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Permalink
https://escholarship.org/uc/item/0tj5c7s8

Journal
Brain, Behavior and Evolution, 88(3-4)

ISSN
0006-8977 1421-9743

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Publication Date
2016

DOI
10.1159/000454797

Peer reviewed

Comparison of Dolphins' Body and Brain Measurements with Four Other Groups of Cetaceans Reveals Great Diversity

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Abstract

We compared mature dolphins with 4 other groupings of mature cetaceans. With a large data set, we found great brain diversity among 5 different taxonomic groupings. The dolphins in our data set ranged in body mass from about 40 to 6,750 kg and in brain mass from 0.4 to 9.3 kg. Dolphin body length ranged from 1.3 to 7.6 m. In our combined data set from the 4 other groups of cetaceans, body mass ranged from about 20 to 120,000 kg and brain mass from about 0.2 to 9.2 kg, while body length varied from 1.21 to 26.8 m. Not all cetaceans have large brains relative to their body size. A few dolphins near human body size have human-sized brains. On the other hand, the absolute brain mass of some other cetaceans is only one-sixth as large. We found that brain volume relative to body mass decreases from Delphinidae to a group of Phocoenidae and Monodontidae, to a group of other odontocetes, to Balaenopteroidea, and finally to Balaenidae. We also found the same general trend when we compared brain volume relative to body length, except that the Delphinidae and Phocoenidae-Monodontidae groups do not differ significantly. The Balaenidae have the smallest relative brain mass and the lowest cerebral cortex surface area. Brain parts also vary. Relative to body mass and to body length, dolphins also have the largest cerebellums. Cortex surface area is isometric with brain size when we exclude the Balaenidae. Our data show that the brains of Balaenidae are less convoluted than those of the other cetaceans measured. Large vascular networks inside the cranial vault may help to maintain brain temperature, and these nonbrain tissues increase in volume with body mass and with body length ranging from 8 to 65% of the endocranial volume. Because endocranial vascular networks and other adnexa, such as the tentorium cerebelli, vary so much in different species, brain size measures from endocasts of some extinct cetaceans may be overestimates. Our regression of body length on endocranial adnexa might be used for better estimates of brain volume from endocasts or from endocranial volume of living species or extinct cetaceans.

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Published by S. Karger AG, Basel

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Introduction

Brain and body size is diverse in our primate family, and we humans have the largest brain by far. From our view as humans, evolution's greatest success is the brain.

Nature presents us with a great variety of mammals with a great variety of brains built upon basic parts [Bullock, 1984]. With few exceptions, the main parts of the human brain are present in the other mammals, including cetaceans. Only among the cetaceans (whales, dolphins, and porpoises) are there many species with brains larger than our own. All cetacean brains that are larger than ours are in larger bodies.

How distinctive are human brains? That question is asked over and over. Ultimately, our driving interest in brain size stems from the large size of our own brain [Deacon, 1990]. There is a huge range of body size among mature cetaceans. The smallest adult La Plata dolphin, *Pontoporia blainvillei*, may weigh as little as 15–20 kg [Kamiya and Yamasaki, 1974; Pirlot and Kamiya, 1975] while the largest blue whale, *Balaenoptera musculus*, may approach 200,000 kg [Lockyer, 1976]. It is obvious from many studies that brain size does not vary strictly with body size [Pilleri and Gihr, 1970; Pirlot and Kamiya, 1975; Miyazaki et al., 1981; Ridgway and Brownson, 1984; Worthy and Hickie, 1986; Marino et al., 2004; Turner et al., 2006; Connor, 2007; Montgomery et al., 2013; Gingerich, 2015; Mallette et al., 2016]. Data on brains of cetaceans of known maturity have been sparse. Brain size is frequently cited in different studies on evolution, ecology, taxonomy, and social organization. To inform such studies, our large data set on brain relations of extant cetaceans should be helpful.

How can brain size be compared across species? Jerison [1973, 1978] reviewed earlier work and introduced an encephalization quotient (EQ) as an improved measure of relative brain size. Jerison's EQ is a number that quantifies how much larger or smaller a brain is relative to the expected brain size based on body size. Among mammals, other than humans, some smaller dolphins have the highest EQ and the highest relative brain size [Jerison, 1973; Ridgway, 1986; Marino, 1998; Marino et al., 2004].

The major divisions among cetaceans are the toothed whales (odontocetes, 10 families and 75 species) and the baleen whales (mysticetes, 4 families and 14 species). Often, broad groups of cetaceans are taken together in studies of encephalization. For example, many studies do not appear to differentiate among toothed whales [Pilleri and Gihr, 1970; Shultz and Dunbar, 2010; Boddy et al., 2012]. Marino et al. [2004] found the EQ among toothed whales

Table 1. Cetacean brains were weighed periodically after immersion in formalin solution

Bin No.	Measurements, n	Range, days	$\log_{10}$ max range	Change, %
1	28	0	0	0
2	26	0.5–3	0.47712	0.99
3	28	4–7	0.8451	0.53
4	24	8–13	1.11394	0.98
5	28	14–28	1.44716	0.44
6	28	29–48	1.68124	0.59
7	26	49–73	1.86332	0.44
8	28	74–99	1.99564	0.22
9	28	100–123	2.08991	0.43
10	27	127–159	2.2014	0.3
11	28	160–192	2.2833	0.17
12	28	193–237	2.37475	0.39
13	28	240–289	2.4609	−0.01
14	27	294–326	2.51322	0.11
15	27	327–364	2.5611	0.09
16	28	365–412	2.6149	0.08
17	28	414–545	2.7364	0.22
18	28	455–501	2.69984	0.08
19	28	502–572	2.7574	0.06
20	28	574–665	2.82282	0.09
21	28	667–741	2.86982	−0.03
22	28	745–825	2.91645	−0.15
23	28	827–973	2.98811	−0.19
24	28	975–1,183	3.07298	−0.13
25	28	1,197–1,524	3.18298	−0.18
26	20	1,533–2,055	3.31281	−0.06

Day 0 is the fresh brain weight (bin 1). Subsequent weights taken during a range of days were averaged. For example, 26 of the 28 brains were measured during the period of 0.5–3 days after day 0 (bin 2) to produce the average % change given in the last column. Twenty-eight brains were weighed during the 4- to 7-day period (bin 3) after day 0 and averaged to give the % change shown in the last column of the next row, and so on.

(odontocetes) was highest in some delphinids. With a smaller data set of living odontocetes than ours, they did not find a significant difference in brain size between different toothed whales. Likewise, Montgomery et al. [2013] did not find a significant difference between Delphinidae and other extant odontocetes for relative body and brain mass. Using the long-lived bowhead whale (*Balaena mysticetus*) as their example, Charvet and Finlay [2012] state that "cetaceans exhibit an extended period of development, an extended lifespan, and a large brain." These simplifications do not apply to all cetaceans. Manger [2013a] explored cetacean brain size and lifespan but found no evidence of a relation.

We often read that the cetacean cerebellum is large. Breathnach [1960] wrote that the mysticete cerebellum is about 20% of total brain size while that of odontocetes represents about 15%. This generalization must be revised. Pilleri and Gihr [1970] and Pilleri [1972] recognized that river dolphins, *Platanista* and *Inia,* differ from the other odontocetes in that they exhibit a lower relative cerebellum weight, which only represents 6.7–11.8% of the total brain weight. In other odontocete brains, Pilleri and Gihr [1970] gave the relative weight of the cerebellum as approximately 15–19% of the total brain weight. Now we know that some previous generalizations about odontocetes are incorrect. For example, there is a large difference in cerebellum size between 2 members of different odontocete families. The largest odontocete, *Physeter macrocephalus,* has a relatively small cerebellum. The largest delphinid, *Orcinus orca*, has a much larger cerebellum [Ridgway and Hanson, 2014]. We wanted to extend these investigations. Our goal was to determine if there were other differences in brain relations within the odontocete suborder and to make some further comparisons with the minimal available data on mysticete whales of the families Balaenopteridae, Eschrichtiidae, and Balaenidae.

Collection of the data reported here began in the 1960s from cetaceans with known mass, length, and maturity. Partial results were reported by Ridgway et al. [1966], Ridgway and Brownson [1984], Ridgway [1981, 1986, 1990], Tarpley and Ridgway [1994], Ridgway and Tarpley [1996], Marino et al. [2000a], Hanson et al. [2013], and Ridgway and Hanson [2014]. We wanted to know if our data might shed light on cetacean brain relationships among the different suborders, families, genera, and species.

Materials and Methods

We have weighed many brains and colleagues have shared many weights. Approximately 20% of the cetacean brains in this study were measured by the authors. Body mass and length measurements were also collected by us. Other researchers contributed about 25% of the measurements, and the remaining 55% were documented in the literature. These brain measurements were taken only from the published scientific literature or from animals that had stranded on beaches, became entrapped in fishing gear, or died of natural causes under human care. The older literature is mostly from whaling and fisheries. Many brains were removed during postmortem examinations. No live animals were used in this research and no animals were killed for the purpose of this study. The original research reported herein (specifically on cetacean brains, the specimen source for much of this study) was performed under guidelines established by the Institutional Animal Care and Use Committee of the US Navy Marine Mammal Program at the Space and Naval Warfare Systems Center Pacific, San Diego, CA, USA.
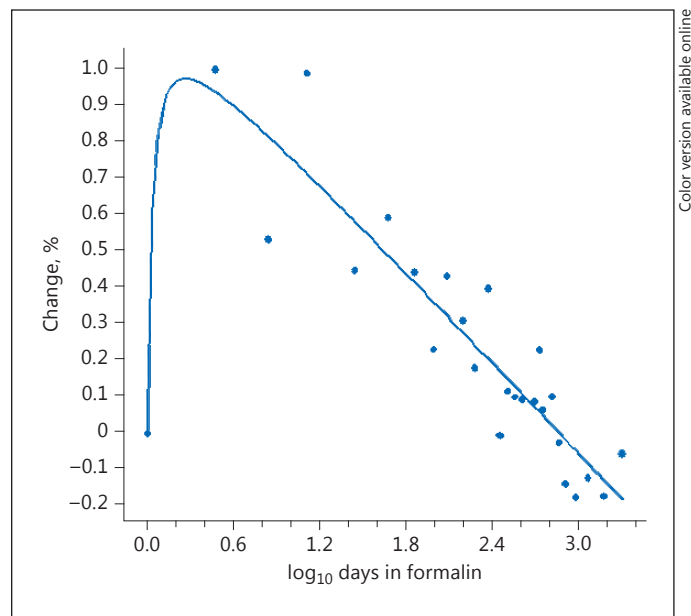

Fig. 1. Average brain mass change for 28 brains weighed fresh after removal and after various periods in phosphate-buffered formalin (10%). Day 0 is the time at which the brain was removed and weighed to establish 0% change.

Data on body length permitted maturity estimation [Perrin et al., 1984], allowing us to restrict our analysis to adult animals with a few exceptions where no adult data were available. In these few cases, we used data from subadult animals that fell just below the cutoff value for mature length.

Specific gravity is important for calculating mass from volume and vice versa. Marino et al. [2004] used a specific gravity of 1.0 to convert endocranial volumes to brain mass. Our mean specific gravity was 1.04. Because cetacean brains may contain slightly more white matter [DeGraaf, 1967], and white matter is heavier than gray matter [Gompertz, 1902], specific gravity of cetacean brains is slightly higher than the 1.036 generally stated for the human brain [Gompertz, 1902]. To remove the brain, numerous blood vessels must be cut allowing some air to enter the brain circulation. This air will have a small effect on the specific gravity. Our preferred method of fixation was to use Ringer's solution to make phosphate-buffered 10% formalin with a specific gravity of 1.029. We suspended cetacean brains in this solution with a thread attached to the blood vessels at the base of the brain. Some postmortem brain tissue may contain gas-producing organisms causing brains to float in formalin. Our analysis did not include any brains that floated.

We weighed brains immediately after removal or, in some cases, after short periods of fixation. Twenty-eight brains were measured fresh and then periodically in formalin. Our measurements during formalin fixation showed some variation. Most of the 28 brains measured during fixation showed an initial increase in mass followed by a steady but relatively small decrease (Fig. 1; Table 1). Thus, we concluded that the change in brain mass due to formalin is variable but not sufficient to affect the comparison of different groups of cetaceans.

Table 2. Total number of individuals for which we have brain mass data and number of species included from each taxonomic family

Taxonomic family and species included	Total, *n*	Author, *n*	Other, *n*	LIT, *n*	Brain mass (species average), g
Delphinidae	564	134	124	306	
Cephalorhynchus commersonii	6	5	0	1	783.17
Delphinus delphis	115	15	7	93	714.61
Feresa attenuata	4	1	1	2	1,144.25
Globicephala macrorhynchus	9	5	2	2	2,679.21
Globicephala melas	6	0	0	6	3,498.67
Grampus griseus	8	3	3	2	2,131.75
Lagenorhynchus acutus	6	0	0	6	1,285.03
Lagenorhynchus albirostris	8	0	7	1	1,372
Lagenorhynchus obliquidens	13	6	5	2	1,198.46
Lissodelphis borealis	2	1	1	0	1,231
Orcinus orca	27	9	3	15	6,621.59
Peponocephala electra	1	0	1	0	1,418
Pseudorca crassidens	7	5	0	2	3,893.43
Sotalia fluviatilis	4	0	0	4	515
Stenella attenuata	125	7	11	107	712.15
Stenella clymene	1	0	1	0	646
Stenella coeruleoalba	57	1	32	24	880.01
Stenella longirostris	57	7	22	28	541.05
Steno bredanensis	16	1	14	1	1,453.9
Tursiops truncatus	92	68	14	10	1,549.9
Monodontidae	16	8	0	8	
Delphinapterus leucas	11	8	0	3	2,086.91
Monodon monoceros	5	0	0	5	2,858
Phocoenidae	29	3	23	3	
Neophocaena phocaenoides	3	0	2	1	546
Phocoena phocoena	2	0	0	2	506
Phocoenoides dalli	24	3	21	0	803.29
Physeteridae	28	0	0	28	
Physeter macrocephalus	28	0	0	28	7,715.64
Kogiidae	14	5	9	0	
Kogia breviceps	12	5	7	0	907
Kogia simus	2	0	2	0	632.5
Iniidae	19	0	0	19	
Inia geoffrensis	19	0	0	19	562.16
Lipotidae	2	0	0	2	
Lipotes vexillifer	2	0	0	2	570
Pontoporiidae	19	0	0	19	
Pontoporia blainvillei	19	0	0	19	223.86
Platanistidae	4	0	0	4	
Platanista gangetica	4	0	0	4	295.25
Ziphiidae	32	1	30	1	
Hyperoodon ampullatus	1	0	0	1	2,720
Berardius bairdii	26	0	26	0	5,284.62
Mesoplodon densirostris	3	0	3	0	1,240
Mesoplodon europaeus	1	0	1	0	1,680
Ziphius cavirostris	1	1	0	0	2,004
Balaenidae	15	6	5	4	
Balaena mysticetus	11	6	5	0	2,795.82
Eubalaena australis	1	0	0	1	2,750
Eubalaena glacialis	3	0	0	3	3,000

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Tarpley

Table 2 (continued)

Taxonomic family and species included	Total, n	Author, n	Other, n	LIT, n	Brain mass (species average), g
Balaenopteridae	32	0	4	28	
Balaenoptera acutorostrata	9	0	4	5	2,227.67
Balaenoptera borealis	2	0	0	2	4,935
Balaenoptera musculus	2	0	0	2	6,716
Balaenoptera physalus	11	0	0	11	~~13,100~~ 6,856
Megaptera novaeangliae	8	0	0	8	5,869.25
Eschrichtiidae	4	0	0	4	
Eschrichtius robustus	4	0	0	4	4,319

"Author," "Other," and "LIT" columns refer to the source of individual data points. "Author" data points were measured directly by the authors listed in this study. "LIT" data points were extracted from the literature. "Other" data points were obtained from personal correspondence, stranding events, etc. All data come from adult individuals, with the exception of 6 subadult *B. mysticetus* and 1 subadult *K. breviceps*, with body lengths just below the mature length cutoff value. Average brain masses for each species are also given.

We used the method of Putnam [1927] to measure the cerebellum. We severed the cerebellar peduncles just above the roots of the 7th and 8th cranial nerves tangential to the brainstem, taking care to leave the posterior quadrigemina and the 4th nerve intact. The volume and mass of 4 sperm whale brains were calculated based on reported measures, drawings, and photographs [Ridgway and Hanson, 2014]. For these rare specimens only, we calculated the cerebellum volume from the length of the cerebellum base, width of the base, and height × 1/3. Kawabe et al. [2009] showed that such measurements could accurately predict brain volume in birds. All the other cerebellums reported here were directly weighed by us or reported in the literature. We did not use some cerebellum data from the literature because values included part of the brainstem [e.g. Schwerdtfeger et al., 1984]. In the case of 1 individual whale, we estimated the brainstem and cerebellum weight of a specimen on which both structures were weighed together. Because in that species (*O. orca*) we had considerable weights of both structures, we estimated the result.

In a subset of our data, we weighed the cerebrum (prosencephalon) by separating it from the brainstem after the cerebellum was removed. To separate the cerebrum, we made a cut from the anterior margin of the superior colliculus down to a point just behind the optic chiasma. These parts were weighed, and then volume was determined from mass using our measured average specific gravity of 1.04.

We measured nonbrain contents of the cranial vault (endocranial adnexa) by 2 different methods. First, after the brain was removed, endocranial adnexa including dura, falx cerebri, tentorium cerebelli, and blood vessels were stripped out and weighed. In 2 bottlenose dolphins, the adnexa volume was calculated by subtracting the in situ brain volume from the volume of the cranium in magnetic resonance images. Other values for endocranial adnexa were taken from the literature [Kojima, 1951; Jacobs and Jensen, 1964; Thewissen et al., 2011; Ridgway and Hanson, 2014].

We estimated the surface area of the cerebral cortex in formalin-fixed brains using stereological methods [Elias and Schwartz, 1969; Ridgway and Brownson, 1984]. Surface area was measured in 31 mature delphinids, 1 mature beaked whale (*Ziphius cavirostris*), and 6 subadult bowhead whales (*B. mysticetus*). Other surface area data were taken from the literature [Elias and Schwartz, 1969; Eriksen and Pakkenberg, 2007].

All statistical comparisons were made using analysis of covariance (ANCOVA) and the Wilcoxon rank sum test in a software program (SAS 9.4; SAS Institute Inc., Cary, NC, USA). All linear regressions, resulting linear equations, and standardized coefficients were generated in XLSTAT (2016.3; Statistical Innovations Inc., Boston, MA, USA).

Results

Total Brain Size Differences relative to Body Size

We categorized our data from each taxonomic family into 1 of 5 groups based on how the individual data points clustered with brain-body size regression analyses. The species and families included in these 5 groups are listed in Table 2. In general, we based the groups in our data analyses on the taxonomy of cetaceans presented by the Taxonomy Committee of the Society for Marine Mammalogy [2016]. Brain to body mass and body length relations in our sample of adult cetaceans represented both odontocetes (9 families, 28 genera, 34 species) and mysticetes (3 families, 5 genera, 9 species). Odontocetes were grouped along 3 regression lines (Fig. 2, 3). The family Delphinidae had larger brains relative to body size, followed by Phocoenidae and Monodontidae, and then by a group of all other odontocetes; these other odontocetes come from the superfamily Physeteroidea (Physeteridae and Kogiidae), family Ziphiidae, superfamily Inioidea
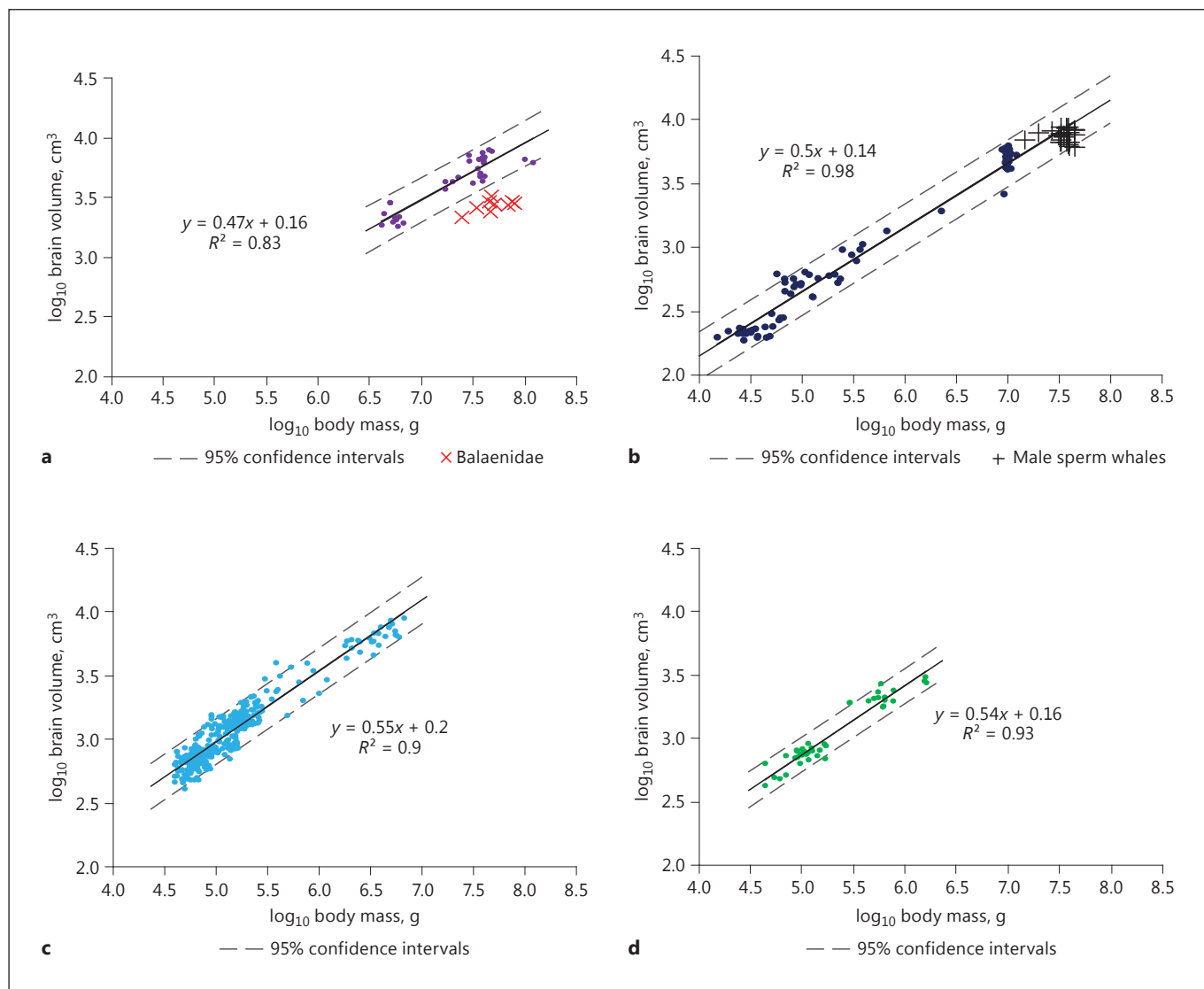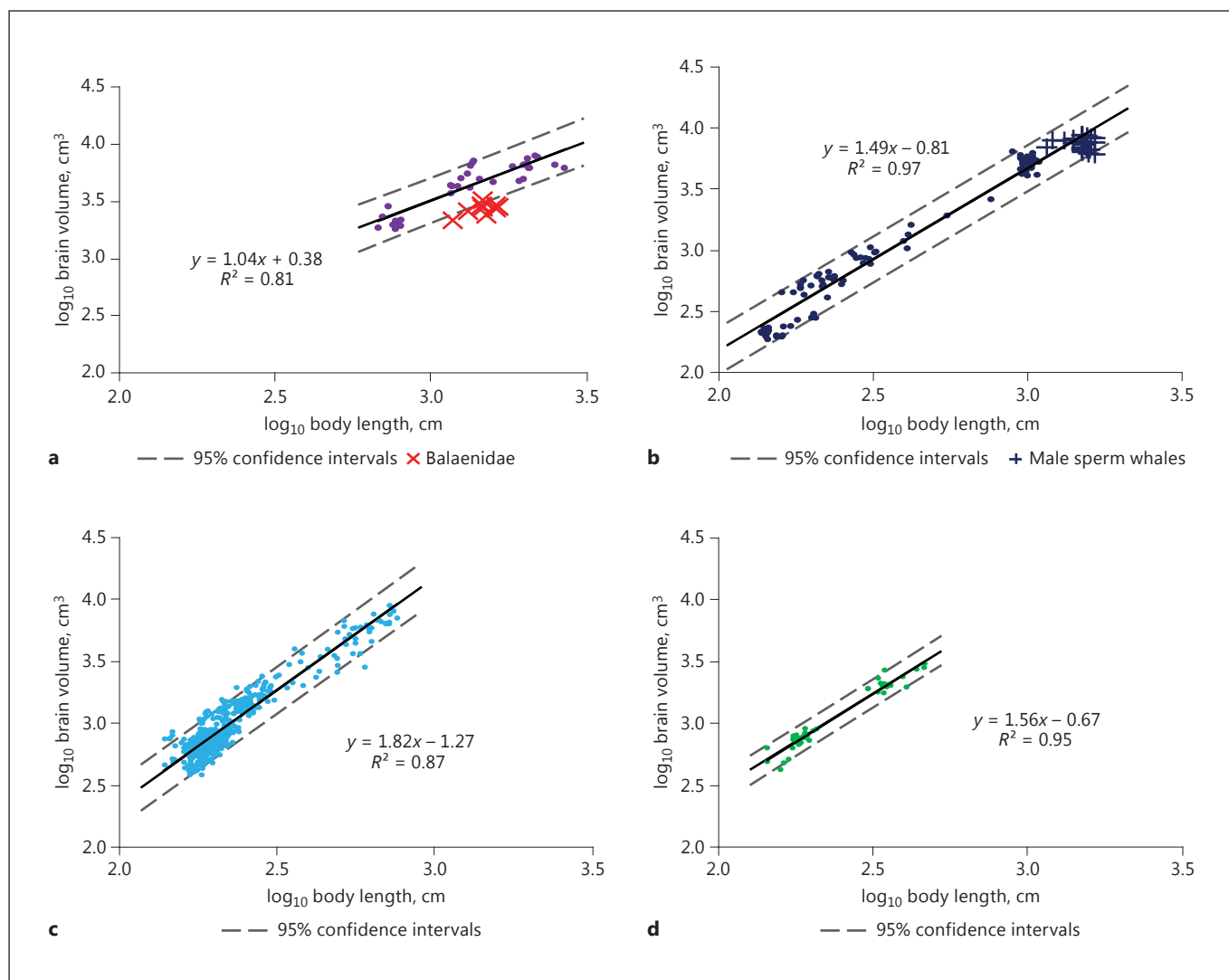
Fig. 2. Regressions of brain volume against body mass among adult cetaceans of 4 groups. All data points represent individual animals. For each plot, the regression trend lines are bound by upper and lower limits using 95% confidence intervals. **a** Balaenopteroidea regression. Balaenidae points were plotted but not included in the regression. **b** PZIP group regression. **c** Delphinidae regression. **d** Phocoenidae-Monodontidae group regression. The Delphinidae group had the largest brains in relation to body mass compared to each of the other groups of animals.

(Iniidae and Pontoporiidae), family Lipotidae, and family Platanistidae. Hereafter, this group of other odontocetes will be referred to as the PZIP group. Animals of the superfamily Balaenopteroidea, which includes the families Balaenopteridae and Eschrichtiidae, had a smaller relative brain size than the 3 odontocete groups but had a larger relative brain size than Balaenidae (Fig. 2, 3).

Figures 2 and 3 include data from 770 adult cetaceans for which we have data on body mass or length and brain volume. These data come from 9 Balaenidae, 36 Balae-

nopteroidea, 563 Delphinidae, 117 PZIP, and 45 Phocoenidae-Monodontidae group members. Individual $\log_{10}$ brain volume versus $\log_{10}$ body mass values for adult cetaceans of each group are plotted in Figure 2, and individual $\log_{10}$ brain volume versus $\log_{10}$ body length values are plotted in Figure 3. Regression lines with R^2 results are displayed for each group except for Balaenidae, which are included with the Balaenopteroidea plots.

Slopes for the Delphinidae, Phocoenidae-Monodontidae, PZIP, and Balaenopteroidea groups (Fig. 2) were

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Fig. 3. Regressions of brain volume against body length among adult cetaceans. All data points represent individual animals. For each plot, the regression trend lines are bound by upper and lower limits using 95% confidence intervals. **a** Balaenopteroidea regres-

sion. Balaenidae points were plotted but not included in the regression. **b** PZIP group regression. **c** Delphinidae regression. **d** Phocoenidae-Monodontidae group regression.

compared and were all equivalent except for the Delphinidae and PZIP groups, which were significantly different ($p < 0.0001$). For the other groups, common slopes were generated using ANCOVA and intercepts for each group were compared. There was a significant difference in mean $\log_{10}$ brain volume between all groups ($p < 0.0001$). Because the slopes were not equal between the Delphinidae and PZIP groups, the magnitude of difference was calculated at several points along the regression lines and was found to be significantly different at all levels ($p < 0.0001$). Thus, $\log_{10}$ brain volume was larger in Delphinidae than in the PZIP group.

Slopes for Delphinidae, Phocoenidae-Monodontidae, PZIP, and Balaenopteroidea (Fig. 3) were compared and were all significantly different from each other ($p < 0.01$), except for the Phocoenidae-Monodontidae and PZIP groups, which were equal. For those 2 groups, common slopes were generated using ANCOVA and intercepts for each group were compared. The mean $\log_{10}$ brain volume was significantly larger for the Phocoenidae-Monodontidae group than for the PZIP group ($p < 0.0001$, LSMean ± SE = 3.37 ± 0.01 and 3.06 ± 0.01, respectively). Since there was so much variation in slopes for the other groups, similar analyses were not utilized.
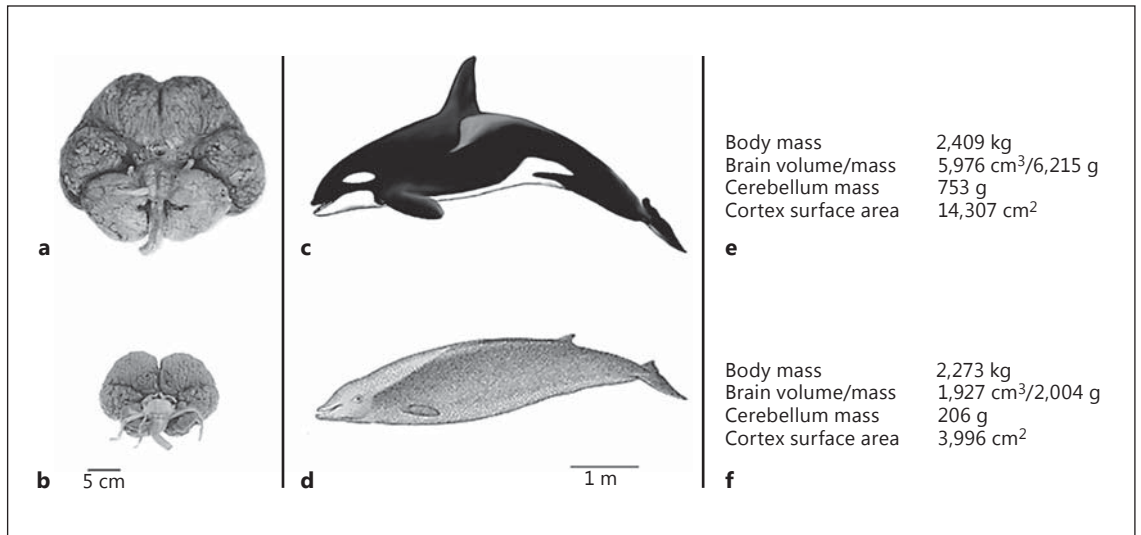
Fig. 4. An illustration of the major difference in brain size between 1 representative adult female delphinid (*O. orca*; **a**, **c**) and 1 member of the PZIP group, an adult female beaked whale (*Z. cavirostris*; **b**, **d**). Brain and body measurements for the delphinid (**e**) and beaked whale (**f**) are also given.
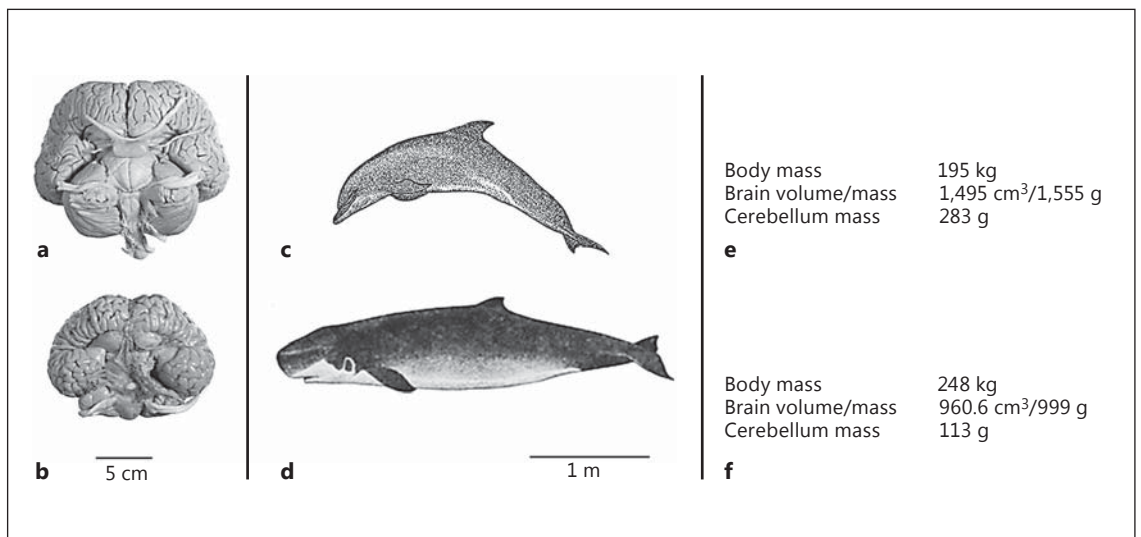

Fig. 5. An illustration of the major difference in brain size between 1 representative adult female delphinid (*T. truncatus*; **a**, **c**) and 1 member of the PZIP group, an adult female pygmy sperm whale (*Kogia breviceps*; **b**, **d**). Brain and body measurements for the delphinid (**e**) and pygmy sperm whale (**f**) are also given.

Instead, adjusted means for all 4 groups were compared. All groups were significantly different from each other ($p < 0.0001$), except for the Delphinidae and Phocoenidae-Monodontidae groups, which were not significantly different.

Figures 4 and 5 give some individual examples of differences in relative brain size between members of the Delphinidae group compared with the PZIP group. Although there is a clear difference in relative brain size between delphinoids of the Delphinidae and Phocoenidae-Monodontidae groups compared with all of the other Odontoceti of the PZIP group, there are also marked differences in brain size within delphinoids of similar body size. Figure 6 shows comparisons of relative brain and
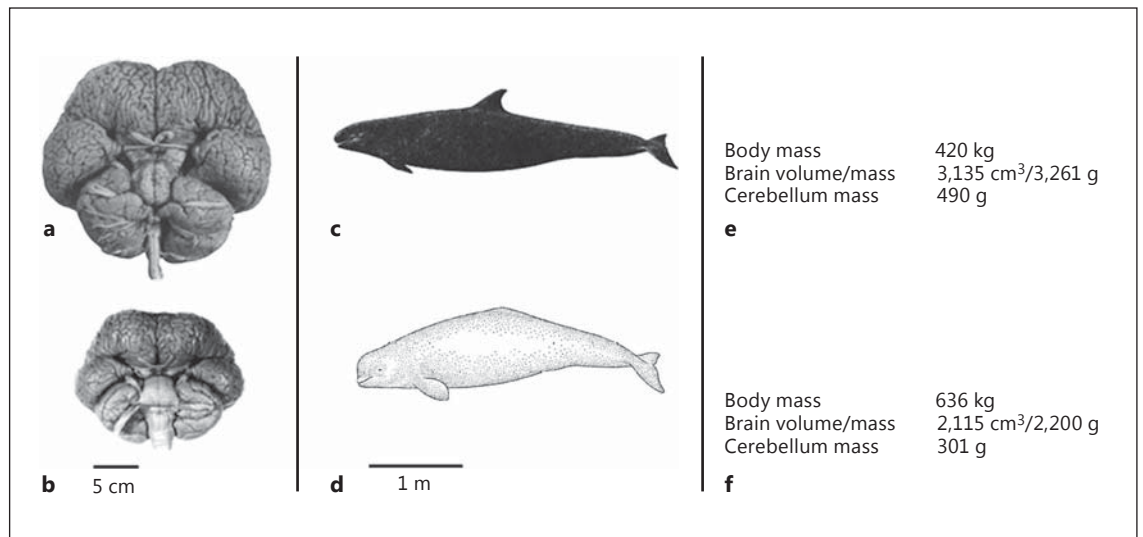
Fig. 6. An illustration of the difference in brain size between 1 adult female delphinid (*P. crassidens*; **a**, **c**) and 1 member of the Phocoenidae-Monodontidae group, an adult female beluga (*D. leucas*; **b**, **d**). Brain and body measurements for the delphinid (**e**) and beluga (**f**) are also given.

body size for individual examples of the Delphinidae and Phocoenidae-Monodontidae groups. Figure 7 shows comparisons of average $\log_{10}$ brain volume and $\log_{10}$ body mass in relation to selected species within the Delphinidae and Phocoenidae-Monodontidae groups. The 4 species representing the Delphinidae group had significantly larger average brain volumes than the 5 species representing the Phocoenidae-Monodontidae group ($p = 0.0148$, LSMean ± SE = 3.22 ± 0.04 and 3.03 ± 0.04, respectively).

We compared 2 North Pacific animals (Fig. 8), the dolphin *Lagenorhynchus obliquidens* of the Delphinidae group [Walker et al., 1986] and the porpoise *Phocoenoides dalli* of the Phocoenidae-Monodontidae group [Ridgway et al., 1966], using ANCOVA and found that adjusted means (± SE) for $\log_{10}$ brain volume were significantly higher in *L. obliquidens* than in *P. dalli* ($p < 0.0001$, 3.06 ± 0.05 vs. 2.89 ± 0.04, respectively). However, brain sizes of 2 species within the dolphin group that did not show up as significantly different from *P. dalli* were *Delphinus delphis* and *Stenella attenuata,* both of which are dolphins with warmer water habitats that occur in large herds. Next, we compared animals of 2 genera from warmer waters, *Steno* and *Stenella* (Fig. 9). ANCOVA was used to compare the 2 groups, and we found that the $\log_{10}$ brain volume in *Steno* was larger compared to *Stenella* ($p < 0.0001$, LSMean ± SE = 3.1 ± 0.02 and 2.85 ± 0.006, respectively).

The Cetacean Cerebellum and Cerebrum

We have data on the cerebellum mass of 101 adult cetaceans, of which 66 were from Delphinidae, 19 were from the PZIP group, 7 were from the Phocoenidae-Monodontidae group, and 9 were Mysticeti (5 from the Balaenopteroidea group and 4 from the Balaenidae group); 6 additional subadult mysticetes were also included in the data (Fig. 10–12). After adjusting for $\log_{10}$ body mass, there was no significant difference in mean $\log_{10}$ cerebellum mass between Mysticeti (Balaenopteroidea and Balaenidae) and the PZIP group.

Figure 10 illustrates $\log_{10}$ cerebellum mass versus $\log_{10}$ body mass values for adult cetaceans. Individuals from the Balaenopteroidea, the PZIP group, and Balaenidae were combined and compared with Delphinidae. Slopes for the 2 groups were not significantly different. Common slopes were generated using ANCOVA and intercepts for each group were compared. There was a significant difference in the mean $\log_{10}$ cerebellum mass between Delphinidae and the Balaenopteroidea, PZIP, and Balaenidae groups with relation to $\log_{10}$ body mass ($p < 0.0001$). The $\log_{10}$ cerebellum mass for Delphinidae was found to be significantly larger than the combined Balaenopteroidea, PZIP, and Balaenidae groups (LSMean ± SE = 2.6 ± 0.02 and 1.98 ± 0.03, respectively).

Using our Delphinoidea data (Delphinidae and Phocoenidae-Monodontidae groups), we regressed cerebellum mass against rest of brain (ROB) mass (total brain

Fig. 7. Average body masses and brain volumes of 4 species from our Delphinidae group and 5 species from our Phocoenidae-Monodontidae group. On average, individuals of the Delphinidae group had larger brain volumes compared to individuals of similar body size from the Phocoenidae-Monodontidae group.
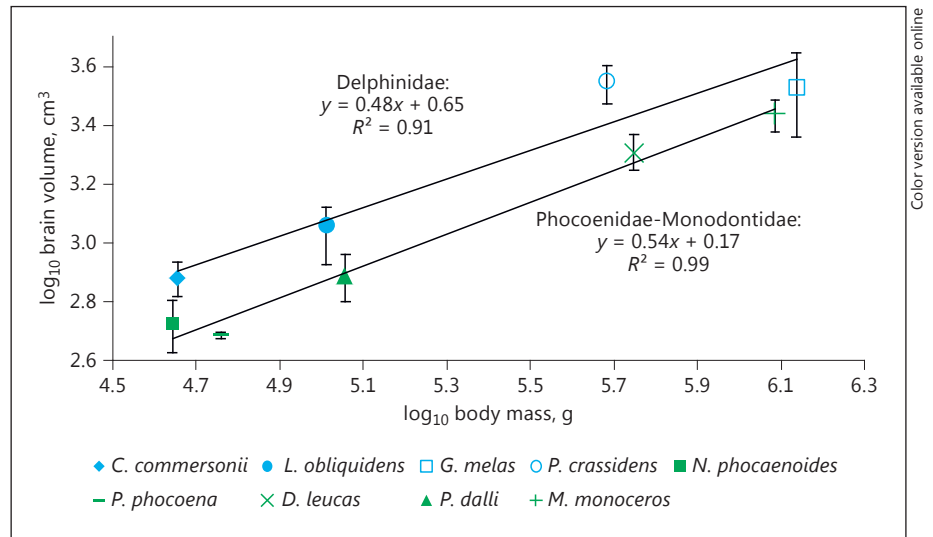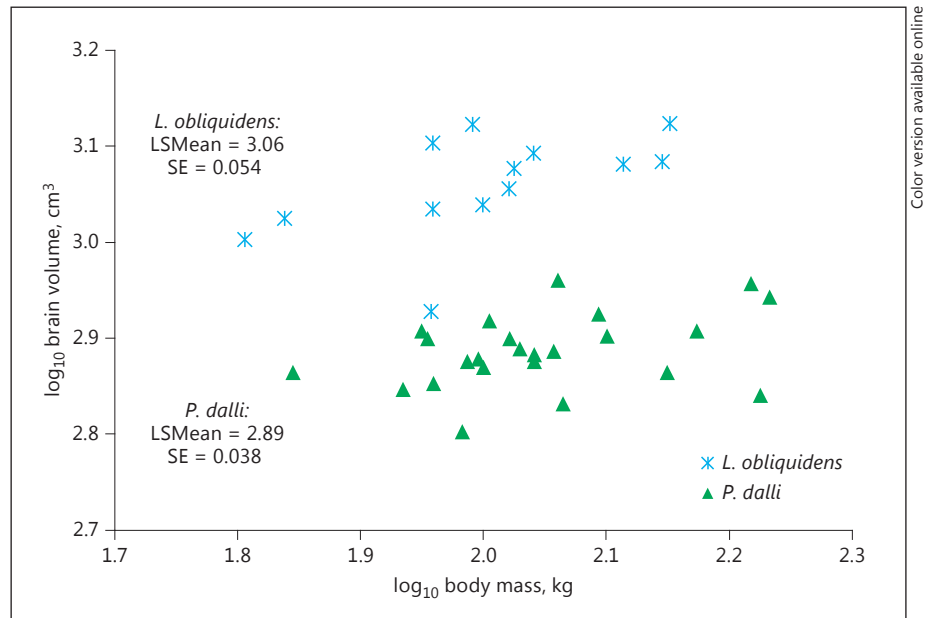

Fig. 8. Comparison of individuals from the Delphinidae and Phocoenidae-Monodontidae groups with different brain sizes and with similar ocean habitats in the North Pacific.

mass – cerebellum mass) with a 95% confidence interval (Fig. 11). The majority of nondelphinoid points fell outside of the limits of the 95% confidence interval for the delphinoid regression; members of the PZIP group generally had a larger ROB, while Balaenopteroidea and Balaenidae group members had a lower ROB compared to the delphinoids.

We measured the cerebrum masses of 62 adult cetaceans (and 6 subadults), of which 53 were from the superfamily Delphinoidea (Delphinidae and Phocoenidae-Monodontidae groups), 6 were from the PZIP group, and 3 (in addition to the 6 subadults) were Mysticeti (Fig. 12–14). Using a multiple linear regression, we regressed cerebellum mass and cerebrum mass against total brain mass with 95% confidence intervals (Fig. 12). The standardized coefficient for cerebellum mass (0.154) was significantly lower than for cerebrum mass (0.855). Thus, a change in cerebrum mass has a greater effect on total brain mass than does a change in cerebellum mass. Figure 13 shows body mass regressed against cerebrum mass with 95% confidence intervals for 42 adults from the Delphinidae group. For delphinids, cerebrum mass scales to approxi-

Fig. 9. Comparison of Delphinidae group dolphins with different brain sizes and with similar tropical ocean habitats. Data on brain size from 3 members of the genus *Stenella* were compared with *Steno* (*S. bredanensis*, also an animal of warmer climes).
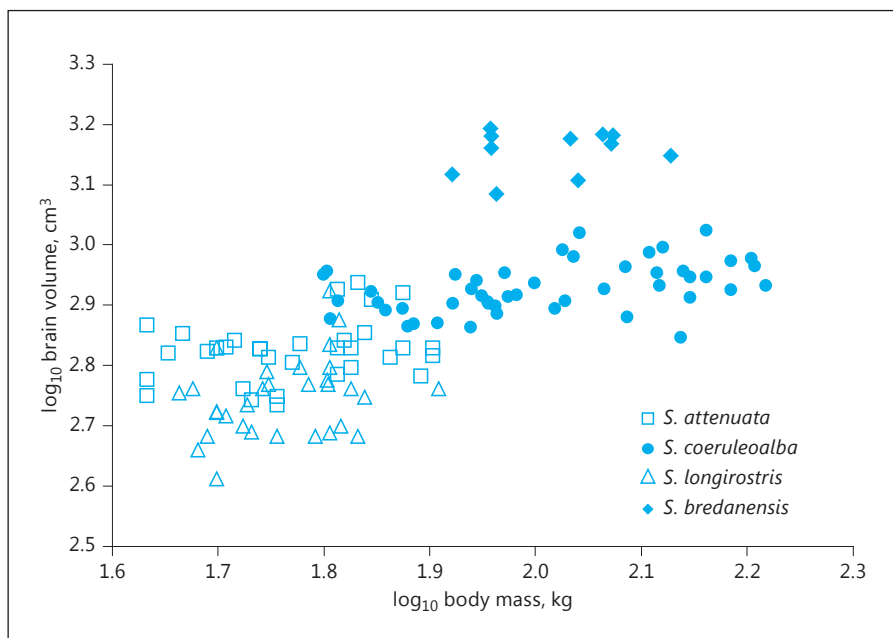

Fig. 10. Cerebellum mass and body mass among individual adult (and 6 subadult *B. mysticetus*) cetaceans from all of our taxonomic groups. The upper regression line shows data for the family Delphinidae with 95% confidence intervals. The lower regression line shows combined data for the Balaenidae, Balaenopteroidea, and PZIP groups. Data for the Phocoenidae-Monodontidae group were plotted, but not included in the Delphinidae regression.
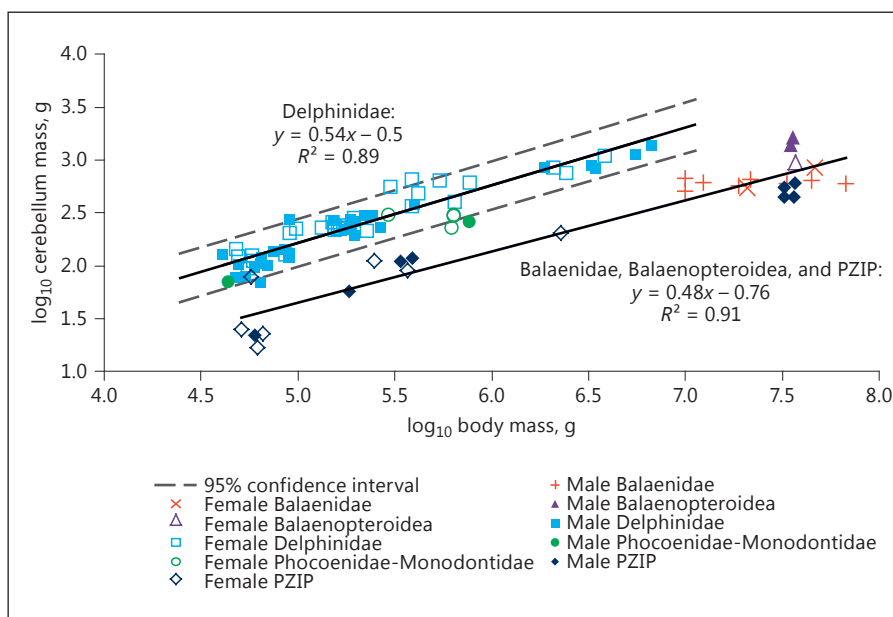
mately the 0.68 power of body mass. All points from the PZIP, Balaenopteroidea, and Balaenidae groups fell below the limits of the 95% confidence interval of the Delphinidae regression. Thus, the individuals in these 3 groups have lower cerebrum masses relative to body size compared to the delphinids.

We used our Delphinoidea data to perform a cerebrum mass versus ROB mass (total brain mass – cerebrum mass) regression (Fig. 14). As with the cerebellum versus ROB regression, the majority of nondelphinoid points fell outside of the limits of the 95% confidence interval for the delphinoid regression. Members of the PZIP group had relatively large cerebrum masses relative to the rest of their brains, while the mysticetes had cerebrums that were slightly smaller than expected based on the Delphinoidea regression. Figure 15 gives an example of the

Fig. 11. Cerebellum mass and ROB mass (cerebellum mass subtracted from total brain mass) among individual adult cetaceans (and 6 subadult *B. mysticetus*) from all of our taxonomic groups. The regression line shows data for Delphinoidea (Delphinidae, Phocoenidae, and Monodontidae) with 95% confidence intervals. Data for the PZIP, Balaenopteroidea, and Balaenidae groups are also plotted, but not included in the regression. As the slope is nearly equal to 1, the relationship between cerebellum mass and the ROB is nearly isometric for the delphinoids.
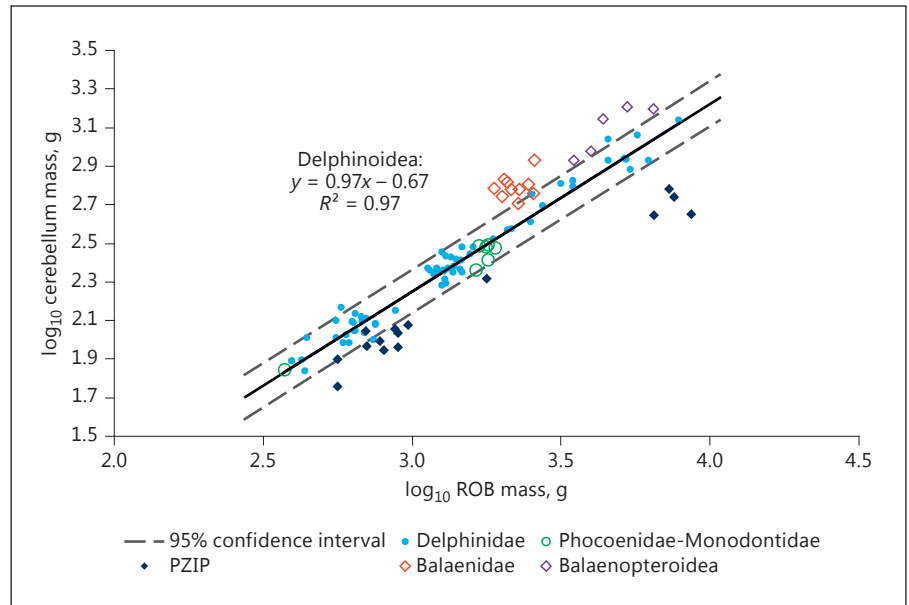
Fig. 12. Cerebrum mass and cerebellum mass regressed against total brain mass among individual adult cetaceans (and 6 subadult *B. mysticetus*) from all of our taxonomic groups. The upper regression line shows data for the cerebrum mass against total brain mass. The lower regression line shows data for the cerebellum mass against total brain mass. Note that the cerebellum data are more scattered about the trendline compared to the cerebrum data points. The 2 prominent outliers in the cerebellum regression represent sperm whales (*P. macrocephalus*), whose cerebellums are much smaller than would be expected for their brain size.
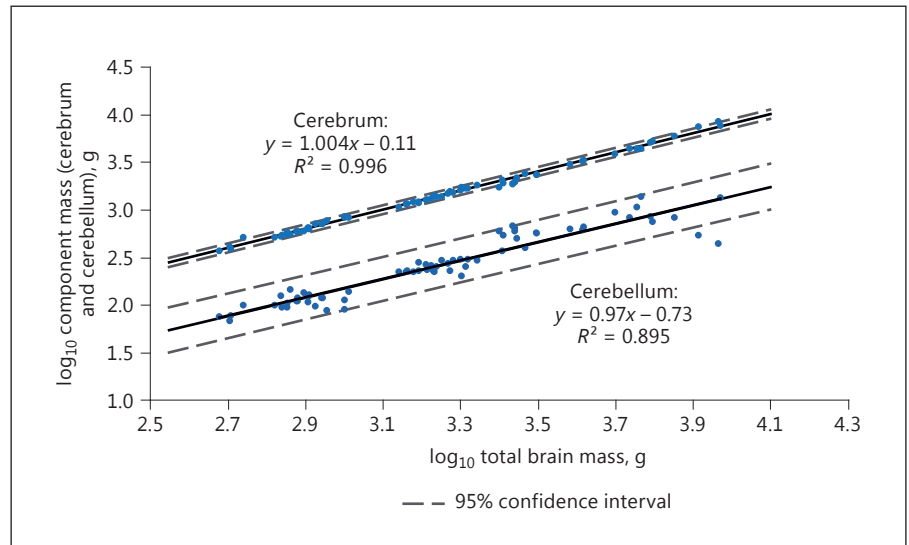
pronounced difference in cerebellum mass and cerebrum mass relative to total brain mass between a member of the Delphinidae group (*O. orca*) and a member of the PZIP group (*P. macrocephalus*).

Surface Area of the Cerebral Cortex

Figure 16 displays data on the surface area of the cerebral cortex in relation to brain volume of 32 adult cetaceans, including 31 Delphinidae and 1 PZIP group member. In addition, we included data from 6 Balaenidae subadults and 1 PZIP group subadult. Thus, 39 individual cetaceans were

used in total. We also plotted male and female averages from the literature for *B. acutorostrata* in order to have representation for Balaenopteroidea [Eriksen and Pakkenberg, 2007]. The Balaenidae had a significantly smaller mean $\log_{10}$ cortex surface area after adjusting for $\log_{10}$ brain volume ($p < 0.0001$). The adjusted means (SE) for $\log_{10}$ cortex surface area are as follows: other cetaceans (Delphinidae and PZIP) = 3.51 (0.008), Balaenidae = 3.36 (0.02). The slope of the regression for our Delphinidae group (Fig. 16) is almost identical to the 0.90 scaling value of terrestrial mammal cortex surface area with brain size reported by Hofman [2012].

Fig. 13. Cerebrum mass and body mass among individual adult (and 6 subadult *B. mysticetus*) cetaceans from all of our taxonomic groups. The regression line shows data for the family Delphinidae with 95% confidence intervals. Data for the Balaenidae, Balaenopteroidea, Phocoenidae-Monodontidae, and PZIP groups were plotted but not included in the regression.
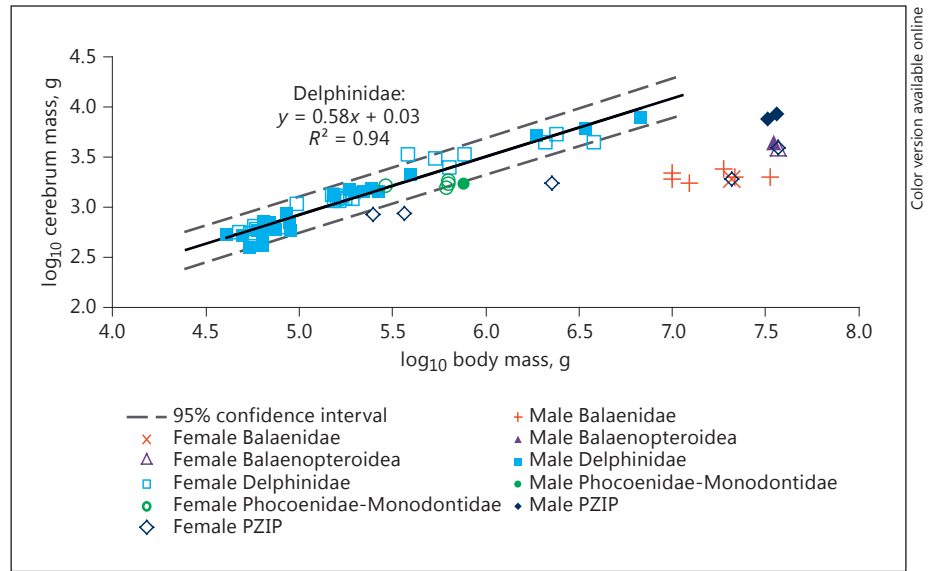

Fig. 14. Cerebrum mass and ROB mass (cerebrum mass subtracted from total brain mass) among individual adult cetaceans (and 6 subadult *B. mysticetus*) from all of our taxonomic groups. The regression line shows data for Delphinoidea (Delphinidae, Phocoenidae, and Monodontidae) with 95% confidence intervals. Data for the PZIP, Balaenopteroidea, and Balaenidae groups are also plotted, but not included in the regression.
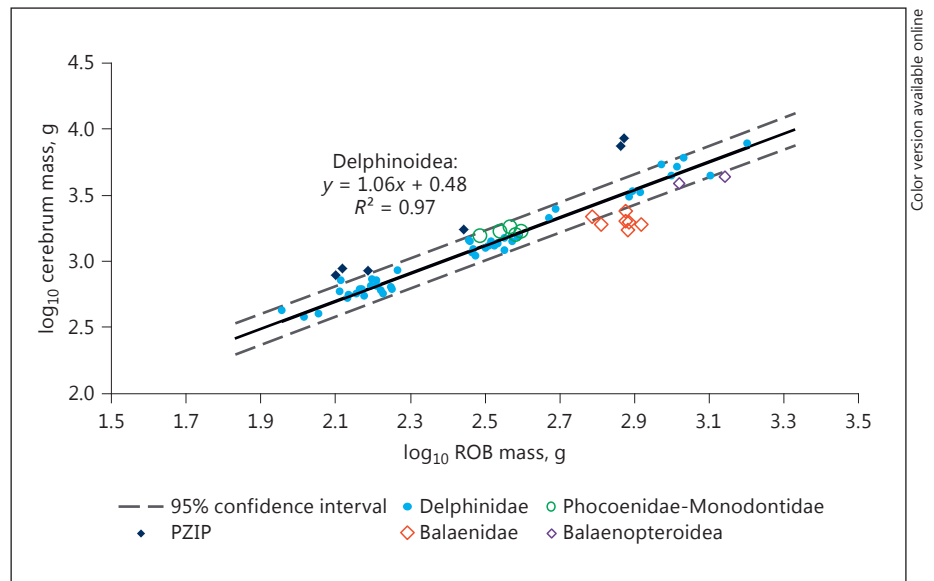
Figure 17 illustrates data for the surface area of the cerebral cortex in relation to the animal's body mass. It includes 35 data points, including 25 adult individuals of the Delphinidae group, 2 adult averages (male and female) for the Balaenopteroidea group, 2 individuals (1 adult and 1 subadult) of the PZIP group, and 6 subadult Balaenidae animals. Similar to the previous analysis, after adjusting for $\log_{10}$ body mass, the Balaenidae had a significantly smaller mean $\log_{10}$ cortex surface area than cetaceans in the other 3 groups combined (3.04 ± 0.1 vs. 3.58 ± 0.03, respectively).

Figure 18 illustrates cerebral cortex surface area data in relation to the animal's body length. Our data include 31 adult individuals of Delphinidae, 2 adult averages (male and female) for Balaenopteroidea, 2 (1 adult and 1 subadult) PZIP group individuals, and 6 subadult Balaenidae animals. Similar to the body mass analysis, the Balaenidae group had a significantly smaller mean $\log_{10}$ cortex surface area compared to the other combined groups after adjusting for $\log_{10}$ body length ($p < 0.0001$, 3.06 ± 0.08 vs. 3.56 ± 0.03, respectively).
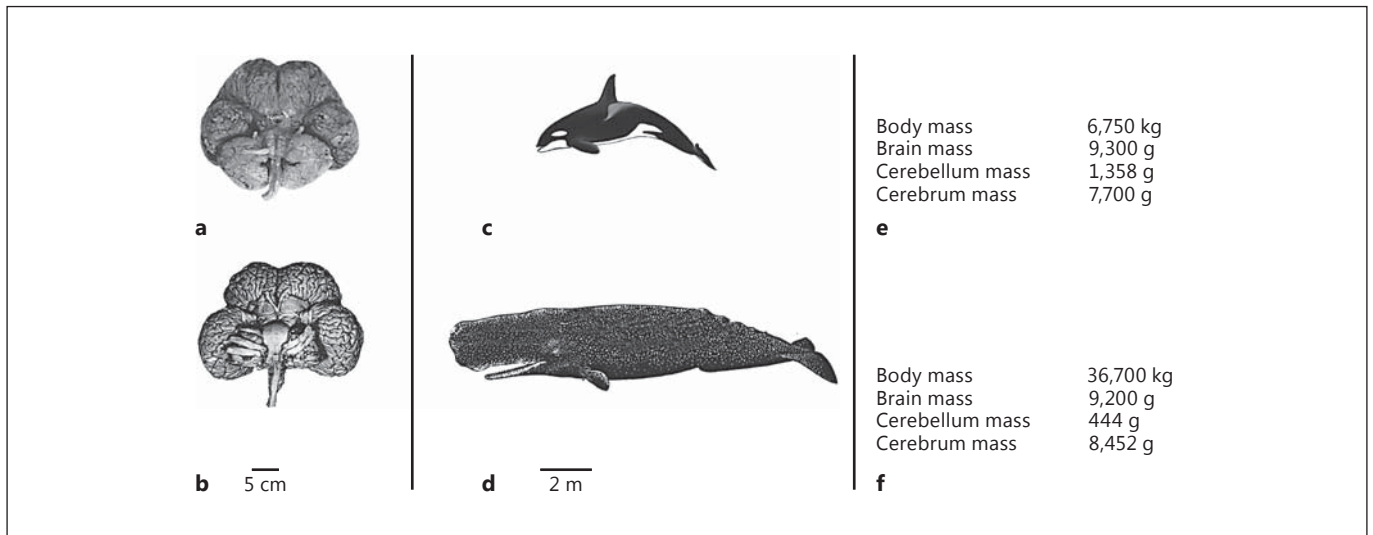
Fig. 15. An illustration of the difference in cerebellum size between 1 adult male delphinid (*O. orca*; **a**, **c**) and 1 member of the PZIP group, an adult male sperm whale (*P. macrocephalus*; **b**, **d**), with similar brain masses. Brain and body measurements for the delphinid (**e**) and sperm whale (**f**) are also given.

Fig. 16. Surface areas of the cerebral cortex and brain volumes of individuals from the Balaenidae, Balaenopteroidea, PZIP, and Delphinidae groups. All data points represent individual animals, except for the 2 *B. acutorostrata* (Balaenopteroidea group) points, which represent male and female averages for the species; these data are from Eriksen and Pakkenberg [2007]. The *B. mysticetus* and *K. breviceps* data come from subadult animals that fell just below the cutoff value for mature length. They are plotted for a visual comparison against the Delphinidae group. All other points come from adult animals. Only the Delphinidae group data were included in the regression.
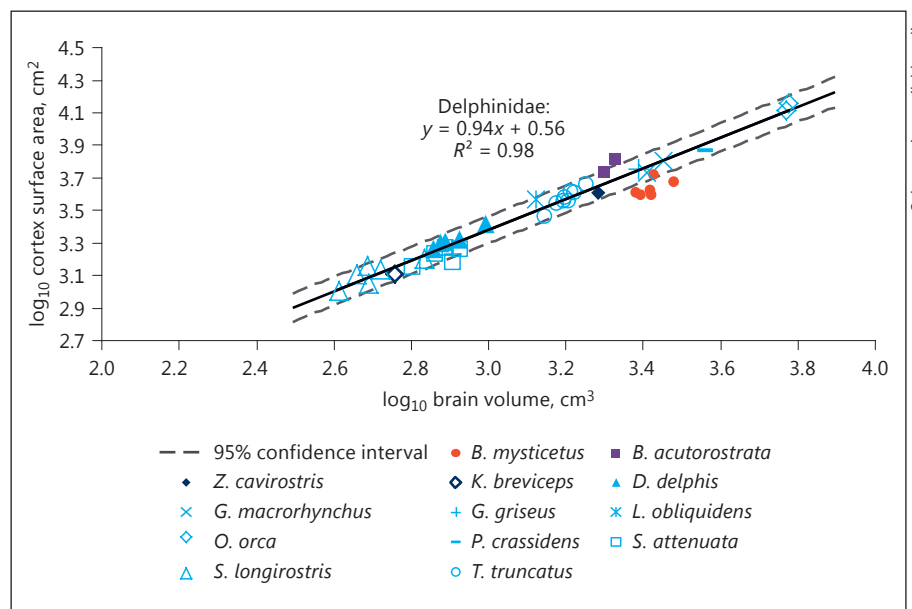
Figure 19 illustrates the variation in cortex surface area between *B. mysticetus,* a member of Balaenidae, and other cetaceans. Except for 2 averages from Eriksen and Pakkenberg [2007], we have no data on cortex surface area in mysticete whales other than *B. mysticetus*. Figure 19 also shows the dorsal surface of 1 brain from each group. From this view it appears that there are variations in the patterns of gyri and sulci of these brains.

EQ and Endocranial Volume

We found 2 problems in using EQ for brain size comparisons across cetaceans. First, EQ cannot be reliably used to compare species of different body size and different degrees of maturity. Second, EQ has often been calculated using endocranial volume [Jerison, 1973; Marino et al., 2000b, 2004; Montgomery et al., 2013]. Because non-brain tissue in the cranial vault varies from around 8–65%

Fig. 17. Surface areas of the cerebral cortex and body masses of individuals from the Balaenidae, Balaenopteroidea, PZIP, and Delphinidae groups. All data points represent individual animals, except for the 2 *B. acutorostrata* (Balaenopteroidea group) points, which represent male and female averages for the species; these data are from Eriksen and Pakkenberg [2007]. The *B. mysticetus* and *K. breviceps* data come from subadult animals that fell just below the cutoff value for mature length. They are plotted for a visual comparison against the Delphinidae group. All other points come from adult animals. Only the Delphinidae group data were included in the regression.
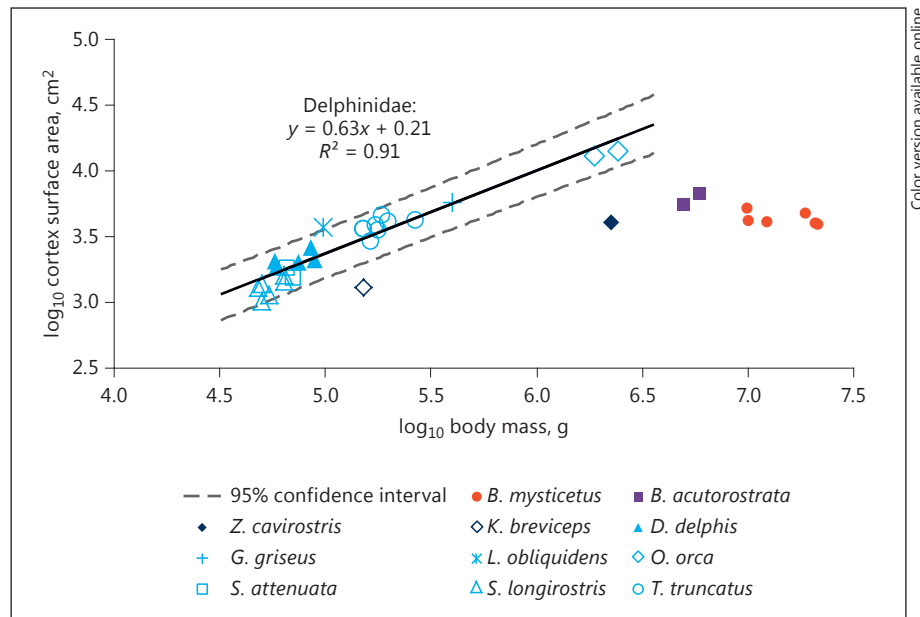

Fig. 18. Surface areas of the cerebral cortex and body lengths of individuals from the Balaenidae, Balaenopteroidea, PZIP, and Delphinidae groups. All data points represent individual animals, except for the 2 *B. acutorostrata* (Balaenopteroidea group) points, which represent male and female averages for the species; these data are from Eriksen and Pakkenberg [2007]. The *B. mysticetus* and *K. breviceps* data come from subadult animals that fell just below the cutoff value for mature length. They are plotted for a visual comparison against the Delphinidae group. All other points come from adult animals. Only the Delphinidae group data were included in the regression.
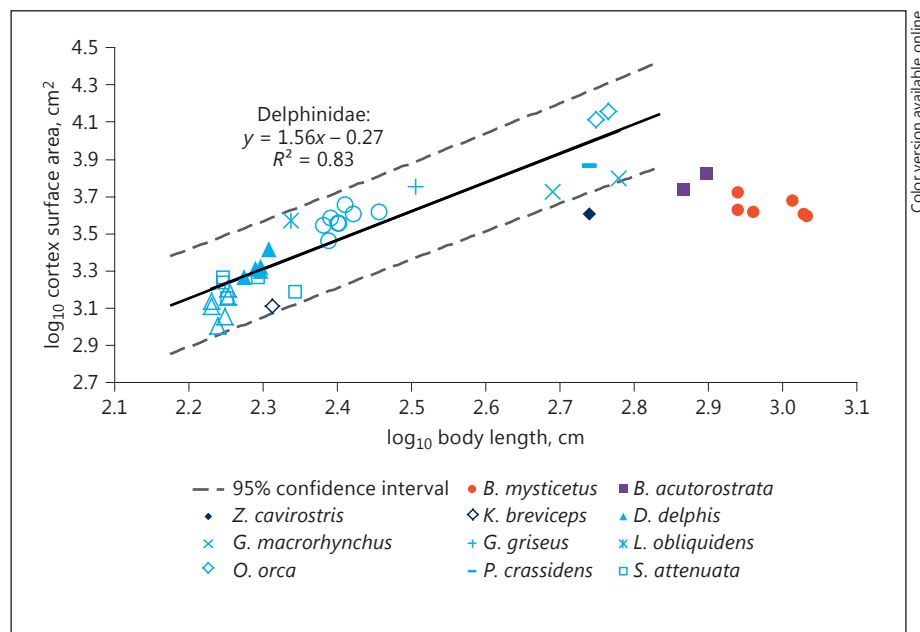
among different cetaceans (Table 3), calculations of brain volume from endocranial volumes are not accurate unless we know the amount of endocranial adnexa (nonbrain tissue). Table 3 and Figures 20–22 give some examples of the proportions of endocranial adnexa in the cranial vault of different cetaceans. To estimate EQ from endocranial volume, one must have a good estimate of nonbrain tissue in the cranial vault.

Discussion

Total Brain Size Differences relative to Body Size

Cetaceans differ greatly in brain volume relative to body mass. Each of our 5 taxonomic groups differed significantly in brain size relative to body size; members of the Delphinidae group had the largest brains relative to body size, followed by the Phocoenidae-Monodontidae
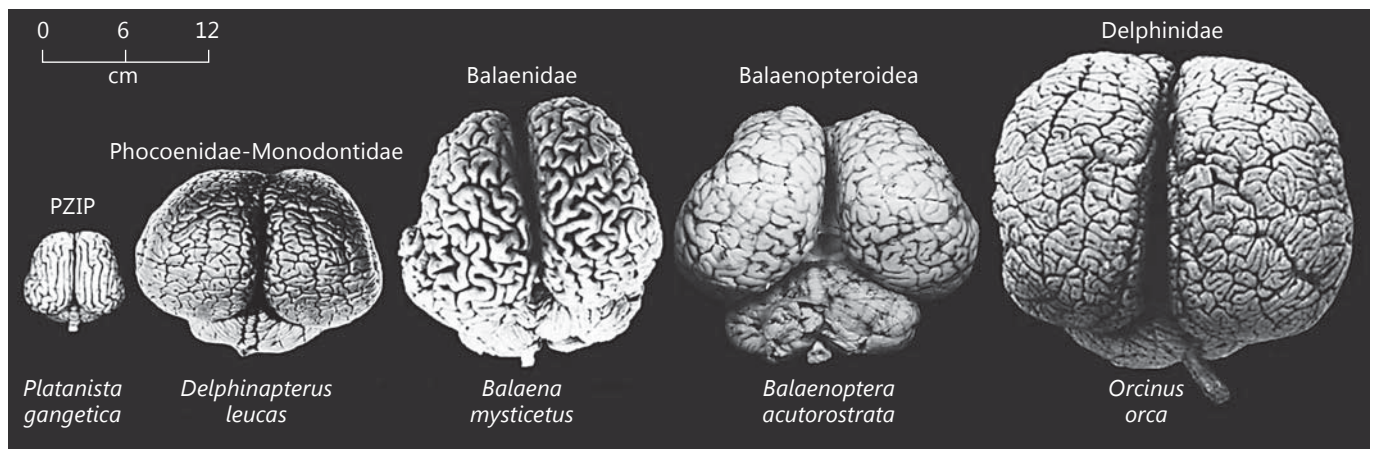
Fig. 19. Five different cetacean brains showing variability of surface configuration. The small *Platanista gangetica* brain on the left has a different pattern of gyri and sulci and appears to be less convoluted than the others. Stereology results showed the brains of *B. mysticetus* (Balaenidae group) to be less convoluted than those from the Phocoenidae-Monodontidae, Balaenopteroidea, and Delphinidae groups.

Table 3. Examples of endocranial adnexa percentages from 6 mysticetes and 4 odontocetes

Cetacean	Tt	Ha	Ba	Oo	Bp	Pm	Bmu	Mn	Pm	Bp	Bmy	Bmy
Brain + adnexa, kg	1.64	3.18	3.46	7.01	7.6	10.7	9.75	8.2	12.9	9.1	8.4	8.9
Brain alone, kg	1.51	2.72	2.74	6.2	5	7.9	6.7	4.7	9.2	5.2	3.05	3.09
Adnexa alone, kg	0.13	0.46	0.72	0.81	2.6	2.8	3.05	3.5	3.7	3.9	5.35	5.81
Adnexa, %	7.9	14.5	21	11.6	34.2	26.2	31.3	42.7	28.7	42.9	63.7	65.3

The table is organized by increasing adnexa mass from left to right. Tt, *T. truncatus* (current study); Ha, *H. ampullatus* [Turner, 1912]; Ba, *B. acutorostrata* [Knudsen et al., 2002], mean data from 35 specimens; Oo, *O. orca* [Ridgway and Hanson, 2014]; Bp, *B. physalus,* Mn, *M. novaeangliae* [Jacobs and Jensen, 1964]; Pm, *P. macrocephalus* [Kojima, 1951]; Bmu, *B. musculus* [Guldberg, 1885]; Bmy, *B.mysticetus* [Thewissen et al., 2011].

group, PZIP group, Balaenopteroidea group, and then the Balaenidae group. They also vary in size of the cerebrum and cerebellum relative to total brain mass and as a function of total body mass. These differences may suggest how brains developed as a result of evolutionary history, their environmental challenges, sensory abilities, and social relations [Schwerdtfeger et al., 1984; Manger, 2006, 2013a; Connor, 2007; Marino et al., 2008; Manger et al., 2013b; Montgomery et al., 2013; Butti et al., 2014; Ridgway and Hanson, 2014].

Marino et al. [2004] and Montgomery et al. [2013] point out that the highest EQ values are found in primates and cetaceans. They suggest that until recent evolutionary history, the most encephalized mammals were odontocetes, not primates. The primate advantage has been attained only in the last few million years [Jerison, 1973;

Montgomery et al., 2013]. These 2 groups have experienced very different evolutionary histories and brain mass trends. The cetacean's continuous life in the sea has freed it from the constraints of gravity. Cetaceans are free to have larger heads, larger bodies, and larger brains. Within Cetacea, mysticete whales experienced more body mass increase than did Odontoceti. Even the giant sperm whale, the largest odontocete, is considerably smaller than the largest mysticete, the blue whale. Yet, the available data suggest that the brain of the large male sperm whale, the largest of the brains in our PZIP group, is larger than any of the Mysticeti brains (Fig. 2b, 3b). Montgomery et al. [2013] suggested that the differences in cetacean EQ are driven mainly by differences in body mass, not dramatic change in brain mass.
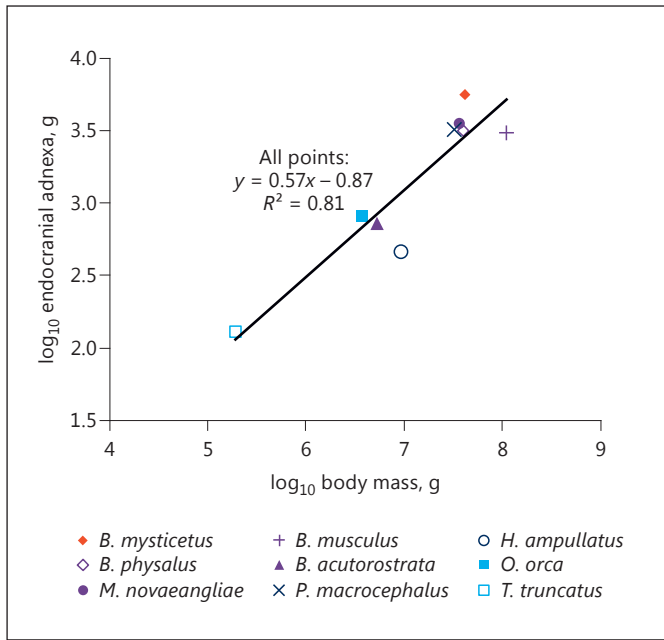
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Tarpley

Fig. 20. Average body masses and endocranial adnexa masses from adults of the Balaenidae, Balaenopteroidea, PZIP, and Delphinidae taxonomic groups. *Hyperoodon ampullatus*, an individual of the PZIP group, has a small brain relative to its body mass. However, *H. ampullatus* has a higher percentage of adnexa material relative to its entire brain compared to *O. orca*, a delphinid of similar body size. The regression includes all data points.
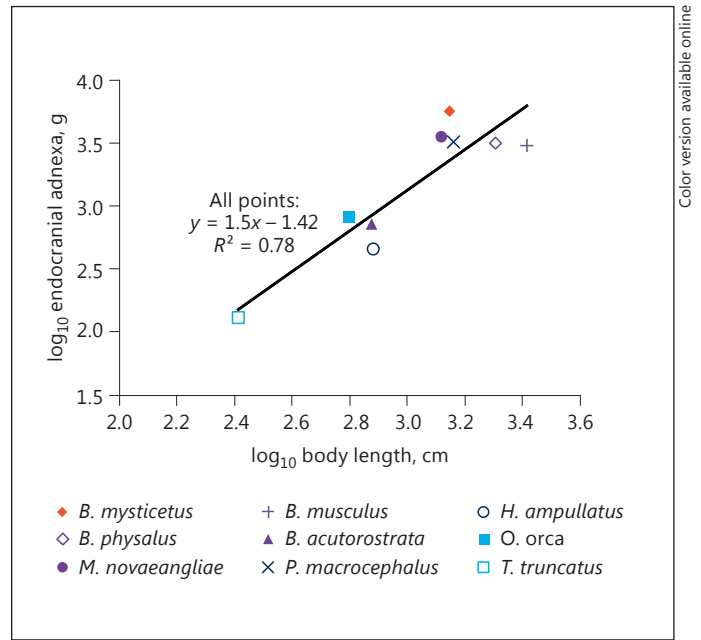
Fig. 21. Average body lengths and endocranial adnexa masses from adults of the Balaenidae, Balaenopteroidea, PZIP, and Delphinidae taxonomic groups. *Hyperoodon ampullatus*, an individual of the PZIP group, has a small brain relative to its body length. However, *H. ampullatus* has a higher percentage of adnexa relative to its entire brain compared to *O. orca*, a delphinid of similar body size. The regression includes all data points.

In evolutionary history, the animals with the largest brains relative to body mass, the Delphinidae, have experienced a large decrease in body mass [Montgomery et al., 2013]. Studies such as Marino et al. [2004] and Montgomery et al. [2013] relied heavily on EQ derived from endocranial volume [also see Gingerich, 2015]. Given the vast differences in nonbrain endocranial tissue, we are skeptical of these results. More investigations are needed in qualitative differences in cetacean brains, apart from quantitative brain mass/body mass relations. For example, the smaller cortex surface area we find in *B. mysticetus* probably represents a qualitative difference. Such differences may be found with other genera, such as *Platanista,* when more data become available. *B. mysticetus* are very large, long-lived whales with relatively small brains. Most cetacean brains are wide relative to their length. *B. mysticetus* brains are longer and narrower [Duffield et al., 1992] (Fig. 19). As shown in Figures 16–18, the surface area of their cortex is smaller than other cetaceans we measured (see further discussion below). Furthermore, the corpus callosum connecting the cerebral hemispheres appears relatively longer than that seen

in other cetacean brains of similar size [Tarpley and Ridgway, 1994]. The corpus callosum of another baleen whale, the Minke whale, *B. acutorostrata*, is also large compared with similar sized Delphinidae group brains [Ratner et al., 2011].

The Cetacean Cerebellum and Cerebrum

Cetacean cerebellum mass relative to total brain mass ranges from approximately 6–22%. Maseko et al. [2012] compared odontocete cetaceans with the elephant and described the elephant as having the largest cerebellum size (relative to its brain size) of all mammals [also see Jacobs et al., 2014]. With regard to previous findings on cetacean relative cerebellum size, we found that some odontocetes (*Platanista*, *Inia*, *Physeter,* and *Kogia*) have relatively small cerebellums compared to their own brains. On the other hand, our data suggest that some large mysticete whales may have relative cerebellum sizes that are comparable to those of the elephant. Some mysticetes may have cerebellums with absolute sizes that are larger than those of elephants. For example, the largest absolute cerebellum volume in our data set (1,557 cm^3)
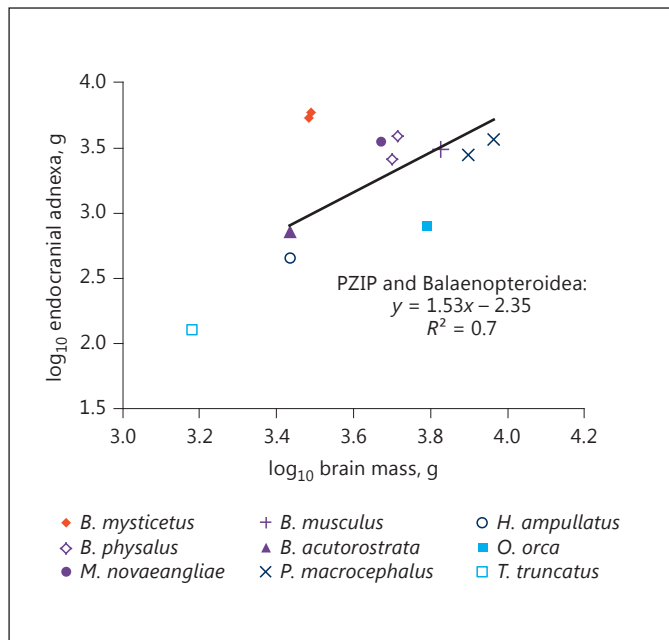

Fig. 22. Individual brain masses and endocranial adnexa masses from adults of the Balaenidae, Balaenopteroidea, PZIP, and Delphinidae taxonomic groups. All data points in this plot come from individual animals, with the exception of the *B. acutorostrata* point, which represents mean brain and endocranial adnexa values from 35 individuals [Knudsen et al., 2002]. The regression includes data from only the Balaenopteroidea and PZIP groups. The *B. mysticetus* individuals (of the Balaenidae group) have more adnexa than would be expected relative to their total brain mass. Conversely, *O. orca* and *T. truncatus* of the Delphinidae group have less adnexa than would be expected relative to their brain mass.

came from an adult fin whale, *B. physalus.* Our data set also included a humpback whale (*Megaptera novaeangliae*) cerebellum with an absolute volume of 1,337.5 cm³. These values exceed the largest cerebellum volume given for *Elephas maximus:* 1,036 cm³ [Maseko et al., 2012]. Thus, the absolute sizes of the mysticete cerebellums in our data set exceed the largest absolute elephant cerebellum size, and some mysticetes rival elephants in terms of cerebellum size relative to brain size. Some of our adult killer whales, *O. orca,* also had absolute cerebellum volumes greater than 1,000 cm³ (online suppl. Table S1; for all online suppl. material, see www.karger.com/doi/10.1159/000454797).

Mysticetes have the largest cetacean cerebellums relative to the size of the rest of their own brains. Relative to their own brains, the PZIP group have small cerebellums, while our Delphinidae and Phocoenidae-Monodontidae groups are intermediate between the PZIP

group odontocetes and the baleen whales (Fig. 11). With allometry, results are different; dolphin cerebellum mass relative to body mass is the highest (Fig. 10). During evolution, the 3 groups of odontocetes developed differently. The cerebellum and cerebrum did not increase together in size.

The members of the PZIP group (nondelphinoid odontocetes) had larger cerebrum masses relative to the rest of their brains compared to the Delphinidae and Phocoenidae-Monodontidae. Conversely, the mysticete whales had slightly smaller cerebrum masses relative to the rest of their brains compared to the delphinoids. However, with allometry, mysticetes and odontocetes of the PZIP group both had smaller cerebrums relative to body mass compared to animals of the Delphinidae and Phocoenidae-Monodontidae groups.

Do cetaceans have complex brains for complex cognition [Marino et al., 2007, see discussion in Ridgway and Hanson, 2014]? If so, cerebellar development must be a key feature of this cognition. We should look at the interconnections between the large cerebellum and the cerebral cortex of delphinids. As suggested in Ridgway and Hanson [2014], there may be a cyclical evolutionary pattern in cetacean cerebellar size. In their comparison of sperm whale and killer whale cerebellums, they found that the largest male killer whales have similar brain sizes to the male sperm whales, but the killer whale cerebellum is much larger (Fig. 15). Females of the 2 species also have equivalent total brain size and cerebellum differences. This discrepancy may be explained by the difference in the rate of total brain development in these 2 taxa. For instance, the sperm whale brain became sufficiently developed for its survival approximately 10 million years ago, while the killer whale brain continued to develop beyond this point in evolutionary history [Ridgway and Hanson, 2014]. In human evolution, fossil evidence suggests early hominids had relatively small cerebellums. Further evolution was characterized by periods of neocortical growth followed by cerebellar growth, in a sort of staggered "catch-up" pattern. This compensatory growth may have allowed an increase in cognitive abilities without requiring more cerebral space [Weaver, 2005]. The more evolutionarily modern delphinoid brain boasts an even larger cerebellum (relative to body mass) compared to other odontocetes or mysticetes (Fig. 10). As killer whales display complex hunting and social behavior and utilize a sophisticated sound repertoire, their relatively large cerebellum size may imply a role in higher level cognitive functioning.

Ridgway/Carlin/Van Alstyne/Hanson/
Tarpley

Surface Area of the Cerebral Cortex

Among delphinoids and members of the PZIP group, the surface area of the cerebral cortex relative to body mass appears isometric [see also Manger et al., 2012]. The cortex surface area for *B. mysticetus* was significantly less than that of odontocetes and of a Balaenopteroidea mysticete, *B. acutorostrata* [Eriksen and Pakkenberg, 2007]. Eriksen and Pakkenberg [2007] measured cerebral cortex surface area using 5 half brains of the minke whale (*B. acutorostrata*), the smallest whale of the family Balaenopteridae. Theirs are the only data on this large baleen whale family. Compared to our values and those of Ridgway and Brownson [1984], they used thicker sections and only measured 1 hemisphere of each brain. However, their mean value of just under 6,000 cm^2 does not appear significantly different from our cortex surface area regression overall, as shown in Figures 16–18. They did find that their mysticete whales had a lower relative surface area when compared with 3 delphinid genera: *Stenella*, *Tursiops*, and *Delphinus*.

Huggenberger [2008] suggested that during evolution dolphins may have increased the computational performance of their cytoarchitecturally "simple" neocortex by a multiplication of relevant structures (resulting in a hypertrophic surface area) instead of increasing its complexity. As we have shown with *B. mysticetus*, some species do not have as much of a hypertrophic surface area. This is apparently the case with genera such as *Platanista* (Fig. 19). There is diversity in this cetacean feature as well as others, such as cortical complexity, relative size of individual brain structures, and neuronal morphology [Hof et al., 2005; Oelschläger et al., 2010; Butti et al., 2014].

We suggest biological features other than total brain size must be considered to understand folding of the cetacean cortex. For example, thickness of the cerebral cortex varies within cetacean brains. In the sperm whale brains studied by Kojima [1951], cortex thickness in different areas ranged from 1.72 to 3 mm. In the smaller odontocetes *Stenella* and *Tursiops*, Ridgway and Brownson [1984] found a variation of 1.3–1.76 mm in cortex thickness. In studies done so far, larger cetacean brains have had progressively thicker cortex values [Furutani, 2008; Kern et al., 2011; Butti et al., 2014]. The crumpled paper model suggested by Mota and Herculano-Houzel [2015] for many other taxa does not apply to cetaceans. In the future, studies of thickness in different functional regions [Brownson et al., 1981] should be instructive for the understanding of brain and biology in diverse cetacean species.

EQ and Endocranial Volume

Endocranial volume includes much nonbrain tissue or adnexa, blood, cerebrospinal fluid, vascular networks, falx cerebri, and tentorium cerebelli. The proportion of brain in the endocranial volume varies between cetaceans. For example, the *B. mysticetus* brain only occupies between 35 and 41% of the volume of the cranial vault [Thewissen et al., 2011]. In fin and humpback whales the brain is closer to 60% of endocranial volume, and it is about 70% in sperm whales [Jacobs and Jensen, 1964]. In large male sperm whales with an average brain mass of 7,800 g, Kojima [1951] estimated that one-third of the cranial vault was filled with dura, blood vessels, and other nonneural material. Without considering nonneural tissue in the cranial vault, endocranial volume would predict a brain mass of over 10.5 kg for the larger sperm whales. Large mysticete whales (Table 3) have even more nonneural tissue in the cranial vault [Jacobs and Jensen, 1964; Thewissen et al., 2011].

Many recent studies have used endocranial volume to compare the brains of living and extinct cetaceans [Marino, 1997, 1998; Marino et al. 2000b, 2004; Montgomery et al., 2013]. Montgomery et al. [2013] point out that the highest EQ values are found in primates and cetaceans. Connor [2007] has cautioned about the use of EQ because of the great body size variation. The mysticetes have a lower EQ than Odontoceti. The sperm whale (*P. macrocephalus*), the largest of the odontocete whales, has a relatively low EQ that is comparable to the mysticetes [Worthy and Hickie, 1986]. However, there is great sexual dimorphism in sperm whales. The EQ of female sperm whales is higher than that of male sperm whales and also higher than equivalent-sized mysticetes [Povinelli et al., 2014]. According to Montgomery et al. [2013], the mysticete whales experienced more body mass increase than did Odontoceti. They suggest that the discrepancy is driven mainly by historic declines in body mass, not dramatic change in brain mass. However, these findings must be viewed with skepticism because they relied heavily on EQ derived from endocranial volumes. It is difficult to assess the accuracy of brain mass from fossil cetaceans considering the great range of cetacean endocranial adnexa (Table 3). In the Delphinidae that we have measured, endocranial volume approximates brain volume with a reduction of 8–12% for endocranial adnexa. For other cetaceans, such as larger members of our PZIP, Balaenopteroidea, and Balaenidae groups, there is a much larger amount of endocranial adnexa which must be considered when comparing cetacean brains based on endocranial volume (Table 3; Fig. 20–22).

Brain mass estimates based on endocasts of ancestors of living cetaceans may be grossly overestimated. EQ was designed to facilitate the comparison of brain size between different species. EQ quantifies the expected brain mass based on body mass. An EQ value of 1 indicates an expected or average brain mass based on the values of all mammals. Values above or below 1 indicate larger or smaller brain sizes, respectively, from those expected [Jerison, 1973]. Though these values are often regarded as a reflection of intelligence [Jerison and Barlow, 1985; Marino et al., 2007], EQ is obviously limited in its usefulness given that it is based solely on brain mass relative to body mass.

Nevertheless, EQ remains one of the main comparative tools, with humans and a few dolphins boasting the highest EQ values. Interestingly, both primates and cetaceans also have the largest range of EQ values [Boddy et al., 2012]. In an analysis of EQ in 630 mammalian species, Boddy et al. [2012] concluded that the "strict correlation" between brain and body mass in most mammalian species appeared to be "relaxed" for primates and cetaceans. Within both of these groups, there are examples of concurrent lineages with decreasing and increasing EQ trends.

Metabolism and Brain Size

When the ancestors of cetaceans entered the ocean, they found rich high-energy food sources – especially fish and squids. Many cetaceans were able to evolve a high-energy lifestyle. Williams et al. [2001] noted that dolphins have high metabolic rates. High metabolic rates have been correlated with brain size across mammalian species [Martin, 1996]. Metabolic rate has been related to intestine length, lactation (rich milk, long periods of lactation), and calories consumed [Williams et al., 2001; Connor, 2007]. The human brain has a high metabolic rate. Available evidence suggests that *Tursiops truncatus* does at least as well [Ridgway, 1990; Ridgway et al., 2006]. Arteriovenous differences in oxygen and glucose across the anesthetized dolphin (*T. truncatus*) brain were as great as, or greater than, those in the brains of anesthetized humans [Ridgway, 1990]. Moreover, positron emission tomography of cooperating dolphins showed marked brain glucose consumption [Ridgway et al., 2006]. Thus, we suspect that the dolphin brain also has a high rate of metabolism.

With its high rate of metabolism, the human brain must be actively cooled by blood flow [Hofman, 2012]. Although water transports heat much faster than air, the insulating blubber over the cranial vault of cetaceans likely precludes significant heat radiation from the brain. Cetaceans may have adapted special means for cooling. The entire blood supply of their brains passes through a large

rete mirabile in the dorsum of the thorax and then into another rete system within the vertebral canal before reaching the cranial vault through the foramen magnum [Nagel et al., 1968; Vogl and Fisher, 1981, 1982]. Such a configuration is well positioned to provide a counter-current heat exchange mechanism capable of regulating temperature in blood reaching the brain. The sperm whale, with a relatively small cerebellum and conversely the largest cetacean cerebrum, has extensive circulation within the cranial vault. In these large whales with thick blubber insulation [Lockyer, 1976], endocranial adnexa, mainly blood vessels, make up a quarter or more of the cranial vault contents (Table 3).

There appears to be a strong relationship between cetacean body length and mass and the amount of endocranial adnexa (Fig. 20, 21). It is interesting that the bowhead whale, *B. mysticetus,* with the largest amount of insulating blubber [George et al., 2007], also has the greatest amount of endocranial adnexa (Table 3; Fig. 20–22). This whale's habitat is restricted to very cold arctic and nearby subarctic waters. The extensive endocranial vascularity and blood flow may be required to cool the brain as these huge, thickly insulated animals feed and migrate along the Arctic ice pack. Although delphinids have much less endocranial adnexa, all have retia around and within the cranial vault.

Manger [2006] posited that the high proportion of glial cells in these large cetacean brains produce considerable heat. The author suggested that this heat production is important for cetaceans to maintain homeostasis in their environment. In fact, the author suggested that thermogenesis drove the evolution of the large cetacean brain. We found a significant difference in brain size between 2 delphinoids of similar body size and similar habitat in the North Pacific Ocean. One was from our Phocoenidae-Monodontidae group, *P. dalli,* and the other from our Delphinidae group, *L. obliquidens.* The Phocoenidae-Monodontidae animal, *P. dalli,* has a larger heart, higher blood volume, more hemoglobin, and a higher metabolic rate [Ridgway and Johnston, 1966], and yet has a significantly smaller brain (Fig. 8). *L. obliquidens* is usually found in larger herds, whereas *P. dalli* is usually seen in smaller groups. *L. obliquidens* has a greater sound repertoire, producing whistles and broadband clicks [Whitten and Thomas, 2001], whereas *P. dalli* produces only narrow-band, high-frequency pulses and no whistle-like sounds [Evans and Awbrey, 1984]. On the other hand, *P. dalli* appears to be a faster swimmer with a larger heart and higher metabolic rate [Ridgway and Johnston, 1966]. This narrow comparison of 2 cetaceans that vary by herd

size and acoustic repertoire suggests that these factors may be more important for a larger brain than habitat or metabolic rate.

We also evaluated the dolphin genus *Stenella* in regard to habitat and water temperatures. It does appear that *S. coeruleoalba,* the *Stenella* species that ventures into colder waters, has a larger brain and body than the more tropical members of the genus (Fig. 9). However, the genus *Steno* shares the tropical habitat [Miyazaki and Perrin, 1994; Baird et al., 2008] and has a significantly larger brain than any of the *Stenella* (Fig. 9) despite its occupation of similar habitats. We cannot reject the thermogenesis hypothesis [Manger, 2006]; however, neither can we claim support for the hypothesis based on our data.

Marino et al. [2008] disagreed with the thermogenesis hypothesis. They posited "that modern cetacean brains are large in order to support complex cognitive abilities driven by social and ecological forces." It may be notable that the large-brained tropical *Steno* in a marine park were impressive in their ability, on cue, to invent and perform new behaviors that had not been trained [Pryor et al., 1969]. Smaller-brained (Fig. 9) tropical *Stenella* kept at the same park never showed such abilities despite their exposure to extensive training at the park. If acoustic repertoire is reflective of cognitive abilities, then a comparison of *Stenella* and *Steno* sound capabilities might be more instructive with regard to their relative brain sizes. The 2 species in these similar habitats do differ in the complexity of their sound production. *Steno* and the *Stenella* both produce whistles and broadband echolocation clicks. In a study of whistle comparisons including these groups in the Tropical Eastern Pacific Ocean, the *Steno* whistles were found to have the highest coefficients of variation for all whistle variables [Oswald et al., 2003]. The greater variation in the *Steno* sound repertoire may contribute to its larger brain relative to *Stenella*.

With their great range of body and brain size, cetaceans show many examples of brain diversity that may derive from their evolution, ecology, taxonomy, and social organization. Our large data set on brain relations of extant cetaceans should be useful to inform such studies (online suppl. Table S1). We recognize that there are many gaps in cetacean brain data. We hope that future research might build on our data (online suppl. Table S1) to fill the numerous gaps and provide a more complete picture of cetacean brain diversity.

Acknowledgements

Disclosure Statement

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