguchi 1992), physical ecology (Mace et al. 1981; Schultz and Dunbar 2006), and sensory specializations (Barton et al. 1995). The original conception of EQ aimed to establish a comparative measure of cognitive ability among species (Jerison 1973), and it has long been assumed that EQ tended to increase through time during mammalian evolution (Jerison 1973; Gould 1988). This progressive view has been challenged (Deacon 1990), and evolutionary trends in relative brain size may be limited to particular clades (Schultz and Dunbar 2010). It is also clear that brain structure can evolve independently of overall changes in brain size (Barton and Harvey 2000) and that shifts in brain architecture are related to ecology (de Winter and Oxnard 2001). Some authors have argued that particular regions of the brain (Reader and Laland 2002), or neuron number irrespective of brain or body mass (Herculano-Houzel 2011), are better predictors of cognitive ability. Undoubtedly both specialization of individual brain components and coevolution among functionally connected structures play major roles in behavioral evolution (Barton 2012). Yet, despite being a somewhat crude measure, there is evidence linking whole brain size to cognitive performance (Deaner et al. 2007; Reader et al. 2011) and survival in novel environments (Sol et al. 2008). Although noncognitive hypotheses have been proposed to explain the large brains of odontocetes (Manger 2006), the consensus is that large brain size is evidence of, or necessary for, the behavioral complexity and cognitive abilities observed in cetaceans (Marino 2002; Simmonds 2006; Connor 2007; Marino et al. 2007).

Primates are one order that shows a strong trend for directional increases in relative brain size (Montgomery et al. 2010). Increases in relative brain size are almost ubiquitous across the primate tree and are produced by directional evolution of increased brain mass in a background of body mass evolution that shows no significant trend to increase through time (Montgomery et al. 2010). This suggests that brain and body mass evolution has become developmentally decoupled in primates (Lande 1979) and that selection may have acted on the developmental mechanisms controlling brain mass (Montgomery et al. 2011; Montgomery and Mundy 2012). Whether the same pattern of evolutionary history and developmental mechanisms are relevant to cetacean brain evolution is not known. A comparison between the evolution of encephalization in primates and cetaceans provides an opportunity to identify shared and clade-specific factors contributing to the evolution of large brains in two orders which differ widely in ecology, anatomy, and evolutionary history (Marino 1996, 1998).

The distribution of EQ values across cetaceans suggests that high levels of encephalization have evolved convergently multiple times (Marino 1998; Marino et al. 2004), but previous tests for directional expansion of cetacean EQ have produced conflicting results (Marino et al. 2004; Schultz and Dunbar 2010) and have not explored the relationship between brain and body mass evolution. This is of particular interest given evidence that brain:body allometry in cetaceans differs significantly from other mammals (Manger 2006; Boddy et al. 2012) and the high discrepancies in EQ between the extremely large-bodied mysticetes, as compared to most smaller-bodied odontocetes (Marino 2004; Tartarelli and Bisconti 2006). Shifts in brain:body scaling toward a lower allometric slope may reflect altered selection pressures shaping one or both traits.

Body mass is likely to be an important adaptive trait in all cetaceans. Comparative analyses suggest that selection on cetacean body mass is related to niche partitioning and diet, which may have played an important role early in cetacean evolution (Slater et al. 2010; but see also Pyenson and Sponberg 2011). Furthermore, the rate of body mass evolution in cetaceans far exceeds that of terrestrial mammals (Evans

et al. 2012) plausibly due to shifts in constraints on body mass due to “aquatic weightlessness” (Marino 1998; Huggenberger 2008), an abundant, nutritious diet (Evans et al. 2012) and selection related to thermoregulation, predator defense, migratory behavior, and feeding ecology (Millar and Hickling 1990; Noren and Williams 2000; Fitzgerald 2006; Demere et al. 2008; Clauset 2013). Given the expected developmental correlation between brain and body size (Atchley et al. 1984; Riska and Atchley 1985), understanding how cetacean-specific selective regimes on body mass have impacted brain evolution is important for understanding the evolution of relative brain size. Although there is some evidence that brains and bodies can evolve independently (Lande 1979; Gonzalez-Voyer et al. 2009; Montgomery et al. 2010, 2011), whether this is generally the case, or if it is necessary for the evolution of high levels of encephalization, is not clear.

In this study we analyze the evolution of brain mass, body mass, relative brain size and the relationships among these traits. We test for macroevolutionary trends, reconstruct ancestral phenotypes and perform a rigorous analysis of the effects of including fossil data in comparative studies. We address a number of debated aspects of cetacean evolution including whether relative brain size has increased through time (Marino et al. 2004; Schultz and Dunbar 2010), whether shifts in EQ are generally due to changes in brain or body mass (Marino et al. 2004), and how allometric shifts in the brain:body mass relationship have influenced the evolution of relative brain size (Manger 2006; Boddy et al. 2012). Through a comparison with primates, our results offer insights into the convergent evolution of large brains in Mammalia.

## Materials and Methods

### *PHENOTYPIC DATA*

Data sets of body mass and brain mass/endocranial volume (ECV) for extant and extinct Cetacea were compiled from published sources (Table S1). Often species data were presented without sample size or gender; we therefore took means of male and female values when presented separately to standardize error introduced by merging data from multiple sources. Data on ECV and brain mass from the same species showed negligible differences (OLS regression:  $P < 0.001$ ,  $ECV = 0.995[\text{mass}] + 0.011$ ) with the slope not significantly different to one ( $P=0.490$ ) and the intercept not significantly different to 0 ( $P = 0.568$ ), and we therefore assumed a 1 g/cc<sup>3</sup> relationship in species for which only volumetric data were available. To avoid the inclusion of juveniles, we took two precautions; where multiple data sets were available for a species, data were taken from the source reporting the largest body mass, and we regressed body mass estimates from the final data set against maximum body masses reported in Reeves et al. (2002) to identify outliers, which were then excluded. Data for extinct species were excluded if the specimen was identified as a juvenile. Where estimates of body mass for extinct taxa differed between sources, the largest estimate was taken. Relative brain size was measured following Jerison (1973):

$$EQ = \text{Brain mass [g]} / (0.12 \times \text{Body mass [g]}^{0.67}).$$

All phenotypic data were log<sub>10</sub>-transformed to improve normality. As we are interested in assessing the interplay between brain and body size through time, we refrained from adding species for which body mass data exist but brain mass data do not as this would yield incomparable metrics that could not be interpreted in a rigorous statistical framework.

In total, our data set includes 42 extant species, ~48% of living species, and 20 extinct species, ~4% of valid extinct species (Supporting Information). The latter value is difficult to gauge; it is likely deflated by counting “valid” species which upon reevaluation will likely prove to be *nomen dubia*, but the discovery of new fossils could render it an underestimation. A more relevant measure of coverage is the phylogenetic

distribution of samples. In this regard our data set includes 13 of 14 extant families (93%) and our fossil taxa span a range of key taxonomic transitions. It is difficult to quantify the proportion of extinct families sampled due to a lack of taxonomic information. Our data set includes the smallest and largest extant genera and a range of extinct body sizes. To begin to explore the stability of our results to variation in sampling, we conducted a series of analyses examining the effects of excluding key taxa, the overall effects of including fossils, and the ability of our model to estimate known species values. The results are stable to the inclusion/exclusion of different extinct taxa and suggest the approach taken is robust (Supporting Information).

## **PHYLOGENY**

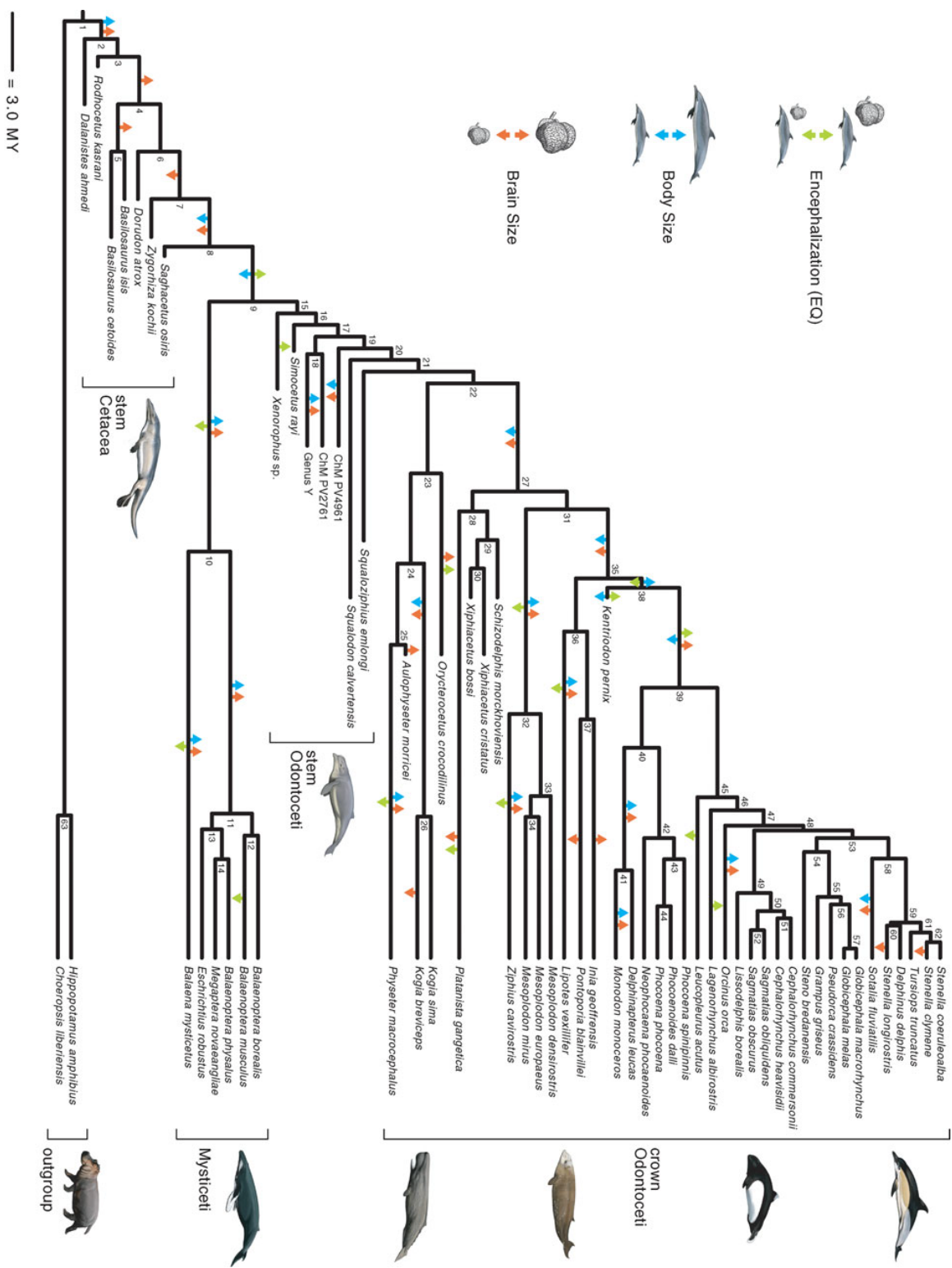
The phylogenetic hypothesis for extant and extinct species is a composite of published molecular (McGowen et al. 2009; McGowen 2011) and morphological trees (Geisler et al. 2011). To construct this phylogenetic framework, we started with a time-calibrated molecular tree (McGowen et al. 2009) and adjusted for relationships within Delphinidae (McGowen 2011). A relaxed clock analysis established divergence points among extant species (Supporting Information). This composite timetree formed the scaffold on which to position extinct taxa. Geisler et al. (2011) conducted a similar analysis and the scaffold they employed is consistent with the calibrated molecular tree of this study, so extinct taxa were positioned as in Geisler et al. (2011). Additional taxa not included in that study, but for which brain and body mass estimates are available, were placed on this tree based on three morphological, cladistic analyses (Uhen 2004; Lambert 2005; Lambert et al. 2010; see Supporting Information).

One challenging issue when incorporating fossils into our analysis is the length of branches leading to, or subdivided by, extinct taxa. Data on the age of the specimens from which the phenotypic data were compiled, and the first appearance of that species or related clade, were used to constrain splitting events and branch lengths of terminal branches leading to extinct taxa. Subdivision of an internal branch bisected by a branching event with an extinct species/clade is more difficult. In the absence of a data driven way to subdivide such branches, we consistently applied a rule throughout the tree which placed branch-splitting events so that the branches on the extant tree were divided into branches of equal duration. To prevent extinct taxon from having an undue influence on our reconstruction of ancestral states, when necessary, we pushed divergences involving fossils back so that terminal branches leading to fossils and internal branches immediately basal to these fossils were each  $\geq 0.5\text{Ma}$  (Fig. 1). Additional information on the construction of the phylogenetic hypothesis is given in the Supporting Information. We refer to “crown Cetacea” as including the common ancestor of Mysticeti and Odontoceti, and “stem Cetacea” as all extinct cetaceans that diverged before the last common ancestor of Mysticeti and Odontoceti (Fig. 1). A similar system is used when referring to Odontoceti.

## **EVOLUTIONARY ANALYSES AND ANCESTRAL STATE RECONSTRUCTIONS**

Evolutionary analyses were performed in Bayes Traits (Pagel et al. 2004; Pagel and Meade 2006). We used phylogenetically corrected *t*-tests (Organ et al. 2007) to explore variation in brain and body size between clades or groups of species. These test for a phylogenetically corrected association between a binary variable (0 or 1), assigned to the two groups under consideration, and the phenotype of interest. Bayes Traits implements phylogenetic least squares to account for phylogenetic non-independence by converting the phylogeny into a variance–covariance matrix, where the diagonal of the matrix gives information on the path length from root to tips (the “variance”) and the off-diagonal values of the matrix provide information on the shared evolutionary history of any pair of species (the “covariance”; Pagel 1997, 1999).

Figure 1. Phylogeny of extant and extinct cetaceans for which brain and body mass estimates are available. Nodes are labeled and referred to throughout the text. Branches which show an increase (upward pointing arrows) or decrease (downward pointing arrows) more than one standard deviation from the mean change across all branches are labeled for body mass (blue), brain mass (red), and encephalization quotient (green). Scale bar for branch lengths (3 million years [MY]) is shown at bottom left. Paintings are by Carl Buell.



Ancestral state reconstructions were performed following Organ et al. (2007) as implemented in Bayes Traits. Bayes Traits assumes a constant-variance Brownian motion model but adopts a model-building approach to test for deviation from the null model. The constant-variance random-walk model has one parameter,  $\alpha$ , which describes the instantaneous variance of evolution (Pagel 1997). This is the default model where all branch length-scaling parameters ( $\lambda$ ,  $\kappa$ ,  $\delta$ ) equal 1 (Pagel 1997). These parameters account for deviation from the null model:  $\lambda$  reveals to what extent the phylogeny predicts the pattern of covariance between species,  $\kappa$  stretches and compresses branch lengths and accounts for stasis in longer branches, and  $\delta$  scales path lengths and accounts for variation in the importance of temporally early or late change. These parameters were estimated using maximum likelihood, and where a parameter was significantly different from 1, as determined using a likelihood ratio test ( $-2(\ln[Lh(\text{null model})] - \ln[Lh(\text{alternative model})])$ ), the value for that parameter was estimated in the final model (Organ et al. 2007).

Using the model with the highest likelihood, one can test if a directional-change random-walk model improves the fit to the data. This is the formal test of whether the trait of interest evolved through time with a directional trend. The directional random walk model has an additional parameter ( $\beta$ ) that captures the directional change using a regression between trait values and the total path length (Pagel 1997, 1999). The harmonic means of the likelihoods of the directional and non-directional random walk models are compared with Bayes Factors (Kass and Raftery 1995; Gilks et al. 1996) to determine which model fits the data best. The Log(Bayes Factor) is computed as:

$$\begin{aligned} & -2(\ln[\text{harmonic mean of } Lh(\text{nullmodel})] \\ & - \ln[\text{harmonic mean of } Lh(\text{alternative model})]). \end{aligned}$$

A Log(Bayes Factor) (BF) greater than 2 is taken as positive evidence for a difference between the two models, greater than 5 represents “strong” evidence, and greater than 10 is “very strong” evidence (Kass and Raftery 1995). This test for directionality was performed for  $\log_{10}(\text{brain mass [g]})$ ,  $\log_{10}(\text{body mass [g]})$ , and  $\log_{10}(\text{EQ})$  within odontocetes and across all cetaceans. Data from Hippopotamidae were excluded to ensure that models, and inferences drawn from them, are specific to Cetacea. Because of the lack of brain size data for extinct mysticetes, we were unable to test for trends in this clade.

Once the final model is obtained it can be used to reconstruct ancestral states. Ancestral state reconstructions were performed for  $\log_{10}(\text{brain mass [g]})$  and  $\log_{10}(\text{body mass [g]})$ . Ancestral states for EQ were calculated from these values. To estimate the ancestral state of the last common ancestor of Cetacea and Hippopotamidae, data for two species of Hippopotamidae were included as outgroups (Weston and Lister 2009). In the Supporting Information we provide a detailed comparison between ancestral state reconstructions for key nodes and evidence from the fossil record.

Changes in brain mass, body mass, and EQ along each branch were calculated by taking the difference between values at consecutive nodes. Rates of evolution for particular branches were calculated by dividing these changes by branch lengths (Gittleman et al. 1996; Organ et al. 2007; Montgomery et al. 2010). This approach has the caveat that it involves many estimated values ( $2n - 1$ ) from only  $n$  data points and risks artificially inflating the degrees of freedom and pseudoreplication (Pagel 1994). However, we use it here as a descriptive tool. Notable branch-specific changes, discussed later as “major decreases/increases,” are branches with changes in  $\log_{10}(\text{phenotype})$  more than one standard deviation from the mean change across the group of interest.

Comparisons between the average rates of evolution in primates and cetaceans were performed using Welch's  $t$ -test as the variance between the two groups was significantly different ( $F$ -test). Data for



primates (Montgomery et al. 2010) were converted to match the units of the current paper (from  $(\Delta\log(\text{mass}[\text{mg}])/\text{branch length}[\text{millions of years}])$  to  $(\Delta\log(\text{mass}[\text{g}])/\text{branch length}[\text{millions of years}])$  for brain mass, and from residual brain size to EQ for relative brain mass). Only branches present in the extant species tree for each clade were considered as Montgomery et al. (2010) assumed fossil lineages formed polytomies with nodes in the extant species tree.

Results of the Bayes Traits analyses were obtained using Markov chain Monte Carlo (MCMC) runs with 3.5 million generations, a conservative burn-in of 500,000 generations, and sampling every 100 generations. These settings were sufficient to achieve chain convergence with acceptable range of data deviation values for all nodes except the basal node for which the MCMC chain was run for 7.5 million generations with a burn-in of 3 million generations. All analyses were performed using the default setting of uniform priors (prior range: -100 to +100). Rate deviation was adjusted to obtain an acceptance of the proposed model parameters between 20% and 40%, and during ancestral state reconstructions the data deviation was adjusted to obtain an acceptance rate for each node's estimate between 20% and 40%. This is the recommended range to ensure that the likelihood surface is efficiently explored (Organ et al. 2007). For full details of rate parameter estimates, see Table S2.

## Results

### VARIATION IN BRAIN AND BODY SIZE AMONG GROUPS

Phylogenetically corrected *t*-tests (Organ et al. 2007) were used to analyze variation in brain and body size between major groups of cetaceans. Extant mysticetes have significantly larger body masses than extant odontocetes ( $t_{40} = 2.079$ ,  $P = 0.044$ ) but do not have significantly larger brain masses ( $t_{40} = 1.000$ ,  $P = 0.323$ ). This results in mysticetes having significantly lower EQs ( $t_{40} = 2.225$ ,  $P = 0.032$ ). The highest EQs in cetaceans are observed among the Delphinoidea, especially among delphinid dolphins (Marino et al. 2004), however, there are no significant differences between the Delphinoidea and other extant odontocetes for body mass ( $t_{34} = 0.107$ ,  $P = 0.916$ ), brain mass ( $t_{34} = 0.669$ ,  $P = 0.508$ ), or EQ ( $t_{34} = 1.227$ ,  $P = 0.228$ ), or between Delphinidae and other extant odontocetes for body mass ( $t_{34} = 0.129$ ,  $P = 0.898$ ), brain mass ( $t_{34} = 0.561$ ,  $P = 0.578$ ) or EQ ( $t_{34} = 1.102$ ,  $P = 0.278$ ).

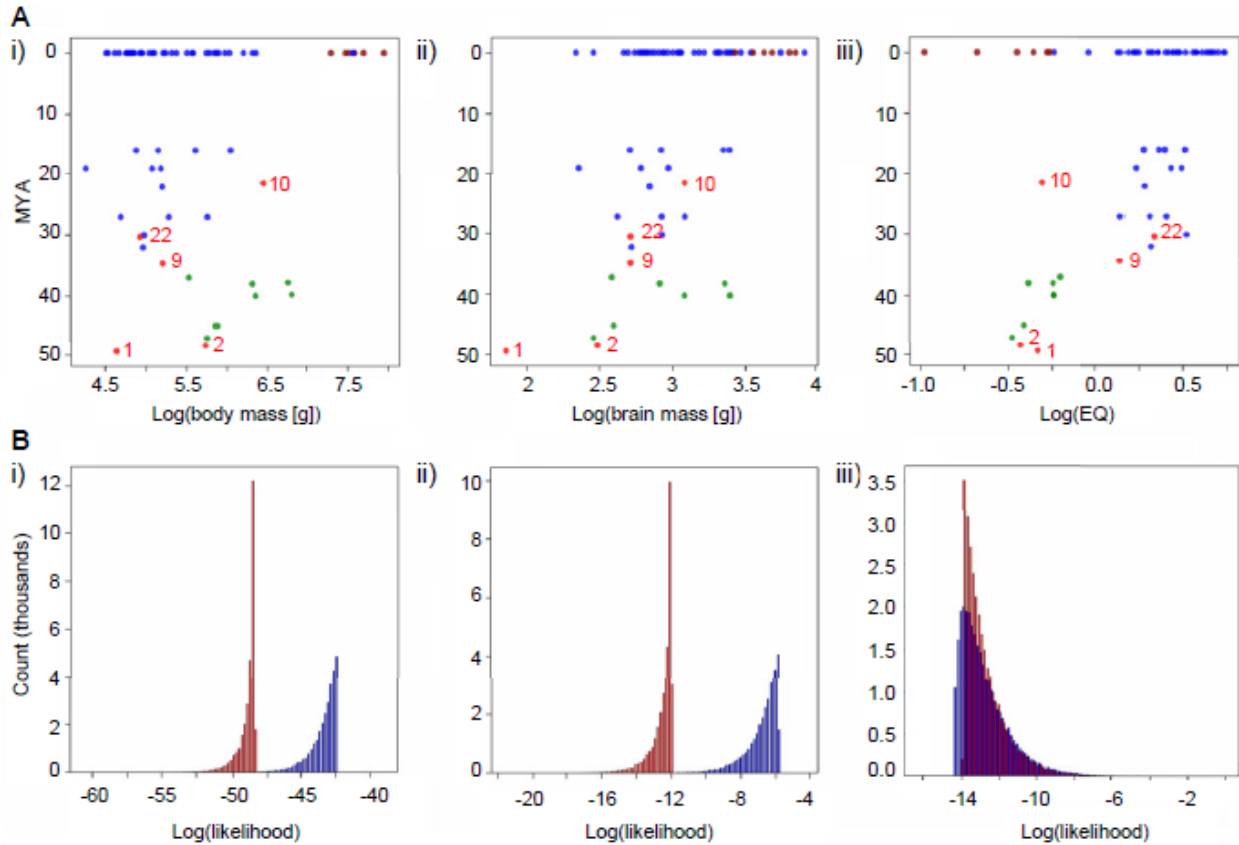
Extinct odontocetes have significantly smaller body masses ( $t_{47} = 2.762$ ,  $P = 0.008$ ) and brain masses ( $t_{47} = 2.147$ ,  $P = 0.037$ ) than the extant odontocetes in the data set, but they do not significantly differ in EQ ( $t_{47} = 1.812$ ,  $P = 0.076$ ). Extant odontocetes do not have significantly different body masses ( $t_{41} = 0.088$ ,  $P = 0.930$ ), brain masses ( $t_{41} = 1.064$ ,  $P = 0.294$ ), or EQs ( $t_{41} = 1.674$ ,  $P = 0.102$ ), than stem Cetacea. In contrast, when extant mysticetes are compared to these early stem cetaceans there are no significant differences for brain mass ( $t_{11} = 1.527$ ,  $P = 0.155$ ) or EQ ( $t_{11} = 1.359$ ,  $P = 0.201$ ) but extant mysticetes do have significantly larger body masses ( $t_{11} = 2.464$ ,  $P = 0.031$ ).

### MACROEVOLUTIONARY TRENDS IN BRAIN AND BODY SIZE

The data set includes fossil taxa that sample a long duration of evolutionary time (Fig. 2A) providing a good basis for testing macroevolutionary trends. There is very strong evidence that the directional model fits both body mass (BF = 10.208) and brain mass (BF=10.167) better than the nondirectional model, suggesting both traits typically increased through time across cetaceans (Fig. 2B and Table 1). However, there is no support for a directional model of evolution when applied to EQ (BF = -0.589). Within odontocetes the same pattern emerges. There is good support for an evolutionary trend to both body mass (BF=5.779) and brain mass (BF=5.336) but not for EQ (BF=-1.106). These results are robust to exclusion of extinct taxa with key phylogenetic positions (Supporting Information). Based on branch-specific estimates of phenotypic change, body mass increased across 78% of evolutionary time (total

time across all branches of the phylogeny), brain mass increased across 74% of evolutionary time, but EQ increased across only 34% of evolutionary time. Because of these trends, the inclusion of fossil data substantially affects estimates of ancestral states compared to analysis of extant species alone (Fig. S1).

**Figure 2. Temporal trajectories in brain and body mass: (A) scatterplots of log<sub>10</sub> (i) body mass, (ii) brain mass, and (iii) encephalization quotient (EQ) against time (millions of years ago [MYA]). Green dots: Archaeoceti, blue dots: Odontoceti, brown dots: Mysticeti, red dots: ancestral state estimates for five key nodes (1 = ancestor of Cetacea + Hippopotamidae, 2 = ancestor of Cetacea, 9 = ancestor of crown Cetacea, 22 = ancestor of crown Odontoceti, 10 = ancestor of crownMysticeti). (B) Posterior distribution of likelihoods for nondirectional (red/brown) and directional (blue) model of evolution for log<sub>10</sub> (i) body mass, (ii) brain mass, and (iii) EQ.**

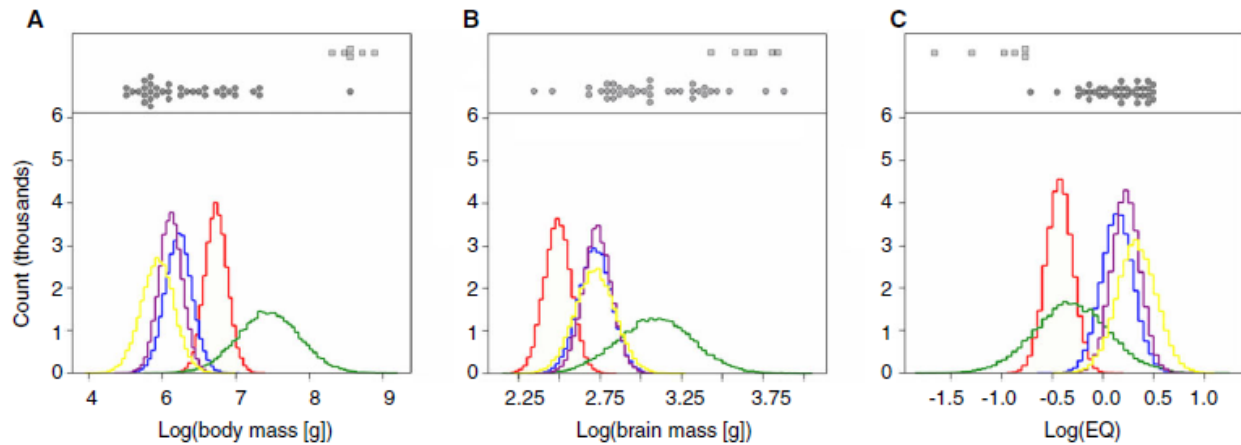


**Table 1. Statistical tests for macroevolutionary trends in brain and body size.**

(a) All cetaceans			
Harmonic mean of log(likelihoods)	Body Mass	Brain mass	Relative brain size (log[EQ])
Nondirectional model	-49.982	-13.474	10.453
Directional model	-44.878	-8.390	10.159
Log(Bayes factor)	10.208	10.167	-0.589
(b) Odontocetes only			
Harmonic mean of log(likelihoods)	Body mass	Brain mass	Relative brain size (log[EQ])
Nondirectional model	-36.281	-8.161	9.724
Directional model	-33.391	-5.493	9.171
Log(Bayes factor)	5.779	5.336	-1.106

EQ = encephalization quotient

**Figure 3. Posterior distribution of ancestral state estimates for five key nodes (red: node 2, blue: node 9, green: node 10, purple: node 15, yellow: node 22) for log<sub>10</sub> (A) body mass, (B) brain mass, and (C) encephalization quotient. The upper panels show dot histograms indicating the distribution of extant phenotypes for odontocetes (dark gray circles) and mysticetes (light gray squares).**



## ORIGINS AND DIVERSIFICATION OF MAJOR GROUPS

### *Evolution of stem Cetacea and the origins of crown Cetacea*

The estimated body and brain masses for the last common ancestor of Cetacea and Hippopotamidae (node 1; Fig. 1) are 43.478 kg and 71.457 g respectively, giving an EQ of 0.465. These estimates have a narrow range (Fig. S2 and Table S3) and should be viewed with some caution given that no close extinct relatives of hippos were included in our study. The most basal node in Cetacea included in our phylogeny (node 2) was probably predominantly aquatic but, like *Dalanistes* and *Rodhocetus* (Gingerich 2003), capable of some terrestrial locomotion. It is estimated to have had a body mass of 541.330 kg (95% confidence interval [CI] = 539.181–543.487 kg), within the range of extant odontocetes and representing over a 10-fold increase in body mass relative to the common ancestor of hippos and whales (Fig. 3A). Brain mass is estimated to be 308.738 g (95% CI = 308.074–309.404 g), a 4.32-fold increase, giving an EQ of 0.371 (Fig. 3A, B). The brain mass is toward the lower end of the range observed within extant odontocetes. The EQ is below the range seen in extant odontocetes but within that of extant mysticetes.

Within stem Cetacea, body and brain mass increased in parallel along the lineages leading to crown Cetacea and *Basilosaurus* (Table S4A). The largest shifts during this early period of cetacean evolution are observed between nodes 3 and 4 when body mass is estimated to have increased from 615.262 kg (95% CI=613.507– 617.022 kg) to 1,275.073 kg (95% CI=1,268.686–1,281.492 kg). A similar increase in brain mass is observed between the same nodes, resulting in a modest increase in EQ (0.356–0.464). Large increases in body mass are observed at the origin of *Basilosaurus* (+41%) and in both terminal *Basilosaurus* branches (*Basilosaurus isis*: +108%, *Basilosaurus cetoides*: +87%). This is accompanied by increases in brain mass such that EQ remains relatively stable. In contrast, body mass is estimated to have decreased from 1,275.073 kg (node 4) to 166.571 kg (node, 9 [95% CI = 165.774–167.371 kg]) after the split between *Basilosaurus* and the lineage leading to crown Cetacea. This is an overall decrease of 87%. Brain mass also decreased, but to a lesser extent, from 685.473 g (95% CI = 683.449–687.391 g) to 522.982 g (95% CI = 521.607–524.360 g). This results in a major increase in EQ from 0.464 to 1.383, well within the range of modern odontocetes. The increase mostly occurred after the divergence of *Saghacetus* (nodes 8–9).

## *Mysticeti*

The last common ancestor of crown mysticetes (node 10) is estimated to have had a body mass of 2800.881 kg (95% CI = 2770.297–2831.803 kg), a brain mass of 1229.946 g (95% CI = 1222.536–1237.402 g), and an EQ of 0.702 (95% CI = 0.694–0.710; Fig. 3). The origin of extant mysticetes from the last common ancestor of crown Cetacea (between nodes 9 and 10) is therefore accompanied by a doubling of brain mass but more notably a 16-fold increase in body mass resulting in a decreased EQ. Continued body mass expansion is observed throughout mysticetes (Fig. 4A and Table S4B). No branch is estimated to have experienced a decrease in brain or body mass, whereas 7 of 11 branches show decreases in EQ. Hence, although we were unable to quantitatively test for directionality due to the lack of brain mass estimates for fossil mysticetes, our ancestral state reconstructions suggest that mysticete brain and body mass evolved with directional trends to increase; but EQ did not. The largest increases are observed on the terminal *Balaena mysticetus* branch, which saw a 32-fold increase in body mass but only a 2.2-fold increase in brain mass, and the stem lineage leading to the last common ancestor of Balaenopteridae and Eschrichtiidae (nodes 10–11), which saw a 6-fold increase in body mass and a 2.7-fold increase in brain mass. These two branches, the stem mysticete branch, and the terminal *Balaenoptera musculus* branch show the highest rates of body mass evolution across cetaceans.

## *Odontoceti*

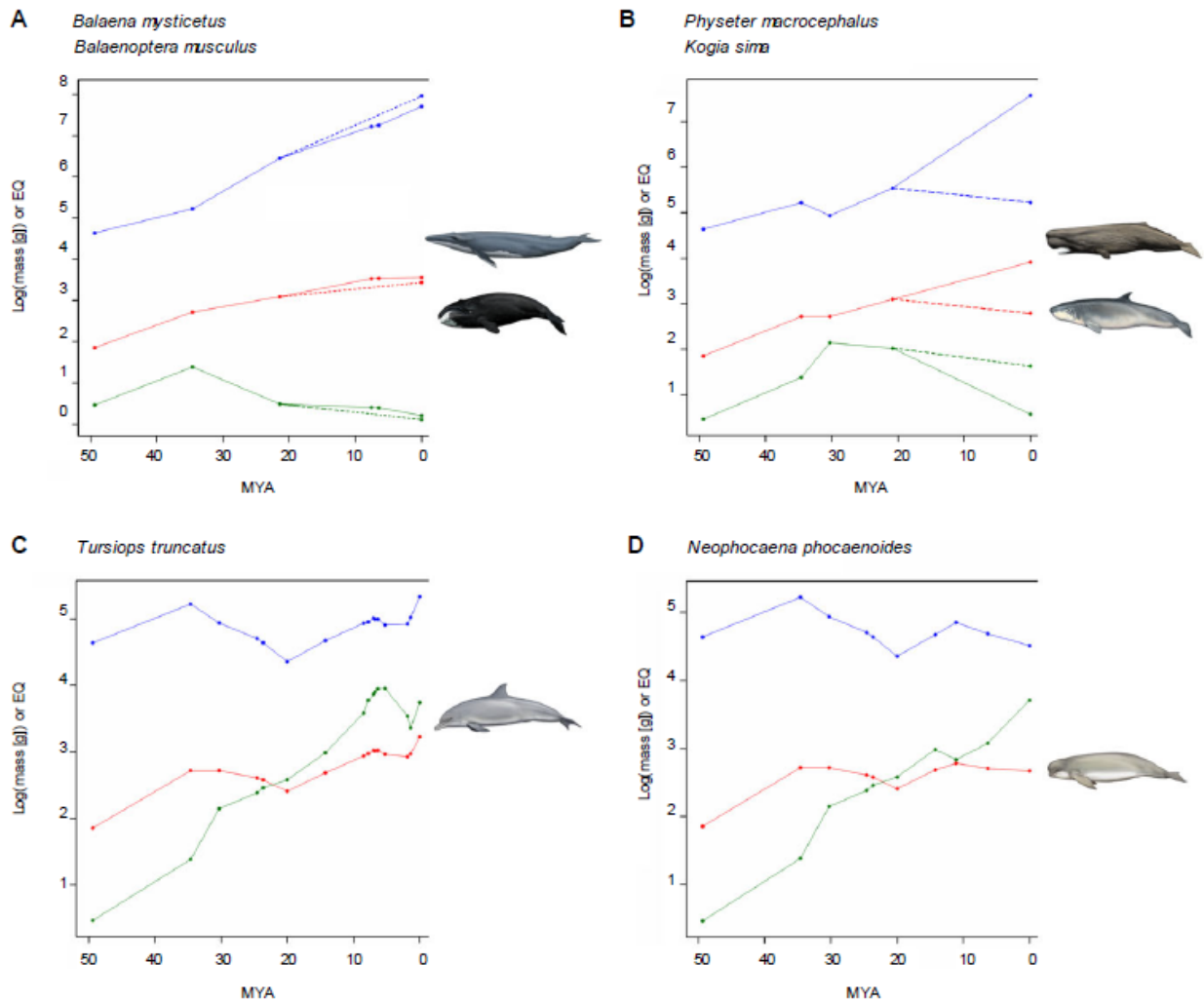
In contrast with mysticetes, the early stages of odontocete evolution are characterized by decreases in body mass. The ancestral odontocete (node 15) had an estimated body mass of 130.472 kg (95% CI=129.927–131.022 kg), a decrease in body mass of 22% from the ancestral crown cetacean (node 9). Brain mass is estimated to have been 539.533 g (95% CI = 538.282–549.787 g), within the 95% CIs for the estimate at node 9. This resulted in an increase in EQ to 1.680 (95% CIs = 1.674–1.687). All three trait estimates are within the range of crown odontocetes (Fig. 3). The reduction in body mass was continuous, with all internal branches estimated to have experienced decreases in body mass between the ancestral crown cetacean (node 9) and the ancestral crown odontocete (node 22), where body mass is 86.471 kg (95% CI = 85.967–86.978 kg). During this period, brain mass remained relatively constant, between 520 and 540 g, and as a result, EQ climbed steadily from 1.383 to 2.146 (node 22; 95% CI= 2.135–2.157). This pattern of decreasing body mass continued on branches leading to the last common ancestors of Synrhina (nodes 22–27), Delphinida+Ziphiidae (nodes 27–31), and Delphinoidea (nodes 31–35). In each case, the decrease in brain mass is limited such that EQ increased. We examined whether this pattern could be due to extant mysticetes inflating the body mass estimate for the ancestral crown cetacean, but even when all mysticetes are excluded from the analysis the same pattern is observed (Supporting Information).

The basal branch of Odontoceti (nodes 9–15) shows a large proportional increase in EQ, from 1.383 (95% CI = 1.377–1.389) to 1.680 (95% CI = 1.674–1.687). This is partly due to a decrease in body mass but also due to a slight increase in brain mass. Some decreases in body mass also occur within the diversification of crown odontocetes, for example, a 41% decrease at the origin of the Kogiidae (dwarf and pygmy sperm whales; nodes 24–26), and a 48% decrease in *Sotalia fluviatilis*, the tucuxi river dolphin.

However, body mass increased across the majority (72%) of evolutionary time during the diversification of the Odontoceti. This compares to 67% for brain mass and just 34% for EQ. Within Odontoceti, the largest increases in body mass are observed on branches leading to *Physeter macrocephalus* (107-fold increase from the last common ancestor of Physeteroidea; Fig. 4B) and *Orcinus orca* (20-fold increase). During the descent of *P. macrocephalus*, brain mass increased by only 6.5-fold, leading to a decrease in EQ from 2.022 (95% CI = 2.009–2.035 g) to 0.575. This is the second largest EQ decrease across cetaceans.

*Orcinus orca* shows a 5.3-fold increase in brain mass, which together with its large body size also leads to a decrease in EQ from 3.867 (95% CI = 3.851–3.883) to 2.764. Branches with the highest rates of body and brain mass evolution are mostly within the Delphinidae. High rates of increase in both traits are estimated on the terminal *Tursiops truncatus* (Fig. 4C) and *O. orca* branches, along the internal branch leading to the last common ancestor of *Tursiops*, *Stenella clymene*, and *Stenella coeruleoalba* (nodes 59–61) and the branch leading to the *Pseudorca/Globicephala* clade (nodes 54–55; nodes 55–56).

Figure 4. Evolutionary trajectories along selected lineages: log(body mass[g]) is shown by the blue lines, log(brain mass[g]) by the red, and encephalization quotient (EQ; not logged) in green. (A) *Balaena mysticetus* (dashed line) and *Balaenoptera musculus* (solid line) provide examples of enormous body mass increases and a falling EQ in spite of an increase in brain mass. (B) *Kogia sima* (dashed line) and *Physeter macrocephalus* (solid line) provide examples of a large-bodied odontocete evolving a small EQ compared to a smaller bodied relative. (C) *Tursiops truncatus* exemplifies a species where EQ has increased rapidly and recently due to brain mass expansion. (D) *Neophocaena phocaenoides* provides an example where brain mass is relatively constant over a long period of time but EQ increases mostly due to decreases in body mass. Where two species are represented in the same panel, the line is solid until the point at which they diverge then one line is dashed and the other remains solid. Dots represent internal nodes from the extant species tree leading from the last common ancestor of Cetacea and Hippopotamidae to each extant species. MYA, millions of years ago. Paintings are by Carl Buell.



Large proportional increases in EQ are observed on the stem lineage to crown Cetacea (nodes 1–9: 0.454–1.383), on the stem to crown Odontoceti (nodes 9–22: 1.383–2.146), and on the terminal branches leading to *Lagenorhynchus albirostris* and *Globicephala macrorhynchus*, both of which show very little change in brain mass. Indeed, body mass decreased on five of six branches identified with major increases in EQ. Similarly, the largest decreases in EQ are associated with large increases in body mass. Only *Platanista gangetica* is estimated to have experienced a decrease in brain mass whereas the terminal *Orycterocetus crocodilinus* branch shows large increases in both EQ and brain mass. High rates of EQ increase are observed on the terminal *Delphinus delphis* and *T. truncatus* branches. High rates of EQ decrease are observed on the branch leading to *S. clymene* and *S. coeruleoalba*, and terminal *S. clymene* and *Globicephala melas* branches (but note the *G. macrorhynchus* body mass estimate lies toward the lower end of the adult range and may be a subadult which could inflate EQ).

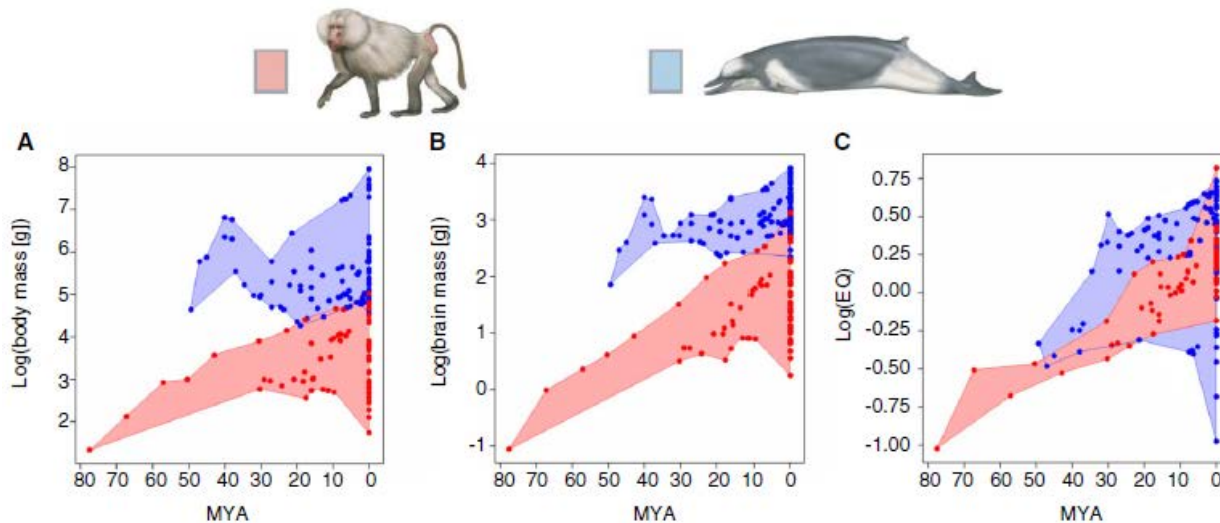
### **BRAIN:BODY ALLOMETRY**

Changes in brain and body mass are significantly correlated ( $t_{81} = 14.670$ ,  $P < 0.001$ ; Fig. S3). We tested whether the discrepancy in EQ values between Mysticeti and Odontoceti reflects a divergence in the allometric relationship between brain and body mass. A similar test was performed between Delphinidae and other Odontoceti, as an allometric shift in delphinids has been suggested (Marino et al. 2004). Based on the available data, the allometric relationship between brain and body mass differs significantly between extant odontocetes and mysticetes ( $t_{40} = 2.146$ ,  $P = 0.038$ ). Within Odontoceti, we find no evidence for an allometric shift in Delphinidae ( $t_{34} = 1.286$ ,  $P = 0.207$ ), or between extant and extinct odontocetes ( $t_{45} = 1.681$ ,  $P = 0.100$ ). Hence, within Odontoceti there is no evidence for shifts in the allometric relationship. However, odontocetes do differ from stem cetaceans ( $t_{54} = 4.291$ ,  $P < 0.001$ ). In contrast, brain:body allometry does not differ significantly between extant mysticetes and stem Cetacea ( $t_{11} = 1.968$ ,  $P = 0.075$ ). This suggests that brain:body allometry shifted at least once during the diversification of cetaceans in Odontoceti.

### **CONVERGENT EVOLUTION OF LARGE BRAINS: A COMPARISON BETWEEN PRIMATES AND CETACEANS**

In contrast to cetaceans, primate evolution has been characterized by a directional trend in brain mass, but not body mass, resulting in a strong trend toward increasing relative brain size (Montgomery et al. 2010). The average rate of body mass evolution is significantly higher in cetaceans than primates ( $t_{97} = 2.152$ ,  $P = 0.034$ ) but the rate of brain mass evolution is significantly higher in primates ( $t_{116} = 4.18$ ,  $P < 0.001$ ). The average rate of change in EQ does not differ between the two orders ( $t_{139} = 1.196$ ,  $P = 0.217$ ). The frequency of decreases in brain mass and EQ is much greater in cetaceans, whereas the frequency of body mass decreases is greater in primates. Across both groups, the branches with the highest rates of body mass increase are dominated by cetaceans. In contrast, when ranked by rate of proportional increase in brain mass, only 8 of the 38 branches in the top 25% are cetacean lineages. When ranked for the rate of increase in EQ, 23 of 38 branches in the top 25% are cetacean lineages. The rate of brain mass evolution along the terminal *Homo* branch is exceeded by five branches; one cetacean and four primate lineages. The rate of increase in EQ along the terminal *Homo* lineage is exceeded by three primate and four cetacean branches; with the terminal *T. truncatus* branch having the highest rate. Cetaceans dominate the highest rates of decreases for EQ, brain, and body mass. To illustrate the distribution of brain and body sizes through time, we plotted data for extinct species and ancestral state estimates for nodes within the extant species tree against time for both primates and cetaceans. It is clear from this that cetaceans reached high levels of encephalization long before primates, and primates only exceeded cetaceans with the emergence of *Homo* (Fig. 5). Similarly, the increased variation in cetacean EQ through time is contrasted with the directional progression inferred in primates.

**Figure 5. Distribution of log(body mass [g]) (A), log(brain mass [g]) (B), and log(EQ) (C) through time for cetaceans (blue) and primates (red) from their origins to present day (x-axis is millions of years ago [MYA]). Scatterplots include data for extant species, extinct taxa, and ancestral states reconstructed at internal nodes of the tree in Figure 1. Paintings are by Carl Buell.**



## Discussion

### *RECONSTRUCTING THE PAST: EFFECTS OF INCORPORATING FOSSILS*

Understanding the evolutionary processes which shaped past diversity is necessary to understand the origin of extant biodiversity. However, this is challenging using only data from extant taxa. If the evolution of a trait was directionally biased, or characterized by heterogeneous evolutionary rates, reconstructions of past events may be unreliable using extant taxa alone (Oakley and Cunningham 2000). Including data from extinct taxa may improve such analyses (Finarelli and Flynn 2006; Montgomery et al. 2010; Slater et al. 2012). Although the fossil record is incomplete, particularly for traits such as brain size that require well preserved specimens, a recent simulation study suggests that the inclusion of even a small proportion of extinct diversity can improve our ability to select the best-fitting model of evolution and obtain improved reconstruction of a trait's evolutionary history (Slater et al. 2012). In this analysis, comparisons of the results obtained with/without fossils and including/excluding taxa in key phylogenetic positions (Supporting Information) suggest that a major factor affecting ancestral state reconstructions in Cetacea is accommodation of directional biases in trait evolution. Hence, in addition to more fully capturing the biological diversity of a group, the inclusion of fossils will improve ancestral state reconstructions if the strength of the directional bias can be reliably estimated from the sample of extinct taxa in the analysis.

Of course this relies on the data set being a phylogenetically unbiased sample of past and present diversity (Ackerly 2000; Freckleton 2009). With fossil taxa it is difficult to ensure that this is the case, as typically only a small proportion are preserved well enough to measure the phenotype of interest, and new discoveries may reveal previously unappreciated levels of diversity. Although we cannot rule this out, for this study, we know of no reason to expect a bias in the extinct taxa sampled, either due to preservation and discovery of specimens or data collection. The most likely bias is against early mysticetes, which are not represented in the data set and could, in theory, result in lower mass estimates

for the last common ancestor of extant cetaceans. However, removal of all extant mysticetes and other selected taxa close to these nodes suggest that these estimates are stable.

## THE EVOLUTIONARY EXPANSION OF THE CETACEAN BRAIN: SHIFTS AND TEMPORAL TRENDS

Increases in both brain and body mass have dominated cetacean evolution. Although EQ has not evolved by a directional, increasing trend in cetaceans, lineage-specific selection pressures presumably resulted in some cetaceans becoming highly encephalized. The initial transition to an obligatory aquatic lifestyle was not accompanied by a marked increase in relative brain size. This contradicts the hypothesis that an aquatic environment was a key selective pressure that initially drove the increase in cetacean EQ (Marino et al. 2004; Tartarelli and Bisconti 2006) and suggests the shift in brain:body allometry at the origin of crown cetaceans was largely due to changes in body mass development well after the move to aquatic habitats (Manger 2006; Boddy et al. 2012). Despite large differences in EQ, both mysticetes and odontocetes show similar patterns of body and brain mass evolution, with both traits generally increasing through time. Our results suggest the difference between these two suborders can largely be explained by a higher rate of body mass evolution in Mysticeti and decreases in body mass at the origin of Odontoceti resulting in an allometric grade-shift between the two suborders.

The expectation that relative brain size tends to increase through time in mammals (Jerison 1973; Gould 1988) is not met in Cetacea as a whole, or within Odontoceti. Although major changes in EQ occurred independently in several lineages, perhaps indicating lineage-specific selection (Marino et al. 2004), the distribution of EQ values across cetaceans is dominated by a major decrease on the stem to crown Mysticeti and a major increase on the stem to crown Odontoceti, in both cases driven by changes in body mass. One hypothesis as to why the brain:body relationship shifted in odontocetes is that selection associated with the evolution of echolocation drove increases in EQ (Marino et al. 2004). The few Oligocene odontocetes whose inner ears have been studied in detail resemble the ears of extant odontocetes (Fleischer 1976; Luo and Eastman 1995), suggesting they were specialized for hearing high-frequency sounds. However, the phylogenetic positions of these Oligocene taxa are unclear, and it is not known whether the most basal odontocetes, according to the phylogeny of Geisler et al. (2011) (e.g., *Xenorophus*, *Simocetus*, *Archaeodelphis*), had inner ears specialized for high-frequency hearing. Although the branch immediately subsequent to the origin of Odontoceti (nodes 9–15) shows a large shift in EQ, shifts in EQ that are caused by major changes in body mass are difficult to interpret. Although we cannot rule out a concurrent remodeling of brain structure, it may be that the stasis in brain size during this period reflects stabilizing selection on brain mass whereas directional selection acted to decrease body mass. If this is the case, the increase in EQ may be neutral with respect to cognition and behavior, although the energetic expense of maintaining a larger relative brain size (Aiello and Wheeler 1995) would suggest that the shift is unlikely to be neutral with respect to overall fitness.

Similarly, whether the decrease in mysticete EQ suggests anything about their cognitive or behavioral flexibility is unclear as the reduction can largely be explained by huge increases in body mass. Data on mysticete behavior are much more limited than for odontocetes. The available information suggests, however, that social communication and structure are often complex in mysticetes, and include long-term social bonds, long-range communication, cooperative hunting, cultural traditions, and fission–fusion like social behavior (Simmonds 2006; Marino et al. 2007; Whitehead 2011). These behaviors are observed in some odontocetes and primates, and are considered cognitively demanding (Barrett et al. 2003; Simmonds 2006).

Mysticete body mass is potentially linked to the ability to ingest and process large aggregations of prey (Fitzgerald 2006; Demere et al. 2008). Although the low EQs of mysticetes have previously been attributed to differences in blubber content, which may deflate EQ in large whales, this appears to have a



minimal effect (Tartarelli and Bisconti 2006). An additional factor may be increased muscle or bone growth. In primates there is some evidence that EQ is negatively correlated with relative amounts of muscle mass (Muchlinski et al. 2012). This has been attributed to potential energetic trade-offs between brain and muscle tissue (Leonard et al. 2007; Muchlinski et al. 2012) but a more parsimonious answer is simply that selection for greater muscle mass acted on postnatal growth and therefore deflated EQ as brain growth ceases earlier in development. Hence, shifts in mysticete development and life history could alter EQ by shaping body mass evolution independently of overall brain mass. Although data are limited, mysticetes do appear to have divergent developmental trajectories compared to odontocetes, with extremely high rates of both pre- and postnatal body growth (Frazer and Hugget 1973). To fully interpret changes in EQ caused by changes in either body mass or brain mass, a better understanding of the mechanisms and selection pressures causing brain:body allometry is required. The allometric relationship between brain and body size has long been interpreted as evidence of functional or developmental constraints (Jerison 1973), but what these constraints are, whether all regions of the brain are affected equally, and how these traits are linked developmentally is poorly understood (Striedter 2005). Recent studies point toward brain and body mass having independent genetic bases and different aspects of brain development evolving independently (Barton and Capellini 2011; Montgomery et al. 2011; Hager et al. 2012), suggesting selection can act on brain size and structure, or body mass, without causing correlated shifts in the other.

Other neuroanatomical features of mysticete brains, for example, level of cortical folding and neocortical architecture (Oelschläger and Oelschläger 2002; Hof and van der Gucht 2007) show that they are at least as complex as the brains of some odontocetes. Although mysticete and odontocete brains show some divergent characteristics, particularly in olfactory centers, both clades possess a highly expanded and convoluted cortex and cerebellum suggesting that either major structural changes occurred in parallel mysticetes and odontocetes or that these changes occurred before the origin of crown Cetacea (Marino et al. 2000; Oelschläger and Oelschläger 2002; Marino 2004; Tartarelli and Bisconti 2006; Hof and van der Gucht 2007). Limited data on neuron numbers suggest that, despite large size differences, mysticete and odontocete brains have similar numbers of neurons (Oelschläger and Oelschläger 2002; Eriksen and Pakkenberg 2007), both being comparable to the number found in an average chimpanzee brain (Huggenberger 2008). Von Economo neurons, which may be linked to some higher cognitive faculties (Allman et al. 2005; Butti et al. 2013), are found in both mysticetes and odontocetes (Butti et al. 2009) and, as in hominoid primates, show a derived regionally specific distribution (Butti and Hoff 2010; Butti et al. 2011). Understanding when and why these structural phenotypes evolved would clearly aid our interpretation of cetacean brain evolution.

## **DISSIMILARITIES IN THE CONVERGENT EVOLUTION OF BIG BRAINS**

Comparing patterns of evolution of cetacean and primate brains provides a potential pathway to uncover shared and divergent evolutionary routes to large brains (Marino 1996, 1998; Tartarelli and Bisconti 2006). We confirm that cetaceans reached high levels of encephalization before primates (Fig. 5; Marino 1998) but our analysis reveals two key differences in brain evolution between primates and cetaceans. First, primates show a strong directional trend for relative brain size to increase through time (Montgomery et al. 2010) whereas cetaceans do not. Second, the discrepancy between the pattern of brain and body mass evolution is much greater in primates than in cetaceans. Whereas cetacean brain:body allometry is predominantly altered during three key periods (the origin of crown cetaceans, the origin of odontocetes, and the origin of mysticetes), primate brain and body mass evolved under contrasting selective regimes across longer periods of time resulting in a continuous allometric change and the expansion of relative brain size (Montgomery et al. 2010). Whether this is due to a general decoupling of the genetic basis of brain and body mass evolution in primates, as predicted by quantitative

genetics models (Lande 1979), or whether this pattern of brain evolution is unique to primates, remains to be tested. Regardless, the patterns of brain and body size evolution in cetaceans and primates suggest that selection can act on brain mass independently from body mass over discrete periods of major change or in a more continuous and accumulative way over longer periods of time, despite the strong genetic covariance between these traits in mammals (Atchley et al. 1984; Riska and Atchley 1985).

Understanding the underlying developmental mechanisms that influence the differences in macroevolutionary trends between primates and cetaceans may ultimately help to identify differences in the constraints and selection pressures acting in these two orders. For example, Lande (1979) postulated that the genetic basis of brain and body mass evolution in primates may have become increasingly decoupled to facilitate an evolutionary expansion of the brain without leading to gigantism and antagonistic selection on body mass. In cetaceans, the evolution of large body masses may have been less of a constraint. Physical constraints acting on body mass may differ between cetaceans and terrestrial mammals as cetaceans experience “aquatic weightlessness” (Marino 1998; Huggenberger 2008). It has been argued that this will lead to underestimates of encephalization for many cetaceans when compared to terrestrial mammals (Harvey and Krebs 1990). It is likely, however, that the aquatic lifestyle of cetaceans also results in altered physical constraints on brain size when compared to arboreal or terrestrial mammals such as primates, for which a larger head may result in substantial costs related to locomotion. Similarly, a trade-off between relative brain size and the amount of adipose depots has recently been demonstrated across mammals (Navarrete et al. 2011). This trade-off is postulated to be due to locomotor constraints associated with carrying fat depots conflicting with the need for fat storage as a means of surviving periods of low food availability. Shifts in such constraints in marine habitats likely results in a rebalancing of this trade-off and may contribute to the altered brain:body allometry seen in cetaceans.

These, or other, differences in constraints, such as the absence of a limiting bony birth canal in cetaceans (Connor 2007), may explain why the evolution of the cetacean brain proceeded along a unique path (Marino 2004b; Hof et al. 2005). Although terrestrial mammals appear to have increased the computational power of their brains by adding new modules to increase structural complexity (Striedter 2005), cetaceans have pursued an alternative route to complexity by multiplying existing structures (Morgane et al. 1990; Marino 2004; Huggenberger 2008) resulting in a thin but highly folded cortex (Morgane et al. 1990; Marino 2004b; Huggenberger 2008). This type of elaboration may have not been available to smaller-bodied terrestrial mammals due to mechanical and gravitational constraints favoring more size-efficient schemes of cortical elaboration.

## **FUTURE DIRECTIONS**

We suggest comparative data on brain structure and neuron numbers (Stephan et al. 1981; Herculano-Houzel et al. 2007) will be a necessary next-step to provide a fuller interpretation of the significance of brain size differences. A complementary approach may be to investigate the genetic basis of cetacean brain and body mass evolution. Comparative genomics could reveal whether the same genes implicated in primate brain evolution have been targeted by selection in cetaceans (McGowen et al. 2011, 2012; Xu et al. 2012), or may reveal categories of genes which evolved adaptively with functional relevance to cetacean-specific neural phenotypes (McGowen et al. 2012). Combining approaches from neuroanatomy, comparative biology, paleontology, and evolutionary genetics will lead to new insights into the origins of behavioral complexity in cetaceans and the convergent evolution of large brains across divergent mammalian orders. Our analysis provides a comparative framework for interpreting future analyses of brain evolution in Cetacea.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Table S1.** Phenotypic data, including notes on compiling the data set.

**Table S2.** Scaling parameters for (a) all cetaceans and (b) odontocetes only.

**Table S3.** Ancestral state reconstructions.

**Table S4.** Changes in phenotypic traits during (a) early cetacean evolution, (b) early odontocete evolution, and (c) extant cetacean evolution.

**Table S5.** Tests of directionality excluding selected taxa.

**Table S6.** Ancestral states of key nodes excluding selected taxa.

**Table S7.** Estimating extinct species traits.

**Table S8.** Measurements and body size estimates for selected fossil cetaceans and raoellids.

**Figure S1.** Scatterplots of ancestral state estimates made with and without fossil data for (a) body mass, (b) brain mass, and (c) encephalization quotient.

**Figure S2.** Posterior distribution of ancestral state reconstructions for node 1, the last common ancestor of Cetacea and Hippopotamidae.

**Figure S3.** Correlations between empirical and estimated data for extinct species traits.

**Figure S4.** Regression between changes in cetacean brain and body mass.