

The Humane Society Institute for Science and Policy
Animal Studies Repository

12-2004

Origin and Evolution of Large Brains in Toothed Whales

Lori Marino
Emory University

Daniel W. McShea
Duke University

Mark D. Uhen
Cranbrook Institute of Science

Follow this and additional works at: https://animalstudiesrepository.org/acwp_vsm

 Part of the [Animal Studies Commons](#), [Other Animal Sciences Commons](#), and the [Other Ecology and Evolutionary Biology Commons](#)

Recommended Citation

Marino, L., McShea, D. W., & Uhen, M. D. (2004). Origin and evolution of large brains in toothed whales. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology*, 281(2), 1247-1255.

This Article is brought to you for free and open access by the Humane Society Institute for Science and Policy. It has been accepted for inclusion by an authorized administrator of the Animal Studies Repository. For more information, please contact eyahner@humanesociety.org.



Origin and Evolution of Large Brains in Toothed Whales

Lori Marino¹, Daniel W. McShea², and Mark D. Uhen³

¹ Emory University

² Duke University

³ Cranbrook Institute of Science

KEYWORDS

cetacean, encephalization, odontocetes

ABSTRACT

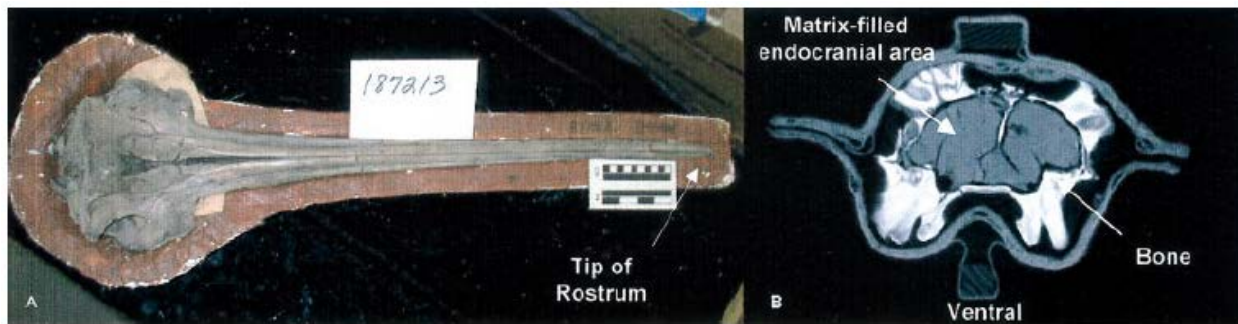
Toothed whales (order Cetacea: suborder Odontoceti) are highly encephalized, possessing brains that are significantly larger than expected for their body sizes. In particular, the odontocete superfamily Delphinoidea (dolphins, porpoises, belugas, and narwhals) comprises numerous species with encephalization levels second only to modern humans and greater than all other mammals. Odontocetes have also demonstrated behavioral faculties previously only ascribed to humans and, to some extent, other great apes. How did the large brains of odontocetes evolve? To begin to investigate this question, we quantified and averaged estimates of brain and body size for 36 fossil cetacean species using computed tomography and analyzed these data along with those for modern odontocetes. We provide the first description and statistical tests of the pattern of change in brain size relative to body size in cetaceans over 47 million years. We show that brain size increased significantly in two critical phases in the evolution of odontocetes. The first increase occurred with the origin of odontocetes from the ancestral group Archaeoceti near the Eocene-Oligocene boundary and was accompanied by a decrease in body size. The second occurred in the origin of Delphinoidea only by 15 million years ago.

Primates are known for their elaborated brains and high encephalization levels, i.e., larger brains than expected for their body sizes (Marino, 1998). The only other mammalian group that rivals primates in this regard is cetaceans (dolphins, porpoises, and whales). Modern cetaceans have been evolving separately from their closest living sister taxa for at least 52 Ma (Gingerich and Uhen, 1998) and from Primates for up to 92 Ma (Kumar and Blair Hedges, 1998). The limited data prior to this study shows that the earliest cetaceans possessed low encephalization levels well below one (Jerison, 1973; Gingerich, 1998; Marino et al., 2000), as was typical of Cretaceous mammals (Jerison, 1973), among which are likely the common ancestor of Primates and Cetacea. Many modern toothed whale (suborder: Odontoceti) species, on the other hand, possess extremely high encephalization levels second only to that of modern humans (Marino, 1998) and therefore have undergone substantial increases in encephalization during their evolutionary history. Likewise, there is evidence for convergent behavioral abilities between odontocetes and humans plus great apes as well (Marino, 2002). These include mirror self-recognition (Reiss and Marino, 2001), comprehension of artificial symbol-based communication systems and abstract concepts

(Herman, 2002), and the learning and intergenerational transmission of behaviors that have been described as cultural (Rendall and Whitehead, 2001).

Despite these commonalities, the odontocete evolutionary pathway has proceeded under a very different selective regime from that of primates. Therefore, the highly expanded brain size and behavioral abilities of odontocetes are, in a sense, convergently shared with humans. A description of the pattern of encephalization in toothed whales has enormous potential to yield new insights into odontocete evolution, whether there are shared features with hominoid brain evolution, and more generally how large brains evolve. Yet, up until now, little has been known about the basic pattern of encephalization that characterized odontocete evolution since their adoption of an aquatic lifestyle. The present study provides the first comprehensive description and statistical tests of the pattern of change in encephalization level in cetaceans over 47 million years.

Fig. 1. **A:** Photograph of early-mid Miocene fossil odontocete (*Rhabdosteus longirostris*, USNM 187213). **B:** Coronal 1.22 mm thick CT image of the same specimen showing differentiation of the hardened matrix that fills the endocranial area and the surrounding bone.



MATERIALS AND METHODS

Scanning and Measurement of Endocranial Volume

Fossil cetacean endocranial volumes were measured from computed tomography (CT) scans acquired with a Siemens Somatom SP scanner at the National Museum of Natural History (USNM), Smithsonian Institution. Image acquisition, analysis, and file conversions were controlled by Siemens SOMARIS software. OSIRIS software was used to convert Siemens image files into DICOM images. Additional scans were obtained at the Medical University of Charleston in Charleston, South Carolina, on a Marconi MX8000 multiple-slice spiral scanner and at Methodist Hospital in Arcadia, California, on a Picker PQ 5000 single-slice spiral scanner. Contiguous 1–2 mm coronal scans of the entire cranium of each specimen were obtained using different scanning parameters depending on the estimated density of the fossil and endocranial matrix, level of permineralization of the bone, and whether the skull was embedded in hardened matrix (Marino et al., 2003).

Each coronal slice through the endocranial cavity was traced manually using Scion Image or ImageJ image analysis software to calculate the area of endocranial space in each slice. The slice areas were then multiplied by the slice thickness and summed to determine the endocranial volume for each specimen, which was used as an estimate of brain mass. Endocranial volume can be converted to mass using the density of brain tissue, approximately 1.0 g/ml, and can be measured directly in modern cetaceans. Previous within-rater and between-rater intraclass correlation coefficients for a subset of archaeocete specimens ranged from 0.91 to 0.98, indicating extremely high agreement across ratings of

these specimens. Figure 1A displays an example of a fossil odontocete cranium from the sample and Figure 1B displays an example of a coronal CT image through a fossil odontocete cranium.

The volume of the endocranial space is an overestimate of brain size because cetaceans have an endocranial vascular structure known as the rete mirabile that also occupies this space. From fossil and recent specimens in which the rete mirabile volume can be measured or accurately estimated, it has been shown that the relative size of the rete mirabile has not systematically changed over time (Marino, 1995; Marino et al., 2000).

A total of 66 fossil cetacean crania were scanned and measured. This subset was added to brain and body weight data from a total of 144 modern cetacean specimens for a total sample in the present study of 210 specimens representing 37 families and 62 species. The data for each modern and fossil species in the present study are displayed in Table 1.

Estimation of Body Mass

Since very few fossil cetacean specimens include entire skeletons from which one can obtain a skeletal length or the multiple anatomical measurements needed to estimate body mass from postcranial elements, we selected the occipital condyle breadth (OCB) to predict body size of odontocetes. OCB was measured on a wide range of modern cetacean specimens with known body masses and was strongly correlated with body mass ($r^2 = 0.79$). This allowed us to use the regression parameters from that analysis to estimate body mass for fossil cetacean specimens when only the cranium was available.

Calculation of Encephalization Quotients

Encephalization is typically expressed as an encephalization quotient (EQ). EQ is an index that quantifies how much larger or smaller a given animal's brain is relative to the expected brain size for an animal at that body size (Jerison, 1973). Brains with EQs larger than 1 are larger than the expected size, while those less than 1 are smaller than the expected size. EQ values were calculated for each specimen in the present study using measured endocranial volumes (or fresh brain weight in some Recent specimens) and estimated body sizes in fossils and actual body weights for all Recent specimens (Marino et al., 2003). The equation $EQ = \text{brain weight}/0.12 (\text{body weight})^{0.67}$ from Jerison (1973) was used to derive EQ values (hereafter referred to as $EQ_{0.67}$) for each genus or, when possible, each species represented in our sample.

Standard EQ values, like most ratios, are not normally distributed. To avoid the problematic statistical properties of ratios and to be able to perform parametric statistical tests on EQ values, $\log_{10}EQ_{0.67}$ values were calculated. All statistical tests were performed on the logged values, which has the same outcome as taking residuals between logged actual and logged expected brain mass values. EQ values can be calculated using alternative methods to that of Jerison (1973). One way is to derive the regression parameters empirically from the actual sample. The resulting regression equation is the following: $EQ = \text{brain weight}/1.6 (\text{body weight})^{0.53}$. Another popular format for EQ is based on the work of Armstrong (1985), Eisenberg (1981), and others. This approach results in a regression equation of $EQ = \text{brain weight}/0.055 (\text{body weight})^{0.75}$. We calculated EQ for our sample based on these two alternative methods, hereafter known as $EQ_{0.53}$ and $EQ_{0.75}$.

TABLE 1. Data plotted in Figure 1. Rows with geomean listed in the Specimen column are geometric mean values for all of the specimens from single species in a time plane

Specimen	Data source	Suborder	Superfamily or Infraorder	Family	Genus	Species
USNM 11121	Gingerich, 1998	Archaeoceti	Basilosauroidea	Basilosauridae	<i>Basilosaurus</i>	<i>cetoides</i>
101222		Archaeoceti	Basilosauridae	Basilosauridae	<i>Basilosaurus</i>	<i>cetoides</i>
geomean	Gingerich, 1998	Archaeoceti	Basilosauroidea	Basilosauridae	<i>Dorudon</i>	<i>atrox</i>
USNM 16638		Archaeoceti	Basilosauroidea	Basilosauridae	<i>Saghacetus</i>	<i>osiris</i>
GSP-UM 3012		Archaeoceti	Protocetoidea	Protocetidae	<i>Zygorhiza</i>	<i>kochii</i>
GSP-UM 3106		Archaeoceti	Protocetoidea	Protocetidae	<i>Rodhocetus</i>	<i>kasrani</i>
USNM 256604		Archaeoceti	Remingtonocetoidea	Remingtonocetidae	<i>Dalanistes</i>	<i>ahmedi</i>
USNM 335240		Odontoceti	incertae sedis	indet.	<i>indet.</i>	indet.
USNM 335502		Odontoceti	incertae sedis	indet.	<i>indet.</i>	indet.
USNM 550067		Odontoceti	incertae sedis	indet.	<i>indet.</i>	indet.
geomean	Pilleri & Busnel, 1969 and Pilleri et al., 1969	Odontoceti	Delphinoidea	Delphinidae	<i>Cephalorhynchus</i>	<i>heavisidii</i>
USNM 21867		Odontoceti	Delphinoidea	Delphinidae	<i>Delphinus</i>	<i>delphis</i>
geomean	USNM 571348, 671349; Pilleri & Gahr, 1970; von Bonin, 1940; Pilleri & Gahr, 1969	Odontoceti	Delphinoidea	Delphinidae	<i>Globicephala</i>	<i>baereckeii</i>
geomean	USNM 55040, Ridgway et al., 1984; Pilleri et al., 1969	Odontoceti	Delphinoidea	Delphinidae	<i>Globicephala</i>	<i>melaena</i>
geomean	USNM 504153, 571326, 571327, 571347, 571391, 571395	Odontoceti	Delphinoidea	Delphinidae	<i>Grampus</i>	<i>griseus</i>
USNM 244317		Odontoceti	Delphinoidea	Delphinidae	<i>Lagenorhynchus</i>	<i>acutus</i>
geomean	Morgane et al., 1979; Pilleri & Gahr, 1970; Ridgway et al., 1966	Odontoceti	Delphinoidea	Delphinidae	<i>Lagenorhynchus</i>	<i>n. sp. H</i>
geomean	USNM 504333, USNM 550549	Odontoceti	Delphinoidea	Delphinidae	<i>Lagenorhynchus</i>	<i>obliquidentis</i>
USNM 206098		Odontoceti	Delphinoidea	Delphinidae	<i>Lagenorhynchus</i>	<i>obscurus</i>
geomean	Pilleri & Gahr, 1970; Lilly, 1964	Odontoceti	Delphinoidea	Delphinidae	<i>Lagenorhynchus</i>	sp.
USNM 501200		Odontoceti	Delphinoidea	Delphinidae	<i>Orcinus</i>	<i>orca</i>
		Odontoceti	Delphinoidea	Delphinidae	<i>Pseudorca</i>	<i>crassidentis</i>
USNM 504408	Morgane & Jacobs, 1979	Odontoceti	Delphinoidea	Delphinidae	<i>Sotalia</i>	<i>fluviatilis</i>
geomean	USNM 504350, 504772, 504773, 550495, 571658	Odontoceti	Delphinoidea	Delphinidae	<i>Stenella</i>	<i>clymene</i>
CAS 2354-16458		Odontoceti	Delphinoidea	Delphinidae	<i>Stenella</i>	<i>coeruleoalba</i>
geomean	USNM 504487, 504489, 504490, 504492, 504493, 504498, 504499	Odontoceti	Delphinoidea	Delphinidae	<i>Stenella</i>	<i>longirostris</i>
geomean	Pilleri & Gahr, 1970; Morgane & Jacobs, 1972; Ridgway et al., 1987; Weber, 1987; Ridgway, 1990; Kruger, 1959; Ridgway et al., 1979	Odontoceti	Delphinoidea	Delphinidae	<i>Steno</i>	<i>bredanensis</i>
USNM 10670		Odontoceti	Delphinoidea	Delphinidae	<i>Tursiops</i>	<i>truncatus</i>
USNM 25005		Odontoceti	Delphinoidea	Kentriodontidae	<i>Kentriodon</i>	<i>pernix</i>
USNM 323772		Odontoceti	Delphinoidea	Kentriodontidae	<i>Kentriodon</i>	<i>pernix</i>
USNM 317882		Odontoceti	Delphinoidea	Kentriodontidae	<i>Kentriodon</i>	sp.
		Odontoceti	Delphinoidea	Kentriodontidae	<i>Kentriodon</i>	n. sp. W
geomean	Ridgway et al., 1984	Odontoceti	Delphinoidea	Monodontidae	<i>Delphinapterus</i>	<i>leucas</i>
geomean	Hay & Mansfield, 1989; Hay et al., 1989	Odontoceti	Delphinoidea	Monodontidae	<i>Monodon</i>	<i>monoceros</i>
geomean	CAS 23161, 23170; UCBMVZ 173468; Anderson, 1968	Odontoceti	Delphinoidea	Phocoenidae	<i>Phocoena</i>	<i>phocoena</i>

Specimen	Data source	Suborder	Superfamily or Infraorder	Family	Genus	Species
USNM 550783		Odontoceti	Delphinoidea	Phocoenidae	<i>Phocoena</i>	<i>spinipinnis</i>
geomean	Pilleri & Gahr, 1969; Pilleri & Gahr, 1970; Ridgway et al., 1966; Ridgway et al., 1966	Odontoceti	Delphinoidea	Phocoenidae	<i>Phocoenoides</i>	<i>dalli</i>
USNM 10714		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	<i>bossi</i>
USNM 20128		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	<i>bossi</i>
geomean	USNM 13436, 13875, 167675	Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	<i>cristatus</i>
USNM 167675		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	<i>cristatus</i>
USNM 167622		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	n. sp. M*
USNM 299947		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	sp.
USNM 214767		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	sp.
USNM 21361		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	n. sp. V*
USNM 175381		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	n. sp. V*
USNM 171103		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Eurhinodelphis</i>	sp.
USNM 187312		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	n. sp. B*
geomean	USNM 187317, 244403, 244409	Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	n. sp. B*
geomean	USNM 13871, 13876	Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	n. sp. H*
geomean	USNM 22804, 187314	Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	n. sp. H*
USNM 187621		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	n. sp. H*
geomean	USNM 175379, 187211, 187212, 187213	Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	<i>longirostris</i>
geomean	USNM 16118, 244413	Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	<i>longirostris</i>
geomean	USNM 187306, 187627	Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	<i>longirostris</i>
USNM 167676		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	<i>longirostris</i>
USNM 187214		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	sp.
USNM 205772		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	<i>Schizodelphis</i>	sp.
PV2757		Odontoceti	incertae sedis	Agorophidae	Genus Y	n. sp.

Species listed with an asterisk () were differentiated in an unpublished dissertation. (A. C. Myrick, Jr., University of California, Los Angeles (1979).) Museum acronyms: CAS, California Academy of Sciences, San Francisco, CA; ChM, Charleston Museum, Charleston, SC; GSP-UM, Geological Survey of Pakistan, University of Michigan collection; USNM, United States National Museum of Natural History, Washington D.C.; YPM, Yale Peabody Museum, New Haven, CT.

TABLE 1. Data plotted in Figure 1. Rows with geomean listed in the Specimen column are geometric mean values for all of the specimens from single species in a time plane (continued)

Brain vol (cc)	Body mass (g)	EQ0.53	EQ0.67	EQ0.75	Log10 (BV)	Log10 (BM)	Log10 (EQ53)	Log10 (EQ67)	Log10 (EQ75)	MaEpoch
2240.0	6480000.0	0.3436	0.5097	0.3171	3.3502	6.8116	-0.4640	-0.2927	-0.4988	39.0 Eocene
302.8	730849.1	0.1476	0.2973	0.2202	2.4811	5.8638	-0.8308	-0.5268	-0.6571	37.0 Eocene
1185.4	2240000.0	0.3192	0.5496	0.3722	3.0739	6.3502	-0.4959	-0.2600	-0.4292	39.0 Eocene
388.0	350000.0	0.2795	0.6239	0.4902	2.5888	5.5441	-0.5537	-0.2049	-0.3096	39.0 Eocene
800.8	2040000.0	0.2266	0.3953	0.2697	2.9035	6.3096	-0.6447	-0.4031	-0.5691	37.0 Eocene
291.0	290000.0	0.2316	0.5308	0.4234	2.4639	5.4624	-0.6353	-0.2751	-0.3733	47.0 Eocene
400.0	750000.0	0.1924	0.3860	0.2854	2.6021	5.8751	-0.7158	-0.4134	-0.5446	45.0 Eocene
256.7	78081.8	0.4096	1.1280	0.9994	2.4095	4.8925	-0.3877	0.0523	-0.0003	27.0 Oligocene
302.4	78081.8	0.4824	1.3287	1.1772	2.4806	4.8925	-0.3166	0.1234	0.0708	17.0 Miocene
507.5	54810.8	0.9766	2.8263	2.5759	2.7054	4.7389	-0.0103	0.4512	0.4109	27.0 Oligocene

Brain vol (cc)	Body mass (g)	EQ0.53	EQ0.67	EQ0.75	Log10 (BV)	Log10 (BM)	Log10 (EQ53)	Log10 (EQ67)	Log10 (EQ75)	MaEpoch
763.0	71000.0	1.2801	3.5727	3.1895	2.8825	4.8513	0.1072	0.5530	0.5037	0.0 Holocene
814.3	59980.7	1.4939	4.2691	3.8629	2.9108	4.7780	0.1743	0.6303	0.5869	0.0 Holocene
4165.9	900766.2	1.8182	3.5558	2.5905	3.6197	5.9546	0.2596	0.5509	0.4134	1.0 Pliocene
2861.7	938074.6	1.2224	2.3771	1.7262	3.4566	5.9722	0.0872	0.3760	0.2371	0.0 Holocene
2384.4	319974.0	1.8011	4.01717	3.2224	3.774	5.5051	0.2555	0.6098	0.5082	0.0 Holocene
1100.5	244217.1	0.9593	2.2521	1.8213	3.0416	5.3878	-0.0181	0.3526	0.2604	0.0 Holocene
1129.2	98673.7	1.5912	4.2411	3.6878	3.0528	4.9942	0.2017	0.6275	0.5668	
1045.0	63500.0	1.8601	5.2732	4.7498	3.0191	4.8028	0.2695	0.7221	0.6767	0.0 Holocene
886.1	58473.1	1.6478	4.7257	4.2848	2.9475	4.7670	0.2169	0.6745	0.6319	0.0 Holocene
1344.0	112804.5	1.7642	4.6149	3.9700	3.1284	5.0523	0.2465	0.6642	0.5988	14.0 Miocene
5028.0	1953201.4	1.4561	2.5551	1.7497	3.7014	6.2907	0.1632	0.4074	0.2430	0.0 Holocene
3512.0	579196.4	1.9370	4.0298	3.0414	3.5456	5.7628	0.2871	0.6053	0.4831	0.0 Holocene
688.0	42200.0	1.5207	4.5651	4.2486	2.8376	4.6253	0.1821	0.6594	0.6282	0.0 Holocene
666.0	86000.0	1.0094	2.7500	2.4112	2.8235	4.9345	0.0041	0.4393	0.3822	0.0 Holocene
938.5	128715.6	1.1488	2.9500	2.5111	2.9725	5.1096	0.0602	0.4698	0.3999	0.0 Holocene
660.0	66200.0	1.1491	3.2388	2.9076	2.8195	4.8209	0.0604	0.5104	0.4635	0.0 Holocene
1541.9	123830.9	1.9264	4.9738	4.2470	3.1881	5.0928	0.2847	0.6967	0.6281	0.0 Holocene
1759.2	206823.8	1.6747	4.0242	3.2980	3.2453	5.3156	0.2239	0.6047	0.5183	0.0 Holocene
230.3	18295.7	0.7928	236754	2.6621	2.3624	4.2623	-0.1008	0.4274	0.4252	18.0 Miocene
276.0	17036.8	0.9866	3.3628	3.3652	2.4409	4.2314	-0.0058	0.5267	0.5270	15.0 Miocene
638.0	41653.3	1.4200	4.2705	3.9786	2.8048	4.6196	0.1523	0.6305	0.5997	14.0 Miocene [
305.1	49277.1	0.6214	1.8262	1.6787	2.4845	4.6922	-0.2065	0.2615	0.2250	14.0 Miocene
2083.0	636000.0	1.0933	2.2449	1.6816	3.3187	5.8035	0.0387	0.3512	0.2257	0.0 Holocene
2993.7	1578116.9	0.9707	1.7550	1.2225	3.4762	6.1981	-0.0129	0.2443	0.0872	0.0 Holocene
522.7	53510.9	1.0188	2.9584	2.7014	2.7183	4.7284	0.0081	0.4711	0.4316	0.0 Holocene
597.0	68041.9	1.0244	2.8763	2.5765	2.7760	4.8328	0.0105	0.4588	0.4110	0.0 Holocene
861.4	85748.3	1.3076	3.5544	3.1255	2.9352	4.9332	0.1165	0.5508	0.4949	0.0 Holocene

Brain vol (cc)	Body mass (g)	EQ0.53	EQ0.67	EQ0.75	Log10 (BV)	Log10 (BM)	Log10 (EQ53)	Log10 (EQ67)	Log10 (EQ75)	MaEpoch
949.3	123019.4	1.1902	3.0758	2.6277	2.9774	5.0900	0.0756	0.4880	0.4196	18.0 Miocene
625.9	90009.0	0.9260	2.5001	2.1900	2.7965	4.9543	-0.0334	0.3980	0.3404	14.0 Miocene
769.7	91675.6	1.1278	3.0370	2.6563	2.8863	4.9623	0.0522	0.4824	0.4243	14.0 Miocene
816.3	191866.9	0.8086	1.9637	1.6190	2.9119	5.2830	-0.0922	0.2931	0.2093	15.0 Miocene
531.8	64044.8	0.9424	2.6684	2.4019	2.7258	4.8065	-0.0258	0.4263	0.3806	14.0 Miocene
431.5	57771.5	0.8075	2.3196	2.1052	2.6349	4.7617	-0.0929	0.3654	0.3233	19.5 Miocene
574.5	98673.7	0.8096	2.1577	1.8762	2.7593	4.9942	-0.0918	0.3340	0.2733	14.0 Miocene
543.1	78081.8	0.8663	2.3859	2.1138	2.7348	4.8925	-0.0623	0.377	0.3251	16.0 Miocene
627.2	184651.4	0.6341	1.5481	1.2803	2.7974	5.2664	-0.1979	0.1898	0.1073	15.0 Miocene
650.8	57771.5	1.2180	3.4989	3.1755	2.8135	4.7617	0.0856	0.5439	0.5018	14.0 Miocene
346.1	74378.7	0.5666	1.5711	1.3973	2.5393	4.8714	-0.2467	0.1962	0.1453	14.0 Miocene
478.9	64903.9	0.8427	2.3816	2.1415	2.6803	4.8123	-0.0743	0.3769	0.3307	15.0 Miocene
642.7	57029.5	1.2110	3.4852	3.1663	2.8080	4.7561	0.0831	0.5422	0.5006	16.0 Miocene
342.1	62426.2	0.6144	1.7461	1.5749	2.5341	4.7954	-0.2115	0.2421	0.1973	14.0 Miocene
476.9	85893.8	0.7232	1.9654	1.7281	2.6784	4.9340	-0.1407	0.2935	0.2376	15.0 Miocene
388.1	94819.0	0.5585	1.4969	1.3058	2.5889	4.9769	-0.2530	0.1752	0.1159	14.0 Miocene
495.1	89983.5	0.7326	1.9781	1.7327	2.6947	4.9542	-0.1351	0.2962	0.2387	15.0 Miocene
595.6	84253.0	0.9125	2.4866	2.1896	2.7749	4.9256	-0.0398	0.3956	0.3404	16.0 Miocene
361.2	90009.0	0.5344	1.4428	1.2338	2.5577	4.9543	-0.2721	0.1592	0.1017	17.0 Miocene
328.0	78081.8	0.5232	1.4409	1.2766	2.5158	4.8925	-0.2813	0.1586	0.1061	14.0 Miocene
416.2	67363.3	0.7179	2.0186	1.8096	2.6193	4.8284	-0.1439	0.3050	0.2576	15.0 Miocene
1234.4	594725.0	0.6713	1.3915	1.0480	3.0914	5.7743	-0.1731	0.1435	0.0203	27.0 Oligocene

Tests of Mean Differences

Each test for a mean difference was conducted using a bootstrap method in which specimens from the groups to be compared were pooled and repeatedly sampled 10,000 times with replacement to produce a distribution of differences between the means. In most comparisons conducted, the actual difference between the two means was outside the range of the bootstrapped distribution of differences.

Tests for Directional Tendencies

A tendency toward increase or decrease in EQ values was tested by reconstructing ancestral states at nodes using parsimony (Maddison and Maddison, 1992), fossil first occurrences (Alroy, 1998), and maximum likelihood (Pagel, 1997) methods using published phylogenies for the Delphinoidea (de Muizon, 1988), Odontoceti (de Muizon, 1991), and Cetacea (Geisler and Sanders, 2003) based on fossil and extant morphology and a phylogeny based on molecular data for Cetacea (Nikaido et al., 2001). For parsimony and fossil first occurrences, nodal states were reconstructed and then compared to the values for adjacent nodes to produce counts of increase and decrease. In the fossil first-occurrence method, each node in the tree was assigned the same state as the descendent taxon with the earliest first occurrence. For maximum likelihood, a likelihood value was calculated for a model of evolution that includes a tendency toward increase or decrease. Then, another likelihood value was calculated for a null

model in which no tendency toward increase or decrease exists. Finally, the likelihood value for the model representing a tendency was compared to the likelihood value for the null model to determine if the first is significantly higher than the second.

TABLE 1. Data plotted in Figure 1. Rows with geomean listed in the Specimen column are geometric mean values for all of the specimens from single species in a time plane (continued)

Specimen	Data source	Suborder	Superfamily or Infraorder	Family	Genus	Species
PV4961		Odontoceti	incertae sedis	Eosqualodontidae	n. gen.	n. sp.
USNM 205491		Odontoceti	Eurhinodelphinoidea	Eurhinodelphidae	n. gen.	n. sp.
geomean	Pilleri & Gahr, 1968; Best & Da Silva, 1989; Best et al., 1989	Odontoceti	incertae sedis	Iniidae	<i>Inia</i>	<i>geoffrensis</i>
		Odontoceti	incertae sedis	Lipotidae	<i>Lipotes</i>	<i>vexillifer</i>
PV2761		Odontoceti	incertae sedis	Patriocetidae	n. gen.	n. sp.
geomean	USNM 501125; 501126; 501168; Pilleri & Gahr, 1970; Kamiya & Yamasaki, 1974; Kamiya et al., 1974	Odontoceti	incertae sedis	Pontoporiidae	<i>Pontoporia</i>	<i>blainvillei</i>
USNM 256517		Odontoceti	incertae sedis	Simocetidae	<i>Simocetus</i>	<i>rayi</i>
PV4266		Odontoceti	incertae sedis	Xenorophidae	<i>Xenorophus</i>	n. sp.
USNM 187015		Odontoceti	Physeteroidea	Kogiidae	n. gen.	n. sp.
geomean	USNM 302040; 550396; Ridgway et al., 1984	Odontoceti	Physeteroidea	Kogiidae	<i>Kogia</i>	<i>breviceps</i>
geomean	USNM 550482; 550487	Odontoceti	Physeteroidea	Kogiidae	<i>Kogia</i>	<i>simus</i>
14730		Odontoceti	Physeteroidea	Physeteridae	<i>Orycterocetus</i>	<i>crocodilinus</i>
geomean	Pilleri & Gahr, 1970	Odontoceti	Physeteroidea	Physeteridae	<i>Physeter</i>	<i>macrocephalus</i>
USNM 425788		Odontoceti	Platanistoidea	indet.	indet.	indet.
YPM 13408		Odontoceti	Platanistoidea	Platanistidae	<i>Allodelphis</i>	<i>pratti</i>
USNM 214911		Odontoceti	Platanistoidea	Platanistidae	indet.	indet.
geomean	Pilleri & Gahr, 1970	Odontoceti	Platanistoidea	Platanistidae	<i>Platanista</i>	<i>gangetica</i>
USNM 323775		Odontoceti	Platanistoidea	Platanistidae	<i>Pomatodelphis?</i>	sp.
USNM 10484		Odontoceti	Platanistoidea	Squalodontidae	<i>Squalodon</i>	<i>calvertensis</i>
USNM 328343		Odontoceti	Platanistoidea	Squalodontidae	<i>Squalodon</i>	<i>calvertensis</i>
geomean	USNM 504217; 550338; 550754	Odontoceti	Ziphioidea	ZZiphiidae	<i>Mesoplodon</i>	<i>densirostris</i>
geomean	USNM 550105; 550390	Odontoceti	Ziphioidea	Ziphiidae	<i>Mesoplodon</i>	<i>europaeus</i>
geomean	USNM 504612; 504724	Odontoceti	Ziphioidea	Ziphiidae	<i>Mesoplodon</i>	<i>mirus</i>
USNM 181528		Odontoceti	Ziphioidea	Ziphiidae	<i>Squaloziphius</i>	<i>emlongi</i>
	Ridgway & Brownson, 1984	Odontoceti	Ziphioidea	Ziphiidae	<i>Ziphius</i>	<i>cavirostris</i>

RESULTS

Figure 2 shows the mean values of $EQ_{0.67}$ and $\log_{10}EQ_{0.67}$ for the modern and fossil genera or species in the present sample. The range of values measured for modern odontocetes is shown at the top of Figure 2, at 0 Ma. Modern odontocetes have $EQ_{0.67}$ values ranging from slightly less than 1 to slightly greater than 5, indicating that most modern odontocetes are more encephalized than average mammals at all body sizes occupied by odontocetes. Humans have an $EQ_{0.67}$ of about 7 on this scale (Marino, 1998).

The most striking finding is that Oligocene odontocetes (mean $\log_{10}EQ_{0.67} = 0.312$) are significantly more highly encephalized (bootstrap test of difference between means, $P < 0.0001$) than the Eocene archaeocetes (mean $\log_{10}EQ_{0.67} = -0.339$), from which they are thought to have been derived (Uhen and Gingerich, 2001). There is no overlap in the range of EQ values between the two groups. The increase in relative brain size from archaeocetes to Oligocene odontocetes reflects both an increase in mean absolute brain size, from 749 (n = 5) to 782 g (n = 5), as well as a decrease in absolute body size, from 1,654 (n = 5) to 207 kg (n = 5).

TABLE 1. Data plotted in Figure 1. Rows with geomean listed in the Specimen column are geometric mean values for all of the specimens from single species in a time plane (continued)

Brain vol (cc)	Body mass (g)	EQ0.53	EQ0.67	EQ0.75	Log10 (BV)	Log10 (BM)	Log10 (EQ53)	Log10 (EQ67)	Log10 (EQ75)	MaEpoch
425.5	50118.1	0.8585	2.5158	2.3094	2.6289	4.7000	-0.0663	0.4007	0.3635	27.0 Oligocene
323.0	88759.5	0.4815	1.3024	1.1421	2.5092	4.9482	-0.3174	0.1148	0.0577	38.0 Eocene
627.8	87935.6	0.9404	2.5473	2.2354	2.7978	4.9442	-0.0267	0.4061	0.3494	0.0 Holocene
510.0	82000.0	0.7927	2.1684	1.9136	2.7076	4.9138	-0.1009	0.3361	0.2818	0.0 Holocene
857.1	197488.1	0.8362	2.0223	1.6635	2.9330	5.2955	-0.0777	0.3059	0.2210	27.0 Oligocene
219.8	33778.3	0.5467	1.6932	1.6041	2.3421	4.5286	-0.2622	0.2287	0.2052	0.0 Holocene
530.6	94267.9	0.7660	2.0548	1.7932	2.7248	4.9744	-0.1158	0.3128	0.2536	33.0 Oligocene
861.4	96849.3	1.2259	3.2759	2.8528	2.9352	4.9861	0.0885	0.5153	0.4553	27.0 Oligocene
2348.4	506744.6	1.3903	2.9470	2.2481	3.3708	5.7048	0.1431	0.4694	0.3518	4.0 Pliocene
1011.5	302214.7	0.7876	1.7946	1.4268	3.0050	5.4803	-0.1037	0.2540	0.1544	0.0 Holocene
621.5	167958.3	0.6606	1.6344	1.3619	2.7934	5.2252	-0.1801	0.2134	0.1342	0.0 Holocene
2188.9	422569.4	1.4268	3.1023	2.4012	3.3402	5.6259	0.1544	0.4917	0.3804	15.0 Miocene
799.4	35632153.77	0.4971	0.5810	0.3154	3.9031	7.5518	-0.3035	-0.2359	-0.5012	0.0 Holocene
613.5	57470.2	1.1512	3.3096	3.0050	2.7878	4.7594	0.0612	0.5198	0.4778	14.0 Miocene
854.8	170823.4	0.9005	2.2227	1.8497	2.9319	5.2325	-0.0455	0.3469	0.2671	24.0 Miocene
486.5	57771.5	0.9105	2.6157	2.3739	2.6871	4.7617	-0.0407	0.4176	0.3755	21.0 Miocene
298.9	61991.5	0.5389	1.5329	1.3834	2.4756	4.7923	-0.2685	0.1855	0.1410	0.0 Holocene
365.3	175573.1	0.3793	0.9325	0.7743	2.5626	5.2445	-0.4211	-0.0304	-0.1111	6.0 Miocene
630.7	151533.8	0.7080	1.7771	1.4931	2.7998	5.1805	-0.1499	0.2497	0.1741	17.0 Miocene
617.2	157774.9	0.6782	1.6926	1.4175	2.7904	5.1980	-0.1687	0.2286	0.1515	19.5 Miocene
1457.5	763334.6	0.6945	1.3900	1.0261	3.1636	5.8827	-0.1584	0.1430	0.0112	0.0 Holocene
2146.7	711655.8	1.0616	2.1457	1.5929	3.3318	5.8523	0.0259	0.3316	0.2022	0.0 Holocene
2354.7	925083.8	1.0133	1.9743	1.4353	3.3719	5.9662	0.0057	0.2954	0.1569	0.0 Holocene
706.9	164203.5	0.7605	1.8875	1.5757	2.8494	5.2154	-0.1189	0.2759	0.1975	22.5 Miocene
2004.0	2273000.0	0.5355	0.9200	0.6224	3.3019	6.3566	-0.2712	-0.0362	-0.2059	0.0 Holocene

The mean EQ value for all odontocetes did not change significantly between the late Oligocene (27 Ma, mean $\log_{10}EQ_{0.67} = 0.312$) and the middle Miocene (14 Ma, mean $\log_{10}EQ_{0.67} = 0.404$), nor between the middle Miocene and the Recent (0 Ma, mean $\log_{10}EQ_{0.67} = 0.402$). Figure 2 also shows that by the middle Miocene, almost the full range of modern odontocete EQ values had been achieved. The upper bound in both time periods is formed exclusively by members of the Delphinoidea; in other words, the highest EQ values in odontocetes were only achieved within this specific superfamily of highly derived odontocetes. Middle Miocene delphinoids have a mean EQ ($\log_{10}EQ_{0.67} = 0.546$) that is significantly higher ($P < 0.02$) than that of the Oligocene odontocetes ($\log_{10}EQ_{0.67} = 0.312$), from which they are thought to have been derived. From the Miocene to the Recent ($\log_{10}EQ_{0.67} = 0.516$), the mean EQ value for delphinoids does not change significantly, although the range increases slightly. Figures 3 and 4 show that the pattern of results yielded by the use of $EQ_{0.53}$ and $EQ_{0.75}$ was indistinguishable from data based on the formula described by Jerison (1973).

The fact that significant increases in EQ occurred in odontocete evolution does not necessarily imply the existence of a general tendency toward an increase over the entire clade. A general tendency is a clade-level property, implying in this case a predominance of increases in EQ over decreases among lineages, which would be the expectation, for example, if natural selection consistently favored increases in EQ. In contrast, the absence of a general tendency, i.e., a roughly equal number of increases and decreases, might be the result of selection acting in different directions in different lineages, with no overall clade-level regularity, that is, no net tendency for selection to favor high EQ (McShea, 1994). The tests did not show any significant general tendency toward increase or decrease in any of the phylogenies explored. Increases were slightly more prevalent, but this tendency was not statistically significant. Nor was there any significant difference in the magnitudes of increases and decreases, on average.

DISCUSSION

The findings of the present study afford the first opportunity to begin to address long-standing hypotheses regarding brain evolution in toothed whales. The results show that encephalization increased in two critical phases in the evolution of Odontoceti. First, the origin of odontocetes from archaeocetes near the Eocene-Oligocene transition occurred contemporaneously with a significant increase in encephalization. Furthermore, because there was no significant increase in brain size over the course of archaeocete evolution, these findings rule out the hypothetical possibility that large relative brain size was associated with the invasion of aquatic habitats.

Another major hypothesis regarding the high encephalization in toothed whales focuses on the neural processing needs associated with either echolocation per se or its elaboration into a complex perceptual system in the suborder Odontoceti (Jerison, 1986; Ridgway, 1986; Oelschläger, 1990). Results here show an increase in encephalization at the origin of Odontoceti that may be related to the emergence and elaboration of the ability to process high-frequency acoustic information associated with echolocation. Echolocation is an ability found in all modern odontocetes, thought to have existed in all known fossil odontocetes (Fleischer, 1976; Fordyce and de Muizon, 2001) and to have been absent in all archaeocetes (Uhen, 2004). Further investigations of echolocatory abilities are currently being undertaken in odontocetes and mysticetes to explore the relationship between changes in encephalization and perception of high-frequency sound as indicated by study of the fine scale anatomy of the internal periotic.

The post-Oligocene period is characterized by little change in the mean encephalization level for Odontoceti as a whole. The origin of Delphinoidea, however, is associated with a significant increase in encephalization over other odontocetes. From the middle Miocene to the Recent, delphinoids form the

upper range of encephalization levels and are the exclusive occupants of the upper third of the range of encephalization levels in the Recent.

Fig. 2. Mean encephalization quotients ($EQ_{0.67}$) of archaeocete and odontocete cetacean species over time. Scales for both raw $EQ_{0.67}$ and $\log_{10} EQ_{0.67}$ are shown across the bottom. Archaeocetes are shown in blue squares; delphinoid odontocetes are shown in green circles; nondelphinoid odontocetes are shown in red triangles. Time scale is in millions of years (Ma). Note the large shift in EQ at the origin of Odontoceti, and that the Delphinoidea form the upper range of odontocete EQ values from the middle Miocene to Recent.

Fig. 3. Mean log encephalization quotients ($EQ_{0.53}$) of archaeocete and odontocete cetaceans species over time. Archaeocetes are shown in blue squares; delphinoid odontocetes are shown in green circles; nondelphinoid odontocetes are shown in red triangles. Time scale is in Ma. $EQ = \text{brain weight (g)}/[1.6 \times \text{body weight (g)}]^{0.53}$.

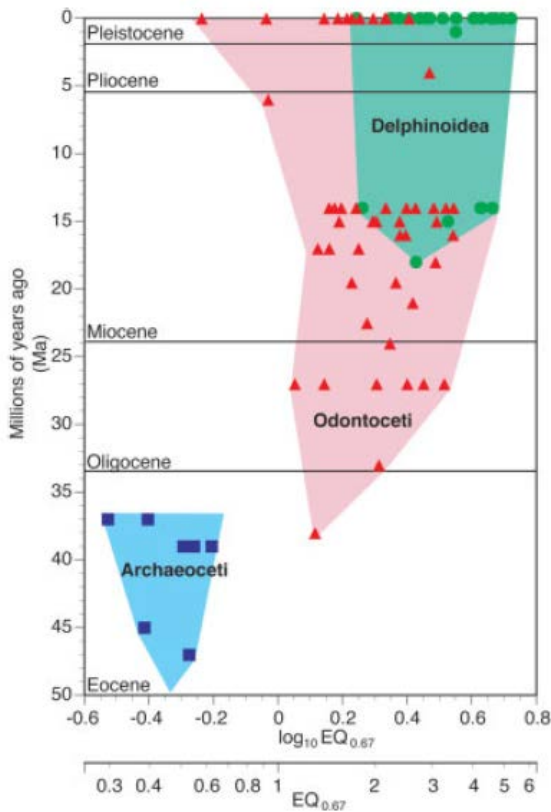


Figure 2

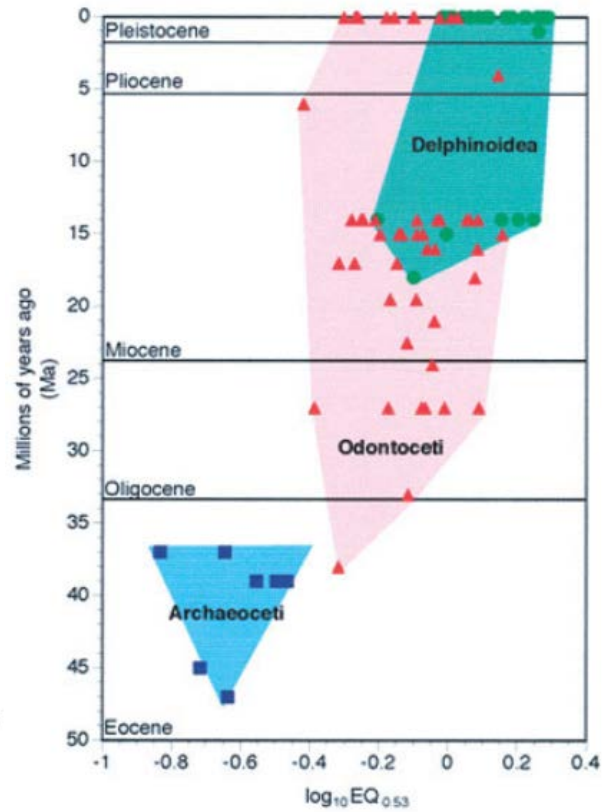


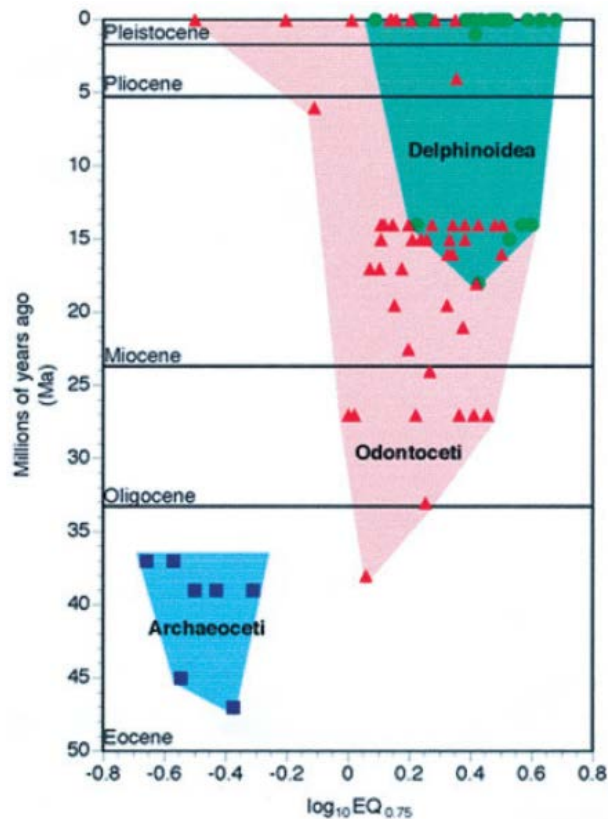
Figure 3

The present findings provide critical data for further investigations of those factors that may have played a role in the increase in encephalization in delphinoids above the encephalization levels achieved by odontocetes in general. Hypothesized causes of increased encephalization in odontocetes include such varied and not altogether independent factors as social ecology (Connor et al., 1998) and communication (Jerison, 1986). Now that the basic pattern of encephalization change for Odontoceti as a whole has been documented, this pattern can be mapped onto an accepted phylogeny and these other factors can be explored as potential causative factors for the documented changes in encephalization.

The conventional wisdom holds that increased encephalization confers a selective advantage and that increases in encephalization should be pervasive across groups and their component lineages (Gould, 1988). The shift to higher encephalization levels within Odontoceti at the origin of Delphinoidea, however, and the continued expansion (toward both higher and lower levels) within Delphinoidea suggests the

absence of an overall drive toward higher levels of encephalization for Delphinoidea as a whole. This does not preclude the possibility that there may have been selective forces acting on individual lineages within the Odontoceti. If increasing encephalization was pervasively advantageous across lineages, however, our tests did not detect it in the available historical record of this group.

Fig. 4. Mean log encephalization quotients ($EQ_{0.75}$) of archaeocete and odontocete cetaceans species over time. Archaeocetes are shown in blue squares; delphinoid odontocetes are shown in green circles; nondelphinoid odontocetes are shown in red triangles. Time scale is in Ma. $EQ = \text{brain weight (g)} / [0.055 \times \text{body weight (g)}]^{0.75}$.



The observation that there is a single remaining human lineage that has been pruned down from a bushier tree has led to a popular view that several species of highly encephalized animal cannot coexist spatially or temporally (Tattersall, 2000). Our results show that not only do multiple highly encephalized delphinoids coexist in similar and overlapping environments today, but this situation arose at least as early as the middle Miocene and has persisted for at least 15 million years.

ACKNOWLEDGMENTS

Specimens and CT scanning facilities were provided by the National Museum of Natural History and D. Bohaska, B. Frolich, J. Mead, C. Potter, F. Whitmore, R. Purdy. Access to additional specimens were provided by A. Sanders, Charleston Museum; P. Gingerich, University of Michigan Museum of Paleontology; L. Barnes and H. Thomas, Natural History Museum of Los Angeles County. Additional CT scanning was provided by the Medical University of South Carolina (Charleston, SC) and Methodist Hospital (Arcadia, CA). Emory University students E. Garafalo, N. Pyenson, S. Rotenberg, and B. Shamsai assisted in endocranial measurements. Special thanks to P.M. Novack-Gottshall for ancestral-state reconstructions and maximum-likelihood analyses and E.P. Venit for assistance with the statistical

analyses. The authors also thank Todd Preuss for his comments on an earlier draft of the manuscript and Louis Lefebvre for his assistance and support. Funding was provided by the National Science Foundation (to L.M. and M.D.U.) and the Center for the Study of Life in the Universe, SETI Institute (to L.M. and D.W.M.).

LITERATURE CITED

- Alroy J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* 280:731–734.
- Armstrong E. 1985. Allometric considerations of the adult mammalian brain with special emphasis on Primates. In: Jungers WL, editor. *Size and scaling in primate biology*. New York: Plenum Press. p 115–146.
- Connor RC, Mann J, Tyack PL, Whitehead H. 1998. Social evolution in toothed whales. *Trends Ecol Evol* 13:228–232.
- Eisenberg JF. 1981. *The mammalian radiations*. Chicago: University of Chicago Press.
- de Muizon C. 1988. Les relations phylogenetiques des Delphinida (Cetacea, mammalia). *Ann Pale'ol* 74:159–227.
- de Muizon C. 1991. A new Ziphiidae (Cetacea) from the early Miocene of Washington State (USA) and phylogenetic analysis of the major groups of odontocetes. *Bull Natl Mus Nat Hist Paris* 12:279–326.
- Fleischer G. 1976. Hearing in extinct cetaceans as determined by cochlear structure. *J Paleo* 50:133–152.
- Fordyce RE, de Muizon C. 2001. Evolutionary history of the cetaceans: a review. In: Mazin JM, Buffre'nil V, editors. *Secondary adaptation of tetrapods to life in water*. Munich: Verlag. p 169–223.
- Geisler J, Sanders AE. 2003. Morphological evidence for the phylogeny of Cetacea. *J Mamm Evol* 10:23–129.
- Gingerich PD. 1998. Paleobiological perspectives on Mesonychia, Archaeoceti, and the origin of whales. In: Thewissen JGM, editor. *The emergence of whales: evolutionary patterns in the origin of Cetacea*. New York: Plenum Press. p 423–449.
- Gingerich PD, Uhen MD. 1998. Likelihood estimation of the time of origin of cetacean and the time of divergence of cetacean and Artiodactyla. *Paleo-electronica* 2:1–47.
- Gould SJ. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. *J Paleontol* 62:319–329.
- Herman LM. 2002. Language learning. In: Perrin WF, Wursig B, Thewissen JGH, editors. *Encyclopedia of marine mammals*. San Diego, CA: Academic Press. p 685–689.
- Jerison HJ. 1973. *Evolution of the brain and intelligence*. New York: Academic Press.

- Jerison HJ. 1986. The perceptual world of dolphins. In: Schusterman R, Thomas JA, Wood FG, editors. *Dolphin cognition and behavior: a comparative approach*. Mahwah, New Jersey: Lawrence Erlbaum. p. 141–166.
- Kumar S, Blair Hedges S 1998. A molecular timescale for vertebrate evolution. *Nature* 392:917–920.
- Maddison WP, Maddison DR. 1992. *MacClade: analysis of phylogeny and character evolution*, version 3.0. Sunderland, MA: Sinauer Associates.
- Marino L. 1995. Brain-behavior relationships in cetaceans and primates: implications for the evolution of complex intelligence. PhD thesis. Albany, NY: State University of New York at Albany.
- Marino L. 1998. A comparison between odontocete cetaceans and anthropoid primates. *Brain Beh Evol* 51:230–238.
- Marino L, Uhen MD, Frohlich B, Aldag JM, Blane C, Bohaska D, Whitmore FC Jr. 2000. Endocranial volume of mid-late Eocene Archaeocetes (order: Cetacea) revealed by computed tomography: implications for cetacean brain evolution. *J Mamm Evol* 7:81–94.
- Marino L. 2002. Convergence in complex cognitive abilities in cetaceans and primates. *Brain Behav Evol* 59:21–32.
- Marino L, Uhen MD, Pyenson ND, Frohlich B. 2003. Reconstructing cetacean brain evolution using computed tomography. *Anat Rec (New Anat)* 272B:107–117.
- McShea DW. 1994. Mechanisms of large-scale evolutionary trends. *Evolution* 48:1747–1763.
- Nikaido M, Matsuno F, Hamilton H, Brownell RL Jr, Cao Y, Ding W, Zuoyan Z, Shedlock AM, Fordyce RE, Hasegawa M, Okada N. 2001. Retroposon analysis of major cetacean lineages: the monophyly of toothed whales and the paraphyly of river dolphins. *Proc Natl Acad Sci USA* 98:7384–7389.
- Oelschläger HA. 1990. Evolutionary morphology and acoustics in the dolphin skull. In: Thomas JA, Kastelein R, editors. *Sensory abilities of cetaceans*. New York: Plenum Press. p 137–162.
- Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zoo Scripta* 26:331–348.
- Reiss D, Marino L. 2001. Self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proc Natl Acad Sci USA* 98:5937–5942.
- Rendell L, Whitehead H. 2001. Culture in whales and dolphins. *Behav Brain Sci* 24:309–382.
- Ridgway SH. 1986. Physiological observations on dolphin brains. In: Schusterman RJ, Thomas TA, Wood FG, editors. *Dolphin cognition and behavior: a comparative approach*. Hillsdale, NJ: Lawrence Erlbaum. p 31–59.
- Tattersall I. 2000. Once we were not alone. *Sci Am* 282:56–62.
- Uhen MD, Gingerich PD. 2001. A new species of dorudontine (Archaeoceti, Cetacea) from the Eocene of South Carolina. *Mar Mamm Sci* 17:1–34.

Uhen MD. 2004. Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): an Archaeocete from the middle to late Eocene of Egypt. *Michigan Mus Paleo Papers on Paleontol* 34: 239.