

Brain size evolution in whales and dolphins: new data from fossil mysticetes

MATTHEW R. MCCURRY^{1,2,3,*}, FELIX G. MARX^{4,5}, ALISTAIR R. EVANS^{6,7}, TRAVIS PARK⁸, NICHOLAS D. PYENSON^{3,9}, NAOKI KOHNO^{10,11}, SILVIA CASTIGLIONE¹² and ERICH M. G. FITZGERALD^{6,7,8}

¹Australian Museum Research Institute, 1 William Street, Sydney, New South Wales 2010, Australia

²Earth and Sustainability Science Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, New South Wales 2052, Australia

³Paleobiology, NMNH, Smithsonian Institution, Washington, DC 20560, USA

⁴Museum of New Zealand Te Papa Tongarewa, Wellington, 6011, New Zealand

⁵Department of Geology, University of Otago, Dunedin, 3054, New Zealand

⁶School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

⁷Geosciences, Museums Victoria, Melbourne, Victoria 3001, Australia

⁸Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

⁹Department of Paleontology and Geology, Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, USA

¹⁰Department of Geology and Palaeontology, National Museum of Nature and Science, Tsukuba, 305-0005, Japan

¹¹Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba, 305-8752, Japan

¹²Department of Earth Sciences, Environment and Resources, University of Naples Federico II, 80138 Napoli, Italy

Received 24 November 2020; revised 4 March 2021; accepted for publication 10 March 2021

Cetaceans (whales and dolphins) have some of the largest and most complex brains in the animal kingdom. When and why this trait evolved remains controversial, with proposed drivers ranging from echolocation to foraging complexity and high-level sociality. This uncertainty partially reflects a lack of data on extinct baleen whales (mysticetes), which has obscured deep-time patterns of brain size evolution in non-echolocating cetaceans. Building on new measurements from mysticete fossils, we show that the evolution of large brains preceded that of echolocation, and subsequently followed a complex trajectory involving several independent increases (e.g. in rorquals and oceanic dolphins) and decreases (e.g. in right whales and ‘river dolphins’). Echolocating whales show a greater tendency towards large brain size, thus reaffirming cognitive demands associated with sound processing as a plausible driver of cetacean encephalization. Nevertheless, our results suggest that other factors such as sociality were also important.

ADDITIONAL KEYWORDS: Cetacea – encephalization – echolocation – Odontoceti – RRphylo.

INTRODUCTION

Cetaceans are renowned for their highly developed brains, which rival those of apes in size, complexity and cognitive ability (Marino *et al.*, 2004). Understanding how, when and why cetaceans acquired this trait promises fundamental insights into the causes and

process of vertebrate encephalization. Yet, despite a substantial body of research (Tartarelli & Bisconti, 2006; Marino *et al.*, 2007; Montgomery *et al.*, 2013; Ridgway *et al.*, 2016; Fox *et al.*, 2017; Serio *et al.*, 2019; Bisconti *et al.*, 2020), an agreement on relevant evolutionary drivers remains elusive.

Some studies detect markedly higher levels of encephalization in toothed whales and dolphins (odontocetes) than baleen whales (mysticetes),

*Corresponding author. E-mail: m.r.mccurry1@gmail.com

perhaps because of their ability to echolocate and/or greater sociality (Marino *et al.*, 2004; Fox *et al.*, 2017; Serio *et al.*, 2019). Others suggest that large brains characterize all cetaceans, and arose from non-social cognitive demands associated with foraging complexity (Muller & Montgomery, 2019). Thermogenesis (Manger, 2006) and deep diving (Robin, 1973) have also been discussed as possible drivers, but generally have found little support (Worthy & Hickie, 1986; Marino *et al.*, 2006, 2008).

Testing these ideas is hindered by a scarcity of observations on extinct baleen whales (Mitchell, 1989; Boessenecker *et al.*, 2017; Bisconti *et al.*, 2020). This is especially problematic in the context of the echolocation hypothesis, which posits that increased brain size evolved to process complex acoustic signals (Marino *et al.*, 2004). Because even the earliest odontocetes show signs of an incipiently developed echolocation apparatus (Fordyce, 2002; Geisler *et al.*, 2014), increased brain size should have characterized their lineage – but not mysticetes or stem cetaceans – to some degree ever since its origin.

Here, we quantify the relative brain size of several archaic baleen whales and integrate our results with existing observations on living and extinct cetaceans. We then analyse this combined data set in a phylogenetic context to test whether early cetacean brain size evolution is consistent with the echolocation hypothesis.

MATERIALS AND METHODS

INSTITUTIONAL ABBREVIATIONS

LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; NMV, Museums Victoria, Melbourne, Australia; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

SPECIMEN SELECTION

We compiled endocranial volumes for stem cetaceans (archaeocetes), odontocetes, extant mysticetes and the stem mysticete *Llanocetus denticrenatus* from the literature (Supporting Information, Table S1), and complemented them with new measurements of five extinct mysticetes: the mammalodontid *Janjucetus hunderi* (NMV P216929); two aetiocetids (*Fucaia goedertorum*, LACM 131146; unnamed species, NMV P252567); the stem presumed stem plicogulan *Parietobalaena palmeri* (USNM 205950); and the cetotheriid *Piscobalaena nana* (MNHN SAS1623). For the sake of completeness, we also included the

previously unmeasured extant pygmy right whale, *Caperea marginata* (NMV C38157).

Endocranial volumes of extinct mysticetes were obtained via computed tomography (CT), using a Siemens combined positron emission tomography/computerized X-ray tomography (PET/CT) system at Melbourne Brain Centre (Melbourne, Australia) for *Janjucetus hunderi*; a Siemens Somatom 128-slice CT device at the Natural History Museum of Los Angeles County (Los Angeles, USA) for *Fucaia*; a 128-slice medical CT device at St Vincent's Hospital (Melbourne, Australia) for the unnamed aetiocetid (NMV P252567); a Nikon Metrology combined 450-kV microfocus walk-in vault system at Chesapeake Testing (Belcamp, USA) for *Parietobalaena*; and a Siemens large-animal CT device at the Werribee Veterinary Centre (Melbourne, Australia) for *Caperea* (NMV C38157). Scan data of the endocranial space for each specimen are available from www.morphosource.org/projects/000347005. CT scanning facilities were not available for *Piscobalaena*, and we therefore measured its endocranial volume by first filling the cranial cavity with moulding clay, and then determining the volume of the clay through its displacement of water in a measuring cup.

ESTIMATION OF BRAIN MASS

We used Mimics (Materialize, v.20) to measure the endocranial cavity of the scanned specimens, defined as ranging from the constriction posterior to the ethmoid canal to the posteriormost coronal slice (following Marino *et al.*, 2000). In *Janjucetus*, the left posterolateral portion of the endocast was missing, and hence had to be reconstructed by mirroring its right counterpart across the sagittal plane.

Next, we inferred the brain mass of all specimens from their endocranial volume (EV). To do so, we first estimated adnexa volume (AV), i.e. the volume of non-brain tissues inside the cranial vault, following Boessenecker *et al.* (2017):

$$AV = 1.7698 \times \log EV - 3EV - 3.4931$$

This equation is based on living toothed and baleen whales, which phylogenetically bracket archaic mysticetes. Finally, we subtracted the adnexa from the endocranial volume, and converted the remainder to brain mass (BrM) assuming a specific gravity of 1.04 (Ridgway *et al.*, 2016).

ESTIMATION OF RELATIVE BRAIN SIZE

To estimate relative brain size, we first calculated the total body length of *Janjucetus*, *Llanocetus*, *Fucaia*, *Parietobalaena*, *Piscobalaena* and NMV P252567 following Pyenson & Sponberg (2011):

$$\log TL = 0.92 \times (\log BIZYG - 1.72) + 2.68$$

where TL is total length and BIZYG is bizygomatic width. TL was then used to estimate body mass (BM), following Uhen (2004):

$$\log BM = (2.966 \times \log TL) - 4.616.$$

Body size data for the remaining taxa were compiled from the literature (Gingerich, 1998; Marino *et al.*, 2004; Manger, 2006; Clauset, 2013; Boessenecker *et al.*, 2017) (Supporting Information, Fig. S1).

Relative brain size is often measured via the encephalization quotient (EQ), or deviation of brain mass of a given species from that predicted by its body size (Jerison, 1973):

$$EQ = BrM / (0.12 \times BM^{0.67}).$$

In cetaceans, however, EQ correlates with body size (Fig. 1A), and therefore fails as a measure of relative brain size. This is because EQ was developed from a primarily terrestrial dataset, and therefore within the limits imposed by life on land. In water, constraints on maximum body size are more relaxed (Clauset, 2013), thus biasing estimates of EQ. To avoid this problem, we instead quantified encephalization via a phylogenetic least squares (PGLS) approach regressing absolute brain mass on body mass under the assumption of Brownian motion.

To provide a framework for this analysis, we created a composite phylogeny following Montgomery *et al.* (2013) for archaeocetes and odontocetes, and Fordyce & Marx (2018) for mysticetes. The stem odontocete *Albertocetus meffordorum* was not included in Montgomery *et al.* (2013), and hence was placed following Boessenecker *et al.* (2017).

Stratigraphic ranges were downloaded from the Paleobiology Database (paleobiodb.org), vetted to remove imprecise estimates (Supporting Information, Table S1), and used to scale the branch lengths of our phylogeny. Scaling was carried out using the timePaleoPhy function of the R (R Development Core Team, 2013) package paleotree (Bapst, 2012), with the minimum age of all nodes with extant descendants constrained to the molecular divergence estimates (six-partition autocorrelated model) of McGowen *et al.* (2020).

EVOLUTIONARY TRENDS AND RATES

We initially compared relative brain size between stem cetaceans, mysticetes and odontocetes via a phylogenetic analysis of variance (ANOVA). This was based on residuals from a linear regression between log brain mass and log body mass, and implemented using the *aov.phylo* function in the geiger v.2.0.6 package of R (Pennell *et al.*, 2014).

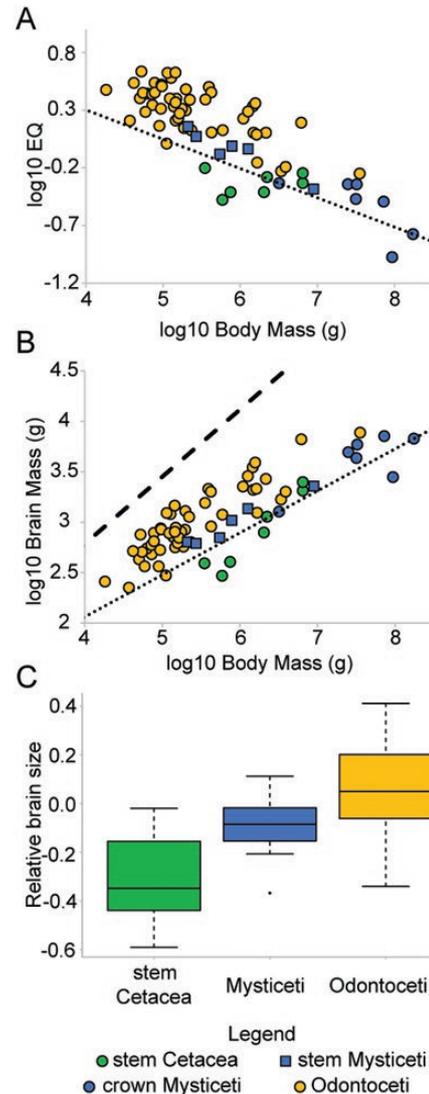


Figure 1. Evolution of relative brain size in whales and dolphins. A, relationship between body size and encephalization quotient (EQ) (PGLS regression, dotted line); green circles denote archaeocetes, yellow circles odontocetes, blue circles extant mysticetes and blue squares extinct mysticetes. B, relationship between body size and brain size (PGLS regression, dotted line); symbols and colours as in A; dashed line represents the scaling relationship between body and brain size in terrestrial tetrapods (Jerison, 1973). C, relative brain size in stem cetaceans, mysticetes and odontocetes.

Next, we tested for trends and shifts in cetacean brain size evolution using phylogenetic ridge regression, as implemented in the R package RRphylo (Castiglione *et al.*, 2018). We searched for trends across all cetaceans, mysticetes and odontocetes via the function *search.trend*, which regresses both phenotypic data (i.e. relative brain size) and rates of brain size evolution against time (Castiglione *et al.*, 2019).

Phenotypic trends were again based on the residuals of a linear regression between log brain mass and log body mass. By contrast, rates were calculated by applying multiple phylogenetic ridge regression to our absolute brain size estimates, while taking into account body size as an additional predictor (Serio *et al.*, 2019; Melchionna *et al.*, 2020).

We searched for potential rate shifts using the function *search.shift* (Castiglione *et al.*, 2018). To test for rate shifts associated with echolocation, we initially ran the function in ‘clade’ mode, which automatically compares the mean absolute rates of all major subclades to the mean absolute rates of the rest of the tree. We hypothesized that, if echolocation drove encephalization, one or more rate shifts should have occurred early in odontocete evolution.

Next, we ran *search.shift* in ‘sparse’ mode, which compares species based on predefined categories (e.g. habitat type or feeding strategy) rather than their phylogenetic position. Specifically, we compared riverine (*Platanista*, *Inia*, *Sotalia fluviatilis* and *Lipotes*) with oceanic taxa as a proxy for foraging complexity, and species forming ephemeral vs. stable pods (data from Fox *et al.*, 2017) as a proxy for sociality. For the latter analysis, we treated extinct taxa as an independent group owing to their lack of behavioural data.

Finally, we tested whether our results are robust to phylogenetic uncertainty and sampling via the function *overfitRR* (Serio *et al.*, 2019). The latter first randomly removes one-fifth of the species in the tree, then partially randomizes the phylogeny (or focal clade), and finally re-analyses it using *search.trend* and *search.shift*. This procedure is repeated 100 times, with the percentage of significant runs providing an estimate of support for particular trends and/or rate shifts.

DATA AVAILABILITY

The data underlying this study are available in the [Supporting Information](#) and at www.morphosource.org/projects/000347005.

RESULTS

ENDOCRANIAL VOLUMES

Reconstructed endocranial volumes range from 618.76 and 640.28 mm³ in the aetiocetids *Fucaia goedertorum* and NMVP252567, to 708.61 mm³ in the mammalodontid *Janjucetus* and, finally, 1073.58, 1329.61 and 1430 mm³ in the baleen-bearing whales *Parietobalaena*, *Caperea* and *Piscobalaena*.

PGLS REGRESSION

Our PGLS analysis of relative brain size in cetaceans yields a substantially lower slope ($y = 0.4164x + 0.3953$, $P < 0.001$, $R^2 = 0.277$) than previous estimates based on terrestrial mammals ($y = 0.666x + 0.12$, $R^2 = 0.96$) (Jerison, 1973), thus corroborating the existence of a different scaling relationship in water (Fig. 1B). Stem mysticetes plot higher than most archaeocetes and broadly fall within the lower part of the range of comparably sized odontocetes. Overall, extinct and living mysticetes follow a similar trend between body mass and brain mass (Fig. 1B), with all but one plotting on or slightly above the line of best fit. Three archaeocetes – *Basilosaurus cetoides*, *B. isis* and *Dorudon atrox* – also fall above this line.

ANOVA

Both mysticetes and odontocetes have notably larger brains than stem cetaceans (Fig. 1C). Nevertheless, our phylogenetic ANOVA reveals no significant difference in encephalization between groups ($P = 0.120$).

PHENOTYPIC AND RATE TRENDS

Visual examination of our results suggests a slight increase in relative brain size in both stem mysticetes and stem odontocetes (Fig. 2). Delphinoids are more highly encephalized than all other cetaceans, with less pronounced increases evident in physeteroids, rorquals and the extinct xenorhids (Figs 2, 3). By contrast, the brains of the ‘river’ (though not necessarily riverine) dolphins *Platanista*, *Pontoporia*, *Lipotes* and *Inia* are notably small, as are those of various baleen whales (*Balaena*, *Caperea* and *Janjucetus*).

Statistically, there are significant trends towards greater encephalization across all cetaceans, mysticetes and odontocetes, but for the latter two only if stem species are included (Table 1). Evolutionary rates also increase across cetaceans, but marginally so and with poor support (Table 2). Better-supported increases characterize odontocetes and crown odontocetes. By contrast, mysticetes show a poorly supported decrease in rates, which again disappears when stem species are excluded (Table 2).

EVOLUTIONARY RATE SHIFTS

In addition to examining overall trends in the rate of brain size evolution, we tested for the presence of distinct, clade-specific rate shifts. In ‘clade’ mode, *search.shift* identifies a significant decrease in the rate of brain size evolution in crown mysticetes ($P = 0.001$; overfit = 100%), and an increase within oceanic dolphins at the node uniting *Steno*, *Globicephala*,

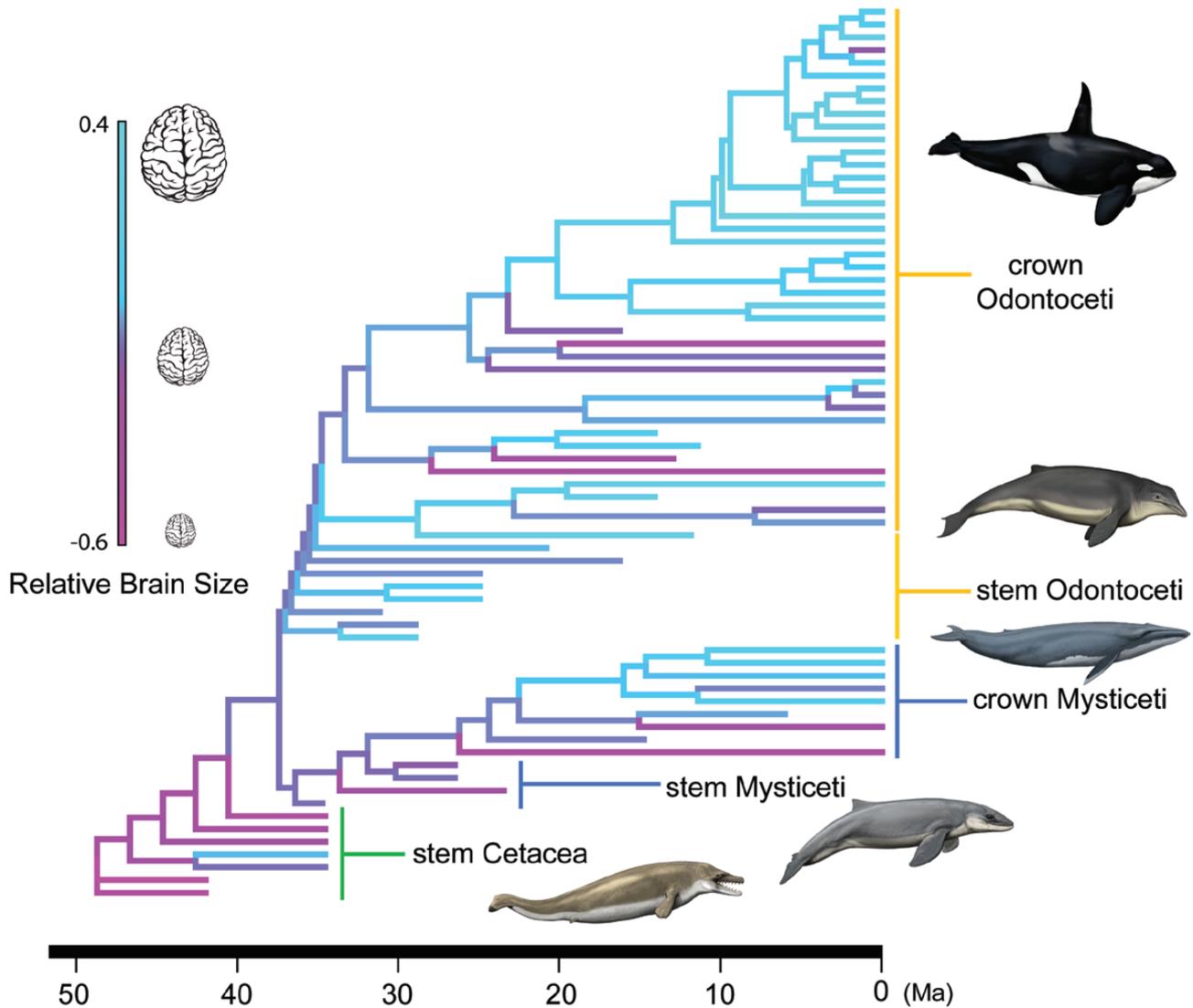


Figure 2. Relative brain size in cetaceans, reconstructed along a time-scaled phylogeny using RRphylo. Drawings of cetaceans by C. Buell.

Pseudorca, *Grampus*, *Sotalia*, *Delphinus*, *Stenella* and *Tursiops* ($P = 1.000$; note that in RRphylo a P -value close to 1 reflects a significant increase in rate; overfit = 95%) (Fig. 3). There are no significant shifts at or near the base of Odontoceti.

In ‘sparse’ mode, there is no significant difference between riverine and oceanic species ($P = 0.206$). By contrast, species aggregating in stable pods do show significantly higher rates of brain size evolution than those forming more ephemeral associations ($P = 0.998$; overfit = 88%).

DISCUSSION

Both baleen and toothed whales are more encephalized than stem cetaceans (Fig. 1), but their respective origins

are not marked by a significant increase in either relative brain size or the rate of brain size evolution (Figs 2, 3). In addition, some of the latest archaeocetes (*Basilosaurus* and *Dorudon*) were under selective pressure towards greater encephalization. Large brains thus preceded, and seemingly were not influenced by, the appearance of echolocation in early odontocetes. Acoustic processing may still explain independent trends towards greater encephalization within some toothed whales – especially delphinoids, as suggested by their enlarged temporal lobe (Bisconti *et al.*, 2020) – but not a similar increase in rorquals (Fig. 2). Likewise, the small brains of ‘river dolphins’, which rely heavily on echolocation to navigate their murky habitat, suggest that even within odontocetes evolutionary drivers other than echolocation must be at work.

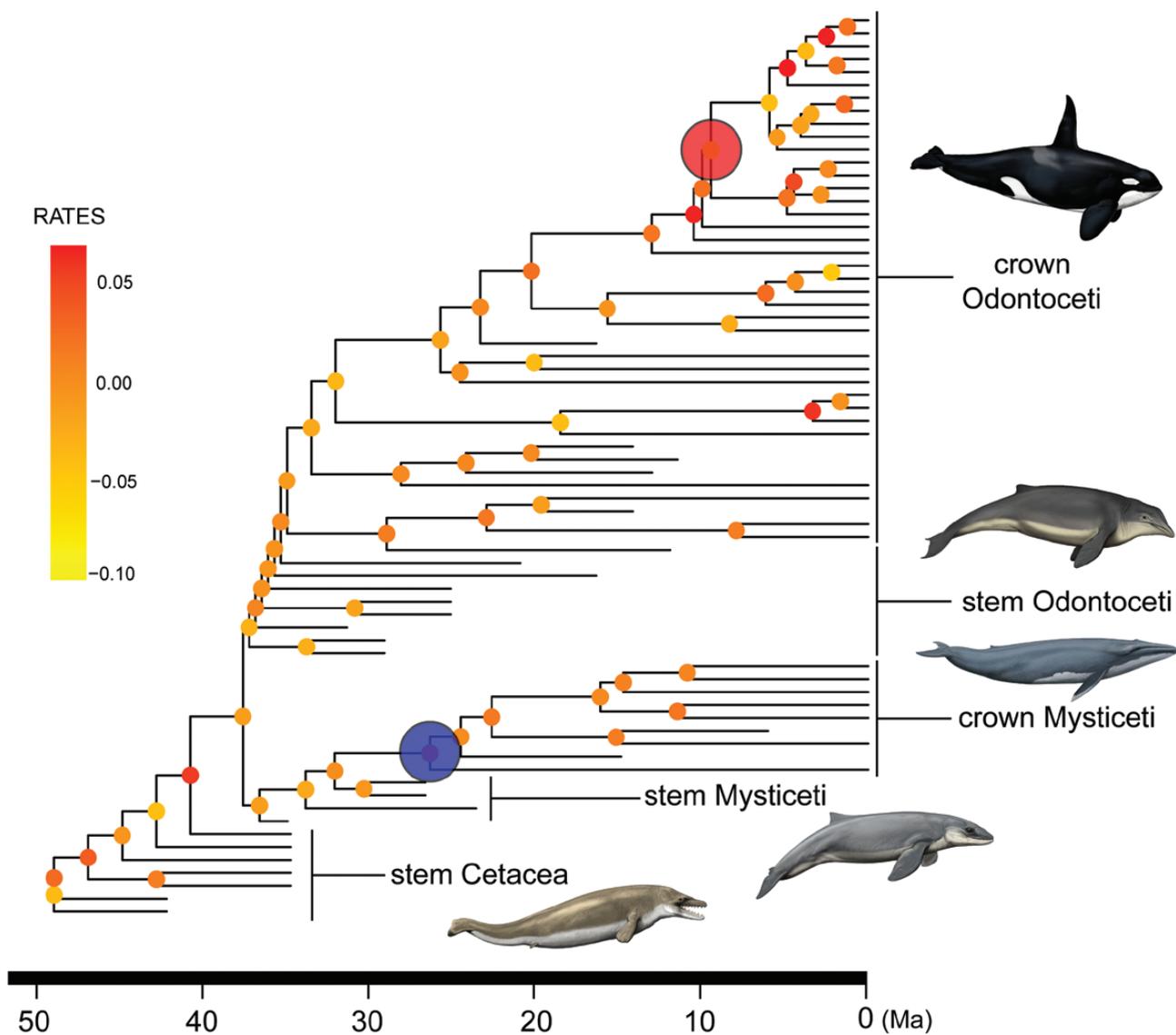


Figure 3. Rate of cetacean brain size evolution, estimated along a time-scaled phylogeny using RRphylo. Red circle, significant increase; blue circle, significant decrease.

Table 1. Phenotypic trends in the evolution of relative brain size across cetaceans, mysticetes and odontocetes

	Slope	<i>P</i> value	Overfit (%)
Cetacea	0.006	0.02	89
Odontoceti	0.005	0.06	42
Crown Odontoceti	0.004	0.16	31
Mysticeti	0.005	0.06	49
Crown Mysticeti	-0.001	0.24	28

Table 2. Trends in the rate of brain size evolution across cetaceans, mysticetes and odontocetes

	Slope	<i>P</i> value	Overfit (%)
Cetacea	0.008	0.05	18
Odontoceti	0.001	<0.001	99
Crown Odontoceti	0.001	<0.001	98
Mysticeti	-0.001	0.006	66
Crown Mysticeti	0	0.398	1

Dietary breadth is another possible driver of brain size (Muller & Montgomery, 2019), yet is difficult to reconcile with the observation that stem

cetaceans retained relatively small brains despite their seemingly varied diets (Fahlke *et al.*, 2013). Nevertheless, encephalization at times may still

reflect concurrent shifts in feeding mode. Thus, long-snouted snap-feeders such as *Inia*, *Lipotes*, *Pontoporia* and *Platanista* and skim-feeders such as *Balaena* and *Caperea* have relatively small brains, whereas those of rorquals increased in tandem with the evolution of lunge feeding (Fig. 2). Such patterns may reflect differences in energy uptake between feeding strategies, which could plausibly constrain brain size (e.g. in primates; Aiello & Wheeler, 1995; Fish & Lockwood, 2003). Comparisons between cetacean energetics and relative brain size may provide a way to test this in the future.

Social complexity is a defining feature of many cetaceans, and along with behavioural richness may have coevolved with their large brains (Fox *et al.*, 2017). Our results support this hypothesis insofar as species forming medium to large pods – all of them odontocetes, and most of them delphinids – appear to experience significantly higher rates of brain size evolution.

Although mysticetes are usually regarded as more solitary, they are still capable of complex social interactions and behaviours. Humpback whales (*Megaptera novaeangliae*), for example, are gregarious, capable of feeding cooperatively, and show cultural transmission of both songs and feeding behaviours (Acevedo-Gutiérrez, 2017). Likewise, long-term bonds between individuals and/or complex socio-sexual behaviours occur in sperm whales and at least some beaked whales and river dolphins (Acevedo-Gutiérrez, 2017; Sutaria *et al.*, 2019). This widespread distribution suggests that sociality is deeply rooted in cetacean evolution, and as such plausibly contributed to the emergence of their large brains. Conversely, reductions in relative brain size might reflect secondary decreases in social complexity, perhaps correlated with feeding strategy (e.g. skim feeding in right whales and *Caperea*) or habitat (e.g. in ‘river’ dolphins).

The relative importance of factors such as sociality and diet are still actively debated in primates (Pontzer *et al.*, 2016; DeCasien *et al.*, 2017; Street *et al.*, 2017), ungulates (Shultz & Dunbar, 2006) and carnivorans (Finarelli & Flynn, 2009; Swanson *et al.*, 2012). As brains are responsible for a complex variety of functions, they are also under a complex array of selective pressures. This matches our results, which suggest that cetacean encephalization cannot be attributed to a single driver. Instead, echolocation, foraging complexity and sociality may all have played a role, albeit at different times and to varying degrees.

ACKNOWLEDGEMENTS

F.G.M. was funded by an Australian Research Council DECRA fellowship (DE190101052) and an

FNRS postdoctoral fellowship (32795797). A.R.E and E.M.G.F. were funded by an ARC Linkage Grant (LP150100403). T.P. was funded by a Marie Skłodowska-Curie Individual Fellowship (748167/ECHO), an ERC Starting Grant (677774/TEMPO) and a Leverhulme Research Project Grant (RPG-2019–323/Back to the water). N.D.P. was funded by the Smithsonian Institution, its Remington Kellogg Fund and with support from the Basis Foundation. We thank O. Lambert as well as two anonymous reviewers for their comments on the manuscript; D. Bohaska, C. de Muizon, S. McLeod and K. Roberts for access to museum collections; and K. Wilson, C. Peredo, R. Peitsch, C. Schueler, R. Williams and St Vincent’s Hospital (Melbourne) for help with scanning specimens. The authors acknowledge the facilities and scientific and technical assistance of the National Imaging Facility, a National Collaborative Research Infrastructure Strategy (NCRIS) capability, at the Melbourne Brain Centre Imaging Unit, the University of Melbourne; A. Giles and P. Smith for helpful discussions; and C. Buell for providing illustrations.

REFERENCES

- Acevedo-Gutiérrez A.** 2017. Group behaviour. In: Würsig B, Thewissen JGM, Kovacs KM, eds. *Encyclopedia of marine mammals*. London: Academic Press, 428–435.
- Aiello LC, Wheeler P.** 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology* **36**: 199–221.
- Bapst DW.** 2012. Paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution* **3**: 803–807.
- Bisconti M, Damarco P, Tartarelli G, Pavia M, Carnevale G.** 2020. A natural endocast of an early Miocene odontocete and its implications in cetacean brain evolution. *The Journal of Comparative Neurology* **529**: 1198–1227.
- Boessenecker RW, Ahmed E, Geisler JH.** 2017. New records of the dolphin *Albertocetus meffordorum* (Odontoceti: Xenorophidae) from the lower Oligocene of South Carolina: encephalization, sensory anatomy, postcranial morphology, and ontogeny of early odontocetes. *PLoS ONE* **12**: e0186476.
- Castiglione S, Serio C, Mondanaro A, Di Febbraro M, Profico A, Girardi G, Raia P.** 2019. Simultaneous detection of macroevolutionary patterns in phenotypic means and rate of change with and within phylogenetic trees including extinct species. *PLoS ONE* **14**: e0210101.
- Castiglione S, Tesone G, Piccolo M, Melchionna M, Mondanaro A, Serio C, Di Febbraro M, Raia P.** 2018. A new method for testing evolutionary rate variation and shifts in phenotypic evolution. *Methods in Ecology and Evolution* **9**: 974–983.
- Clauset A.** 2013. How large should whales be? *PLoS ONE* **8**: e53967.

- DeCasien AR, Williams SA, Higham JP. 2017.** Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution* **1**: 1–7.
- Fahlke JM, Bastl KA, Semprebon GM, Gingerich PD. 2013.** Paleoeology of archaeocete whales throughout the Eocene: dietary adaptations revealed by microwear analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* **386**: 690–701.
- Finarelli JA, Flynn JJ. 2009.** Brain-size evolution and sociality in Carnivora. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 9345–9349.
- Fish JL, Lockwood CA. 2003.** Dietary constraints on encephalization in primates. *American Journal of Physical Anthropology* **120**: 171–181.
- Fordyce RE, Marx FG. 2018.** Gigantism precedes filter feeding in baleen whale evolution. *Current Biology* **28**: 1670–1676.e1672.
- Fordyce RE. 2002.** *Simocetus rayi* (Odontoceti: Simocetidae, new family): a bizarre new archaic Oligocene dolphin from the eastern North Pacific. *Smithsonian Contributions to Paleobiology* **93**: 185–222.
- Fox KCR, Muthukrishna M, Shultz S. 2017.** The social and cultural roots of whale and dolphin brains. *Nature Ecology & Evolution* **1**: 1699–1705.
- Geisler JH, Colbert MW, Carew JL. 2014.** A new fossil species supports an early origin for toothed whale echolocation. *Nature* **508**: 383–386.
- Gingerich PD. 1998.** Paleobiological perspectives on Mesonychia, Archaeoceti, and the origin of whales. In: *The emergence of whales*. Boston: Springer, 423–449.
- Jerison HJ. 1973.** *Evolution of the brain and intelligence*. New York: Academic Press.
- Manger PR. 2006.** An examination of cetacean brain structure with a novel hypothesis correlating thermogenesis to the evolution of a big brain. *Biological Reviews of the Cambridge Philosophical Society* **81**: 293–338.
- Marino L, Butti C, Connor RC, Fordyce RE, Herman LM, Hof PR, Lefebvre L, Lusseau D, McCowan B, Nimchinsky EA, Pack AA, Reidenberg JS, Reiss D, Rendell L, Uhen MD, Van der Gucht E, Whitehead H. 2008.** A claim in search of evidence: reply to Manger's thermogenesis hypothesis of cetacean brain structure. *Biological Reviews of the Cambridge Philosophical Society* **83**: 417–440.
- Marino L, Connor RC, Fordyce RE, Herman LM, Hof PR, Lefebvre L, Lusseau D, McCowan B, Nimchinsky EA, Pack AA, Rendell L, Reidenberg JS, Reiss D, Uhen MD, Van der Gucht E, Whitehead H. 2007.** Cetaceans have complex brains for complex cognition. *PLoS Biology* **5**: e139.
- Marino L, McShea DW, Uhen MD. 2004.** Origin and evolution of large brains in toothed whales. *The Anatomical Record. Part A, Discoveries in Molecular, Cellular, and Evolutionary Biology* **281**: 1247–1255.
- Marino L, Sol D, Toren K, Lefebvre L. 2006.** Does diving limit brain size in cetaceans? *Marine Mammal Science* **22**: 413–425.
- Marino L, Uhen MD, Frohlich B, Aldag JM, Blane C, Bohaska D, Whitmore FC. 2000.** Endocranial volume of Mid-Late Eocene archaeocetes (Order: Cetacea) revealed by computed tomography: implications for cetacean brain evolution. *Journal of Mammalian Evolution* **7**: 81–94.
- McGowen MR, Tsagkogeorga G, Álvarez-Carretero S, Dos Reis M, Struebig M, Deaville R, Jepson PD, Jarman S, Polanowski A, Morin PA, Rossiter SJ. 2020.** Phylogenomic resolution of the cetacean tree of life using target sequence capture. *Systematic Biology* **69**: 479–501.
- Melchionna M, Mondanaro A, Serio C, Castiglione S, Di Febbraro M, Rook L, Diniz-Filho J, Manzi G, Profico A, Sansalone G. 2020.** Macroevolutionary trends of brain mass in Primates. *Biological Journal of the Linnean Society* **129**: 14–25.
- Mitchell ED. 1989.** A new cetacean from the Late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 2219–2235.
- Montgomery SH, Geisler JH, McGowen MR, Fox C, Marino L, Gatesy J. 2013.** The evolutionary history of cetacean brain and body size. *Evolution; International Journal of Organic Evolution* **67**: 3339–3353.
- Muller AS, Montgomery SH. 2019.** Co-evolution of cerebral and cerebellar expansion in cetaceans. *Journal of Evolutionary Biology* **32**: 1418–1431.
- Pennell MW, Eastman JM, Slater GJ, Brown JW, Uyeda JC, FitzJohn RG, Alfaro ME, Harmon LJ. 2014.** geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics (Oxford, England)* **30**: 2216–2218.
- Pontzer H, Brown MH, Raichlen DA, Dunsworth H, Hare B, Walker K, Luke A, Dugas LR, Durazo-Arvizu R, Schoeller D, Plange-Rhule J, Bovet P, Forrester TE, Lambert EV, Thompson ME, Shumaker RW, Ross SR. 2016.** Metabolic acceleration and the evolution of human brain size and life history. *Nature* **533**: 390–392.
- Pyenson ND, Sponberg SN. 2011.** Reconstructing body size in extinct crown Cetacea (Neoceti) using allometry, phylogenetic methods and tests from the fossil record. *Journal of Mammalian Evolution* **18**: 269–288.
- R Development Core Team. 2013.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Ridgway SH, Carlin KP, Van Alstyne KR, Hanson AC, Tarpley RJ. 2016.** Comparison of dolphins' body and brain measurements with four other groups of cetaceans reveals great diversity. *Brain, Behavior and Evolution* **88**: 235–257.
- Robin ED. 1973.** The evolutionary advantages of being stupid. *Perspectives in Biology and Medicine* **16**: 369–380.
- Serio C, Castiglione S, Tesone G, Piccolo M, Melchionna M, Mondanaro A, Di Febbraro M, Raia P. 2019.** Macroevolution of toothed whales exceptional relative brain size. *Evolutionary Biology* **46**: 332–342.
- Shultz S, Dunbar RI. 2006.** Both social and ecological factors predict ungulate brain size. *Proceedings of the Royal Society of London B: Biological Sciences* **273**: 207–215.

- Street SE, Navarrete AF, Reader SM, Laland KN. 2017.** Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America* **114**: 7908–7914.
- Sutaria D, Kelkar N, Araújo-Wang C, Santos M. 2019.** Cetacean sociality in rivers, lagoons, and estuaries. In: Würsig B, ed. *Ethology and behavioral ecology of odontocetes*. Cham: Springer International Publishing, 413–434.
- Swanson EM, Holekamp KE, Lundrigan BL, Arsznov BM, Sakai ST. 2012.** Multiple determinants of whole and regional brain volume among terrestrial carnivorans. *PLoS ONE* **7**: e38447.
- Tartarelli G, Bisconti M. 2006.** Trajectories and constraints in brain evolution in primates and cetaceans. *Human Evolution* **21**: 275–287.
- Uhen MD. 2004.** Form, function and anatomy of *Dorudon atrox* (Mammalia: Cetacea): an archaeocete from the Middle to Late Eocene of Egypt. *University of Michigan Papers on Paleontology* **34**: 1–222.
- Worthy GAJ, Hickie JP. 1986.** Relative brain size in marine mammals. *The American Naturalist* **128**: 445–459.

SUPPORTING INFORMATION

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

Table S1. Supplementary data including phenotypic data, tip dates and node dates.

Figure S1. Plot of \log_{10} body mass across the phylogeny.